
SYSTEMATIC REVISION OF THE ASIAN FOREST
SCORPIONS (HETEROMETRINAE SIMON, 1879),
REVISED SUPRAGENERIC CLASSIFICATION
OF SCORPIONIDAE LATREILLE, 1802, AND
REVALIDATION OF RUGODENTIDAE
BASTAWADE ET AL., 2005

LORENZO PRENDINI AND STEPHANIE F. LORIA



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BULLETIN OF THE AMERICAN MUSEUM OF NATURAL HISTORY

Number 442, 480 pp., 251 figures, 5 tables

Issued October 14, 2020

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ABSTRACT

The genera and species of the Asian forest scorpions (Scorpionidae Latreille, 1802) are revised based on a phylogenetic analysis of 186 morphological characters and 4188 base pairs of concatenated DNA sequence from three mitochondrial loci and two nuclear loci. Revision of the Asian scorpionids required a critical reappraisal of the suprageneric classification of Scorpionidae, on the basis of which the monotypic Indian scorpionoid genus, *Rugodentus* Bastawade et al., 2005, stat. rev., and its type species, *Rugodentus keralaensis* Bastawade et al., 2005, stat. rev., are revalidated, and subfamily Rugodentinae Bastawade et al., 2005, revalidated and elevated to the rank of family, Rugodentidae Bastawade et al., 2005, stat. nov. et stat. rev.; Heterometrinae Simon, 1879, stat. nov., and Opisthophthalminae Rossi, 2016, stat. nov., are elevated to the rank of subfamily; *Pandinopsis* Vachon, 1974, stat. nov., and *Pandipalpus* Rossi, 2015, stat. nov., are elevated to the rank of genus, resulting in two new combinations: *Pandinopsis dictator* (Pocock, 1888), comb. nov., and *Pandipalpus viatoris* (Pocock, 1890), comb. nov.; and 10 new synonyms are presented: Pandinopsini Rossi, 2016 = Pandininae Thorell, 1876, syn. nov.; Protophthalmini Rossi, 2016 = Opisthophthalminae Rossi, 2016, syn. nov.; *Protophthalmus* Lawrence, 1969 = *Opisthophthalmus* C.L. Koch, 1837, syn. nov.; *Pandinoides* (*Dunlopandinoides*) Rossi, 2016 = *Pandinoides* Fet, 2000, syn. nov.; *Pandinurus* (*Pandicaporiaccous*) Rossi, 2015 = *Pandiborellius* Rossi, 2015, syn. nov.; *Buthus defensor* C.L. Koch, 1837 = *Pandinurus gregoryi* (Pocock, 1896), syn. nov.; *Buthus heros* C.L. Koch, 1837 = *Pandinurus exitialis* (Pocock, 1888), syn. nov.; *Pandinus lowei* Kovařík, 2012 = *Pandipalpus viatoris* (Pocock, 1890), syn. nov.; *Pandinurus* (*Pandipalpus*) *pygmaeus* Rossi, 2015 = *Pandipalpus viatoris* (Pocock, 1890), syn. nov.; *Pandinus intermedius* Borelli, 1919 = *Pandinurus citernii* (Borelli, 1919), syn. nov. The following revisions are implemented to the classification of the Asian forest scorpions (Heterometrinae). Three former subgenera of *Heterometrus* Ehrenberg, 1828 are revalidated and elevated to the rank of genus: *Chersonesometrus* Couzijn, 1978, stat. nov. et stat. rev.; *Javanimetrus* Couzijn, 1981, stat. nov. et stat. rev.; and *Srilankametrus* Couzijn, 1981, stat. nov. et stat. rev. One subgenus is elevated to the rank of genus: *Gigantometrus* Couzijn, 1978, stat. nov. Two new genera and eight new species are described: *Deccanometrus*, gen. nov.; *Sahyadrimetrus*, gen. nov.; *Chersonesometrus bastawadei*, sp. nov.; *Chersonesometrus hendersoni*, sp. nov.; *Chersonesometrus nathanorum*, sp. nov.; *Chersonesometrus shivashankari*, sp. nov.; *Sahyadrimetrus mathewi*, gen. et sp. nov.; *Sahyadrimetrus tikaderi*, gen. et sp. nov.; *Srilankametrus couzijni*, sp. nov.; *Srilankametrus pococki*, sp. nov. *Heterometrus* sensu stricto is restricted to eight species of the nominotypical subgenus, all other species, formerly placed in *Heterometrus*, are transferred to appropriate genera, five species are revalidated, and two subspecies elevated to the rank of species, resulting in 28 new combinations: *Chersonesometrus beccaloniae* (Kovařík, 2004), comb. nov.; *Chersonesometrus fulvipes* (C.L. Koch, 1837), comb. nov.; *Chersonesometrus madraspatensis* (Pocock, 1900), comb. nov.; *Chersonesometrus pelekomanus* (Couzijn, 1981), comb. nov. et stat. rev.; *Chersonesometrus tristis* (Henderson, 1919), comb. nov.; *Chersonesometrus wroughtoni* (Pocock, 1899), comb. nov.; *Deccanometrus bengalensis* (C.L. Koch, 1841), comb. nov.; *Deccanometrus latimanus* (Pocock, 1894), comb. nov.; *Deccanometrus liurus* (Pocock, 1897), comb. nov.; *Deccanometrus obscurus* (Couzijn, 1981), comb. et stat. nov.; *Deccanometrus phipsoni* (Pocock, 1893), comb. nov.; *Deccanometrus ubicki* (Kovařík, 2004), comb. nov.; *Deccanometrus xanthopus* (Pocock, 1897), comb. nov.; *Gigantometrus swammerdami* (Simon, 1872), comb. nov.; *Gigantometrus titanicus* (Couzijn, 1981), comb. nov. et stat. rev.; *Heterometrus glaucus* (Thorell, 1876), comb. nov. et stat. rev.; *Heterometrus laevigatus* (Thorell, 1876), comb. nov. et stat. rev.; *Heterometrus silenus* (Simon, 1884), comb. nov. et stat. rev.; *Javanimetrus cyaneus* (C.L. Koch, 1836), comb. nov.; *Sahyadrimetrus barberi* (Pocock, 1900), comb. nov.; *Sahyadrimetrus kanarensis* (Pocock, 1900), comb. nov.; *Sahyadrimetrus rugosus* (Couzijn, 1981), comb. et stat. nov.; *Sahyadrimetrus scaber* (Thorell, 1876), comb. nov.; *Srilankametrus caesar* (C.L. Koch, 1841), comb. nov. et stat. rev.; *Srilankametrus gravimanus* (Pocock, 1894), comb. nov.; *Srilankametrus indus* (DeGeer, 1778),

comb. nov.; *Srilankametrus serratus* (Pocock, 1900), comb. nov.; *Srilankametrus yaleensis* (Kovařík et al., 2019), comb. nov. Twenty-seven new synonyms are presented: *Scorpio leioderma* Dufour, 1856 = *Sahyadrimetrus scaber* (Thorell, 1876), syn. nov.; *Palamnaeus costimanus* var. β *borneensis* Thorell, 1876 = *Heterometrus longimanus* (Herbst, 1800), syn. nov.; *Palamnaeus liophysa* Thorell, 1888 = *Heterometrus longimanus* (Herbst, 1800), syn. nov.; *Palamnaeus oatesii* Pocock, 1900 = *Heterometrus petersii* (Thorell, 1876), syn. nov.; *Palamnaeus swammerdami flavimanus* Pocock, 1900 = *Gigantometrus swammerdami* (Simon, 1872), syn. nov.; *Heterometrus liophysa* var. *madoerensis* Kopstein, 1921 = *Heterometrus glaucus* (Thorell, 1876), syn. nov.; *Heterometrus laevifrons* Roewer, 1943 = *Heterometrus glaucus* (Thorell, 1876), syn. nov.; *Heterometrus* (*Chersonesometrus*) *granulomanus* Couzijn, 1981 = *Srilankametrus caesar* (C.L. Koch, 1841), syn. nov.; *Heterometrus* (*Heterometrus*) *liophysa separatus* Couzijn, 1981 = *Heterometrus glaucus* (Thorell, 1876), syn. nov.; *Heterometrus* (*Heterometrus*) *liophysa spartanicus* Couzijn, 1981 = *Heterometrus glaucus* (Thorell, 1876), syn. nov.; *Heterometrus* (*Heterometrus*) *longimanus bengkalitensis* Couzijn, 1981 = *Heterometrus longimanus* (Herbst, 1800), syn. nov.; *Heterometrus* (*Heterometrus*) *longimanus marmoratus* Couzijn, 1981 = *Heterometrus longimanus* (Herbst, 1800), syn. nov.; *Heterometrus* (*Heterometrus*) *petersii mindanaensis* Couzijn, 1981 = *Heterometrus silenus* (Simon, 1884), syn. nov.; *Heterometrus* (*Heterometrus*) *spinifer solitarius* Couzijn, 1981 = *Heterometrus spinifer* (Ehrenberg, 1828), syn. nov.; *Heterometrus* (*Srilankametrus*) *indus laevitensus* Couzijn, 1981 = *Srilankametrus indus* (DeGeer, 1778), syn. nov.; *Heterometrus* (*Heterometrus*) *keralaensis* Tikader and Bastawade, 1983 = *Sahyadrimetrus rugosus* (Couzijn, 1981), syn. nov.; *Heterometrus cimrmani* Kovařík, 2004 = *Heterometrus laevigatus* (Thorell, 1876), syn. nov.; *Heterometrus mysorensis* Kovařík, 2004 = *Chersonesometrus tristis* (Henderson, 1919), syn. nov.; *Heterometrus nepalensis* Kovařík, 2004 = *Deccanometrus bengalensis* (Pocock, 1900), syn. nov.; *Heterometrus rolciki* Kovařík, 2004 = *Sahyadrimetrus scaber* (Thorell, 1876), syn. nov.; *Heterometrus sejnai* Kovařík, 2004 = *Javanimetrus cyaneus* (C.L. Koch, 1836), syn. nov.; *Heterometrus tibetanus* Lourenço et al., 2005 = *Deccanometrus bengalensis* (Pocock, 1900), syn. nov.; *Heterometrus liangi* Zhu and Yang, 2007 = *Heterometrus silenus* (Simon, 1884), syn. nov.; *Heterometrus telanganaensis* Javed et al., 2010 = *Deccanometrus xanthopus* (Pocock, 1897), syn. nov.; *Heterometrus atrascorpius* Mirza et al., 2012 = *Chersonesometrus beccaloniae* (Kovařík, 2004), syn. nov.; *Heterometrus minotaurus* Plíšková et al., 2016 = *Heterometrus laevigatus* (Thorell, 1876), syn. nov.; *Heterometrus bastawadei* Rossi, 2016 = *Rugodentus keralaensis* Bastawade et al., 2005, syn. nov. Another 25 synonyms by previous authors are confirmed, for a total of 51 synonyms in subfamily Heterometrinae. Revised diagnoses with comparative images, and a key and distributional atlas of the genera and species are provided, along with a summary of available data for their ecology and conservation status, where applicable.

INTRODUCTION

Asian forest scorpions (Scorpionidae Latreille, 1802) are distributed across southern Asia from Pakistan, India, and Sri Lanka to Wallace's Line in the Indonesian archipelago (figs. 1–6; tables 1, 2), where they are common throughout tropical and subtropical rainforests, moist and dry tropical deciduous forests, and tropical thorn forests (Prendini et al., 2003; Tahir and Prendini, 2014; figs. 7, 8). These scorpions are among the largest in the world, some species reaching almost 180

mm in length (Pocock, 1900a; Couzijn, 1981; Tikader and Bastawade, 1983; Sissom, 1990). Whereas most are entirely black in color, some are brown or reddish brown, and others bicolored, their pale (reddish or yellowish) legs and/or telson contrasting with the dark prosoma and opisthosoma (fig. 9). Although their venom is relatively mild, Asian forest scorpions deter attackers by snapping with their powerful pedipalp chelae, lunging with the metasoma and telson, and stridulation, an audible rasping hiss created by rubbing together the opposing sur-

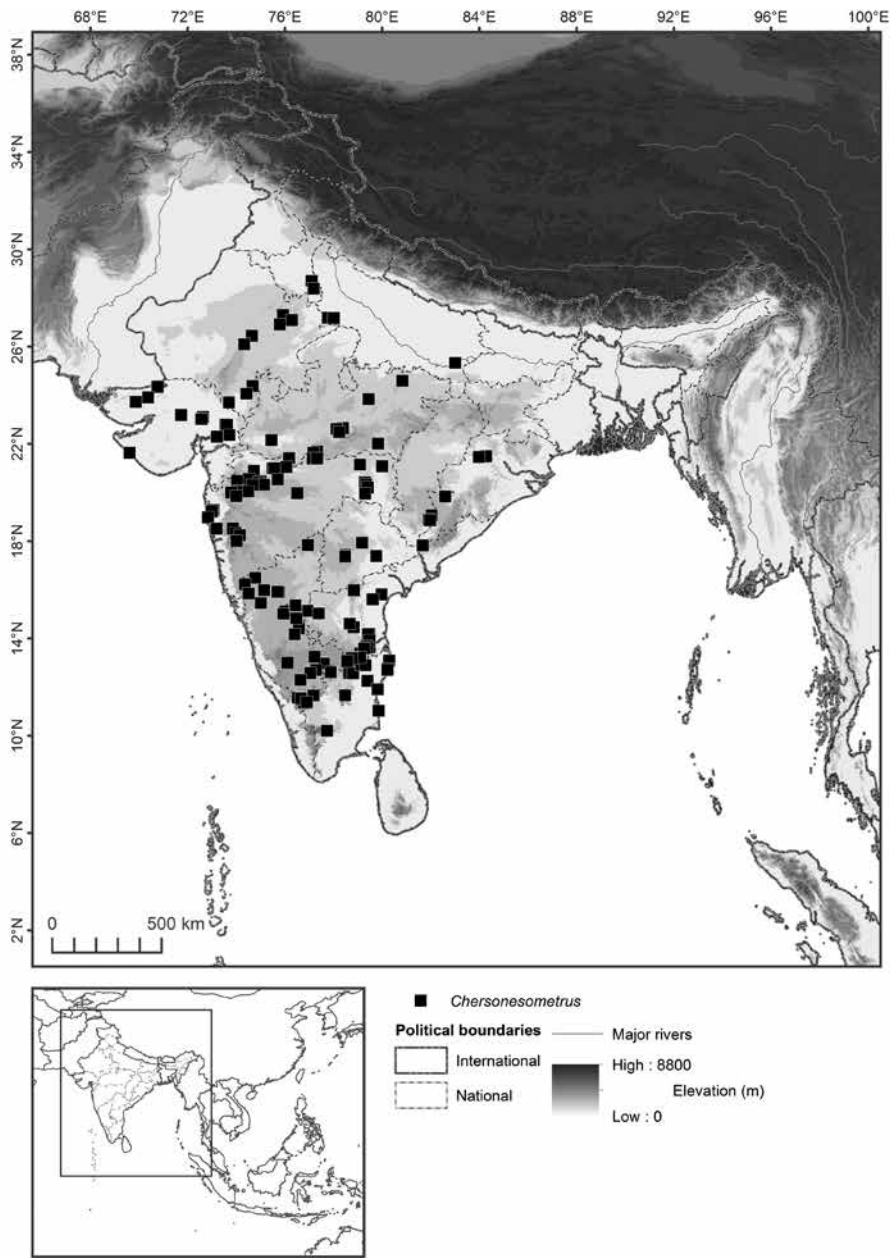


FIGURE 1. Map of South Asia, plotting known locality records of *Chersonesometrus* Couzijn, 1978, stat. nov. et stat. rev., based on material examined, and verified records from virtual museums and the literature.

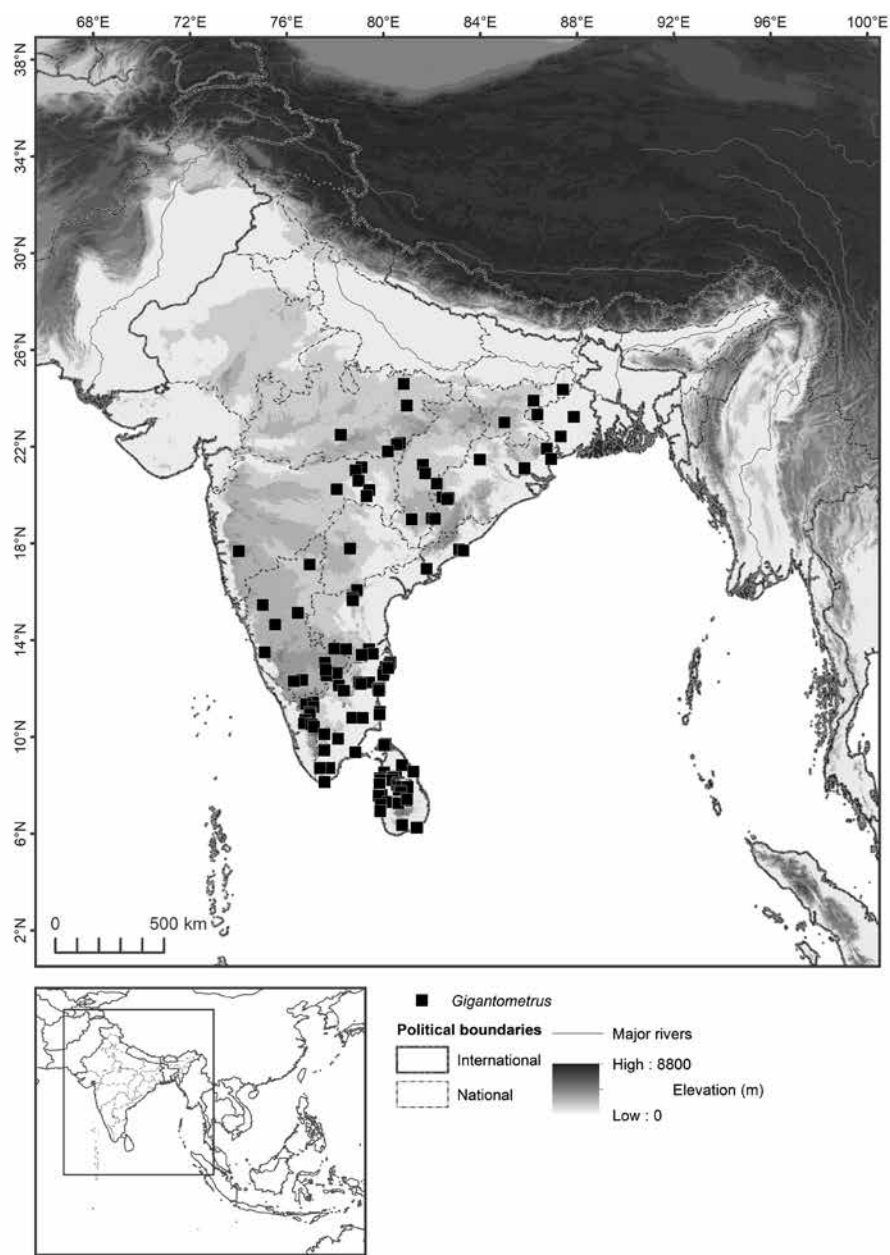


FIGURE 2. Map of South Asia, plotting known locality records *Gigantometrus* Couzijn, 1978, stat. nov., based on material examined, and verified records from virtual museums and the literature.

faces of the cheliceral coxae and the coxae of the first pair of walking legs (Prendini et al., 2003).

Like other Scorpionidae, Asian forest scorpions are fossorial, constructing burrows in loamy riverbanks and other sloping ground, in open ground, at the base of stones or among the roots of trees (Prendini et al., 2003; Bastawade, 2004, 2005, 2006a, 2006b, 2008, 2009; Sureshan et al., 2007a; Bastawade and Borkar, 2008; Javed et al., 2010a; Mirza et al., 2012; Pande et al., 2012; Tahir and Prendini, 2014; fig. 8). Composite, multi-entranced burrows containing up to fifteen related individuals of overlapping generations have been recorded in some species (Shivashankar, 1994; Javed et al., 2010a) whereas others live subsocially within large termitaria (Hull-Williams, 1986). The thickened metasoma and robust legs with stout, spiniform macrosetae distributed laterally and distally on the basitarsi, and curved telotarsal ungues, of most species are used to excavate burrows in the hard, clayey or loamy substrata of their habitats. Although all Asian forest scorpions burrow, many opportunistically inhabit holes in rock walls, tree trunks and logs, enabling them to survive in and around human habitation even when their natural forest habitat is degraded.

Asian forest scorpions are harvested and consumed for food in Southeast Asia, and for narcotic or medicinal purposes in India and Pakistan (Majumder and Dey, 2005; Tahir and Prendini, 2014). They are also harvested and exported in large numbers from several countries for the commercial trade in exotic pets (Prendini et al., 2003). The impact on wild populations is unknown but several factors suggest they may be slow to repopulate and vulnerable to overharvesting (Prendini et al., 2003; Tahir and Prendini, 2014). Females have gestation periods up to 12 months and produce rather small broods (30–35 young) compared with other scorpions. Young are relatively altricial, spending several months in the maternal burrow before dispersing, protracting the period before a female can give birth to her next brood. Age to sexual maturity is 4–7 years in these scorpions

(Prendini et al., 2003), during which period most juveniles experience natural predation (including cannibalism). The relatively restricted distributional ranges of many species provide further cause for concern, given that wild populations are threatened not only by harvesting but also by continued habitat destruction (e.g., agriculture, deforestation, mining and urbanization). Many Asian forest scorpions appear to be restricted to primary forest and may be regarded as equilibrium species. Despite the threats to these remarkable scorpions, no formal assessment of their conservation status has been presented (Prendini et al., 2003). This may, in part, be attributed to the chaotic state of their classification, and the absence of reliable keys for their identification by wildlife conservation officials.

Almost two centuries after the first Asian forest scorpion, *Heterometrus spinifer* Ehrenberg, 1828, was described, and despite several revisions, there remains little consensus about the number of species or supraspecific taxa in the group. The genus with which most Asian forest scorpions have long been associated, *Heterometrus* Ehrenberg, 1828, was first created, as a subgenus of *Buthus* Leach, 1815, to accommodate *H. spinifer* and *Scorpio maurus palmatus* (Ehrenberg, 1828). Thorell (1876a) regarded the morphological differences between *H. spinifer* and *Scorpio maurus* Linnaeus, 1758 (then considered a senior synonym of *S. m. palmatus*), to justify their placement in separate genera and created *Palamnaeus* Thorell, 1876, to accommodate *H. spinifer*. Karsch (1879a) disagreed, returned *S. maurus* to *Scorpio* Linnaeus, 1758, designated *H. spinifer* as type species of *Heterometrus*, and synonymized *Palamnaeus* with *Heterometrus*. Although Karsch's (1879a) decisions were supported by Pocock (1888) and Kraepelin (1899), most subsequent authors, including Birula (1898), Davydov (1898), Gough and Hirst (1927), Henderson (1919), Kraepelin (1894), Laurie (1896a, 1896b), Lönnberg (1897a), Pallary (1929, 1934, 1938), Pavesi (1880, 1884, 1895a, 1895b), Peters (1861), Pocock (1892, 1893, 1896a, 1896b, 1897, 1899, 1900a, 1900b), Sergeant

(1938, 1941), Simon (1872a, 1879, 1880, 1884a, 1884b, 1885, 1892, 1910), and Thorell (1876b, 1888, 1893) followed Thorell's (1876a) generic classification.

Kraepelin (1899) presented the first revision of *Heterometrus*, wherein 13 species were recognized. Pocock (1900a) provided diagnoses for 16 species and six subspecies from British India, including three new species and five new subspecies. After these early studies, the taxonomy of Asian forest scorpions was ignored for almost a century until interest renewed in the 1970s.

Couzijn (1978, 1981) published the first modern revision with keys, wherein 21 species and 31 subspecies (including nine nominotypical forms) were recognized and classified into five subgenera (*Chersonesometrus* Couzijn, 1978, *Gigantometrus* Couzijn, 1978, *Javanimetrus* Couzijn, 1981, *Srilankametrus* Couzijn, 1981, and the nominotypical *Heterometrus*) based on a phenetic cluster analysis. Couzijn's (1981) attempt to partition the morphological variation into widespread polymorphic species with many subspecies was less successful than his subgeneric classification, however. Subsequent attempts, describing new species and elevating subspecies based on small samples comprising few or no adult male specimens from a limited number of populations (e.g., Tikader and Bastawade, 1983; Kovařík, 2004; Lourenço et al., 2005; Zhu and Yang, 2007; Javed et al., 2010a; Mirza et al., 2012; Plíšková et al., 2016) fared little better.

Tikader and Bastawade (1983) published redescrptions and keys for all the Indian species and described two new ones. Despite examining many of the same specimens, and adopting Couzijn's (1981) subgeneric classification, Tikader and Bastawade (1983) differed from Couzijn (1981) in their opinions on the rank or validity of various taxa such that 30 species and 27 subspecies (including eight nominotypical forms) were subsequently recognized (Fet, 2000).

The first quantitative phylogenetic analyses to test the monophyly of Asian forest scorpions, using morphology and multilocus DNA sequence data for exemplar species, were pre-

sented by Prendini (2000a) and Prendini et al. (2003), who also provided the first comprehensive morphological diagnosis of *Heterometrus*, and synthesized what was known about the biology of its species. *Heterometrus* was separated from *Pandinus* Thorell, 1876 by orthobothriotaxic pedipalps, with 26 trichobothria (patella with 13 trichobothria in the *e* series and three trichobothria in the *v* series; chela with four trichobothria in the *V* series and two trichobothria in the *i* series); and the granular tubercles of the "rasp" and stridulatory setae (scaphotrix) of the "scraper" respectively situated on the coxae of the first leg and pedipalp. *Heterometrus* was separated from *Opisthophthalmus* C.L. Koch, 1837 by orthobothriotaxic pedipalps, with 26 trichobothria (including 13 trichobothria in the *e* series of the patella); and cheliceral coxae without stridulatory setae (scaphotrix) on the dorsointernal surfaces and chemoreceptive lamelliform setae (trichocopae) on the internommedian surfaces. *Heterometrus* was separated from *Scorpio* by the obsolete digital carina of the pedipalp chela; and usually by the absence of paired ventrosubmedian and ventrolateral carinae on sternite VII.

Kovařík (2004) presented the third revision of *Heterometrus* in which many of the same specimens were again reexamined. Kovařík (2004) ignored the work of Prendini et al. (2003) and disagreed with many of the taxonomic decisions of Couzijn (1981). Couzijn's (1981) subgenera were synonymized, along with five species and six subspecies, seven new species were described, and one species revalidated, leaving the genus with 31 species and without subspecies.

A further six species of *Heterometrus* were described since 2004 (Lourenço et al., 2005; Zhu and Yang, 2007; Kovařík, 2009; Javed et al., 2010a; Mirza et al., 2012; Plíšková et al., 2016; Kovařík et al., 2019a), the poorly known *Heterometrus latimanus* (Pocock, 1894) was redescrbed (Tahir and Prendini, 2014), and *Heterometrus serratus* (Pocock, 1900) revalidated (Kovařík et al., 2016). Additionally, subgenus *Gigantometrus* was revalidated (Rossi, 2016a)

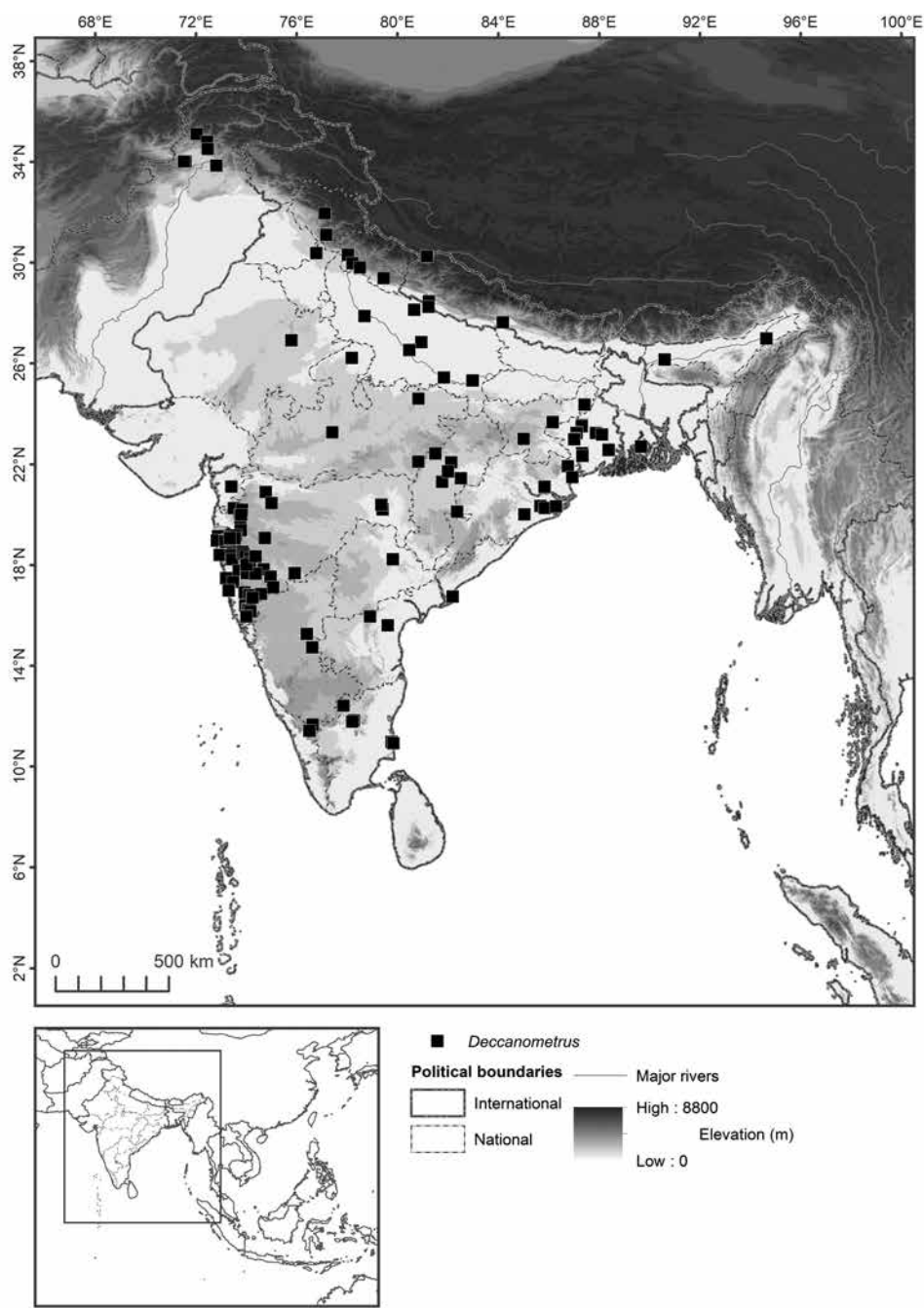


FIGURE 3. Map of South Asia, plotting known locality records of *Deccanometrus*, gen. nov., based on material examined, and verified records from virtual museums and the literature.

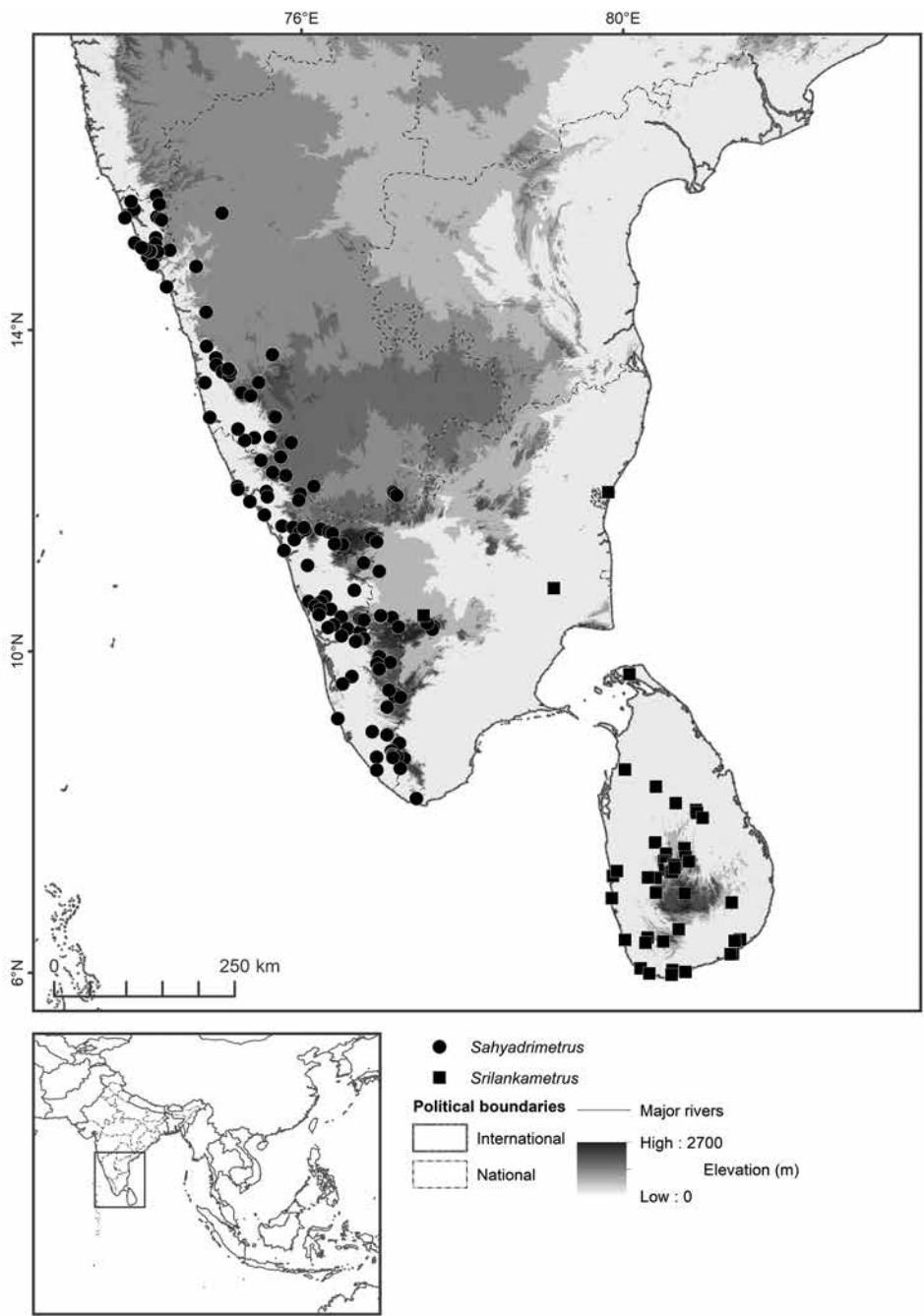


FIGURE 4. Map of South India and Sri Lanka, plotting known locality records of *Sahyadrimetrus*, gen. nov., and *Srilankametrus* Couzijn, 1981, stat. nov. et stat. rev., based on material examined, and verified records from virtual museums and the literature.

and the monotypic Indian scorpionoid genus, *Rugodentus* Bastawade et al., 2005, synonymized with *Heterometrus*, resulting in a new homonym, *Heterometrus keralaensis* (Bastawade et al., 2005), for which the name, *Heterometrus bastawadei* Rossi, 2016, was created. Rossi (2016a) also revalidated *Heterometrus* Simon, 1879, to accommodate the Asian scorpionids within the otherwise exclusively African subfamily Pandininae Thorell, 1876.

When the present study commenced, the classification of Asian forest scorpions did not accurately reflect either the taxonomic or cladistic diversity in the group. Many of the problems with previous studies arose from the small samples of material examined (typically fewer than five, but often singletons, female or immature), the propensity for sexual dimorphism among many species (Prendini et al., 2003; Tahir and Prendini, 2014), high levels of morphological convergence, and a general failure by previous workers to adequately consider these issues. As in other scorpionid taxa, adult males are important for species identification and delimitation in Asian forest scorpions, and there are several species complexes comprising morphologically similar, range-restricted or narrowly endemic species (Prendini, 2001a). Some species, especially those occurring in Southeast Asia, are extremely difficult to determine from females or immature stages. Without series, especially adult males, the diagnostic characters (coloration, granulation, meristic variation) often presented to justify putative new species are unreliable and comparisons made with other species, the adults of which may or may not have been described, invalid. As Prendini et al. (2003: 218) pointed out, when contrasting the decisions taken by Tikader and Bastawade (1983) vs. Couzijn (1981):

The small sample size of specimens examined by Tikader and Bastawade (usually one or two at most) and the propensity for marked sexual dimorphism in many species of *Heterometrus*, as in *Opisthophthalmus* (Prendini 2001), suggests that many of the synonyms resurrected, and subspecies elevated by those authors may be synonymous with one another or with existing species. That said, Couzijn's approach of retaining

numerous subspecies within existing species is equally inadequate.... Simply partitioning the morphological variation into a few widespread polymorphic species with many subspecies (e.g., Couzijn 1981) will not alleviate the taxonomic problems. Obviously, subspecies cannot be elevated on the basis of one or a few specimens (e.g., Tikader and Bastawade 1983) either. A thorough revision, involving the examination of many specimens, in order to determine which characters are consistent across the range of the various taxa, is required. Subspecies that can be consistently differentiated from other subspecies by means of a diagnostic character combination should be elevated to the rank of species. If they cannot be consistently differentiated, then they should be synonymised. Molecular data (e.g., DNA sequences) may also help to clarify species limits within *Heterometrus*, as has been found in other complex scorpion genera.... Finally, a computational cladistic analysis of relationships among the species of *Heterometrus* remains to be presented.... This should help to clarify the validity of the five subgenera currently recognised.

Similar points were reiterated by Tahir and Prendini (2014: 3):

As Prendini et al. (2003) suggested, a thorough revision, involving the examination of many specimens to determine which morphological characters are consistent across the range of the various taxa, and augmented by DNA sequence data, is required to address the confusion.... When this is accomplished, many of the putative new species described, subspecies elevated, and synonyms resurrected by previous authors will likely prove synonymous with one another or with species described decades earlier. A quantitative cladistic analysis of relationships among the species.... is also needed to reassess Couzijn's (1981) five subgenera, which were rather arbitrarily synonymized.

In the present contribution, the Asian forest scorpions are revised based on a phylogenetic analysis of 186 morphological characters (appendices 1, 2) and 4188 base pairs of concatenated DNA sequence from two nuclear and three mitochondrial loci (fig. 10; appendix 3), presented elsewhere (Loria and Prendini, in press). Revision of the Asian scorpionids required a critical reappraisal of the suprageneric classification of Scorpionidae that was self-published, without peer review, by Rossi (2016a), on the basis of which the monotypic Indian scorpionoid genus, *Rugodentus* Bastawade et al., 2005, stat. rev., and its type species, *Rugodentus keralaensis* Bastawade

et al., 2005, stat. rev., are revalidated, and subfamily Rugodentinae Bastawade et al., 2005, revalidated and elevated to the rank of family, Rugodentidae Bastawade et al., 2005, stat. nov. et stat. rev.; Heterometrinae Simon, 1879, stat. nov., and Opisthophthalminae Rossi, 2016, stat. nov., are elevated to the rank of subfamily; *Pandinopsis* Vachon, 1974, stat. nov., and *Pandipalpus* Rossi, 2015, stat. nov., are elevated to the rank of genus, resulting in two new combinations; and 10 new synonyms are presented: *Pandinopsini* Rossi, 2016 = *Pandininae* Thorell, 1876, syn. nov.; *Protophthalmini* Rossi, 2016 = *Opisthophthalminae* Rossi, 2016, syn. nov.; *Protophthalmus* Lawrence, 1969 = *Opisthophthalmus* C.L. Koch, 1837, syn. nov.; *Pandinoides* (*Dunlopandinoides*) Rossi, 2016 = *Pandinoides* Fet, 2000, syn. nov.; *Pandinurus* (*Pandicaporiaccous*) Rossi, 2015 = *Pandiborellius* Rossi, 2015, syn. nov.; *Buthus defensor* C.L. Koch, 1837 = *Pandinurus gregoryi* (Pocock, 1896), syn. nov.; *Buthus heros* C.L. Koch, 1837 = *Pandinurus exitialis* (Pocock, 1888), syn. nov.; *Pandinus lowei* Kovařík, 2012 = *Pandipalpus viatoris* (Pocock, 1890), syn. nov.; *Pandinurus* (*Pandipalpus*) *pygmaeus* Rossi, 2015 = *Pandipalpus viatoris* (Pocock, 1890), syn. nov.; *Pandinus intermedius* Borelli, 1919 = *Pandinurus citernii* (Borelli, 1919), syn. nov. The following revisions are implemented to the classification of the Asian forest scorpions (Heterometrinae). Three former subgenera of *Heterometrus* are revalidated and elevated to the rank of genus: *Chersonesometrus* Couzijn, 1978, stat. nov. et stat. rev.; *Javanimetrus* Couzijn, 1981, stat. nov. et stat. rev.; *Srilankametrus* Couzijn, 1981, stat. nov. et stat. rev. One subgenus is elevated to the rank of genus: *Gigantometrus* Couzijn, 1978, stat. nov. Two new genera and eight new species are described: *Deccanometrus*, gen. nov.; *Sahyadrimetrus*, gen. nov.; *Chersonesometrus bastawadei*, sp. nov.; *Chersonesometrus hendersoni*, sp. nov.; *Chersonesometrus nathanorum*, sp. nov.; *Chersonesometrus shivashankari*, sp. nov.; *Sahyadrimetrus mathewi*, gen. et sp. nov.; *Sahyadrimetrus tika-deri*, gen. et sp. nov.; *Srilankametrus couzijni*, sp. nov.; *Srilankametrus pococki*, sp. nov. *Heterome-*

trus sensu stricto is restricted to eight species of the nominotypical subgenus (appendix 4). All other species, formerly placed in *Heterometrus*, are transferred to appropriate genera, five species are revalidated, and two subspecies elevated to the rank of species, resulting in 28 new combinations. Twenty-seven new synonyms are presented. Another 25 synonyms by previous authors are confirmed, for a total of 51 synonyms in subfamily Heterometrinae. Revised diagnoses with comparative images, a key and distributional atlas of the genera and species of Asian forest scorpions are also provided, along with a summary of available data for their ecology and conservation status, where applicable.

MATERIAL AND METHODS

FIELD COLLECTIONS: Scorpions were collected by turning logs and stones or excavating burrows during the day or searching at night using portable ultraviolet (UV) lamps, comprising a pair of mercury-vapor tubes attached to a chromium parabolic reflector and powered by a rechargeable 7 Amp/hr, 12 V battery, or UV light-emitting diode (LED) flashlights. Material collected was preserved and injected with 95% ethanol. A portable Garmin™ GPS etrex 30 device was used for recording the geographical coordinates (WGS84 datum) of some collection localities in the field; others were retroactively georeferenced using Google Earth.

MATERIAL REPOSITORIES: Type and nontype material is deposited in the following collections: American Museum of Natural History (AMNH), including the Alexis Harington Collection (AH), New York; Natural History Museum (BMNH), London, U.K.; Bombay Natural History Society (BNHS), Mumbai, India; California Academy of Sciences (CAS), San Francisco; Faculty of Science, Charles University, Prague (CUP), Czech Republic; František Kovařík Private Collection (FKPC), Prague, Czech Republic; Institute of Fundamental Studies (IFS), Kandy, Sri Lanka; Field Museum of Natural History (FMNH), Chicago; Lee Kong Chian Natural History Museum (LKC), National

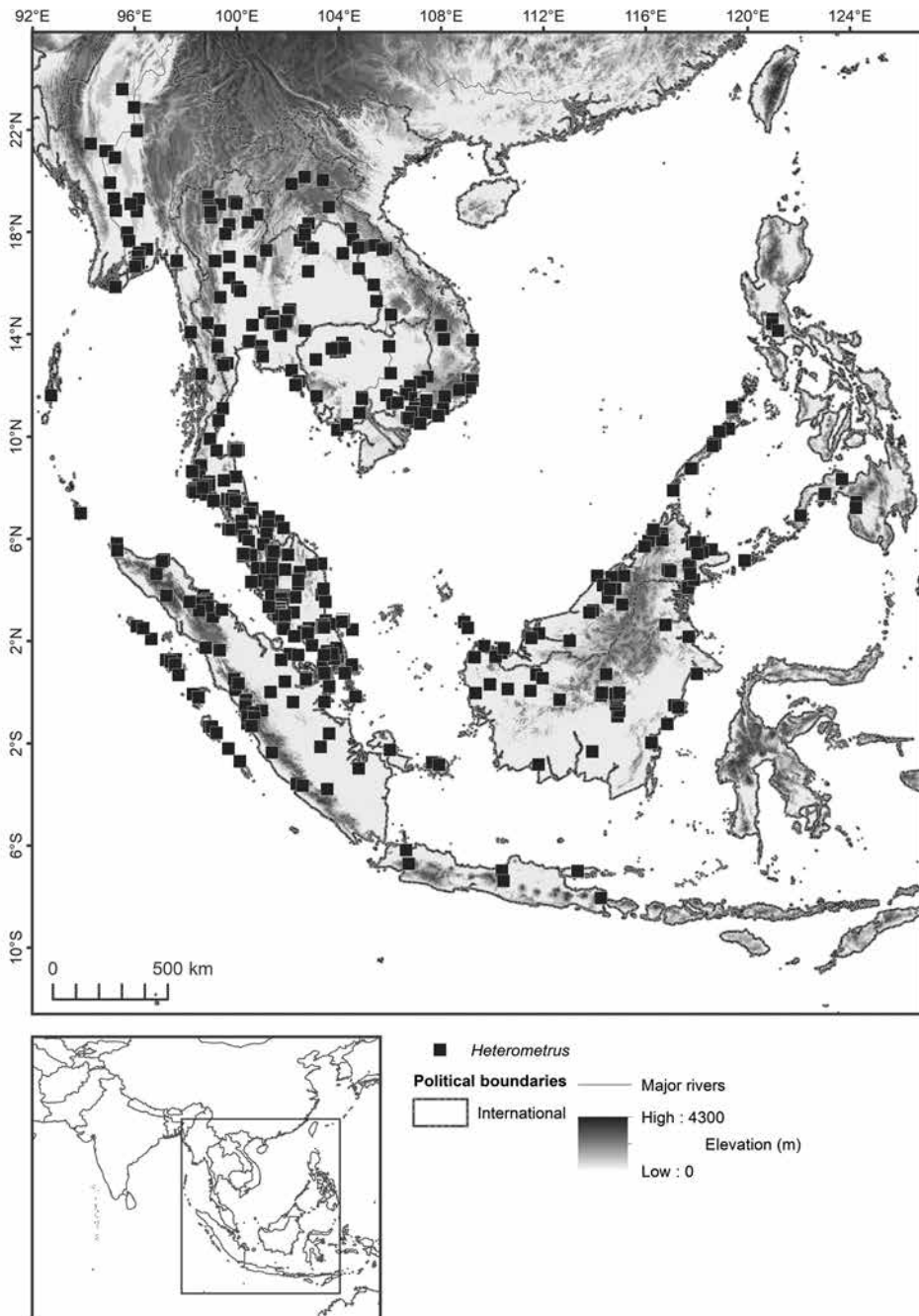


FIGURE 5. Map of Southeast Asia, plotting known locality records of all species of *Heterometrus* Ehrenberg, 1828, based on material examined, and verified records from virtual museums and the literature.

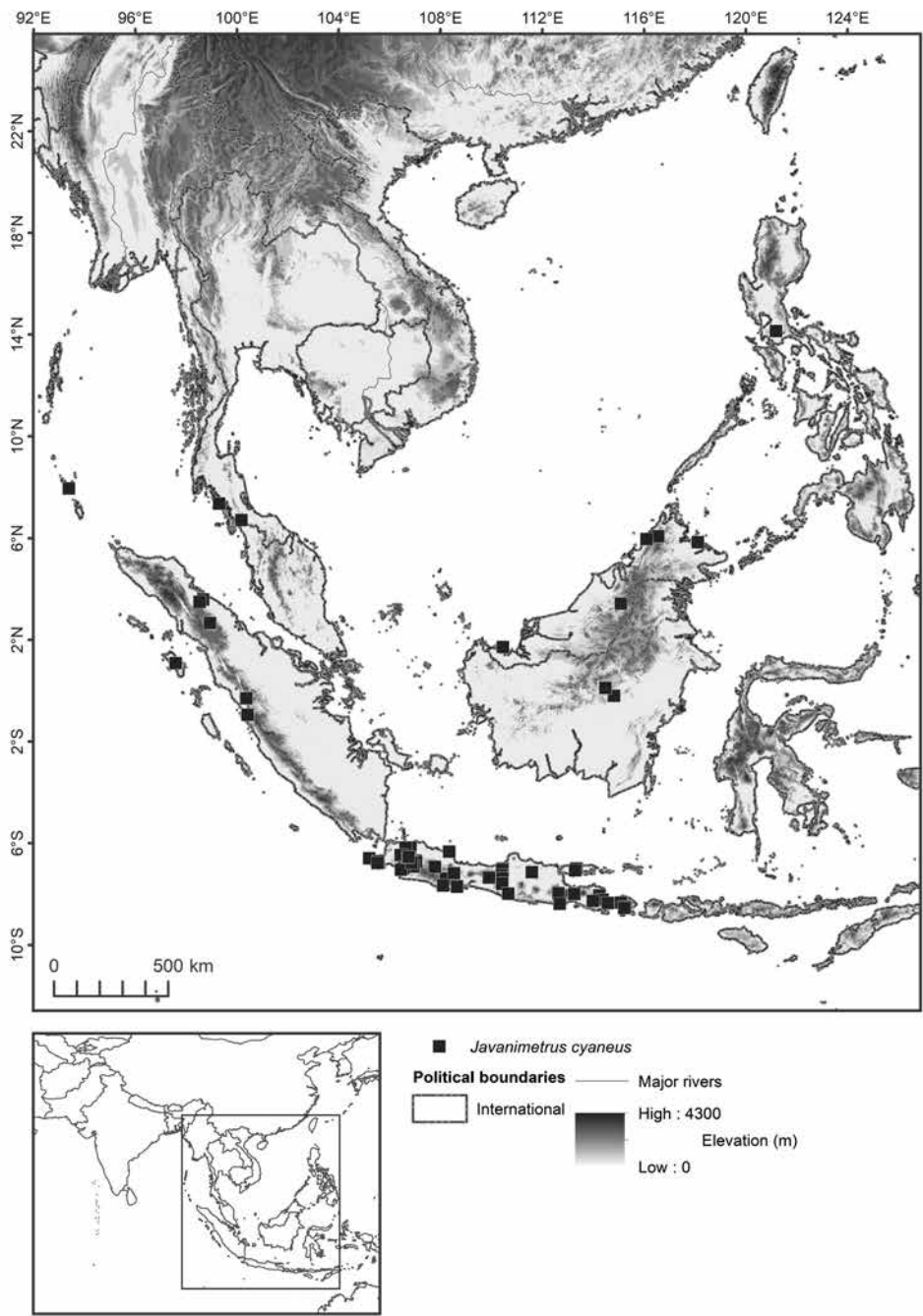


FIGURE 6. Map of Southeast Asia, plotting known locality records of *Javanimetrus cyaneus* (C.L. Koch, 1836), comb. nov., based on material examined, and verified records from virtual museums and the literature.

University of Singapore; Museo Civico di Storia Naturale "Giacomo Doria," Genoa (MCSNG), Italy; Museum of Comparative Zoology (MCZ), Harvard University, Cambridge, MA; Museum of Hebei University (MHU), China; Muséum National d'Histoire Naturelle (MNHN), Paris, France; Musée Royal d'Histoire Naturelle de Belgique (MRHNB), Brussels, Belgium; Naturhistorisches Museum Wien (NHMW), Vienna, Austria; KwaZulu-Natal Museum (NM), Pietermaritzburg, South Africa; Naturhistoriska Museet, Göteborg (NMG), Sweden; Naturhistoriska Riksmuseet (NRS), including the Julio Ferrer Collection (JF), Stockholm, Sweden; Pakistan Museum of Natural History (PMNH), Islamabad; Naturalis, the Rijksmuseum van Natuurlijke Historie (RMNH), Leiden, incorporating the collection of the Instituut voor Taxonomische Zoologie (Zoologisch Museum), Amsterdam (ZMA), the Netherlands; Iziko South African Museum (SAM), Cape Town, including the John Visser Collection (JV); Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt (SMF), Germany; Ditsong National Museum of Natural History (former Transvaal Museum) (TM), Pretoria, South Africa; United States National Museum of Natural History (USNM), Smithsonian Institution, Washington, DC; Western Australian Museum (WAM), Perth; Museum für Naturkunde, Berlin (ZMB), Germany; Zoologisches Institut und Zoologisches Museum, Universität Hamburg (ZMH), Hamburg, Germany; Natural History Museum of Denmark, Copenhagen (ZMUC); Zoological Survey of India (ZSI), Kolkata; Zoological Survey of India, Freshwater Biological Regional Center, Arachnid Section (ZSI/FBRC/A), Hyderabad. Tissue samples are stored at -150°C in the Ambrose Monell

Cryocollection for Molecular and Microbial Research (AMCC) at the AMNH.

GEOREFERENCING: All records of sufficient accuracy were isolated from the material examined, published literature, and virtual museums, e.g., iNaturalist (<https://www.inaturalist.org>), to create a point locality geographical dataset for mapping distributional ranges. Records for which geographical coordinates were previously entered by the collector were checked for accuracy and the remaining records georeferenced using the GEONet Names Server (<http://earth-info.nga.mil/gns/html/namefiles.htm>), Fuzzy Gazetteer (<http://isodp.hof-university.de/fuzzyg/query>) and Google Earth. Distribution maps were produced using ArcMap version 10.1 (Environmental Systems Research Institute, Redlands, CA), by superimposing point locality records on the GTOPO30 global digital elevation model (<https://lta.cr.usgs.gov/GTOPO30> from http://webmap.ornl.gov/wcs-down/wcsdown.jsp?dg_id=10003_1).

MICROSCOPY AND IMAGING: Specimens were examined with Nikon SMZ1500 and Leica MZ16 stereo dissecting microscopes. Photographs were taken in visible light as well as under long-wave UV light using a Microoptics™ ML-1000 digital photomicrography system.

MORPHOLOGY: The key and diagnoses are based on characters of the external morphology considered informative among the Asian scorpionid taxa. For example, unlike most African Scorpionidae, trichobothrial counts and patterns are rather uninformative among Asian Scorpionidae (Prendini et al., 2003). Male hemispermatophores were also not studied in detail among the Asian Scorpionidae due to the limited number of adult males, which are unknown for

FIGURE 7. Representative habitats of Asian forest scorpions (Scorpionidae: Heterometrinae Simon, 1879, stat. nov.). **A.** Khambatki Ghat, India, habitat of *Chersonesometrus fulvipes* (C.L. Koch, 1837), comb. nov., and *Deccanometrus xanthopus* (Pocock, 1897), comb. nov. **B.** Tirumalai Hills, India, habitat of *Chersonesometrus tristis* (Henderson, 1919), comb. nov. **C.** Sanapura, India, habitat of *Chersonesometrus hendersoni*, sp. nov. **D.** Mayureshwar, India, habitat of *Deccanometrus xanthopus* (Pocock, 1897), comb. nov. **E.** Sai Yok, Thailand, habitat of *Heterometrus laevigatus* (Thorell, 1876), comb. nov. et stat. rev. **F.** Tham Xe Bang Fai, Laos, habitat of *Heterometrus laoticus* Couzijn, 1981. **G.** Achanakmar Tiger Reserve, India, habitat of *Deccanometrus phipsoni* (Pocock, 1893), comb. nov. **H.** Udawattakele, Sri Lanka, habitat of *Srilankametrus indus* (DeGeer, 1778), comb. nov.



TABLE 2

Southeast Asian Countries, Major Islands, and Archipelagoes with Records of Asian Forest Scorpions
(Scorpionidae: Heterometrinae Simon, 1879, stat. nov.)

		<i>Heterometrus glaucus</i>	<i>Heterometrus laevigatus</i>	<i>Heterometrus laoticus</i>	<i>Heterometrus longimanus</i>	<i>Heterometrus petersii</i>	<i>Heterometrus silenus</i>	<i>Heterometrus spinifer</i>	<i>Heterometrus thorelli</i>	<i>Javaninetrus cyaneus</i>
Brunei					X					
Cambodia				X			X			
China	Hainan						?			
India	Andaman Islands				X					
	Nicobar Islands	X								X
Indonesia	Babi	X								
	Bali									X
	Bangka				X					
	Batu Islands	X								
	Belitung, Bengkalis				X					
	Borneo (Kalimantan)				X					
	Java, Madura				X					X
	Mentawai Islands	X								
	Miang-Besar				X					
	Nias	X								X
	Riau Islands				X					
	Siberut, Weh	X								
	Simeulue	X			X					
	Sumatra	X			X					X
Laos				X						
Malaysia	mainland				X			X		
	Borneo (Sarawak, Sabah)				X					X
	Langkawi		X							
	Penang					X				
	Tinggi				X					
	Tioman							X		
Myanmar	mainland		X						X	
	Myeik (Mergui) Islands		X							
Philippines	Balabac				X					
	Luzon				X					X
	Mindanao, Palawan, Panay				X					
	Sulu Islands (Tawi Tawi)				X					
Singapore						X				
	Pulau Ubin				X					
Thailand	mainland		X	X						X
	Ko Chang			X						
	Ko Lanta		X							
	Ko Muk									X
	Ko Samui, Phi Phi Islands, Phuket		X							
Vietnam	mainland						X			
	Phù Quoc Island						X			



several species or represented only by type material, which could not be dissected.

Morphological terminology follows previous papers on Scorpionidae Latreille, 1802, by the first author (e.g., Prendini, 2000b, 2001a; Prendini et al., 2003; Tahir and Prendini, 2014; Prendini, 2016). The terminology applied in the new trichobothrial interpretation of *R. keralaensis*, proposed here, follows Vachon (1974).

A morphological data matrix, comprising 186 morphological characters (appendices 1, 2) scored for 132 terminals (including four outgroups) and incorporating characters from previously published matrices by Lamoral (1979), Couzijn (1981), Prendini (2000a), and Prendini et al. (2003), was prepared using WinClada ver. 1.00.08 (Nixon, 2002), and deposited in Morphobank (<http://morphobank.org/permalink/P3719>). Characters scored in the matrix included a variety of traits capturing the morphological diversity within Scorpionidae, most pertaining to the adult stage: total length, 1 (0.5%); chelicerae, 4 (2%); carapace, 30 (16%); pedipalps, 61 (32.5%); coxosternum, 1 (0.5%); legs, 33 (18%); genital operculum, 1 (0.5%); hemispermatophore, 3 (1.5%); pectines, 5 (3%); tergites, 5 (3%); sternites, 4 (2%); metasoma, 29 (16%); telson, 5 (3%); ecology and behavior, 3 (1.5%). The breakdown of morphological characters by character system is as follows: surface macrosculpture, 70 (38%); macrosetae, 32 (17%); color patterns, 19 (10%); shape and size, 29 (16%); surface topography, 13 (7%); trichobothria, 9 (5%); genitalia, 4 (2%); unguis, 3 (2%); sutures, 3 (2%); dentition, 1 (1%). Forty-seven (25%) multistate characters were treated as unordered/nonadditive (Fitch, 1971) to avoid a priori character state transformations.

DNA SEQUENCING: Two loci in the nuclear genome, the 18S rDNA (18S) and 28S rDNA (28S), and three loci in the mitochondrial genome, 12S rDNA (12S), 16S rDNA (16S), and cytochrome c oxidase subunit I (COI) were Sanger dideoxy sequenced using an ABI Prism 3730 XL DNA Sequencer (Perkin-Elmer, Melville, NY) at the AMNH Sackler Institute of Comparative Genomics. Double-stranded sequences were edited and assembled into consensus sequences using Sequencher ver. 5.4.6 (Gene Codes Corporation, Ann Arbor, MI), and deposited in GenBank (<https://www.ncbi.nlm.nih.gov/genbank>) (appendix 3). Sequences of the 18S, 28S, and COI loci were length invariant, respectively comprising 1761 nucleotide base pairs (bp), 514 bp, and 1078 bp in all terminals, except *Nebo hierichonticus* (Simon, 1872), which was 515 bp for 28S. Sequences of the 12S locus varied from 328–335 bp with a mode of 333 bp and the 16S locus from 481–487 bp with a mode of 481 bp. DNA sequences were unavailable for 10 species, for which samples could not be obtained; these were represented in the analyses by morphological characters only.

DNA SEQUENCE ALIGNMENT: DNA sequence alignment was performed with MAFFT ver. 7.429 by auto-aligning with the “leavegapregion” option selected (Katoh et al., 2002; Katoh and Standley, 2013). The aligned sequences were concatenated to produce a matrix of 4188 bp. The concatenated alignment contained 925 variable sites and 769 parsimony-informative sites. Considered as a percentage of the alignment length of each locus, the numbers of variable positions and parsimony-informative sites were highest for 12S (variable, 56%; parsimony informative, 48%), followed by 16S (49%, 40%), COI (40%, 36%), 28S (6%, 2%) and 18S (2%, 0.3%). As expected for a protein-cod-

FIGURE 8. Burrow entrances of selected species of Asian forest scorpions (Scorpionidae: Heterometrinae Simon, 1879, stat. nov.). **A.** *Deccanometrus obscurus* (Couzijn, 1981), comb. nov., Amboli, India. **B.** *Srilankametrus pococki*, sp. nov., Kodigala, Sri Lanka. **C.** *Chersonesometrus pelekomanus* (Couzijn, 1981), comb. nov. et stat. rev., Chitradurga, India. **D.** *Sahyadrimetrus rugosus* (Couzijn, 1981), comb. et stat. nov., Wayanad, India. **E.** *Chersonesometrus madraspatensis* (Pocock, 1900), comb. nov., Chittoor, India. **F.** *Heterometrus laoticus* Couzijn, 1981, Thakek, Laos. **G, I.** *Srilankametrus indus* (DeGeer, 1778), comb. nov., Udawattakele, Sri Lanka, multiple entrances (**G**), single entrance close-up (**I**). **H.** *Deccanometrus xanthopus* (Pocock, 1897), comb. nov., Mayureshwar, India.

ing gene, the third codon position of the COI was the most informative, containing 77% and 82% of the variable and parsimony-informative sites in the locus, followed by the first codon position, containing 19% and 15%, respectively.

PHYLOGENETIC ANALYSIS: The morphological character matrix and the concatenated dataset of aligned nuclear and mitochondrial DNA sequences (hereafter, “the molecular dataset”) were analyzed simultaneously using maximum likelihood (ML), Bayesian inference (BI), and parsimony with equal weighting and implied weighting (Goloboff, 1993), applying five values for the concavity constant, k , ranging from strong to mild ($k = 1, 3, 10, 60, 100$). The morphological and molecular datasets were also analyzed separately using parsimony with equal weighting and implied weighting with $k = 1, 3, 10, 60, 100$, and the molecular dataset was analyzed separately using ML and BI.

Parsimony analyses were performed using TNT ver. 1.1 (Goloboff et al., 2003, 2008), with a script from Dimitrov et al. (2012, 2013) modified by Santibáñez-López et al. (2014a), which includes tree drifting, mixed sectorial search, and tree fusing for the tree search. Gaps were treated as missing data and uninformative characters deactivated. A jackknife analysis was performed to evaluate nodal support using another script modified from Dimitrov et al. (2012). A bootstrap analysis was performed for comparison with 1000 pseudoreplicates.

The ML analysis was conducted using RAXML-HPC ver. 8.2.12 on the CIPRES gateway (<https://www.phylo.org>; Stamatakis, 2006, 2014). The dataset was partitioned by loci, a MULTIGAMMA model was implemented, and an ascertainment bias applied to the Mk model (Lewis, 2001) for the morphological partition. A rapid bootstrap analysis with 1000 replicates (Stamatakis, 2014) was used to search for the ML tree.

Twenty-four nucleotide substitution models were tested for each locus using JModeltest ver. 2.1.6 (Guindon and Gascuel, 2003; Darriba et al., 2012) on the CIPRES gateway. Models were selected using the Akaike information criterion (AIC) and a gamma distribution assumed for the morphological dataset (Lewis, 2001). Using these models, BI

was conducted in MrBayes v. 3.2.7 on the CIPRES gateway (Ronquist and Huelsenbeck, 2003) with unlinked parameters for all partitions. The analysis was terminated after 25 million generations when the standard deviation of the split frequencies was below 0.01. The preferred hypothesis for the phylogeny of Heterometrinae, with unambiguous morphological synapomorphies optimized, is presented in fig. 10. A more detailed explanation of the methods and results of the phylogenetic analyses is provided by Loria and Prendini (in press).

SYSTEMATICS

Family Rugodentidae Bastawade et al., 2005, stat. nov. et stat. rev.

Figures 11–14

Rugodentinae Bastawade et al., 2005: 77, 82, type genus by original designation: *Rugodentus* Bastawade et al., 2005; Sureshan et al., 2007a: 2903, 2905, 2908; Kovařík, 2009: 6, 28; Aswathi and Sureshan, 2017: 9844.
Pandininae: Rossi, 2016a: 7–9, 19 (part).

DIAGNOSIS: Rugodentidae can be placed unequivocally in the superfamily Scorpionioidea Latreille, 1802, based on the following combination of characters (Prendini, 2000a; Prendini et al., 2003): cheliceral movable finger with one subdistal tooth and without serrula; pedipalps with Type C trichobothrial pattern (femur with three trichobothria; patella with 19 or more; chela with 26 or more); retrolateral pedal spurs of telotarsi absent; pro- and retroventral macrosetae of telotarsi spiniform; genital opercula (♀) fused along the midline.

Rugodentidae can be separated from other scorpionoid families by the following combination of characters: pedipalp chela fingers with multiple primary rows of denticles; pedipalps Type C, neobothriotaxic major, with accessory trichobothrium in *e* series of patella; chela manus, trichobothrium *Db* located on dorsal surface; chela fixed finger, trichobothria *Dt* and *ib* located proximally, *it* distally, *db* on prolateral

surface, *eb* midway on finger, and *esb* in distal third; telotarsi I–IV each with pro- and retroventral rows of spiniform macrosetae, laterodistal lobes rounded; metasomal segments I–IV each with paired ventrosubmedian carinae, segment V with transverse carina; telson vesicle not laterally compressed, without anterodorsal lateral lobes and subaculear tubercle.

SUPPLEMENTARY DESCRIPTION: The following summary is based on a reinterpretation of the description and illustrations of Bastawade et al. (2005), reproduced in figs. 11 and 12, supplemented by images 24 and 25 in Aswathi and Sureshan (2017: 9849) and live habitus (fig. 13). Carapace with median notch in anterior margin; median longitudinal sulcus narrow, with anterior bifurcation. Three pairs of lateral ocelli (MLMa, PLMa, PDMi). Median ocular tubercle raised. Cheliceral movable finger prodistal (DI) and retrodistal (DE) teeth unequal, DE tooth considerably smaller than DI tooth (less than half its length), aligned longitudinally and not opposable. Pedipalp patella prolateral process obsolete; retrodorsal and retrolateral carinae obsolete. Pedipalp chela dorsal secondary, subdigital, digital, retromedian, ventromedian, proventral and promedian carinae obsolete; retroventral carina distinct, parallel to longitudinal axis of chela, with distal edge directed toward a point between pro- and retroventral movable finger condyles, but closer to retroventral condyle. Pedipalp chela fingers with multiple primary rows of denticles. Pedipalps Type C, neobothriotaxic major, with accessory trichobothrium in *e* series of patella. Pedipalp chela with trichobothrium *Db* located on dorsal surface of manus; *Et*₂ located on retrolateral surface of manus; *db* located on prolateral surface of fixed finger; *Est* located distally on manus; *Dt* and *ib* located proximally on fixed finger; *eb* located midway on fixed finger, proximal to or aligned with *db* and dorsal to *esb*–*est*–*et* axis; *esb* located in distal third of fixed finger, aligned with *est*–*et* axis; *it* located distally on fixed finger. Sternum longer than wide, pentagonal. Telotarsi I–IV each with pro- and ret-

roventral rows of spiniform macrosetae; laterodistal lobes rounded; retrolateral pedal spurs absent. Metasomal segments I–IV each with paired ventrosubmedian carinae; segment V with transverse carina. Telson vesicle not laterally compressed and without anterodorsal lateral lobes; aculeus long, shallowly curved, without subaculear tubercle.

INCLUDED TAXA: This family accommodates the monotypic genus, *Rugodentus* Bastawade et al., 2005, stat. rev.

DISTRIBUTION: This family is endemic to the state of Kerala, India (fig. 14).

REMARKS: The monotypic Indian scorpionoid genus, *Rugodentus*, was recently synonymized with *Heterometrus*, creating a new homonym, *Heterometrus keralaensis* Bastawade et al., 2005, for which the name *Heterometrus bastawadei* Rossi, 2016, was devised. Rossi (2016a: 19) presented the following argument for synonymizing *Rugodentus*:

the subfamily Rugodentinae and its unique genus *Rugodentus* Bastawade, Sureshan et Radhakrishnan, 2005 are rejected and synonymized respectively with subfamily Pandininae and genus *Heterometrus* because the only difference proposed by their authors, e. g., the granulation on pedipalp chela fingers (Bastawade et al., 2005), is a character usually present in many species of the family Scorpionidae, confirmed by the great number of specimens and species examined during the present study.

This argument is inconsistent with other changes in Rossi's (2016a) "revised classification" of Scorpionidae, among them the revalidation of *Protophthalmus* Lawrence, 1969, which contradicts the phylogenetic analyses of Lamoral (1978a, 1979), based on morphology, and subsequent analyses of Prendini et al. (2003), based on morphology and DNA sequences from the nuclear and mitochondrial genomes. Furthermore, Rossi's (2016a) arguments are unsupported by the evidence. The diagnostic characters of *Rugodentus* are inconsistent not only with the diagnosis of *Heterometrus* but with the diagnosis of Scorpionidae (Prendini, 2000a; Prendini et al., 2003), revealing that *Rugodentus* lacks the syn-

apomorphies of either, and shares potential synapomorphies with several other families.

Although a comparative diagnosis was not presented, Bastawade et al. (2005: 82) justified the new subfamily, genus, and species as follows:

Rugodentus keralaensis is described as a new species under a new genus and a new subfamily on the basis of the peculiar dentition on pedipalp fingers, which is apparently unknown in the known subfamily Scorpioninae. None of the Indian species show such character. Based on the pedipalp character, a new subfamily Rugodentinae is described with the new type genus *Rugodentus*. The genus has been designated based on a new type species *Rugodentus keralaensis*.

As correctly described and illustrated (fig. 11B) by Bastawade et al. (2005: 79, 80, figs. 2, 10, 14, 16), the dentition of the pedipalp chela fingers is indeed unlike that observed in *Heterometrus* or other Scorpionidae:

immovable finger ... scalloped at the base and lined with irregularly spread granular teeth in a band (Fig. 16); movable finger ... inner surface with a band of granular dentition, scalloped deeply at the base (Fig. 2).

This was confirmed in photographs published subsequently by Aswathi and Sureshan (2017: 9847, 9849, images 24, 25), who described the dentition as “rugously granular ... in a band along the interior surface.”

The dentition described and illustrated (fig. 11B) most closely resembles the “multiple rows” condition (Stockwell, 1989; Prendini, 2000a) observed in three genera of Bothriuridae Simon, 1880, i.e., the Australian *Cercophonius* Peters, 1861, and South American *Centromachetes* Lönnberg, 1897, and *Urophonius* Pocock, 1893, and in the Australian Urodacidae Pocock, 1893, and Malagasy Heteroscorpionidae Kraepelin,

1905, two families erroneously synonymized by Soleglad et al. (2005), as discussed by Volschenk and Prendini (2008). Additionally, the dentate margins of the fixed and movable fingers (gently scalloped, with lobes and corresponding notches conspicuously absent) of *Rugodentus* (Bastawade et al., 2005: 79, 80, figs. 2, 10, 14, 16; Aswathi and Sureshan, 2017: 9849, image 25) are unlike those of *Heterometrus* or other Scorpionidae, in which a series of pronounced lobes and corresponding notches are evident in the fixed and movable fingers (Prendini, 2000a, 2016; Prendini et al., 2003). The dentate margins of the fixed and movable fingers of *Rugodentus* are more akin to those observed in other families, e.g., Bothriuridae, Heteroscorpionidae, Urodacidae, and the Middle Eastern Hemiscorpiidae Pocock, 1893, another family misconstrued by Soleglad and Fet (2003a), Fet and Soleglad (2005), and Soleglad et al. (2005), as discussed by Monod and Prendini (2014).

Furthermore, unlike *Heterometrus*, in which the pedipalps are orthobothriotaxic (Prendini et al., 2003), the pedipalps of *Rugodentus* are neobothriotaxic (fig. 12), with an accessory *e* trichobothrium on the patella (14 trichobothria are present on the retrolateral surface in *Rugodentus* whereas only 13 are present in *Heterometrus*). Accessory *e* trichobothria on the pedipalp patella occur in all African scorpionid genera except *Scorpio* as well as in Heteroscorpionidae and Urodacidae, some Iranian species of Hemiscorpiidae, the South American bothriurid genera, *Timogenes* Simon, 1880, and *Vachonia* Abalos, 1954, the Mexican diplocentrid genus, *Kolotl* Santibáñez-López et al., 2014, the African hormurid genus, *Hadogenes* Kraepelin, 1894, and

FIGURE 9. Representative species of Asian forest scorpions (Scorpionidae: Heterometrinae Simon, 1879, stat. nov.), habitus in life. **A.** *Chersonesometrus fulvipes* (C.L. Koch, 1837), comb. nov., ♂, Jaipur, Rajasthan, India. **B.** *Chersonesometrus tristis* (Henderson, 1919), comb. nov., ♂, Chittoor, Andhra Pradesh, India. **C.** *Deccanometrus xanthopus* (Pocock, 1897), comb. nov., ♂, Andori, Maharashtra, India. **D.** *Gigantometrus swammerdami* (Simon, 1872), comb. nov., ♂, Korpall, Chhattisgarh, India. **E.** *Heterometrus laevigatus* (Thorell, 1876), comb. nov. et stat. rev., ♂, Dawei, Tanintharyi Region, Myanmar. **F.** *Javanimetrus cyaneus* (C.L. Koch, 1836), comb. nov., ♂, Pangandaran National Park, West Java Prov., Indonesia. **G.** *Sahyadrimetrus kanarensis* (Pocock, 1900), comb. nov., ♂, Fort Cabo de Rama, Goa, India. **H.** *Srilankametrus indus* (DeGeer, 1778), comb. nov., ♀, Laggala-Pallegama, Matale, Central Prov., Sri Lanka.



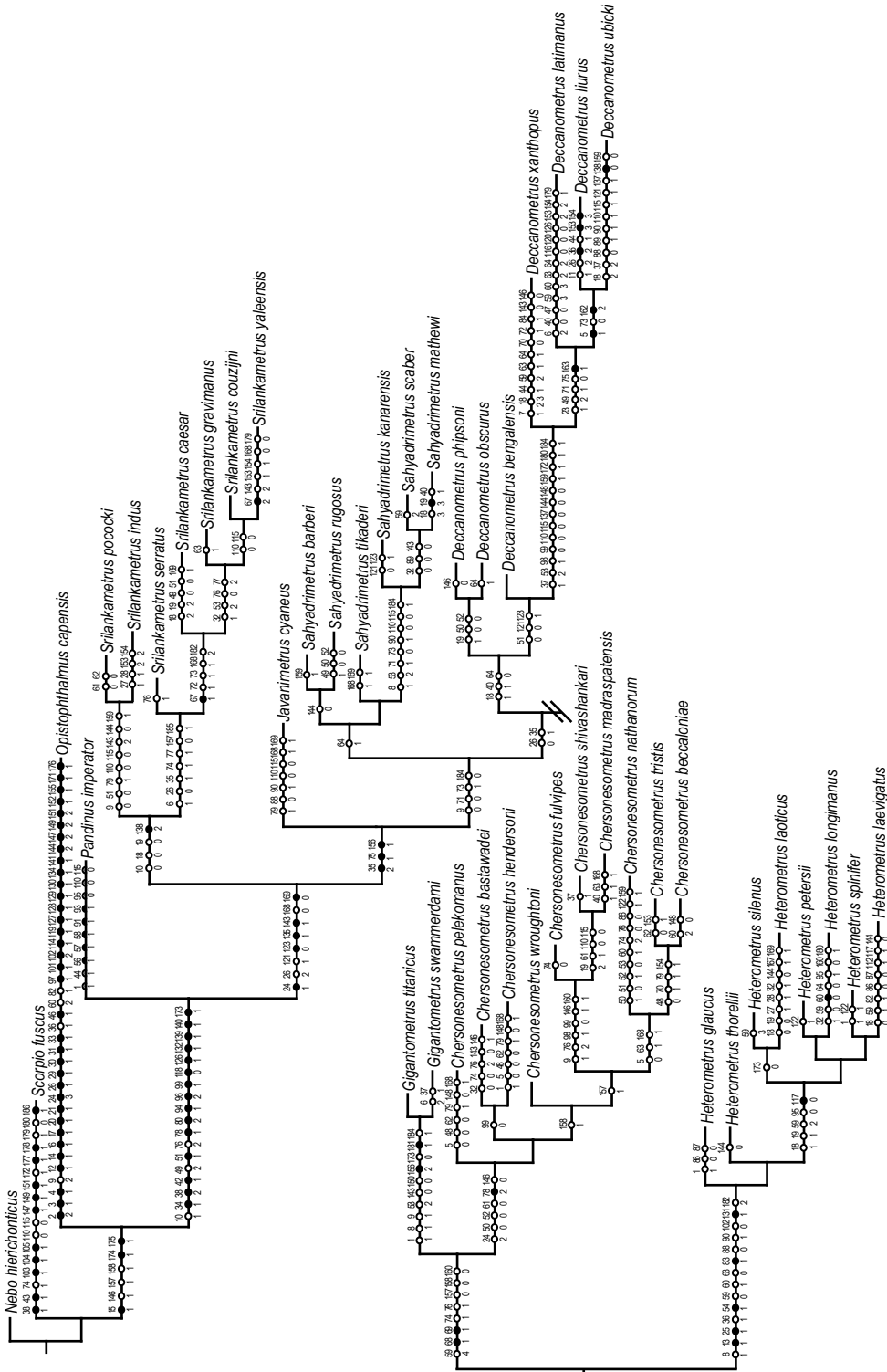


FIGURE 10. Phylogeny of Asian forest scorpions (Scorpionidae: Heterometrinae Simon, 1879, stat. nov.), obtained by simultaneous phylogenetic analysis of 186 morphological characters and 4188 aligned DNA nucleotides from three mitochondrial and two nuclear gene loci (Loria and Prendini, in press). Maximum likelihood tree with unambiguous morphological synapomorphies optimized. Black circles indicate uniquely derived apomorphic states, white circles parallel derivations of apomorphic states. Numbers above circles indicate characters, numbers below indicate states (appendix 1).

some Neotropical species of the hormurid genus, *Opisthacanthus* Peters, 1861 (Prendini, 2000a; Monod and Lourenço, 2005; Santibáñez-López et al., 2014b; Kovařík et al., 2017a).

Indeed, the trichobothrial pattern of the pedipalp chela appears to be unique to *Rugodentus*. *Rugodentus* (fig. 12) is unlike any other scorpionoid in the relatively distal positions of trichobothria *eb* and *esb*, situated midway on the fixed finger and in its distal third, respectively. *Rugodentus* is also the only scorpionoid in which trichobothrium *Dt* is situated proximally on the fixed finger, as in Diplocentridae Karsch, 1880, and Hemiscorpiidae, and *it* situated distally on the fixed finger, as in the Middle Eastern diplocentrid genus, *Nebo* Simon, 1878. Neither character is exhibited by Scorpionidae (Prendini, 2000a), with which Diplocentridae was erroneously synonymized by Soleglad and Fet (2003a) and Fet and Soleglad (2005). Additionally, trichobothrium *Db* is situated on the dorsal surface of the manus in *Rugodentus*, a character otherwise unique to Hemiscorpiidae and Scorpionidae, whereas *db* is situated on the prolateral surface of the fixed finger in *Rugodentus*, as in Diplocentridae, Hemiscorpiidae, Scorpionidae, and most Hormuridae Laurie, 1896, rather than on its dorsal surface, as in Bothriuridae, Heteroscorpionidae, Urodacidae, and some Hormuridae (Prendini, 2000a).

Finally, the ventral surface of metasomal segment V bears a distinct transverse carina in *Rugodentus* (fig. 11I), described as a “granular transverse submarginal ridge present only on inferior portion,” and illustrated by Bastawade et al. (2005: 79, 81, fig. 9). This character, observed in most genera of Diplocentridae and some Bothriuridae, e.g., *Bothriurus* Peters, 1861, *Timo- genes* and *Vachonia*, is also absent among Scorpionidae (Prendini, 2000a, 2003).

Rugodentus lacks a key diagnostic character of Scorpionidae (Prendini, 2000a; Prendini et al., 2003): i.e., pedipalp chela dorsal secondary carina partially developed, extending partway across dorsal surface of manus, subdigital carina

partially developed, extending partway across manus in opposite direction.

One character that *Rugodentus* shares with Scorpionidae is the presence of rounded laterodistal lobes on the leg telotarsi (fig. 11D), described as “tarsus ... lateral distal margin partly overlapping the base” and illustrated by Bastawade et al. (2005: 79, 81, fig. 4), but this character also occurs in Diplocentridae and Urodacidae (Prendini, 2000a).

Several other aspects of the habitus of *Rugodentus* are also noteworthy (figs. 11–13). The shape of the carapace (e.g., the truncate anterior margin) and the pedipalp chelae (described as “globular” by Aswathi and Sureshan, 2017: 9849) resemble some Bothriuridae and Urodacidae, rather than Scorpionidae, and the robust metasoma and shape of the telson also resemble some Bothriuridae, e.g., *Centromachetes*.

It is clear from the preceding discussion that *Rugodentus* is a valid genus that is neither con-familial with Scorpionidae nor with any other scorpionoid family but appears most closely allied to Diplocentridae, Scorpionidae, and Urodacidae. Kovařík (2009: 6, 28) likewise doubted the placement of *Rugodentus* in Scorpionidae but failed to suggest an alternative:

The key does not include the genus *Rugodentus* Bastawade et al., 2005 from India, for which the authors formed the subfamily Rugodentinae and assigned it to the family Scorpionidae Latreille, 1802. Unfortunately, the original description does not contain characters which would allow to place this genus in the key. The validity and taxonomic position of this genus can be ascertained only upon examination and redescription of the types.

Subfamily Rugodentinae Bastawade et al., 2005, is hereby elevated to the rank of family, Rugodentidae Bastawade et al., 2005, genus *Rugodentus* Bastawade et al., 2005, and its type species *Rugodentus keralaensis* Bastawade et al., 2005, are revalidated, and the following new synonym is presented: *Heterometrus bastawadei* Rossi, 2016 = *Rugodentus keralaensis* Bastawade et al., 2005.

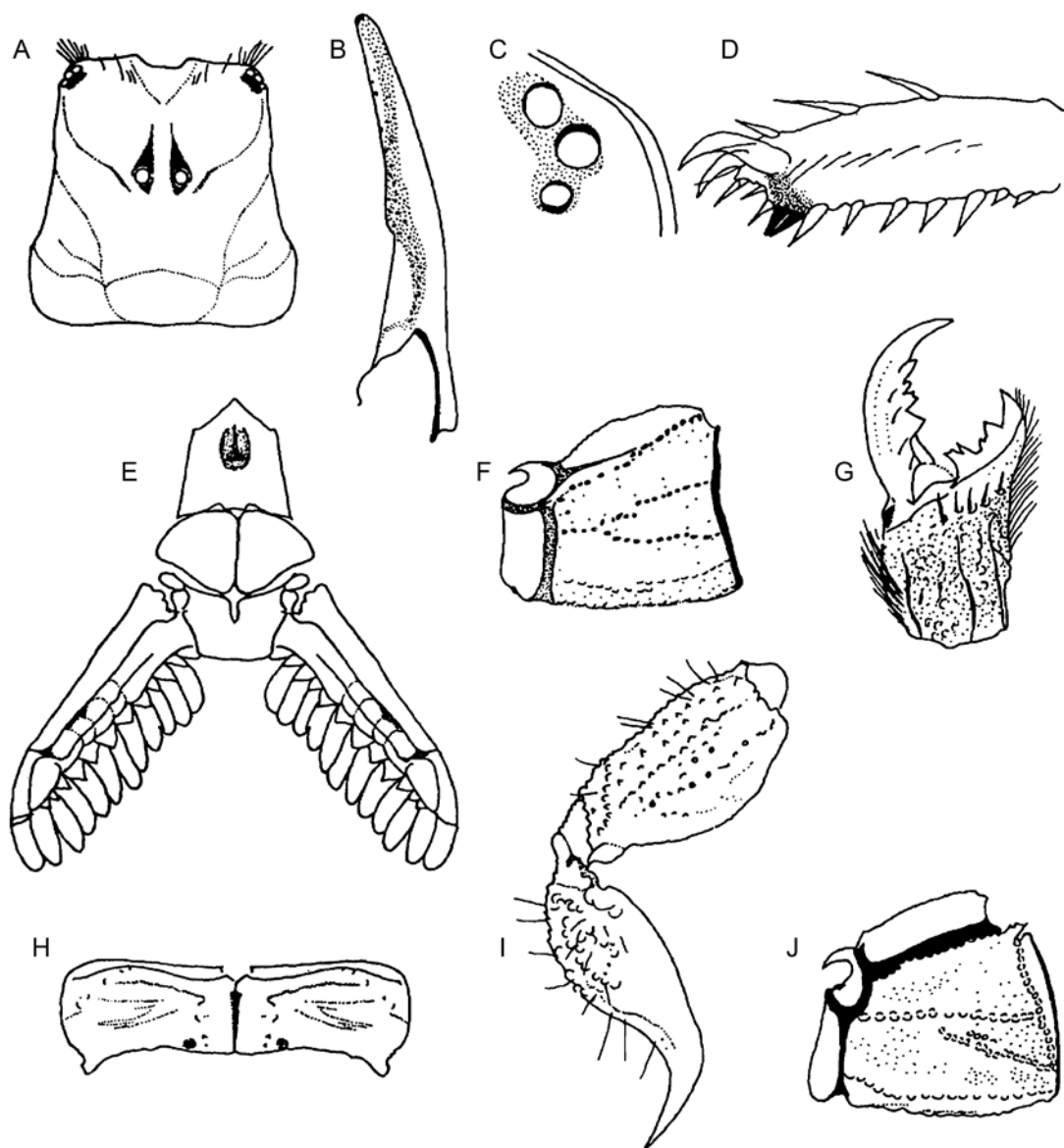


FIGURE 11. *Rugodentus keralaensis* Bastawade et al., 2005, stat. rev., holotype ♂ (ZSI 11002), diagnostic characters reproduced from Bastawade et al. (2005: 79, figs. 1–11). **A**. Carapace, dorsal aspect. **B**. Dextral pedipalp chela movable finger, dorsal aspect. **C**. Carapace, lateral ocelli, prodorsal aspect. **D**. Telotarsus, retrolateral aspect. **E**. Sternum, genital operculum and pectines, ventral aspect. **F**. Metasomal segment I, lateral aspect. **G**. Sinistral chelicera, dorsal aspect. **H**. Mesosomal tergite, dorsal aspect. **I**. Metasomal segment V and telson, lateral aspect. **J**. Metasomal segment II, lateral aspect.

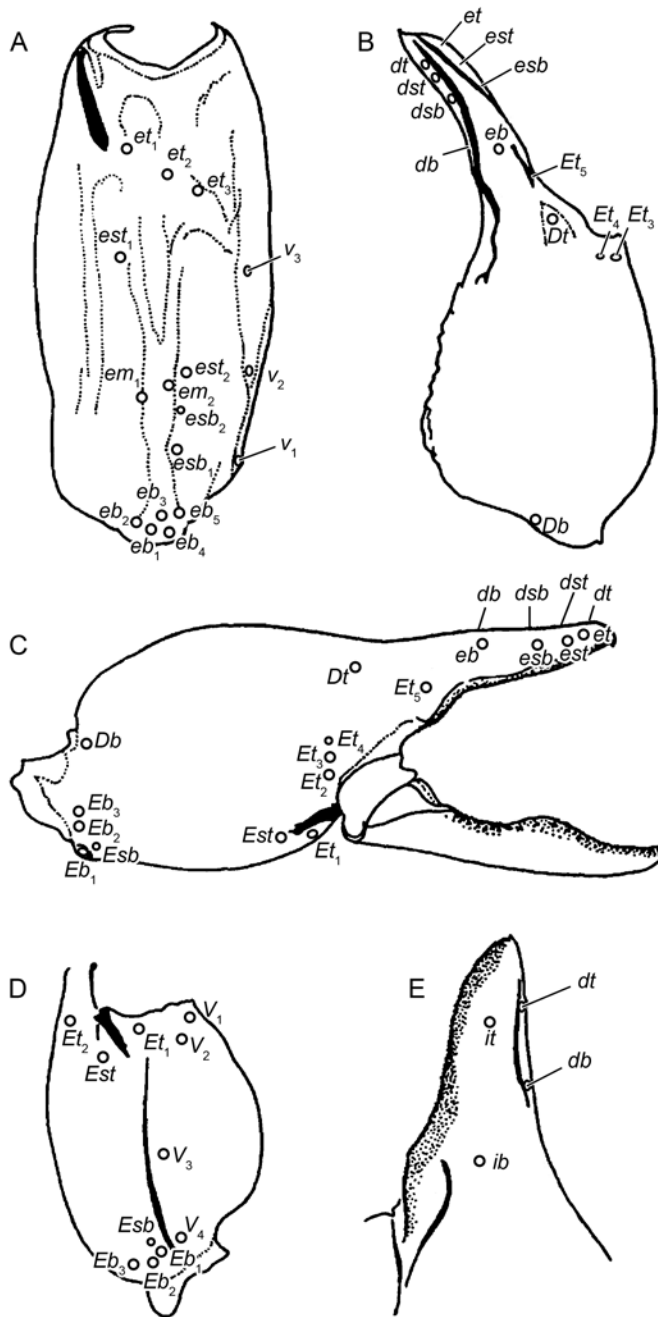


FIGURE 12. *Rugodentus keralaensis* Bastawade et al., 2005, stat. rev., holotype ♂ (ZSI 11002), dextral pedipalp patella (A) and chela (B–E), reproduced from Bastawade et al. (2005: 80, figs. 12–16), with new trichobothrial interpretation proposed here (terminology follows Vachon, 1974). A, C. Retrolateral aspect. B. Dorsal aspect. D. Ventral aspect. E. Prolateral aspect.

Rugodentus Bastawade et al., 2005, stat. rev.

Figures 11–14

Rugodentus Bastawade et al., 2005: 77–82, type species by original designation: *Rugodentus keralaensis* Bastawade et al., 2005; Sureshan et al., 2007a: 2903, 2908; Kovařík, 2009: 6, 28; Javed et al., 2010a: 143; Mirza et al., 2012: 1; Aswathi and Sureshan, 2017: 9844, 9847.

Heterometrus: Rossi, 2016a: 6–9, 15, 19, 20, 25 (misidentification).

DIAGNOSIS: As for family.

INCLUDED SPECIES: *Rugodentus keralaensis* Bastawade et al., 2005, stat. rev.

DISTRIBUTION: As for family.

Rugodentus keralaensis Bastawade et al., 2005, stat. rev.

Figures 11–14

Rugodentus keralaensis Bastawade et al., 2005: 77–82, figs. 1–16, photo 1; Sureshan et al., 2007a: 2903, 2905–2908, fig. 1; Aswathi and Sureshan, 2017: 9844, 9847, 9849, images 24, 25.

Heterometrus bastawadei Rossi, 2016a: 7–9, 25, syn. nov.

TYPE MATERIAL: **INDIA: Kerala:** *Ernakulam Distr.*: Holotype ♂ (ZSI 11002), Kodanad [10°11'N 76°31'E], Mallana Reserve Forest, 12.ii.1999, P.M. Sureshan.

It is unclear whether the holotype is lost. Attempts to locate it in the ZSI collections (D.B. Bastawade, in litt.) were unsuccessful.

DIAGNOSIS: As for family.

DISTRIBUTION: This species is endemic to India and currently known only from the Ernakulam District of Kerala (fig. 14).

ECOLOGY: The known localities are situated in wet, lowland rainforest in the foothills of the Western Ghats. According to P. Jain (personal commun.), these fossorial scorpions were

observed retreating into burrows at night under UV light. The habitat and habitus (Bastawade et al., 2005: 83, pl. 1; fig. 12) are consistent with the pelophilous ecomorphotype (Prendini, 2001b), like most Diplocentridae, Scorpionidae, and Urodacidae, and many Bothriuridae. This species is sympatric with the buthid *Reddyanus brachycentrus* (Pocock, 1899) and the scorpionid *Sahyadrimetrus mathewi* gen. et sp. nov.

Family Scorpionidae Latreille, 1802

Figures 1–10, 15–251, tables 1–5

Scorpionides Latreille, 1802: 46, 47 (part), type genus: *Scorpio* Linnaeus, 1758; 1804: 110 (part); 1806: 130 (part); 1810: 116, 118 (part); Leach, 1814: 412; 1815: 390; Sundevall, 1833: 29 (part).

Scorpiones: Ehrenberg in Hemprich and Ehrenberg, 1828, pl. I, figs. 1, 2 (family, part).

Buthides: C.L. Koch, 1837: 36, 37 (part).

Centrurides C.L. Koch, 1837: 38 (part), type genus: *Centrurus* Ehrenberg, 1829 [= *Heterometrus* Ehrenberg, 1828].

Pandinoidae Thorell, 1876a: 11 (part), type genus: *Pandinus* Thorell, 1876; 1876b: 83 (part); Karsch, 1879a: 19 (part); Thorell and Lindström, 1885: 25 (part).

Heterometridae Simon, 1879: 92, 115, type genus: *Heterometrus* Ehrenberg, 1828 (part) [= *Scorpio* Linnaeus, 1758].

Scorpionidae: Lankester, 1885: 379 (part); Pocock, 1893: 305, 306 (part); Kraepelin, 1894: 8 (part); Laurie, 1896b: 128 (part); Kraepelin, 1899: 96 (part); Pocock, 1900a: 11, 84; Kraepelin, 1901: 270 (part); 1905: 343 (part); 1913: 165; Birula, 1917a: 161 (part); 1917b: 58, 59 (part); Kopstein, 1921: 128; Pavlovsky, 1924a: 78 (part); 1925: 190, 191, 195 (part); Kopstein, 1926: 111; Fage, 1933: 27; Werner, 1934: 275 (part); Fage, 1936: 179, 181; Kästner, 1941: 232 (part); Fage, 1946: 73; Millot and Vachon, 1949: 428 (part); Petrunkevitch, 1955: 75; Bücherl,

1964: 59 (part); 1967: 114 (part); Tikader, 1973: 263; Stahnke, 1974: 339 (part); L.E. Koch, 1977: 159 (part); Lamoral, 1980: 440 (part); Levy and Amitai, 1980: 102 (part); Couzijn, 1981: 4, 5, 20; Francke, 1982: 75 (part); Tikader and Bastawade, 1983: 2, 3, 27, 32, 517, 518, fig. 45; Biswas, 1984: 318, 320, 321; Francke, 1985: 18; Lourenço, 1989: 161, 174; Sissom, 1990: 131; Nenilin and Fet, 1992: 5 (part); Kovařík, 1997: 183; 1998: 136; Lourenço, 1999: 929 (part); Fet, 2000: 427, 428 (part); Lourenço, 2000: 25; Prendini, 2000a: 34, 35, 39, 44; Indra, 2001: 55, 56; Bastawade, 2002: 295; Lourenço and Huber, 2002: 273; Kovařík, 2003: 136, table 1; Prendini et al., 2003: 185–189, 192–194, 206, 209, 210, 212, 217, 220, 223, 226, 230, 235, 250, 252–259, tables 1, 3, 4, 6, figs. 1–3, 8, appendices 1, 2; Soleglad and Fet, 2003a: 1, 3, 4, 5, 8, 29, 56, 58, 59, 61, 67, 71, 75, 84, 86, 88, 111–117, 119–121, 138, 139, 141, 145, 148, tables 1, 9, 11, figs. 114, 126, appendices A, B (part); 2003b: 2, 5, 8, 18, 25, 31, table 1, figs. 5, 22; Bastawade, 2004: 286, 290; Bastawade et al., 2004: 43, 44, 47, 49, 56, 57, figs. 6, 10; Bastawade, 2005: 411, 417; Fet and Soleglad, 2005: 9, 13 (part); Prendini, 2005: 28, 29, 32–36, tables 1, 2, figs. 1, 2; Prendini and Wheeler, 2005: 447, 448, 449, 471, 477, 481, 482, 491, tables 2, 10, appendix 1; Soleglad et al., 2005: 1, 2, 4, 6, 8, 14–17, 19, 20, 21, 23–26, 28–30, 32, 33–35, tables 1, 4, 6, figs. 37–39, 68–70, 72–74 (part); Thulsi Rao et al., 2005: 3, 8; Bastawade, 2006a: 131; Indra, 2006: 197, 199; Sureshan et al., 2007a: 2903, 2905; 2007b: 49, 52; Wirkner and Prendini, 2007: 402; Bastawade, 2008: 133, 136; Bastawade and Borkar, 2008: 212, 215, 218; Kamenz and Prendini, 2008: 6, 31, 33, table 1; Prendini and Bird, 2008: 77; Volschenk and Prendini, 2008: 242, 249; Volschenk et al., 2008: 653, 656, 669; Bastawade, 2009: 215, 219; Indra, 2009: 141; Kovařík, 2009: 6, 14,

15, 17, 18, 27, 28, 33 (part), fig. 8, pl. J; Prendini, 2009: 12; 16, 17, 22, 32, 34, 40, tables 1, 3, fig. 6; Javed et al., 2010a: 143; 2010b: 785; Michalik and Mercati, 2010: 96; Prendini, 2011: 117; Klußmann-Fricke et al., 2012: 549, 555, fig. 2; Mirza et al., 2012: 1; Di et al., 2013: 52, 86, 94; Veronika et al., 2013: 72, 76; Loria and Prendini, 2014: 5, 7, 12, 14, 16, 20, 21, 23, tables 2–4; Lourenço, 2014: 141; Amr et al., 2015: 30, 31; Rossi, 2015a: 11, 16, 21; Sharma et al., 2015: 2, 4, 5, 7, 8, table 1, figs. 1–4; Adams et al., 2016: 1, 7; Janion-Scheepers et al., 2016: 147; Rossi, 2016a: 7–9, 18, 20, 26; 2016b: 47; Aswathi and Sureshan, 2017: 9845, 9847; Esposito et al., 2017: 4, 14; Pham et al., 2017: 136; Esposito et al., 2018: 89, 90, 115, 116, appendix 1.

Pandinidae: Marx, 1890: 211.

DIAGNOSIS: Members of the family Scorpionidae can be placed unequivocally in the superfamily Scorpionoidea on the basis of the following characters (Prendini, 2000a; Prendini et al., 2003): retrolateral pedal spurs of telotarsi absent; pro- and retroventral macrosetae of telotarsi spiniform; genital opercula (♀) fused along the midline; paraxial organ (♂) with an internobasal reflection of the sperm duct. Additional characters that, in combination, place Scorpionidae unequivocally in the Scorpionoidea, are as follows (Prendini, 2000a; Prendini et al., 2003): cheliceral movable finger with one subdistal tooth and without serrula; pedipalps with Type C trichobothrial pattern (femur with three trichobothria; patella with 19 or more; chela with 26 or more); hemispermatophore lamelliform with distinct truncal flexure.

Scorpionidae can be separated from all other scorpionoid taxa by the following character: pedipalp chela with dorsal secondary carina partially developed, extending partway across dorsal surface of manus, and subdigital carina partially developed, extending partway across in opposite direction. Scorpionidae can also be separated

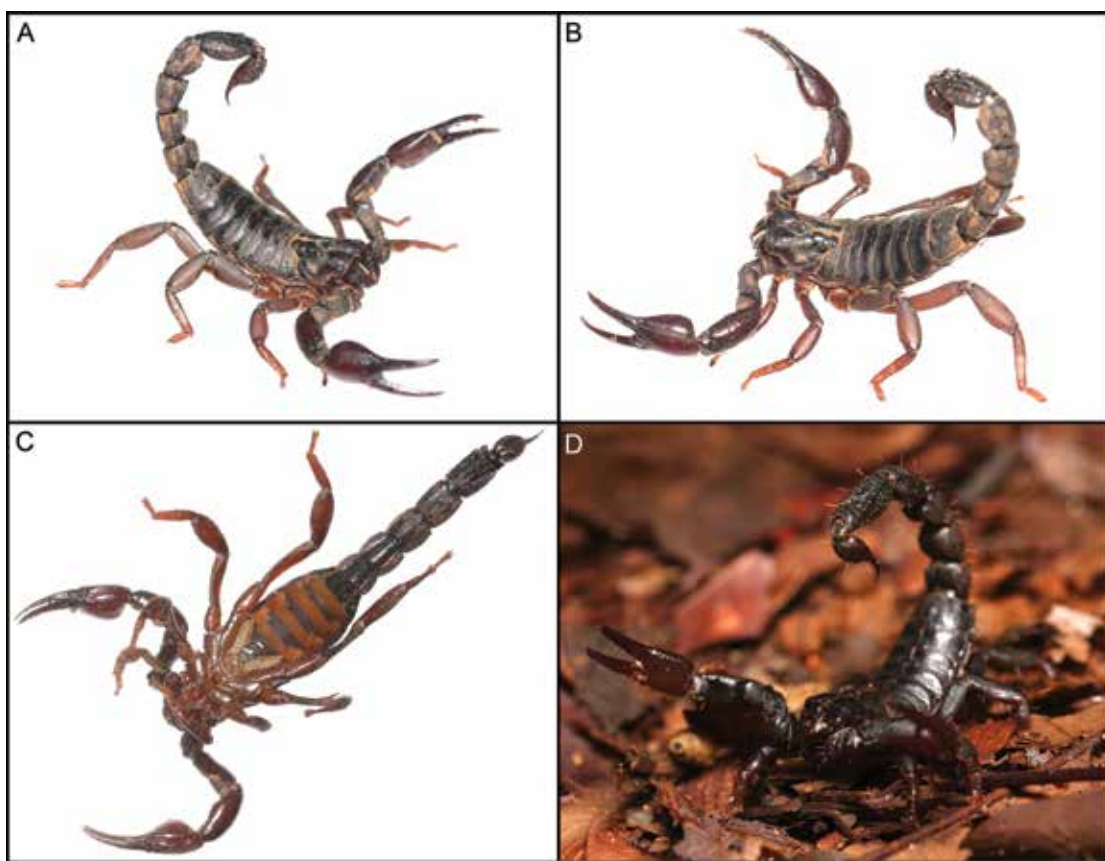


FIGURE 13. *Rugodentus keralaensis* Bastawade et al., 2005, stat. rev., ♀, Idukki, Kerala, India, habitus in life. **A, B.** Dorsolateral aspect. **C.** Ventral aspect. **D.** Anterolateral aspect, in vivo.

from all other scorpionoid taxa, except the diplocentrid subfamily Diplocentrinae Karsch, 1880, by the following characters: pedipalp chela with ventromedian carina more strongly developed than proventral and promedian carinae; promedian and proventral carinae equally developed (often obsolete); pedipalp patella with trichobothrium d_2 located on prolateral surface.

Characters separating Scorpionidae from particular scorpionoid families are as follows (Prendini, 2000a; Prendini et al., 2003): paired ventrosubmedian carinae of metasomal segments I–IV separate Scorpionidae from Hemiscorpiidae, Heteroscorpionidae and Urodacidae; rounded laterodistal lobes of the telotarsi separate Scorpionidae from Heteroscorpionidae and

Hormuridae; absence of a subaculear tubercle on the telson vesicle separates Scorpionidae from Diplocentrinae.

INCLUDED TAXA: As redefined in the present contribution, Scorpionidae comprises 18 genera and 152 species grouped into four extant subfamilies: Heterometrinae Simon, 1879, stat. nov.; Opisthophthalminae Rossi, 2016, stat. nov.; Pandininae Thorell, 1876; Scorpioninae Latreille, 1802.

DISTRIBUTION: Africa: Algeria, Angola, Benin, Botswana, Burkina Faso, Cameroon, Central African Republic, Chad, Congo, Côte d'Ivoire, Democratic Republic of Congo, Egypt, Equatorial Guinea (including Bioko Island), Eritrea, Ethiopia, Gabon, the Gambia, Ghana, Guinea, Guinea-Bissau, Kenya, Lesotho, Liberia, Libya, Malawi, Mali, Mauritania,

Morocco, Mozambique, Namibia, Nigeria, Senegal, Sierra Leone, Somalia, South Africa, Sudan, Swaziland, Tanzania, Togo, Tunisia, Zambia, Zimbabwe. Asia: Bangladesh, Brunei, Cambodia, India (including the Andaman and Nicobar islands), Indonesia, Iran, Iraq, Israel and the Palestinian territories, Jordan, Kuwait, Laos, Lebanon, Malaysia, Myanmar, Nepal, the Philippines, Qatar, Saudi Arabia, Somalia, Singapore, Sri Lanka, Syria, Thailand, Turkey, Vietnam, Yemen.

Heterometrinae are endemic to Asia, with greatest species richness and endemism in India, followed by Indonesia. Opisthophthalminae are endemic to Africa, with greatest species richness and endemism in South Africa, followed by Namibia. Pandininae are near endemic to Africa (including the Arabian Peninsula), with greatest species richness and endemism in Somalia. Scorpioninae is the most widespread scorpionid subfamily, extending from the West African countries of Benin and Senegal, across North Africa to Iran, but the greatest species richness and endemism occurs in Morocco. Only two scorpionid subfamilies occur in the same country and the greatest scorpionid species richness and endemism occurs in South Africa.

Key to the Subfamilies of Scorpionidae Latreille, 1802

1. Stridulatory organs, comprising a “rasp” (granular tubercles) and “scrapper” (stridulatory setae or scaphotrix), present on opposing surfaces of coxae of pedipalps and first pair of legs; counts of pro- and retroventral spiniform macrosetae similar on telotarsi I and II and on III and IV. 2
- Stridulatory organs absent from opposing surfaces of coxae of pedipalps and first pair of legs; counts of pro- and retroventral spiniform macrosetae increasing from telotarsi I and II to III and IV. 3
2. Pedipalps orthobothriotaxic, with 26 trichobothria (patella with 13 trichobothria in *e* series and 3 trichobothria in *v* series; chela with 4 trichobothria in *V* series and 2

trichobothria in *i* series); granular tubercles of “rasp” and stridulatory setae (scaphotrix) of “scrapper” situated on coxae of first leg and pedipalp, respectively.

- Heterometrinae Simon, 1879, stat. nov.
- Pedipalps neobothriotaxic major, with more than 26 trichobothria (patella with more than 13 trichobothria in *e* series and more than 3 trichobothria in *v* series; chela usually with more than 4 trichobothria in *V* series and often with more than 2 trichobothria in *i* series); granular tubercles of “rasp” and stridulatory setae (scaphotrix) of “scrapper” situated on coxae of pedipalp and first leg, respectively. Pandininae Thorell, 1876
- 3. Pedipalps neobothriotaxic, with more than 26 trichobothria (patella with more than 13 trichobothria in *e* series and often more than 3 trichobothria in *v* series; chela rarely with more than 4 trichobothria in *V* series); cheliceral coxae usually with stridulatory setae (scaphotrix) on prodorsal surfaces and chemoreceptive lamelliform setae (trichocopae) on promedian surfaces.
- ... Opisthophthalminae Rossi, 2016, stat. nov.
- Pedipalps orthobothriotaxic, with 26 trichobothria (patella with 13 trichobothria in *e* series and 3 trichobothria in *v* series; chela with 4 trichobothria in *V* series); cheliceral coxae without stridulatory setae (scaphotrix) on prodorsal surfaces and without chemoreceptive lamelliform setae (trichocopae) on promedian surfaces.
- Scorpioninae Latreille, 1802

Subfamily Heterometrinae Simon, 1879,
stat. nov.

Figures 1–10, 15–251, tables 1–5

- Heterometridae Simon, 1879: 92, 115,
type genus: *Heterometrus* Ehrenberg, 1828
(part) [= *Scorpio* Linnaeus, 1758].
Pandininae: Rossi, 2016a: 19, 20, 22, 26 (part).
Heterometrini: Rossi, 2016a: 19, 20, 25, 26.

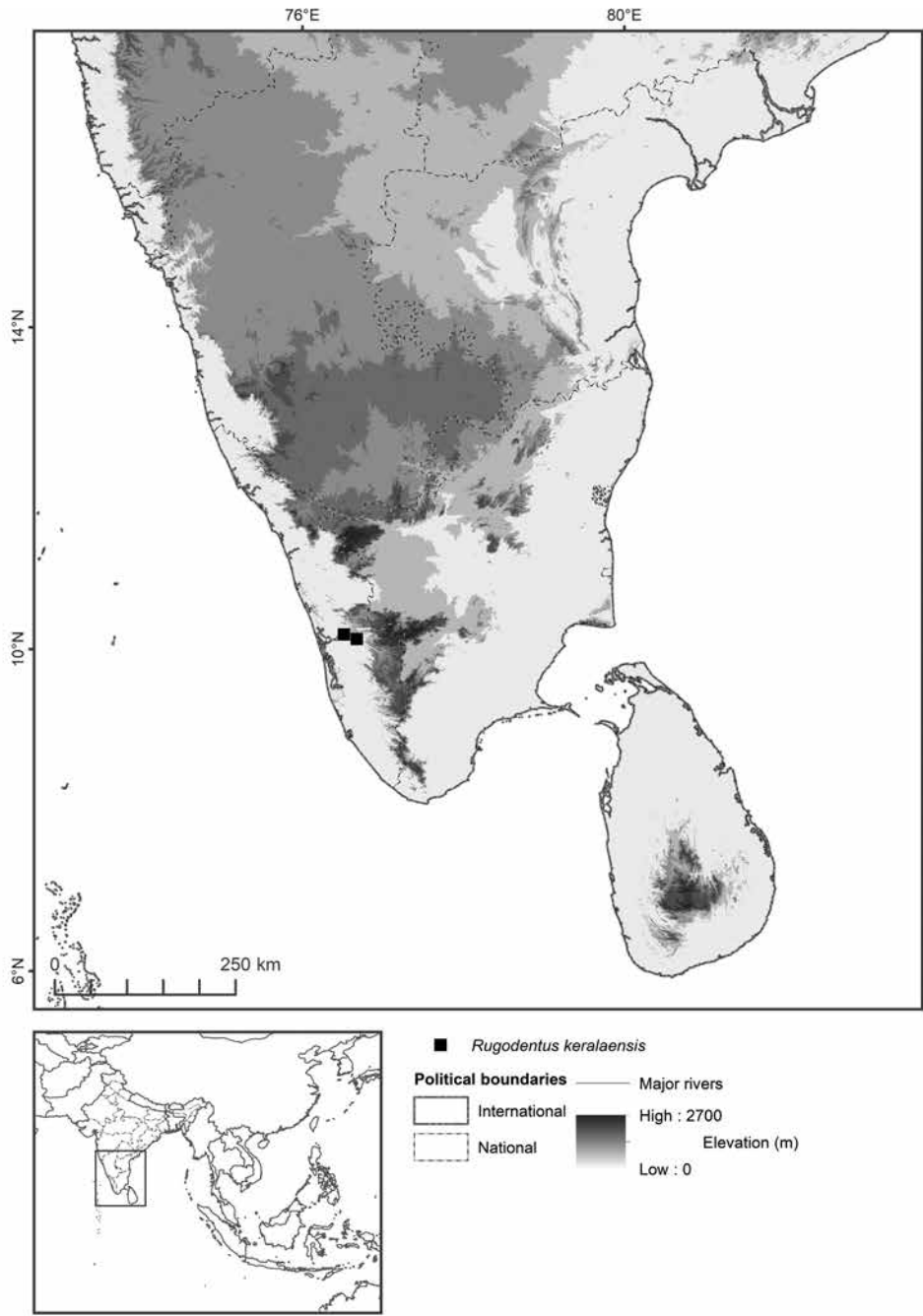


FIGURE 14. Map of South India and Sri Lanka, plotting known locality records of *Rugodentus keralaensis* Bastawade et al., 2005, stat. rev., based on verified records from virtual museums and the literature.

DIAGNOSIS: Heterometrinae are the sister group of Pandininae (Prendini, 2000a; Prendini et al., 2003). Both subfamilies share the following characters, by means of which they can be separated from Opisthophthalminae and Scorpioninae: presence of a stridulatory organ, comprising a “rasp” (granular tubercles) and “scraper” (stridulatory setae or scaphotrix), on opposing surfaces of the coxae of the pedipalps and the first pair of legs; similar counts of pro- and retroventral spiniform macrosetae on telotarsi I and II and on III and IV. Heterometrinae can be separated from Pandininae by means of the following characters: pedipalps orthobothriotaxic, with 26 trichobothria (patella with 13 trichobothria in *e* series and 3 trichobothria in *v* series; chela with 4 trichobothria in *V* series and 2 trichobothria in *i* series); granular tubercles of “rasp” and stridulatory setae (scaphotrix) of “scraper” situated on coxae of first leg and pedipalp, respectively. Heterometrinae can be further separated from Opisthophthalminae by means of the following characters: pedipalps orthobothriotaxic, with 26 trichobothria (including 13 trichobothria in *e* series of patella); cheliceral coxae without stridulatory setae (scaphotrix) on prodorsal surfaces and chemoreceptive lamelliform setae (trichocopae) on promedian surfaces. Heterometrinae can be further separated from Scorpioninae by means of the following characters: digital carina of pedipalp chela obsolete; mesosomal sternite VII usually without paired ventrosubmedian and ventrolateral carinae.

INCLUDED TAXA: As redefined in the present contribution, Heterometrinae includes seven genera and 41 species: *Chersonesometrus* Couzijn, 1978, stat. nov. et stat. rev.; *Deccanometrus*, gen. nov.; *Gigantometrus* Couzijn, 1978, stat. nov.; *Heterometrus* Ehrenberg, 1828; *Javanimetrus* Couzijn, 1981, stat. nov. et stat. rev.; *Sahyadrimetrus*, gen. nov.; *Srilankametrus* Couzijn, 1981, stat. nov. et stat. rev.

DISTRIBUTION: Asia: Bangladesh, Brunei, Cambodia, China (including Hainan Island and

Tibet Autonomous Region), India (including the Andaman and Nicobar Islands), Indonesia (Babi, Bali, Bangka, Batu Islands, Belitung, Bengkalis, Java, Kalimantan, Madura, Mentawai Islands, Miang-Besar, Nias, Riau Islands, Siberut, Simeulue, Sumatra, Weh), Laos, Malaysia (mainland, Langkawi, Penang, Tinggi, and Tioman islands, Sabah and Sarawak), Myanmar (mainland, Myeik Islands), Nepal, Pakistan, the Philippines (Balabac, Luzon, Mindanao, Palawan, Panay, Tawi Tawi), Singapore, Sri Lanka, Thailand (mainland, Ko Chang, Ko Lanta, Ko Muk, Ko Samui, Phi Phi islands and Phuket), Vietnam (mainland, Phú Quoc Island).

Heterometrinae are distributed from India and Sri Lanka throughout the Southeast Asian mainland and archipelagos as far as Wallace's Line (Vachon, 1953; Couzijn, 1981; Prendini et al., 2003), where they mostly inhabit tropical and subtropical rainforests, moist and dry tropical deciduous forests, and tropical thorn forests (Couzijn, 1981; Tikader and Bastawade, 1983; Sissom, 1990). Reports of *Heterometrus* from the Indonesian islands of Sulawesi and Halmahera (Meise, 1932: 662; Takashima, 1945: 90), to the east of Wallace's Line, have never been confirmed (Couzijn, 1981: 175, 178).

ECOLOGY: The ability to construct burrows has been confirmed in all genera of Heterometrinae (Couzijn, 1981; Hull-Williams, 1989; Khataavkar and More, 1990; Shivashankar and Veeresh, 1991; Shivashankar, 1992, 1994; Tare et al., 1993; Prendini et al., 2003; Javed et al., 2010a; Pande et al., 2012; Tahir and Prendini, 2014). Burrows are constructed in loamy riverbanks and other sloping ground, at the base of stones and among the roots of trees (Couzijn, 1981; Shivashankar, 1994; fig. 12). As in some species of Pandininae, composite, multi-entranced burrows containing multiple (up to 15) related individuals of different ages have been recorded in some species, e.g., *Chersonesometrus madraspatensis* and *Deccanometrus xanthopus* (Shivashankar, 1994; Prendini et al., 2003; Javed et al., 2010a). In others, e.g., *Heterometrus longimanus* (Herbst, 1800) and *H.*

spinifer, mixed age groups of related and unrelated individuals cohabit with minimal aggression or cannibalism in laboratory terraria (Harrison, 1954; Polis and Lourenço, 1986) and, according to some evidence, this also occurs in the wild (Schultze, 1927).

Few ecological data are available for most Heterometrinae. However, the thickened metasoma, short, robust legs with stout, spiniform macrosetae distributed laterally and distally on the basitarsi, and curved telotarsal unguis of most genera occurring in South Asia, as well as the Southeast Asian *Javanimetrus*, are consistent with the fossorial, pelophilous ecomorphotype (Prendini, 2001b). *Gigantometrus* often inhabits termitaria and most if not all species of *Heterometrus* appear to be lapidicolous or corticolous as well as fossorial. For example, *H. longimanus* is often found under the loose bark of dead standing trees, under decaying trunks and logs, or in the cavities of rotten tree stumps (Schultze, 1927; Prendini et al., 2003). Furthermore, the morphology of the species of *Heterometrus* differs from that of most South Asian genera in elongation of the legs, absence of a retrolateral row of spiniform macrosetae on the leg tibia, presence of strongly curved unguis and an enlarged, curved pseudonychium (dactyl) on the telotarsi, and enlarged median ocelli. Although such characters are uncommon among scorpionids, they occur in arboreal chactids (e.g., *Chactas* Gervais, 1844) and hormurids (e.g., *Hormurus* Thorell, 1876, and some species of *Opisthacanthus*), and are regarded as corticolous adaptations to an arboreal habitat (Prendini, 2001b). Although some species of *Chersonesometrus* and *Deccanometrus* are dorsoventrally compressed and evidently semilithophilous, inhabiting the cracks and crevices of rock outcrops, no Heterometrinae exhibit psammophilous adaptations.

CONSERVATION STATUS: Several species of Heterometrinae are harvested and consumed for food in Southeast Asia and for narcotic or medicinal purposes in India and Pakistan (Men-

zel and D'Aluisio, 1998; Prendini et al., 2003; Majumder and Dey, 2005; Tahir and Prendini, 2014).

Various species of Heterometrinae are readily available in Europe, the United States, China, and Japan for the exotic pet trade because their impressive size and fearsome appearance are highly prized by collectors. An extensive literature exists on the captive husbandry of Asian forest scorpions (e.g., Nemenz and Gruber, 1967; Hull-Williams, 1986; Hosoi, 1990; Dupré, 1993; Gopalakrishnakone et al., 1995; Condevaux-Lanloy, 1996; Mahsberg et al., 1999; Rubio, 2000). The following species and countries of origin have been personally recorded in the trade: *C. fulvipes* (India, Pakistan); *C. madraspatensis* (India); *D. bengalensis* (India); *D. obscurus* (India); *G. swammerdami* (India); *H. laevigatus* (Myanmar, Thailand); *H. petersii* (Singapore); *H. silenus* (Vietnam); *H. spinifer* (Malaysia); *J. cyaneus* (Indonesia). Due to the difficulties involved in the identification of *Heterometrus* species, especially those occurring in Southeast Asia (Dupré, 1989), species are often advertised under false or erroneous names.

In addition to being sold alive as pets, many Southeast Asian *Heterometrus* are dried and mounted in glass cases or set in resin to be sold as curios. *Heterometrus laoticus*, *H. silenus*, and *H. spinifer* have been observed for sale as curios in the United States, U.K. and South Africa.

Unfortunately, wild populations of Heterometrinae are expected to be slow to repopulate after harvesting for the following reasons. Females have gestation periods up to 12 months (Subburam and Reddy, 1978a) and produce rather small broods (30–35) compared with other scorpions (Schultze, 1927; Mathew, 1956; Polis and Sissom, 1990; Shivashankar, 1994; Condevaux-Lanloy, 1996). Young are relatively altricial, spending several months in the maternal burrow before dispersing (Schultze, 1927; Shivashankar, 1994), thereby further protracting the period before a female can give birth to her next brood. Age to sexual maturity is 4–7 yr in these scorpions (Polis and Lourenço,

1986; Polis and Sissom, 1990), during which period most juveniles experience natural predation (including cannibalism).

These factors suggest that species of Heterometrinae are extremely vulnerable to overharvesting and, unlike Pandininae, three species of which receive CITES protection (IUCN, 1994; Lourenço and Cloudsley-Thompson, 1996), no species of Heterometrinae is currently CITES listed. The apparently restricted distributional ranges of many species provide further cause for concern, given that the remaining wild populations are threatened not only by overexploitation but also by continued habitat destruction (e.g., through deforestation). Many Heterometrinae appear to be restricted to virgin habitat (e.g., Schultze, 1927) and may thus be regarded as equilibrium species.

REMARKS: Rossi (2016a) recognized the Asian scorpionids as a tribe of Pandininae Thorell, 1876, for reasons unspecified. The two lineages are sister taxa, with similar levels of taxonomic and morphological diversity, hence it is appropriate to elevate Heterometrini to the rank of subfamily, i.e., Heterometrinae Simon, 1879, stat. nov.

Key to the Genera and Species of Asian Forest Scorpions (Heterometrinae Simon, 1879, stat. nov.)

1. Carapace rostrolateral margin distinctly incised adjacent to posterior lateral ocelli; median ocelli relatively large, distance between them less than an ocellus width (fig. 23B, C); pedipalp patella proventral carina with prominent spiniform granule (fig. 186); pedipalp chela manus dorsal surface (adult ♂) depression proximal to fixed finger present and distinct (fig. 187B); legs I and II tibiae, pro- and retrolateral surfaces with scattered, setiform macrosetae, not arranged in definite row; legs I–IV telotarsi, pseudonychium (dactyl) prominent and acuminate (fig. 50E–H). 2 (*Heterometrus* Ehrenberg, 1828)
- Carapace rostrolateral margin entire; median ocelli relatively small, distance between them equal to or greater than an ocellus width (figs. 17A, B, 18A, B, 19C, D, 25A, B, 26E, F, 28A, B); pedipalp patella proventral carina without prominent spiniform granule (figs. 89, 132, 149, 195, 217, 240); pedipalp chela manus dorsal surface (adult ♂) depression proximal to fixed finger absent or obsolete (figs. 90, 133, 150, 196, 218, 241); legs I and II tibiae, pro- and retrolateral surfaces with row of two or three spiniform macrosetae; legs I–IV telotarsi, pseudonychium (dactyl) usually reduced and rounded (figs. 45A–D, 46E–H, 49A–D, 53E–H, 55I–L, 57A–D). 8
2. Telson dark reddish brown, paler than metasomal segment V. 3
 - Telson blackish, as dark as metasomal segment V. 5
3. Pedipalp (♂) short, femur length : posterior carapace width ratio (FL:PCW) < 0.77 and femur length : carapace length ratio (FL:CL) < 0.74 (fig. 184); chela movable finger, second (subproximal) lobe (♂) more strongly developed than other lobes on movable finger, with correspondingly well-developed notch in fixed finger (figs. 187B, 188B); leg II basitarsus proventral surface, macroseta *st* setiform (fig. 50F). *Heterometrus petersii* (Thorell, 1876) and *Heterometrus spinifer* (Ehrenberg, 1828)
- Pedipalp (♂) long, FL:PCW ≥ 0.80 and FL:CL ≥ 0.76 (figs. 159, 174); chela movable finger, second (subproximal) lobe (♂) similar to or barely larger than other lobes on movable finger (figs. 162A, 177B, D); leg II basitarsus proventral surface, macroseta *st* usually spiniform (fig. 52B, F). 4
4. Carapace interocular surface (♂) frontal lobes and medial region granular, with smooth areas (fig. 22A); posterolateral surfaces (♀) granular (fig. 22B); pedipalp chela manus dorsal surface shallowly reticulate (figs. 162A, 163A); leg III basitarsus retroventral surface, macroseta *sb* spiniform (fig.

- 52C). *Heterometrus glaucus* (Thorell, 1876), comb. nov. et stat. rev.
- Carapace interocular surface (δ) granular along median longitudinal and anterior bifurcated sulci only (fig. 22C); posterolateral surfaces (φ) smooth or nearly so (fig. 22D); pedipalp chela manus dorsal surface smooth or nearly so (fig. 177A, B); leg III basitarsus retroventral surface, macroseta *sb* setiform (fig. 52G).
- ... *Heterometrus longimanus* (Herbst, 1800)
5. Pedipalp (δ) long, FL:PCW ≥ 0.80 and FL:CL ≥ 0.76 (figs. 164, 189A, B); legs I and II basitarsi proventral surfaces, macroseta *st* spiniform (figs. 50A, B, 53A, B). 6
 - Pedipalp (δ) short, FL:PCW < 0.77 and FL:CL < 0.74 (figs. 169, 179A, 180A); legs I and II basitarsi proventral surfaces, macroseta *st* setiform (fig. 51A, B, E, F). 7
 6. Carapace interocular surface entirely smooth (δ) (fig. 23A) or granular along median longitudinal and anterior bifurcated sulci only (φ) (fig. 23B); pedipalp chela manus promedian carina (φ) absent or obsolete; chela movable finger, second (subproximal) lobe (δ) more strongly developed than other lobes on movable finger, with correspondingly well-developed notch in fixed finger (figs. 167B, 168B).
- ... *Heterometrus laevigatus* (Thorell, 1876), comb. nov. et stat. rev.
- Carapace interocular surface frontal lobes and medial region granular, with smooth areas (δ , φ) (fig. 22E, F); pedipalp chela manus promedian carina (φ) present, granular (fig. 192B); chela movable finger, second (subproximal) lobe (δ) similar to or barely larger than other lobes on finger (fig. 191A).
- ... *Heterometrus thorellii* (Pocock, 1892)
7. Carapace interocular surface entirely smooth (fig. 24A, B); anterolateral, mediolateral, and posterolateral surfaces (φ) smooth or nearly so (fig. 24B); mesosomal tergites I–VI (φ), mesial and lateral surfaces smooth.
- ... *Heterometrus laoticus* Couzijn, 1981
- Carapace interocular surface often granular along median longitudinal and anterior bifurcated sulci only (fig. 24C, D); anterolateral, mediolateral, and posterolateral surfaces (φ) granular (fig. 24D); mesosomal tergites I–VI (φ), mesial surfaces smooth and lateral surfaces granular.
- ... *Heterometrus silenus* (Simon, 1884), comb. nov. et stat. rev.
8. Pedipalp chela manus dorsal secondary, digital and retromedian carinae distinct from intercarinal surfaces, entirely to predominantly granular or entirely to predominantly costate, and/or dorsal intercarinal surface granular, without reticulation (figs. 90A, 91A, 150A, 151A, 241A, 242A). 9
 - Pedipalp chela manus dorsal secondary, digital and retromedian carinae absent or obsolete, not distinct from intercarinal surfaces, and/or dorsal intercarinal surface smooth or granular, and shallowly reticulate (figs. 133A, 134A, 196A, 197A, 218A, 219A). 27
 9. Carapace median ocular tubercle posteromedial (fig. 17A, B), distance from carapace anterior margin : carapace length (CAM:CL) 0.51–0.62; pedipalp chela manus retromedian carina more pronounced than digital carina (figs. 90A, 91A). 10
- ... *Chersonesometrus* Couzijn, 1978, stat. nov. et stat. rev.)
- Carapace median ocular tubercle anteromedial to medial (figs. 18A, B, 28A, B), CAM:CL 0.40–0.50; pedipalp chela manus digital and retromedian carinae similarly developed, may be absent or obsolete (figs. 150A, 151A, 241A, 242A). 19
 - 10. Cheliceral movable finger prodistal (DI) and retrodistal (DE) teeth unequal, with DE tooth considerably smaller than DI tooth, aligned longitudinally and not opposable; pedipalp chela (adult δ) sparsely setose (figs. 90, 97, 108). 11
 - Cheliceral movable finger, prodistal (DI) and retrodistal (DE) teeth subequal, with DE tooth only slightly smaller than DI tooth, and opposable, i.e., forming a bicus; pedi-

- palp chela (adult ♂) moderately to densely setose (figs. 87, 100, 104, 113A) 15
11. Carapace dorsoventrally compressed, lateral surfaces sloping gently (fig. 16A, B); metasomal segment V dorsal intercarinal surface (♂) granular. 12
 - Carapace vaulted, lateral surfaces sloping moderately to steeply (figs. 16C, D, 17); metasomal segment V dorsal intercarinal surface (♂) smooth (fig. 61A, C) 13
 12. Carapace interocular surface (♀) frontal lobes and medial region granular, with smooth areas (fig. 16A); pedipalp chela manus dorsal secondary, subdigital, and digital carinae (♂) absent or obsolete; legs pale or very lightly infusate (fig. 81A, B); mesosomal tergites I–VI, mesial surfaces granular *Chersonesometrus bastawadei*, sp. nov.
 - Carapace interocular surface (♀) granular along median longitudinal and anterior bifurcated sulci only (fig. 16B); pedipalp chela manus dorsal secondary, subdigital, and digital carinae (♂) present and entirely to predominantly granular; legs dark or heavily infusate (fig. 81C, D); mesosomal tergites I–VI, mesial surfaces smooth *Chersonesometrus wroughtoni* (Pocock, 1899), comb. nov.
 13. Carapace interocular surface (♀) entirely smooth (fig. 17B); pedipalp chela manus dorsal surface (between dorsomedian and digital carinae) relatively flat (figs. 90A, 91A); dorsal secondary and subdigital carinae (♂) absent or obsolete; legs I and II basitarsi retroventral surfaces, macroseta *st* spiniform (fig. 45A, B) ... *Chersonesometrus fulvipes* (C.L. Koch, 1837), comb. nov.
 - Carapace interocular surface (♀) granular along median longitudinal and anterior furcated sulci only (figs. 16D, 17D); pedipalp chela manus manus dorsal surface (between dorsomedian and digital carinae) curved, slightly to markedly convex (figs. 97A, 98A, 108A, 109A); dorsal secondary and subdigital carinae (♂) present and entirely to predominantly granular; legs I and II basitarsi retroventral surfaces, macroseta *st* setiform (fig. 45E, F, I, J) 14
 14. Carapace posterolateral surfaces (♀) granular (fig. 17D); pedipalp (♂) long, FL:PCW ≥ 0.80 and FL:CL ≥ 0.76 (fig. 95A, B); chela manus (♂) narrow, dorsal intercarinal surface, maximum distance between dorsomedian and dorsal secondary carinae (DMC–DSC) similar to maximum distance between dorsal secondary and digital carinae (DSC–DC); chela infusate, similar in color to femur and patella. *Chersonesometrus madraspatensis* (C.L. Koch, 1837), comb. nov.
 - Carapace posterolateral surfaces (♀) smooth or nearly so (fig. 16D); pedipalp (♂) short, FL:PCW < 0.77 and FL:CL < 0.74 (fig. 106A, B); chela manus (♂) broad, dorsal intercarinal surface, DMC–DSC greater than DSC–DC; chela immaculate, paler than femur and patella. *Chersonesometrus shivashankari*, sp. nov.
 15. Pedipalp chela manus dorsal surface, proximal margin (lobe) markedly curved (figs. 94A, 104A, 105A), proximal to proximal margin of manus condyle (articulation with patella); chela manus (♂) broad, dorsal intercarinal surface, DMC–DSC greater than DSC–DC; metasomal segment V dorsal intercarinal surface (♂) granular 16
 - Pedipalp chela manus dorsal surface, proximal margin (lobe) moderately curved (figs. 86A, 87A, 100A, 113), aligned with or proximal to proximal margin of retrolateral surface, or aligned with proximal margin of manus condyle; chela manus (♂) narrow, dorsal intercarinal surface, DMC–DSC similar to DSC–DC; metasomal segment V dorsal intercarinal surface (♂) smooth 17
 16. Carapace interocular surface frontal lobes and medial region granular, with smooth areas (♂), granular along median longitudinal and anterior bifurcated sulci only (♀) (fig. 16F); legs pale or very lightly infusate (fig. 92) *Chersonesometrus hendersoni*, sp. nov.

- Carapace interocular surface granular along medial longitudinal and anterior bifurcated sulci only (♂) (fig. 15C) or frontal lobes and medial region granular, with smooth areas (♂, ♀) (fig. 15C, D); legs dark or heavily infusate (figs. 101, 102).....
.....*Chersonesometrus pelekomanus* (Couzijn, 1981), comb. nov. et stat. rev.
- 17. Pedipalp chela manus dorsal secondary, subdigital, and digital carinae (♂), and patella retromedian carinae (♀) entirely to predominantly costate; manus dorsal surface granular and shallowly reticulate (fig. 100A); patella dorsal surface convex, axis of dorsomedian carina dorsal to axis of retrodorsal carina (fig. 99A, B); leg III basitarsus retroventral surface, macroseta *sb* spiniform; metasomal segments dorsosubmedian carinae (♀) granular or costate-granular on segments I-IV.....
.....*Chersonesometrus nathanorum*, sp. nov.
- Pedipalp chela manus dorsal secondary, subdigital, and digital carinae (♂), and patella retromedian carinae (♀) entirely to predominantly granular; manus dorsal surface predominantly granular (figs. 86A, 87A, 113); patella dorsal surface flat (or nearly so), axes of dorsomedian and retrodorsal carinae in same plane (figs. 85, 112); leg III basitarsus retroventral surface, macroseta *sb* setiform (fig. 43C, K); metasomal segments dorsosubmedian carinae (♀) granular or costate-granular on segments III and IV or IV, costate on I and II or I-III (fig. 58B, E)..... 18
- 18. Pedipalp chela manus manus dorsal surface (between dorsomedian and digital carinae) curved, slightly convex (figs. 86A, 87A); mesosomal tergites I-VI (♀), lateral surfaces granular; sternite VII, ventral surface with moderately to strongly developed pairs of ventrosubmedian and ventrolateral carinae; metasomal segments I-IV dorsosubmedian carinae (♂) granular or costate-granular on segments I-IV.....*Chersonesometrus beccaloniae* (Kovářík, 2004), comb. nov.
- Pedipalp chela manus dorsal surface (between dorsomedian and digital carinae) flat (fig. 113); mesosomal tergites I-VI (♀), lateral surfaces smooth; sternite VII, ventral surface with pair of weakly developed ventrolateral carinae; metasomal segments I-IV dorso-submedian carinae (♂) granular or costate-granular on segments III and IV or IV, costate on I and II or I-III.....*Chersonesometrus tristis* (Henderson, 1919), comb. nov.
- 19. Carapace anterolateral margins, dorsal aspect, converging gradually anteriorly (fig. 18A, B); superciliary carinae with anterocular extensions; interocular surface frontal lobes and medial region granular with smooth areas; pedipalp chela manus dorsomedian carina continuous to proximal margin (figs. 150A, 151A); pecten first proximal median lamella (scape) (♀) distinctly angular, > 90° but < 180° (fig. 32B); metasomal segments I and II, length markedly greater than width (figs. 67A, 69A); segment V dorsosubmedian carinae partially developed (fig. 67A); telson vesicle (♀), width greater than metasomal segment V width..... 20
(*Gigantometrus* Couzijn, 1978, stat. nov.)
- Carapace anterolateral margins, dorsal aspect, converging slightly to subparallel anteriorly (fig. 28A, B); superciliary carinae without anterocular extensions; interocular surface usually entirely smooth; pedipalp chela manus dorsomedian carina becoming obsolete proximally (figs. 241A, 242A); pecten first proximal median lamella (scape) (♀) straight or shallowly curved (fig. 42B); metasomal segments I and II, length approximately equal to or less than width (figs. 76D, 78D); segment V dorsosubmedian carinae absent or vestigial (fig. 76D); telson vesicle (♀), width approximately equal to or less than metasomal segment V width..... 21 (*Srilankametrus* Couzijn, 1981, stat. nov. et stat. rev.)
- 20. Carapace, pedipalps, tergites and metasoma dark reddish brown; pedipalp chela immac-

- ulate, paler than femur and patella; chela manus prodorsal margin sloping gently to low hump proximal to base of fixed finger (figs. 150, 151); fixed finger markedly curved; legs pale, lightly infusate or dark, heavily infusate (figs. 147, 148); metasomal segments robust (figs. 147, 148)..... *Gigantometrus swammerdami* (Simon, 1872), comb. nov.
- Carapace, pedipalps, tergites and metasoma very dark reddish or brownish black; pedipalp chela infusate, similar in color to femur and patella; chela manus prodorsal margin sloping steeply and continuously to base of fixed finger (figs. 155, 156); fixed finger gently curved; legs very dark, heavily infusate (figs. 152, 153); metasomal segments relatively slender (figs. 152, 153)..... *Gigantometrus titanicus* (Couzijn, 1981), comb. nov. et stat. rev.
21. Carapace slightly to markedly dorsoventrally compressed, lateral surfaces sloping gently (fig. 28); pedipalp chela dorsomedian carina obsolete on fixed finger and manus (figs. 241A, 242A, 246A, 248A, 250A, 251A); telson vesicle globose (figs. 238, 239, 243, 244)..... 22
 - Carapace vaulted, lateral surfaces sloping moderately to steeply (fig. 27); pedipalp chela dorsomedian carina pronounced, costate on fixed finger and distally on manus (figs. 228A, 229A, 232A, 233A, 236A, 237A); telson vesicle elongate (figs. 225, 226, 230, 234). 24
 22. Pedipalp chela (adult ♂) sparsely setose (figs. 248, 250); chela manus dorsal secondary, subdigital, digital, and retromedian carinae entirely to predominantly granular; legs I and II basitarsi retroventral surfaces, macroseta *st* spiniform (fig. 57I, J); mesosomal tergites I–VI, lateral surfaces granular; telson usually dark reddish brown, paler than metasomal segment V. *Srilankametrus serratus* (Pocock, 1900), comb. nov.
 - Pedipalp chela (adult ♂) moderately to densely setose (fig. 241); chela manus dorsal secondary, subdigital, digital, and retromedian carinae absent or obsolete; legs I and II basitarsi retroventral surfaces, macroseta *st* setiform (fig. 57A, B, E, F); mesosomal tergites I–VI, lateral surfaces smooth; telson blackish, as dark as metasomal segment V..... 23
 23. Carapace anterolateral and mediolateral surfaces entirely smooth (fig. 28A, B); pedipalp chela manus dorsal surface (between dorso-median and digital carinae) curved, slightly to markedly convex (figs. 241A, 242A); metasomal segments I–IV dorsosubmedian carinae costate on segments I–IV (fig. 76D)..... *Srilankametrus indus* (DeGeer, 1778), comb. nov.
 - Carapace anterolateral and mediolateral surfaces granular (fig. 28D); pedipalp chela manus dorsal surface (between dorsomedian and digital carinae) flat (fig. 246A); metasomal segments I–IV dorsosubmedian carinae granular or costate-granular on segments I–IV (fig. 76E) *Srilankametrus pococki*, sp. nov.
 24. Pedipalp chela manus dorsal secondary and subdigital carinae entirely to predominantly granular (figs. 228A, 229A, 232A, 233A)..... 25
 - Pedipalp chela manus dorsal secondary and subdigital carinae entirely to predominantly costate (figs. 236A, 237A)..... 26
 25. Carapace interocular surface (♂, ♀) frontal lobes and medial region granular, with smooth areas (fig. 27A, B); pedipalp chela manus digital carina (♂, ♀) absent or obsolete (figs. 228A, 229A); retromedian carina (♂) entirely to predominantly granular; legs I and II basitarsi retroventral surfaces, macroseta *st* spiniform (fig. 56A, B)..... *Srilankametrus caesar* (C.L. Koch, 1841), comb. nov. et stat. rev.
 - Carapace interocular surface (♂) entirely smooth (fig. 27C); pedipalp chela manus digital and retromedian carinae (♂) entirely to predominantly costate (fig. 232A); legs I and II basitarsi retroventral surfaces, macroseta *st* setiform (fig. 56E, F)..... *Srilankametrus couzijni*, sp. nov.
 26. Pedipalp chela dorsomedian carina pronounced, costate on fixed finger and distally

- on manus (figs. 236A, 237A); legs I and II basitarsi retroventral surfaces, macroseta *st* spiniform (fig. 56I, J); mesosomal tergites I–VI, lateral surfaces granular; metasomal segments I–IV dorsosubmedian carinae granular or costate-granular on segments I and IV (fig. 76C); telson blackish, as dark as metasomal segment V. *Srilankametrus gravimanus* (Pocock, 1894), comb. nov.
- Pedipalp chela dorsomedian carina pronounced, costate on fixed finger and distal three-quarters of manus; legs I and II basitarsi retroventral surfaces, macroseta *st* setiform; mesosomal tergites I–VI, lateral surfaces smooth; metasomal segments I–IV dorsosubmedian carinae granular or costate-granular on segments III and IV or IV, costate on I and II or I–III; telson dark reddish brown, paler than metasomal segment V. *Srilankametrus yaleensis* (Kovářík et al., 2019), comb. nov.
27. Carapace, pedipalps, tergites, and metasoma black or greenish black; legs very dark or heavily infuscate (figs. 193, 194, 216); carapace interocular and posterior sutures absent; telson vesicle elongate. 28
- Carapace, pedipalps, tergites, and metasoma dark reddish or brownish black, dark reddish brown, pale yellowish brown or yellowish; legs often pale or lightly infuscate (figs. 130, 131); carapace interocular suture present; posterior sutures present and extending past median ocular tubercle; telson vesicle globose. 34 (*Deccanometrus*, gen. nov.)
28. Carapace anterolateral margins, dorsal aspect, converging slightly to subparallel anteriorly (fig. 25A, B); pedipalp chela (adult ♂) sparsely setose (fig. 196); chela manus (♂) broad, dorsal intercarinal surface, DMC–DSC greater than DSC–DC; manus ventral surface angled, axis of retroventral carina ventral to axis of ventromedian carina; metasomal segment IV, ventral intercarinal surfaces sparsely granular (fig. 72E). *Javanimetrus cyaneus* (C.L. Koch, 1836), comb. nov.
- Carapace anterolateral margins, dorsal aspect, converging gradually anteriorly (fig. 26E, F); pedipalp chela (adult ♂) moderately to densely setose (fig. 218); chela manus (♂) narrow, dorsal intercarinal surface, DMC–DSC similar to or less than DSC–DC; manus ventral surface flat, axes of retroventral and ventromedian carinae in approximately same plane; metasomal segment IV, ventral intercarinal surfaces smooth (fig. 75E). 29 (*Sahyadrimetrus*, gen. nov.)
29. Pedipalp patella retrodorsal carina (♀) absent or obsolete, retromedian carinae (♀) present and granular (figs. 201, 214); pedipalp chela manus retrolateral intercarinal surfaces (♀) granular (figs. 202A, 215A, 224A); legs I and II basitarsi retroventral surfaces, macroseta *st* spiniform (fig. 54); mesosomal tergites I–VI (♀) lateral surfaces often smooth. 30
- Pedipalp patella retrodorsal carina (♀) present, as strongly developed as or more strongly developed than retromedian carinae (♀), which are absent or obsolete (fig. 205); pedipalp chela manus retrolateral intercarinal surfaces (♀) smooth or nearly so (figs. 207A, 212A, 219A); legs I and II basitarsi retroventral surfaces, macroseta *st* setiform (fig. 55); mesosomal tergites I–VI (♀) lateral surfaces granular. 32
30. Pedipalp (♂) long, FL:PCW ≥ 0.80 and FL:CL ≥ 0.76 ; patella dorsomedian carina (♀) present and entirely to predominantly granular, and dorsal, retrodorsal, and retroventral intercarinal surfaces (♀) granular (fig. 214). *Sahyadrimetrus rugosus* (Couzijn, 1981), comb. et stat. nov.
- Pedipalp (♂) short, FL:PCW < 0.77 and FL:CL < 0.74 (fig. 220); patella dorsomedian carina (♀) absent or obsolete and dorsal, retrodorsal, and retroventral intercarinal surfaces (♀) smooth or nearly so (fig. 201). 31
31. Pedipalp chela manus dorsal intercarinal surface (♀) finely to coarsely granular (fig. 202A); mesosomal tergites I–VI

- (♀), lateral surfaces smooth; metasomal segment IV ventral surface (♀) smooth (fig. 75A); segment V, dorsolateral carinae weak and discontinuous to absent (fig. 73A) *Sahyadrimetrus barberi* (Pocock, 1900), comb. nov.
- Pedipalp chela manus dorsal intercarinal surface (♀) smooth (fig. 224A); mesosomal tergites I–VI (♀), lateral surfaces granular; metasomal segment IV ventral surface (♀) granular; segment V, dorsolateral carinae strong and continuous (fig. 73F) *Sahyadrimetrus tikaderi*, sp. nov.
32. Carapace moderately dorsoventrally compressed (fig. 26A, B); posterolateral surfaces (♀) smooth or nearly so; pedipalp chela manus dorsal surface (♀) (fig. 207A) and retrolateral intercarinal surfaces (♂) smooth or nearly so (fig. 206A); leg III basitarsi proventral surfaces, macroseta *st* spiniform and retroventral surfaces, macroseta *st* setiform (fig. 55C); mesosomal tergites I–VI (♂), mesial surfaces smooth. *Sahyadrimetrus kanarensis* (Pocock, 1900), comb. nov.
- Carapace vaulted (fig. 26C–F); posterolateral surfaces (♀) granular; pedipalp chela manus dorsal surface (♀) (figs. 212A, 219A) and retrolateral intercarinal surfaces (♂) granular or granulo-reticulate (figs. 211A, 218A); leg III basitarsi proventral surfaces, macroseta *st* setiform and retroventral surfaces, macroseta *st* spiniform (fig. 55G, K); mesosomal tergites I–VI (♂), mesial surfaces granular. 33
33. Carapace lateral surfaces sloping very steeply (fig. 26C, D); interocular surface entirely uniformly granular; pedipalp (♂) long, FL:PCW ≥ 0.80 and FL:CL ≥ 0.76 (fig. 208); chela manus narrow, dorsal intercarinal surface, DMC–DSC less than DSC–DC. *Sahyadrimetrus mathewi*, sp. nov.
- Carapace lateral surfaces sloping steeply (fig. 26E, F); interocular surface frontal lobes and medial region granular with smooth areas; pedipalp (♂) short, FL:PCW < 0.77 and FL:CL < 0.74 (fig. 216A, B); chela manus broad, dorsal intercarinal surface, DMC–DSC similar to DSC–DC. *Sahyadrimetrus scaber* (Thorell, 1876), comb. nov.
34. Legs very dark or heavily infusate (figs. 119, 120, 130, 131, 135); pedipalp patella retromedian carinae (♀) present and granular; mesosomal tergites I–VI (♀) lateral surfaces usually granular; metasomal segments I–IV, ventrosubmedian and ventrolateral carinae more strongly developed on III and IV than on I and II (fig. 66A–C); segment V lateral carinae often partial (fig. 65A–C); telson vesicle (♂) width less than or equal to metasomal segment V width (fig. 64A–C) 35
- Legs pale or very lightly infusate (figs. 123, 127, 139); pedipalp patella retromedian carinae (♀) absent or obsolete (figs. 124, 128, 140, 142); mesosomal tergites I–VI (♀) lateral surfaces smooth; metasomal segments I–IV, ventrosubmedian and ventrolateral carinae more strongly developed on I and II than on III and IV (fig. 66D–G); segment V lateral carinae often absent or obsolete (fig. 65D–G); telson vesicle (♂) width greater than metasomal segment V width (fig. 64D–G) 37
35. Carapace posterolateral surfaces (♀) granular (fig. 19B); pedipalp patella retrodorsal carina (♀) absent or obsolete; patella dorsal, retrodorsal, and retroventral intercarinal surfaces (♀) smooth or nearly so; chela manus, dorsal surface granular and shallowly reticulate (fig. 122A, B); leg III basitarsus retroventral surfaces, macroseta *st* setiform (fig. 46C) *Deccanometrus bengalensis* (C.L. Koch, 1841), comb. nov.
- Carapace posterolateral surfaces (♀) smooth or nearly so (fig. 19D, F); pedipalp patella retrodorsal carina (♀) present, as strongly developed as, or more strongly developed than retromedian carinae; patella dorsal, retrodorsal, and retroventral intercarinal surfaces (♀) granular; chela manus, dorsal surface granular (figs. 133A, 134A, 137A, 138A); leg III basitarsus retroventral

- surfaces, macroseta *st* spiniform (fig. 46G, K)..... 36
36. Carapace moderately dorsoventrally compressed (fig. 19C, D); pedipalp chela manus dorsal surface (between dorsomedian and digital carinae) curved, slightly to markedly convex; chela manus (♀) broad (figs. 133A, 134A), dorsal intercarinal surface, DMC–DSC similar to DSC–DC; surface mostly covered in rounded granules..... *Deccanometrus obscurus* (Couzijn, 1981), comb. et stat. nov.
- Carapace markedly dorsoventrally compressed (fig. 19E, F); pedipalp chela manus dorsal surface (between dorsomedian and digital carinae) relatively flat; chela manus (♀) narrow (figs. 137A, 138A), dorsal intercarinal surface, DMC–DSC less than DSC–DC; surface entirely covered in pointed granules..... *Deccanometrus phipsoni* (Pocock, 1893), comb. nov.
37. Carapace vaulted, lateral surfaces sloping steeply (fig. 20); cheliceral movable finger prodistal (DI) and retrodistal (DE) teeth aligned longitudinally and not opposable; pedipalp chela manus broad (figs. 125A, 126A, 143), dorsal intercarinal surface, DMC–DSC similar to or greater than DSC–DC; manus promedian carina (♀) absent or obsolete; metasomal segment I lateral carinae partial (fig. 65D, G)..... 38
- Carapace dorsoventrally compressed, lateral surfaces sloping gently (fig. 21); cheliceral movable finger, prodistal (DI) and retrodistal (DE) teeth opposable, i.e., forming a bicuspid; pedipalp chela manus narrow (figs. 129A, 141A, B), dorsal intercarinal surface, DMC–DSC less than DSC–DC; manus promedian carina (♀) present and granular; metasomal segment I lateral carinae vestigial (fig. 65E, F)..... 39
38. Carapace interocular surface granular along median longitudinal and anterior bifurcated sulci only (♂, ♀) (fig. 20A, B) posterolateral surfaces (♀) granular (fig. 20B); pedipalp (♂) short, FL:PCW < 0.77 and FL:CL < 0.74 (fig. 123A, B); pedipalp femur prodorsal carina present and distinct; patella dorsomedian carina (♀) absent or obsolete (fig. 124A); chela (adult ♂) moderately to densely setose; leg III basitarsus retrolateral surface, macroseta *sb* setiform (fig. 47C); leg telotarsi laterodistal lobes each with three or more spiniform macrosetae (fig. 47A–D); mesosomal tergites I–VI (♂), mesial surfaces smooth; metasomal segments I–IV dorso-submedian carinae costate (fig. 64D); telson as dark as metasomal segment V..... *Deccanometrus latimanus* (Pocock, 1894), comb. nov.
- Carapace interocular surface mostly or entirely granular (♂) (fig. 20C) or frontal lobes and medial region granular, with smooth areas (♀) (fig. 20D), posterolateral surfaces (♀) smooth (fig. 20D); pedipalp (♂) long, FL:PCW ≥ 0.80 and FL:CL ≥ 0.76 (fig. 127C, D); pedipalp femur prodorsal carina absent or obsolete; patella dorsomedian carina (♀) present and entirely to predominantly granular (fig. 142A); chela (adult ♂) moderately to densely setose; leg III basitarsus retrolateral surface, macroseta *sb* setiform (fig. 47G); leg telotarsi laterodistal lobes each with only two spiniform macrosetae (fig. 47E–H); mesosomal tergites I–VI (♂), mesial surfaces granular; metasomal segments I–IV dorsosubmedian carinae granular or costate-granular (fig. 64G); telson paler than metasomal segment V..... *Deccanometrus xanthopus* (Pocock, 1897), comb. nov.
39. Carapace anterior margin, median notch shallow (fig. 21C); interocular surface granular along median longitudinal and anterior bifurcated sulci only, posterolateral surfaces (♀) granular (fig. 21C); interocular suture absent; pedipalp femur prodorsal carina absent or obsolete; pedipalp chela immaculate, paler than femur and patella; manus dorsal intercarinal surface (♀) and retrolateral intercarinal surfaces (♂, ♀), finely granular (fig. 129A); legs I–III basitarsi retroventral surfaces, macroseta *st* setiform (fig. 48A–C);

metasomal segments I–IV dorsosubmedian carinae obsolete (fig. 64E); segment V, dorso-lateral carinae weak and discontinuous to absent. *Deccanometrus liurus* (Pocock, 1897), comb. nov.

- Carapace anterior margin, median notch deeply excavated (fig. 21A, B); interocular surface frontal lobes and medial region granular with smooth areas, posterolateral surfaces (♀) smooth (fig. 21B); interocular suture present; pedipalp femur prodorsal carina present and distinct; pedipalp chela infusate, similar in color to femur and patella; manus dorsal intercarinal surface (♀) and retrolateral intercarinal surfaces (♂, ♀), smooth (fig. 141A, B); legs I–III basitarsi retroventral surfaces, macroseta *st* spiniform (fig. 48E–G); metasomal segments I–IV dorsosubmedian carinae distinct, granular or costate-granular (fig. 64F); segment V, dorsolateral carinae strong and continuous. *Deccanometrus ubicki* (Kovařík, 2004), comb. nov.

Chersonesometrus Couzijn, 1978,
stat. nov. et stat. rev.

Figures 1, 7A, B, D, 8C, E, 9A, B, 10, 15–17,
29–31, 43–45, 58–63, 79–116, tables 1, 3, 4

Heterometrus (*Chersonesometrus*) Couzijn, 1978:

330, type species by original designation:
Buthus fulvipes C.L. Koch, 1837
[= *Chersonesometrus fulvipes* (C.L. Koch, 1837)]; 1981: 80, 83, 131, 133, 161, 169–171, 180, 182, 184, 186–188, 192, figs. 21, 57–59, 66b, 68, 69 (part); Tikader and Bastawade, 1983: 519, 520, 573 (part); Fet, 2000: 438; Francke, 1985: 8, 18; Prendini, 2000a: 44; Prendini et al., 2003: 222, 252, appendix 1; Bastawade, 2004: 290 (part); Bastawade et al., 2004: 48 (part); Kovařík, 2004: 1; Bastawade, 2005: 417; Bastawade and Borkar, 2008: 212, 219.

Heterometrus: Kovařík, 2004: 1, 2, 7, 49, 51, tables
1, 2 (part); 2009: 34, 35, table 1 (part); Mirza

et al., 2012: 1, 2 (part); Kovařík et al., 2016: 96,
100 (part); Rossi, 2016a: 6–9, 15, 19, 20, 25 (part);
Aswathi and Sureshan, 2017: 9847 (part).

DIAGNOSIS: Species of *Chersonesometrus* may be separated from other Asian scorpionid genera as follows. The carapace is slightly to markedly dorsoventrally compressed, the lateral surfaces sloping gently (figs. 15, 16A, B, E, F), in all except three species of *Chersonesometrus*, *C. fulvipes*, *C. madraspatensis*, and *C. shivashankari*, in which the carapace is vaulted, the lateral surfaces sloping steeply (figs. 16C, D, 17), as in *Gigantometrus*, *Heterometrus*, *Javanimetrus*, two species of *Deccanometrus*, *D. latimanus* and *D. xanthopus*, two species of *Sahyadrimetrus*, *S. mathewi* and *S. scaber*, and all except three species of *Srilankametrus*, *S. indus*, *S. pococki*, and *S. serratus*. The carapace anterolateral margins converge gradually anteriorly (figs. 15–17) in *Chersonesometrus* but are subparallel anteriorly in *Javanimetrus* and *Srilankametrus*; the mediolateral margins diverge or converge slightly posteriorly (at the posterolateral sulci) in *Chersonesometrus*, but converge markedly posteriorly (at the posterolateral sulci) in *Gigantometrus*, *Heterometrus*, and three species of *Sahyadrimetrus*, *S. kanarensis*, *S. mathewi*, and *S. scaber*. The carapace rostrrolateral margin is entire in *Chersonesometrus* but distinctly incised adjacent to the posterior lateral ocelli in *Heterometrus*. Anterocular extensions of the superciliary carinae are present in *Chersonesometrus* but absent in *Srilankametrus*. The median ocelli are relatively small, the distance between them equal to or greater than the width of an ocellus in *Chersonesometrus* but relatively large, the distance between them less than the width of an ocellus in *Heterometrus*; the median ocular tubercle is situated posteromedially, the distance from carapace anterior margin : carapace length (CAM:CL) 0.51–0.62 in *Chersonesometrus*, but anteromedially to medially, CAM:CL 0.40–0.50 in all other genera. The interocular suture is present in *Chersonesometrus* but absent in *Heterometrus*, *Javanimetrus*, *Sahyadrimetrus*, one species of *Deccanometrus*, and two species of

Srilankametrus. The carapace posterior sutures are present, extending past the median ocular tubercle, and connected anteriorly to the posterior bifurcations of the interocular suture in *Chersonesometrus*; present, extending to the median ocular tubercle, and connected by a short cross-suture anterior to the postocular depression in *Heterometrus*; and absent in *Javanimetrus*, *Sahyadrimetrus*, and two species of *Srilankametrus*. The cheliceral movable finger prodistal (DI) and retrodistal (DE) teeth are unequal, with the DE tooth considerably smaller than the DI tooth, aligned longitudinally and not opposable in some species of *Chersonesometrus*, as in *Gigantometrus*, *Javanimetrus*, *Sahyadrimetrus*, *Srilankametrus*, and most *Deccanometrus*, but subequal, with the DE tooth only slightly smaller than the DI tooth, and opposable, i.e., forming a bicusps, in other species, as in *Heterometrus*. The pedipalp patella dorsomedian carina of the female is entirely to predominantly granular or costate in *Chersonesometrus*, but absent or obsolete in *Heterometrus*, *Javanimetrus*, all except one species of *Sahyadrimetrus*, *S. rugosus*, and all except one species of *Srilankametrus*, *S. caesar*. The patella retromedian carinae of the female are granular or costate (figs. 82, 85, 93, 103, 112, 115) in *Chersonesometrus*, but absent or obsolete in *Gigantometrus*, *Heterometrus*, *Javanimetrus*, all except three species of *Deccanometrus*, *D. bengalensis*, *D. obscurus*, and *D. phipsoni*, all except two species of *Srilankametrus*, *S. gravimanus* and *S. yaleensis*, and three species of *Sahyadrimetrus*, *S. kanarensis*, *S. mathewi*, and *S. scaber*. The prominent spiniform granule of the patella proventral carina is absent (figs. 82, 85, 89, 93, 96, 99, 103, 107, 112, 115) in *Chersonesometrus* but present in *Heterometrus*. The patella dorsal, retrodorsal, and retroventral intercarinal surfaces of the female are granular (figs. 82, 85, 93, 103, 112, 115) in all species of *Chersonesometrus* except *C. nathanorum*, in which the surfaces are smooth or nearly so, as in *Gigantometrus*, *Heterometrus*, *Javanimetrus*, *Srilankametrus*, all species of *Deccanometrus* except *D. obscurus* and *D. phipsoni*, and all species of

Sahyadrimetrus except *S. rugosus*. The distance between the chela manus dorsomedian and promedian carinae or setal rows (DMC-PMC) is slightly to markedly greater than the distance between the promedian and proventral carinae or setal rows (PMC-PVC) in *Chersonesometrus* whereas the DMC-PMC is similar to the PMC-PVC in *Heterometrus*. The dorsomedian carina is continuous to the proximal edge of the manus in *Chersonesometrus* but becomes obsolete proximally in *Heterometrus*, *Javanimetrus*, *Sahyadrimetrus*, *Srilankametrus*, and all species of *Deccanometrus* except *D. obscurus* and *D. phipsoni*. The proximal half of the chela manus dorsal secondary carina, distal half of the subdigital carina and distal third of the digital carina are closely adjacent in *Chersonesometrus* whereas the dorsal secondary, subdigital and digital carinae (or setal rows) are well separated along their entire length in all the other genera except *Gigantometrus*. The dorsal secondary and subdigital carinae of the male are present and entirely to predominantly granular or costate (figs. 87, 97, 100, 104, 108, 113A) in all species of *Chersonesometrus*, except *C. bastawadei* and *C. fulvipes*, in which the carinae are absent or obsolete (fig. 90), as in *Deccanometrus*, *Heterometrus*, *Javanimetrus*, *Sahyadrimetrus*, and two species of *Srilankametrus*, *S. indus* and *S. pococki*. The dorsal secondary carina comprises a double row of separate or confluent granules in *Chersonesometrus* whereas it comprises a single row in *Srilankametrus*. The chela manus retromedian carina is more pronounced than the digital carina (figs. 83, 86, 87, 90, 91, 94, 97, 98, 100, 104, 105, 108, 109, 113, 116) in *Chersonesometrus* whereas the digital and retromedian carinae are similarly developed in all the other genera. The retromedian carina of the male is entirely to predominantly costate in *Chersonesometrus* but entirely to predominantly granular in *Gigantometrus*, *Srilankametrus caesar* and *S. serratus*, and absent or obsolete in *Deccanometrus*, *Heterometrus*, *Javanimetrus*, *Sahyadrimetrus*, *Srilankametrus indus*, and *S. pococki*. The depression in the dorsal surface of the chela manus, proxi-

mal to the fixed finger of the adult male, is absent or obsolete (figs. 87, 90, 97, 100, 104, 108, 113A) in *Chersonesometrus* but present and distinct in *Heterometrus*. The chela manus dorsal surface is usually without reticulation in *Chersonesometrus* but shallowly reticulate in *Javanimetrus*, *Sahyadrimetrus*, all except two species of *Deccanometrus*, *D. obscurus* and *D. phipsoni*, and three species of *Heterometrus*, *H. glaucus*, *H. longimanus* and *H. thorellii*; the dorsal surface is finely to coarsely granular in *Chersonesometrus* but smooth in *Heterometrus*, *Javanimetrus*, two species of *Sahyadrimetrus*, *S. kanarensis* and *S. tikaderi*, and one species of *Deccanometrus*, *D. ubicki*. The chela manus retrolateral intercarinal surfaces are granular in *Chersonesometrus* but smooth or nearly so in *Heterometrus*, *Javanimetrus*, and some species of *Sahyadrimetrus*. The chela manus ventral surface is flat, with the axes of the retroventral and ventromedian carinae in approximately the same plane, in all except four species of *Chersonesometrus*, *C. beccaloniae*, *C. hendersoni*, *C. pelekomanus*, and *C. tristis*, in which it is angled, with the axis of the retroventral carina ventral to the axis of the ventromedian carina, as in *Javanimetrus* and two species of *Srilankametrus*, *S. indus* and *S. pococki*. The pro- and retrolateral surfaces of the tibiae of legs I and II each bear a row of two or three spiniform macrosetae in *Chersonesometrus* and scattered, setiform macrosetae, not arranged in a definite row, in *Heterometrus*. Macroseta *st* on the retroventral surface of the basitarsus of leg I is spiniform (figs. 43–45) in *Chersonesometrus* but usually setiform in *Heterometrus*, and *sb* on the retroventral surface of the basitarsus of leg III is usually setiform in *Chersonesometrus* but spiniform in *Javanimetrus* and *Sahyadrimetrus*. The pseudonychium (dactyl) of the telotarsi of legs I–IV is reduced and rounded in *Chersonesometrus* but prominent and acuminate in *Heterometrus*. The pectinal first proximal median lamella (scape) of the female is distinctly angular, $> 90^\circ$ but $< 180^\circ$ (figs. 29–31) in *Chersonesometrus* but straight or shallowly curved in *Srilankametrus*. The lengths of metasomal segments I and II are approximately equal

to or less than their respective widths (figs. 58–63) in *Chersonesometrus* but markedly greater than their respective widths in *Gigantometrus*. The ventrosubmedian and ventrolateral carinae are granular or costate-granular on metasomal segment IV only and costate on segments I–III (figs. 59, 60, 62, 63) in *Chersonesometrus* but granular on segments I–IV, II–IV (costate on I), or III and IV (costate on I and II) in *Gigantometrus*. The dorsosubmedian carinae of metasomal segment V are vestigial (figs. 58, 61) in *Chersonesometrus* but partial in *Gigantometrus* and absent in *Heterometrus*. The telson is paler than metasomal segment V in *Chersonesometrus* but as dark as segment V in most species of *Srilankametrus* and some species of *Deccanometrus* and *Heterometrus*. The width of the telson vesicle is approximately equal to or less than the width of metasomal segment V in the female of *Chersonesometrus* but greater than the width of segment V in the female of *Gigantometrus* and the vesicle is globose in *Chersonesometrus* but elongate in *Heterometrus*, *Javanimetrus*, *Sahyadrimetrus*, and all except three species of *Srilankametrus*, *S. indus*, *S. pococki*, and *S. serratus*.

INCLUDED SPECIES: As redefined in the present contribution, *Chersonesometrus* accommodates 10 species, five of which were formerly assigned to subgenus *Chersonesometrus* of *Heterometrus* by various authors (Couzijn, 1981; Tikader and Bastawade, 1983; Fet, 2000), whereas four are newly described, recovered as a monophyletic group by phylogenetic analysis of morphological characters and DNA sequences from the nuclear and mitochondrial genomes (fig. 10): *Chersonesometrus bastawadei*, sp. nov.; *Chersonesometrus beccaloniae* (Kovářík, 2004), comb. nov.; *Chersonesometrus fulvipes* (C.L. Koch, 1837), comb. nov.; *Chersonesometrus hendersoni*, sp. nov.; *Chersonesometrus madraspatensis* (Pocock, 1900), comb. nov.; *Chersonesometrus nathanorum*, sp. nov.; *Chersonesometrus pelekomanus* (Couzijn, 1981), comb. nov. et stat. rev.; *Chersonesometrus shivashankari*, sp. nov.; *Chersonesometrus tristis* (Henderson, 1919), comb. nov.; and *Chersonesometrus wroughtoni* (Pocock, 1899), comb. nov.

DISTRIBUTION: *Chersonesometrus* is endemic to India (figs. 1, 79, 80) and has been recorded in the states of Andhra Pradesh, Gujarat, Haryana, Karnataka, Madhya Pradesh, Maharashtra, National Capital Territory of Delhi, Odisha, Rajasthan, Tamil Nadu, Telangana, Uttar Pradesh, and the union territory of Puducherry (table 1). A single record of *C. fulvipes* from Sindh, south-eastern Pakistan, on the border with India (Kovářík, 2009) requires confirmation (Tahir and Prendini, 2014).

ECOLOGY: The species of *Chersonesometrus* for which data are available, occur in semiarid savanna or deciduous woodland, mostly on the Deccan Plateau or in the rain shadow of the Western Ghats (Sahyadri), at elevations of 150–1020 m above sea level. Based on morphology and available habitat data, all species of the genus appear to be pelophilous and fossorial, constructing shallow burrows under stones, or semilithophilous, inhabiting rock crevices or scrapes under stones.

CONSERVATION STATUS: *Chersonesometrus fulvipes* and *C. tristis*, traded as *Heterometrus mysorensis*, are occasionally harvested for the commercial trade in exotic pets.

REMARKS: *Chersonesometrus* Couzijn, 1978, stat. nov., originally created as a subgenus of *Heterometrus*, and subsequently synonymized with the latter (Kovářík, 2004), is hereby revalidated and elevated to the rank of genus.

***Chersonesometrus bastawadei*, sp. nov.**

Figures 10, 16A, 30A, 44A–D, 58A, 59A, 60A, 80, 81A, B, 82, 83, tables 1, 3, 4

Palamnaeus fulvipes madraspatensis: Pocock, 1900a: 89 (misidentification, part).

TYPE MATERIAL: INDIA: Karnataka: *Bagalkot Distr.*: Holotype ♀, paratypes: 7 ♀, 5 subad. ♂, 1 subad. ♀, 11 juv. ♂, 4 juv. ♀ (AMNH), 2 juv. ♂, 1 juv. ♀ (AMCC [LP 16787]), Naganath Temple, NW of Navilahole, 15°54'N 75°44'E, 541 m, 23.xi.2009, R. Datta,

narrow valley between ridges, degraded savanna with plantations, mixed broadleaf woodland with moderate to sparse grass layer on sandy loam, many loose or embedded quartzite stones, in shallow burrows (ca. 10–40 cm deep) or scrapes under stones; 1 subad. ♂ paratype (AMCC [LP 16785]), Badami, Bhootnath Temple, Badami–Mahakoota Path, 15°55'N 75°41'E, 607 m, 23.xi.2009, R. Datta, sandstone plateau, fairly degraded, mixed savanna on sandy-loam with many sandstone outcrops, loose and embedded stones, in shallow burrow (ca. 10 cm deep) under stone.

ETYMOLOGY: The specific epithet is a patronym honoring Deshbhushan B. Bastawade, formerly of the Zoological Survey of India, Poona, and widely known as D.B. Bastawade, who contributed significantly to knowledge of Indian scorpions (e.g., Tikader and Bastawade, 1983) and other arachnids over the course of his career.

DIAGNOSIS: *Chersonesometrus bastawadei* may be separated from other species of *Chersonesometrus* as follows. The carapace is slightly dorsoventrally compressed, the lateral surfaces sloping gently (fig. 16A), in *C. bastawadei*, but vaulted, the lateral surfaces sloping steeply, in *C. fulvipes*, *C. madraspatensis*, and *C. shivashankari*. The frontal lobes and medial region of the carapace interocular surface are granular with smooth areas in the female (fig. 16A) of *C. bastawadei* whereas the interocular surface is granular along the median longitudinal and anterior bifurcated sulci only in the female of all other species except *C. madraspatensis*, *C. pelekomanus*, and *C. shivashankari*. The carapace posterolateral surfaces of the female are granular in *C. bastawadei* but smooth or nearly so in all other species except *C. fulvipes* and *C. madraspatensis*. The cheliceral movable finger prodistal (DI) and retrodistal (DE) teeth are unequal, with the DE tooth considerably smaller than the DI tooth, aligned longitudinally and not opposable in *C. bastawadei*, but subequal, with the DE tooth only slightly smaller than the DI tooth, and opposable, i.e., forming a bicuspid, in

C. beccaloniae, *C. hendersoni*, *C. nathanorum*, *C. pelekomanus*, and *C. tristis*. The pedipalp patella dorsal surface is convex, with the axis of the dorsomedian carina dorsal to the axis of the retrodorsal carina (fig. 82), in *C. bastawadei* but flat or nearly so, with the axes of the dorsomedian and retrodorsal carinae in the same plane, in *C. beccaloniae*, *C. hendersoni*, *C. pelekomanus*, and *C. tristis*. The patella retrodorsal carina of the female is as strongly developed as or more strongly developed than the retromedian carinae in *C. bastawadei* but absent or obsolete in *C. nathanorum*. The retromedian carinae are granular in *C. bastawadei* but costate in *C. nathanorum*. The patella dorsal, retrodorsal, and retroventral intercarinal surfaces of the female are granular (fig. 82) in *C. bastawadei* but smooth or nearly so in *C. nathanorum*. The pedipalp chela is infusate and similar in color to the femur and patella in *C. bastawadei* but immaculate and paler than the femur and patella in *C. shivashankari*. The chela manus dorsal surface (between the dorsomedian and digital carinae) is flat in the male and curved, i.e., slightly to markedly convex, in the female of *C. bastawadei*, flat in the male and female of *C. hendersoni*, *C. pelekomanus*, and *C. tristis*, and curved in the male and female of *C. madraspatensis* and *C. shivashankari*. The proximal margin (lobe) of the chela manus dorsal surface is moderately curved and proximal to the proximal margin of the retrolateral surface in the male or aligned with the proximal margin of the condyle (articulation with patella) in the female (fig. 83) of *C. bastawadei*; moderately curved and aligned with the proximal margin of the retrolateral surface in the male or aligned with or proximal to the proximal margin of the retrolateral surface in the female of *C. beccaloniae* and *C. nathanorum*; and markedly curved and proximal to the proximal margin of the condyle in the male and female of *C. hendersoni* and *C. pelekomanus*. The maximum distance between the dorsomedian and dorsal secondary carinae (DMC–DSC) of the chela manus is greater

than the maximum distance between the dorsal secondary and digital carinae (DSC–DC) in the male of *C. bastawadei*, but greater than the DSC–DC in the male of *C. beccaloniae*, *C. madraspatensis*, *C. nathanorum*, and *C. tristis*. The dorsal secondary and subdigital carinae of the male are absent or obsolete in *C. bastawadei* but entirely to predominantly granular or costate in all other species except *C. fulvipes*. The digital carina is absent or obsolete (fig. 83) in *C. bastawadei*, but entirely to predominantly granular in *C. beccaloniae*, *C. hendersoni*, *C. pelekomanus*, *C. tristis*, and *C. wroughtoni*, and entirely to predominantly costate in *C. nathanorum*. The manus dorsal intercarinal surface is without reticulation in *C. bastawadei* but shallowly reticulate in *C. nathanorum*. The manus ventral surface is flat, with the axes of the retroventral and ventromedian carinae in approximately the same plane in *C. bastawadei* but angled, with the axis of the retroventral carina ventral to the axis of the ventromedian carina in *C. beccaloniae*, *C. hendersoni*, *C. pelekomanus*, and *C. tristis*. The legs are pale or very lightly infusate (fig. 81A, B) in *C. bastawadei* but very dark or heavily infusate in *C. beccaloniae*, *C. nathanorum*, *C. pelekomanus*, *C. tristis*, and *C. wroughtoni*. Macroseta *st* on the retroventral surfaces of the basitarsi of legs I and II is spiniform (fig. 44A–D) in *C. bastawadei* but setiform in *C. nathanorum* and *C. shivashankari*. The mesial surfaces of mesosomal tergites I–VI are granular in the male and the lateral surfaces granular in the female of *C. bastawadei*, whereas the mesial surfaces are smooth in the male of *C. beccaloniae*, *C. hendersoni*, *C. pelekomanus*, and *C. wroughtoni*, the mesial surfaces smooth in the male and the lateral surfaces smooth in the female of *C. tristis*, and the lateral surfaces smooth in the female of *C. nathanorum*. The ventral surface of mesosomal sternite VII bears a pair of weakly developed ventrolateral carinae in *C. bastawadei* and two pairs of moderately to strongly developed ventrosubmedian and ventrolateral carinae in *C.*

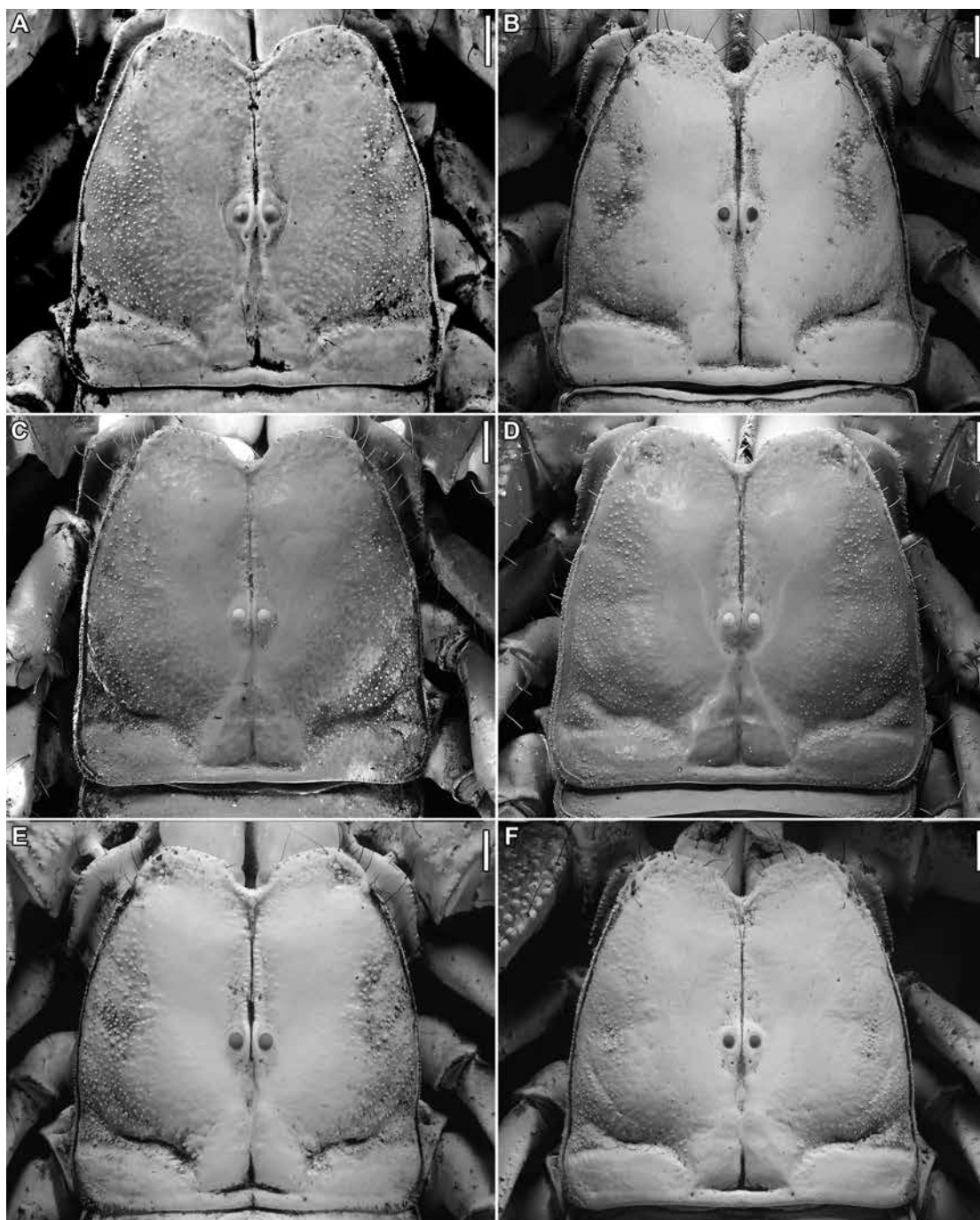


FIGURE 15. *Chersonesometrus* Couzijn, 1978, stat. nov. et stat. rev., carapace, dorsal aspect. **A, B.** *Chersonesometrus beccaloniae* (Kovářík, 2004), comb. nov., **A.** ♂ (ZMH), Ootacalum, India, **B.** ♀ (AMNH), Yelagiri Hills, India. **C, D.** *Chersonesometrus pelekomanus* (Couzijn, 1981), comb. nov. et stat. rev., **C.** holotype ♂ (SMF RII/1088/19), **D.** paratype ♀ (SMF RII/329). **E, F.** *Chersonesometrus tristis* (Henderson, 1919), comb. nov. **E.** ♂ (AMNH), Ithepalli, India, **F.** ♀ (AMNH), Maddur, India. Scale bars = 2 mm.

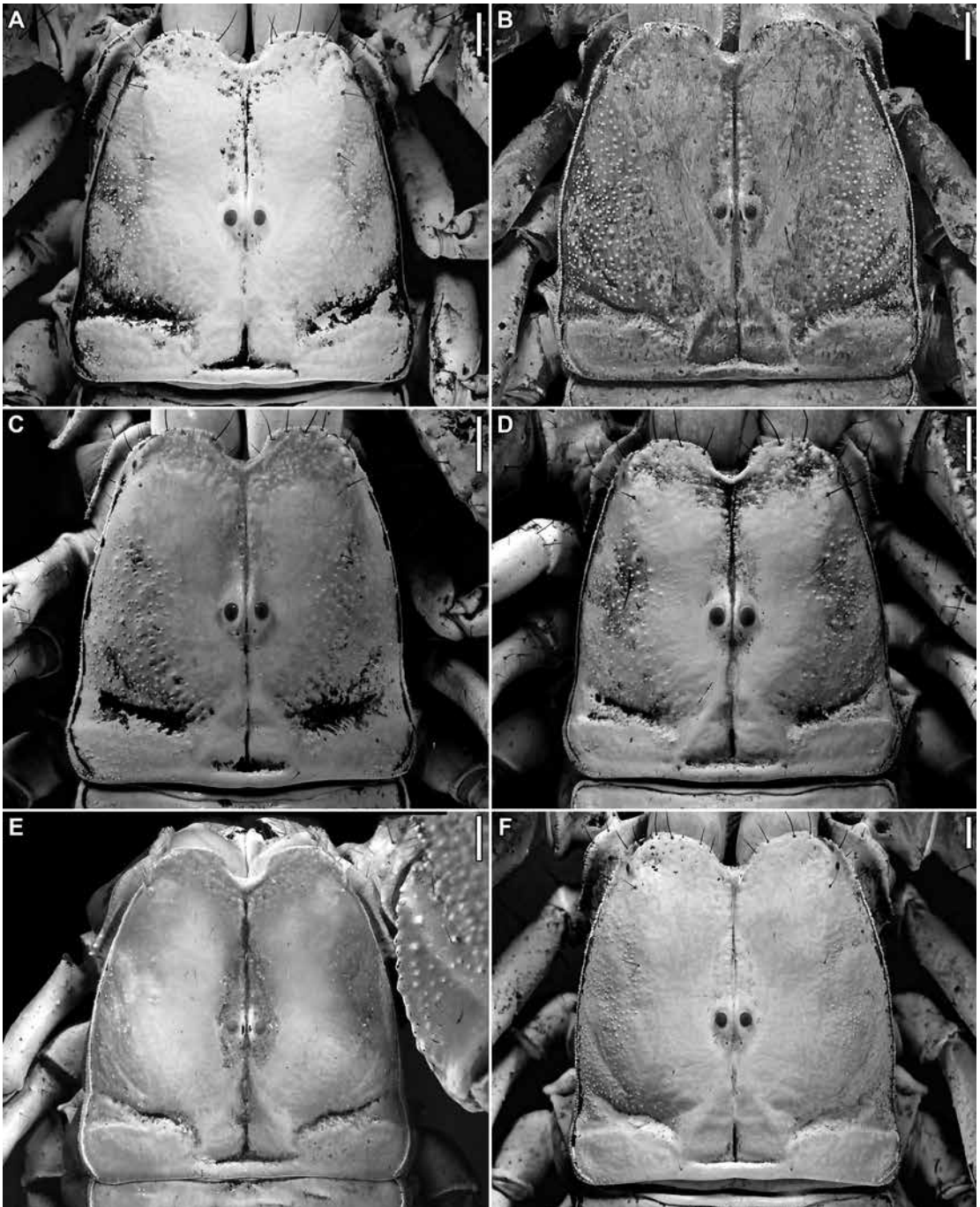


FIGURE 16. *Chersonesometrus* Couzijn, 1978, stat. nov. et stat. rev., carapace, dorsal aspect. **A.** *Chersonesometrus bastawadei*, sp. nov., holotype ♀ (AMNH), Naganath Temple, India. **B.** *Chersonesometrus wroughtoni* (Pocock, 1899), comb. nov., paralectotype ♀ (BMNH 1897.9.17.1-4, 11, 20). **C, D.** *Chersonesometrus shivashankari*, sp. nov., **C.** holotype ♂ (BMNH), Bellahunsi, India, **D.** paratype ♀ (BMNH), Hampasagar, India. **E.** *Chersonesometrus nathanorum*, sp. nov., subad. ♂ holotype (MNHN RS 3145). **F.** *Chersonesometrus hendersoni*, sp. nov., holotype ♀ (AMNH), Sanapura, India. Scale bars = 2 mm.

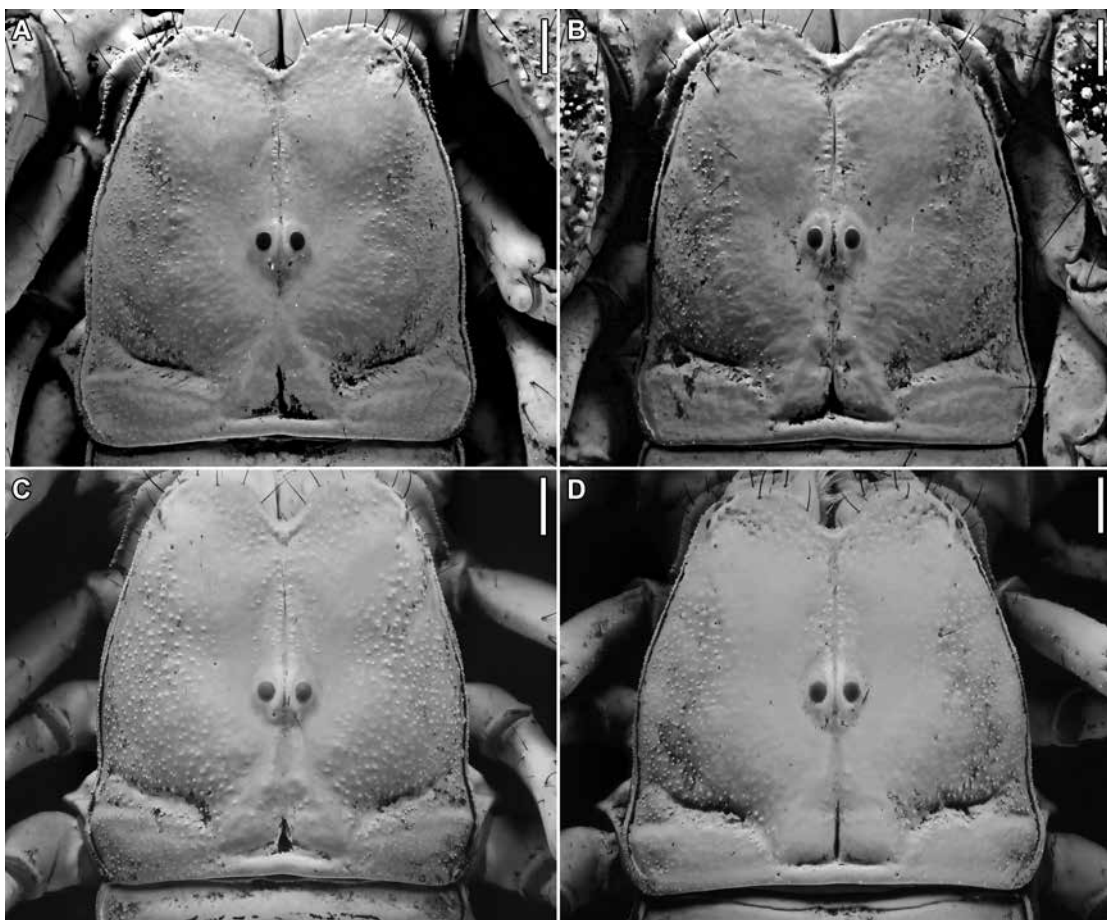


FIGURE 17. *Chersonesometrus* Couzijn, 1978, stat. nov. et stat. rev., carapace, dorsal aspect. **A, B.** *Chersonesometrus fulvipes* (C.L. Koch, 1837), comb. nov., **A.** ♂, **B.** ♀ (AMNH), Khambatki Ghat, India. **C, D.** *Chersonesometrus madraspatensis* (Pocock, 1900), comb. nov., **C.** ♂ (CAS 9071142), **D.** ♀ (CAS 9071143). Scale bars = 2 mm.

beccaloniae, *C. hendersoni*, and *C. pelekomanus*. The dorsosubmedian carinae are granular or costate-granular on metasomal segments I–IV (fig. 58A) in *C. bastawadei* but costate on segments I and II or I–III and granular or costate-granular on III and IV or IV in *C. tristis* and the female of *C. beccaloniae*. The ventral intercarinal surfaces of segment IV are smooth in the male and granular in the female (fig. 60A) of *C. bastawadei* but granular in the male and smooth in the female of *C. beccaloniae* and *C. nathanorum*, granular in the male of *C. hendersoni*, *C. madraspatensis*, *C. pelekomanus*,

and *C. tristis*, and smooth in the female of *C. wroughtoni*. The dorsolateral carinae of metasomal segment V are strong and continuous in *C. bastawadei* but weak and discontinuous to absent in *C. nathanorum*. The dorsal intercarinal surface of segment V is granular in the male and female of *C. bastawadei*, smooth in the female of *C. wroughtoni*, and smooth in the male and female of all other species except *C. hendersoni* and *C. pelekomanus*.

DESCRIPTION: The following description is based on the holotype and paratypes. Meristic data are presented in table 3. The adult male is

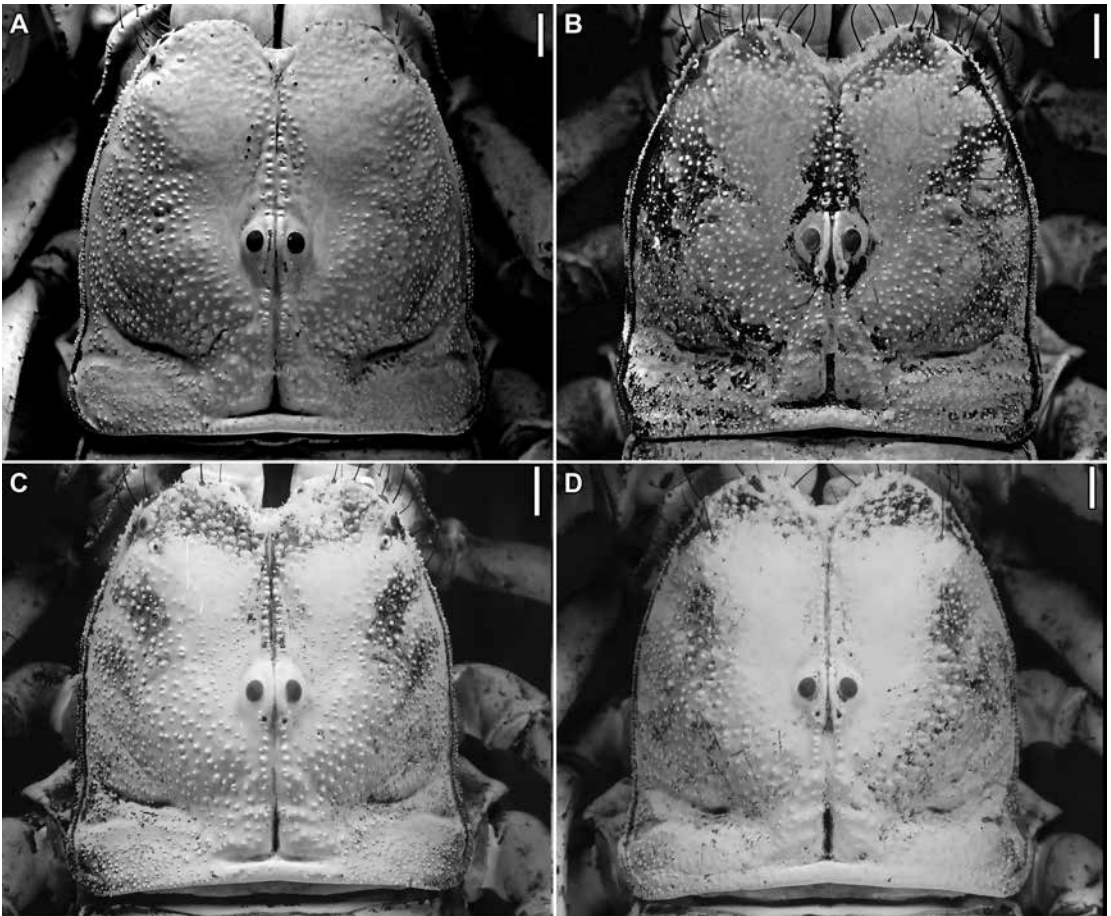


FIGURE 18. *Gigantometrus* Couzijn, 1978, stat. nov., carapace, dorsal aspect. **A, B.** *Gigantometrus swammerdami* (Simon, 1872), comb. nov., **A.** lectotype ♂ (*Palamnaeus swammerdami flavimanus* Pocock, 1900, syn. nov.) (BMNH 1899.11.2.292-3), **B.** ♀ (FMNH 086 257). **C, D.** *Gigantometrus titanicus* (Couzijn, 1981), comb. nov. et stat. rev., **C.** ♂, **D.** ♀ (AMNH), Polonnaruwa, Sri Lanka.

unknown, hence measurements are presented only for the adult female (table 4).

Total length: Adult medium sized, maximum length, measured from anterior margin of carapace to tip of aculeus, 107 mm (100–115 mm, $n = 5$) (♀).

Color: Chelicerae, dorsal surfaces bicolored, mostly to entirely immaculate prodorsal half of manus paler than infuscate retrodorsal half of manus and fingers; manus markedly paler than carapace interocular surface. Carapace, pedipalps, tergites, and metasoma entirely infuscate, uniformly dark reddish black. Sternites III–VI immaculate or partially infuscate, VII mostly or

entirely infuscate, dark olive to brownish black, becoming darker posteriorly. Coxosternal region infuscate, brownish, maxillary lobes darker. Legs lightly infuscate, uniformly yellow to light brown, contrasting with carapace, pedipalps, tergites, and metasoma (fig. 81A, B). Genital opercula and pectines uniformly pale cream. Metasomal segments I–V similar to one another; carinae infuscate, darker than intercarinal surfaces; dorsal intercarinal surfaces similar to tergites; ventral intercarinal surfaces darker than sternites. Telson vesicle immaculate, light yellowish, markedly paler than metasomal segment V; aculeus black.

Chelicerae: Movable finger prodistal (DI) and retrodistal (DE) teeth unequal, with DE tooth considerably smaller than DI tooth, aligned longitudinally and not opposable. Fingers and manus, proventral surfaces with long, dense vestiture of macrosetae. Coxae, prodorsal surfaces without stridulatory setae (scaphotrix); promedian surfaces without chemoreceptive lamelliform setae (trichocopae).

Carapace: Carapace slightly dorsoventrally compressed, lateral surfaces sloping gently. Anterior margin straight, frontal lobes evenly rounded or truncate, with deep median notch, without median projection or median depression (fig. 16A). Anterolateral margins converging gradually anteriorly, without distinct notch adjacent to posterior lateral ocelli; mediolateral margins diverging or converging slightly posteriorly (at posterolateral sulci). Anterior width of posterior width, 64% (62%–58%, $n = 5$) (♀); posterior width of length, 94% (91%–97%, $n = 5$) (♀). Three pairs of lateral ocelli (MLMa, PLMa, PDMi), all similar in size, two anterior pairs situated anteriorly, well separated from posterior pair, situated laterally. Median ocelli slightly larger than lateral ocelli, distance between ocelli greater than or equal to width of ocellus; median ocular tubercle situated posteromedially, distance from anterior carapace margin, 52% (51%–53%, $n = 5$) (♀). Median longitudinal sulcus narrow, suturiform; continuous from median notch to interocular sulcus; with obsolete anterior furcation; without anterocular depression. Anterior furcated sulci diverging broadly from anterior edge of median longitudinal sulcus. Median ocular tubercle raised, superciliary carinae higher than ocelli, extended anteriorly, subparallel. Interocular sulcus present. Circumocular depressions completely encircling median ocular tubercle, converging anteriorly. Posteromedian and posteromarginal sulci deep. Paired mediolateral and posterolateral sulci shallow. Median longitudinal suture continuous from median notch to median ocular tubercle, equally strong along entire length; not extending to anterior margin of carapace, terminating at or posterior to

median notch. Anterior furcated sutures absent or obsolete. Anterocular furcated sutures absent. Interocular suture present, slender. Posterior sutures present but indistinct, converging on median ocular tubercle; connected anteriorly to posterior furcations of interocular suture and extending anteriorly beyond median ocular tubercle. Frontal lobes and medial region of interocular surface finely granular with smooth areas (fig. 16A); anterolateral, mediolateral, and posterolateral surfaces uniformly finely granular; posteromedian surface smooth.

Pedipalps: Pedipalp short, pedipalp femur length : posterior carapace width ratio (FL:PCW) < 0.77, femur length : carapace length ratio (FL:CL) < 0.74. Femur width of length, 49% (47%–51%, $n = 5$) (♀). Retrodorsal carina complete, costate-granular, similar to or more strongly developed than prodorsal carina. Dorsal secondary carina comprising scattered granules, becoming obsolete distally. Dorsomedian carina vestigial, reduced to prominent granule demarcated by conspicuous macroseta. Prodorsal carina complete, granular. Promedian carina complete, comprising row of spiniform or subspiniform granules (several demarcated by conspicuous macrosetae), oriented diagonally between prodorsal and proventral carinae. Proventral carina complete, granular, as strongly developed as or more strongly developed than retroventral carina. Ventromedian and secondary accessory carinae absent. Retroventral carina extending partly or entirely to distal edge of segment. Retromedian carinae absent, indicated only by macrosetal rows. Dorsal and prolateral intercarinal surfaces finely granular; ventral and retrolateral surfaces smooth. Patella width of length, 51% (49%–54%, $n = 5$) (♀). Dorsal surface convex, axis of dorsomedian carina dorsal to axis of retrodorsal carina. Dorsomedian carina entirely to predominantly costate (fig. 82). Retrodorsal carina predominantly costate-granular, more strongly developed than granular retromedian carinae. Retroventral carina distinct, costate to costate-granular. Promedian carina and promedian process absent. Other

carinae absent. Dorsal and prolateral intercarinal surfaces finely granular, other surfaces smooth. Chela short, broad (fig. 83); manus height of width, 82% (78%–85%, $n = 5$) (♀); manus length along retroventral carina of manus width, 89% (89%–93%, $n = 5$) (♀); manus length along retroventral carina of movable finger length, 72% (69%–75%, $n = 5$) (♀). Chela sparsely setose. Manus dorsal surface (between dorsomedian and digital carinae) flat (♂) or curved, i.e., slightly to markedly convex (♀); proximal margin (lobe) of dorsal surface moderately curved and proximal to proximal margin of retrolateral surface (♂) or aligned with proximal margin of condyle (articulation with patella) (♀). Dorsomedian carina obsolete, costate on fixed finger and comprising regular row of spiniform granules along entire length of manus. Dorsal secondary, subdigital, and digital carinae absent or obsolete. Maximum distance between dorsomedian carina and setal row demarcating dorsal secondary carina (DMC–DSC) greater than maximum distance between setal rows demarcating dorsal secondary and digital carinae (DSC–DC). Retromedian carina complete, predominantly costate, more strongly developed than digital carina. Retrolateral secondary and secondary accessory carinae vestigial, proximal to condyle of movable finger. Retroventral and ventromedian carina distinct, costate, but retroventral carina more strongly developed. Proventral and promedian carinae similarly developed, each comprising row of spiniform granules and associated macrosetae. Prodorsal carina obsolete, comprising few spiniform granules and associated macrosetae. Distance between dorsomedian and promedian carinae (DMC–PMC) slightly to markedly greater than distance between promedian and proventral carinae (PMC–PVC). Manus, dorsal and retrolateral intercarinal surfaces densely and coarsely granular except for smooth depression at base of fixed finger; ventral intercarinal surface granular; prolateral intercarinal surfaces sparsely finely and coarsely granular, more densely dorsally and distally. Manus ventral surface flat, axes of retroventral and ventromedian

carinae in approximately same plane. Fixed and movable fingers, intercarinal surfaces smooth; median denticle rows each with six enlarged retrolateral denticles (including terminal denticle), proximal three situated on lobes; first (proximal) lobe of fixed finger and second lobe of movable finger larger than others, with correspondingly deeper notches in movable and fixed fingers, respectively; terminal denticles of fingers interlocking unevenly when closed, movable finger displaced retrolaterally; distinct notch near tip of fixed finger to accommodate terminal denticle of movable finger.

Trichobothria: Orthobothriotaxic, Type C, with the following segment totals ($n = 20$): femur, 3 (1 d , 1 i , 1 e); patella, 19 (2 d , 1 i , 3 v , 13 e , comprising 3 et , 1 est , 2 em , 2 esb , 5 eb); chela, 26 (manus, 16, comprising 2 D , 10 E , 4 V ; fixed finger, 10, comprising 4 d , 4 e , 2 i). Total count of trichobothria per pedipalp: 48. Femur, i situated on dorsal surface. Patella, d_2 situated on internal surface, slightly closer to d_1 than to i ; distance v_2 – v_3 ca. one-third distance v_1 – v_2 . Chela, distance et – est less than half distance est – esb ; distance est – esb greater than half distance esb – eb ; est distal to dst ; V_3 situated in proximal third of manus V_3 , closer to V_4 than V_2 .

Legs: First pair of maxillary lobes (coxapophyses) tapering anteriorly, longer than and encircling second pair. Stridulatory organs, comprising “rasp” (granular tubercles) and “scraper” (stridulatory setae or scaphotrix), present on opposing surfaces of coxae of first pair of legs and pedipalps, respectively. Legs I–IV acarinate, except femora, with distinct pro- and retrolateral surfaces demarcated by partial, granular prodorsal and complete, costate-granular proventral carinae. Femora, patellae, and tibiae, pro- and retrolateral surfaces each with scattered setiform macrosetae. Tibiae, prolateral surfaces, without spiniform macrosetae; I and II, retrolateral surfaces, each with two spiniform (t , st) macrosetae; III and IV, retrolateral surfaces, without spiniform macrosetae. Basitarsi I–IV, slightly dorsoventrally compressed; retrolateral margins similar, unmodi-

fied, rounded; prolateral pedal spurs present (fig. 44A–D); retrolateral pedal spurs absent. Basitarsi, pro- and retrolateral surfaces, each with scattered long and short setiform macrosetae, and spiniform macrosetae, more numerous on I and II than III and IV. Basitarsi, spiniform macrosetae, I, retrolateral: *t*, *sb*; retroventral: *t*, *st*, *sb*; proventral: *t*, *st*; II, retrolateral: *t*, *sb*; retroventral: *t*, *st*, *sb*; proventral: *t*, *st*; III, retrolateral: *t*, *sb*; retroventral: *t*, *st*; proventral: *t*; prolateral: *t*, *st*; IV, retrolateral: *t*; retroventral: *t*; proventral: *t*, *st*; prolateral: *t*, *st*. Telotarsi I–IV short, stout and distally broadened in dorsal and lateral views. Laterodistal lobes rounded. Dorsomedian lobes approximately equal to laterodistal lobes; each terminating in single setiform macroseta. Telotarsi, pro- and retrolateral surfaces, each with long and short, scattered macrosetae, not arranged in definite row. Telotarsi each with pro- and retroventral rows of spiniform macrosetae, two inserted on laterodistal lobes; macrosetal counts in pro- and retroventral rows similar on I and II, and on III and IV ($n = 20$): I, proventral: 3 (3 or 4), retroventral: 6 (5 or 6); II, 4 (3 or 4), 6 (5 or 6); III and IV, 4, 6. Telotarsal unguis short, curved, equal to subequal; pseudonychium (dactyl) reduced, rounded.

Sternum: Shape subpentagonal (fig. 30A). Median longitudinal sulcus shallow anteriorly, deep and narrow posteriorly.

Genital operculum: Genital opercula suboval, completely divided longitudinally, partially overlapping, genital papillae present (δ); subcordate, fused, genital papillae absent (φ) (fig. 30A).

Hemispermaphore: Unknown.

Pectines: Distal edge extending past distal edge of coxa IV but not reaching distal edge of trochanter IV (fig. 30A). First proximal median lamella (scape) of each pecten with mesial margin angular, approximately 90° (δ) or obtusely angular, greater than 90° but less than 180° (φ). Pectinal teeth straight and elongate (δ) or shorter and curved (φ), present along entire posterior margin; sinistral/dextral tooth count, 17/17 (16–18/16–18, $n = 12$) (δ), 15/15 (15 or

16/15–17, $n = 12$) (φ). Fulcra smooth proximally but densely setose (microsetae only) distally.

Mesosoma: Tergites each with shallow pair of submedian depressions, without obsolete median carina. Pretergites smooth and glabrous. Posttergites finely granular (δ) or smooth and glabrous (φ) medially, unevenly finely and coarsely granular to predominantly coarsely granular laterally. Sternites IV–VI, each with paired longitudinal depressions prolateral to spiracles, absent on VII. Surface, sternites III–VII, smooth; VII with pair of weakly developed, costate ventrolateral carinae only, without posteromarginal carina. Sternite VII, length of width, 65% (61%–72%, $n = 5$) (φ).

Metasoma and telson: Metasomal segments I–V progressively increasing in length, decreasing in width; segment V, width of segment I, width, 73% (72%–76%, $n = 5$) (φ). Metasoma robust, width of length, segment I, 90% (85%–98%, $n = 5$) (φ); II, 72% (69%–74%) (φ); III, 64% (62%–66%) (φ); IV, 53% (51%–54%) (φ); V, 39% (38%–40%) (φ). Telson vesicle, width of metasomal segment V, width, 94% (90%–95%, $n = 5$) (φ); vesicle globose, height of length, 55% (53%–57%, $n = 5$) (φ); dorsal surface flat; ventral surface evenly curved. Aculeus relatively long, gently curved, length of vesicle length, 57% (56%–60%, $n = 5$) (φ). Length metasoma and telson, of total length, 55% (54%–56%, $n = 5$) (φ). Dorsosubmedian carinae, segments I–IV, distinct, complete, granular or costate-granular, posterior spiniform granules obsolete (fig. 58A); V, vestigial. Dorsolateral carinae, segments I–V, distinct, complete, costate-granular on I–IV, costate-granular to granular on V. Median lateral carinae, segment I, incomplete, reduced to granular row in posterior half, diagonally oriented between dorso-lateral and ventrolateral carinae (fig. 59A); II–IV, obsolete row of granules posteriorly; V, incomplete, granular row, restricted to anterior two-thirds. Ventrolateral and ventrosobmedian carinae, I–IV, distinct, complete, costate on I–III, granular or costate-granular on IV, more strongly developed on III and IV than on I and II (fig. 60A). Ventrolateral carinae, V, distinct, complete, comprising spiniform granules, diverging posteriorly, terminal granule slightly larger than preceding granules.

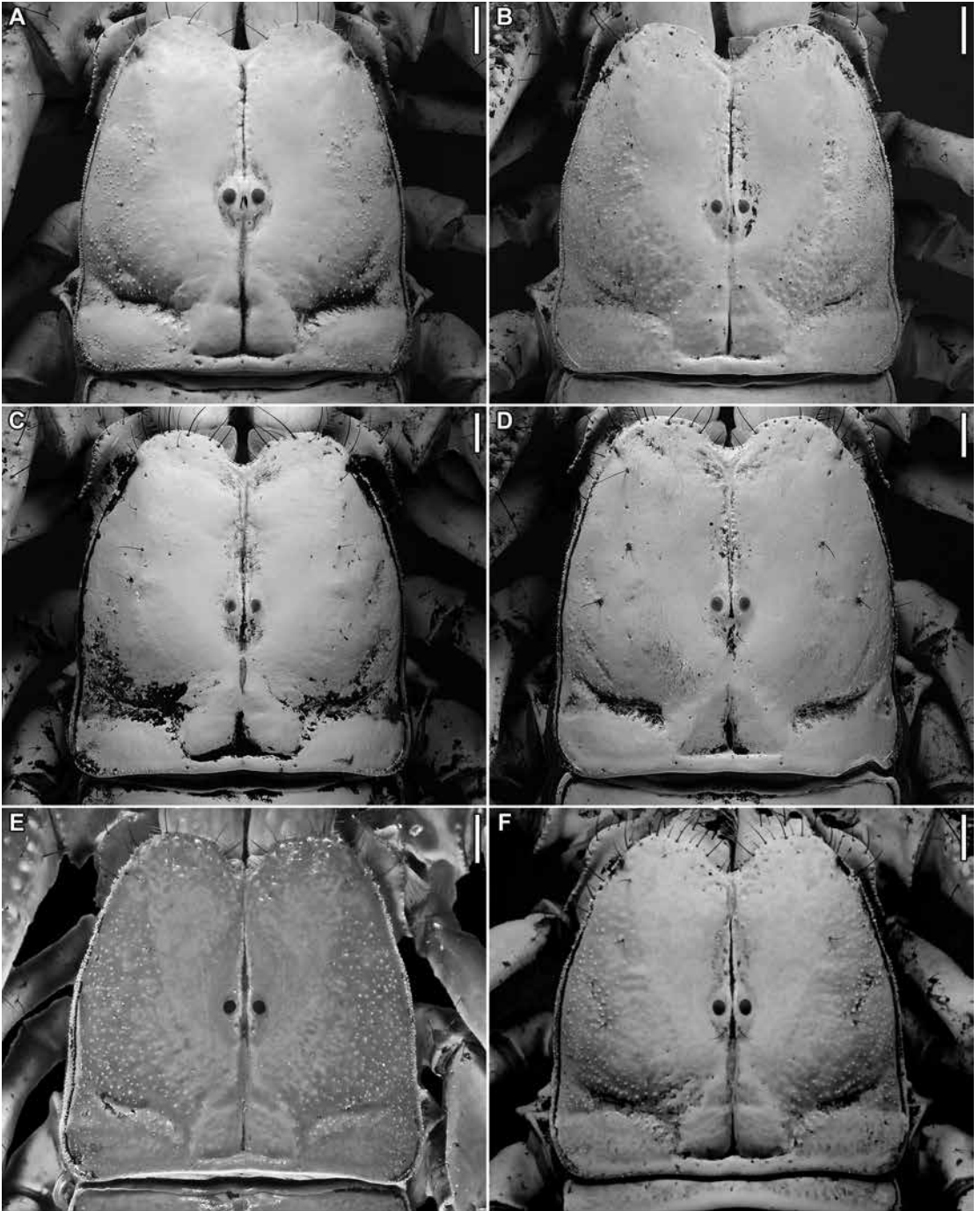


FIGURE 19. *Deccanometrus*, gen. nov., carapace, dorsal aspect. **A, B.** *Deccanometrus bengalensis* (C.L. Koch, 1841), comb. nov., **A.** ♂ (BMNH 1913.1.6.3), **B.** ♀ (BMNH 1896.8.15.4). **C, D.** *Deccanometrus obscurus* (Couzijn, 1981), comb. et stat. nov., **C.** ♂, **D.** ♀ (AMNH), Bhimashankar, India. **E, F.** *Deccanometrus phipsoni* (Pocock, 1893), comb. nov., **E.** ♂, **F.** ♀ (MNHN RS 0080). Scale bars = 2 mm.

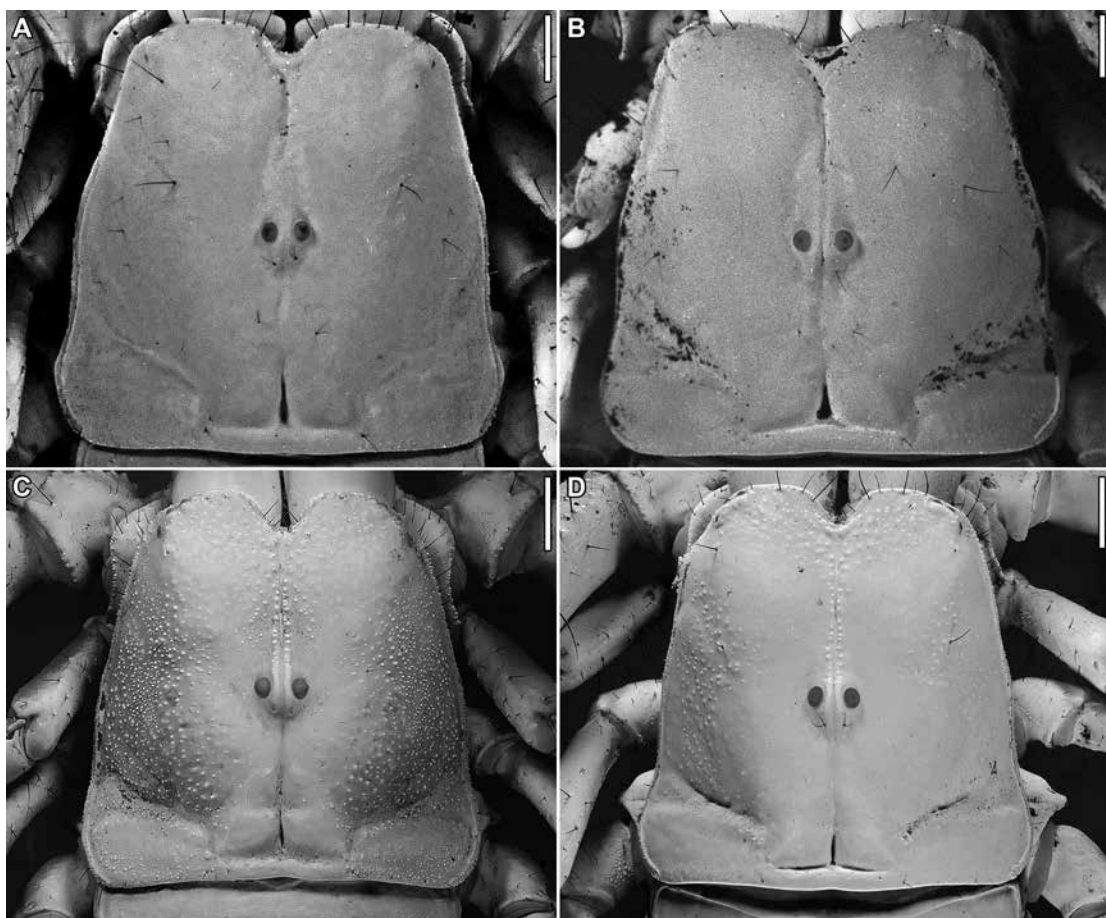


FIGURE 20. *Deccanometrus*, gen. nov., carapace, dorsal aspect. **A, B.** *Deccanometrus latimanus* (Pocock, 1894), comb. nov., **A.** ♂ (AMNH), Charbagh, Pakistan, **B.** ♀ (AMNH), Daggar, Pakistan. **C, D.** *Deccanometrus xanthopus* (Pocock, 1897), comb. nov., **C.** lectotype ♂ (BMNH 1896.9.26.88-91), **D.** ♀ (AMNH), Khambatki Ghat, India. Scale bars = 2 mm.

Ventrosubmedian carinae, segment V, vestigial, each reduced to one or two isolated spiniform granules, demarcated by conspicuous macrosetae. Ventromedian carina, segment V comprising single row of spiniform granules, unmodified posteriorly. Anal arch, segment V, dorsal carina, costate; ventral carina comprising subspiniform granules. Dorsal intercarinal surfaces, segments I–V, granular. Lateral intercarinal surfaces, segments I–IV, granular, V, smooth. Ventral intercarinal surfaces, segments I–III, smooth, IV and V, smooth (♂) or granular (♀). Ventral surface, lateral aspect, segment IV, shallowly convex. Telson vesicle, dorsal and lateral

surfaces smooth; ventral surface with four longitudinal carinae, each comprising spiniform granules.

DISTRIBUTION: This species is endemic to India and presently recorded only from the state of Karnataka (fig. 80, table 1). Its distribution is allopatric with the morphologically similar *C. fulvipes*, *C. madraspatensis*, *C. shivashankari*, and *C. wroughtoni*.

ECOLOGY: The known locality records of this species occur in semiarid savanna dominated by *Acacia* Martius, 1829, *Euphorbia* Linnaeus, 1753, and broadleaf bushes

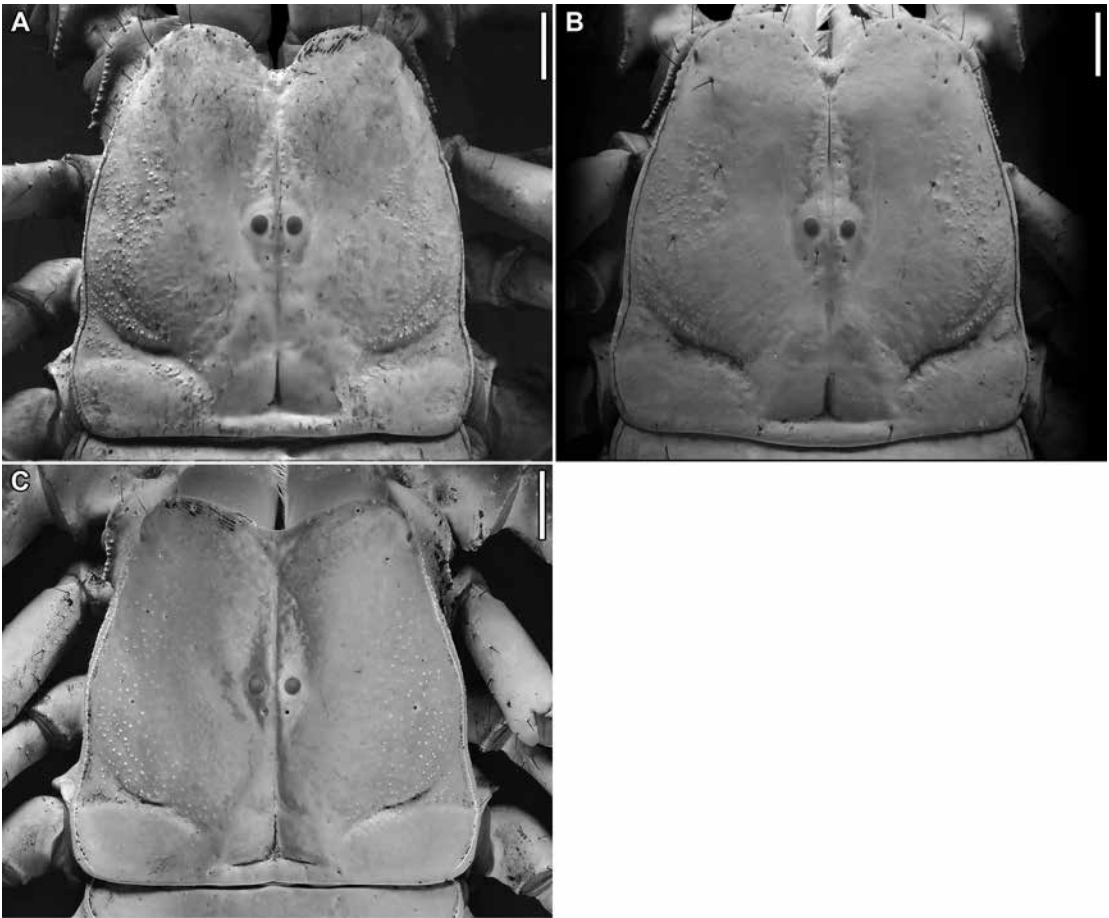


FIGURE 21. *Deccanometrus*, gen. nov., carapace, dorsal aspect. **A, B.** *Deccanometrus ubicki* (Kovářík, 2004), comb. nov., **A.** paratype ♂ (CAS 9071136), **B.** paratype ♀ (CAS 9071135). **C.** *Deccanometrus liurus* (Pocock, 1897), comb. nov., paralectotype ♀ (BMNH 1896.12.15.20-25). Scale bars = 2 mm.

(*Dichrostachys* (DC.) Wight and Arnott, 1834, *Grewia* Linnaeus, 1753, *Ziziphus* Miller, 1754), with sparse grass on rocky sandstone or quartzite hills, at elevations of 540–610 m. The specimens for which data are available were collected from shallow burrows or scrapes (10–40 cm deep) under stones or boulders, embedded in hard, sandy loam. The habitat and habitus are consistent with the pelophilous, fossorial and semilithophilous ecomorphotypes (Prendini, 2001b). This species is sympatric with *Charmus indicus* Hirst, 1915, *Hottentotta rugiscutis* (Pocock, 1897) and *Lychas tricarinatus* (Simon, 1884).

Chersonesometrus beccaloniae (Kovářík, 2004),
comb. nov.

Figures 10, 15A, B, 29A, B, 43A–D, 58B, 59B,
60B, 80, 84–87, table 1

Heterometrus indus: Roewer, 1929: 612
(misidentification, part).

Heterometrus liurus: Roewer, 1929: 613
(misidentification, part).

Heterometrus phipsoni: Roewer, 1929: 612
(misidentification, part).

Heterometrus (*Chersonesometrus*) *palekomanus*:
Indra, 2001: 56, 58 (misidentification, part).

TABLE 3 continued

Species	Type	Sex	Collection	Pro. I	Retro. I	Pro. II	Retro. II	Pro. III	Retro. III	Pro. IV	Retro. IV	Pectines
<i>Chersonesometrus shivashankari</i>	Holo.	♂	BMNH	4/3	6/6	4/3	6/5	4/4	6/6	4/4	6/6	15/16
	Para.	♀	BMNH	3/3	6/6	4/4	6/6	4/4	6/6	4/4	6/6	15/15
	Para.	subad. ♀	MNHN RS 0093	3/3	5/5	4/-	5/-	4/-	5/-	4/4	5/5	13/13
<i>Sahyadrimetrus mathewi</i>	Holo.	♂	AMNH	3/3	5/5	3/3	5/5	4/4	5/5	4/4	5/5	12/12
	Para.	♂	AMNH	3/3	6/5	3/3	5/5	4/3	5/5	4/4	5/5	11/9
	Para.	♂	AMNH	3/3	5/5	3/3	5/5	4/4	5/4	4/4	5/5	11/12
	Para.	subad. ♂	AMNH	3/3	4/4	3/3	5/5	4/4	5/5	4/4	5/5	12/12
	Para.	subad. ♂	AMNH	3/3	4/4	3/3	5/5	4/4	5/5	4/4	5/5	12/12
	Para.	♀	AMNH	3/3	5/5	3/3	5/5	4/4	6/5	4/4	5/6	10/10
	Para.	♀	AMNH	3/-	5/-	4/3	6/5	3/4	6/5	4/4	5/6	11/11
	Para.	subad. ♀	AMNH	3/3	4/4	3/3	5/5	3/3	5/5	3/3	5/5	11/12
<i>Sahyadrimetrus tikaderi</i>	Para.	subad. ♀	AMNH	3/3	4/5	3/3	5/5	4/4	5/5	4/4	5/5	9/10
	Holo.	♂	MNHN RS 3265	3/3	6/5	3/3	6/6	4/4	6/6	4/4	6/6	11/11
	Para.	♂	MNHN RS 3266	3/4	6/6	4/3	6/6	4/4	6/6	4/4	6/6	12/12
	Para.	♀	MNHN RS 3265	3/3	6/5	4/4	6/6	4/4	6/6	4/4	6/6	11/11
	Para.	♀	MNHN RS 3265	-/3	-/6	-/4	-/6	4/4	6/6	4/4	6/6	11/11
<i>Srilankametrus couzijni</i>	Holo.	♂	BMNH 18967.30.121	3/3	4/4	2/2	4/4	3/3	5/5	4/4	5/5	14/14
	Para.	♂	SMF 5332/1	3/3	4/4	3/3	4/4	4/3	5/5	4/4	5/5	14 ² /14
<i>Srilankametrus pococki</i>	Holo.	♀	AMNH	3/3	4/4	4/4	4/4	4/4	5/5	4/4	5/5	12/12 ²
	Para.	subad. ♀	AMNH	3/3	4/4	3/3	4/4	3/4	5/5	4/4	5/4	12/11
	Para.	subad. ♀	AMNH	3/3	4/4	3/4	4/4	4/4	5/5	4/4	5/5	12/12
	Para.	subad. ♂	AMNH	3/3	4/4	3/4	4/4	4/4	5/5	4/4	5/5	13/12
	Para.	subad. ♂	AMNH	3/3	4/4	3/3	4/4	4/4	5/5	4/4	5/5	12/13
	Para.	subad. ♂	AMNH	3/3	4/4	4/-	4/-	4/4	5/5	4/4	5/5	12/12

TABLE 4
Measurement Data for Type Specimens of Three New Species of *Chersonesometrus* Couzijn, 1978, stat. nov. et stat. rev.
Material deposited at the American Museum of Natural History (AMNH), New York, and the Natural History Museum (BMNH), London.
Measurements (mm) follow Prendini (2000b): ¹sum of carapace, tergites I–VII, metasomal segments I–V, and telson; ²distance from anterior carapace margin; ³sum of metasomal segments I–V and telson; ⁴distance from base of condyle to tip of fixed finger.

Species	<i>Chersonesometrus bastawadei</i>						<i>Chersonesometrus hendersoni</i>						<i>Chersonesometrus shivashankari</i>	
Type	Holo.	Para.	Para.	Para.	Para.	Para.	Holo.	Para.	Para.	Para.	Para.	Holo.	Holo.	Para.
Sex	♀	♀	♀	♀	♀	♀	♀	♀	♀	♀	♀	♂	♂	♀
Collection	AMNH	AMNH	AMNH	AMNH	AMNH	AMNH	AMNH	AMNH	AMNH	AMNH	AMNH	BMNH	BMNH	BMNH
Total length ¹	112.1	114.9	101.5	105.6	99.8	156.1	125.9	129.3				85.7	82.1	
Carapace														
anterior width	9.8	10.0	8.5	8.8	8.9	13.8	11.6	11.8				7.4	7.3	
posterior width	15.2	16.0	13.6	13.5	13.1	21.5	17.9	18.2				11.6	11.1	
length	15.9	16.4	14.3	14.6	14.4	22.6	18.2	18.8				12.0	11.8	
median ocelli ²	8.3	8.6	7.6	7.5	7.5	11.7	9.5	9.6				6.2	5.9	
Tergite I														
length	2.5	2.6	1.9	2.5	2.3	3.3	2.6	2.7				2.3	2.2	
Tergite II														
length	2.8	3.1	2.9	2.7	2.6	3.9	3.5	3.3				3.0	2.3	
Tergite III														
length	4.3	4.2	4.0	3.7	3.7	5.8	4.8	4.7				3.3	3.1	
Tergite IV														
length	5.5	5.1	4.2	4.9	4.4	7.5	5.8	6.1				4.1	3.5	
Tergite V														
length	5.9	5.8	5.1	5.2	4.8	8.4	6.8	6.6				4.3	4.2	
Tergite VI														
length	6.7	6.4	6.3	6.1	5.4	8.8	7.5	7.7				4.4	4.8	
Tergite VII														
length	8.3	8.3	7.0	7.4	6.7	10.9	9.7	9.5				4.9	5.2	
Sternite VII														
length	8.1	8.4	6.9	7.3	7.5	11.8	9.0	10.0				6.1	5.8	
width	12.6	11.7	11.2	11.9	11.4	18.5	14.0	14.4				8.9	9.7	
Mesosoma														
total length (tergites)	36.0	35.5	31.4	32.4	29.9	48.7	40.7	40.6				26.4	25.3	
Metasoma I														
length	7.1	8.2	6.9	7.0	7.2	11.4	8.4	8.9				6.0	5.8	
width	6.9	6.9	6.3	6.4	6.1	8.9	7.2	7.5				5.7	5.4	
Metasoma II														
length	8.9	8.9	7.7	8.0	8.0	12.1	9.8	9.6				6.3	6.4	
width	6.4	6.2	5.7	5.9	5.5	7.7	6.7	6.7				5.2	5.0	

TABLE 4 continued

Species	<i>Chersonesometrus bastawadei</i>						<i>Chersonesometrus hendersoni</i>				<i>Chersonesometrus shivashankari</i>			
Type	Holo.	Para.	Para.	Para.	Para.	Para.	Holo.	Para.	Para.	Para.	Holo.	Para.	Para.	Para.
Sex	♀	♀	♀	♀	♀	♀	♀	♀	♀	♀	♂	♂	♀	♀
Collection	AMNH	AMNH	AMNH	AMNH	AMNH	AMNH	AMNH	AMNH	AMNH	AMNH	BMNH	BMNH	BMNH	BMNH
Metasoma III	length	9.1	9.5	8.6	8.9	8.3	12.6	10.0	10.0	10.0	6.9	6.9	6.6	6.6
	width	6.0	6.0	5.5	5.7	5.2	7.1	6.3	6.4	6.4	5.0	5.0	4.7	4.7
Metasoma IV	length	10.0	10.5	9.7	10.1	9.5	13.6	11.0	11.2	11.2	7.7	7.7	7.4	7.4
	width	5.5	5.5	5.2	5.3	4.9	6.6	5.6	5.4	5.4	4.7	4.7	4.4	4.4
Metasoma V	length	12.6	13.2	11.8	12.5	11.6	17.2	13.9	15.0	15.0	10.4	10.4	9.1	9.1
	width	5.0	5.0	4.6	4.8	4.4	6.0	5.1	5.1	5.1	4.3	4.3	3.8	3.8
Telson	vesicle length	8.1	8.0	7.1	7.6	7.0	10.6	8.6	9.2	9.2	6.0	6.0	6.2	6.2
	vesicle width	4.8	4.8	4.1	4.5	4.2	6.1	5.4	5.1	5.1	4.0	4.0	3.3	3.3
	vesicle height	4.4	4.5	3.9	4.1	3.8	5.6	4.6	4.7	4.7	3.6	3.6	2.9	2.9
	aculeus length	4.5	4.6	4.1	4.6	4.0	7.6	5.4	6.0	6.0	3.8	3.8	3.6	3.6
	total length	12.6	12.6	11.2	12.2	11.0	18.2	14.0	15.3	15.3	9.9	9.9	9.8	9.8
	total length ³	60.2	62.9	55.8	58.7	55.5	84.9	67.1	69.9	69.9	47.2	47.2	45.0	45.0
Metasoma														
Femur	length	11.7	11.4	9.8	10.8	10.0	18.5	14.1	14.4	14.4	9.1	9.1	8.1	8.1
	width	5.5	5.8	5.0	5.2	4.7	8.4	6.5	7.3	7.3	4.0	4.0	3.7	3.7
Patella	length	12.3	12.4	10.5	11.1	10.7	18.8	14.9	14.9	14.9	10.1	10.1	8.4	8.4
	width	6.1	6.1	5.7	5.8	5.5	9.5	7.5	7.9	7.9	4.6	4.6	4.6	4.6
Chela	length ⁴	26.1	26.0	22.1	23.8	23.0	41.5	32.7	32.4	32.4	18.9	18.9	18.5	18.5
	width	12.0	11.5	11.0	10.3	10.3	20.3	16.4	15.5	15.5	5.0	5.0	6.1	6.1
	height	9.3	9.8	9.3	8.5	8.4	13.7	11.1	9.4	9.4	10.3	10.3	10.9	10.9
	length retrovent. carina	10.7	10.3	9.3	9.5	9.2	17.4	13.1	14.3	14.3	7.5	7.5	7.0	7.0
Pecten	length movable finger	14.3	14.8	12.9	13.4	13.0	24.7	18.0	18.2	18.2	11.5	11.5	10.2	10.2
	total length	8.3	8.9	6.8	7.3	7.4	11.0	9.4	9.9	9.9	6.4	6.4	5.9	5.9
	length dentate margin	6.6	6.2	5.3	5.6	5.4	7.8	7.1	7.9	7.9	5.9	5.9	4.9	4.9

Heterometrus beccaloniae Kovařík, 2004: 1, 4, 6, 7, 51, 52, tables 1–3, fig. 9; 2009: 34–36, 47, 49, 73, 101, tables 1, 2, figs. 5–7, 217; Mirza et al., 2012: 1, 3, 6, 7, table 1.

Heterometrus (Chersonesometrus) pelekomanus: Indra, 2009: 141 (misidentification, part).

Heterometrus atrascorpius Mirza et al., 2012: 1–8, table 1, figs. 1–10; syn. nov.

TYPE MATERIAL: **INDIA: Tamil Nadu:** *Nilgiris Distr.*: *Heterometrus atrascorpius*: Holotype: 1 [subad.] ♀ (BNHS Sc-55), Bokkapuram village near Masinagudi, 11°33'N 76°40'E, 912 m, 25.i.2011, G. Desouza and N.S. Chithyuan; paratypes: 1 [imm.] ♂ (BNHS Sc-56), same data except: R. Sanap and Z. Mirza, 1 imm. paratype ♀ (BNHS Sc-57), same data except: D. Joshi and S. Chikane. *Heterometrus beccaloniae*: Paratypes: 1 imm., 7 juv. (FKPC), Nilgiri hills, Mudumalai National Park [11°34'N 76°32'E], 6.v.2000, Rolčík. *Vellore Distr.*: *Heterometrus beccaloniae*: Holotype ♀ (FKPC), Kavalore [Kavalur, 12°35'N 78°49'E], Javadu Hills [Jawadhu Hills], 2000 ft., v.2003, T.R.S.N.

DIAGNOSIS: *Chersonesometrus beccaloniae* may be separated from other species of *Chersonesometrus* as follows. The carapace is markedly dorsoventrally compressed, the lateral surfaces sloping gently (fig. 15A, B), in *C. beccaloniae*, but vaulted, the lateral surfaces sloping steeply, in *C. fulvipes*, *C. madraspatensis*, and *C. shivashankari*. The carapace interocular surface is granular along the median longitudinal and anterior bifurcated sulci only in the female (fig. 15B) of *C. beccaloniae* whereas the frontal lobes and medial region of the interocular surface are granular with smooth areas in the female of *C. bastawadei*, *C. madraspatensis*, *C. pelekomanus*, and *C. shivashankari*. The carapace posterolateral surfaces of the female are usually smooth in *C. beccaloniae* but granular in *C. bastawadei*, *C. fulvipes*, and *C. madraspatensis*. The cheliceral movable finger prodistal (DI) and retrodistal (DE) teeth are subequal, with the DE tooth only slightly smaller than the DI tooth, and opposable, i.e., forming a bicuspid, in *C. beccaloniae* but unequal, with the DE tooth considerably

smaller than the DI tooth, aligned longitudinally and not opposable in *C. bastawadei*, *C. fulvipes*, *C. madraspatensis*, *C. shivashankari*, and *C. wroughtoni*. The pedipalps of the adult male are long, with femur length : posterior carapace width ratio (FL:PCW) ≥ 0.80 and femur length : carapace length ratio (FL:CL) ≥ 0.76 (fig. 84A, B) in *C. beccaloniae* but short, with FL:PCW < 0.77 , FL:CL < 0.74 in all other species except *C. madraspatensis* and *C. tristis*. The pedipalp patella dorsal surface is flat or nearly so, with the axes of the dorsomedian and retrodorsal carinae in the same plane (fig. 85), in *C. beccaloniae* but convex, with the axis of the dorsomedian carina dorsal to the axis of the retrodorsal carina, in all other species except *C. hendersoni*, *C. pelekomanus*, and *C. tristis*. The patella retrodorsal carina of the female is as strongly developed as or more strongly developed than the retromedian carinae in *C. beccaloniae* but absent or obsolete in *C. nathanorum*. The retromedian carinae are granular in *C. beccaloniae* but costate in *C. nathanorum*. The patella dorsal, retrodorsal, and retroventral intercarinal surfaces of the female are granular (fig. 85) in *C. beccaloniae* but smooth or nearly so in *C. nathanorum*. The pedipalp chela is infusate and similar in color to the femur and patella in *C. beccaloniae* but immaculate and paler than the femur and patella in *C. shivashankari*. The chela of the adult male is moderately to densely setose in *C. beccaloniae* but sparsely setose in *C. fulvipes*, *C. madraspatensis*, and *C. shivashankari*. The chela manus dorsal surface (between the dorsomedian and digital carinae) is flat in the male and curved, i.e., slightly to markedly convex, in the female of *C. beccaloniae*, flat in the male and female of *C. hendersoni*, *C. pelekomanus*, and *C. tristis*, and curved in the male and female of *C. madraspatensis* and *C. shivashankari*. The proximal margin (lobe) of the chela manus dorsal surface is moderately curved and aligned with the proximal margin of the retrolateral surface in the male (fig. 87), or aligned with or proximal to the proximal margin of the retrolateral surface in the female (fig. 86) of *C. beccaloniae*; moderately curved and proximal to the proximal margin of the retrolateral surface

in the male, or aligned with the proximal margin of the condyle (articulation with patella) in the female of *C. bastawadei*, *C. fulvipes*, *C. madraspatensis*, *C. shivashankari*, *C. tristis*, and *C. wroughtoni*; and markedly curved and proximal to the proximal margin of the condyle in the male and female of *C. hendersoni* and *C. pelekomanus*. The maximum distance between the dorsomedian and dorsal secondary carinae (DMC–DSC) of the chela manus is similar to the maximum distance between the dorsal secondary and digital carinae (DSC–DC) in the male of *C. beccaloniae*, but greater than the DSC–DC in the male of all other species except *C. madraspatensis*, *C. nathanorum*, and *C. tristis*. The dorsal secondary and subdigital carinae of the male (fig. 87) are entirely to predominantly granular in *C. beccaloniae*, entirely to predominantly costate in *C. nathanorum*, and absent or obsolete in *C. bastawadei* and *C. fulvipes*. The digital carina is entirely to predominantly granular in *C. beccaloniae*, entirely to predominantly costate in *C. nathanorum*, and absent or obsolete in *C. bastawadei*, *C. fulvipes*, *C. madraspatensis*, and *C. shivashankari*. The manus dorsal intercarinal surface is without reticulation in *C. beccaloniae* but shallowly reticulate in *C. nathanorum*. The manus ventral surface is angled, with the axis of the retroventral carina ventral to the axis of the ventromedian carina in *C. beccaloniae* but flat, with the axes of the retroventral and ventromedian carinae in approximately the same plane in all other species except *C. hendersoni*, *C. pelekomanus*, and *C. tristis*. The legs are very dark or heavily infusate (fig. 84) in *C. beccaloniae* but pale or very lightly infusate in *C. bastawadei*, *C. fulvipes*, *C. hendersoni*, *C. madraspatensis*, and *C. shivashankari*. Macroseta *st* on the retroventral surfaces of the basitarsi of legs I and II is spini-form (fig. 43A–D) in *C. beccaloniae* but setiform in *C. nathanorum* and *C. shivashankari*. The mesial surfaces of mesosomal tergites I–VI are smooth in the male and the lateral surfaces granular in the female of *C. beccaloniae*, whereas the mesial surfaces are granular in the male of *C. bastawadei*, *C. fulvipes*, *C. madraspatensis*, and *C. shivashankari*, the mesial surfaces granular in the

male and the lateral surfaces smooth in the female of *C. nathanorum*, and the lateral surfaces smooth in the female of *C. tristis*. The ventral surface of mesosomal sternite VII bears two pairs of moderately to strongly developed ventrosubmedian and ventrolateral carinae in *C. beccaloniae* and a pair of weakly developed ventrolateral carinae in all other species except *C. hendersoni* and *C. pelekomanus*. The dorsosubmedian carinae are granular or costate-granular on metasomal segments I–IV in the male but costate on segments I and II or I–III and granular or costate-granular on III and IV or IV in the female (fig. 58B) of *C. beccaloniae*, whereas the dorsosubmedian carinae are granular or costate-granular on segments I–IV in all other species, except *C. tristis*. The ventral intercarinal surfaces of segment IV are granular in the male and smooth in the female (fig. 60B) of *C. beccaloniae* but smooth in the male and granular in the female of *C. bastawadei*, *C. fulvipes*, and *C. shivashankari*, smooth in the male of *C. wroughtoni*, and granular in the female of *C. hendersoni*, *C. madraspatensis*, *C. pelekomanus*, and *C. tristis*. The dorsolateral carinae of metasomal segment V are strong and continuous in *C. beccaloniae* but weak and discontinuous to absent in *C. nathanorum*. The dorsal intercarinal surface of segment V is smooth in the male and female of *C. beccaloniae*, granular in the male and female of *C. bastawadei*, *C. hendersoni*, and *C. pelekomanus*, and granular in the male of *C. wroughtoni*.

DISTRIBUTION: This species is endemic to India and recorded from the Javadu Hills, the Nilgiri Hills, and the Yelagiri Hills in the state of Tamil Nadu (fig. 80, table 1).

ECOLOGY: The known locality records of this species occur in semiarid savanna and deciduous woodland dominated by thorn bushes (*Acacia* and *Ziziphus*) and sparse grass on rocky granite hills, at elevations of 305–1020 m (Mirza et al., 2012). The specimens for which data are available were collected from shallow burrows or scrapes (10–20 cm long) under large stones or boulders, embedded in hard clayey or gravelly-loam soils. Burrow entrances, below stones, are crescent shaped (Mirza et al., 2012). The habitat

and habitus are consistent with the pelophilous, fossorial and semilithophilous ecomorphotypes (Prendini, 2001b). This species is sympatric with the buthids, *Hottentotta rugiscutis*, *Isometrus sankeriensis* Tikader and Bastawade, 1983, and *Lychas tricarinatus* (Mirza et al., 2012).

REMARKS: This species is newly accommodated in *Chersonesometrus*, stat. nov. et stat. rev., based on a phylogenetic analysis (fig. 10).

The description of *H. beccaloniae* was based on a female holotype. The diagnosis of *H. beccaloniae* compared it to *H. wroughtoni*, for which the adult male is unknown, but not to *H. phipsoni*, which was described from an adult male, occurs in geographical proximity, and resembles *H. beccaloniae* in several respects, including dark coloration; length, 115 mm in the type of *H. beccaloniae* compared with 101 mm in the type of *Scorpio phipsoni*; pectinal tooth count, 14–16 in *H. beccaloniae* compared with 15/15 in *S. phipsoni*; and pro- and retroventral spiniform macrosetal counts on the leg telotarsi, 5–6/6–7 on legs III and IV in *H. beccaloniae* compared with 5/7 on I–IV in *S. phipsoni*. Nevertheless, based on comparison of type and nontype material, including an adult male of *C. beccaloniae*, during the present investigation, *C. beccaloniae* is evidently distinct from both *C. wroughtoni* and *D. phipsoni*, in which the pedipalp chela manus is much more granular, among other differences recounted in the key and diagnoses.

Heterometrus atrascorpius was distinguished from *H. beccaloniae* by the following characters: moderate size, 91.7 mm; coloration dark blackish brown, with the exception of the vesicle, which is yellowish white, and the leg tarsi, which are paler; pectines, sternum, and pectinal basal piece yellowish brown; pedipalp chela manus tuberculate with carina; patella and femur dorsally tuberculate; pedipalp femur longer than twice as wide; manus length/width ratio 3.22; pectines with 16–16 teeth. However, as noted by Tahir and Prendini (2014), it is evident that none of the type specimens are adult. The holotype illustrated in figures 1–9 (Mirza et al., 2012: 4, 5) is subadult. Consequently, the diagnostic characters (coloration, granulation, meristic variation) presented to justify this putative new species

are unreliable and the comparisons made with other species, described on the basis of adults, invalid. Based on both the description and the type locality, *H. atrascorpius* is assessed to be conspecific with *C. beccaloniae* and the following new synonym presented: *Heterometrus atrascorpius* Mirza et al., 2012 = *Chersonesometrus beccaloniae* (Kovařík, 2004), syn. nov.

MATERIAL EXAMINED: **INDIA: Tamil Nadu:** *Nilgiris Distr.*: Ootacamund [Ooty, 11°25'N 76°42'E], 1 ♂ (ZMH); Vibudhi Malai Murugan Temple, Bokkapuram, 11°33'N 76°39'E, 1023 m, 27.xi.2004, S. Basi, rocky hill, savanna-grassland on hard clay, many granite stones and boulders, in shallow scrapes under stones, 1 ♀, 1 subad. ♂, 7 juv. ♂, 6 juv. ♀ (AMNH), 2 juv. ♂ (AMCC [LP 13133]). *Vellore Distr.*: Javadu Hills, S of Madanur on Highway 46 (Ambur–Vellore), 12°51'N 78°49'E, 306 m, 30.xi.2004, S. Basi, dense broadleaf savanna-woodland at base of large mountain with scattered granite stones, in shallow scrape (ca. 20 cm long), under large stone in gravelly loam, 1 ♀ (AMNH); Yelagiri Hills, Mangalam Road, Yelagiri, 12°35'N 78°39'E, 1000 m, 29.xi.2004, S. Basi, savanna-grassland on rocky hillside with many large granite stones, burrow entrances under very large stones in hard gravelly loam, 1 ♀, 1 juv. ♂, 3 juv. ♀, 1 ♀ carapace and sinistral pedipalp segments (AMNH), 1 juv. ♂, 1 juv. ♀ (AMCC [LP 13134]); Yelagiri Hills, Yelagiri Road, 12°36'N 78°37'E, 773 m, 30.xi.2004, S. Basi, steep rocky slope, savanna-woodland with many granite stones embedded in hard gravelly loam, in shallow scrape (ca. 10 cm long) under stone, 1 subad. ♂ (AMNH).

Chersonesometrus fulvipes (C.L. Koch, 1837),
comb. nov.

Figures 7A, 9A, 10, 17A, B, 31A, B, 45A–D,
61A, 62A, 63A, 79, 88–91, table 1

Buthus fulvipes C.L. Koch, 1837: 45, 46, pl.

CXXI, fig. 278; 1850: 87; Couzijn, 1981: 133,
136; Kovařík, 2004: 2, 15; 2009: 38.

Pandinus fulvipes: Karsch, 1884: 67, 68; Thorell,
1888: 329, 338.

Scorpio fulvipes: Pocock, 1893: 304–307, 309
(part); Kraepelin, 1894: 31, 43–46, 52,
59–61, 246, pl. I, figs. 22, 28, 37 (part).

Heterometrus fulvipes: Kraepelin, 1899: 109, 112,
113, 115 (part); Masi, 1912: 124 (part);

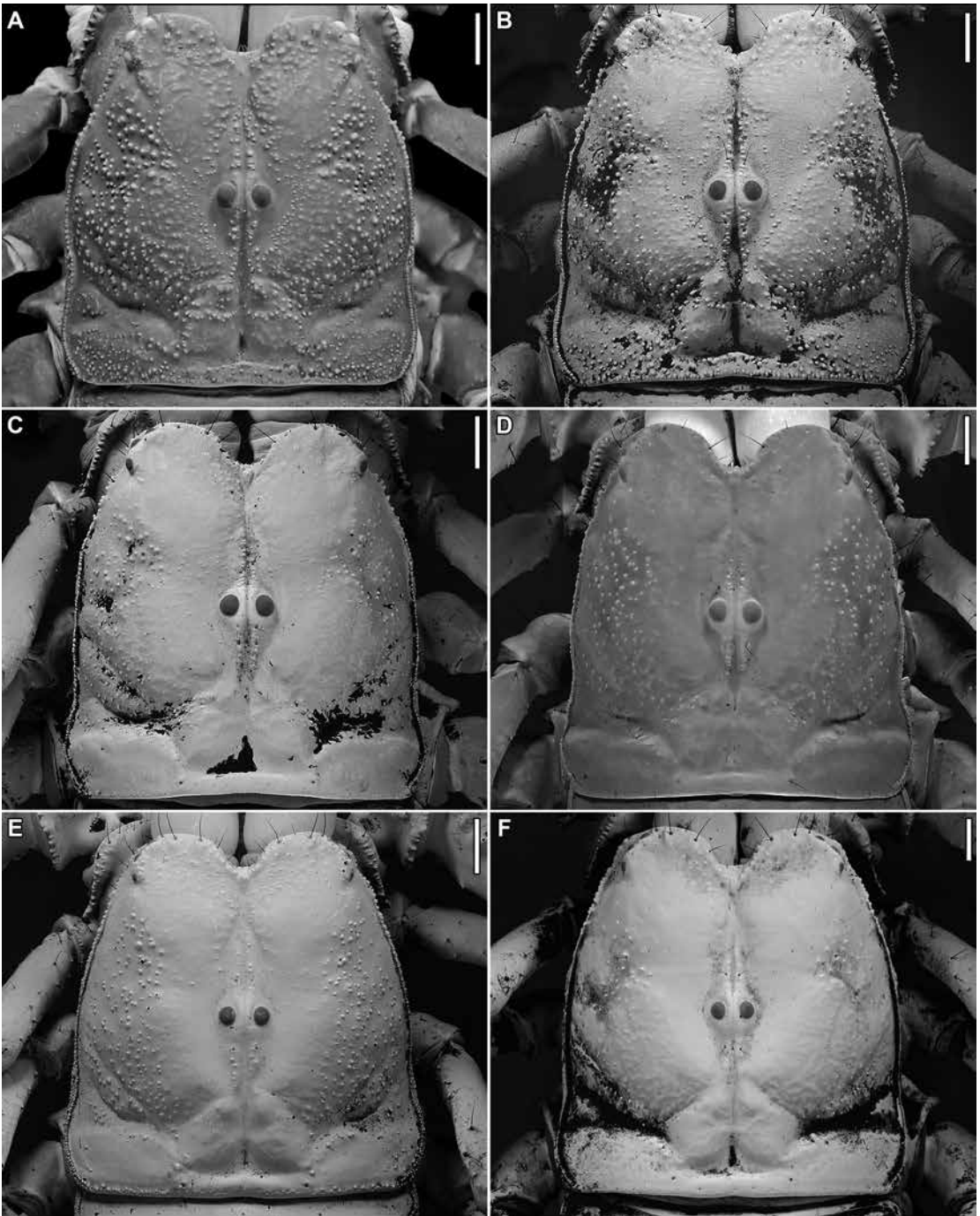


FIGURE 22. *Heterometrus* Ehrenberg, 1828, carapace, dorsal aspect. **A, B.** *Heterometrus glaucus* (Thorell, 1876), comb. nov. et stat. rev., **A.** ♂ (ZMH 3966), **B.** ♀ (AMNH), Nias Island, Indonesia. **C, D.** *Heterometrus longimanus* (Herbst, 1800), **C.** ♂, **D.** ♀ (AMNH), Kuching, Malaysia. **E, F.** *Heterometrus thorellii* (Pocock, 1892), **E.** ♂ (AMNH), Mandalay, Myanmar, **F.** ♀ (AMNH), Pho Kyar Elephant Camp, Yedashe, Myanmar. Scale bars = 2 mm.

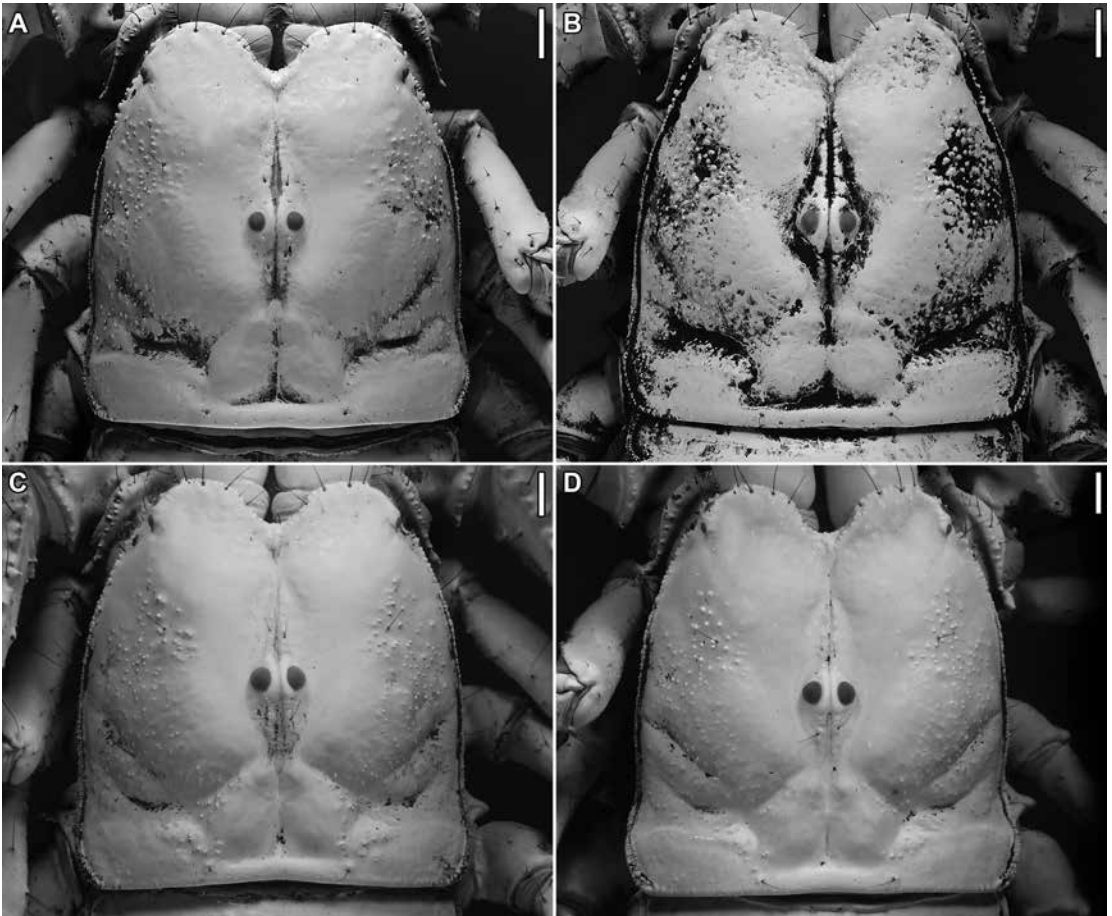


FIGURE 23. *Heterometrus* Ehrenberg, 1828, carapace, dorsal aspect. **A, B.** *Heterometrus laevigatus* (Thorell, 1876), comb. nov. et stat. rev., **A.** ♂ (AMNH), Thale Ban, Thailand, **B.** ♀ (AMNH), Khao Pu-Khao Ya, Thailand. **C, D.** *Heterometrus spinifer* (Ehrenberg, 1828), **C.** ♂ (AMNH), **D.** ♀ (AMNH), Cameron Highlands, Malaysia. Scale bars = 2 mm.

Kraepelin, 1913: 166 (part); Kopstein, 1921: 119, 133 (part); 1923: 186, 187 (part); 1926: 111, 112; 1927: 107; Giltay, 1931: 9; Werner, 1934: 277 (part); Takashima, 1945: 91, 92 (part); Vyas, 1971: 65–79, figs. 1–6; Vyas and Laliwala, 1972: 267–271, figs. 1, 2; Devarajulu Naidu and Venkatachari, 1974: 539–541, figs. 1–4; Vyas, 1974: 9–14; Darlingwater, 1980: 285–289, figs. 1c, 2, 3; Brignoli, 1985: 415; Hjelle, 1990: 17, 26, 48; Polis and Sissom, 1990: 179 (part); Sissom, 1990: 80, 81, 133, figs. 3.13G, 3.28B–E; Pointer, 1991: 24; Tare et al., 1993: 102, 103,

table 1; Dupré et al., 1998: 13; Prendini et al., 2003: 192, 202, 205, 208, 209, 218, 222, 252, 254, 255, 259, table 3, figs. 4, 6, 7, appendices 1, 2 (part); Kovařík, 2004: 1, 15, 16, 29, 44, 49, 51, 52, tables 2, 3 (part), fig. 14; 2009: 35–38, 48 (part), 49, 78, 100, 104, tables 1, 2 (part), figs. 32–39, 206, 207, 246–248; Javed et al., 2010a: 144, 147; Warburg, 2010: 1746, 1750, tables 2, 3 (part); 2012a: 82, 83, 85, table 1 (part); 2013: 152, 153, 155 (part); Tahir and Prendini, 2014: 2, 9.
Palamnaeus fulvipes: Pocock, 1900a: 85, 87–89, 92, 96, figs. 25A, 29B; Bardi and George,

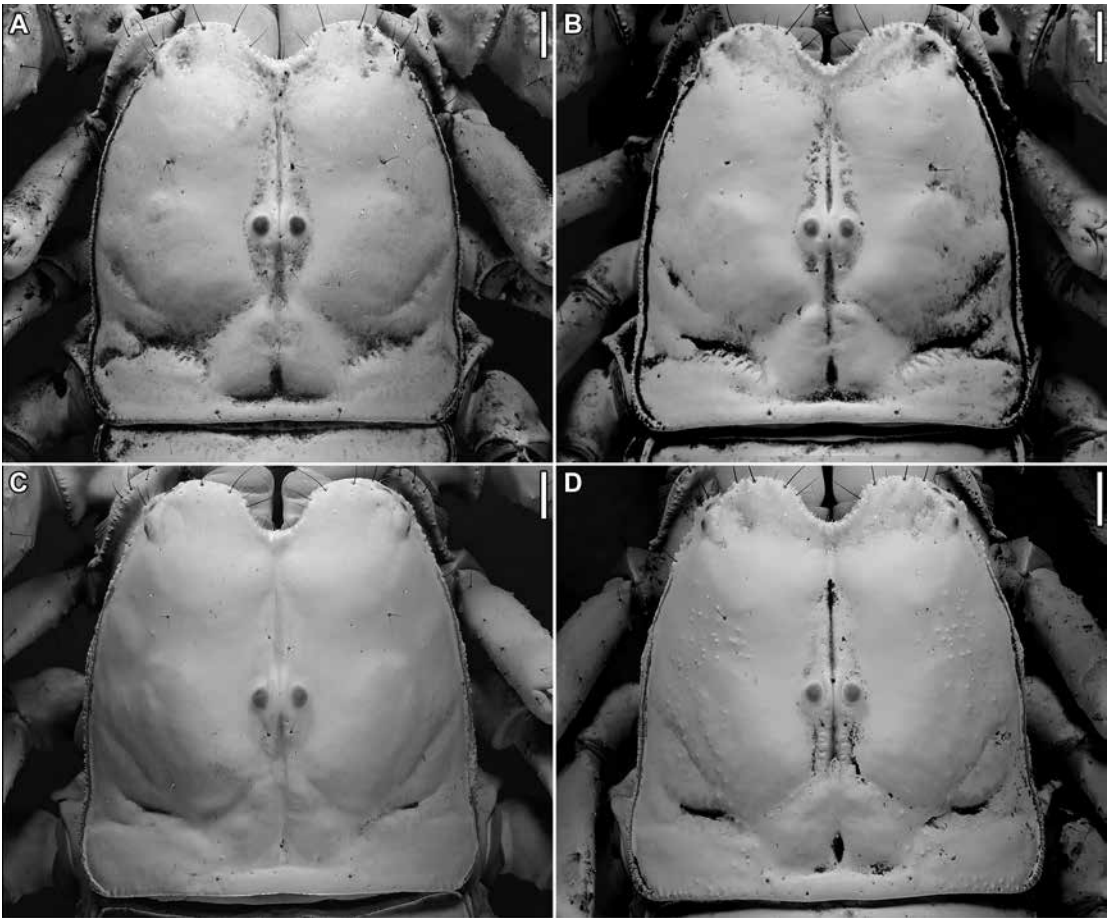


FIGURE 24. *Heterometrus* Ehrenberg, 1828, carapace, dorsal aspect. **A, B.** *Heterometrus laoticus* Couzijn, 1981, **A.** ♂ (AMNH), Phahom Camp, Laos, **B.** ♀ (AMNH), Tham Pha In, Laos. **C, D.** *Heterometrus silenus* (Simon, 1884), comb. nov. et stat. rev. **C.** ♂, **D.** ♀ (AMNH), Ta Kou Mountain Nature Reserve, Vietnam. Scale bars = 2 mm.

1943: 91–115, figs. 1, 3, 4; Sareen and Monga, 1973: 281, 282, fig. 1; Cekalovic, 1982: 191 (misidentification); Warburg, 2012a: 79, 82, table 1.

Palamnaeus fulvipes bombayensis Pocock, 1900a: 89 (synonymized by Couzijn, 1981: 133–136); Tikader, 1973: 263; Couzijn, 1981: 134–136; Kovařík, 2004: 15; 2009: 37.

Heterometrus phipsoni: Kraepelin, 1913: 166 (misidentification, part); Pande et al., 2012: 2383–2385, 2387, table 1, fig. 1, images 11a, b (misidentification).

Heterometrus sp.: Dubale and Vyas, 1968: 240–244.

Heterometrus (*Chersonesometrus*) *fulvipes*: Couzijn, 1981: 18, 23, 24, 26, 40, 88, 123, 133–136, 139, 140, 142, 149, 169, 192, table 7, figs. 1b–f, 5c, 6c, 8b, 57 (part); Tikader and Bastawade, 1983: 575, 599–603, figs. 1581–1594; Kovařík, 1997: 183; 1998: 136 (part); Fet, 2000: 439 (part); Bastawade, 2002: 296; 2004: 286, 290, 291; 2005: 411, 417, 418.

Heterometrus (*Chersonesometrus*) *granulomanus*: Couzijn, 1981: 142, 143 (misidentification, part); Bastawade, 2004: 286, 291, 292 (mis-

identification, part); Thulsi Rao et al., 2005: 3, 9 (misidentification, part); Bastawade, 2008: 133, 136, 137 (misidentification, part).

Heterometrus (Chersonesometrus) pelekomanus:

Bastawade, 2002: 296 (misidentification).

Heterometrus (Gigantometrus) swammerdami:

Thulsi Rao et al., 2005: 3, 8 (misidentification, part).

TYPE MATERIAL: *Buthus fulvipes*: Holotype ? ♀ [lost], "Java." **INDIA: Maharashtra:** Chandrapur Distr.: *Heterometrus (Chersonesometrus) fulvipes*: Neotype [= *Palamnaeus fulvipes bombayensis* holotype]: 1 ♀ (BMNH 1913.1.6.2 ex BNHS), Chanda [Chandrapur, 19°58'N 79°18'E], Central Provinces [examined].

Buthus fulvipes was described from a holotype female with erroneous locality data (i.e., "Java"). The holotype was subsequently lost, leading Couzijn (1981: 136) to designate the holotype of *Palamnaeus fulvipes bombayensis*, a junior synonym, as the neotype. Couzijn (1981: 136), Fet (2000: 439), and Kovařík (2004: 15) mistakenly referred to syntypes of *P. f. bombayensis*. Pocock (1900a: 89) explicitly mentioned a "type from Násik."

DIAGNOSIS: *Chersonesometrus fulvipes* may be separated from other species of *Chersonesometrus* as follows. The carapace is vaulted, the lateral surfaces sloping steeply (fig. 17A, B), in *C. fulvipes* but slightly to markedly dorsoventrally compressed, the lateral surfaces sloping gently, in all other species except *C. madraspatensis* and *C. shivashankari*. The carapace interocular surface is granular along the median longitudinal and anterior bifurcated sulci only in the female (fig. 17B) of *C. fulvipes* whereas the frontal lobes and medial region of the interocular surface are granular with smooth areas in the female of *C. bastawadei*, *C. madraspatensis*, *C. pelekomanus*, and *C. shivashankari*. The carapace posterolateral surfaces of the female are granular in *C. fulvipes* but smooth or nearly so in all other species except *C. bastawadei* and *C. madraspatensis*. The cheliceral movable finger prodistal (DI) and retrodistal (DE) teeth are unequal, with the DE tooth considerably smaller than the DI tooth, aligned longitudinally and not

opposable in *C. fulvipes*, but subequal, with the DE tooth only slightly smaller than the DI tooth, and opposable, i.e., forming a bicuspid, in *C. beccaloniae*, *C. hendersoni*, *C. nathanorum*, *C. pelekomanus*, and *C. tristis*. The pedipalps of the adult male are short, with femur length : posterior carapace width ratio (FL:PCW) < 0.77 and femur length : carapace length ratio (FL:CL) < 0.74 (fig. 88A, B) in *C. fulvipes* but long, with FL:PCW ≥ 0.80, FL:CL ≥ 0.76 in *C. beccaloniae*, *C. madraspatensis*, and *C. tristis*. The pedipalp patella dorsal surface is convex, with the axis of the dorsomedian carina dorsal to the axis of the retrodorsal carina (fig. 89), in *C. fulvipes* but flat or nearly so, with the axes of the dorsomedian and retrodorsal carinae in the same plane, in *C. beccaloniae*, *C. hendersoni*, *C. pelekomanus*, and *C. tristis*. The patella retrodorsal carina of the female is as strongly developed as or more strongly developed than the retromedian carinae in *C. fulvipes* but absent or obsolete in *C. nathanorum*. The retromedian carinae are granular in *C. fulvipes* but costate in *C. nathanorum*. The patella dorsal, retrodorsal, and retroventral intercarinal surfaces of the female are granular in *C. fulvipes* but smooth or nearly so in *C. nathanorum*. The pedipalp chela is infusate and similar in color to the femur and patella in *C. fulvipes* but immaculate and paler than the femur and patella in *C. shivashankari*. The chela of the adult male is sparsely setose in *C. fulvipes* but moderately to densely setose in *C. beccaloniae*, *C. pelekomanus*, and *C. tristis*. The chela manus dorsal surface (between the dorsomedian and digital carinae) is flat in the male and curved, i.e., slightly to markedly convex, in the female of *C. fulvipes*, flat in the male and female of *C. hendersoni*, *C. pelekomanus*, and *C. tristis*, and curved in the male and female of *C. madraspatensis* and *C. shivashankari*. The proximal margin (lobe) of the chela manus dorsal surface is moderately curved and proximal to the proximal margin of the retrolateral surface in the male (fig. 90), or aligned with the proximal margin of the condyle (articulation with patella) in the female (fig. 91) of *C. fulvipes*; moderately curved and aligned with the proximal margin of the ret-

rolateral surface in the male, or aligned with or proximal to the proximal margin of the retrolateral surface in the female of *C. beccaloniae* and *C. nathanorum*; and markedly curved and proximal to the proximal margin of the condyle in the male and female of *C. hendersoni* and *C. pelekomanus*. The maximum distance between the dorsomedian and dorsal secondary carinae (DMC–DSC) of the chela manus is greater than the maximum distance between the dorsal secondary and digital carinae (DSC–DC) in the male of *C. fulvipes*, but greater than the DSC–DC in the male of *C. beccaloniae*, *C. madraspatensis*, *C. nathanorum*, and *C. tristis*. The dorsal secondary and subdigital carinae of the male are absent or obsolete (fig. 90) in *C. fulvipes* but entirely to predominantly granular or costate in all other species except *C. bastawadei*. The digital carina is absent or obsolete in *C. fulvipes*, but entirely to predominantly granular in *C. beccaloniae*, *C. hendersoni*, *C. pelekomanus*, *C. tristis*, and *C. wroughtoni*, and entirely to predominantly costate in *C. nathanorum*. The manus dorsal intercarinal surface is without reticulation in *C. fulvipes* but shallowly reticulate in *C. nathanorum*. The manus ventral surface is flat, with the axes of the retroventral and ventromedian carinae in approximately the same plane in *C. fulvipes* but angled, with the axis of the retroventral carina ventral to the axis of the ventromedian carina in *C. beccaloniae*, *C. hendersoni*, *C. pelekomanus*, and *C. tristis*. The legs are pale or very lightly infuscate (figs. 9A, 88) in *C. fulvipes* but very dark or heavily infuscate in *C. beccaloniae*, *C. nathanorum*, *C. pelekomanus*, *C. tristis*, and *C. wroughtoni*. Macroseta *st* on the retroventral surfaces of the basitarsi of legs I and II is spiniform (fig. 45A–D) in *C. fulvipes* but setiform in *C. nathanorum* and *C. shivashankari*. The mesial surfaces of mesosomal tergites I–VI are granular in the male and the lateral surfaces granular in the female of *C. fulvipes*, whereas the mesial surfaces are smooth in the male of *C. beccaloniae*, *C. hendersoni*, *C. pelekomanus*, and *C. wroughtoni*, the mesial surfaces smooth in the male and the lateral surfaces smooth in the female of *C. tristis*, and the lateral surfaces smooth in the female of *C. natha-*

norum. The ventral surface of mesosomal sternite VII bears a pair of weakly developed ventrolateral carinae in *C. fulvipes* and two pairs of moderately to strongly developed ventrosubmedian and ventrolateral carinae in *C. beccaloniae*, *C. hendersoni*, and *C. pelekomanus*. The dorsosubmedian carinae are granular or costate-granular on metasomal segments I–IV (fig. 61A) in *C. fulvipes* but costate on segments I and II or I–III and granular or costate-granular on III and IV or IV in *C. tristis*, and the female of *C. beccaloniae*. The ventral intercarinal surfaces of segment IV are smooth in the male (fig. 63A) and granular in the female of *C. fulvipes* but granular in the male and smooth in the female of *C. beccaloniae* and *C. nathanorum*, granular in the male of *C. hendersoni*, *C. madraspatensis*, *C. pelekomanus*, and *C. tristis*, and smooth in the female of *C. wroughtoni*. The dorsolateral carinae of metasomal segment V are strong and continuous in *C. fulvipes* but weak and discontinuous to absent in *C. nathanorum*. The dorsal intercarinal surface of segment V is smooth in the male and female of *C. fulvipes*, granular in the male and female of *C. bastawadei*, *C. hendersoni*, and *C. pelekomanus*, and granular in the male of *C. wroughtoni*.

DISTRIBUTION: *Chersonesometrus fulvipes* is widely distributed across northwestern India (fig. 79) and has been recorded from the following states: Gujarat, Haryana, Karnataka, Madhya Pradesh, Maharashtra, National Capital Territory of Delhi, Rajasthan, Uttar Pradesh (table 1). A single record from Sindh, southeastern Pakistan, on the border with India (Kovářík, 2009) requires confirmation (Tahir and Prendini, 2014). The distribution of *C. fulvipes* is parapatric with that of its sister species, *C. madraspatensis*, and allopatric with the morphologically similar *C. bastawadei*, *C. shivashankari*, and *C. wroughtoni*.

ECOLOGY: *Chersonesometrus fulvipes* inhabits deciduous forest, broadleaf woodland and semi-arid savanna, dominated by *Acacia*, *Commiphora* Jacquin, 1797, *Sterculia* Linnaeus, 1753, and *Euphorbia* trees, on clayey to sandy-loam soils, at elevations of 250–940 m (fig. 7A; Pande et al., 2012). As with other species of the genus, *C. ful-*

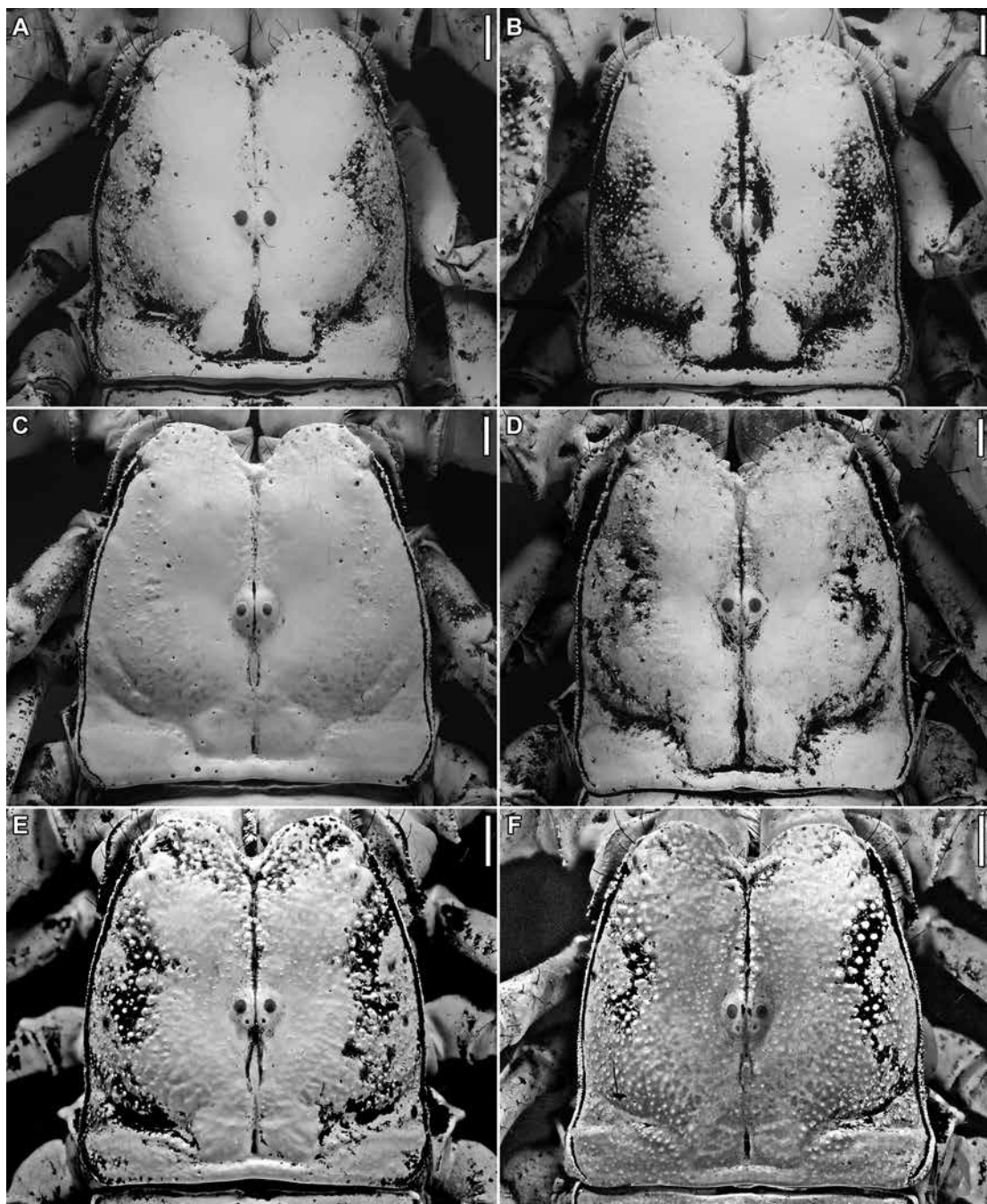


FIGURE 25. **A, B.** *Javanimetrus* Couzijn, 1981, stat. nov. et stat. rev., and **C–F.** *Sahyadrimetrus*, gen. nov., carapace, dorsal aspect. **A, B.** *Javanimetrus cyaneus* (Simon, 1872), comb. nov., **A.** ♂, **B.** ♀ (AMNH), Ujung Kulon, Indonesia. **C.** *Sahyadrimetrus barberi* (Pocock, 1900), comb. nov., holotype ♀ (BMNH 1899.9.24.1). **D.** *Sahyadrimetrus rugosus* (Couzijn, 1981), comb. et stat. nov., ♀ (AMNH), Chaliyar River, India. **E, F.** *Sahyadrimetrus tikaderi*, gen. et sp. nov., **E.** holotype ♂, **F.** paratype ♀ (MNHN RS 3265). Scale bars = 2 mm.

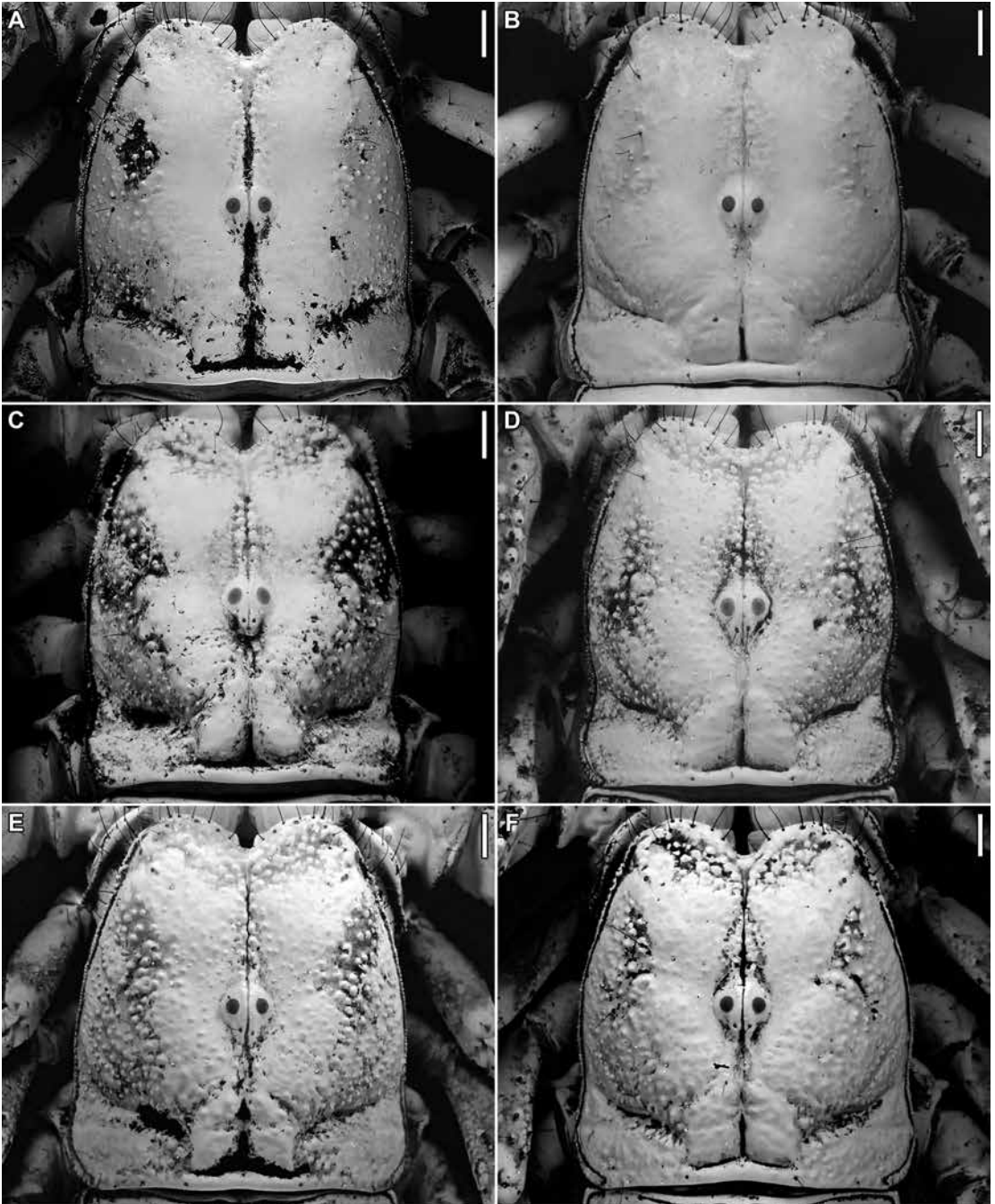


FIGURE 26. *Sahyadrimetrus*, gen. nov., carapace, dorsal aspect. **A, B.** *Sahyadrimetrus kanarensis* (Pocock, 1900), comb. nov., **A.** ♂, **B.** ♀ (AMNH), Chaudi, India. **C, D.** *Sahyadrimetrus mathewi*, gen. et sp. nov., **C.** holotype ♂, **D.** paratype ♀ (AMNH), Poomala, India. **E, F.** *Sahyadrimetrus scaber* (Thorell, 1876), comb. nov., **E.** ♂ (AMNH), Nadpalu, India, **F.** ♀ (AMNH), Sitha River, India. Scale bars = 2 mm.

vipes, is usually found in rocky habitats, often on wooded hill slopes, gulleys, or ravines where the humidity is slightly higher (P. Jain, personal commun.). The burrowing biology of this fossorial, pelophilous species was described by Tare et al. (1993), Bastawade (2004, 2005, 2008), and Pande et al. (2012), the latter misidentified as *H. phipsoni*. The burrows, constructed in open ground or under moderate to large stones, have oval or crescent-shaped entrances and are almost vertical or gradually sloping to a terminal chamber at a depth of 10–30 cm. Across its distribution, *C. fulvipes* occurs in sympatry with the buthids *Hottentotta pachyurus* (Pocock, 1897), *Hottentotta tamulus* (Fabricius, 1798), *Lychas tricarinatus*, and *Orthochirus bicolor* (Pocock, 1897), the hormurid *Liocheles nigripes* (Pocock, 1897), the scoriopid *Neoscorpiops satarensis* (Pocock, 1900), and the scorpionids *Deccanometrus xanthopus* and *Gigantometrus swammerdami* (Bastawade, 2004, 2005, 2008; Pande et al., 2012).

CONSERVATION STATUS: *Chersonesometrus fulvipes* is occasionally available in the exotic pet trade under the name *Heterometrus xanthopus*. Material offered for sale appears to have originated from India, regardless of the alleged country of origin.

REMARKS: This species was previously accommodated in subgenus *Chersonesometrus* of *Heterometrus* by various authors (e.g., Couzijn, 1981; Tikader and Bastawade, 1983; Fet, 2000). The following synonym is confirmed: *Palamnaeus fulvipes bombayensis* Pocock, 1900 = *Chersonesometrus fulvipes* (C.L. Koch, 1837), comb. nov., synonymized by Couzijn (1981). *Buthus caesar*, synonymized with *H. (C.) fulvipes* by Couzijn (1981), is revalidated as *Srilankametrus caesar*, comb. nov. et stat. rev.

MATERIAL EXAMINED: 1 ♂, 1 subad. ♂ (MCZ). **Gujarat:** *Panch Mahals Distr.:* Panch Mahals [22°48'N 73°34'E], W.A. Wallinger, 2 ♂ (BMNH 1896.10.20.68–69 [BNHS 421, 425]). *Sunrendranagar Distr.:* Karaghora [Kharaghoda, 23°11'N 71°44'E], in Kathiawar, H. Bulkley, 1 ♂ (BMNH 1896.7.30.100 [BNHS 442]); Kathiawar, 1 ♂ (BMNH 1897.9.17.16). **Haryana:** *Faridabad Distr.:* Aravalli Hills, NNE of Mangar, 28°23'N 77°11'E, 252 m, 14.xi.2006, P. Menon, savanna in ravine

on summit of rocky hill, in burrows (ca. 20 cm deep) under stones, 1 ♀, 6 juv. ♀ (AMNH), 1 juv. ♀ (AMCC [LP 13990]). **Madhya Pradesh:** *Hoshangabad Distr.:* Satpura, Pipariya Road 19, between Matkuli and Pipariya, 22°39'N 78°23'E, 364 m, 6.xii.2006, P. Menon, dry broadleaf forest on plain with gulleys, excavated from burrows in open ground, ca. 15 cm long, in hard, sandy-clay bank, 1 ♀ (AMNH), 1 juv. ♂ (AMCC [LP 14031]); Raini Pani, 22°37'N 78°07'E, 385 m, 4.xii.2006, P. Menon, deciduous forest on low hills, excavated from shallow burrows (ca. 10 cm deep) in sandy-clay under stones, 1 ♀, 1 juv. ♀ (AMNH), 1 juv. ♀ (AMCC [LP 13997]); Raini Pani road, 22°37'N 78°08'E, 369 m, 5.xii.2006, P. Menon, deciduous forest along dry gully, excavated from burrows in open ground or under sandstones, in very hard sandy-clay, 3 ♀, 1 juv. ♀ (AMNH), 1 juv. ♀ (AMCC [LP 13981]). **Satna Distr.:** Satna [24°36'N 80°50'E], Sarg. Maj. Prinlette, 1 juv. ♂, 1 juv. ♀ (BMNH 1896.8.15.1–2 [BNHS 593]). **Maharashtra:** *East Khandesh, R.H. Medan, 1 ♂ [BNHS 228], 1 juv. ♀ [BNHS 224] (BMNH 1896.7.30.89); East Satpura Hills [21°25'N 76°10'E], Khandesh, J.H. Du Boulay, 1 ♂ [BNHS 132], 1 ♀ [BNHS 128], 1 subad. ♂ [BNHS 138], 1 subad. ♀ [BNHS 137] (BMNH 1896.7.95–98); Khandesh, R.H. Madan, 1 ♀, 1 juv. ♂, 1 juv. ♀, 1 subad. ♂ [BNHS 126] (BMNH 1896.7.30.93–94); Talgaum [Talegaon, 20°24'N 74°55'E], East Khandesh, R.H. Madan, 1 ♂ [BNHS 234], 1 ♀ [BNHS 235] (BMNH 1896.7.30.91–92). **Nashik Distr.:** Kalwan [20°29'N 74°02'E], Nasik, J. Duxburg, 1 ♂ (BMNH 1897.9.5.32 [BNHS 1148]); Malegaum [Malegaon, 20°33'N 74°31'E], Nasik, J. Duxburg, 1 ♀ (BMNH 1897.9.5.28 [BNHS 1146]); Nandgaum [Nandgaon, 20°19'N 74°40'E], Nasik, J. Duxburg, 1 ♀ (BMNH 1897.9.5.29 [BNHS 1150]); Sinnar [19°51'N 74°00'E], Nasik, J. Duxburg, 1 ♂ (BMNH 1897.9.5.33 [BNHS 1152]); Yeola [20°03'N 74°29'E], Nasik, J. Duxburg, 1 ♂ (BMNH 1897.9.5.30 [BNHS 1158]); Kalwan [20°29'N 74°02'E], Nasik, J. Duxburg, 1 ♂ (BMNH 1897.9.5.32 [BNHS 1148]). **Satara Distr.:** Khambatki Ghat, S of Khandala, on M.B.T. Road (Highway 47), 18°01'N 74°01'E, 928 m, 17.xi.2004, S. Basi, steep slopes of rocky ridge, mixed, semiarid savanna, in scrapes under basalt stones in rocky ravine, 2 pedipalp chelae (AMNH), 1 juv. ♀ (AMCC [LP 13125]), 18°01'N 74°00'E, 937 m, 30.xi.2006, P. Menon, dry savanna woodland (mostly broadleaf) on steep mountain slope with basalt outcrops, excavated from shallow burrows (ca. 10–20 cm long) under stones in clayey-loam, 2 ♂, 1 ♀, 9 juv. ♂, 5 juv. ♀ (AMNH), 1 juv. ♂, 1 juv. ♀ (AMCC [LP 13957]), 902 m, 29.xi.2009, R. Datta,*

broadleaf woodland on fairly steep slope of large mountain, clayey-loam with many loose/embedded volcanic (basalt) stones, excavated from shallow burrows (ca. 10–15 cm deep) under embedded stones, 2 ♂, 1 ♀ (AMNH), 2 juv. ♂, 1 juv. ♀ (AMCC [LP 16812]). **Rajasthan:** *Ajmer Distr.:* Ajmeer [Ajmer, 26°27'N 74°38'E], H.M. Phipson, 1 ♂ (BMNH 1893.12.20.17); Beawar [26°06'N 74°19'E], Rajputana, R.G. Robson, 4 ♂, 1 ♀ (MNHN RS 0157). *Jaipur Distr.:* Jeypore [Jaipur, 26°55'N 75°47'E], 1 ♀ (MCZ), Jeypore [Jaipur], Rajputana, x.1912, 2 ♂, 3 ♀ (ZMH ex Mus. Calcutta). **Uttar Pradesh:** *Agra Distr.:* Agmeza [27°11'N 77°46'E], 15.v.1899, 2 ♀ (ZMH ex Mus. Brussel). *Varanasi Distr.:* Benares [25°20'N 83°00'E], 1 juv. ♂, 1 juv. ♀ (MCZ). **PAKISTAN:** [alleged], iii.2008, ex pet trade, 1 ♂ (AMNH [LP 8268]), [pedipalp chela] (AMCC [LP 8268]).

Chersonesometrus hendersoni, sp. nov.

Figures 7D, 10, 16F, 30F, 44E–H, 58C, 59C, 60C, 80, 92–94, tables 1, 3, 4

TYPE MATERIAL: **INDIA:** **Karnataka:** *Balari Distr.:* Holotype ♀, paratypes: 1 subad. ♀, 7 juv. ♂, 6 juv. ♀ (AMNH), 2 juv. ♀ (AMCC [LP 16776]), Sanapur Lake, Sanapura, 15°22'N 76°26'E, 477–478 m, 22.xi.2009, R. Datta, dry riverbed on rocky hills, slightly disturbed mixed-broadleaf savanna on coarse granitic sandy-loam with many granite outcrops and embedded stones, in scrapes or shallow burrows under stones below canopy; paratypes: 2 ♀, 2 subad. ♂, 1 subad. ♀, 6 juv. ♂, 1 juv. ♀ (AMNH), 2 juv. ♂ (AMCC [LP 16782]), Tungabhadra River, Narayanpet, 15°20'N 76°25'E, 448 m, 22.xi.2009, R. Datta, riverine dry forest with thickets of spiny bamboo and thorn trees, on granite outcrops along permanent river, dense canopy and litter in places, from shallow scrapes in coarse granitic sandy-loam, under large, flat, embedded rocks.

ETYMOLOGY: The specific epithet is a patronym honoring John Robertson Henderson (1863–1925), a Scottish zoologist who served as Superintendent of the Government Museum in Madras, British India, from 1908 to 1920, in recognition of his contributions to the scorpions and other arachnids of India.

DIAGNOSIS: *Chersonesometrus hendersoni* may be separated from other species of *Chersonesometrus* as follows. The carapace is markedly dorso-ventrally compressed, the lateral surfaces sloping gently (fig. 16F), in *C. hendersoni*, but vaulted, the lateral surfaces sloping steeply, in *C. fulvipes*, *C. madraspatensis*, and *C. shivashankari*. The carapace interocular surface is granular along the median longitudinal and anterior bifurcated sulci only in the female (fig. 16F) of *C. hendersoni*, whereas the frontal lobes and medial region of the interocular surface are granular with smooth areas in the female of *C. bastawadei*, *C. madraspatensis*, *C. pelekomanus*, and *C. shivashankari*. The carapace posterolateral surfaces of the female are smooth in *C. hendersoni* but granular in *C. bastawadei*, *C. fulvipes*, and *C. madraspatensis*. The cheliceral movable finger prodistal (DI) and retrodistal (DE) teeth are subequal, with the DE tooth only slightly smaller than the DI tooth, and opposable, i.e., forming a bicus, in *C. hendersoni* but unequal, with the DE tooth considerably smaller than the DI tooth, aligned longitudinally and not opposable in *C. bastawadei*, *C. fulvipes*, *C. madraspatensis*, *C. shivashankari*, and *C. wroughtoni*. The pedipalp patella dorsal surface is flat or nearly so, with the axes of the dorsomedian and retrodorsal carinae in the same plane (fig. 93), in *C. hendersoni* but convex, with the axis of the dorsomedian carina dorsal to the axis of the retrodorsal carina in all other species except *C. beccaloninae*, *C. pelekomanus*, and *C. tristis*. The patella retrodorsal carina of the female is as strongly developed as or more strongly developed than the retromedian carinae in *C. hendersoni* but absent or obsolete in *C. nathanorum*. The retromedian carinae are granular in *C. hendersoni* but costate in *C. nathanorum*. The patella dorsal, retrodorsal, and retroventral intercarinal surfaces of the female (fig. 93) are granular in *C. hendersoni* but smooth or nearly so in *C. nathanorum*. The pedipalp chela is infusate and similar in color to the femur and patella in *C. hendersoni* but immaculate and paler than the femur and patella in *C. shivashankari*. The chela manus dorsal surface (between the dorsomedian and digital carinae) is flat in the male

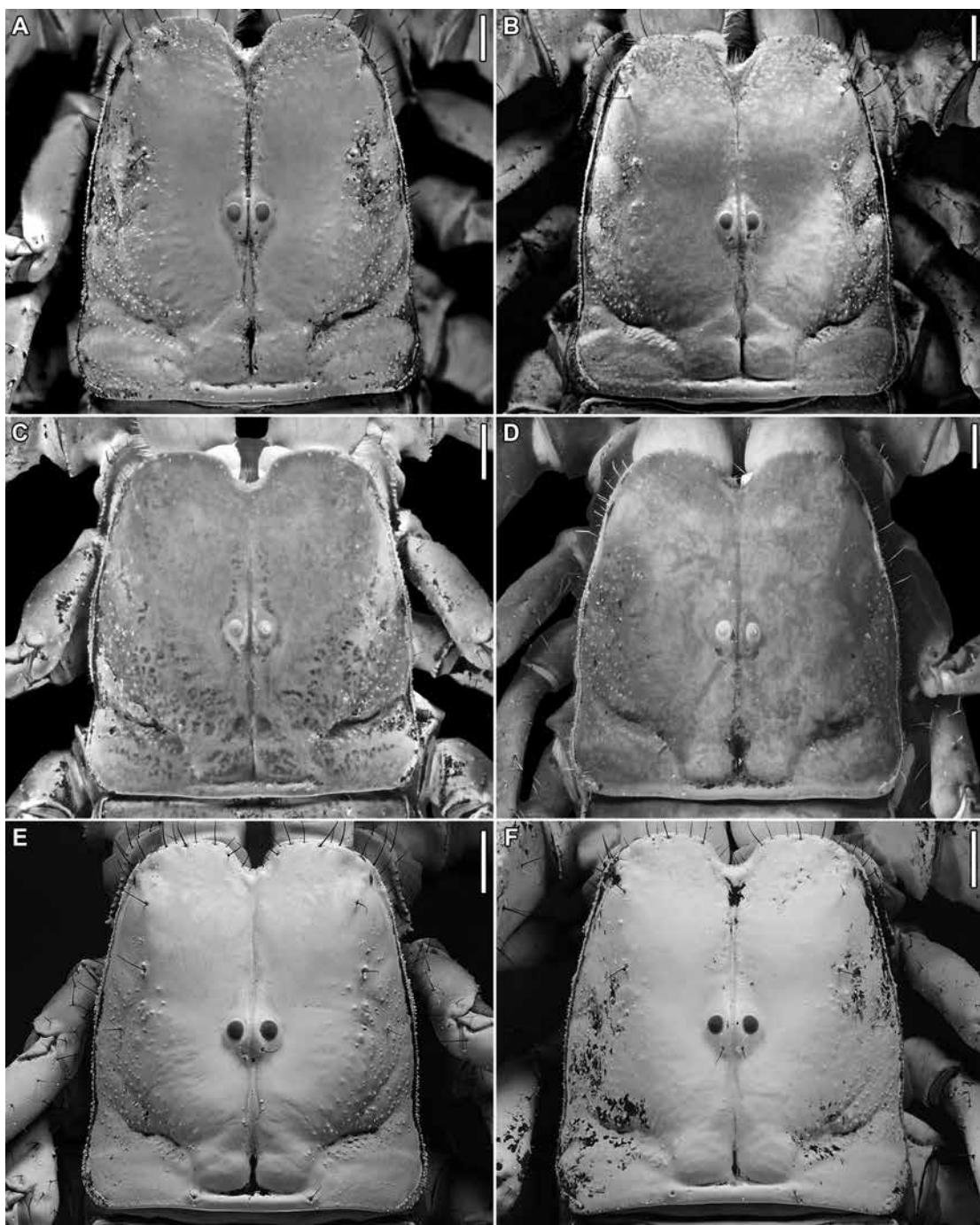


FIGURE 27. *Srilankametrus* Couzijn, 1981, stat. nov. et stat. rev., carapace, dorsal aspect. **A, B.** *Srilankametrus caesar* (C.L. Koch, 1841), comb. nov. et stat. rev., **A.** ♂, **B.** ♀ (MNHN RS 0079). **C, D.** *Srilankametrus couzijni*, sp. nov., **C.** holotype ♂ (BMNH 1896.7.30.121), **D.** paratype ♂ (SMF 5332/1). **E, F.** *Srilankametrus gravimanus* (Pocock, 1894), comb. nov., **E.** ♂, **F.** ♀ (AMNH), Kokmotte, Sri Lanka. Scale bars = 2 mm.

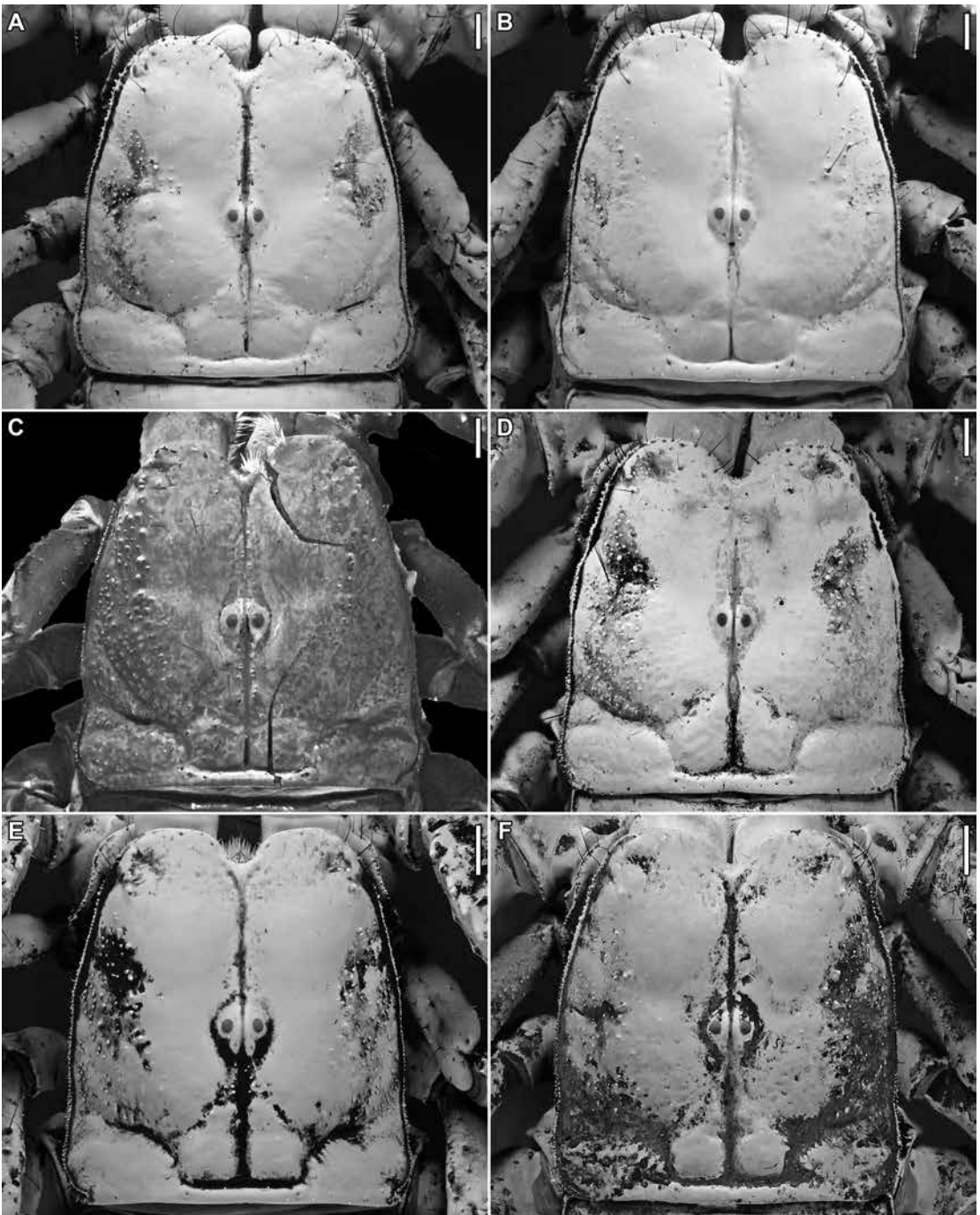


FIGURE 28. *Srilankametrus* Couzijn, 1981, stat. nov. et stat. rev., carapace, dorsal aspect. **A, B.** *Srilankametrus indus* (DeGeer, 1778), comb. nov., **A.** ♂, **B.** ♀ (AMNH), Kandy, Sri Lanka. **C, E, F.** *Srilankametrus serratus* (Pocock, 1900), comb. nov., **C.** holotype ♂ (BMNH 1888.55), **E.** ♂ (FMNH 086 916), **F.** ♀ (ZMH), Ceylon [Sri Lanka]. **D.** *Srilankametrus pococki*, sp. nov., holotype ♀ (AMNH), Kodigala, Sri Lanka. Scale bars = 2 mm.

and female of *C. hendersoni*, flat in the male and curved, i.e., slightly to markedly convex, in the female of *C. bastawadei*, *C. beccaloniae*, *C. fulvipes*, *C. nathanorum*, and *C. wroughtoni*, and curved in the male and female of *C. madraspatensis* and *C. shivashankari*. The proximal margin (lobe) of the chela manus dorsal surface is markedly curved and proximal to the proximal margin of the condyle (articulation with patella) in the male and female (fig. 94) of *C. hendersoni* but moderately curved and aligned with or proximal to the proximal margin of the retrolateral surface, or aligned with the proximal margin of the condyle in all other species except *C. pelekomanus*. The maximum distance between the dorsomedian and dorsal secondary carinae (DMC–DSC) of the chela manus is greater than the maximum distance between the dorsal secondary and digital carinae (DSC–DC) in the male of *C. hendersoni*, but greater than the DSC–DC in the male of *C. beccaloniae*, *C. madraspatensis*, *C. nathanorum*, and *C. tristis*. The dorsal secondary and subdigital carinae of the male are entirely to predominantly granular in *C. hendersoni*, entirely to predominantly costate in *C. nathanorum*, and absent or obsolete in *C. bastawadei* and *C. fulvipes*. The digital carina is entirely to predominantly granular (fig. 94) in *C. hendersoni*, entirely to predominantly costate in *C. nathanorum*, and absent or obsolete in *C. bastawadei*, *C. fulvipes*, *C. madraspatensis*, and *C. shivashankari*. The manus dorsal intercarinal surface is without reticulation in *C. hendersoni* but shallowly reticulate in *C. nathanorum*. The manus ventral surface is angled, with the axis of the retroventral carina ventral to the axis of the ventromedian carina in *C. hendersoni* but flat, with the axes of the retroventral and ventromedian carinae in approximately the same plane in all other species except *C. beccaloniae*, *C. pelekomanus*, and *C. tristis*. The legs are pale or very lightly infusate (fig. 92) in *C. hendersoni* but very dark or heavily infusate in *C. beccaloniae*, *C. nathanorum*, *C. pelekomanus*, *C. tristis*, and *C. wroughtoni*. Macroseta *st* on the retroventral surfaces of the basitarsi of legs I and II is spiniform (fig. 44E–H) in *C. hendersoni* but setiform in *C.*

nathanorum and *C. shivashankari*. The mesial surfaces of mesosomal tergites I–VI are smooth in the male and the lateral surfaces granular in the female of *C. hendersoni*, whereas the mesial surfaces are granular in the male of *C. bastawadei*, *C. fulvipes*, *C. madraspatensis*, and *C. shivashankari*, the mesial surfaces granular in the male and the lateral surfaces smooth in the female of *C. nathanorum*, and the lateral surfaces smooth in the female of *C. tristis*. The ventral surface of mesosomal sternite VII bears two pairs of moderately to strongly developed ventrosubmedian and ventrolateral carinae in *C. hendersoni* and a pair of weakly developed ventrolateral carinae in all other species except *C. beccaloniae* and *C. pelekomanus*. The dorsosubmedian carinae are granular or costate-granular on metasomal segments I–IV (fig. 58C) in *C. hendersoni* but costate on segments I and II or I–III and granular or costate-granular on III and IV or IV in *C. tristis*, and the female of *C. beccaloniae*. The ventral intercarinal surfaces of segment IV are granular in the male and female (fig. 60C) of *C. hendersoni* but smooth in the male and female of *C. wroughtoni*, the male of *C. bastawadei*, *C. fulvipes*, and *C. shivashankari*, and the female of *C. beccaloniae* and *C. nathanorum*. The dorsolateral carinae of metasomal segment V are strong and continuous in *C. hendersoni* but weak and discontinuous to absent in *C. nathanorum*. The dorsal intercarinal surface of segment V is granular in the male and female of *C. hendersoni*, smooth in the female of *C. wroughtoni*, and smooth in the male and female of all other species except *C. bastawadei* and *C. pelekomanus*.

DESCRIPTION: The following description is based on the holotype and paratypes. Meristic data are presented in table 3. The adult male is unknown hence measurements are presented only for the adult female (table 4).

Total length: Adult large, maximum length, measured from anterior margin of carapace to tip of aculeus, 137 mm (126–156 mm, $n = 3$) (♀).

Color: Chelicerae, dorsal surfaces bicolored, mostly to entirely immaculate prodorsal half of manus paler than infusate retrodorsal half of manus and fingers; manus markedly paler than

carapace interocular surface. Carapace, pedipalps, tergites, and metasoma entirely infusate, uniformly dark reddish brown to reddish black. Sternites III–VI immaculate, VII immaculate to slightly infusate, dark olive to blackish brown, becoming darker posteriorly. Coxosternal region infusate, brownish, maxillary lobes darker. Legs lightly infusate, uniformly yellow to light brown, contrasting with carapace, pedipalps, tergites, and metasoma (fig. 92). Genital opercula and pectines uniformly pale cream. Metasomal segments I–V similar to one another; carinae infusate, darker than intercarinal surfaces; dorsal intercarinal surfaces similar to tergites; ventral intercarinal surfaces darker than sternites. Telson vesicle immaculate, light yellowish, markedly paler than metasomal segment V; aculeus black.

Chelicerae: Movable finger prodistal (DI) and retrodistal (DE) teeth subequal, with DE tooth only slightly smaller than DI tooth, and opposable, i.e., forming a bicuspid. Fingers and manus, proventral surfaces with long, dense vestiture of macrosetae. Coxae, prodorsal surfaces without stridulatory setae (scaphotrix); promedian surfaces without chemoreceptive lamelliform setae (trichocapae).

Carapace: Carapace markedly dorsoventrally compressed, lateral surfaces sloping gently. Anterior margin concave, frontal lobes uneven, sloping medially toward deep median notch, without median projection or median depression (fig. 16F). Anterolateral margins converging gradually anteriorly, without distinct notch adjacent to posterior lateral ocelli; mediolateral margins diverging or converging slightly posteriorly (at posterolateral sulci). Anterior width of posterior width, 65% (64%–65%, $n = 3$) (♀); posterior width of length, 97% (95%–98%, $n = 3$) (♀). Three pairs of lateral ocelli (MLMa, PLMa, PDMi), all similar in size, two anterior pairs situated anteriorly, well separated from posterior pair, situated laterally. Median ocelli slightly larger than lateral ocelli, distance between ocelli slightly less than width of ocellus; median ocular tubercle situated posteromedially, distance from anterior carapace margin,

52% (51%–52%, $n = 3$) (♀). Median longitudinal sulcus narrow, suturiform; continuous from median notch to interocular sulcus; anteriorly furcated; without anterocular depression. Anterior furcated sulci diverging broadly from anterior edge of median longitudinal sulcus. Median ocular tubercle raised, superciliary carinae higher than ocelli, extended anteriorly, subparallel. Interocular sulcus present. Circumocular depressions completely encircling median ocular tubercle, converging anteriorly. Posteromedian and posteromarginal sulci deep. Paired mediolateral and posterolateral sulci shallow. Median longitudinal suture continuous from median notch to median ocular tubercle, equally strong along entire length; not extending to anterior margin of carapace, terminating at or posterior to median notch. Anterior furcated sutures absent or obsolete. Anterocular furcated sutures absent. Interocular suture present, slender. Posterior sutures present but indistinct, converging on median ocular tubercle; connected anteriorly to posterior furcations of interocular suture and extending anteriorly beyond median ocular tubercle. Frontal lobes and medial region of interocular surface finely granular with smooth areas (♂) or finely granular along median longitudinal and anterior furcated sulci only, elsewhere smooth (♀) (fig. 16F); anterolateral and mediolateral surfaces uniformly finely granular; posterolateral surfaces uniformly finely granular (♂) or smooth (♀); posteromedian surfaces smooth.

Pedipalps: Femur width of length, 47% (45%–51%, $n = 3$) (♀). Retrodorsal carina complete, costate-granular, similar to or more strongly developed than prodorsal carina. Dorsal secondary carina partial, reduced to granular row in anterior quarter, becoming obsolete distally. Dorsomedian carina partial, reduced to granular row in anterior quarter. Prodorsal carina complete, granular. Promedian carina complete, comprising row of spiniform or subspiniform granules (several demarcated by conspicuous macrosetae), oriented diagonally between prodorsal and proventral carinae. Proventral carina complete, granular as

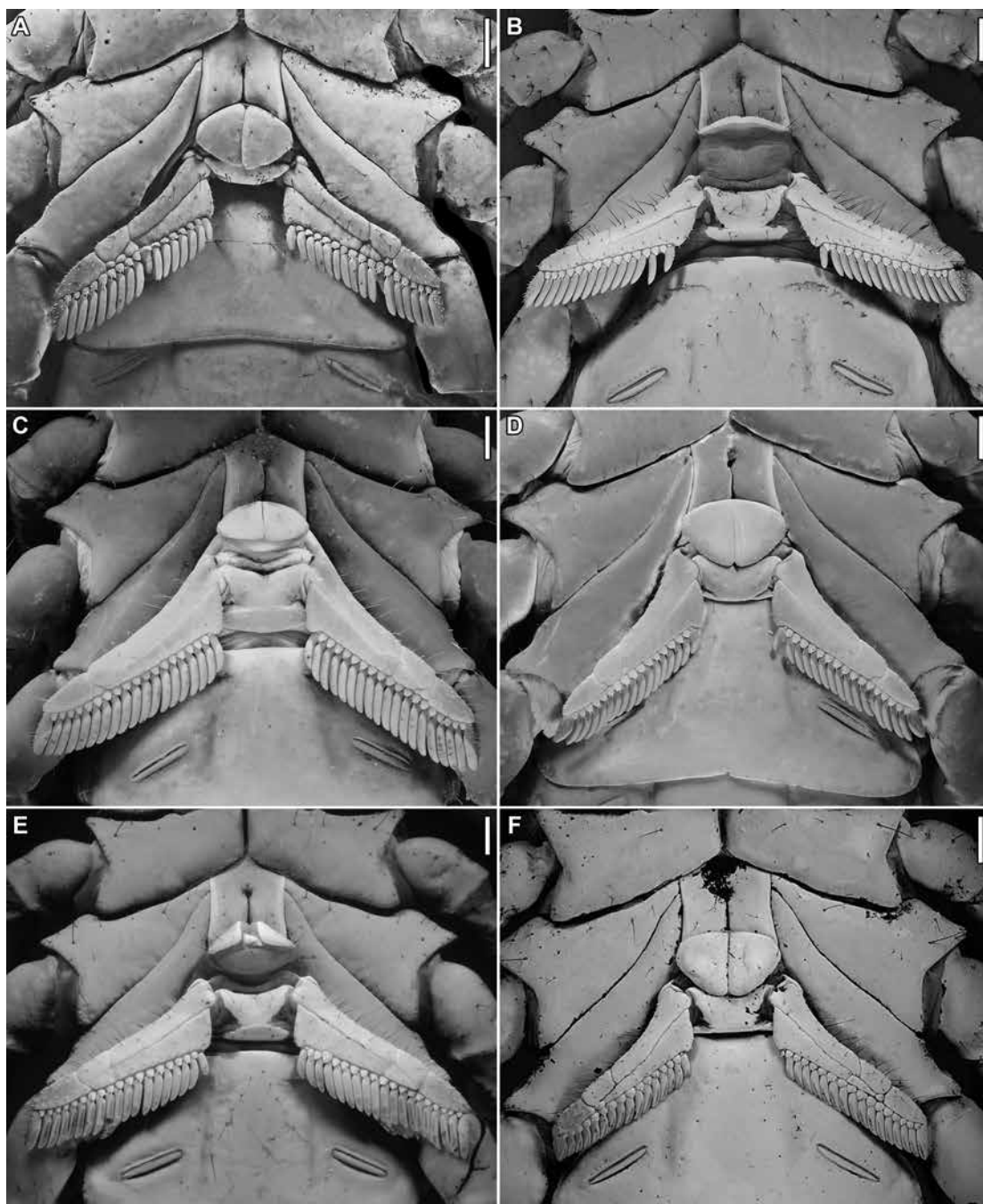


FIGURE 29. *Chersonesometrus* Couzijn, 1978, stat. nov. et stat. rev., sternum and pectines, ventral aspect. **A, B.** *Chersonesometrus beccaloniae* (Kovářík, 2004), comb. nov., **A.** ♂ (ZMH), Ootacalum, India, **B.** ♀ (AMNH), Yelagiri Hills, India. **C, D.** *Chersonesometrus pelekomanus* (Couzijn, 1981), comb. nov., **C.** holotype ♂ (SMF RII/1088/19), **D.** paratype ♀ (SMF RII/329). **E, F.** *Chersonesometrus tristis* (Henderson, 1919), comb. nov. **E.** ♂ (AMNH), Ithepalli, India, **F.** ♀ (AMNH), Maddur, India. Scale bars = 2 mm.

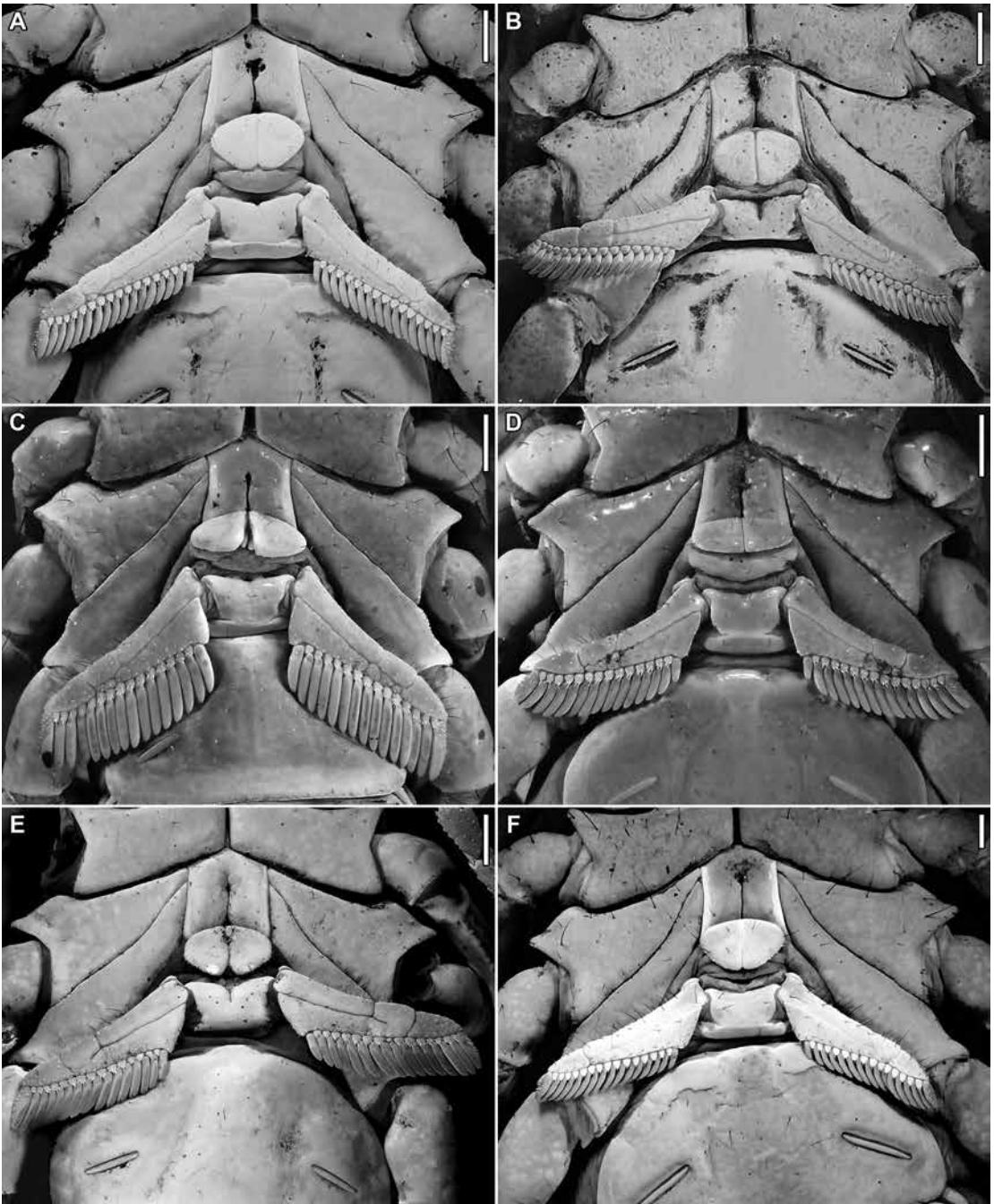


FIGURE 30. *Chersonesometrus* Couzijn, 1978, stat. nov. et stat. rev., sternum and pectines, ventral aspect. **A.** *Chersonesometrus bastawadei*, sp. nov., holotype ♀ (AMNH), Naganath Temple, India. **B.** *Chersonesometrus wroughtoni* (Pocock, 1899), comb. nov., paralectotype ♀ (BMNH 1897.9.17.1-4, 11, 20). **C, D.** *Chersonesometrus shivashankari*, sp. nov., **C.** holotype ♂ (BMNH), Bellahunsi, India, **D.** paratype ♀ (BMNH), Hampasagar, India. **E.** *Chersonesometrus nathanorum*, sp. nov., subad. ♂ holotype (MNHN RS 3145). **F.** *Chersonesometrus hender-soni*, sp. nov., holotype ♀ (AMNH), Sanapura, India. Scale bars = 2 mm.

strongly developed as or more strongly developed than retroventral carina. Ventromedian and secondary accessory carinae absent. Retroventral carina extending partly or entirely to distal edge of segment. Retromedian carinae absent, indicated only by macrosetal rows. Dorsal and prolateral intercarinal surfaces finely granular; ventral and retrolateral surfaces smooth. Patella width of length, 51% (50%–53%, $n = 3$) (♀). Dorsal surface flat, axes of dorsomedian and retrodorsal carinae in same plane. Dorsomedian carina entirely to predominantly costate-granular (fig. 93). Retrodorsal carina predominantly costate-granular, more strongly developed than granular retromedian carinae. Retroventral carina distinct, costate-granular. Promedian carina and promedian process absent. Other carinae absent. Dorsal and retrolateral intercarinal surfaces finely granular, other surfaces smooth. Chela short, broad (fig. 94); manus height of width, 65% (60%–67%, $n = 3$) (♀); manus length along retroventral carina of manus width, 86% (80%–92%, $n = 3$) (♀); manus length along retroventral carina of movable finger length, 74% (70%–79%, $n = 3$) (♀). Chela moderately (♂) to sparsely (♀) setose. Manus dorsal surface (between dorsomedian and digital carinae) flat; proximal margin (lobe) of dorsal surface markedly curved and proximal to proximal margin of condyle (articulation with patella); proximal margin (lobe) of dorsal surface moderately curved and aligned with (♂) or proximal to (♀) proximal margin of retrolateral surface. Dorsomedian carina obsolete, costate on fixed finger and comprising regular row of spiniform granules along entire length of manus. Dorsal secondary, subdigital, and digital carinae incomplete, entirely to predominantly granular; dorsal secondary carina comprising double row of granules in proximal two-thirds; proximal half of dorsal secondary carina, distal half of subdigital carina and distal third of digital carina closely adjacent. Maximum distance between dorsomedian and dorsal secondary carinae (DMC–DSC) greater than maximum distance between dorsal secondary and digital carinae (DSC–DC). Retromedian carina complete, predominantly costate, more strongly

developed than digital carina. Retrolateral secondary and secondary accessory carinae vestigial, proximal to condyle of movable finger. Retroventral carina distinct, costate. Ventromedian carina obsolete, costate. Proventral and promedian carinae similarly developed, each comprising row of spiniform granules and associated macrosetae. Prodorsal carina obsolete, comprising few spiniform granules and associated macrosetae. Distance between dorsomedian and promedian carinae (DMC–PMC) slightly to markedly greater than distance between promedian and proventral carinae (PMC–PVC). Manus, dorsal and retrolateral intercarinal surfaces densely and coarsely granular except for smooth depression at base of fixed finger; ventral intercarinal surface smooth or nearly so; prolateral intercarinal surfaces very sparsely and finely granular, more densely dorsally and distally. Manus ventral surface angled, axis of retroventral carina ventral to axis of ventromedian carina. Fixed and movable fingers, intercarinal surfaces smooth; median denticle rows each with six enlarged retrolateral denticles (including terminal denticle), proximal three situated on lobes; first (proximal) lobe of fixed finger and second lobe of movable finger larger than others, with correspondingly deeper notches in movable and fixed fingers, respectively; terminal denticles of fingers interlocking unevenly when closed, movable finger displaced retrolaterally; distinct notch near tip of fixed finger to accommodate terminal denticle of movable finger.

Trichobothria: Orthobothriotaxic, Type C, with the following segment totals ($n = 12$): femur, 3 (1 d , 1 i , 1 e); patella, 19 (2 d , 1 i , 3 v , 13 e , comprising 3 et , 1 est , 2 em , 2 esb , 5 eb); chela, 26 (manus, 16, comprising 2 D , 10 E , 4 V ; fixed finger, 10, comprising 4 d , 4 e , 2 i). Total count of trichobothria per pedipalp: 48. Femur, i situated on dorsal surface. Patella, d_2 situated on internal surface, slightly closer to d_1 than to i ; distance v_2 – v_3 ca. one-third distance v_1 – v_2 . Chela, distance et – est ca. half distance est – esb ; distance est – esb greater than half distance esb – eb ; est distal to dst ; V_3 situated in proximal third of manus, closer to V_4 than V_2 .

Legs: First pair of maxillary lobes (coxapophyses) tapering anteriorly, longer than and encircling second pair. Stridulatory organs, comprising “rasp” (granular tubercles) and “scraper” (stridulatory setae or scaphotrix), present on opposing surfaces of coxae of first pair of legs and pedipalps, respectively. Legs I–IV acarinate, except femora, with distinct pro- and retrolateral surfaces demarcated by partial, granular prodorsal and complete, costate-granular proventral carinae. Femora, patellae, and tibiae, pro- and retrolateral surfaces each with scattered setiform macrosetae. Tibiae, prolateral surfaces, without spiniform macrosetae; I and II, retrolateral surfaces, each with two spiniform (*t*, *st*) macrosetae; III and IV, retrolateral surfaces, without spiniform macrosetae. Basitarsi I–IV, slightly dorsoventrally compressed; retrolateral margins similar, unmodified, rounded; prolateral pedal spurs present (fig. 44E–H); retrolateral pedal spurs absent. Basitarsi, pro- and retrolateral surfaces, each with scattered long and short setiform macrosetae, and spiniform macrosetae, more numerous on I and II than III and IV. Basitarsi, spiniform macrosetae, I, retrolateral: *t*, *sb*; retroventral: *t*, *st*, *sb*; proventral: *t*, *st*; II, retrolateral: *t*, *sb*; retroventral: *t*, *st*, *sb*; proventral: *t*, *st*; III, retrolateral: *t*, *sb*; retroventral: *t*, *st*; proventral: *t*; prolateral: *t*, *st*; IV, retrolateral: *t*; retroventral: *t*; proventral: *t*, *st*; prolateral: *t*, *st*. Telotarsi I–IV short, stout and distally broadened in dorsal and lateral views. Laterodistal lobes rounded. Dorsomedian lobes approximately equal to laterodistal lobes; each terminating in single setiform macroseta. Telotarsi, pro- and retrolateral surfaces, each with long and short, scattered macrosetae, not arranged in definite row. Telotarsi each with pro- and retroventral rows of spiniform macrosetae, two inserted on laterodistal lobes; counts in pro- and retroventral rows similar on I and II, and on III and IV ($n = 16$): I, proventral: 4, retroventral: 6; II, 4 (4 or 5), 6 (6 or 7); III and IV, 5, 6 (6 or 7). Telotarsal ungues short, curved, equal to subequal; pseudonychium (dactyl) reduced, rounded.

Sternum: Shape subpentagonal (fig. 30F). Median longitudinal sulcus shallow anteriorly, deep and narrow posteriorly.

Genital operculum: Genital opercula suboval, completely divided longitudinally, partially overlapping, genital papillae present (δ); subcordate, fused, genital papillae absent (φ) (fig. 30F).

Hemispermaphore: Unknown.

Pectines: Distal edge extending past distal edge of coxa IV but not reaching distal edge of trochanter IV (δ) or reaching to distal edge of coxa IV (φ) (fig. 30F). First proximal median lamella (scape) of each pecten with mesial margin angular, approximately 90° (δ) or obtusely angular, greater than 90° but less than 180° (φ). Pectinal teeth straight and elongate (δ) or shorter and curved (φ), present along entire posterior margin; sinistral/dextral tooth count, 19/19 (17–19/18 or 19, $n = 6$) (δ), 16/16 (16 or 17/16 or 17, $n = 10$) (φ). Fulcra smooth proximally but densely setose (microsetae only) distally.

Mesosoma: Tergites each with shallow pair of submedian depressions, without obsolete median carina. Pretergites smooth and glabrous. Posttergites smooth and glabrous medially, unevenly finely and coarsely granular to predominantly coarsely granular laterally. Sternites IV–VI, each with paired longitudinal depressions prolateral to spiracles, absent on VII. Surface, sternites III–VII, smooth; VII with two pairs of moderately to strongly developed, costate ventrosubmedian and ventrolateral carinae. Sternite VII, length of width, 66% (64%–70%, $n = 3$) (φ).

Metasoma and telson: Metasomal segments I–V progressively increasing in length, decreasing in width; segment V, width of segment I, width, 69% (67%–71%, $n = 3$) (φ). Metasoma fairly robust, width of length, segment I, 83% (79%–86%, $n = 3$) (φ); II, 67% (63%–70%) (φ); III, 61% (56%–64%) (φ); IV, 49% (48%–51%) (φ); V, 35% (34%–37%) (φ). Telson vesicle, width of metasomal segment V, width, 102% (100%–105%, $n = 3$) (φ); vesicle globose, height of length, 52% (51%–53%, $n = 3$) (φ); dorsal surface flat; ventral surface evenly curved. Aculeus relatively long, gently curved, length of vesicle length, 67% (63%–72%, $n = 3$) (φ). Length metasoma and telson, of total length, 54% (53%–54%, $n = 3$) (φ). Dorso-submedian carinae, segments I–IV, distinct, com-

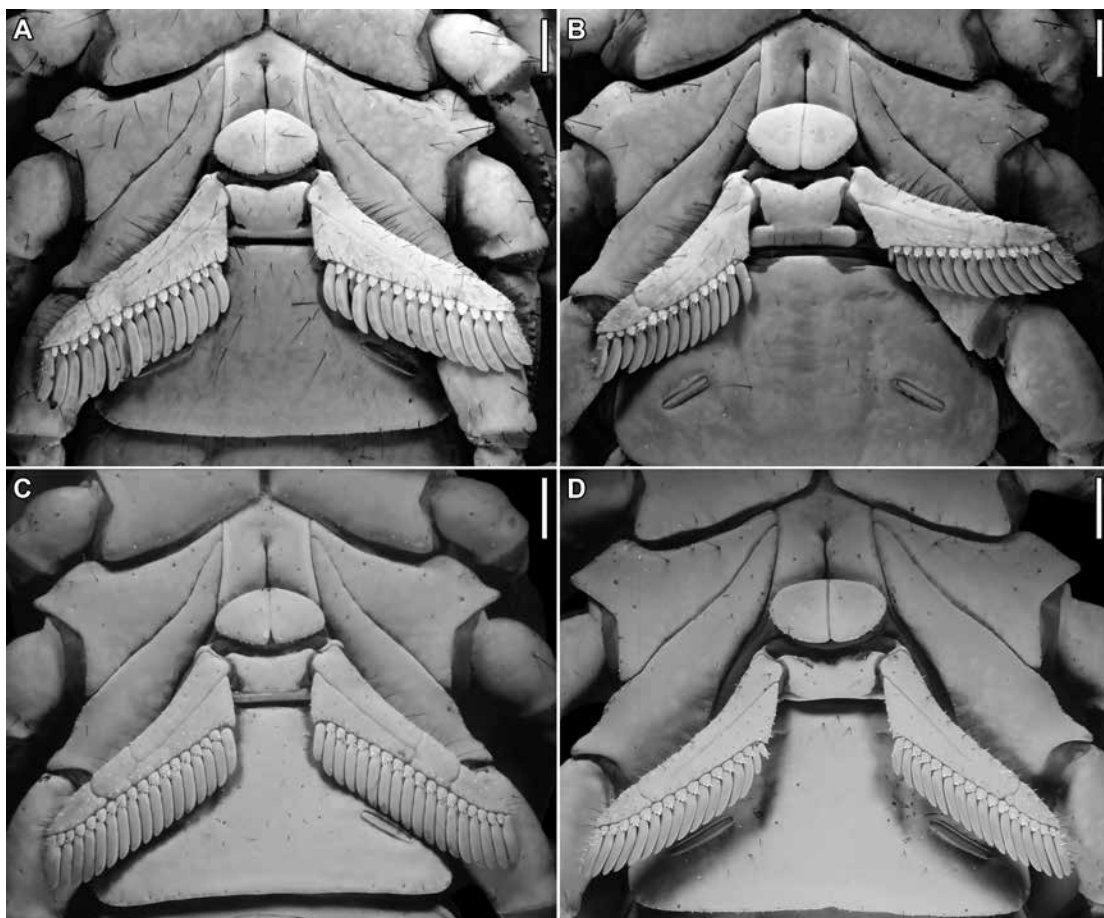


FIGURE 31. *Chersonesometrus* Couzijn, 1978, stat. nov. et stat. rev., sternum and pectines, ventral aspect. **A**, **B**. *Chersonesometrus fulvipes* (C.L. Koch, 1837), comb. nov., **A**. ♂, **B**. ♀ (AMNH), Khambatki Ghat, India. **C**, **D**. *Chersonesometrus madraspatensis* (Pocock, 1900), comb. nov., **C**. ♂ (CAS 9071142), **D**. ♀ (CAS 9071143). Scale bars = 2 mm.

plete, granular or costate-granular, posterior spiniform granules obsolete (fig. 58C); V, vestigial. Dorsolateral carinae, segments I–V, distinct, complete, costate-granular on I–IV, costate-granular to granular on V. Median lateral carinae, segment I, incomplete, reduced to granular row in posterior half, diagonally oriented between dorsolateral and ventrolateral carinae (fig. 59C); II–IV, obsolete row of granules posteriorly; V, incomplete, granular row, restricted to anterior two-thirds. Ventrolateral and ventrosubmedian carinae, segments I–IV, distinct, complete, costate on I–III, granular or costate-granular on IV, more strongly devel-

oped on III and IV than on I and II (fig. 60C). Ventrolateral carinae, segment V, distinct, complete, comprising spiniform granules, diverging posteriorly, terminal granule slightly larger than preceding granules. Ventrosubmedian carinae, segment V, vestigial, each reduced to one or two isolated spiniform granules, demarcated by conspicuous macrosetae. Ventromedian carina, segment V comprising single row of spiniform granules, unmodified posteriorly. Anal arch, segment V, dorsal carina, costate; ventral carina comprising subspiniform granules. Lateral intercarinal surfaces, segments I–IV, granular, V, smooth. Ven-

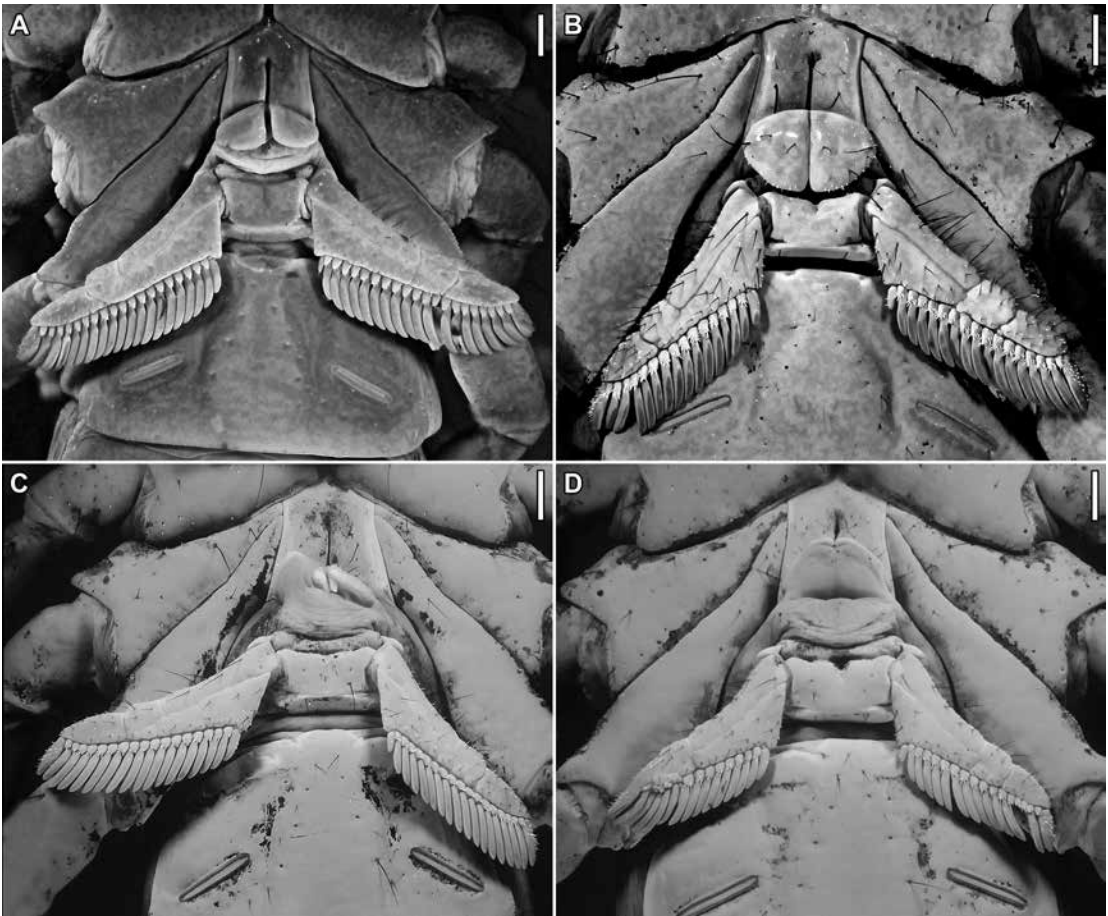


FIGURE 32. *Gigantometrus* Couzijn, 1978, stat. nov., sternum and pectines, ventral aspect. **A, B.** *Gigantometrus swammerdami* (Simon, 1872), comb. nov., **A.** lectotype ♂ (*Palamnaeus swammerdami flavimanus* Pocock, 1900, syn. nov.) (BMNH 1899.11.2.292-3), **B.** ♀ (FMNH 086 257). **C, D.** *Gigantometrus titanicus* (Couzijn, 1981), comb. nov. et stat. rev., **C.** ♂, **D.** ♀ (AMNH), Polonnaruwa, Sri Lanka.

tral intercarinal surfaces, segments I–III, smooth, IV and V, granular. Telson vesicle, dorsal and lateral surfaces smooth; ventral surface with four longitudinal carinae, each comprising spiniform granules.

DISTRIBUTION: This species is endemic to India and presently recorded only from the state of Karnataka (fig. 80, table 1).

ECOLOGY: The known locality records of this species occur in semiarid savanna and deciduous riverine forest dominated by *Acacia*, *Euphorbia*, and broadleaf bushes (*Grewia*, *Ziziphus*), with

bamboo, along riverbeds in rocky granite hills, at elevations of 450–480 m (fig. 7D). The specimens for which data are available were collected from shallow scrapes in coarse granitic sandy-loam soil under large, flat, embedded rocks. The habitat and habitus are consistent with the pelophilous, fossorial and semilithophilous ecomorphotypes (Prendini, 2001b). This species is sympatric with *Charmus indicus*, *Hottentotta rugiscutis*, *Lychas scaber* (Pocock, 1893), *L. tricarinatus*, and an undetermined species of *Reddyanus* Vachon, 1972.

Chersonesometrus madraspatensis

(Pocock, 1900), comb. nov.

Figures 8E, 10, 17C, D, 31C, D, 45I–L, 61C, 62C, 63C, 79, 95–98, table 1

Scorpio (Buthus) fulvipes: Laurie, 1890: 105.

Scorpio fulvipes: Laurie, 1891: 587–597, pl. XL, figs. 1–18; Pocock, 1893: 304–307, 309 (part); Kraepelin, 1894: 31, 43–46, 52, 59–61, 246, pl. I, figs. 22, 28, 37 (part); Laurie, 1896a: 187, 188, 192, 194, pl. IX, figs. 3, 6; Warburg, 2010: 1749; 2012b: 60.

Heterometrus fulvipes: Kraepelin, 1899: 109, 112, 113, 115 (part); Masi, 1912: 124 (part); Kraepelin, 1913: 166 (part); Giltay, 1931: 9; Sasirababu, 1961: 11–17, pl. I, figs. 1, 2 (misidentification); Pampapathi Rao, 1964: 133–141, fig. 1 (misidentification); Laverack, 1966: 241, 244, 250 (misidentification); Pampapathi Rao and Murthy, 1966: 520, 521 (misidentification); Sasirababu and Venkatachari, 1966: 22–32, figs. 1–4 (misidentification); Venkateswara Rao and Sepur Govindappa, 1967: 243–249, tables I, II, pl. XIII, figs. 1–3 (misidentification); Venkatachari and Murali-krishna Dass, 1968: 617–620, graph (misidentification); Devarajulu Naidu, 1969: 1274, figs. 1, 2 (misidentification); Chengal Raju et al., 1973: 964, 965, fig. (misidentification); Geethabali and Pampathi Rao, 1973: 189–196, figs. 2, 3, 4C, 4D, 5, 6 (misidentification); Devarajulu Naidu and Padmanabhanaidu, 1976: 1–5, tables 1, 2, figs. 1–4 (misidentification); Geethabali, 1976: 345–347, table, figs. 1–3 (misidentification); Chandrasekara Reddy and Padmanabhanaidu, 1977: 217, 218, fig. 1 (misidentification); Mastanaiah et al., 1977: 1051, 1052, fig. (misidentification); Chengal Raju et al., 1978: 111–113, table I (misidentification); Jayaram et al., 1978: 1184, 1185, table, fig. (misidentification); Mastanaiah et al., 1978: 130, 131, fig. 1 (misidentification); Subburam and Gopalakrishna Reddy, 1978a: 513, 514, table

I (misidentification); 1978b: 665, 666, figs. 1–4 (misidentification); Jayaram and Padmanabhanaidu, 1979: 6–8, tables I, II (misidentification); Mastanaiah et al., 1979: 69, 70, fig. (misidentification); Subburam and Gopalakrishna Reddy, 1979: 853–855, table I (misidentification); Uthaman and Srinivasa Reddy, 1979: 347–352, tables 1, 2, fig. 1 (misidentification); Jayaram and Padmanabhanaidu, 1980: 109–112, table 1 (misidentification); Subburam and Gopalakrishna Reddy, 1980a: 658–661, tables I, II (misidentification); 1980b: 138, 139, figs. 1–4 (misidentification); Yellamma et al., 1980: 29–37, figs. 1–7 (misidentification); Subburam and Gopalakrishna Reddy, 1981: 275–281, figs. 1–31 (misidentification); Yellamma et al., 1982: 225–233, tables 1–3, fig. 1 (misidentification); Subburam and Gopalakrishna Reddy, 1989: 329–333, figs. 1–3 (misidentification); Root, 1990: 354, 365, 368, 396, 404–410, figs. 9.24, 9.29 (misidentification); Polis and Sissom, 1990: 179 (part); Simard and Watt, 1990: 419 (misidentification); Warburg and Polis, 1990: 229, 235 table 5.2 (misidentification); Pointer, 1991: 24; Rajyalakshmi et al., 1991: 429–432, fig. 1 (misidentification); Shivashankar and Veeresh, 1991: 697–702 (misidentification); Kalarani et al., 1992: 141–146, tables 1–3, fig. 1 (misidentification); Shivashankar, 1992: 134–138 (misidentification); 1994: 81–90, tables 1–3, figs. 1–3 (misidentification); Prendini et al., 2003: 192, 193, 202, 203, 205, 208, 209, 218, 222, 252, 254, 255, 259, tables 3, 4, figs. 4–7, appendices 1, 2 (misidentification, part); Kovařík, 2004: 1, 15, 29, 49, 51, 52, tables 2, 3 (misidentification, part); Mirza and Sanap, 2009: 488, 490 (misidentification); Javed et al., 2010b: 785, table 1 (misidentification); Warburg, 2010: 1739, 1749, 1750, table 3 (misidentification, part); 2012a: 82, 83, 85, table 1 (part); 2012b: 60, 61, 63, 64 (misidentification); 2013: 152, 153, 155 (misidentification, part).

- Palamnaeus fulvipes madraspatensis* Pocock, 1900a: 88, 89 (part), fig. 25B; Tikader, 1973: 263; Couzijn, 1981: 135; Fet, 2000: 439, 440; Kovařík, 2004: 29.
- Heterometrus (Scorpio) fulvipes*: Kraepelin, 1901: 271 (misidentification, part).
- Pandinus fulvipes*: Simon, 1905: 161 (misidentification).
- Heterometrus (Chersonesometrus) fulvipes*: Couzijn, 1981: 23, 40, 88, 123, 132–136, 139, 140, 142, 149, 169, 192, table 7, figs. 39, 57 (misidentification, part); Kovařík, 1998: 136 (part); 2002: 17 (misidentification).
- Heterometrus (Chersonesometrus) madraspatensis*: Tikader and Bastawade, 1983: 576, 630–635, figs. 1668–1682; Fet, 2000: 440; Indra, 2009: 142.
- Heterometrus madraspatensis*: Kovařík, 2004: 1, 2, 27–29, 51, 52, tables 2, 3 (part), fig. 20; 2009: 35, 36, 41, 48, 49, 85, 100, 108, tables 1, 2 (part), figs. 83–88, 208, 209, 257, 258; Javed et al., 2010b: 785, table 1; Tahir and Prendini, 2014: 9.
- Heterometrus (Chersonesometrus) granulomanus*: Thulsi Rao et al., 2005: 3, 9 (misidentification, part).

TYPE MATERIAL: INDIA: Andhra Pradesh:

Kadapa Distr.: *Palamnaeus fulvipes madraspatensis*: Paralectotype [sex?] (BMNH), Cuddapah [Kadapa, 14°28'N 78°49'E], Popert. **Tamil Nadu:** **Chennai Distr.:** *P. f. madraspatensis*: Lectotype ♂, paralectotype ♂ (BMNH), Madras [Chennai, 13°05'N 80°17'E], Henderson [examined]. **Telangana:** **Hyderabad Distr.:** *P. f. madraspatensis*: Paralectotype [sex?] (BMNH), Secunderabad [17°26'N 78°30'E], Ricardo.

In the description of *Palamnaeus fulvipes madraspatensis*, Pocock (1900a: 88, 89) referred to specimens from three localities, Madras, Cuddapah, and Secunderabad, but did not specify a “type,” hence all specimens listed are syntypes. Couzijn (1981: 133–136) mistakenly referred to a holotype of *P. f. madraspatensis*, Tikader and

Bastawade (1983: 630–635), referred to two male type specimens and mistakenly listed Madras as the type locality, and Fet (2000: 440) followed these authors in incorrectly referring to a male holotype from Madras and paratypes from Madras, Cuddapah, and Secunderbad. Kovařík (2004) correctly designated a male lectotype and male paralectotype from Madras but failed to mention the specimens from Cuddapah and Secunderabad, which are therefore also paralectotypes.

DIAGNOSIS: *Chersonesometrus madraspatensis* may be separated from other species of *Chersonesometrus* as follows. The carapace is vaulted, the lateral surfaces sloping steeply (fig. 17C, D), in *C. madraspatensis*, but slightly to markedly dorso-ventrally compressed, the lateral surfaces sloping gently in all other species except *C. fulvipes* and *C. shivashankari*. The frontal lobes and medial region of the carapace interocular surface are granular with smooth areas in the female (fig. 17D) of *C. madraspatensis* whereas the interocular surface is granular along the median longitudinal and anterior bifurcated sulci only in the female of all other species except *C. bastawadei*, *C. pelekomanus*, and *C. shivashankari*. The carapace posterolateral surfaces of the female are granular in *C. madraspatensis* but smooth or nearly so in all other species except *C. bastawadei* and *C. fulvipes*. The cheliceral movable finger prodistal (DI) and retrodistal (DE) teeth are unequal, with the DE tooth considerably smaller than the DI tooth, aligned longitudinally and not opposable in *C. madraspatensis*, but subequal, with the DE tooth only slightly smaller than the DI tooth, and opposable, i.e., forming a bicuspid, in *C. beccaloniae*, *C. hendersoni*, *C. nathanorum*, *C. pelekomanus*, and *C. tristis*. The pedipalps of the adult male are long, with femur length : posterior carapace width ratio (FL:PCW) ≥ 0.80 and femur length : carapace length ratio (FL:CL) ≥ 0.76 (fig. 95A, B) in *C. madraspatensis* but short, with FL:PCW < 0.77 , FL:CL < 0.74 in all other species except *C. beccaloniae* and *C. tristis*. The pedipalp patella dorsal surface is convex, with the axis of the dorsomedian carina dorsal to the axis of the retrodorsal carina (fig. 96) in *C.*

madraspatensis but flat or nearly so, with the axes of the dorsomedian and retrodorsal carinae in the same plane, in *C. beccaloniae*, *C. hendersoni*, *C. pelekomanus*, and *C. tristis*. The patella retrodorsal carina of the female is as strongly developed as or more strongly developed than the retromedian carinae in *C. madraspatensis* but absent or obsolete in *C. nathanorum*. The retromedian carinae are granular in *C. madraspatensis* but costate in *C. nathanorum*. The patella dorsal, retrodorsal, and retroventral intercarinal surfaces of the female are granular in *C. madraspatensis* but smooth or nearly so in *C. nathanorum*. The pedipalp chela is infusate and similar in color to the femur and patella in *C. madraspatensis* but immaculate and paler than the femur and patella in *C. shivashankari*. The chela of the adult male is sparsely setose in *C. madraspatensis* but moderately to densely setose in *C. beccaloniae*, *C. pelekomanus*, and *C. tristis*. The chela manus dorsal surface (between the dorsomedian and digital carinae) is curved, i.e., slightly to markedly convex, in the male and female of *C. madraspatensis*, flat in the male and curved in the female of *C. bastawadei*, *C. beccaloniae*, *C. fulvipes*, *C. nathanorum*, and *C. wroughtoni*, and flat in the male and female of *C. hendersoni*, *C. pelekomanus*, and *C. tristis*. The proximal margin (lobe) of the chela manus dorsal surface is moderately curved and proximal to the proximal margin of the retrolateral surface in the male (fig. 97), or aligned with the proximal margin of the condyle (articulation with patella) in the female (fig. 98) of *C. madraspatensis*; moderately curved and aligned with the proximal margin of the retrolateral surface in the male, or aligned with or proximal to the proximal margin of the retrolateral surface in the female of *C. beccaloniae* and *C. nathanorum*; and markedly curved and proximal to the proximal margin of the condyle in the male and female of *C. hendersoni* and *C. pelekomanus*. The maximum distance between the dorsomedian and dorsal secondary carinae (DMC–DSC) of the chela manus is similar to the maximum distance between the dorsal secondary and digital carinae (DSC–DC) in the male of *C. madraspatensis*, but greater than the DSC–

DC in the male of all other species except *C. beccaloniae*, *C. nathanorum*, and *C. tristis*. The dorsal secondary and subdigital carinae of the male are entirely to predominantly granular (fig. 97) in *C. madraspatensis*, entirely to predominantly costate in *C. nathanorum*, and absent or obsolete in *C. bastawadei* and *C. fulvipes*. The digital carina is absent or obsolete in *C. madraspatensis*, but entirely to predominantly granular in *C. beccaloniae*, *C. hendersoni*, *C. pelekomanus*, *C. tristis*, and *C. wroughtoni*, and entirely to predominantly costate in *C. nathanorum*. The manus dorsal intercarinal surface is without reticulation in *C. madraspatensis* but shallowly reticulate in *C. nathanorum*. The manus ventral surface is flat, with the axes of the retroventral and ventromedian carinae in approximately the same plane in *C. madraspatensis* but angled, with the axis of the retroventral carina ventral to the axis of the ventromedian carina in *C. beccaloniae*, *C. hendersoni*, *C. pelekomanus*, and *C. tristis*. The legs are pale or very lightly infusate (fig. 95) in *C. madraspatensis* but very dark or heavily infusate in *C. beccaloniae*, *C. nathanorum*, *C. pelekomanus*, *C. tristis*, and *C. wroughtoni*. Macroseta *st* on the retroventral surfaces of the basitarsi of legs I and II is spiniform (fig. 45I–L) in *C. madraspatensis* but setiform in *C. nathanorum* and *C. shivashankari*. The mesial surfaces of mesosomal tergites I–VI are granular in the male and the lateral surfaces granular in the female of *C. madraspatensis*, whereas the mesial surfaces are smooth in the male of *C. beccaloniae*, *C. hendersoni*, *C. pelekomanus*, and *C. wroughtoni*, the mesial surfaces smooth in the male and the lateral surfaces smooth in the female of *C. tristis*, and the lateral surfaces smooth in the female of *C. nathanorum*. The ventral surface of mesosomal sternite VII bears a pair of weakly developed ventrolateral carinae in *C. madraspatensis* and two pairs of moderately to strongly developed ventrosubmedian and ventrolateral carinae in *C. beccaloniae*, *C. hendersoni*, and *C. pelekomanus*. The dorsosubmedian carinae are granular or costate-granular on metasomal segments I–IV (fig. 61C) in *C. madraspatensis* but costate on segments I and II

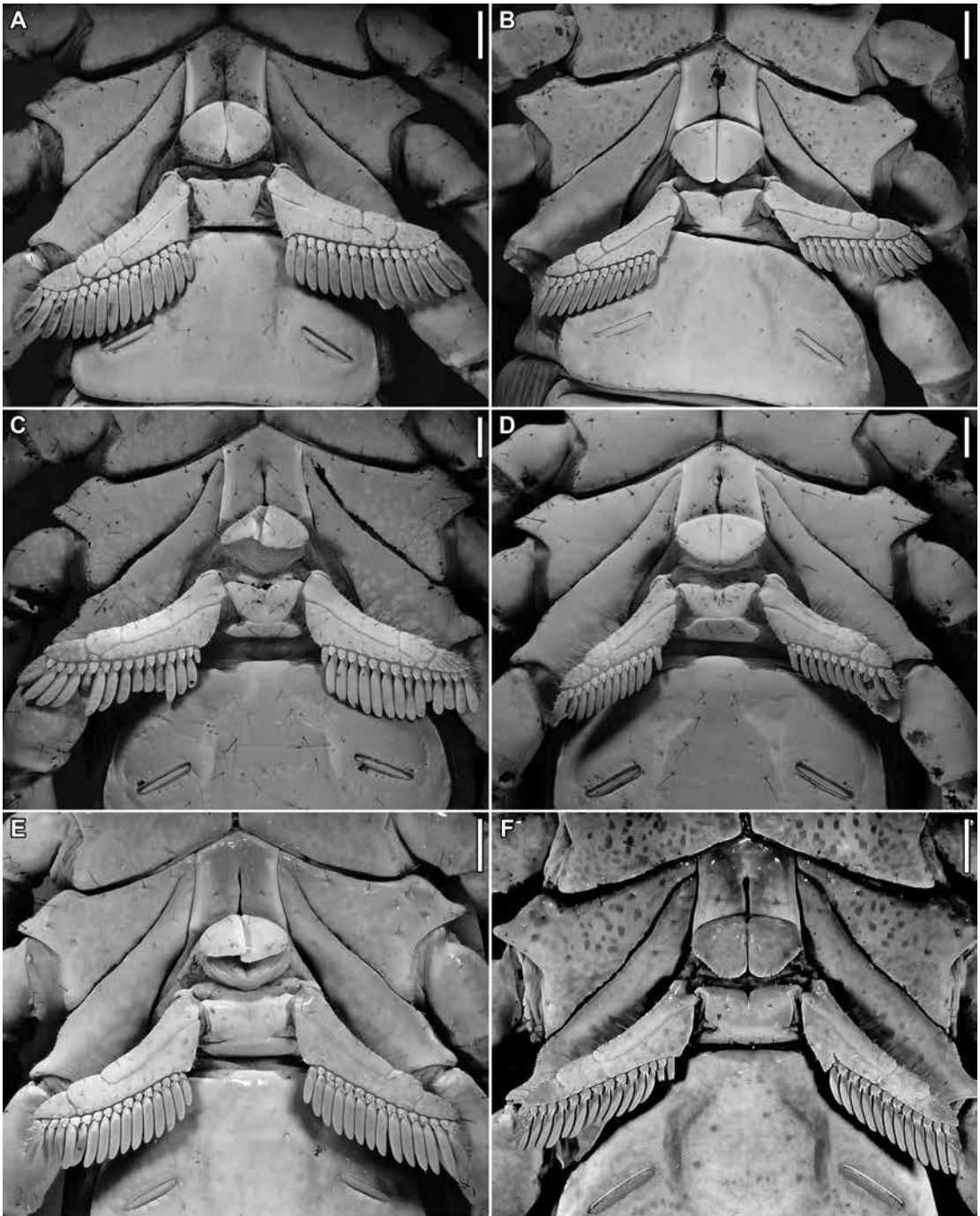


FIGURE 33. *Deccanometrus*, gen. nov., sternum and pectines, ventral aspect. **A, B.** *Deccanometrus bengalensis* (C.L. Koch, 1841), comb. nov., **A.** ♂ (BMNH 1913.1.6.3), **B.** ♀ (BMNH 1896.8.15.4). **C, D.** *Deccanometrus obscurus* (Couzijn, 1981), comb. et stat. nov., **C.** ♂, **D.** ♀ (AMNH), Bhimashankar, India. **E, F.** *Deccanometrus phipsoni* (Pocock, 1893), comb. nov., **E.** ♂, **F.** ♀ (MNHN RS 0080). Scale bars = 2 mm.

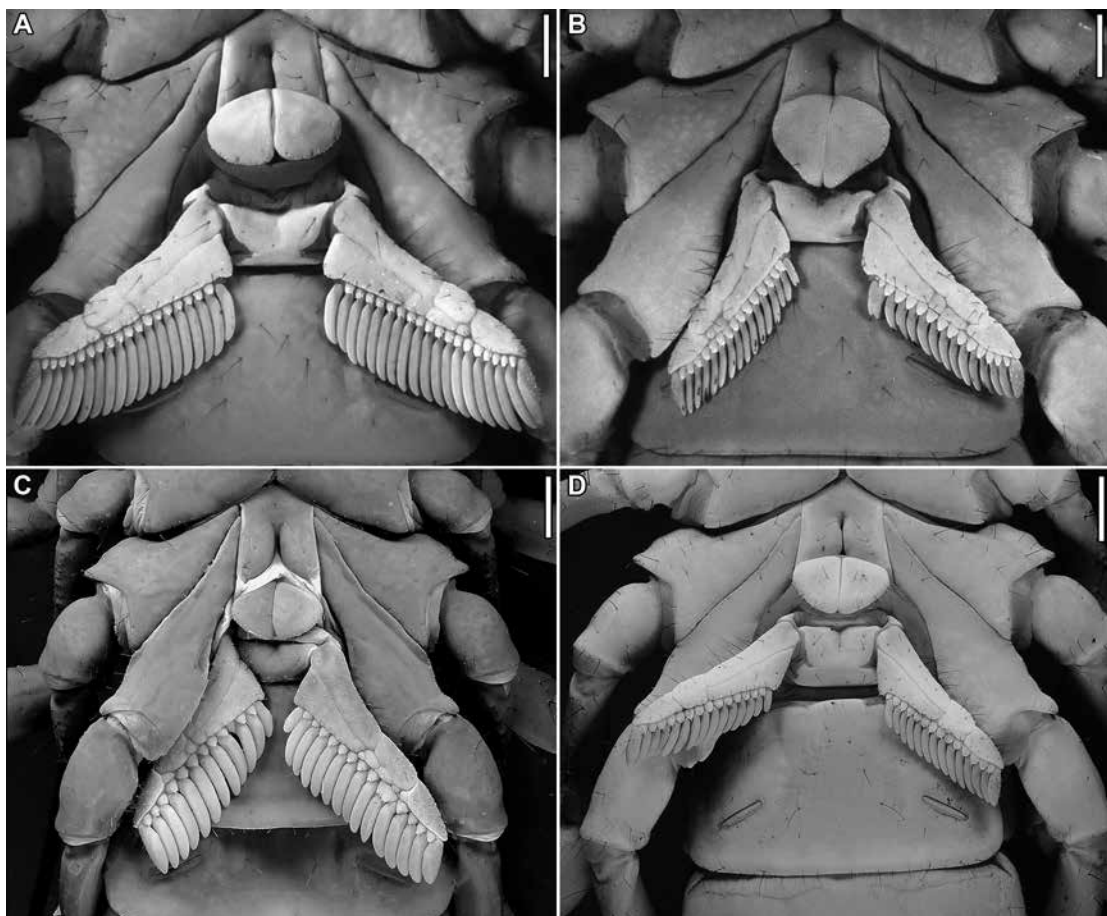


FIGURE 34. *Deccanometrus*, gen. nov., sternum and pectines, ventral aspect. **A, B.** *Deccanometrus latimanus* (Pocock, 1894), comb. nov., **A.** ♂ (AMNH), Charbagh, Pakistan, **B.** ♀ (AMNH), Daggar, Pakistan. **C, D.** *Deccanometrus xanthopus* (Pocock, 1897), comb. nov., **C.** lectotype ♂ (BMNH 1896.9.26.88-91), **D.** ♀ (AMNH), Khambatki Ghat, India. Scale bars = 2 mm.

or I–III and granular or costate-granular on III and IV or IV in *C. tristis*, and the female of *C. beccaloniae*. The ventral intercarinal surfaces of segment IV are granular in the male and female (fig. 63C) of *C. madraspatensis* but smooth in the male and female of *C. wroughtoni*, the male of *C. bastawadei*, *C. fulvipes*, and *C. shivashankari*, and the female of *C. beccaloniae* and *C. nathanorum*. The dorsolateral carinae of metasomal segment V are strong and continuous in *C. madraspatensis* but weak and discontinuous to absent in *C. nathanorum*. The dorsal intercarinal surface of segment V is smooth in the male and female of *C. madras-*

patensis, granular in the male and female of *C. bastawadei*, *C. hendersoni*, and *C. pelekomanus*, and granular in the male of *C. wroughtoni*.

DISTRIBUTION: *Chersonesometrus madraspatensis* is widely distributed across eastern India (fig. 79) and has been recorded from the following states: Andhra Pradesh, Chhattisgarh, Karnataka, Odisha, Tamil Nadu, Telangana, and the union territory of Puducherry (table 1). Its distribution is parapatric with that of its sister species, *C. fulvipes*, and allopatric with the morphologically similar *C. bastawadei*, *C. shivashankari*, and *C. wroughtoni*.

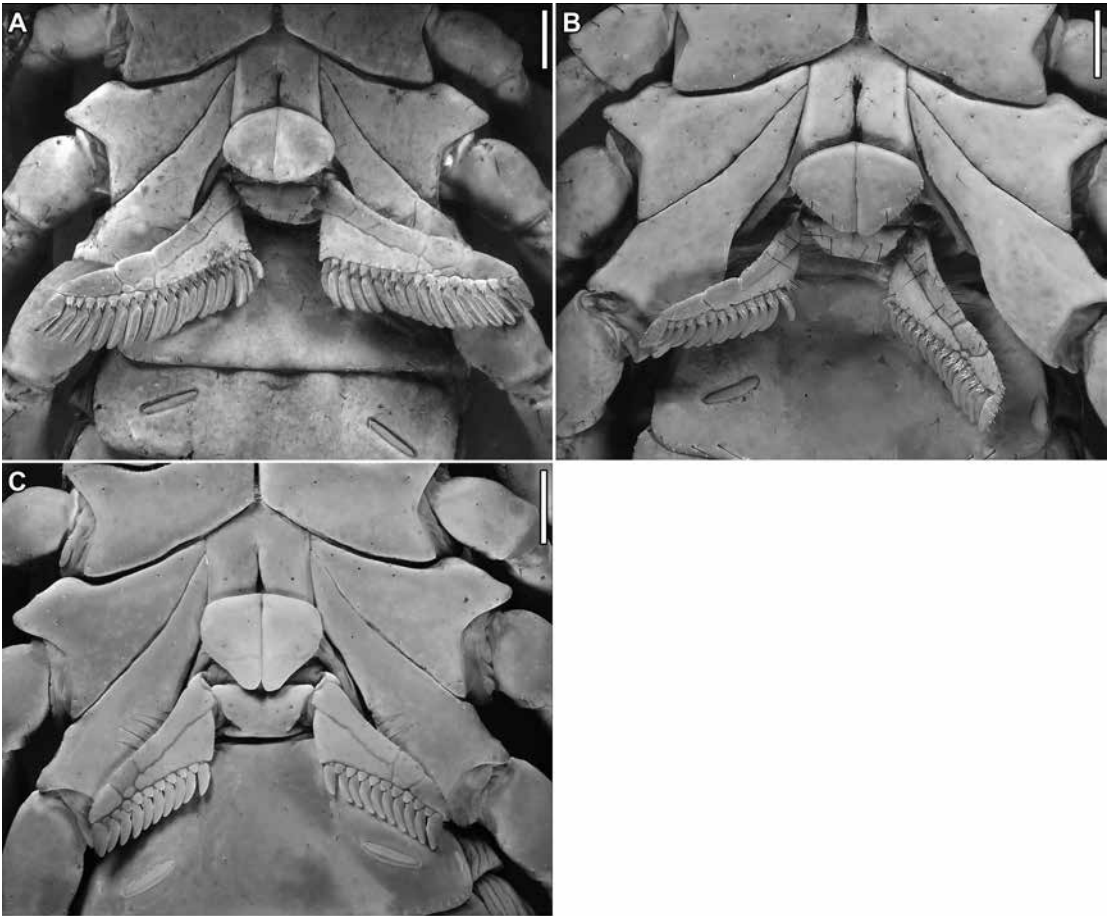


FIGURE 35. *Deccanometrus*, gen. nov., sternum and pectines, ventral aspect. **A, B.** *Deccanometrus ubicki* (Kovářík, 2004), comb. nov., **A.** paratype ♂ (CAS 9071136), **B.** paratype ♀ (CAS 9071135). **C.** *Deccanometrus liurus* (Pocock, 1897), comb. nov., paralectotype ♀ (BMNH 1896.12.15.20-25). Scale bars = 2 mm.

ECOLOGY: *Chersonesometrus madraspatensis* inhabits deciduous forest and broadleaf woodland, on sandy- to gravelly-loam soils, at elevations of 370 m. As with other species of the genus, *C. madraspatensis* is usually found in rocky habitats, often on wooded hill slopes, gulleys, or ravines where the humidity is slightly higher. The burrowing biology of this fossorial, pelophilous species was described by Shivashankar and Veeresh (1991) and Shivashankar (1992, 1994), misidentified as *H. fulvipes*. The burrows, constructed in open ground or under moderate to large stones (fig. 8E), have oval or crescent-shaped entrances and are almost vertical or

gradually sloping to a terminal chamber at a depth of 10–20 cm. Across its distribution, *C. madraspatensis* occurs in sympatry with the buthids *Hottentotta rugiscutis* and *Lychas tricarinatus* and the scorpionid *Gigantometrus swammerdami*.

CONSERVATION STATUS: *Chersonesometrus madraspatensis* is occasionally available in the exotic pet trade under the name *Heterometrus xanthopus*.

REMARKS: Pocock (1900a: 88, 89) based two subspecies of *Palamnaeus fulvipes*, i.e., *P. f. bombayensis* and *P. f. madraspatensis*, on a difference in the shape of the male pedipalps:

chela shorter with hand flatter above and wider, its width equal to the median length of the carapace and much greater than length of underhand, and the brachium [patella] much shorter than carapace in *P. f. bombayensis*, whereas chela long, flat, and narrower, its width only equal to length of underhand, and less than median length of carapace, and the brachium as long as carapace, in *P. f. madraspatensis*.

Couzijn (1981) synonymized both subspecies with the nominotypical form of *Heterometrus* (*Chersonesometrus*) *fulvipes* whereas Tikader and Bastawade (1983) elevated *P. f. madraspatensis* to the rank of species as *Heterometrus* (*Chersonesometrus*) *madraspatensis*, a decision upheld by Fet (2000) and Kovařík (2004). In discussing the question, Prendini et al. (2003: 218) remarked:

[Tikader and Bastawade (1983)] rejected Couzijn's (1981) synonymy of *Palamnaeus fulvipes madraspatensis* Pocock, 1900 with *H. fulvipes*, instead elevating the subspecies to the rank of species. Tikader and Bastawade's redescription of *H. madraspatensis* was based on two adult ♂, whereas their redescription of *H. fulvipes* was based on an adult ♀. During the course of the present investigation, the type specimens of *P. fulvipes madraspatensis* (previously examined by Tikader and Bastawade) were re-examined and compared with specimens of *H. fulvipes*, including some from the type locality of *P. fulvipes madraspatensis*. On the basis of this comparison there is no doubt that *P. fulvipes madraspatensis* is conspecific with *H. fulvipes*. This is a yet another example where the adults of a sexually dimorphic species of scorpion have been classified as different species, a conclusion also reached by Couzijn (1981: 135–136), who stated: "The subspecies *P. fulvipes madraspatensis* ... [does] not show other differences from *B. fulvipes* Koch than the ... ratio of length and width of the male's pedipalp hand.

Previous opinions that *H. fulvipes* and *H. madraspatensis* are conspecific (Couzijn, 1981; Prendini et al., 2003) were based on their very similar morphology. Indeed, Kovařík (2004: 15, 27) referred specimens (including adult males) from Podili (CAS) to both species. The counts of pro- and retroventral spiniform macrosetae on the leg telotarsi provided for *H. fulvipes* and *H. madraspatensis* by Tikader and Bastawade (1983) and Kovařík (2004) are identical. Tikader and Bastawade (1983) cite counts of 3/5 on legs I and II, 4/5 on III, and 4/6 on IV for *H. fulvipes* and counts of 3–4/5 on I and 4/6 on II–IV for

H. madraspatensis whereas Kovařík (2004) cites counts of 4/5–6 on III and IV for both taxa. The primary character justifying the distinction between *H. fulvipes* and *H. madraspatensis* is the shape (width) of the male chela manus first proposed by Pocock (1900a). As described in the key of Kovařík (2004: 52) for *H. fulvipes* "male and female chela differently shaped but of about the same width, its length to width ratio 1.7–1.9 in both sexes," and for *H. madraspatensis* "chela narrower in male than in female, its length to width ratio 2.0–2.5 in males and 1.7–1.9 in females." Following an examination of material from across the distribution of both taxa during the present investigation, this difference, albeit subtle, appears to consistently separate *H. fulvipes* in the northwest of India from *H. madraspatensis* in the southeast (fig. 79). Additional diagnostic characters identified during the present investigation, e.g., the greater length of the male pedipalp patella and femur, the more convex female pedipalp chela manus, and the more convex carapace of *H. madraspatensis*, taken together with genetic divergence supporting reciprocal monophyly of samples assigned to the two taxa based on morphology, justifies the continued recognition of *H. madraspatensis* as distinct from *H. fulvipes*, hence: *Chersonesometrus madraspatensis* (Pocock, 1900), comb. nov.

MATERIAL EXAMINED: **INDIA:** 4 ♂, 6 ♀, 2 subad. ♂, 1 subad. ♀ (AMNH); vi.1999, ex F. Somma, 1 ♀ (AMCC 101695 [LP 1533]). **Andhra Pradesh:** *Chittoor Distr.:* Kothakota, on Chittoor–Tirupati Road 61, 13°23'N 79°06'E, 372 m, 30.xii.2004, S. Basi, ravine between rocky ridges, broadleaf thicket, in shallow burrow (ca. 10 cm deep) under large stone, 1 subad. ♂ (AMCC [LP 13127]); Madireddy Palem [Madired-dypalem, 15°37'N 79°35'E], 1.i.1967, D.E. Johnson, ex Stahnke coll., 2 ♂, 3 ♀, 2 subad. ♂ (CAS [ASU 67-053, 54, 58–60, 62, 63]). *Prakasam Distr.:* Podili [15°36'N 79°37'E], 1.i.1967, Johnson and Guruiyah, ex Stahnke coll., 2 ♀, 1 juv. ♀ (CAS 9071141 [ASU 67-040, 56]), 13.ii.1967, D.E. Johnson, ex Stahnke coll., 2 ♂ (CAS 9071142 [ASU 67-352, 363]), 11 ♀ (CAS 9071142 [ASU 67-358, 366, 368], 9071143 [ASU 67-359–361, 364, 369–371, 373]), 1 subad. ♀ (CAS 9071143 [ASU 67-365]). **Karnataka:** *Bengaluru Distr.:* Mysore state,

env. Bangalore [Bengaluru, 12°59'N 77°35'E], 8.v.1974, Geethamali, 5 ♀ (MNHN RS 7798–7802), 1 juv. ♂ (MNHN RS 7803). **Odisha:** *Sambalpur Distr.:* Badrama [21°29'N 84°17'E], Orissa, 1100 ft., 20–26.ii.1975, M.L. Ripley, 1 juv. ♀ (USNM). **Tamil Nadu:** *Chennai Distr.:* Madras [Chennai, 13°05'N 80°17'E], viii.1999, T. Kolb, 1 ♀ (ZMH ex SMF); Madras, J.R. Henderson, 2 ♂, 3 ♀ (BMNH 1892.2.15.1–3); Madras and Callula, J.R. Henderson, 2 ♂, 1 subad. ♂, 10 juv. ♂ (BMNH 1894.10.24.5–8). *Kancheepuram Distr.:* Nemmeli [Nemmeli, 12°43'N 80°13'E], 45 km from Chennai, on eastern coastline, 30.v.2005, H.A. Vadivelu, A. and R. Ali, and F. Paul, 4 ♂, 4 ♀, 1 juv. ♂, 1 juv. ♀ (AMCC [LP 4324]). *Villupuram Distr.:* Genji [Gingi/Gingee, 12°15'N 79°24'E], Coromandel, 25.viii–12.ix.1901, M. Maindron, 4 ♂, 6 ♀, 2 subad. ♀, 1 juv. ♀ (MNHN RS 0113), M. Maindron, 2 ♂, 3 ♀ (MNHN RS 0085).

***Chersonesometrus nathanorum*, sp. nov.**

Figures 10, 16E, 30E, 61D, 62D, 63D, 80, 99, 100, tables 1, 3

TYPE MATERIAL: **INDIA:** **Tamil Nadu:** *Theni Distr.:* Holotype: 1 subad. ♂, paratype: 1 juv. ♀ (MNHN RS 3145), India, Monts Palni, 8 km NE Ganguvarpatti [Genguvarpatti] village [10°12'N 77°44'E], 20.ii.1943, Dr. K. Lindberg, se pente en montant [upper slope].

ETYMOLOGY: The specific epithet is a patronym honoring Prabala Susai Nathan (1891–1976), widely known as P. Susai Nathan, and his daughter-in-law, Theresa Rajabi Susai Nathan, widely known as T.R.S. Nathan or T.R.S.N., Indian entomologists and natural history dealers from Kurumbagaram, Puducherry, who provided many museums with important arthropod collections from India between 1945 and 1975 (Hincks, 1960; Brindle, 1965; Miles, 2015), including much of the heterometrine material in the Herbert L. Stahnke Collection, presently deposited at the CAS. Handwritten labels bearing the unpublished name “*Heterometrus nathani*” accompany the type material of *Decanometrus ubicki* (Kovářík, 2004), comb. nov. at the CAS.

DIAGNOSIS: *Chersonesometrus nathanorum* may be separated from other species of *Chersone-*

sometrus as follows. The carapace is markedly dorsoventrally compressed, the lateral surfaces sloping gently (fig. 16E) in *C. nathanorum*, but vaulted, the lateral surfaces sloping steeply, in *C. fulvipes*, *C. madraspatensis*, and *C. shivashankari*. The carapace interocular surface is granular along the median longitudinal and anterior bifurcated sulci only in the female of *C. nathanorum*, whereas the frontal lobes and medial region of the interocular surface are granular with smooth areas in the female of *C. bastawadei*, *C. madraspatensis*, *C. pelekomanus*, and *C. shivashankari*. The carapace posterolateral surfaces of the female are smooth in *C. nathanorum* but granular in *C. bastawadei*, *C. fulvipes*, and *C. madraspatensis*. The cheliceral movable finger prodistal (DI) and retrodistal (DE) teeth are subequal, with the DE tooth only slightly smaller than the DI tooth, and opposable, i.e., forming a bicuspid, in *C. nathanorum* but unequal, with the DE tooth considerably smaller than the DI tooth, aligned longitudinally and not opposable in *C. bastawadei*, *C. fulvipes*, *C. madraspatensis*, *C. shivashankari*, and *C. wroughtoni*. The pedipalp patella dorsal surface is convex, with the axis of the dorsomedian carina dorsal to the axis of the retrodorsal carina (fig. 99) in *C. nathanorum* but flat or nearly so, with the axes of the dorsomedian and retrodorsal carinae in the same plane, in *C. beccaloniae*, *C. hendersoni*, *C. pelekomanus*, and *C. tristis*. The patella retrodorsal carina of the female is absent or obsolete in *C. nathanorum* but as strongly developed as or more strongly developed than the retromedian carinae in all other species. The retromedian carinae are costate in *C. nathanorum* but granular in all other species. The patella dorsal, retrodorsal, and retroventral intercarinal surfaces of the female are smooth or nearly so in *C. nathanorum* but granular in all other species. The pedipalp chela is infusate and similar in color to the femur and patella in *C. nathanorum* but immaculate and paler than the femur and patella in *C. shivashankari*. The chela manus dorsal surface (between the dorso-medial and digital carinae) is flat in the male and curved, i.e., slightly to markedly convex, in

the female of *C. nathanorum*, flat in the male and female of *C. hendersoni*, *C. pelekomanus*, and *C. tristis*, and curved in the male and female of *C. madraspatensis* and *C. shivashankari*. The proximal margin (lobe) of the chela manus dorsal surface is moderately curved and aligned with the proximal margin of the retrolateral surface in the male (fig. 100), or aligned with or proximal to the proximal margin of the retrolateral surface in the female of *C. nathanorum*; moderately curved and proximal to the proximal margin of the retrolateral surface in the male, or aligned with the proximal margin of the condyle (articulation with patella) in the female of *C. bastawadei*, *C. fulvipes*, *C. madraspatensis*, *C. shivashankari*, *C. tristis*, and *C. wroughtoni*; and markedly curved and proximal to the proximal margin of the condyle in the male and female of *C. hendersoni* and *C. pelekomanus*. The maximum distance between the dorsomedian and dorsal secondary carinae (DMC–DSC) of the chela manus is similar to the maximum distance between the dorsal secondary and digital carinae (DSC–DC) in the male of *C. nathanorum*, but greater than the DSC–DC in the male of all other species except *C. beccaloniae*, *C. madraspatensis*, and *C. tristis*. The dorsal secondary and subdigital carinae of the male (fig. 100) are entirely to predominantly costate in *C. nathanorum*, absent or obsolete in *C. bastawadei* and *C. fulvipes*, and entirely to predominantly granular in all other species of *Chersonesometrus*. The digital carina is entirely to predominantly costate in *C. nathanorum*, entirely to predominantly granular in *C. beccaloniae*, *C. hendersoni*, *C. pelekomanus*, *C. tristis*, and *C. wroughtoni*, and absent or obsolete in *C. bastawadei*, *C. fulvipes*, *C. madraspatensis*, and *C. shivashankari*. The manus dorsal intercarinal surface is shallowly reticulate in *C. nathanorum* but without reticulation in all other species. The manus ventral surface is flat, with the axis of the retroventral and ventromedian carinae in approximately the same plane, in *C. nathanorum* but angled, with the axis of the retroventral carina ventral to the axis of the ventromedian carina, in *C. beccaloniae*, *C. hendersoni*, *C. pelekomanus*, and *C.*

tristis. The legs are very dark or heavily infusate in *C. nathanorum* but pale or very lightly infusate in *C. bastawadei*, *C. fulvipes*, *C. hendersoni*, *C. madraspatensis*, and *C. shivashankari*. Macroseta *st* on the retroventral surfaces of the basitarsi of legs I and II is setiform in *C. nathanorum* but spiniform in all other species except *C. shivashankari*. The mesial surfaces of mesosomal tergites I–VI are granular in the male and the lateral surfaces smooth in the female of *C. nathanorum*, whereas the mesial surfaces are smooth in the male of *C. tristis*, the mesial surfaces smooth in the male and the lateral surfaces granular in the female of *C. beccaloniae*, *C. hendersoni*, *C. pelekomanus*, and *C. wroughtoni*, and the lateral surfaces granular in the female of *C. bastawadei*, *C. fulvipes*, *C. madraspatensis*, and *C. shivashankari*. The ventral surface of mesosomal sternite VII bears a pair of weakly developed ventrolateral carinae in *C. nathanorum* and two pairs of moderately to strongly developed ventrosubmedian and ventrolateral carinae in *C. beccaloniae*, *C. hendersoni*, and *C. pelekomanus*. The dorsosubmedian carinae are granular or costate-granular on metasomal segments I–IV (fig. 61D) in *C. nathanorum* but costate on segments I and II or I–III and granular or costate-granular on III and IV or IV in *C. tristis* and the female of *C. beccaloniae*. The ventral intercarinal surfaces of segment IV are granular in the male (fig. 63D) and smooth in the female of *C. nathanorum* but smooth in the male and granular in the female of *C. bastawadei*, *C. fulvipes*, and *C. shivashankari*, smooth in the male of *C. wroughtoni*, and granular in the female of *C. hendersoni*, *C. madraspatensis*, *C. pelekomanus*, and *C. tristis*. The dorsolateral carinae of metasomal segment V are weak and discontinuous to absent in *C. nathanorum* but strong and continuous in all other species. The dorsal intercarinal surface of segment V is smooth in the male and female of *C. nathanorum*, granular in the male and female of *C. bastawadei*, *C. hendersoni*, and *C. pelekomanus*, and granular in the male of *C. wroughtoni*.

DESCRIPTION: The following description is based on the holotype and paratype. Meristic

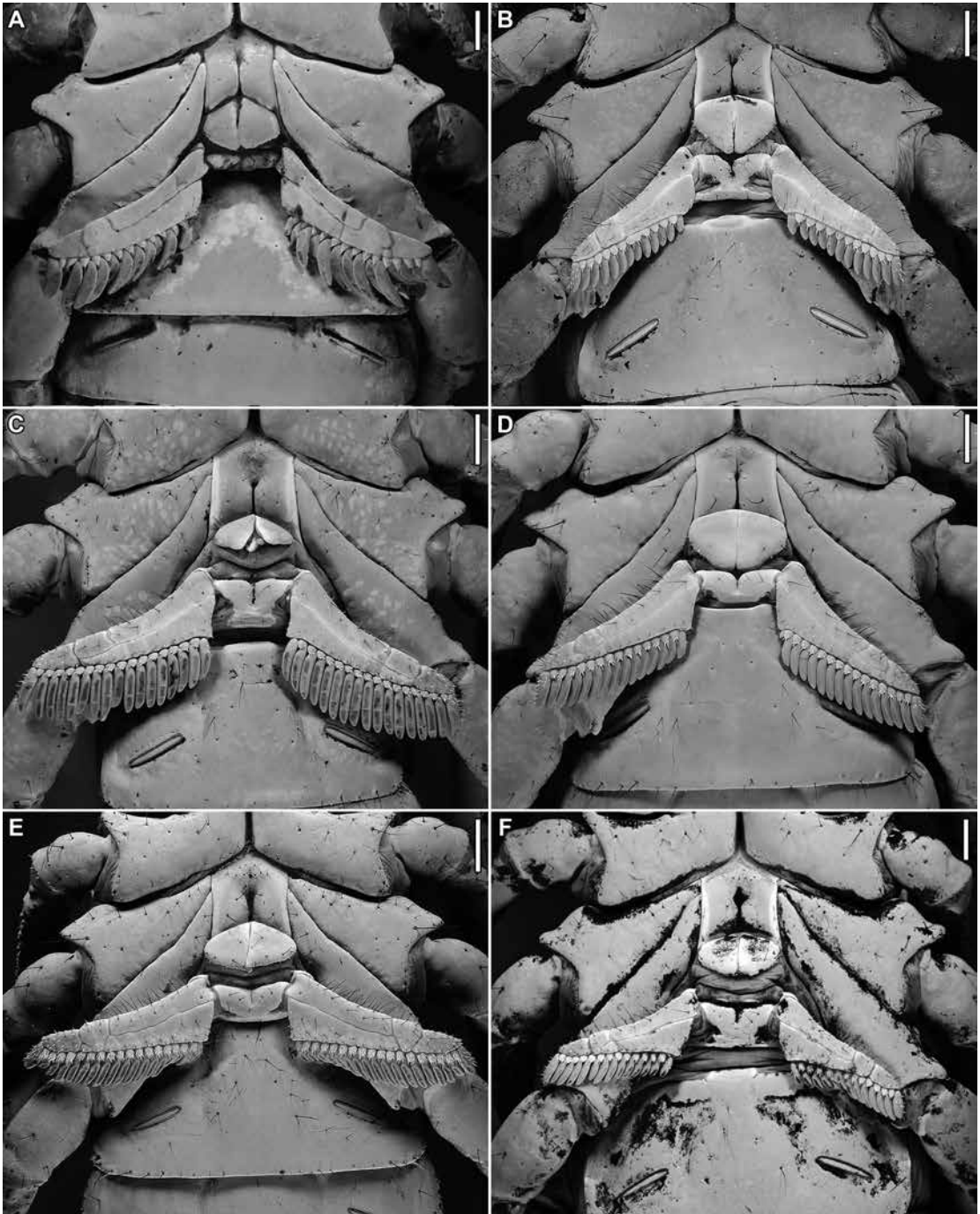


FIGURE 36. *Heterometrus* Ehrenberg, 1828, sternum and pectines, ventral aspect. **A, B.** *Heterometrus glaucus* (Thorell, 1876), comb. nov. et stat. rev., **A.** ♂ (ZMH), Padang, West Sumatra, Indonesia. **B.** ♀ (AMNH), Nias Island, Indonesia. **C, D.** *Heterometrus longimanus* (Herbst, 1800), **C.** ♂, **D.** ♀ (AMNH), Kuching, Malaysia. **E, F.** *Heterometrus thorellii* (Pocock, 1892), **E.** ♂ (AMNH), Mandalay, Myanmar, **F.** ♀ (AMNH), Pho Kyar Elephant Camp, Yedashe, Myanmar. Scale bars = 2 mm.

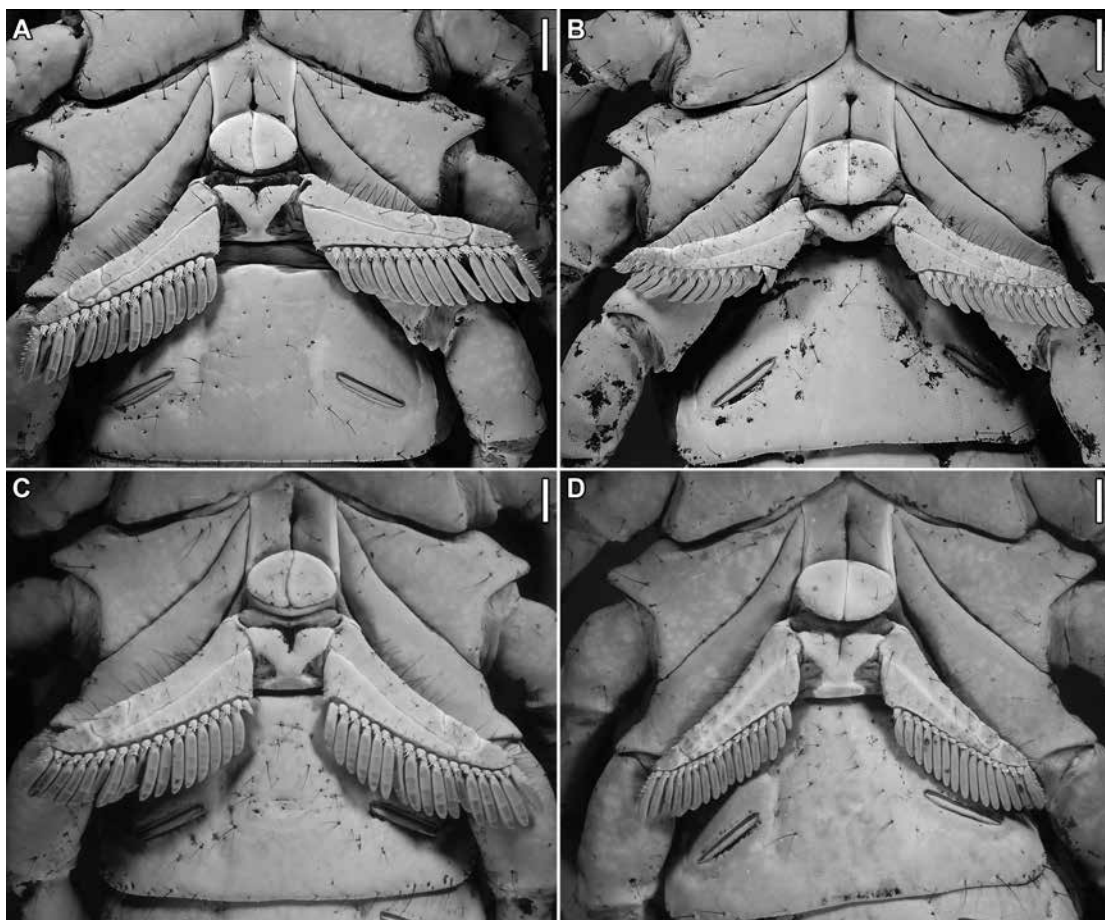


FIGURE 37. *Heterometrus* Ehrenberg, 1828, sternum and pectines, ventral aspect. **A, B.** *Heterometrus laevigatus* (Thorell, 1876), comb. nov. et stat. rev., **A.** ♂ (AMNH), Thale Ban, Thailand, **B.** ♀ (AMNH), Khao Pu-Khao Ya National Park, Thailand. **C, D.** *Heterometrus spinifer* (Ehrenberg, 1828), **C.** ♂, **D.** ♀ (AMNH), Cameron Highlands, Malaysia. Scale bars = 2 mm.

data are presented in table 3. Measurements are not presented as none of the type specimens are sexually mature.

Total length: Adults unknown.

Color: Chelicerae, dorsal surfaces bicolored, mostly to entirely immaculate prodorsal half of manus paler than infusate retrodorsal half of manus and fingers; manus markedly paler than carapace interocular surface. Carapace, pedipalps, tergites, and metasoma entirely infusate, uniformly dark brown. Sternites III–VI immaculate, VII immaculate to slightly infusate, dark brown, becoming darker posteriorly. Coxosternal region

infusate, brownish, maxillary lobes darker. Legs infusate, uniformly dark brown, similar to carapace, pedipalps, tergites, and metasoma. Genital opercula and pectines uniformly pale cream. Metasomal segments I–V similar to one another; carinae infusate, darker than intercarinal surfaces; dorsal intercarinal surfaces similar to tergites; ventral intercarinal surfaces darker than sternites. Telson vesicle immaculate, light yellowish, markedly paler than metasomal segment V; aculeus black.

Chelicerae: Movable finger prodistal (DI) and retrodistal (DE) teeth subequal, with DE tooth only slightly smaller than DI tooth, and oppos-

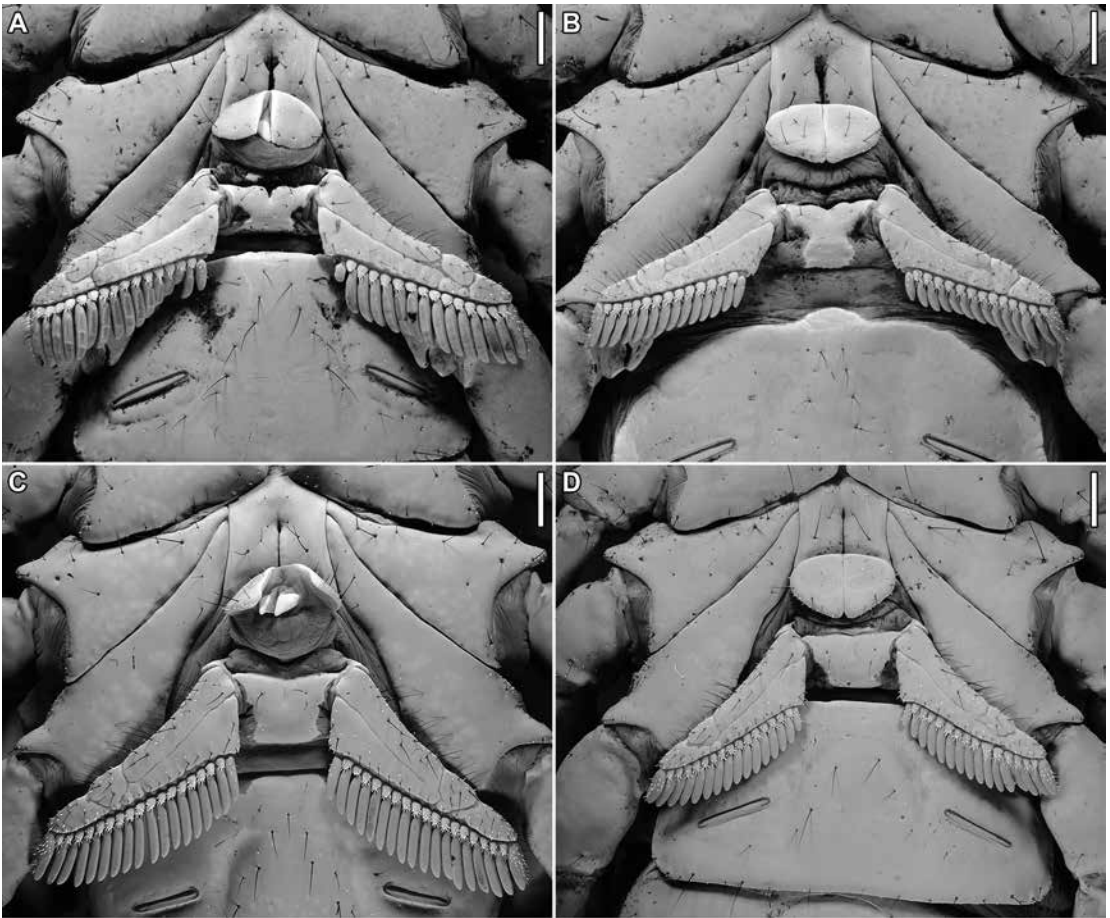


FIGURE 38. *Heterometrus* Ehrenberg, 1828, sternum and pectines, ventral aspect. **A, B.** *Heterometrus laoticus* Couzijn, 1981, **A.** ♂ (AMNH), Phahom Camp, Laos, **B.** ♀ (AMNH), Tham Pha In, Laos. **C, D.** *Heterometrus silenus* (Simon, 1884), comb. nov. et stat. rev. **C.** ♂, **D.** ♀ (AMNH), Ta Kou Mountain Nature Reserve, Vietnam. Scale bars = 2 mm.

able, i.e., forming a bicusp. Fingers and manus, proventral surfaces with long, dense vestiture of macrosetae. Coxae, prodorsal surfaces without stridulatory setae (scaphotrix); promedian surfaces without chemoreceptive lamelliform setae (trichocopae).

Carapace: Carapace markedly dorsoventrally compressed, lateral surfaces sloping gently. Anterior margin concave, frontal lobes uneven, sloping medially toward deep median notch, without median projection or median depression (fig. 16E). Anterolateral margins converging gradually anteriorly, without distinct notch

adjacent to posterior lateral ocelli; mediolateral margins diverging or converging slightly posteriorly (at posterolateral sulci). Three pairs of lateral ocelli (MLMa, PLMa, PDMi), all similar in size, two anterior pairs situated anteriorly, well separated from posterior pair, situated laterally. Median ocelli slightly larger than lateral ocelli, distance between ocelli greater than or equal to width of ocellus; median ocular tubercle situated posteromedially, distance from anterior carapace margin, 53% (♂), 55% (♀). Median longitudinal sulcus narrow, suturiform; continuous from median notch to interocular sulcus;

anteriorly furcated; without anterocular depression. Anterior furcated sulci diverging broadly from anterior edge of median longitudinal sulcus. Median ocular tubercle raised, superciliary carinae higher than ocelli, extended anteriorly, subparallel. Interocular sulcus present. Circumocular depressions completely encircling median ocular tubercle, converging anteriorly. Posteromedian and posteromarginal sulci deep. Paired mediolateral and posterolateral sulci shallow. Median longitudinal suture continuous from median notch to median ocular tubercle, equally strong along entire length; not extending to anterior margin of carapace, terminating at or posterior to median notch. Anterior furcated sutures absent or obsolete. Anterocular furcated sutures absent. Interocular suture present, slender. Posterior sutures present but indistinct, converging on median ocular tubercle; connected anteriorly to posterior furcations of interocular suture and extending anteriorly beyond median ocular tubercle. Frontal lobes and medial region of interocular surface finely granular with smooth areas (δ) (fig. 16E) or finely granular along median longitudinal and anterior furcated sulci only, elsewhere smooth (φ); anterolateral and mediolateral surfaces uniformly finely granular; posterolateral surfaces uniformly finely granular (δ) or smooth (φ); posteromedian surfaces smooth.

Pedipalps: Pedipalp short, pedipalp femur length : posterior carapace width ratio (FL:PCW) < 0.77 , femur length : carapace length ratio (FL:CL) < 0.74 . Femur retrodorsal carina complete, costate-granular, similar to or more strongly developed than prodorsal carina. Dorsal secondary carina comprising scattered granules, becoming obsolete distally. Dorsomedian carina vestigial, reduced to two prominent granules, one demarcated by conspicuous macroseta. Prodorsal carina complete, granular. Promedian carina complete, comprising row of spiniform or subspiniform granules (several demarcated by conspicuous macrosetae), oriented diagonally between prodorsal and proventral carinae. Proventral carina complete, granular, as strongly

developed as or more strongly developed than retroventral carina. Ventromedian and secondary accessory carinae absent. Retroventral carina extending partly or entirely to distal edge of segment. Retromedian carinae absent, indicated only by macrosetal rows. Dorsal intercarinal surfaces finely granular; other surfaces smooth. Patella dorsal surface convex, axis of dorsomedian carina dorsal to axis of retrodorsal carina. Dorsomedian carina entirely to predominantly costate (fig. 99). Retrodorsal carina obsolete, less strongly developed than costate retromedian carinae. Retroventral carina distinct, costate. Promedian carina and promedian process absent. Other carinae absent. Intercarinal surfaces smooth. Chela short, narrow (fig. 100); moderately (δ) to sparsely (φ) setose. Manus dorsal surface (between dorsomedian and digital carinae) flat (δ) or curved, i.e., slightly to markedly convex (φ); proximal margin (lobe) of dorsal surface moderately curved and aligned with proximal margin of retrolateral surface. Dorso-median carina obsolete, costate on fixed finger and comprising irregular row of spiniform granules along entire length of manus. Dorsal secondary, digital, and subdigital carinae incomplete, costate-granular to costate; dorsal secondary carina comprising double row of confluent granules in proximal half; proximal half of dorsal secondary carina, distal half of subdigital carina and distal third of digital carina closely adjacent. Maximum distance between dorsomedian and dorsal secondary carinae (DMC–DSC) similar to (δ) or greater than (φ) maximum distance between dorsal secondary and digital carinae (DSC–DC). Retromedian carina complete, entirely to predominantly costate, more strongly developed than digital carina. Retrolateral secondary and secondary accessory carinae vestigial, proximal to condyle of movable finger. Retroventral and ventromedian carina distinct, costate, but retroventral carina more strongly developed. Proventral and promedian carinae similarly developed, each comprising row of spiniform granules and associated macrosetae. Prodorsal carina comprising irregular row of

prominent spiniform granules and associated macrosetae. Distance between dorsomedian and promedian carinae (DMC–PMC) slightly to markedly greater than distance between promedian and proventral carinae (PMC–PVC). Manus, dorsal intercarinal surfaces densely and finely granulo-reticulate except for smooth depression at base of fixed finger; retrolateral intercarinal surfaces densely and finely granular; ventral intercarinal surface smooth; prolateral intercarinal surfaces smooth, except for few scattered spiniform granules dorsally and distally. Manus ventral surface flat, axes of retroventral and ventromedian carinae in approximately same plane. Fixed and movable fingers, intercarinal surfaces smooth; median denticle rows each with six enlarged retrolateral denticles (including terminal denticle), proximal three situated on lobes; first (proximal) lobe of fixed finger and second lobe of movable finger larger than others, with correspondingly deeper notches in movable and fixed fingers, respectively; terminal denticles of fingers interlocking unevenly when closed, movable finger displaced retrolaterally; distinct notch near tip of fixed finger to accommodate terminal denticle of movable finger.

Trichobothria: Orthobothriotaxic, Type C, with the following segment totals ($n = 4$): femur, 3 (1 d , 1 i , 1 e); patella, 19 (2 d , 1 i , 3 v , 13 e , comprising 3 et , 1 est , 2 em , 2 esb , 5 eb); chela, 26 (manus, 16, comprising 2 D , 10 E , 4 V ; fixed finger, 10, comprising 4 d , 4 e , 2 i). Total count of trichobothria per pedipalp: 48. Femur, i situated on dorsal surface. Patella, d_2 situated on internal surface, slightly closer to d_1 than to i ; distance v_2 – v_3 ca. half distance v_1 – v_2 . Chela, distance et – est ca. half distance est – esb ; distance est – esb greater than half distance esb – eb ; est aligned with dst ; V_3 situated in proximal third of manus, closer to V_4 than V_2 .

Legs: First pair of maxillary lobes (coxapophyses) tapering anteriorly, longer than and encircling second pair. Stridulatory organs, comprising “rasp” (granular tubercles) and “scraper” (stridulatory setae or scaphotrix), present on opposing surfaces of coxae of first pair of legs and pedi-

palps, respectively. Legs I–IV acarinate, except femora, with distinct pro- and retrolateral surfaces demarcated by complete, costate-granular proventral carinae. Femora, patellae, and tibiae, pro- and retrolateral surfaces each with scattered setiform macrosetae. Tibiae, prolateral surfaces, without spiniform macrosetae; I and II, retrolateral surfaces, each with two spiniform (t , st) macrosetae; III and IV, retrolateral surfaces, without spiniform macrosetae. Basitarsi I–IV, slightly dorsoventrally compressed; retrolateral margins similar, unmodified, rounded; prolateral pedal spurs present; retrolateral pedal spurs absent. Basitarsi, pro- and retrolateral surfaces, each with scattered long and short setiform macrosetae, and spiniform macrosetae, more numerous on I and II than on III and IV. Basitarsi, spiniform macrosetae, I, retrolateral: t , sb ; retroventral: t , st , sb ; proventral: t , st ; II, retrolateral: t , sb ; retroventral: t , st , sb ; proventral: t , st ; III, retrolateral: t , sb ; retroventral: t , st , sb ; proventral: t ; prolateral: t , st ; IV, retrolateral: t ; retroventral: t ; proventral: t , st ; prolateral: t , st . Telotarsi I–IV short, stout and distally broadened in dorsal and lateral views. Laterodistal lobes rounded. Dorsomedian lobes approximately equal to laterodistal lobes; each terminating in single setiform macroseta. Telotarsi, pro- and retrolateral surfaces, each with long and short, scattered macrosetae, not arranged in definite row. Telotarsi each with pro- and retroventral rows of spiniform macrosetae, two inserted on laterodistal lobes; counts in pro- and retroventral rows similar on I and II, and on III and IV ($n = 4$): I, proventral: 4, retroventral: 5 or 6; II, 4, 6 or 7; III, 4, 6 (6 or 7); IV, 4, 6. Telotarsal ungues short, curved, equal to subequal; pseudonychium (dactyl) reduced, rounded.

Sternum: Shape subpentagonal (fig. 30E). Median longitudinal sulcus shallow anteriorly, deep and narrow posteriorly.

Genital operculum: Genital opercula suboval, completely divided longitudinally, partially overlapping, genital papillae present (σ) (fig. 30E); subcordate, fused, genital papillae absent (φ).

Hemispermatorphore: Unknown.

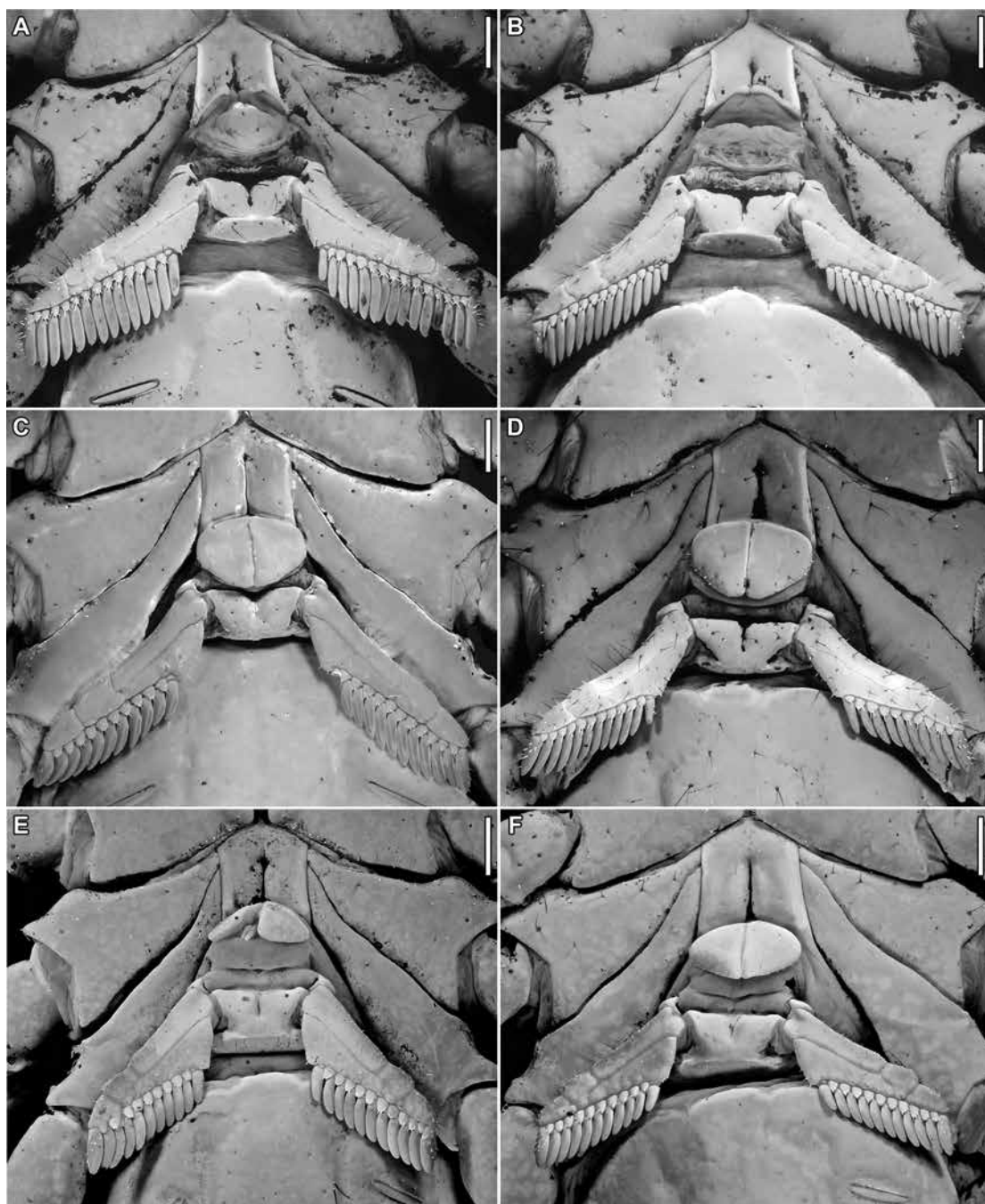


FIGURE 39. *Javanimetrus* Couzijn, 1981, stat. nov. et stat. rev. (A, B), and *Sahyadrimetrus*, gen. nov. (C–F), sternum and pectines, ventral aspect. A, B. *Javanimetrus cyaneus* (Simon, 1872), comb. nov., A. ♂, B. ♀ (AMNH), Ujung Kulon, Indonesia. C. *Sahyadrimetrus barberi* (Pocock, 1900), comb. nov., holotype ♀ (BMNH 1899.9.24.1). D. *Sahyadrimetrus rugosus* (Couzijn, 1981), comb. et stat. nov., ♀ (AMNH), Chaliyar River, India. E, F. *Sahyadrimetrus tikaderi*, gen. et sp. nov., E. holotype ♂, F. paratype ♀ (MNHN RS 3265). Scale bars = 2 mm.

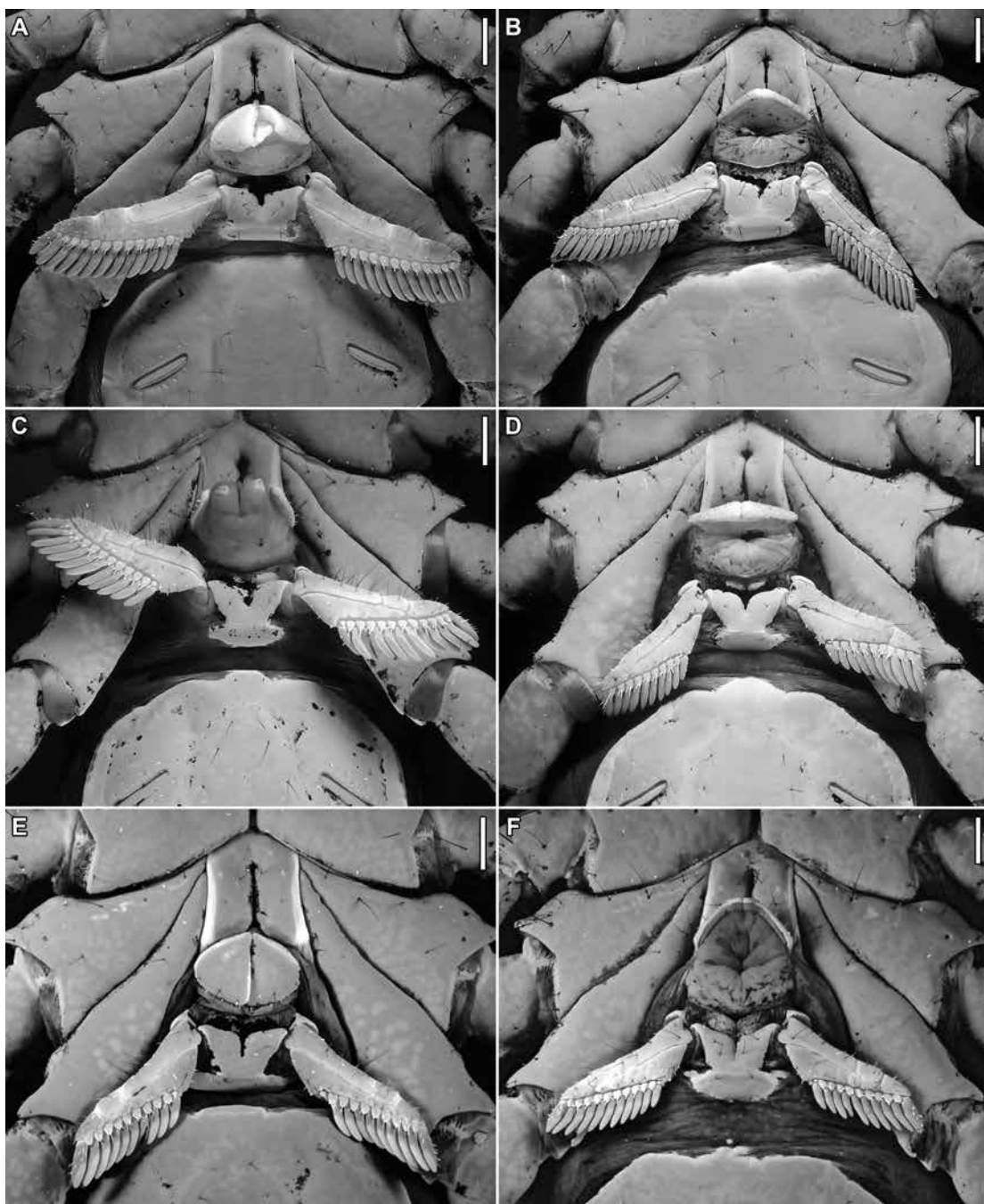


FIGURE 40. *Sahyadrimetrus*, gen. nov., sternum and pectines, ventral aspect. **A, B.** *Sahyadrimetrus kanarensis* (Pocock, 1900), comb. nov., **A.** ♂, **B.** ♀ (AMNH), Chaudi, India. **C, D.** *Sahyadrimetrus mathewi*, gen. et sp. nov., **C.** holotype ♂, **D.** paratype ♀ (AMNH), Poomala, India. **E, F.** *Sahyadrimetrus scaber* (Thorell, 1876), comb. nov., **E.** ♂ (AMNH), Nadpalu, India, **F.** ♀ (AMNH), Sitha River, India. Scale bars = 2 mm.

Pectines: Distal edge extending past distal edge of coxa IV but not reaching distal edge of trochanter IV (♂) (fig. 30E) or reaching to distal edge of coxa IV (♀). First proximal median lamella (scape) of each pecten with mesial margin angular, approximately 90° (♂) or obtusely angular, greater than 90° but less than 180° (♀). Pectinal teeth straight and elongate (♂) or shorter and curved (♀), present along entire posterior margin; sinistral/dextral tooth count, 16/16 (♂), 15/15 (♀). Fulcra smooth proximally but densely setose (microsetae only) distally.

Mesosoma: Tergites each with shallow pair of submedian depressions, without obsolete median carina. Pretergites smooth and glabrous. Posttergites finely granular medially and unevenly finely and coarsely granular laterally (♂) or entirely smooth and glabrous (♀). Sternites IV–VI, each with paired longitudinal depressions prolateral to spiracles, absent on VII. Surface, sternites III–VII, smooth; VII with pair of weakly developed, costate ventrolateral carinae only, without postermarginal carina.

Metasoma and telson: Metasoma fairly robust. Telson vesicle globose; dorsal surface flat; ventral surface evenly curved. Aculeus relatively long, gently curved. Dorsosubmedian carinae, segments I–IV, distinct, complete, granular or costate-granular; posterior spiniform granules obsolete (fig. 61D); V, absent. Dorsolateral carinae, segments I–IV, distinct, complete, costate-granular; V, obsolete, incomplete, reduced to few spiniform granules. Median lateral carinae, segment I, incomplete, reduced to granular row in posterior half, diagonally oriented between dorsolateral and ventrolateral carinae (fig. 62D); II–IV, obsolete row of granules posteriorly; V, incomplete, granular row, restricted to anterior two-thirds. Ventrolateral and ventrosubmedian carinae, I–IV, distinct, complete, costate on I–III, granular or costate-granular on IV, more strongly developed on III and IV than on I and II (fig. 63D). Ventrolateral carinae, segment V, distinct, complete, comprising spiniform granules, diverging posteriorly, terminal granule slightly larger than preceding granules. Ventrosubmedian carinae, segment V, vestigial, each reduced to one

or two isolated spiniform granules, demarcated by conspicuous macrosetae. Ventromedian carina, segment V comprising single row of spiniform granules, unmodified posteriorly. Anal arch, segment V, dorsal carina, costate; ventral carina comprising subspiniform granules. Dorsal intercarinal surfaces, segments I–V, smooth. Lateral intercarinal surfaces, segments I–IV, granular, V, smooth. Ventral intercarinal surfaces, segments I–III, smooth, IV and V, granular (♂) or smooth (♀). Ventral surface, lateral aspect, segment IV, shallowly convex. Telson vesicle, dorsal and lateral surfaces smooth; ventral surface with four longitudinal carinae, each comprising spiniform granules.

DISTRIBUTION: This species is endemic to India and known only from the type locality in the state of Tamil Nadu (fig. 80, table 1).

ECOLOGY: Although no data are available on the ecology of this species, the habitus is consistent with the fossorial, pelophilous and semi-lithophilous ecomorphotypes (Prendini, 2001b). The dorsoventral compression of this species suggests that it excavates burrows under stones.

Chersonesometrus pelekomanus (Couzijn, 1981),
comb. nov. et stat. rev.

Figures 8C, 10, 15C, D, 29C, D, 43E–H, 58D,
59D, 60D, 80, 101–105, table 1

Heterometrus indus: Roewer, 1943: 226
(misidentification, part).

Heterometrus phipsoni Roewer, 1943: 228
(misidentification).

Heterometrus (Chersonesometrus) pelekomanus
Couzijn, 1981: 19, 41, 75, 86, 137–139, 169,
170, 192, table 7, figs. 2f, 41, 58 (part);
Tikader and Bastawade, 1983: 577, 641–646
(part), figs. 1696–1709; Kovařík, 1998: 136;
Fet, 2000: 440 (part); Bastawade, 2002: 296;
Kovařík, 2002: 17; 2004: 49; Indra, 2009: 142.

Heterometrus (Chersonesometrus) palekomanus:
Indra, 2001: 58 (part).

Heterometrus pelekomanus: Kovařík, 2004: 49;
2009: 28, pl. J.

Heterometrus wroughtoni: Kovařík, 2004: 1, 3, 7, 46, 49, 51, 52, tables 2, 3 (misidentification, part), figs. 1–7 (misidentification); 2009: 28, 35, 36, 45, 48, tables 1, 2 (misidentification, part), pl. J (misidentification); Javed et al., 2010b: 785, table 1 (misidentification).
Heterometrus swammerdami: Nagaraj et al., 2015: 1–5, table 1, fig. 1d (misidentification).

TYPE MATERIAL: INDIA: *Heterometrus* (*Chersonesometrus*) *pelekomanus*: Holotype ♂ (SMF RII/1088/19), Nilgiris, Deccan [examined]. Paratype ♀ (SMF RII/329), Bombay [Bombay Presidency], Deccan [examined].

Couzijn (1981: 137) specifically indicated a holotype and paratype in the original description:

Material – Maharashtra: Nilgiris, Deccan (2 ♂ ad. including holotype, leg. unknown, SMF II/1088/19), Bombay, Deccan (1 ♂ ad., 2 ♀ ad. including allotype, 10 ♂ juv., 8 ♀ juv., SMF II/329/3); Karnataka: Mysore, environs of Bangalore (1 ♀ juv., RS 7804); Andhra Pradesh: Tirumalai Hills, Tirupati (1 ♂ juv., 1 ♀ juv., RS 4499).

Fet (2000) erroneously listed all material in Couzijn's (1981) description as paratypes.

DIAGNOSIS: *Chersonesometrus pelekomanus* may be separated from other species of *Chersonesometrus* as follows. The carapace is markedly dorsoventrally compressed, the lateral surfaces sloping gently (fig. 15C, D) in *C. pelekomanus*, but vaulted, the lateral surfaces sloping steeply, in *C. fulvipes*, *C. madraspatensis*, and *C. shivashankari*. The frontal lobes and medial region of the carapace interocular surface are granular with smooth areas in the female (fig. 15D) of *C. pelekomanus* whereas the interocular surface is granular along the median longitudinal and anterior bifurcated sulci only in the female of all other species except *C. bastawadei*, *C. madraspatensis*, and *C. shivashankari*. The carapace posterolateral surfaces of the female are smooth in *C. pelekomanus* but granular in *C. bastawadei*, *C. fulvipes*, and *C. madraspatensis*. The cheliceral movable finger prodistal (DI) and retrodistal (DE) teeth are subequal, with the DE

tooth only slightly smaller than the DI tooth, and opposable, i.e., forming a bicusps, in *C. pelekomanus* but unequal, with the DE tooth considerably smaller than the DI tooth, aligned longitudinally and not opposable in *C. bastawadei*, *C. fulvipes*, *C. madraspatensis*, *C. shivashankari*, and *C. wroughtoni*. The pedipalps of the adult male are short, with femur length : posterior carapace width ratio (FL:PCW) < 0.77 and femur length : carapace length ratio (FL:CL) < 0.74 (fig. 101) in *C. pelekomanus* but long, with FL:PCW ≥ 0.80, FL:CL ≥ 0.76 in *C. beccaloninae*, *C. madraspatensis*, and *C. tristis*. The pedipalp patella dorsal surface is flat or nearly so, with the axes of the dorsomedian and retrodorsal carinae in the same plane (fig. 103), in *C. pelekomanus* but convex, with the axis of the dorsomedian carina dorsal to the axis of the retrodorsal carina in all other species except *C. beccaloninae*, *C. hendersoni*, and *C. tristis*. The patella retrodorsal carina of the female is as strongly developed as or more strongly developed than the retromedian carinae in *C. pelekomanus* but absent or obsolete in *C. nathanorum*. The retromedian carinae are granular in *C. pelekomanus* but costate in *C. nathanorum*. The patella dorsal, retrodorsal, and retroventral intercarinal surfaces of the female (fig. 103) are granular in *C. pelekomanus* but smooth or nearly so in *C. nathanorum*. The pedipalp chela is infusate and similar in color to the femur and patella in *C. pelekomanus* but immaculate and paler than the femur and patella in *C. shivashankari*. The chela of the adult male is moderately to densely setose in *C. pelekomanus* but sparsely setose in *C. fulvipes*, *C. madraspatensis*, and *C. shivashankari*. The chela manus dorsal surface (between the dorsomedian and digital carinae) is flat in the male and female of *C. pelekomanus*, flat in the male and curved, i.e., slightly to markedly convex, in the female of *C. bastawadei*, *C. beccaloninae*, *C. fulvipes*, *C. nathanorum*, and *C. wroughtoni*, and curved in the male and female of *C. madraspatensis* and *C. shivashankari*. The proximal margin (lobe) of the chela manus dorsal surface is markedly curved and proximal to the proximal margin of the con-

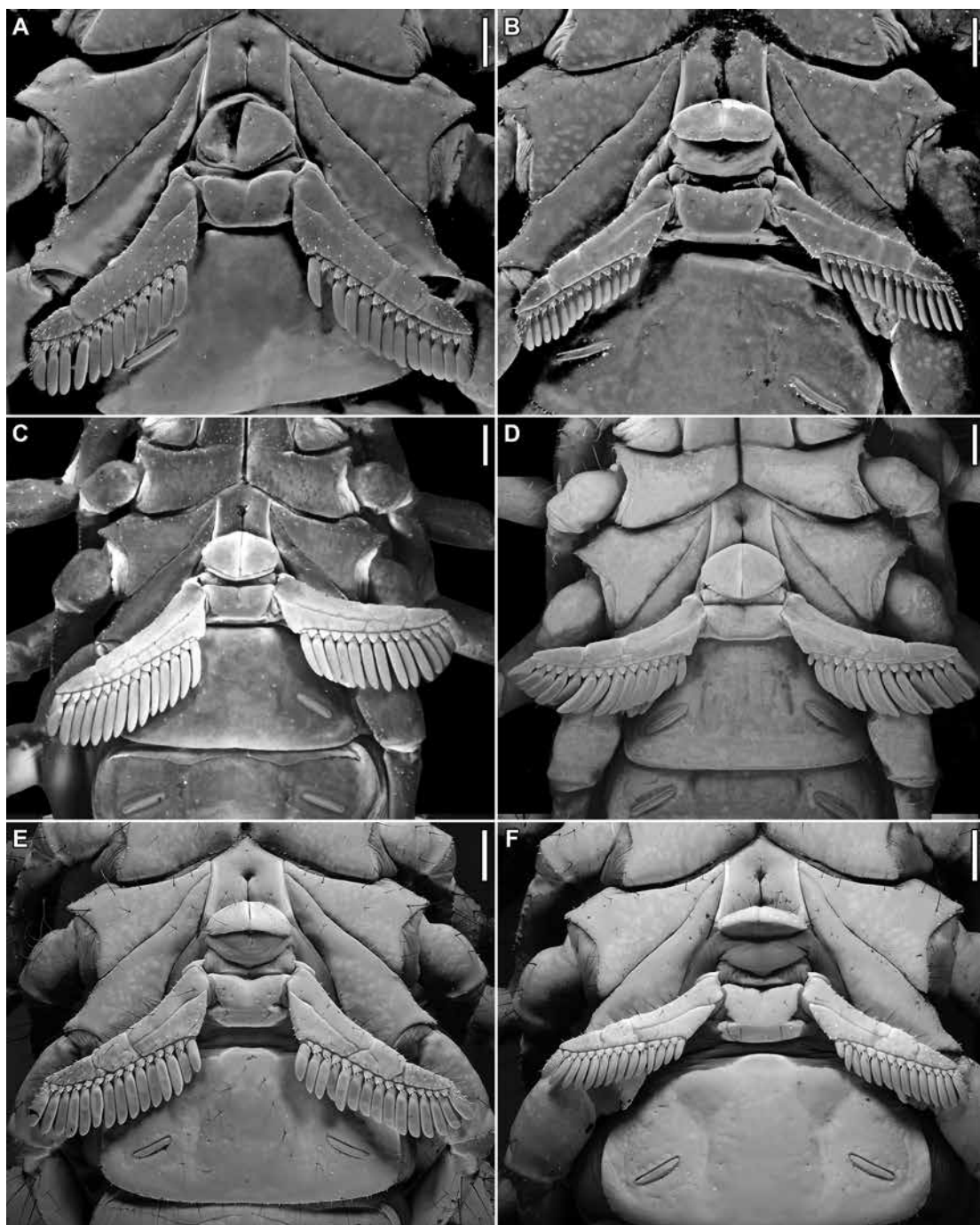


FIGURE 41. *Srilankametrus* Couzijn, 1981, stat. nov. et stat. rev., sternum and pectines, ventral aspect. **A, B.** *Srilankametrus caesar* (C.L. Koch, 1841), comb. nov. et stat. rev., **A.** ♂, **B.** ♀ (MNHN RS 0079). **C, D.** *Srilankametrus couzijni*, sp. nov., **C.** holotype ♂ (BMNH 1896.7.30.121), **D.** paratype ♂ (SMF 5332/1). **E, F.** *Srilankametrus gravimanus* (Pocock, 1894), comb. nov., **E.** ♂, **F.** ♀ (AMNH), Kokmotte, Sri Lanka. Scale bars = 2 mm.

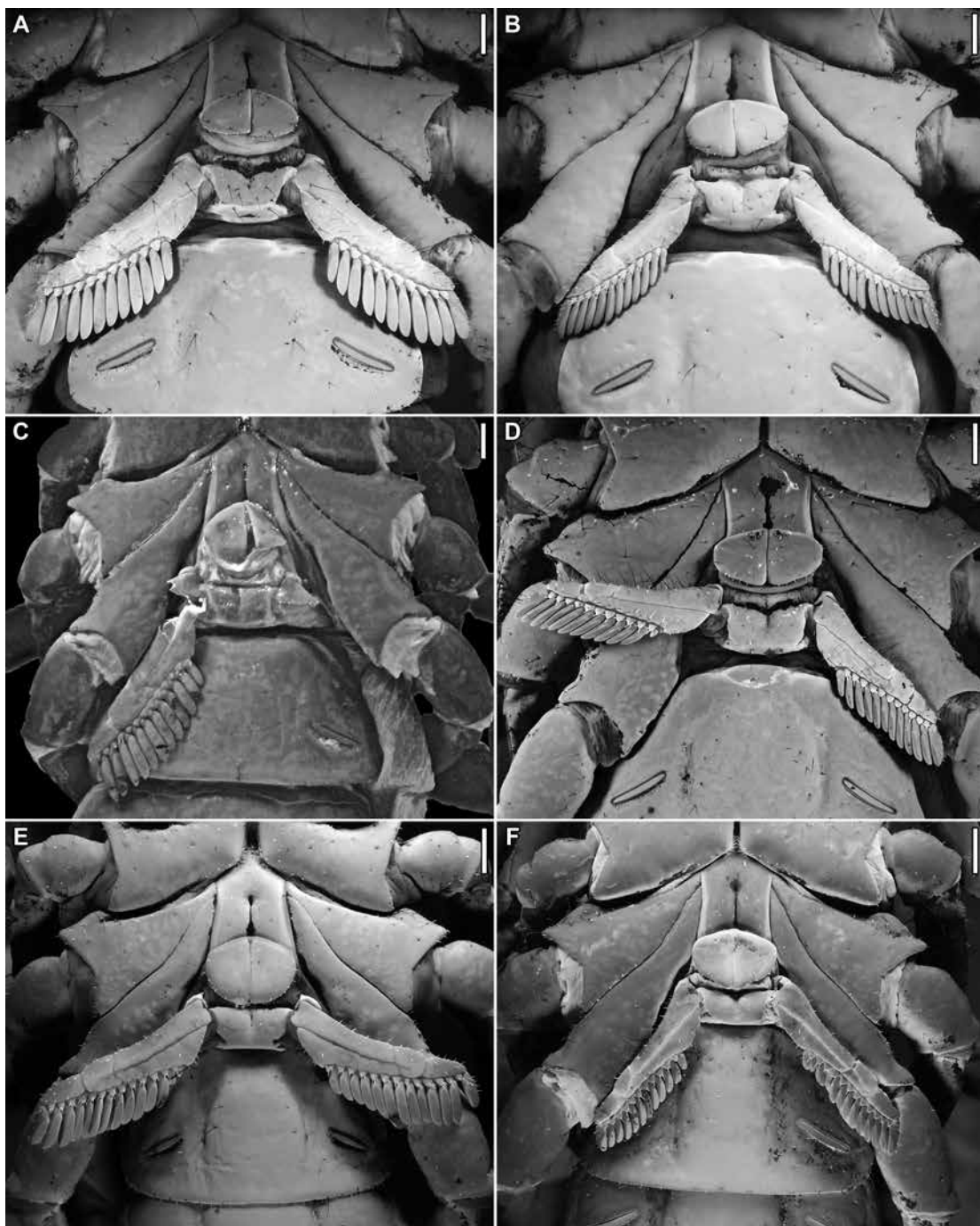


FIGURE 42. *Srilankametrus* Couzijn, 1981, stat. nov. et stat. rev., sternum and pectines, ventral aspect. **A, B.** *Srilankametrus indus* (DeGeer, 1778), comb. nov., **A.** ♂, **B.** ♀ (AMNH), Kandy, Sri Lanka. **C, E, F.** *Srilankametrus serratus* (Pocock, 1900), comb. nov., **C.** holotype ♂ (BMNH 1888.55), **E.** ♂ (FMNH 086 916), **F.** ♀ (ZMH), Ceylon [Sri Lanka]. **D.** *Srilankametrus pococki*, sp. nov., holotype ♀ (AMNH), Kodigala, Sri Lanka. Scale bars = 2 mm.

dyle (articulation with patella) in the male and female (figs. 104, 105) of *C. pelekomanus* but moderately curved and aligned with or proximal to the proximal margin of the retrolateral surface, or aligned with the proximal margin of the condyle in all other species except *C. hendersoni*. The maximum distance between the dorsomedian and dorsal secondary carinae (DMC–DSC) of the chela manus is greater than the maximum distance between the dorsal secondary and digital carinae (DSC–DC) in the male of *C. pelekomanus*, but greater than the DSC–DC in the male of *C. beccaloniae*, *C. madraspatensis*, *C. nathanorum*, and *C. tristis*. The dorsal secondary and subdigital carinae of the male are entirely to predominantly granular (fig. 104) in *C. pelekomanus*, entirely to predominantly costate in *C. nathanorum*, and absent or obsolete in *C. bastawadei* and *C. fulvipes*. The digital carina is entirely to predominantly granular in *C. pelekomanus*, entirely to predominantly costate in *C. nathanorum*, and absent or obsolete in *C. bastawadei*, *C. fulvipes*, *C. madraspatensis*, and *C. shivashankari*. The manus dorsal intercarinal surface is without reticulation in *C. pelekomanus* but shallowly reticulate in *C. nathanorum*. The manus ventral surface is angled, with the axis of the retroventral carina ventral to the axis of the ventromedian carina in *C. pelekomanus* but flat, with the axes of the retroventral and ventromedian carinae in approximately the same plane in all other species except *C. beccaloniae*, *C. hendersoni*, and *C. tristis*. The legs are very dark or heavily infusate (figs. 101, 102) in *C. pelekomanus* but pale or very lightly infusate in *C. bastawadei*, *C. fulvipes*, *C. hendersoni*, *C. madraspatensis*, and *C. shivashankari*. Macroseta *st* on the retroventral surfaces of the basitarsi of legs I and II is spiniform (fig. 43E–H) in *C. pelekomanus* but setiform in *C. nathanorum* and *C. shivashankari*. The mesial surfaces of mesosomal tergites I–VI are smooth in the male and the lateral surfaces granular in the female of *C. pelekomanus*, whereas the mesial surfaces are granular in the male of *C. bastawadei*, *C. fulvipes*, *C. madraspatensis*, and *C. shivashankari*, the

mesial surfaces granular in the male and the lateral surfaces smooth in the female of *C. nathanorum*, and the lateral surfaces smooth in the female of *C. tristis*. The ventral surface of mesosomal sternite VII bears two pairs of moderately to strongly developed ventrosubmedian and ventrolateral carinae in *C. pelekomanus* and a pair of weakly developed ventrolateral carinae in all other species except *C. beccaloniae* and *C. hendersoni*. The dorsosubmedian carinae are granular or costate-granular on metasomal segments I–IV (fig. 58D) in *C. pelekomanus* but costate on segments I and II or I–III and granular or costate-granular on III and IV or IV in *C. tristis* and the female of *C. beccaloniae*. The ventral intercarinal surfaces of segment IV are granular in the male and female (fig. 60D) of *C. pelekomanus* but smooth in the male and female of *C. wroughtoni*, the male of *C. bastawadei*, *C. fulvipes*, and *C. shivashankari*, and the female of *C. beccaloniae* and *C. nathanorum*. The dorsolateral carinae of metasomal segment V are strong and continuous in *C. pelekomanus* but weak and discontinuous to absent in *C. nathanorum*. The dorsal intercarinal surface of segment V is granular in the male and female of *C. pelekomanus*, smooth in the female of *C. wroughtoni*, and smooth in the male and female of all other species except *C. bastawadei* and *C. hendersoni*.

DISTRIBUTION: This species is endemic to India, but the full extent of its distribution is unclear. The type localities are imprecisely indicated “Nilgiris, Deccan” and “Bombay, Deccan” (presumably, the former Bombay Presidency, as this species does not occur in the vicinity of present-day Mumbai). The Nilgiri Hills occur in the state of Tamil Nadu, not Maharashtra, as implied by Couzijn (1981), and the records from Mysore, environs of Bangalore (MNHN RS 7804) in Karnataka, and the Tirumalai Hills, Tirupati (MNHN RS 4499) in Andhra Pradesh, cited by Couzijn (1981) are referable to *C. tristis*. Material that most closely matches the types originates from the Ballari and Chitradurga districts of Karnataka (fig. 80, table 1).

ECOLOGY: The known locality records of this species occur in semiarid, mixed savanna dominated by *Acacia*, *Euphorbia*, and broadleaf bushes (*Grewia*, *Ziziphus*), with bamboo thickets and moderate to thick grass on rocky granite hills, at elevations of 675–1000 m. The specimens for which data are available were collected from shallow scrapes in hard sandy-clay or sandy-loam soil under large granite boulders (fig. 8C). The habitat and habitus, especially the dorsoventrally compressed carapace and pedipalp chelae, are consistent with the pelophilous, fossorial and semilithophilous ecomorphotypes (Prendini, 2001b).

REMARKS: This species was previously accommodated in subgenus *Chersonesometrus* of *Heterometrus* by various authors (e.g., Couzijn, 1981; Tikader and Bastawade, 1983; Fet, 2000).

Heterometrus pelekomanus, described by Couzijn (1981) and upheld by Tikader and Bastawade (1983), was mistakenly synonymized with *H. wroughtoni* by Kovařík (2004), based on the alleged absence of sexual dimorphism in the shape of the pedipalp chela manus, which was cited as a putative diagnostic difference between *H. wroughtoni* and *H. mysorensis* (the latter regarded as junior synonym of *C. tristis* in the present contribution). However, as noted below, the absence of adult males in the type series of *C. wroughtoni*, the adult male of which is unknown, suggests that Kovařík (2004) mistook ontogenetic character states for diagnostic character states. Comparison of types of *C. pelekomanus* and *C. wroughtoni* revealed that the two species are not closely related.

MATERIAL EXAMINED: **INDIA:** Bombay [Bombay Presidency], Deccan, 1 subad. ♀, 10 juv. ♂, 8 juv. ♀ (SMF RII/329). Nilgiris, Deccan, 1 ♂ (SMF RII/1088/19). **Karnataka:** *Ballari* *Distr.*: Jarmali, NW of Jarmali Durgamma Temple, 14°50'N 76°28'E, 675 m, 22.xi.2009, R. Datta, degraded broadleaf savanna with euphorbias on low, rocky hills with many granite outcrops and embedded stones, in scrapes under stones in coarse, granitic sandy loam, 1 juv. ♂ (AMCC [LP 16774]), 1 juv. ♂ (AMNH). *Chitradurga* *Distr.*: Chitradurga, Jogi Matti Road, 14°11'N 76°24'E, 1000 m, 21.xi.2009, R. Datta, mixed savanna with broadleaf trees, bamboo thickets

and *Acacia* on rocky hills, moderate to thick grass layer on hard sandy clay with many granite outcrops and embedded stones, in shallow scrapes under large boulders, 1 ♂, 2 ♀, 1 subad. ♀, 19 juv. ♂, 15 juv. ♀ (AMNH), 1 juv. ♂, 2 juv. ♀ (AMCC [LP 16773]).

ERRONEOUS RECORD: **Puducherry:** *Puducherry* *Distr.*: Pondichéry [Pondicherry/Puduchcheri/Puducherry, 11°59'N 79°49'E], M. Maindron, 1 ♀ (MNHN RS 0141 [Simon coll. 19501]).

Chersonesometrus shivashankari, sp. nov.

Figures 10, 16C, D, 30C, D, 45E–H, 61B, 62B, 63B, 80, 106–109, tables 1, 3, 4

Scorpio fulvipes: Simon, 1885: 23 (misidentification); Pocock, 1893: 304–307, 309 (misidentification, part).

Palamnaeus fulvipes madraspatensis: Pocock, 1900a: 89 (misidentification, part).

Heterometrus (Scorpio) fulvipes: Kraepelin, 1901: 271 (misidentification, part).

TYPE MATERIAL: **INDIA:** **Karnataka:** *Ballari* *Distr.*: Holotype ♂, 1 juv. ♂, 2 juv. ♀ paratypes (BMNH), Bellahunsi [Bellahunshi, 15°10'N 76°16'E], 30.viii.1912, Fletcher, under stones; 1 ♀, 4 juv. ♀ paratypes (BMNH), near road from Hampasagar [Hampasagara/Hampasagaram, 15°07'N 76°01'E] to Hadagalli [Hadagali, 15°01'N 75°56'E], 1.ix.1912, Y.R., under stones; 2 juv. ♀ paratypes (BMNH), Hospet [15°16'N 76°24'E], 30.viii.1912, Fletcher, under stones. **Andhra Pradesh:** *Anantapur* *Distr.*: Paratype ♂ (MNHN RS 0083 [Simon coll. 7015]), Wagra Karoor/Wagra Karur/Wagra Karour [Vajrakarur, 15°02'N 77°23'E], Chaper, 1 ♂, 1 ♀, 2 juv. ♂ paratypes (MNHN RS 0093), same data, except: 1893, Chaper.

ETYMOLOGY: The specific epithet is a patronym honoring the Indian biologist, Tirumani Shivashankar, formerly of the University of Agricultural Sciences, Arsiker, for his pioneering contributions to the knowledge of burrowing biology and sociality in the closely related species, *Chersonesometrus madraspatensis* (as *H. fulvipes*) (Shivashankar and Veeresh, 1991; Shivashankar, 1992, 1994).

DIAGNOSIS: *Chersonesometrus shivashankari* may be separated from other species of *Chersonesometrus* as follows. The carapace is vaulted, the lateral surfaces sloping steeply (fig. 16C, D), in *C. shivashankari* but slightly to markedly dorsoventrally compressed, the lateral surfaces sloping gently in all other species except *C. fulvipes* and *C. madraspatensis*. The frontal lobes and medial region of the carapace interocular surface are granular with smooth areas in the female (fig. 16D) of *C. shivashankari*, whereas the interocular surface is granular along the median longitudinal and anterior bifurcated sulci only in the female of all other species except *C. bastawadei*, *C. madraspatensis*, and *C. pelekomanus*. The carapace posterolateral surfaces of the female are smooth in *C. shivashankari* but granular in *C. bastawadei*, *C. fulvipes*, and *C. madraspatensis*. The cheliceral movable finger prodistal (DI) and retrodistal (DE) teeth are unequal, with the DE tooth considerably smaller than the DI tooth, aligned longitudinally and not opposable in *C. shivashankari*, but subequal, with the DE tooth only slightly smaller than the DI tooth, and opposable, i.e., forming a bicuspid, in *C. beccaloniae*, *C. hendersoni*, *C. nathanorum*, *C. pelekomanus*, and *C. tristis*. The pedipalps of the adult male are short, with femur length : posterior carapace width ratio (FL:PCW) < 0.77 and femur length : carapace length ratio (FL:CL) < 0.74 (fig. 106A, B) in *C. shivashankari* but long, with FL:PCW $\geq$ 0.80, FL:CL $\geq$ 0.76 in *C. beccaloniae*, *C. madraspatensis*, and *C. tristis*. The pedipalp patella dorsal surface is convex, with the axis of the dorsomedian carina dorsal to the axis of the retrodorsal carina (fig. 107), in *C. shivashankari* but flat or nearly so, with the axes of the dorsomedian and retrodorsal carinae in the same plane, in *C. beccaloniae*, *C. hendersoni*, *C. pelekomanus*, and *C. tristis*. The patella retrodorsal carina of the female is as strongly developed as or more strongly developed than the retromedian carinae in *C. shivashankari* but absent or obsolete in *C. nathanorum*. The retromedian carinae are granular in *C. shivashankari* but costate in *C. nathanorum*. The patella dorsal, retrodorsal, and retroventral intercarinal surfaces of the female are granular in *C. shivashan-*

kari but smooth or nearly so in *C. nathanorum*. The pedipalp chela is immaculate and paler than the femur and patella in *C. shivashankari* but infusate and similar in color to the femur and patella in all other species. The chela of the adult male is sparsely setose in *C. shivashankari* but moderately to densely setose in *C. beccaloniae*, *C. pelekomanus*, and *C. tristis*. The chela manus dorsal surface (between the dorsomedian and digital carinae) is curved, i.e., slightly to markedly convex, in the male and female of *C. shivashankari*, flat in the male and curved in the female of *C. bastawadei*, *C. beccaloniae*, *C. fulvipes*, *C. nathanorum*, and *C. wroughtoni*, and flat in the male and female of *C. hendersoni*, *C. pelekomanus*, and *C. tristis*. The proximal margin (lobe) of the chela manus dorsal surface is moderately curved and proximal to the proximal margin of the retrolateral surface in the male (fig. 108), or aligned with the proximal margin of the condyle (articulation with patella) in the female (fig. 109) of *C. shivashankari*; moderately curved and aligned with the proximal margin of the retrolateral surface in the male, or aligned with or proximal to the proximal margin of the retrolateral surface in the female of *C. beccaloniae* and *C. nathanorum*; and markedly curved and proximal to the proximal margin of the condyle in the male and female of *C. hendersoni* and *C. pelekomanus*. The maximum distance between the dorsomedian and dorsal secondary carinae (DMC–DSC) of the chela manus is greater than the maximum distance between the dorsal secondary and digital carinae (DSC–DC) in the male of *C. shivashankari*, but greater than the DSC–DC in the male of *C. beccaloniae*, *C. madraspatensis*, *C. nathanorum*, and *C. tristis*. The dorsal secondary and subdigital carinae of the male (fig. 108) are entirely to predominantly granular in *C. shivashankari*, entirely to predominantly costate in *C. nathanorum*, and absent or obsolete in *C. bastawadei* and *C. fulvipes*. The digital carina is absent or obsolete in *C. shivashankari*, but entirely to predominantly granular in *C. beccaloniae*, *C. hendersoni*, *C. pelekomanus*, *C. tristis*, and *C. wroughtoni*, and entirely to predominantly costate in *C. nathanorum*. The manus dorsal intercarinal surface is without reticulation in *C.*

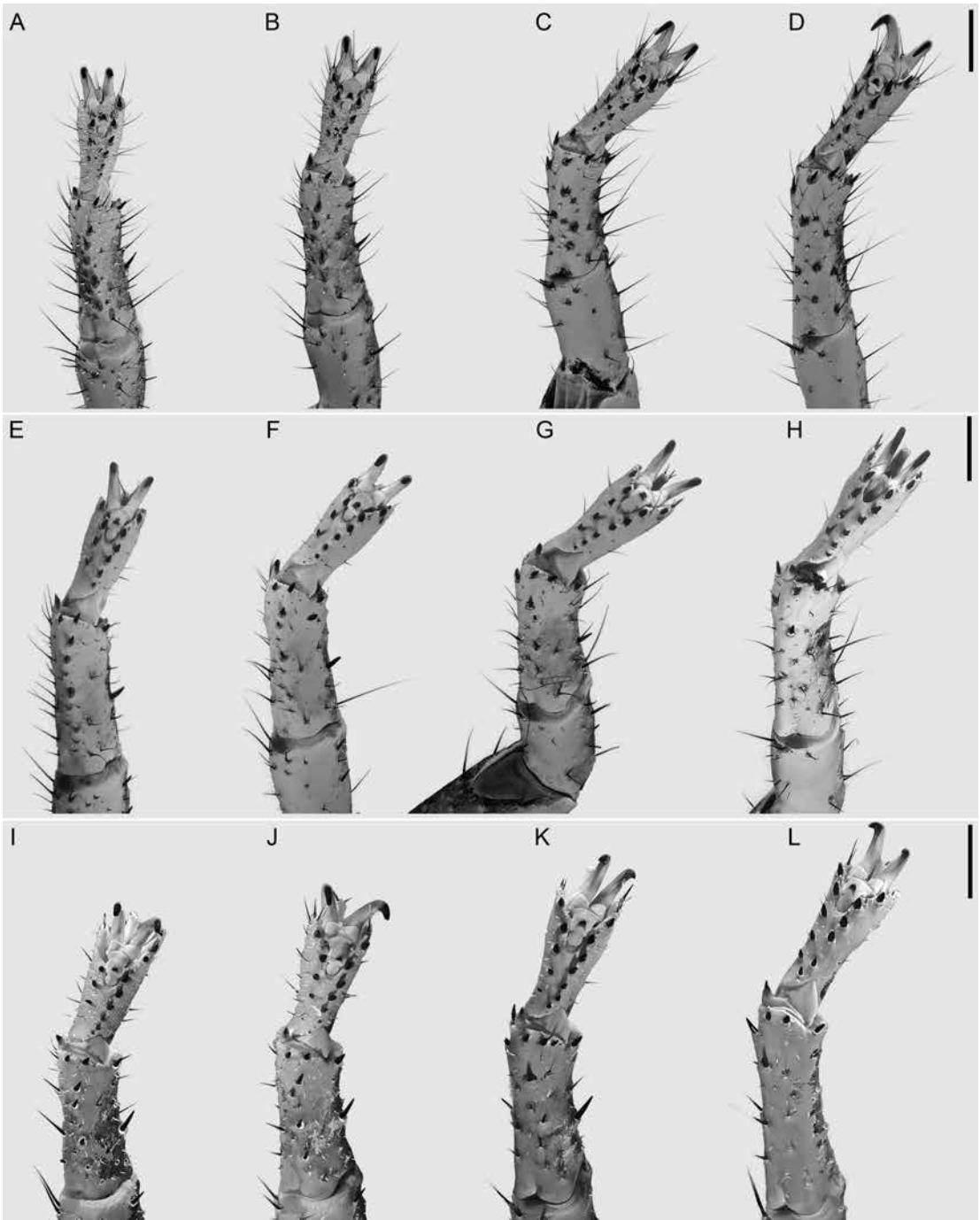


FIGURE 43. *Chersonesometrus* Couzijn, 1978, stat. nov. et stat. rev., legs I–IV, tibiae, basitarsi and telotarsi, ventral aspect. A–D. *Chersonesometrus beccaloniae* (Kovařík, 2004), comb. nov., ♀ (AMNH), Yelagiri Hills, India. E–H. *Chersonesometrus pelekomanus* (Couzijn, 1981), comb. nov., paratype ♀ (SMF RII/329). I–L. *Chersonesometrus tristis* (Henderson, 1919), comb. nov., ♀ (AMNH), Maddur, India. Scale bars = 2 mm.

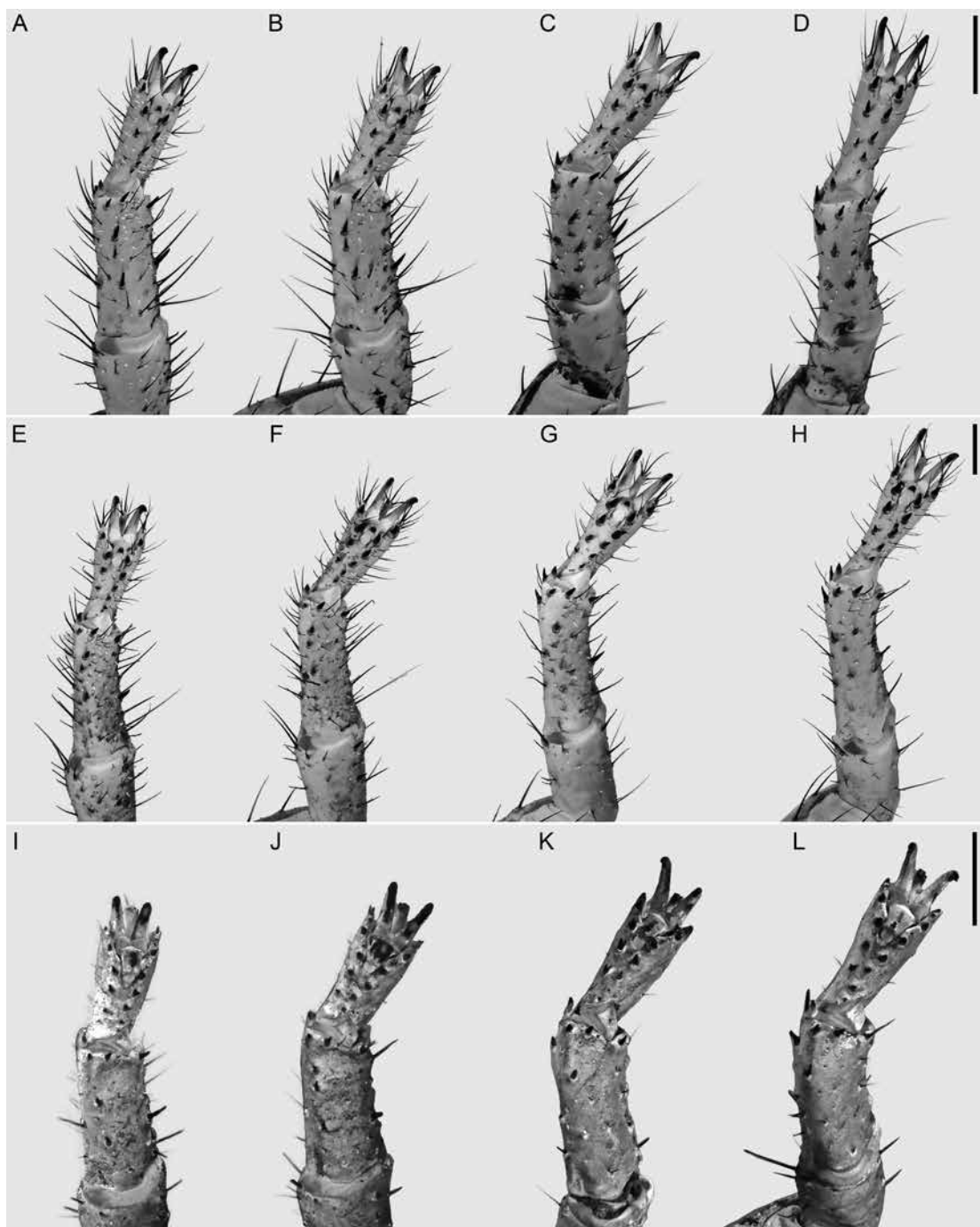


FIGURE 44. *Chersonesometrus* Couzijn, 1978, stat. nov. et stat. rev., legs I-IV, tibiae, basitarsi and telotarsi, ventral aspect. A-D. *Chersonesometrus bastawadei*, sp. nov., holotype ♀ (AMNH), Naganath Temple, India. E-H. *Chersonesometrus hendersoni*, sp. nov., holotype ♀ (AMNH), Sanapura, India. I-L. *Chersonesometrus wroughntoni* (Pocock, 1899), comb. nov., paralectotype ♀ (BMNH 1897.9.17.1-4, 11, 20). Scale bars = 2 mm.

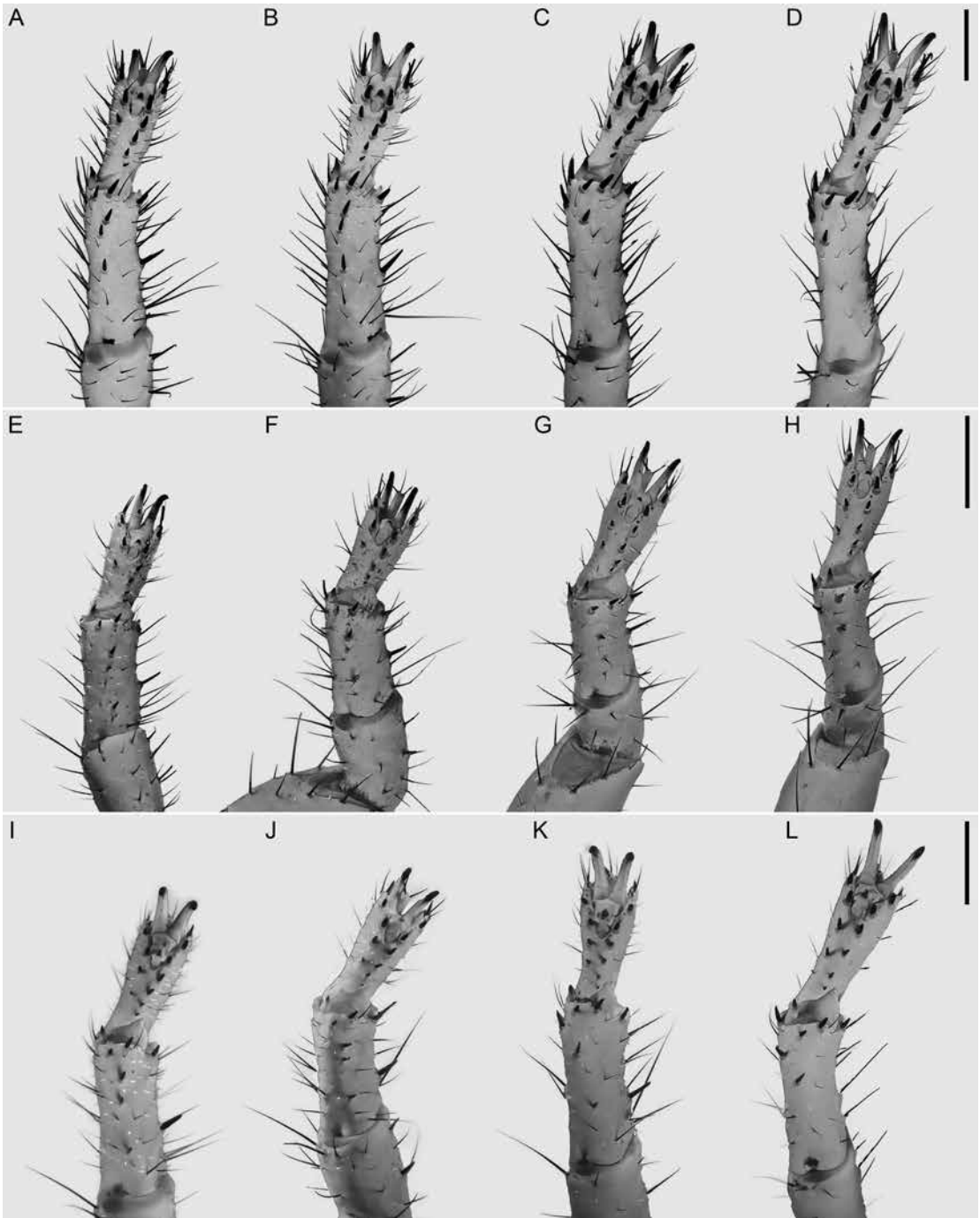


FIGURE 45. *Chersonesometrus* Couzijn, 1978, stat. nov. et stat. rev., legs I–IV, tibiae, basitarsi and telotarsi, ventral aspect. A–D. *Chersonesometrus fulvipes* (C.L. Koch, 1837), comb. nov., ♂ (AMNH), Khambatki Ghat, India. E–H. *Chersonesometrus shivashankari*, sp. nov., paratype ♀ (BMNH), Hampasagar, India. I–L. *Chersonesometrus madraspatensis* (Pocock, 1900), comb. nov., ♂ (CAS 9071142). Scale bars = 2 mm.

shivashankari but shallowly reticulate in *C. nathanorum*. The manus ventral surface is flat, with the axes of the retroventral and ventromedian carinae in approximately the same plane in *C. shivashankari* but angled, with the axis of the retroventral carina ventral to the axis of the ventromedian carina in *C. beccaloniae*, *C. hendersoni*, *C. pelekomanus*, and *C. tristis*. The legs are pale or very lightly infusate (fig. 106) in *C. shivashankari* but very dark or heavily infusate in *C. beccaloniae*, *C. nathanorum*, *C. pelekomanus*, *C. tristis*, and *C. wroughtoni*. Macroseta *st* on the retroventral surfaces of the basitarsi of legs I and II is setiform (fig. 45E–H) in *C. shivashankari* but spiniform in all other species except *C. nathanorum*. The mesial surfaces of mesosomal tergites I–VI are granular in the male and the lateral surfaces granular in the female of *C. shivashankari*, whereas the mesial surfaces are smooth in the male of *C. beccaloniae*, *C. hendersoni*, *C. pelekomanus*, and *C. wroughtoni*, the mesial surfaces smooth in the male and the lateral surfaces smooth in the female of *C. tristis*, and the lateral surfaces smooth in the female of *C. nathanorum*. The ventral surface of mesosomal sternite VII bears a pair of weakly developed ventrolateral carinae in *C. shivashankari* and two pairs of moderately to strongly developed ventrosulmedian and ventrolateral carinae in *C. beccaloniae*, *C. hendersoni*, and *C. pelekomanus*. The dorsosulmedian carinae are granular or costate-granular on metasomal segments I–IV (fig. 61B) in *C. shivashankari* but costate on segments I and II or I–III and granular or costate-granular on III and IV or IV in *C. tristis* and the female of *C. beccaloniae*. The ventral intercarinal surfaces of segment IV are smooth in the male and granular in the female (fig. 63B) of *C. shivashankari* but granular in the male and smooth in the female of *C. beccaloniae* and *C. nathanorum*, granular in the male of *C. hendersoni*, *C. madraspatensis*, *C. pelekomanus*, and *C. tristis*, and smooth in the female of *C. wroughtoni*. The dorsolateral carinae of metasomal segment V are strong and continuous in *C. shivashankari* but weak and discontinuous to absent in *C. nathanorum*. The dorsal intercarinal surface of segment V is smooth in the male and female of *C. shivashankari*, granular in

the male and female of *C. bastawadei*, *C. hendersoni*, and *C. pelekomanus*, and granular in the male of *C. wroughtoni*.

DESCRIPTION: The following description is based on the holotype and paratypes. Meristic data are presented in table 3 and measurements in table 4.

Total length: Adult small, maximum length, measured from anterior margin of carapace to tip of aculeus, 86 mm (♂), 82 mm (♀).

Color: Chelicerae, dorsal surfaces bicolored, mostly to entirely immaculate prodorsal half of manus paler than infusate retrodorsal half of manus and fingers; manus markedly paler than carapace interocular surface. Carapace, tergites, and metasoma entirely infusate, uniformly dark reddish black; pedipalp trochanter, femur, and patella, entirely infusate, uniformly dark reddish brown to reddish black, chela immaculate, manus yellowish to reddish brown with darker fingers. Sternites III–VI immaculate or partially infusate, VII mostly or entirely infusate, dark brownish black, becoming darker posteriorly. Coxosternal region infusate, brownish, maxillary lobes darker. Legs immaculate, uniformly pale yellow, contrasting with carapace, pedipalps, tergites, and metasoma (fig. 106). Genital opercula and pectines uniformly pale yellow. Metasomal segments I–V entirely infusate, similar to one another; carinae infusate, darker than intercarinal surfaces; dorsal intercarinal surfaces similar to tergites; ventral intercarinal surfaces darker than sternites. Telson vesicle immaculate, light yellowish, markedly paler than metasomal segment V; aculeus black.

Chelicerae: Movable finger prodistal (DI) and retrodistal (DE) teeth unequal, with DE tooth considerably smaller than DI tooth, aligned longitudinally and not opposable. Fingers and manus, proventral surfaces with long, dense vestiture of macrosetae. Coxae, prodorsal surfaces without stridulatory setae (scaphotrix); promedian surfaces without chemoreceptive lamelliform setae (trichocopae).

Carapace: Carapace vaulted, lateral surfaces sloping steeply. Anterior margin straight, frontal

lobes evenly rounded or truncate, with deep median notch, without median projection or median depression (fig. 16C, D). Anterolateral margins converging gradually anteriorly, without distinct notch adjacent to posterior lateral ocelli; mediolateral margins diverging or converging slightly posteriorly (at posterolateral sulci). Anterior width of posterior width, 64% (♂), 65% (♀); posterior width of length, 96% (♂), 94% (♀). Three pairs of lateral ocelli (MLMa, PLMa, PDMi), all similar in size, two anterior pairs situated anteriorly, well separated from posterior pair, situated laterally. Median ocelli moderately larger than lateral ocelli, distance between ocelli slightly less than width of ocellus; median ocular tubercle situated posteromedially, distance from anterior carapace margin, 52% (♂), 50% (♀). Median longitudinal sulcus narrow, suturiform; continuous from median notch to interocular sulcus; anteriorly furcated; without anterocular depression. Anterior furcated sulci diverging broadly from anterior edge of median longitudinal sulcus. Median ocular tubercle raised, superciliary carinae higher than ocelli, extended anteriorly, subparallel. Interocular sulcus present. Circumocular depressions completely encircling median ocular tubercle, converging anteriorly. Posteromedian and posteromarginal sulci deep. Paired mediolateral and posterolateral sulci shallow. Median longitudinal suture continuous from median notch to median ocular tubercle, equally strong along entire length; not extending to anterior margin of carapace, terminating at or posterior to median notch. Anterior furcated sutures absent or obsolete. Anterocular furcated sutures absent. Interocular suture present, slender. Posterior sutures present but indistinct, converging on median ocular tubercle; connected anteriorly to posterior furcations of interocular suture and extending anteriorly beyond median ocular tubercle. Frontal lobes and medial region of interocular surface finely granular with smooth areas (fig. 16C, D); anterolateral and mediolateral surfaces uniformly finely granular; posterolateral surfaces uniformly finely granular (♂) or smooth (♀); posteromedian surfaces smooth.

Pedipalps: Pedipalp short, pedipalp femur length : posterior carapace width ratio (FL:PCW) < 0.77, pedipalp femur length : carapace length (FL:CL) < 0.74. Femur width of length, 43% (♂), 45% (♀). Retrodorsal carina complete, granular, similar to or more strongly developed than prodorsal carina. Dorsal secondary carina comprising scattered granules, becoming obsolete distally. Dorsomedian carina vestigial, reduced to prominent granule demarcated by conspicuous macroseta. Prodorsal carina complete, granular. Promedian carina complete, comprising row of spiniform or subspiniform granules (several demarcated by conspicuous macrosetae), oriented diagonally between prodorsal and proventral carinae. Proventral carina complete, granular, as strongly developed as or more strongly developed than retroventral carina. Ventromedian and secondary accessory carinae absent. Retroventral carina extending partly or entirely to distal edge of segment. Retromedian carinae absent, indicated only by macrosetal rows. Dorsal intercarinal surfaces finely granular; other surfaces smooth. Patella width of length, 46% (♂), 54% (♀). Dorsal surface convex, axis of dorsomedian carina dorsal to axis of retrodorsal carina. Dorsomedian carina granular to costate-granular (fig. 107). Retrodorsal carina granular, similarly developed to granular retromedian carinae. Retroventral carina obsolete, granular. Promedian carina and promedian process absent. Other carinae absent. Dorsal and retrolateral intercarinal surfaces finely granular, other surfaces smooth. Chela short, broad (figs. 108, 109); manus height of width, 206% (♂), 180% (♀); manus length along retroventral carina of manus width, 150% (♂), 116% (♀); manus length along retroventral carina of movable finger length, 66% (♂), 69% (♀). Chela sparsely setose. Manus dorsal surface (between dorsomedian and digital carinae) curved, i.e., slightly to markedly convex; proximal margin (lobe) of dorsal surface moderately curved and proximal to proximal margin of retrolateral surface (♂) or aligned with proximal margin of condyle (articulation with patella) (♀). Dorsomedian carina obsolete, costate on fixed finger and comprising regular row of spi-

niform granules along entire length of manus. Dorsal secondary and subdigital carinae incomplete, granular; digital carina obsolete, granular; distal half of subdigital carina and distal third of digital carina closely adjacent. Maximum distance between dorsomedian and dorsal secondary carinae (DMC–DSC) greater than maximum distance between dorsal secondary and digital carinae (DSC–DC). Retromedian carina complete, entirely to predominantly costate, more strongly developed than digital carina. Retrolateral secondary and secondary accessory carinae vestigial, proximal to condyle of movable finger. Retroventral and ventromedian carina distinct, costate, but retroventral carina more strongly developed. Proventral and promedian carinae similarly developed, each comprising few spiniform granules and associated macrosetae. Prodorsal carina obsolete, comprising few spiniform granules and associated macrosetae. Distance between dorsomedian and promedian carinae (DMC–PMC) slightly to markedly greater than distance between promedian and proventral carinae (PMC–PVC). Manus, dorsal intercarinal and retrolateral intercarinal surfaces densely and coarsely granular except for smooth depression at base of fixed finger; ventral intercarinal surface smooth; prolateral intercarinal surfaces very sparsely and finely granular, more densely dorsally and distally. Manus ventral surface flat, axes of retroventral and ventromedian carinae in approximately same plane. Fixed and movable fingers, intercarinal surfaces finely granular (♂) to smooth (♀); median denticle rows each with six enlarged retrolateral denticles (including terminal denticle), proximal three situated on lobes; first (proximal) lobe of fixed finger and second lobe of movable finger larger than others, with correspondingly deeper notches in movable and fixed fingers, respectively; terminal denticles of fingers interlocking unevenly when closed, movable finger displaced retrolaterally; distinct notch near tip of fixed finger to accommodate terminal denticle of movable finger.

Trichobothria: Orthobothriotaxic, Type C, with the following segment totals ($n = 4$): femur, 3 (1 *d*, 1 *i*, 1 *e*); patella, 19 (2 *d*, 1 *i*, 3 *v*, 13 *e*,

comprising 3 *et*, 1 *est*, 2 *em*, 2 *esb*, 5 *eb*); chela, 26 (manus, 16, comprising 2 *D*, 10 *E*, 4 *V*; fixed finger, 10, comprising 4 *d*, 4 *e*, 2 *i*). Total count of trichobothria per pedipalp: 48. Femur, *i* situated on dorsal surface. Patella, *d*₂ situated on internal surface, slightly closer to *d*₁ than to *i*; distance v_2-v_3 ca. one-third distance v_1-v_2 . Chela, distance *et*–*est* ca. half distance *est*–*esb*; distance *est*–*esb* greater than half distance *esb*–*eb*; *est* aligned with *dst*; *V*₃ situated in proximal third of manus, closer to *V*₄ than *V*₂.

Legs: First pair of maxillary lobes (coxapophyses) tapering anteriorly, longer than and encircling second pair. Stridulatory organs, comprising “rasp” (granular tubercles) and “scraper” (stridulatory setae or scaphotrix), present on opposing surfaces of coxae of first pair of legs and pedipalps, respectively. Legs I–IV acarinate, except femora, with distinct pro- and retrolateral surfaces demarcated by partial, granular proventral carinae. Femora, patellae, and tibiae, pro- and retrolateral surfaces each with scattered setiform macrosetae. Tibiae, prolateral surfaces, without spiniform macrosetae; I and II, retrolateral surfaces, each with two spiniform (*t*, *st*) macrosetae; III and IV, retrolateral surfaces, without spiniform macrosetae. Basitarsi I–IV, slightly dorsoventrally compressed; retrolateral margins similar, unmodified, rounded; prolateral pedal spurs present (fig. 45E–H); retrolateral pedal spurs absent. Basitarsi, pro- and retrolateral surfaces, each with scattered long and short setiform macrosetae, and spiniform macrosetae, more numerous on I and II than III and IV. Basitarsi, spiniform macrosetae, I, retrolateral: *t*, *sb*; retroventral: *t*, *sb*; proventral: *t*, *st*; II, retrolateral: *t*, *sb*; retroventral: *t*, *sb*; proventral: *t*, *st*; III, retrolateral: *t*, *sb*; retroventral: *t*, *st*; proventral: *t*; prolateral: *t*, *st*; IV, retrolateral: *t*; retroventral: *t*; proventral: *t*, *st*; prolateral: *t*, *st*. Telotarsi I–IV short, stout and distally broadened in dorsal and lateral views. Laterodistal lobes rounded. Dorsomedian lobes approximately equal to laterodistal lobes; each terminating in single setiform macroseta. Telotarsi, pro- and retrolateral surfaces, each with long and short, scattered macrosetae, not arranged in definite row. Telotarsi each

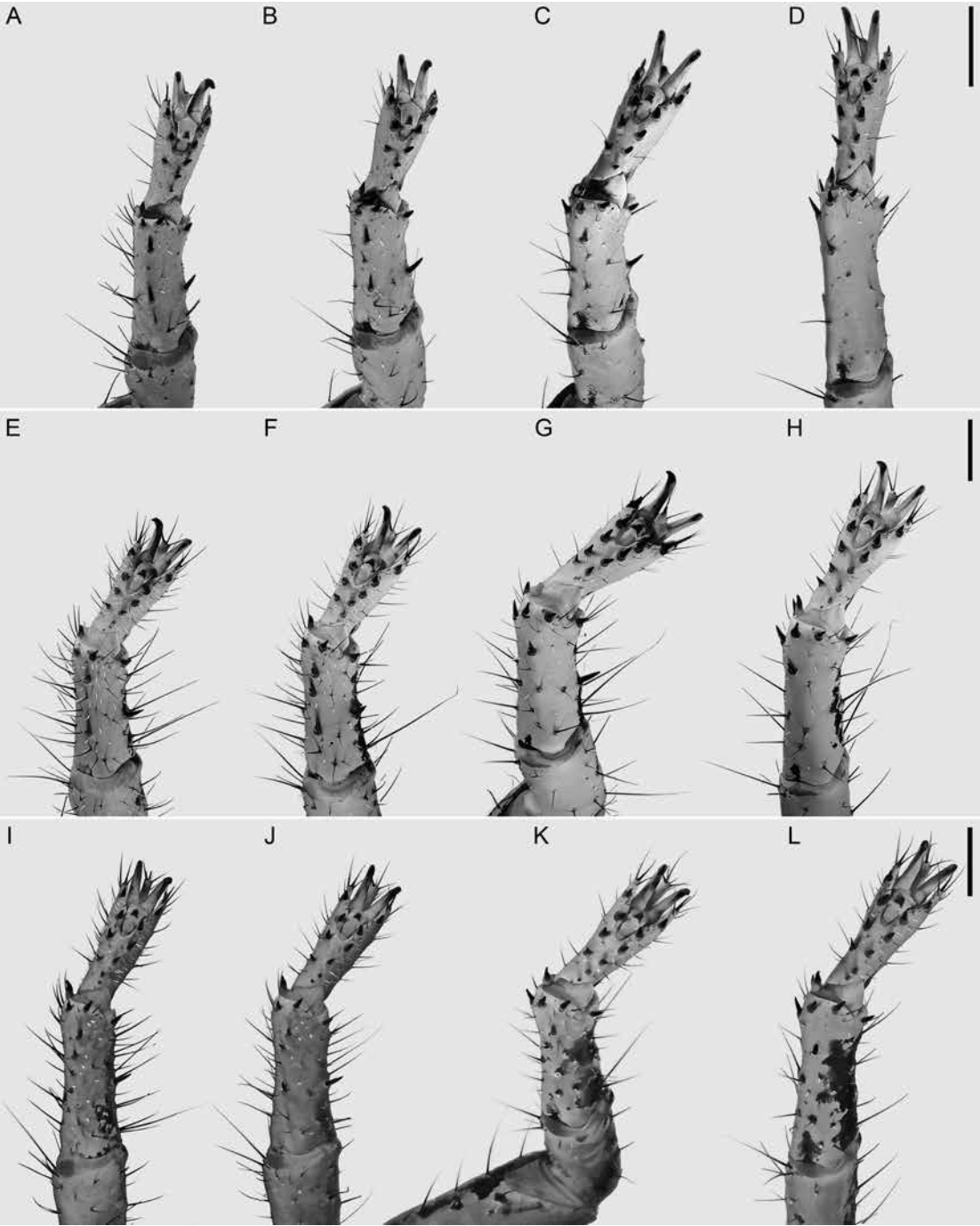


FIGURE 46. *Deccanometrus*, gen. nov., legs I-IV, tibiae, basitarsi and telotarsi, ventral aspect. A-D. *Deccanometrus bengalensis* (C.L. Koch, 1841), comb. nov., ♂ (BMNH 1913.1.6.3). E-H. *Deccanometrus obscurus* (Couzijn, 1981), comb. et stat. nov., ♂ (AMNH), Bhimashankar, India. I-L. *Deccanometrus phipsoni* (Pocock, 1893), comb. nov., ♂ (MNHN RS 0080). Scale bars = 2 mm.

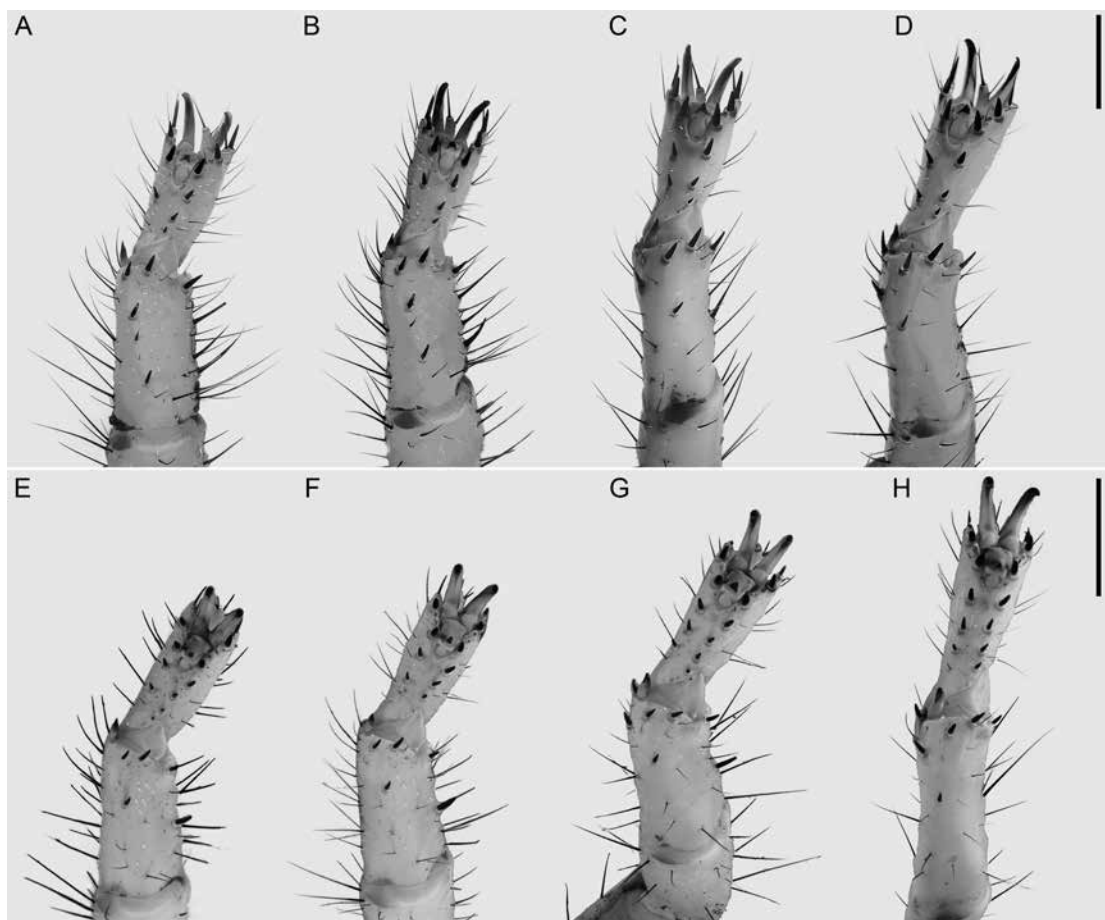


FIGURE 47. *Deccanometrus*, gen. nov., legs I-IV, tibiae, basitarsi and telotarsi, ventral aspect. **A-D.** *Deccanometrus latimanus* (Pocock, 1894), comb. nov., ♀ (AMNH), Daggar, Pakistan. **E-H.** *Deccanometrus xanthopus* (Pocock, 1897), comb. nov., ♀ (AMNH), Khambatki Ghat, India. Scale bars = 2 mm (**A-D**) or 1 mm (**E-H**).

with pro- and retroventral rows of spiniform macrosetae, two inserted on laterodistal lobes; counts in pro- and retroventral rows similar on I and II, and on III and IV ($n = 6$): I, proventral: 3 (3 or 4), retroventral: 6 (5 or 6); II, 4 (3 or 4), 6 (5 or 6); III and IV, 4, 6 (5 or 6). Telotarsal ungues short, curved, equal to subequal; pseudonychium (dactyl) reduced, rounded.

Sternum: Shape subpentagonal (fig. 30C, D). Median longitudinal sulcus shallow anteriorly, deep and narrow posteriorly.

Genital operculum: Genital opercula suboval, completely divided longitudinally, partially overlapping, genital papillae present (♂) (fig. 30C);

subcordate, fused, genital papillae absent (♀) (fig. 30D).

Hemispermaphore: Lamelliform, with complex, folded capsule and accessory distal lobe protruding between articular suture and distal lobe (hook). Distal lamina with distal crest truncate, unfolded.

Pectines: Distal edge extending past distal edge of coxa IV but not reaching distal edge of trochanter IV (fig. 30C, D). First proximal median lamella (scape) of each pecten with mesial margin angular, approximately 90° (♂) or obtusely angular, greater than 90° but less than 180° (♀). Pectinal teeth straight and elongate

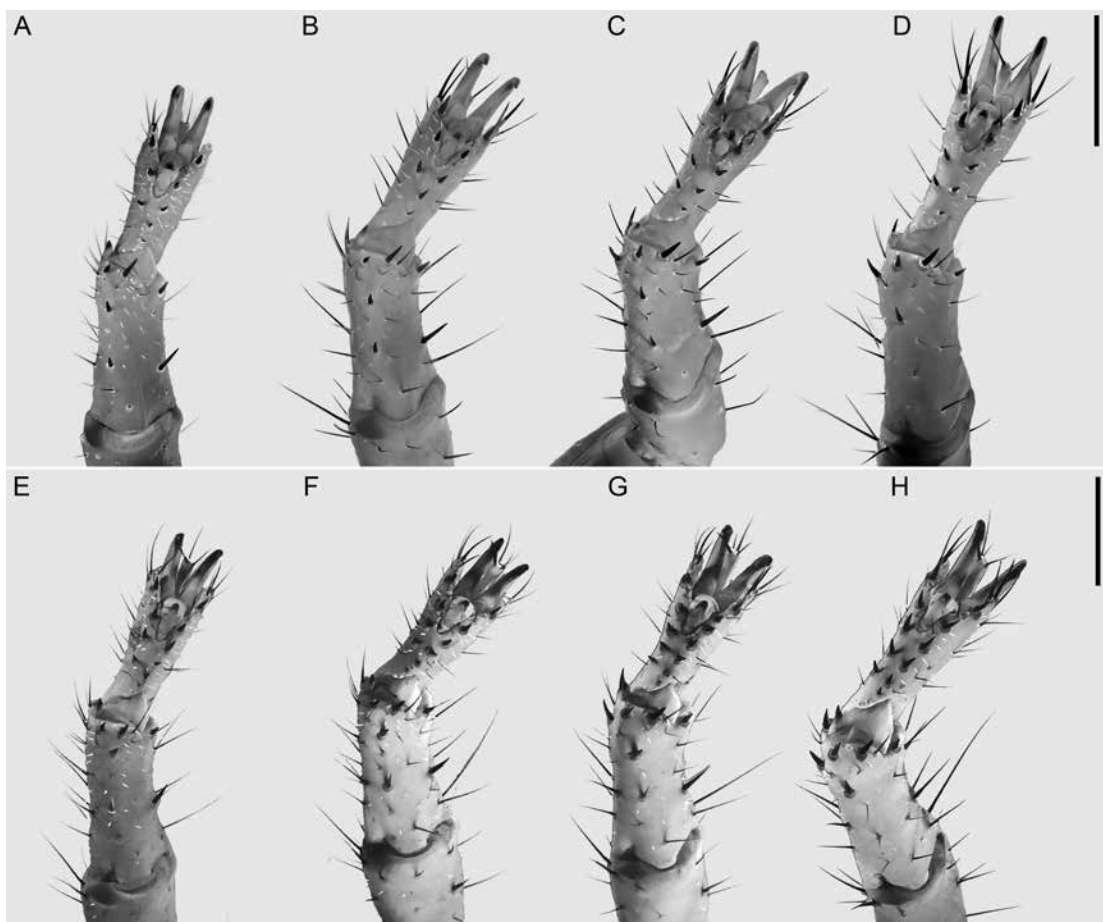


FIGURE 48. *Deccanometrus*, gen. nov., legs I–IV, tibiae, basitarsi and telotarsi, ventral aspect. **A–D.** *Deccanometrus liurus* (Pocock, 1897), comb. nov., paralectotype ♀ (BMNH 1896.12.15.20–25). **E–H.** *Deccanometrus ubicki* (Kovařík, 2004), comb. nov., paratype ♀ (CAS 9071135). Scale bars = 1 mm (A–D) or 2 mm (E–H).

(♂) or shorter and curved (♀), present along entire posterior margin; sinistral/dextral tooth count, 15/16 (♂), 13–15/13–15 ($n = 2$) (♀). Fulcra smooth proximally but densely setose (microsetae only) distally.

Mesosoma: Tergites each with shallow pair of submedian depressions, without obsolete median carina. Pretergites smooth and glabrous. Posttergites finely granular (♂) or smooth and glabrous (♀) medially, unevenly finely and coarsely granular to predominantly coarsely granular laterally. Sternites IV–VI, each with paired longitudinal depressions prolateral to spiracles, absent on VII. Surface, sternites

III–VII, smooth; VII with pair of weakly developed, costate ventrolateral carinae only, without posteromarginal carina. Sternite VII, length of width, 69% (♂), 60% (♀).

Metasoma and telson: Metasomal segments I–V progressively increasing in length, decreasing in width; segment V, width of segment I, width, 76% (♂), 70% (♀). Metasoma fairly robust, width of length, segment I, 94% (♂), 93% (♀); II, 83% (♂), 78% (♀); III, 72% (♂, ♀); IV, 61% (♂), 59% (♀); V, 41% (♂), 42% (♀). Telson vesicle, width of metasomal segment V, width, 93% (♂), 86% (♀); vesicle globose, height of length, 59% (♂), 47% (♀); dorsal surface flat;

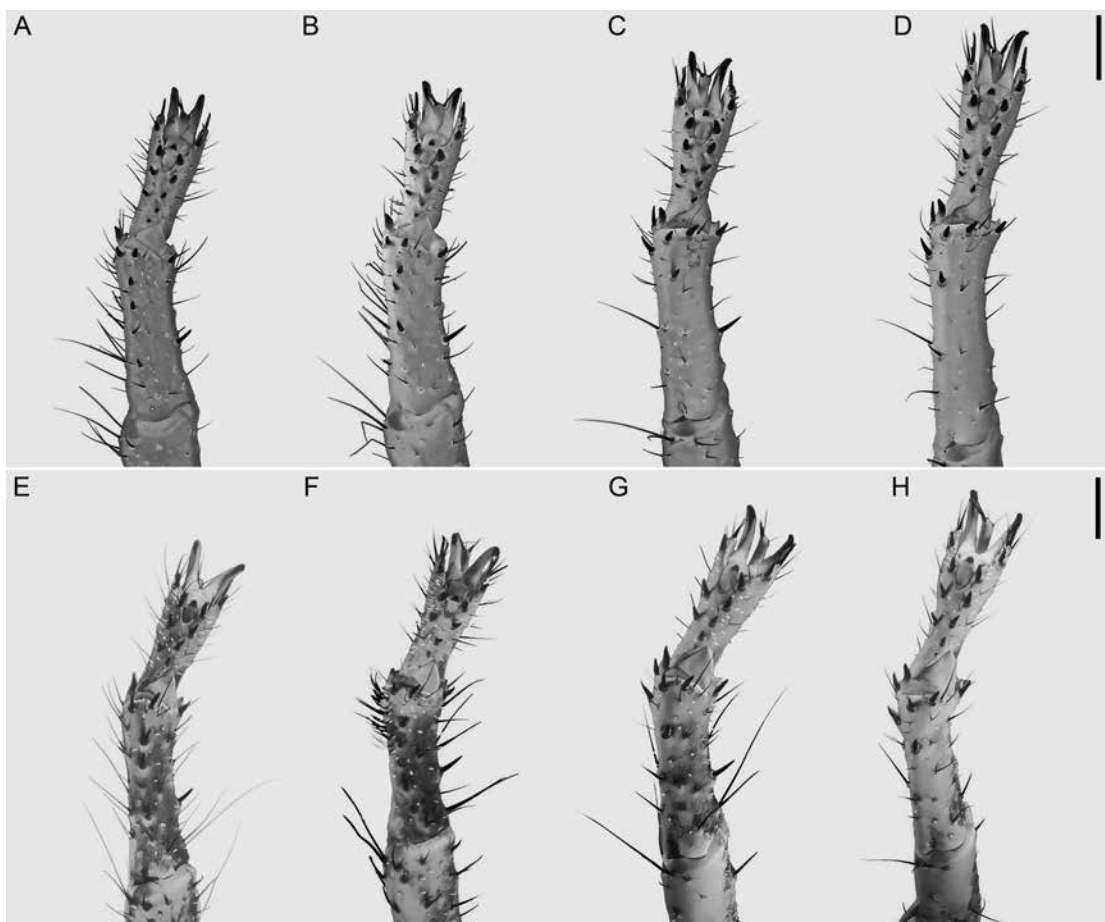


FIGURE 49. *Gigantometrus* Couzijn, 1978, stat. nov., legs I-IV, tibiae, basitarsi and telotarsi, ventral aspect. **A-D.** *Gigantometrus swammerdami* (Simon, 1872), comb. nov., lectotype ♂ (*Palamnaeus swammerdami flavimanus* Pocock, 1900, syn. nov.) (BMNH 1899.11.2.292-3). **E-H.** *Gigantometrus titanicus* (Couzijn, 1981), comb. nov. et stat. rev., ♂ (AMNH), Polonnaruwa, Sri Lanka. Scale bars = 2 mm.

ventral surface evenly curved. Aculeus relatively long, gently curved, length of vesicle length, 64% (♂), 58% (♀). Length metasoma and telson, of total length, 55% (♂, ♀). Dorsosubmedian carinae, segments I-IV, distinct, complete, granular or costate-granular, posterior spiniform granules obsolete (fig. 61B); V, vestigial. Dorsolateral carinae, segments I-V, distinct, complete, costate to costate-granular. Median lateral carinae, segment I, incomplete, reduced to granular row in posterior half, diagonally oriented between dorsolateral and ventrolateral carinae (fig. 62B); II-IV, obsolete row of granules posteriorly; V, incom-

plete, granular row, restricted to anterior two-thirds. Ventrolateral and ventrosubmedian carinae, segments I-IV, distinct, complete, costate on I-III, granular or costate-granular on IV, more strongly developed on III and IV than on I and II (fig. 63B). Ventrolateral carinae, segment V, distinct, complete, comprising spiniform granules, diverging posteriorly, terminal granule slightly larger than preceding granules. Ventrosubmedian carinae, segment V, vestigial, each reduced to one or two isolated spiniform granules, demarcated by conspicuous macrosetae. Ventromedian carina, segment V comprising

single row of spiniform granules, unmodified posteriorly. Anal arch, segment V, dorsal carina, costate; ventral carina comprising subspiniform granules. Dorsal and lateral intercarinal surfaces, segments I–V, smooth. Ventral intercarinal surfaces, segments I–III, smooth, IV and V, smooth (♂) or granular (♀). Ventral surface, lateral aspect, segment IV, shallowly convex. Telson vesicle, dorsal and lateral surfaces smooth; ventral surface with four longitudinal carinae, each comprising spiniform granules.

DISTRIBUTION: This species is endemic to India and presently recorded only from the states of Andhra Pradesh and Karnataka (fig. 80, table 1). Its distribution is allopatric with the morphologically similar *C. bastawadei*, *C. fulvipes*, *C. madraspatensis*, and *C. wroughtoni*.

ECOLOGY: The habitus is consistent with the fossorial, pelophilous ecomorphotype (Prendini, 2001b) and the limited data available suggest it constructs burrows under stones.

Chersonesometrus tristis (Henderson, 1919),
comb. nov.

Figures 7B, 9B, 10, 15E, F, 29E, F, 43I–L, 58E,
59E, 60E, 80, 110–114, table 1

Palamnaeus tristis Henderson, 1919: 380–381,
pl. XXI, figs. 3, 4.

Heterometrus tristis: Takashima, 1945: 94;
Kovářík, 2004: 1, 44, 49, 51, 52, tables 2, 3;
2009: 35, 36, 45, tables 1, 2; Javed et al.,
2010b: 785, table 1.

Heterometrus (Chersonesometrus) pelekomanus:
Couzijn, 1981: 137, 139, 169, 170, fig. 58
(misidentification, part); Tikader and
Bastawade, 1983: 577, 641, 642, 644, 646
(part); Fet, 2000: 440 (part).

Heterometrus (Chersonesometrus) tristis:
Couzijn, 1981: 42, 87, 156–158, 169, 171,
192, table 7, figs. 51, 59; Tikader and
Bastawade, 1983: 574, 582–587, figs. 1539–
1552; Kovářík, 1998: 137; Fet, 2000: 442;
Indra, 2009: 141.

Heterometrus (Chersonesometrus) palekomanus:

Indra, 2001: 56, 58 (misidentification, part).

Heterometrus mysorensis Kovářík, 2004: 1, 7, 29,
30, 51, 52, tables 1–3, fig. 21; 2009: 35, 36,
42, 46, 48, 49, 86, 101, 109, tables 1, 2, figs.
89–94, 215, 216, 259–262; syn. nov.

Heterometrus wroughtoni: Kovářík, 2004: 1, 7,
46, 49, 51, 52, tables 2, 3 (misidentification,
part); 2009: 35, 36, tables 1, 2 (misidentifica-
tion, part).

Heterometrus (Chersonesometrus) pelekomanus:

Indra, 2009: 141 (misidentification, part).

Heterometrus (Chersonesometrus) tristis: Indra,
2009: 141.

TYPE MATERIAL: INDIA: Karnataka: Mandya
Distr.: Heterometrus mysorensis: Holotype ♂
(FKPC), Mysore, Maddur env. [Madduru,
12°35'N 77°03'E], ca. 900 m, 1983. **Andhra**
Pradesh: Arcot Distr.: Palamnaeus tristis: Holo-
type ♂ (ZSI 2422/17), Tirupati Hills [13°39'N
79°25'E], North Arcot District, S.K.
Sundaracharlu.

Although Henderson (1919: 380) listed two males from the Tirupati Hills, North Arcot District, and two females and one immature male from the Venkatagiri Hills, Nellore District, the description was based on an adult male, and the “type-specimen” explicitly identified as ZSI 2422/17. Therefore, one of the two males from the Tirupati Hills is the holotype and no other specimens are types. Couzijn (1981: 157) mistakenly listed an adult male holotype and adult male paratype from the Tirupati Hills, and an allotype female from the Venkatagiri Hills, all with the number ZSI 2160/18. Tikader and Bastawade (1983: 587), mistakenly listed a male and a female “type specimens” (ZSI 2160/18), and Fet (2000: 442) followed Couzijn (1981).

DIAGNOSIS: *Chersonesometrus tristis* may be separated from other species of *Chersonesometrus* as follows. The carapace is markedly dorso-ventrally compressed, the lateral surfaces sloping gently (fig. 15E, F) in *C. tristis*, but vaulted, the lateral surfaces sloping steeply, in *C. fulvipes*, *C.*

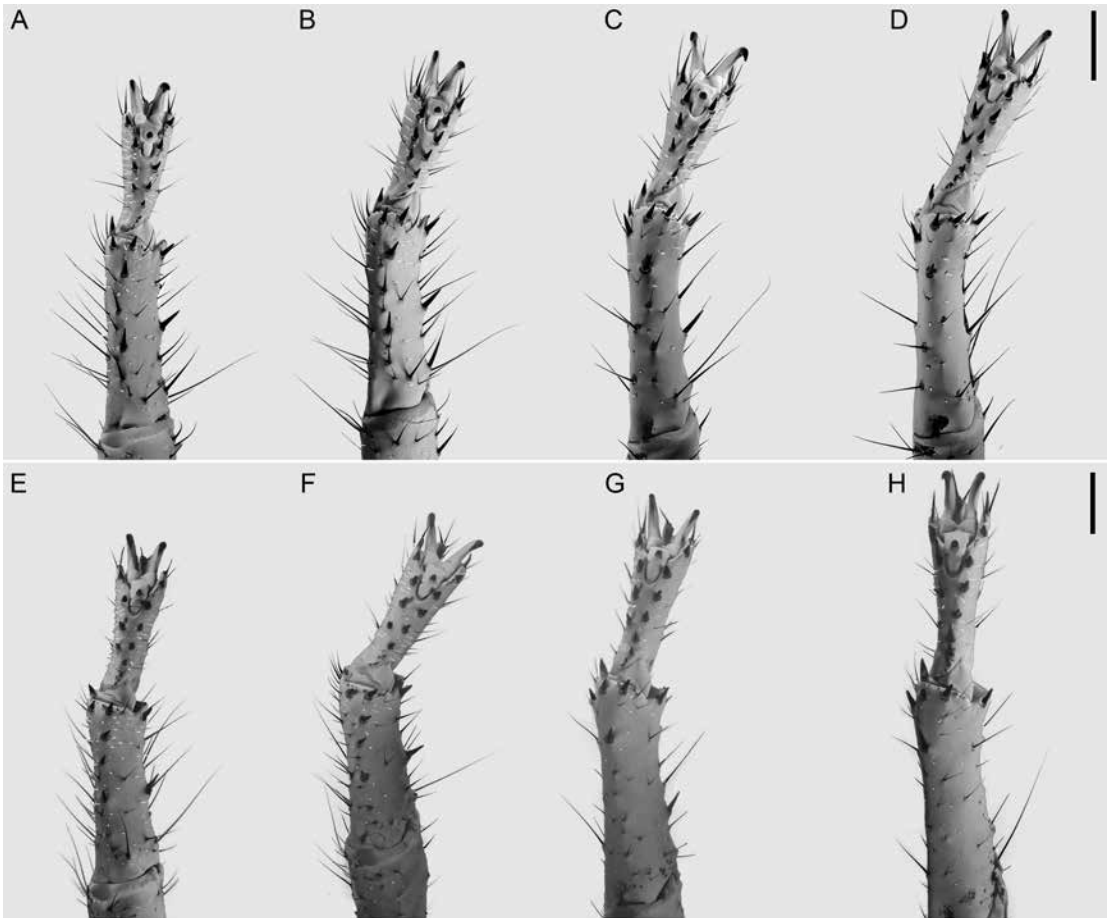


FIGURE 50. *Heterometrus* Ehrenberg, 1828, legs I–IV, tibiae, basitarsi and telotarsi, ventral aspect. **A–D.** *Heterometrus laevigatus* (Thorell, 1876), comb. nov. et stat. rev., ♂ (AMNH), Thale Ban, Thailand. **E–H.** *Heterometrus spinifer* (Ehrenberg, 1828), ♂ (AMNH), Cameron Highlands, Malaysia. Scale bars = 2 mm.

madraspatensis, and *C. shivashankari*. The carapace interocular surface is granular along the median longitudinal and anterior bifurcated sulci only in the female (fig. 15F) of *C. tristis*, whereas the frontal lobes and medial region of the interocular surface are granular with smooth areas in the female of *C. bastawadei*, *C. madraspatensis*, *C. pelekomanus*, and *C. shivashankari*. The carapace posterolateral surfaces of the female are smooth in *C. tristis* but granular in *C. bastawadei*, *C. fulvipes*, and *C. madraspatensis*. The cheliceral movable finger prodistal (DI) and retrodistal (DE) teeth are subequal, with the DE tooth only slightly smaller than the DI tooth, and

opposable, i.e., forming a bicuspid, in *C. tristis* but unequal, with the DE tooth considerably smaller than the DI tooth, aligned longitudinally and not opposable in *C. bastawadei*, *C. fulvipes*, *C. madraspatensis*, *C. shivashankari*, and *C. wrough-toni*. The pedipalps of the adult male are long, with femur length : posterior carapace width ratio (FL:PCW) ≥ 0.80 and femur length : carapace length ratio (FL:CL) ≥ 0.76 (fig. 110) in *C. tristis* but short, with FL:PCW < 0.77 , FL:CL < 0.74 in all other species except *C. beccaloniae* and *C. madraspatensis*. The pedipalp patella dorsal surface is flat or nearly so, with the axes of the dorsomedian and retrodorsal carinae in the same

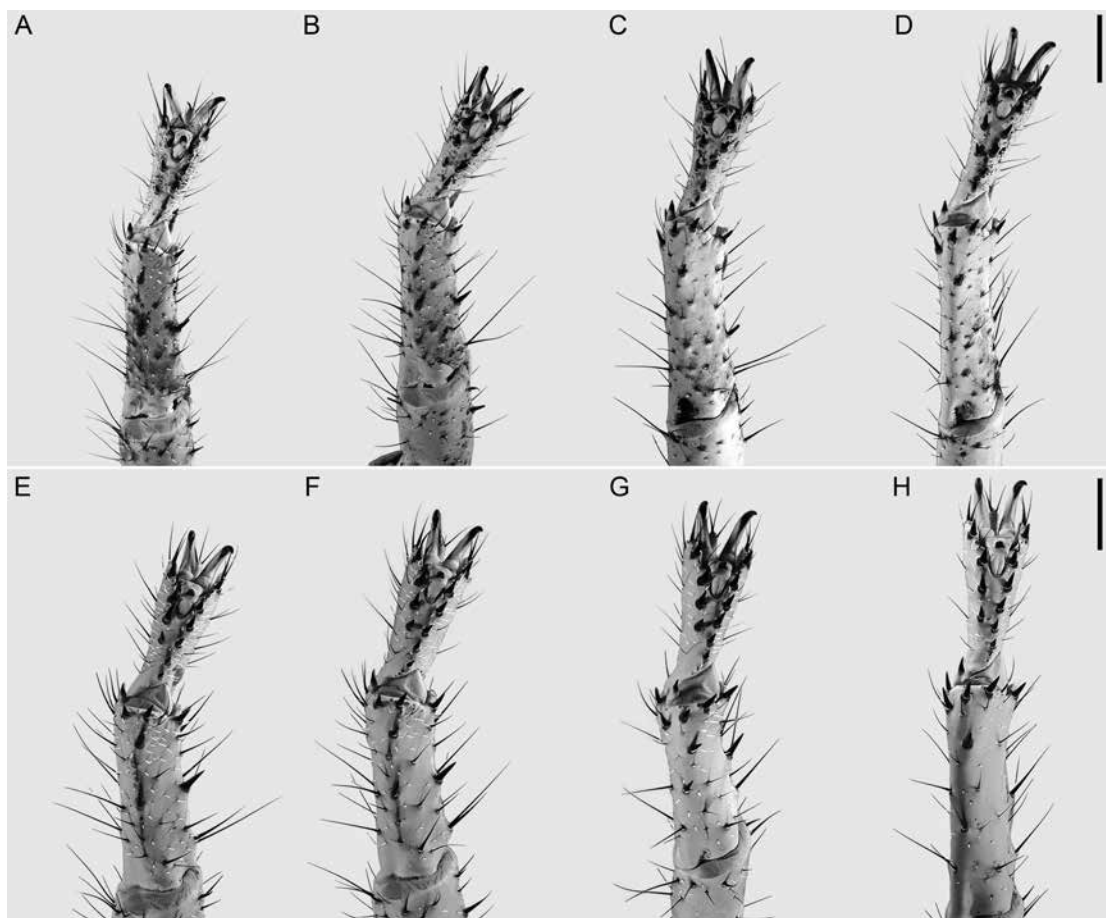


FIGURE 51. *Heterometrus* Ehrenberg, 1828, legs I–IV, tibiae, basitarsi and telotarsi, ventral aspect. **A–D.** *Heterometrus laoticus* Couzijn, 1981, ♂ (AMNH), Phahom Camp, Laos. **E–H.** *Heterometrus silenus* (Simon, 1884), comb. nov. et stat. rev., ♂ (AMNH), Ta Kou Mountain Nature Reserve, Vietnam. Scale bars = 2 mm.

plane (fig. 112), in *C. tristis* but convex, with the axis of the dorsomedian carina dorsal to the axis of the retrodorsal carina in all other species except *C. beccaloniae*, *C. hendersoni*, and *C. pelekomanus*. The patella retrodorsal carina of the female is as strongly developed as or more strongly developed than the retromedian carinae in *C. tristis* but absent or obsolete in *C. nathanorum*. The retromedian carinae are granular in *C. tristis* but costate in *C. nathanorum*. The patella dorsal, retrodorsal, and retroventral intercarinal surfaces of the female (fig. 112) are granular in *C. tristis* but smooth or nearly so in *C. nathanorum*. The pedipalp chela is infusate and similar

in color to the femur and patella in *C. tristis* but immaculate and paler than the femur and patella in *C. shivashankari*. The chela of the adult male is moderately to densely setose in *C. tristis* but sparsely setose in *C. fulvipes*, *C. madraspatensis*, and *C. shivashankari*. The chela manus dorsal surface (between the dorsomedian and digital carinae) is flat in the male and female of *C. tristis*, flat in the male and curved, i.e., slightly to markedly convex, in the female of *C. bastawadei*, *C. beccaloniae*, *C. fulvipes*, *C. nathanorum*, and *C. wroughtoni*, and curved in the male and female of *C. madraspatensis* and *C. shivashankari*. The proximal margin (lobe) of the chela

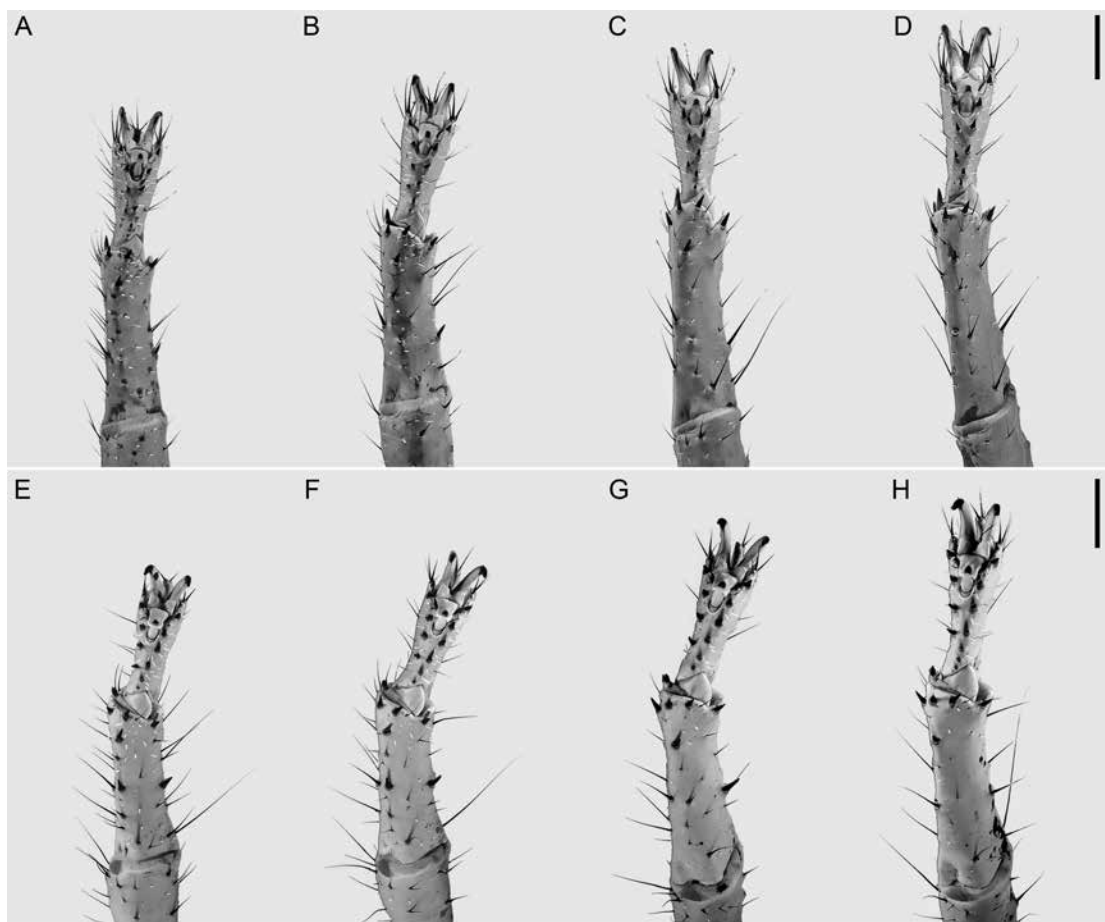


FIGURE 52. *Heterometrus* Ehrenberg, 1828, legs I–IV, tibiae, basitarsi and telotarsi, ventral aspect. **A–D.** *Heterometrus glaucus* (Thorell, 1876), comb. nov. et stat. rev., ♀ (AMNH), Nias Island, Indonesia. **E–H.** *Heterometrus longimanus* (Herbst, 1800), ♂ (AMNH), Kuching, Malaysia. Scale bars = 2 mm.

manus dorsal surface is moderately curved and proximal to the proximal margin of the retrolateral surface in the male (fig. 113A), or aligned with the proximal margin of the condyle (articulation with patella) in the female (fig. 113B) of *C. tristis*; moderately curved and aligned with the proximal margin of the retrolateral surface in the male, or aligned with or proximal to the proximal margin of the retrolateral surface in the female of *C. beccaloniae* and *C. nathanorum*; and markedly curved and proximal to the proximal margin of the condyle in the male and female of *C. hendersoni* and *C. pelekomanus*. The maximum distance between the dorsomedian and

dorsal secondary carinae (DMC–DSC) of the chela manus is similar to the maximum distance between the dorsal secondary and digital carinae (DSC–DC) in the male of *C. tristis*, but greater than the DSC–DC in the male of all other species except *C. beccaloniae*, *C. madraspatensis*, *C. nathanorum*. The dorsal secondary and subdigital carinae of the male are entirely to predominantly granular (fig. 113A) in *C. tristis*, entirely to predominantly costate in *C. nathanorum*, and absent or obsolete in *C. bastawadei* and *C. fulvipes*. The digital carina is entirely to predominantly granular in *C. tristis*, entirely to predominantly costate in *C. nathanorum*, and

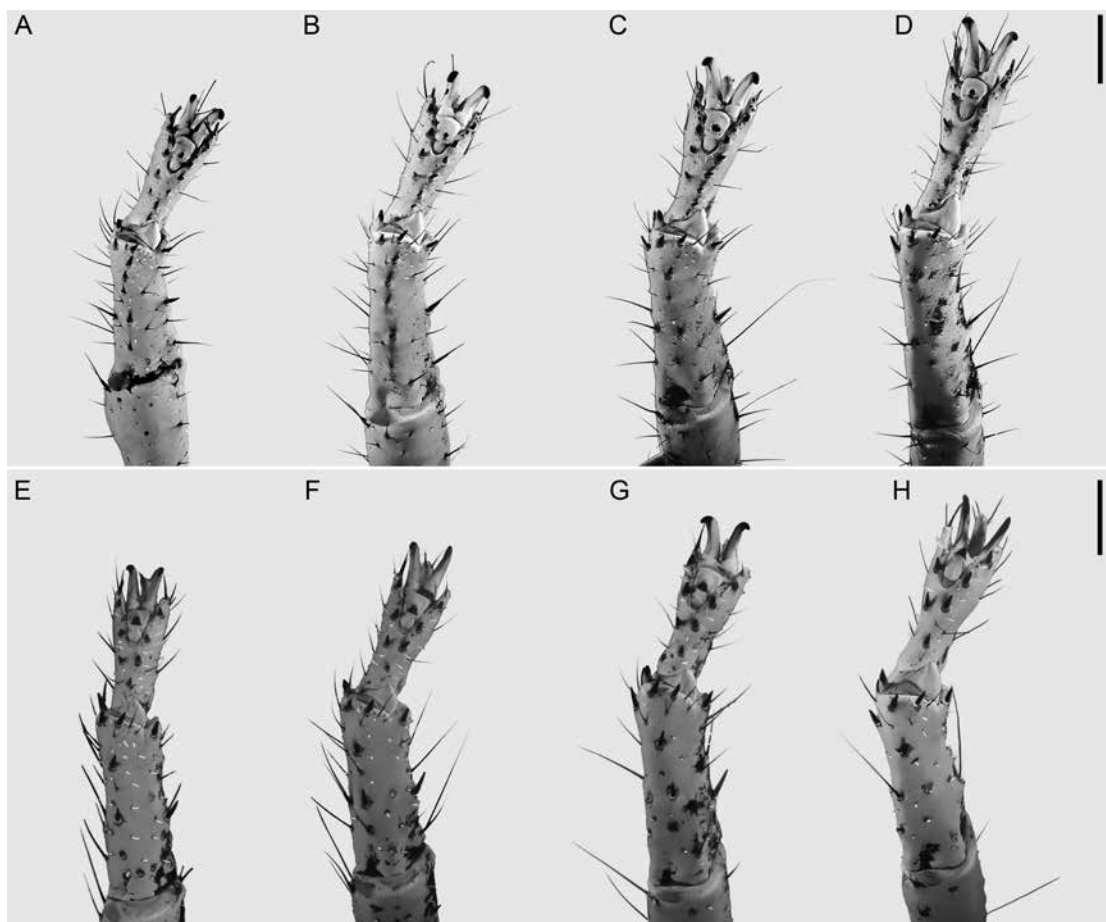


FIGURE 53. *Heterometrus* Ehrenberg, 1828 (A–D), and *Javanimetrus* Couzijn, 1981, stat. nov. et stat. rev. (E–H), legs I–IV, tibiae, basitarsi, and telotarsi, ventral aspect. A–D. *Heterometrus thorellii* (Pocock, 1892), ♀ (AMNH), Pho Kyar Elephant Camp, Yedashe, Myanmar. E–H. *Javanimetrus cyaneus* (Simon, 1872), comb. nov., ♂ (AMNH), Ujung Kulon, Indonesia. Scale bars = 2 mm.

absent or obsolete in *C. bastawadei*, *C. fulvipes*, *C. madraspatensis*, and *C. shivashankari*. The manus dorsal intercarinal surface is without reticulation in *C. tristis* but shallowly reticulate in *C. nathanorum*. The manus ventral surface is angled, with the axis of the retroventral carina ventral to the axis of the ventromedian carina in *C. tristis* but flat, with the axes of the retroventral and ventromedian carinae in approximately the same plane in all other species except *C. beccaloniae*, *C. hendersoni*, and *C. pelekomanus*. The legs are very dark or heavily infusate (figs. 9B, 110, 111) in *C. tristis* but pale or very lightly

infusate in *C. bastawadei*, *C. fulvipes*, *C. hendersoni*, *C. madraspatensis*, and *C. shivashankari*. Macroseta *st* on the retroventral surfaces of the basitarsi of legs I and II is spiniform (fig. 43I–L) in *C. tristis* but setiform in *C. nathanorum* and *C. shivashankari*. The mesial surfaces of mesosomal tergites I–VI are smooth in the male and the lateral surfaces smooth in the female of *C. tristis*, whereas the mesial surfaces are granular in the male of *C. nathanorum*, the lateral surfaces granular in the female of *C. beccaloniae*, *C. hendersoni*, *C. pelekomanus*, and *C. wroughtoni*, and the mesial surfaces granular in the male and the

lateral surfaces granular in the female of *C. bastawadei*, *C. fulvipes*, *C. madraspatensis*, and *C. shivashankari*. The ventral surface of mesosomal sternite VII bears a pair of weakly developed ventrolateral carinae in *C. tristis* and two pairs of moderately to strongly developed ventrosubmedian and ventrolateral carinae in *C. beccaloniae*, *C. hendersoni*, and *C. pelekomanus*. The dorso-submedian carinae are costate on metasomal segments I and II or I–III and granular or costate-granular on III and IV or IV (fig. 58E) in *C. tristis* but granular or costate-granular on segments I–IV in all other species, except the female of *C. beccaloniae*. The ventral intercarinal surfaces of segment IV are granular in the male and female (fig. 60E) of *C. tristis* but smooth in the male and female of *C. wroughtoni*, the male of *C. bastawadei*, *C. fulvipes*, and *C. shivashankari*, and the female of *C. beccaloniae* and *C. nathanorum*. The dorsolateral carinae of metasomal segment V are strong and continuous in *C. tristis* but weak and discontinuous to absent in *C. nathanorum*. The dorsal intercarinal surface of segment V is smooth in the male and female of *C. tristis*, granular in the male and female of *C. bastawadei*, *C. hendersoni*, and *C. pelekomanus*, and granular in the male of *C. wroughtoni*.

DISTRIBUTION: This species is endemic to India and has been recorded in the states of Andhra Pradesh, Karnataka, and Tamil Nadu (fig. 80, table 1). Records of *H. pelekomanus* from Mysore, environs of Bangalore (MNHN RS 7804) in Karnataka, and the Tirumalai Hills, Tirupati (MNHN RS 4499) in Andhra Pradesh, cited by Couzijn (1981), are referable to *C. tristis*.

ECOLOGY: *Chersonesometrus tristis* inhabits the rocky granite or quartzite/sandstone slopes and ravines of several small mountain ranges, e.g., the Tirumalai Hills and the Venkatagiri Hills, at elevations of 150–915 m on the Deccan Plateau (fig. 7B). The known locality records occur in arid to semiarid areas of deciduous broadleaf woodland on clayey to sandy-loam soils. As noted by Henderson (1919: 380), this species inhabits “short burrows,” or scrapes, under large stones, as well as the cracks and crevices of rock and earthen walls,

usually in humid, shaded locations. Specimens observed with UV light detection were abundant in suitable habitat at night and under stones during daytime (P. Jain, personal commun.). The habitat and habitus, especially the dorsoventrally compressed carapace and pedipalp chelae, are consistent with the pelophilous, fossorial and semilithophilous ecomorphotypes (Prendini, 2001b). This species is sympatric with the buthids *Charmus indicus*, *Hottentotta rugiscutis*, and *Lychas tricarinatus* and several species of *Reddyanus* across its distribution.

CONSERVATION STATUS: *Chersonesometrus tristis* is occasionally offered in the exotic pet trade, under the name *H. mysorensis*.

REMARKS: This species was previously accommodated in subgenus *Chersonesometrus* of *Heterometrus* by various authors (e.g., Couzijn, 1981; Tikader and Bastawade, 1983; Fet, 2000).

Kovářík (2004: 29) described *H. mysorensis*, collected in Mysore and Chittoor, and compared it with *H. phipsoni*, noting that *H. mysorensis* “is close to *H. phipsoni*, but has conspicuous rows of granules (carinae) on the chela and only slightly tuberculate patella of pedipalp, whereas in *H. phipsoni* the chela is strongly granulose.”

Kovářík (2004: 29) did not examine the holotype of *Palamnaeus tristis* but suggested based on Henderson’s (1919: 380) figure 3 that it could be a junior synonym of *H. gravimanus* “with which it shares the shape of pedipalps and the presence of carinae on the chela.” However, Couzijn (1981) and Tikader and Bastawade (1983) each presented detailed redescriptions of *H. tristis*, based on the holotype, accompanied by illustrations in the case of Tikader and Bastawade (1983), from which it is clear that *H. mysorensis* is conspecific with *C. tristis*, based on the similar carapace shape and granulation, chela shape, granulation, and carination, as well as metric and meristic data. For example, the total length of the male of *H. mysorensis* is 118 mm, the total length of the male of *C. tristis* is 116 mm, according to Henderson (1919), or 120 mm according to Couzijn (1981), and the total length of the female is 110 mm (Couzijn, 1981). The pectinal tooth count is 16/17 in the male of *H. mysorensis*.

rensis, compared with 17/17 in the male and 14/15 in the female of *C. tristis*. The counts of pro- and retroventral spiniform macrosetae on the leg telotarsi are 5–6/6–7 on legs III and IV in *H. mysorensis*, 4/6, 4–5/6–7, 5/6–7, 5/7 on legs I–IV in the male and 4/5–6, 4/6, 5/6–7, 5/7 on legs I–IV in the female of *C. tristis*. Kovařík (2004) distinguished *H. mysorensis* from *H. wroughtoni* and *H. pelekomanus*, which was regarded as a junior synonym of the latter, by the sexual dimorphism in the pedipalp shape: the pedipalps of the male are longer and narrower than those of the female in *H. mysorensis* unlike *H. pelekomanus*, in which they are similar (this character cannot be evaluated for *H. wroughtoni*, as the adult male of that species is unknown). However, adult male specimens from the vicinity of the type locality of *P. tristis*, in the Chittoor area, examined during the present investigation (fig. 80), which appear to be conspecific with adult female specimens from Chittoor identified as *H. mysorensis* by Kovařík (2009: 42, 86, figs. 92–94) display sexually dimorphic pedipalps, proving that the character cited as diagnostic for *H. mysorensis* by Kovařík (2004, 2009) occurs in *C. tristis*. DNA sequence data obtained from samples originating from the vicinities of the type localities of *H. mysorensis* and *C. tristis* also failed to differentiate among the two species. The combination of evidence leads to the inescapable conclusion that *H. mysorensis* and *C. tristis* are conspecific and the following new synonym is therefore presented: *Heterometrus mysorensis* Kovařík, 2004 = *Chersonesometrus tristis* (Henderson, 1919), syn. nov.

MATERIAL EXAMINED: **INDIA:** viii.1973, Chowdaiah, 1 subad. ♀, 2 juv. ♂ (MNHN RS 6558). **Andhra Pradesh:** *Chittoor Distr.:* Ithepalli/Agarala, NW of, 13°35'N 79°15'E, 340 m, 1.xii.2004, S. Basi, rocky granite hillslopes and ravine, broadleaf savanna with moderate grass layer on sandy loam, many large and small granite boulders, in crevices or cracks in earthen and rock walls in ravine, 2 ♂ [1 ♂ remains], 1 subad. ♂, 1 juv. ♂ (AMNH), 1 juv. ♂ (AMCC [LP 13135]); Palmaner [13°12'N 78°45'E], 6 mi. W, 725 m, 26.ii.1962, E.S. Ross and D.Q. Cavagnaro, 1 juv. ♀ (CAS 9070407); Tirumalai Hills [Tirumala, 13°41'N 79°21'E], Tirupati, R.P. Sreenivasa-Reddy, 1 subad. ♀, 2 juv. ♂, 2 juv. ♀, 1

subad. (MNHN RS 4499). *Kadapa Distr.:* Highway 58, between Rajukunta and Rapur, 14°11'N 79°25'E, 289 m, 12.ii.2004, S. Basi, steep mountain slope, semideciduous broadleaf forest with shale outcrops and loose stones on clayey-loam, in scrape under stone, 1 juv. ♂ (AMCC [LP 13136]), 14°12'N 79°28'E, 148 m, 12.ii.2004, S. Basi, slopes of small rocky hill, semideciduous broadleaf woodland on clayey loam, many quartzite/sandstone outcrops and loose stones, in shallow scrape under stone, 1 juv. ♀ (AMNH). **Karnataka:** *Bengaluru Distr.:* Mysore state, env. Bangalore [Bengaluru, 12°59'N 77°35'E], 8.v.1974, Geethamali, 1 juv. ♀ (MNHN RS 7804). *Cud-dapah Distr.:* Mysore, Kamalapuram [14°37'N 78°40'E], 6.ix.1912, Y.R. C.M., 1 juv. ♀ (BMNH). *Mandya Distr.:* Maddur [Madduru, 12°35'N 77°03'E], iii.2003 [juv. born in captivity on 26.ix.2001], 1 ♀ (AMNH), 1 juv. ♂ (AMCC [LP 2275]), 1 juv. ♀ (AMCC [LP 2276]). *Mysore Distr.:* Mysore [Mysuru, 12°18'N 76°38'E], M. Seiter, 1 ♂, 1 ♀, 1 juv. (NHMW 28529).

Chersonesometrus wroughtoni (Pocock, 1899),
comb. nov.

Figures 10, 16B, 30B, 44I–L, 61E, 62E, 63E, 80,
81C, D, 115, 116, table 1

Palamnaeus wroughtoni Pocock, 1899: 745;
1900a: 85, 89, fig. 26; Henderson, 1919: 381;
Tikader, 1973: 263.

Heterometrus wroughtoni Takashima, 1945: 93;
Kovařík, 2004: 1, 7, 46, 48, 49, 51, 52, tables
2, 3 (part), fig. 31; 2009: 35, 36, 45, 48, 49,
97, 101, tables 1, 2 (part), figs. 168–173, 218,
219; Tahir and Prendini, 2014: 1, 2, 6, 9.

Heterometrus (Chersonesometrus) wroughtoni:
Couzijn, 1981: 16, 44, 88, 158–160, 171, 192,
table 7, figs. 52, 59; Tikader and Bastawade,
1983: 575, 593–598, figs. 1566–1580;
Kovařík, 1998: 137; Fet, 2000: 443.

Heterometrus (Chersonesometrus) wroughtoni:
Bastawade, 2002: 296.

Heterometrus (Chersonesometrus) wroughtoni:
Bastawade and Borkar, 2008: 212, 219, 220
(part).

TYPE MATERIAL: **INDIA:** **Karnataka:** *Bel-gaum Distr.:* *Palamnaeus wroughtoni:* Lectotype

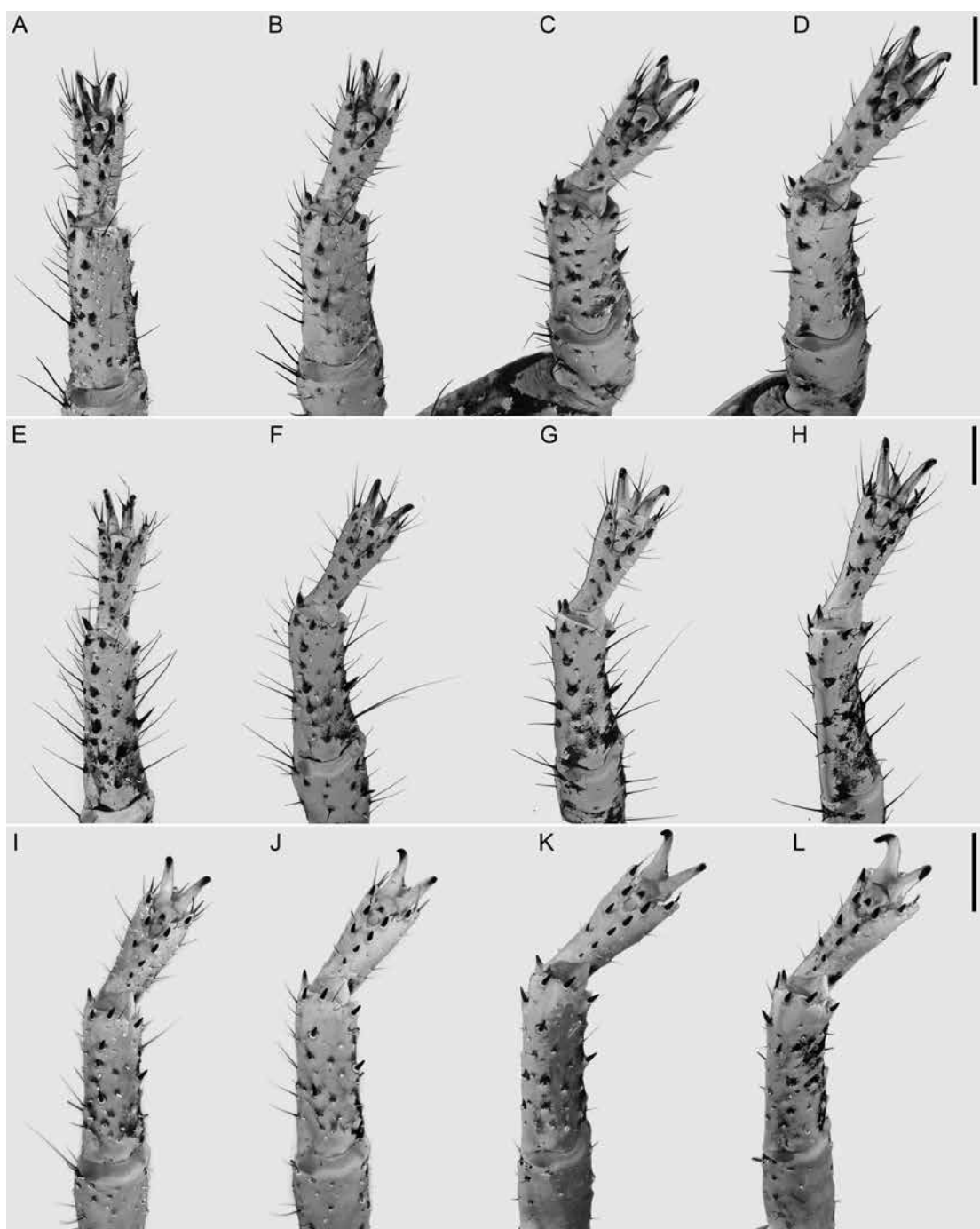


FIGURE 54. *Sahyadrimetrus*, gen. nov., legs I-IV, tibiae, basitarsi and telotarsi, ventral aspect. **A-D.** *Sahyadrimetrus barberi* (Pocock, 1900), comb. nov., holotype ♀ (BMNH 1899.9.24.1). **E-H.** *Sahyadrimetrus rugosus* (Couzijn, 1981), comb. et stat. nov., ♀ (AMNH), Chaliyar River, India. **I-L.** *Sahyadrimetrus tikaderi*, gen. et sp. nov., holotype ♂ (MNHN RS 3265). Scale bars = 2 mm.

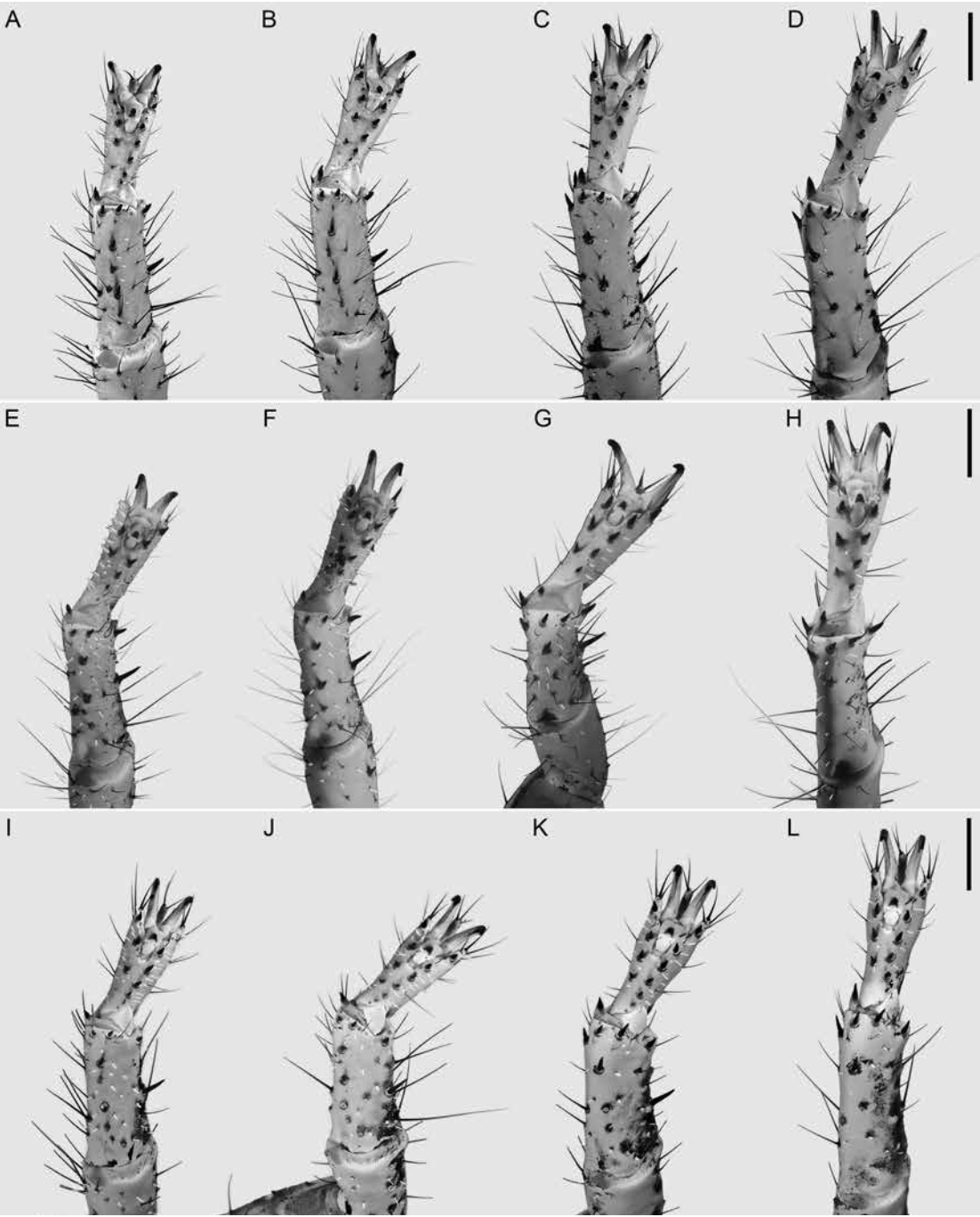


FIGURE 55. *Sahyadrimetrus*, gen. nov., legs I–IV, tibiae, basitarsi and telotarsi, ventral aspect. A–D. *Sahyadrimetrus kanarensis* (Pocock, 1900), comb. nov., ♀ (AMNH), Chaudi, India. E–H. *Sahyadrimetrus mathewi*, gen. et sp. nov., holotype ♂, (AMNH), Poomala, India. I–L. *Sahyadrimetrus scaber* (Thorell, 1876), comb. nov., ♂ (AMNH), Nadpalu, India. Scale bars = 2 mm.

♀, paralectotypes: 3 ♀, 3 juv. ♂, 1 juv. ♀ (BMNH 1897.9.17.1-4.11.20 [BNHS 1163, 1165, 1168, 1169, 1171]), Belgaum [Belagavi, 15°52'N 74°30'E], W.A. Talbot [examined]. **Maharashtra:** *Kolhapur Distr.:* *P. wroughtoni*: Paralectotype ♀ (BMNH 1897.9.5.2 [BNHS 1027]), Gadingal [Gadhinglaj, 16°14'N 74°21'E], Kolhapur, Wray [examined].

Pocock (1899) did not specify types among the material listed from Belgaum and Gadingal, hence all specimens in the original description are syntypes. A single type specimen from Gadingal is numbered BMNH 1897.9.5.2 [BNHS 1027]. However, Couzijn (1981: 158) mistakenly identified one specimen as the holotype: "Maharashtra: Gadingal (Gad-Hinglaj), Belgaum (1 ♀ ad. Holotype, 3 ♂ juv., 4 ♀ juv., leg W.A. Talbot, BM 1897.9.17.1-4.11.20)." Tikader and Bastawade (1983: 598) again referred to "the type specimen 1 ♀" and the type locality as Belgaum. Fet (2000: 443) followed by referring incorrectly to the "holotype: ♀ (BMNH 1897.9.17.1-4.11.20), Gadingal (Gad-Hinglaj), Kolhapur District, Maharashtra; Belgaum, Karnataka, India" and seven paratypes with the same data and number. Examination of the BMNH specimens during the present investigation revealed that all specimens numbered BMNH 1897.17.1-4.11.20 are from Belgaum not Gadingal. Kovařík (2004: 46) correctly designated a lectotype female and the remaining specimens of BMNH 1897.17.1-4.11.20 as paralectotypes, but misidentified the three immature males as adults, and failed to mention the specimen from Gadingal, which is also a paralectotype.

DIAGNOSIS: *Chersonesometrus wroughtoni* may be separated from other species of *Chersonesometrus* as follows. The carapace is markedly dorsoventrally compressed, the lateral surfaces sloping gently (fig. 16B), in *C. wroughtoni*, but vaulted, the lateral surfaces sloping steeply, in *C. fulvipes*, *C. madraspatensis*, and *C. shivashankari*. The carapace interocular surface is granular along the median longitudinal and anterior bifurcated sulci only in the female (fig. 16B) of *C. wroughtoni*, whereas the frontal lobes and medial region of the

interocular surface are granular with smooth areas in the female of *C. bastawadei*, *C. madraspatensis*, *C. pelekomanus*, and *C. shivashankari*. The carapace posterolateral surfaces of the female are smooth in *C. wroughtoni* but granular in *C. bastawadei*, *C. fulvipes*, and *C. madraspatensis*. The cheliceral movable finger prodistal (DI) and retrodistal (DE) teeth are unequal, with the DE tooth considerably smaller than the DI tooth, aligned longitudinally and not opposable in *C. wroughtoni*, but subequal, with the DE tooth only slightly smaller than the DI tooth, and opposable, i.e., forming a bicuspid, in *C. beccaloninae*, *C. hendersoni*, *C. nathanorum*, *C. pelekomanus*, and *C. tristis*. The pedipalp patella dorsal surface is convex, with the axis of the dorsomedian carina dorsal to the axis of the retrodorsal carina (fig. 115) in *C. wroughtoni* but flat or nearly so, with the axes of the dorsomedian and retrodorsal carinae in the same plane, in *C. beccaloninae*, *C. hendersoni*, *C. pelekomanus*, and *C. tristis*. The patella retrodorsal carina of the female is as strongly developed as or more strongly developed than the retromedian carinae in *C. wroughtoni* but absent or obsolete in *C. nathanorum*. The retromedian carinae are granular in *C. wroughtoni* but costate in *C. nathanorum*. The patella dorsal, retrodorsal, and retroventral intercarinal surfaces of the female (fig. 115) are granular in *C. wroughtoni* but smooth or nearly so in *C. nathanorum*. The pedipalp chela is infusate and similar in color to the femur and patella in *C. wroughtoni* but immaculate and paler than the femur and patella in *C. shivashankari*. The chela manus dorsal surface (between the dorsomedian and digital carinae) is flat in the male and curved, i.e., slightly to markedly convex, in the female of *C. wroughtoni*, flat in the male and female of *C. hendersoni*, *C. pelekomanus*, and *C. tristis*, and curved in the male and female of *C. madraspatensis* and *C. shivashankari*. The proximal margin (lobe) of the chela manus dorsal surface is moderately curved and proximal to the proximal margin of the retrolateral surface in the male, or aligned with the proximal margin of the condyle (articulation with patella) in the female (fig. 116) of *C. wroughtoni*; moderately curved and

aligned with the proximal margin of the retrolateral surface in the male, or aligned with or proximal to the proximal margin of the retrolateral surface in the female of *C. beccaloniae* and *C. nathanorum*; and markedly curved and proximal to the proximal margin of the condyle in the male and female of *C. hendersoni* and *C. pelekomanus*. The maximum distance between the dorsomedian and dorsal secondary carinae (DMC–DSC) of the chela manus is greater than the maximum distance between the dorsal secondary and digital carinae (DSC–DC) in the male of *C. wroughtoni*, but greater than the DSC–DC in the male of *C. beccaloniae*, *C. madraspatensis*, *C. nathanorum*, and *C. tristis*. The dorsal secondary and subdigital carinae of the male are entirely to predominantly granular in *C. wroughtoni*, entirely to predominantly costate in *C. nathanorum*, and absent or obsolete in *C. bastawadei* and *C. fulvipes*. The digital carina is entirely to predominantly granular in *C. wroughtoni*, entirely to predominantly costate in *C. nathanorum*, and absent or obsolete in *C. bastawadei*, *C. fulvipes*, *C. madraspatensis*, and *C. shivashankari*. The manus dorsal intercarinal surface is without reticulation in *C. wroughtoni* but shallowly reticulate in *C. nathanorum*. The manus ventral surface is flat, with the axes of the retroventral and ventromedian carinae in approximately the same plane in *C. wroughtoni* but angled, with the axis of the retroventral carina ventral to the axis of the ventromedian carina in *C. beccaloniae*, *C. hendersoni*, *C. pelekomanus*, and *C. tristis*. The legs are very dark or heavily infuscate (fig. 81C, D) in *C. wroughtoni* but pale or very lightly infuscate in *C. bastawadei*, *C. fulvipes*, *C. hendersoni*, *C. madraspatensis*, and *C. shivashankari*. Macroseta *st* on the retroventral surfaces of the basitarsi of legs I and II is spiniform (fig. 44I–L) in *C. wroughtoni* but setiform in *C. nathanorum* and *C. shivashankari*. The mesial surfaces of mesosomal tergites I–VI are smooth in the male and the lateral surfaces granular in the female of *C. wroughtoni*, whereas the mesial surfaces are granular in the male of *C. bastawadei*, *C. fulvipes*, *C. madraspatensis*, and *C. shivashankari*, the mesial surfaces granular in the male and the lat-

eral surfaces smooth in the female of *C. nathanorum*, and the lateral surfaces smooth in the female of *C. tristis*. The ventral surface of mesosomal sternite VII bears a pair of weakly developed ventrolateral carinae in *C. wroughtoni* and two pairs of moderately to strongly developed ventrosubmedian and ventrolateral carinae in *C. beccaloniae*, *C. hendersoni*, and *C. pelekomanus*. The dorsosubmedian carinae are granular or costate-granular on metasomal segments I–IV (fig. 61E) in *C. wroughtoni* but costate on segments I and II or I–III and granular or costate-granular on III and IV or IV in *C. tristis*, and the female of *C. beccaloniae*. The ventral intercarinal surfaces of segment IV are smooth in the male and female (fig. 63E) of *C. wroughtoni* but granular in the male and female of *C. hendersoni*, *C. madraspatensis*, *C. pelekomanus*, and *C. tristis*, the male of *C. beccaloniae* and *C. nathanorum*, and the female of *C. bastawadei*, *C. fulvipes*, and *C. shivashankari*. The dorsolateral carinae of metasomal segment V are strong and continuous in *C. wroughtoni* but weak and discontinuous to absent in *C. nathanorum*. The dorsal intercarinal surface of segment V is granular in the male and smooth in the female of *C. wroughtoni*, granular in female of *C. bastawadei*, *C. hendersoni* and *C. pelekomanus*, and smooth in the male of all other species.

DISTRIBUTION: This species is endemic to India and known from only two localities in the states of Karnataka and Maharashtra (fig. 80, table 1).

ECOLOGY: Little ecological data are available for this species, the known records of which occur on arid, rocky hills on the Deccan Plateau. This species probably constructs burrows under stones, similar to *C. bastawadei* and *C. fulvipes*. The habitus is consistent with the pelophilous, fossorial ecomorphotype (Prendini, 2001b).

CONSERVATION STATUS: This species has not been seen in over a century. Its habitat has been extensively modified and it may be extinct.

REMARKS: This species was previously accommodated in subgenus *Chersonesometrus* of *Heterometrus* by various authors (e.g., Couzijn, 1981; Tikader and Bastawade, 1983; Fet, 2000). *Het-*

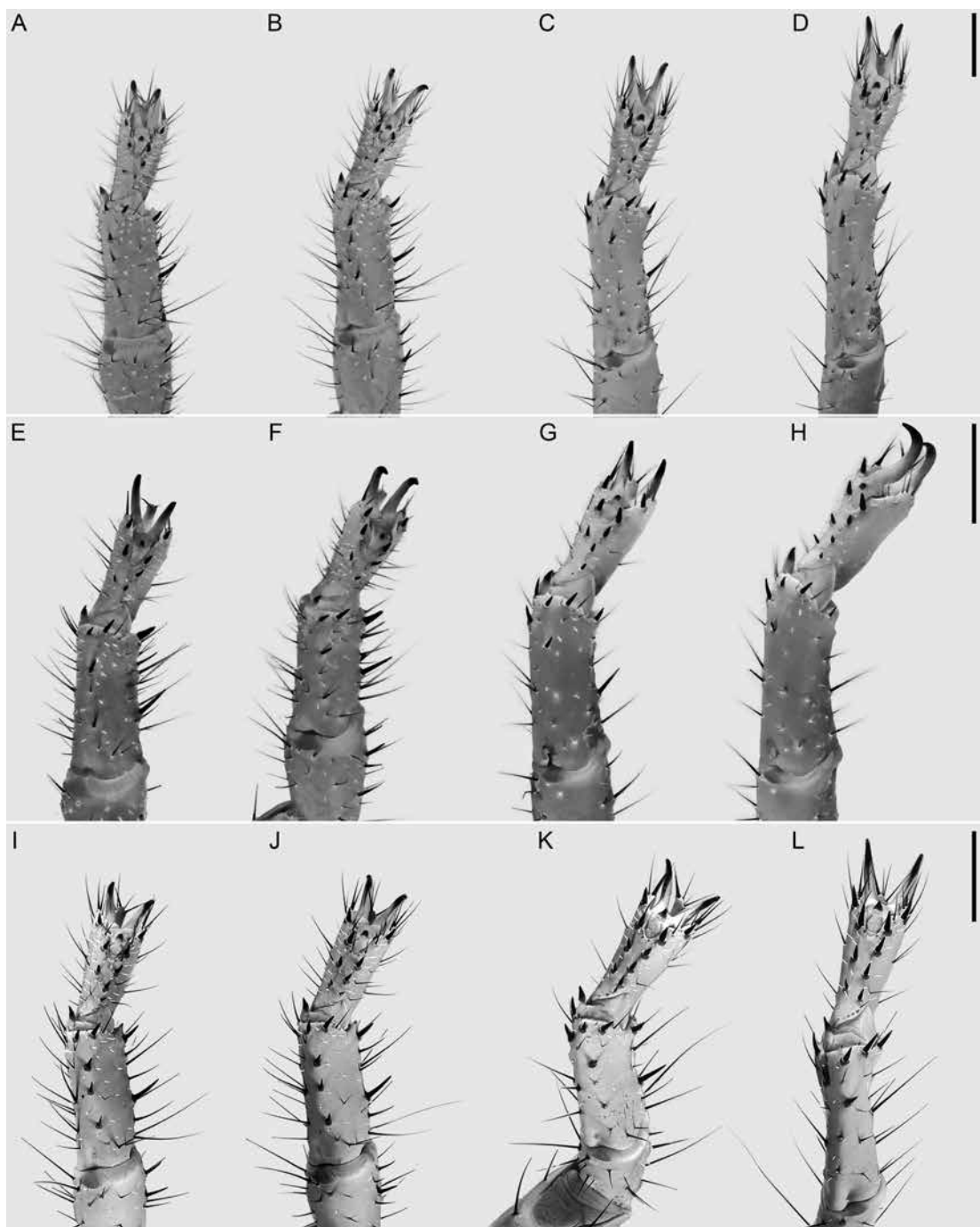


FIGURE 56. *Srilankametrus* Couzijn, 1981, stat. nov. et stat. rev., legs I-IV, tibiae, basitarsi and telotarsi, ventral aspect. **A-D.** *Srilankametrus caesar* (C.L. Koch, 1841), comb. nov. et stat. rev., ♂ (MNHN RS 0079). **E-H.** *Srilankametrus couzijni*, sp. nov., holotype ♂ (BMNH 1896.7.30.121). **I-L.** *Srilankametrus gravimanus* (Pocock, 1894), comb. nov., ♂ (AMNH), Kokmotte, Sri Lanka. Scale bars = 2 mm.

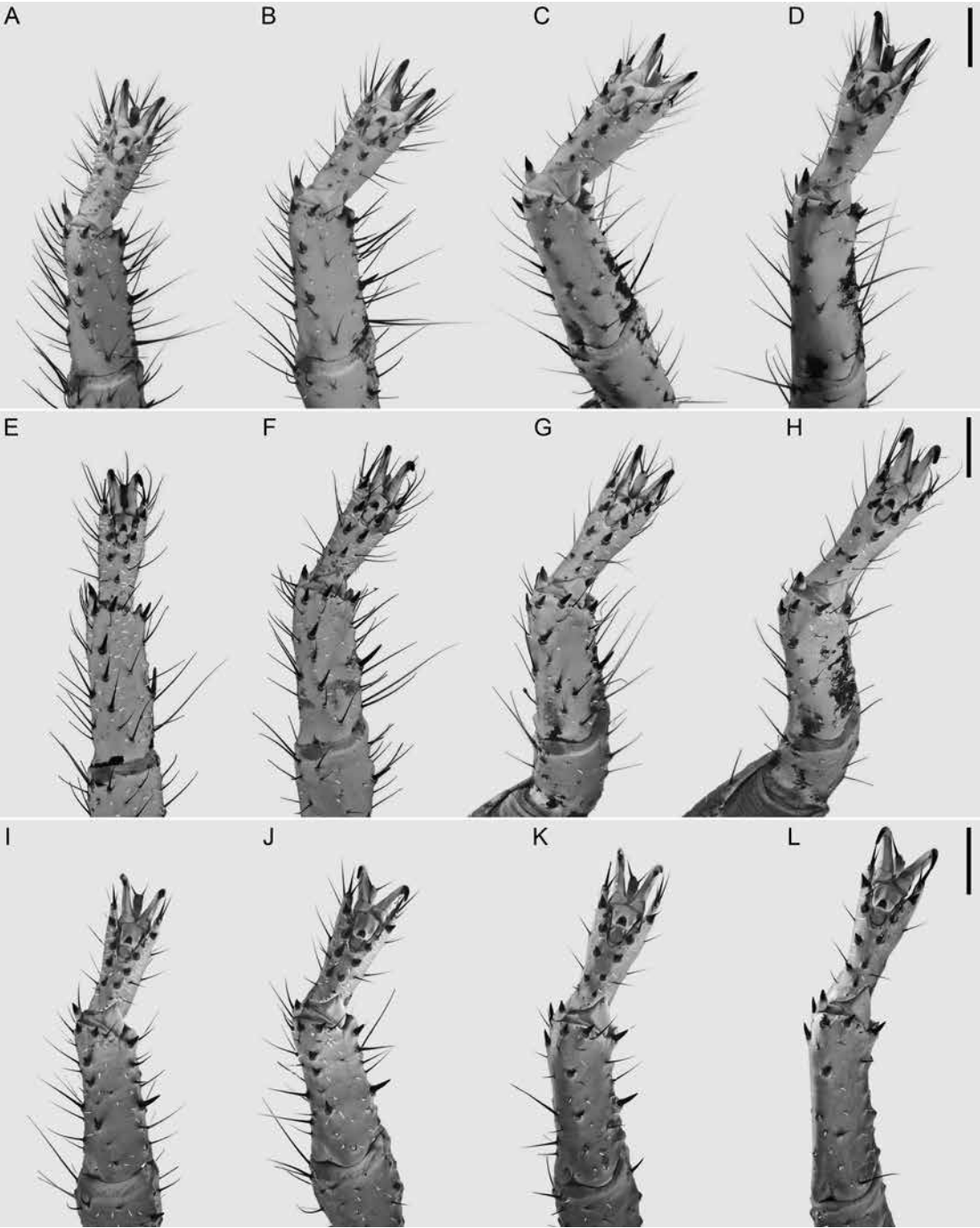


FIGURE 57. *Srilankametrus* Couzijn, 1981, stat. nov. et stat. rev., legs I–IV, tibiae, basitarsi and telotarsi, ventral aspect. A–D. *Srilankametrus indus* (DeGeer, 1778), comb. nov., ♂ (AMNH), Kandy, Sri Lanka. E–H. *Srilankametrus pococki*, sp. nov., holotype ♀ (AMNH), Kodigala, Sri Lanka. I–L. *Srilankametrus serratus* (Pocock, 1900), comb. nov., ♂ (ZMH), Ceylon [Sri Lanka]. Scale bars = 2 mm.

erometrus pelekomanus, described by Couzijn (1981), and upheld by Tikader and Bastawade (1983), was mistakenly synonymized with *H. wroughtoni* by Kovařík (2004) based on the absence of sexual dimorphism in the shape of the pedipalp chela manus, cited as a putative diagnostic difference between *H. wroughtoni* and *H. mysorensis* (= *C. tristis*). The absence of adult males in the type series of *C. wroughtoni*, the adult male of which remains unknown, suggests that Kovařík (2004) mistook ontogenetic character states for diagnostic character states.

***Deccanometrus*, gen. nov.**

Figures 3, 7A, C, G, 8A, H, 9C, 10, 19–21, 33–35, 46–48, 64–66, 117–144, table 1

Type species: *Heterometrus* (*Chersonesometrus*) *scaber obscurus* Couzijn, 1981: 87, 146–149, 170, figs. 46, 58 [= *Deccanometrus obscurus* (Couzijn, 1981), comb. et stat. nov.], here designated.

Heterometrus (*Chersonesometrus*): Couzijn, 1981: 80, 83, 131, 133, 161, 169–171, 173, 182, 184, 186–188, 192, figs. 21, 57–59, 66b, 68, 69 (part); Tikader and Bastawade, 1983: 519, 520, 573 (part); Kovařík, 2004: 1.

Heterometrus: Kovařík, 2004: 1, 2, 49, 51, tables 1, 2 (part); 2009: 34, 35, table 1 (part); Mirza and Sanap, 2009: 486 (part); Javed et al., 2010a: 143 (part); Tahir and Prendini, 2014: 1–5, 11, 20, 21, fig. 1 (part); Aswathi and Sureshan, 2017: 9847 (part).

DIAGNOSIS: Species of *Deccanometrus* may be separated from other Asian scorpionid genera as follows. The carapace is slightly to markedly dorsoventrally compressed, the lateral surfaces sloping gently (figs. 19, 21), in all except two species of *Deccanometrus*, *D. latimanus* and *D. xanthopus*, in which the carapace is vaulted, the lateral surfaces sloping steeply (fig. 20), as in *Gigantometrus*, *Heterometrus*, *Javanimetrus*, three species of *Chersonesometrus*, *C. fulvipes*, *C. madraspatensis*, and *C. shivashankari*, two spe-

cies of *Sahyadrimetrus*, *S. mathewi* and *S. scaber*, and all except three species of *Srilankametrus*, *S. indus*, *S. pococki*, and *S. serratus*. The carapace anterior margin is concave, with the frontal lobes uneven and sloping medially, in all except two species of *Deccanometrus*, *D. latimanus* and *D. xanthopus*, in which the anterior margin is straight, with the frontal lobes evenly rounded or truncate (fig. 20), as in *Gigantometrus*, *Sahyadrimetrus*, and some species of *Chersonesometrus*. The carapace anterolateral margins converge gradually anteriorly in *Deccanometrus* but are subparallel anteriorly in *Javanimetrus* and *Srilankametrus*; the mediolateral margins diverge or converge slightly posteriorly (at the posterolateral sulci) in *Deccanometrus*, but converge markedly posteriorly (at the posterolateral sulci) in *Gigantometrus*, *Heterometrus*, and three species of *Sahyadrimetrus*, *S. kanarensis*, *S. mathewi*, and *S. scaber*. The carapace rostrolateral margin is entire in *Deccanometrus* but distinctly incised adjacent to the posterior lateral ocelli in *Heterometrus*. Anterocular extensions of the superciliary carinae are present in *Deccanometrus* but absent in *Srilankametrus*. The median ocelli are relatively small, the distance between them equal to or greater than the width of an ocellus in *Deccanometrus* but relatively large, the distance between them less than the width of an ocellus in *Heterometrus*; the median ocular tubercle is situated anteromedially to medially, the distance from carapace anterior margin : carapace length (CAM:CL) 0.40–0.50 in *Deccanometrus*, but posteromedially, CAM:CL 0.51–0.62 in *Chersonesometrus*. The interocular suture is present in all species of *Deccanometrus* except *D. liurus*, in which it is absent, as in *Heterometrus*, *Javanimetrus*, *Sahyadrimetrus*, and two species of *Srilankametrus*. The carapace posterior sutures are present, extending past the median ocular tubercle, and connected anteriorly to the posterior bifurcations of the interocular suture in all species of *Deccanometrus* except *D. liurus*, in which the posterior sutures and posterior bifurcations of the interocular suture are disconnected; present, extending to the

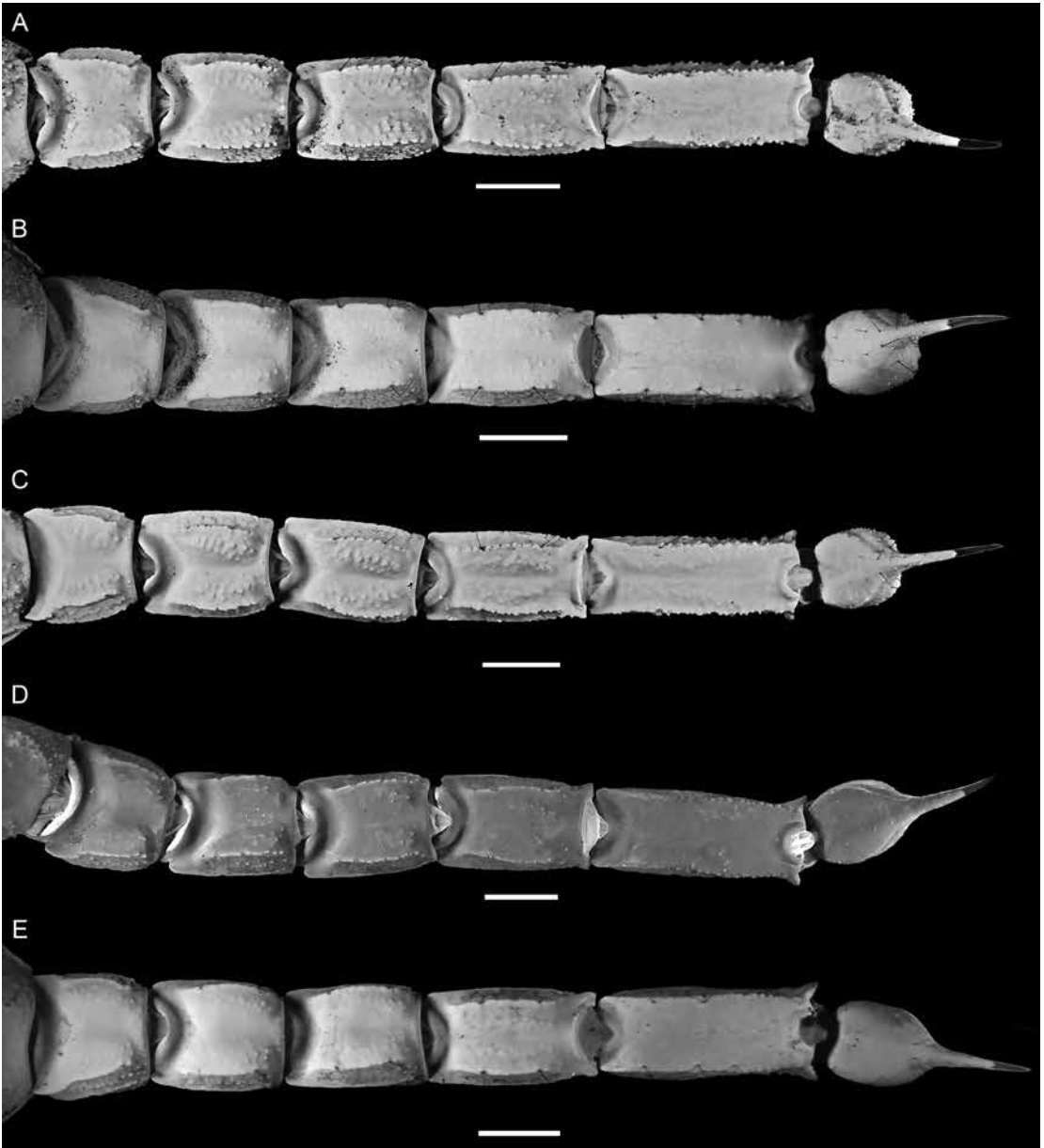


FIGURE 58. *Chersonesometrus* Couzijn, 1978, stat. nov. et stat. rev., metasoma and telson, dorsal aspect. **A.** *Chersonesometrus bastawadei*, sp. nov., holotype ♀ (AMNH), Naganath Temple, India. **B.** *Chersonesometrus beccaloniae* (Kovařík, 2004), comb. nov., ♀ (AMNH), Yelagiri Hills, India. **C.** *Chersonesometrus hendersoni*, sp. nov., paratype ♀ (AMNH), Tungabhadra River, India. **D.** *Chersonesometrus pelekomanus* (Couzijn, 1981), comb. nov., paratype ♀ (SMF RII/329). **E.** *Chersonesometrus tristis* (Henderson, 1919), comb. nov., ♀ (AMNH), Maddur, India. Scale bars = 5 mm.

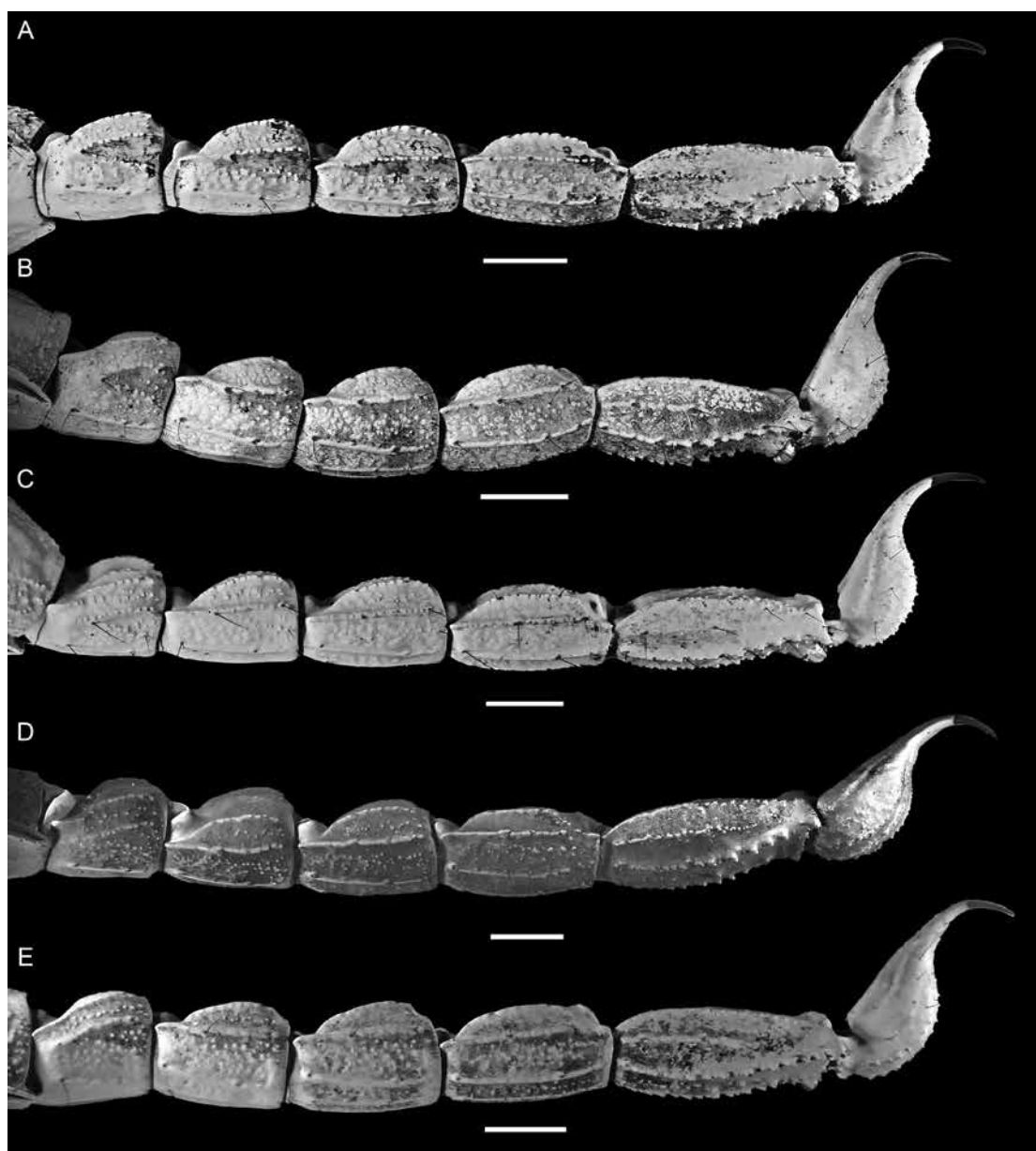


FIGURE 59. *Chersonesometrus* Couzijn, 1978, stat. nov. et stat. rev., metasoma and telson, lateral aspect. **A.** *Chersonesometrus bastawadei*, sp. nov., holotype ♀ (AMNH), Naganath Temple, India. **B.** *Chersonesometrus beccaloniae* (Kovářík, 2004), comb. nov., ♀ (AMNH), Yelagiri Hills, India. **C.** *Chersonesometrus hendersoni*, sp. nov., paratype ♀ (AMNH), Tungabhadra River, India. **D.** *Chersonesometrus pelekomanus* (Couzijn, 1981), comb. nov., paratype ♀ (SMF RII/329). **E.** *Chersonesometrus tristis* (Henderson, 1919), comb. nov., ♀ (AMNH), Maddur, India. Scale bars = 5 mm.

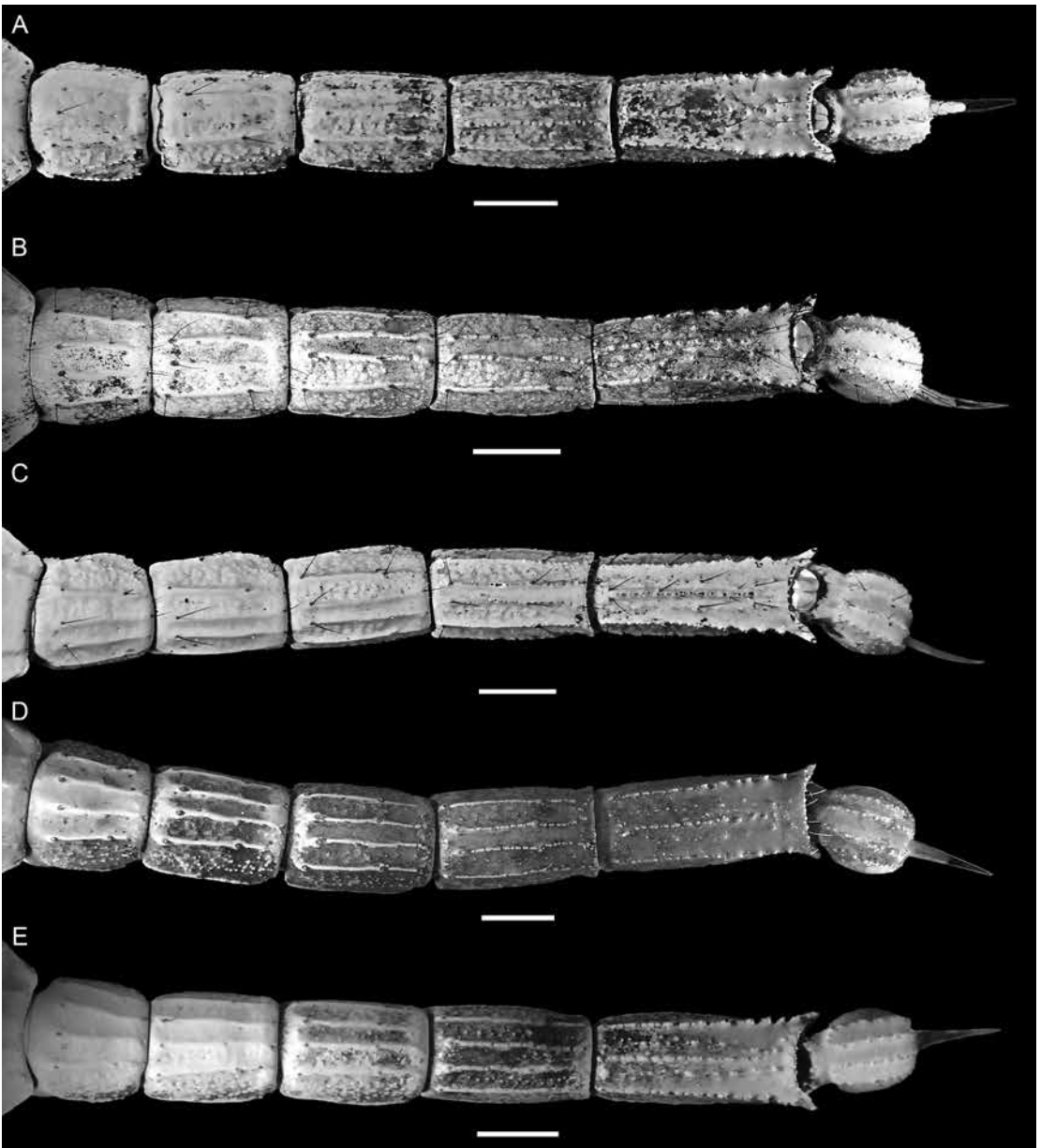


FIGURE 60. *Chersonesometrus* Couzijn, 1978, stat. nov. et stat. rev., metasoma and telson, ventral aspect. **A.** *Chersonesometrus bastawadei*, sp. nov., holotype ♀ (AMNH), Naganath Temple, India. **B.** *Chersonesometrus beccaloniae* (Kovářík, 2004), comb. nov., ♀ (AMNH), Yelagiri Hills, India. **C.** *Chersonesometrus hendersoni*, sp. nov., paratype ♀ (AMNH), Tungabhadra River, India. **D.** *Chersonesometrus pelekomanus* (Couzijn, 1981), comb. nov., paratype ♀ (SMF RII/329). **E.** *Chersonesometrus tristis* (Henderson, 1919), comb. nov., ♀ (AMNH), Maddur, India. Scale bars = 5 mm.

median ocular tubercle, and connected by a short cross-suture anterior to the postocular depression in *Heterometrus*; and absent in *Javanimetrus*, *Sahyadrimetrus*, and two species of *Srilankametrus*. The cheliceral movable finger prodistal (DI) and retrodistal (DE) teeth are unequal, with the DE tooth considerably smaller than the DI tooth, aligned longitudinally and not opposable, in all *Deccanometrus* except *D. liurus* and *D. ubicki*, in which the DI and DE teeth are opposable, i.e., forming a bicusps, resembling *Heterometrus* and some species of *Chersonesometrus*, in which the DI and DE teeth are subequal, with the DE tooth only slightly smaller than the DI tooth, and opposable. The pedipalp patella dorsomedian carina of the female is entirely to predominantly granular or costate (fig. 142) in all except three species of *Deccanometrus*, *D. latimanus*, *D. liurus*, and *D. ubicki*, in which the carina is absent or obsolete (figs. 124, 128, 140), as in *Heterometrus*, *Javanimetrus*, all except one species of *Sahyadrime-trus*, *S. rugosus*, and all except one species of *Srilankametrus*, *S. caesar*. The patella retromedian carinae of the female are absent or obsolete (figs. 124, 128, 140, 142) in all except three species of *Deccanometrus*, *D. bengalensis*, *D. obscurus*, and *D. phipsoni*, in which the carinae are granular or costate, as in *Chersonesometrus*, three species of *Sahyadrimetrus*, *S. barberi*, *S. rugosus*, and *S. tikaderi*, and two species of *Srilankametrus*, *S. gravimanus* and *S. yaleensis*. The prominent spiniform granule of the patella proventral carina is absent in *Deccanometrus* (figs. 121, 124, 128, 132, 136, 140, 142) but present in *Heterometrus*. The patella dorsal, retrodorsal, and retroventral intercarinal surfaces of the female are smooth or nearly so (figs. 124, 128, 140, 142) in all species of *Deccanometrus* except *D. obscurus* and *D. phipsoni*, in which the surfaces are granular, as in all species of *Chersonesometrus* except *C. nathanorum*. The pedipalp chela of the adult male is moderately to densely setose (figs. 122B–D, 125, 133, 137, 141A) in all species of *Deccanometrus* except *D. xanthopus*, in which the chela is sparsely setose (fig. 143A),

as in *Gigantometrus*, *Heterometrus*, *Javanimetrus*, most species of *Srilankametrus*, and some species *Chersonesometrus*. The distance between the chela manus dorsomedian and promedian carinae or setal rows (DMC–PMC) is slightly to markedly greater than the distance between the promedian and proventral carinae or setal rows (PMC–PVC) in *Deccanometrus* whereas the DMC–PMC is similar to the PMC–PVC in *Heterometrus*. The dorsomedian carina becomes obsolete proximally in all except two species of *Deccanometrus*, *D. obscurus* and *D. phipsoni*, in which the carina is continuous to the proximal edge of the manus (figs. 133, 134, 137, 138), as in *Chersonesometrus* and *Gigantometrus*. The dorsal secondary, subdigital, and digital carinae (setal rows) are well separated along their entire length in *Deccanometrus*, whereas the proximal half of the dorsal secondary carina, distal half of the subdigital carina and distal third of the digital carina are closely adjacent in *Chersonesometrus* and *Gigantometrus*. The dorsal secondary and subdigital carinae of the male are absent or obsolete in *Deccanometrus* but present and entirely to predominantly granular or costate in *Gigantometrus*, all species of *Chersonesometrus* except *C. bastawadei* and *C. fulvipes*, and all species of *Srilankametrus* except *S. indus* and *S. pococki*. The chela manus digital and retromedian carinae are similarly developed (figs. 122, 125, 126, 129, 133, 134, 137, 138, 141, 143, 144) in *Deccanometrus*, whereas the retromedian carina is more pronounced than the digital carina in *Chersonesometrus*. The retromedian carina of the male is absent or obsolete in *Deccanometrus* but entirely to predominantly granular in *Gigantometrus*, *Srilankametrus caesar*, and *S. serratus*, and entirely to predominantly costate in *Chersonesometrus*, *Srilankametrus couzijni*, *S. gravimanus*, and *S. yaleensis*. The depression in the dorsal surface of the chela manus, proximal to the fixed finger of the adult male, is absent or obsolete (figs. 122B–D, 125, 133, 137, 141A, 143A) in *Deccanometrus* but present and distinct in *Heterometrus*. The chela manus dorsal surface is shallowly reticulate (figs. 122, 125, 126, 129,

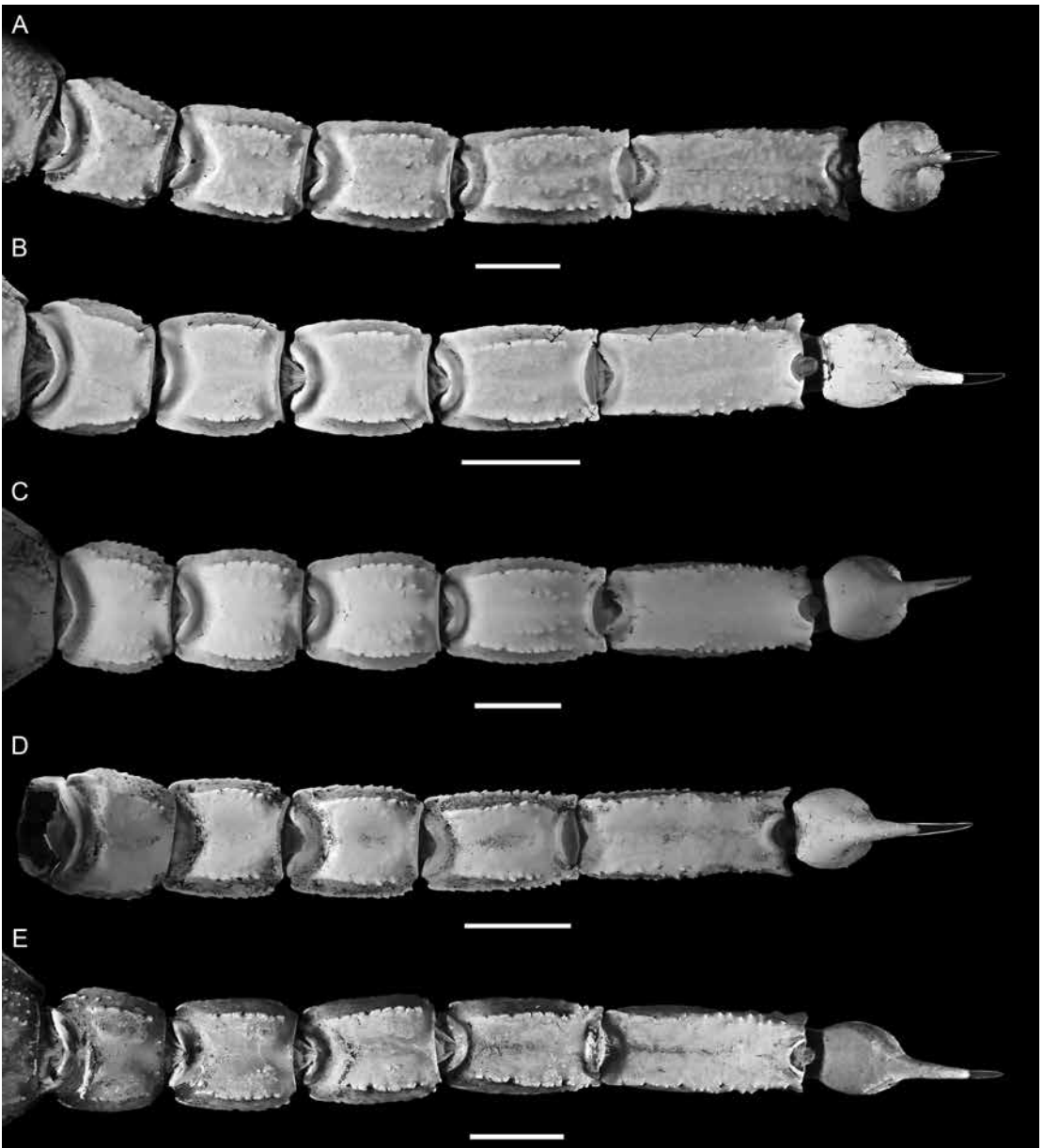


FIGURE 61. *Chersonesometrus* Couzijn, 1978, stat. nov. et stat. rev., metasoma and telson, dorsal aspect. **A.** *Chersonesometrus fulvipes* (C.L. Koch, 1837), comb. nov., ♂ (BMNH 1896.7.30.91-92). **B.** *Chersonesometrus shivashankari*, sp. nov., paratype ♀ (BMNH), Hampasagar, India. **C.** *Chersonesometrus madraspatensis* (Pocock, 1900), comb. nov., ♂ (CAS 9071142). **D.** *Chersonesometrus nathanorum*, sp. nov., subad. ♂ holotype (MNHN RS 3145). **E.** *Chersonesometrus wroughtoni* (Pocock, 1899), comb. nov., paralectotype ♀ (BMNH 1897.9.17.1-4, 11, 20). Scale bars = 5 mm.

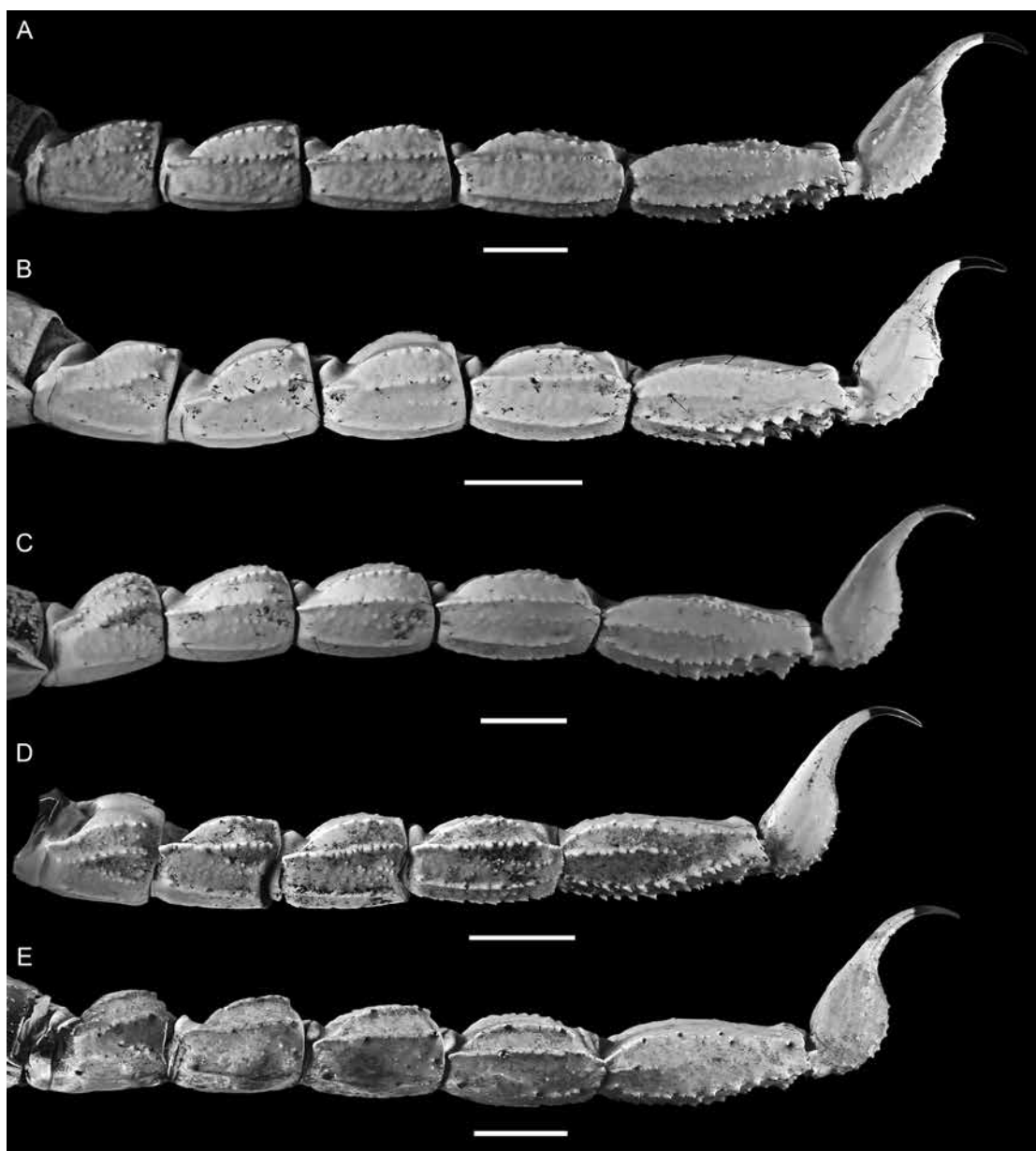


FIGURE 62. *Chersonesometrus* Couzijn, 1978, stat. nov. et stat. rev., metasoma and telson, lateral aspect. **A.** *Chersonesometrus fulvipes* (C.L. Koch, 1837), comb. nov., ♂ (BMNH 1896.7.30.91-92). **B.** *Chersonesometrus shivashankari*, sp. nov., paratype ♀ (BMNH), Hampasagar, India. **C.** *Chersonesometrus madraspatensis* (Pocock, 1900), comb. nov., ♂ (CAS 9071142). **D.** *Chersonesometrus nathanorum*, sp. nov., subad. ♂ holotype (MNHN RS 3145). **E.** *Chersonesometrus wroughtoni* (Pocock, 1899), comb. nov., paralectotype ♀ (BMNH 1897.9.17.1-4, 11, 20). Scale bars = 5 mm.

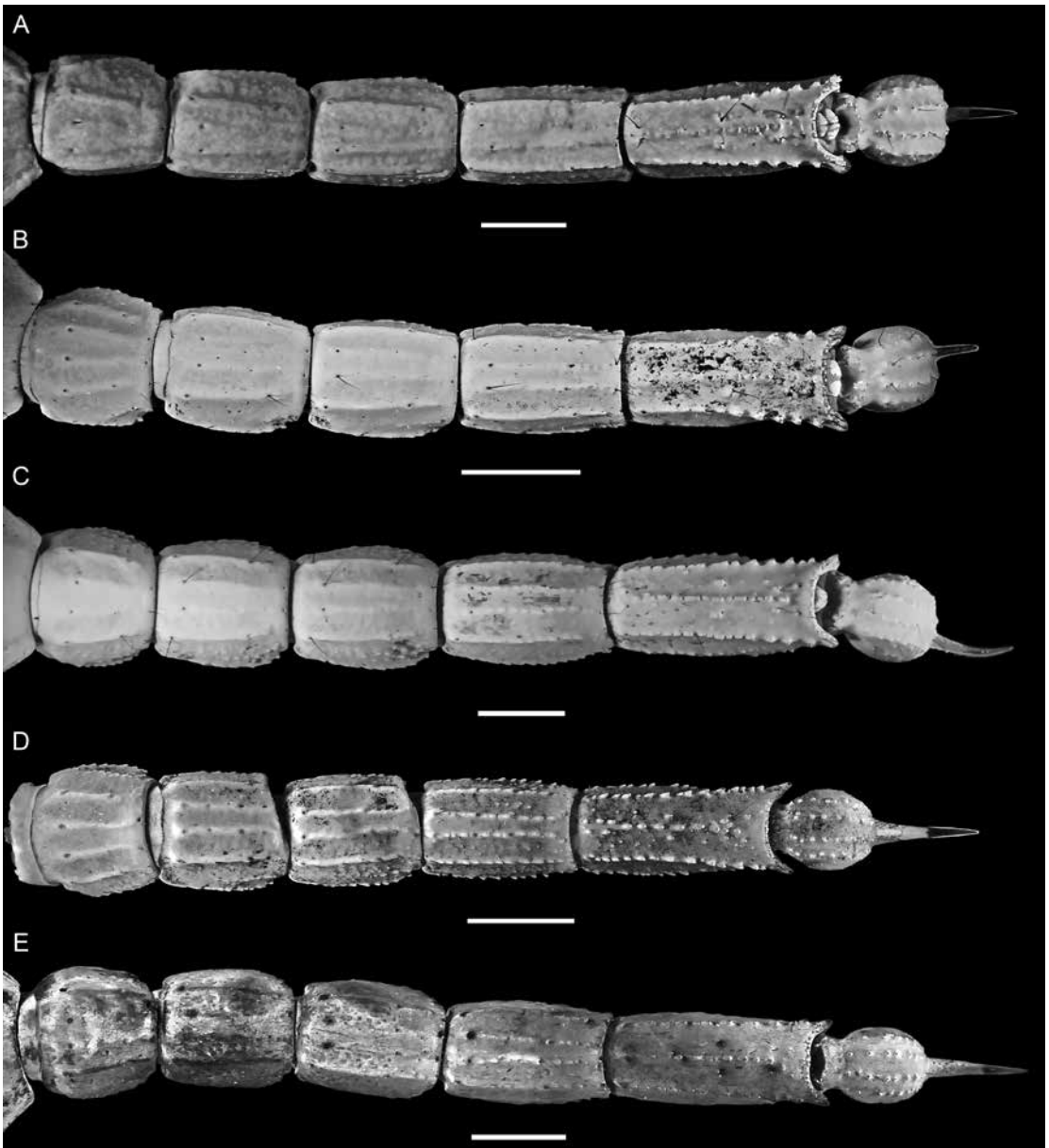


FIGURE 63. *Chersonesometrus* Couzijn, 1978, stat. nov. et stat. rev., metasoma and telson, ventral aspect. **A.** *Chersonesometrus fulvipes* (C.L. Koch, 1837), comb. nov., ♂ (BMNH 1896.7.30.91-92). **B.** *Chersonesometrus shivashankari*, sp. nov., paratype ♀ (BMNH), Hampasagar, India. **C.** *Chersonesometrus madraspatensis* (Pocock, 1900), comb. nov., ♂ (CAS 9071142). **D.** *Chersonesometrus nathanorum*, sp. nov., subad. ♂ holotype (MNHN RS 3145). **E.** *Chersonesometrus wroughtoni* (Pocock, 1899), comb. nov., paralectotype ♀ (BMNH 1897.9.17.1-4, 11, 20). Scale bars = 5 mm.

141, 143, 144) in all except two species of *Deccanometrus*, *D. obscurus* and *D. phipsoni*, in which the surface is without reticulation (figs. 133, 134, 137, 138), as in *Gigantometrus*, *Srilankametrus*, most species of *Chersonesometrus*, and all except three species of *Heterometrus*, *H. glaucus*, *H. laevigatus*, and *H. thorellii*; the dorsal surface is finely to coarsely granular in all species of *Deccanometrus* except *D. ubicki*, in which the surface is smooth, as in *Heterometrus*, *Javanimetrus*, and two species of *Sahyadrimetrus*, *S. kanarensis* and *S. tikaderi*. The chela manus retrolateral intercarinal surfaces are granular (figs. 122, 125, 126, 129, 133, 134, 137, 138, 143) in all species of *Deccanometrus* except *D. ubicki*, in which the surfaces are smooth or nearly so (fig. 141), as in *Heterometrus*, *Javanimetrus* and some species of *Sahyadrimetrus*. The chela manus ventral surface is flat, with the axes of the retroventral and ventromedian carinae in approximately the same plane in *Deccanometrus* but angled, with the axis of the retroventral carina ventral to the axis of the ventromedian carina in *Javanimetrus*, four species of *Chersonesometrus*, *C. beccaloniae*, *C. hendersoni*, *C. pelekomanus*, and *C. tristis*, and two species of *Srilankametrus*, *S. indus* and *S. pococki*. The pro- and retrolateral surfaces of the tibiae of legs I and II each bear a row of two or three spiniform macrosetae (figs. 46–48) in *Deccanometrus* and scattered, setiform macrosetae, not arranged in a definite row, in *Heterometrus*. The pseudonychium (dactyl) of the telotarsi of legs I–IV is reduced and rounded (figs. 46–48) in *Deccanometrus* but prominent and acuminate in *Heterometrus*. Macroseta *st* on the retroventral surface of the basitarsus of leg I is spiniform (figs. 46–48) in *Deccanometrus* but usually setiform in *Heterometrus*, and *sb* on the retroventral surface of the basitarsus of leg III is setiform in *Deccanometrus* but spiniform in *Javanimetrus* and *Sahyadrimetrus*. The pectinal first proximal median lamella (scape) of the female is distinctly angular, $\geq 90^\circ$ but $< 180^\circ$ (figs. 33–35) in *Deccanometrus* but straight or shallowly curved in *Srilankametrus*. The mesial surfaces of mesosomal tergites I–VI of the male

are smooth (figs. 119, 123A, B, 130, 135A, B, 139A, B) in all except one species of *Deccanometrus*, *D. xanthopus*, in which the surfaces are granular (fig. 127C, D), as in *Gigantometrus*, some species of *Chersonesometrus*, and two species of *Sahyadrimetrus*, *S. mathewi* and *S. scaber*. The lengths of metasomal segments I and II are approximately equal to or less than their respective widths (figs. 64–66) in *Deccanometrus* but markedly greater than their respective widths in *Gigantometrus*. The ventrosubmedian and ventrolateral carinae are granular or costate-granular on metasomal segment IV only and costate on segments I–III (figs. 65, 66) in *Deccanometrus* but granular on segments I–IV, II–IV (costate on I), or III and IV (costate on I and II) in *Gigantometrus*. The ventral intercarinal surfaces of metasomal segment IV are smooth in *Deccanometrus* but sparsely granular in *Javanimetrus*. The dorsosubmedian carinae of metasomal segment V are vestigial (fig. 64) in *Deccanometrus* but partial in *Gigantometrus* and absent in *Heterometrus*. The dorsal intercarinal surface of segment V is smooth in *Deccanometrus* but granular in *Gigantometrus*, and some species of *Chersonesometrus* and *Srilankametrus*. The width of the telson vesicle is approximately equal to or less than the width of metasomal segment V in the female of *Deccanometrus* but greater than the width of segment V in the female of *Gigantometrus* and the vesicle is globose in *Deccanometrus* but elongate in *Heterometrus*, *Javanimetrus*, *Sahyadrimetrus*, and all except three species of *Srilankametrus*, *S. indus*, *S. pococki*, and *S. serratus*.

ETYMOLOGY: The generic name refers to the Deccan Plateau, covering an area of approximately 422,000 km² between the Western Ghats and the Eastern Ghats of the Indian subcontinent, and traversing the central Indian states of Maharashtra, Karnataka, Telangana, and Andhra Pradesh. Along with many other taxa, most species of the genus are endemic to or associated with the Deccan Plateau.

INCLUDED SPECIES: *Deccanometrus*, gen. nov., is hereby created to accommodate seven

species, formerly assigned to subgenera *Cheronesometrus*, *Heterometrus*, and *Srilankametrus* of *Heterometrus* by various authors (Couzijn, 1981; Tikader and Bastawade, 1983; Fet, 2000), one of which was formerly recognized at the rank of subspecies, recovered as a monophyletic group by phylogenetic analysis of morphological characters and DNA sequences from the nuclear and mitochondrial genomes (fig. 10): *Deccanometrus bengalensis* (C.L. Koch, 1841), comb. nov.; *Deccanometrus latimanus* (Pocock, 1894), comb. nov.; *Deccanometrus liurus* (Pocock, 1897), comb. nov.; *Deccanometrus obscurus* (Couzijn, 1981), comb. et stat. nov.; *Deccanometrus phipsoni* (Pocock, 1893), comb. nov.; *Deccanometrus ubicki* (Kovářík, 2004), comb. nov.; and *Deccanometrus xanthopus* (Pocock, 1897), comb. nov.

DISTRIBUTION: *Deccanometrus*, gen. nov., is distributed across the Indian subcontinent (figs. 3, 117, 118, table 1), with records confirmed from China (in the Tibet Autonomous Region only), India (Andhra Pradesh, Assam, Chhattisgarh, Gujarat, Haryana, Himachal Pradesh, Karnataka, Jharkhand, Madhya Pradesh, Maharashtra, Odisha, Rajasthan, Tamil Nadu, Telangana, Uttarakhand, Uttar Pradesh, West Bengal, and the union territory of Puducherry), Nepal and Pakistan (in Khyber Pakhtoon Khwa and perhaps Azad Kashmir). The presence of this genus in Bangladesh, while likely, requires confirmation.

ECOLOGY: The species of *Deccanometrus* for which data are available, occur in habitats ranging from evergreen forest, through deciduous woodland to semiarid savanna, at elevations of 300–1030 m above sea level. Based on morphology and available habitat data, all species of the genus appear to be pelophilous and fossorial, constructing burrows under stones or, in the case of *D. xanthopus*, in open ground. Some species, e.g., *D. liurus* and *D. phipsoni*, are markedly dorsoventrally compressed, suggesting a semilithophilous habit.

CONSERVATION STATUS: *Deccanometrus bengalensis* and *D. latimanus* are harvested, dried, and consumed for medicinal purposes in India

(Majumder and Dey, 2005) and Pakistan (Tahir and Prendini, 2014), respectively, and *D. bengalensis* is occasionally harvested for the commercial trade in exotic pets.

Deccanometrus bengalensis (C.L. Koch, 1841),
comb. nov.

Figures 10, 19A, B, 33A, B, 46A–D, 64A, 65A,
66A, 117, 119–122, table 1

Buthus bengalensis C.L. Koch, 1841b: 3–5, pl.
CCXC, fig. 696; 1850: 88; Thorell, 1876b:
220; Moritz and Fischer, 1980: 310; Couzijn,
1981: 142; Kovářík, 2004: 7, 9.

Palamnaeus spinifer: Pocock, 1892: 38–41
(misidentification, part); 1894c: 316
(misidentification, part).

Scorpio bengalensis: Pocock, 1892: 39; 1893: 310,
312; Kraepelin, 1894: 25, 31, 37, 46, 47, 49,
51–53, pl. I, fig. 30 (part); Pocock, 1894a: 72.

Heterometrus bengalensis: Kraepelin, 1899: 110,
114, 115 (part); Werner, 1902: 601; Kraepelin,
1913: 166 (part); Borelli, 1915: 463;
Lampe, 1918: 198; Roewer, 1943: 228;
Takashima, 1945: 93; Pérez Minnocci, 1974:
38; Brignoli, 1985: 415; Hjelle, 1990: 51, fig.
2.24; McCormick and Polis, 1990: 298;
Kovářík, 2004: 1, 7–9 (part), 44, 51–53,
tables 2, 3, fig. 10; 2009: 34–36, 48, 49, 74,
99, tables 1, 2, figs. 8–13, 180, 181; Warburg,
2012a: 85.

Palamnaeus bengalensis: Pocock, 1900a: 85,
94–96; Kanungo, 1954: 536–539, figs. 1, 2;
Srivastava, 1955: 85–91, text-figs. 1–5;
Sinha, 1966: 221, 222, table; Srivastava and
Kanungo, 1966: 629–632, tables 1–3; Sinha
and Kanungo, 1967: 386–390, figs. 1–3;
Kovářík, 2004: 44; Warburg, 2012a: 82, 85,
table 1.

Palamnaeus phipsoni: Pocock, 1900a: 85, 94–96
(misidentification, part).

Heterometrus (Scorpio) bengalensis: Kraepelin,
1901: 271.

Heterometrus longimanus: Kraepelin, 1913: 166 (misidentification, part); Kopstein, 1921: 129 (misidentification, part).

Heterometrus longimanus longimanus: Giltay, 1935: 2 (part); Takashima, 1945: 90 (part).

Heterometrus (Heterometrus) bengalensis: Couzijn, 1981: 38, 73, 75–77, 80, 85, 88, 89, 117–120, 167, 173, 174, 177, 178, 183, 184, 189–191, table 7, figs. 17b, 18, 19, 21, 62, 63, 71 (part); Tikader and Bastawade, 1983: 522, 538–544 (part), figs. 1445–1457; Biswas, 1984: 320, 321; Kovařík, 1998: 137 (part); Fet, 2000: 432 (part); Majumder and Dey, 2005: 13, 14.

Heterometrus (Chersonesometrus) fastigosus: Couzijn, 1981: 22, 41, 87, 120, 140–142, 169, 170, 192, table 7, figs. 4d, 42, 57 (synonymized by Kovařík, 2004: 1, 7, 9, 44); Tikader and Bastawade, 1983: 574, 587–593, figs. 1553–1565; Kovařík, 1998: 136; Fet, 2000: 432, 438, 439; Kovařík, 2002: 3, 17; 2004: 1, 9, 44.

Heterometrus (Chersonesometrus) phipsoni: Couzijn, 1981: 153, 155, 157–159, 169, 180 (misidentification, part); Fet, 2000: 442 (part).

Heterometrus (Chersonesometrus) phipsoni phipsoni: Couzijn, 1981: 43, 87, 149–151, 153, 170, 192, table 7 (misidentification, part).

Heterometrus cf. (*Chersonesometrus*) *hipponi*: Kovařík, 1997: 183 (misidentification).

Heterometrus fastigosus: Kovařík, 2004: 7, 9; Zhu and Yang, 2007: 95.

Heterometrus nepalensis Kovařík, 2004: 1, 7, 29, 31, 32, 51, 52, tables 1, 2, fig. 22; 2009: 35, 42, 48, 49, 79, 100, table 1, figs. 47–49, 205; syn. nov.

Heterometrus phipsoni: Kovařík, 2004: 1, 4, 29, 34, 44, 49, 51, 52, tables 2, 3 (part); 2009: 35, 36, 42, 43, 48, tables 1, 2 (part).

Heterometrus tibetanus Lourenço et al., 2005: 1, 5, 10–14, table 1, figs. 18–35; Zhu and Yang, 2007: 95; Kovařík, 2009: 35, 45, table 1; Di et al., 2013: 52, 86, 88, 94, 95, fig. 138; syn. nov.

Heterometrus phipsoni: Mirza and Sanap, 2009: 488 (part); Aswathi and Sureshan, 2017: 9847 (part).

TYPE MATERIAL: CHINA: Tibet Autonomous Region: Ngari Prefecture: *Heterometrus tibetanus*: Holotype ♂ (MNHN RS 8608) [examined], 2 ♂ paratypes (MNHN) [1 ♂ paratype (MNHN RS 8726) examined], Tibet, south region of Pulan [Purang/Burang Xian, 30°15'N 81°10'E], low valley of Kongque He River, near border with Nepal, vii.1931. **INDIA: Assam:** *Heterometrus (Chersonesometrus) fastigosus*: Holotype ♂, paratypes: 1 ♀, 1 subad. ♂ (SMF II/8886/228), Assam [examined]. **West Bengal:** *Buthus bengalensis*: Lectotype [= *Heterometrus (Chersonesometrus) fastigosus* paratype]: 1 ♂ (ZMB 70/2), paralectotypes [= *H. (C.) fastigosus* paratypes]: 1 ♂ (ZMB 70/1), 3 ♂ (ZMB 70/4, 5, 7), 1 ♀ (ZMB 70/3), 1 subad. ♀ (ZMB 70/6), Bengal, Lam [examined]. **NEPAL:** *Heterometrus nepalensis*: Holotype ♀ [not ♂] (FKPC), Royal Chitwan National Park, Island Jungle Resort [27°38'N 84°10'E], Nepal, vi.1993, Csorba.

Buthus bengalensis was based on seven syntypes deposited at the ZMB (C.L. Koch, 1841b). According to Couzijn (1981: 120, 142) these syntypes were destroyed during World War II (unlikely as the arachnid collection at ZMB was not destroyed in the war, unlike those of some other German museums). Couzijn (1981: 142) examined two of the specimens, but speculated that they did not match Koch's (1841) original description: "they do not fit the description of *B. bengalensis* by the absence of external keels on the pedipalp hands and the different internal denticulation on the fourth pedipalp segment." Couzijn (1981) designated the two syntypes of *B. bengalensis* as paratypes of a new species, *Heterometrus (Chersonesometrus) fastigosus*, and designated a neotype, deposited at MNHN, for *H. bengalensis*, which was in fact conspecific with another species, *Heterometrus thorellii*.

Kovařík (2004: 9) considered Couzijn's (1981) taxonomic decision "entirely invalid and incomprehensible." As all seven syntypes of *B. benga-*

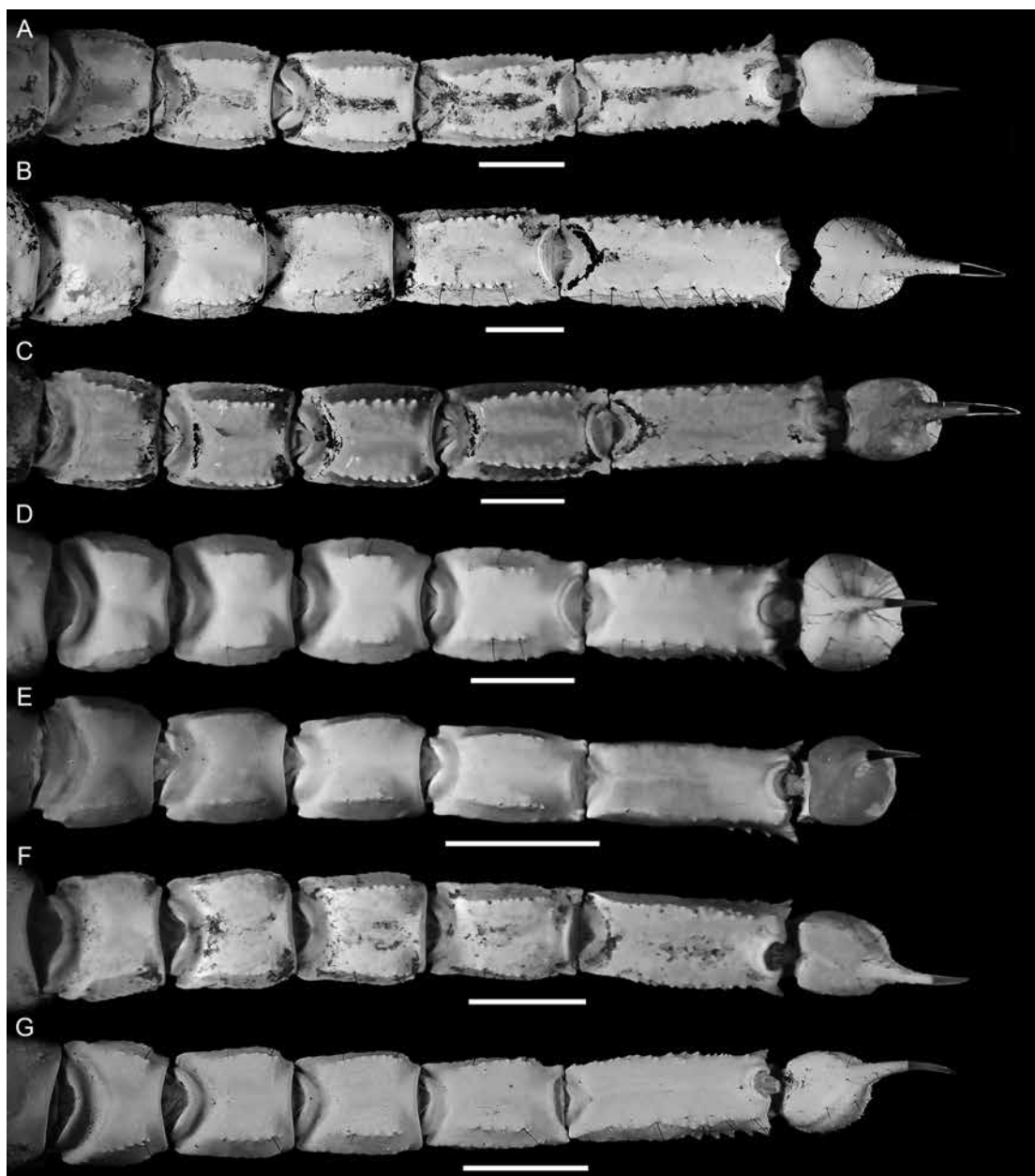


FIGURE 64. *Deccanometrus*, gen. nov., metasoma and telson, dorsal aspect. **A.** *Deccanometrus bengalensis* (C.L. Koch, 1841), comb. nov., ♂ (BMNH 1913.1.6.3). **B.** *Deccanometrus obscurus* (Couzijn, 1981), comb. et stat. nov., ♂ (AMNH), Bhimashankar, India. **C.** *Deccanometrus phipsoni* (Pocock, 1893), comb. nov., ♂ (MNHN 0080). **D.** *Deccanometrus latimanus* (Pocock, 1894), comb. nov., ♂ (AMNH), Charbagh, Pakistan. **E.** *Deccanometrus liurus* (Pocock, 1897), comb. nov., paralectotype ♀ (BMNH 1896.12.15.20-25). **F.** *Deccanometrus ubicki* (Kovářík, 2004), comb. nov., paratype ♀ (CAS 9071135). **G.** *Deccanometrus xanthopus* (Pocock, 1897), comb. nov., ♀ (AMNH), Khambatki Ghat, India. Scale bars = 5 mm.



FIGURE 65. *Deccanometrus*, gen. nov., metasoma and telson, lateral aspect. **A.** *Deccanometrus bengalensis* (C.L. Koch, 1841), comb. nov., ♂ (BMNH 1913.1.6.3). **B.** *Deccanometrus obscurus* (Couzijn, 1981), comb. et stat. nov., ♂ (AMNH), Bhimashankar, India. **C.** *Deccanometrus phipsoni* (Pocock, 1893), comb. nov., ♂ (MNHN 0080). **D.** *Deccanometrus latimanus* (Pocock, 1894), comb. nov., ♂ (AMNH), Charbagh, Pakistan. **E.** *Deccanometrus liurus* (Pocock, 1897), comb. nov., paralectotype ♀ (BMNH 1896.12.15.20-25). **F.** *Deccanometrus ubicki* (Kovařík, 2004), comb. nov., paratype ♀ (CAS 9071135). **G.** *Deccanometrus xanthopus* (Pocock, 1897), comb. nov., ♀ (AMNH), Khambatki Ghat, India. Scale bars = 5 mm.

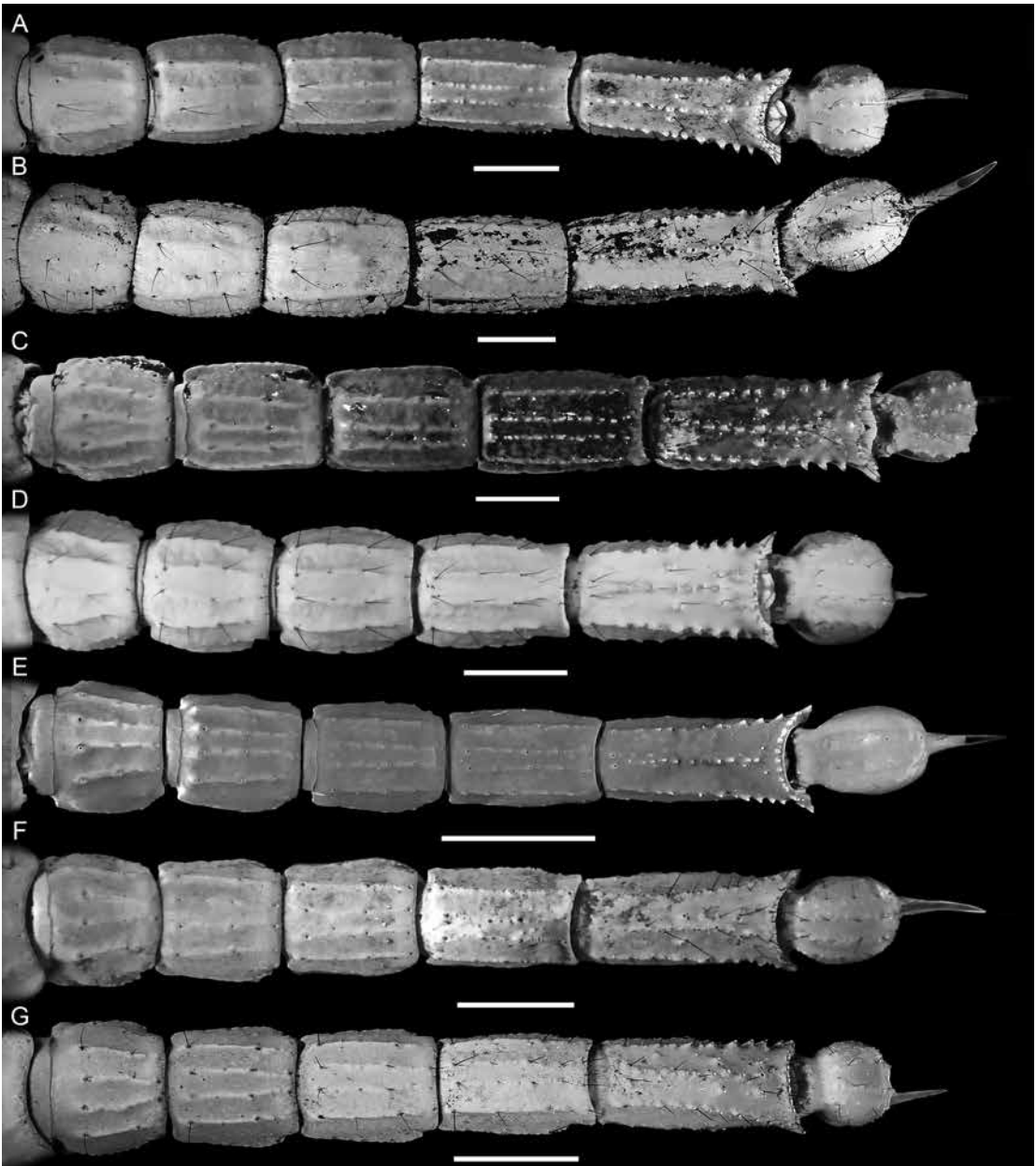


FIGURE 66. *Deccanometrus*, gen. nov., metasoma and telson, ventral aspect. **A.** *Deccanometrus bengalensis* (C.L. Koch, 1841), comb. nov., ♂ (BMNH 1913.1.6.3). **B.** *Deccanometrus obscurus* (Couzijn, 1981), comb. et stat. nov., ♂ (AMNH), Bhimashankar, India. **C.** *Deccanometrus phipsoni* (Pocock, 1893), comb. nov., ♂ (MNHN 0080). **D.** *Deccanometrus latimanus* (Pocock, 1894), comb. nov., ♂ (AMNH), Charbagh, Pakistan. **E.** *Deccanometrus liurus* (Pocock, 1897), comb. nov., paralectotype ♀ (BMNH 1896.12.15.20-25). **F.** *Deccanometrus ubicki* (Kovářík, 2004), comb. nov., paratype ♀ (CAS 9071135). **G.** *Deccanometrus xanthopus* (Pocock, 1897), comb. nov., ♀ (AMNH), Khambatki Ghat, India. Scale bars = 5 mm.

lensis are still extant at the ZMB, Kovařík (2004) designated one as lectotype, invalidating Couzin's (1981) designation of the neotype in accordance with ICZN Article 75.8.

DIAGNOSIS: *Deccanometrus bengalensis* may be separated from other species of *Deccanometrus* as follows. The carapace is slightly dorsoventrally compressed, the lateral surfaces sloping gently (fig. 19A, B), in *D. bengalensis* but vaulted, the lateral surfaces sloping moderately, in *D. latimanus* and *D. xanthopus*. The median notch in the carapace anterior margin is deeply excavated in *D. bengalensis* but shallow in *D. liurus*. The superciliary carinae are higher than the median ocelli in *D. bengalensis*, but lower than the ocelli in all other species except *D. latimanus*, *D. liurus*, and *D. ubicki*. The interocular suture is present in *D. bengalensis* but absent in *D. liurus*. The carapace interocular surface is granular along the median longitudinal and anterior bifurcated sulci only in the male (fig. 19A), and the frontal lobes and medial region are granular, with smooth areas, in the female (fig. 19B) of *D. bengalensis*, whereas the interocular surface is granular along the median longitudinal and anterior bifurcated sulci only in the female of *D. latimanus*, *D. liurus*, *D. obscurus*, and *D. phipsoni*, and the frontal lobes and medial region are granular, with smooth areas, in the male of *D. ubicki* or partially to entirely granular in the male of *D. xanthopus*. The carapace posterolateral surfaces of the female are granular in *D. bengalensis* but smooth or nearly so in *D. obscurus*, *D. phipsoni*, *D. ubicki*, and *D. xanthopus*. The cheliceral movable finger prodistal (DI) and retrodistal (DE) teeth are aligned longitudinally and not opposable in *D. bengalensis* but opposable, i.e., forming a bicusps, in *D. liurus* and *D. ubicki*. The pedipalps of the adult male are long, with femur length : posterior carapace width ratio (FL:PCW) ≥ 0.80 and femur length : carapace length ratio (FL:CL) ≥ 0.76 (fig. 119) in *D. bengalensis* but short, with FL:PCW < 0.77 , FL:CL < 0.74 in *D. latimanus*. The pedipalp femur prodorsal carina is present and distinct in *D. bengalensis* but absent or obsolete in *D. liurus* and *D. xanthopus*. The pedipalp patella dorsomedian carina of the female is entirely to predominantly granular in *D. bengalensis* but absent or

obsolete in *D. latimanus*, *D. liurus*, and *D. ubicki*. The patella retrodorsal carina of the female is absent or obsolete in *D. bengalensis* but as strongly developed as or more strongly developed than the retromedian carinae in *D. obscurus* and *D. phipsoni*. The retromedian carinae of the female are granular in *D. bengalensis* but absent or obsolete in *D. latimanus*, *D. liurus*, *D. ubicki*, and *D. xanthopus*. The patella dorsal, retrodorsal, and retroventral intercarinal surfaces of the female are smooth or nearly so in *D. bengalensis* but granular in *D. obscurus* and *D. phipsoni*. The pedipalp chela is infusate and similar in color to the femur and patella in *D. bengalensis* but immaculate and paler than the femur and patella in *D. latimanus*, *D. liurus*, and *D. xanthopus*. The chela of the adult male is moderately to densely setose (fig. 122B–D) in *D. bengalensis* but sparsely setose in *D. xanthopus*. The chela manus promedian carina of the female is granular in *D. bengalensis* but absent or obsolete in *D. latimanus* and *D. xanthopus*. The maximum distance between the dorsomedian and dorsal secondary carinae (DMC–DSC) of the chela manus is less than the maximum distance between the dorsal secondary and digital carinae (DSC–DC) in the male and female of *D. bengalensis* whereas the DMC–DSC is similar to the DSC–DC in the male and female of *D. xanthopus*, and the female of *D. obscurus*, and greater than the DSC–DC in the male and female of *D. latimanus*. The chela manus dorsal intercarinal surface is finely to coarsely granular and shallowly reticulate (fig. 122) in *D. bengalensis*, smooth and shallowly reticulate in *D. ubicki*, and finely to coarsely granular, without reticulation in *D. obscurus* and *D. phipsoni*. The manus retrolateral intercarinal surfaces are granular in *D. bengalensis* but smooth or nearly so in *D. ubicki*. The legs are very dark or heavily infusate (figs. 119, 120) in *D. bengalensis* but pale or very lightly infusate in *D. latimanus*, *D. liurus*, *D. ubicki*, and *D. xanthopus*. Macroseta *st* on the retroventral surfaces of the basitarsi is spiniform on legs I and II and setiform on III (fig. 46A–D) in *D. bengalensis*, spiniform on legs I–III in *D. obscurus*, *D. phipsoni*, and *D. ubicki*, and setiform on legs I–III in *D. latimanus*, *D. liurus*, and *D. xanthopus*; *sb* on the retroventral surfaces of

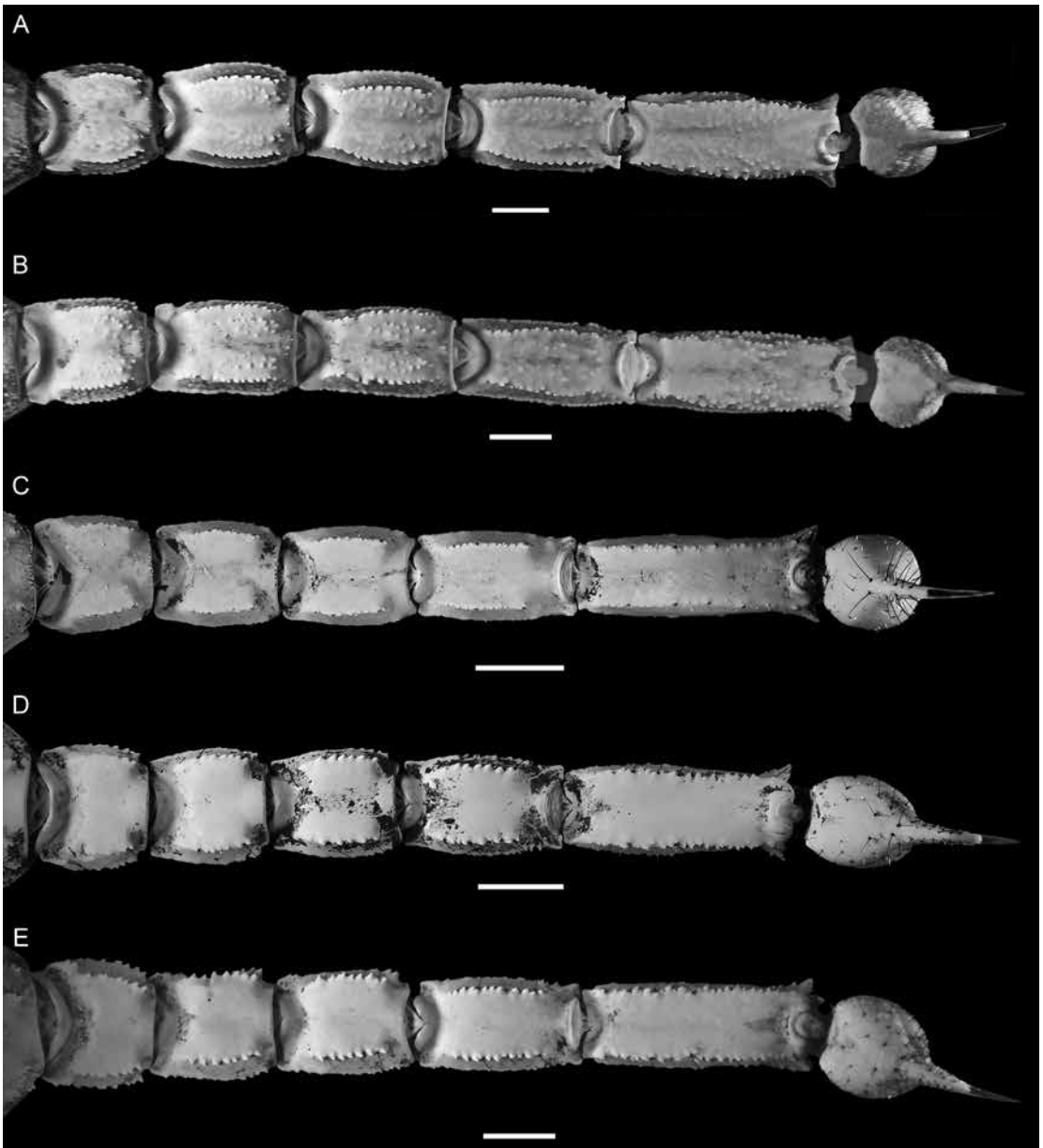


FIGURE 67. **A, B.** *Gigantometrus* Couzijn, 1978, stat. nov., and **C–E.** *Heterometrus* Ehrenberg, 1828, metasoma and telson, dorsal aspect. **A.** *Gigantometrus swammerdami* (Simon, 1872), comb. nov., lectotype ♂ (*Palamnaeus swammerdami flavimanus* Pocock, 1900, syn. nov.) (BMNH 1899.11.2.292-3). **B.** *Gigantometrus titanicus* (Couzijn, 1981), comb. nov. et stat. rev., ♂ (AMNH), Polonnaruwa, Sri Lanka. **C.** *Heterometrus glaucus* (Thorell, 1876), comb. nov. et stat. rev., ♀ (AMNH), Nias Island, Indonesia. **D.** *Heterometrus laevigatus* (Thorell, 1876), comb. nov. et stat. rev., ♂ (AMNH), Thale Ban, Thailand. **E.** *Heterometrus spinifer* (Ehrenberg, 1828), ♂ (AMNH), Cameron Highlands, Malaysia. Scale bars = 5 mm.

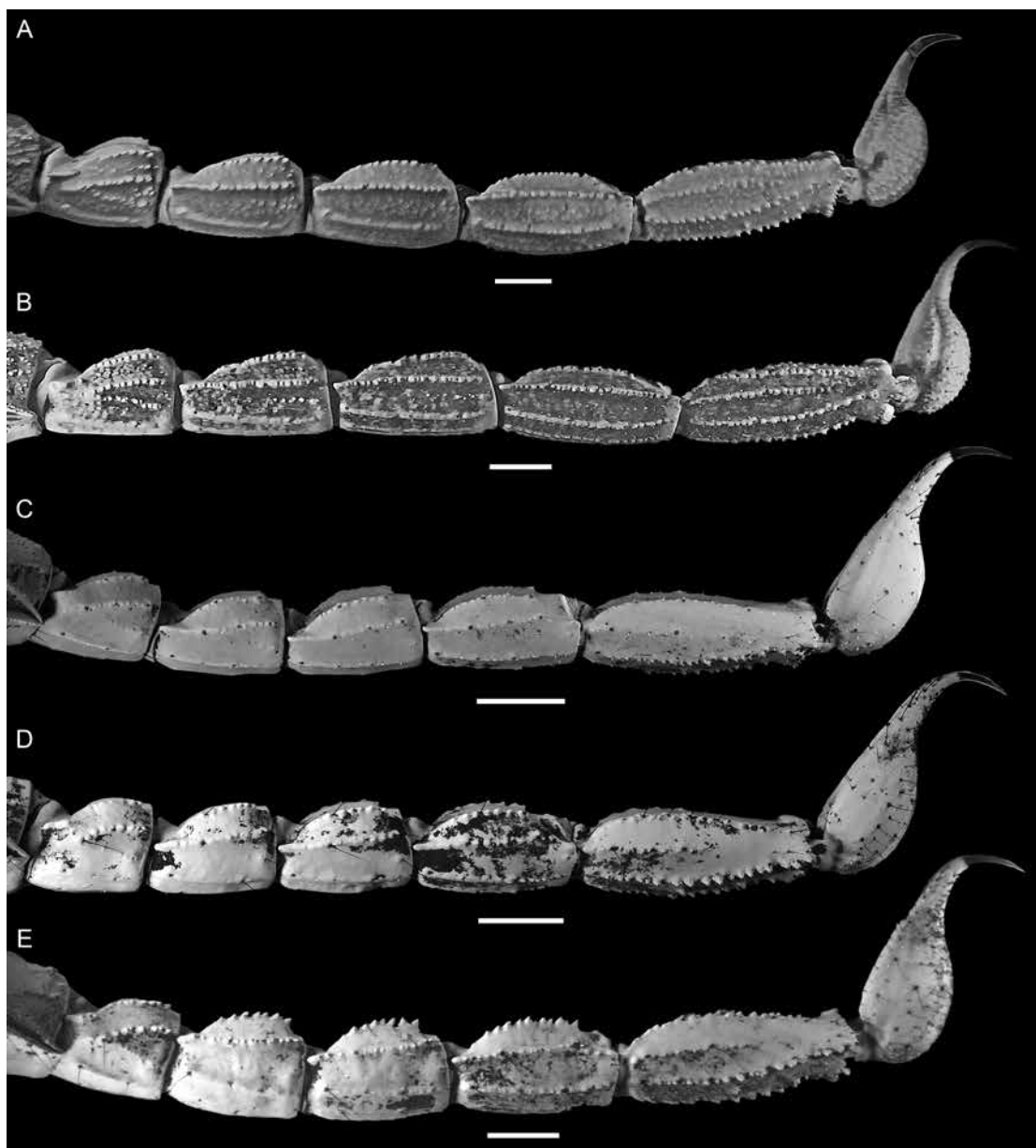


FIGURE 68. **A, B.** *Gigantometrus* Couzijn, 1978, stat. nov., and **C–E.** *Heterometrus* Ehrenberg, 1828, metasoma and telson, lateral aspect. **A.** *Gigantometrus swammerdami* (Simon, 1872), comb. nov., lectotype ♂ (*Palamnaeus swammerdami flavimanus* Pocock, 1900, syn. nov.) (BMNH 1899.11.2.292-3). **B.** *Gigantometrus titanicus* (Couzijn, 1981), comb. nov. et stat. rev., ♂ (AMNH), Polonnaruwa, Sri Lanka. **C.** *Heterometrus glaucus* (Thorell, 1876), comb. nov. et stat. rev., ♀ (AMNH), Nias Island, Indonesia. **D.** *Heterometrus laevigatus* (Thorell, 1876), comb. nov. et stat. rev., ♂ (AMNH), Thale Ban, Thailand. **E.** *Heterometrus spinifer* (Ehrenberg, 1828), ♂ (AMNH), Cameron Highlands, Malaysia. Scale bars = 5 mm.

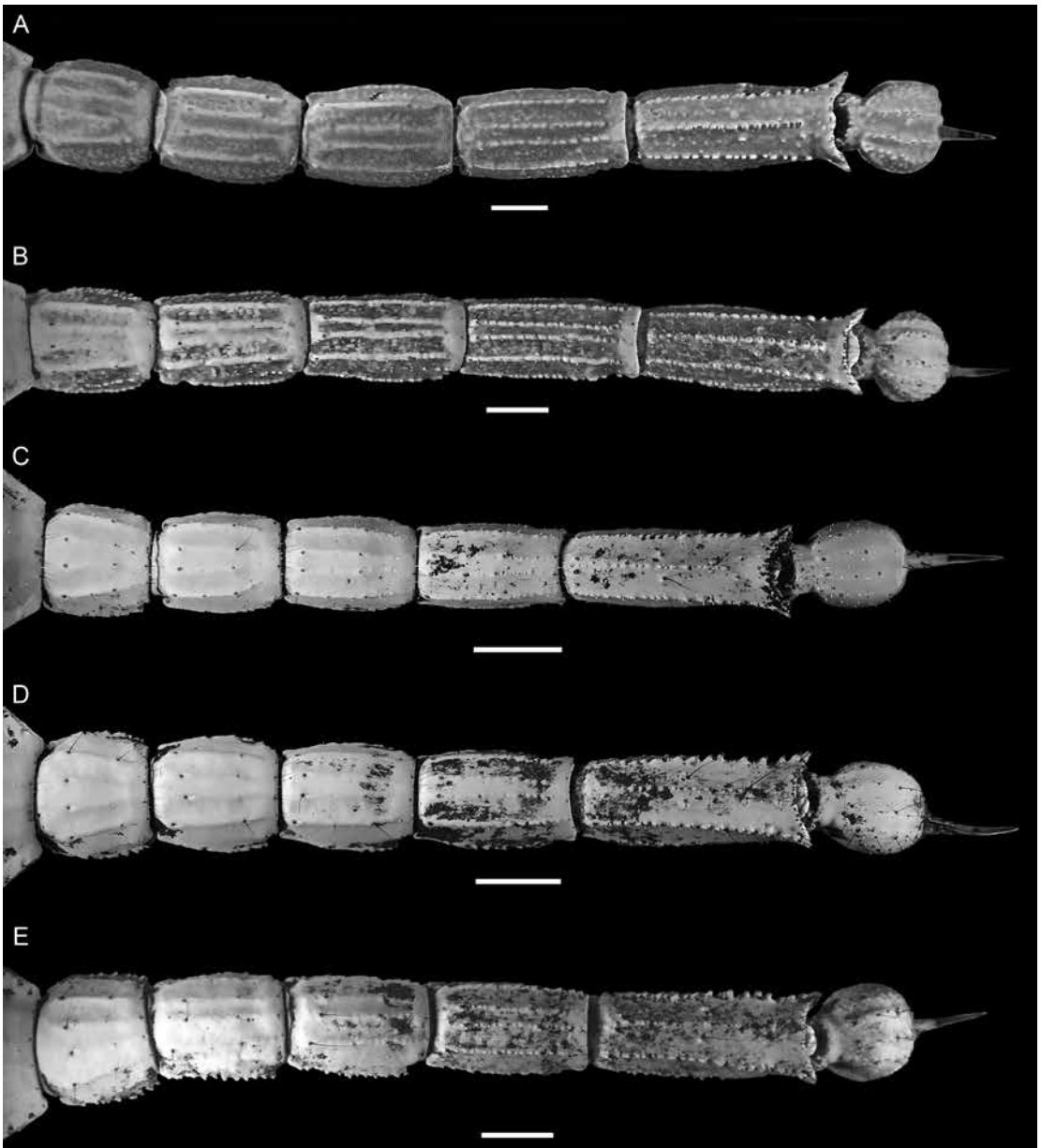


FIGURE 69. **A, B.** *Gigantometrus* Couzijn, 1978, stat. nov., and **C–E.** *Heterometrus* Ehrenberg, 1828, metasoma and telson, ventral aspect. **A.** *Gigantometrus swammerdami* (Simon, 1872), comb. nov., lectotype ♂ (*Palamnaeus swammerdami flavimanus* Pocock, 1900, syn. nov.) (BMNH 1899.11.2.292-3). **B.** *Gigantometrus titanicus* (Couzijn, 1981), comb. nov. et stat. rev., ♂ (AMNH), Polonnaruwa, Sri Lanka. **C.** *Heterometrus glaucus* (Thorell, 1876), comb. nov. et stat. rev., ♀ (AMNH), Nias Island, Indonesia. **D.** *Heterometrus laevigatus* (Thorell, 1876), comb. nov. et stat. rev., ♂ (AMNH), Thale Ban, Thailand. **E.** *Heterometrus spinifer* (Ehrenberg, 1828), ♂ (AMNH), Cameron Highlands, Malaysia. Scale bars = 5 mm.

the basitarsi is spiniform on legs I and II in *D. bengalensis*, setiform on legs I and II in *D. latimanus*, and setiform on leg I, and setiform or spiniform on leg II in *D. xanthopus*; *st* on the proventral surface of the basitarsus of leg III is spiniform in *D. bengalensis* but setiform in *D. obscurus* and *D. phipsoni*; *sb* on the retrolateral surface of the basitarsus of leg III is spiniform in *D. bengalensis* but setiform in *D. latimanus*. The laterodistal lobes on the telotarsi of legs I–IV each bear only two spiniform macrosetae in *D. bengalensis* but three or more in *D. latimanus*. The angle of the pectinal first proximal median lamella (scape) is $> 90^\circ$ but $< 180^\circ$ in the male and female (fig. 33A, B) of *D. bengalensis*, and approximately 90° in the male of *D. latimanus*, *D. liurus*, and *D. xanthopus*, and the male and female of *D. ubicki*. The mesial surfaces of mesosomal tergites I–VI are smooth in the male and the lateral surfaces granular in the female of *D. bengalensis*, whereas the mesial surfaces are granular in the male of *D. xanthopus*, and the lateral surfaces smooth in the female of *D. latimanus*, *D. liurus*, *D. ubicki*, and *D. xanthopus*. The ventral surface of mesosomal sternite VII bears a pair of weakly developed ventrolateral carinae in *D. bengalensis* but two pairs of moderately to strongly developed ventrosulmedian and ventrolateral carinae in *D. latimanus*, *D. liurus*, *D. ubicki*, and *D. xanthopus*. The dorsosulmedian carinae of metasomal segments I–IV are granular or costate-granular (fig. 64A) in *D. bengalensis*, costate in *D. latimanus*, and obsolete in *D. liurus*. The ventrosulmedian and ventrolateral carinae of metasomal segments I–IV are more strongly developed on segments III and IV than on I and II (fig. 66A) in *D. bengalensis* but more strongly developed on segments I and II than on III and IV in *D. latimanus*, *D. liurus*, *D. ubicki*, and *D. xanthopus*. The lateral carinae are partial on metasomal segments I and V (fig. 65A) in *D. bengalensis* but vestigial on I in *D. liurus* and *D. ubicki*, and absent or obsolete on V in *D. latimanus*, *D. liurus*, and *D. ubicki*. The dorsolateral carinae of metasomal segment V are strong and continuous in *D. bengalensis* but weak and discontinuous to absent in *D. latimanus*, *D. liurus*, and *D. xanthopus*. The width of the telson vesicle is approximately

equal to or less than the width of metasomal segment V in the male (figs. 64A, 66A) of *D. bengalensis* but greater than the width of segment V in the male of *D. latimanus*, *D. liurus*, *D. ubicki*, and *D. xanthopus*.

DISTRIBUTION: This species has been recorded in China (in the Tibet Autonomous Region only), India (in the states of Assam, Haryana, Himachal Pradesh, Jharkhand, Madhya Pradesh, Odisha, Rajasthan, Uttar Pradesh, Uttarakhand, and West Bengal) and Nepal (fig. 117, table 1). Its presence in Bangladesh, based on a record from the Ganges Delta (Kraepelin, 1913), while likely, requires confirmation. Records of this species and its junior synonym, *H. fastigosus*, from Maharashtra, India (Tikader and Bastawade, 1983; Bastawade, 2002) are referable to *D. phipsoni*.

ECOLOGY: Surprisingly little is known about the ecology of this widespread species. The known records occur in areas of deciduous forest on the plains south of the Himalayas and valleys in the Himalayan foothills. Specimens from Rajaji National Park in Uttar Pradesh, India, were found in a deciduous forest with Sal, *Shorea robusta* C.F. Gaertner, 1805 (Biswas, 1984). The burrowing biology of this species was described by Kanungo (1954). The burrows are constructed in open ground on shaded slopes of low, vegetated ridges ("bunds"). The crescentic entrance, 5.1–7.6 cm x 1.3–3.8 cm, leads via a sinuous passage, almost circular in cross-section, to a terminal chamber, ca. 30 cm below the surface. As with other species of the genus, the habitus is consistent with the fossorial, pelophilous ecomorphotype (Prendini, 2001b). *Deccanometrus bengalensis* is sympatric with the buthid *Hottentotta tamulus*, and the hormurid *Liocheles nigripes* (Kanungo, 1954).

CONSERVATION STATUS: *Deccanometrus bengalensis* is harvested for medicinal purposes (Majumder and Dey, 2005) and occasionally for the exotic pet trade.

REMARKS: This species, previously placed in the nominal subgenus of *Heterometrus* by various authors (e.g., Couzijn, 1981; Tikader and Bastawade, 1983; Fet, 2000), is newly accommo-

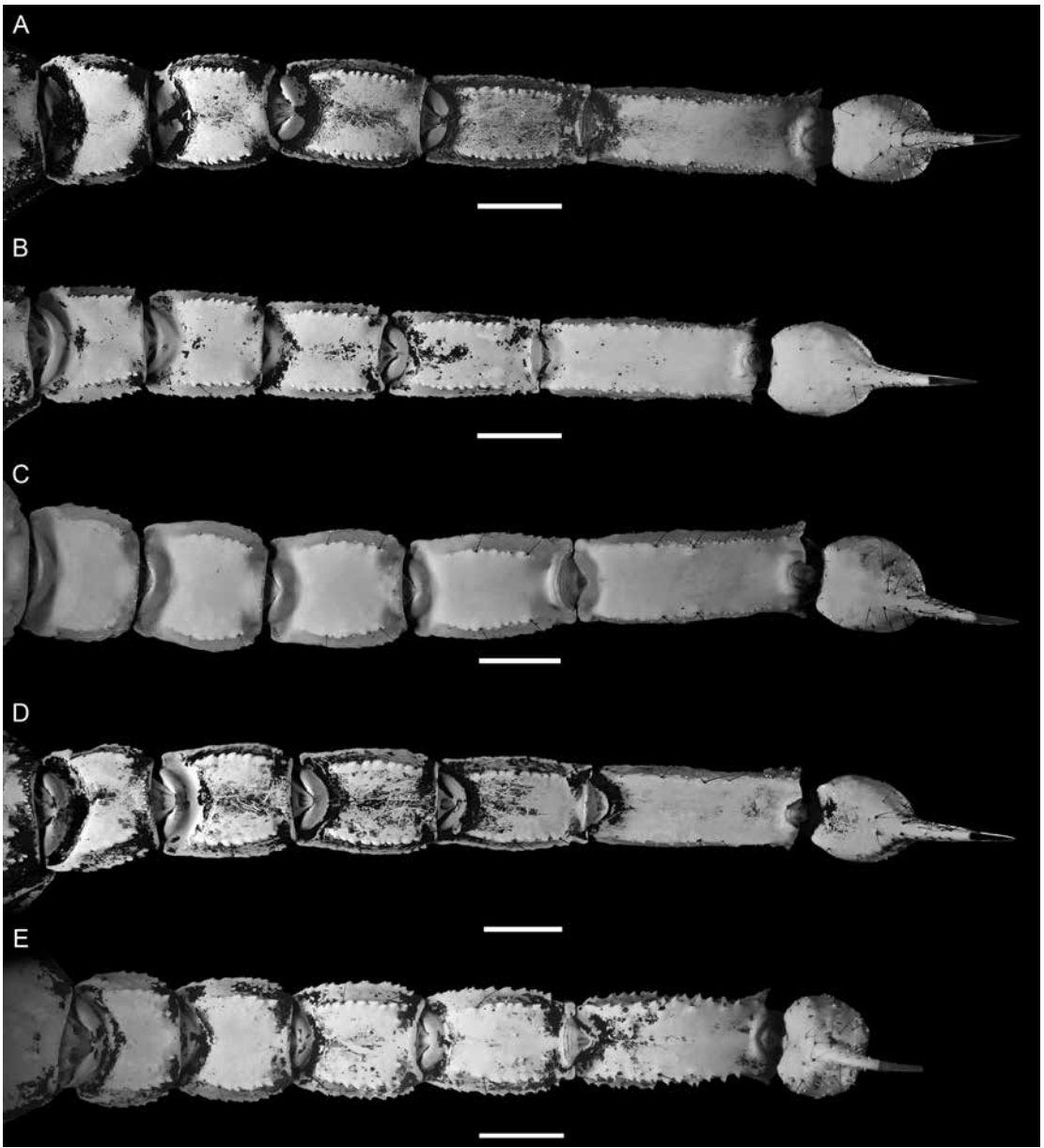


FIGURE 70. A–D. *Heterometrus* Ehrenberg, 1828, and E. *Javanimetrus* Couzijn, 1981, stat. nov. et stat. rev., metasoma and telson, dorsal aspect. A. *Heterometrus laoticus* Couzijn, 1981, ♂ (AMNH), Phahom Camp, Laos. B. *Heterometrus longimanus* (Herbst, 1800), ♂ (AMNH), Kuching, Malaysia. C. *Heterometrus silenus* (Simon, 1884), comb. nov. et stat. rev., ♂ (AMNH), Ta Kou Mountain Nature Reserve, Vietnam. D. *Heterometrus thorellii* (Pocock, 1892), ♀ (AMNH), Pho Kyar Elephant Camp, Yedashe, Myanmar. E. *Javanimetrus cyaneus* (Simon, 1872), comb. nov., ♂ (AMNH), Ujung Kulon, Indonesia. Scale bars = 5 mm.



FIGURE 71. A–D. *Heterometrus* Ehrenberg, 1828, and E. *Javanimetrus* Couzijn, 1981, stat. nov. et stat. rev., metasoma and telson, lateral aspect. A. *Heterometrus laoticus* Couzijn, 1981, ♂ (AMNH), Phahom Camp, Laos. B. *Heterometrus longimanus* (Herbst, 1800), ♂ (AMNH), Kuching, Malaysia. C. *Heterometrus silenus* (Simon, 1884), comb. nov. et stat. rev., ♂ (AMNH), Ta Kou Mountain Nature Reserve, Vietnam. D. *Heterometrus thorellii* (Pocock, 1892), ♀ (AMNH), Pho Kyar Elephant Camp, Yedashe, Myanmar. E. *Javanimetrus cyaneus* (Simon, 1872), comb. nov., ♂ (AMNH), Ujung Kulon, Indonesia. Scale bars = 5 mm.

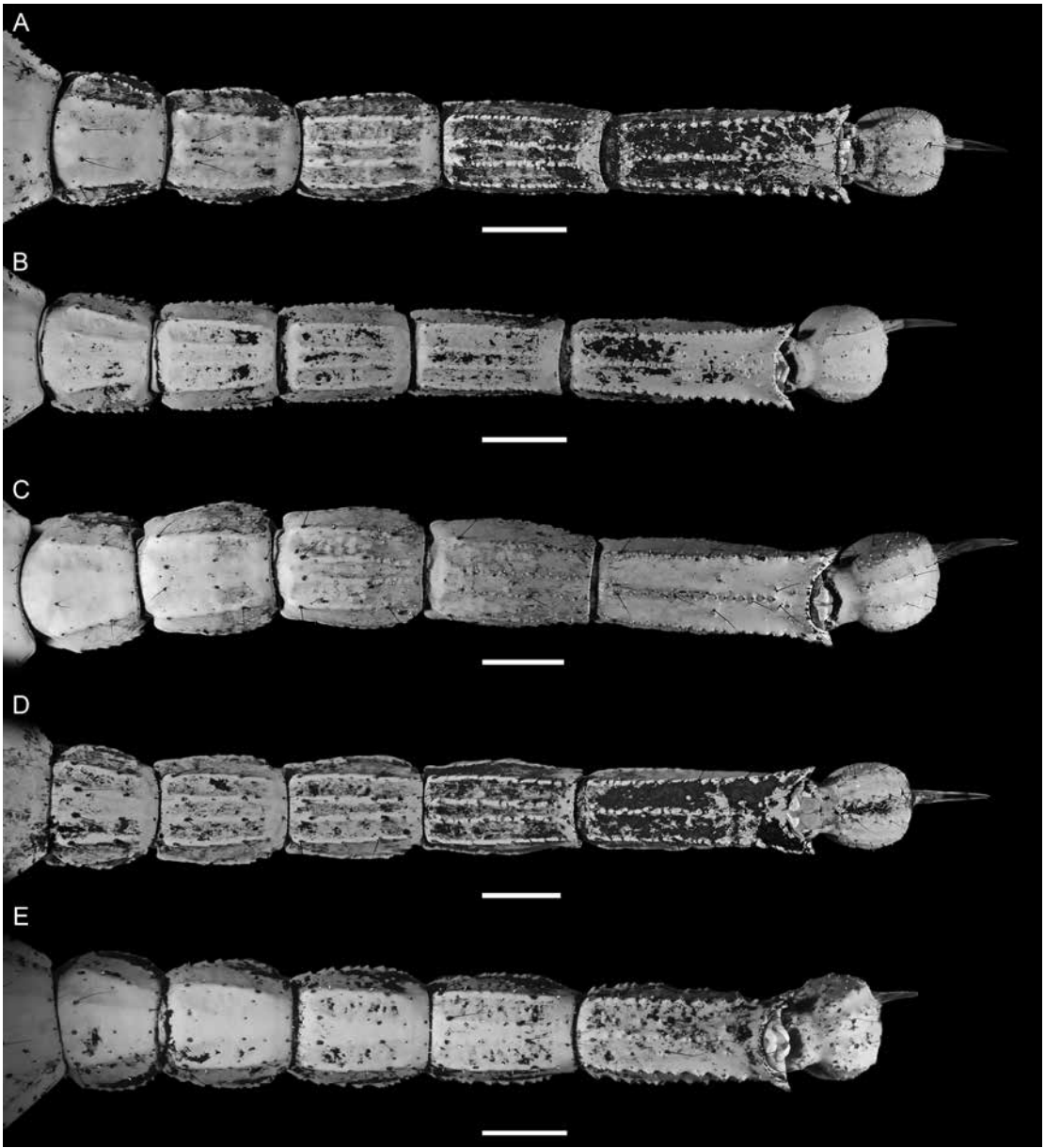


FIGURE 72. A–D. *Heterometrus* Ehrenberg, 1828, and E. *Javanimetrus* Couzijn, 1981, stat. nov. et stat. rev., metasoma and telson, ventral aspect. A. *Heterometrus laoticus* Couzijn, 1981, ♂ (AMNH), Phahom Camp, Laos. B. *Heterometrus longimanus* (Herbst, 1800), ♂ (AMNH), Kuching, Malaysia. C. *Heterometrus silenus* (Simon, 1884), comb. nov. et stat. rev., ♂ (AMNH), Ta Kou Mountain Nature Reserve, Vietnam. D. *Heterometrus thorellii* (Pocock, 1892), ♀ (AMNH), Pho Kyar Elephant Camp, Yedashe, Myanmar. E. *Javanimetrus cyaneus* (Simon, 1872), comb. nov., ♂ (AMNH), Ujung Kulon, Indonesia. Scale bars = 5 mm.

dated in *Deccanometrus*, gen. nov., based on a phylogenetic analysis (fig. 10).

Couzijn (1981: 117) examined the syntypes of *Palamnaeus costimanus* var. γ *glaucus*, allegedly from "Bengal," and synonymized the taxon with *Heterometrus* (H.) *bengalensis*. Fet (2000: 432) and Kovařík (2004: 7) followed Couzijn (1981). Reexamination of the types during the present investigation demonstrated that they are neither conspecific with one another nor with *D. bengalensis*, however.

Kovařík (2004) examined the holotype and paratypes of *H. (C.) fastigosus*, concluded they were conspecific with *H. bengalensis*, and synonymized *H. (C.) fastigosus* with the latter. Based on Koch's (1841b) original description of *Buthus bengalensis* and examination of the types of *B. bengalensis* and *H. (C.) fastigosus*, Kovařík's (2004) conclusions, that Couzijn (1981) erroneously synonymized *H. thorellii* with *H. bengalensis* and redescribed *B. bengalensis* as *H. (C.) fastigosus*, are upheld. Koch's (1841b) original illustration of the male and the pedipalp chela of the female of *B. bengalensis* reveals that the type specimens do not match *H. thorellii*, i.e., Couzijn's (1981) concept of *D. bengalensis*, because the chela manus is granular and relatively shorter than that of *H. thorellii*, and a prominent spini-form granule is absent from the proventral surface of the patella. Therefore, the following synonym is confirmed: *Heterometrus* (*Chersone-sometrus*) *fastigosus* Couzijn, 1981 = *Deccanometrus bengalensis* (C.L. Koch, 1841), comb. nov., synonymized by Kovařík (2004).

Heterometrus nepalensis is known only from the holotype, a dry specimen that is allegedly male, but judging from Kovařík's (2009: 79) figures 47–49 closely matches the female of *D. bengalensis*. Although Kovařík (2004: 32) cites a close relationship to *Srilankametrus indus* (as *H. indus*), the following putatively diagnostic characters are a precise match for *D. bengalensis* (Kovařík, 2004: 9, 32), which occurs in close geographical proximity to the type locality of *H. nepalensis*: carapace smooth, with granules only at margins; pedipalp patella without pronounced

internal tubercle; chela hirsute, "lobiform," its adult length to width ratio 2.2, as in the female of *D. bengalensis*, for which Kovařík (2004: 9) gives a ratio of 2.2, and Tikader and Bastawade (1983: 541) describe the chela manus of *D. bengalensis* as "lobate"; pectinal tooth count 14–15 compared with 14–17 in both sexes of *D. bengalensis* (Tikader and Bastawade, 1983; Kovařík, 2004); "spine formula" of legs III and IV, 4/5 compared with 4–6/4–6 in *D. bengalensis*, based on data in Tikader and Bastawade (1983) and Kovařík (2004); telson bulbous, vesicle longer than aculeus. Many specimens of *D. bengalensis* (e.g., figs. 119, 120) are "uniformly reddish black, only telson lighter colored" (Kovařík, 2004: 32) and the length of the holotype of *H. nepalensis* (83 mm) falls within the range of 78–115 mm for *D. bengalensis* based on data from Couzijn (1981), Tikader and Bastawade (1983) and Kovařík (2004). The granular pedipalp chela manus described for *H. nepalensis* is also observed in *D. bengalensis* and was described as "covered with obsolete granules" by Tikader and Bastawade (1983: 542) and as "sparsely tuberculate, uneven" by Kovařík (2004: 9). Finally, the suggestion that sexual dimorphism in the proportions of the pedipalps is "probably not noticeable" (Kovařík, 2004: 32) rests on the assumption that the holotype is an adult male, which has not been demonstrated.

Heterometrus tibetanus was described from three males (Lourenço et al., 2005). The diagnosis of *H. tibetanus* compares it with *H. nepalensis* and lists the following differences: much paler coloration in *H. tibetanus* than *H. nepalensis* which is reddish black; pedipalps and chela strongly elongated in *H. tibetanus* but hirsute "lobiform" chela in *H. nepalensis*; second metasomal segment longer than wide in *H. tibetanus* but wider than long in *H. nepalensis*; telson aculeus same length as vesicle in *H. tibetanus* but longer than aculeus in *H. nepalensis*. Setting aside the low sample sizes for both species ($n = 1$ for *H. nepalensis*; $n = 3$ for *H. tibetanus*), it is apparent that several putative diagnostic differences, e.g., the differences

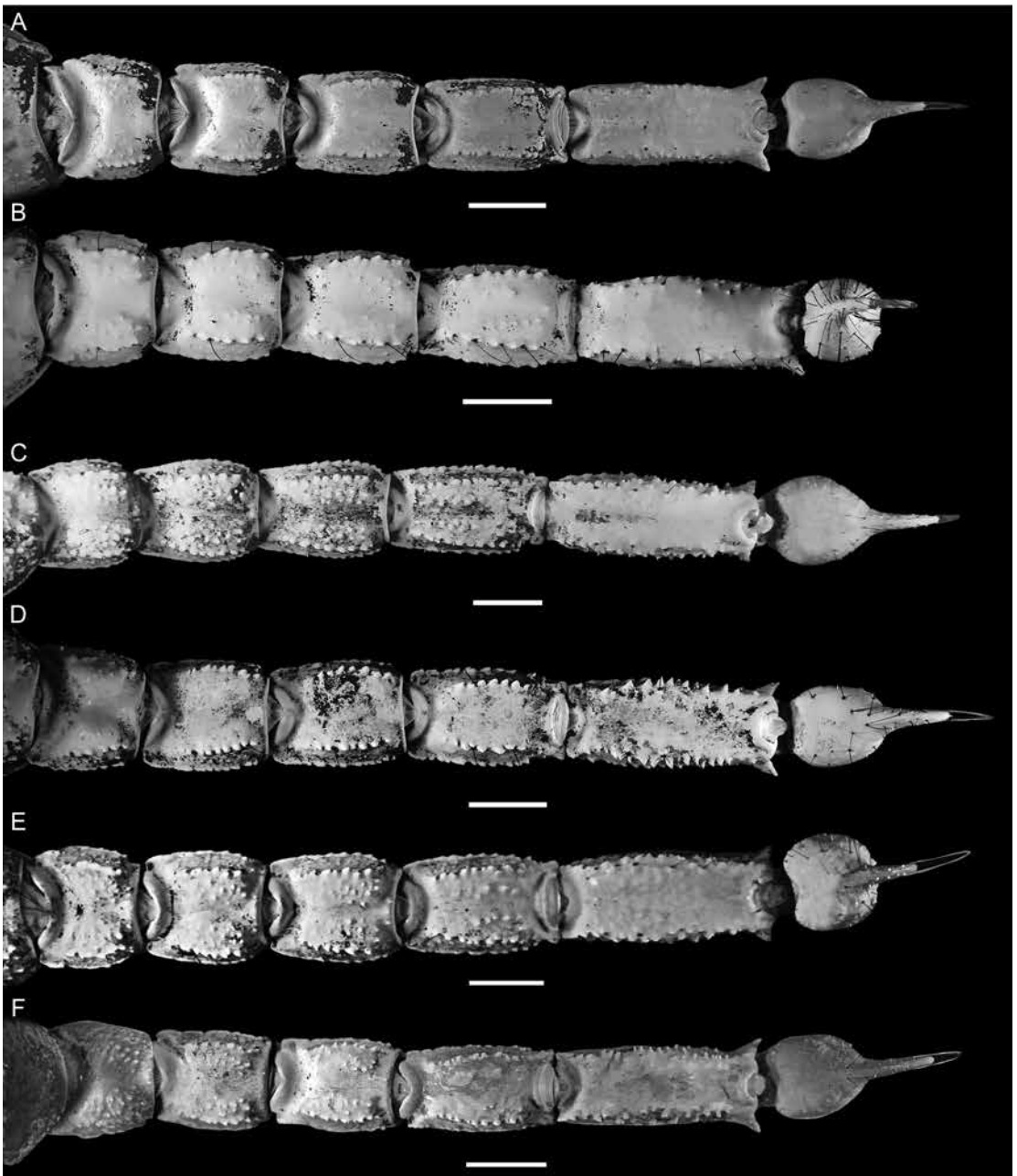


FIGURE 73. *Sahyadrimetrus*, gen. nov., metasoma and telson, dorsal aspect. **A.** *Sahyadrimetrus barberi* (Pocock, 1900), comb. nov., holotype ♀ (BMNH 1899.9.24.1), **B.** *Sahyadrimetrus kanarensis* (Pocock, 1900), comb. nov., ♀ (AMNH), Chaudi, India. **C.** *Sahyadrimetrus mathewi*, sp. nov., holotype ♂ (AMNH), Poomala, India. **D.** *Sahyadrimetrus rugosus* (Couzijn, 1981), comb. et stat. nov., ♀ (AMNH), Chaliyar River, India. **E.** *Sahyadrimetrus scaber* (Thorell, 1876), comb. nov., ♂ (AMNH), Nadpalu, India. **F.** *Sahyadrimetrus tikaderi*, gen. et sp. nov., paratype ♂ (MNHN RS 3266). Scale bars = 5 mm.



FIGURE 74. *Sahyadrimetrus*, gen. nov., metasoma and telson, lateral aspect. **A.** *Sahyadrimetrus barberi* (Pocock, 1900), comb. nov., holotype ♀ (BMNH 1899.9.24.1), **B.** *Sahyadrimetrus kanarensis* (Pocock, 1900), comb. nov., ♀ (AMNH), Chaudi, India. **C.** *Sahyadrimetrus mathewi*, sp. nov., holotype ♂ (AMNH), Poomala, India. **D.** *Sahyadrimetrus rugosus* (Couzijn, 1981), comb. et stat. nov., ♀ (AMNH), Chaliyar River, India. **E.** *Sahyadrimetrus scaber* (Thorell, 1876), comb. nov., ♂ (AMNH), Nadpalu, India. **F.** *Sahyadrimetrus tikaderi*, gen. et sp. nov., paratype ♂ (MNHN RS 3266). Scale bars = 5 mm.

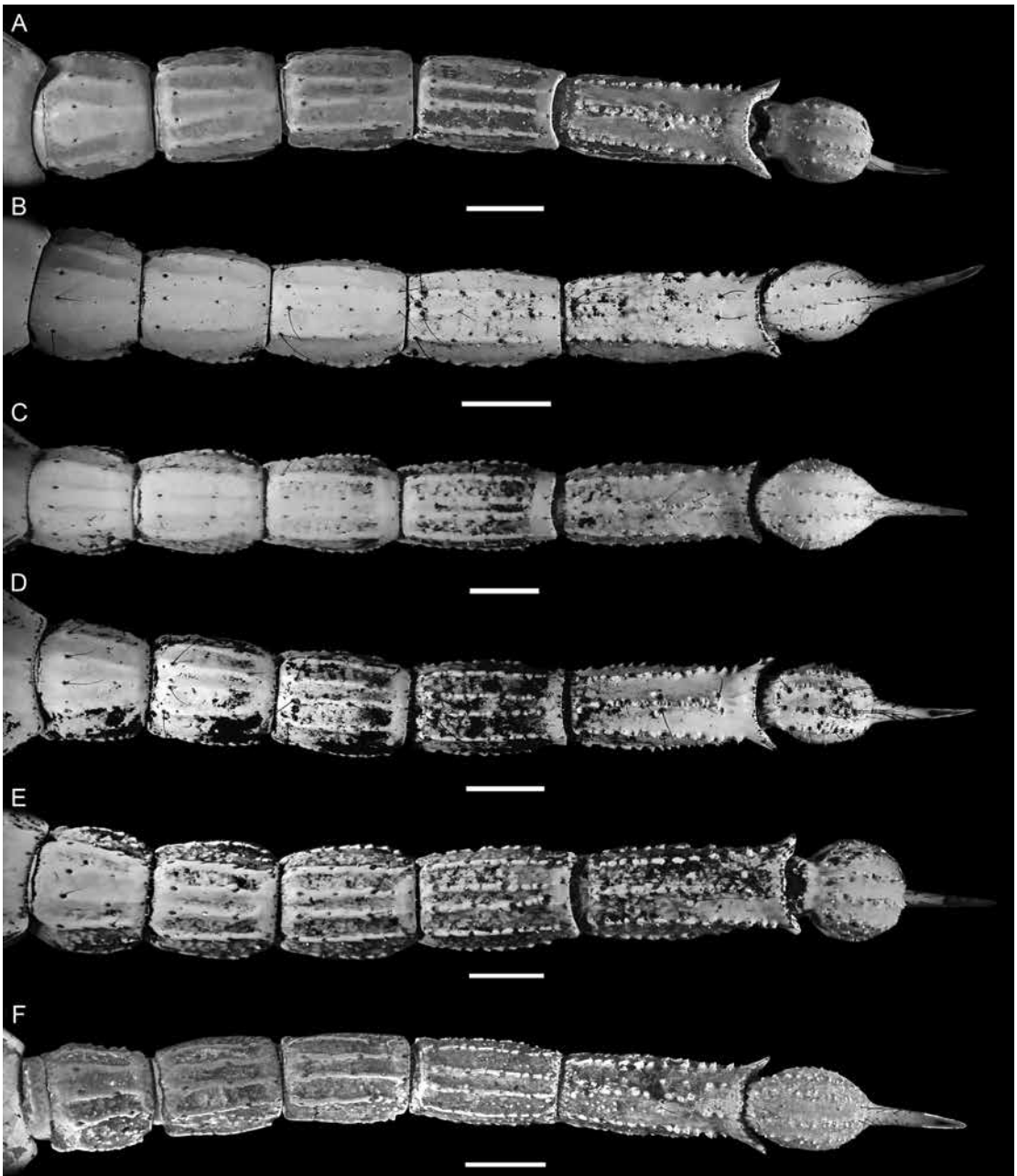


FIGURE 75. *Sahyadrimetrus*, gen. nov., metasoma and telson, ventral aspect. **A.** *Sahyadrimetrus barberi* (Pocock, 1900), comb. nov., holotype ♀ (BMNH 1899.9.24.1), **B.** *Sahyadrimetrus kanarensis* (Pocock, 1900), comb. nov., ♀ (AMNH), Chaudi, India. **C.** *Sahyadrimetrus mathewi*, sp. nov., holotype ♂ (AMNH), Poomala, India. **D.** *Sahyadrimetrus rugosus* (Couzijn, 1981), comb. et stat. nov., ♀ (AMNH), Chaliyar River, India. **E.** *Sahyadrimetrus scaber* (Thorell, 1876), comb. nov., ♂ (AMNH), Nadpalu, India. **F.** *Sahyadrimetrus tikaderi*, gen. et sp. nov., paratype ♂ (MNHN RS 3266). Scale bars = 5 mm.

in the shape of the pedipalps, metasoma, and telson, reflect sexual dimorphism. Although the diagnoses of *H. nepalensis* and *H. tibetanus* do not compare either species to *D. bengalensis*, the figures and diagnostic characters closely match the latter, with which they are clearly conspecific. Kovařík (2009: 45) suggests further that *H. nepalensis* may be a senior synonym of *H. tibetanus*. As *H. tibetanus* is undoubtedly a male of *D. bengalensis*, Kovařík's (2009) observation reinforces the conclusion that *H. nepalensis* is a female, conspecific with *D. bengalensis*.

The total length of *H. tibetanus* (85–88 mm) is close to the length of the holotype of *H. nepalensis* (83 mm) and falls within the range of *D. bengalensis*, which is 78–115 mm based on data from Tikader and Bastawade (1983) and Kovařík (2004). The pectinal tooth count of *H. tibetanus* (15–16 teeth) falls within the range of *D. bengalensis*, which has 14–17 teeth in both sexes (Tikader and Bastawade, 1983; Kovařík, 2004). The character “pedipalps, especially the chela strongly elongated and rather slender” (Lourenço et al., 2005: 11) exactly matches the male of *D. bengalensis* as do the characters “chela manus with strong spinoid granules on the dorsointernal aspect” and “second metasomal segment longer than wide (7.1/5.9).” The coloration “reddish-yellow to reddish-brown ... legs, chelicerae and telson paler than the body” is commonly observed in *D. bengalensis* which varies from reddish yellow to reddish black across its distribution; Tikader and Bastawade (1983: 539) described the color as “entirely brown with reddish tint.” The counts of proventral and retroventral spiniform macrosetae on the telotarsi, 3/4 on legs I and II in *H. tibetanus* (Lourenço et al., 2005), and 4/5 on legs III and IV in *H. nepalensis* (Kovařík, 2004) fall within the ranges of corresponding counts for *D. bengalensis*, i.e., 3/5 on I and II, and 4–6/4–6 on III and IV (Tikader and Bastawade, 1983; Kovařík, 2004). Based on the evidence, there is little doubt that *H. nepalensis* and *H. tibetanus* are conspecific with *D. bengalensis* and represent the sexually dimorphic

female and male of that species, respectively. This conclusion was reinforced by examination of the type material of *D. bengalensis* and *H. tibetanus*. The following new synonyms are proposed accordingly: *Heterometrus nepalensis* Kovařík, 2004 = *Deccanometrus bengalensis* (C.L. Koch, 1841), syn. nov.; *Heterometrus tibetanus* Lourenço et al., 2005 = *D. bengalensis*, syn. nov.

MATERIAL EXAMINED: **INDIA:** Dr. C.J. Marin-kelle, ex Stahnke coll., 1 ♀ (CAS 9071132 [ASU 61-11/65-0121]); northern India, 22.xi.1873, M.M. Carleton, 1 ♀, 1 subad. ♀ (MCZ 88170). **Assam:** Coremia, Assam, O.P. Cambridge, 1 ♂ (BMNH 1896.10... [illegible]). **Haryana:** Ambala Distr.: Amballa [Ambala, 30°23'N 76°47'E], plains 70 mi. SW, M.M. Carleton, 1874, 1 ♂, 1 ♀, 1 subad. ♂, subad. ♀ (MCZ 88169). Karnal Distr.: Nokheri [Nilokheri, 29°50'N 76°56'E], Faunthorpe-Vernay Expedition, 29.iv.1923, 1 ♀ (AMNH [24381]). **Himachal Pradesh:** Kullu Distr.: Koolloo [Kullu, 31°57'N 77°07'E], 1876, 1 ♀ (MCZ 88164). **Jharkhand:** Chota Nagpur [Chota Nagpur Plateau, ca. 23°N 85°E], D. Winffin, 1 ♂ (BMNH 1896.9.26-92 [BNHS 662]). Dumka Distr.: KathiKund (Bihar) [Kathikund, 24°22'N 87°25'E], viii.1967, R. Heim, voisinage immediate de la forêt (*Shorea*), 1 ♂ (MNHN RS 5325). **Madhya Pradesh:** Gwalior Distr.: Gwalior [26°13'N 78°11'E], 1 ♂ (BMNH 1896.12.15-19 [BNHS 185]). Satna Distr.: Satna [24°36'N 80°50'E], central India, R. Wroughton, 1 ♂ [BNHS 576], 1 ♀, 1 subad. ♀ [BNHS 814] (BMNH 1896.8.15.4). **Odisha:** Majurbanj Distr.: Rangamatia Village, near Baripada, 21°55'N 86°45'E, T. Kroes, 1 ♂, 1 ♀ (AMNH), 3 juv. (AMCC [LP 14238]). **Uttar Pradesh:** Allahabad Distr.: Allahabad [25°26'N 81°51'E], E.W. Oates, 2 subad. ♂, 2 subad. ♀ (BMNH 1897.7.5.10.218-221). Unnao Distr.: Shakpur [26°32'N 80°28'E], near Unao, Punjab, H.W. Waite, 15.vi.1912, 1 ♂ (BMNH 1913.1.6.3). **Uttarakhand:** Dehradun Distr.: Dehra Dun [30°19'N 78°02'E], 1 ♂ (BMNH 1897.9.17.5 [BNHS 1236]), F. Gleadow, 1 ♂ (BMNH 1896.10.20.70 [BNHS 843]), Gamble, 2 ♂, 1 ♀ (BMNH 1896.2.2.1-2). Pauri Garhwal Distr.: Munala [Mundala, 29°48'N 78°31'E], A.N. Cassia, 1 juv. ♂, 1 juv. ♀ (BMNH 1896.9.26.85,86 [BNHS 764]). **West Bengal:** Bengal, 1 ♂, 1 ♀ (BMNH 1860.15); West Bengal, 13.iii.1968, received from Zafer's Export Centre, ex Stahnke coll., 8 ♂, 5 ♀, 1 subad. ♂, 1 subad. ♀ (CAS [ASU 68-0178, 180, 182, 184, 186, 187, 191, 192, 194, 224, 226, 245, 251–253]), 13.iii.1968, Zafer's Export Centre, ex Stahnke coll., 2 ♀ (CAS 9071130 [ASU 68-0227], 9071131 [ASU 68-0223]). Kolkata Distr.: Cal-

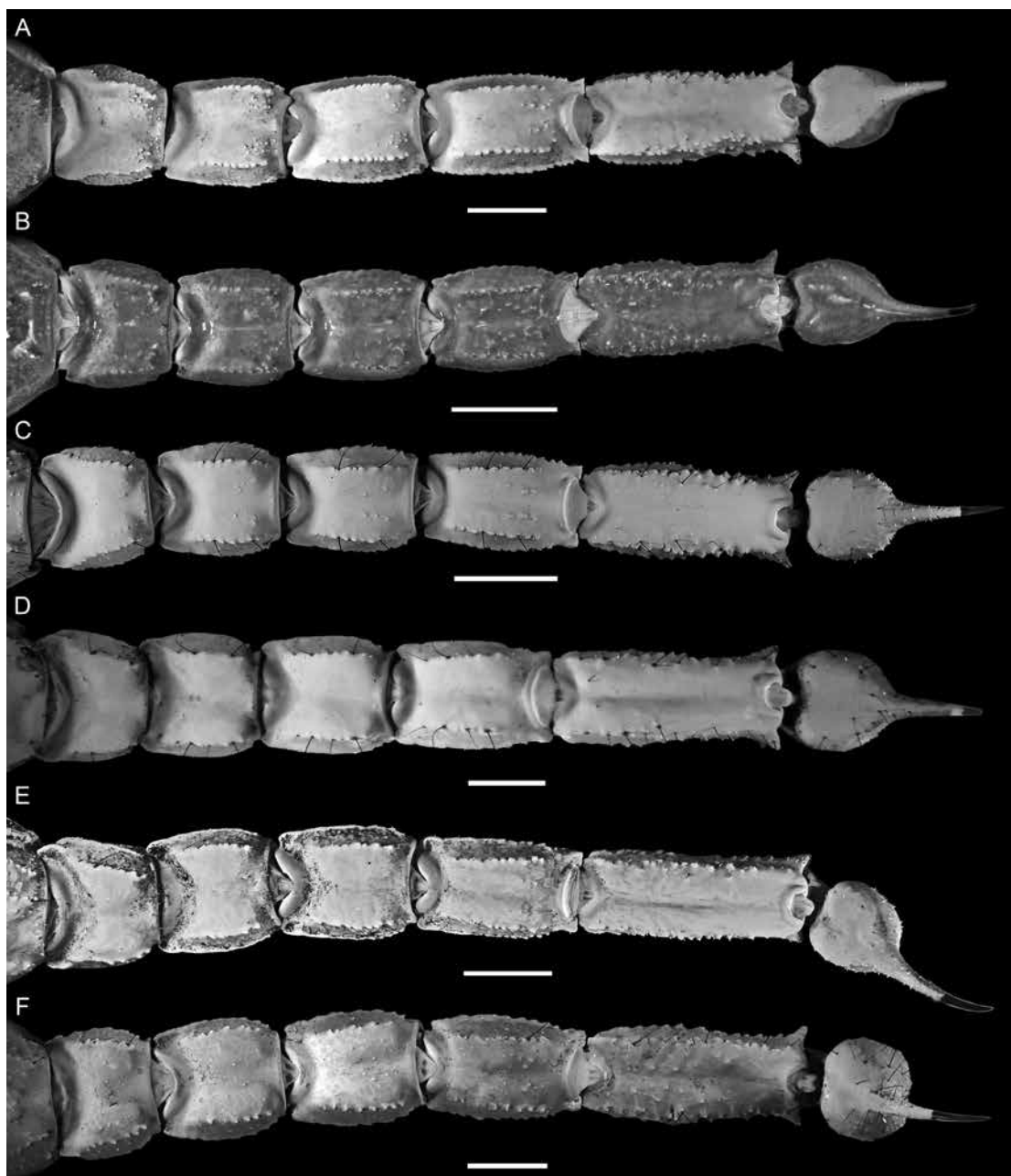


FIGURE 76. *Srilankametrus* Couzijn, 1978, stat. nov. et stat. rev., metasoma and telson, dorsal aspect. **A.** *Srilankametrus caesar* (C.L. Koch, 1841), comb. nov. et stat. rev., ♂ (MNHN RS 0079). **B.** *Srilankametrus couzijni*, sp. nov., holotype ♂ (BMNH 1896.7.30.121). **C.** *Srilankametrus gravimanus* (Pocock, 1894), comb. nov., ♂ (AMNH), Kokmotte, Sri Lanka. **D.** *Srilankametrus indus* (DeGeer, 1778), comb. nov., ♂ (AMNH), Kandy, Sri Lanka. **E.** *Srilankametrus pococki*, sp. nov., holotype ♀ (AMNH), Kodigala, Sri Lanka. **F.** *Srilankametrus serratus* (Pocock, 1900), comb. nov., ♂ (ZMH), Ceylon [Sri Lanka]. Scale bars = 5 mm



FIGURE 77. *Srilankametrus* Couzijn, 1978, stat. nov. et stat. rev., metasoma and telson, lateral aspect. **A.** *Srilankametrus caesar* (C.L. Koch, 1841), comb. nov. et stat. rev., ♂ (MNHN RS 0079). **B.** *Srilankametrus couzijni*, sp. nov., holotype ♂ (BMNH 1896.7.30.121). **C.** *Srilankametrus gravimanus* (Pocock, 1894), comb. nov., ♂ (AMNH), Kokmotte, Sri Lanka. **D.** *Srilankametrus indus* (DeGeer, 1778), comb. nov., ♂ (AMNH), Kandy, Sri Lanka. **E.** *Srilankametrus pococki*, sp. nov., holotype ♀ (AMNH), Kodigala, Sri Lanka. **F.** *Srilankametrus serratus* (Pocock, 1900), comb. nov., ♂ (ZMH), Ceylon [Sri Lanka]. Scale bars = 5 mm.

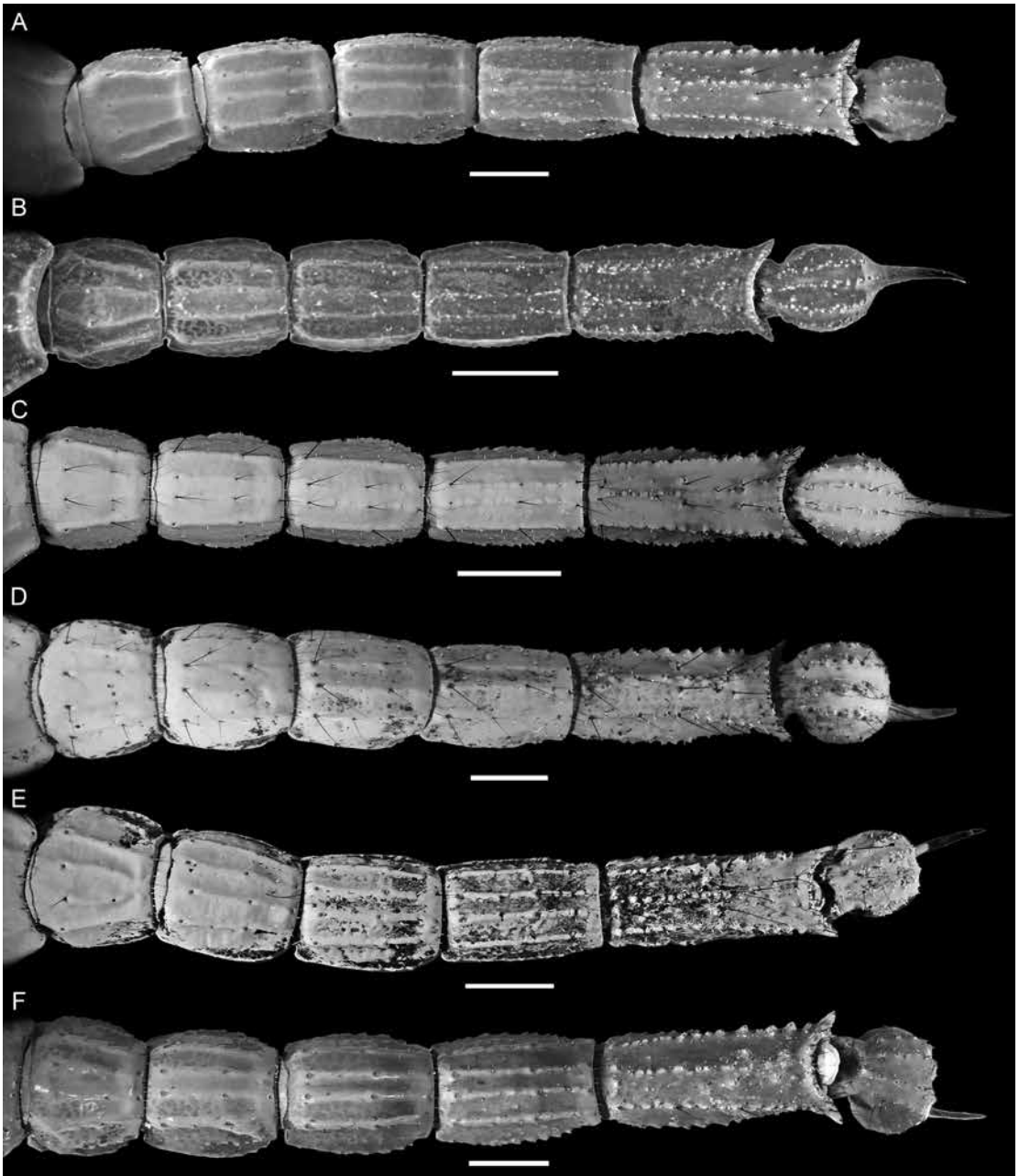


FIGURE 78. *Srilankametrus* Couzijn, 1978, stat. nov. et stat. rev., metasoma and telson, ventral aspect. **A.** *Srilankametrus caesar* (C.L. Koch, 1841), comb. nov. et stat. rev., ♂ (MNH RS 0079). **B.** *Srilankametrus couzijni*, sp. nov., holotype ♂ (BMNH 1896.7.30.121). **C.** *Srilankametrus gravimanus* (Pocock, 1894), comb. nov., ♂ (AMNH), Kokmotte, Sri Lanka. **D.** *Srilankametrus indus* (DeGeer, 1778), comb. nov., ♂ (AMNH), Kandy, Sri Lanka. **E.** *Srilankametrus pococki*, sp. nov., holotype ♀ (AMNH), Kodigala, Sri Lanka. **F.** *Srilankametrus serratus* (Pocock, 1900), comb. nov., ♂ (ZMH), Ceylon [Sri Lanka]. Scale bars = 5 mm.

cutta [Kolkata, 22°34'N 88°22'E], Barabank?, B.V. College, rec. P.K. Sina, 17.viii.1965, ex Stahnke coll., 1 ♀ (CAS 9071134 [ASU 60-271/75-0321]). *Paschim Medinipur Distr.*: Kharqpur [Kharagpur, 22°20'N 87°20'E], 30 m, 20.vi.1960, L. Murmu, in yard, 1 ♂ (CAS 9071140), 17.ii.1961, C.L. Kau, engine room by tin, 1 ♀ (CAS 9071133). *Purba Bardhaman Distr.*: Talpata village [23°11'N 88°07'E], near Saktigarh [23°12'N 87°58'E], ca. 100 km W of Calcutta, xi.1973, Prof. Lahiri, 1 ♀, 2 subad. ♂ (MNHN).

Deccanometrus latimanus (Pocock, 1894),
comb. nov.

Figures 10, 20A, B, 34A, B, 47A–D, 64D, 65D,
66D, 118, 123–126, table 1

Scorpio latimanus Pocock, 1894a: 74, 75;
Kovařík, 2004: 21.

Heterometrus latimanus: Kraepelin, 1899: 113;
Takashima, 1945: 92; Pérez Minnocci, 1974:
38; Kovařík, 2004: 21, 51, table 2 (part);
2009: 35, 39, 47, table 1 (part); Tahir and
Prendini, 2014: 1–23, tables 1, 2, figs. 1–8.

Palamnaeus latimanus: Pocock, 1900a: 85, 90,
fig. 27; Tikader, 1973: 263.

Heterometrus (Srilankametrus) indus: Couzijn,
1981: 82, 94, 121, 123 (misidentification,
part); Kovařík, 1998: 137, 138 (part).

Heterometrus (Srilankametrus) indus indus:
Couzijn, 1981: 39, 82, 121–124, 129, table 7
(misidentification, part).

Heterometrus (Srilankametrus) latimanus:
Tikader and Bastawade, 1983: 544–550, figs.
1458–1468; Fet, 2000: 448.

Heterometrus wroughtoni: Khatoon, 1999: 223, 224,
fig. 12 (misidentification); Kovařík, 2004: 49,
51, table 2 (part); 2009: 35, table 1 (part).

TYPE MATERIAL: Holotype ♀ (BMNH
1879.7.3.1 old 1859/88), India [examined].

DIAGNOSIS: *Deccanometrus latimanus* may be separated from other species of *Deccanometrus* as follows. The carapace is vaulted, the lateral surfaces sloping moderately (fig. 20A, B), in *D. latimanus* but slightly to markedly dorsoventrally

compressed, the lateral surfaces sloping gently, in all other species except *D. xanthopus*. The median notch in the carapace anterior margin is deeply excavated in *D. latimanus* but shallow in *D. liurus*. The superciliary carinae are lower than the median ocelli in *D. latimanus*, but higher than the ocelli in all other species except *D. liurus* and *D. ubicki*. The interocular suture is present in *D. latimanus* but absent in *D. liurus*. The carapace interocular surface is granular along the median longitudinal and anterior bifurcated sulci only in the male and female (fig. 20A, B) of *D. latimanus*, whereas the frontal lobes and medial region are granular, with smooth areas, in the male and female of *D. ubicki*, and the female of *D. bengalensis* and *D. xanthopus*, or partially to entirely granular in the male of *D. xanthopus*. The carapace posterolateral surfaces of the female are granular in *D. latimanus* but smooth or nearly so in *D. obscurus*, *D. phipsoni*, *D. ubicki*, and *D. xanthopus*. The cheliceral movable finger prodistal (DI) and retrodistal (DE) teeth are aligned longitudinally and not opposable in *D. latimanus*, but opposable, i.e., forming a bicuspid, in *D. liurus* and *D. ubicki*. The pedipalps of the adult male are short, with femur length : posterior carapace width ratio (FL:PCW) < 0.77 and femur length : carapace length ratio (FL:CL) < 0.74 (fig. 123A, B) in *D. latimanus* but long, with FL:PCW ≥ 0.80, FL:CL ≥ 0.76 in all other species. The pedipalp femur prodorsal carina is present and distinct in *D. latimanus* but absent or obsolete in *D. liurus* and *D. xanthopus*. The pedipalp patella dorsomedian carina of the female (fig. 124) is absent or obsolete in *D. latimanus*, but entirely to predominantly granular in *D. bengalensis*, *D. obscurus*, *D. phipsoni*, and *D. xanthopus*. The patella retrodorsal carina of the female (fig. 124) is absent or obsolete in *D. latimanus* but as strongly developed as or more strongly developed than the retromedian carinae in *D. obscurus* and *D. phipsoni*. The retromedian carinae of the female are absent or obsolete in *D. latimanus* but granular in *D. bengalensis*, *D. obscurus*, and *D. phipsoni*. The patella dorsal, retrodorsal, and retroventral intercarinal surfaces of the female are smooth or nearly so in *D. latimanus* but granular in *D. obscurus* and *D.*

phipsoni. The pedipalp chela is immaculate and paler than the femur and patella in *D. latimanus* but infusate and similar in color to the femur and patella in *D. bengalensis*, *D. obscurus*, *D. phipsoni*, and *D. ubicki*. The chela of the adult male is moderately to densely setose (fig. 125) in *D. latimanus* but sparsely setose in *D. xanthopus*. The chela manus promedian carina of the female is absent or obsolete in *D. latimanus* (fig. 126) but granular in all other species except *D. xanthopus*. The maximum distance between the dorsomedian and dorsal secondary carinae (DMC–DSC) of the chela manus is greater than the maximum distance between the dorsal secondary and digital carinae (DSC–DC) in the male and female of *D. latimanus* whereas the DMC–DSC is similar to the DSC–DC in the male and female of *D. xanthopus*, and the female of *D. obscurus*, and less than the DSC–DC in the male of *D. obscurus*, and the male and female of *D. bengalensis*, *D. liurus*, *D. phipsoni*, and *D. ubicki*. The chela manus dorsal intercarinal surface is finely to coarsely granular and shallowly reticulate (figs. 125, 126) in *D. latimanus*, smooth and shallowly reticulate in *D. ubicki*, and finely to coarsely granular, without reticulation in *D. obscurus* and *D. phipsoni*. The manus retrolateral intercarinal surfaces are granular in *D. latimanus* but smooth or nearly so in *D. ubicki*. The legs are pale or very lightly infusate (fig. 123) in *D. latimanus* but very dark or heavily infusate in *D. bengalensis*, *D. obscurus*, and *D. phipsoni*. Macroseta *st* on the retroventral surfaces of the basitarsi is setiform on legs I–III (fig. 47A–D) in *D. latimanus* but spiniform on legs I–III in *D. obscurus*, *D. phipsoni*, and *D. ubicki*, and spiniform on legs I and II and setiform on III in *D. bengalensis*; *sb* on the retroventral surfaces of the basitarsi is setiform on legs I and II in *D. latimanus*, setiform on leg I, and setiform or spiniform on leg II in *D. xanthopus*, and spiniform on legs I and II in the other species; *st* on the proventral surface of the basitarsus of leg III is spiniform in *D. latimanus* but setiform in *D. obscurus* and *D. phipsoni*; *sb* on the retrolateral surface of the basitarsus of leg III is setiform in *D. latimanus* but spiniform in the other species. The laterodistal

lobes on the telotarsi of legs I–IV each bear three or more spiniform macrosetae in *D. latimanus* but only two in all other species. The angle of the pectinal first proximal median lamella (scape) is approximately 90° in the male (fig. 34A) and > 90° but < 180° in the female (fig. 34B) of *D. latimanus*, > 90° but < 180° in the male of *D. bengalensis*, *D. obscurus*, and *D. phipsoni*, and approximately 90° in the female of *D. ubicki*. The mesial surfaces of mesosomal tergites I–VI are smooth in the male and the lateral surfaces smooth in the female of *D. latimanus*, whereas the mesial surfaces are granular in the male of *D. xanthopus*, and the lateral surfaces granular in the female of *D. bengalensis*, *D. obscurus*, and *D. phipsoni*. The ventral surface of mesosomal sternite VII bears two pairs of moderately to strongly developed ventrosubmedian and ventrolateral carinae in *D. latimanus* and a pair of weakly developed ventrolateral carinae in *D. bengalensis*, *D. obscurus*, and *D. phipsoni*. The dorsosubmedian carinae of metasomal segments I–IV are costate (fig. 64D) in *D. latimanus*, obsolete in *D. liurus*, and granular or costate-granular in the other species. The ventrosubmedian and ventrolateral carinae of metasomal segments I–IV are more strongly developed on segments I and II than on III and IV (fig. 66D) in *D. latimanus* but more strongly developed on segments III and IV than on I and II in *D. bengalensis*, *D. obscurus*, and *D. phipsoni*. The lateral carinae are partial on metasomal segment I and absent or obsolete on segment V (fig. 65D) in *D. latimanus* but vestigial on I in *D. liurus* and *D. ubicki*, and partial on V in *D. bengalensis*, *D. obscurus*, *D. phipsoni*, and *D. xanthopus*. The dorsolateral carinae of metasomal segment V are weak and discontinuous to absent in *D. latimanus* but strong and continuous in all other species except *D. liurus* and *D. xanthopus*. The telson is as dark as metasomal segment V in *D. latimanus* but paler than segment V in *D. liurus*, *D. ubicki*, and *D. xanthopus*. The width of the telson vesicle is greater than the width of metasomal segment V in the male (figs. 64D, 66D) of *D. latimanus* but approximately equal to or less than the width of segment V in the male of *D. bengalensis*, *D. obscurus*, and *D. phipsoni*.

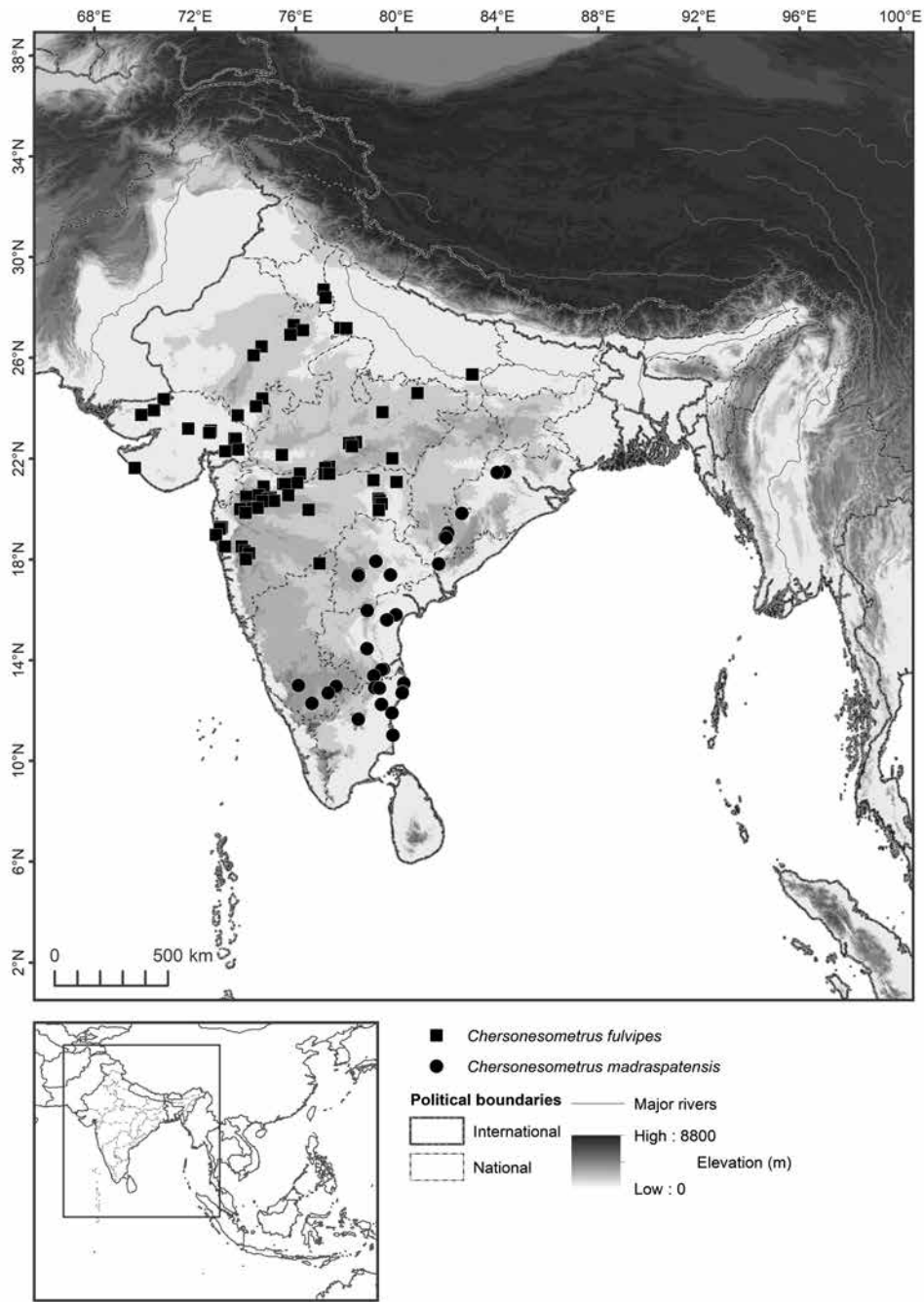


FIGURE 79. Map of South Asia, plotting known locality records of two species of *Chersonesometrus* Couzijn, 1978, stat. nov. et stat. rev., based on material examined, and verified records from virtual museums and the literature: *Chersonesometrus fulvipes* (C.L. Koch, 1837), comb. nov.; *Chersonesometrus madraspatensis* (Pocock, 1900), comb. nov.

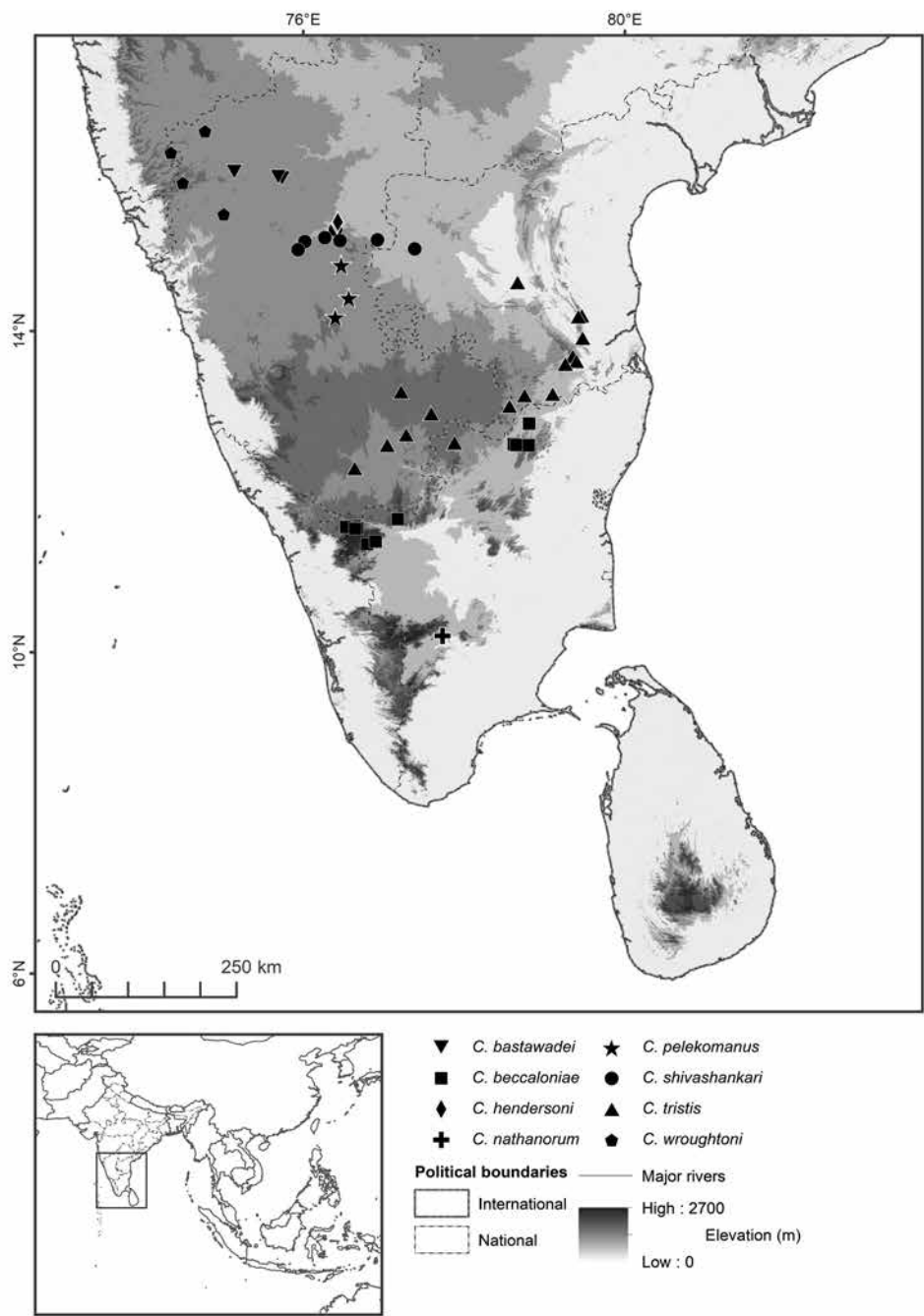


FIGURE 80. Map of South India and Sri Lanka, plotting known locality records of eight species of *Chersonesometrus* Couzijn, 1978, stat. nov. et stat. rev., based on material examined, and verified records from virtual museums and the literature: *Chersonesometrus bastawadei*, sp. nov.; *Chersonesometrus beccaloniae* (Kovářík, 2004), comb. nov.; *Chersonesometrus hendersoni*, sp. nov.; *Chersonesometrus nathanorum*, sp. nov.; *Chersonesometrus pelekomanus* (Couzijn, 1981), comb. nov.; *Chersonesometrus shivashankari*, sp. nov.; *Chersonesometrus tristis* (Henderson, 1919), comb. nov.; *Chersonesometrus wroughtoni* (Pocock, 1899), comb. nov.

DISTRIBUTION: The type locality of *D. latimanus* was indefinitely located in British India (Pocock, 1894a: 74) which, at the time of its description, also included Pakistani territory. It is presently unknown whether the distribution of this species extends into India or whether it is endemic to Pakistan (Tahir and Prendini, 2014). The known locality records are situated in Khyber Pakhtoon Khawa and Azad Kashmir, Pakistan (fig. 118, table 1). Khatoon's (1999) poorly preserved juvenile specimen (PMNH 52) is tentatively assigned to *D. latimanus*. However, this identification requires confirmation by the collection of additional, adult specimens from Azad Kashmir.

ECOLOGY: The specimens for which ecological data are available were collected under stones or on the surface at night, in rocky, forested, mountainous terrain at 350–1030 m elevation. The habitat and habitus of this species are consistent with the pelophilous ecomorphotype (Prendini, 2001b), and suggests that this species is fossorial, although the burrows were not observed (Tahir and Prendini, 2014).

CONSERVATION STATUS: *Deccanometrus latimanus* is harvested, dried, and consumed for medicinal and narcotic purposes in Pakistan (Tahir and Prendini, 2014).

REMARKS: This species, previously placed in subgenus *Srilankametrus* of *Heterometrus* by Tikader and Bastawade (1983) and Fet (2000), is newly accommodated in *Deccanometrus*, gen. nov., based on a phylogenetic analysis (fig. 10).

The two female specimens identified as *H. latimanus* by Kovařík (2004: 21, 51, table 2; 2009: 35, 39, 47, 49, 73, 100, table 1, figs. 3, 4, 198), from "India," are not conspecific with the latter (Tahir and Prendini, 2014). The most obvious differences between these specimens and *D. latimanus* are their larger size (70–105 mm), darker coloration, apparently with dark legs (although this is difficult to tell given the poor condition of the specimen illustrated), more densely granular frontal lobes of the carapace interocular surface, and the uniformly coarsely and densely granular dorsal surface of the pedipalp chela manus. The characters, locality data, and state of preservation

are a precise match for the lectotype of *Buthus caesar*, suggesting they could be part of the original syntype series.

MATERIAL EXAMINED: **PAKISTAN: Khyber Pakhtoon Khawa:** Boner Distr.: Daggar Tehsil, Daggar, 34°31'N 72°28'E, 27.ix.2012, M. Shahid, M. Ahsan, and A. Khan, rocky area with stones, 1 ♀ (AMNH), 1 subad. ♂ (AMCC [LP 11569]), x.2012, M. Azhar, rocky area with stones, collected by turning stones, 2 ♂, 4 ♀, 4 subad. ♂, 2 subad. ♀ (AMNH), 1 subad. ♀ (AMCC [LP 11601]); Boner Tehsil, Daggar, 3 km W of Rega village, 33°51'N 72°48'E, 2257 ft., 13.ix.2012, M. Ahsan, rocky hilly area, collected with UV lamps, 1 ♂, 1 ♀ (AMNH). **Peshawar Distr.:** Peshawar Tehsil, Peshawar, 15 km W on road to Landi Kotal, 34°01'N 71°35'E, 1158 ft., 24.ix.2012, M. Shahid, M. Ahsan, and A. Khan, rocky area with little vegetation, collected by turning stones, 4 PM, 3 ♀ (AMNH), 1 subad. ♀ (AMCC [LP 11568]). **Swat Distr.:** Charbagh Tehsil, Charbagh village, 5 km W, 34°48'N 72°26'E, 3377 ft., 25.ix.2012, M. Shahid, M. Ahsan and A. Khan, rocky area with little vegetation, collected by turning stones, 3–6 PM, 2 ♂, 2 ♀ (AMNH). **Upper Dir Distr.:** Barawal Tehsil, Barawal town, 7 km W, 35°07'N 72°02'E, 14.viii.2012, M. Ahsan, M. Irfan, M. Hussain, and M. Ayyub, hilly area with little vegetation, collected with UV lamps, 10 PM, 3 ♂, 1 juv. ♀ (AMNH), Barawal town, 9 km W, 35°06'N 72°01'E, 14.viii.2012, M. Ahsan, M. Irfan, M. Hussain, and M. Ayyub, hilly area with little vegetation, collected with UV lamps, 10 PM, 3 ♂ (AMNH).

Deccanometrus liurus (Pocock, 1897), comb. nov.

Figures 10, 21C, 35C, 48A–D, 64E, 65E, 66E, 118, 127A, B, 128, 129, table 1

Palamnaeus liurus Pocock, 1897: 114, 115; 1900a: 85, 91, 92.

Heterometrus liurus: Kraepelin, 1899: 110, 115; Roewer, 1929: 613 (part); Fage, 1936: 181 (part); Takashima, 1945: 93; Bücherl, 1964: 59; Pérez Minnocci, 1974: 38; Kovařík, 2004: 23–25, 51, 52, tables 2, 3, fig. 18; 2009: 35, 36, 40, 48, 49, 79, 100, tables 1, 2, figs. 43–46, 204.

Heterometrus (Chersonometrus) liurus: Couzijn, 1981: 42, 86, 133, 152–154, 157, 169–171, 192, table 7, figs. 49, 59; Tikader and Bastawade,



FIGURE 81. *Chersonesometrus* Couzijn, 1978, stat. nov. et stat. rev., habitus, **A, C**, dorsal and **B, D**, ventral aspects. **A, B**, *Chersonesometrus bastawadei*, sp. nov., holotype ♀ (AMNH), Naganath Temple, India. **C, D**, *Chersonesometrus wroughtoni* (Pocock, 1899), comb. nov., paralectotype ♀ (BMNH 1897.9.17.1-4, 11, 20). Scale bars = 10 mm.

1983: 575, 604–608, figs. 1595–1608; Kovařík, 1998: 136 (part); Fet, 2000: 442.

TYPE MATERIAL: INDIA: Madhya Pradesh:

Gwalior Distr.: Palamnaeus liurus: Lectotype ♀ [BNHS 995], paralectotypes: 2 ♀ [BNHS 992,

944], 1 subad. ♂ [BNHS 987], 4 juv. ♂ (BMNH 1896.12.15.20-25), Gwalior [26°13'N 78°11'E], Dane (Medical Officer of Makarajah Scindia) [examined].

DIAGNOSIS: *Deccanometrus liurus* may be separated from other species of *Deccanometrus* as

follows. The carapace is markedly dorsoventrally compressed, the lateral surfaces sloping gently (fig. 21C), in *D. liurus* but vaulted, the lateral surfaces sloping moderately, in *D. latimanus* and *D. xanthopus*. The median notch in the carapace anterior margin is shallow in *D. liurus* but deeply excavated in all other species. The superciliary carinae are lower than the median ocelli in *D. liurus*, but higher than the ocelli in all other species except *D. latimanus* and *D. ubicki*. The interocular suture is absent in *D. liurus* but present in the other species. The carapace interocular surface is granular along the median longitudinal and anterior bifurcated sulci only in the male and female (fig. 21C) of *D. liurus*, whereas the frontal lobes and medial region are granular, with smooth areas, in the male and female of *D. ubicki*, and the female of *D. bengalensis* and *D. xanthopus*, or partially to entirely granular in the male of *D. xanthopus*. The carapace posterolateral surfaces of the female are granular in *D. liurus* but smooth or nearly so in *D. obscurus*, *D. phipsoni*, *D. ubicki* and *D. xanthopus*. The cheliceral movable finger prodistal (DI) and retrodistal (DE) teeth are opposable, i.e., forming a bicusps, in *D. liurus*, but aligned longitudinally and not opposable in all other species except *D. ubicki*. The pedipalp femur prodorsal carina is absent or obsolete in *D. liurus* but present and distinct in all other species except *D. xanthopus*. The pedipalp patella dorsomedian carina of the female (fig. 128) is absent or obsolete in *D. liurus*, but entirely to predominantly granular in *D. bengalensis*, *D. obscurus*, *D. phipsoni* and *D. xanthopus*. The patella retrodorsal carina of the female (fig. 128) is absent or obsolete in *D. liurus* but as strongly developed as or more strongly developed than the retromedian carinae in *D. obscurus* and *D. phipsoni*. The retromedian carinae of the female are absent or obsolete in *D. liurus* but granular in *D. bengalensis*, *D. obscurus*, and *D. phipsoni*. The patella dorsal, retrodorsal, and retroventral intercarinal surfaces of the female are smooth or nearly so in *D. liurus* but granular in *D. obscurus* and *D. phipsoni*. The pedipalp chela is immaculate and paler than the femur and

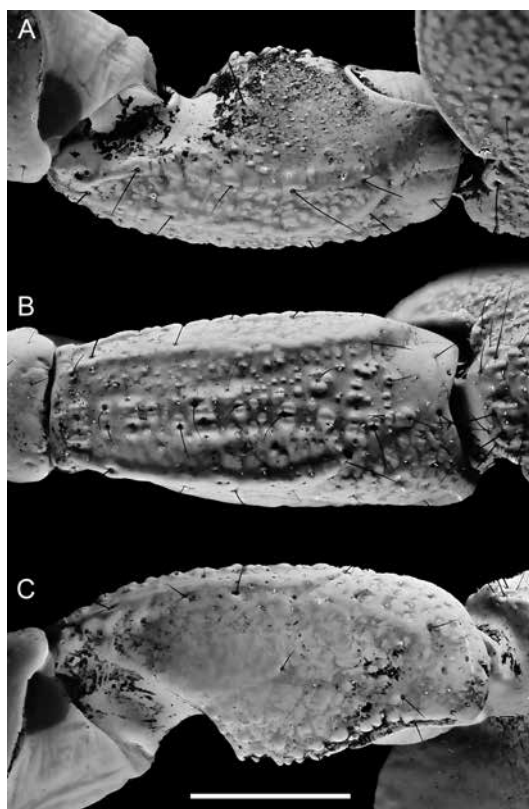


FIGURE 82. *Chersonesometrus bastawadei*, sp. nov., holotype ♀ (AMNH), Naganath Temple, India, pedipalp patella: A. dorsal, B. retrolateral, and C. ventral aspects. Scale bar = 5 mm.

patella in *D. liurus* but infusate and similar in color to the femur and patella in *D. bengalensis*, *D. obscurus*, *D. phipsoni*, and *D. ubicki*. The chela manus promedian carina of the female is granular (fig. 129) in *D. liurus* but absent or obsolete in *D. latimanus* and *D. xanthopus*. The maximum distance between the dorsomedian and dorsal secondary carinae (DMC–DSC) of the chela manus is less than the maximum distance between the dorsal secondary and digital carinae (DSC–DC) in the male and female of *D. liurus* whereas the DMC–DSC is similar to the DSC–DC in the male and female of *D. xanthopus* and the female of *D. obscurus*, and greater than the DSC–DC in the male and female of *D. latimanus*. The chela

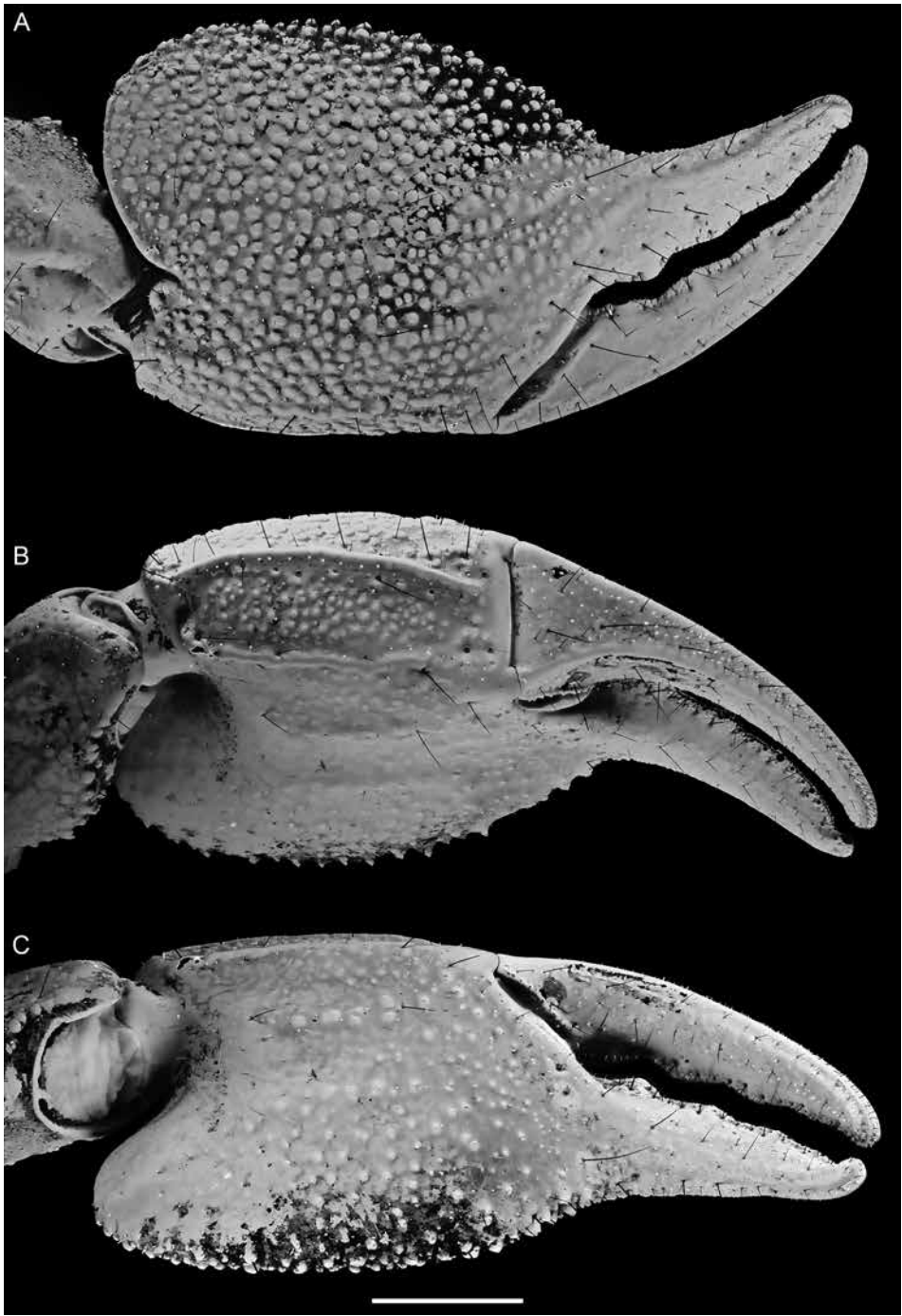


FIGURE 83. *Chersonesometrus bastawadei*, sp. nov., holotype ♀ (AMNH), Naganath Temple, India, pedipalp chela: **A.** retrodorsal, **B.** ventral, and **C.** prolateral aspects. Scale bar = 5 mm.

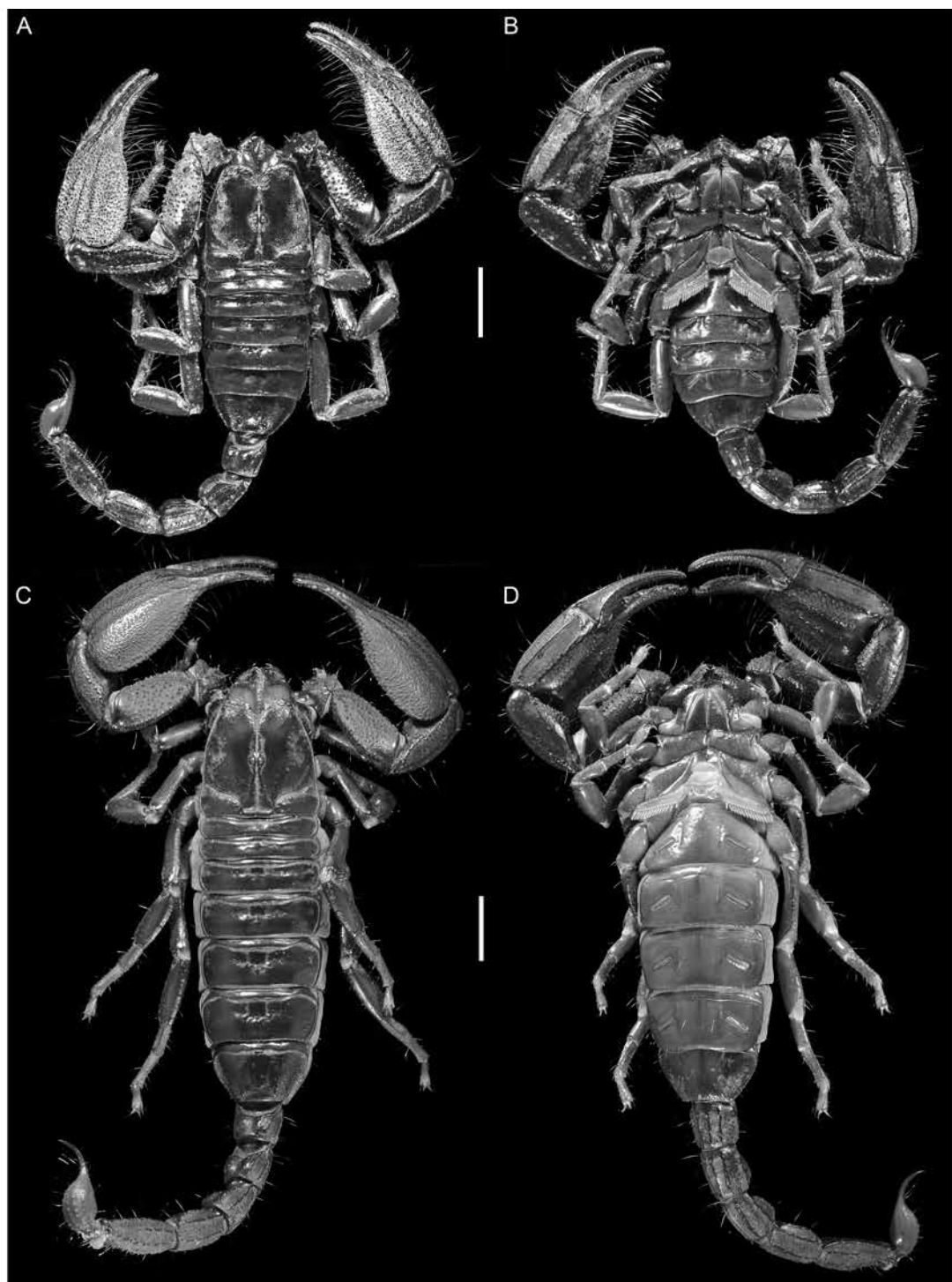


FIGURE 84. *Chersonesometrus beccaloniae* (Kovářík, 2004), comb. nov., habitus: **A, C.** dorsal and **B, D.** ventral aspects. **A, B.** ♂ (ZMH), Ootacalum, India. **C, D.** ♀ (AMNH), Yelagiri Hills, India. Scale bars = 10 mm.

manus dorsal intercarinal surface is finely to coarsely granular and shallowly reticulate (fig. 129) in *D. liurus*, smooth and shallowly reticulate in *D. ubicki*, and finely to coarsely granular, without reticulation in *D. obscurus* and *D. phipsoni*. The manus retrolateral intercarinal surfaces are granular in *D. liurus* but smooth or nearly so in *D. ubicki*. The legs are pale or very lightly infuscate (fig. 127A, B) in *D. liurus* but very dark or heavily infuscate in *D. bengalensis*, *D. obscurus*, and *D. phipsoni*. Macroseta *st* on the retroventral surfaces of the basitarsi is setiform on legs I–III (fig. 48A–D) in *D. liurus* but spiniform on legs I–III in *D. obscurus*, *D. phipsoni*, and *D. ubicki* and spiniform on legs I and II, and setiform on III in *D. bengalensis*; *sb* on the retroventral surfaces of the basitarsi is spiniform on legs I and II in *D. liurus*, setiform on legs I and II in *D. latimanus*, and setiform on leg I, and setiform or spiniform on leg II in *D. xanthopus*; *st* on the proventral surface of the basitarsus of leg III is spiniform in *D. liurus* but setiform in *D. obscurus* and *D. phipsoni*; *sb* on the retrolateral surface of the basitarsus of leg III is spiniform in *D. liurus* but setiform in *D. latimanus*. The laterodistal lobes on the telotarsi of legs I–IV each bear only two spiniform macrosetae in *D. liurus* but three or more in *D. latimanus*. The angle of the pectinal first proximal median lamella (scape) is approximately 90° in the male and > 90° but < 180° in the female (fig. 35C) of *D. liurus*, > 90° but < 180° in the male of *D. bengalensis*, *D. obscurus*, and *D. phipsoni*, and approximately 90° in the female of *D. ubicki*. The mesial surfaces of mesosomal tergites I–VI are smooth in the male and the lateral surfaces smooth in the female of *D. liurus*, whereas the mesial surfaces are granular in the male of *D. xanthopus*, and the lateral surfaces granular in the female of *D. bengalensis*, *D. obscurus*, and *D. phipsoni*. The ventral surface of mesosomal sternite VII bears two pairs of moderately to strongly developed ventrosubmedian and ventrolateral carinae in *D. liurus* and a pair of weakly developed ventrolateral carinae in *D. bengalensis*, *D. obscurus*, and *D. phipsoni*. The dorsosubmedian carinae of metasomal segments I–IV are obsolete

(fig. 64E) in *D. liurus*, costate in *D. latimanus*, and granular or costate-granular in the other species. The ventrosubmedian and ventrolateral carinae of metasomal segments I–IV are more strongly developed on segments I and II than on III and IV (fig. 66E) in *D. liurus* but more strongly developed on segments III and IV than on I and II in *D. bengalensis*, *D. obscurus*, and *D. phipsoni*. The lateral carinae are vestigial on metasomal segment I and absent or obsolete on segment V (fig. 65E) in *D. liurus* but partial on I in *D. latimanus*, and on I and V in *D. bengalensis*, *D. obscurus*, *D. phipsoni*, and *D. xanthopus*. The dorsolateral carinae of metasomal segment V are weak and discontinuous to absent in *D. liurus* but strong and continuous in all other species except *D. latimanus* and *D. xanthopus*. The telson is paler than metasomal segment V in *D. liurus* but as dark as segment V in *D. latimanus*. The width of the telson vesicle is greater than the width of metasomal segment V in the male of *D. liurus* but approximately equal to or less than the width of segment V in the male of *D. bengalensis*, *D. obscurus*, and *D. phipsoni*.

DISTRIBUTION: This species is endemic to India and known from only two localities, Gwalior and Bhopal, in the state of Madhya Pradesh (fig. 118, table 1).

ECOLOGY: The known locality records are situated in a region of arid savanna with low rocky hills and ridges. Although no data are available on the ecology of this species, the habitus is consistent with fossorial, semilithophilous ecomorphotype (Prendini, 2001b). The dorsoventral compression and short metasoma of this species suggest that it inhabits rock crevices or scrapes under stones.

CONSERVATION STATUS: This species has not been seen in over a century and its status is unknown.

REMARKS: This species, previously placed in subgenus *Chersonesometrus* of *Heterometrus* by various authors (e.g., Couzijn, 1981; Tikader and Bastawade, 1983; Fet, 2000), is newly accommodated in *Deccanometrus*, gen. nov., based on a phylogenetic analysis (fig. 10).

- Deccanometrus obscurus* (Couzijn, 1981),
comb. et stat. nov.
Figures 8A, 10, 19C, D, 33C, D, 46E–H, 64B,
65B, 66B, 117, 130–134, table 1
- Pandinus megacephalus*: Thorell, 1893: 381, 382
(part).
- Scorpio phipsoni*: Pocock, 1894a: 73, 74
(misidentification, part).
- Palamnaeus phipsoni*: Pocock, 1900a: 94, 95
(misidentification, part); Tikader, 1973: 263
(misidentification).
- Heterometrus (Scorpio) longimanus*: Kraepelin,
1901: 271 (misidentification, part).
- Heterometrus (Scorpio) phipsoni*: Kraepelin,
1901: 271 (misidentification).
- Heterometrus phipsoni*: Kraepelin, 1913: 166
(misidentification, part); Kovařík, 2004: 4,
29, 34, 44, 49, 51, 52, tables 2, 3 (misidenti-
fication, part); 2009: 35, 36, 42, 43, 48, 49,
88, 99, tables 1, 2 (misidentification, part),
figs. 103–110, 188, 189 (misidentification);
Mirza and Sanap, 2009: 488–490, table 1,
fig. 1, images 1–7 (misidentification, part);
Javed et al., 2010a: 147 (misidentification);
Mirza et al., 2012: 7 (misidentification); Patil
and Shah, 2013: 33–35 (misidentification);
Aswathi and Sureshan, 2017: 9847 (misiden-
tification, part).
- Heterometrus scaber*: Kraepelin, 1913: 166 (mis-
identification, part); Aswathi and Sureshan,
2017: 9847 (misidentification, part).
- Palamnaeus scaber*: Tikader, 1973: 263
(misidentification).
- Palamnaeus scaber kanarensis*: Tikader, 1973:
263 (misidentification).
- Heterometrus (Chersonesometrus) phipsoni*:
Couzijn, 1981: 153, 155, 157–159, 169, 171,
180, fig. 59 (misidentification, part); Tikader
and Bastawade, 1983: 577, 646–648, 651
(misidentification, part); Bastawade, 2002:
296 (part); 2006a: 131, 134, 135
(misidentification); 2009: 215, 219, 220
(misidentification).
- Heterometrus (Chersonesometrus) phipsoni*
phipsoni: Couzijn, 1981: 43, 87, 149–151,
153, 170, 171, 192, table 7, fig. 59 (misiden-
tification, part).
- Heterometrus (Chersonesometrus) scaber*
obscurus Couzijn, 1981: 87, 146–149, 170,
192, figs. 46, 58; Kovařík, 1998: 136; Fet,
2000: 440.
- Heterometrus (Chersonesometrus) kanaraensis*:
Tikader and Bastawade, 1983: 577, 636, 638,
640, 641 (misidentification, part);
Bastawade, 2002: 296 (misidentification);
Bastawade et al., 2004: 56 (misidentification,
part).
- Heterometrus (Heterometrus) bengalensis*:
Tikader and Bastawade, 1983: 522, 528,
539–544 (part).
- Heterometrus indus*: Tare et al., 1993: 102–104,
tables 1, 2, figs. 1–3 (misidentification).
- Heterometrus (Chersonesometrus) fastigosus*:
Bastawade, 2002: 295 (misidentification).
- Heterometrus (Heterometrus) keralaensis*:
Bastawade, 2002: 295 (misidentification).
- Heterometrus keralaensis*: Kovařík, 2004: 20,
51–53, tables 2, 3 (part); 2009: 35, 36, 39,
48, tables 1, 2 (part).
- Heterometrus scaber*: Kovařík, 2004: 1, 35, 38,
51–53, tables 2, 3 (misidentification, part);
2009: 35, 36, 43, 48, tables 1, 2 (misidentifi-
cation, part).
- Heterometrus scaber obscurus*: Kovařík, 2004: 38.
- Heterometrus (Heterometrus) keralensis*:
Bastawade, 2006a: 131, 135, 136 (misidenti-
fication, part); 2009: 215, 220, 221 (misiden-
tification, part).
- Heterometrus (Chersonesometrus) kanarensis*:
Sureshan et al., 2007b: 52, 53, photo 5
(misidentification, part).
- Heterometrus keralaensis*: Aswathi and Sureshan,
2017: 9847 (misidentification, part).

TYPE MATERIAL: **INDIA: Maharashtra:**
Raigad Distr.: Heterometrus (Chersonesometrus)
scaber obscurus: Holotype ♀ (MNHN RS 0107),

Matheran [18°59'N 73°16'E], near Bombay [Mumbai], xi.1896, M. Maindron [examined].

DIAGNOSIS: *Deccanometrus obscurus* may be separated from other species of *Deccanometrus* as follows. The carapace is moderately dorsoventrally compressed, the lateral surfaces sloping gently (fig. 19C, D), in *D. obscurus* but markedly dorsoventrally compressed in *D. phipsoni* and vaulted, the lateral surfaces sloping moderately, in *D. latimanus* and *D. xanthopus*. The median notch in the carapace anterior margin is deeply excavated in *D. obscurus* but shallow in *D. liurus*. The superciliary carinae are higher than the median ocelli in *D. obscurus*, but lower than the ocelli in all other species except *D. latimanus*, *D. liurus*, and *D. ubicki*. The interocular suture is present in *D. obscurus* but absent in *D. liurus*. The carapace interocular surface is granular along the median longitudinal and anterior bifurcated sulci only in the male and female (fig. 19C, D) of *D. obscurus*, whereas the frontal lobes and medial region are granular, with smooth areas, in the male and female of *D. ubicki*, and the female of *D. bengalensis* and *D. xanthopus*, or partially to entirely granular in the male of *D. xanthopus*. The carapace posterolateral surfaces of the female are smooth or nearly so in *D. obscurus* but granular in *D. bengalensis*, *D. latimanus*, and *D. liurus*. The chelicer al movable finger prodistal (DI) and retrodistal (DE) teeth are aligned longitudinally and not opposable in *D. obscurus*, but opposable, i.e., forming a bicusps, in *D. liurus* and *D. ubicki*. The pedipalps of the adult male are long, with femur length : posterior carapace width ratio (FL:PCW) ≥ 0.80 and femur length : carapace length ratio (FL:CL) ≥ 0.76 (fig. 130) in *D. obscurus* but short, with FL:PCW < 0.77 , FL:CL < 0.74 in *D. latimanus*. The pedipalp femur prodorsal carina is present and distinct in *D. obscurus* but absent or obsolete in *D. liurus* and *D. xanthopus*. The pedipalp patella dorsomedian carina of the female is entirely to predominantly granular in *D. obscurus* but absent or obsolete in *D. latimanus*, *D. liurus*, and *D. ubicki*. The patella retrodorsal carina of the female is as strongly developed as or more strongly developed than the retromedian carinae in *D. obscurus* but absent or obsolete in all other spe-

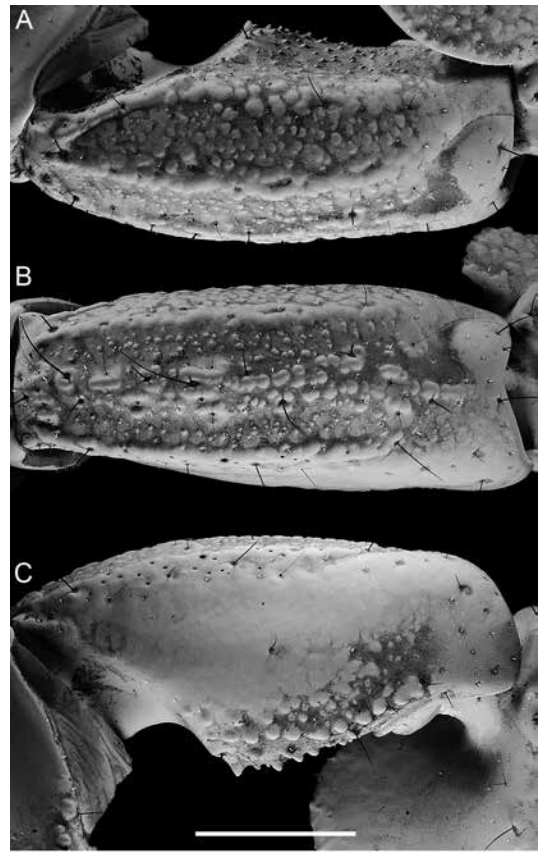


FIGURE 85. *Chersonesometrus beccaloniae* (Kovařík, 2004), comb. nov., ♀ (AMNH), Yelagiri Hills, India, pedipalp patella: A. dorsal, B. retrolateral, and C. ventral aspects. Scale bar = 5 mm.

cies except *D. phipsoni*. The retromedian carinae of the female are granular in *D. obscurus* but absent or obsolete in *D. latimanus*, *D. liurus*, *D. ubicki*, and *D. xanthopus*. The patella dorsal, retrodorsal and retroventral intercarinal surfaces are granular (fig. 132) in *D. obscurus* but smooth or nearly so in all other species except *D. phipsoni*. The pedipalp chela is infusate and similar in color to the femur and patella in *D. obscurus* but immaculate and paler than the femur and patella in *D. latimanus*, *D. liurus*, and *D. xanthopus*. The chela of the adult male is moderately to densely setose (fig. 133) in *D. obscurus* but sparsely setose in *D. xanthopus*. The chela manus promedian carina of the female is granular

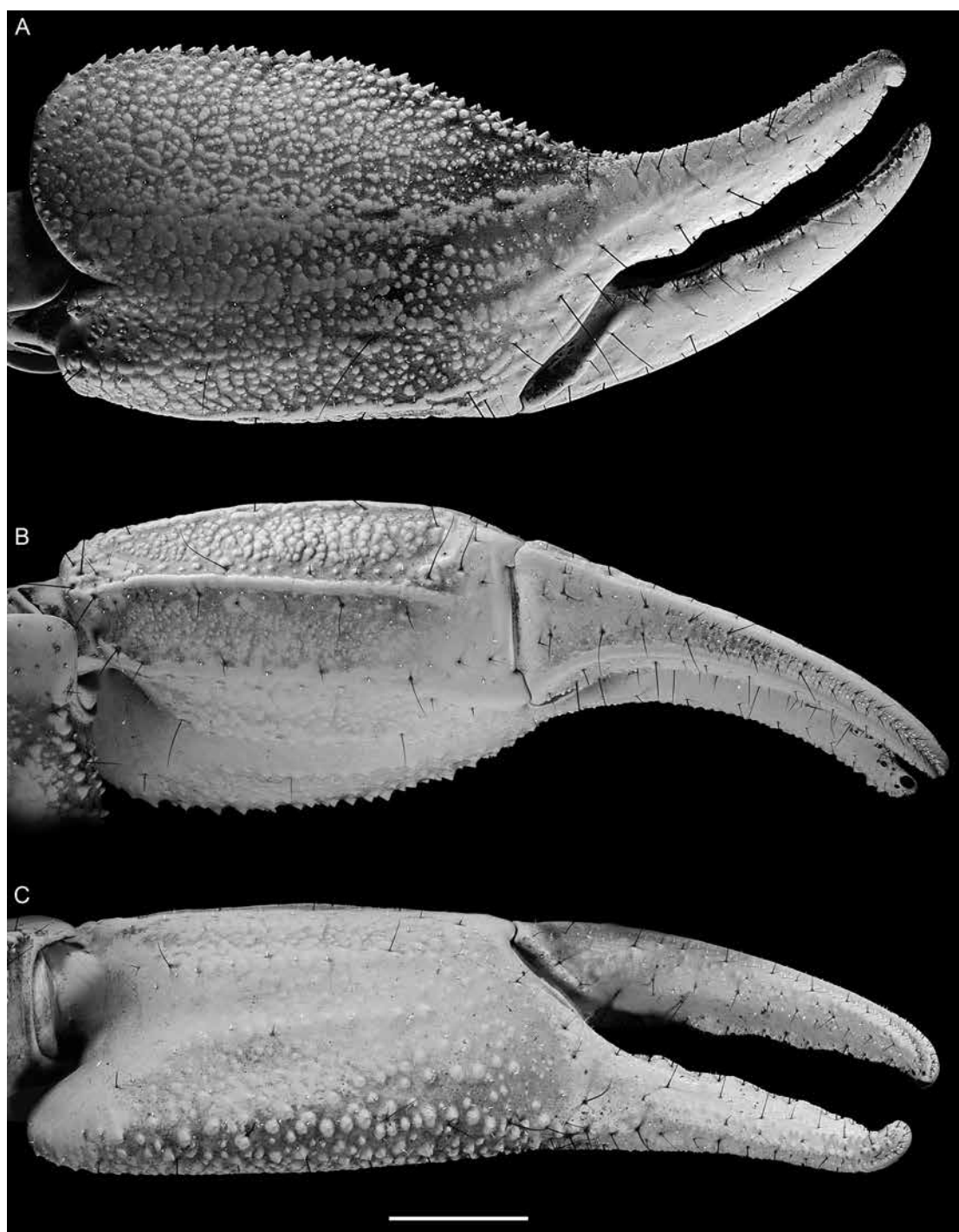


FIGURE 86. *Chersonesometrus beccaloniae* (Kovařík, 2004), comb. nov., ♀ (AMNH), Yelagiri Hills, India, pedipalp chela: A. retrodorsal, B. ventral, and C. prolateral aspects. Scale bar = 5 mm.



FIGURE 87. *Chersonesometrus beccaloniae* (Kovářík, 2004), comb. nov., ♂ (ZMH), Ootacalum, India, pedipalpal chela: A. retrodorsal, B. ventral, and C. prolateral aspects. Scale bar = 5 mm.

(fig. 134) in *D. obscurus* but absent or obsolete in *D. latimanus* and *D. xanthopus*. The maximum distance between the dorsomedian and dorsal secondary carinae (DMC–DSC) of the chela manus is less than the maximum distance between the dorsal secondary and digital carinae (DSC–DC) in the male and similar to the DSC–DC in the female of

D. obscurus whereas the DMC–DSC is less than the DSC–DC in the female of *D. bengalensis*, *D. liurus*, *D. phipsoni*, and *D. ubicki*, similar to the DSC–DC in the male and female of *D. xanthopus*, and greater than the DSC–DC in the male and female of *D. latimanus*. The chela manus dorsal intercarinal surface is finely to coarsely granular, without reticulation

(figs. 133, 134) in *D. obscurus*, finely to coarsely granular and shallowly reticulate in *D. bengalensis*, *D. latimanus*, *D. liurus*, and *D. xanthopus*, and smooth and shallowly reticulate in *D. ubicki*. The manus retrolateral intercarinal surfaces are granular in *D. obscurus* but smooth or nearly so in *D. ubicki*. The legs are very dark or heavily infusate (figs. 130, 131) in *D. obscurus* but pale or very lightly infusate in *D. latimanus*, *D. liurus*, *D. ubicki*, and *D. xanthopus*. Macroseta *st* on the retroventral surfaces of the basitarsi is spiniform on legs I–III (fig. 46E–H) in *D. obscurus* and on legs I and II in *D. bengalensis* but setiform on legs I–III in *D. latimanus*, *D. liurus*, and *D. xanthopus* and on leg III in *D. bengalensis*; *sb* on the retroventral surfaces of the basitarsi is spiniform on legs I and II in *D. obscurus*, setiform on legs I and II in *D. latimanus*, and setiform on leg I, and setiform or spiniform on leg II in *D. xanthopus*; *st* on the proventral surface of the basitarsus of leg III is setiform in *D. obscurus* but spiniform in all other species except *D. phipsoni*; *sb* on the retrolateral surface of the basitarsus of leg III is spiniform in *D. obscurus* but setiform in *D. latimanus*. The laterodistal lobes on the telotarsi of legs I–IV each bear only two spiniform macrosetae in *D. obscurus* but three or more in *D. latimanus*. The laterodistal lobes on the telotarsi of legs I–IV each bear only two spiniform macrosetae in *D. obscurus* but three or more in *D. latimanus*. The angle of the pectinal first proximal median lamella (scape) is $> 90^\circ$ but $< 180^\circ$ in the male and female (fig. 33C, D) of *D. obscurus*, and approximately 90° in the male of *D. latimanus*, *D. liurus*, and *D. xanthopus* and the male and female of *D. ubicki*. The mesial surfaces of mesosomal tergites I–VI are smooth in the male and the lateral surfaces granular in the female of *D. obscurus*, whereas the mesial surfaces are granular in the male of *D. xanthopus*, and the lateral surfaces smooth in the female of *D. latimanus*, *D. liurus*, *D. ubicki*, and *D. xanthopus*. The ventral surface of mesosomal sternite VII bears a pair of weakly developed ventrolateral carinae in *D. obscurus* but two pairs of moderately to strongly developed ventrosulmedian and ventrolateral carinae in *D. latimanus*, *D. liurus*, *D. ubicki*, and *D. xanthopus*. The dorsosulmedian carinae of metasomal segments I–IV are granular or

costate-granular (fig. 64B) in *D. obscurus*, costate in *D. latimanus*, and obsolete in *D. liurus*. The ventrosulmedian and ventrolateral carinae of metasomal segments I–IV are more strongly developed on segments III and IV than on I and II (fig. 66B) in *D. obscurus* but more strongly developed on segments I and II than on III and IV in *D. latimanus*, *D. liurus*, *D. ubicki*, and *D. xanthopus*. The lateral carinae are partial on metasomal segments I and V (fig. 65B) in *D. obscurus* but vestigial on I in *D. liurus* and *D. ubicki*, and absent or obsolete on V in *D. latimanus*, *D. liurus*, and *D. ubicki*. The dorsolateral carinae of metasomal segment V are strong and continuous in *D. obscurus* but weak and discontinuous to absent in *D. latimanus*, *D. liurus*, and *D. xanthopus*. The width of the telson vesicle is approximately equal to or less than the width of metasomal segment V in the male (figs. 64B, 66B) of *D. obscurus* but greater than the width of segment V in the male of *D. latimanus*, *D. liurus*, *D. ubicki*, and *D. xanthopus*.

DISTRIBUTION: This species is endemic to India (fig. 117) and appears to be restricted to the states of Gujarat and Maharashtra (table 1). Its distribution is allopatric with that of the closely related *D. phipsoni*.

ECOLOGY: *Deccanometrus obscurus* inhabits primary evergreen forests at 550–1000 m elevation on the slopes of the Western Ghats (Sahyadri). The burrowing biology of this fossorial, pelophilous species was described by Tare et al. (1993), as *H. indus*, and Mirza and Sanap (2009), as *H. phipsoni*. The burrows, constructed under stones (fig. 8A) or in open ground in clayey-loam soil, have oval, semicircular or crescent-shaped entrances, 4–5.5 cm x 2–3.3 cm. The burrows are 30–50 cm deep and descend gradually, often with a gentle turn, but sometimes straight or tortuous, leading to a terminal chamber (Bastawade, 2006, 2009; Mirza and Sanap, 2009). Burrows are usually occupied by a single individual and have a single entrance, even when occupied by a mother and her brood (Tare et al., 1993). The habitat and habitus are consistent with the fossorial, pelophilous ecomorphotype (Prendini, 2001b). This species is sympatric with the buthids *Hottentotta rugiscutis*, *Isometrus sankeriensis*, *Reddyanus acan-*

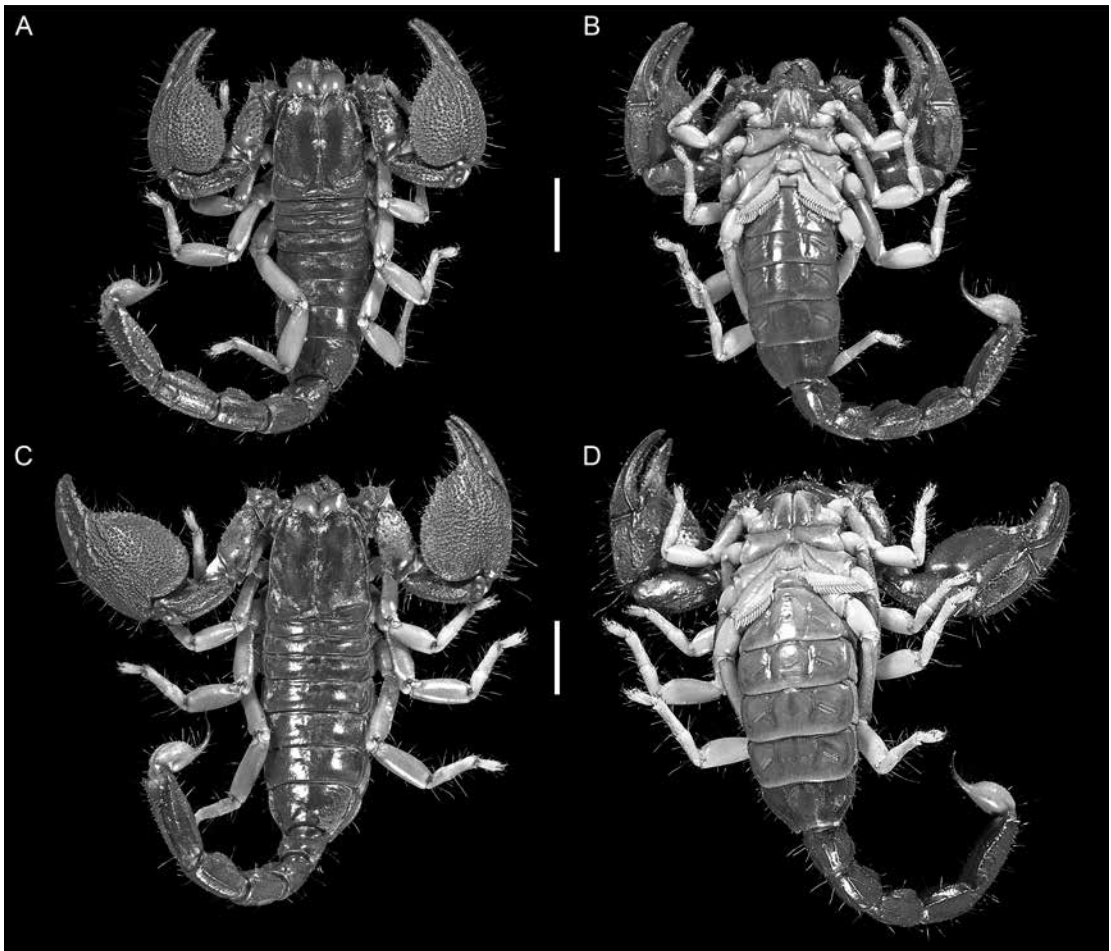


FIGURE 88. *Chersonesometrus fulvipes* (C.L. Koch, 1837), comb. nov., habitus: A, C. dorsal and B, D. ventral aspects. A, B. ♂, C, D. ♀ (AMNH), Khambatki Ghat, India. Scale bars = 10 mm.

thurus (Pocock, 1899), and *Reddyanus rigidulus* (Pocock, 1897), the scorpionid *Chersonesometrus fulvipes*, and the scoriopids *Neoscorpiops deccanensis* (Tikader and Bastawade, 1977) and *Neoscorpiops tenuicauda* (Pocock, 1894).

CONSERVATION STATUS: *Deccanometrus obscurus* is occasionally available in the exotic pet trade, under the name *H. phipsoni*.

REMARKS: This species, previously placed in subgenus *Chersonesometrus* of *Heterometrus* by various authors (e.g., Couzijn, 1981; Fet, 2000), is newly accommodated in *Deccanometrus*, gen. nov., based on a phylogenetic analysis (fig. 10).

Couzijn (1981) described *H. (C.) scaber obscurus* from Matheran, a hill station near Mumbai, in the state of Maharashtra. The subspecies was not mentioned by Tikader and Bastawade (1983) but was listed by Fet (2000). Kovařík (2004: 35, 38; 2009: 43) listed the subspecies under *H. scaber* but did not formally synonymize it, being unable to examine the holotype. The holotype was examined during the present investigation, and the diagnostic characters mentioned by Couzijn (1981: 147, 148) are consistent with material from Maharashtra identified as *H. phipsoni* by subsequent authors (e.g., Tikader

and Bastawade, 1983; Kovařík, 2004, 2009; Mirza and Sanap, 2009; Javed et al., 2010a; Mirza et al., 2012). These characters include carination and surface macrosculpture of the pedipalp chela, described as “external hand surface covered with low and stout granules, no keels present”; counts of 5/6 pro- and retroventral spiniform macrosetae on the telotarsi of legs III and IV; and pectinal tooth counts of 12/12. Comparison of specimens from across the distributions of *H. (C.) s. obscurus* and *H. phipsoni*, including the types of both taxa, during the present investigation identified subtle but consistent differences between the two taxa, e.g., the more convex carapace and pedipalp chela manus (more obvious in the female), less coarsely granular chela manus, and proportionally shorter, more robust metasoma of *H. (C.) s. obscurus*. These differences, taken together with reciprocal monophyly of specimens from the two areas in the phylogenetic analysis, justify the elevation of *H. (C.) s. obscurus* to the rank of species as *Deccanometrus obscurus* (Couzijn, 1981), comb. et stat. nov.

MATERIAL EXAMINED: **Maharashtra:** N Konkan, R.C. Wroughton, 1 ♂ [BNHS 49], 1 ♀ [BNHS 47], 1 juv. ♀ [BNHS 2] (BMNH 1896.7.30.101-103). S Konkan, W.H. Drew, 1 ♀ [BNHS 186], 1 subad. ♂ [BNHS 193], 1 subad. ♀ [BNHS 188], 3 juv. ♂ [BNHS 201, 205, 210], 4 juv. ♀ [BNHS 196, 197, 204, 208] (BMNH 1896.7.3.104-113). **Kolhapur Distr.:** Budhargad [Bhudargad, 16°14'N 74°03'E], Kolhapur St., 1 ♀ (BMNH 1897.9.5.1 [BNHS 1009]), 1 juv. ♂ (BMNH 1897.9.5.15 [BNHS 1010]), 1 juv. ♀ (BMNH 1897.9.5.14 [BNHS 1012]); Kolhapur [16°42'N 74°14'E], 1 ♀ (BMNH 1897.9.5.12 [BNHS 1052]); Panala [Panhala, 16°49'N 74°07'E], Kolhapur St., 1 subad. ♂ (BMNH 1897.9.5.13 [BNHS 1024]), 1 juv. ♂, 3 juv. ♀ (BMNH 1897.9.5.14 [BNHS 1025]). **Mumbai City Distr.:** Bombay [Mumbai, 18°59'N 72°50'E], 6.iii.1967, S.R. Sane, ex Stahnke coll., 4 ♂ (CAS 9070410 [ASU 67-351], 9070414 [ASU 67-317, 322], 9070415 [ASU 67-301]), 8 ♀ (CAS 9070408 [ASU 67-311], 9070412 [ASU 67-313], 9070413 [ASU 67-309, 315], 9070414 [ASU 67-302, 312], 9070415 [ASU 67-304, 306]), 11 subad. ♂ (CAS 9070413 [ASU 67-328, 332, 340-342], 9070414 [ASU 67-314, 336, 337], 9070415 [ASU 67-310, 343, 344]), 12 subad. ♀ (CAS 9070413 [ASU 67-324, 330, 339], 9070414 [ASU 67-303, 321, 326, 332, 333, 335, 338], 9070415 [ASU

67-345, 346]), 8 juv. ♂ (CAS 9070413 [ASU 67-308, 329], 9070414 [ASU 67-331, 334], 9070415 [ASU 67-347-350]), 5 juv. ♀ (CAS 9070414 [ASU 67-318], 9070415 [ASU 67-316, 323, 325, 327]). **Mumbai Suburban Distr.:** Sanjay Ghandi Park, Kanheri caves [19°12'N 72°54'E], Bombay [Mumbai], 24.v.2006, S. Huber, under big stone, mother and juveniles, 1 ♀ (AMNH), 1 juv. ♂ (AMCC [LP 6225]). **Nashik Distr.:** Dindori [20°12'N 73°50'E], Nasik, 1 ♀ (BMNH 1897.9.5.11 [BNHS 1142]); Nasik [20°00'N 73°47'48"E], Lina, 1 juv. ♀ (BMNH 1897.9.5.5 [BNHS 1135]), N. Peinth, 1 ♂ (BMNH 1897.9.5.9 [BNHS 1131]), 1 ♀ (BMNH 1897.9.5.10 [BNHS 1132]), S. Peinth, 1 subad. ♀ (BMNH 1897.9.5.7 [BNHS 1157]), 1 juv. ♀ (BMNH 1897.9.5.3.11 [BNHS 1160]); Nasik Ghat [20°00'N 73°47'E], 1 ♀ (BMNH 1897.9.5.4 [BNHS 1151]). **Pune Distr.:** Bhimashankar, near Maa Anjani Temple, 19°04'N 73°32'E, 942-956 m, 30. xi.2009, R. Datta, evergreen forest with patches of grassland, on rocky mountain slope, volcanic (basalt) outcrops, loose and embedded stones, burrows (ca. 20 cm deep) in clayey-loam soil under stones along forest margins, 2 ♀ (AMNH), 1 juv. ♂ (AMCC [LP 16817]); Bhimashankar, path to Hanuman Temple, 19°04'N 73°32'E, 900 m, 1.xii.2006, P. Menon, in burrows, ca. 30-50 cm deep, under basalt stones in forest or on forest margins, 2 ♂, 2 ♀, 1 subad. ♂, 1 subad. ♀, 8 juv. ♂, 14 juv. ♀ (AMNH), 1 juv. ♂, 2 juv. ♀ (AMCC [LP 13974]). **Raigad Distr.:** Matheran [18°59'N 73°16'E], near Bombay [Mumbai], xi.1896, M. Maindron, 1 juv. ♂, 1 juv. ♀ (MNHN RS 0107). **Sindhudurg Distr.:** Amboli, ca. 300 m S, 15°58'N 74°00'E, 699 m, 26. xi.2009, R. Datta, evergreen dry forest with open grassy areas between forest patches, scattered volcanic (basalt) stones, in shallow burrows (ca. 15 cm deep) in clayey-loam soil under large stones, 2 ♂, 1 ♀, 1 subad. ♀, 1 juv. ♂, 1 juv. ♀, 1 ♀ dextral pedipalp patella and chela (AMNH), 1 juv. ♂, 1 juv. ♀ (AMCC [LP 16800]). **Thane Distr.:** Bhiwandi [19°18'N 73°03'E], 15 mi. N Bombay, F.B. Steiner, xii.1964, 2 ♀, 1 subad. ♂, 2 subad. ♀ (CAS 9070420).

Deccanometrus phipsoni (Pocock, 1893),
comb. nov.

Figures 7G, 10, 19E, F, 33E, F, 46I-L, 64C, 65C, 66C, 117, 135-138, table 1

Scorpio phipsoni Pocock, 1893: 307-310;

Kraepelin, 1894: 48; Kovařík, 2004: 34.

Scorpio ceylonicus: Kraepelin, 1894: 31, 46–51, 54, 55, 57, 240 (misidentification, part).

Scorpio megacephalus: Pocock, 1894a: 74 (misidentification).

Heterometrus phipsoni: Kraepelin, 1899: 109, 114; 1913: 166 (part); Werner, 1936: 186 (part); Takashima, 1945: 92 (part); Pointer, 1991: 24; Kovařík, 2004: 1, 4, 29, 34, 44, 49, 51, 52, tables 2, 3 (part); 2009: 35, 36, 42, 43, 48, tables 1, 2 (part); Mirza and Sanap, 2009: 488 (part); Aswathi and Sureshan, 2017: 9847 (part).

Palamnaeus phipsoni: Pocock, 1900a: 85, 94–96 (misidentification, part); Kovařík, 2004: 34.

Palamnaeus phipsoni carnaticus: Pocock, 1900a: 95; Kovařík, 2004: 34.

Palamnaeus phipsoni collinus Pocock, 1900a: 95 (synonymized by Kovařík, 2004: 1, 34); Kovařík, 2004: 34.

Heterometrus (Scorpio) longimanus: Kraepelin, 1901: 271 (misidentification, part).

Heterometrus (Scorpio) scaber: Kraepelin, 1901: 271 (misidentification, part).

Heterometrus (Chersonesometrus) phipsoni: Couzijn, 1978: 330, table 1; 1981: 153, 155, 157–159, 169, 171, 180, fig. 59 (part); Tikader and Bastawade, 1983: 577, 646–651 (part), figs. 1710–1724; Kovařík, 1992: 185; 1998: 136 (part); Fet, 2000: 442 (part); Bastawade, 2002: 296 (part); Indra, 2009: 142.

Heterometrus (Chersonesometrus) collinus: Couzijn, 1981: 42, 75, 86, 155–157, 169, 171, 192, table 7, figs. 50, 59; Tikader and Bastawade, 1983: 576, 625–630, figs. 1653–1667; Kovařík, 1998: 136; Fet, 2000: 441; Indra, 2001: 56, 58; 2009: 142.

Heterometrus (Chersonesometrus) fulvipes: Couzijn, 1981: 40, 88, 123, 133–136, 139, 140, 142, 149, 169, table 7, fig. 57 (misidentification, part).

Heterometrus (Chersonesometrus) phipsoni phipsoni: 1981: 43, 87, 148–151, 153, 170, 171, 192, table 7 (part), figs. 47, 59 (part).

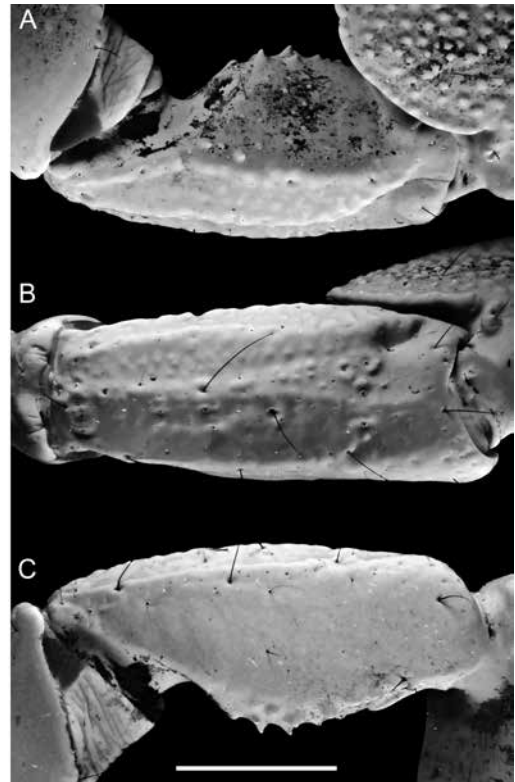


FIGURE 89. *Chersonesometrus fulvipes* (C.L. Koch, 1837), comb. nov., ♂ (AMNH), Khambatki Ghat, India, pedipalp patella: A. dorsal, B. retrolateral, and C. ventral aspects. Scale bar = 5 mm.

TYPE MATERIAL: **INDIA**: *Scorpio phipsoni*: Lectotype [here designated]: 1 ♂ (BMNH 1879.7.3.2-3), Madras [Madras Presidency] [examined]. **Tamil Nadu**: *Nilgiris Distr.*: *Palamnaeus phipsoni collinus*: Holotype ♀, paratypes: 1 ♀, 2 juv. ♂ (BMNH 1894.8.21.4-7), Nilgiri Hills [11°25'N 76°30'E], W.M. Daly [examined]. *Salem Distr.*: *Scorpio phipsoni*: Paralectotype [here designated]: 1 subad. ♂ (BMNH 1879.7.3.2-3), Shevaroy Hills [11°47'N 78°12'E] [examined].

The type series of *Scorpio phipsoni* (BMNH 1879.7.3.2-3) comprises two specimens, an adult male from “Madras” (presumably referring to the former Madras Presidency) and labelled “Type male” and a subadult male from the Shevaroy Hills. Although Pocock (1893:

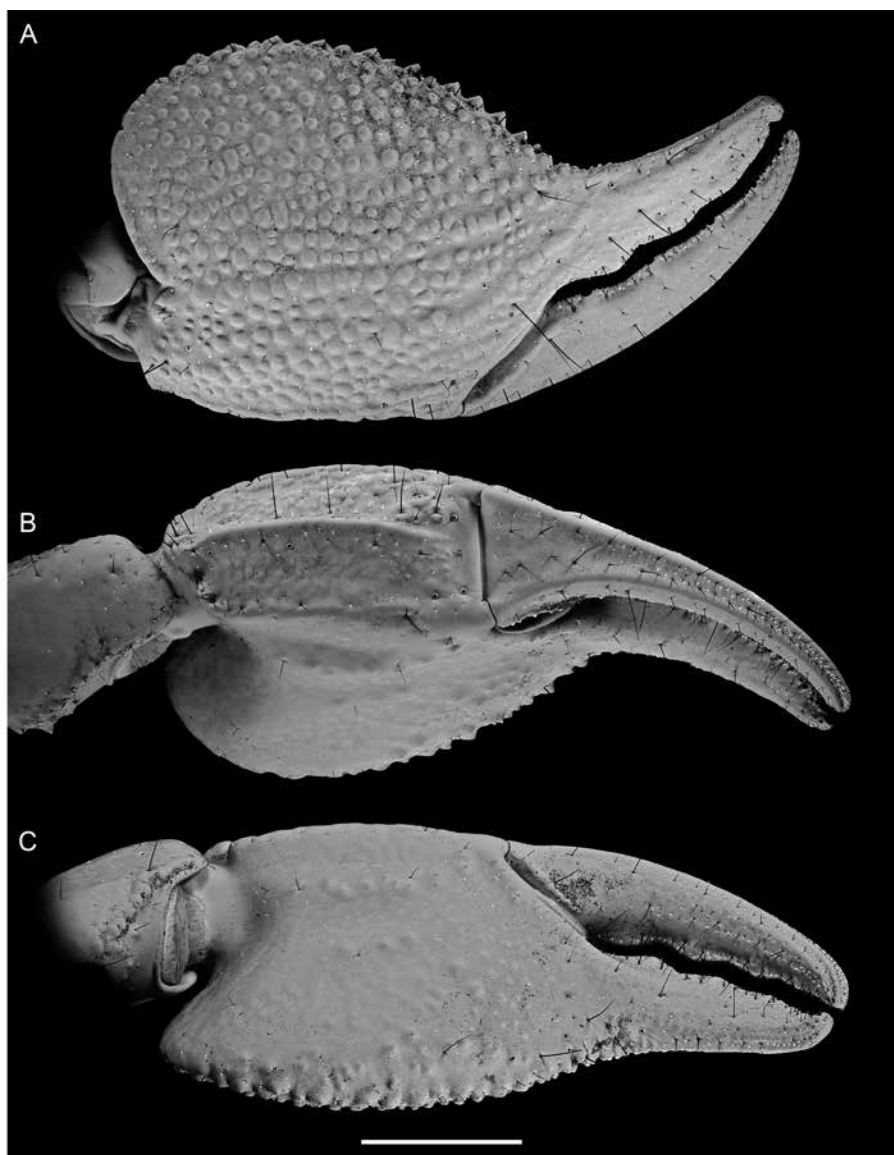


FIGURE 90. *Chersonesometrus fulvipes* (C.L. Koch, 1837), comb. nov., ♂ (AMNH), Khambatki Ghat, India, pedipalp chela: **A.** retrodorsal, **B.** ventral, and **C.** prolateral aspects. Scale bar = 5 mm.

307–309) referred to both specimens in the description of *S. phipsoni*, a type was not specified. Therefore, the two specimens are syntypes, as correctly noted by Fet (2000: 442). Couzijn (1981: 149) and Kovařík (2004: 34) incorrectly referred to the Madras specimen as the holotype of *S. phipsoni*, Couzijn (1981: 134) incorrectly listed the subadult male from Shevaroy

Hills under *H. (C.) fulvipes* (i.e., a misidentification) and referred to it as a type of *S. phipsoni* (an opinion repeated by Fet, 2000: 439), and Kovařík (2004: 34) incorrectly referred to the specimen as a paratype female of *S. phipsoni*. The adult male and subadult male are hereby designated as the lectotype and paralectotype of *Scorpio phipsoni*.

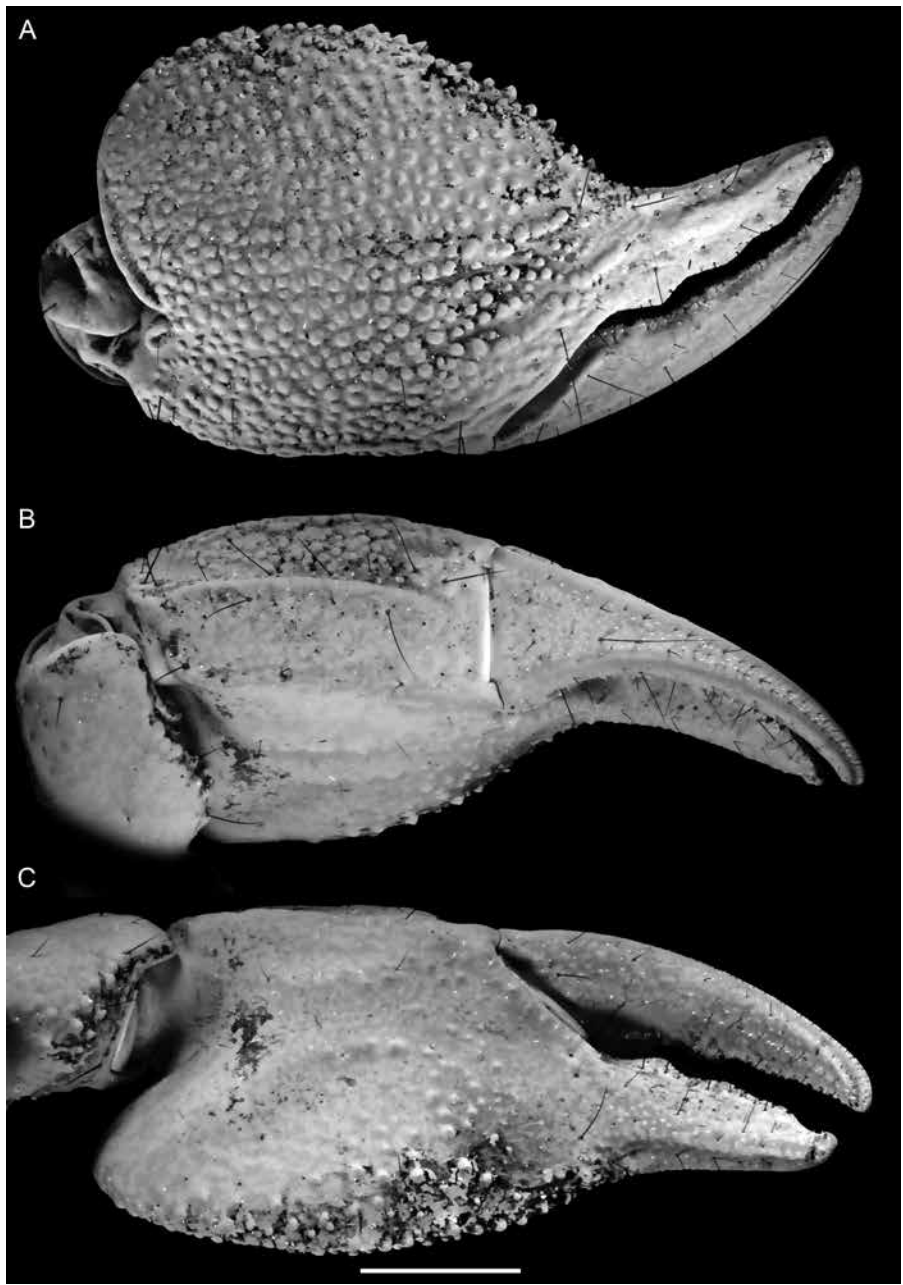


FIGURE 91. *Chersonesometrus fulvipes* (C.L. Koch, 1837), comb. nov., ♀ (AMNH), Khambatki Ghat, India, pedipalp chela: **A.** retrodorsal, **B.** ventral, and **C.** prolateral aspects. Scale bar = 5 mm.

The type series of *Palamnaeus phipsoni collinus* (BMNH 1894.8.21.4-7) comprises two females and two juvenile males from the Nilgiri Hills. In the brief original description, Pocock (1900a: 95) provided measurements of the total length, carapace, and metasoma for the "type from Nilgiri Hills" but did not specify which specimen was the holotype. Pocock (1900a) also compared characters of the male and female. Couzijn (1981: 155), Fet (2000: 441) and Kovařík (2004: 34) referred to a holotype female and a paratype female. Fet (2000) noted "also description of ♂." In the absence of evidence to the contrary, it is assumed that the holotype female was correctly identified by previous workers and the two juvenile males are paratypes of *P. p. collinus*.

DIAGNOSIS: *Deccanometrus phipsoni* may be separated from other species of *Deccanometrus* as follows. The carapace is markedly dorsoventrally compressed (fig. 19E, F) in *D. phipsoni* but moderately dorsoventrally compressed, the lateral surfaces sloping gently in *D. obscurus* and vaulted, the lateral surfaces sloping moderately, in *D. latimanus* and *D. xanthopus*. The median notch in the carapace anterior margin is deeply excavated in *D. phipsoni* but shallow in *D. liurus*. The superciliary carinae are higher than the median ocelli in *D. phipsoni*, but lower than the ocelli in all other species except *D. latimanus*, *D. liurus*, and *D. ubicki*. The interocular suture is present in *D. phipsoni* but absent in *D. liurus*. The carapace interocular surface is granular along the median longitudinal and anterior bifurcated sulci only in the male and female (fig. 19E, F) of *D. phipsoni*, whereas the frontal lobes and medial region are granular, with smooth areas, in the male and female of *D. ubicki*, and the female of *D. bengalensis* and *D. xanthopus*, or partially to entirely granular in the male of *D. xanthopus*. The carapace posterolateral surfaces of the female are smooth or nearly so in *D. phipsoni* but granular in *D. bengalensis*, *D. latimanus*, and *D. liurus*. The cheliceral movable finger prodistal (DI) and retrodistal (DE) teeth are aligned longitudinally and not opposable in *D. phipsoni*, but oppos-

able, i.e., forming a bicuspid, in *D. liurus* and *D. ubicki*. The pedipalps of the adult male are long, with femur length : posterior carapace width ratio (FL:PCW) ≥ 0.80 and femur length : carapace length ratio (FL:CL) ≥ 0.76 (fig. 135A, B) in *D. phipsoni* but short, with FL:PCW < 0.77 , FL:CL < 0.74 in *D. latimanus*. The pedipalp femur prodorsal carina is present and distinct in *D. phipsoni* but absent or obsolete in *D. liurus* and *D. xanthopus*. The pedipalp patella dorso-median carina of the female is entirely to predominantly granular in *D. phipsoni* but absent or obsolete in *D. latimanus*, *D. liurus*, and *D. ubicki*. The patella retrodorsal carina of the female is as strongly developed as or more strongly developed than the retromedian carinae in *D. phipsoni* but absent or obsolete in all other species except *D. obscurus*. The retromedian carinae of the female are granular in *D. phipsoni* but absent or obsolete in *D. latimanus*, *D. liurus*, *D. ubicki*, and *D. xanthopus*. The patella dorsal, retrodorsal, and retroventral intercarinal surfaces are granular (fig. 136) in *D. phipsoni* but smooth or nearly so in all other species except *D. obscurus*. The pedipalp chela is infusate and similar in color to the femur and patella in *D. phipsoni* but immaculate and paler than the femur and patella in *D. latimanus*, *D. liurus*, and *D. xanthopus*. The chela of the adult male is moderately to densely setose (fig. 137) in *D. phipsoni* but sparsely setose in *D. latimanus*. The chela manus promedian carina of the female is granular (fig. 138) in *D. phipsoni* but absent or obsolete in *D. latimanus* and *D. xanthopus*. The maximum distance between the dorsomedian and dorsal secondary carinae (DMC–DSC) of the chela manus is less than the maximum distance between the dorsal secondary and digital carinae (DSC–DC) in the male and female of *D. phipsoni* whereas the DMC–DSC is similar to the DSC–DC in the male and female of *D. xanthopus*, and the female of *D. obscurus*, and greater than the DSC–DC in the male and female of *D. latimanus*. The chela manus dorsal intercarinal surface is finely to coarsely granular, without reticulation (figs.

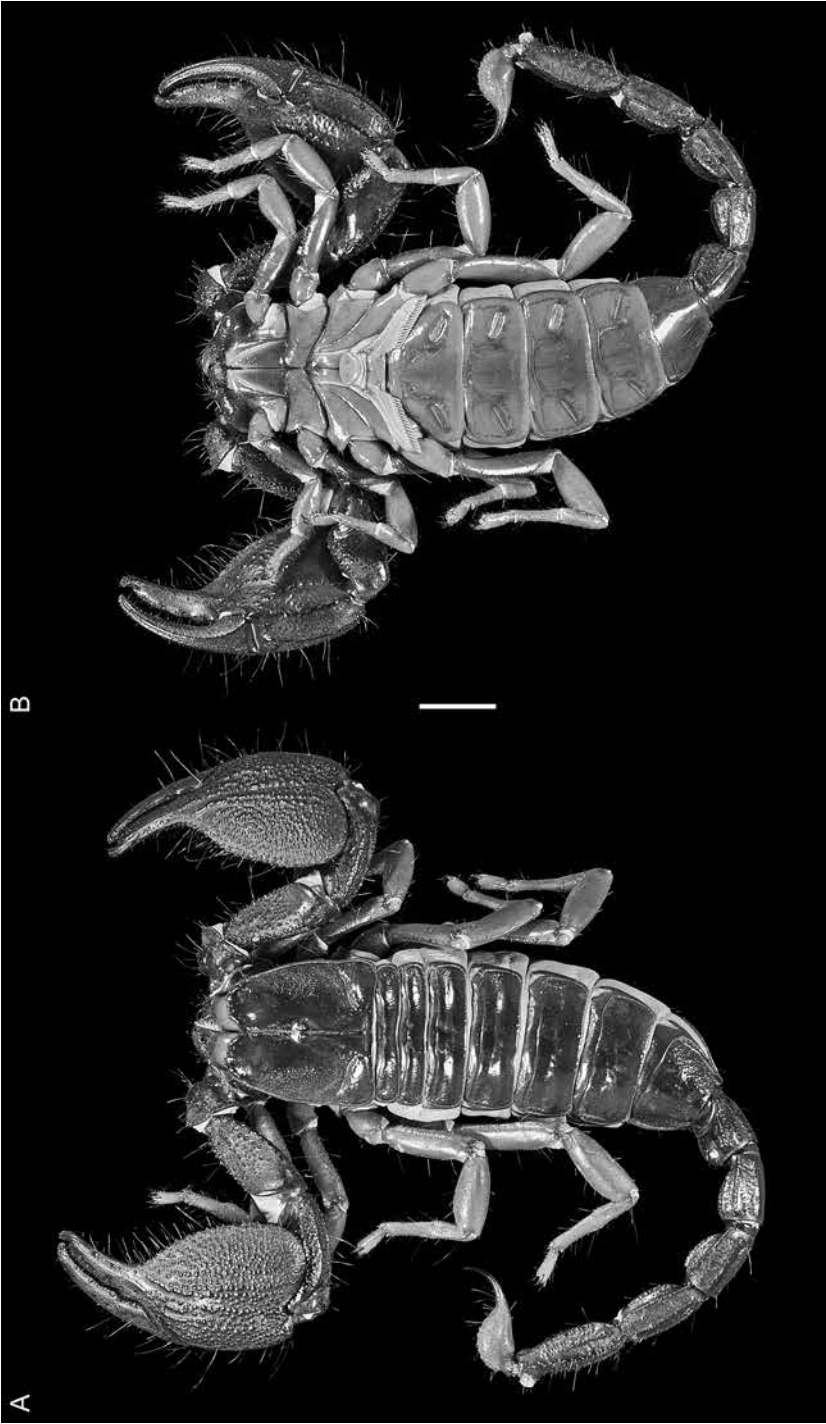


FIGURE 92. *Chersonesometrus hendersoni*, sp. nov., paratype ♀ (AMNH), Tungabhadra River, India, habitus. A. dorsal and B. ventral aspects. Scale bar = 10 mm.

137, 138) in *D. phipsoni*, finely to coarsely granular and shallowly reticulate in *D. bengalensis*, *D. latimanus*, *D. liurus*, and *D. xanthopus*, and smooth and shallowly reticulate in *D. ubicki*. The manus retrolateral intercarinal surfaces are granular in *D. phipsoni* but smooth or nearly so in *D. ubicki*. The legs are very dark or heavily infusate (fig. 135) in *D. phipsoni* but pale or very lightly infusate in *D. latimanus*, *D. liurus*, *D. ubicki*, and *D. xanthopus*. Macroseta *st* on the retroventral surfaces of the basitarsi is spiniform on legs I–III (fig. 46I–L) in *D. phipsoni* and on legs I and II in *D. bengalensis* but setiform on legs I–III in *D. latimanus*, *D. liurus*, and *D. xanthopus* and on leg III in *D. bengalensis*; *sb* on the retroventral surfaces of the basitarsi is spiniform on legs I and II in *D. phipsoni*, setiform on legs I and II in *D. latimanus*, and setiform on leg I, and setiform or spiniform on leg II in *D. xanthopus*; *st* on the proventral surface of the basitarsus of leg III is setiform in *D. phipsoni* but spiniform in all other species except *D. obscurus*; *sb* on the retrolateral surface of the basitarsus of leg III is spiniform in *D. phipsoni* but setiform in *D. latimanus*. The latero-distal lobes on the telotarsi of legs I–IV each bear only two spiniform macrosetae in *D. phipsoni* but three or more in *D. latimanus*. The angle of the pectinal first proximal median lamella (scape) is $> 90^\circ$ but $< 180^\circ$ in the male and female (fig. 33E, F) of *D. phipsoni*, and approximately 90° in the male of *D. latimanus*, *D. liurus*, and *D. xanthopus*, and the male and female of *D. ubicki*. The mesial surfaces of mesosomal tergites I–VI are smooth in the male and the lateral surfaces granular in the female of *D. phipsoni*, whereas the mesial surfaces are granular in the male of *D. xanthopus*, and the lateral surfaces smooth in the female of *D. latimanus*, *D. liurus*, *D. ubicki*, and *D. xanthopus*. The ventral surface of mesosomal sternite VII bears a pair of weakly developed ventrolateral carinae in *D. phipsoni* but two pairs of moderately to strongly developed ventrosubmedian and ventrolateral carinae in *D. latimanus*, *D. liurus*, *D. ubicki*, and *D. xanthopus*. The dorso-

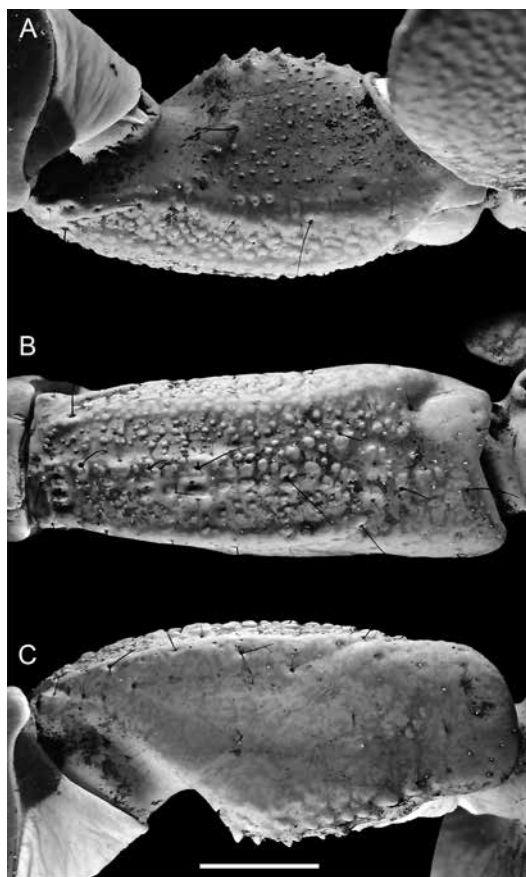


FIGURE 93. *Chersonesometrus hendersoni*, sp. nov., holotype ♀ (AMNH), Sanapura, India, pedipalp patella: A. dorsal, B. retrolateral, and C. ventral aspects. Scale bar = 5 mm.

submedian carinae of metasomal segments I–IV are granular or costate-granular (fig. 64C) in *D. phipsoni*, costate in *D. latimanus*, and obsolete in *D. liurus*. The ventrosubmedian and ventrolateral carinae of metasomal segments I–IV are more strongly developed on segments III and IV than on I and II (fig. 66C) in *D. phipsoni* but more strongly developed on segments I and II than on III and IV in *D. latimanus*, *D. liurus*, *D. ubicki*, and *D. xanthopus*. The lateral carinae are partial on metasomal segments I and V (fig. 65C) in *D. phipsoni* but vestigial on I in *D. liurus* and *D. ubicki*, and absent or obsolete on V in *D. latimanus*, *D. liurus*, and *D. ubicki*. The



FIGURE 94. *Chersonesometrus hendersoni*, sp. nov., holotype ♀ (AMNH), Sanapura, India, pedipalp chela: A. retrodorsal, B. ventral, and C. prolateral aspects. Scale bar = 5 mm.

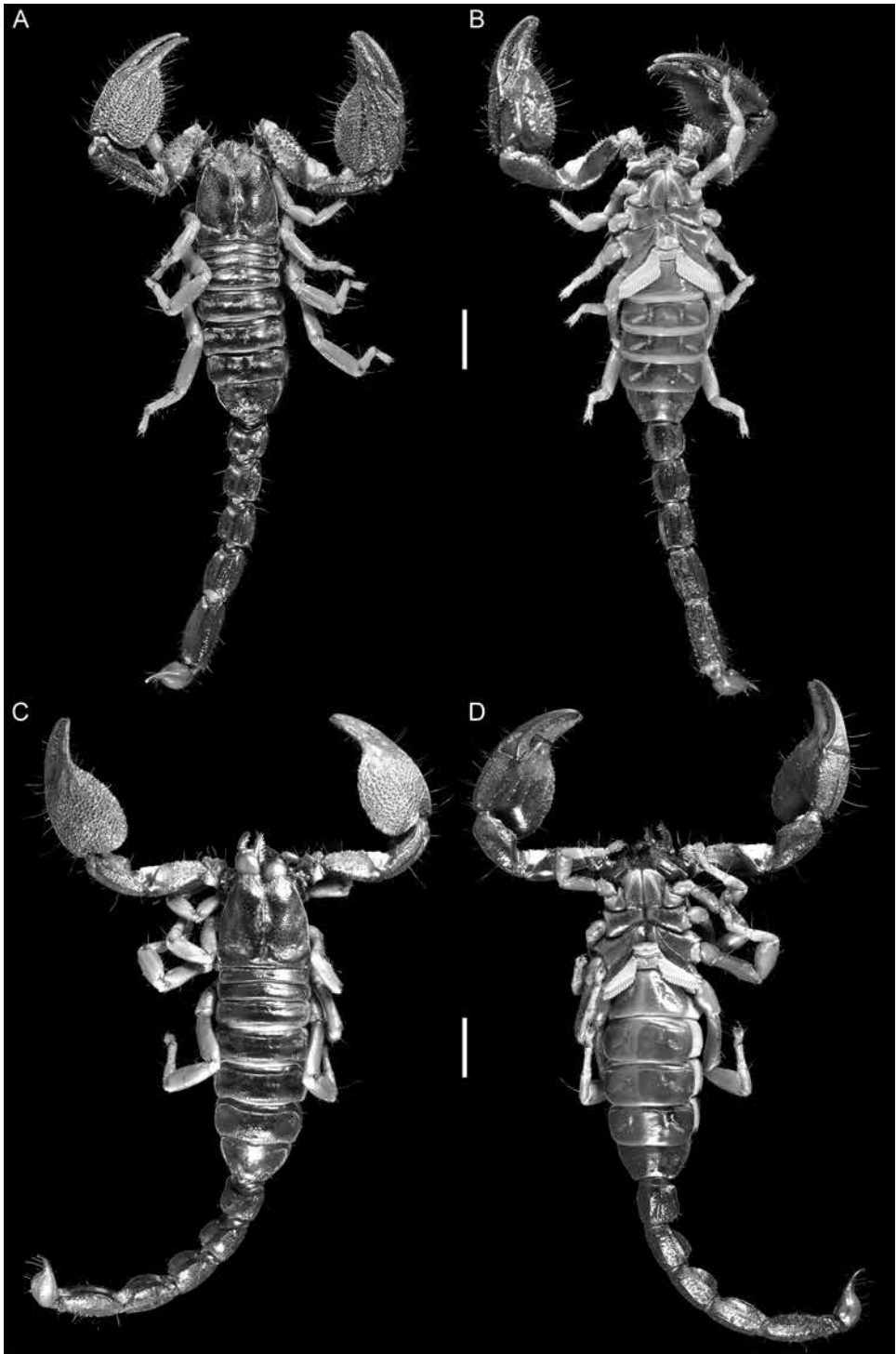


FIGURE 95. *Chersonesometrus madraspatensis* (Pocock, 1900), comb. nov., habitus: A, C. dorsal and B, D. ventral aspects. A, B. ♂ (CAS 9071142). C, D. ♀ (CAS 9071143). Scale bars = 10 mm.

dorsolateral carinae of metasomal segment V are strong and continuous in *D. phipsoni* but weak and discontinuous to absent in *D. latimanus*, *D. liurus*, and *D. xanthopus*. The width of the telson vesicle is approximately equal to or less than the width of metasomal segment V in the male (figs. 64C, 66C) of *D. phipsoni* but greater than the width of segment V in the male of *D. latimanus*, *D. liurus*, *D. ubicki*, and *D. xanthopus*.

DISTRIBUTION: This species is endemic to India (fig. 117) and has been recorded in the states of Andhra Pradesh, Chhattisgarh, Karnataka, Madhya Pradesh, Maharashtra, and Tamil Nadu (table 1). Its distribution is allopatric with that of *D. obscurus*.

ECOLOGY: *Deccanometrus phipsoni* inhabits primary evergreen forests at 550–900 m elevation on the slopes of the Western Ghats and the Eastern Ghats (fig. 7G). The habitus is consistent with the fossorial, semilithophilous ecomorphotype (Prendini, 2001b). The dorsoventral compression of this species is consistent with observations that it constructs scrapes or shallow burrows under stones (Z. Mirza, personal commun.).

REMARKS: This species, previously placed in subgenus *Chersonesometrus* of *Heterometrus* by various authors (e.g., Couzijn, 1981; Tikader and Bastawade, 1983; Fet, 2000), is newly accommodated in *Deccanometrus*, gen. nov., based on a phylogenetic analysis (fig. 10).

The following synonym is currently recognized: *Palamnaeus phipsoni collinus* Pocock, 1900 = *Deccanometrus phipsoni* (Pocock, 1893), comb. nov., synonymized by Kovařík (2004). Although described as a subspecies, *P. p. collinus* was elevated to the rank of species, as *Heterometrus* (*Chersonesometrus*) *collinus*, by Couzijn (1981), a decision upheld by Tikader and Bastawade (1983) and Fet (2000) until it was synonymized with *H. phipsoni* by Kovařík (2004). According to Pocock (1900a) and confirmed in the redescription of Tikader and Bastawade (1983), *P. p. collinus* is smaller (the holotype is 81.75 mm total length) with a shorter

metasoma and more granular pedipalp chela than *Scorpio phipsoni*. Other differences include a lower pectinal tooth count in *P. p. collinus*, with 12/12 or 12/13 teeth according to Couzijn (1981) compared to *S. phipsoni*, with 13–15 teeth; and lower counts of pro- and retroventral spiniform macrosetae on the telotarsi, with 4/5 and 4/5–6 on legs III and IV, respectively, in *P. p. collinus* compared to 5–7 on legs I–IV in *S. phipsoni*, according to Tikader and Bastawade (1983), differences that do not merit their recognition as distinct taxa. Comparison of the type series of *S. phipsoni* and *P. p. collinus* reinforced the conclusion that they are conspecific.

MATERIAL EXAMINED: **INDIA:** 1 ♂, 1 subad. ♀ (BMNH), 1 ♀ (BMNH 1891.8.27.1), 1 ♂ (ZMH A939 ex BMNH). **Andhra Pradesh:** *Prakasam Distr.:* Podili [15°36'N 79°37'E], 16.i.1967, D.E. Johnson, ex Stahnke coll., 1 ♂ (CAS 9070409 [ASU 67-104]). **Chhattisgarh:** “Indes anglaises (Provinces centrales)” [Central Provinces of British India], 1915, G. Babault, 2 ♂, 6 ♀, 1 subad. ♂, 2 subad. ♀, 1 juv. ♂ (MNHN RS 0080), Chilpy, 19.iii.1914, G. Babault, 24 juv. (MNHN RS 0103); Rajadhar [21°43'N 82°00'E], 1915, G. Babault, 1 juv. ♀ (MNHN RS 0111). *Bilaspur Distr.:* Billespoor [Bilaspur, 22°05'N 82°08'E], northern India, iv.1871, M.M. Carleton, 1 ♀ (MCZ 88165). **Odisha:** *Koraput Distr.:* Pottangi [18°34'N 82°58'E], 13 mi. SE, 550 m, 4.ii.1962, E.S. Ross and D.Q. Cavagnaro, 1 subad. ♂ (CAS 9070417). **Tamil Nadu:** *Salem Distr.:* Yercauda, Sheveroy Hills [11°47'N 78°12'E], J.R. Henderson, 1 ♀, 1 subad. ♂, 2 juv. ♂, 2 juv. ♀ (BMNH 1894.10.24.9-12); Yercaud [11°46'N 78°14'E], 4000 ft., 6.iii.1962, E.S. Ross and D.Q. Cavagnaro, 1 subad. ♂, 1 juv. ♂, 1 juv. ♀ (CAS 9070416).

Deccanometrus ubicki (Kovařík, 2004),
comb. nov.

Figures 10, 21A, B, 35A, B, 48E–H, 64F, 65F,
66F, 118, 139–141, table 1

Heterometrus ubicki Kovařík, 2004: 1, 7, 46, 47,
51–53, tables 1–3, fig. 30; 2009: 35, 36, 45, 48,
49, 96, 99, tables 1, 2, figs. 160–167, 186, 187.

TYPE MATERIAL: **INDIA:** **Puducherry:** *Karaikal Distr.:* *Heterometrus ubicki:* Holotype ♂ (FKPC), Karaikal [10°56'N 79°50'E], 2003,

T.R.S.N. Paratypes: 1 ♀ (CAS); 1 ♀ (FKPC), Karaikal, 2003, T.R.S.N., 9 ♂, 2 ♀ paratypes (FKPC), same data, except: 2002–2003, 8 ♂, 15 ♀, 2 im., 1 juv. (FKPC), same data, except: x.2003–v.2004; 1 ♀ (CAS 9071138 [ASU 63-1114]), Karikal [Karaikal], Madras, viii.1962, P.S. Nathan, ex Stahnke coll. [examined], 1 ♀ (CAS 9071135 [ASU 63-1122]), same data, except: ix.1962 [examined], 2 ♀ (CAS), same data, except: x.1962, 1 ♂ (CAS 9081136 [ASU 63-1138]), same data, except: vi.1963 [examined], 3 ♀, 1 subad. ♀ (CAS 90711339 [ASU 63-1142/46/47]), same data, except: vii.1963 [examined], 2 ♀ (CAS), same data, except: viii.1963, 1 ♀ (CAS), same data, except: viii.1964; 1 ♀ (CAS 9071137 [ASU 63-1114]), Karikal territory, Kurumbargum [Kurumbagaram, 10°59'N 79°46'E] P.O. [Post Office], Tanjore Distr., i.1954, P.S. Nathan, ex Stahnke coll. [examined], 3 juv. (CAS), same data, except: vii.1954, 1 ♀ (CAS), same data, except: 12.vii.1954.

Kovářík (2004) lists two female paratypes collected on viii.1962 and deposited in CAS. However, only one specimen with that date could be found in the CAS collection and the 2002–2004 collection dates cited for the 39 specimens labelled “FKPC” are at least 25 years after the collector, T.R. Susai Nathan (T.R.S.N.), ceased to be active (L.A. Esposito and D. Ubick, personal commun.).

DIAGNOSIS: *Deccanometrus ubicki* may be separated from other species of *Deccanometrus* as follows. The carapace is moderately dorso-ventrally compressed, the lateral surfaces sloping gently (fig. 21A, B), in *D. ubicki* but vaulted, the lateral surfaces sloping moderately, in *D. latimanus* and *D. xanthopus*. The median notch in the carapace anterior margin is deeply excavated in *D. ubicki* but shallow in *D. liurus*. The superciliary carinae are lower than the median ocelli in *D. ubicki*, but higher than the ocelli in all other species except *D. latimanus* and *D. liurus*. The interocular suture is present in *D. ubicki* but absent in *D. liurus*. The frontal lobes and medial region of the carapace interocular surface are granular, with smooth areas, in the male and female (fig.

21A, B) of *D. ubicki*, whereas the interocular surface is granular along the median longitudinal and anterior bifurcated sulci only in the male and female of *D. latimanus*, *D. liurus*, *D. obscurus*, and *D. phipsoni*, and the male of *D. bengalensis*, and the frontal lobes and medial region are partially to entirely granular in the male of *D. xanthopus*. The carapace posterolateral surfaces of the female are smooth or nearly so in *D. ubicki* but granular in *D. bengalensis*, *D. latimanus*, and *D. liurus*. The cheliceral movable finger prodistal (DI) and retrodistal (DE) teeth are opposable, i.e., forming a bicus, in *D. ubicki*, but aligned longitudinally and not opposable in all other species except *D. liurus*. The pedipalps of the adult male are long, with femur length : posterior carapace width ratio (FL:PCW) ≥ 0.80 and femur length : carapace length ratio (FL:CL) ≥ 0.76 (fig. 139A, B) in *D. ubicki* but short, with FL:PCW < 0.77 , FL:CL < 0.74 in *D. latimanus*. The pedipalp femur prodorsal carina is present and distinct in *D. ubicki* but absent or obsolete in *D. liurus* and *D. xanthopus*. The pedipalp patella dorsomedian carina of the female (fig. 140) is absent or obsolete in *D. ubicki*, but entirely to predominantly granular in *D. bengalensis*, *D. obscurus*, *D. phipsoni*, and *D. xanthopus*. The patella retrodorsal carina of the female (fig. 140) is absent or obsolete in *D. ubicki* but as strongly developed as or more strongly developed than the retromedian carinae in *D. obscurus* and *D. phipsoni*. The retromedian carinae of the female are absent or obsolete in *D. ubicki* but granular in *D. bengalensis*, *D. obscurus*, and *D. phipsoni*. The patella dorsal, retrodorsal, and retroventral intercarnal surfaces of the female are smooth or nearly so in *D. ubicki* but granular in *D. obscurus* and *D. phipsoni*. The pedipalp chela is infusate and similar in color to the femur and patella in *D. ubicki* but immaculate and paler than the femur and patella in *D. latimanus*, *D. liurus*, and *D. xanthopus*. The pedipalp chela of the adult male is moderately to densely setose (fig. 141A) in *D. ubicki* but sparsely setose in *D.*

xanthopus. The chela manus promedian carina of the female is granular (fig. 141B–D) in *D. ubicki* but absent or obsolete in *D. latimanus* and *D. xanthopus*. The maximum distance between the dorsomedian and dorsal secondary carinae (DMC–DSC) of the chela manus is less than the maximum distance between the dorsal secondary and digital carinae (DSC–DC) in the male and female of *D. ubicki* whereas the DMC–DSC is similar to the DSC–DC in the male and female of *D. xanthopus*, and the female of *D. obscurus*, and greater than the DSC–DC in the male and female of *D. latimanus*. The chela manus dorsal intercarinal surface is smooth and shallowly reticulate (fig. 141) in *D. ubicki*, finely to coarsely granular and shallowly reticulate in *D. bengalensis*, *D. latimanus*, *D. liurus*, and *D. xanthopus*, and finely to coarsely granular, without reticulation in *D. obscurus* and *D. phipsoni*. The manus retrolateral intercarinal surfaces are smooth or nearly so in *D. ubicki* but granular in all other species. The legs are pale or very lightly infusate (fig. 139) in *D. ubicki* but very dark or heavily infusate in *D. bengalensis*, *D. obscurus*, and *D. phipsoni*. Macroseta *st* on the retroventral surfaces of the basitarsi is spiniform on legs I–III (fig. 48E–H) in *D. ubicki* and on legs I and II in *D. bengalensis* but setiform on legs I–III in *D. latimanus*, *D. liurus* and *D. xanthopus* and on leg III in *D. bengalensis*; *sb* on the retroventral surfaces of the basitarsi is spiniform on legs I and II in *D. ubicki*, setiform on legs I and II in *D. latimanus*, and setiform on leg I, and setiform or spiniform on leg II in *D. xanthopus*; *st* on the proventral surface of the basitarsus of leg III is spiniform in *D. ubicki* but setiform in *D. obscurus* and *D. phipsoni*; *sb* on the retrolateral surface of the basitarsus of leg III is spiniform in *D. ubicki* but setiform in *D. latimanus*. The laterodistal lobes on the telotarsi of legs I–IV each bear only two spiniform macrosetae in *D. ubicki* but three or more in *D. latimanus*. The angle of the pectinal first proximal median lamella (scape) is approximately 90° in the male and female

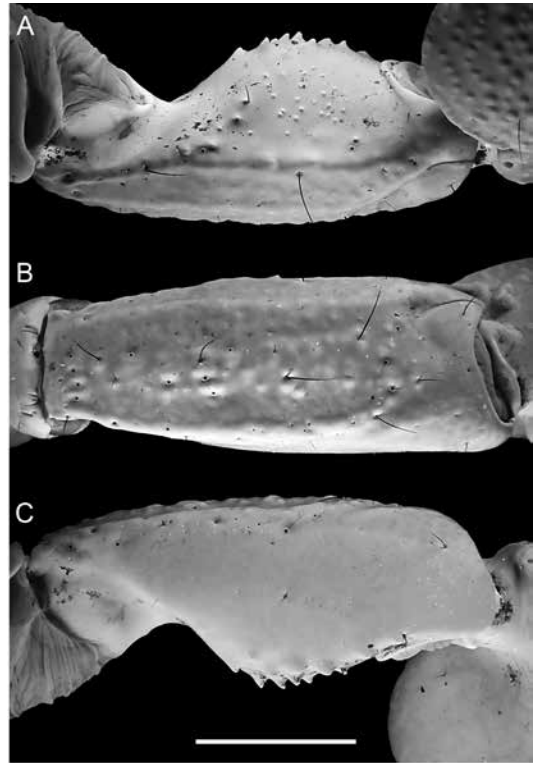


FIGURE 96. *Chersonesometrus madraspatensis* (Pocock, 1900), comb. nov., ♂ (CAS 9071142), pedipalp patella: A. dorsal, B. retrolateral, and C. ventral aspects. Scale bar = 5 mm.

(fig. 35A, B) of *D. ubicki*, > 90° but < 180° in the male and female of *D. bengalensis*, *D. obscurus*, and *D. phipsoni*, and the female of *D. latimanus* and *D. liurus*, and 90° to 180° in the female of *D. xanthopus*. The mesial surfaces of mesosomal tergites I–VI are smooth in the male and the lateral surfaces smooth in the female of *D. ubicki*, whereas the mesial surfaces are granular in the male of *D. xanthopus*, and the lateral surfaces granular in the female of *D. bengalensis*, *D. obscurus* and *D. phipsoni*. The ventral surface of mesosomal sternite VII bears two pairs of moderately to strongly developed ventrosubmedian and ventrolateral carinae in *D. ubicki* and a pair of weakly developed ventrolateral carinae in *D. bengalensis*, *D. obscurus*, and *D. phipsoni*. The dorsosubmedian carinae of metasomal segments I–IV are



FIGURE 97. *Chersonesometrus madraspatensis* (Pocock, 1900), comb. nov., ♂ (CAS 9071142), pedipalp chela: A. retrodorsal, B. ventral, and C. prolateral aspects. Scale bar = 5 mm.

granular or costate-granular (fig. 64F) in *D. ubicki*, costate in *D. latimanus*, and obsolete in *D. liurus*. The ventrosubmedian and ventrolateral carinae of metasomal segments I–IV are more strongly developed on segments I and II than on III and IV (fig. 66F) in *D. ubicki* but more strongly developed on segments III and IV than on I and II in *D. bengalensis*, *D. obscurus* and *D. phipsoni*. The lateral carinae are vestigial on metasomal segment I and absent or obsolete on segment V (fig. 65F) in *D.*

ubicki but partial on I in *D. latimanus*, and on I and V in *D. bengalensis*, *D. obscurus*, *D. phipsoni*, and *D. xanthopus*. The dorsolateral carinae of metasomal segment V are strong and continuous in *D. ubicki* but weak and discontinuous to absent in *D. latimanus*, *D. liurus*, and *D. xanthopus*. The telson is paler than metasomal segment V in *D. ubicki* but as dark as segment V in *D. latimanus*. The width of the telson vesicle is greater than the width of metasomal segment V in the male of *D. ubicki*



FIGURE 98. *Chersonesometrus madraspatensis* (Pocock, 1900), comb. nov., ♀ (CAS 9071143), pedipalp chela: A. retrodorsal, B. ventral, and C. prolateral aspects. Scale bar = 5 mm.

but approximately equal to or less than the width of segment V in the male of *D. bengalensis*, *D. obscurus*, and *D. phipsoni*.

REMARKS: This species is newly accommodated in *Deccanometrus*, gen. nov., based on a phylogenetic analysis (fig. 10).

DISTRIBUTION: This species is only known from the Karaikal District of the union territory of Puducherry, India (fig. 118, table 1).

ECOLOGY: Although no data are available on the ecology of this species, the habitus is consistent with the fossorial, pelophilous ecomorphot-

ype (Prendini, 2001b). The dorsoventral compression of this species suggests that it excavates burrows under stones.

CONSERVATION STATUS: This habitat of this species has been extensively modified and it may be extinct.

MATERIAL EXAMINED: INDIA: Puducherry: Karaikal Distr.: Karum, Kurum Bagaram [Kurumbagar, 10°59'N 79°46'E], 7.ii.1947, P.S. Nathan, 1 subad. ♀ (AMNH).

Deccanometrus xanthopus (Pocock, 1897),
comb. nov.

Figures 7A, C, 8H, 9C, 10, 20C, D, 34C, D, 47E–H, 64G, 65G, 66G, 118, 127C–F, 142–144, table 1

Palamnaeus xanthopus Pocock, 1897: 116; 1900a: 85, 92; Tikader, 1973: 263.

Heterometrus xanthopus: Kraepelin, 1899: 110, 115; Takashima, 1945: 93; Khatavkar and More, 1990: 79–81, figs. 1–4; Kovařík, 2004: 1, 49–52, tables 2, 3, fig. 32; 2009: 35, 36, 46, 48, 49, 98, 100, tables 1, 2, figs. 174–179, 202, 203; Javed et al., 2010a: 147; Pande et al., 2012: 2382–2385, 2387, table 1, image 10; Patil and Shah, 2012a: 139–141, figs. 1–7; 2012b: 491–493, fig. 1; Tahir and Prendini, 2014: 9.

Heterometrus (Chersonesometrus) xanthopus: Couzijn, 1981: 41, 87, 133, 136–138, 169, 192, table 7, figs. 40, 57; Tikader and Bastawade, 1983: 576, 609–614, figs. 1609–1624; Kovařík, 1998: 137; Fet, 2000: 441; Bastawade, 2002: 296.

Heterometrus telanganaensis Javed et al., 2010a: 143–148, table 1, figs. 1–8; syn. nov.

TYPE MATERIAL: INDIA: Maharashtra: Satara Distr.: *Palamnaeus xanthopus*: Lectotype ♂, paralectotypes: 1 ♀, 2 subad. ♂ [BNHS 707], 1 subad. ♀ [BNHS 703] (BMNH 1896.9.26.88–91 [BNHS 700, 703]), Kadao Tal (Satara) [Khatav, 17°39'N 74°22'E], S. Dekhan, Bombay [Bombay

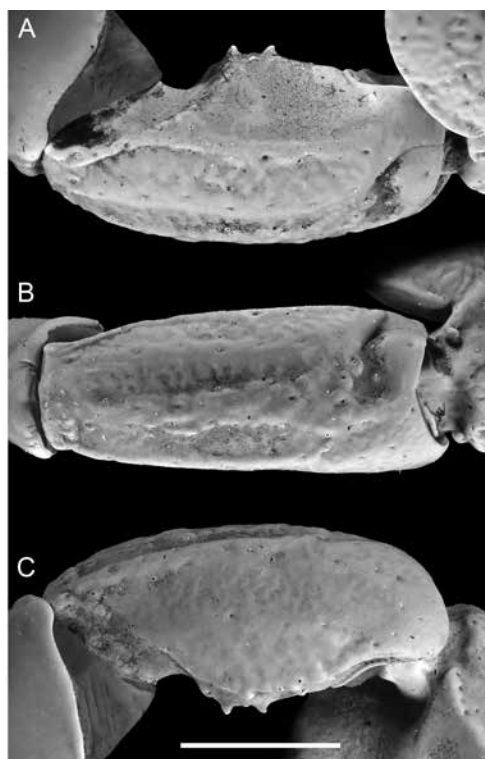


FIGURE 99. *Chersonesometrus nathanorum*, sp. nov., subad. ♂ holotype (MNHN RS 3145), pedipalp patella: **A.** dorsal, **B.** retrolateral, and **C.** ventral aspects. Scale bar = 5 mm.

Presidency], A.D. Wilkins [examined]. **Telangana:** Jayashankar Bhupalpally Distr.: *Heterometrus telanganaensis*: Holotype ♀, paratypes: 1 subad. ♂, 1 subad. ♀ (ZSI/FBRC/A-30-32), Regonda, 18°14'N 79°49'E, Warangal District, 24.ix.2010 and 27.x.2010, N. Goud.

DIAGNOSIS: *Deccanometrus xanthopus* may be separated from other species of *Deccanometrus* as follows. The carapace is vaulted, the lateral surfaces sloping moderately (fig. 20C, D), in *D. xanthopus* but slightly to markedly dorsoventrally compressed, the lateral surfaces sloping gently, in all other species except *D. latimanus*. The median notch in the carapace anterior margin is deeply excavated in *D. xanthopus* but shallow in *D. liurus*. The superciliary carinae are higher than the median ocelli in *D. xanthopus*, but lower than the ocelli in all other



FIGURE 100. *Chersonesometrus nathanorum*, sp. nov., subad. ♂ holotype (MNHN RS 3145), pedipalp pedipalp chela: A. retrodorsal, B. ventral, and C. prolateral aspects. Scale bar = 5 mm.

species except *D. latimanus*, *D. liurus* and *D. ubicki*. The interocular suture is present in *D. xanthopus* but absent in *D. liurus*. The frontal lobes and medial region of the carapace interocular surface are partially to entirely granular in the male (fig. 20C) or granular, with smooth areas, in the female (fig. 20D) of *D. xanthopus*, whereas the interocular surface is granular

along the median longitudinal and anterior bifurcated sulci only in the male and female of *D. latimanus*, *D. liurus*, *D. obscurus*, and *D. phipsoni*, and the male of *D. bengalensis*, and the frontal lobes and medial region are granular, with smooth areas, in the male of *D. ubicki*. The carapace posterolateral surfaces of the female are smooth or nearly so in *D. xanthopus* but

granular in *D. bengalensis*, *D. latimanus*, and *D. liurus*. The cheliceral movable finger prodistal (DI) and retrodistal (DE) teeth are aligned longitudinally and not opposable in *D. xanthopus*, but opposable, i.e., forming a bicusps, in *D. liurus* and *D. ubicki*. The pedipalps of the adult male are long, with femur length : posterior carapace width ratio (FL:PCW) ≥ 0.80 and femur length : carapace length ratio (FL:CL) ≥ 0.76 (fig. 127C, D) in *D. xanthopus* but short, with FL:PCW < 0.77 , FL:CL < 0.74 in *D. latimanus*. The pedipalp femur prodorsal carina is absent or obsolete in *D. xanthopus* but present and distinct in all other species except *D. liurus*. The pedipalp patella dorsomedian carina of the female (fig. 142) is entirely to predominantly granular in *D. xanthopus* but absent or obsolete in *D. latimanus*, *D. liurus*, and *D. ubicki*. The patella retrodorsal carina of the female (fig. 142) is absent or obsolete in *D. xanthopus* but as strongly developed as or more strongly developed than the retromedian carinae in *D. obscurus* and *D. phipsoni*. The retromedian carinae of the female are absent or obsolete in *D. xanthopus* but granular in *D. bengalensis*, *D. obscurus*, and *D. phipsoni*. The patella dorsal, retrodorsal, and retroventral intercarinal surfaces of the female are smooth or nearly so in *D. xanthopus* but granular in *D. obscurus* and *D. phipsoni*. The pedipalp chela is immaculate and paler than the femur and patella in *D. xanthopus* but infusate and similar in color to the femur and patella in *D. bengalensis*, *D. obscurus*, *D. phipsoni* and *D. ubicki*. The pedipalp chela of the adult male is sparsely setose (fig. 143A) in *D. xanthopus* but moderately to densely setose in all other species. The chela manus promedian carina of the female is absent or obsolete in *D. xanthopus* (fig. 144B) but present and granular in all other species except *D. latimanus*. The maximum distance between the dorsomedian and dorsal secondary carinae (DMC–DSC) of the chela manus is similar to the maximum distance between the dorsal secondary and digital carinae (DSC–DC) in the male and female of *D. xanthopus* whereas the DMC–DSC is less than

the DSC–DC in the male of *D. obscurus*, and the male and female of *D. bengalensis*, *D. liurus*, *D. phipsoni*, and *D. ubicki*, and greater than the DSC–DC in the male and female of *D. latimanus*. The chela manus dorsal intercarinal surface is finely to coarsely granular and shallowly reticulate (fig. 143) in *D. xanthopus*, smooth and shallowly reticulate in *D. ubicki*, and finely to coarsely granular, without reticulation in *D. obscurus* and *D. phipsoni*. The manus retrolateral intercarinal surfaces are granular in *D. xanthopus* but smooth or nearly so in *D. ubicki*. The legs are pale or very lightly infusate (figs. 9C, 127C–F) in *D. xanthopus* but very dark or heavily infusate in *D. bengalensis*, *D. obscurus*, and *D. phipsoni*. Macroseta *st* on the retroventral surfaces of the basitarsi is setiform on legs I–III (fig. 47E–H) in *D. xanthopus* but spiniform on legs I–III in *D. obscurus*, *D. phipsoni*, and *D. ubicki*, and spiniform on legs I and II and setiform on III in *D. bengalensis*; *sb* on the retroventral surfaces of the basitarsi is setiform on leg I, and setiform or spiniform on leg II in *D. xanthopus*, setiform on legs I and II in *D. latimanus*, and spiniform on legs I and II in the other species; *st* on the proventral surface of the basitarsus of leg III is spiniform in *D. xanthopus* but setiform in *D. obscurus* and *D. phipsoni*; *sb* on the retrolateral surface of the basitarsus of leg III is spiniform in *D. xanthopus* but setiform in *D. latimanus*. The laterodistal lobes on the telotarsi of legs I–IV each bear only two spiniform macrosetae in *D. xanthopus* but three or more in *D. latimanus*. The angle of the pectinal first proximal median lamella (scape) is approximately 90° in the male (fig. 34C) of *D. xanthopus* and $> 90^\circ$ but $< 180^\circ$ in the male of *D. bengalensis*, *D. obscurus*, and *D. phipsoni*. The mesial surfaces of mesosomal tergites I–VI are granular in the male and the lateral surfaces smooth in the female of *D. xanthopus*, whereas the mesial surfaces are smooth in the male and the lateral surfaces granular in the female of *D. bengalensis*, *D. obscurus*, and *D. phipsoni*, and the mesial surfaces smooth in the male of *D. latimanus*, *D. liurus*, and *D. ubicki*. The ventral

surface of mesosomal sternite VII bears two pairs of moderately to strongly developed ventrosubmedian and ventrolateral carinae in *D. xanthopus* and a pair of weakly developed ventrolateral carinae in *D. bengalensis*, *D. obscurus*, and *D. phipsoni*. The dorsosubmedian carinae of metasomal segments I–IV are granular or costate-granular (fig. 64G) in *D. xanthopus*, costate in *D. latimanus*, and obsolete in *D. liurus*. The ventrosubmedian and ventrolateral carinae of metasomal segments I–IV are more strongly developed on segments I and II than on III and IV (fig. 66G) in *D. xanthopus* but more strongly developed on segments III and IV than on I and II in *D. bengalensis*, *D. obscurus*, and *D. phipsoni*. The lateral carinae are partial on metasomal segments I and V (fig. 65G) in *D. xanthopus* but vestigial on I in *D. liurus* and *D. ubicki*, and absent or obsolete on V in *D. latimanus*, *D. liurus*, and *D. ubicki*. The dorso-lateral carinae of metasomal segment V are weak and discontinuous to absent (fig. 64G) in *D. xanthopus* but strong and continuous in all other species except *D. latimanus* and *D. liurus*. The telson is paler than metasomal segment V in *D. xanthopus* but as dark as segment V in *D. latimanus*. The width of the telson vesicle is greater than the width of metasomal segment V in the male of *D. xanthopus* but approximately equal to or less than the width of segment V in the male of *D. bengalensis*, *D. obscurus*, and *D. phipsoni*.

DISTRIBUTION: This species is endemic to India (fig. 118) and has been recorded only in the states of Maharashtra and Telangana (table 1).

ECOLOGY: *Deccanometrus xanthopus* inhabits a region of semiarid savanna, dominated by *Acacia*, *Commiphora*, *Euphorbia*, *Sterculia*, and *Ziziphus* trees, with a sparse grass layer on clayey-loam soils derived from volcanic basalt on the Deccan Plateau, at elevations of 300–930 m (fig. 7A, C; Javed et al., 2010a). The climate is predominately hot and dry, receiving approximately 550 mm of precipitation annually, during the monsoon season from June to September. The burrowing biology of this fossorial, pelophi-

lous species was described by Khatavkar and More (1990), Javed et al. (2010a) and Pande et al. (2012). The burrows, constructed in open ground, have oval, semicircular or crescent-shaped entrances, 2–2.5 cm x 1.5 cm (fig. 8H), and are 10–50 cm deep, usually almost vertical with a gradual turn, but sometimes tortuous, leading to a terminal chamber 8 cm in diameter. Whereas burrows are usually occupied by a single individual, those containing a female with her brood may have multiple entrances, each connecting, via a separate tunnel, to the main tunnel and terminal chamber (Javed et al., 2010a). This species occurs in sympatry with the buthids *Hottentotta pachyurus*, *Hottentotta tamulus*, and *Orthochirus bicolor*, the scorpionid *Chersonesometrus fulvipes*, and the scorpipid *Neoscorpiops satarensis*.

REMARKS: This species, previously placed in subgenus *Chersonesometrus* of *Heterometrus* by various authors (e.g., Couzijn, 1981; Tikader and Bastawade, 1983; Fet, 2000), is newly accommodated in *Deccanometrus*, gen. nov., based on a phylogenetic analysis (fig. 10).

Although the type material of *H. telanganaensis*, described from Telangana, was not examined and compared directly with *D. xanthopus*, described from Maharashtra, it is clearly conspecific with the latter, matching closely in size, coloration, shape and surface macrosculpture of the carapace and telson, and shape, carination, and surface macrosculpture of the pedipalp chela. The only apparent morphological differences, in pectinal tooth counts (*H. telanganaensis*: ♂, 13/13, ♀, 10/10; *D. xanthopus*: ♂, 16/16, ♀, 14/14) and pro- and retroventral spiniform macrosetal counts of the leg telotarsi (*H. telanganaensis*: 3–4/4 on legs I and II, 4/4–5 on III and IV; *D. xanthopus*: 4/5 on I and II, and 4/6 on III and IV), fall within the normal range of geographical variation for Scorpionidae (Prendini, 2001a). The burrowing biology described for *H. telanganaensis* is also a precise match for *D. xanthopus* (Khatavkar and More, 1990; Javed et al., 2010a; Pande et al., 2012). Based on these deductions, the following new synonym is pre-

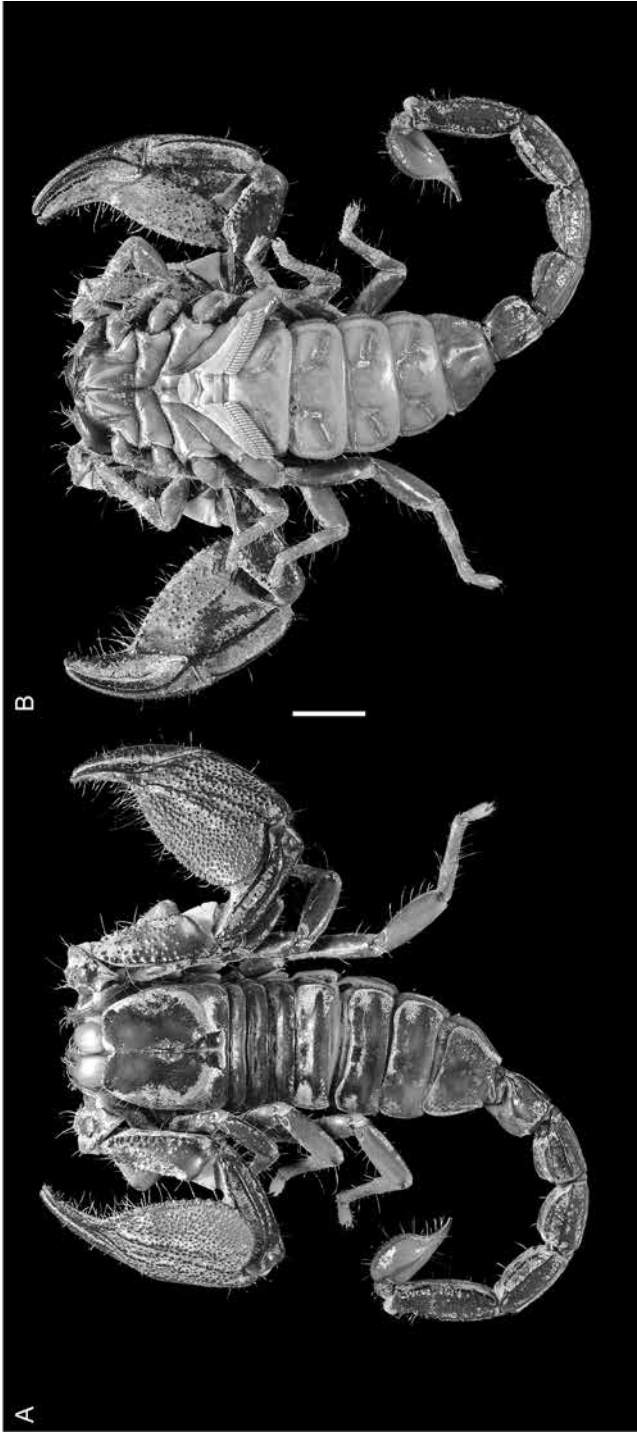


FIGURE 101. *Chersonesometrus pelekomanus* (Couzijn, 1981), comb. nov., holotype ♂ (SMF RII/1088/19), habitus: **A.** dorsal and **B.** ventral aspects. Scale bars = 10 mm.



FIGURE 102. *Chersonesometrus pelekomanus* (Couzijn, 1981), comb. nov., paratype ♀ (SMF RII/329), habitus: **A.** dorsal and **B.** ventral aspects. Scale bar = 10 mm.

sented: *Heterometrus telanganaensis* Javed et al., 2010 = *Deccanometrus xanthopus* (Pocock, 1897), syn. nov.

MATERIAL EXAMINED: INDIA: Maharashtra:
Pune Distr.: Mayureshwar, ca. 2 km NW of Supe, 18°21'N 74°22'E, 644–646 m, 29.xi.2009, R. Datta, mixed savanna on plain intersected by episodic washes, excavated from vertical burrows (ca. 30–50 cm deep) in open ground, clayey soil along drainage lines or near riverbed, 1 ♂, 1 ♀ (AMNH), same data, except: 676 m, 1 juv. ♀ (AMCC [LP 16814]). **Satara Distr.:** Khambatki Ghat, S of Khandala, on M.B.T. Road (Highway 47), 18°01'N 74°01'E, 928 m, 17.xi.2004, S. Basi, steep slopes of rocky ridge, mixed, semiarid savanna, excavated from near-vertical burrows (ca. 15 cm deep) in open ground, 1 ♀ (AMNH), 1 juv. ♂ (AMCC [LP 13126]), 18°01'N 74°01'E, 937 m, dry savanna woodland (mostly broadleaf) on steep mountain slope, excavated from burrows ca. 15 cm deep, almost vertical with gradual turn, in hard, reddish clayey-loam, 30.xi.2006, P. Menon, 3 ♀, 1 subad. ♀, 1 juv. ♀ (AMNH), 1 juv. ♂ (AMCC [LP 13971]), 902 m, 29.xi.2009, R. Datta, broadleaf woodland with dense grass layer on clayey-loam soil, excavated from near vertical burrows (ca. 10–20 cm deep) in open ground on steep slope, 1 ♂, 4 ♀, 1 juv. ♂ (AMNH), 1 juv. ♂ (AMCC [LP 16813]).

Gigantometrus Couzijn, 1978, stat. nov.

Figures 2, 9D, 10, 18, 32, 49, 67A, B, 68A, B, 69A, B, 145–156, table 1

Heterometrus (*Gigantometrus*) Couzijn, 1978:

330, type species by monotypy: *Heterometrus swammerdami* Simon, 1872 [= *Gigantometrus swammerdami* (Simon, 1872)]; 1981: 80, 81, 159, 161, 167, 168, 179–181, 183, 186, 187, 192, table 14, figs. 21, 56, 66, 68a; Tikader and Bastawade, 1983: 519, 520, 561; Francke, 1985: 8, 18; Fet, 2000: 443; Prendini, 2000a: 44; Prendini et al., 2003: 222, 252, appendix 1; Kovařík, 2004: 1, 2; Rossi, 2016a: 6–9, 25, figs. 3, 23.

Heterometrus: Lourenço and Huber, 2002: 273;

Kovařík, 2004: 1, 2, 49, 51, table 2 (part); 2009: 34, 35, table 1 (part); Veronika et al.,

2013: 70; Kovařík et al., 2016: 96, 100 (part); Aswathi and Sureshan, 2017: 9847 (part); Kovařík et al., 2019a: 1, 9, 12, fig. 53 (part).

DIAGNOSIS: *Gigantometrus* may be separated from other Asian scorpionid genera as follows. The carapace is vaulted, the lateral surfaces sloping steeply (fig. 18) in *Gigantometrus*, but slightly to markedly dorsoventrally compressed, the lateral surfaces sloping gently, in all except two species of *Deccanometrus*, *D. latimanus*, and *D. xanthopus*, all except two species of *Sahyadrimetrus*, *S. mathewi*, and *S. scaber*, all except three species of *Chersonesometrus*, *C. fulvipes*, *C. madraspatensis*, and *C. shivashankari*, and three species of *Srilankametrus*, *S. indus*, *S. pococki*, and *S. serratus*. The carapace anterior margin is straight, with the frontal lobes evenly rounded or truncate (fig. 18) in *Gigantometrus*, whereas the anterior margin is concave, with the frontal lobes uneven and sloping medially in *Heterometrus*, *Javanimetrus*, *Sahyadrimetrus*, all except two species of *Deccanometrus*, *D. latimanus* and *D. xanthopus*, and some species of *Chersonesometrus*. The carapace anterolateral margins converge gradually anteriorly in *Gigantometrus* but are subparallel anteriorly in *Javanimetrus* and *Srilankametrus*; the mediolateral margins converge markedly posteriorly (at the posterolateral sulci) in *Gigantometrus* but diverge or converge slightly posteriorly (at the posterolateral sulci) in all other genera, and three species of *Sahyadrimetrus*, *S. barberi*, *S. rugosus*, and *S. tikaderi*. The carapace rostrolateral margin is entire in *Gigantometrus* but distinctly incised adjacent to the posterior lateral ocelli in *Heterometrus*. Anterocular extensions of the superciliary carinae are present in *Gigantometrus* but absent in *Srilankametrus*. The median ocelli are relatively small, the distance between them equal to or greater than the width of an ocellus in *Gigantometrus* but relatively large, the distance between them less than the width of an ocellus in *Heterometrus*; the median ocular tubercle is situated anteromedially to medially, the distance from carapace anterior margin : carapace length (CAM:CL) 0.40–0.50 in *Gigantometrus*, but pos-

teromedially, CAM:CL 0.51–0.62 in *Chersonesometrus*. The interocular suture is present in *Gigantometrus* but absent in *Heterometrus*, *Javanimetrus*, *Sahyadrimetrus*, one species of *Deccanometrus*, and two species of *Srilankametrus*. The carapace posterior sutures are present, extending past the median ocular tubercle, and connected anteriorly to the posterior bifurcations of the interocular suture in *Gigantometrus*; present, extending to the median ocular tubercle, and connected by a short cross-suture anterior to the postocular depression in *Heterometrus*; and absent in *Javanimetrus*, *Sahyadrimetrus*, and two species of *Srilankametrus*. The frontal lobes and medial region of the carapace interocular surface are granular with smooth areas in *Gigantometrus* whereas the interocular surface is entirely smooth in all except one species of *Srilankametrus* and some species of *Heterometrus*. The chelical movable finger prodistal (DI) and retrodistal (DE) teeth are unequal, with the DE tooth considerably smaller than the DI tooth, aligned longitudinally and not opposable in *Gigantometrus*, but opposable, i.e., forming a bicusps, in two species of *Deccanometrus*, *D. liurus* and *D. ubicki*, and subequal, with the DE tooth only slightly smaller than the DI tooth, and opposable in *Heterometrus* and some species of *Chersonesometrus*. The pedipalp patella dorsomedian carina of the female is entirely to predominantly granular or costate in *Gigantometrus*, but absent or obsolete in *Heterometrus*, *Javanimetrus*, all except one species of *Sahyadrimetrus*, *S. rugosus*, and all except one species of *Srilankametrus*, *S. caesar*. The patella retromedian carinae of the female are absent or obsolete in *Gigantometrus*, but granular or costate in *Chersonesometrus*, three species of *Deccanometrus*, *D. bengalensis*, *D. obscurus*, and *D. phipsoni*, two species of *Srilankametrus*, *S. gravimanus* and *S. yaleensis*, and three species of *Sahyadrimetrus*, *S. barberi*, *S. rugosus*, and *S. tikaderi*. The prominent spiniform granule of the patella proventral carina is absent (figs. 149, 154) in *Gigantometrus* but present in *Heterometrus*. The patella dorsal, retrodorsal, and retroventral intercarinal surfaces of the female are smooth or nearly so in *Gigan-*

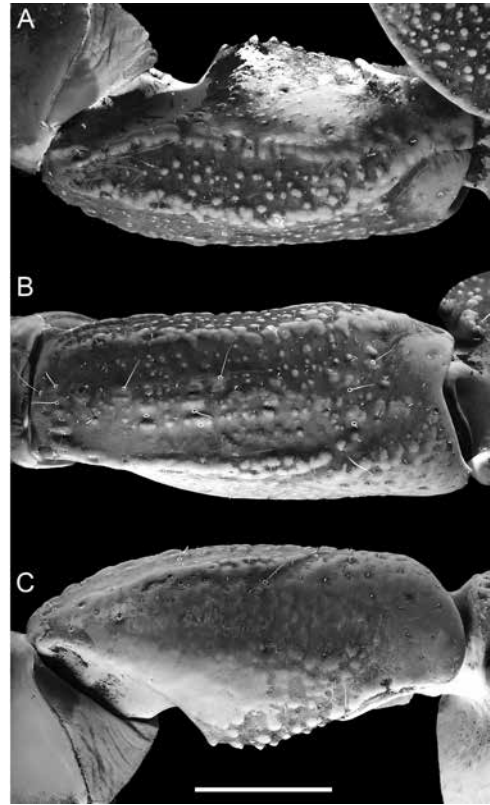


FIGURE 103. *Chersonesometrus pelekomanus* (Couzijn, 1981), comb. nov., paratype ♀ (SMF RII/329), pedipalp patella: A. dorsal, B. retrolateral, and C. ventral aspects. Scale bar = 5 mm.

tometrus but granular in all species of *Chersonesometrus* except *C. nathanorum*. The pedipalp chela of the adult male is sparsely setose in *Gigantometrus* but moderately to densely setose in *Sahyadrimetrus*, all species of *Deccanometrus* except *D. xanthopus*, one species of *Srilankametrus*, and some species of *Chersonesometrus*. The distance between the chela manus dorsomedian and promedian carinae or setal rows (DMC–PMC) is slightly to markedly greater than the distance between the promedian and proventral carinae or setal rows (PMC–PVC) in *Gigantometrus* whereas the DMC–PMC is similar to the PMC–PVC in *Heterometrus*. The dorsomedian carina is continuous to the proximal edge of the manus in *Gigantometrus* but becomes obsolete proximally in *Heterometrus*, *Javanimetrus*, *Sahyadrimetrus*, *Sri-*



FIGURE 104. *Chersonesometrus pelekomanus* (Cousijn, 1981), comb. nov., holotype ♂ (SMF RII/1088/19), pedipalp chela: **A.** retrodorsal, **B.** ventral, and **C.** prolateral aspects. Scale bar = 5 mm.



FIGURE 105. *Chersonesometrus pelekomanus* (Couzijn, 1981), comb. nov., paratype ♀ (SMF RII/329), pedipalp chela: A. retrodorsal, B. ventral, and C. prolateral aspects. Scale bar = 5 mm.

lankametrus, and all species of *Deccanometrus* except *D. obscurus* and *D. phipsoni*. The proximal half of the chela manus dorsal secondary carina, distal half of the subdigital carina and distal third of the digital carina are closely adjacent in *Gigantometrus* whereas the dorsal secondary, subdigital, and digital carinae (or setal rows) are well separated along their entire length in all the other genera except *Chersonesometrus*. The dorsal secondary and subdigital carinae of the male are present and entirely to predominantly granular in *Gigantometrus* but absent or obsolete in *Deccanometrus*, *Heterometrus*, *Javanimetrus*, *Sahyadrimetrus*, two species of *Chersonesometrus*, *C. bastawadei* and *C. fulvipes*, and two species of *Srilankametrus*, *S. indus* and *S. pococki*. The dorsal secondary carina comprises a double row of separate or confluent granules in *Gigantometrus* whereas it comprises a single row in *Srilankametrus*. The chela manus digital and retromedian carinae are similarly developed (figs. 150, 151, 155, 156) in *Gigantometrus* whereas the retromedian carina is more pronounced than the digital carina in *Chersonesometrus*. The retromedian carina of the male is entirely to predominantly granular in *Gigantometrus* but entirely to predominantly costate in *Chersonesometrus*, *Srilankametrus couzijni*, *S. gravimanus*, and *S. yaleensis*, and absent or obsolete in *Deccanometrus*, *Heterometrus*, *Javanimetrus*, *Sahyadrimetrus*, *Srilankametrus indus*, and *S. pococki*. The depression in the dorsal surface of the chela manus, proximal to the fixed finger of the adult male, is absent or obsolete (figs. 150, 155) in *Gigantometrus* but present and distinct in *Heterometrus*. The chela manus dorsal surface is without reticulation in *Gigantometrus* but shallowly reticulate in *Javanimetrus*, *Sahyadrimetrus*, all except two species of *Deccanometrus*, *D. obscurus* and *D. phipsoni*, and three species of *Heterometrus*, *H. glaucus*, *H. laevigatus*, and *H. thorellii*; the dorsal surface is finely to coarsely granular in *Gigantometrus* but smooth in *Heterometrus*, *Javanimetrus*, two species of *Sahyadrimetrus*, *S. kanarensis* and *S. tikaderi*, and one species of *Deccanometrus*, *D. ubicki*. The chela manus retrolateral intercarinal surfaces are granu-

lar in *Gigantometrus* but smooth or nearly so in *Heterometrus*, *Javanimetrus*, and some species of *Sahyadrimetrus*. The chela manus ventral surface is flat, with the axes of the retroventral and ventromedian carinae in approximately the same plane in *Gigantometrus* but angled, with the axis of the retroventral carina ventral to the axis of the ventromedian carina in *Javanimetrus*, four species of *Chersonesometrus*, *C. beccaloniae*, *C. hendersoni*, *C. pelekomanus*, and *C. tristis*, and two species of *Srilankametrus*, *S. indus* and *S. pococki*. The pro- and retrolateral surfaces of the tibiae of legs I and II each bear a row of two or three spiniform macrosetae in *Gigantometrus* and scattered, setiform macrosetae, not arranged in a definite row, in *Heterometrus*. Macroseta *st* on the retroventral surface of the basitarsus of leg I is spiniform (fig. 49) in *Gigantometrus* but usually setiform in *Heterometrus*, and *sb* on the retroventral surface of the basitarsus of leg III is setiform in *Deccanometrus* but spiniform in *Javanimetrus* and *Sahyadrimetrus*. The pectinal first proximal median lamella (scape) of the female is distinctly angular, $> 90^\circ$ but $< 180^\circ$ (fig. 32) in *Gigantometrus* but straight or shallowly curved in *Srilankametrus*. The mesial surfaces of mesosomal tergites I–VI of the male are granular in *Gigantometrus*, but smooth in *Heterometrus*, *Javanimetrus*, *Srilankametrus*, all except one species of *Deccanometrus*, *D. xanthopus*, all except two species of *Sahyadrimetrus*, *S. mathewi* and *S. scaber*, and some species of *Chersonesometrus*. The lengths of metasomal segments I and II are markedly greater than their respective widths (figs. 67A, B, 68A, B, 69A, B) in *Gigantometrus* but approximately equal to or less than their respective widths in all other genera. The ventrosubmedian and ventrolateral carinae are granular on metasomal segments I–IV, II–IV (costate on I), or III and IV (costate on I and II) (fig. 69A, B) in *Gigantometrus* but granular or costate-granular on segment IV only and costate on segments I–III in all other genera, except two species of *Heterometrus*, *H. laoticus* and *H. silenus*. The ventral intercarinal surfaces of metasomal segment IV are smooth in *Gigantometrus* but sparsely granular in *Javanimetrus*. The dorso-

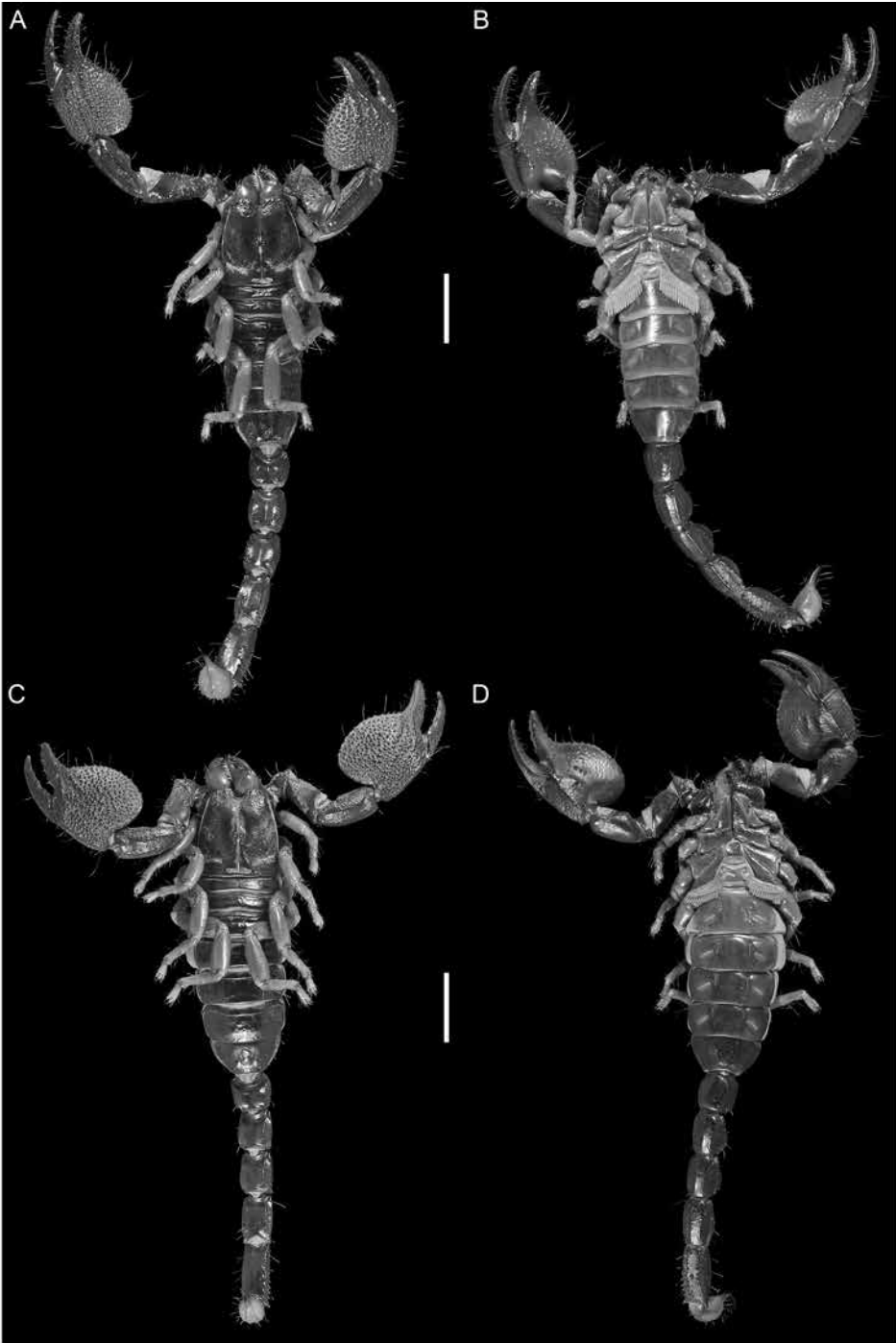


FIGURE 106. *Chersonesometrus shivashankari*, sp. nov., habitus: A, C. dorsal and B, D. ventral aspects. A, B. holotype ♂ (BMNH), Bellahunsi, India. C, D. paratype ♀ (BMNH), Hampasagar, India. Scale bar = 10 mm.

submedian carinae of metasomal segment V are partial (fig. 67A, B) in *Gigantometrus* but vestigial or absent in all other genera. The dorsal intercarnal surface of segment V is granular in *Gigantometrus* but smooth in *Deccanometrus*, *Heterometrus*, *Javanimetrus*, *Sahyadrimetrus*, and some species of *Chersonesometrus* and *Srilankametrus*. The telson is paler than metasomal segment V in *Gigantometrus* but as dark as segment V in most species of *Srilankametrus*, and some species of *Deccanometrus* and *Heterometrus*. The width of the telson vesicle is greater than the width of metasomal segment V in the female of *Gigantometrus* but approximately equal to or less than the width of segment V in the female of all other genera, and the vesicle is globose in *Gigantometrus* but elongate in *Heterometrus*, *Javanimetrus*, *Sahyadrimetrus*, and all except three species of *Srilankametrus*, *S. indus*, *S. pococki*, and *S. serratus*.

INCLUDED SPECIES: This genus accommodates two species, formerly assigned to subgenus *Gigantometrus* of *Heterometrus* by various authors (Couzijn, 1981; Tikader and Bastawade, 1983; Fet, 2000; Rossi, 2016a), that was recovered as a distinct lineage by phylogenetic analysis of morphological characters and DNA sequences from the nuclear and mitochondrial genomes (fig. 10): *Gigantometrus swammerdami* (Simon, 1872), comb. nov., and *Gigantometrus titanicus* (Couzijn, 1981), comb. nov. et stat. rev.

DISTRIBUTION: The genus *Gigantometrus* is endemic to India and Sri Lanka (figs. 2, 145, 146, table 1). Its distribution overlaps those of most species of *Deccanometrus* except *D. latimanus*, and most species of *Chersonesometrus* and *Srilankametrus*, but appears to be allopatric with the species of *Sahyadrimetrus*.

ECOLOGY: The species of *Gigantometrus* inhabit broadleaf savanna, riverine thicket, scrub jungle, dry deciduous forest with bamboo thickets, subtropical lowland rainforest, and plantations at low elevations ranging from 30–375 m above sea level. Both are fossorial and pelophilous (Prendini, 2001b), excavating steep burrows, ca. 30–50 cm deep, in hard, sandy- or clayey-

loam soils, under or at the base of large stones, among the roots of trees, in earthen banks or rock walls, or inhabiting rock crevices, holes in tree trunks, or the burrows of other animals (Hull-Williams, 1986; Kovařík et al., 2016; Aswathi and Sureshan, 2017). Colonies of *G. titanicus*, comprising multiple individuals of both sexes and different ages, presumably kin, are commonly found inhabiting the shafts of large termitaria, often at considerable depths, and have been observed emerging to the surface en masse to gorge on winged alates leaving the nest after rain (unpublished data).

CONSERVATION STATUS: One species, *G. swammerdami*, is occasionally available in the exotic pet trade.

REMARKS: *Gigantometrus* Couzijn, 1978, stat. nov., originally created as a subgenus of *Heterometrus*, subsequently synonymized with the latter (Kovařík, 2004), and then revalidated (Rossi, 2016a), is newly elevated to the rank of genus. This decision is based on phylogenetic position and not on “the larger chela” suggested as a diagnostic character by Rossi (2016a: 19).

Gigantometrus swammerdami (Simon, 1872),
comb. nov.

Figures 9D, 10, 18A, B, 32A, B, 49A–D, 67A,
68A, 69A, 145–151, table 1

Scorpio afer (nec *Scorpio afer* Linnaeus, 1758):

Herbst, 1800: 38–42, pl. I, fig. 1 (misidentification, part); Latreille, 1804: 120–122 (part).

Buthus afer (nec *Scorpio afer* Linnaeus, 1758):

C.L. Koch, 1836: 17–19, pl. LXXIX, fig. 175 (misidentification, part); 1850: 87 (misidentification, part); Bellevoye, 1870: 112.

Scorpio (Buthus) afer: Gervais, 1844a: 60 (part).

Heterometrus swammerdami Simon, 1872b: 54, 56–59, 97, 100, pl. VI, fig. 3; Kraepelin, 1899: 106, 108, 112, fig. 34 (part); 1913: 166 (part); Roewer, 1929: 612 (part); Werner, 1934: 278 (part); 1936: 186; Kästner, 1941: 233, 234 (part); Roewer, 1943: 228 (part);

Takashima, 1945: 91; Sasirababu, 1961: 11; Pampapathi Rao, 1964: 134; Pampapathi Rao and Habibulla, 1973: 148–154, tables 1, 2; Pérez Minnocci, 1974: 38 (part); Cloudsley-Thompson, 1981: 328, 331–333, fig. 3, pl. 1d; Hjelle, 1990: 49; Polis, 1990: 267; Root, 1990: 398, 401, 404, fig. 9.27; Warburg and Polis, 1990: 229, 234, table 5.2; Prendini et al., 2003: 192, 193, 202, 203, 205, 208, 209, 218, 222, 252–255, 259, tables 3, 4, figs. 4–7, appendices 1, 2 (part); Kovařík, 2004: 1, 2, 42–44, 49, 51, 52, table 2 (part), table 3, fig. 28; 2009: 16, 35, 36, 44, 47, 49, 93, 101, 113, table 1 (part), table 2, figs. 139–145, 222, 223, 275–283; Javed et al., 2010a: 147; 2010b: 785, table 1; Veronika et al., 2013: 73; Warburg, 2013: 152; Tahir and Prendini, 2014: 2 (part); Kovařík et al., 2016: 10, 111, 113 (part); Aswathi and Sureshan, 2017: 9847.

Pandinus asper Thorell, 1876b: 199–202

(synonymized by Pocock, 1890: 237–239).

Pandinus kochii Karsch, 1879b: 127 (synonymized by Pocock, 1890: 237, 239); Moritz and Fischer, 1980: 316.

Pandinus (Heterometrus) swammerdami: Karsch, 1879b: 127.

Pandinus kochii: Karsch, 1884: 68, 69; Moritz and Fischer, 1980: 316.

Scorpio lucidipes Simon, 1885: 38, 39 (synonymized by Pocock, 1890: 237, 239, 240).

Scorpio swammerdami: Simon, 1885: 39; Pocock, 1890: 237–241, table; 1893: 304, 309 (part); Kraepelin, 1894: 25, 42–44, 46, 47, 60, 62, 246, pl. I, figs. 9, 24 (part).

Scorpio fulvipes: Pocock, 1893: 304–307, 309 (part).

Pandinus megacephalus: Thorell, 1893: 381, 382 (part).

Pandinus swammerdami: Thorell, 1893: 379, 380; Simon, 1905: 161.

Palamnaeus swammerdami: Pocock, 1900a: 8, 85–88, 93, fig. 4B (part); Tikader, 1973: 263; Govindarajan and Rajulu, 1974: 908, 909;

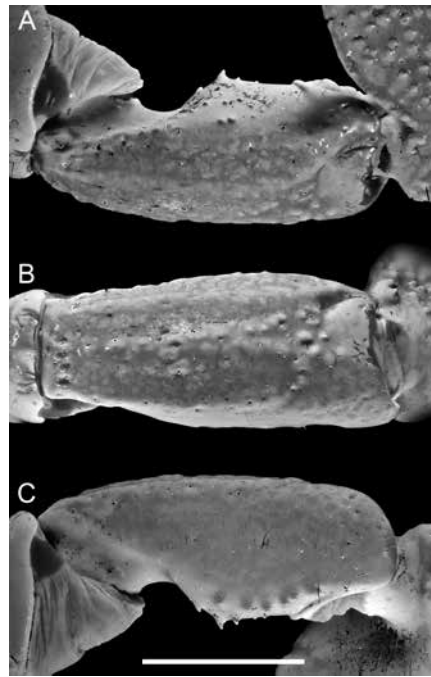


FIGURE 107. *Chersonesometrus shivashankari*, sp. nov., holotype ♂ (BMNH), Bellahunsi, India, pedipalp patella: A. dorsal, B. retrolateral, and C. ventral aspects. Scale bar = 5 mm.

Ravindranath, 1974: 1–5, 8, 9, pl. I; Tikader, 1987: 37.

Palamnaeus swammerdami flavimanus Pocock, 1900a: 87, 96; syn. nov.

Palamnaeus swammerdami lucidipes: Pocock, 1900a: 87; Couzijn, 1981: 163.

Heterometrus (Scorpio) swammerdami: Kraepelin, 1901: 271 (part).

Heterometrus schwammerdami: Borelli, 1915: 463.

Heterometrus (Gigantometrus) swammerdami: Couzijn, 1978: 330, 331 table 1 (part); 1981: 80, 81, 161, 168, 178, 179, 181, figs. 21, 66a; Tikader and Bastawade, 1983: 561–567 (part), figs. 1497–1510; Sissom, 1990: 131 (part); Kovařík, 1997: 183; 1998: 137 (part); Fet, 2000: 443 (part); Prendini, 2000a: 44; Indra, 2001: 56, 57 (part); Bastawade, 2002: 295; Kovařík, 2002: 17 (part); Lourenço and Huber, 2002: 273; Thulsi Rao et al., 2005: 3,

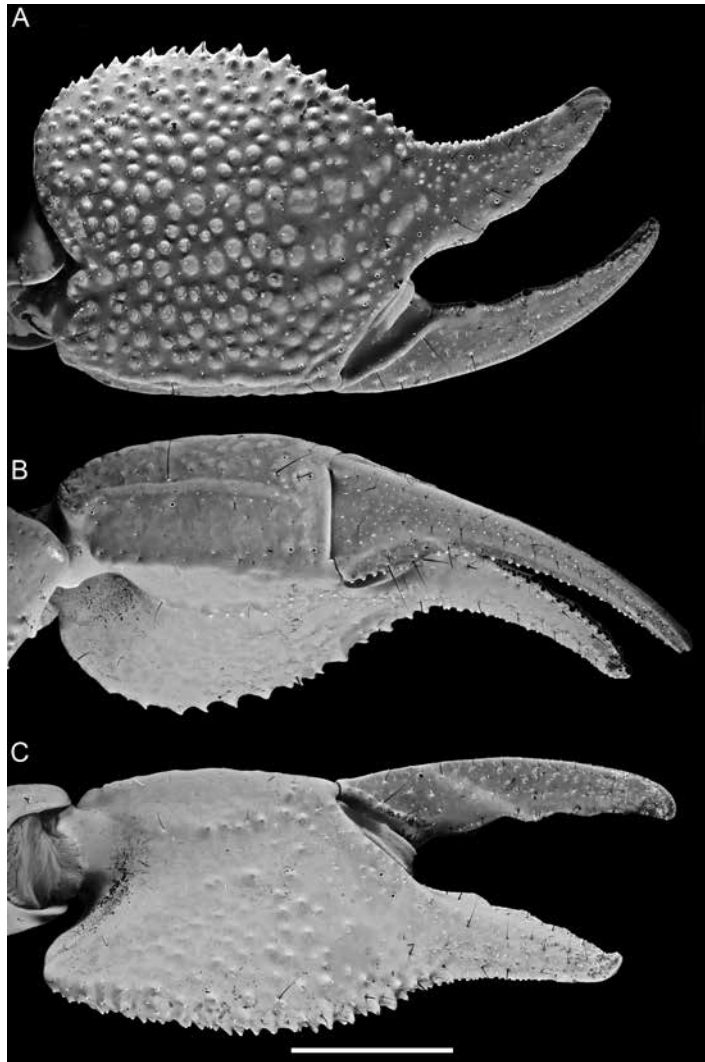


FIGURE 108. *Chersonesometrus shivashankari*, sp. nov., holotype ♂ (BMNH), Bellahunsi, India, pedipalp chela: A. retrodorsal, B. ventral, and C. prolateral aspects. Scale bar = 5 mm.

8, 9 (part); Indra, 2009: 141; Rossi, 2016a: 4, 6, 15, 25 (part), figs. 3, 23.

Heterometrus (Gigantometrus) swammerdami flavimanus: Couzijn, 1981: 19, 45, 81, 162, 164, 165, 168, 192, table 7, figs. 2a, 54, 56.

Heterometrus (Gigantometrus) swammerdami swammerdami: Couzijn, 1981: 45, 81, 160, 162–165, 167, 168, 192, table 7, figs. 53, 56 (part); Fet, 2000: 444 (part).

Heterometrus (Gigantometrus) flavimanus:

Tikader and Bastawade, 1983: 562, 568–573, figs. 1511–1524; Tikader, 1987: 36, fig. 28; Kovařík, 1998: 137; Fet, 2000: 443; Indra, 2009: 141; Rossi, 2016a: 4, 25.

Heterometrus swammerdammi: Pointer, 1991: 24.

Heterometrus (Chersonesometrus) fulvipes: Kovařík, 1998: 136 (part).

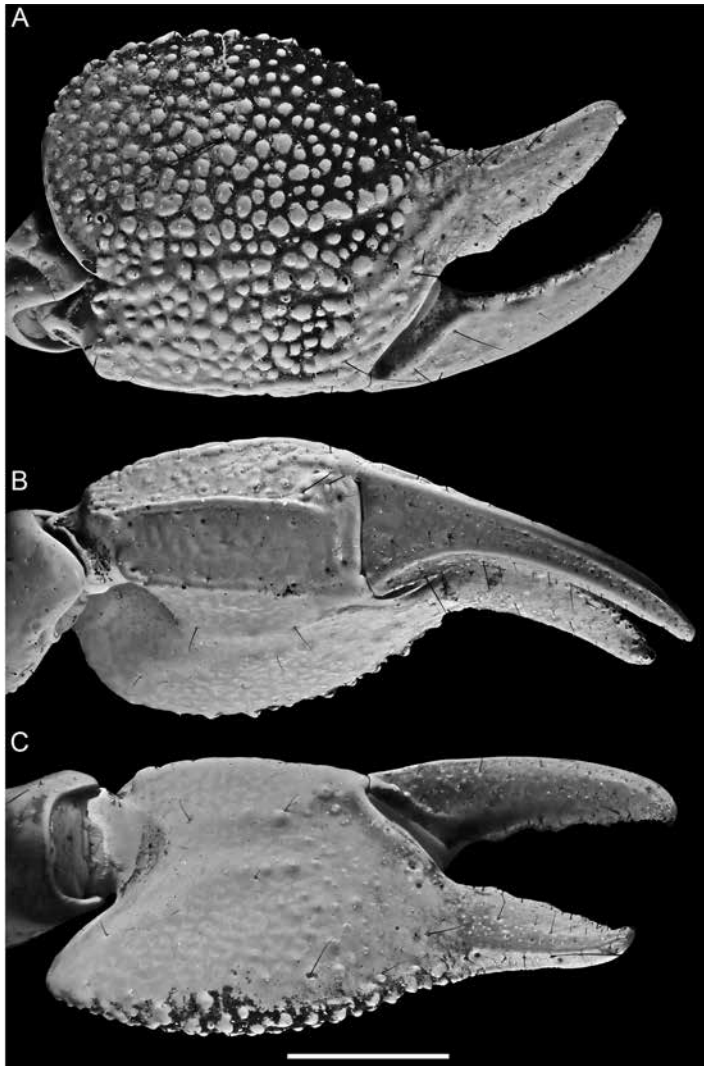


FIGURE 109. *Chersonesometrus shivashankari*, sp. nov., paratype ♀ (BMNH), Hampasagar, India, pedipalp chela: **A.** retrodorsal, **B.** ventral, and **C.** prolateral aspects. Scale bar = 5 mm.

Heterometrus flavimanus: Kovařík, 2004: 13, 14, 49, 51, 52, tables 2, 3, fig. 13; 2009: 35–37, 47, 49, 77, 101, tables 1, 2, figs. 26–31, 220, 221; Aswathi and Sureshan, 2017: 9844, 9845, 9847–9849, images 1, 6, 18.

Palamnaeus flavimanus: Kovařík, 2004: 4.

TYPE MATERIAL: *Heterometrus swammerdami*: Holotype ♀ [examined], paratype ♀ (MNH RS

0110 [Simon coll. 1500]), “India Orientalis” [East Indies]. *Pandinus asper*: Holotype: 1 subad. ♂ (NMG 92), 16.iv.1875, G.N. Westring [examined]. *Pandinus kochii*: 2 ♀ syntypes (ZMB 62), “Java,” Dupont [examined]. **INDIA: Tamil Nadu: Coimbatore Distr.: Palamnaeus swammerdami flavimanus: Lectotype ♀, paralectotype ♂ (BMNH 1899.11.2.292-3), Coimbatore [11°00′N 76°58′E], W. Brady [examined]. *Ramanthapuram Distr.:***

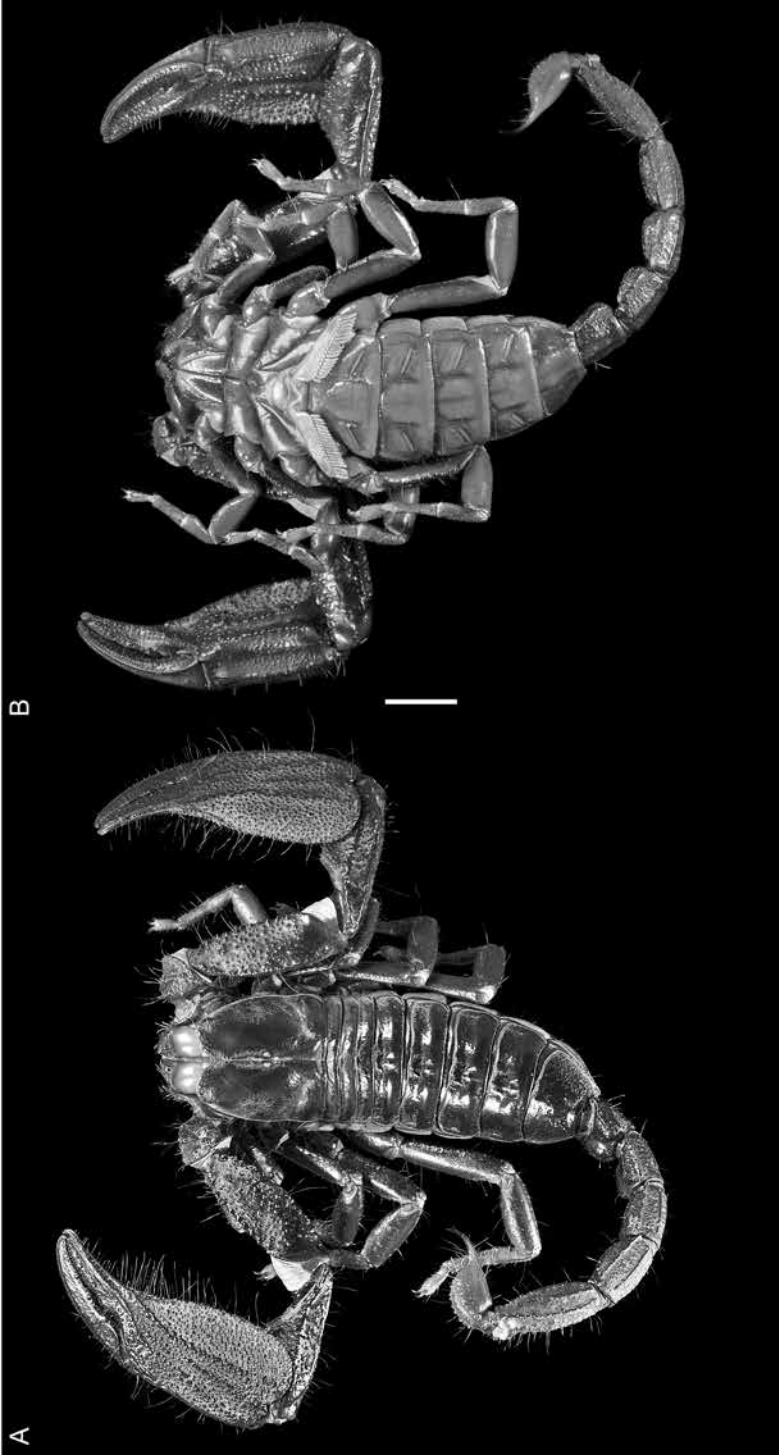


FIGURE 110. *Chersonesometrus tristis* (Henderson, 1919), comb. nov., ♂ (AMNH), Ithepalli, India, habitus: A, dorsal and B, ventral aspects. Scale bar = 10 mm.

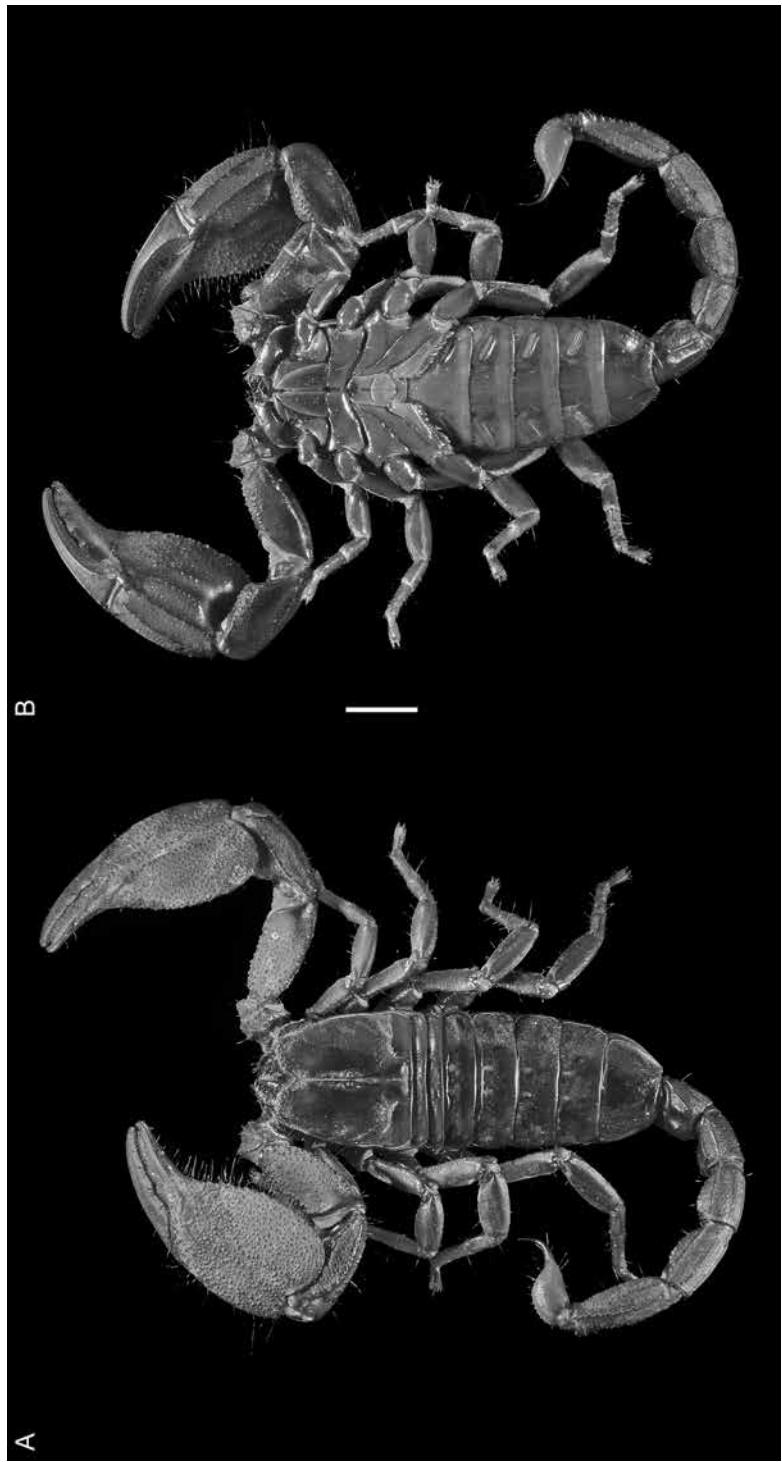


FIGURE 111. *Chersonesometrus tristis* (Henderson, 1919), comb. nov., ♀ (AMNH), Maddur, India, habitus: A. dorsal and B. ventral aspects. Scale bar = 10 mm.

Scorpio lucidipes: Holotype ♂ (MNHN RS 0112 [Simon coll. 1542]), Ramnad [Ramanthapuram, 09°22'N 78°50'E] [examined].

In the description of *P. s. flavimanus*, Pocock (1900a: 87) stated “Coimbatore (Brady, type)” but did not indicate whether the male or female was the type. Couzijn (1981: 164) designated the female as “hololectotype” (lectotype) and the male as “allolectotype” (paralectotype).

DIAGNOSIS: *Gigantometrus swammerdami* may be separated from *G. titanicus* as follows. The carapace, pedipalps, tergites and metasoma are dark reddish brown in *G. swammerdami* but very dark reddish or brownish black in *G. titanicus*. The pedipalp chela is often immaculate and paler than the femur and patella in *G. swammerdami* but infusate and similar in color to the femur and patella in *G. titanicus*. The chela is broader, with fixed finger proportionally shorter and more markedly curved (figs. 150, 151), in *G. swammerdami* than *G. titanicus*. The prodorsal margin of the chela manus slopes gently to a low hump proximal to the base of the fixed finger in *G. swammerdami* but steeply and continuously to the base of the fixed finger in *G. titanicus*. The legs are pale, lightly infusate or dark, heavily infusate (figs. 9D, 147, 148) in *G. swammerdami* but very dark, heavily infusate in *G. titanicus*. The metasoma is shorter and more robust, with the segments proportionally shorter and broader (figs. 67A, 69A), in *G. swammerdami* than *G. titanicus*. The telson is less setose in *G. swammerdami* than *G. titanicus*.

DISTRIBUTION: *Gigantometrus swammerdami* is endemic to India, where it has been recorded in the states of Andhra Pradesh, Chhattisgarh, Jharkhand, Karnataka, Kerala, Madhya Pradesh, Maharashtra, Odisha, Tamil Nadu, Telangana, West Bengal, and the union territory of Puducherry (figs. 145, 146, table 1). A record from Dehra Dun (BMNH) is doubtful. Its distribution is allopatric with *G. titanicus* but overlaps those of most species of *Deccanometrus* except *D. latimanus*, most species of *Chersonesometrus* and the Indian species of *Srilankametrus* but appears to be allopatric with the species of *Sahyadrimetrus*.

ECOLOGY: *Gigantometrus swammerdami* inhabits broadleaf savanna, riverine thicket, scrub jungle, dry deciduous forest with bamboo thickets, and plantations at low elevations ranging from 40–375 m above sea level. This species is fossorial and pelophilous (Prendini, 2001b), excavating steep burrows, ca. 30–50 cm deep, in hard, sandy- or clayey-loam soils, under or at the base of large stones, among the roots of trees, in earthen banks or rock walls, or inhabiting rock crevices, holes in tree trunks, and the burrows of other animals (Aswathi and Sureshan, 2017). The following scorpions have been recorded in sympatry with *G. swammerdami*: the buthids *Buthoscorpio politus* (Pocock, 1899), *Charmus indicus*, *Hottentotta rugiscutis*, *Isometrus thurstoni* Pocock, 1893, and *Lychas tricarinatus*; the hormurid *Iomachus laeviceps* (Pocock, 1890); and the scorpionids *C. fulvipes* and *C. madraspatensis*.

CONSERVATION STATUS: *Gigantometrus swammerdami* is occasionally available in the exotic pet trade.

REMARKS: This species was previously accommodated in subgenus *Gigantometrus* of *Heterometrus* by various authors (e.g., Couzijn, 1981; Tikader and Bastawade, 1983; Fet, 2000; Rossi, 2016a).

The following synonyms are currently recognized: *Pandinus asper* Thorell, 1876 = *Gigantometrus swammerdami* (Simon, 1872), comb. nov., synonymized by Pocock (1890); *Pandinus kochii* Karsch, 1879 = *G. swammerdami*, synonymized by Pocock (1890); *Scorpio lucidipes* Simon, 1885 = *G. swammerdami*, synonymized by Pocock (1890).

Fet (2000: 443) stated that Thorell (1893: 379) synonymized *P. asper*, *P. kochii*, and *S. lucidipes* with *H. swammerdami*, but Pocock (1890: 237, 239) was the first to do so, as noted by Kovařík (2004, 2009). Pocock's (1890) synonymies of *P. asper* and *S. lucidipes* were confirmed by examination of the types during the present investigation.

Pocock (1900a: 87) distinguished *P. s. flavimanus* from the typical form of *P. swammerdami* by “having the hands of the chelae clear red or yellow, and contrasting strongly with the dark tint of the body.” Although maintained as a subspecies

by Couzijn (1981), *H. (G.) s. flavimanus* was elevated to the rank of species by Tikader and Bastawade (1983), a decision approved by Kovařík (2004). However, *P. s. flavimanus*, described from the vicinity of Coimbatore, Tamil Nadu, appears to differ from *G. swammerdami* solely on the paler color of the pedipalp chela manus, as noted by Kovařík (2004: 49): “chela of pedipalp of adults yellow to yellowish or reddish-brown, always lighter colored than body” in *H. flavimanus* compared to “chela of pedipalp of adults colored similarly to body” in *H. swammerdami*. In the absence of other differences, this character alone cannot be considered diagnostic because color is known to vary across the distribution of *G. swammerdami* as in many Scorpionidae (Prendini, 2001a). Other putative differences in granulation and carination of the chela mentioned by Couzijn (1981) and Tikader and Bastawade (1983) fall well within the range of geographical variation for *G. swammerdami*. Based on the abundant evidence that *P. s. flavimanus* is conspecific with *G. swammerdami*, reinforced by comparison of the type material, the following new synonym is presented: *Palamnaeus swammerdami flavimanus* Pocock, 1900 = *Gigantometrus swammerdami* (Simon, 1872), syn. nov.

MATERIAL EXAMINED: 1 ♂ (AMNH). **INDIA:** ix.2001, T. Gearheart, ex pet trade, 1 ♂ (AMNH), [leg] (AMCC 101700 [LP 1607]). “India Orient.,” 1 subad. ♂, 1 subad. ♀, 1 juv. ♀ (ZMB 2284). **Andhra Pradesh:** Chittoor Distr.: Kothakota, on Chittoor–Tirupati Road 61, 13°23'N 79°06'E, 372 m, 30.xi.2004, S. Basi, shallow ravine between rocky ridges, broadleaf thicket with scattered granite and basalt outcrops on coarse gravelly loam, excavated from shallow burrow under stone on rocky slope, 1 subad. ♂ (AMCC [LP 13128]); Puttur Chittoor [Puttur, 12°46'N 75°13'E], E. Chell, xi.1952, 1 ♂ (USNM). **Karnataka:** Dharwad Distr.: Dekan, Dharwar [Dharwad, 15°28'N 75°00'E], 24.ii.1897, Lüshy, 1 ♀ (ZMH ex Mus. Bern). **Maharashtra:** Chandrapur Distr.: Chaudh [Chanda, 19°58'N 79°18'E], Central Province, 1925, J. Simpson-Roosevelt Exped., 1 ♂ (FMNH 086 256). Balaghat Distr.: Baihar [22°06'N 80°33'E], 1.ii.1949, R.L. Fleming, 1 ♀ (FMNH 086 257); Mukhi-Balagash [Mukhi-Balaghat, 22°09'N 80°41'E], 27.viii.1957, G.A. Frhr. V. Maydell, 1 ♀ (ZMH). **Puducherry:** Puducherry Distr.: Pondichéry [Pondicherry/Puduchcheri/Puducherry,

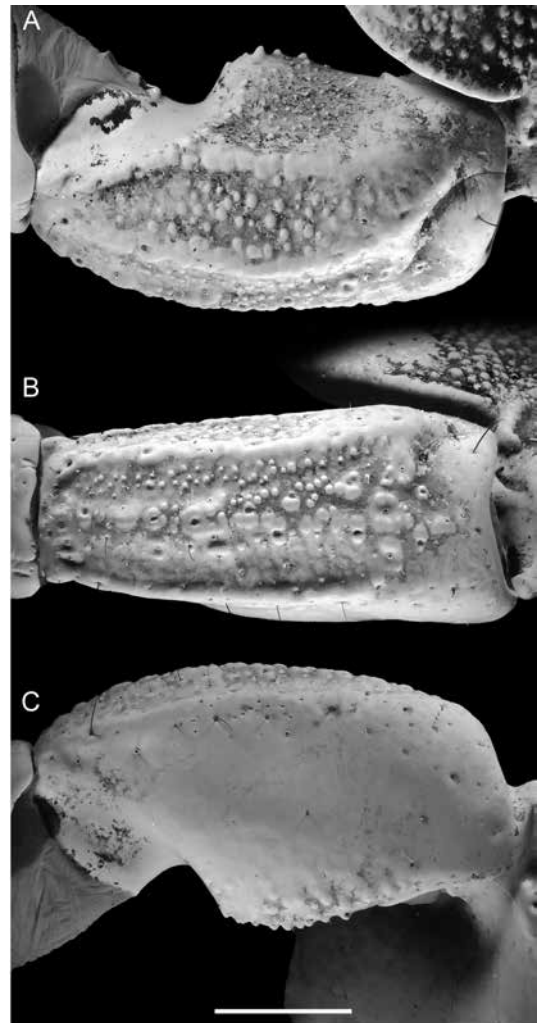


FIGURE 112. *Chersonesometrus tristis* (Henderson, 1919), comb. nov., ♀ (AMNH), Maddur, India, pedipalp patella: A. dorsal, B. retrolateral, and C. ventral aspects. Scale bar = 5 mm.

11°59'N 79°49'E], M. Maindron, 1 juv. ♂ (MNHN RS 0141 [Simon coll. 19501]), Perotet, 1 subad. ♀ (MNHN RS 0105). **Rajasthan:** Jaipur Distr.: Jeypore [Jaipur, 26°55'N 75°47'E], Rajputana, vii.1913, 1 ♀ (ZMH [Mus. Calcutta]). **Tamil Nadu:** Coimbatore Distr.: Coimbatore [11°00'N 76°58'E], vi.1954, P.S. Nathan, ex Stahnke coll., 2 ♂ [ASU 1454.1, 2], 1 subad. ♂ [ASU 1454.5] (CAS 9070406), 2.vii.1954, P.S. Nathan, ex Stahnke coll., 1 ♂ (CAS 9070418 [ASU 1451]), viii.1957, P.S. Nathan, ex Stahnke coll., 1 ♂ [ASU 58-78], 1 ♀ [ASU 58-75] (CAS 9070402). **Erode Distr.:** Bhabanisagar (plain) [Bhavāni



FIGURE 113. *Chersonesometrus tristis* (Henderson, 1919), comb. nov., pedipalp chela, retrodorsal aspect. **A.** ♂ (AMNH), Ithepalli, India. **B.** ♀ (AMNH), Maddur, India. Scale bar = 5 mm.

Sāgar, 11°25'N 77°05'E], Madras, 21.v.1963, P.S. Nathan, ex Stahnke coll., 1 ♂ (CAS 9070411 [ASU 63-1165]). *Kanchipuram Distr.*: Echankaranai, 12°41'N 80°02'E, 43 m, 2-3.xii.2004, S. Basi, flat plain below low rocky granite hills, dry forest with broadleaf trees and bamboo thickets on coarse granitic sandy-loam, moderate canopy layer, doorkeeping at burrow entrances in earthen banks, ♂ excavated from burrow (ca. 50 cm deep) in open

ground, subad. ♂ excavated from burrow (ca. 30 cm deep) under large stone, 1 ♂, 2 subad. pedipalp chelae (AMNH), 1 subad. ♂ (AMCC [LP 13129]). *Theni Distr.*: Periaculam [Periyakulam, 10°07'N 77°33'E], S. India, v.1963, Mrs D.C. Scudder, 2 ♂, 1 subad. ♀ (MCZ). *Vil-lupuram Distr.*: Genji [Gingi/Gingee, 12°15'N 79°24'E], Coromandel, 25.viii-12.ix.1901, M. Maindron, 2 juv. ♂ (MNHN RS 0113).



FIGURE 114. *Chersonesometrus tristis* (Henderson, 1919), comb. nov., ♀ (AMNH), Maddur, India, pedipalp chela: **A.** ventral and **B.** prolateral aspects. Scale bar = 5 mm.

Gigantometrus titanicus (Couzijn, 1981),
comb. nov. et stat. rev.

Figures 10, 18C, D, 32C, D, 49E–H, 67B, 68B,
69B, 145, 146, 152–156, table 1

Buthus ceylonicus (nec *Scorpio ceylonicus* Herbst,
1800): C.L. Koch, 1841b: 9–11, pl. CCXCI, fig.

698 (misidentification); Couzijn, 1981: 58.

Buthus ceylanicus: C.L. Koch, 1850: 88
(misidentification).

Pandinus ceylonicus: Karsch, 1891: 307
(misidentification).

Pandinus kochi: Karsch, 1892: 307
(misidentification).

- Scorpio ceylonicus*: Pocock, 1893: 309 (misidentification, part).
- Scorpio swammerdami*: Pocock, 1893: 304, 309 (misidentification, part); Kraepelin, 1894: 25, 42–46, 47, 60, 62, 246, pl. I, figs. 9, 24 (misidentification, part); Lönnberg, 1897b: 186 (misidentification).
- Heterometrus swammerdami*: Kraepelin, 1899: 106, 108, 112, fig. 34 (misidentification, part); Werner, 1902: 601 (misidentification); Kraepelin, 1913: 166 (misidentification, part); Lampe, 1918: 198 (misidentification); Roewer, 1929: 612 (part); Werner, 1934: 278 (part); Kästner, 1941: 233, 234 (part); Roewer, 1943: 228 (misidentification, part); Takashima, 1945: 91 (part); Pérez Minnocci, 1974: 38 (part); Root, 1990: 358, 367 (misidentification); Kovařík 2002: 20 (misidentification); Prendini et al., 2003: 192, 202, 205, 208, 209, 218, 222, 252–255, 259, table 3, figs. 4, 6, 7, appendices 1, 2 (misidentification, part); Kovařík, 2004: 1, 2, 42, 44, 49, 51, table 2 (misidentification, part); 2009: 16, 35, 44, 47, table 1 (misidentification, part); Veronika et al., 2013: 70–73, 76, table 1, figs. 1, 2a, 3–8 (misidentification); Kovařík et al., 2016: 2, 4, 5, 10, 106, 109, 110–113, 117, 118, 120, 122–125, figs. 4, 15, 535–546, 575, 576, 579, 580, 586, 587, 589, 591, 592–594 (misidentification, part); 2019a: 12, fig. 53 (misidentification).
- Palamnaeus swammerdami*: Pocock, 1900a: 8, 85–88, fig. 4B (misidentification, part).
- Heterometrus (Scorpio) swammerdami*: Kraepelin, 1901: 271 (misidentification, part).
- Heterometrus liurus*: Roewer, 1943: 228 (misidentification, part).
- Heterometrus (Palamnaeus) swammerdami*: Pringle, 1955: 271 (misidentification).
- Heterometrus (Gigantometrus) swammerdami titanicus*: Couzijn, 1981: 22, 46, 82, 165–168, 192, table 7, figs. 4f, 55, 56; Vachon, 1982: 78, 79, 96, 110, fig. 50; Kovařík, 1997: 183; 1998: 137; Fet, 2000: 444; Kovařík, 2004: 42.
- Heterometrus (Gigantometrus) swammerdami*: Tikader and Bastawade, 1983: 561, 562, 564–567 (misidentification, part); Kovařík, 1992: 185 (misidentification); 1998: 137 (misidentification, part); Fet, 2000: 443 (part); Indra, 2001: 56, 57 (misidentification, part); Kovařík, 2002: 17 (misidentification, part); Thulsi Rao et al., 2005: 3, 8, 9 (part); Rossi, 2016a: 4 (part).
- Heterometrus (Chersonesometrus) liurus*: Kovařík, 1998: 136 (part).
- Heterometrus (Gigantometrus) titanicus*: Lourenço and Huber, 2002: 273.
- TYPE MATERIAL: SRI LANKA: Western Prov.: Colombo Distr.: *Heterometrus (Gigantometrus) swammerdami titanicus*:** Holotype ♀ (MNHN RS 0084), Colombo [06°56'N 79°52'E], 1900, E. de la Croix [examined]. **Gampaha Distr.: *H. (G.) s. titanicus*:** Paratype ♂ (MNHN RS 7759), Negombo [07°12'N 79°52'E], west coast, N of Colombo, 26.iv.1974, Dr. J. Balazuc, la nuit près des paillotes [examined].
- Couzijn (1981: 165) based the description of *H. (G.) s. titanicus* on five specimens, but clearly specified a holotype and allotype (paratype) among them:
- Colombo (1 ♀ adult holotype, leg. Errington de la Croix 1900, [MNHN] RS 0084), Negombo, West coast, North of Colombo (1 ♂ ad. allotype, leg. Dr. J. Balazuc, the largest of two specimens sharing number [MNHN] RS 7759).
- Fet (2000: 444) incorrectly cited all specimens in Couzijn's (1981) list as type material for *H. (G.) s. titanicus*.
- DIAGNOSIS:** *Gigantometrus titanicus* may be separated from *G. swammerdami* as follows. The carapace, pedipalps, tergites, and metasoma are very dark reddish or brownish black in *G. titanicus* but dark reddish brown in *G. swammerdami*. The pedipalp chela is infusate and similar in color to the femur and patella in *G. titanicus* but often immaculate and paler than the femur and patella in *G. swammerdami*. The chela is narrower, with the fixed finger proportionally longer and more gently curved (figs. 155, 156), in *G. titanicus* than *G.*

swammerdami. The prodorsal margin of the chela manus slopes steeply and continuously to the base of the fixed finger in *G. titanicus* but gently to a low hump proximal to the base of the fixed finger in *G. swammerdami*. The legs are very dark, heavily infusate (figs. 152, 153) in *G. titanicus* but pale, lightly infusate, or dark, heavily infusate in *G. swammerdami*. The metasoma is longer and more slender, with the segments proportionally longer and narrower (figs. 67B, 69B), in *G. titanicus* than *G. swammerdami*. The telson is more setose in *G. titanicus* than *G. swammerdami*.

DISTRIBUTION: *Gigantometrus titanicus* is endemic to Sri Lanka. It has been recorded across the island in the Central, Eastern, North Central, North Western, Northern, Southern, and Western provinces (figs. 145, 146, table 1). Its distribution is allopatric with *G. swammerdami* but overlaps those of most species of *Srilankametrus* occurring in Sri Lanka.

ECOLOGY: *Gigantometrus titanicus* inhabits broadleaf savanna, riverine thicket, dry deciduous forest with bamboo thickets, subtropical lowland rainforest, and plantations mostly at low elevations ranging from 30–200 m above sea level. This species is fossorial and pelophilous (Prendini, 2001b), excavating steep burrows, ca. 30–50 cm deep, in hard, sandy- or clayey-loam soils, under or at the base of large stones, among the roots of trees, in earthen banks, or inhabiting rock crevices, holes in tree trunks, the burrows of other animals, and the shafts of large termitaria (Hull-Williams, 1986; Kovařík et al., 2016). The following scorpions have been recorded in sympatry with *G. titanicus* (Kovařík et al., 2016): the buthids *Buthoscorpio politus*, *Charmus laneus* Karsch, 1879, *Charmus sara-dielii* Kovařík et al., 2016, *Isometrus maculatus* (DeGeer, 1778), *Isometrus thwaitesii* Pocock, 1897, *Lychas srilankensis* Lourenço, 1997, *Reddyanus besucheti* (Vachon, 1982), *Reddyanus ceylonensis* Kovařík et al., 2016, and *Reddyanus loebli* (Vachon, 1982); the chaerilid *Chaerilus ceylonensis* Pocock, 1894; and the scorpionid *S. gravimanus*.

REMARKS: Couzijn (1981) created the subspecies, *H. (G.) s. titanicus*, to accommodate the population of *H. swammerdami* occurring in Sri Lanka,

Lourenço and Huber (2002) elevated it to the rank of species, and Kovařík (2004) synonymized it with *H. swammerdami*. An assessment of the original description and comparison of specimens from India and Sri Lanka, including the types of both taxa, during the present investigation revealed subtle but consistent differences between the two taxa, e.g., the proportionally narrower metasoma of *H. (G.) s. titanicus*. These differences, taken together with genetic divergence supporting reciprocal monophyly of samples from the two areas, supports the revalidation of *H. (G.) s. titanicus* and its elevation to the rank of species as *Gigantometrus titanicus* (Couzijn, 1981), comb. nov. et stat. rev.

MATERIAL EXAMINED: **SRI LANKA:** Ceylon, E.C. Fernando, 1 ♂ (FMNH 086 264). **Central Prov.:** Kandy Distr.: Hasalaka, SE of Rathna Ella Falls, 07°22'N 80°56'E, 200 m, 3.ii.2014, L. Prendini and P. Horsley, subtropical forest along small river, steep slopes, rocky in places, very muddy soil, dense canopy layer, sparse to moderate understorey, moderate to sparse litter layer, doorkeeping at burrow entrances at base of stones, tree roots or in earthen banks or termitaria, one in hole in tree trunk, several “colonies” of multiple individuals of different ages observed, ♂, juv. ♀ at burrow entrances, ♀ excavated from burrow ca. 50 cm long, 1 ♂, 1 ♀ (AMNH), 1 juv. ♀ (AMCC [LP 12288]). **Eastern Prov.:** Trincomalee Distr.: Trincomali [Trincomalee, 08°34'N 81°14'E], P.W. Bassett-Smith, 1 subad. ♂ (BMNH 1898.4.203). **North Central Prov.:** Polonnaruwa Distr.: Giritale, roadside, 07°59'N 80°55'E, 173 m, 27–29.i.2014, L. Prendini and P. Horsley, dry forest on gently sloping hill, moderate canopy with sparse understorey and moderate leaf-litter layer, doorkeeping at burrow entrances (one at base of large boulders, other in termitarium), 1 ♀ (AMNH); Polonnaruwa [07°56'N 81°00'E], 29.i.2014, local villagers, excavated from termitaria, 1 ♂, 1 ♀, 2 subad. ♂, 4 subad. ♀, 2 juv. ♂, 3 juv. ♀ (AMNH), 1 juv. ♀ (AMCC [LP 12287]); Polonnaruwa, Sudu Araliya, 07°55'24.3"N 81°00'E, 65 m, 27.i.2014, L. Prendini and P. Horsley, sinistral pedipalp segments (AMNH). **Northern Prov.:** Jaffna Distr.: Jaffnapatam [Jaffna, 09°40'N 80°02'E], Dr. A.E.S. Twynam, 1 ♀ (BMNH). **North Western Prov.:** Puttalam Distr.: Chilaw [07°34'N 79°48'E], near sea-level, 13.v.1965, C.M. Bogert, in house at coconut plantation, 1 ♂ (AMNH); Wilpattu, Kokmotte on Modaragam Aru River, 08°32'N 80°01'E, 30 m, 24–25.i.2014, L. Prendini and P. Horsley, mesic savanna/thicket and riverine forest near perennial river, many small lakes, moderate canopy, sparse understorey with leaf litter in places, sandy-loam soil, doorkeep-

ing at entrance to almost vertical burrow in termitarium, 1 subad. ♂ (AMNH).

Heterometrus Ehrenberg, 1828

Figures 5, 7E, F, 8F, 9E, 10, 22–24, 36–38, 50–52, 53A–D, 67C–E, 68C–E, 69C–E, 70A–D, 71A–D, 72A–D, 157–192, table 2

Buthus (*Heterometrus*) Ehrenberg in Hemprich and Ehrenberg, 1828, pl. I, figs. 1, 2 (part), type species by subsequent designation (Karsch, 1879a: 20): *Buthus* (*Heterometrus*) *spinifer* Ehrenberg, 1828 [= *Heterometrus spinifer* (Ehrenberg, 1828)]; Hemprich and Ehrenberg, 1829: 351, 352; 1831 [pages unnumbered].

Buthus (*Heterometrus*): Hemprich and Ehrenberg, 1829: 351.

Centrurus Ehrenberg in Hemprich and Ehrenberg, 1829: 350, type species by subsequent monotypy: *Centrurus galbineus* C.L. Koch, 1838 [= *Heterometrus longimanus* (Herbst, 1800)] (synonymized by Kraepelin, 1894: 34).

Palamnaeus Thorell, 1876a: 13, type species by original designation: *Palamnaeus petersii* Thorell, 1876; 1876b: 84; Pocock, 1892: 38 (part); 1893b: 307 (part); Laurie, 1896a: 193; 1896b: 128; Pocock, 1896a: 77; 1900a: 84; Tikader, 1973: 263; Couzijn, 1981: 5, 75, 86.

Caucon Karsch, 1879a: 14, type species by original designation: *Centrurus galbineus* C.L. Koch, 1838 [= *Heterometrus longimanus* (Herbst, 1800)] (synonymized by Kraepelin, 1894: 34).

Heterometrus: Karsch, 1879a: 20; Ausser, 1880: 466; Laurie, 1896a: 193; 1896b: 128; Kraepelin, 1899: 106, 107; 1904: 198, 199; 1905: 344; 1913: 165; Birula, 1917a: 161; 1917b: 59; Kopstein, 1921: 128, 129; 1927: 107; Fage, 1933: 27, 28; Werner, 1934: 277; Fage, 1936: 179, 180; Kästner, 1941: 233; Vachon, 1953c: 9, fig. 1; 1963: 162, fig. 4; Bücherl, 1964: 59; Couzijn, 1978: 327, 331; Daling-

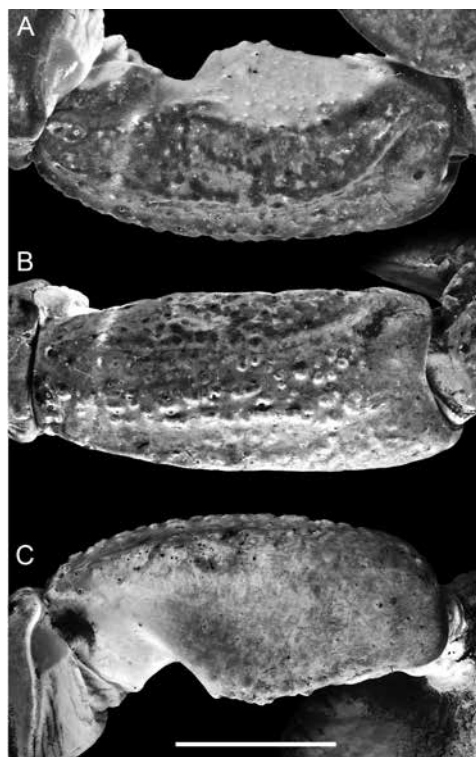


FIGURE 115. *Chersonesometrus wroughtoni* (Pocock, 1899), comb. nov., paralectotype ♀ (BMNH 1897.9.17.1-4, 11, 20), pedipalp patella: A. dorsal, B. retrolateral, and C. ventral aspects, Scale bar = 5 mm.

water, 1980: 286; Couzijn, 1981: 3–6, 8, 26, 32, 47, 48, 50, 52, 60, 64, 65, 69, 73, 74, 81, 101, 130, 133, 145, 167, 178, 179, 181, 183–189, 191, tables 7, 8, 9, figs. 66a, 68, 70, 71; Tikader and Bastawade, 1983: 2, 6, 7, 518, 519; Biswas, 1984: 320; Francke, 1985: 8, 18; Lourenço, 1989: 174; Mahsberg, 1990: 269, 271; Sissom, 1990a: 136; Nenilin and Fet, 1992: 19, 20; Braunwalder and Fet, 1998: 31; Kovařík, 1998: 136; Fet, 2000: 431; Lourenço, 2000: 25; Prendini, 2000a: 2, 4, 27, 28, 34, 35, 44, 50, 53, 57, 61, 62, 70, tables 1, 2, 10; Indra, 2001: 55; Bastawade, 2002: 95, 295; Lourenço and Huber, 2002: 273; Prendini et al., 2003: 185–191, 194, 199, 200, 202–206, 208–210, 212–214, 217, 218, 220, 222, 223, 226, 229, 230, 234, 235, 237, 250–



FIGURE 116. *Chersonesometrus wroughtoni* (Pocock, 1899), comb. nov., paralectotype ♀ (BMNH 1897.9.17.1-4, 11, 20), pedipalp chela: **A.** retrodorsal, **B.** ventral, and **C.** prolateral aspects, Scale bar = 5 mm.

259, tables 1, 2, 6, 8, 9, figs. 1, 3, appendices 1, 2 (part); Soleglad and Fet, 2003a: 58, 88, 113, 115, 116, table 9; Bastawade et al., 2004: 47; Kovařík, 2004: 1, 2, 4, 7, 49, 51, 53 tables 2, 3 (part); Bastawade et al., 2005: 77;

Prendini and Wheeler, 2005: 460, 477, 482; Bastawade, 2006a: 134; Booncham et al., 2007: 43 (part); Shultz, 2007: 78, 84, 86–91, table 1, figs. 2–5; Bastawade, 2008: 133, 136; Bastawade and Borkar, 2008: 212;

- Bastawade, 2009: 215; Kovařík, 2009: 1–3, 14–16, 28, 33, 34, 46, 49, 99–101 (part); Mirza and Sanap, 2009: 486 (part); Javed et al., 2010a: 143; Mirza et al., 2012: 1, 2 (part); Di et al., 2013: 86, 88, 94, 96; Tahir and Prendini, 2014: 1–5, 11, 20, 21, fig. 1 (part); Kovařík et al., 2016: 96, 100; Plíšková et al., 2016: 467–469, 474; Rossi, 2016a: 6–9, 15, 19, 20, 25 (part); Aswathi and Sureshan, 2017: 9847; Esposito et al., 2017: 4, 14; Pham et al., 2017: 133, 136; Esposito et al., 2018: 89, 90, 110, 115, appendix 1.
- Scorpio (Buthus)* (nec Leach, 1815): Lankester, 1885: 379.
- Scorpio* (nec Linnaeus, 1758): Laurie, 1896a: 193; Lönnberg, 1897a: 197 (part).
- Heterometrus (Heterometrus)*: Couzijn, 1978: 330; 1981: 80, 83, 86, 121, 161, 173–177, 180, 182–184, 186–188, 191, table 14, figs. 62–65, 66b, 69, 70; Tikader and Bastawade, 1983: 519, 520 (part); Biswas, 1984: 320; Francke, 1985: 8, 18; Fet, 2000: 431, 432; Prendini, 2000a: 44; Prendini et al., 2003: 222, 252, appendix 1; Bastawade et al., 2004: 47; Bastawade and Borkar, 2008: 212, 218.
- Herometrus*: Bastawade and Borkar, 2008: 218.
- Heterometrus*: Bastawade, 2009: 218.

DIAGNOSIS: Species of *Heterometrus* may be separated from other Asian scorpionid genera as follows. The carapace is vaulted, the lateral surfaces sloping steeply (figs. 22–24) in *Heterometrus*, but slightly to markedly dorsoventrally compressed, the lateral surfaces sloping gently, in all except two species of *Deccanometrus*, *D. latimanus* and *D. xanthopus*, all except two species of *Sahyadrimetrus*, *S. mathewi* and *S. scaber*, all except three species of *Chersonesometrus*, *C. fulvipes*, *C. madraspatensis*, and *C. shivashankari*, and three species of *Srilankametrus*, *S. indus*, *S. pococki*, and *S. serratus*. The carapace anterior margin is concave, with the frontal lobes uneven and sloping medially in *Heterometrus*, whereas the anterior margin is straight, with the frontal lobes evenly rounded or truncate in *Gigantome-*

trus, *Srilankametrus*, two species of *Deccanometrus*, *D. latimanus* and *D. xanthopus*, and some species of *Chersonesometrus*. The carapace anterolateral margins converge gradually anteriorly in *Heterometrus* but are subparallel anteriorly in *Javanimetrus* and *Srilankametrus*; the medio-lateral margins converge markedly posteriorly (at the posterolateral sulci) in *Heterometrus* but diverge or converge slightly posteriorly (at the posterolateral sulci) in all other genera, and three species of *Sahyadrimetrus*, *S. barberi*, *S. rugosus*, and *S. tikaderi*. The carapace rostrrolateral margin is distinctly incised adjacent to the posterior lateral ocelli in *Heterometrus* but entire in all the other genera. Anterocular extensions of the superciliary carinae are present in *Heterometrus* but absent in *Srilankametrus*. The median ocelli are relatively large, the distance between them less than the width of an ocellus in *Heterometrus* but relatively small, the distance between them equal to or greater than the width of an ocellus in the other genera; the median ocular tubercle is situated anteromedially to medially, the distance from carapace anterior margin : carapace length (CAM:CL) 0.40–0.50 in *Heterometrus*, but posteromedially, CAM:CL 0.51–0.62 in *Chersonesometrus*. The interocular suture is absent in *Heterometrus* but present in *Chersonesometrus*, *Gigantometrus*, and all except one species of *Deccanometrus*, and two species of *Srilankametrus*. The carapace posterior sutures are present, extending to the median ocular tubercle, and connected by a short cross-suture anterior to the postocular depression in *Heterometrus*; present, extending past the median ocular tubercle, and connected anteriorly to the posterior bifurcations of the interocular suture or disconnected in *Chersonesometrus*, *Deccanometrus*, *Gigantometrus*, and most species of *Srilankametrus*; and absent in *Javanimetrus*, *Sahyadrimetrus*, and two species of *Srilankametrus*. The cheliceral movable finger prodistal (DI) and retrodistal (DE) teeth are subequal, with the DE tooth only slightly smaller than the DI tooth, and opposable, i.e., forming a bicuspid in *Heterometrus* but unequal, with the DE tooth considerably smaller than the DI tooth,

aligned longitudinally and not opposable in *Gigantometrus*, *Javanimetrus*, *Sahyadrimetrus*, *Srilankametrus*, most *Deccanometrus*, and some *Chersonesometrus*. The pedipalp patella dorsomedian carina of the female is absent or obsolete (figs. 161, 190) in *Heterometrus*, but predominantly granular or costate in *Chersonesometrus*, *Gigantometrus*, and all except three species of *Deccanometrus*, *D. latimanus*, *D. liurus*, and *D. ubicki*. The patella retromedian carinae of the female are absent or obsolete in *Heterometrus*, but granular or costate in *Chersonesometrus*, three species of *Deccanometrus*, *D. bengalensis*, *D. obscurus*, and *D. phipsoni*, three species of *Sahyadrimetrus*, *S. barberi*, *S. rugosus*, and *S. tikaderi*, and two species of *Srilankametrus*, *S. gravimanus* and *S. yaleensis*. The prominent spiniform granule of the patella proventral carina is present (figs. 161, 166, 171, 176, 181, 186, 190) in *Heterometrus* but absent in all the other genera. The patella dorsal, retrodorsal, and retroventral intercarinal surfaces of the female are smooth or nearly so (figs. 161, 190) in *Heterometrus* but granular in all species of *Chersonesometrus* except *C. nathanorum*. The pedipalp chela of the adult male is sparsely setose (figs. 162, 167B, 168, 172, 177B–D, 182B, 183, 187B, 188, 191A) in *Heterometrus* but moderately to densely setose in *Sahyadrimetrus*, all species of *Deccanometrus* except *D. xanthopus*, one species of *Srilankametrus*, and some species of *Chersonesometrus*. The distance between the chela manus dorsomedian and promedian carinae or setal rows (DMC–PMC) is similar to the distance between the promedian and proventral carinae or setal rows (PMC–PVC) in *Heterometrus* whereas the DMC–PMC is slightly to markedly greater than the PMC–PVC in all other genera. The dorsomedian carina becomes obsolete proximally in *Heterometrus* but is continuous to the proximal edge of the manus in *Chersonesometrus*, *Gigantometrus*, and two species of *Deccanometrus*, *D. obscurus* and *D. phipsoni*. The chela manus dorsal secondary, subdigital, and digital carinae (setal rows) are well separated along their entire length in *Heterometrus* whereas the proximal half of the dorsal secondary carina,

distal half of the subdigital carina and distal third of the digital carina are closely adjacent in *Chersonesometrus* and *Gigantometrus*. The dorsal secondary and subdigital carinae of the male are absent or obsolete in *Heterometrus* but present and entirely to predominantly granular or costate in *Gigantometrus*, all species of *Chersonesometrus* except *C. bastawadei* and *C. fulvipes*, and all species of *Srilankametrus* except *S. indus* and *S. pococki*. The chela manus digital and retromedian carinae are similarly developed (figs. 162, 163, 167, 172, 173, 177, 182, 187, 191) in *Heterometrus* whereas the retromedian carina is more pronounced than the digital carina in *Chersonesometrus*. The retromedian carina of the male is absent or obsolete in *Heterometrus* but entirely to predominantly granular in *Gigantometrus*, *Srilankametrus caesar*, and *S. serratus*, and entirely to predominantly costate in *Chersonesometrus*, *Srilankametrus couzijni*, *S. gravimanus*, and *S. yaleensis*. The depression in the dorsal surface of the chela manus, proximal to the fixed finger of the adult male, is present and distinct (figs. 162, 167B, 172, 177B–D, 182B, 187B, 191A) in *Heterometrus* but absent or obsolete in all the other genera. The chela manus dorsal surface is without reticulation (figs. 172, 173, 177, 182, 187) in all except three species of *Heterometrus*, *H. glaucus*, *H. laevigatus*, and *H. thorellii*, in which the dorsal surface is shallowly reticulate (figs. 162, 163, 167, 191) as in *Javanimetrus*, *Sahyadrimetrus*, and all except two species of *Deccanometrus*, *D. obscurus* and *D. phipsoni*; the dorsal surface is smooth in *Heterometrus* but finely to coarsely granular in *Chersonesometrus*, *Gigantometrus*, *Srilankametrus*, all species of *Deccanometrus* except *D. ubicki*, and all except two species of *Sahyadrimetrus*, *S. kanarensis* and *S. tikaderi*. The chela manus retrolateral intercarinal surfaces are smooth or nearly so in *Heterometrus* but granular in *Chersonesometrus*, *Gigantometrus*, *Srilankametrus*, all species of *Deccanometrus* except *D. ubicki*, and some species of *Sahyadrimetrus*. The chela manus ventral surface is flat, with the axes of the retroventral and ventromedian carinae in approximately the same plane in *Heterometrus*

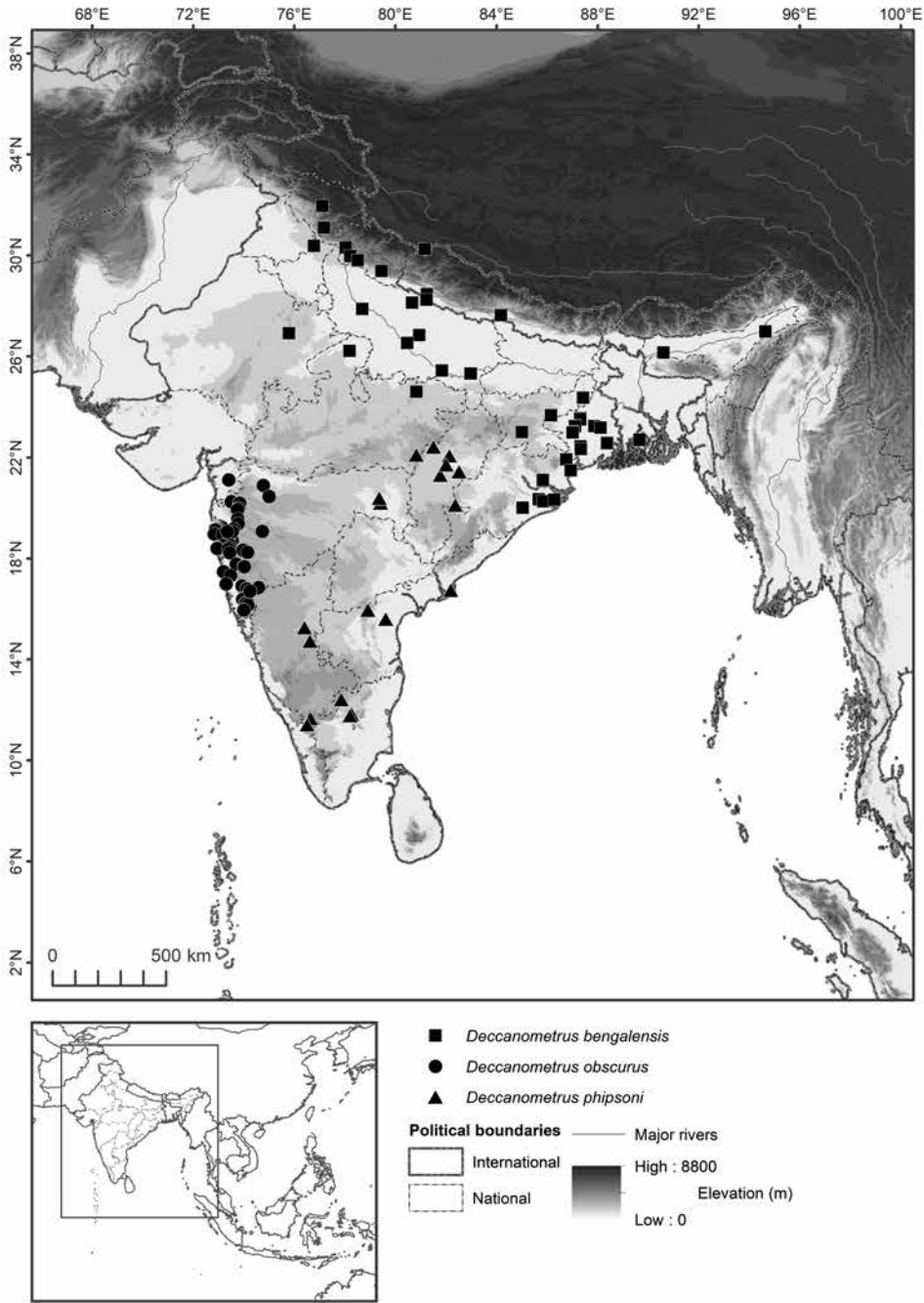


FIGURE 117. Map of South Asia, plotting known locality records of two species of *Deccanometrus*, gen. nov., based on material examined, and verified records from virtual museums and the literature: *Deccanometrus bengalensis* (C.L. Koch, 1841), comb. nov.; *Deccanometrus obscurus* (Couzijn, 1981), comb. et stat. nov.; *Deccanometrus phipsoni* (Pocock, 1893), comb. nov.

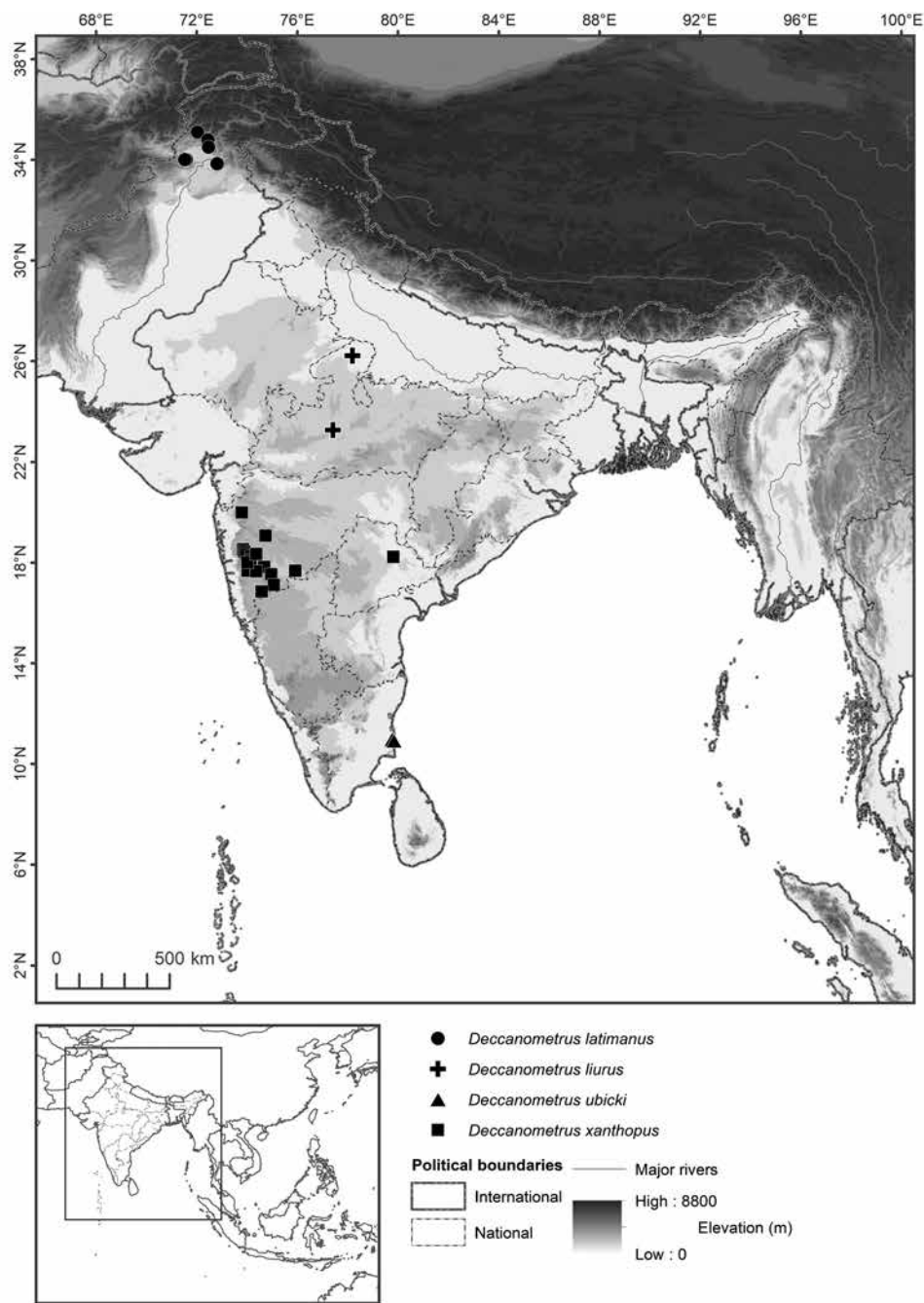


FIGURE 118. Map of South Asia, plotting known locality records of four species of *Deccanometrus*, gen. nov., based on material examined, and verified records from virtual museums and the literature: *Deccanometrus latimanus* (Pocock, 1894), comb. nov.; *Deccanometrus liurus* (Pocock, 1897), comb. nov.; *Deccanometrus ubicki* (Kovářík, 2004), comb. nov.; *Deccanometrus xanthopus* (Pocock, 1897), comb. nov.

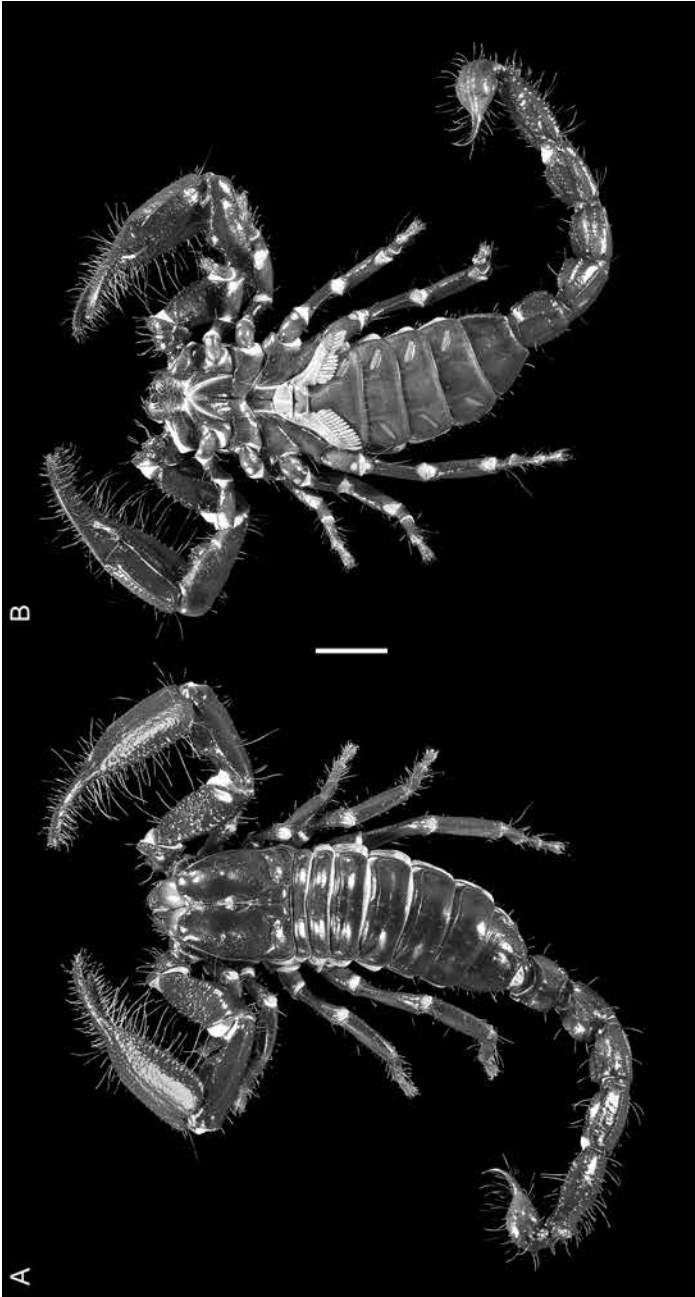


FIGURE 119. *Deccanometrus bengalensis* (C.L. Koch, 1841), comb. nov., ♂ (AMNH), Rangamatia, India, habitus: **A**, dorsal and **B**, ventral aspects. Scale bar = 10 mm.

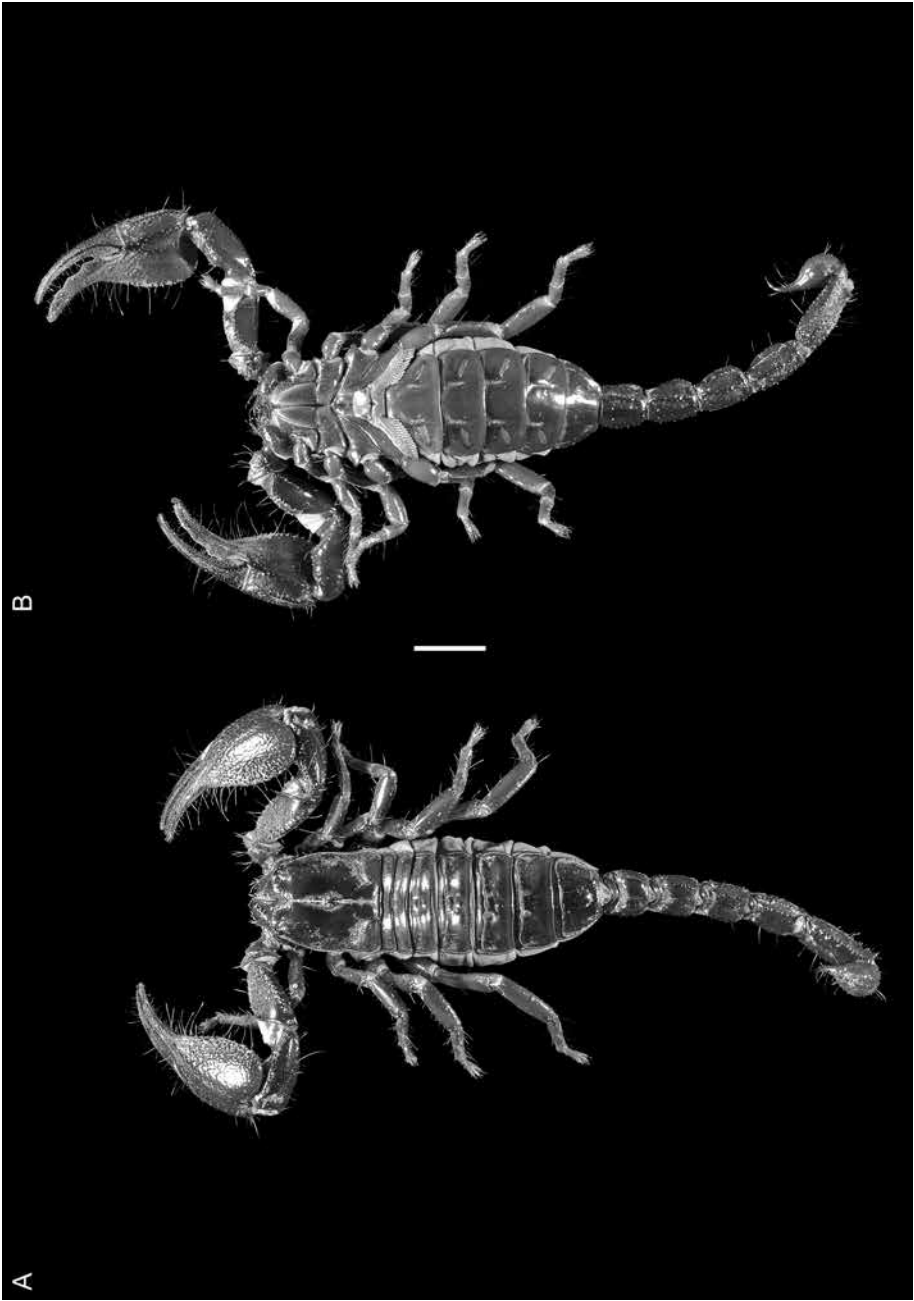


FIGURE 120. *Deccanometrus bengalensis* (C.L. Koch, 1841), comb. nov., ♀ (CAS 9071133), habitus: **A.** dorsal and **B.** ventral aspects. Scale bar = 10 mm.

but angled, with the axis of the retroventral carina ventral to the axis of the ventromedian carina in *Javanimetrus*, four species of *Chersonesometrus*, *C. beccaloniae*, *C. hendersoni*, *C. pelekomanus*, and *C. tristis*, and two species of *Srilankametrus*, *S. indus* and *S. pococki*. The pro- and retrolateral surfaces of the tibiae of legs I and II each bear scattered, setiform macrosetae, not arranged in a definite row, in *Heterometrus* and a row of two or three spiniform macrosetae in all the other genera. Macroseta *st* on the retroventral surface of the basitarsus of leg I is usually setiform (figs. 50–52, 53A–D) in *Heterometrus* but spiniform in all the other genera, and *sb* on the retroventral surface of the basitarsus of leg III is often setiform in *Heterometrus* but spiniform in *Javanimetrus* and *Sahyadrimetrus*. The pseudonychium (dactyl) of the telotarsi of legs I–IV is prominent and acuminate in *Heterometrus* but usually reduced and rounded in the other genera. The pectinal first proximal median lamella (scape) of the female is distinctly angular, $> 90^\circ$ but $< 180^\circ$ (figs. 36–38) in *Heterometrus* but straight or shallowly curved in *Srilankametrus*. The mesial surfaces of mesosomal tergites I–VI of the male are smooth in *Heterometrus*, but granular in *Gigantometrus*, one species of *Deccanometrus*, *D. xanthopus*, two species of *Sahyadrimetrus*, *S. mathewi* and *S. scaber*, and some species of *Chersonesometrus*. The lengths of metasomal segments I and II are approximately equal to or less than their respective widths (figs. 67C–E, 69C–E, 70A–D, 72A–D) in *Heterometrus* but markedly greater than their respective widths in *Gigantometrus*. The ventro-submedian and ventrolateral carinae are granular or costate-granular on metasomal segment IV only and costate on segments I–III (figs. 68C–E, 69C–E, 71B, D, 72B, D) in all except two species of *Heterometrus*, *H. laoticus* and *H. silenus*, in which the carinae are granular on segments I–IV, II–IV (costate on I), or III and IV (costate on I and II) (figs. 71A, C, 72A, C), as in *Gigantometrus*. The ventral intercarinal surfaces of metasomal segment IV are usually smooth (figs. 69C–E, 72A–D) in *Heterometrus* but sparsely granular in *Javanimetrus*. The dorsosubmedian

carinae of metasomal segment V are absent (figs. 67C–E, 70A–D) in *Heterometrus* but vestigial or partial in all other genera. The dorsal intercarinal surface of segment V is smooth in *Heterometrus* but granular in *Gigantometrus*, and some species of *Chersonesometrus* and *Srilankametrus*. The width of the telson vesicle is approximately equal to or less than the width of metasomal segment V in the female of *Heterometrus* but greater than the width of segment V in the female of *Gigantometrus* and the vesicle is elongate in *Heterometrus* but globose in *Chersonesometrus*, *Deccanometrus*, *Gigantometrus*, and three species of *Srilankametrus*, *S. indus*, *S. pococki*, and *S. serratus*.

INCLUDED SPECIES: As redefined in the present contribution, *Heterometrus* accommodates eight species formerly assigned to the nominotypical subgenus by various authors (Couzijn, 1981; Tikader and Bastawade, 1983; Fet, 2000), that were recovered as a monophyletic group by phylogenetic analysis of morphological characters and DNA sequences from the nuclear and mitochondrial genomes (fig. 10): *Heterometrus glaucus* (Thorell, 1876), comb. nov. et stat. rev.; *Heterometrus laevigatus* (Thorell, 1876), comb. nov. et stat. rev.; *Heterometrus laoticus* Couzijn, 1981; *Heterometrus longimanus* (Herbst, 1800); *Heterometrus petersii* (Thorell, 1876); *Heterometrus silenus* (Simon, 1884), comb. nov. et stat. rev.; *Heterometrus spinifer* (Ehrenberg, 1828); *Heterometrus thorellii* (Pocock, 1892).

DISTRIBUTION: The genus *Heterometrus* is distributed throughout Southeast Asia (figs. 5, 157, 158), from the Andaman and Nicobar Islands, throughout Indochina, the Thai-Malay Peninsula and offshore islands (Ko Chang, Ko Lanta, Ko Muk, Ko Samui, Langkawi, the Myeik archipelago, Penang, the Phi Phi Islands, Phuket, Phú Quoc Island, Tioman, Tinggi and Singapore), the Riau archipelago, Sumatra, Weh, Simeulue, Babi, Nias, the Batu archipelago, Siberut, the Mentawai archipelago, Bangka, Belitung, Java, Madura, Bali, Borneo, Miang-Besar, and the Philippine islands of Balabac, Mindanao, Luzon, Palawan, Panay, and Tawi Tawi in the

Sulu archipelago, to Wallace's Line (table 2). Reports of *Heterometrus* from the Indonesian islands of Sulawesi and Halmahera (Meise, 1932: 662; Takashima, 1945: 90), to the east of Wallace's Line, have never been confirmed (Couzijn, 1981: 175). The genus has been recorded from the following countries: Brunei, Cambodia, India, Indonesia, Laos, Malaysia, Myanmar, the Philippines, Singapore, Thailand and Vietnam. Its distribution overlaps with that of *Javanimetrus* in Borneo, Luzon, Nias, the Nicobar Islands, Sumatra, and Thailand.

ECOLOGY: *Heterometrus* species occur in primary and secondary evergreen rainforests, deciduous and semideciduous forests, plantations, agricultural fields, and backyards, from sea level to 1315 m elevation. Most species of the genus are fossorial and pelophilous, although some appear to be lapidicolous or corticolous (Prendini, 2001b). Whereas some *Heterometrus* were collected under stones or logs during daytime, most were collected with UV detection or flashlights at night, doorkeeping at or near burrow entrances, or walking on the ground after rains. Many *Heterometrus* appear to vacate their burrows during the monsoon season.

In several species of *Heterometrus*, e.g., *H. longimanus* and *H. spinifer*, mixed age groups of related and unrelated individuals cohabit with minimal aggression or cannibalism in laboratory terraria (Harrison, 1954; Polis and Lourenço, 1986) and, according to some evidence, this also occurs in the wild (Schultze, 1927).

CONSERVATION STATUS: Several species of *Heterometrus* are extensively harvested for the commercial trade in exotic pets. The most commonly traded species are *H. silenus*, apparently exported from Vietnam and, to a lesser extent, *H. spinifer*, exported from Malaysia, and *H. petersii*, exported from Malaysia and Singapore. *Heterometrus spinifer* is now protected in Malaysia. *Heterometrus laevigatus* and *H. laoticus* are occasionally available, apparently exported from Thailand, where *H. laoticus* is also harvested for consumption (Menzel and D'Aluisio, 1998).

Heterometrus glaucus (Thorell, 1876),
comb. nov. et stat. rev.

Figures 10, 22A, B, 36A, B, 52A–D, 67C, 68C,
69C, 157, 159–163, table 2

Palamnaeus costimanus var. γ *glaucus* Thorell,
1876b: 219–221 (part).

Palamnaeus liophysa: Thorell, 1890: 90–94, 1049,
figs. 1–4 (misidentification, part).

Scorpio longimanus liophysa: Kraepelin, 1894: 35,
36, 41 (misidentification).

Heterometrus liophysa: Kraepelin, 1899: 108, 112
(misidentification); Werner, 1916: 91 (mis-
identification); Lampe, 1918: 198 (misiden-
tification); Kopstein, 1921: 118, 119,
131–133; 1923: 184, 186, 187 (misidentifica-
tion, part); 1929: 124 (misidentification);
Giltay, 1931: 18; Takashima, 1945: 91 (part);
Kovařík, 2004: 1, 2, 21–23, 51, 53, table 2,
fig. 17 (misidentification, part); 2009: 35, 40,
48, 49, 83, 99, table 1, figs. 71–76, 192, 193
(misidentification, part).

Heterometrus liophysa var. *madoerensis* Kopstein,
1921: 119, 132, 133; syn. nov.

Heterometrus liophysa liophysa: Giltay, 1931: 9.

Heterometrus liophysa madoerensis: Giltay, 1931:
9, 18; Kovařík, 2004: 23.

Heterometrus laevifrons Roewer, 1943: 227–229,
pl. 4, fig. 8a–c; Kovařík, 2004: 23; 2009: 40;
syn. nov.

Heterometrus (Heterometrus) bengalensis:

Couzijn 1981: 38, 73, 75–77, 80, 85, 88, 89,
117–120, 182, 184, 191, table 7, figs. 17b, 18,
19, 21, 66b (misidentification, part).

Heterometrus (Heterometrus) liophysa: Couzijn,
1981: 80, 116–118, 173, 177, 178, 182, 184,
189, 190, figs. 21, 62, 65, 66b, 71 (misidenti-
fication, part); Kovařík, 1998: 137; Fet, 2000:
433 (part); Kovařík, 2002: 17
(misidentification).

Heterometrus (Heterometrus) liophysa laevifrons:
Couzijn, 1981: 37, 86, 88, 113–115, 177, 191,
table 7, figs. 33, 65; Kovařík, 1998: 137; Fet,
2000: 433; Kovařík, 2002: 17.

Heterometrus (Heterometrus) liophysa liophysa

Couzijn, 1981: 37, 86, 88, 111–116, 177, 191, table 7, figs. 32, 65 (misidentification, part); Fet, 2000: 433 (part).

Heterometrus (Heterometrus) liophysa separatus

Couzijn, 1981: 22, 38, 86, 115, 116, 177, 191, table 7, figs. 4b, 65; Kovařík, 1998: 137; Fet, 2000: 433, 434; syn. nov.

Heterometrus (Heterometrus) liophysa spartanicus

Couzijn, 1981: 37, 86, 88, 115, 177, 191, table 7, fig. 65; Kovařík, 1998: 137; Fet, 2000: 434; syn. nov.

Heterometrus (Heterometrus) madoerensis

Couzijn, 1981: 22, 38, 80, 85, 88, 89, 116, 117, 173, 177, 178, 182, 184, 189–191, table 7, figs. 4e, 21, 62, 66b, 71; Kovařík, 1998: 137; Fet, 2000: 436.

Heterometrus bengalensis: Kovařík, 2004: 7, 9 (part); 2009: 34 (part).

Heterometrus liophysa separatus: Kovařík, 2004: 23; 2009: 40, 41, 83, figs. 73, 74.

Heterometrus liophysa spartanicus: Kovařík, 2004: 23; 2009: 40.

Heterometrus madoerensis: Kovařík, 2004: 23.

Heterometrus longimanus: Kovařík, 2009: 40, 41 (misidentification, part).

TYPE MATERIAL: *Palamnaeus costimanus* var. γ *glaucus*: Lectotype [here designated]: 1 ♀ (NMG 88), “Bengal,” 7.viii.1868, G. Litman [examined]. **INDONESIA: Aceh Prov.: Sabang City Reg.:** *Heterometrus (H.) liophysa separatus*: Holotype ♂, paratype ♀ (RMNH 185), Poeloe Weh [Pulau Weh, 05°49'N 95°18'E], 1919, P. Buitendijk [examined]. *Simeulue Reg.:* *Heterometrus (H.) liophysa spartanicus*: Holotype: 1 subad. ♂ (RMNH 187), Poeloe Babi [Babi Island, 02°05'N 96°39'E], W coast of Sumatra, ii.1908, P. Buitendijk [examined]. **East Java Prov.:** *Heterometrus liophysa* var. *madoerensis*: Holotype: 1 juv. ♀ (RMNH 188), Madoera [Madura, 07°00'S 113°20'E], v.1910, P. Buitendijk [examined]. **West Sumatra Prov.: Mentawai Islands Reg.:** *Heterometrus laevifrons*: Holotype: 1 juv. ♂, paratype: 1 juv. ♀ (SMF

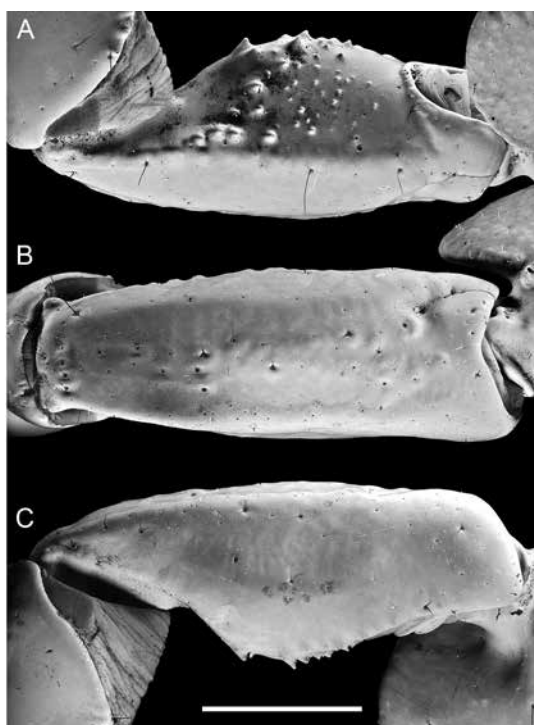


FIGURE 121. *Deccanometrus bengalensis* (C.L. Koch, 1841), comb. nov., ♂ (BMNH 1913.1.6.3), pedipalp patella: A. dorsal, B. retrolateral, and C. ventral aspects. Scale bar = 5 mm.

8883/225), Mentawai Islands, Siberut [Siberoet Island, 01°20'S 98°55'E] [examined]. *Padang Pariaman Reg.:* *Heterometrus (H.) liophysa*: Neotype ♂ (RMNH 78), Padang, Sumatra, J. van den Hoeven [examined].

Thorell (1876b) based *Palamnaeus costimanus* var. γ *glaucus* on two female syntypes, allegedly from Bengal, and did not specify a type. However, Couzijn (1981: 117, 118) referred to one of the specimens as the “type”: “Bengal (2 ♀ ad. including type of *P. costimanus glaucus* Thorell, NMG Scorp. 88).” Fet (2000: 432) correctly listed “Syntypes: 2 ♀ (NMG Scorp. 88), Bengal, India.” Examination of the types during the present investigation revealed that the two specimens are not conspecific. The specimen erroneously labelled “Holotype” by H.W.C. Couzijn is conspecific with *H. longimanus*, the specimen labelled “Paratype” with the species formerly referred to as *H. liophysa*



FIGURE 122. *Deccanometrus bengalensis* (C.L. Koch, 1841), comb. nov., pedipalp chela: A, B. retrodorsal, C. ventral, and D. prolateral aspects. A. ♀ (BMNH 1896.8.15.4). B–D. ♂ (BMNH 1913.1.6.3). Scale bar = 5 mm.

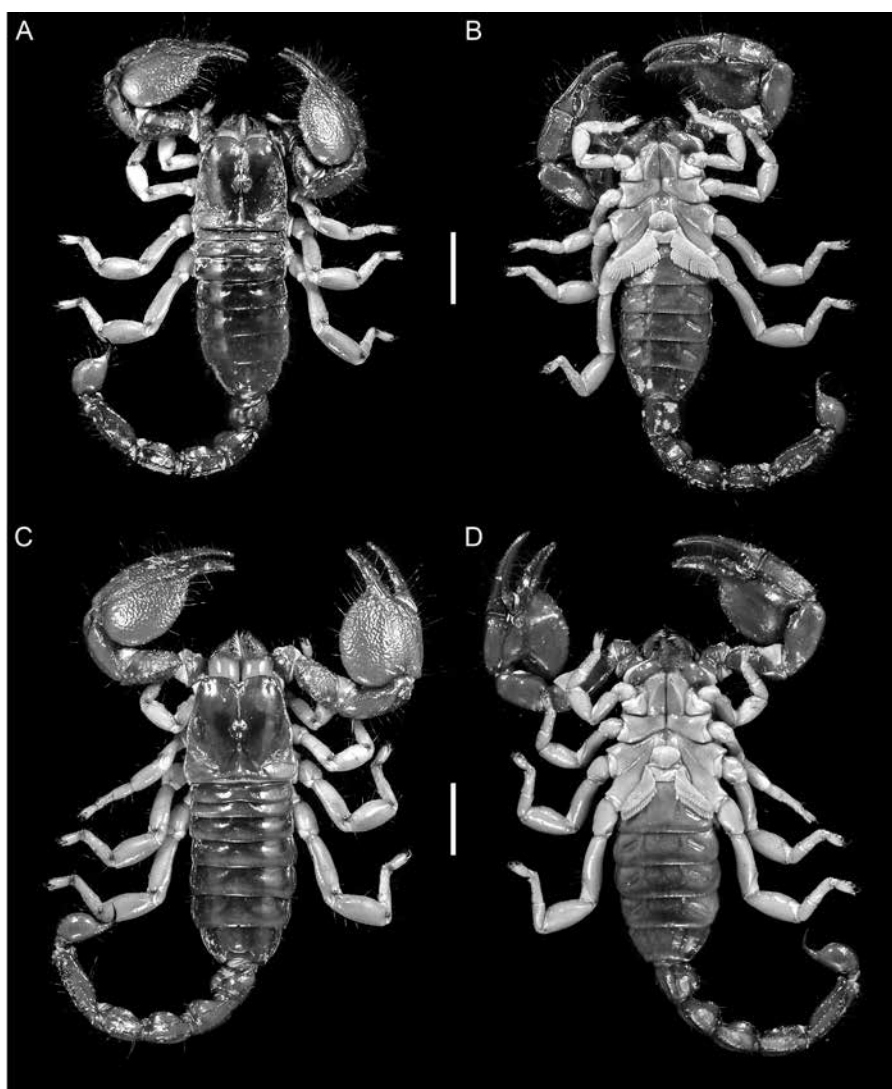


FIGURE 123. *Deccanometrus latimanus* (Pocock, 1894), comb. nov., habitus: **A**, **C**. dorsal and **B**, **D**. ventral aspects. **A**, **B**. ♂ (AMNH), **C**, **D**. ♀ (AMNH), Daggar, Pakistan. Scale bars = 10 mm.

(Couzijn, 1981; Fet, 2000; Kovařík, 1998, 2002, 2004, 2009). These two species appear to be sympatric in some areas, e.g., western Sumatra, and may have been collected at the same locality. H.L. Stahnke, who examined the specimens at an unspecified date (possibly 1962), also concluded that the two specimens were heterospecific. Stahnke labelled Couzijn's "Holotype" with number 62-579 and the determination "*Heterometrus [spinifer] spinifer* H&E"; Couzijn's "Paratype" was

labelled with number 62-580 and the determination "*Heterometrus [spinifer] liophysa costamanus* Koch." The specimen numbered 62-580 is hereby designated the lectotype of *H. glaucus*, fixing the name of the species, whereas the specimen numbered 62-579, and conspecific with *H. longimanus*, is designated the paralectotype.

Roewer (1943: 229) listed the collection data for the type of *H. laevifrons* as follows: "Mentawai-Inseln: Siberut – 2 ♀ ... Typus und Paratyp-

oid: Senck.-Mus. (Coll. Roewer) Nr. 8883/225." Couzijn (1981: 114) listed the data as: "Mentawai islands, Siberut (1 ♀ juv. holotype, 1 ♂ juv. allotype, leg. unknown, SMF II/883/225)." Fet (2000: 433) listed the data as follows: "Holotype: juv. ♀ (SMF/88/225), Saibi Siberut Island, Mentawai Islands, Indonesia. Paratype: juv. ♂ (SMF II/88/225; allotype), same locality as holotype."

DIAGNOSIS: *Heterometrus glaucus* may be separated from other species of *Heterometrus* as follows. The frontal lobes and medial region of the carapace interocular surface are granular with smooth areas in the male and female (fig. 22A, B) of *H. glaucus* whereas the interocular surface is granular along the median longitudinal and anterior bifurcated sulci only in the female of *H. laevigatus* and the male and female of *H. longimanus*, *H. petersii*, *H. silenus*, and *H. spinifer*, and the interocular surface is entirely smooth in the male of *H. laevigatus* and the male and female *H. laoticus*. The carapace anterolateral, mediolateral, and posterolateral surfaces of the female (fig. 22B) are granular in *H. glaucus* but smooth or nearly so in *H. laoticus*, and the posterolateral surfaces of the female smooth or nearly so in *H. longimanus*. The pedipalps of the adult male are long, with femur length : posterior carapace width ratio (FL:PCW) ≥ 0.80 and femur length : carapace length ratio (FL:CL) ≥ 0.76 (fig. 159) in *H. glaucus* but short, with FL:PCW < 0.77 , FL:CL < 0.74 in *H. laoticus*, *H. petersii*, *H. silenus* and *H. spinifer*. The pedipalp chela manus promedian carina of the female (fig. 163) is present and granular in *H. glaucus* but absent or obsolete in *H. laevigatus*. The maximum distance between the dorsomedian and dorsal secondary carinae (DMC–DSC) of the chela manus is less than the maximum distance between the dorsal secondary and digital carinae (DSC–DC) in the male (fig. 162) and similar to the DSC–DC in the female (fig. 163) of *H. glaucus* whereas the DMC–DSC is greater than the DSC–DC in the male of *H. silenus*, similar to the DSC–DC in the male of *H. laoticus*, *H. petersii* and *H. spinifer*, and less than the DSC–DC in the female of *H. longimanus*. The chela manus dorsal intercarinal surface is shallowly reticulate (figs. 162, 163) in *H. glaucus*

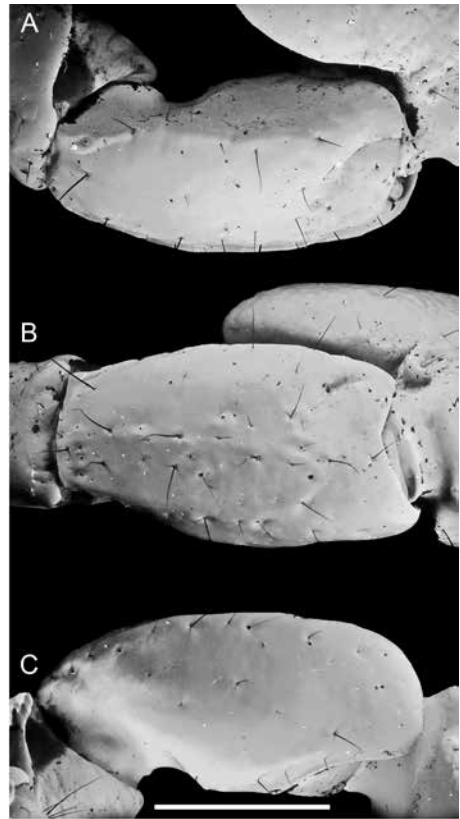


FIGURE 124. *Deccanometrus latimanus* (Pocock, 1894), comb. nov., ♀ (AMNH), Daggar, Pakistan, pedipalp patella: A. dorsal, B. retrolateral, and C. ventral aspects. Scale bar = 5 mm.

but smooth or nearly so in all other species except *H. laevigatus* and, often, *H. thorellii*. The second (subproximal) lobe of the chela movable finger of the adult male (fig. 162) is similar to or barely larger than other lobes on the finger in *H. glaucus* but more strongly developed than other lobes on the finger, with a correspondingly well-developed notch in the fixed finger in all other species except *H. longimanus* and *H. thorellii*. Macroseta *st* on the proventral surface of the basitarsus of leg I is setiform (fig. 52A) in *H. glaucus* but spiniform in *H. laevigatus* and *H. thorellii*; *st* on the proventral surface of the basitarsus of leg II is spiniform (fig. 52B) in *H. glaucus* but setiform in all other species except *H. laevigatus*, *H. thorellii* and, usually, *H. longimanus*; *sb* on the proventral surface of the

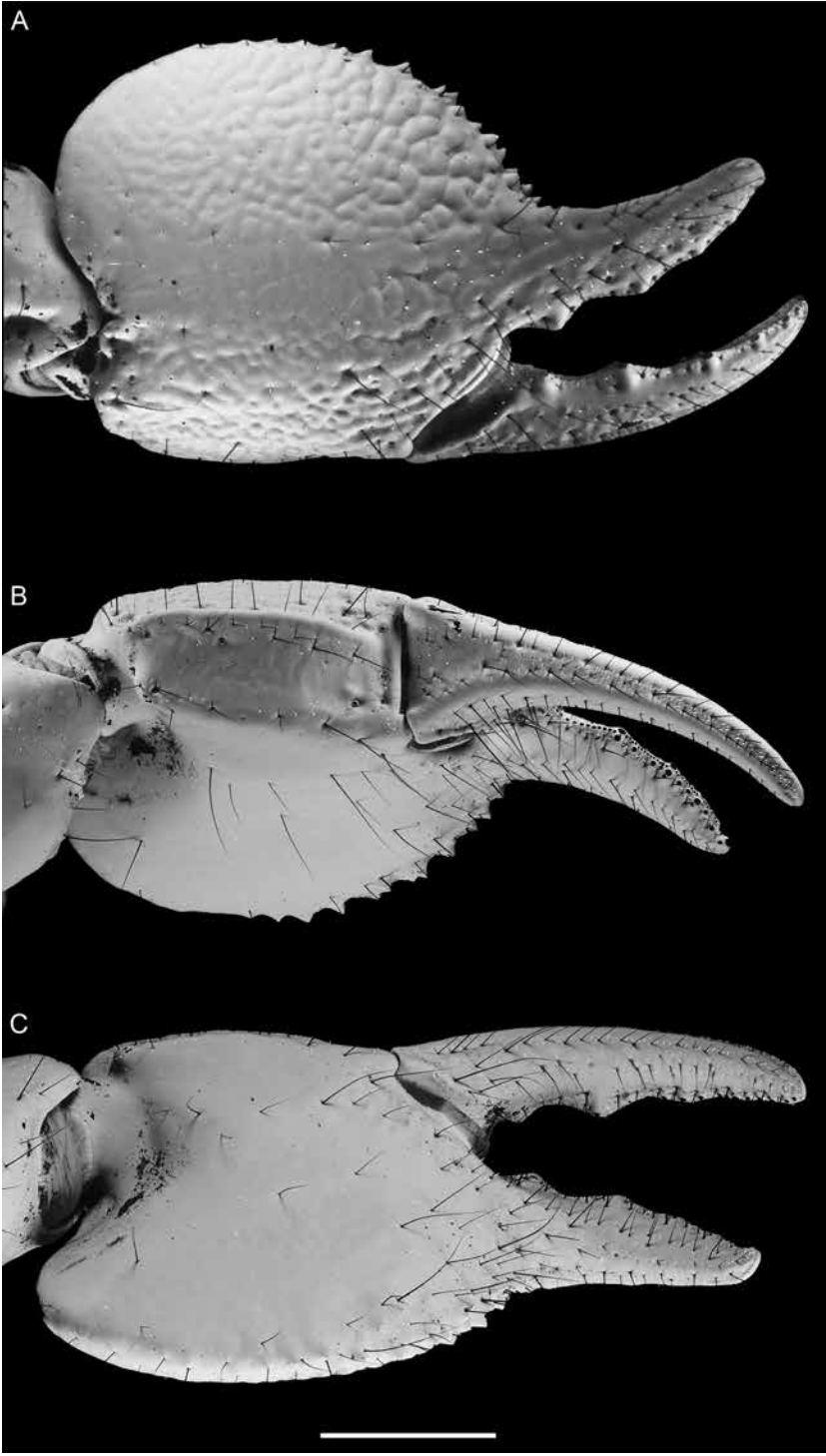


FIGURE 125. *Deccanometrus latimanus* (Pocock, 1894), comb. nov., ♂ (AMNH), Daggar, Pakistan, pedipalp chela: **A.** retrodorsal, **B.** ventral, and **C.** prolateral aspects. Scale bar = 5 mm.



FIGURE 126. *Deccanometrus latimanus* (Pocock, 1894), comb. nov., ♀ (AMNH), Daggar, Pakistan, pedipalp chela: A. retrodorsal, B. retrolateral, C. ventral, and D. prodorsal aspects. Scale bar = 5 mm.

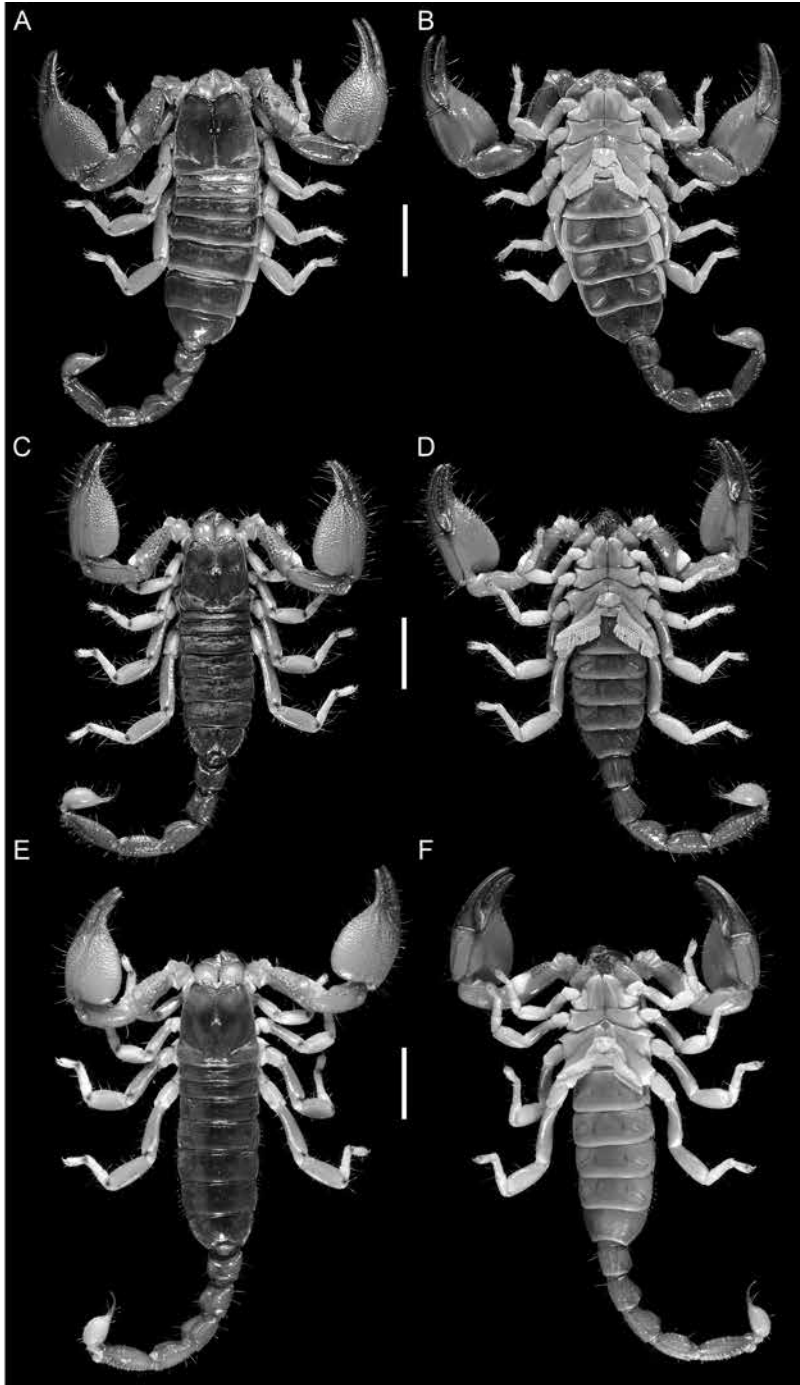


FIGURE 127. *Deccanometrus*, gen. nov., habitus: **A**, **C**, **E**, dorsal and **B**, **D**, **F**, ventral aspects. **A**, **B**. *Deccanometrus liurus* (Pocock, 1897), comb. nov., paralectotype ♀ (BMNH 1896.12.15.20-25). **C**–**F**. *Deccanometrus xanthopus* (Pocock, 1897), comb. nov., **C**, **D**. ♂ (AMNH), **E**, **F**. ♀ (AMNH), Khambatki Ghat, India. Scale bars = 10 mm.

basitarsus of leg III is spiniform (fig. 52C) in *H. glaucus* but setiform in all other species except *H. petersii* and *H. spinifer*. The lateral surfaces of mesosomal tergites I–VI in the female (fig. 160A) are granular in *H. glaucus* but smooth in *H. laevigatus*, *H. laoticus*, and *H. thorellii*. The ventrosubmedian and ventrolateral carinae of metasomal segments I–IV are granular or costate-granular on segment IV only and costate on segments I–III (fig. 69C) in *H. glaucus* but granular on segments I–IV, II–IV (costate on I), or III and IV (costate on I and II) in *H. laoticus* and *H. silenus*. The ventral intercarinal surfaces of segments III and IV of the female (fig. 69C) are smooth in *H. glaucus* but granular in *H. laoticus*. The telson is dark reddish brown and paler than metasomal segment V in *H. glaucus* (figs. 159, 160) but blackish and as dark as segment V in *H. laevigatus*, *H. laoticus*, *H. silenus*, and *H. thorellii*. The width of the telson vesicle is greater than the width of metasomal segment V in the male of *H. glaucus* but approximately equal to or less than the width of segment V in the male of all other species except *H. longimanus*. Additionally, the ventral surface of the telson vesicle is usually completely smooth in *H. glaucus*, whereas granular rows are present, at least anteroventrally, on the vesicle of other species of the genus.

DISTRIBUTION: *Heterometrus glaucus* occurs in the Nicobar Islands of India (recorded from Great Nicobar) and the Indonesian islands of Sumatra (mostly in the Barisan Mountains along the western margin of the island in the provinces of Aceh, North Sumatra, and West Sumatra), Weh, Simeulue, Babi, Nias, Siberut, the Batu archipelago, and the Mentawai archipelago (fig. 157, table 2). Its distribution overlaps that of *H. longimanus* in Sumatra and the Simeulue Islands. The presence of this species on Madura (type locality of the junior synonym, *H. liophysa* var. *madoerensis*) is doubtful, given “the long distance between Madura and the distributional area of *H. liophysa* on W Sumatra and the islands along the coast” previously noted by Couzijn (1981: 117).

ECOLOGY: *Heterometrus glaucus* has been recorded in primary and secondary rainforests at elevations of 20–120 m above sea level. Specimens

were observed with UV detection at night, doorkeeping from burrow entrances in earthen walls or near the bases of trees. It is unclear whether this species constructs its own burrows or inhabits the burrows of other animals. The habitat and habitus are consistent with the lapidicolous and corticolous ecomorphotypes (Prendini, 2001b).

REMARKS: Couzijn (1981: 117) examined the syntypes of *Palamnaeus costimanus* var. γ *glaucus*, allegedly from “Bengal,” and synonymized the taxon with *H. (H.) bengalensis*. Fet (2000: 432) and Kovařík (2004: 7) followed Couzijn (1981). Reexamination of the types during the present investigation demonstrated that they are neither conspecific with one another nor with *D. bengalensis*, however. The lectotype, here designated, is conspecific with the species formerly referred to as *H. liophysa* (Couzijn, 1981; Fet, 2000; Kovařík, 1998, 2002, 2004, 2009). However, as discussed further below, the types of *Palamnaeus liophysa*, thought to be lost and not examined by Couzijn (1981) or Kovařík (2004), were rediscovered and examined during the present investigation, revealing *P. liophysa* to be a junior synonym of *H. longimanus*. As the name *P. costimanus* var. γ *glaucus* is available and has priority, it is hereby revalidated. The name is henceforth cited as *H. glaucus*, for the following reasons:

First, Thorell (1888) published the name as *Palamnaeus costimanus* var. γ *glaucus*. According to ICZN Article 11.2, a scientific name must, when first published, have been spelled only in the 26 letters of the Latin alphabet and, according to Article 11.9.1, a species group name must be a word of two or more letters. The Greek letter “ γ ” fulfills neither of these requirements. Even if transliterated to “gamma,” that was not the original spelling. Therefore, the name “gamma” is unavailable.

Second, according to ICZN Article 45.6.4, varietal names published before 1961 are available if determined to be subspecific, and a name is deemed subspecific if its author used the terms “variety” (including “var.”) or “form,” unless the author also expressly gave it infrasubspecific

rank, or the content of the work unambiguously reveals that the name was proposed for an infrasubspecific entity, in which case it is infrasubspecific. There is little doubt “*glaucus*” was intended as a subspecies of *P. costimanus*. The use of “ α , β , γ ,” etc. by Thorell (1888) and others of the time is not unlike how modern taxonomists might use “sp. 1, sp. 2, sp. a, sp. b” to sort apparent species into groups while working through unidentified material. Even today, some workers might publish such, sometimes with some characters, in a revision. For example, the name “*Pseudobledius* A, n. sp.” would not lead anyone to conclude that a new species was published.

Heterometrus laevifrons was relegated to a subspecies of *H. liophysa* by Couzijn (1981: 114), where it remained (Fet, 2000; Kovařík, 1998, 2002) until being synonymized with the latter by Kovařík (2004: 23). As the types of *H. laevifrons* are conspecific with the lectotype of *P. costimanus* var. γ *glaucus*, and not with the types of *P. liophysa*, Kovařík’s (2004) synonym is rejected and the following new synonym presented: *Heterometrus laevifrons* Roewer, 1943 = *Heterometrus glaucus* (Thorell, 1876), syn. nov.

Heterometrus liophysa var. *madoerensis*, based on an immature specimen allegedly from the island of Madura, Indonesia, was elevated to the rank of species by Couzijn (1981: 116) but subsequently synonymized with *H. liophysa* by Kovařík (2004: 23):

Couzijn (1981: 116) elevated *H. l. madoerensis* Kopstein, 1921 to species, although it is known only by an immature female from Madura (Indonesia). I have not been able to study this specimen, but I have seen many females of *H. cimrmani* sp. n., *H. liophysa*, *H. longimanus*, and *H. spinifer* and have to say that distinguishing these valid taxa on solitary, lest immature, females is very difficult and often impossible. For this reason, I place *H. madoerensis* in synonymy of *H. liophysa*.

The holotype of *H. liophysa* var. *madoerensis* was examined during the present investigation and determined to be conspecific with the lectotype of *P. costimanus* var. γ *glaucus*, rather than the types of *P. liophysa*. Kovařík’s (2004) synonym is therefore rejected and the following new synonym presented: *Heterometrus liophysa* var.

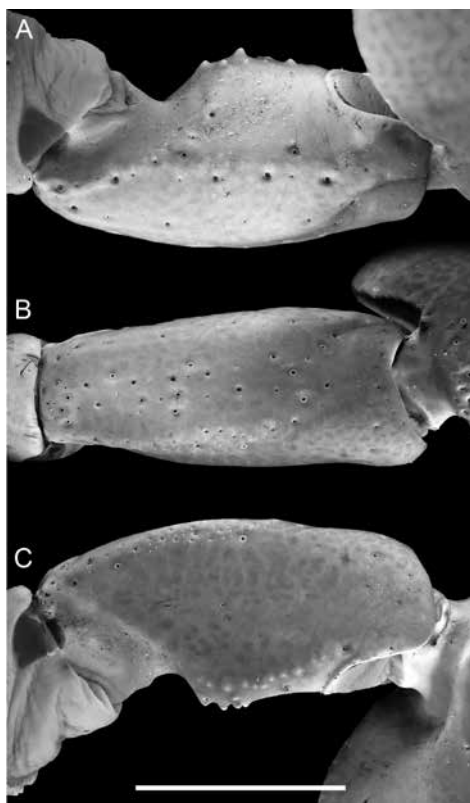


FIGURE 128. *Deccanometrus liurus* (Pocock, 1897), comb. nov., paralectotype ♀ (BMNH 1896.12.15.20-25), pedipalp patella: A. dorsal, B. retrolateral, and C. ventral aspects. Scale bar = 5 mm.

madoerensis Kopstein, 1921 = *Heterometrus glaucus* (Thorell, 1876), syn. nov.

Kovařík (2004: 23) was unable to verify the status of *H. (H.) liophysa separatus*, described from Pulau Weh near the northwest tip of Sumatra, Indonesia (Couzijn, 1981), but subsequently (Kovařík, 2009: 40) synonymized it with *H. longimanus*, noting that this “confirms a similarity of *H. liophysa* and *H. longimanus* so close that they invite the term sibling species.” Despite listing the holotype and allotype of *H. (H.) liophysa separatus* as material examined under *H. longimanus*, Kovařík (2009: 41, 83, figs. 73, 74) identified habitus photos of the female allotype of *H. (H.) liophysa separatus* as *H. liophysa*. During the present investigation, the types of *H. (H.)*



FIGURE 129. *Deccanometrus liurus* (Pocock, 1897), comb. nov., paralectotype ♀ (BMNH 1896.12.15.20-25), pedipalp pedipalp chela: A. retrodorsal, B. ventral, and C. prolateral aspects. Scale bar = 5 mm.

liophysa separatus were reexamined and found to be conspecific with the lectotype of *P. costimanus* var. γ *glaucus*. Kovařík's (2009) synonym is therefore rejected and the following new synonym presented: *Heterometrus* (*H.*) *liophysa separatus* Couzijn, 1981 = *Heterometrus glaucus* (Thorell, 1876), syn. nov.

Kovařík (2004: 23) was also unable to verify the status of *H. (H.) liophysa spartanicus*, based on a subadult male from Babi Island, between the islands of Simeulue and Nias, off the west coast of Sumatra (Couzijn, 1981). Kovařík (2009: 40) later synonymized it with *H. liophysa*, however, suggesting the differences that led Couzijn

(1981) to create the subspecies were “due to its immaturity.” As the types of *H. (H.) liophysa spartanicus* are conspecific with the lectotype of *P. costimanus* var. γ *glaucus*, and not with the types of *P. liophysa*, Kovařík's (2009) synonym is again rejected and the following new synonym presented: *Heterometrus (H.) liophysa spartanicus* Couzijn, 1981 = *Heterometrus glaucus* (Thorell, 1876), syn. nov.

MATERIAL EXAMINED: INDONESIA: 3 ♀ (BMNH). Sumatra, 1 ♂, 1 ♀ (AMNH [3178]), 1 ♂ (ZMH 3966), R. Weber, 1 ♀ (AMNH); Sumatra, W Coast, 1909, P. Serre, 1 ♀ (MNHN RS 3460). **Aceh Prov.:** *Sabang City Reg.:* Poeloe Weh [Pulau Weh, 05°49'N 95°18'E], 1919, P. Buitendijk, 2 ♂ [1 ♂ pedipalp chelae only], 1 ♀ (RMNH 185). *Simeulue Reg.:* Simalur Island (Simeuluë Island) [Simeulue Island, 02°35'N 96°05'E], 14–15.xii.1901, W.L. Abbott, 1 ♀ (USNM 57-110), 1 juv. (USNM 57-1109), xii.1901, W.L. Abbott, 1 ♀ (USNM), 2 ♀ (USNM 57-1083, 1084), 1 juv. (USNM 57-111). **North Sumatra Prov.:** Deli [Medan, 03°35'N 98°41'E], Sumatra, 1893, 1 ♀ (ZMH ex Mus. Leiden). *North Nias Reg.:* Nias [Nias Island, 01°05'N 97°35'E], Sumatra, P. Beyer, 1 ♀ (SMF 5322); Nias, Dr. Schrieber, 1 ♂, 1 ♀ (BMNH 1885.29), 1 ♂ (BMNH 1885.54); Pulo [Pulau] Nias Island, 24.iii.1903, W.L. Abbott, 1 ♀ (USNM 57-593); Nias Island, Alasa Village, 01°12'N 97°25'E, 136 m, 3.xi.2006, S.F. Loria and M. Roppo, in burrows, 3 ♀, 1 subad. ♀ (AMNH), 1 juv. ♂, 1 juv. ♀ (AMCC [LP 13922]); Afulu Retreat, 01°15'N 97°14'E, ca. 18 m, 2.xi.2006, S.F. Loria and M. Roppo, blacklight at night, in burrows, near bases of trees, 1 juv. ♂, 1 juv. ♀ (AMCC [LP 13928]). *Simalungun Reg.:* Dolok Merangis [Dolok Merangir, 03°07'N 99°07'E], E coast of Sumatra, 1932, W.H. Bangham, 1 ♂ (MCZ 103090), near Pematangsiantar [02°57'N 99°03'E], Sumatra, C.T. Brues, 2 ♂ (MCZ 103088). *South Tapanuli Reg.:* Bunga Bondar [01°39'N 99°20'E], W Sumatra, 1911, 1 ♂ (SMF 5323), 28.x.1911, Schütze, 1 ♂, 1 subad. ♂ (SMF 18158/2). **West Sumatra Prov.:** *Mentawai Islands Reg.:* Mentawai Islands, Siberut [Siberoet Island, 01°20'N 98°55'E], 1 juv. ♂, 1 juv. ♀ (SMF 8883/225); Siberut, Mentawai Islands, ix.1924, C.B. Kloss and N. Smedley, 1 ♂ pedipalp chelae, 1 subad. ♀ (LKC ZRC-ARA 778). *Padang Pariaman Reg.:* Padang [00°57'S 100°25'E], Sumatra, 2 juv. ♀ (SMF 5278), 20.ii.1908, Rolle, 1 ♂ (ZMH). *Pesisir Selatan Reg.:* Tarussan [Tarusan] Bay [01°13'S 100°25'E], W Sumatra, 25.xii.1904, W.L. Abbott, 1 ♂ (USNM

57-895), 29.xii.1904, W.L. Abbott, 1 ♀ (USNM 57-896), 18.i.1905, W.L. Abbott, 1 ♀ (USNM 57-815).

ERRONEOUS RECORD: Laos, 1884–1899, Neis, 2 ♂ (MNHN RS 0030).

Heterometrus laevigatus (Thorell, 1876),
comb. nov. et stat. rev.

Figures 7E, 9E, 10, 23A, B, 37A, B, 50A–D, 67D, 68D, 69D, 158, 164–168, table 2

Palamnaeus laevigatus Thorell, 1876b: 221, 222;
Keyserling, 1885: 39; Couzijn, 1981: 93.

Palamnaeus oatesii: Pocock, 1900a: 84, 98, 99
(misidentification, part).

Heterometrus longimanus angustimanus: Simon,
1901: 78 (misidentification).

Heterometrus longimanus thorelli: Simon, 1901:
78 (misidentification).

Heterometrus (Heterometrus) bengalensis:
Couzijn, 1981: 117–120, 173, 177, 178, 184,
190, figs. 62, 71 (part).

Heterometrus (Heterometrus) spinifer: Couzijn,
1981: 73, 80, 94, 96, 173, 175, 187, 189, 190,
figs. 21, 62 (misidentification, part); Fet,
2000: 437, 438 (part).

Heterometrus (Heterometrus) spinifer spinifer:
Couzijn, 1981: 19, 32, 75–77, 83, 89–93, 167,
174, 191, table 7, figs. 2b, 17b, 18, 19, 63 (mis-
identification, part); Kovařík, 1995: 203, 204
(misidentification, part); Fet, 2000: 438 (part).

Heterometrus cimrmani Kovařík, 2004: 1, 2, 7,
9–11, 23, 42, 51, 53 (part), tables 1, 2 (part),
fig. 11; 2009: 35, 36, 46, 48, 49, 75, 99, 102
(part), table 1 (part), figs. 14–19, 194, 195,
232–237; Booncham et al., 2007: 43; syn. nov.

Heterometrus laoticus: Kovařík, 2004: 20, 21
(misidentification, part).

Heterometrus spinifer: Kovařík, 2004: 9, 11, 23,
34, 40, 42, 51, 53, table 2 (misidentification,
part); 2009: 35, 44, 48, table 1 (part);
Booncham et al., 2007: 43 (part).

Heterometrus minotaurus Plíšková et al., 2016:
467–474, figs. 1–23; syn. nov.

TYPE MATERIAL: *Palamnaeus laevigatus*: Holotype: 1 subad. ♀ (NMG 90), “Nova Hollandia [Australia], Melbourne,” 11.ix.1860, G.E. Bothen [examined]. **THAILAND: Trang Prov.: Mueang Trang Distr.: Heterometrus cimrmani**: Holotype ♂, 5 ♀, 2 imm., 5 juv. paratypes, Trang env. [Trang, 07°34'N 99°37'E], paratype ♂ (FKPC), Trang env., 1980; paratype ♀ (FKPC), Trang, 20 km E, 1999, Komzík. **Na Yong Distr.: H. cimrmani**: Paratypes: 4 ♀ (FKPC), Khao Chong (Trang) [Khao Chong Wildlife Development and Conservation Promotion Station, 07°33'N 99°47'E], x.1998, V. Šejna, 1 juv. (FKPC), Trang-Kao Chong [Khao Chong Wildlife Development and Conservation Promotion Station], 10.ix.1993, M. Veselý. **Nakhon Si Thammarat Prov.: Mueang Nakhon Si Thammarat Distr.: H. cimrmani**: Paratype: 1 imm. ♀, Ban Huai Phan env. [Ban Huai, 08°29'N 99°51'E], 12.vi.1996, F. Kantner. **Satun Prov.: Khuan Don Distr.: H. cimrmani**: Paratype ♂ (FKPC), Thaleban [Thale Ban National Park, 06°43'N 100°10'E, 30 km SW near Satun, 20.ix.1993. **Surat Thani Prov.: Phanom Distr.: Heterometrus minotaurus**: Holotype ♂ (CUP-S651), 08°52'N 98°36'E, 395 m, trail along rubber plantation and water stream, 11.vii.2014, O. Košulič.

A single paratype ♀ of *H. cimrmani* in the FKPC, allegedly from Vietnam, is either mislabeled or misidentified (i.e., conspecific with *H. silenus*).

DIAGNOSIS: *Heterometrus laevigatus* may be separated from other species of *Heterometrus* as follows. The carapace interocular surface is entirely smooth in the male (fig. 23A), and granular along the median longitudinal and anterior bifurcated sulci only in the female (fig. 23B), of *H. laevigatus* whereas the interocular surface is granular along the median longitudinal and anterior bifurcated sulci only in the male of *H. longimanus*, *H. petersii*, *H. silenus*, and *H. spinifer*, the frontal lobes and medial region of the interocular surface are granular with smooth areas in the male and female of *H. glaucus* and *H. thorellii*, and the interocular surface is entirely smooth in the female of *H. laoticus*. The carapace anterolateral, mediolateral, and posterolateral surfaces of the female are granular (fig. 23B) in

H. laevigatus but smooth or nearly so in *H. laoticus*, and the posterolateral surfaces of the female smooth or nearly so in *H. longimanus*. The pedipalps of the adult male are long, with femur length : posterior carapace width ratio (FL:PCW) ≥ 0.80 and femur length : carapace length ratio (FL:CL) ≥ 0.76 (fig. 164) in *H. laevigatus* but short, with FL:PCW < 0.77 , FL:CL < 0.74 in *H. laoticus*, *H. petersii*, *H. silenus*, and *H. spinifer*. The pedipalp chela manus promedian carina of the female is absent or obsolete in *H. laevigatus* but present and granular in all other species. The maximum distance between the dorsomedian and dorsal secondary carinae (DMC–DSC) of the chela manus is less than the maximum distance between the dorsal secondary and digital carinae (DSC–DC) in the male (fig. 167B) and similar to the DSC–DC in the female (fig. 167A) of *H. laevigatus* whereas the DMC–DSC is greater than the DSC–DC in the male of *H. silenus*, similar to the DSC–DC in the male of *H. laoticus*, *H. petersii*, and *H. spinifer*, and less than the DSC–DC in the female of *H. longimanus*. The chela manus dorsal intercarinal surface is shallowly reticulate (fig. 167) in *H. laevigatus* but smooth or nearly so in all other species except *H. glaucus* and, often, *H. thorellii*. The second (subproximal) lobe of the chela movable finger of the adult male is more strongly developed than other lobes on the finger, with a correspondingly well-developed notch in the fixed finger (figs. 167B, 168) in *H. laevigatus* but similar to or barely larger than other lobes on the finger in *H. glaucus*, *H. longimanus*, and *H. thorellii*. Macroseta *st* on the proventral surface of the basitarsus of leg I is spiniform (fig. 50A) in *H. laevigatus* but setiform in all other species except *H. thorellii*; *st* on the proventral surface of the basitarsus of leg II is spiniform (fig. 50B) in *H. laevigatus* but setiform in all other species except *H. glaucus*, *H. thorellii*, and, usually, *H. longimanus*; *sb* on the proventral surface of the basitarsus of leg III is setiform (fig. 50C) in *H. laevigatus* but spiniform in *H. glaucus*, *H. petersii*, and *H. spinifer*. The lateral surfaces of mesosomal tergites I–VI in the female are smooth (fig. 165A) in *H. laevigatus* but granular in all other species except *H. laoticus* and *H. thorellii*. The ventro-submedian and ventrolateral carinae of metasomal

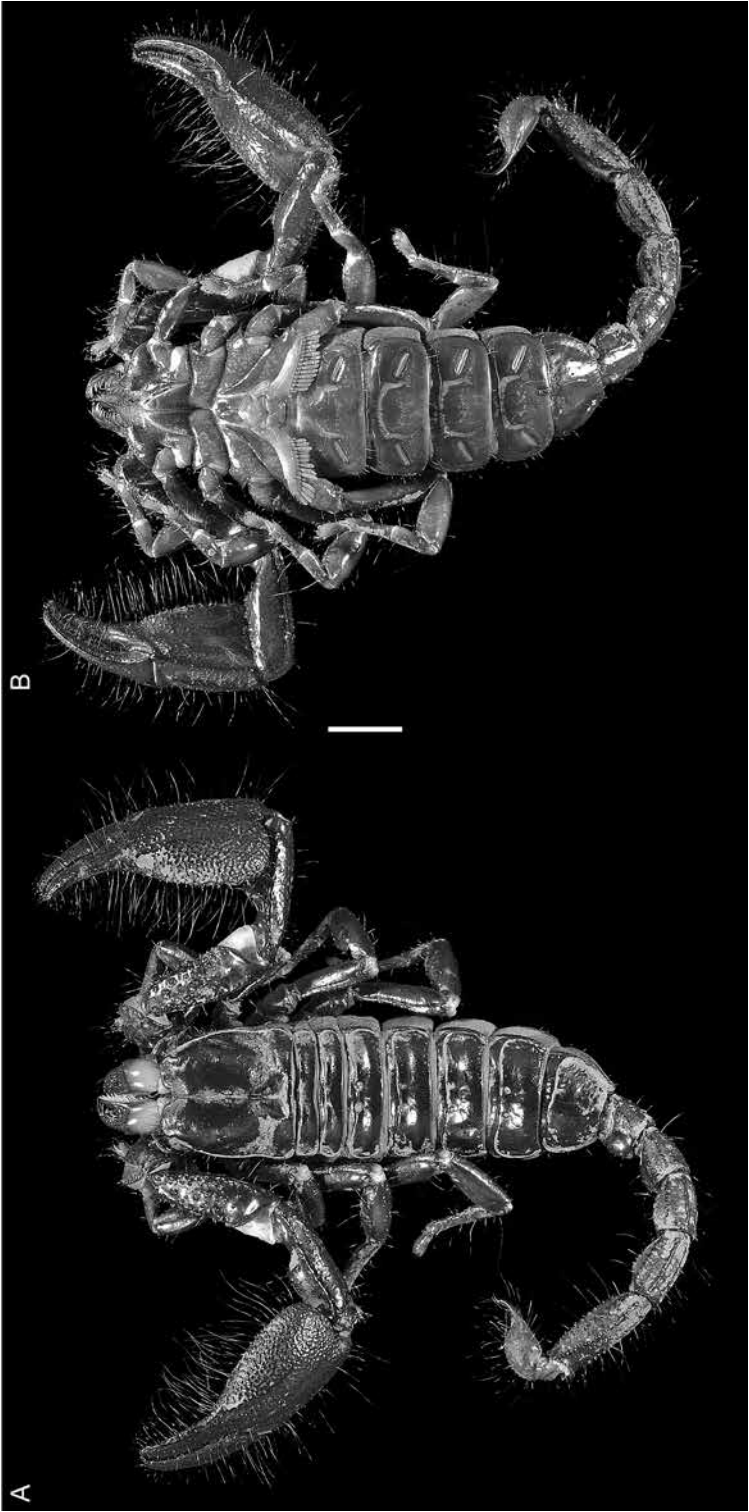


FIGURE 130. *Deccanometrus obscurus* (Coutzjin, 1981), comb. et stat. nov., ♂ (AMNH), Bhimashankar, India, habitus: A. dorsal and B. ventral aspects. Scale bar = 10 mm.

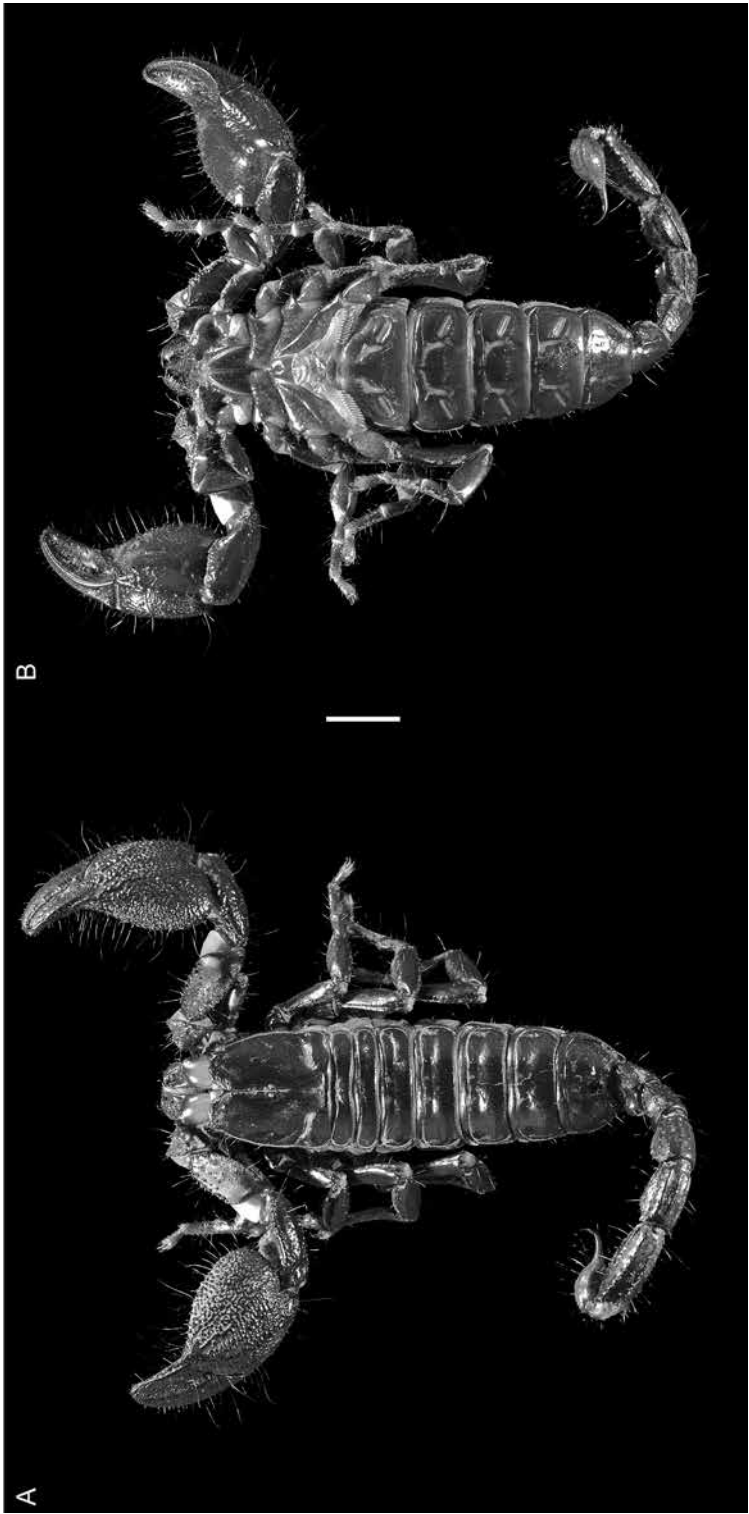


FIGURE 131. *Deccanometrus obscurus* (Couzijn, 1981), comb. et stat. nov., ♀ (AMNH), Bhimashankar, India, habitus: **A.** dorsal and **B.** ventral aspects. Scale bar = 10 mm.

segments I–IV are granular or costate-granular on segment IV only and costate on segments I–III (fig. 69D) in *H. laevigatus* but granular on segments I–IV, II–IV (costate on I), or III and IV (costate on I and II) in *H. laoticus* and *H. silenus*. The ventral intercarinal surfaces of segments III and IV of the female are smooth in *H. laevigatus* but granular in *H. laoticus*. The telson is blackish and as dark as metasomal segment V in *H. laevigatus* (figs. 9E, 164, 165) but dark reddish brown and paler than segment V in *H. glaucus*, *H. longimanus*, *H. petersii*, and *H. spinifer*. The width of the telson vesicle is approximately equal to or less than the width of metasomal segment V (figs. 67D, 69D) in the male of *H. laevigatus* but greater than the width of segment V in the male of *H. glaucus* and *H. longimanus*.

DISTRIBUTION: This species is recorded from the Tanintharyi Region of southwestern Myanmar, including the Myeik archipelago, southern Thailand (recorded in the provinces of Chumphon, Kanchanaburi, Krabi, Nakhon Si Thammarat, Narathiwat, Phang-Nga, Phattalung, Pattani, Phetchaburi, Satun, Songkhla, Surat Thani, and Trang), including the islands of Ko Lanta, Ko Muk, Ko Samui, the Phi Phi archipelago, and Phuket, and Langkawi island in the state of Kedah, Malaysia (fig. 158, table 2). Its distribution overlaps those of *H. laoticus* in central Thailand and *J. cyaneus* in southern Thailand. *Heterometrus spinifer* is allopatric to the south of the Sankalakhiri (Titiwangsa) Mountains, in Malaysia.

ECOLOGY: *Heterometrus laevigatus* has been collected in primary and secondary tropical rainforest and rubber plantations at elevations of 30–395 m above sea level (fig. 7E). Most specimens, including the holotype of *H. minotaurus*, were collected with UV detection at night, door-keeping in or near burrows or walking on the ground. Some were collected by overturning stones and logs during the day. The habitat and habitus of this species are consistent with the fossorial, pelophilous, lapidicolous, and corticolous ecomorphotypes (Prendini, 2001b). The following scorpions were found in sympatry with *H. laevigatus*: the buthids *Lychas mucronatus* (Fabricius,

1798), *Lychas krali* Kovařík, 1995, *Lychas scutillus* C.L. Koch, 1845, and *Thaicharmus mahunkai* Kovařík, 1995; an undetermined chaerilid, genus *Chaerilus* Simon, 1877; undetermined scorpionids of the genera *Alloscorpiops* Vachon, 1980, and *Euscorpiops* Vachon, 1980; and the hormurids *Liocheles australasiae* (Fabricius, 1775) and undetermined species of *Liocheles* Sundevall, 1883.

CONSERVATION STATUS: *Heterometrus laevigatus* is occasionally available in the exotic pet trade. Material offered for sale is believed to have originated from Thailand or Myanmar.

REMARKS: *Palamnaeus laevigatus* Thorell, 1876, was based on an adult female from “Melbourne, Nova Hollandia” [Australia], although the type locality is erroneous and may refer to the transportation (Couzijn, 1981). Couzijn (1981: 93) synonymized *P. laevigatus* with *H. spinifer* but noted differences including coarse reticulation on the pedipalp chela manus and two meristic characters (the sum of the lengths of metasomal segments I–V and the distance between pedipalp chela trichobothria V_1 and V_4 as a ratio of the distance between V_3 and V_4) differing from typical values.

Whereas Fet (2000: 438) correctly credited Couzijn (1981) as the first to synonymize *P. laevigatus* with *H. spinifer*, Kovařík (2004) incorrectly listed Kraepelin (1894) as the first to do so. Kraepelin (1894) listed both *H. spinifer* and *P. laevigatus* as synonyms of *Scorpio longimanus* (i.e., *Heterometrus longimanus*).

Examination of the holotype of *P. laevigatus* during the present investigation demonstrated that, although it is a subadult female with erroneous locality data, the specimen is unequivocally conspecific with *H. cimrmani*, not *H. spinifer*, consistent with Couzijn’s (1981) assessment that the specimen differed from “typical” *H. spinifer* in several respects. Characters consistent with *H. cimrmani* and differing from *H. spinifer* include the dark blackish telson (yellowish in immature stages and reddish brown in adults of *H. spinifer*), the more elongated shape of the pedipalp chela manus and, especially, the pronounced reticulation on its dorsal and retrodor-



FIGURE 132. *Deccanometrus obscurus* (Couzijn, 1981), comb. et stat. nov., ♂ (AMNH), Bhimashankar, India, pedipalp patella: A. dorsal, B. retrolateral, and C. ventral aspects. Scale bar = 5 mm.

sal surfaces (smooth in *H. spinifer*), as well as the shape and granulation of the carapace, the shape of the pectinal scape, and the two meristic characters mentioned by Couzijn (1981). Based on the evidence, *P. laevigatus* is indisputably conspecific with *H. cimrmani*, hence *Heterometrus cimrmani* Kovařík, 2004 = *Heterometrus laevigatus* (Thorell, 1876), syn. nov.

Heterometrus minotaurus was based on a holotype male from Surat Thani Province, southern Thailand. The description and figures of *H. minotaurus* closely match the male of *H. cimrmani*, and the type locality falls within the known range of *H. cimrmani*, only a short distance north of localities of *H. cimrmani* specimens identified by Kovařík (2004), e.g., Phang

Nga. No diagnostic characters were provided to separate *H. minotaurus* from *H. cimrmani* in the original description, Plíšková et al. (2016) compared *H. minotaurus* only with *H. longimanus*, a species that does not overlap in distribution. As *H. cimrmani* is a junior synonym of *H. laevigatus*, the same is true for *H. minotaurus*, hence *Heterometrus minotaurus* Plíšková et al., 2016 = *Heterometrus laevigatus* (Thorell, 1876), syn. nov.

MATERIAL EXAMINED: ex pet trade, xii.2000, 1 ♂, 1 ♀ (AMNH). Myanmar [alleged]: ex pet trade, 2002, 1 ♀ (AMNH [LP 1789]), 1 juv. ♂ (AMCC [LP 1789]). **MALAYSIA: Kedah:** Langkawi, D'Coconut Hill Resort [06°22'N 99°49'E], 16.vii.2017, M.S. Foo, 1 ♀ (LKC ZRC-ENT 915); Langkawi, Lubuk Somilang [Semilang, 06°22'N 99°48'E], 15.vii.2017, M.S. Foo, 1 ♂ (LKC

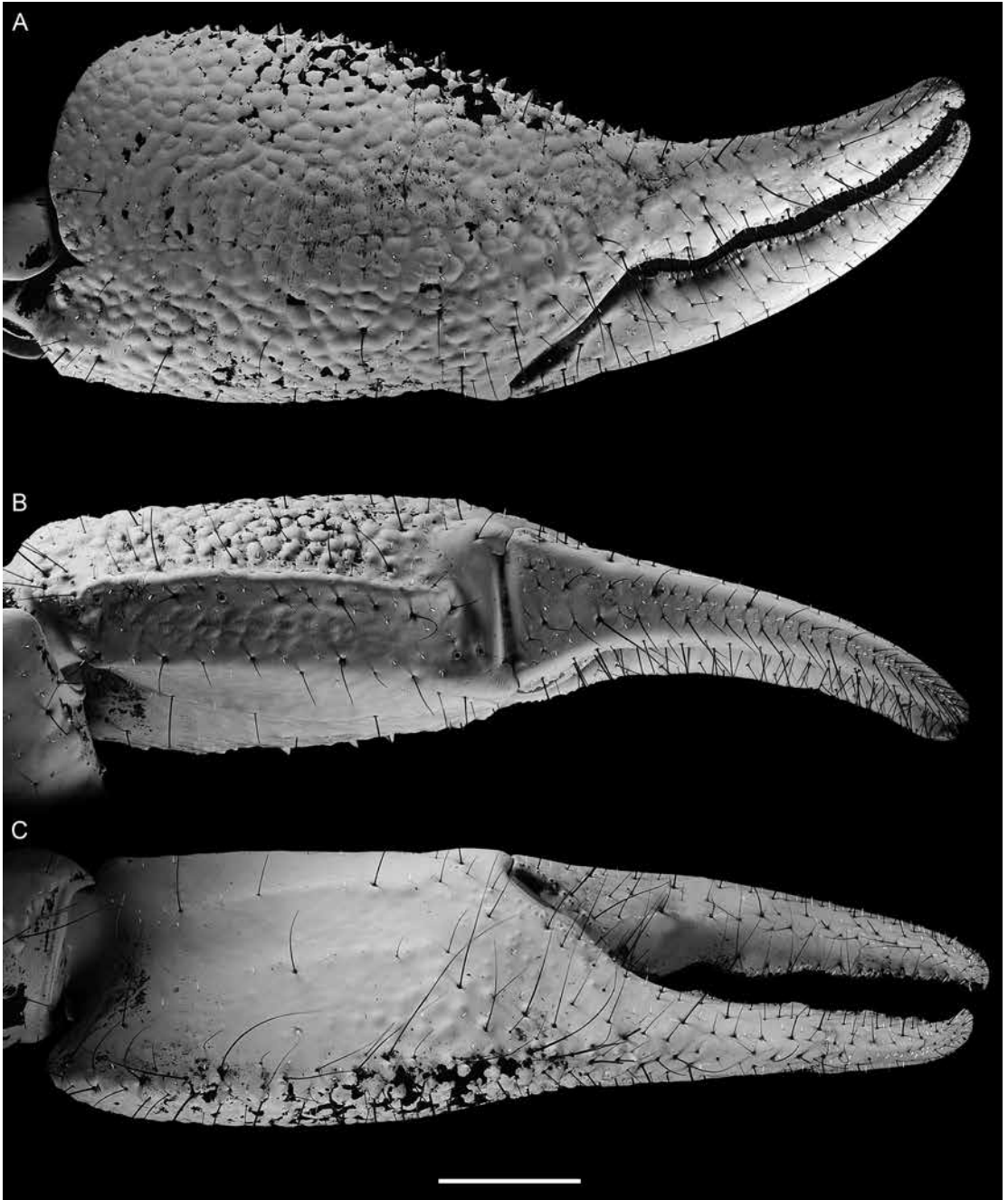


FIGURE 133. *Deccanometrus obscurus* (Couzijn, 1981), comb. et stat. nov., ♂ (AMNH), Bhimashankar, India, pedipalp chela: **A.** retrodorsal, **B.** ventral, and **C.** prolateral aspects. Scale bar = 5 mm.

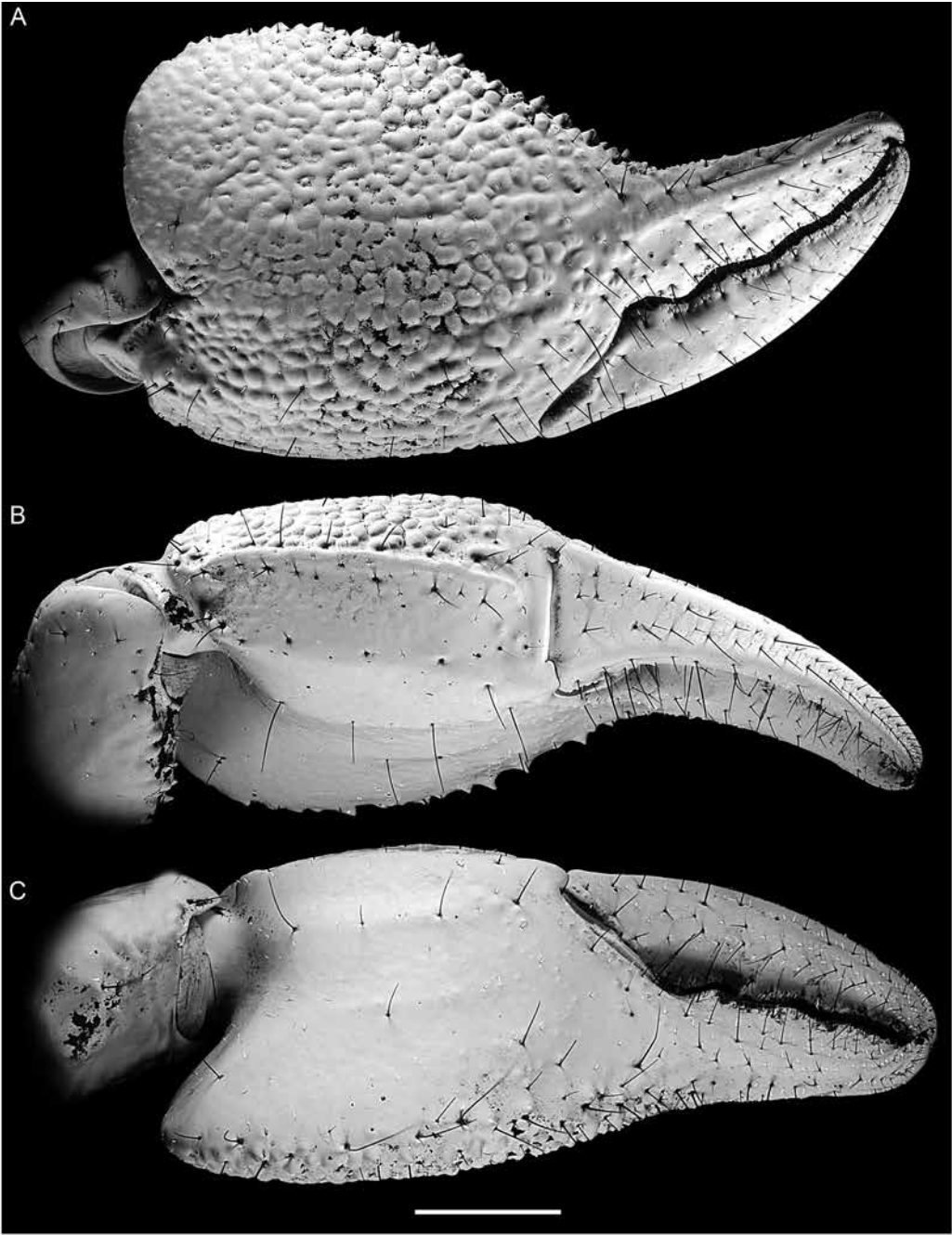


FIGURE 134. *Deccanometrus obscurus* (Couzijn, 1981), comb. et stat. nov., ♀ (AMNH), Bhimashankar, India, pedipalp chela: **A.** retrodorsal, **B.** ventral, and **C.** prolateral aspects. Scale bar = 5 mm.

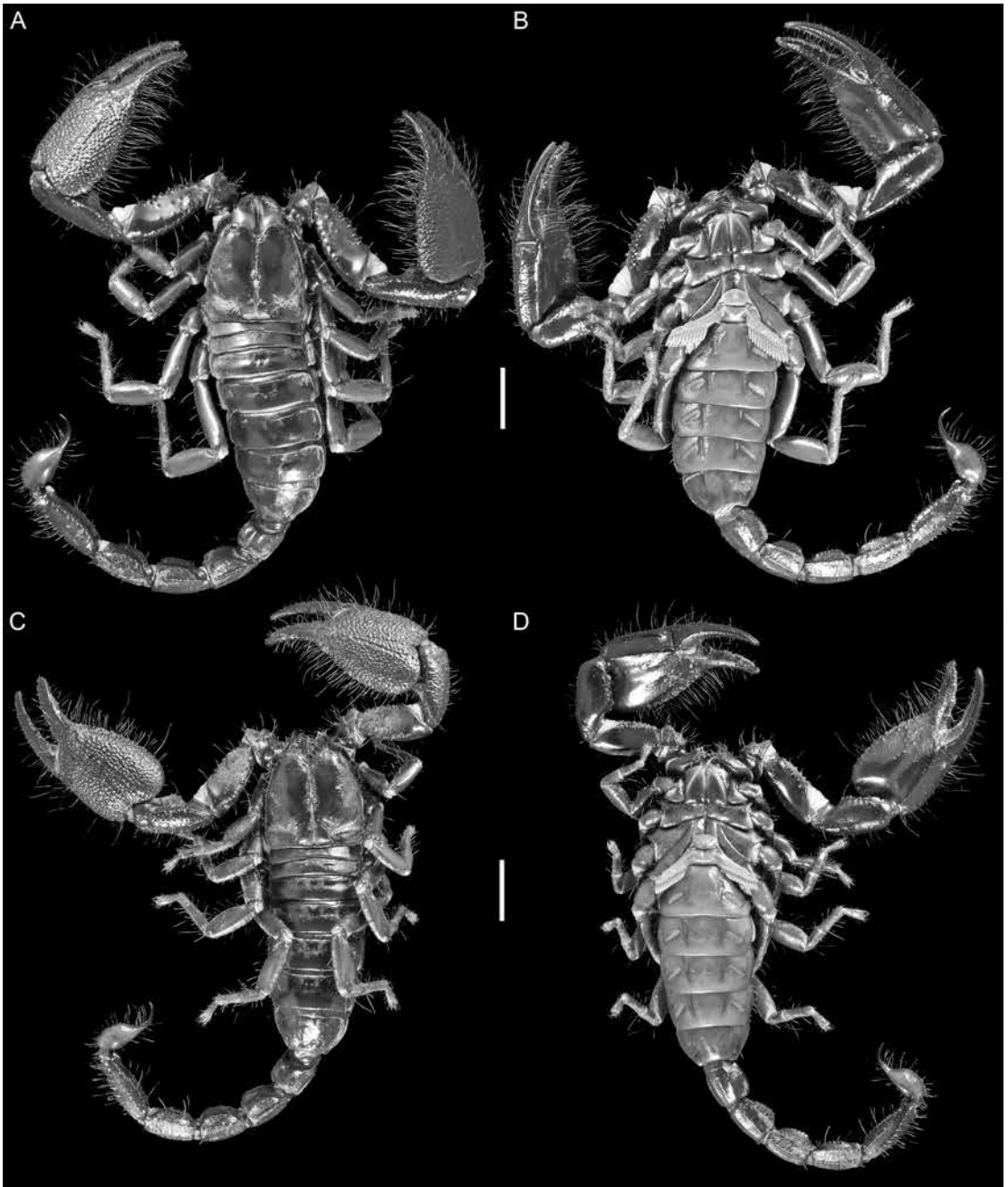


FIGURE 135. *Deccanometrus phipsoni* (Pocock, 1893), comb. nov., habitus: A, C. dorsal and B, D. ventral aspects. A, B. ♂, C, D. ♀ (MNHN 0080). Scale bar = 10 mm.

ZRC-ENT 916). **THAILAND:** F. Odendaal, 1 ♂ (TM 20261), G. Newlands, 2 ♀ (SAM C4511 [JV 2210]). **Bangkok Prov.:** Bangkok [13°45'N 100°31'E], 1956, G. Alexander, 1 ♂ (FMNH [086 252]). **Chumphon Prov.:** *Phato Distr.:* Khao Kai Jae Waterfall, along main road/trail leading toward waterfall, 09°55'N 98°57'E, 26.iv.2014, S.F. Loria and P. Horsley, blacklight at night, 1 ♀ (AMNH), 1 juv. ♂ (AMCC [LP 12337]). **Krabi Prov.:** *Krabi Distr.:* Khao Phanom Bencha, around bungalows, 08°14'N 98°55'E, 126 m, 25–26.xi.2014, S.F. Loria and M.M. Locke, on ground, 1 juv. ♀ (AMCC [LP 13048]). **Narathiwat Prov.:** *Mueang Narathiwat Distr.:* Baugnara, Navaddivas [06°25'N 101°49'E], 13.x.1940, Dr. Hemmingsen, rubber plantations, 1 ♂, 1 ♀ (AMNH). **Phattalung Prov.:** *Si Banphot Distr.:* Khao Pu-Khao Ya, 07°41'N 99°52'E, 186 m, 24.xi.2014, S.F. Loria and M.M. Locke, blacklight at night, 3 ♀, 1 subad. ♂, 1 juv. ♂ (AMNH), 1 juv. ♀ (AMCC [LP 13047]), on hill along nature trail, 07°41'N 99°53'E, 219 m, 24.xii.2014, S.F. Loria and M.M. Locke, under rotting log, 1 juv. ♀ (AMNH). **Phetchaburi Prov.:** *Kaeng Krachan Distr.:* Kaeng Krachan, around lake, near road, 12°53'N 99°38'E, 100 m, 24.iv.2014, S.F. Loria and P. Horsley, 3 ♂, 2 juv. ♂, 2 juv. ♀ (AMNH), 1 juv. ♀ (AMCC [LP 12335]). **Satun Prov.:** *Khuan Don Distr.:* Thale Ban, along road and trails, 06°43'N 100°10'E, 163 m, 23.xi.2014, S.F. Loria and M.M. Locke, in burrows, 1 ♂, 1 ♀, 1 subad. ♂, 1 subad. ♀ (AMNH), 1 juv. ♂ (AMCC [LP 13045]). **Surat Thani Prov.:** *Ko Samui Distr.:* Koh Samui (Samui Island), Na Mueang-1 Waterfall, around grounds of waterfall, 09°28'N 99°59'E, 30 m, 15.xii.2018, S.F. Loria, under rocks and logs, 2 ♂, 1 ♀ (AMNH). **Trang Prov.:** *Mueang Trang Distr.:* Kao Chong [Khao Chong, 07°33'N 99°47'E], 1000 ft., 24.viii.1933, H.M. Smith, 1 ♂ (USNM); Trong [Trang, 07°34'N 99°37'E], lower Siam, W.L. Abbott, 4 ♂, 3 ♀ (USNM).

Heterometrus laoticus Couzijn, 1981

Figures 7F, 8F, 10, 24A, B, 38A, B, 51A–D, 70A, 71A, 72A, 157, 169–173, table 2

Palamnaeus silenus Simon, 1884a: 361 (misidentification, part); Thorell, 1889: 588 (misidentification, part); Flower, 1901: 35, 36 (misidentification); Simon, 1904: 293 (misidentification, part).

Heterometrus (Scorpio) longimanus: Kraepelin, 1901: 271 (misidentification, part).

Heterometrus (Scorpio) longimanus var. *silenus*: Kraepelin, 1901: 271 (misidentification, part).

Heterometrus longimanus petersi: Fage, 1933: 25, 27 (misidentification, part); 1936: 180, 181 (misidentification, part); 1946: 73 (misidentification part).

Heterometrus longimanus petersii: Nemenz and Gruber, 1967: 1–24, tables 1–3, figs. 1–7 (misidentification).

Heterometrus (Heterometrus) laotianus: Couzijn, 1981: 173, fig. 62 (part).

Heterometrus (Heterometrus) laoticus Couzijn, 1981: 22, 32, 73, 75–77, 80, 83, 89, 94–96, 174, 175, 182, 184, 185, 189, 191, table 7, figs. 4a, 17b, 18, 19, 21, 24, 63, 66b (part); Kovařík, 1995: 202 (part); 1997: 183; Hue et al., 1998: 8 (part); Kovařík, 1998: 137 (part); Fet, 2000: 433 (part); Kovařík, 2002: 17.

Heterometrus (Heterometrus) petersii: Couzijn, 1981: 73, 173, 175, 185, 187–189, figs. 62, 70 (misidentification, part); Fet, 2000: 437 (part).

Heterometrus (Heterometrus) petersii petersii: Couzijn, 1981: 32, 76, 77, 83, 88, 89, 96–99, 174, table 7, figs. 18, 19, 63 (misidentification, part); Hue et al., 1998: 7, 8 (misidentification, part); Fet, 2000: 437 (part).

Heterometrus (Heterometrus) spinifer: Couzijn, 1981: 73, 94, 96, 173, 175, 187, 189, 190, fig. 62 (misidentification, part).

Heterometrus (Heterometrus) spinifer spinifer: Couzijn, 1981: 19, 32, 76, 77, 83, 89–93, 167, 174, 191, table 7, figs. 2b, 18, 19, 63 (misidentification, part).

Heterometrus longimanus: Warburg and Polis, 1990: 233 (misidentification).

Heterometrus petersii petersii: Warburg and Polis, 1990: 225 (misidentification).

Heterometrus spinifer: Delfosse, 1998: 30 (misidentification); Robert, 1999: 19–27 (misidentification, part).

Heterometrus (Heterometrus) petersi: Kovařík, 1998: 137 (part).

Heterometrus laoticus: Prendini et al., 2003: 188, 192, 202, 205, 208, 209, 222, 252–259, table 3, figs. 2, 4, 6, 7, appendices 1, 2 (part); Kovařík, 2004: 2, 20, 21, 34, 51, 53, table 2 (part); Booncham et al., 2007: 42–50, table 1, figs. 1–6; Wirkner and Prendini, 2007: 402, table 1; Kovařík, 2009: 35, 39, 47–49, 82, 87, 101, 106, table 1 (part), figs. 63–70, 102, 228, 229, 253, 254; Klußmann-Fricke et al., 2012: 546, table 1; Pham et al., 2017: 136, fig. 5.

Heterometrus petersii: Kovařík, 2004: 2, 13, 21, 32, 34, 42, 51, 53, table 2 (misidentification, part); Booncham et al., 2007: 43; Kovařík, 2009: 35, 42, 48, table 1 (part): 3.

TYPE MATERIAL: **LAOS**: Holotype ♂, paratype ♀ (MNHN RS 0030), 1884–1899, Neis [examined].

Couzijn (1981: 94) based the description of *H. (H.) laoticus* on multiple specimens, but clearly specified a holotype and allotype (paratype) among them: “Laos (3 ♂ ad. including holotype, 1 ♀ ad. allotype, leg. Neis 1884–1899, [MNHN] RS 0030 ...)”. Fet (2000: 433) incorrectly cited all specimens in Couzijn’s (1981) list as type material for *H. (H.) laoticus*.

DIAGNOSIS: *Heterometrus laoticus* may be separated from other species of *Heterometrus* as follows. The carapace interocular surface is entirely smooth in the male and female (fig. 24A, B) of *H. laoticus* whereas the interocular surface is granular along the median longitudinal and anterior bifurcated sulci only in the male and female of *H. longimanus*, *H. petersii*, *H. silenus*, and *H. spinifer*, and the female of *H. laevigatus*, and the frontal lobes and medial region of the interocular surface are granular with smooth areas in the male and female of *H. glaucus* and *H. thorellii*. The carapace anterolateral, mediolateral, and posterolateral surfaces of the female (fig. 24B) are smooth or nearly so in *H. laoticus*, the anterolateral and mediolateral surfaces of the female granular in all other species, and the posterolateral surfaces of the female granular in all other species except *H. longimanus*. The pedipalps of the adult male are short, with femur length : pos-

terior carapace width ratio (FL:PCW) < 0.77 and femur length : carapace length ratio (FL:CL) < 0.74 (fig. 169) in *H. laoticus* but long, with FL:PCW ≥ 0.80 and FL:CL ≥ 0.76 in *H. glaucus*, *H. laevigatus*, *H. longimanus*, and *H. thorellii*. The pedipalp chela manus promedian carina of the female (fig. 173) is present and granular in *H. laoticus* but absent or obsolete in *H. laevigatus*. The maximum distance between the dorsomedian and dorsal secondary carinae (DMC–DSC) of the chela manus is similar to the maximum distance between the dorsal secondary and digital carinae (DSC–DC) in the male and female (figs. 172, 173) of *H. laoticus* whereas the DMC–DSC is less than the DSC–DC in the male of *H. glaucus*, *H. laevigatus* and *H. thorellii*, greater than the DSC–DC in the male of *H. silenus*, and less than the DSC–DC in the male and female of *H. longimanus*. The chela manus dorsal intercarnal surface is smooth or nearly so (figs. 172, 173) in *H. laoticus* but shallowly reticulate in *H. glaucus*, *H. laevigatus* and, often, *H. thorellii*. The second (subproximal) lobe of the chela movable finger of the adult male is more strongly developed than other lobes on the finger, with a correspondingly well-developed notch in the fixed finger (fig. 172) in *H. laoticus* but similar to or barely larger than other lobes on the finger in *H. glaucus*, *H. longimanus*, and *H. thorellii*. Macroseta *st* on the proventral surface of the basitarsus of leg I is setiform (fig. 51A) in *H. laoticus* but spiniform in *H. laevigatus* and *H. thorellii*; *st* on the proventral surface of the basitarsus of leg II is setiform (fig. 51B) in *H. laoticus* but spiniform in *H. glaucus*, *H. laevigatus*, *H. thorellii*, and, usually, *H. longimanus*; *sb* on the proventral surface of the basitarsus of leg III is setiform (fig. 51C) in *H. laoticus* but spiniform in *H. glaucus*, *H. petersii*, and *H. spinifer*. The lateral surfaces of mesosomal tergites I–VI in the female are smooth (fig. 170A) in *H. laoticus* but granular in all other species except *H. laevigatus* and *H. thorellii*. The ventrosubmedian and ventrolateral carinae of metasomal segments I–IV are granular on segments I–IV, II–IV (costate on I), or III and IV (costate on I and II) (fig. 72A) in *H. laoticus* but granular or costate-granular on segment IV only and costate on segments I–III in *H. glaucus*. The

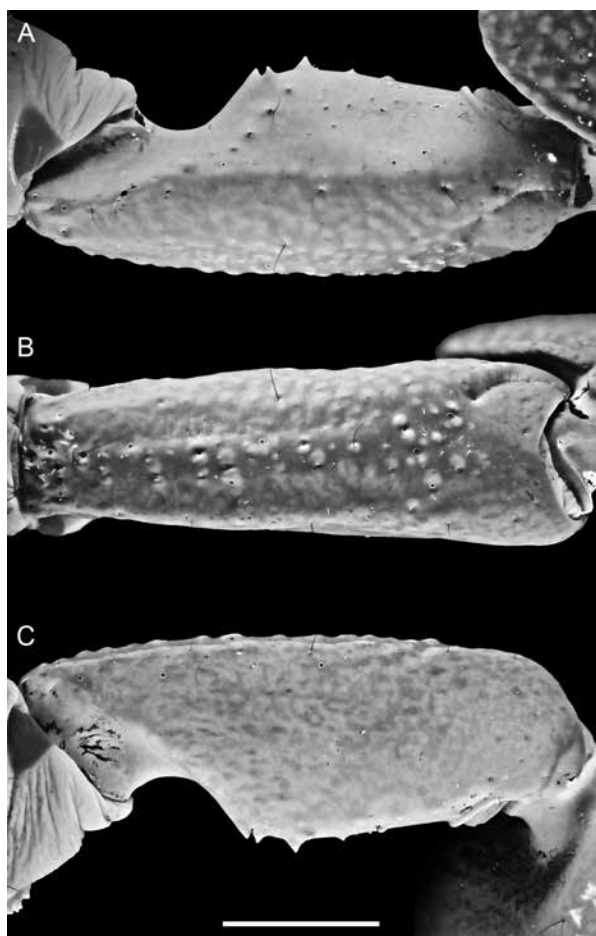


FIGURE 136. *Deccanometrus phipsoni* (Pocock, 1893), comb. nov., ♂ (MNHN 0080), pedipalp patella: **A.** dorsal, **B.** retrolateral, and **C.** ventral aspects. Scale bar = 5 mm.

ventral intercarinal surfaces of segments III and IV of the female are granular in *H. laoticus* but smooth in all other species. The telson is blackish and as dark as metasomal segment V in *H. laoticus* (figs. 169, 170) but dark reddish brown and paler than segment V in *H. glaucus*, *H. longimanus*, *H. petersii*, and *H. spinifer*. The width of the telson vesicle is approximately equal to or less than the width of metasomal segment V (figs. 70A, 72A) in the male of *H. laoticus* but greater than the width of segment V in the male of *H. glaucus* and *H. longimanus*.

DISTRIBUTION: This species is distributed across Thailand (recorded in the provinces of Bangkok, Chanthaburi, Chiang Mai, Chonburi,

Kampheng Phet, Kanchanaburi, Lampang, Lamphun, Lopburi, Nakhon Phanom, Nakhon Ratchasima, Nakhon Sawan, Nan, Phetchabun, Prachinburi, Phrae, Sakon Nakhon, Tak, Trat, Ubon Ratchathani, and Udon Thani), including Ko Chang island, Laos (recorded in Vientiane Prefecture and the provinces of Bolikhamxa, Chachoengsao, Khammouane, Luang Prabang, Salavan, Savannakhet, Vientiane, and Xiengkhouang), and northwestern Cambodia (recorded only in Siem Reap Province). Its distribution overlaps that of *H. laevigatus* in central Thailand and appears to be bounded in the east by the Annamite Mountain range (fig. 157, table 2). Its

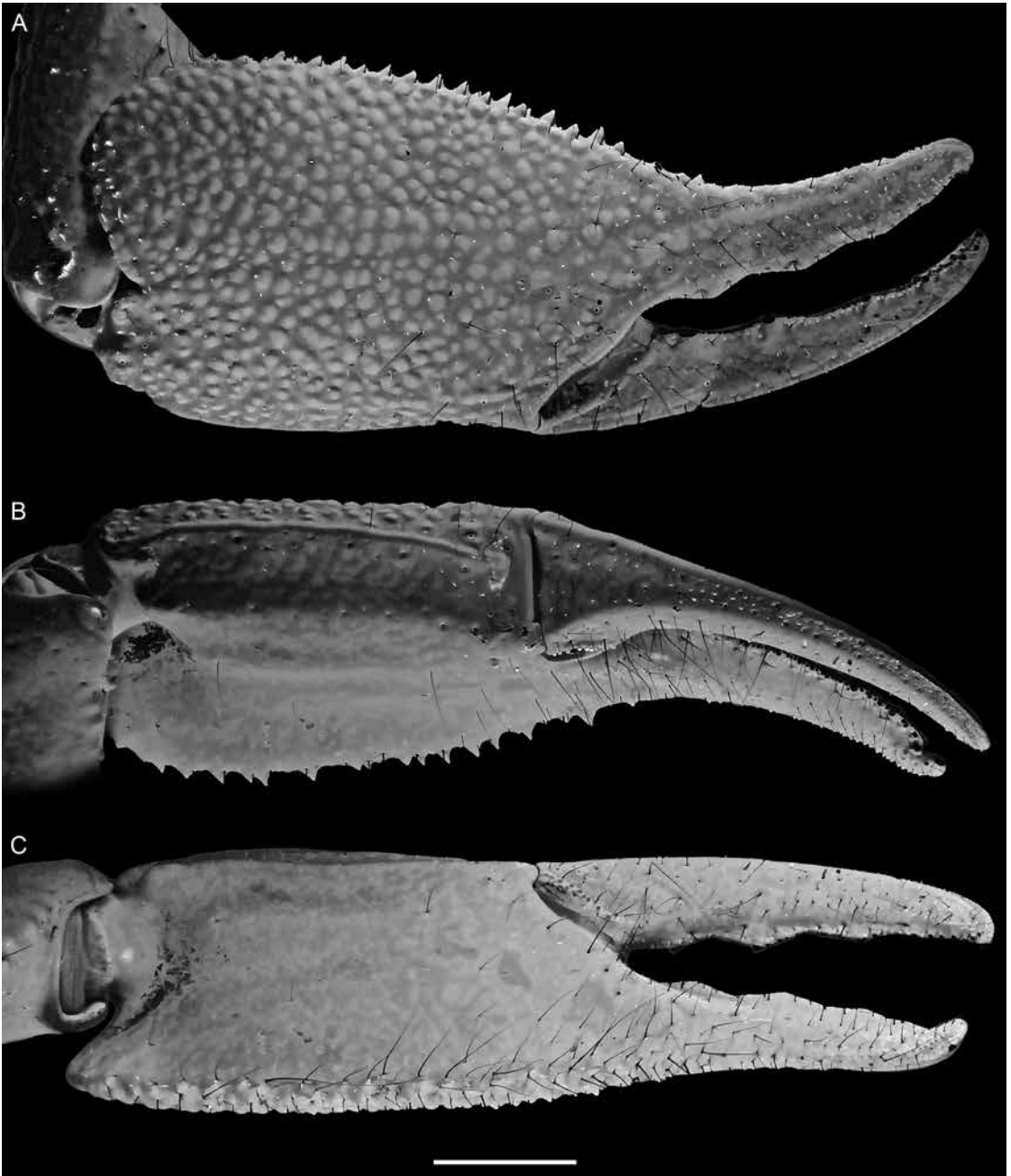


FIGURE 137. *Deccanometrus phipsoni* (Pocock, 1893), comb. nov., ♂ (MNHN 0080), pedipalp chela: **A.** retro-dorsal, **B.** ventral, and **C.** prolateral aspects. Scale bar = 5 mm.

sister species, *H. silenus* is allopatric, distributed to the east of the Annamite Mountains.

ECOLOGY: Specimens of *H. laoticus* with ecological data were collected in or near primary

deciduous forests, mesic savanna on flat plains, limestone formations, gardens, and rice fields at elevations of 10–1220 m above sea level (fig. 7F). Most specimens were collected with UV detec-

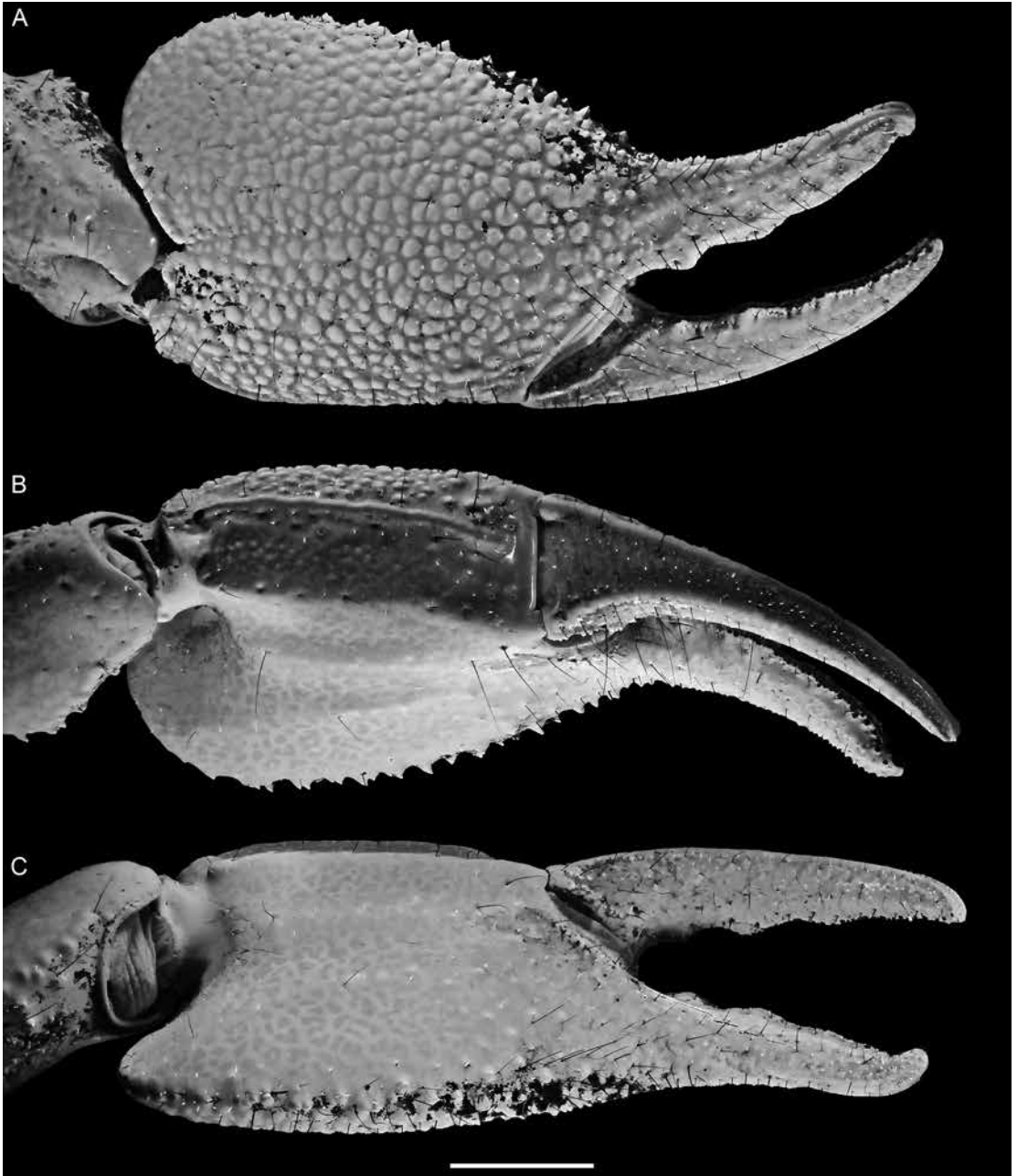


FIGURE 138. *Deccanometrus phipsoni* (Pocock, 1893), comb. nov., ♀ (MNHN 0080), pedipalp chela: **A.** retro-dorsal, **B.** ventral, and **C.** prolateral aspects. Scale bar = 5 mm.

tion at night, doorkeeping at burrow entrances (fig. 8F). Some burrows were located under rocks and specimens were occasionally observed walking on the ground. The habitat and habitus of

this species are consistent with the fossorial, pelophilous ecomorphotype (Prendini, 2001b). The following scorpions were collected in sympatry: the buthids *Lychas aberlenci* Lourenço,

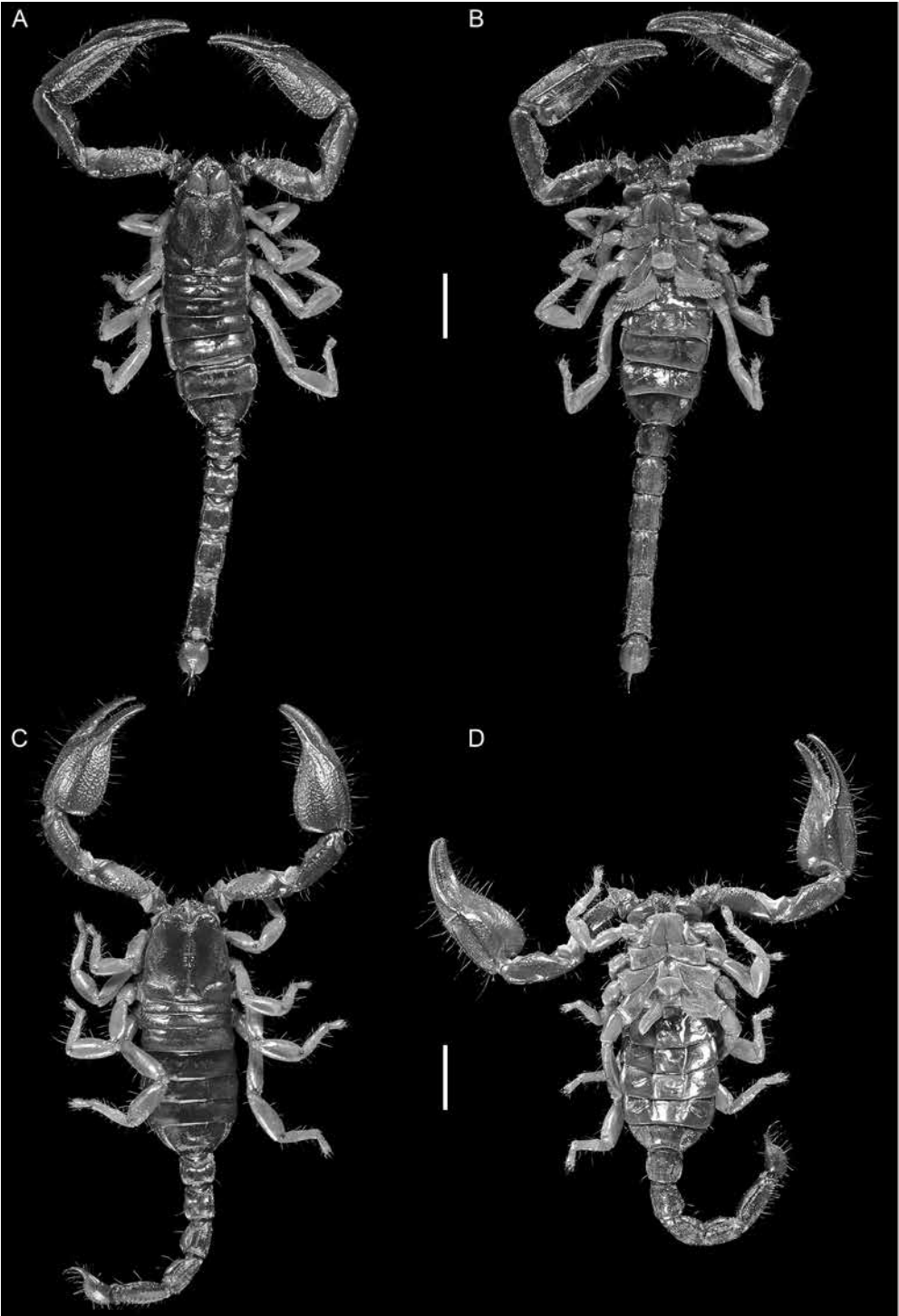


FIGURE 139. *Deccanometrus ubicki* (Kovařík, 2004), comb. nov., habitus: A, C. dorsal and B, D. ventral aspects. A, B. Paratype ♂ (CAS 9071136). C, D. Paratype ♀ (CAS 9071135). Scale bars = 10 mm.

2013, *Lychas cernickai* Kovařík, 2013, *Lychas mucronatus*, and an undetermined species of *Lychas* C.L. Koch, 1845; the hormurid *Liocheles australasiae*; and the scoriopids *Alloscorpiops calmonti* Lourenço, 2013, and *Alloscorpiops wongpromi* Kovařík et al., 2013.

CONSERVATION STATUS: *Heterometrus laoticus* is occasionally available in the exotic pet trade. Material offered for sale is believed to have originated from Thailand, where the species is also harvested for consumption.

REMARKS: This species was previously accommodated in the nominal subgenus of *Heterometrus* by Couzijn (1981) and Fet (2000).

MATERIAL EXAMINED: 1 ♀ (AMNH), > 1990, 1 ♂ (TM 20261). **CAMBODIA:** **Siem Reap Prov.:** *Bakorng Distr.:* Kantrieng Commune, Tatrow Village, 13°20'N 104°02'E, > 10 m, vii.1999, B.L. Stuart, 12 PM under water tank next to house, 1 ♀, 1 subad. ♀, 1 juv. ♂ (FMNH 086 259 [408]). Siem Reap, Angkor Wat, 13°24'N 103°52'E, 36 m, 15.vii.2017, P. Jäger, tree trunks, shrubs, forest floor, at night, by hand at roadside, 1 ♂ (SMF). **LAOS:** 1884–1899, Neis, 6 ♂, 2 subad. ♂, 1 subad. ♀, 1 juv. ♀, 1 juv. (MNHN RS 0030). **Champasak Prov.:** *Pathoumphone Distr.:* Ban Kiet Ngong, near Vanhna Ban Xang Restaurant and Guesthouse, 14°46'N 106°02'E, 177 m, 21.v.2018, S.F. Loria, L. Ngo and S.T. Kangnavong, blacklight at night in burrows under rocks, 1 ♂, 1 subad. ♂ (AMNH), Ban Kiet Ngong, behind house in disturbed forest, 14°47'N 106°02'E, 161 m, 22.v.2018, S.F. Loria, L. Ngo, S.T. Kangnavong and V. Keosopha, in burrows under volcanic rocks, 2 ♂, 1 ♀ (AMNH). **Khammouane Prov.:** *Boualapha Distr.:* between Boualapha [17°19'N 105°43'E] and Ban Nong Ping, 3.v.2012, P. Jäger, by hand at night, 1 ♀ (SMF), 1 ♀ (AMCC [LP 11330]); Hin Namno National Biodiversity Conservation Area: Tham Xe Bang Fai (Xe Bang Fai River Cave), 17°22'N 105°50'E, 159 m, 19–20.ii.2012, L. Prendini and P. Kanyavong, beach at bottom of “Balcony Passage,” right bank of river, ca. 300–500 m from downstream entrance of cave, UV detection, dextral pedipalp patella (AMNH), 19–21.ii.2012, L. Prendini, P. Kanyavong, and W. Phimmathong, beach between “Balcony Passage” and “Stairway to Heaven,” right bank of river, UV detection, sinistral pedipalp chela (AMNH), 20–21.ii.2012, L. Prendini, P. Kanyavong and W. Phimmathong, beach midway through cave, left bank of river, UV detection, dextral pedipalp chela (AMNH). *Gnommalath Distr.:* Tham Makhang near Ban Naden village, 17°29'N 105°24'E, 159 m, 13.vi.2012, L. Prendini, S.F. Loria and P. Kanyavong, limestone cave in savanna, inside cave, 1 ♂ pedipalp chela

(AMNH); Tham Nam Lot (Lod) near Ban Naden village, 17°30'N 105°23'E, 260 m, 13–14.vi.2012, L. Prendini, S.F. Loria, and P. Kanyavong, outside entrance to limestone cave in primary rainforest at base of limestone mountain, UV light detection on hot, very humid night after late afternoon rainfall, doorkeeping at burrow entrances in open ground or under stones, excavated from shallow burrows (ca. 20 cm) in clayey-loam soil, 3 ♂, 2 subad. ♂, 1 subad. ♀, 2 juv. ♀, two pedipalp chelae (AMNH), 1 juv. ♀ (AMCC [LP 11352]); Tham Nam Lot (Lod), near Ban Naden village, outside cave, 17°30'N 105°23'E, 260 m, 19.v.2018, S.F. Loria, L. Ngo, S.T. Kangnavong, and P.T. Thon Thondet, blacklight at night, on ground outside cave, 1 ♂ (AMNH). *Thakhek Distr.:* Phou Hin Boun National Biodiversity Conservation Area, Phahom Camp, ca. 12 km E Thakhek on road to Gnommalath, 17°27'N 104°55'E, 151 m, 14–15.vi.2012, L. Prendini and S.F. Loria, primary rainforest/mesic savanna on flat plains around bases of steep limestone mountains, lush vegetation after recent rains, clayey-loam soil, UV light detection on hot, humid, dark night following showers of rainfall, walking on ground in open, 1 ♂ (AMNH); Phou Hin Boun National Biodiversity Conservation Area, Tham Pha In, ca. 12 km E Thakhek on road to Gnommalath, 17°28'N 104°55'E, 143 m, 14–15.vi.2012, L. Prendini and S.F. Loria, primary rainforest/mesic savanna on plains around bases of steep limestone mountains, lush vegetation after recent rains, clayey-loam soil, UV light detection on hot, humid, dark night following showers of rainfall, walking on ground in open, 1 ♀ (AMNH); Thakhek, 17°24'N 104°48'E, 15.vi.2012, P. Kanyavong, in garden, 1 subad. ♂ (AMNH); Thakek [17°24'N 104°50'E], 9–13 road km E, 25–27. iv.2012, P. Jäger, limestones, at night, 1 subad. ♂ (SMF), 1 subad. ♂ (AMCC [LP 11331]). **Luang Prabang Prov.:** *Pak Seng Distr.:* Pak-Xeng town, on Pak Xeng–Sam Soun Road, 20°10'N 102°39'E, 13.v.2018, S.F. Loria, L. Ngo and S.T. Kangnavong, blacklight at night, under rock in house garden, 1 ♂ (AMNH), sitting on wall, 1 ♀ (AMNH), 1 ♀ pedipalp chela (AMCC [LP 15584]). **Vientiane Prefecture:** Vientiane vicinity [17°58'N 102°36'E], 28.iv.1965, L.G. Bush, 1 ♂ (AMNH). **Vientiane Prov.:** *Thoulakhom Distr.:* Phou Khao Khouay NBCA, Ban Vangheua (Khua) school, 18°20'N 102°49'E, 775 m, 25–30.v.2008, A. Newton, M. Thayer et al., settlement near forests and rice fields, at light (UV and MV), FMHD 2008-018, 1 juv. ♂ (FMNH 129 144). **THAILAND:** 1 ♂ (AMNH), F.J. Odendaal, 2 ♀ (AMNH [AH 803, 804]), Eisenhofer, 6 ♂, 1 subad. ♂, 1 subad. ♀ (ZMB 14928), 23.vi.1900, H. Zimmermann, 3 ♂, 1 juv. ♀ (ZMB 14929), 1996, C.K. Wee, 1 ♀ (LKC ZRC-ARA 680). **Bangkok Prov.:** Bangkok [13°45'N 100°31'E], 29.xi.1929, H.M. Smith, 1 ♂, 1 ♀ (USNM). **Chiang Mai Prov.:** *Chiang Dao Distr.:* Doi Chang Dao [Doi Chiang

Dao, 19°24'N 98°53'E], April, Asiatic Primate Expedition, 1 ♀ (MCZ 10381); Doi Chiang Dao [Doi Chiang Dao], northern Siam, 29.i.1932, H.M. Smith, 2 ♂, 2 subad. ♀ (USNM). **Mae Taeng Distr.:** Khun Tan Mts. [19°05'N 99°21'E], northern Siam, 4000 ft., 16.v.1933, H.M. Smith, 1 ♀ (USNM); Sanpayang [San Payang, 19°02'N 98°52'E], northern Siam, 30.xii.1932, 1 juv. ♀ (USNM). **Mueang Chiang Mai Distr.:** Chiangmai [Chiang Mai, 18°48'N 99°00'E], vi.1952, D.C. and E. Thurman, 1 ♀ (USNM); Chiang Mai [Chiang Mai, 18°48'N 99°00'E], 12.x.1966, G. Dingerkus, 1 subad. ♂ (AMNH [GD 10.007.1]). **Kam Peng Pet Prov.:** **Khlong Khlung Distr.:** Klong Klung River [Ban Klong Klung (Khlong Khlung), 16°13'N 99°42'E], 20.vi.1949, C.C. Sanborn (CNHM-Rush Watkins Zool. Exped. 1949), 1 ♂, 1 ♀ (FMNH 086 262). **Kanchanaburi Prov.:** **Sai Yok Distr.:** Sai Yok, 14°26'N 98°51'E, 88 m, 22.iv.2014, S.F. Loria and P. Horsley, in forest patch near open area, in/near burrows, 1 ♀, 1 juv. ♂ (AMNH), 1 ♀, 1 juv. ♀ (AMCC [LP 12336]). **Lampang Prov.:** **Mae Mo Distr.:** Maemo [Mae Mo, 18°16'N 99°42'E], 2.vi.1994, J. Nielsen, 1 ♀ (NRS [JF 175]). **Loei Prov.:** **Dan Sai Distr.:** Loei Ransai [Dan Sai, 17°17'N 101°10'E], Sakon Nakhon, 29.v.1954, R.E. Elbel, 1 ♀ (USNM). **Lopburi Prov.:** **Chai Badan Distr.:** Tha-Manao [15°11'N 101°10'E], 30 km NW Kanchanaburi, 145 km NW Bangkok, 120 m, W. Thielen, 3 ♂, 2 ♀, 1 subad. ♂ (ZHM A32/90). **Nakhon Ratchasima Prov.:** **Kao Liao Distr.:** Khao-Din (Kao-Liau) [Ban Khao Din, 15°48'N 100°05'E], Nakhon Sawan, 11.xi.1984, R. Meunier, 1 ♀ (AMNH [AH 4649]), 3 subad. ♂ (AMNH [AH 4651, 4654, 4658]), 2 subad. ♀ (AMNH [AH 4657, 4659]), 3 juv. ♂ (AMNH [AH 4650, 4652, 4655]), 2 juv. ♀ (AMNH [AH 4653, 4656]). **Pak Chong Distr.:** Pak Jong [Pak Djong, 14°42'N 101°25'E], eastern Siam, 18.v.1925, H.M. Smith, 1 subad. ♂ (USNM 92/528). **Nakhon Si Thammarat Prov.:** **Nakhon Si Thammarat Distr.:** Nakhon Sritamarat [Nakhon Si Thammarat, 08°26'N 99°58'E], 8.vii.1928, 1 ♂ (USNM 103/537). **Phrae Prov.:** **Rong Kwang Distr.:** Ban Phai Thon [18°23'N 100°26'E] or **Nan Prov.:** **Sa Distr.:** Ban Pha Hang [Ban Pha Han, 18°28'N 100°43'E], xii.1961, K. Thonglongy, 1 subad. ♀, 1 juv. ♀ (USNM). **Phetchabun Prov.:** **Chon Daen Distr.:** Takaw, Pasak River [Ban Ta Kam (Tha Kham), 16°09'N 100°48'E], 20.x.1932, H.M. Smith, 1 ♂, 1 subad. ♀ (USNM). **Sakon Nakhon Prov.:** **Mueang Sakon Nakhon Distr.:** Pak Nam Po [Pak Nam Pho, 15°43'N 100°09'E], Pak Nam Po Prov., 11.vi.1949, F. Wonder (CNHM-Rush Watkins Zool. Exped. 1949), 1 ♂, 1 juv. ♂, 3 juv. ♀ (FMNH 086 253), 12.vi.1949, F. Wonder (CNHM-Rush Watkins Zool. Exped. 1949), 1 ♀, 1 juv. ♂, 1 juv. ♀ (FMNH 086 263); Sakon Nakhon [Sakon Nakhon, 17°10'N 104°09'E], E Siam, 16.iii.1929, 2 ♀ (USNM). **Ratchaburi Prov.:** **Suan Phueng Distr.:** Suan Phueng Nature Education Park, 13°31'N

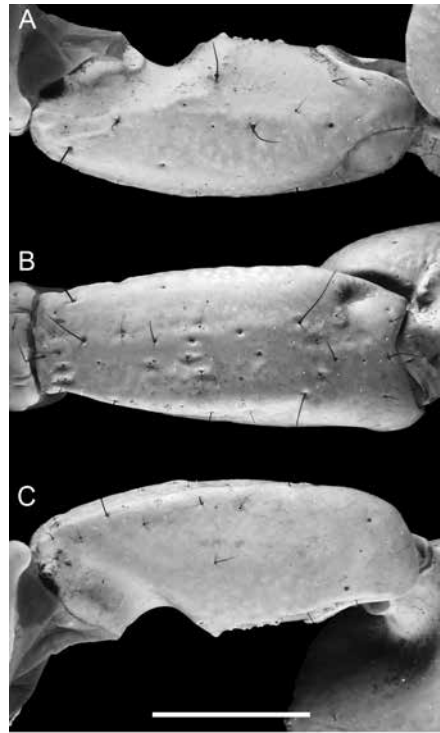


FIGURE 140. *Deccanometrus ubicki* (Kovářík, 2004), comb. nov., paratype ♀ (CAS 9071135), pedipalp patella: A. dorsal, B. retrolateral, and C. ventral aspects. Scale bar = 5 mm.

99°14'E, 21.xi.2018, 5th ASA Congress Attendees, 1 juv. ♂ (AMCC [LP 16489]). **Ubon Ratchathani Prov.:** **Khong Chiam Distr.:** Kaeng Tana, trail to Pra Cave and Phaphueng Rock Garden, 15°18'N 105°28'E, 112 m, 7.xii.2014, S.F. Loria and M.M. Locke, blacklight at night, on ground, 1 ♀ sinistral pedipalp chela (AMNH), 15°18'N 105°29'E, 112 m, 8.xii.2014, S.F. Loria and M.M. Locke, in burrow, 1 ♂ (AMNH), [tissue] (AMCC [LP 13046]).

DUBIOUS RECORDS: Ipoh [Malaysia: Perak: Kinta Distr.], ix.1971, 1 ♂ (AMNH [GD 10.003.3]). Burma [Myanmar], 15.x.1972, 1 ♀ (AMNH).

Heterometrus longimanus (Herbst, 1800)

Figures 10, 22C, D, 36C, D, 52E–H, 70B, 71B, 72B, 158, 174–177, table 2

Scorpio longimanus Herbst, 1800: 42–44, pl. II, fig. 1; Latreille, 1804: 122; Kraepelin, 1894: 29, 30, 34–39, 41, 49, 51–53, 55, 57, 246, pl.

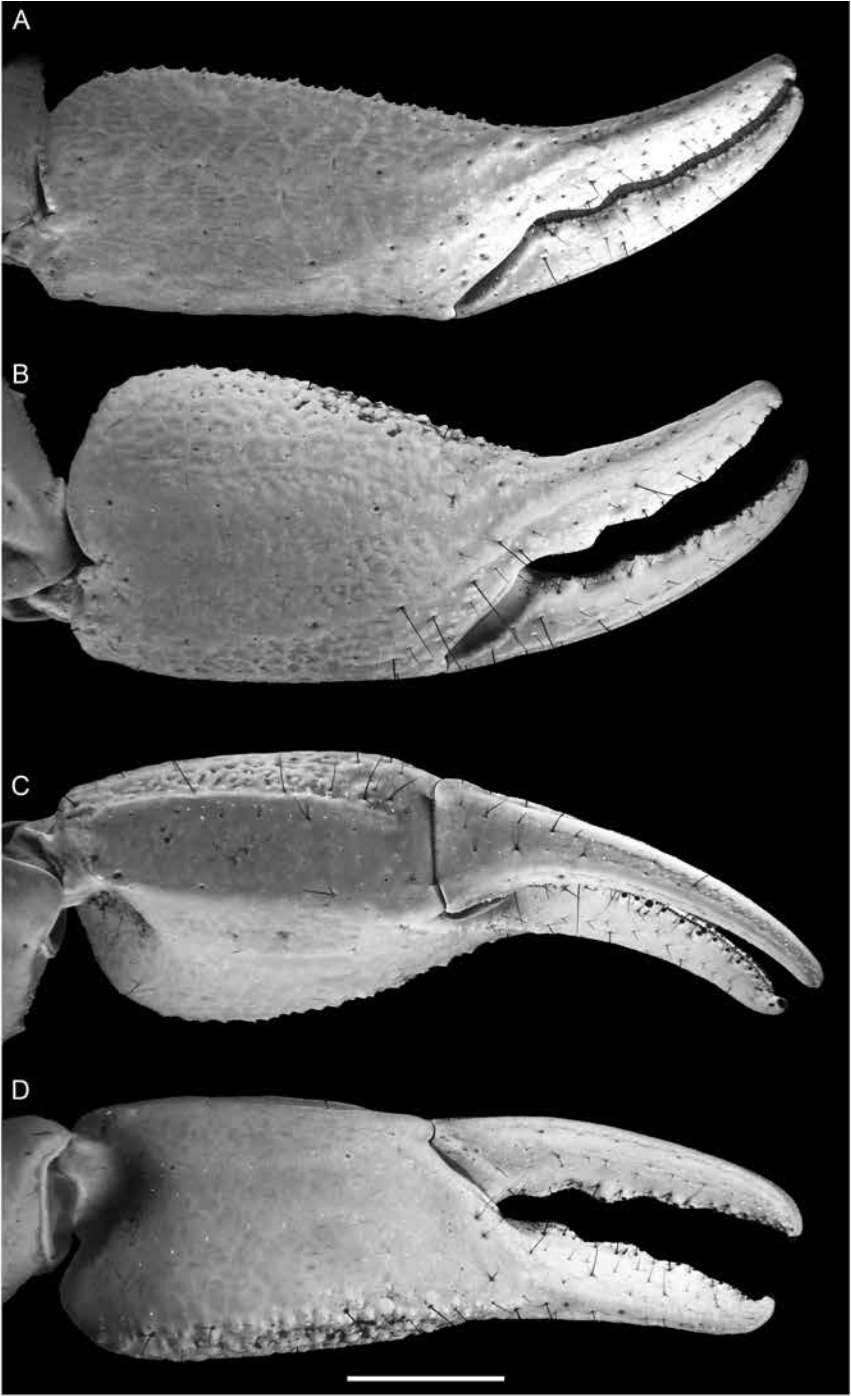


FIGURE 141. *Deccanometrus ubicki* (Kovařík, 2004), comb. nov., pedipalp chela: **A**, **B**. retrodorsal, **C**. ventral, and **D**. prolateral aspects. **A**. Paratype ♂ (CAS 9071136). **B–D**. Paratype ♀ (CAS 9071136). Scale bar = 5 mm.

- I, figs. 20, 21 (part); 1897: 537; Lönnberg, 1897b: 186; Kraepelin, 1908: 191, fig. 15.
- Buthus costimanus* C.L. Koch, 1837: 27–29, pl. CXVI, fig. 266 (synonymized by Kraepelin, 1894: 34); Newport, 1843: 295; C.L. Koch, 1850: 88.
- Centrurus galbineus* C.L. Koch, 1838: 110–112, pl. CXXXIX, fig. 320 (synonymized by Kraepelin, 1894: 34); Gervais, 1844a: 50; C.L. Koch, 1850: 89; Pocock, 1902: 365; Braunwalder and Fet, 1998: 33; Couzijn, 1981: 58.
- Buthus longimanus*: C.L. Koch, 1840: 1–3, pl. CCLIII, fig. 595; 1850: 88.
- Scorpio (Ischnurus) longimanus*: Gervais, 1844a: 69 (part).
- Palamnaeus angustimanus* Thorell, 1876b: 211–214 (synonymized by Kraepelin, 1894: 34); Pocock, 1892: 41, 42.
- Palamnaeus costimanus* var. β *borneensis* Thorell, 1876b: 217–220; 1888: 338, 414; syn. nov.
- Palamnaeus costimanus* var. γ *glauca* Thorell, 1876b: 219–221 (misidentification, part).
- Pandinus humilis* Simon, 1877: 94, 95 (synonymized by Kraepelin, 1894: 34).
- Palamnaeus longimanus*: Simon, 1884a: 361; Pocock, 1892: 41, 42; Simon, 1893: 328; 1899: 120; 1900a: 84, 97–99 (part); Schultze, 1927: 375–388, table 1, pl. 1–4; Auber, 1963: 273; Kovařík, 2004: 44.
- Palamnaeus costimanus*: Thorell, 1888: 329.
- Palamnaeus liophysa* Thorell, 1888: 338, 415–419; 1890: 90–94 (part); syn. nov.
- Palamnaeus spinifer*: Pocock, 1892: 38–42 (misidentification, part); 1894b: 85, 96.
- Palamnaeus (Scorpio) longimanus*: Pavesi, 1898: 94.
- Heterometrus longimanus*: Kraepelin, 1899: 108, 111 (part); Werner, 1902: 601; Masi, 1912: 123, 124 (part); Scheuring, 1912: 370–374, figs. 1–5; Lampe, 1918: 197; Kopstein, 1921: 118, 119, 129, 130 (part); 1923: 186, 187; Pavlovsky, 1924a: 78, pl. I, fig. 13; Kopstein, 1926: 111, 112, 115; 1927: 107; Banks, 1928: 505; Werner, 1932: 576; 1934: 277 (part), 278, fig. 348; 1936: 186; Kästner, 1941: 210, 233, fig. 192; Roewer, 1943: 228 (part); Vachon, 1952a: 37, fig. 34; Rosin and Shulov, 1963: 570; Bücherl, 1964: 59; Vachon et al., 1970: 426; Stockmann, 1979: 405; Francke and Sissom, 1984: 12, table 6; Casper, 1985: 281, 282; McCormick and Polis, 1990: 301, table 7.1; Polis and Sissom, 1990: 187, 199, 202, tables 4.2, 4.4; Pointer, 1991: 24; Lourenço, 2002: 75, table 1; Soleglad and Fet, 2003a: 8, 158, appendix C; 2003b: 5, 20, fig. 22; Kovařík, 2004: 1, 2, 23, 25–27, 44, 51, 53, table 2, fig. 19; 2009: 35, 40, 41, 48, 49, 84, 99, 107, table 1 (part), figs. 77–82, 190, 191, 255; Mirza and Sanap, 2009: 488, 490; Warburg, 2013: 152; Plíšková et al., 2016: 467, 469, 470, 473, 474; Rossi, 2016a: 15; Esposito et al., 2017: 14; 2018: 115, appendix 1.
- Heterometrus (Scorpio) longimanus*: Kraepelin, 1901: 271 (part).
- Heterometrus (Scorpio) longimanus* var. *silenus*: Kraepelin, 1901: 271 (misidentification, part).
- Heterometrus longimanus typicus*: Masi, 1912: 123 (part).
- Heterometrus liophysa*: Kopstein, 1921: 131 (part); 1923: 186 (part); Bücherl, 1964: 59; Kovařík, 2004: 1, 2, 21, 23, 51, 53, table 2 (part); 2009: 35, 40, 48, table 1 (part).
- Palamnaeus oatesii*: Schultze, 1927: 375 (misidentification).
- Heterometrus longimanus longimanus*: Giltay, 1931: 3 (part); 1935: 2 (part); Takashima, 1945: 90 (part).
- Heterometrus (Heterometrus) bengalensis*: Couzijn, 1981: 38, 73, 75–77, 80, 85, 88, 89, 117–120, 178, 182, 184, 191, table 7, figs. 17b, 18, 19, 21, 66b (misidentification, part).
- Heterometrus (Heterometrus) liophysa*: Couzijn, 1981: 116–118, 173, 184 (part); Kovařík, 1998: 137; Fet, 2000: 433 (part).
- Heterometrus (Heterometrus) liophysa liophysa*: Couzijn, 1981: 111–114, 191 (part); Fet, 2000: 433 (part).

Heterometrus (Heterometrus) longimanus: Couzijn, 1981: 6, 69, 80, 108, 111, 167, 173, 175–178, 182, 184, 188–190, figs. 21, 62, 64, 66b, 70, 71; Tikader and Bastawade, 1983: 519–521 (part); Vachon and Lourenço, 1985: 9; Kovařík, 1992: 185; 1994: 197; 1997: 183; 1998: 137 (part); Fet, 2000: 434; Kovařík, 2002: 17.

Heterometrus (Heterometrus) longimanus angustimanus: Couzijn, 1981: 34, 85, 88, 102, 103, 173, 175, 176, 189–191, table 7, figs. 29, 64; Kovařík, 1998: 137; Fet, 2000: 435.

Heterometrus (Heterometrus) longimanus belitungensis Couzijn, 1981: 35, 84, 105, 106, 176, 191, table 7, fig. 64 (synonymized by Kovařík, 2004: 1, 25, 27); Kovařík, 1998: 137; Fet, 2000: 435; Kovařík, 2002: 17; 2004: 1, 25.

Heterometrus (Heterometrus) longimanus bengkalitensis Couzijn, 1981: 35, 85, 106–108, 176, 191, table 7, fig. 64; Kovařík, 1998: 137; Fet, 2000: 435; Kovařík, 2004: 25; 2009: 40, 41; syn. nov.

Heterometrus (Heterometrus) longimanus borneensis: Couzijn, 1981: 34, 85, 104–109, 175, 176, 191, table 7, figs. 30, 64; Kovařík, 1997: 183; 1998: 137; Fet, 2000: 435; Kovařík, 2004: 25; 2009: 40.

Heterometrus (Heterometrus) longimanus humilis: Couzijn, 1981: 36, 84, 107, 109–111, 176, 177, 191, table 7, figs. 31, 64; Kovařík, 1998: 137; Fet, 2000: 435, 436.

Heterometrus (Heterometrus) longimanus longimanus: Couzijn, 1981: 6, 19, 21, 23–26, 34, 67–72, 85, 100–104, 108, 110, 111, 175, 176, 191, table 7, figs. 2d, 5d, 6d, 7a–d, 8c, 12–15, 16c, 28, 64; Tikader and Bastawade, 1983: 522–528, 533 (part), figs. 1403–1416; Fet, 2000: 435.

Heterometrus (Heterometrus) longimanus marmoratus Couzijn, 1981: 36, 85, 109, 176, 177, 191, table 7, fig. 64; Kovařík, 1998: 137; Fet, 2000: 436; Kovařík, 2004: 25; 2009: 40; syn. nov.

Heterometrus (Heterometrus) longimanus parisis Couzijn, 1981: 19, 35, 84, 88, 106, 176, 191, table 7, figs. 2e, 64 (synonymized by

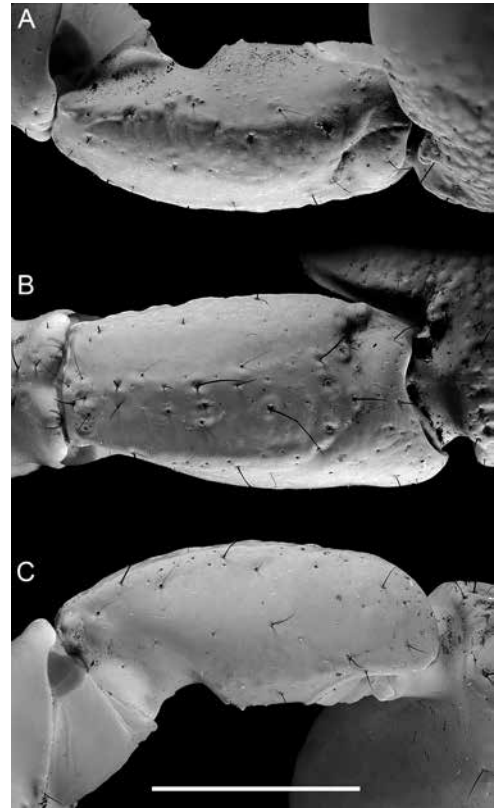


FIGURE 142. *Deccanometrus xanthopus* (Pocock, 1897), comb. nov., ♀ (AMNH), Khambatki Ghat, India, pedipalp patella: A. dorsal, B. retrolateral, and C. ventral aspects. Scale bar = 5 mm.

Kovařík, 2009: 40, 41); Kovařík, 1998: 137; Fet, 2000: 436; Kovařík, 2004: 25.

Heterometrus (Heterometrus) longimanus tarawakanensis Couzijn, 1981: 36, 84, 89, 101, 108, 176, 177, 191, table 7, fig. 64 (synonymized by Kovařík, 2004: 1, 25, 27); Kovařík, 1998: 137; Fet, 2000: 436; Kovařík, 2004: 1.

Heterometrus bengalensis: Kovařík, 2004: 1, 7, 9, 44, 53 (part); 2009: 34, 36 (part).

Heterometrus longimanus belitungensis: Kovařík, 2004: 27; 2009: 41, 84, figs. 79, 80.

Heterometrus longimanus tarawakanensis: Kovařík, 2004: 27.

Heterometrus petersii: Soleglad and Fet, 2003a: 8 (misidentification); 2003b: 5 (misidentification).

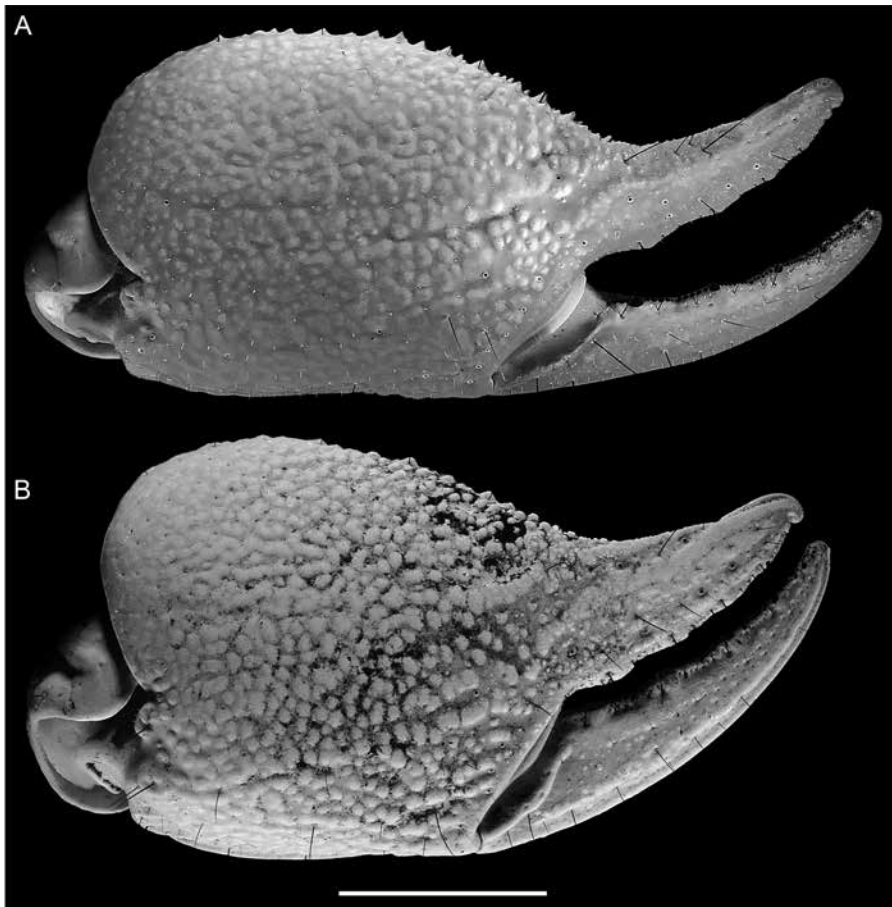


FIGURE 143. *Deccanometrus xanthopus* (Pocock, 1897), comb. nov., pedipalp chela, retrodorsal aspect. **A.** Lectotype ♂ (BMNH 1896.9.26.88-91). **B.** ♀ (AMNH), Khambatki Ghat, India. Scale bar = 5 mm.

Heterometrus longimanus paris: Kovařík, 2009: 41, 84, fig. 77.

TYPE MATERIAL: *Scorpio longimanus*: Holotype ♂, "Africa" [lost]. *Palamnaeus angustimanus*: Holotype ♂ (NMG 87), East Indies, 26.x.1843, J. Hall [examined]. *Palamnaeus costimanus* var. *γ glaucus*: Paralectotype [here designated]: 1 ♀ (NMG 88), "Bengal," 7.viii.1868, G. Litman [examined]. **INDONESIA:** *Buthus costimanus*: Holotype ♀?, Java [lost]. *Centrurus galbineus*: Holotype [sex?] [lost]. **Bangka-Belitung Islands Prov.:** *Heterometrus* (*H.*) *longimanus belitungensis*: Holotype ♂ (RMNH 786), paratype ♀ (RMNH 86), Bangka [Pulau Bangka, 02°15'S 106°00'E],

Vosmaer and Budding [examined]. **Riau Prov.:** *Heterometrus* (*H.*) *longimanus paris*: Holotype ♂, paratype ♀ (RMNH 83), Riouw [Riau], A.H.G. Blokzeyl [examined]. **Bengkalis Reg.:** *Heterometrus* (*H.*) *longimanus bengkalitensis*: Holotype ♂, paratype ♀ (MNHN RS 0048), Bengkalis [Bengkalis Island, 01°27'N 102°24'E], M. Maindron [examined]. **West Sumatra Prov.:** *Padang Panjang Reg.:* *Palamnaeus liophysa*: Syntypes: 1 juv. ♂, 1 juv. ♀ (MCSNG), Ajer Mantcior [Ajermantsjur/Ajer Mantjoer, near Padang Panjang, 00°28'S 100°24'E], Sumatra, viii.1878, O. Beccari [examined]. **Solok Reg.:** *Heterometrus* (*H.*) *longimanus*: Neotype ♂ (RMNH 291), Gunung Talang [00°59'S 100°41'E], 1000 m, 1926, V. Duivenbode



FIGURE 144. *Deccanometrus xanthopus* (Pocock, 1897), comb. nov., ♀ (AMNH), Khambatki Ghat, India, pedipalp chela: **A.** ventral, and **B.** prolateral aspects. Scale bar = 5 mm.

and E. Jacobson [examined]. **MALAYSIA: Sarawak:** *Palamnaeus costimanus* var. β *borneensis*: Syntypes: 1 ♂, 1 ♀, 1 juv. ♂ (MCSNG), Sarawak, Borneo, Doria and Beccari [examined]. **PHILIPPINES: National Capital Region:** *Pandinus humilis*: Syntypes: 3 juv. ♀ (MNHN RS 0021 [Simon coll. 2499]), Manille [Manila, 14°36'N 120°59'E], Laglaise, M.N. [examined]. **Palawan Prov.:** *Heterometrus* (*H.*) *longimanus marmoratus*: Holotype ♂, paratype ♀ (ZMUC 24639), Balabac, Dalawan Bay [07°54'N 117°05'E], 9.x.1961, Noona Danish Expedition 1961–1962 [examined]. **Tawi Tawi Prov.:** *Heterometrus* (*H.*) *longimanus tarawakanensis*: Holotype ♀, 1 subad. ♂ paratype (ZMUC 24641), Tarawakan [05°09'N

119°53'E], Tawi Tawi Island (Sulu Islands), Philippines, 7.xi.1961, Noona Danish Expedition 1961–1962 [examined].

Herbst (1800: 42) described *S. longimanus* from a male, allegedly from Africa, that belonged to the Museum of Baron de Block. Couzijn (1981: 102) was unable to locate the specimen, despite consulting several arachnologists and German museums, and therefore designated an adult male (RMNH 291) from Gunung Talang, Sumatra, Indonesia as neotype.

Simon (1877: 94, 95) based the description of *P. humilis* on an unspecified number of specimens with the data “Manila (Laglaise) (M.N.)”; a

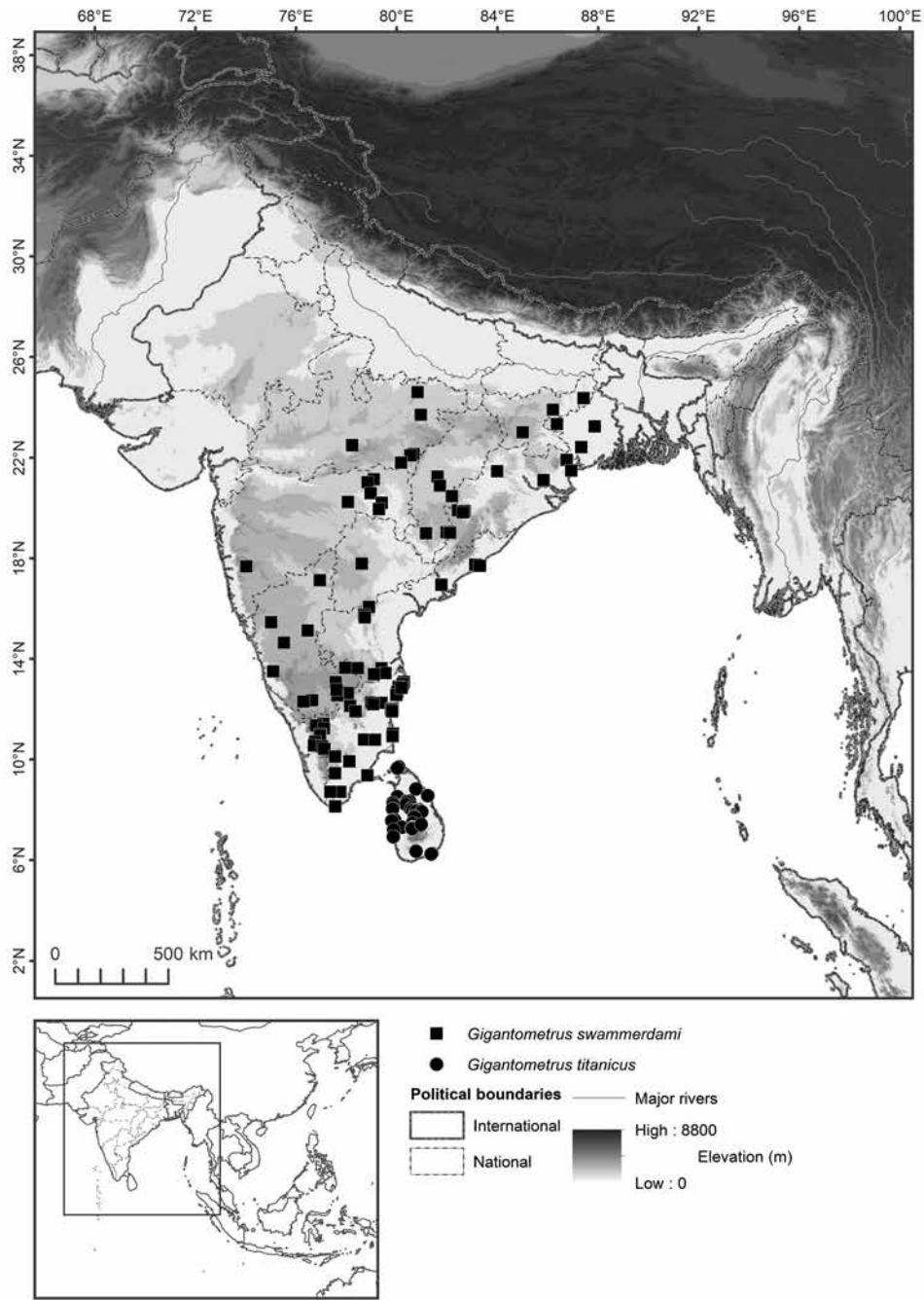


FIGURE 145. Map of South Asia, plotting known locality records of two species of *Gigantometrus* Couzijn, 1978, stat. nov., based on material examined, and verified records from virtual museums and the literature: *Gigantometrus swammerdami* (Simon, 1872); *Gigantometrus titanicus* (Couzijn, 1981), comb. nov. et stat. rev.

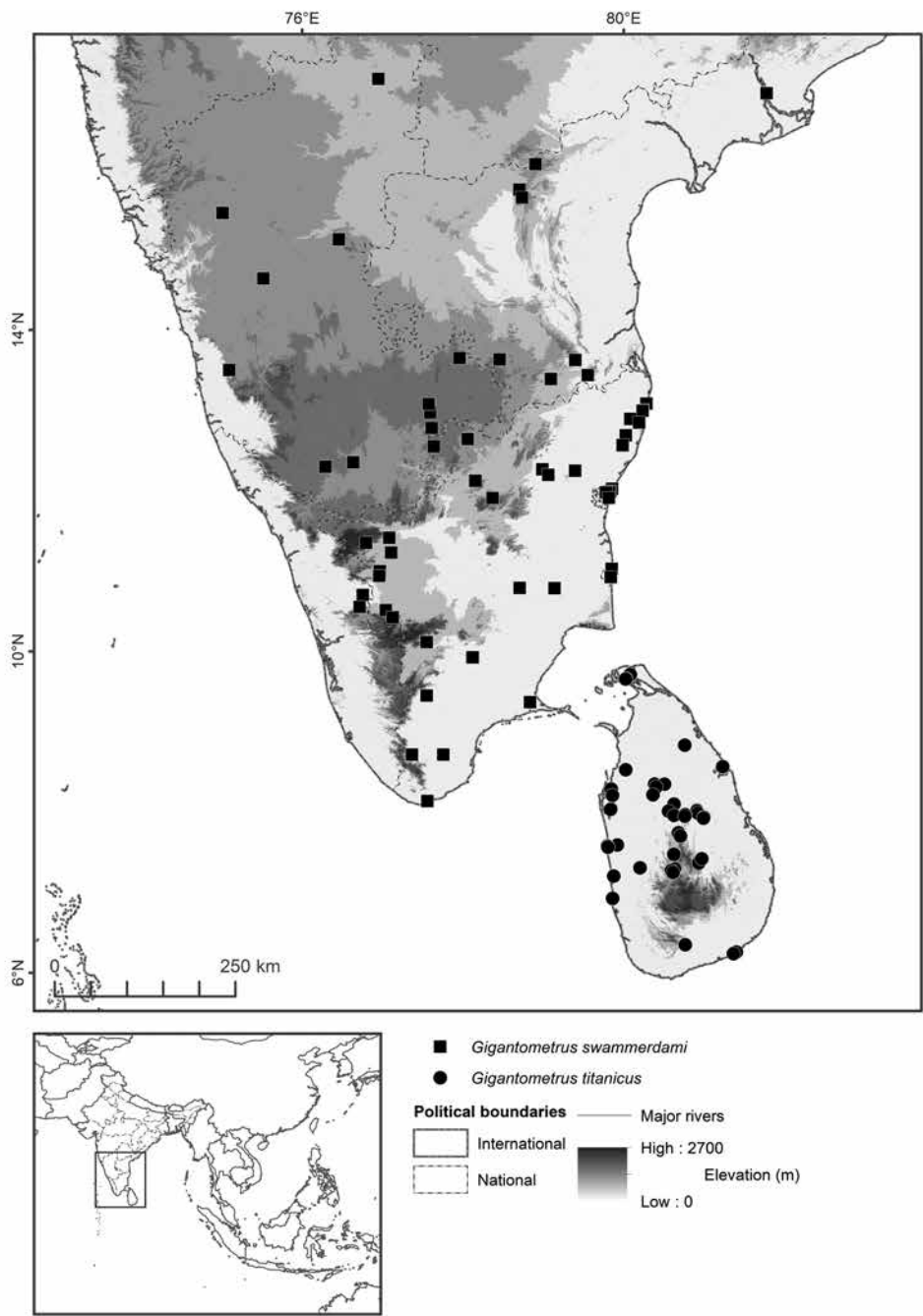


FIGURE 146. Map of South India and Sri Lanka, plotting known locality records of two species of *Gigantometrus* Couzijn, 1978, stat. nov., based on material examined, and verified records from virtual museums and the literature: *Gigantometrus swammerdami* (Simon, 1872); *Gigantometrus titanicus* (Couzijn, 1981), comb. nov. et stat. rev.

type or types were not specified. Fet (2000: 434) and Couzijn (1981: 109) mistakenly referred to the syntypes of *P. humilis* as a holotype and paratypes.

Thorell (1888) based *P. liophysa* on three syntypes from Ajer Mantcior, Sumatra, collected by Beccari. Thorell (1888: 415, 419) suggested the specimens were adult and might be male: “♂ (?) ad.” but later (Thorell, 1890: 91) stated the types were undoubtedly immature “juniores, haud dubie,” consistent with the lengths (53–67 mm) mentioned in the original description. Couzijn (1981: 113, 114) could not locate the types and therefore designated a neotype for *H. (H.) liophysa*. According to the curator (M. Tavano, in litt.), a flood damaged the MCSNG in 1970. The basement, where the arachnological collection was stored, was submerged by water and mud, gravely damaging the collections. Many jars were broken and specimens lost. It took years to recover and reorganize the collections. Presumably for this reason, the types could not be located when requested by H.W.C. Couzijn in the 1970s, leading to the conclusion they were lost. However, two of Thorell's (1888) original specimens have since been located and were examined during the present investigation. There is no doubt these specimens are part of the original series, for the following reasons. Firstly, the label data indicate they are syntypes and match the data in Thorell's (1888) description: “Ajer Mantcior, viii.1878, O. Beccari.” Secondly, although only one is male, both specimens are immature and match the size range (53–67 mm), pectinal tooth counts (12–15), and other descriptive details (e.g., telson vesicle reddish-brown) provided by Thorell (1888). The rediscovery of two of the original syntypes (the third, presumably lost in the flood) invalidates Couzijn's (1981) neotype designation in accordance with ICZN Article 75.8.

DIAGNOSIS: *Heterometrus longimanus* may be separated from other species of *Heterometrus* as follows. The carapace interocular surface is usually granular along the medial longitudinal and anterior bifurcated sulci in the male and female

(fig. 22C, D) of *H. longimanus*, whereas the frontal lobes and medial region of the interocular surface are granular with smooth areas in the male and female of *H. glaucus* and *H. thorellii*, and the interocular surface is entirely smooth in the male of *H. laevigatus* and the male and female of *H. laoticus*. The carapace anterolateral and mediolateral surfaces of the female (fig. 22D) are granular in *H. longimanus* but smooth or nearly so in *H. laoticus*, and the posterolateral surfaces of the female smooth or nearly so in *H. longimanus* but granular in all other species except *H. laoticus*. The pedipalps of the adult male are long, with femur length : posterior carapace width ratio (FL:PCW) ≥ 0.80 and femur length : carapace length ratio (FL:CL) ≥ 0.76 (fig. 174) in *H. longimanus* but short, with FL:PCW < 0.77 , FL:CL < 0.74 in *H. laoticus*, *H. petersii*, *H. silenus*, and *H. spinifer*. The pedipalp chela manus promedian carina of the female is present and granular in *H. longimanus* but absent or obsolete in *H. laevigatus*. The maximum distance between the dorsomedian and dorsal secondary carinae (DMC–DSC) of the chela manus is less than the maximum distance between the dorsal secondary and digital carinae (DSC–DC) in the male and female (fig. 177) of *H. longimanus* whereas the DMC–DSC is similar to the DSC–DC in the female of *H. glaucus*, *H. laevigatus*, and *H. thorellii*, greater than the DSC–DC in the male and similar to the DSC–DC in the female of *H. silenus*, and similar to the DSC–DC in the male and female of *H. laoticus*, *H. petersii*, and *H. spinifer*. The chela manus dorsal intercarinal surface is smooth or nearly so (fig. 177) in *H. longimanus* but shallowly reticulate in *H. glaucus*, *H. laevigatus*, and, often, *H. thorellii*. The second (subproximal) lobe of the chela movable finger of the adult male is similar to or barely larger than other lobes on the finger (fig. 177B–D) in *H. longimanus* but more strongly developed than other lobes on the finger, with a correspondingly well-developed notch in the fixed finger in all other species except *H. glaucus* and *H. thorellii*. Macroseta *st* on the proventral surface of the basitarsus of leg I is setiform (fig. 52E) in *H.*

longimanus but spiniform in *H. laevigatus* and *H. thorellii*; *st* on the proventral surface of the basitarsus of leg II is usually spiniform (fig. 52F) in *H. longimanus* but setiform in all other species except *H. laevigatus*, *H. glaucus*, and *H. thorellii*; *sb* on the proventral surface of the basitarsus of leg III is setiform (fig. 52G) in *H. longimanus* but spiniform in *H. glaucus*, *H. petersii*, and *H. spinifer*. The lateral surfaces of mesosomal tergites I–VI in the female (fig. 175A) are granular in *H. longimanus* but smooth in *H. laevigatus*, *H. laoticus*, and *H. thorellii*. The ventrosubmedian and ventrolateral carinae of metasomal segments I–IV are granular or costate-granular on segment IV only and costate on segments I–III (fig. 72B) in *H. longimanus* but granular on segments I–IV, II–IV (costate on I), or III and IV (costate on I and II) in *H. laoticus* and *H. silenus*. The ventral intercarinal surfaces of segments III and IV of the female are smooth in *H. longimanus* but granular in *H. laoticus*. The telson is dark reddish brown and paler than metasomal segment V in *H. longimanus* (figs. 174, 175) but blackish and as dark as segment V in *H. laevigatus*, *H. laoticus*, *H. silenus*, and *H. thorellii*. The width of the telson vesicle is greater than the width of metasomal segment V in the male (figs. 70B, 72B) of *H. longimanus* but approximately equal to or less than the width of segment V in the male of all other species except *H. glaucus*.

DISTRIBUTION: This species has the broadest distribution in the genus (fig. 158, table 2), occurring from the Andaman Islands of India (recorded from South Andaman), through peninsular Malaysia and Tinggi Island (recorded in the states of Johor, Pahang and Selangor), Singapore (including Pulau Ubin), the Riau archipelago, and the islands of Sumatra, Simeulue, Bangka, Belitung, Bengkalis, Java, Madura, Miang-Besar, and Borneo (recorded in Brunei, the Indonesian provinces of Aceh, Bangka-Belitung Islands, East Java, East Kalimantan, Lampung, North Kalimantan, North Sumatra, Riau, South Sumatra, West Kalimantan, and West Sumatra, and the Malaysian states of Sabah and Sarawak), to the Philippine islands of Balabac, Luzon, Mindanao, Palawan, Panay, and

Tawi Tawi in the Sulu archipelago (recorded in the National Capital Region and the provinces of Cotabato, Maguindanao, Misamis Occidental, Palawan, Tawi Tawi, and Zamboanga). The distribution of *H. longimanus* overlaps those of *H. glaucus* in Sumatra and the Simeulue Islands, *H. petersii* in Singapore, *H. spinifer* in southern peninsular Malaysia, and *J. cyaneus* in Luzon.

Couzijn (1981: 178) and Fet (2000: 434) suggested that records of *H. longimanus* from the Andaman Islands, Nicobar Islands, and Burma “do not belong to this species ... [and] may be misidentified *H. bengalensis*.” Records of *H. longimanus* from the Andaman Islands have been verified, whereas records from the Nicobar Islands are referable to *H. glaucus*. Records of *H. longimanus* from the Mergui (Myeik) archipelago, Myanmar are referable to *H. laevigatus*, and from the Burmese (Myanmar) mainland, to *H. laevigatus* and *H. thorellii*.

An unconfirmed record of *H. longimanus* from the Sula Islands, in the Moluccas, east of Wallace’s Line (Couzijn, 1981: 178), probably refers to the Sulu archipelago between northeastern Borneo and Mindanao, where *H. longimanus* has been recorded (Prendini et al., 2003).

ECOLOGY: Specimens with ecological data were collected from sea level to 657 m elevation in or near backyards, in primary or secondary forest on small hills, limestone formations, coconut plantations, tree holes, and rock walls. In the Philippines, two or more specimens were often found together under loose bark or in the cavities of dead standing trees and stumps, or under rotting logs, in damp, humid primary forest (Schultze, 1927). It is unclear whether this species constructs burrows. The habitat and habitus are consistent with the lapidicolous and corticolous ecomorphotypes (Prendini, 2001b). The following scorpions were found in sympatry: the buthids *Lychas hosei* (Pocock, 1891) and *Lychas shelfordi* (Borelli, 1904); the hormurid *Liocheles australasiae*; the scorpiopid *Parascorpiops montana* Banks, 1928, and an undetermined chaerilid, genus *Chaerilus*.



FIGURE 147. *Gigantometrus swammerdami* (Simon, 1872), comb. nov., lectotype ♂ (*Palamnaeus swammerdami flavimanus* Pocock, 1900, syn. nov.) (BMNH 1899.11.2.292-3), habitus: **A.** dorsal and **B.** ventral aspects. Scale bar = 10 mm.

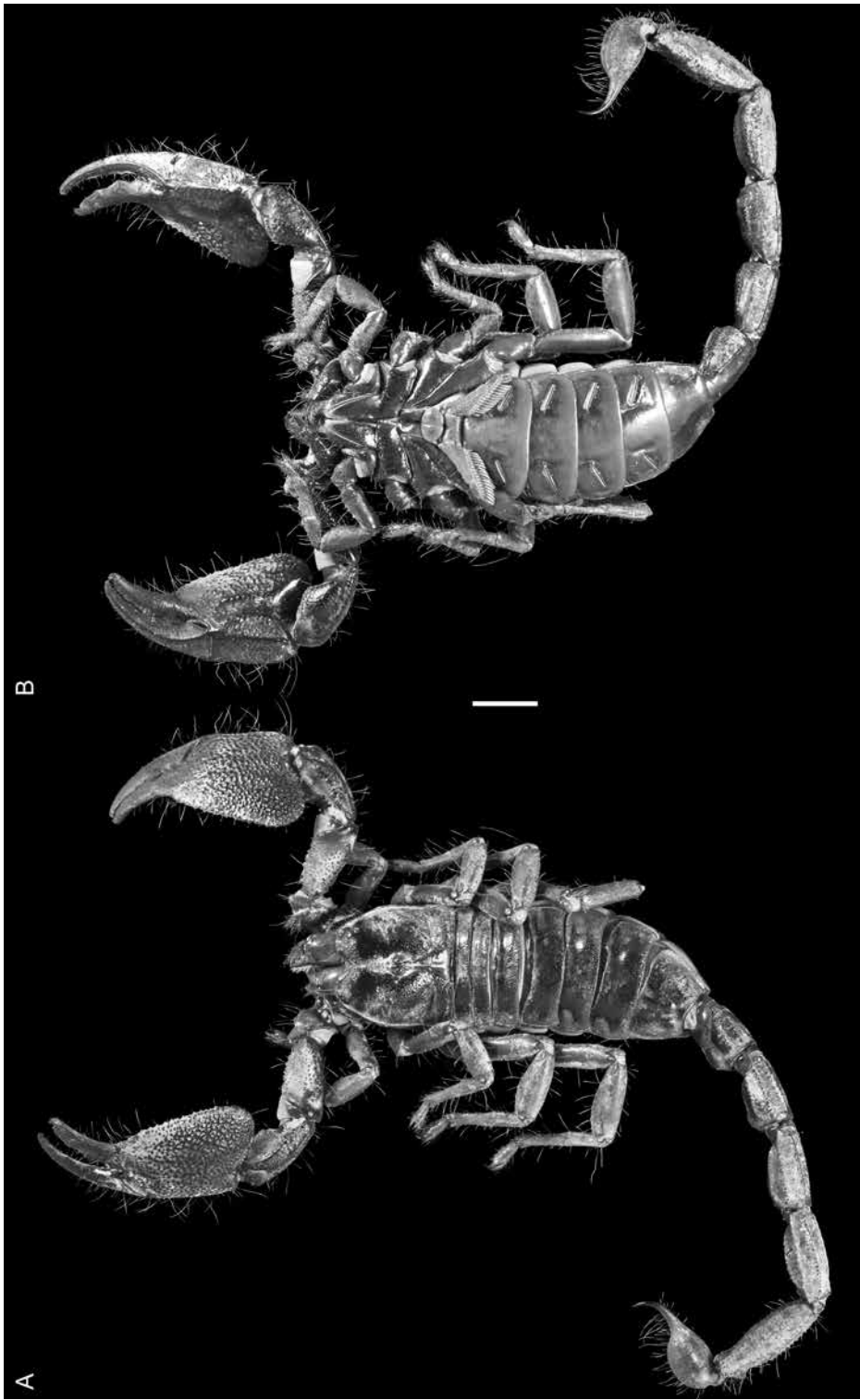


FIGURE 148. *Gigantometrus swammerdami* (Simon, 1872), comb. nov., ♀ (FMNH 086 257), habitus: A. dorsal and B. ventral aspects. Scale bar = 10 mm.

REMARKS: This species was previously accommodated in the nominal subgenus of *Heterometrus* by various authors (e.g., Couzijn, 1981; Fet, 2000; Kovařík, 1992, 2002). Fet (2000) and Kovařík (2004, 2009) followed Kraepelin (1894) in listing *Buthus costimanus*, *Centrurus galbinus*, and *Pandinus humilis* as junior synonyms of *H. longimanus*. Whereas Kovařík (2004: 25) listed Simon (1901: 78) as the first to synonymize *Palamnaeus angustimanus* with *H. longimanus*, Fet (2000: 434) correctly listed Kraepelin (1894: 34) as the first to do so.

Neither Couzijn (1981: 113) nor Kovařík (2004: 23) examined the types of *Palamnaeus liophysa* which were presumed to be lost. Consequently, their concepts of the species were based on the assessments of previous workers, most if not all of whom appear to have followed Thorell (1888, 1890). Thorell (1888) based *P. liophysa* on three immatures (53–67 mm in length) from Ajer Mantcior, Sumatra, but subsequently (Thorell, 1890: 94) redescribed the species from several larger, allegedly adult specimens including a male (100 mm in length) and female (132 mm in length) from the island of Nias, considered to be conspecific with the syntypes from Sumatra:

Cel. Modigliani exempla feminea adulta sat multa et masculum adultum singulum in Nias ad Gunung Sitoli et Lelemboli collegit. Cum iis tria juniora cepit, quae hujus certe sunt speciei, et quae ab exemplo *P. liophysae* Thor., distinguere nequeo; quam ob rem credo, speciem illam Sumatranam nihil nisi juniores speciei Niasensis jam a me adumbratae esse. Pullulos, de quibus supra locutus sum, ad Lelemboli et Fadoro in Nias invenit Modigliani.

Rediscovery and examination of the two remaining syntypes of *P. liophysa* during the present investigation revealed they are conspecific with *H. longimanus*, and not with the species occurring on Nias, for which an earlier, available name, *Palamnaeus costimanus* var. γ *glaucus*, is revalidated. Accordingly, the following new synonym is presented: *Palamnaeus liophysa* Thorell, 1888 = *Heterometrus longimanus* (Herbst, 1800), syn. nov.

Eight subspecies of *H. longimanus* were listed by Couzijn (1981), and followed by Fet (2000), who treated *P. angustimanus*, *P. humilis*, and *Palamnaeus costimanus* var. β *borneensis* as *H. l. angustimanus*, *H. l. humilis*, and *H. l. borneensis*, respectively. The other five subspecies were described by Couzijn (1981): *H. (H.) l. belitungensis*; *H. (H.) l. bengkalitensis*; *H. (H.) l. marmoratus*; *H. (H.) l. paris*; *H. (H.) l. tarawakensis*.

Kovařík (2004, 2009) followed earlier authors (Kraepelin, 1894; Simon, 1901) in listing *P. angustimanus* and *P. humilis* as synonyms of *H. longimanus*, and Kovařík (2004: 25) synonymized *H. (H.) l. belitungensis* and *H. (H.) l. tarawakensis* with the nominotypical form, noting:

This species is known under a number of older names and as many as eight subspecies. I have studied the paratypes of *H. l. belitungensis* Couzijn, 1981 and specimens from nearly the entire area of known distribution of the species and have not found any morphological differences indicating the existence of any subspecies. I have examined also [CAS] specimens from the type locality of *H. l. tarawakanensis* Couzijn, 1981 and have not found them to differ in any way from the nominotypical subspecies. However, I have not studied the types of all the subspecies.

Kovařík (2004: 25, 2009: 40) listed *Palamnaeus costimanus borneensis*, *Heterometrus (H.) l. bengkalitensis*, and *H. (H.) l. marmoratus* under *H. longimanus* but did not formally synonymize these taxa. Kovařík (2004: 25) also listed *H. (H.) l. paris* under *H. longimanus* but later synonymized it (Kovařík, 2009: 40).

Based on the examination of material from across the distribution of *H. longimanus*, including the types of *P. angustimanus*, *P. costimanus* var. β *borneensis*, *P. humilis*, *P. liophysa*, *H. (H.) l. belitungensis*, *H. (H.) l. bengkalitensis*, *H. (H.) l. marmoratus*, *H. (H.) l. paris*, and *H. (H.) l. tarawakensis*, the opinion of Kovařík (2004: 25) that there is no evidence for subspecies is upheld. The following synonyms are confirmed: *Buthus costimanus* C.L. Koch, 1837 = *Heterometrus longimanus* (Herbst, 1800), synonymized by Kraepelin (1894); *Centrurus galbinus* C.L. Koch, 1838 = *H. longimanus*, synonymized by Kraepelin (1894); *Palamnaeus angustima-*

nus Thorell, 1876 = *H. longimanus*, synonymized by Kraepelin (1894); *Pandinus humilis* Simon, 1877 = *H. longimanus*, synonymized by Kraepelin (1894); *Heterometrus* (*H.*) *longimanus belitungensis* Couzijn, 1981 = *H. longimanus*, synonymized by Kovařík (2004); *Heterometrus* (*H.*) *longimanus paris* Couzijn, 1981 = *H. longimanus*, synonymized by Kovařík (2009); *Heterometrus* (*H.*) *longimanus tarawakanensis* Couzijn, 1981 = *H. longimanus*, synonymized by Kovařík (2004). Additionally, the following new synonyms are presented: *Palamnaeus costimanus* var. *β borneensis* Thorell, 1876 = *H. longimanus*, syn. nov.; *Palamnaeus liophysa* Thorell, 1888 = *H. longimanus*, syn. nov.; *Heterometrus* (*H.*) *longimanus bengkalitensis* Couzijn, 1981 = *H. longimanus*, syn. nov.; *Heterometrus* (*H.*) *longimanus marmoratus* Couzijn, 1981 = *H. longimanus*, syn. nov.

MATERIAL EXAMINED: 1 ♀ (AMNH), 1 ♀ (LKC ZRC-ARA 678), 1 subad. ♀, 1 juv. ♀ (LKC ZRC-ARA 810), 1 ♂, 3 ♀ (MCZ), 2 ♂ (MCZ 103093); iii.2008, ex pet trade, 1 subad. ♂ (AMNH [LP 8269]), pedipalp chela (AMCC [LP 8269]). Borneo, H.W. Smith, 1 ♀ (MCZ 103089), 1898, 1 ♂, 2 ♀ (MCZ 103094), 1989, 1 ♂ (LKC ZRC-ARA 684). Philippines, Burma, etc., 1 ♂ (AMNH [3236]). **BRUNEI:** Brunei [04°30'N 114°40'E], 2.vi.1989, confiscated by Paya Labor custom, 1 ♂ (LKC ZRC-ARA 685). **INDONESIA:** 1 ♂, 1 ♀ (ZMH); Java, 1 subad. ♂ (MCZ 12577 ex Nathan Banks coll.); Krapoh, vi.1892, Kannegijeter, 1 ♂, 5 ♀, 2 juv. ♂, 2 juv. ♀ (RMNH 85); Parnok Meja (Thomas' Chicken Farm), 29.xi.1996, 1 ♂, 1 juv. ♀ (LKC ZRC-ARA 662); Sumatra, 1927, W.M. Mann (National Geographic Society–Smithsonian Institution Expedition), 1 ♂ (USNM 145/564), 1 subad. ♀ (USNM); West Sumatra, 1899, 1 ♂, 1 juv. ♂ (SAM 5106 ex ZMH). **Bangka-Belitung Islands Prov.:** Bangka [Pulau Bangka, 02°15'S 106°00'E], Vosmaer and Budding, 10 ♂, 5 ♀ (RMNH 86), 1933, F. Kopstein, 1 ♂ (LKC ZRC-ENT 7966). **East Kalimantan Prov.:** *East Kutai Reg.:* Poeloe Miang Island [Miang-Besar Island, 00°43'N 118°00'E], Borneo, 2.xii.1902, Dr. T. Lorenz, 3 ♀ (ZMH). **North Sumatra Prov.:** *Deli Serdang Reg.:* Bandar Kwalu [03°21'N 98°52'E], Geli, 7.viii.1913, Van Outtfarken, 2 ♂, 3 ♀ (ZMH). **Riau Islands Prov.:** Little Siak River, E Sumatra, 11.iv.1906, W.L. Abbott, 1 subad. ♂ (USNM 57-582). Riouw [Riau], A.H.G. Blokzeyl, 2 ♂ (RMNH 83). **Batam City Reg.:** Pulau Grallang [Galang], Rhio [Riau] Archipelago, ix.1926, C.P. Brooke, 4 ♀ (LKC ZRC-ARA 665, ZRC-ENT 7973–7975), 1 subad. ♂ (LKC

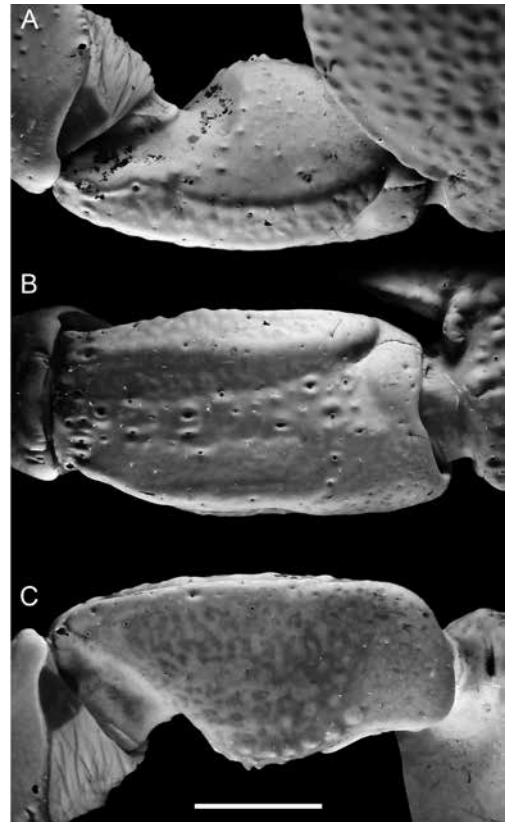


FIGURE 149. *Gigantometrus swammerdami* (Simon, 1872), comb. nov., lectotype ♂ (*Palamnaeus swammerdami flavimanus* Pocock, 1900, syn. nov.) (BMNH 1899.11.2.292-3), pedipalp patella: **A.** dorsal, **B.** retro-lateral, and **C.** ventral aspects. Scale bar = 5 mm.

ZRC-ENT 7972), 1 juv. ♂ (LKC ZRC-ARA 777). **Bengkalis Reg.:** Bengkalis [Bengkalis Island, 01°27'N 102°24'E], M. Maindron, 2 ♀, 1 juv. ♀ (MNHN RS 0048), Bengkalis, Rijk Siak, P.J. Losgert/Loschert, 3 ♂, 4 ♀, 1 subad. ♂ (RMNH 82). *Indragiri Hulu Reg.:* Somgei [Sangei] Lalah [Sungai Lala, 0°25'S 102°14'E], Judragiri, Sumatra, 26.viii.1901, W. Burchard, 2 ♂, 1 subad. ♂ (ZMH). *Lingga Reg.:* Lingga Island [00°10'S 104°39'E], 26.viii.1901, 1 ♀ (USNM). *Natuna Reg.:* Pulau Panjang [02°45'N 108°55'E], 11.viii.1931, Pur, 1 ♀ (LKC ZRC-ENT 7650 [ZRC-ENT 7221]); Pulau Perassan [Serasan], Natuna Islands [02°31'N 109°03'E], 19.viii.1931, 1 ♀ (LKC ZRC-ENT 7221), 29.viii.1931, 1 ♀ (LKC ZRC-ENT 7220). **West Kalimantan Prov.:** *Pontianak City:* Pontianak [00°05'S 109°16'E], 1893, F. Will, 2 subad. ♀, 1 juv. ♀ (NM 10333 ex SMF). **West Sumatra Prov.:** *Solok Reg.:* Gunung Talang [00°59'S 100°41'E], 1000 m,



FIGURE 150. *Gigantometrus swammerdami* (Simon, 1872), comb. nov., lectotype ♂ (*Palamnaeus swammerdami flavimanus* Pocock, 1900, syn. nov.) (BMNH 1899.11.2.292-3), pedipalp chela: A. retrodorsal, B. ventral, and C. prolateral aspects. Scale bar = 5 mm.



FIGURE 151. *Gigantometrus swammerdami* (Simon, 1872), comb. nov., paralectotype ♀ (*Palamnaeus swammerdami flavimanus* Pocock, 1900, syn. nov.) (BMNH 1899.11.2.292-3), pedipalp chela: **A.** retrodorsal, **B.** ventral, and **C.** prolateral aspects. Scale bar = 5 mm.

1926, V. Duivenbode and E. Jacobson, 2 ♀ (RMNH 291). **MALAYSIA: Johor:** *Mersing Distr.*: Aor Island, South China Sea [Pulau Aur, 02°27'N 104°31'E], vi.1938, 1 ♀ (LKC ZRC-ENT 7957), 1 juv. ♀ (LKC ZRC-ENT 7956). *Tangkak Distr.*: Mt. Ophir [Gunung Ledang, 02°22'N 102°37'E], viii.1905, 2 ♂ (LKC ZRC-ENT 7968, 7969), 2 ♀ (LKC ZRC-ENT 7970, 7971). **Pahang:** Pahang [03°49'N 103°19'E], 15.viii.1907, 1 subad. ♂ (LKC ZRC-ENT 7958), 1 juv. ♂, 2 juv. ♀ (LKC ZRC-ENT 7959). **Sabah:** *Sandakan Div.*: Bettotan [Batatan, 05°47'N 117°50'E], iv–viii.1927, S. Fize, 3 juv. ♂ (LKC ZRC-ARA 771, 773, 776), 6.viii.1927, S. Fize, 1 juv. ♀ (LKC ZRC-ENT 772), 7.viii.1927, S. Fize, 1 ♂ (LKC ZRC-ENT 774), 8.viii.1927, S. Fize, 1 ♂ (LKC ZRC-ENT 775); Danum [Danum Valley, 04°58'N 117°41'E], Borneo, 1.x.1996, H.H. Tan et al., 1 ♂ pedipalp chela (LKC ZRC-ARA 660); Kinabatangan Distr., Kampung Bilit, Myne Resort, near Kinabatangan River, 05°29'N 118°14'E, 20–66 m, 22–23.vii.2013, S.F. Loria and J. Huff, 1 ♂, 1 subad. ♂, 1 juv. ♀ (AMNH), 1 juv. ♂ (AMCC [LP 12114]); Kinabatangan Distr., northern Borneo, SE end of Dewhurst Bay [05°35'N 118°35'E], 6.v–15.vi.1950, R.F. Inger and D.D. Davis, 1 ♀ (FMNH 086 267); Pasir [Bukit Pasir, 05°37'N 117°44'E], eastern Borneo, 1926, T. Barbour, 1 subad. ♀ (MCZ); Sandakan [05°50'N 118°07'E], northern Borneo, 10.vii.1929, K.P. Schmidt, 1 ♂, 2 juv. ♀ (FMNH 086 266). *West Coast Div.*: Kasigui [05°55'N 116°07'E], northern Borneo, 16.ix.1960, 1 ♂ (USNM); Ranau [05°57'N 116°40'E], northern Borneo, 29. viii.1953, B.C. Walton, 2 ♀ (USNM); Ranau vicinity, northern Borneo, viii.1953, R. Traub, 1 ♀ (USNM). **Sarawak:** Sarawack, Borneo, 1 subad. ♀ (AMNH); Sarawak, Borneo, 1 ♂ (AMNH); Sundu [Sunda, Borneo], 1920, H.W. Smith, 1 ♀, 2 subad. ♂, 2 juv. ♂ (MCZ); Baram [04°33'N 114°06'E], ix.1920, 1 ♀, 1 subad. ♀, 1 juv. ♀ (LKC ZRC-ARA 667), v.1920, H.W. Smith, 1 subad. ♂, 1 juv. ♂ (MCZ 103097); Baram River, Borneo, Dr. E. Mjöberg, 1 ♂ (MCZ). *Bintulu Div.*: Belaga [03°12'N 113°56'E], vi.1967, S. Thomas, 3 ♂ (USNM); Pesu Stream [03°07'N 113°42'E], 1 subad. ♀, 1 juv. ♀ (FMNH 086 242). *Kuching Div.*: Bau Distr., Fairy Cave, 01°23'N 110°07'E, 44 m, 8.viii.2013, J. Huff, A. Ang, and L. Qie, under limestone outside cave, 1 ♂ (AMNH); Goebilt [01°38'N 110°28'E], Borneo, Roger and Hornby, 1 ♀ (MCZ); Kubah National Park, Matang, 4.2 km from front gate, 01°36'N 110°12'E, 657 m, 5–6.viii.2013, J. Huff and A. Ang, rock wall with minimal moss growth, 1 ♂ (AMNH), 1 juv. ♀ (AMCC [LP 12116]); Kuching, Reservoir Park [04°33'N 110°21'E], 18.viii.2002, I. Das, 1 subad. ♀ (LKC ZRC-ARA 668); Kuching, 8 Jalan Ong Kwan Hin, 01°33'N 110°21'E, 29 m, 6.viii.2013, J. Huff

and A. Ang, in backyard under rocks and debris, 1 juv. ♀ (AMNH), 1 juv. ♂ (AMCC [LP 12139]); Kuching, in overgrown residential area between Taman Bunga Teratai and inner recesses of Lintang Park, within central city area, 01°32'N 110°21'E, 1–20.viii.2010, A. Ang, found perched face down on trunk of tree roughly 2 ft. above ground level, gave birth in captivity on 14.iv.2011 and 18.iv.2012, 5 ♂, 5 ♀ (AMNH); residential property off Jalan Mendu, 2.5 km from Kuching City Centre, 01°33'N 110°22'E, 27.xi.2010, A. Ang, garden shed, 5 ♂, 5 ♀ (AMNH); Mt. Matang [01°35'N 110°13'E], 500 ft., vii.1956, R. Inger, 1 juv. ♀ (FMNH 086 254); Mt. Poe [Mt. Pueh, 01°48'N 109°41'E], iv.1923, 3500 ft., 1 ♂ (LKC ZRC-ENT 7967). *Miri Div.*: Gunung Mulu National Park, trails around park headquarters, 04°03'N 114°49'E, 58 m, 6.v.2014, S.F. Loria and P. Horsley, 1 ♀, 1 subad. ♂, 1 subad. ♀, 1 juv. ♂ (AMNH), trails near research headquarters, 04°03'N 114°49'E, 40 m, 29.vii–5. viii.2013, J. Huff and A. Ang, 1 ♂, 1 subad. ♀, 2 juv. ♀ (AMNH), 1 juv. ♀ (AMCC [LP 12115]); Racer Cave, 04°04'N 114°50'E, 34 m, 2–3.viii.2013, L. Qie, J. Huff, L. Kumpang, M. Peter and A. Ang, pedipalp chela (AMNH). Marudi [03°42'N 114°31'E], Peat Swamp Forest, ix.1998, found smashed on fallen log, 1 ♂ (LKC ZRC-ENT 7038). **Selangor:** *Kuala Selangor Distr.*: Bukit Malawati, Kuala Selangor, 03°20'N 101°15'E, 8–12 m, 9.vi.2013, L. Prendini and S.F. Loria, graveyard with secondary forest on slope of small hill, granitic outcrops under moderate canopy, under stones and old concrete blocks around graves, 1 ♀, 1 juv. ♀ (AMNH), 1 juv. ♀ (AMCC [LP 11948]). **PHILIPPINES:** 2 ♀ (USNM); 1884, M. Mareke, 2 ♀ (MNHN RS 0054); Philippinae ins., 1 ♂, 1 juv. ♀ (MNHN RS 0153 [Simon coll. 2499]); Mindanao, T.B. McCown, 1 ♀ (USNM). **Capiz Prov.**: *First Distr.*, Roxas City: near Rokas City [Roxas City, 11°35'N 122°45'E], Palawan, ix.1975, 1 juv. ♀ (AMNH). **Cotabato Prov.**: *First Distr.*, Cotabato City: Cotabato City [07°13'N 124°15'E], Mindanao, near sea level, 28. xii.1946, F.G. Werner, Philippine Zool. Exped., 1 ♀ (FMNH 086 249), 29.xii.1946, F.G. Werner, Philippine Zool. Exped., 1 juv. ♀ (FMNH 086 240). *First Distr.*, Parang Municip.: Bugasan [07°27'N 124°16'E], Parang, Mindanao, near sea level, 12.xii.1946, F.G. Werner, Philippine Zool. Exped., 1 ♀ (FMNH 086 243). **Laguna Prov.**: *First Distr.*, Los Baños Municip.: Mt. Makiling [14°08'N 121°12'E], Luzon, Baker, 1 ♀, 1 subad. ♀, 9 juv. ♀, 2 juv. (AMNH), 1 ♀ (MCZ 103099 ex Nathan Banks coll.). **Palawan Prov.**: *Second Distr.*: Puerto Princesa City: Iwahig [09°45'N 118°40'E], near sea level, ii.1947, F.G. Werner, Philippine Zool. Exped., 1 juv. ♀ (FMNH 086 241); P. Princess [Puerto Princesa, 09°44'N

118°44'E], Palawan, Baker, 3 ♀ (MCZ); Puerto Princessa [Puerto Princessa], Palawan, 3 juv. ♂ (MCZ 59304). *Brooke's Point Municip.*: Brooke's Point [08°49'N 117°47'E], Palawan Island, near sea level, 28.iv.1947, Philippine Zool. Exped., secondary coconut growth, 5 subad. ♀, 34 juv. ♀ (FMNH 086 244), 1 ♀, 7 subad. ♀, 24 juv. ♀ (FMNH 086 245), 1 ♀, 5 subad. ♀, 29 juv. ♀ (FMNH 086 247), same data, except: 7.v.1947, 1 ♀, 2 subad. ♀, 2 juv. ♂, 40 juv. ♀ (FMNH 086 246), same data, except: 8.v.1947, 1 subad. ♀, 1 juv. ♀ (FMNH 086 258). **Tawi Tawi Prov.**: Tarawakan [05°09'N 119°53'E], Tawi Tawi Island, Philippines (Sulu Islands), 7.xi.1961, Noona Danish Expedition 1961–1962, 1 juv. ♀ (ZMUC 24641). **Zamboanga Prov.**: *Zamboanga City*: Zamboanga [06°55'N 122°04'E], Mindanao Island, B.P. Clark, 1 ♀, 1 subad. ♀ (MCZ 103085). **SINGAPORE**: Singapore [01°22'N 103°48'E], 1 ♀ (MCZ 12553), 1903, 1 ♂ (LKC ZRC-ENT 7984), xi.1932, C.H. Kay, 1 ♂ (LKC ZRC-ARA 674); Pulau Ubin [01°24'N 103°58'E], ii.1927, 2 ♂ (LKC ZRC-ENT 7980, 7982), 1 ♀ (LKC ZRC-ENT 7983), 1 subad. ♂ (LKC ZRC-ENT 7981).

DUBIOUS RECORDS: "Africa," 1 ♀ (MCZ 103086). Amballa [India: Haryana: Ambala Distr.: Ambala, 30°23'N 76°47'E], 70 mi. S, 1 ♀ (MCZ 88162).

Heterometrus petersii (Thorell, 1876)

Figures 10, 158, 178, table 2

- Palamnaeus petersii* Thorell, 1876a: 13, nomen nudum; 1876b: 214–217; 1888: 335, 338, 339, 414; 1889: 588–590 (part).
Palamnaeus petersii: Thorell, 1876b: 164.
Palamnaeus petersii: Simon, 1884a: 361.
Palamnaeus petersii: Pocock, 1892: 38–40 (part); Kovařík, 2004: 2.
Palamnaeus spinifer: Pocock, 1892: 39–42 (misidentification, part); 1894b: 316 (misidentification, part).
Scorpio longimanus: Kraepelin, 1894: 34–39 (misidentification, part).
Palamnaeus petersii: Kraepelin, 1894: 35.
Heterometrus longimanus: Kraepelin, 1899: 108, 111 (misidentification, part).
Palamnaeus oatesii Pocock, 1900a: 84, 98, 99 (misidentification, part); Flower, 1901: 34, 35 (misidentification, part); Kovařík, 2004: 41, fig. 27; syn. nov.

- Heterometrus (Scorpio) longimanus*: Kraepelin, 1901: 271 (misidentification, part).
Heterometrus oatesii: Kraepelin, 1913: 167 (misidentification, part).
Heterometrus longimanus petersii: Giltay, 1931: 4 (part).
Heterometrus oatesii: Giltay, 1931: 4 (part); Takashima, 1945: 94 (part).
Heterometrus longimanus petersii: Fage, 1933: 27 (part).
Heterometrus longimanus petersii: Takashima, 1945: 90, 91 (part); 1952: 34 (part).
Heterometrus (Heterometrus) spinifer: Couzijn, 1981: 73, 94, 96, 173, 175, 182, 187, 189, 190, figs. 62, 66b (misidentification, part); Fet, 2000: 437, 438 (part).
Heterometrus (Heterometrus) spinifer spinifer: Couzijn, 1981: 19, 32, 75–77, 83, 89–93, 167, 174, 191 table 7, figs. 2b, 17b, 18, 19, 63 (misidentification, part); Fet, 2000: 438 (part).
Heterometrus longimanus: Gopalakrishnakone et al., 1995: 456–458, figs. 3, 4 (misidentification).
Heterometrus spinifer: Robert, 1999: 19 (misidentification, part); Prendini et al., 2003: 192, 193, 202, 203, 205, 208, 209, 218, 222, 252–259, tables 3, 4, figs. 4–7, appendices 1, 2 (misidentification, part); Kovařík, 2004: 9, 11, 23, 34, 40–42, 51, 53, table 2, fig. 27 (misidentification, part); 2009: 35, 44, 48, table 1 (misidentification, part).

TYPE MATERIAL: *Palamnaeus oatesii*: Syntypes?: 3 ♂, 2 ♀, 1 juv. ♂ (BMNH), Hardwicke [examined]. **SINGAPORE**: *P. oatesii*: Syntype: [sex?] (BMNH), Singapore. *Palamnaeus petersii*: Holotype ♀ (NMG 91), "India Orientalis, ex Singapore," 22.iv.1852, J.F. Lijbeck [examined].

Six specimens (3 ♂, 2 ♀, 1 juv. ♂) in the BMNH, apparently transferred to ethanol from dry storage, with the determination label "*Palamnaeus oatesii*," but without any other data, appears to be all that remains of the type material of *P. oatesii*. Although no other specimens so labeled have been



FIGURE 152. *Gigantometrus titanicus* (Couzijn, 1981), comb. nov. et stat. rev., ♂ (AMNH), Polonnaruwa, Sri Lanka, habitus: A. dorsal and B. ventral aspects. Scale bar = 10 mm.

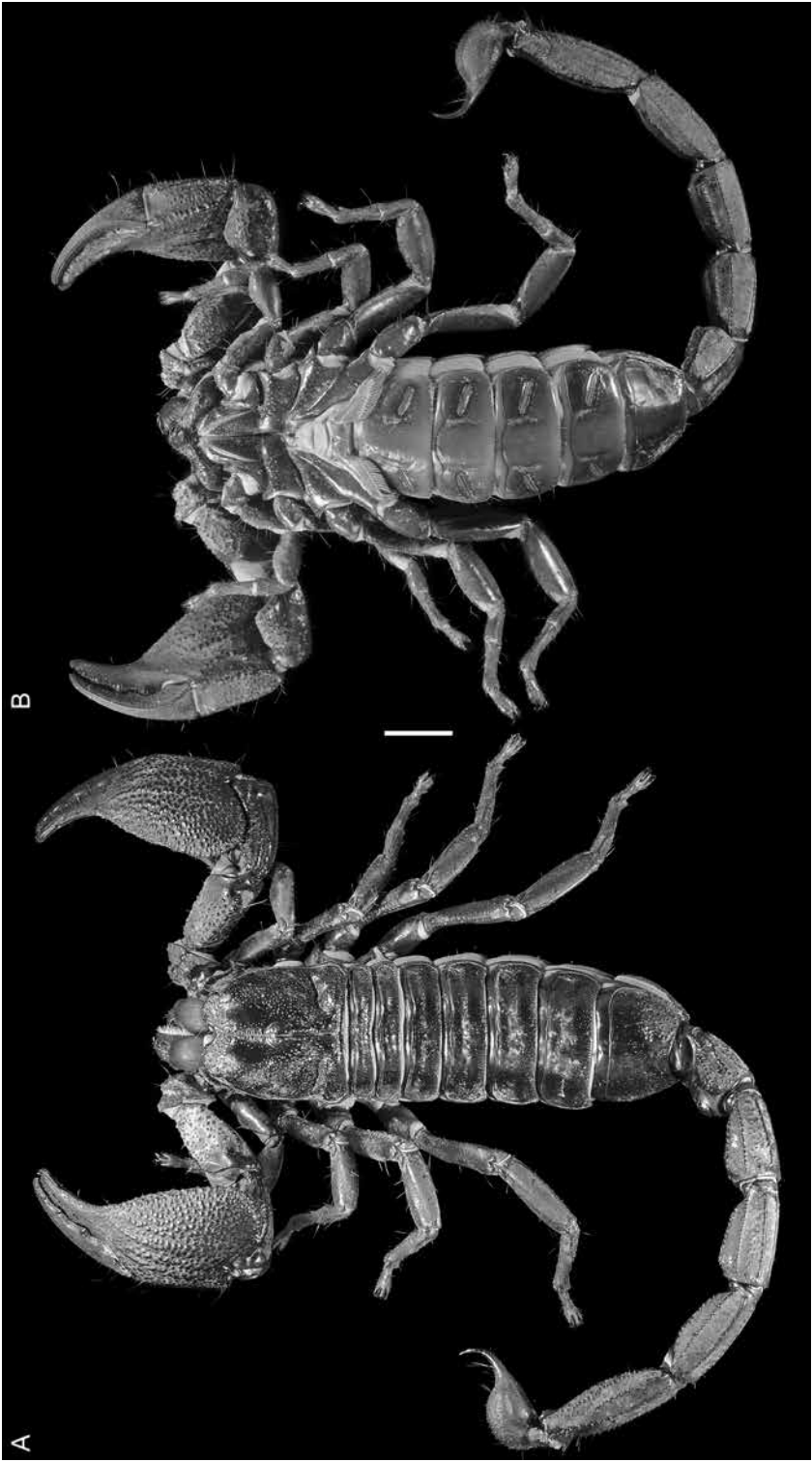


FIGURE 153. *Gigantometrus titanicus* (Couzijn, 1981), comb. nov. et stat. rev., ♀ (AMNH), Polonnaruwa, Sri Lanka, habitus: **A.** dorsal and **B.** ventral aspects. Scale bar = 10 mm.

found at BMNH, it is impossible to know whether these specimens really are syntypes, as noted by Kovařík (2004). Therefore, following Kovařík (2004), a lectotype is not designated. Whereas the six putative syntypes remaining at the BMNH are conspecific with *H. petersii*, with which *P. oatesii* is therefore synonymized below, the following syntypes, listed in the original description of *P. oatesii*, all of which appear to be lost, were probably conspecific with other species of *Heterometrus*: [sex?] (BMNH), "Bengal"; *H. laevigatus*: [sex?] (BMNH), Siam [Thailand], 1 ♀? (BMNH), Mergui, Burma [Myanmar: Tanintharyi Reg.: Myeik Archipelago, 12°27'N 98°37'E], Anderson; *H. thorellii*: 1 ♂? (BMNH), Rangoon, Burma [Myanmar: Yangon Reg.: Yangon, 16°47'N 96°10'E], Oates.

DIAGNOSIS: *Heterometrus petersii* may be separated from other species of *Heterometrus*, except *H. spinifer*, as follows. The carapace interocular surface is granular along the median longitudinal and anterior bifurcated sulci only in the male and female of *H. petersii* whereas the frontal lobes and medial region of the interocular surface are granular with smooth areas in the male and female of *H. glaucus* and *H. thorellii*, and the interocular surface is entirely smooth in the male of *H. laevigatus* and the male and female of *H. laoticus*. The carapace anterolateral, mediolateral and posterolateral surfaces of the female are granular in *H. petersii* but smooth or nearly so in *H. laoticus*, and the posterolateral surfaces of the female smooth or nearly so in *H. longimanus*. The pedipalps of the adult male are short, with femur length : posterior carapace width ratio (FL:PCW) < 0.77 and femur length : carapace length ratio (FL:CL) < 0.74 in *H. petersii* but long, with FL:PCW ≥ 0.80 and FL:CL ≥ 0.76 in *H. glaucus*, *H. laevigatus*, *H. longimanus*, and *H. thorellii*. The pedipalp chela manus promedian carina of the female is present and granular in *H. petersii* but absent or obsolete in *H. laevigatus*. The maximum distance between the dorsomedian and dorsal secondary carinae (DMC–DSC) of the chela manus is similar to the maximum distance between the dorsal secondary and digital carinae (DSC–DC) in the male

and female of *H. petersii* whereas the DMC–DSC is less than the DSC–DC in the male of *H. glaucus*, *H. laevigatus*, and *H. thorellii*, greater than the DSC–DC in the male of *H. silenus*, and less than the DSC–DC in the male and female of *H. longimanus*. The chela manus dorsal intercarinal surface is smooth or nearly so in *H. petersii* but shallowly reticulate in *H. glaucus*, *H. laevigatus*, and, often, *H. thorellii*. The second (subproximal) lobe of the chela movable finger of the adult male is more strongly developed than other lobes on the finger, with a correspondingly well-developed notch in the fixed finger in *H. petersii* but similar to or barely larger than other lobes on the finger in *H. glaucus*, *H. longimanus*, and *H. thorellii*. Macroseta *st* on the proventral surface of the basitarsus of leg I is setiform in *H. petersii* but spiniform in *H. laevigatus* and *H. thorellii*; *st* on the proventral surface of the basitarsus of leg II is setiform in *H. petersii* but spiniform in *H. glaucus*, *H. laevigatus*, *H. thorellii*, and, usually, *H. longimanus*; *sb* on the proventral surface of the basitarsus of leg III is spiniform in *H. petersii* but setiform in all other species except *H. glaucus* and *H. spinifer*. The lateral surfaces of mesosomal tergites I–VI in the female are granular (fig. 178) in *H. petersii* but smooth in *H. laevigatus*, *H. laoticus*, and *H. thorellii*. The ventrosubmedian and ventrolateral carinae of metasomal segments I–IV are granular or costate-granular on segment IV only and costate on segments I–III in *H. petersii* but granular on segments I–IV, II–IV (costate on I), or III and IV (costate on I and II) in *H. laoticus* and *H. silenus*. The ventral intercarinal surfaces of segments III and IV of the female are smooth in *H. petersii* but granular in *H. laoticus*. The telson is dark reddish brown and paler than metasomal segment V in *H. petersii* but blackish and as dark as segment V in *H. laevigatus*, *H. laoticus*, *H. silenus*, and *H. thorellii*. The width of the telson vesicle is approximately equal to or less than the width of metasomal segment V in the male of *H. petersii* but greater than the width of segment V in the male of *H. glaucus* and *H. longimanus*. No consistent morphological differences between *H.*

petersii and *H. spinifer* were identified in the present investigation.

DISTRIBUTION: The full extent of the distribution of *H. petersii* is currently unknown as many specimens have doubtless been mistaken for *H. spinifer*. The only confirmed records of this cryptic species are from Singapore and the Malaysian island of Penang (Penang state) (fig. 158, table 2). Its distribution overlaps that of *H. longimanus* in Singapore. *Heterometrus laevigatus* and *H. spinifer* appear to be allopatric with *H. petersii* in Thailand and peninsular Malaysia, respectively.

ECOLOGY: *Heterometrus petersii* inhabits wet primary and secondary rainforest. Recently collected specimens were found doorkeeping at burrow entrances and sometimes under or in logs, or under stones with UV detection at night. Burrows were constructed in open ground or at the base of logs, roots, or stones in clayey soils. The habitat and habitus of this species are consistent with the fossorial, pelophilous ecomorphotype (Prendini, 2001b). The following scorpions were found in sympatry: the buthid *Lychas scutillus* and two chaerilids, *Chaerilus rectimanus* Pocock, 1899, and an undetermined species of *Chaerilus*.

CONSERVATION STATUS: Material originating from Singapore, and misidentified as *H. spinifer*, has been offered in the exotic pet trade.

REMARKS: As noted by Fet (2000: 437), *Palamnaeus petersii* and *Palamnaeus silenus* were introduced as replacement names for a species based on specimens originating from Cochin China [Vietnam] in the MNHN. Simon (1872b: 97, 98) misidentified these specimens as *Heterometrus megacephalus*, itself a junior synonym of *Srilankametrus indus*, that was originally described as *Buthus megacephalus* C.L. Koch, 1836 (see below). Thorell (1876a, 1876b) realized that the specimens described as *H. megacephalus* by Simon (1872b) were misidentified and assigned them to a new species, *P. petersii*. However, Thorell (1876a, 1876b) did not examine the MNHN material described by Simon (1872b), and based *P. petersii* on a specimen from Singapore, in the NMG (Thorell, 1876b: 216). Simon

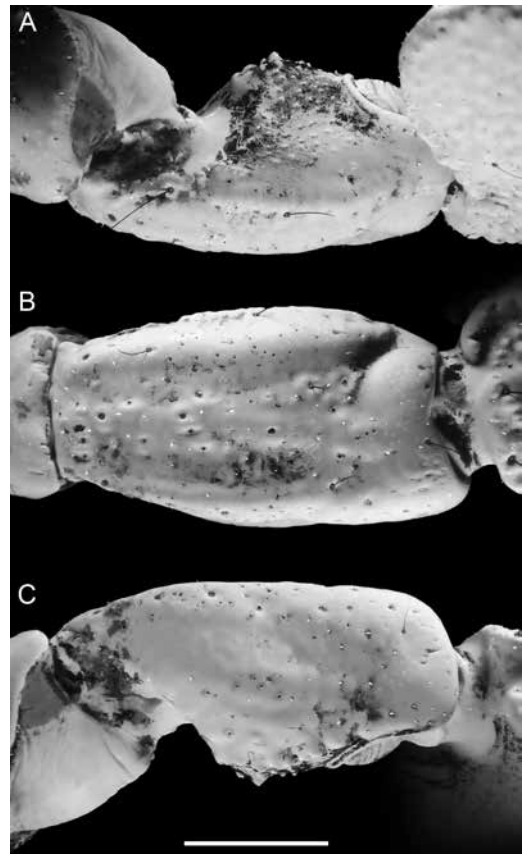


FIGURE 154. *Gigantometrus titanicus* (Couzijn, 1981), comb. nov. et stat. rev., ♂ (AMNH), Polonnaruwa, Sri Lanka, pedipalp patella: A. dorsal, B. retrolateral, and C. ventral aspects. Scale bar = 5 mm.

(1884a) agreed with Thorell (1876a, 1876b) that the MNHN material previously examined (Simon, 1872b) from Cochin China [Vietnam] was not conspecific with *B. megacephalus*. However, Simon (1884a: 361) suggested that *P. petersii* was a different species, occurring on the Malaysian Peninsula and adjacent islands, and possibly the female of *H. longimanus*, and was not conspecific with the MNHN specimens from Cochin China, which were therefore described as another new species, *P. silenus*:

L'espèce que nous avons décrite (Etudes sur les Scorp., p. 3, pl. 6, f. 2, 1872) sous le nom de *Het. megacephalus* C. Koch, est sans doute différente de *Buthus megacephalus* C. Koch, comme le Dr. Thorell l'a déjà fait



FIGURE 155. *Gigantometrus titanicus* (Couzijn, 1981), comb. nov. et stat. rev., ♂ (AMNH), Polonnaruwa, Sri Lanka, pedipalp chela: A. retrodorsal, B. ventral, and C. prolateral aspects. Scale bar = 5 mm.



FIGURE 156. *Gigantometrus titanicus* (Couzijn, 1981), comb. nov. et stat. rev., ♀ (AMNH), Polonnaruwa, Sri Lanka, pedipalp chela: A. retrodorsal, B. ventral, and C. prolateral aspects. Scale bar = 5 mm.

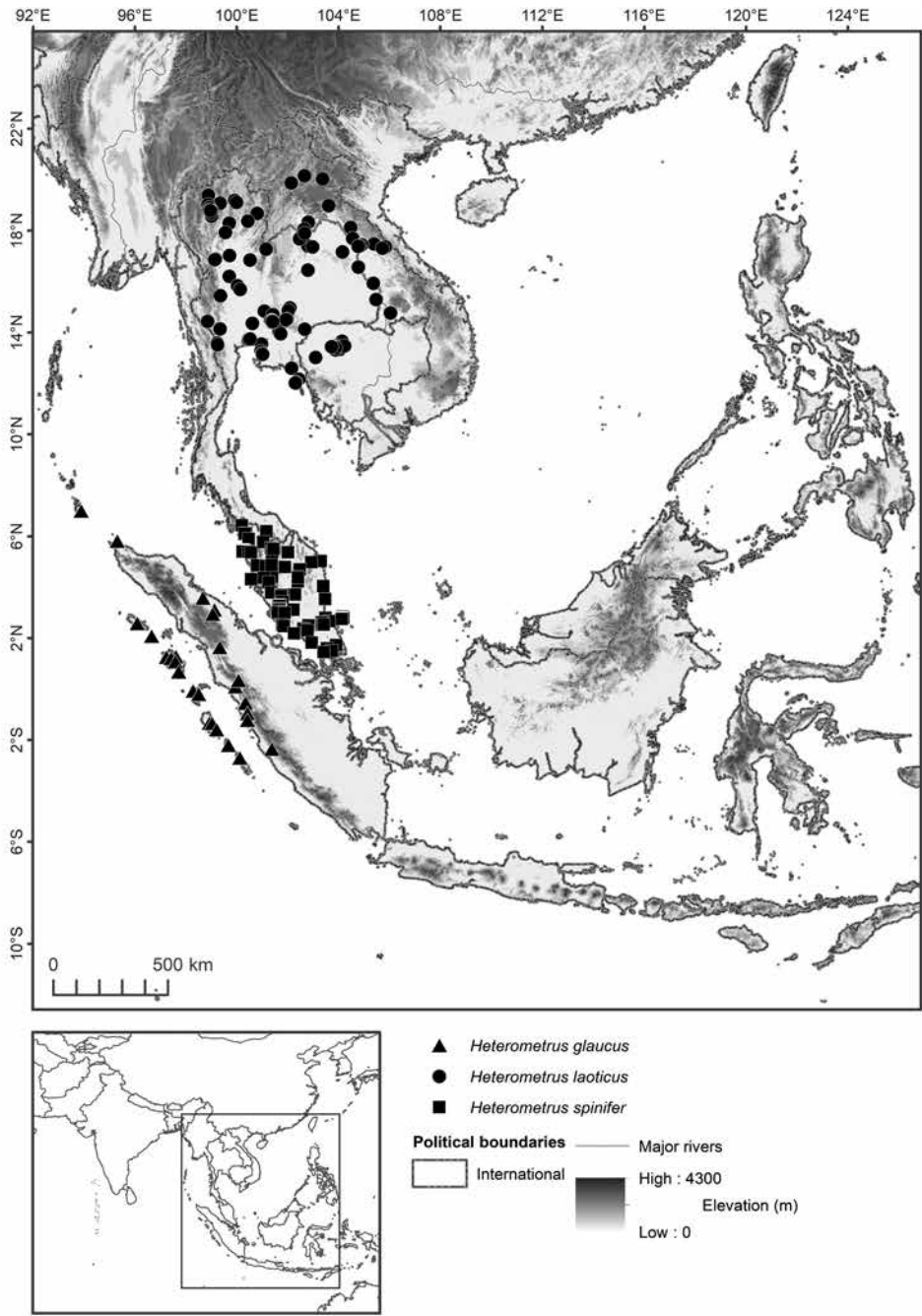


FIGURE 157. Map of Southeast Asia, plotting known locality records of three species of *Heterometrus* Ehrenberg, 1828, based on material examined, and verified records from virtual museums and the literature: *Heterometrus glaucus* (Thorell, 1876), comb. nov. et stat. rev.; *Heterometrus laoticus* Couzijn, 1981; *Heterometrus spinifer* (Ehrenberg, 1828).

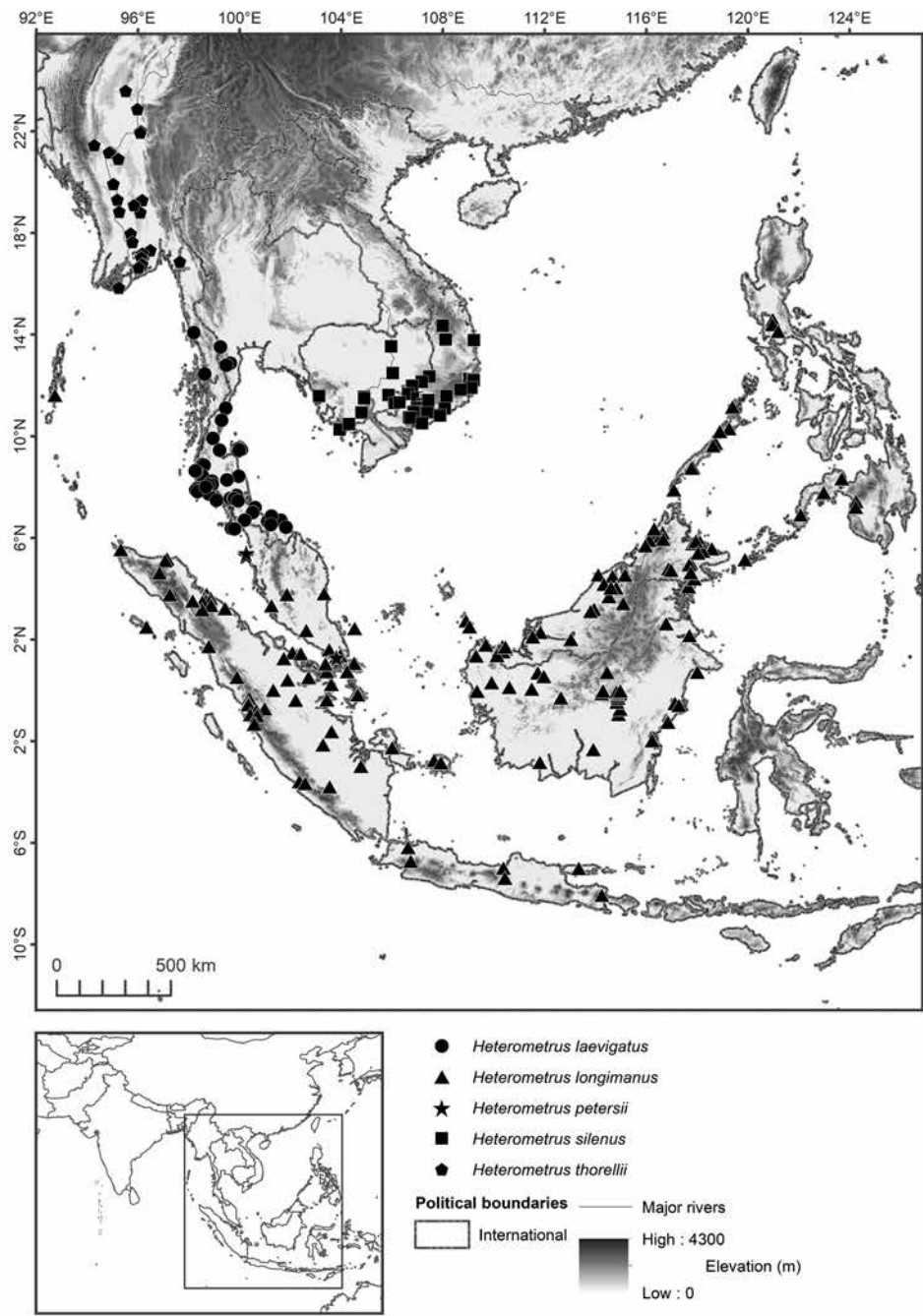


FIGURE 158. Map of Southeast Asia, plotting known locality records of five species of *Heterometrus* Ehrenberg, 1828, based on material examined, and verified records from virtual museums and the literature: *Heterometrus laevigatus* (Thorell, 1876), comb. nov. et stat. rev.; *Heterometrus longimanus* (Herbst, 1800); *Heterometrus petersii* (Thorell, 1876); *Heterometrus silenus* (Simon, 1884), comb. nov. et stat. rev.; *Heterometrus thorellii* (Pocock, 1892).

observer; le Dr. Thorell propose pour cette espèce le nom de *P. petersi* (Et. Scorp. p. 140) mais la description qu'il en donne ne s'applique aucunement au *megacephalus* Simon et désigne une espèce beaucoup plus grande, propre à la presqu'île de la Malacca et aux îles voisines. Chez *petersi* en effet la main est de moitié plus longue que large, sensiblement atténuée jusqu'à la base des doigts, en dessus lisse brillante très finement réticulée-rugueuse non ponctuée, tandis que chez *megacephalus* Simon, qui habite Siam, la Cochinchine, et l'Annam, la main est à peine plus longue que large, plus convexe, nullement réticulée mais parsemée de points enfoncés. *P. petersi* est peut-être le femelle de *P. longimanus* Herbst, nous avons reçu les deux formes de l'île Bintang; quant au *megacephalus* Simon (non C. Koch) nous proposons pour lui le nom nouveau de *P. silenus*. (Simon 1884: 361)

Pocock (1892: 38–40; 1894b: 316) initially synonymized *P. petersii* with *H. spinifer* but, later (Pocock, 1900a: 84, 98), synonymized *P. silenus* with *P. petersii*, noting:

The name *petersii* was originally applied by Thorell in 1876 to the Cochin China form which Simon in 1872 had erroneously described and figured as *megacephalus*, C. Koch, and which he subsequently in 1882 renamed *silenus*.

Although Pocock (1892, 1900a) apparently did not examine the types of either, his synonymy of *P. silenus* with *P. petersii* has persisted until today (Couzijn, 1981; Kovařík, 2004, 2009). Fet (2000: 437) mistakenly credited the synonymy to Couzijn (1981: 89), who also continued to list *P. silenus* in synonymy with *H. petersii*, despite examining the types of both taxa, and listing the holotype of *H. petersii* among the material examined for *H. spinifer*.

The types of *P. petersii*, *P. silenus*, and *H. longimanus* and its junior synonyms were examined during the present investigation. *Palamnaeus petersii* was not found to be conspecific with *H. longimanus*, as suggested by Simon (1884a) or *H. silenus*, as assumed ever since the latter was synonymized by Pocock (1900a), justifying the revalidation of *H. silenus*, below.

In agreement with Pocock (1892: 38–40; 1894b: 316) and Couzijn (1981: 89), the adult female holotype of *P. petersii*, which originated from Singapore, was morphologically indistinguishable from the neotype of *H. spinifer*, and

nontype material, previously identified as *H. spinifer*, from Singapore and elsewhere (e.g., the Malaysian mainland and the islands of Penang and Tioman). However, nontype material from Singapore and Penang, assessed to be conspecific with the holotype of *P. petersii* based on morphological similarity, was genetically more closely related to *H. longimanus* than to morphologically indistinguishable material of *H. spinifer* from the Malaysian mainland and Tioman (Loria and Prendini, in press), leading to the conclusion that *H. petersii* is a cryptic species.

Palamnaeus oatesii was described from an unknown series of specimens from Rangoon and Mergui, Burma [Myanmar], Siam [Thailand], Singapore, and “Bengal” although Pocock (1900a: 99) doubted the accuracy of the latter. Pocock (1900a: 98) listed *P. spinifer* and *P. petersii* among the synonyms of *P. oatesii*. Couzijn (1981: 89) synonymized *P. oatesii* with *H. spinifer*, a decision upheld by Fet (2000) and Kovařík (2004, 2009). Reexamination of putative syntypes in the BMNH during the present investigation, taken together with the original description (Pocock, 1900a: 98, 99), which mentions characters such as “vesicle generally reddish yellow and much paler ... than the segments of the tail” and “♂ ... with secondary sexual characters poorly developed” confirmed the morphological similarity of *P. oatesii* and *H. spinifer* which formed the basis of Couzijn's (1981) synonymy. The morphology is also consistent with *H. petersii*, however, in which the males closely resemble the females. Pocock's (1900a) original series evidently included several species, e.g., *H. laevigatus* from Mergui, *H. petersii* from Singapore, and *H. thorellii* from Rangoon. None of the type localities cited by Pocock (1900a) matches the known distribution of *H. spinifer*, however, and the sexually dimorphic species, *H. laevigatus* and *H. thorellii*, do not match the original description or the BMNH specimens, in which the males resemble the females. Therefore, by a process of elimination, and absent evidence to the contrary, the following new synonym is proposed: *Palamnaeus oatesii* Pocock, 1900 = *Heterometrus petersii* (Thorell, 1876), syn. nov.

MATERIAL EXAMINED: MALAYSIA: Penang: Penang [Penang Island, 05°24'N 100°14'E], i.1862, M.D. Parker, 1 ♂ (MCZ); Pulo Penang [Pulau Penang (Penang Island)], vii.1860, W.H.A. Putnam, 1 ♂, 1 ♀ (MCZ); Penang Island, Bukit Bendera/Penang Hill, Moniot Road, 05°25'N 100°15'E, and grounds of Monkey Cup Cafe, 05°25'N 100°16'E, 16–27.x.2017, L. Esposito and S.F. Loria, night collecting with UV, 3 ♂, 2 ♀ (CAS 9080783), 1 ♂ [leg] (AMCC [LP 16458]), 1 ♀ [leg] (AMCC [LP 16459]). **SINGAPORE:** Singapore [01°22'N 103°48'E], 1889, Dr. Hamlin, 1 ♂ (MCZ 14970), 1921, 1 subad. ♂ (LKC ZRC-ENT 7964), xii.1921, 1 subad. ♂ (LKC ZRC-ENT 7960), 1 subad. ♀ (LKC ZRC-ENT 7963), xi.2004, captive bred, 1 subad. ♀, 2 juv. ♀ (LKC ZRC-ARA 677); 8th Mile Old Upper Thomson Road/6th Mile Thomson Road [01°23'N 103°49'E], 16–17.ii.1963, K.O. Yee, 1 juv. ♀ (LKC ZRC-ENT 7229 [ZRC-ARA 731]); Gardens [Singapore Botanic Gardens, 01°19'N 103°49'E], 7.viii.1921, 1 ♂ (LKC ZRC-ENT 7961), xii.1921, 1 ♂ (LKC ZRC-ENT 7962), Botanical Gardens, 13.iv.1960, S.C. Keong, 1 ♀ (LKC ZRC-ARA 675), Botanic Gardens, National Orchid Garden, 2010, K. Lin, 1 ♂ (LKC ZRC-ENT 7239); Bukit Kallang, track near [01°22'N 103°49'E], 23.v.1994, C.H. Yeow and J. Choo P.S., 1 subad. ♀ (LKC ZRC-ARA 676); [probably Mandai, 01°25'N 103°47'E], ix.1998, C.K. Wee, 1 ♀ (AMNH [LP 1604]), legs (AMCC 101699 [LP 1604]); Mandai [01°25'N 103°47'E], 1998, C.K. Wee, 1 juv. ♀ (LKC RC-ARA 679); SADA Hill [Singapore Air Defence Artillery, 01°26'N 103°50'E], 1 ♂ (LKC ZRC-ENT 7965).

Heterometrus silenus (Simon, 1884),
comb. nov. et stat. rev.

Figures 10, 24C, D, 38C, D, 51E–H, 70C, 71C,
72C, 158, 179–183, table 2

Heterometrus megacephalus (nec *Buthus megacephalus* C.L. Koch, 1836: 73): Simon, 1872b: 53, 97, 98, 100, pl. VI, fig. 2.

Palamnaeus silenus Simon, 1884a: 361 (part); Thorell, 1889: 588 (part); Kraepelin, 1894: 35, 37, 41, 42; Simon, 1904: 293 (part); Meise, 1932: 666.

Scorpio longimanus silenus: Kraepelin, 1894: 41, 42.

Heterometrus longimanus: Kraepelin, 1899: 108 (part); Bücherl, 1959: 269 (misidentifica-

tion); Zhu and Yang, 2007: 95, 96 (misidentification).

Heterometrus longimanus silenus: Kraepelin, 1899: 111, 112; 1904: 199; Masi, 1912: 123; Takashima, 1941: 281.

Palamnaeus petersii: Pocock, 1900a: 84, 98 (misidentification).

Heterometrus (Scorpio) longimanus: Kraepelin, 1901: 271 (misidentification, part).

Heterometrus (Scorpio) longimanus var. *silenus*: Kraepelin, 1901: 271 (part).

Heterometrus longimanus petersi: Kraepelin, 1904: 199; Giltay, 1931: 4 (misidentification, part); Fage, 1933: 25, 27 (misidentification, part); 1936: 180, 181 (misidentification, part); 1946: 73 (misidentification, part).

Heterometrus longimanus silenus: Masi, 1912: 123.

Heterometrus cyaneus: Fage, 1936: 181 (misidentification, part); 1946: 73 (misidentification).

Heterometrus liurus: Fage, 1936: 180, 181 (misidentification, part); 1946: 73 (misidentification).

Heterometrus silenus: Kishida, 1939: 45.

Heterometrus longimanus petersii: Takashima, 1945: 90, 91 (part); 1952: 34 (part).

Heterometrus (Heterometrus) laotianus: Couzijn, 1981: 173, fig. 62 (misidentification, part).

Heterometrus (Heterometrus) laoticus Couzijn, 1981: 32, 73, 75–77, 80, 83, 89, 94, 96, 174, 175, 182, 184, 185, 189, 191, table 7, figs. 17b, 18, 19, 21, 63, 66b (misidentification, part); Kovařík, 1995: 202 (misidentification, part); Hue et al., 1998: 8 (misidentification, part); Kovařík, 1998: 137 (part); Fet, 2000: 433 (part).

Heterometrus (Heterometrus) petersii: Couzijn, 1981: 73, 80, 173, 175, 182, 185, 187–189, figs. 21, 62, 66b, 70 (misidentification, part); Fet, 2000: 437 (part); Kovařík, 2002: 17 (misidentification).

Heterometrus (Heterometrus) petersii mindanais Couzijn, 1981: 19, 33, 84, 88, 97–99, 175, 187, 189, 191, table 7, figs. 2c, 26;



FIGURE 159. *Heterometrus glaucus* (Thorell, 1876), comb. nov. et stat. rev., ♂ (BMNH 1885.54), habitus: A. dorsal and B. ventral aspects. Scale bar = 10 mm.

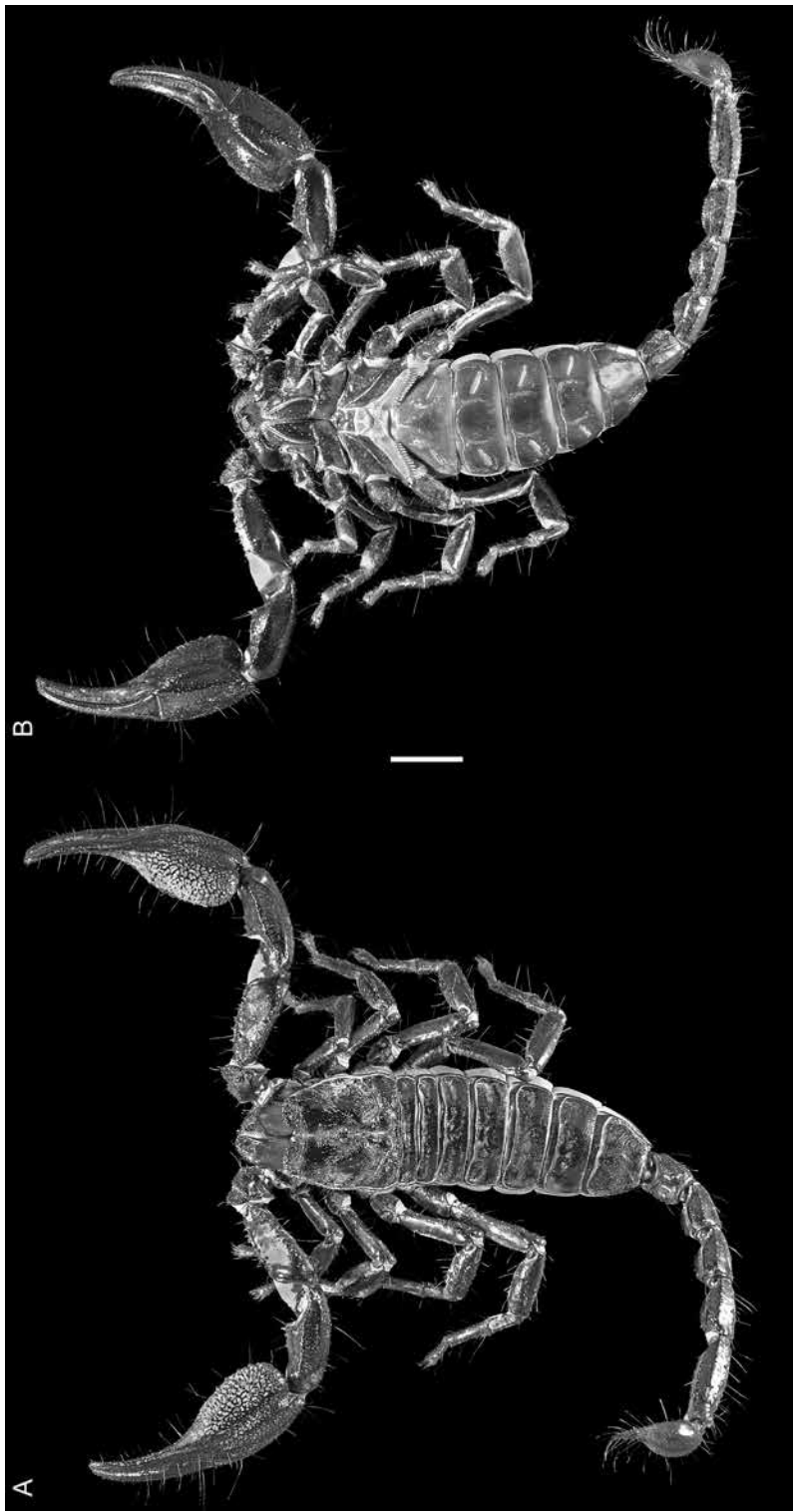


FIGURE 160. *Heterometrus glaucus* (Thorell, 1876), comb. nov. et stat. rev., ♀ (AMNH), Nias Island, Indonesia, habitus: A. dorsal and B. ventral aspects. Scale bar = 10 mm.

- Kovařík, 1998: 137; Fet, 2000: 437; Kovařík, 2004: 32, 34; 2009: 42; syn. nov.
- Heterometrus (Heterometrus) petersii petersii*: Couzijn, 1981: 32, 75–77, 83, 88, 89, 95–99, 174, 191, table 7, figs. 17b, 18, 19, 25, 63 (misidentification, part); Hue et al., 1998: 7, 8 (misidentification, part); Fet, 2000: 437 (part).
- Heterometrus (Heterometrus) spinifer*: Couzijn, 1981: 73, 94, 96, 173, 175, 182, 187, 189, 190, figs. 62, 66b (misidentification, part); Kovařík, 1992: 185 (misidentification); Fet, 2000: 437, 438 (part).
- Heterometrus (Heterometrus) spinifer spinifer*: Couzijn, 1981: 19, 32, 75–77, 83, 89–93, 167, 174, 191, table 7, figs. 2b, 17b, 18, 19, 63 (misidentification, part); Hue et al., 1998: 7 (misidentification, part); Fet, 2000: 138 (part).
- Heterometrus (Javanimetrus) cyaneus*: Hue et al., 1998: 8 (misidentification, part).
- Heterometrus (Heterometrus) longimanus silenus*: Kovařík, 1998: 137 (part).
- Heterometrus (Heterometrus) petersi*: Kovařík, 1998: 137 (part).
- Heterometrus laoticus*: Prendini et al., 2003: 192, 193, 202, 203, 205, 208, 209, 222, 252–259, tables 3, 4, figs. 4–7, appendices 1, 2 (misidentification, part); Kovařík, 2004: 2, 20, 21, 34, 51, 53, table 2 (misidentification, part); Zhu and Yang, 2007: 96 (misidentification); Kovařík, 2009: 35, 39, 48, table 1 (part); Pham et al., 2017: 134, 136 (misidentification), fig. 1.
- Heterometrus cimrmani*: Kovařík, 2004: 1, 2, 9, 11, 23, 42, 51, 53, table 2 (misidentification, part); Zhu and Yang, 2007: 96 (misidentification); Kovařík, 2009: 35, 36, 48, table 1 (part); Pham et al., 2017: 134, 136, fig. 1 (misidentification).
- Heterometrus petersii*: Kovařík, 2004: 2, 13, 21, 32–34, 42, 51, 53, table 2, fig. 23 (misidentification, part); Zhu and Yang, 2007: 92–97, 101–103, table 1, figs. 28–54 (misidentification); Kovařík, 2009: 35, 42, 48, 49, 87, 101, 110, table 1 (misidentification, part), figs. 95–101, 230, 231, 263, 264; Pham et al., 2017: 134, 136, fig. 1 (misidentification); Wang et al., 2019: 76–87, figs. 2–8 (misidentification).
- Heterometrus petersii mindanaensis*: Kovařík, 2004: 34.
- Heterometrus liangi* Zhu and Yang, 2007: 92–100, table 1, figs. 1–27; syn. nov.
- Heterometrus spinifer*: Zhu and Yang, 2007: 96 (misidentification); Pham et al., 2017: 134, 136, fig. 1 (misidentification).
- Heterometrus petersii*: Di et al., 2013: 52.
- TYPE MATERIAL: PHILIPPINES:** *Heterometrus (H.) petersii mindanaensis*: Holotype ♂ (MNHN RS 0023), Mindanao, Mantano and Rey [examined, erroneous locality]. **VIETNAM:** *Palamnaeus silenus*: Lectotype [here designated]: 1 ♂ (MNHN RS 0020) [examined], paralectotype [here designated]: 1 ♂ (MNHN RS 8903 ex 0020), Cochinchina, Germain. **Ho Chi Minh City Prov.:** *Heterometrus cimrmani*: Paratype ♀ (FKPC), Saigon [Ho Chi Minh City, 10°45'N 106°40'E], 1940. **Tây Ninh Prov.:** *Heterometrus liangi*: Holotype ♂, paratypes: 2 ♂, 2 ♀ (MHU), Tây Ninh Prov., ex Mr. Y.-M. Liang.
- In the original descriptions of *H. megacephalus*, *P. petersii*, and *P. silenus*, neither Simon (1872b, 1884a) nor Thorell (1876a) specified a type, nor referred to the number of specimens examined. Couzijn (1981: 96) examined the MNHN types of *P. silenus*, originally misidentified as *Heterometrus megacephalus* by Simon (1872b), and incorrectly listed a holotype and paratype under *H. (H.) p. petersii*: “Cochinchina (2 ♂ ad., holotype and paratype, leg. Germain, [MNHN] RS 0020).” Fet (2000: 437) followed Couzijn (1981), incorrectly listing the same type specimens for *P. petersii* and *P. silenus*. The syntypes of *P. silenus* are hereby designated as lectotype (MNHN RS 0020) and paralectotype (MNHN RS 8903 ex 0020). However, the type specimens of *P. silenus* are not the same as the

holotype of *P. petersii*, as implied by Couzijn (1981) and explicitly stated by Fet (2000: 437). The types of *P. silenus* are deposited in the MNHN, whereas the holotype of *P. petersii* is deposited in NMG, as indicated by Thorell (1876b: 216): “Mus. Gothob. exemplum singulum ex Singapore.”

DIAGNOSIS: *Heterometrus silenus* may be separated from other species of *Heterometrus* as follows. The carapace interocular surface is granular along the medial longitudinal and anterior bifurcated sulci only in the male and female (fig. 24C, D) of *H. silenus* whereas the frontal lobes and medial region of the interocular surface are granular with smooth areas in the male and female of *H. glaucus* and *H. thorellii*, and the interocular surface is entirely smooth in the male of *H. laevigatus* and the male and female of *H. laoticus*. The carapace anterolateral, mediolateral, and posterolateral surfaces of the female are granular (fig. 24D) in *H. silenus* but smooth or nearly so in *H. laoticus*, and the posterolateral surfaces of the female smooth or nearly so in *H. longimanus*. The pedipalps of the adult male are short, with femur length : posterior carapace width ratio (FL:PCW) < 0.77 and femur length : carapace length ratio (FL:CL) < 0.74 (figs. 179A, 180A) in *H. silenus* but long, with FL:PCW ≥ 0.80 and FL:CL ≥ 0.76 in *H. glaucus*, *H. laevigatus*, *H. longimanus*, and *H. thorellii*. The pedipalp chela manus promedian carina of the female is present and granular in *H. silenus* but absent or obsolete in *H. laevigatus*. The maximum distance between the dorsomedian and dorsal secondary carinae (DMC–DSC) of the chela manus is greater than the maximum distance between the dorsal secondary and digital carinae (DSC–DC) in the male (fig. 182B) and similar to the DSC–DC in the female (fig. 182A) of *H. silenus* whereas the DMC–DSC is less than the DSC–DC in the male of *H. glaucus*, *H. laevigatus*, and *H. thorellii*, similar to the DSC–DC in the male of *H. laoticus*, *H. petersii*, and *H. spinifer*, and less than the DSC–DC in the male and female of *H. longimanus*. The chela manus dorsal intercarinal surface is smooth or nearly so (fig. 182) in *H.*



FIGURE 161. *Heterometrus glaucus* (Thorell, 1876), comb. nov. et stat. rev., ♀ (AMNH), Nias Island, Indonesia, pedipalp patella: A. dorsal, B. retrolateral, and C. ventral aspects. Scale bar = 5 mm.

silenus but shallowly reticulate in *H. glaucus*, *H. laevigatus*, and, often, *H. thorellii*. The second (subproximal) lobe of the chela movable finger of the adult male is more strongly developed than other lobes on the finger, with a correspondingly well-developed notch in the fixed finger (figs. 182B, 183) in *H. silenus* but similar to or barely larger than other lobes on the finger in *H. glaucus*, *H. longimanus*, and *H. thorellii*. Macroseta *st* on the proventral surface of the basitarsus of leg I is setiform (fig. 51E) in *H. silenus* but spiniform in *H. laevigatus* and *H. thorellii*; *st* on the proventral surface of the basitarsus of leg II is setiform (fig. 51F) in *H. silenus* but spiniform in *H. glaucus*, *H. laevigatus*, *H. thorellii*.



FIGURE 162. *Heterometrus glaucus* (Thorell, 1876), comb. nov. et stat. rev., ♂ (ZMH 3966), pedipalp chela: A. retrodorsal, B. ventral, and C. prolateral aspects. Scale bar = 5 mm.



FIGURE 163. *Heterometrus glaucus* (Thorell, 1876), comb. nov. et stat. rev., ♀ (AMNH), Nias Island, Indonesia, pedipalp chela: A. retrodorsal, B. ventral, and C. prolateral aspects. Scale bar = 5 mm.

lii, and, usually, *H. longimanus*; *sb* on the proven-tral surface of the basitarsus of leg III is setiform (fig. 51G) in *H. silenus* but spiniform in *H. glaucus*, *H. petersii*, and *H. spinifer*. The lateral surfaces of mesosomal tergites I–VI in the female (fig. 179B) are granular in *H. silenus* but smooth in *H. laevigatus*, *H. laoticus*, and *H. thorellii*. The ventrosubmedian and ventrolateral carinae of metasomal segments I–IV are granular on segments I–IV, II–IV (costate on I), or III and IV (costate on I and II) (fig. 72C) in *H. silenus* but granular or costate-granular on segment IV only and costate on segments I–III in *H. glaucus*. The ventral intercarinal surfaces of segments III and IV of the female are smooth in *H. silenus* but granular in *H. laoticus*. The telson is blackish and as dark as metasomal segment V in *H. silenus* (figs. 179, 180) but dark reddish brown and paler than segment V in *H. glaucus*, *H. longimanus*, *H. petersii*, and *H. spinifer*. The width of the telson vesicle is approximately equal to or less than the width of metasomal segment V in the male (figs. 70C, 72C) of *H. silenus* but greater than the width of segment V in the male of *H. glaucus* and *H. longimanus*.

DISTRIBUTION: *Heterometrus silenus* is endemic to western Cambodia (recorded from Phnom Penh Municipality and the Kratié, Mondulhiri, Phnom Penh, and Takéo provinces) and southern Vietnam including Phú Quốc Island (recorded from Ho Chi Minh City and the Bà Rịa–Vũng Tàu, Bin Dinh, Bình Phước, Bình Thuận, Dong Nai, Khanh Hoa, Ninh Thuận, Quảng Trị, and Tây Ninh provinces). Its distribution appears to be bounded by the Annamite Mountains in the north, and the Mekong River in the west, although individuals have been collected on both sides of the river (fig. 158, table 2). Its sister species, *H. laoticus*, is allopatric, distributed to the west of the Annamite Mountains. Records of *H. silenus* from mainland China (former Manchukuo) are erroneous (Couzijn, 1981: 97; Fet, 2000: 437) whereas records from the island of Hainan require confirmation (Takashima, 1941: 281; Couzijn, 1981: 97, 175; Wang et al.,

2019). A record from the Philippine island of Mindanao, the type locality of *H. (H.) petersii mindanaensis*, is either erroneous or the result of an introduction.

ECOLOGY: This species inhabits primary and secondary forests between 135–1000 m elevation. Specimens were collected under logs and rocks during the day, or doorkeeping at burrow entrances using UV detection at night. Whereas juveniles were found on the surface or under stones, adults were excavated from burrows 10–30 cm deep, situated at the base of rocks or tree roots in sandy-loam soil. A few adults were collected wandering into homes after a heavy monsoon downpour. The habitat and habitus of this species are consistent with the fossorial, pelophilous ecomorphotype (Prendini, 2001b). The following scorpions were found in sympatry: the buthids *Lychas mucronatus*, *Reddyanus petrzekai* (Kovářik, 2003), and an undetermined species of *Thaicharmus* Kovářik, 1995; the chaerilids *Chaerilus kampuchea* Lourenço, 2012, *Chaerilus juliettae* Lourenço, 2011, and *Chaerilus petrzekai* Kovářik, 2000; and the hormurids *Liocheles australasiae* and two undetermined species of *Liocheles*.

CONSERVATION STATUS: *Heterometrus silenus* is the most commonly available species of the genus in the exotic pet trade. Material offered for sale appears to have originated from Vietnam, regardless of the alleged country of origin.

REMARKS: Pocock (1900a) synonymized *Palamnaeus silenus* with *Palamnaeus petersii* but did not examine the types of either. Couzijn (1981: 89, 96) examined the types of both taxa but continued to list *P. silenus* in synonymy with *H. petersii*, while also listing the holotype of *H. petersii* among the material examined for *H. spinifer*. Fet (2000: 437) mistakenly credited Pocock's (1900a) synonymy to Couzijn (1981). Kovářik (2004, 2009) followed previous authors in treating *P. silenus* as a junior synonym of *H. petersii*, again without examining the types of either. As discussed above, examination of the types during the present investigation demonstrated that *P. silenus* is not conspecific with *H.*

petersii (or *H. longimanus*), justifying its revalidation.

Couzijn (1981) described two subspecies of *H. petersii* from the Philippines, *H. (H.) p. luzonensis*, from the island of Luzon, and *H. (H.) p. mindanaensis*, from the island of Mindanao, also listed by Fet (2000: 437). Kovařík (2002) synonymized *H. (H.) p. luzonensis* with *H. cyaneus*, and Kovařík (2004, 2009) listed *H. (H.) p. mindanaensis* under *H. petersii* but did not formally synonymize it because the holotype was not examined. As discussed below, examination of the types during the present investigation confirmed that *H. (H.) p. luzonensis* is conspecific with *Javanimetrus cyaneus*. The holotype of *H. (H.) p. mindanaensis* was found to be conspecific with *H. silenus*, and not with the holotype of *H. petersii*, however. The following new synonym is therefore presented: *Heterometrus (Heterometrus) petersii mindanaensis* Couzijn, 1981 = *Heterometrus silenus*, syn. nov.

Heterometrus liangi was described from three males and two females from Tây Ninh Province, Vietnam (Zhu and Yang, 2007), an area just north of Ho Chi Minh City and well within the known distributional range of *H. silenus* (fig. 158). In the diagnosis, Zhu and Yang (2007) compared *H. liangi* with *H. laoticus*, noting a similarity in the shape of the pedipalp chela but contrasting the two species based on differences in surface macrosculpture of the carapace, mesosomal tergites, and shape and surface macrosculpture of the pedipalp chela. According to Zhu and Yang (2007: 96), the dorsal surfaces of the carapace, including the median ocular carinae, and the mesosoma are granular in *H. liangi* but smooth in *H. laoticus*; the prodorsal surface of the pedipalp chela manus bears spiniform granules in *H. liangi* but is smooth in *H. laoticus*; and the length : width ratio of the chela is 2.10–2.14 in the male and 2.00–2.10 in the female of *H. liangi* whereas the ratio is 2.00–2.30 in both sexes of *H. laoticus*. Although the presence of spiniform granules on the prodorsal surface of the chela manus applies to *H. laoticus* and *H. silenus*, the other characters cited as diagnostic for *H. liangi* are typical of *H. silenus*. Although no illustrations or photographs

of the habitus of the type specimens of *H. liangi* were presented, three characters in the description suggest they are subadults of *H. silenus*. The total length of 82–98 mm given for *H. liangi* falls within the range of 88–122 mm for *H. silenus* specimens from Tây Ninh Province, Vietnam examined by Zhu and Yang (2007). However, the smaller total length of *H. liangi*, compared to the lengths of adult males (93–110 mm) and females (107–122 mm) of *H. silenus* from the same locality, are consistent with the type series of *H. liangi* being subadults of *H. silenus* (Zhu and Yang, 2007: 97, table 1). The length : width ratio of the pedipalp chela 2.1–2.14 (males) and 2–2.1 (females) of *H. liangi*, indicates that it is sexually dimorphic, consistent with *H. silenus* but unlike *H. laoticus*, in which the ratio is 2–2.3 in both sexes. Lastly, the similarity in the shape of the chela of *H. liangi* to that of *H. laoticus* is consistent with the subadult of *H. silenus*. Importantly, although Zhu and Yang (2007: 96) distinguish *H. liangi*, in which a difference in the chela movable finger “is not noticeable in either sex,” from *H. silenus*, in which the “chela movable finger of male exhibits a strong knob the middle,” this comparison is odious as the median lobe on the chela movable finger of the male of *H. silenus* appears only in sexual maturity and would not be developed in the subadult male types of *H. liangi*. No evidence of sexual maturity, e.g., hemispermatophores or mating plugs, was presented to refute the hypothesis that the types of *H. liangi* are immature. In view of the evidence that the types of *H. liangi* are conspecific with *H. silenus*, the following new synonym is presented: *Heterometrus liangi* Zhu and Yang, 2007 = *H. silenus* (Simon, 1884), syn. nov.

MATERIAL EXAMINED: 2 ♂ (MCZ 88175), 1 ♂ (MCZ 103100). viii.1999, ex pet trade, 1 ♂ (AMNH/AMCC [LP 1888]), xii.2000, ex pet trade, 1 ♀ (AMNH). **CAMBODIA: Kep Prov.:** *Kep Distr.:* Kep National Park, 10°29'N 104°18'E, 72 m, 24.v.2018, S.F. Loria, T. Chea, and V. Khem, on trail, near stream under log/rock, 2 juv. ♀ (AMCC [LP 15590]). **Mondulhiri Prov.:** *Pichrada Distr.:* Phnom Nam Lyr Wildlife Sanctuary [12°28'N 107°30'E], 500–1000 m, vi.2000, B.L. Stuart, 2 ♂, 2 ♀, 1 subad. ♀ (FMNH 086 265 [411]). **Phnom Penh Prov.:** *Phnom Penh Municip.:* Phnom Penh City [11°33'N

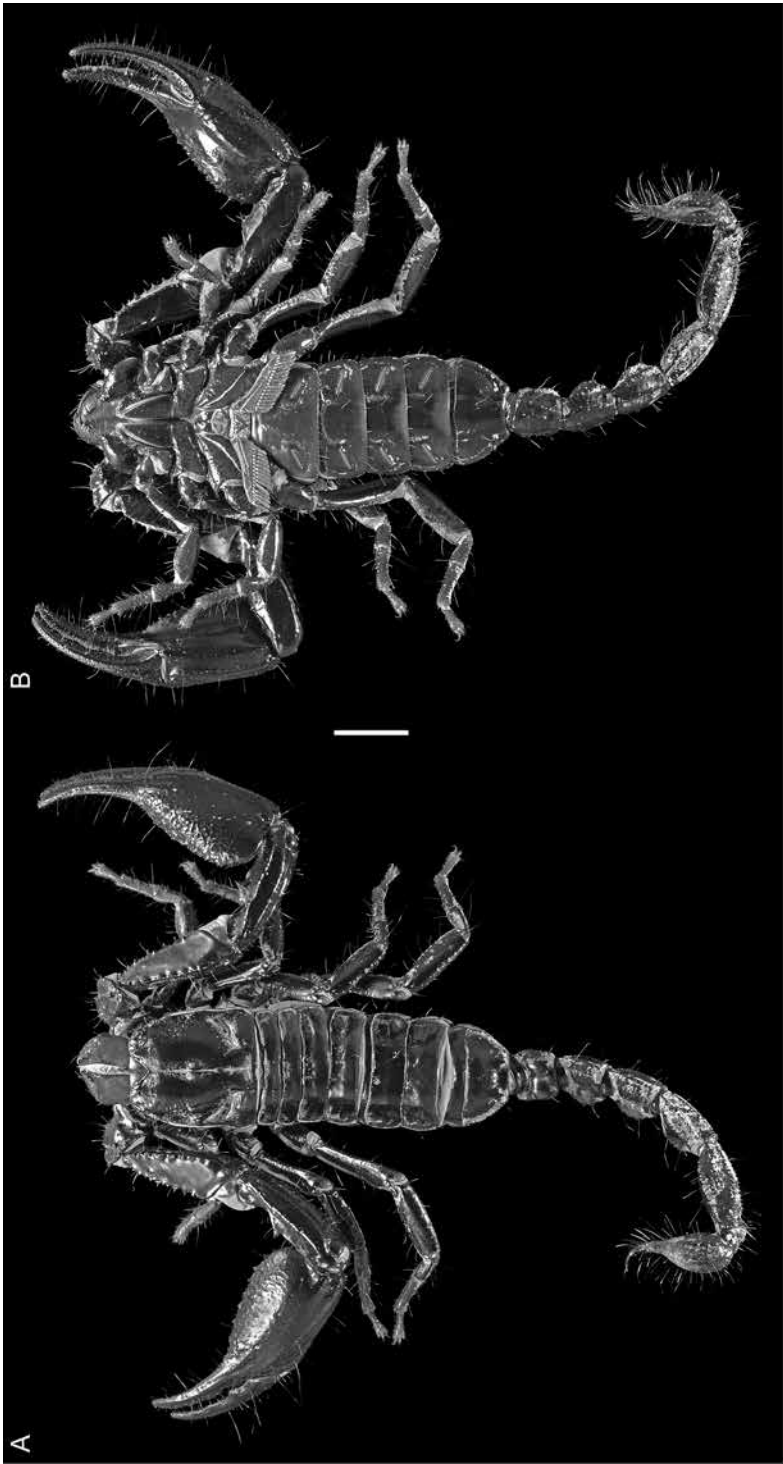


FIGURE 164. *Heterometrus laevigatus* (Thorell, 1876), comb. nov. et stat. rev., ♂ (AMNH), Thale Ban, Thailand, habitus: A. dorsal and B. ventral aspects. Scale bar = 10 mm.



FIGURE 165. *Heterometrus laevigatus* (Thorell, 1876), comb. nov. et stat. rev., ♀ (AMNH), Khao Pu-Khao Ya, Thailand, habitus: A. dorsal and B. ventral aspects. Scale bar = 10 mm.

104°54'E], vi.2000, B.L. Stuart, on bedroom floor, 1 ♂ (FMNH 086 261 [409]). **VIETNAM:** x.1997, 1 ♂ (AMCC [LP 1602]), 1 ♀ (AMCC 101697 [LP 1603]), x.1997, D. Taylor, 1 ♂ (AMNH), xii.2000, ex pet trade, 1 ♂ (AMNH), ix.2002, 1 ♂ (AMCC [LP 2163]), 1 ♀ (AMCC [LP 2162]), viii.2004, 1 ♂ pedipalps and legs (AMCC [LP 3089]), 1 ♀ pedipalp and legs (AMCC [LP 3090]), iii.2010, R. Loon, 1 ♂ (AMNH); Vietnam?, 2004, 1 ♂ (AMNH). **Bin Thuan Prov.: Ham Thuan Nam Distr.:** Ta Kou Mountain Nature Reserve, Ta Kou Mountain (Nui Ta Kou), trail above pagoda, 10°49'N 107°54'E, 540 m, 22–23.vi.2012, L. Prendini and S.F. Loria, primary rainforest with dense stands of bamboo close to summit of inselberg surrounded by farmland, moderate to dense canopy with sparse to moderate understorey, sandy/clayey-loam with sandstone outcrops and scattered boulders, moderate leaf-litter layer, moist soil, under stone, 1 ♂ (AMNH), trail below guesthouse and upper cable station, 10°49'N 107°54'E, 383 m, 22–23.vi.2012, L. Prendini and S.F. Loria, primary rainforest with dense stands of bamboo, moderate to dense canopy with sparse to moderate understorey, many sandstone outcrops, sandy/clayey-loam soil, UV light detection on cool, still, dark night after rainshower, doorkeeping at burrow entrances, usually under large stones or in earthen banks, several excavated from burrows ca. 20 cm long, 1 ♂, 2 ♀, 3 juv. ♂, 7 juv. ♀, 1 ♀ pedipalp chela (AMNH), 1 juv. ♀ (AMCC [LP 11353]), 10°49'N 107°53'E, 356 m, 23.vi.2012, L. Prendini and S.F. Loria, primary rainforest with bamboo, moderate canopy cover with sparse to moderate understorey, many sandstone outcrops, dense leaf-litter layer on steep slope alongside path, sandy-loam soil, UV light detection on cool, still, dark, humid night, doorkeeping at burrow entrances in open, or at base of rocks or tree roots, 1 ♂, 2 ♀ excavated from burrows ca. 20–30 cm deep, juveniles on surface or under stones, 1 ♂, 2 ♀, 1 subad. ♂, 2 juv. ♀ (AMNH). **Quy Nho'n City:** Qui Nhon [Qui Nhan, 13°46'N 109°14'E] (Phutai), 5.viii.1965, L.J. Barrier, under debris, ex Stahnke coll., 1 ♂ (CAS [ASU 66-1051]). **Dong Nai Prov.: Din Quan Distr.:** Din Quan [11°09'N 107°16'E], Bienhoa, 18.xii.1932, M. Poilane, 1 ♀ (USNM); Dinh Quan, outskirts of town, 11°16'N 107°25'E, 139 m, 16.ii.2012, L. Prendini and D.P. Phu, very degraded rainforest on outskirts of town, old cultivated lands among outcrops of large pumice (lava) stones on moist clayey-loam soil, specimens excavated from shallow burrows (ca. 10–20 cm deep) under stones and in open ground, 1 ♂ in scrape under stone, 1 ♂, 1 ♀, 1 subad. ♂, 2 juv. ♂, 2 juv. ♀ (AMNH), 1 juv. ♂ (AMCC [LP 11252]). **Tan Phu Distr.:** Nam Cat Tien

National Park, forest trail to Bau Sau [11°28'N 107°20'E], 6–8.v.2001, H.H. Tan et al., 1 ♂ (LKC ZRC-ARA 652); Cat Tien, camp and trail to Big Tree, 11°25'N 107°26'E, 135 m, 16.ii.2012, L. Prendini, primary rainforest with moderate to dense canopy and moderate to sparse understorey, moist clayey loam with pumice (lava) rock outcrops (under canopy cover) and moderate leaf-litter layer, in burrows under stones, most collected with UV detection on warm, dark, humid night with periodic rainshowers, many doorkeeping at burrow entrances at base of stones or roots, rarely in the open, several excavated from shallow (ca. 10–20 cm deep) burrows, two contained 1 ♂ and 1 subad. ♀, juveniles in communal burrows, 1 ♂, 1 ♀ walking on ground after rainshower at night, 4 ♂, 3 ♀, 1 subad. ♂, 1 subad. ♀, 3 juv. ♂ (AMNH); Kat Tien National Park, *Lagerstroemia* site, 11°26'N 107°25'E, 7.xii.2011, A. Goncharov, 4 juv. ♂ (AMNH, AMCC [LP 11243, 11246]), 8 juv. ♀ (AMNH, AMCC [LP 11242, 11244, 11245, 11247]), *Afzelia* site, 11°26'N 107°26'E, 24.xi.2011, A. Goncharov, 2 juv. ♂ (AMNH, AMCC [LP 11250]), 2 juv. ♀ (AMNH, AMCC [LP 11249]), 2 juv. (AMNH, AMCC [LP 11248]). **Trang Bom Distr.:** Trang Bom [10°58'N 107°02'E], 9.x.1932, M. Poilane, 1 ♀ (USNM); Trang Bom [10°58'N 107°02'E], Arboretum, 26.viii.1932, M. Poilane, 1 ♂ (USNM). **Ho Chi Minh City Prov.:** Saigon [Ho Chi Minh City, 10°45'N 106°40'E], 1908, Kraft, 1 ♀, 1 juv. ♂ (ZMB 14930), 27.i.1965, Robinson, 1 ♂ (USNM).

Heterometrus spinifer (Ehrenberg, 1828)

Figures 10, 23C, D, 37C, D, 50E–H, 67E, 68E, 69E, 157, 184–188, table 2

Buthus (Heterometrus) spinifer Ehrenberg in

Hemprich and Ehrenberg, 1828: pl. 1, fig. 2; Hemprich and Ehrenberg, 1829: 352; 1831 [p. 3, no page numbers]; Gervais, 1844a: 60, 61 (misidentification, part); Moritz and Fischer, 1980: 324; Braunwalder and Fet, 1998: 32; Kovařík, 2004: 2; 2009: 34.

Scorpio (Buthus) spinifer: Gervais, 1844b: 210.

Scorpio (Buthus) spinifer: Gervais, 1844b: 240, pl. 12, figs. 33, 34.

Heterometrus spinifer: Karsch, 1879a: 16, 20;

Ausserer, 1880: 466; Mahsberg, 1990: 271; Pointer, 1991: 24; Braunwalder and Fet, 1998: 32; Dupré et al., 1998: 63; Robert, 1999: 19 (part); Prendini et al., 2003: 192, 202, 203, 205,

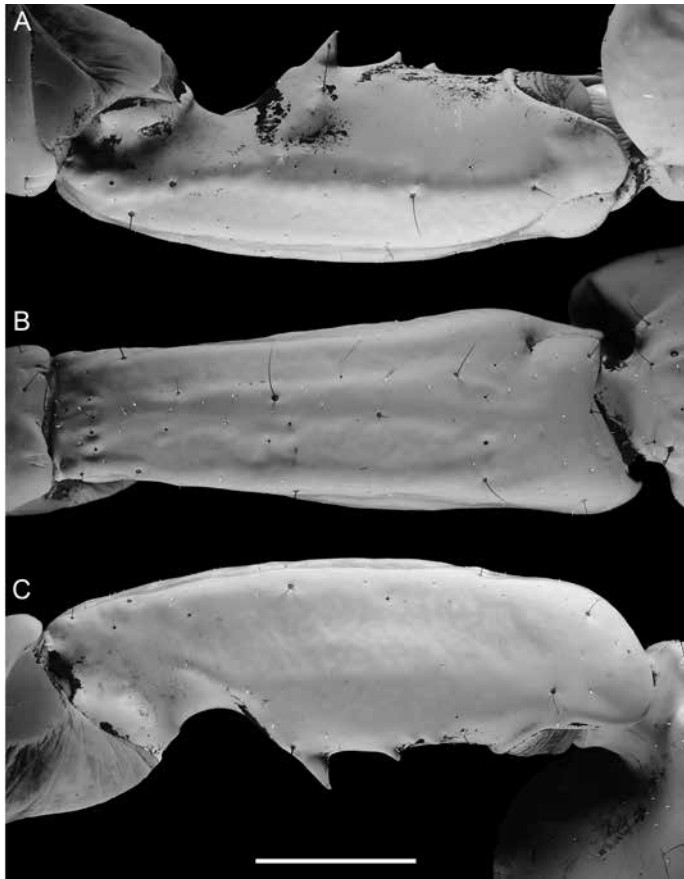


FIGURE 166. *Heterometrus laevigatus* (Thorell, 1876), comb. nov. et stat. rev., ♂ (AMNH), Thale Ban, Thailand, pedipalp patella: A. dorsal, B. retrolateral, and C. ventral aspects. Scale bar = 5 mm.

208, 209, 211, 213, 215, 218, 222, 224, 228, 232, 236, 252–259, table 3, figs. 4, 6, 7, 9A, 10A, B, 11, 15A, C, 17A, B, 19A–D, 21A, appendices 1, 2: (part); Kovařík, 2004: 2, 9, 11, 23, 34, 40, 42, 51, 53, table 2 (part); Shultz, 2007: 78, 86–91, figs. 2, 3A, 4, 5A, B; Kovařík, 2009: 35, 44, 46–49, 92, 99, 112, table 1 (part), figs. 133–138, 196, 197, 268–274.

Palamnaeus spinifer: Pocock, 1892: 38–42 (part); 1894b: 316 (part).

Scorpio longimanus: Kraepelin, 1894: 29, 30, 34–39, 41, 49, 51–53, 55, 57 (misidentification, part).

Heterometrus longimanus: Kraepelin, 1899: 108, 111 (misidentification, part); Giltay, 1931: 4–6.

Palamnaeus oatesii: Flower, 1901: 34, 35 (misidentification, part).

Heterometrus longimanus longimanus: Giltay, 1931: 3 (part); Takashima, 1945: 90 (misidentification, part).

Heterometrus (Heterometrus) spinifer: Couzijn, 1978: 330, table 1; 1981: 73, 80, 94, 96, 173, 175, 182, 187, 189, 190, figs. 21, 62, 66b (part); Kovařík, 1998: 137 (part); Fet, 2000: 437, 438 (part); Prendini, 2000a: 44.

Heterometrus (Heterometrus) spinifer solitarius: Couzijn, 1981: 33, 83, 92–94, 167, 173, 187, 191, table 7, figs. 23, 62; Vachon, 1982: 78, 96, 110, fig. 50; Kovařík, 1998: 137; Fet, 2000: 438; syn. nov.



FIGURE 167. *Heterometrus laevigatus* (Thorell, 1876), comb. nov. et stat. rev., pedipalp chela, retrodorsal aspect. **A.** ♀ (AMNH), Khao Pu-Khao Ya, Thailand. **B.** ♂ (AMNH), Thale Ban, Thailand. Scale bar = 5 mm.



FIGURE 168. *Heterometrus laevigatus* (Thorell, 1876), comb. nov. et stat. rev., ♂ (AMNH), Thale Ban, Thailand, pedipalp chela: **A**, ventral and **B**, prolateral aspects. Scale bar = 5 mm.

Heterometrus (Heterometrus) spinifer spinifer:

Couzijn, 1981: 19, 32, 75–77, 83, 89–93, 167, 174, 191, table 7, figs. 2b, 17b, 18, 19, 22, 63 (part); Kovařík, 1995: 203 (part); Hue et al., 1998: 7 (part); Fet, 2000: 438 (part).

Heterometrus spinifer solitarius: Kovařík, 2004: 42.

Heterometrus indus: Kovařík et al., 2016: 1, 10, 103 (part).

TYPE MATERIAL: *Buthus (Heterometrus) spinifer*: Holotype?: 1 ♂ (ZMB 67), “India” [examined]. **MALAYSIA: Kedah**: *Heterometrus (H.) spinifer*: Neotype ♂ (RMNH 290), Sult. Kadeh [Kedah], Malacca, 1900, Jhr. A. van de Does de Bij/Bye [examined]. *Heterometrus (H.) spinifer solitarius*: Holotype ♀ (MNHN RS 2866), Peradeniya [erroneous] [examined].

Ehrenberg (1828) described the type of *Buthus (Heterometrus) spinifer* from a specimen collected in India by Morpurgo, most likely deposited in ZMB. Couzijn (1981: 91) could not locate the holotype in ZMB or any other German museum and speculated it was probably destroyed during World War II (unlikely as the arachnid collection at ZMB was not destroyed in the war, unlike those of some other German museums). Couzijn (1981) examined an old adult male specimen in the SMF, which resembled the illustration and description of the holotype and was labeled “B.” for *Buthus* and collected in “India.” However, Couzijn (1981: 92) doubted this specimen was the holotype, as it was collected by Biedermann not Morpurgo, its sinistral chelicera was wide open (rather than closed as in the holotype), and the positions of the sinistral pedipalp chela, the patella and chela of the dextral pedipalp, and the metasoma differed from the original illustrations. Couzijn (1981) therefore designated an adult male (RMNH 290) from Kedah, Malaysia, as neotype. However, Braunwalder and Fet (1998: 32), followed by Fet (2000: 437), listed the holotype male of *Buthus (Heterometrus) spinifer* as “?ZMB 67” and Kovařík (2004) examined the specimen and concluded it was the holotype. ZMB 67, an

adult male, was reexamined during the present investigation and found to match existing concepts of *H. spinifer*. In the absence of evidence to the contrary, it is assumed to be the holotype of the latter, supporting Kovařík’s (2004: 40) conclusion that “in accordance with ICZN Article 75.8, Couzijn’s neotype designation is invalid.”

As noted above, the holotype of *Palamnaeus petersii* is not the same as the type specimens of *Palamnaeus silenus*, as implied by Couzijn (1981) and explicitly stated by Fet (2000: 437). Thorell (1876a: 2) neither specified a type nor listed the material on which *P. petersii* was based, merely stating it was deposited in Sweden. However, Thorell (1876b: 216) explicitly stated that *P. petersii* was based on a single specimen from Singapore, deposited in Göteborg (NMG). Couzijn (1981) listed the holotype of *P. petersii* among the material examined for *H. spinifer* but neglected to refer to it as a type.

DIAGNOSIS: *Heterometrus spinifer* may be separated from other species of *Heterometrus*, except *H. petersii*, as follows. The carapace interocular surface is granular along the median longitudinal and anterior bifurcated sulci only in the male and female (fig. 23C, D) of *H. spinifer*, whereas the frontal lobes and medial region of the interocular surface are granular with smooth areas in the male and female of *H. glaucus* and *H. thorellii*, and the interocular surface is entirely smooth in the male of *H. laevigatus* and the male and female of *H. laoticus*. The carapace anterolateral, mediolateral, and posterolateral surfaces of the female (fig. 23D) are granular in *H. spinifer* but smooth or nearly so in *H. laoticus*, and the posterolateral surfaces of the female smooth or nearly so in *H. longimanus*. The pedipalps of the adult male are short, with femur length : posterior carapace width ratio (FL:PCW) < 0.77 and femur length : carapace length ratio (FL:CL) < 0.74 (fig. 184) in *H. spinifer* but long, with FL:PCW ≥ 0.80 and FL:CL ≥ 0.76 in *H. glaucus*, *H. laevigatus*, *H. longimanus*, and *H. thorellii*. The pedipalp chela manus promedian carina of the female is present and granular in *H. spinifer* but absent or obsolete in *H. laevigatus*. The maximum distance between

the dorsomedian and dorsal secondary carinae (DMC–DSC) of the chela manus is similar to the maximum distance between the dorsal secondary and digital carinae (DSC–DC) in the male and female (fig. 187) of *H. spinifer* whereas the DMC–DSC is less than the DSC–DC in the male of *H. glaucus*, *H. laevigatus*, and *H. thorellii*, greater than the DSC–DC in the male of *H. silenus*, and less than the DSC–DC in the male and female of *H. longimanus*. The chela manus dorsal intercarinal surface is smooth or nearly so (fig. 187) in *H. spinifer* but shallowly reticulate in *H. glaucus*, *H. laevigatus*, and, often, *H. thorellii*. The second (subproximal) lobe of the chela movable finger of the adult male is more strongly developed than other lobes on the finger, with a correspondingly well-developed notch in the fixed finger (figs. 187B, 188) in *H. spinifer* but similar to or barely larger than other lobes on the finger in *H. glaucus*, *H. longimanus*, and *H. thorellii*. Macroseta *st* on the proventral surface of the basitarsus of leg I is setiform (fig. 50E) in *H. spinifer* but spiniform in *H. laevigatus* and *H. thorellii*; *st* on the proventral surface of the basitarsus of leg II is setiform (fig. 50F) in *H. spinifer* but spiniform in *H. glaucus*, *H. laevigatus*, *H. thorellii*, and, usually, *H. longimanus*; *sb* on the proventral surface of the basitarsus of leg III is spiniform (fig. 50G) in *H. spinifer* but setiform in all other species except *H. glaucus* and *H. petersii*. The lateral surfaces of mesosomal tergites I–VI in the female (fig. 185A) are granular in *H. spinifer* but smooth in *H. laevigatus*, *H. laoticus*, and *H. thorellii*. The ventrosubmedian and ventrolateral carinae of metasomal segments I–IV are granular or costate-granular on segment IV only and costate on segments I–III (fig. 69E) in *H. spinifer* but granular on segments I–IV, II–IV (costate on I), or III and IV (costate on I and II) in *H. laoticus* and *H. silenus*. The ventral intercarinal surfaces of segments III and IV of the female are smooth in *H. spinifer* but granular in *H. laoticus*. The telson is dark reddish brown and paler than metasomal segment V in *H. spinifer* (figs. 184, 185) but blackish and as dark as segment V in *H. laevigatus*, *H. laoticus*, *H. silenus*, and *H. thorellii*. The width of the telson

vesicle is approximately equal to or less than the width of metasomal segment V in the male (figs. 67E, 69E) of *H. spinifer* but greater than the width of segment V in the male of *H. glaucus* and *H. longimanus*. No morphological differences between *H. spinifer* and *H. petersii* were identified in the present investigation.

DISTRIBUTION: This species is distributed throughout peninsular Malaysia (recorded from the Federal Territory of Kuala Lumpur and the states of Johor, Kedah, Kelantan, Melaka, Negeri Sembilan, Pahang, Perak, Perlis, Selangor, and Terengganu) and also recorded from Tioman Island (fig. 157, table 2). Its distribution overlaps that of *H. longimanus* in southern peninsular Malaysia. *Heterometrus laevigatus* is allopatric to the north of the Sankalakhiri (Titiwangsa) Mountains, in Thailand. *Heterometrus petersii* appears to be allopatric on the islands of Penang and Singapore. The record from Peradeniya (Sri Lanka), the type locality of *H. (H.) spinifer solitarius*, is erroneous.

ECOLOGY: *Heterometrus spinifer* inhabits wet or dry primary and secondary rainforest from 40–1315 m on plains, in valleys and near rivers, at the base and on the lower slopes of mountains, and on plateaus. Recently collected specimens were mostly found doorkeeping at burrow entrances and sometimes under or in logs, or under stones using UV detection at night. Burrows were constructed in open ground or at the base of logs, roots, or stones in clayey-loam, sandy-clay and sandy-loam soils. The habitat and habitus of this species are consistent with the fossorial, pelophilous ecomorphotype (Prendini, 2001b). The following scorpions were found in sympatry: the buthids *Lychas scutillus* and *Reddyanus zideki* (Kovářík, 1994); the chaerilids *Chaerilus ojangureni* Kovářík, 2005, *Chaerilus tichyi* Kovářík, 2000, and several undetermined species of *Chaerilus*; and the hormurids *Hormiops infulcra* Monod, 2014, *Liocheles australasiae*, and two undetermined species of *Liocheles*.

CONSERVATION STATUS: *Heterometrus spinifer* was commonly available in the exotic pet trade until recently. Material offered for sale appears to

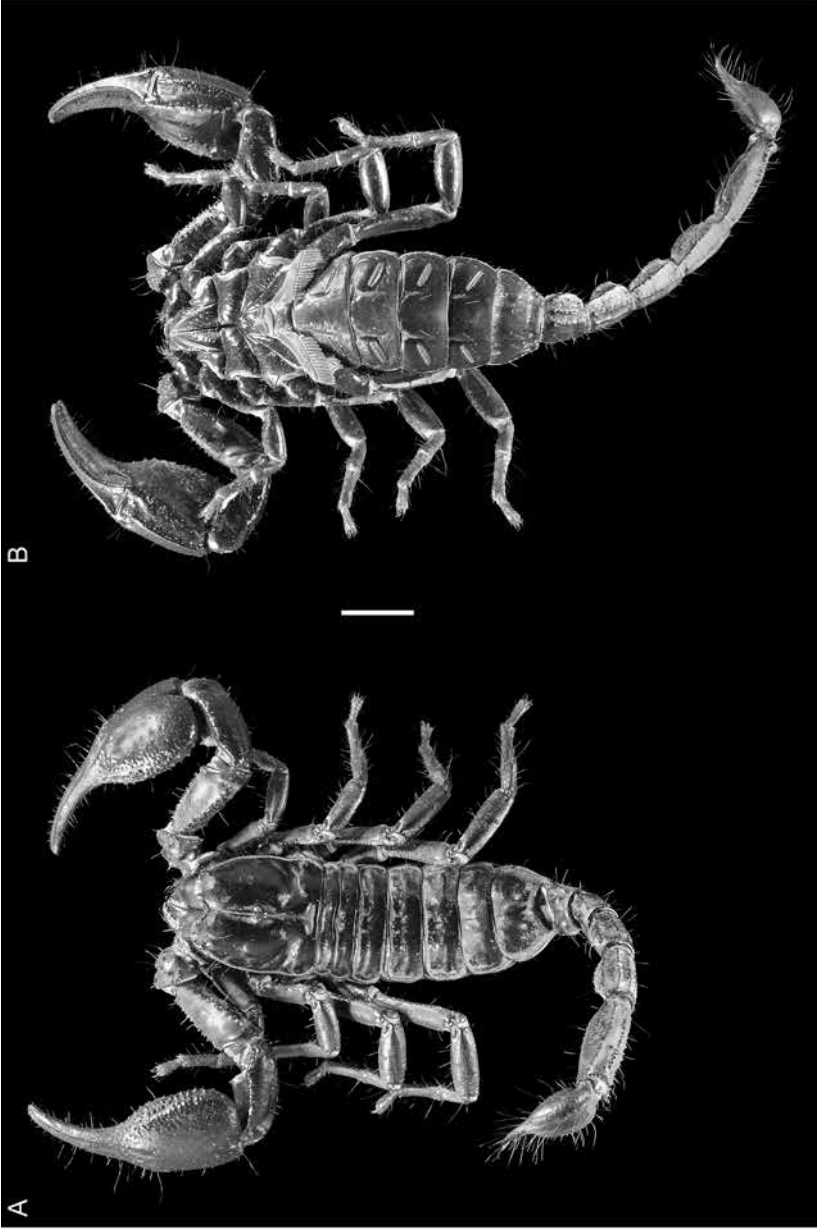


FIGURE 169. *Heterometrus laoticus* Couzijn, 1981, ♂ (AMNH), Phahom Camp, Laos, habitus: A. dorsal and B. ventral aspects. Scale bar = 10 mm.

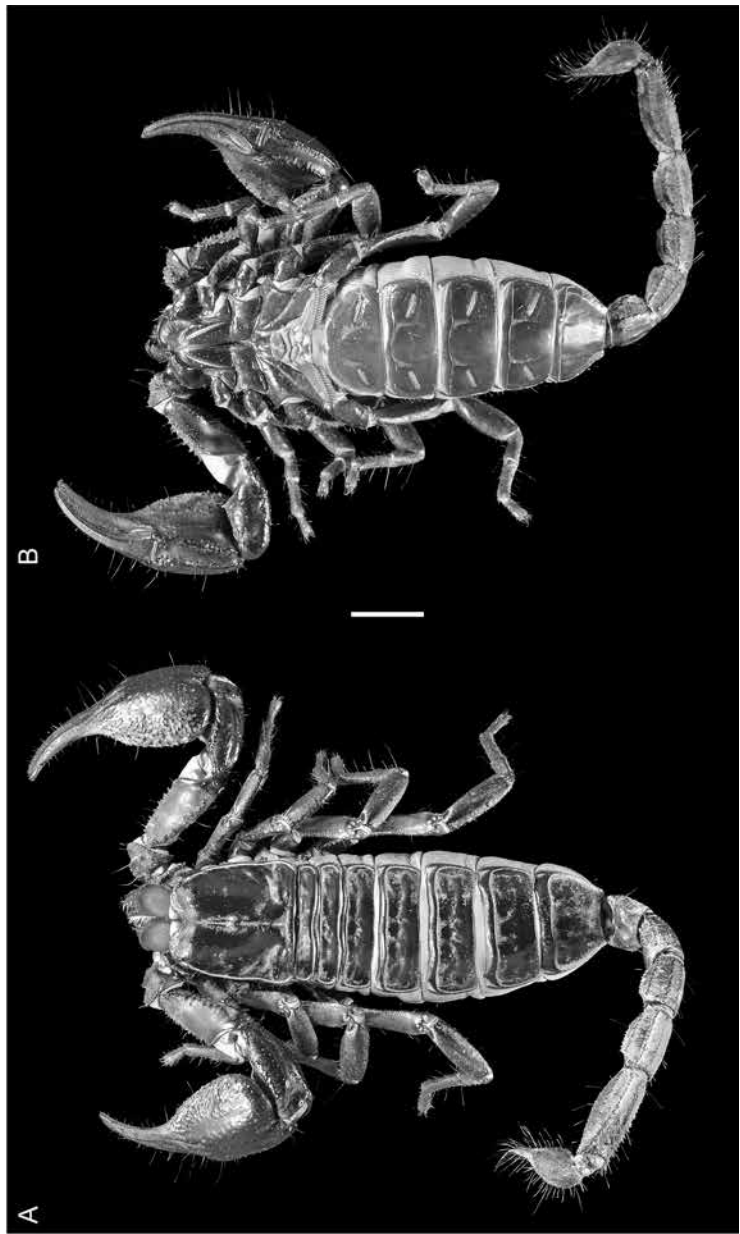


FIGURE 170. *Heterometrus laoticus* Couzijn, 1981, ♀ (AMNH), Tham Pha In, Laos, habitus: **A.** dorsal and **B.** ventral aspects. Scale bar = 10 mm.

have originated from Malaysia, where the species is now protected from commercial exploitation.

REMARKS: As discussed above, material from Penang and Singapore, previously identified as *H. spinifer* and assessed to be conspecific with the holotype of *Palamnaeus petersii* (also from Singapore), based on morphological similarity, was found to be more closely related genetically to *H. longimanus* from the Malaysian mainland and Borneo than to morphologically similar material of *H. spinifer* from the Malaysian mainland and Tioman, including the neotype of *H. spinifer* (Loria and Prendini, in press), leading to the conclusion that *H. petersii* is a cryptic species. This discovery, in turn, leads to the synonymy of *Palamnaeus oatesii* with *H. petersii*, rather than with *H. spinifer*, as proposed by Couzijn (1981) and upheld by Fet (2000) and Kovařík (2004, 2009).

Couzijn (1981) described *H. (H.) spinifer solitarius* from Peradeniya, Sri Lanka, an area in which *Srilankametrus indus* is the dominant species, on an island from which no species of the nominotypical subgenus of *Heterometrus* were recorded. Kovařík (2004: 42) listed *H. s. solitarius* under *H. spinifer* but did not formally synonymize the subspecies and doubted the accuracy of the type locality. Recently, Kovařík et al. (2016: 106, 107) synonymized *H. s. solitarius* with *S. indus* (as *H. indus*) on the grounds that the original description of *H. spinifer solitarius* “lacks clear diagnostic characters and any connection to *H. spinifer*” and *H. indus* is common, whereas *H. swammerdami* is uncommon, at the type locality of *H. s. solitarius*, Peradeniya. Contrary to the assertion of Kovařík (2004), it is abundantly clear from Couzijn’s (1981: 17, 93) description that *H. s. solitarius* is not conspecific with *S. indus* but closely allied to *H. spinifer* and other species of *Heterometrus*, vide “7–10 small teeth (besides the stout and sharp tooth) on the internal surface of segment 4 [pedipalp patella] ... Pedipalp hand relief type 15 [granulation absent, surface smooth].” Examination of the holotype of *H. s. solitarius* during the present investigation confirmed that it is conspecific with *H. spinifer*, regardless of the type locality, which is obviously erroneous. Therefore, the synonymy of

Kovařík et al. (2016) is rejected, and the following new synonym presented: *Heterometrus (Heterometrus) spinifer solitarius* Couzijn, 1981 = *Heterometrus spinifer* (Ehrenberg, 1828), syn nov.

MATERIAL EXAMINED: 1 ♂ (AMNH), 2 ♂ (AMNH [JV 7139, 7141]), 1 ♀ (AMNH [JV 7410]), [leg] [JV 8559] (AMCC [LP 11879]); 11.x.1940, 1 subad. ♂ (LKC ZRC-ARA 687). “East India,” 2 ♂ (MCZ). “Indonesia,” T.W. Tylor, 1 ♂ (NRS [JF 67]). Thailand, Burma, Southeast Asia, 1949, 1 ♂ (AMNH). **MALAYSIA:** xii.2000, ex pet trade, 1 ♀ (AMNH); most probably Malaysian import, 1990, ex pet trade, donated from Bronx Zoo, New York, U.S.A., 1 ♂ (AMNH). Peninsular Malaysia, 1988, Gopal, 2 ♂, 1 ♀ (LKC ZRC-ARA 666). **Johor:** *Johore Baru Distr.*: Johore, S. Malakka [Malacca, Johore Baru, 01°30′N 103°44′E], 9.viii.1910, F. Diehl, 6 ♂, 2 ♀ (ZMH). *Ledang Distr.*: Bukit Serampang [02°18′N 102°47′E], 1–3.i.1959, D.D. Davis, Malayan Zool. Exped., logged forest, 1 ♀ (FMNH 086 255); Taman Hutan Lagenda Gunung Ledang (Gunung Ledang Recreational Park), trail around camp, 02°20′N 102°37′E, 43 m, 19.vi.2013, L. Prendini and S.F. Loria, primary/secondary rainforest at base of large mountain (Gunung Ledang/Mt. Ophir), canopy partially open, moderate leaf-litter layer, large granite boulders, sandy-loam soil, fairly dry, moderate to sparse understorey, 1 ♀ under large stone during day, others observed with UV detection on warm, still night, doorkeeping at burrow entrances, 1 ♀ inside log, 1 ♂, 2 ♀ (AMNH). *Mersing Distr.*: Endau-Rompin National Park: Chalet area, 02°32′N 103°25′E, 53 m, 29.vi.2010, M.S. Harvey, K.L. Edward, R. Hashim, and S. Dzarawi, rainforest, from burrow, 1 subad. ♂ (WAM Ta209), [leg] (AMCC [LP 10581]); Kuala Jasin camp, trail to Janing Barat Plateau, 02°32′N 103°22′E, 37 m, 16–17. vi.2013, L. Prendini and S.F. Loria, primary rainforest at foot and lower slopes of Janing Barat Plateau, near confluence of Sungai Endau and Sungai Jasin rivers, thick canopy and sparse understorey with moderate to thick leaf-litter layer, clayey loam soil, UV detection on warm, still night, doorkeeping at burrow entrances in open or at base of logs/roots, 1 ♀ (AMNH), trail Denai Kecemasan, first 500 m, 02°32′N 103°22′E, 48 m, 17.vi.2013, L. Prendini and S.F. Loria, id., doorkeeping at burrow entrances, 1 subad. ♀ (AMNH). *Pontian Distr.*: Pontian, Sri Bunian, Kampung PT. Tekong (Pt. 112), 01°27′N 103°25′E, 8.v.1992, P.K.L. Ng, 1 subad. ♂ (LKC ZRC-ARA 672). *Segamat Distr.*: Segamat [02°30′N 102°49′E], 1 ♀ (LKC ZRC-ARA 681). **Kedah:** Sult. Kadeh [Kedah], Malacca, 1900, Jhr. A. van de Does de Bijé/Bye, 3 ♂, 4 ♀, 1 subad. ♂, 2 subad. ♀ (RMNH 290); Kedah, xi.1915, 1 juv. ♂ (LKC ZRC-ENT 7986). **Kuala Lumpur Federal Territory:** Kuala Lumpur [03°10′N 101°42′E], 2 ♂ (AMNH [JV 7116, 7117]), 1 ♀

(AMNH [JV 7007]); Kuala Lumpur, Pahang Road, 2.v.1949, U.S. Scrub Typhus Unit, 2 ♂ (USNM). **Pahang:** *Cameron Highlands Distr.:* Cameron Highlands [04°29'N 101°23'E], 1930–1931, K.B.N., 4500 ft., 1 subad. ♀ (LKC ZRC-ARA 683); Cameron Highlands, Tanah Rata [04°28'N 101°23'E], 21.i.1993, J. Nielsen, 1 ♂ (NRS [JF 50]). *Kuala Krau Distr.:* Krau Game Preserve, Kuala Lompat Ranger Post [03°43'N 102°17'E], at junction Lompat and Krau rivers (ca. 90 mi E Kuala Lumpur), ix.1972, J. Fleagle, 1 ♂ (MCZ). *Raub Distr.:* The “Gap” [03°42'N 101°45'E], Fraser’s Hill, R.C. West, 10.iv.2001, 1 ♂ (AMNH), [leg] (AMCC [LP 1906]). *Rompin Distr.:* Endau-Rompin National Park, Sungai Kinchin Base Camp, 02°37'N 103°20'E, 38 m, 18.vi.2013, L. Prendini and S.F. Loria, primary to secondary rainforest on flat plain near Kinchin River, closed canopy, moderate understorey, moderate to thick leaf-litter layer, clayey-loam soil, doorkeeping at burrow entrances with UV detection on warm, still night (moon > 50%), 1 juv. under rotten logs on forest floor, 1 juv. ♂, 1 juv. ♀ (AMNH), 1 juv. ♀ (AMCC [LP 11950]); Pulau Tioman (Tioman Island): trail between Kampung Genting and Kampung Paya, 02°46'N 104°07'E, 35–41 m, 11.vi.2013, L. Prendini and S.F. Loria, primary rainforest near seashore, moderately open canopy, sparse understorey, moderate leaf-litter layer, many large granite boulders, often with exfoliating flakes, clayey granitic loam, UV light detection on warm, dark, humid night, doorkeeping at burrow entrances, 1 ♀, 1 juv. ♀ (AMNH), 1 juv. ♂ (AMCC [LP 11920]), between 02°45'N 104°07'E and 02°47'N 104°07'E, 28–31 m, 12.vi.2013, L. Prendini and S.F. Loria, primary rainforest close to seashore, moderately open canopy, sparse understorey, moderate leaf-litter layer, many large granite boulders, often with exfoliating flakes, clayey granitic loam, under stone, 1 juv. sinistral pedipalp chela (AMNH); trail from Air Batang to Salang via Monkey Bay, 02°51'N 104°09'E, 48 m, 13.vi.2013, L. Prendini and S.F. Loria, primary rainforest near seashore, moderately open canopy, sparse understorey, moderate leaf-litter layer, many large granite boulders, often with exfoliating flakes, clayey granitic loam, under stone, 1 juv. ♀ (AMCC [LP 11974]); trail from Juara to Tekek, between 02°49'N 104°10'E and 02°49'N 104°11'E, 301–305 m, 15.vi.2013, L. Prendini and S.F. Loria, primary rainforest with closed canopy, moderate to dense leaf-litter layer, limestone rocks on summit, becoming sandstone and then granite lower down, under log, 1 juv. ♂ (AMNH). **Perak:** K. Legap [Kampung Legap], iii.1933, S. Plus, 1 juv. ♂, 2 juv. ♀ (LKC ZRC-ENT 7985). *Batang Padang Distr.:* Kampung Batu Tujoh [04°15'N 101°19'E], Cameron Highlands, vi.2013, ex. Penang Butterfly Farm, 11 ♂, 9 ♀ (AMNH). *Bukit Bakri Distr.:* Tanjong Hantu [Tanjong Hantu, 04°19'N

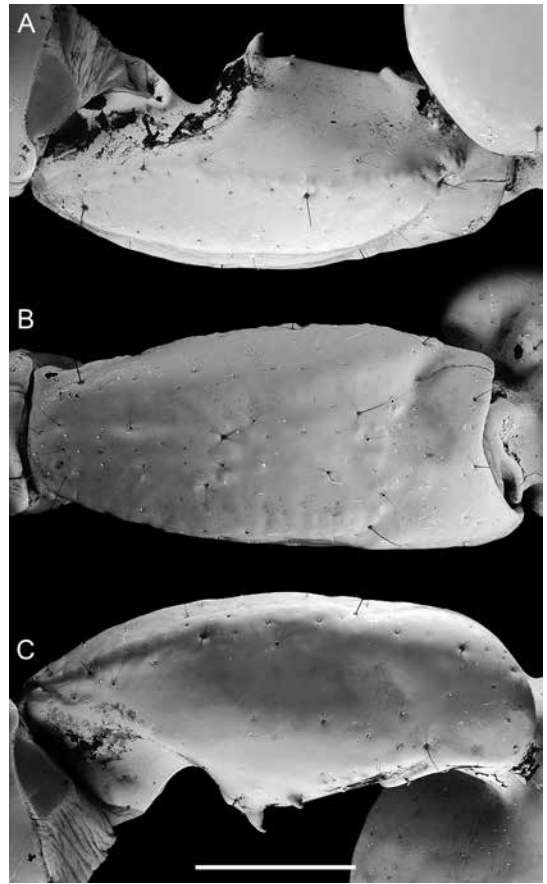


FIGURE 171. *Heterometrus laoticus* Couzijn, 1981, ♂ (AMNH), Phahom Camp, Laos, pedipalp patella: **A.** dorsal, **B.** retrolateral, and **C.** ventral aspects. Scale bar = 5 mm.

100°34'E], ii.1913, 2 ♂ (LKC ZRC-ENT 7976, 7978), 1 ♀ (LKC ZRC-ENT 7977), 1 subad. ♀ (LKC ZRC-ENT 7979). *Hulu Perak Distr.:* Upper Perak, Ulu Belum (MNS Exp. Base camp) [Sungai Halong Base Camp, Belum, 05°22'N 101°23'E], 9.ix.1993, I. Turner and J. Yong, 1 ♀ (LKC ZRC-ARA 670). *Kuala Kangsar Distr.:* Jalong [Kampung Jalong, 04°50'N 101°09'E], viii.1938, 1 subad. ♀ (LKC ZRC-ARA 682). *Larut, Matang and Selama Distr.:* Maxwell Hill [Bukit Larut, 04°52'N 100°48'E], 9.iv.1940, Yeo, 2850 ft., 1 ♀ (LKC ZRC-ARA 671). **Selangor:** *Gombak Distr.:* Taman Negeri Selangor (Selangor State Park), 03°18'N 101°42'E, 1314 m, 7.vi.2013, L. Prendini and S.F. Loria, primary rainforest in valley near river, very wet, sandy-loam soil, moderate leaf-litter layer, UV detection on warm night after heavy downpour, doorkeeping at burrow entrances in



FIGURE 172. *Heterometrus laoticus* Couzijn, 1981, ♂ (AMNH), Phahom Camp, Laos, pedipalp chela: A. retrodorsal, B. ventral, and C. prolateral aspects. Scale bar = 5 mm.



FIGURE 173. *Heterometrus laoticus* Couzijn, 1981, ♀ (AMNH), Tham Pha In, Laos, pedipalp chela: **A.** retro-dorsal, **B.** ventral, and **C.** prolateral aspects. Scale bar = 5 mm.

ground, 1 subad. ♀ (AMNH), 1 juv. ♀ (AMCC [LP 11949]); Taman Rimba Templar, 03°17'N 101°39'E, 94 m, 10.vi.2013, L. Prendini and S.F. Loria, primary rainforest on moderate slope along river, thick bamboo stands, under rotten log along trail, 1 juv. ♂ (AMNH). **Terengganu:** *Hulu Terengganu Distr.*: Sekayu Waterfall Park [04°59'N 102°56'E], 29.x.1998, H.H. Tan, 1 ♂ (LKC ZRC-ARA 669).

Heterometrus thorellii (Pocock, 1892)

Figures 10, 22E, F, 36E, F, 53A–D, 70D, 71D, 72D, 158, 189–192, table 2

Palamnaeus bengalensis: Simon, 1884a: 360–362 (misidentification, part); 1887: 112 (misidentification, part).

Palamnaeus petersii: Thorell, 1889: 588–590 (misidentification, part).

Palamnaeus spinifer: Pocock, 1892: 38–42 (misidentification, part); 1894b: 316 (misidentification, part).

Palamnaeus thorelli: Pocock, 1892: 40; Weidner, 1959: 103.

Palamnaeus thorellii Pocock, 1892: 39–41, 43; Laurie, 1896a: 187–190, 192, 193, pl. IX, fig. 2; 1896b: 127, 133, pl. IX, fig. 6.

Palamnaeus thorellii: Kraepelin, 1894: 35.

Scorpio bengalensis: Kraepelin, 1894: 25, 31, 37, 46, 47, 49, 51–53 (misidentification, part).

Scorpio longimanus: Kraepelin, 1894: 30, 34–39, 41, 49, 51–53, 55, 57 (misidentification, part).

Scorpio longimanus thorellii: Kraepelin, 1894: 40, 41.

Heterometrus bengalensis: Kraepelin, 1899: 110, 114, 115 (misidentification, part).

Heterometrus fulvipes: Kraepelin, 1899: 109, 112, 113, 115 (misidentification, part); Masi, 1912: 124 (part); Kopstein, 1921: 133 (part); Werner, 1934: 277 (part); Takashima, 1945: 91, 92 (part).

Heterometrus longimanus: Kraepelin, 1899: 108, 111 (misidentification, part); Masi, 1912: 123 (part); Kraepelin, 1913: 166 (misidentification, part); Kopstein, 1921: 129 (part); Werner, 1934: 277 (part); Roewer, 1943: 228 (misidentification, part).

Palamnaeus longimanus: Pocock, 1900a: 84, 97–99 (misidentification, part); Kovařík, 2004: 44.

Palamnaeus oatesii Pocock, 1900a: 84, 93, 98, 99 (misidentification, part); Flower, 1901: 35 (part).

Heterometrus longimanus typicus: Masi, 1912: 123 (part).

Heterometrus longimanus longimanus: Giltay, 1935: 2 (part).

Heterometrus oatesii: Takashima, 1945: 94 (part).

Heterometrus (Heterometrus) longimanus longimanus: Tikader and Bastawade, 1983: 519–522, 524, 526–528 (misidentification, part).

Heterometrus (Heterometrus) bengalensis: Couzijn, 1981: 38, 73, 75–77, 80, 85, 88, 89, 117–120, 167, 173, 174, 177, 178, 182–184, 189–191, table 7, figs. 17b, 18, 19, 21, 34, 62, 63, 66b, 71 (misidentification, part); Kovařík, 1998: 137 (part); Fet, 2000: 432, 434 (part); Kovařík, 2002: 17 (misidentification).

Heterometrus (Heterometrus) longimanus: Kovařík, 1998: 137 (part).

Heterometrus thorellii: Kovařík, 2004: 1, 20, 44–46, 51, 53, table 2, fig. 29; 2009: 35, 39, 44, 45, 48, 49, 94, 95, 99, table 1, figs. 146–159, 182–185.

TYPE MATERIAL: **MYANMAR**: *Palamnaeus thorellii*: Syntypes: 2 ♂, 3 ♀ (BMNH), Burma. *Heterometrus (H.) bengalensis*: Neotype ♂ (MNHN RS 0045), Irouaddy [Irrawaddy], Vossoin [examined].

Pocock (1892) based *H. thorellii* on two males and three females from Burma. A single adult male from Tharrawaddy ex BNHS 504, with a handwritten label that reads “*Palamnaeus thorelli* [sic] Pocock (= *Heterometrus*) ♂ lectotype dsq Kovařík, 2011” was examined in the BMNH. Given that the data for this specimen do not match the data in Pocock’s (1892) original description, it is doubtful that this specimen is one of the original syntypes. Therefore, it is not considered the lectotype of *P. thorellii* in the present contribution. The neotype

of *H. (H.) bengalensis*, designated by Couzijn (1981), is conspecific with the latter.

DIAGNOSIS: *Heterometrus thorellii* may be separated from other species of *Heterometrus* as follows. The frontal lobes and medial region of the carapace interocular surface are granular with smooth areas in the male and female (fig. 22E, F) of *H. thorellii* whereas the interocular surface is granular along the median longitudinal and anterior bifurcated sulci only in the female of *H. laevigatus* and the male and female of *H. longimanus*, *H. petersii*, *H. silenus*, and *H. spinifer*, and the interocular surface is entirely smooth in the male of *H. laevigatus* and the male and female of *H. laoticus*. The carapace anterolateral, mediolateral, and posterolateral surfaces of the female (fig. 22F) are granular in *H. thorellii* but smooth or nearly so in *H. laoticus*, and the posterolateral surfaces of the female smooth or nearly so in *H. longimanus*. The pedipalps of the adult male are long, with femur length : posterior carapace width ratio (FL:PCW) ≥ 0.80 and femur length : carapace length ratio (FL:CL) ≥ 0.76 (fig. 189A, B) in *H. thorellii* but short, with FL:PCW < 0.77 , FL:CL < 0.74 in *H. laoticus*, *H. petersii*, *H. silenus*, and *H. spinifer*. The pedipalp chela manus promedian carina of the female (fig. 192) is present and granular in *H. thorellii* but absent or obsolete in *H. laevigatus*. The maximum distance between the dorsomedian and dorsal secondary carinae (DMC–DSC) of the chela manus is less than the maximum distance between the dorsal secondary and digital carinae (DSC–DC) in the male (fig. 191A) and similar to the DSC–DC in the female (fig. 191B) of *H. thorellii* whereas the DMC–DSC is greater than the DSC–DC in the male of *H. silenus*, similar to the DSC–DC in the male of *H. laoticus*, *H. petersii*, and *H. spinifer*, and less than the DSC–DC in the female of *H. longimanus*. The chela manus dorsal intercarinal surface is often shallowly reticulate (fig. 191) in *H. thorellii* but smooth or nearly so in all other species except *H. glaucus* and *H. laevigatus*. The second (subproximal) lobe of the chela movable finger of the adult male is similar to or barely larger than other lobes

on the finger (fig. 191A) in *H. thorellii* but more strongly developed than other lobes on the finger, with a correspondingly well-developed notch in the fixed finger in all other species except *H. glaucus* and *H. longimanus*. Macroseta *st* on the proventral surface of the basitarsus of leg I is spiniform (fig. 53A) in *H. thorellii* but setiform in all other species except *H. laevigatus*; *st* on the proventral surface of the basitarsus of leg II is spiniform (fig. 53B) in *H. thorellii* but setiform in all other species except *H. glaucus*, *H. laevigatus*, and, usually, *H. longimanus*; *sb* on the proventral surface of the basitarsus of leg III is setiform (fig. 53C) in *H. thorellii* but spiniform in *H. glaucus*, *H. petersii*, and *H. spinifer*. The lateral surfaces surfaces of mesosomal tergites I–VI in the female are smooth (fig. 189C) in *H. thorellii* but granular in all other species except *H. glaucus* and *H. longimanus*. The ventrosubmedian and ventrolateral carinae of metasomal segments I–IV are granular or costate-granular on segment IV only and costate on segments I–III (fig. 72D) in *H. thorellii* but granular on segments I–IV, II–IV (costate on I), or III and IV (costate on I and II) in *H. laoticus* and *H. silenus*. The ventral intercarinal surfaces of segments III and IV of the female (fig. 72D) are smooth in *H. thorellii* but granular in *H. laoticus*. The telson is blackish and as dark as metasomal segment V in *H. thorellii* (fig. 189) but dark reddish brown and paler than segment V in *H. glaucus*, *H. longimanus*, *H. petersii*, and *H. spinifer*. The width of the telson vesicle is approximately equal to or less than the width of metasomal segment V in the male of *H. thorellii* but greater than the width of segment V in the male of *H. glaucus* and *H. longimanus*.

DISTRIBUTION: This species is endemic to central and northern Myanmar where it has been recorded in the Bago, Magway, Mandalay, Sagaing, and Yangon regions (fig. 158, table 2). Its distribution appears to be bounded in the east by the Shan Hills, Karen Hills, Dawna Range, and Tenasserim Hills, along the border with Thailand. *Heterometrus laevigatus* is allopatric, occurring further southwest in the Tanintharyi Region of Myanmar and in Thailand.

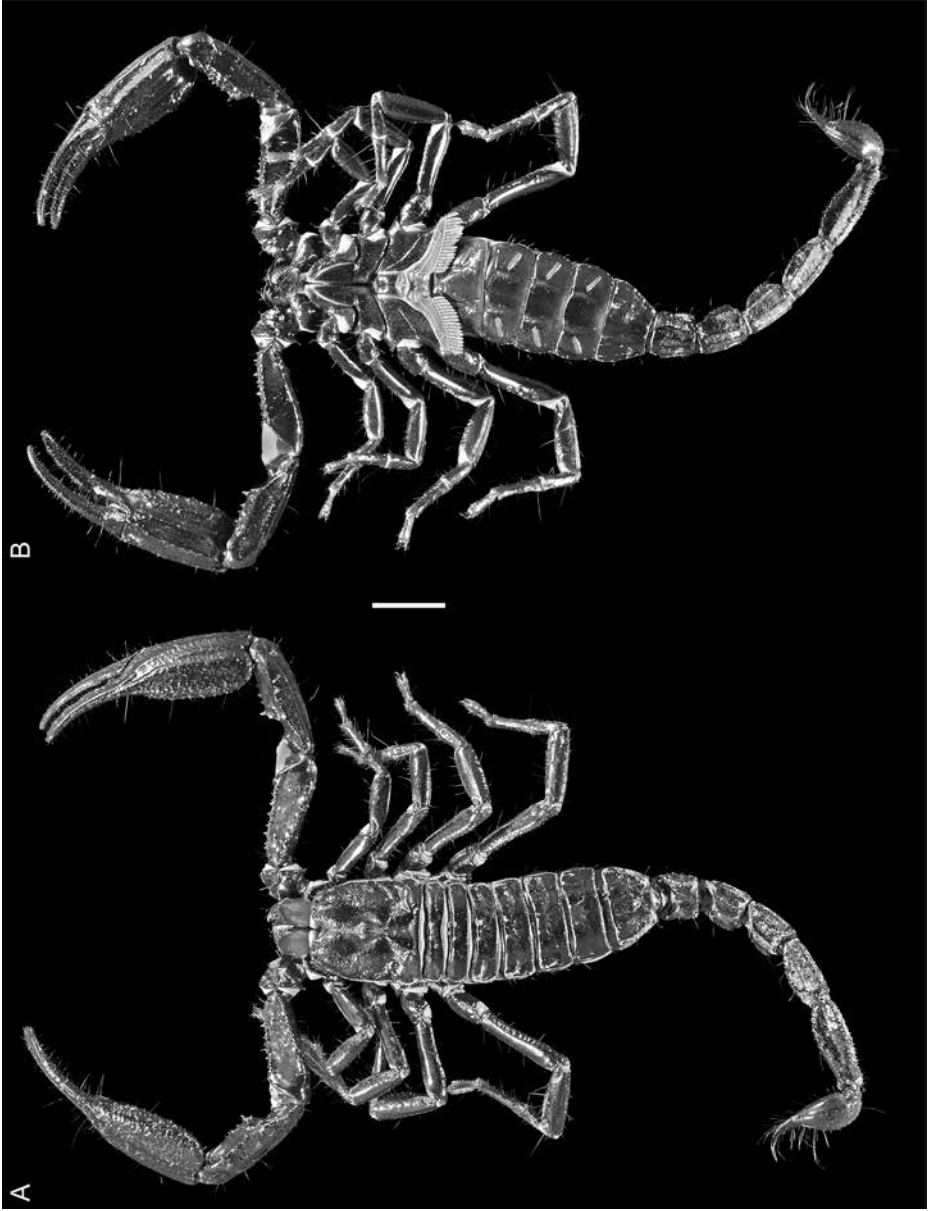


FIGURE 174. *Heterometrus longimanus* (Herbst, 1800), ♂ (AMNH), Kuching, Malaysia, habitus: **A.** dorsal and **B.** ventral aspects. Scale bar = 10 mm.

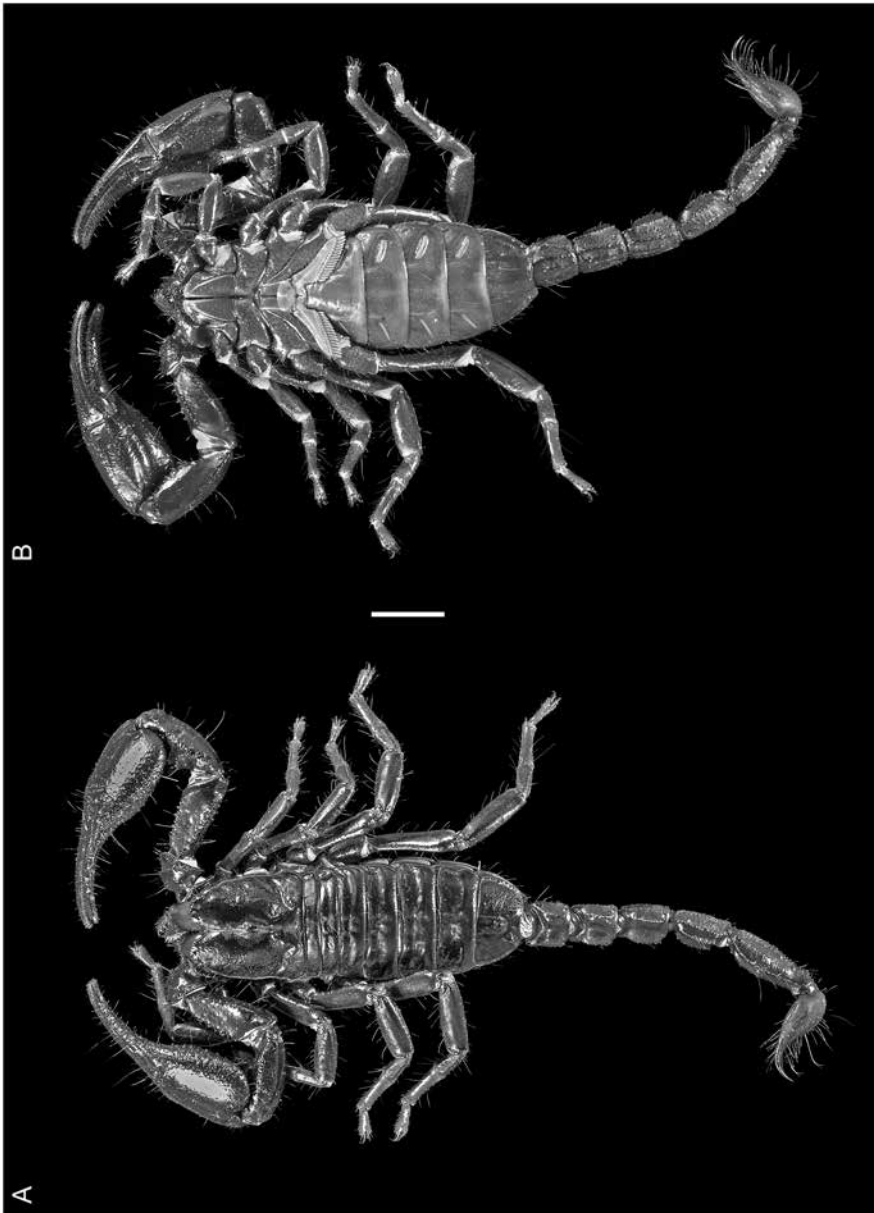


FIGURE 175. *Heterometrus longimanus* (Herbst, 1800), ♀ (AMNH), Kuching, Malaysia, habitus: A. dorsal and B. ventral aspects. Scale bar = 10 mm.

ECOLOGY: *Heterometrus thorellii* inhabits deciduous forest and savanna, and has also been found in backyards, at elevations of 55–815 m above sea level. Most specimens were collected at night with UV detection, doorkeeping at burrow entrances or under wood piles during the day. The habitat and habitus are consistent with the fossorial, pelophilous ecomorphotype (Prendini, 2001b). The following scorpions were collected in sympatry: the buthids *Lychas mucronatus*, *Lychas shoplanti* (Oates, 1888), and an undetermined species of *Lychas*; an undetermined chaerilid, genus *Chaerilus*; two undetermined hormurids of the genus *Liocheles*; and the scorpionid *Alloscorpions viktoriae* Lourenço and Košulic, 2018.

REMARKS: This species was previously accommodated in the nominal subgenus of *Heterometrus* by various authors (e.g., Couzijn, 1981; Tikader and Bastawade, 1983; Fet, 2000).

In the original description, Pocock (1892: 40) first used the specific epithet, *thorelli*, to refer to the new species, but later used the spelling, *thorellii*, more than once. The more commonly used spelling is applied in the present contribution, following Fet (2000) and Kovařík (2004, 2009).

As noted by Kovařík (2004: 44), the taxonomy of this species has a complex history. Simon (1884a: 36–38) believed it to be *Palamnaeus bengalensis*. Pocock (1892: 40) subsequently described it as *P. thorellii* and distinguished it from the similar *P. longimanus*, but later synonymized it with the latter (Pocock, 1900a). As with all other species of *Heterometrus*, *H. thorellii* is easily distinguished from *D. bengalensis* and other species of *Deccanometrus* by the presence of a prominent spiniform granule on the proventral carina of the pedipalp patella, referred to by Kovařík (2004: 44) as a “pronounced internal tubercle on the patella.” *Heterometrus thorellii* resembles *H. longimanus* but has a different geographical distribution and differs, among other characters cited in the key and diagnosis, in the blackish telson, which is dark reddish brown in *H. longimanus*. Couzijn (1981: 117) was apparently aware of some of the differences but refused to accept the authenticity of the original type series of *P. bengalensis* and based on it a new species, *H. (C.)*

fastigosus that was eventually synonymized by Kovařík (2004: 44). Therefore, most references to and identifications of *H. bengalensis* between 1981 and 2002 are mistaken and pertain to *H. thorellii*.

MATERIAL EXAMINED: 1 ♂, 2 ♀ (MNHN RS 0122 [Simon coll. 3276]); Cochinchina, 1 ♀ (MNHN RS 0155 [Simon coll. 1510]); Burma, India, 20.ix.1923, Faunthorpe-Vernay Expedition, 2 ♂, 1 ♀, 1 subad. ♀ (AMNH). **MYANMAR:** Thormann, 1 ♂ (ZMB 8072); Irouaddy [Irrawaddy], Vossoin, 1 ♂ (MNHN RS 0045); Tharrawaddy [Thayarwaddy, 17°39'N 95°47'E], 1 ♂ (BMNH [BNHS 504]); Burma, brought in U.S. by dealer, 15.x.1972, 1 ♀ (AMNH). **Bago Reg.:** Bago Distr.: Pegu [Bago, 17°20'N 96°29'E], Burma, C.H. Carpenter, xi.1966, 2 ♂, 3 ♀, 6 subad. ♂, 1 subad. ♀, 1 juv. ♀ (MCZ 103067). **Taungoo Distr.:** Bago (East) Region, Pho Kyar Elephant Camp, Yedashe, on trails near bungalows, 19°18'N 96°10'E, 127 m, 20.ix.2014, S.F. Loria and M.M. Locke, in burrows, 2 ♀, 1 juv. ♀ (AMNH), 1 juv. ♀ (AMCC [LP 13049]). **Kayin Reg.:** Hpa-An Distr.: Hpa-An Township, ca. 10 mi. E of Hpa-An Kalauk Htaung Village [16°53'N 97°39'E], v.2018, H.T. Bone, 3 ♂ (AMNH), 1 juv. ♀ (AMCC [LP 15604]). **Magway Reg.:** Thayet Distr.: Thayetinyo [Thayet, 19°19'N 95°11'E], Oates, 1 subad. ♂, 2 subad. ♀, 7 juv. ♂, 6 juv. ♀ (BMNH). **Mandalay Reg.:** Mandalay Distr.: Mandalay, 22°01'N 96°07'E, 20.ii.2014, M. Roppo, 1 ♂ (AMNH), 1 subad. ♀ (AMCC [LP 13155]). **Myingyan Distr.:** Mt. Popa, Popa Mountain Resort, 20°55'N 95°13'E, 777–815 m 16–17.xi.2014, S.F. Loria and M.M. Locke, blacklight at night, in burrows, 5 ♀, 3 subad. ♂, 3 subad. ♀, 2 juv. ♂, 1 juv. ♀ (AMNH), 1 juv. ♂ (AMCC [LP 13051]). **Nyaung-U Distr.:** Kyauk Kuumin Pagoda, near Nyaung-U, 21°12'N 94°56'E, 58 m, 18.xi.2014, S.F. Loria and M.M. Locke, desert, very dry, blacklight at night, in burrows, 1 subad. ♂, 12 juv. ♂, 9 juv. ♀ (AMNH), 1 juv. ♀ (AMCC [LP 13052]); Nyaung-U, on dirt road toward Kyauk Kuumin Pagoda, 21°12'N 94°56'E, 81–101 m, 18.xi.2014, S.F. Loria and M.M. Locke, desert, very dry, blacklight at night, on ground, 1 ♀, 4 juv. ♂, 4 juv. ♀ (AMNH), 1 juv. ♂ (AMCC [LP 13153]). **Pyin Oo Lwin Distr.:** Thaybeikyni [Thabeikkyin, 22°53'N 95°59'E], Burma, 1 ♀ (MCZ 103068). **Sagaing Reg.:** Shwebo Distr.: Chatten Wildlife Sanctuary, San Mydung, Chattung Wildlife Sanctuary, [23°12'N 95°33'E], 14.x.1998, at night, 1 ♀, 1 juv. ♂, 2 juv. ♀ (USNM 2050033). **Yangon Reg.:** Pane Ne Gone village, ca. 18 mi. S of Yangon, v.2018, Y.Z. Nyunt, 2 ♂ (AMNH); Rangoon [Yangon, 16°47'N 96°10'E], 1902, J. Claire, 2 ♂, 2 ♀ (MNHN RS 3447). **Yangon North Distr.:** Hlawga National Park, 23 km NNW Yangon, 17°03'N 96°06'E, 16–20.ix.2003, C. Gris-

wold, 1 ♂ (CAS 9019143), [leg] (AMCC [LP 2704]); Hlawga National Park, 17°03'N 96°07'E, 55 m, 22.xi.2014, S.F. Loria and M.M. Locke, blacklight at night, in burrows, 2 ♀, 1 subad. ♂, 3 juv. ♂, 4 juv. ♀ (AMNH), 1 juv. ♂ (AMCC [LP 13053]); Yangon, plantation on outskirts, 17°12'N 96°10'E, 56 m, 22.xi.2014, S.F. Loria and M.M. Locke, under wood pile, 1 ♀, 1 juv. ♀ (AMNH), 1 juv. ♂ (AMCC [LP 13050]).

Javanimetrus Couzijn, 1981,
stat. nov. et stat. rev.

Figures 6, 9F, 10, 25A, B, 39A, B, 53E–H, 70E,
71E, 72E, 193–197, table 2

Heterometrus (*Javanimetrus*) Couzijn, 1981: 80,
82, 120, 125, 126, 133, 161, 172–174, 180,
181, 183, 184, 186–189, 192, table 14, figs.
21, 61, 66a, 68–70, type species by original
designation: *Buthus cyaneus* C.L. Koch, 1836
[= *Javanimetrus cyaneus* (C.L. Koch, 1836)];
Tikader and Bastawade, 1983: 519, 520;
Francke, 1985: 8; Fet, 2000: 444; Prendini,
2000a: 44; Prendini et al., 2003: 222, 252,
appendix 1; Kovařík, 2004: 1, 2.

Heterometrus: Kovařík, 2004: 1, 2, 7, 49, 51, table
2 (part); 2009: 34, 35, table 1 (part); Kovařík
et al., 2016: 96, 100 (part); Rossi, 2016a:
6–9, 15, 19, 20, 25 (part).

DIAGNOSIS: *Javanimetrus cyaneus* may be separated from other Asian scorpionid genera as follows. The carapace is vaulted, the lateral surfaces sloping steeply (fig. 25A, B) in *Javanimetrus*, but slightly to markedly dorsoventrally compressed, the lateral surfaces sloping gently, in all except two species of *Deccanometrus*, *D. latimanus* and *D. xanthopus*, all except two species of *Sahyadrimetrus*, *S. mathewi* and *S. scaber*, all except three species of *Chersonesometrus*, *C. fulvipes*, *C. madraspatensis*, and *C. shivashankari*, and three species of *Srilankametrus*, *S. indus*, *S. pococki*, and *S. serratus*. The carapace anterior margin is concave, with the frontal lobes uneven and sloping medially in *Javanimetrus*, whereas the anterior margin is straight, with the frontal lobes evenly rounded or truncate in *Gigantometrus*, *Srilanka-*

metrus, two species of *Deccanometrus*, *D. latimanus* and *D. xanthopus*, and some species of *Chersonesometrus*. The carapace anterolateral margins are subparallel anteriorly in *Javanimetrus* but converge gradually anteriorly in all other genera except *Srilankametrus*; the mediolateral margins diverge or converge slightly posteriorly (at the posterolateral sulci) in *Javanimetrus*, but converge markedly posteriorly (at the posterolateral sulci) in *Gigantometrus*, *Heterometrus*, and three species of *Sahyadrimetrus*, *S. kanarensis*, *S. mathewi*, and *S. scaber*. The carapace rostrrolateral margin is entire in *Javanimetrus* but distinctly incised adjacent to the posterior lateral ocelli in *Heterometrus*. Anterocular extensions of the superciliary carinae are present in *Javanimetrus* but absent in *Srilankametrus*. The median ocelli are relatively small, the distance between them equal to or greater than the width of an ocellus in *Javanimetrus* but relatively large, the distance between them less than the width of an ocellus in *Heterometrus*; the median ocular tubercle is situated anteromedially to medially, the distance from carapace anterior margin : carapace length (CAM:CL) 0.40–0.50 in *Javanimetrus*, but posteromedially, CAM:CL 0.51–0.62 in *Chersonesometrus*. The interocular suture is absent in *Javanimetrus* but present in *Chersonesometrus*, *Gigantometrus*, and all except one species of *Deccanometrus*, and two species of *Srilankametrus*. The carapace posterior sutures are absent in *Javanimetrus*; present, extending to the median ocular tubercle, and connected by a short cross-suture anterior to the postocular depression in *Heterometrus*; and present, extending past the median ocular tubercle, and connected anteriorly to the posterior bifurcations of the interocular suture or disconnected in *Chersonesometrus*, *Deccanometrus*, *Gigantometrus*, and most species of *Srilankametrus*. The frontal lobes and medial region of the carapace interocular surface are granular with smooth areas in *Javanimetrus* whereas the interocular surface is entirely smooth in all except one species of *Srilankametrus* and some species of *Heterometrus*. The cheliceral movable finger prodistal (DI) and retrodistal (DE) teeth are unequal,

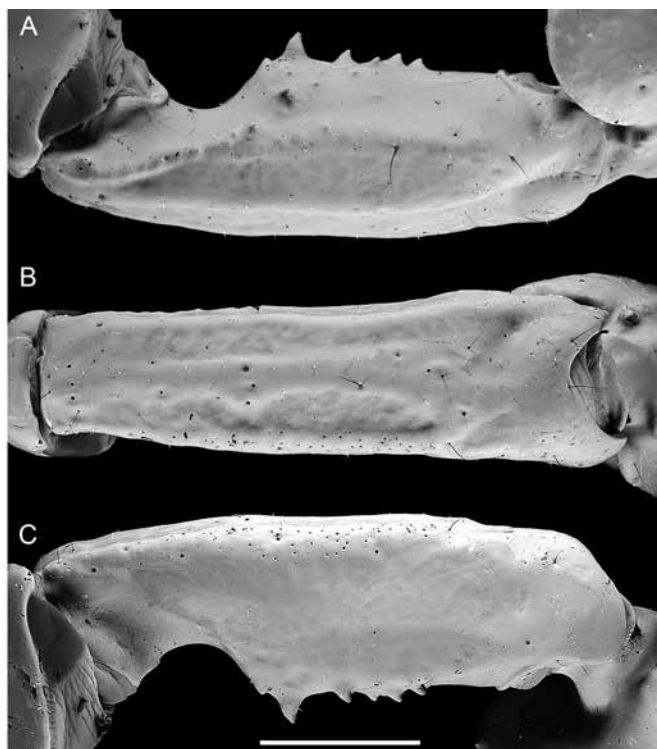


FIGURE 176. *Heterometrus longimanus* (Herbst, 1800), ♂ (AMNH), Kuching, Malaysia, pedipalp patella: A. dorsal, B. retrolateral, and C. ventral aspects. Scale bar = 5 mm.

with the DE tooth considerably smaller than the DI tooth, aligned longitudinally and not opposable in *Javanimetrus*, but opposable in two species of *Deccanometrus*, and subequal, with the DE tooth only slightly smaller than the DI tooth, and opposable, i.e., forming a bicuspid in *Heterometrus* and some species of *Chersonesometrus*. The pedipalp patella dorsomedian carina of the female is absent or obsolete in *Javanimetrus*, but predominantly granular or costate in *Chersonesometrus*, *Gigantometrus*, and all except three species of *Deccanometrus*, *D. latimanus*, *D. liurus*, and *D. ubicki*. The patella retromedian carinae of the female are absent or obsolete in *Javanimetrus*, but granular or costate in *Chersonesometrus*, three species of *Deccanometrus*, *D. bengalensis*, *D. obscurus*, and *D. phipsoni*, two species of *Srilankametrus*, *S. gravimanus* and *S. yaleensis*, and three species of *Sahyadrimetrus*, *S. barberi*, *S. rugosus*, and *S. tikaderi*.

The prominent spiniform granule of the patella proventral carina is absent (fig. 195) in *Javanimetrus* but present in *Heterometrus*. The patella dorsal, retrodorsal, and retroventral intercarinal surfaces of the female are smooth or nearly so in *Javanimetrus* but granular in all species of *Chersonesometrus* except *C. nathanorum*. The pedipalp chela of the adult male is sparsely setose (fig. 196) in *Javanimetrus* but moderately to densely setose in *Sahyadrimetrus*, all species of *Deccanometrus* except *D. xanthopus*, one species of *Srilankametrus*, and some species of *Chersonesometrus*. The distance between the chela manus dorsomedian and promedian carinae or setal rows (DMC-PMC) is slightly to markedly greater than the distance between the promedian and proventral carinae or setal rows (PMC-PVC) in *Javanimetrus* whereas the DMC-PMC is similar to the PMC-PVC in *Heterometrus*. The dorsomedian carina



FIGURE 177. *Heterometrus longimanus* (Herbst, 1800), pedipalp chela: **A**, **B**. retrodorsal, **C**. ventral, and **D**. prolateral aspects. **A**. ♀ (AMNH), **B–D**. ♂ (AMNH), Kuching, Malaysia. Scale bar = 5 mm.

becomes obsolete proximally in *Javanimetrus* but is continuous to the proximal edge of the manus in *Chersonesometrus*, *Gigantometrus*, and two species of *Deccanometrus*, *D. obscurus* and *D. phipsoni*. The chela manus dorsal secondary, subdigital, and digital carinae (setal rows) are well separated along their entire length in *Javanimetrus* whereas the proximal half of the dorsal secondary carina, distal half of the subdigital carina and distal third of the digital carina are closely adjacent in *Chersonesometrus* and *Gigantometrus*. The dorsal secondary and subdigital carinae of the male are absent or obsolete in *Javanimetrus* but present and entirely to predominantly granular or costate in *Gigantometrus*, all species of *Chersonesometrus* except *C. bastawadei* and *C. fulvipes*, and all species of *Srilankametrus* except *S. indus* and *S. pococki*. The chela manus digital and retromedian carinae are similarly developed (figs. 196, 197) in *Javanimetrus* whereas the retromedian carina is more pronounced than the digital carina in *Chersonesometrus*. The retromedian carina of the male is absent or obsolete in *Javanimetrus* but entirely to predominantly granular in *Gigantometrus*, *Srilankametrus caesar*, and *S. serratus*, and entirely to predominantly costate in *Chersonesometrus*, *Srilankametrus couzijni*, *S. gravimanus*, and *S. yaleensis*. The depression in the dorsal surface of the chela manus, proximal to the fixed finger of the adult male, is absent or obsolete (fig. 196) in *Javanimetrus* but present and distinct in *Heterometrus*. The chela manus dorsal surface is shallowly reticulate in *Javanimetrus* but without reticulation in *Gigantometrus*, *Srilankametrus*, most species of *Chersonesometrus*, all except three species of *Heterometrus*, *H. glaucus*, *H. laevigatus*, and *H. thorellii*, and two species of *Deccanometrus*, *D. obscurus* and *D. phipsoni*; the dorsal surface is smooth in *Javanimetrus* but finely to coarsely granular in *Chersonesometrus*, *Gigantometrus*, *Srilankametrus*, all species of *Deccanometrus* except *D. ubicki*, and all except two species of *Sahyadrimetrus*, *S. kanarensis* and *S. tikaderi*. The chela manus retrolateral intercarinal surfaces are smooth or nearly so in *Javanimetrus* but granular in *Chersonesometrus*, *Gigantometrus*, *Srilankametrus*, all species of *Dec-*

canometrus except *D. ubicki*, and some species of *Sahyadrimetrus*. The chela manus ventral surface is angled, with the axis of the retroventral carina ventral to the axis of the ventromedian carina in *Javanimetrus* but flat, with the axes of the retroventral and ventromedian carinae in approximately the same plane in *Deccanometrus*, *Gigantometrus*, *Heterometrus*, *Sahyadrimetrus*, all except four species of *Chersonesometrus*, *C. beccaloniae*, *C. hendersoni*, *C. pelekomanus*, and *C. tristis*, and all except two species of *Srilankametrus*, *S. indus* and *S. pococki*. The pro- and retrolateral surfaces of the tibiae of legs I and II each bear a row of two or three spiniform macrosetae in *Javanimetrus* and scattered, setiform macrosetae, not arranged in a definite row, in *Heterometrus*. Macroseta *st* on the retroventral surface of the basitarsus of leg I is spiniform (fig. 53E–H) in *Javanimetrus* but usually setiform in *Heterometrus*, and *sb* on the retroventral surface of the basitarsus of leg III is spiniform in *Javanimetrus* but setiform in *Deccanometrus*, *Gigantometrus*, *Srilankametrus*, and most species of *Chersonesometrus* and *Heterometrus*. The pseudonychium (dactyl) of the telotarsi of legs I–IV is reduced and rounded in *Javanimetrus* but prominent and acuminate in *Heterometrus*. The pectinal first proximal median lamella (scape) of the female is distinctly angular, $>90^\circ$ but $<180^\circ$ (fig. 39B) in *Javanimetrus* but straight or shallowly curved in *Srilankametrus*. The mesial surfaces of mesosomal tergites I–VI of the male are smooth in *Javanimetrus*, but granular in *Gigantometrus*, one species of *Deccanometrus*, *D. xanthopus*, two species of *Sahyadrimetrus*, *S. mathewi* and *S. scaber*, and some species of *Chersonesometrus*. The lengths of metasomal segments I and II are approximately equal to or less than their respective widths (figs. 70E, 72E) in *Javanimetrus* but markedly greater than their respective widths in *Gigantometrus*. The ventrosubmedian and ventrolateral carinae are granular or costate-granular on metasomal segment IV only and costate on segments I–III (figs. 71E, 72E) in *Javanimetrus* but granular on segments I–IV, II–IV (costate on I), or III and IV (costate on I and II) in *Gigantometrus*. The ventral



FIGURE 178. *Heterometrus petersii* (Thorell, 1876), holotype ♀ (NMG 91), habitus: **A.** dorsal and **B.** ventral aspects. Scale bar = 10 mm.



FIGURE 179. *Heterometrus silenus* (Simon, 1884), comb. nov. et stat. rev., habitus, dorsal aspect: **A.** ♂ (AMNH), **B.** ♀ (AMNH), Ta Kou Mountain Nature Reserve, Vietnam. Scale bars = 10 mm.

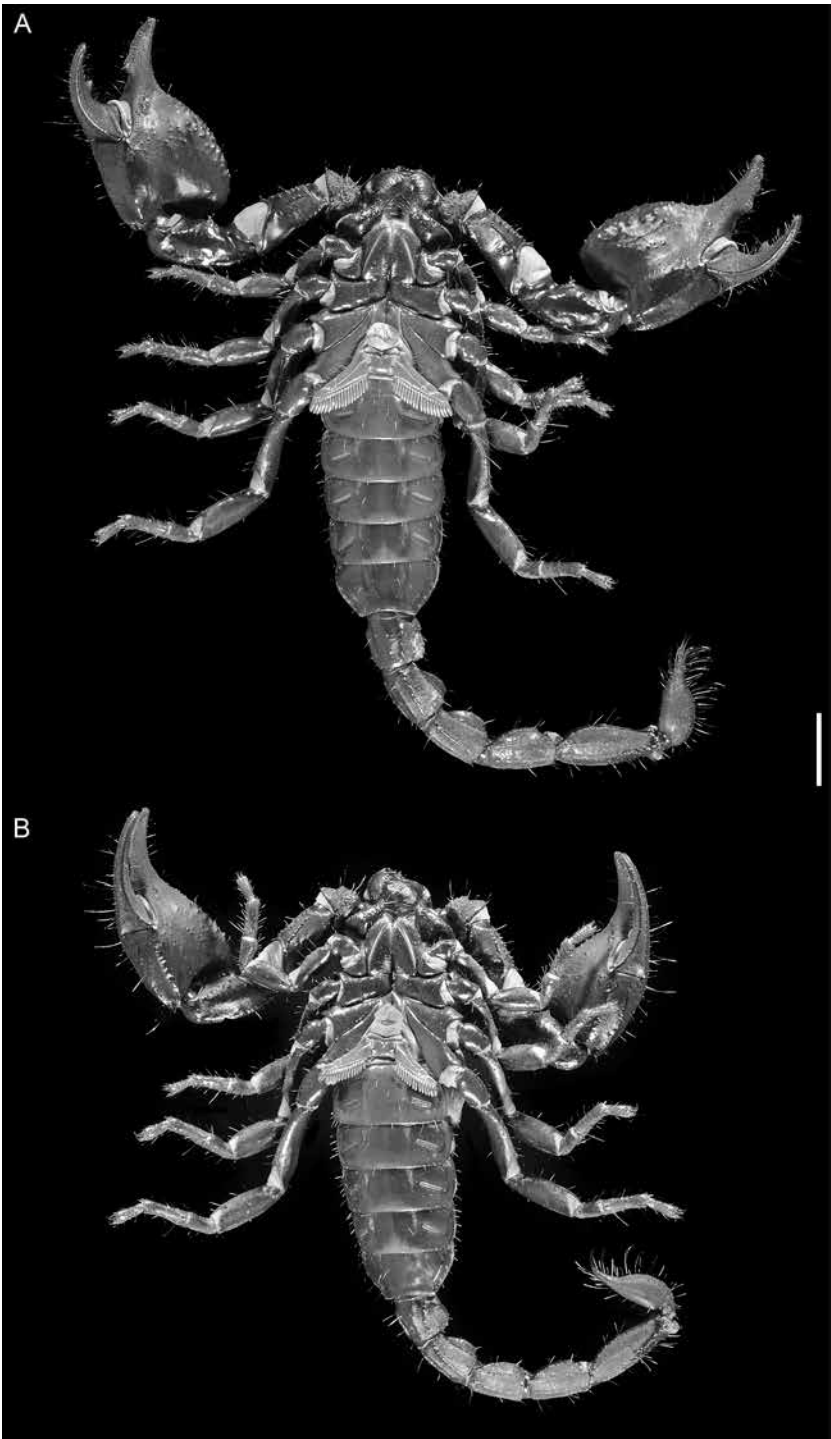


FIGURE 180. *Heterometrus silenus* (Simon, 1884), comb. nov. et stat. rev., habitus, ventral aspect: **A.** ♂ (AMNH), **B.** ♀ (AMNH), Ta Kou Mountain Nature Reserve, Vietnam. Scale bars = 10 mm.

intercarinal surfaces of metasomal segment IV are sparsely granular in *Javanimetrus* but smooth in *Deccanometrus*, *Gigantometrus*, *Heterometrus*, all except one species of *Sahyadrimetrus*, *S. tikaderi*, and all species of *Srilankametrus* except *S. caesar* and the males of *S. couzijni* and *S. gravimanus*. The dorsosubmedian carinae of metasomal segment V are vestigial (fig. 70E) in *Javanimetrus* but partial in *Gigantometrus* and absent in *Heterometrus*. The dorsal intercarinal surface of segment V is smooth in *Javanimetrus* but granular in *Gigantometrus* and some species of *Chersonesometrus* and *Srilankametrus*. The telson is usually paler than segment V in *Javanimetrus* (fig. 9F) but as dark as segment V in most species of *Srilankametrus* and some species of *Deccanometrus* and *Heterometrus*. The width of the telson vesicle is approximately equal to or less than the width of metasomal segment V in the female of *Javanimetrus* but greater than the width of segment V in the female of *Gigantometrus* and the vesicle is elongate in *Javanimetrus* but globose in *Chersonesometrus*, *Deccanometrus*, *Gigantometrus*, and three species of *Srilankametrus*, *S. indus*, *S. pococki*, and *S. serratus*.

INCLUDED SPECIES: *Javanimetrus* accommodates the single species formerly assigned to subgenus *Javanimetrus* of *Heterometrus* by various authors (Couzijn, 1981; Tikader and Bastawade, 1983; Fet, 2000), which was recovered as a distinct lineage by phylogenetic analysis of morphological characters and DNA sequences from the nuclear and mitochondrial genomes (fig. 10): *Javanimetrus cyaneus* (C.L. Koch, 1836).

DISTRIBUTION: The monotypic genus *Javanimetrus* exhibits a disjunct distribution across Southeast Asia (fig. 6, table 2) from the Nicobar Islands of India through Thailand (recorded on the island of Ko Muk and on the peninsula in Satun Province), the islands of Madura, Nias, Sumatra, Java, Bali, Borneo (recorded in the Indonesian provinces of Bali, Banten, Central Java, East Java, Jakarta Special Capital Region, Lampung, North Sumatra, West Java, and West Sumatra, and the Malaysian states of Sabah and Sarawak) to the Philippine island of Luzon

(recorded only in Laguan Province). Records from Singapore are unconfirmed (Kovářík, 1997: 183; 2004: 13) whereas records from Vietnam (Xuân Long), New Guinea (Merauke and Jayapura in Irian Jaya) and Japan are erroneous or based on misidentifications (Couzijn, 1981: 128; Kovářík, 2004: 13). The distribution of *Javanimetrus* overlaps those of *Heterometrus glaucus* in the Nicobar Islands, *H. laevigatus* in Thailand, *H. glaucus* and *H. longimanus* in Nias and Sumatra, and *H. longimanus* in Borneo and Luzon.

ECOLOGY: As for species.

CONSERVATION STATUS: As for species.

REMARKS: *Javanimetrus* Couzijn, 1981, stat. nov., originally created as a subgenus of *Heterometrus*, and subsequently synonymized with the latter (Kovářík, 2004), is hereby revalidated and elevated to the rank of genus.

Javanimetrus cyaneus (C.L. Koch, 1836),
comb. nov.

Figures 6, 9F, 10, 25A, B, 39A, B, 53E–H, 70E, 71E, 72E, 193–197, table 2

Scorpio afer Linnaeus, 1758: 624 (part; synonymized by Thorell, 1876b: 205–211); 1767: 1038 (part); 1775: 1091 (part); Fabricius, 1775: 399 (part); 1781: 550 (part); 1787: 348 (part); 1793: 434 (part); Herbst, 1800: 38–42 (part); Latreille, 1803: 267 (part); 1804: 120–122 (part); 1817: 106 (part); Dufour, 1856: 563, 571, 573, 574, 584, 590, 593, 614, 615, 622, 629, 631, 632, 641, 642, 644, 645, 648 (part); Lönnberg, 1897b: 176, 178, 179, 182, 186, 187 (part); 1898a: 82–86 (part); Couzijn, 1981: 129.

Buthus (Heterometrus) afer: Sundevall, 1833: 32 (part).

Buthus cyaneus C.L. Koch, 1836: 75–78, pl. XCVIII, fig. 225; 1850: 88; Doleschall, 1857: 404; Simon, 1872b: 98; Karsch, 1884: 69; Couzijn, 1981: 130; Kovářík, 2004: 2; 2009: 36, 37.

Buthus reticulatus C.L. Koch, 1837: 25–27, pl. CXV, fig. 265 (synonymized by Simon,

1872b: 98); 1850: 88; Doleschall, 1857: 404, 405.

Buthus setosus C.L. Koch, 1841a: 87, 88, pl. CCLXXVII, fig. 657 (synonymized by Kraepelin, 1899: 115); 1850: 88; Couzijn, 1981: 58.

Heterometrus reticulatus: Peters, 1861: 515.

Heterometrus cyaneus: Simon, 1872b: 54, 98, 99; Kraepelin, 1899: 110, 115, 116; Werner, 1902: 602; Domaniewski, 1913: 251–272, tables 1, 2, pl. XXVIII, figs. 1–4; Borelli, 1915: 463; Lampe, 1918: 198; Kopstein, 1921: 118, 119, 133, 134; 1923: 185, 186, 187; Pavlovsky, 1924a: 78; 1925: 152; Kopstein, 1926: 111–117, figs. 4–6; 1927: 105–108, 110; Giltay, 1931: 6–8, 18, figs. 2, 3; Kästner, 1931: 738; Werner, 1932: 576; 1934: 278; Giltay, 1935: 1, 2; Fage, 1936: 181 (part); Werner, 1936: 186; Kästner, 1941: 233; Roewer, 1943: 226; Takashima, 1945: 93; 1952: 27, 29; Bücherl, 1959: 269; Rosin and Shulov, 1963: 568; Bücherl, 1964: 59; Sreenivasa-Reddy, 1968: 760; Soleglad and Fet, 2003a: 59, tables 1, 2; Kovařík, 2004: 11–13, 34, 40, 51, 53, table 2, fig. 12 (part); Volschenk et al., 2008: 655, table 1; Kovařík, 2009: 3, 35–37, 46–49, 76, 101, 103, table 1, figs. 20–25, 226, 227, 238–245; Warburg, 2012b: 60, 63; Loria and Prendini, 2014: appendix S1: 10, appendix S2: 7.

Pandinus indicus (*nomen nudum*): Thorell, 1876b: 204, 209.

Pandinus indicus Karsch, 1884: 68, 69 (replacement name for *Scorpio afer* Linnaeus, 1758; synonymized by Couzijn, 1981: 126); Thorell, 1888: 329, 332, 333, 335, 337, 412–414; 1893: 380, 381; 1894: 15.

Pandinus setosus: Karsch, 1884: 67, 68.

Scorpio (*Buthus*) *cyaneus*: Lankester, 1885: 379, 382, 384, pl. LXXX, figs. 13, 14, pl. LXXXII, figs. 1, 10, 19, LXXXIII, figs. 17, 24.

Scorpio indicus: Pocock, 1893: 311, 312 (part); Kraepelin, 1894: 36, 49, 50, 52–58, 63, 246,

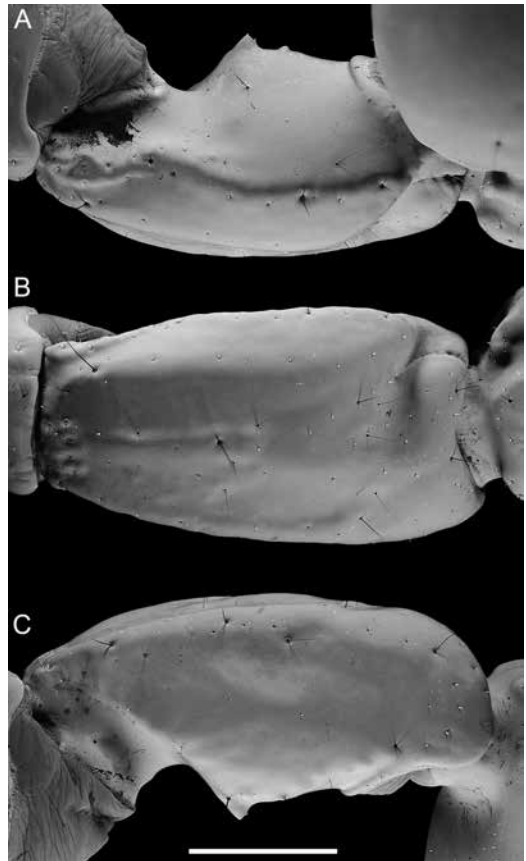


FIGURE 181. *Heterometrus silenus* (Simon, 1884), comb. nov. et stat. rev., ♂ (AMNH), Ta Kou Mountain Nature Reserve, Vietnam, pedipalp patella: **A.** dorsal, **B.** retrolateral, and **C.** ventral aspects. Scale bar = 5 mm.

pl. I, figs. 18, 19, 26, 27; Pocock, 1894c: 95, 96; Poljansky, 1903: 49–58, fig.; Couzijn, 1981: 58, 129; Warburg, 2012b: 60, 63.

Palamnaeus cyaneus: Kraepelin, 1898: 439.

Pandinus (*Scorpio*) *indicus*: Pavesi, 1898: 93, 94.

Heterometrus (*Scorpio*) *cyaneus*: Kraepelin, 1901: 271.

Heterometrus (*Heterometrus*) *cyaneus*: Couzijn, 1978: 330, table 1.

Heterometrus (*Heterometrus*) *petersii*: Couzijn, 1981: 73, 173, 175, 185, 187–189, figs. 62, 70 (misidentification, part); Fet, 2000: 437 (part).

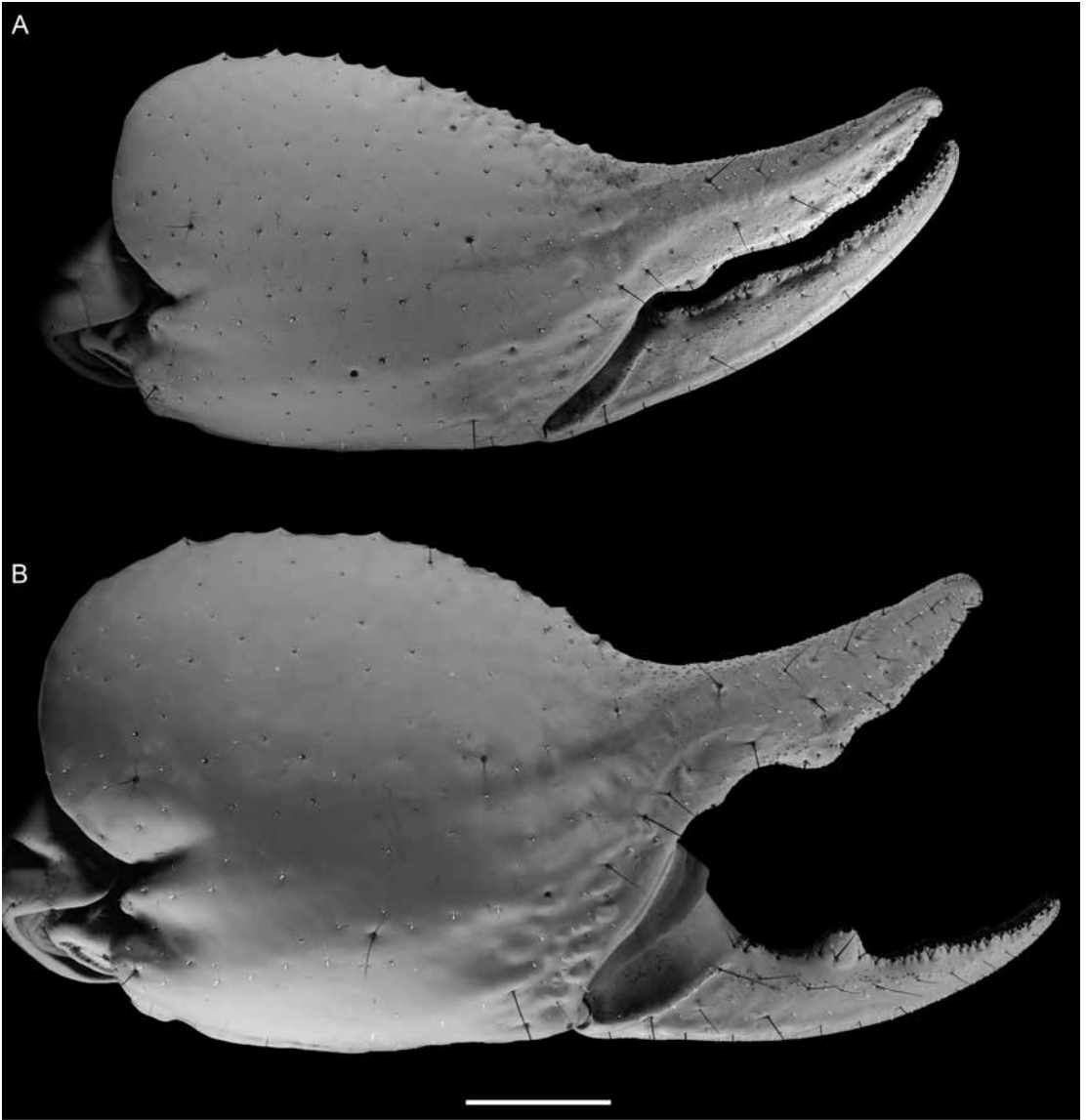


FIGURE 182. *Heterometrus silenus* (Simon, 1884), comb. nov. et stat. rev., pedipalp chela, retrodorsal aspect. A. ♀ (AMNH), B. ♂ (AMNH), Ta Kou Mountain Nature Reserve, Vietnam. Scale bar = 5 mm.



FIGURE 183. *Heterometrus silenus* (Simon, 1884), comb. nov. et stat. rev., ♂ (AMNH), Ta Kou Mountain Nature Reserve, Vietnam, pedipalp chela: **A.** ventral and **B.** nrolateral aspects. Scale bar = 5 mm.

Heterometrus (Heterometrus) petersii luzonensis
Couzijn, 1981: 33, 83, 88, 89, 98, 99, 175,
189, 191, table 7, fig. 27 (*Heterometrus (Het-*
erometrus) petersi luzonensis synonymized
by Kovařík, 2002: 3, 17; Kovařík, 1998: 137;
Fet, 2000: 437.

Heterometrus (Javanimetrus) cyaneus: Couzijn,
1981: 69, 80, 82, 94, 126, 129, 167, 172, 175,
178, 181, figs. 21, 61, 66a; Vachon and Abe,
1988: 27; Kovařík, 1992: 185; 1997: 183;
1998: 137; Fet, 2000: 444–446 (part);
Kovařík, 2002: 17.

Heterometrus (Javanimetrus) cyaneus cyaneus
Couzijn, 1981: 5, 8, 18, 21, 23–26, 44, 72,
78, 82, 124, 126–131, 172, 192, table 7, figs.
1a, 5a, b, 6a, b, 7e, f, 8a, 16a, 20, 37, 61; Hue
et al., 1998: 8 (part); Fet, 2000: 446.

Heterometrus (Javanimetrus) cyaneus insulanus
Couzijn, 1981: 45, 82, 125, 131, 172, 177,
192, table 7, fig. 61 (synonymized by
Kovařík, 2009: 36); Kovařík, 1998: 137; Fet,
2000: 446; Kovařík, 2004: 11; 2009: 37.

Heterometrus (Javanimetrus) cyaneus sumatrensis
Couzijn, 1981: 44, 82, 130–132, 172, 192,
table 7, figs. 38, 61 (synonymized by
Kovařík, 2009: 36); Kovařík, 1998: 137; Fet,
2000: 446; Kovařík, 2004: 11; 2009: 37.

Scorpio javanicus: Couzijn, 1981: 129.

Heterometrus (Srilankametrus) indus: Kovařík,
1997: 183 (misidentification).

Heterometrus petersi luzonensis: Kovařík, 2002:
17; 2004: 13; 2009: 37.

Heterometrus cyaneus insulanus: Kovařík, 2004:
13; 2009: 37.

Heterometrus cyaneus sumatrensis: Kovařík,
2004: 13; 2009: 37.

Heterometrus petersii luzonensis: Kovařík, 2004:
12, 34, fig. 12.

Heterometrus sejnai Kovařík, 2004: 1, 7, 38–40,
51, 53, tables 1, 2, fig. 26; 2009: 35, 43, 44,
48, 49, 91, 101, 111, table 1, figs. 124–132,
224, 225, 266, 267; Booncham et al., 2007:
43; syn. nov.

Heterometrus indus: Warburg, 2012b: 60, 63.

TYPE MATERIAL: *Buthus setosus*: Holotype
[lost]. *Scorpio afer* [= *Pandinus indicus*]: Syntypes
[sex?], “Africa” [lost]. **INDONESIA**: *Buthus cya-*
neus: Holotype [sex?], Java [lost]. *Buthus reticula-*
tus: Holotype ♀?, Java [lost]. **East Java Prov.:**
Banjuwangi Reg.: Heterometrus (Javanimetrus) c.
cyaneus: Neotype ♂ (RMNH 139), Kalie Baroe/
Kali Baru [Kalibaru, 08°16'S 113°59'E], Banjoe-
wangi/Banjuwangi, Java, viii.1902, M.A.J. Fokker
[examined]. *H. (J.) c. insulanus*: Holotype ♂, para-
type ♀ (RMNH 272), Central Madura [07°00'S
113°20'E], x.1903, G.J.A. Steen [examined]. **West**
Sumatra Prov.: *H. (J.) c. sumatrensis*: Holotype ♂,
paratype ♀ (RMNH 267), Padang [00°57'S
100°25'E], Sumatra, Muller [examined]. **PHILIP-**
PINES: Laguna Prov.: *First Distr., Los Baños*
Municipality: Heterometrus (H.) petersii luzonen-
sis: Holotype ♀, paratype ♀ (SMF RII/8882/24),
Mt. Makiling [14°08'N 121°12'E], Luzon [exam-
ined]. **THAILAND: Satun Prov.:** *Khuan Don*
Distr.: Heterometrus sejnai: Holotype ♂, para-
types: 1 ♀, 3 imm. (FKPC), Thaleban National
Park [06°43'N 100°10'E], x.1998, V. Šejna.

Koch (1836: 75) based *Buthus cyaneus* on an
adult from Java, Indonesia, in the collection of J.
Sturm in Nürnberg. As noted by Couzijn (1981:
129) it is impossible to deduce the sex of the
holotype from the description, because sexual
dimorphism is hardly developed in this species
and the primary sexual characters were not yet
known in the 19th century. Couzijn (1981) could
not locate the holotype and designated a neotype
male from Kali Baru, Banjuwangi (Java), col-
lected by M.A.J. Fokker (RMNH 139).

DIAGNOSIS: As for genus.

DISTRIBUTION: As for genus.

ECOLOGY: *Javanimetrus cyaneus* inhabits pri-
mary and secondary rainforest but has also been
collected in agricultural fields. The known local-
ity records occur at elevations between 75–1115
m above sea level. This pelophilous, fossorial
species constructs burrows in hard, clayey soil in
earthen banks, or under stones or logs. Specimens
were collected at night with UV light, door-
keeping at burrow entrances, or under rocks
during daytime. This species was collected in

sympatry with the chaerilid, *Chaerilus variegatus* Simon, 1877.

CONSERVATION STATUS: *Javanimetrus cyaneus* is extensively harvested for the commercial trade in exotic pets. Material offered for sale appears to have originated from the Indonesian island of Java.

REMARKS: This species was previously accommodated in subgenus *Javanimetrus* of *Heterometrus* by Couzijn (1981) and Fet (2000). The following synonyms are currently recognized: *Scorpio afer* Linnaeus, 1758 (part) = *Javanimetrus cyaneus* (C.L. Koch, 1836), comb. nov., synonymized by Thorell (1876b); *Buthus reticulatus* C.L. Koch, 1837 = *J. cyaneus*, synonymized by Simon (1872b), not Thorell (1893), as suggested by others (see Fet, 2000); *Buthus setosus* C.L. Koch, 1841 = *J. cyaneus*, synonymized by Kraepelin (1899); *Pandinus indicus* Karsch, 1884 = *J. cyaneus*, synonymized by Couzijn (1981); *Heterometrus (Javanimetrus) cyaneus insulanus* Couzijn, 1981 = *J. cyaneus*, synonymized by Kovařík (2009); *Heterometrus (Javanimetrus) cyaneus sumatrensis* Couzijn, 1981 = *J. cyaneus*, synonymized by Kovařík (2009); *Heterometrus (H.) petersii luzonensis* Couzijn, 1981 = *J. cyaneus*, synonymized by Kovařík (2002).

Although Kovařík (2004: 11) credited Thorell (1893: 381) for synonymizing *Scorpio afer* with *H. cyaneus*, the synonymy was published earlier by Thorell (1876b: 205–211), as noted by Couzijn (1981: 129) and Fet (2000: 445). The validity of *S. afer* is unclear (Fet, 2000). As noted by Couzijn (1981: 129) the name *S. afer* (Linnaeus, 1758: 624) was published as a substitute for earlier names used by Linnaeus (1746: 45): *Scorpio javanicus* (= *Buthus cyaneus*), *Scorpio indicus*, and *Scorpio ceylonicus* (= *Scorpio indus*). Its brief description may be that of a *Heterometrus* species, but it refers to a scorpion from Africa which is probably a mistake (Fet, 2000), and its types are probably lost (Couzijn, 1981; Fet, 2000). The two “Linnean types” in the Zoological Museum of Uppsala University, Sweden, were examined by Couzijn (1981: 129) and identified as *H. i. indus* and *H. c. cyaneus*, in accordance with Thorell (1876b: 205–211). It is probable, however, that these specimens are not

the genuine type specimens described by Linnaeus (Couzijn, 1981; Wallin, 1994; Fet, 2000); they may have been replaced later by C.P. Thunberg. The name *S. afer* has not been used since Lönnberg (1897b, 1898a) but was not formally suppressed (Fet, 2000). Couzijn (1981) recommended using the younger, well-established name, *H. cyaneus*, frequently used in publications since Kraepelin (1899).

Fet (2000: 445) stated that Thorell (1893: 380) synonymized *Buthus reticulatus* with *H. cyaneus* but, as noted by Kovařík (2004, 2009), Simon (1872b: 98) was the first to do so.

Buthus defensor C.L. Koch, 1837, and *Buthus heros* C.L. Koch, 1837, first listed in synonymy with *H. cyaneus* by Kraepelin (1899: 115), an opinion accepted uncritically by various authors (Couzijn, 1981: 126; Fet, 2000: 444–446; Kovařík, 2004: 11, 2009: 3, 36), are not conspecific with *J. cyaneus*, let alone *Heterometrinae*, as pointed out early on by Karsch (1879b: 128, 1884). Although the types of both taxa are apparently lost (Fet, 2000), they are evidently congeneric with the African *Pandinurus* Fet, 1997; indeed, Koch (1837: 3) notes the origin of *B. heros* as Africa, whereas *B. defensor* is supposedly from Mexico, clearly erroneous. The descriptions and illustrations of *B. defensor* and *B. heros* closely match *Pandinurus gregoryi* (Pocock, 1896) and *Pandinurus exitialis* (Pocock, 1888), respectively, justifying the following new synonyms: *Buthus heros* C.L. Koch, 1837 = *Pandinurus exitialis* (Pocock, 1888), syn. nov.; *Buthus defensor* C.L. Koch, 1837 = *Pandinurus gregoryi* (Pocock, 1896), syn. nov. Although *B. defensor* and *B. heros* have nomenclatural priority, these names have not been used in publications since Kraepelin (1899) but, more importantly, the absence of types and accurate type localities prevents their taxonomic identities from ever being verified. Therefore, it seems prudent to retain the more recent names of Pocock (1888, 1896c).

Due to loss of the holotype and an inadequate original description, the status of *Buthus setosus* remains uncertain and it was listed under *H. cyaneus* with a questionmark by Kraepelin (1899: 115) and Kovařík (2004: 11).

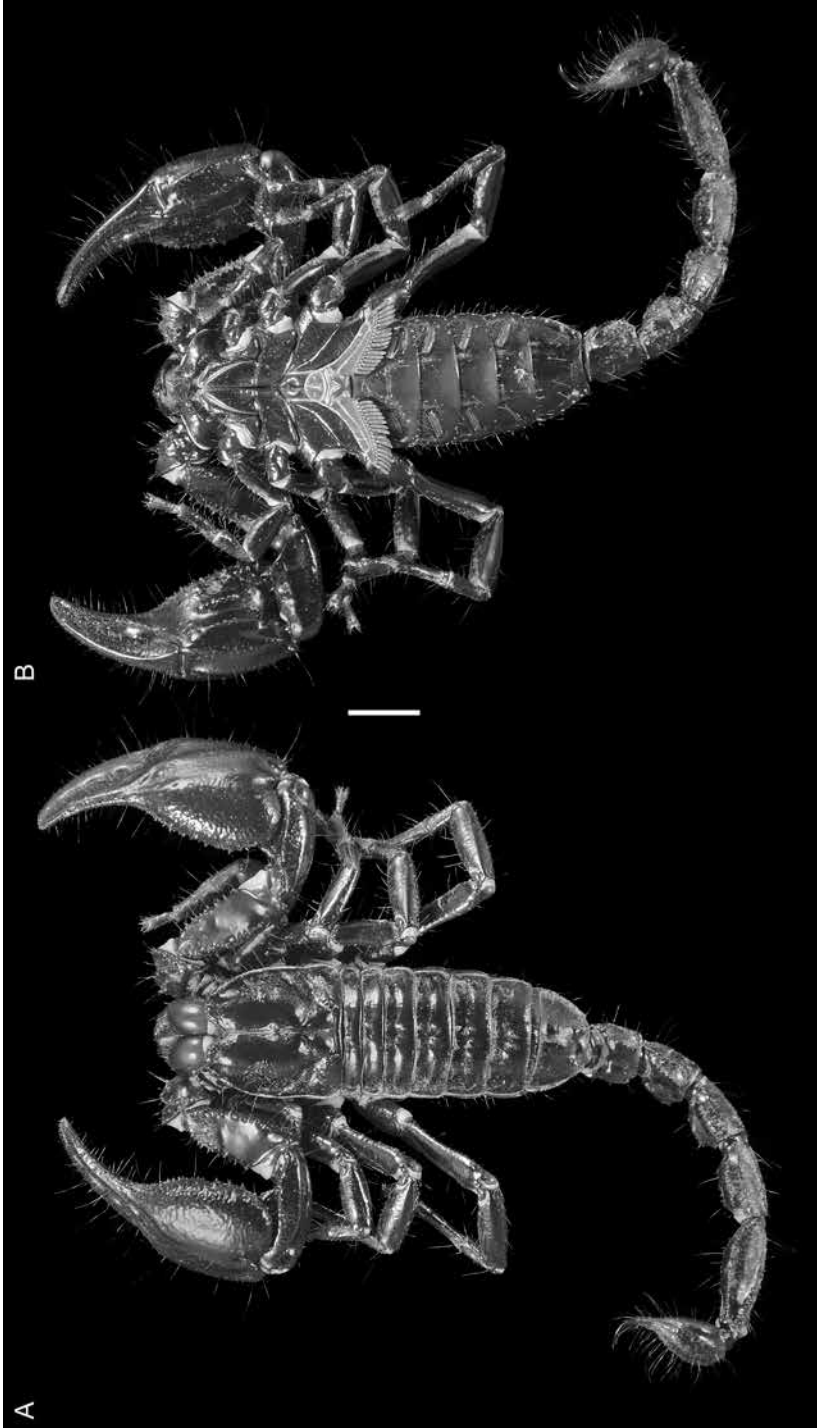


FIGURE 184. *Heterometrus spinifer* (Ehrenberg, 1828), ♂ (AMNH), Cameron Highlands, Malaysia, Scale bar = 10 mm.

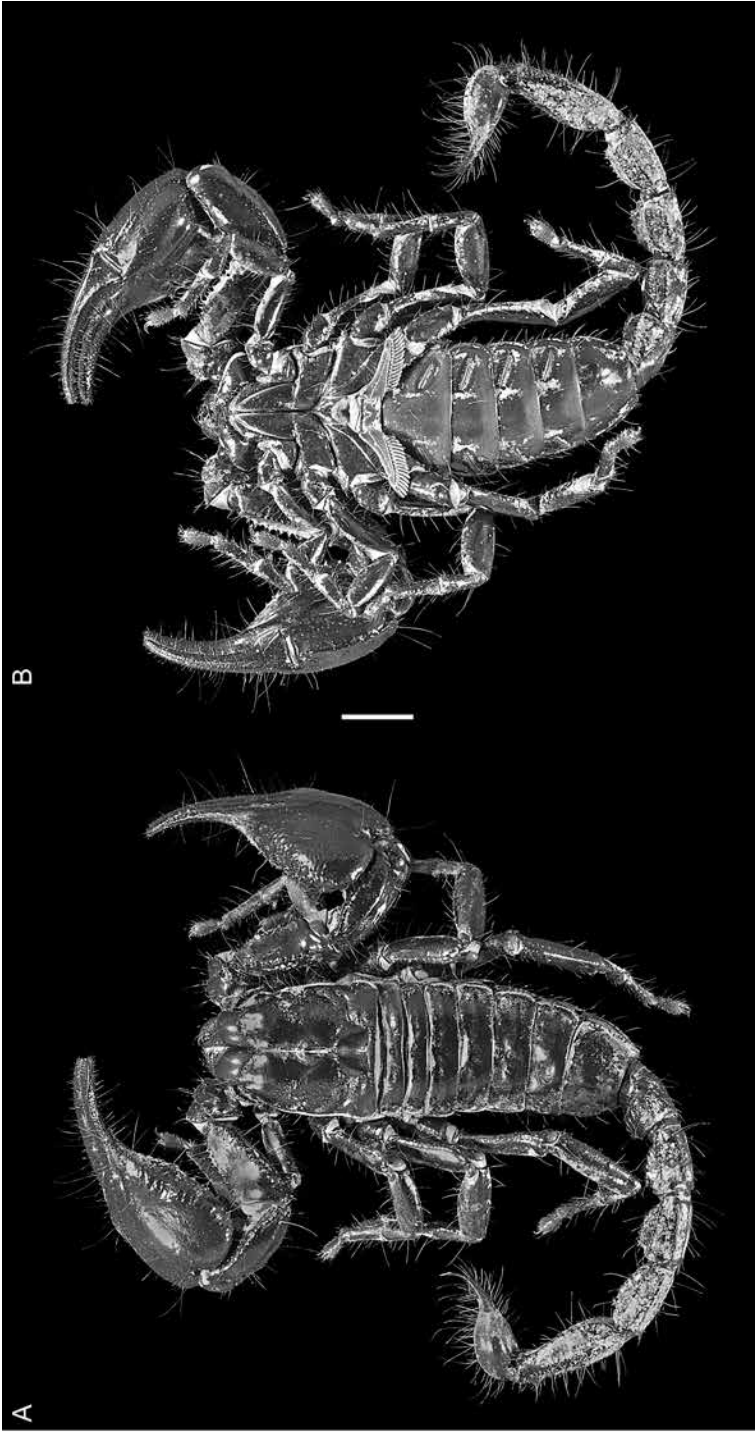


FIGURE 185. *Heterometrus spinifer* (Ehrenberg, 1828), ♀ (AMNH), Cameron Highlands, Malaysia, A. dorsal and B. ventral aspects. Scale bar = 10 mm.

As noted by Fet (2000: 445), *Scorpio indicus* is a “pre-1758” binomen, used by Linnaeus (1748) but not later. Karsch (1884: 68) was the first to use it in reference to the Linnean species in combination with a description, inadvertently creating an available name, *Pandinus indicus*. In the same work, Karsch (1884: 69) stated that *P. indicus* is identical with *Buthus reticulatus*, synonymized with *H. cyaneus* by Simon (1872b).

Couzijn (1981) described two subspecies of *H. (J.) cyaneus*, *H. (J.) c. insulanus* from Madura, Indonesia, and *H. (J.) c. sumatrensis*, from Sumatra, Indonesia, and the Lesser Nicobar Islands, India. Kovařík (2004: 11, 13) listed both subspecies under *H. cyaneus*, but did not formally synonymize them because the types were not examined. After examining the types of these subspecies and the neotype of *H. cyaneus*, Kovařík (2009: 36, 37) subsequently synonymized the subspecies on the grounds that the characters Couzijn (1981) used to define these subspecies represented intraspecific variation and were therefore “taxonomically meaningless” (Kovařík, 2009: 37). During the present investigation, both synonyms were verified by examination of the type material. Kovařík’s (2002) synonymy of *H. (H.) petersii luzonensis* with *H. cyaneus* was also confirmed by examination of the types of *H. (H.) p. luzonensis*.

Heterometrus sejnai was based on five specimens from Thaleban National Park in Satun Province, Thailand. According to the original description (Kovařík, 2004: 40), *H. sejnai* “is close to *H. cyaneus* but its smaller size causes some morphological differences [and the] two species also differ in geographic distribution.” Although localized, *Javanimetrus cyaneus* appears to be widely distributed. Besides Java, it has been recorded from Madura, Borneo, Sumatra, the Philippines, and the Lesser Nicobar Islands. Therefore, its presence in Thailand is plausible. Kovařík’s (2004: 53) key separates the two species solely on the total length of the adults being less than 80 mm in *H. sejnai* but more than 95 mm in *H. cyaneus*. However, the diagnosis of *H. sejnai* states: “Adult male holo-

type 78 mm long. Other adults 95–117 mm long” (Kovařík, 2004: 38). The diagnosis of *H. cyaneus* states: “Adults 95–115 mm long” (Kovařík, 2004: 9). Other characters presented in the diagnosis of *H. sejnai* are either typical of *H. cyaneus* or fall within the range of variation for that species (Kovařík, 2004: 9, 38): base color of adults uniformly reddish black with telson reddish brown in *H. sejnai* but uniformly black to greenish black with telson reddish brown in *H. cyaneus*; carapace entirely granular or “disc” smooth in *H. sejnai* compared with “disc” smooth, “sides” may be granular in *H. cyaneus*; without noticeable sexual dimorphism in proportions of pedipalps (both species); pedipalp patella without pronounced internal tubercle (both species); pedipalp chela “lobiform” (both species), its length : width ratio in adults ca. 2.2 in both sexes of *H. sejnai* and 2.0–2.3 in both sexes of *H. cyaneus*; chela manus dorsal surface tuberculate and without carinae in *H. sejnai* and tuberculate with carinae weakly indicated in *H. cyaneus*; pectinal tooth count 13–14 in both sexes of *H. sejnai* and 12–16 in both sexes of *H. cyaneus*; telson hirsute and bulbous (both species), vesicle as long as aculeus in *H. sejnai* or longer than aculeus in *H. cyaneus*. In synonymizing Couzijn’s (1981) two subspecies of *H. (J.) cyaneus* from Madura and Sumatra, Kovařík (2009: 37) stated that “the minor features on which these taxa are based clearly fall within the limits of intraspecific variation and as such are taxonomically meaningless” yet recognized *H. sejnai* as distinct from *H. cyaneus* without stipulating any meaningful differences. Although the types of *H. sejnai* were not examined during the present investigation, sufficient evidence is available from the descriptions and illustrations of Kovařík (2004, 2009) to justify the following new synonym: *Heterometrus sejnai* Kovařík, 2004 = *J. cyaneus*, syn. nov.

MATERIAL EXAMINED: 1 ♂, 1 ♀ (MCZ). **INDONESIA:** Indes néerlandaises [Netherlands Indies], Suykerbuyk, 2 ♂, 2 ♀, 1 subad. ♂, 1 juv. ♂, 1 juv. ♀ (MRHNB [S.G. 30]). Java, 1 ♀ (NRS [JF 51]), Steenstra Toussaint, 2 ♀ (MNHN RS 0088), 1.x.1899, T. Mann, 3 ♀, 1 subad. ♀, 1 juv. ♂ (AMNH), 10.x.1899, 1 ♂, 1 ♀ (ZMH ex

Mus. Tubingen), 1909, C. de Bearn, 2 ♀ (MNHN RS 3481), 14.ii.1924, S. Rich, 4 ♀ (AMNH [24849]), xii.2002, 1 ♂ (AMNH), [leg] (AMCC [LP 2309]), iii.2008, ex pet trade, 1 ♀ (AMNH), [pedipalp] (AMCC [LP 8270]). **Banten Prov.: Pandeglang Reg.:** Ujung Kulon National Park: Ujung Jaya, Cibiuk TNUK, 06°47'S 105°31'E, 80–103 m, 17.vii.2013, Loria and Sarino, under rocks, 1 juv. ♀ (AMCC [LP 12117]); Kertamukti, Mountain Honje, 06°43'S 105°34'E, 74 m, 18.vii.2013, Loria, Sarino and Oman, under rocks, 2 ♂, 3 ♀, 1 subad. ♀, 3 juv. ♂, 7 juv. ♀ (AMNH), 1 juv. ♀ (AMCC [LP 12113]). **East Java Prov.: Banjuwangi Reg.:** Kalie Baroe/Kali Baru [Kalibaru, 08°16'S 113°59'E], Banjoewangi/Banjuwangi, Java, viii.1902, M.A.J. Fokker, 1 ♀ (RMNH 139). **North Sumatra Prov.: Deli Serdang Reg.:** Deli [Medan, 03°35'N 98°41'E], L. van Heyden, 1 ♀ (NM 10332 ex SMF). **West Java Prov.:** Padang [00°57'S 100°25'E], Sumatra, Muller, 1 ♂ (RMNH 267). **Bogor City Reg.:** Buitenzorg [Bogor, 06°36'S 106°48'E], 24.xii.1890, O. Warburg, 2 ♂, 5 ♀, 1 subad. ♂, 4 juv. ♀ (ZMH), 1899, 1 ♀, 1 subad. ♀, 1 juv. ♂ (SAM 5110), 1906–1907, T. Barbour, 2 ♂, 6 ♀, 1 juv. ♂, 1 juv. ♀ (MCZ), iii.1909, Palmer and Bryant, 2 ♂, 11 ♀, 2 subad. ♀, 2 juv. ♂, 7 juv. (MCZ), v.1921, 2 ♂ (AMNH); Buitenzorg, Botanical Garden [Bogor Botanical Gardens], 21.i.1925, H. Winkler, 1 ♂, 2 ♀, 1 juv. ♀ (ZMH). **Cianjur Reg.:** Ciseureuh, 06°42'S 107°02'E, 1115 m, 4.vii.2013, S.F. Loria, in tea plantation in burrow, 1 subad. ♂, 1 subad. ♀, 1 juv. ♂ (AMNH), 1 juv. ♀ (AMCC [LP 12112]). **East Parahyangan Reg.:** Tasik Malaju [Tasikmalaja, 07°20'S 108°12'E], Java, x.1925, Kopstein, 1 juv. ♀ (LKC ZRC-ARA 664). **Sukabumi Reg.:** Pelaboean Ratoe [Pelabuhanratu, 06°59'S 106°32'E], Java, x.1909, Palmer and Bryant, 1 ♂, 2 ♀ (MCZ), xii.1909, O. Bryant, 2 ♀, 1 juv. ♀ (MCZ); Sukabumi [06°56'S 106°56'E], Java, xi.1999, F. Yunono, 1 ♂, 1 ♀ (LKC ZRC-ARA 663). **Yogyakarta Special Region: Sleman Reg.:** Yogyakarta, Kaliurang village [Kaliurang, 07°36'S 110°25'E], Java, 1000 m, 18.x.1996, Kuntner and Sereg, 1 juv. ♀ (USNM).

ERRONEOUS RECORD: Ceylon [Sri Lanka], 1 ♂ (BMNH 1870.7.1.197).

Sahyadrimetrus, gen. nov.

Figures 4, 8D, 9G, 10, 25C–F, 26, 39C–F, 40, 54, 55, 73–75, 198–224, tables 1, 3, 5

Type species: *Pandinus scaber* Thorell, 1876b: 202 [= *Sahyadrimetrus scaber* (Thorell, 1876), comb. nov.], here designated.

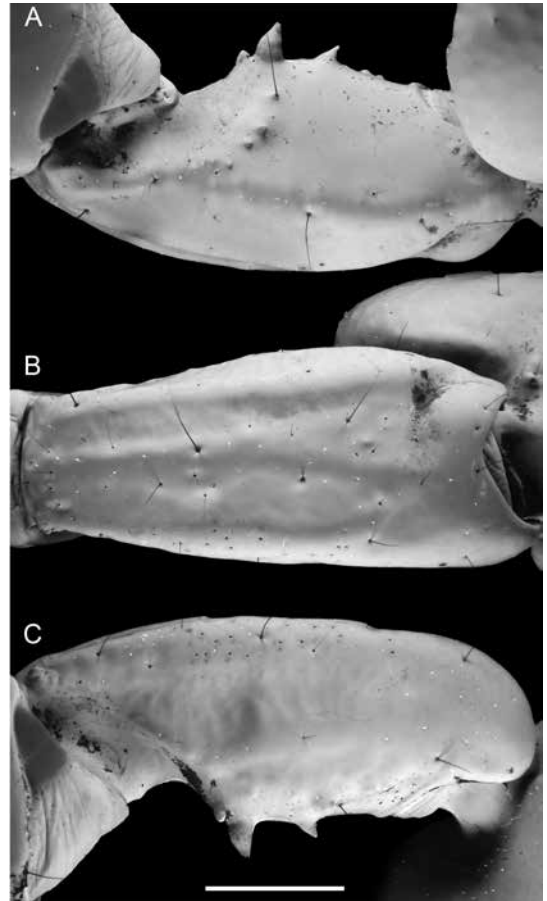


FIGURE 186. *Heterometrus spinifer* (Ehrenberg, 1828), ♂ (AMNH), Cameron Highlands, Malaysia, pedipalp patella: **A.** dorsal, **B.** retrolateral, and **C.** ventral aspects. Scale bar = 5 mm.

Heterometrus (*Chersonesometrus*): Couzijn, 1981: 80, 83, 131, 133, 161, 169–171, 173, 182, 184, 186–188, 192, figs. 21, 57–59, 66b, 68, 69 (part); Tikader and Bastawade, 1983: 519, 520, 573 (part).

Heterometrus (*Heterometrus*): Tikader and Bastawade, 1983: 519, 520 (part); Biswas, 1984: 320; Bastawade et al., 2004: 47; Bastawade and Borkar, 2008: 212, 218; Aswathi and Sureshan, 2017: 9847 (part).

Heterometrus: Kovařík, 2004: 1, 2, 7, 49, 51, tables 1, 2 (part); 2009: 34, 35, table 1 (part).



FIGURE 187. *Heterometrus spinifer* (Ehrenberg, 1828), pedipalp chela, retrodorsal aspect. **A.** ♀ (AMNH), **B.** ♂ (AMNH), Cameron Highlands, Malaysia. Scale bar = 5 mm.



FIGURE 188. *Heterometrus spinifer* (Ehrenberg, 1828), ♂ (AMNH), Cameron Highlands, Malaysia, pedipalp chela: **A.** ventral and **B.** prolateral aspects. Scale bar = 5 mm.

DIAGNOSIS: Species of *Sahyadrimetrus* may be separated from other Asian scorpionid genera as follows. The carapace is moderately to markedly dorsoventrally compressed, the lateral surfaces sloping gently (figs. 25C–F, 26A, B), in all except two species of *Sahyadrimetrus*, *S. mathewi* and *S. scaber*, in which the carapace is vaulted, the lateral surfaces sloping steeply (fig. 26C–F), as in *Gigantometrus*, *Heterometrus*, *Javanimetrus*, two species of *Deccanometrus*, *D. latimanus* and *D. xanthopus*, three species of *Chersonesometrus*, *C. fulvipes*, *C. madraspatensis*, and *C. shivashankari*, and all except three species of *Srilankametrus*, *S. indus*, *S. pococki*, and *S. serratus*. The carapace anterior margin is concave, with the frontal lobes uneven and sloping medially (figs. 25C–F, 26) in *Sahyadrimetrus*, whereas the anterior margin is straight, with the frontal lobes evenly rounded or truncate in *Gigantometrus*, *Srilankametrus*, two species of *Deccanometrus*, *D. latimanus* and *D. xanthopus*, and some species of *Chersonesometrus*. The carapace anterolateral margins converge gradually anteriorly in *Sahyadrimetrus* but are subparallel anteriorly in *Javanimetrus* and *Srilankametrus*. The carapace rostrolateral margin is entire in *Sahyadrimetrus* but distinctly incised adjacent to the posterior lateral ocelli in *Heterometrus*. Anterocular extensions of the superciliary carinae are present in *Sahyadrimetrus* but absent in *Srilankametrus*. The median ocelli are relatively small, the distance between them equal to or greater than the width of an ocellus in *Sahyadrimetrus* but relatively large, the distance between them less than the width of an ocellus in *Heterometrus*; the median ocular tubercle is situated anteromedially to medially, the distance from carapace anterior margin : carapace length (CAM:CL) 0.40–0.50 in *Sahyadrimetrus*, but posteromedially, CAM:CL 0.51–0.62 in *Chersonesometrus*. The interocular suture is absent in *Sahyadrimetrus* but present in *Chersonesometrus*, *Gigantometrus*, and all except one species of *Deccanometrus*, and two species of *Srilankametrus*. The carapace posterior sutures are absent in *Sahyadrimetrus*; present, extending to the median ocular tubercle, and connected by a short cross-suture

anterior to the postocular depression in *Heterometrus*; and present, extending past the median ocular tubercle, and connected anteriorly to the posterior bifurcations of the interocular suture or disconnected in *Chersonesometrus*, *Deccanometrus*, *Gigantometrus*, and most species of *Srilankametrus*. The frontal lobes and medial region of the carapace interocular surface are mostly to entirely granular in *Sahyadrimetrus*, whereas the interocular surface is entirely smooth in all species of *Srilankametrus* except *S. caesar* and some species of *Heterometrus*. The cheliceral movable finger prodistal (DI) and retrodistal (DE) teeth are unequal, with the DE tooth considerably smaller than the DI tooth, aligned longitudinally and not opposable in *Sahyadrimetrus*, but opposable in two species of *Deccanometrus*, and subequal, with the DE tooth only slightly smaller than the DI tooth, and opposable, i.e., forming a bicuspid, in *Heterometrus* and some species of *Chersonesometrus*. The pedipalp patella dorsomedian carina of the female is absent or obsolete (figs. 201, 205) in all except one species of *Sahyadrimetrus*, *S. rugosus*, in which the carina is predominantly granular or costate (fig. 214), as in *Chersonesometrus*, *Gigantometrus*, and all except three species of *Deccanometrus*, *D. latimanus*, *D. liurus*, and *D. ubicki*. The prominent spiniform granule of the patella proventral carina is absent (figs. 201, 205, 210, 214, 217, 222) in *Sahyadrimetrus* but present in *Heterometrus*. The patella dorsal, retrodorsal, and retroventral intercarinal surfaces of the female are smooth or nearly so (figs. 201, 205) in all species of *Sahyadrimetrus* except *S. rugosus*, in which the surfaces are granular (fig. 214), as in all species of *Chersonesometrus* except *C. nathanorum*. The pedipalp chela of the adult male is moderately to densely setose (figs. 206, 211, 218, 223) in *Sahyadrimetrus* but sparsely setose in *Gigantometrus*, *Heterometrus*, *Javanimetrus*, most species of *Srilankametrus*, and some species *Chersonesometrus*. The distance between the chela manus dorsomedian and promedian carinae or setal rows (DMC–PMC) is slightly to markedly greater than the distance between the promedian and proventral carinae or setal rows (PMC–PVC) in *Sahyadrimetrus* whereas the



FIGURE 189. *Heterometrus thorellii* (Pocock, 1892), habitus: **A, C.** dorsal and **B, D.** ventral aspects. **A, B.** ♂ (AMNH), Mandalay, Myanmar. **C, D.** ♀ (AMNH), Pho Kyar Elephant Camp, Yedashe, Myanmar. Scale bars = 10 mm.

DMC-PMC is similar to the PMC-PVC in *Heterometrus*. The dorsomedian carina becomes obsolete proximally in *Sahyadrimetrus* but is continuous to the proximal edge of the manus in *Chersonesometrus*, *Gigantometrus*, and two species of *Deccanometrus*, *D. obscurus* and *D. phipsoni*. The chela manus dorsal secondary, subdigital, and digital carinae (setal rows) are well separated along their entire length in *Sahyadrimetrus* whereas the proximal half of the dorsal secondary carina, distal half of the subdigital carina and distal third of the digital carina are closely adjacent in *Chersonesometrus* and *Gigantometrus*. The dorsal secondary and subdigital carinae of the male are absent or obsolete in *Sahyadrimetrus* but present and entirely to predominantly granular or costate in *Gigantometrus*, all species of *Chersonesometrus* except *C. bastawadei* and *C. fulvipes*, and all species of *Srilankametrus* except *S. indus* and *S. pococki*. The chela manus digital and retromedian carinae are similarly developed (figs. 202, 206, 207, 211, 212, 215, 218, 219, 223, 224) in *Sahyadrimetrus* whereas the retromedian carina is more pronounced than the digital carina in *Chersonesometrus*. The retromedian carina of the male is absent or obsolete in *Sahyadrimetrus* but entirely to predominantly granular in *Gigantometrus*, *Srilankametrus caesar*, and *S. serratus*, and entirely to predominantly costate in *Chersonesometrus*, *Srilankametrus couzijni*, *S. gravimanus*, and *S. yaleensis*. The depression in the dorsal surface of the chela manus, proximal to the fixed finger of the adult male, is absent or obsolete (figs. 206, 211, 218, 223) in *Sahyadrimetrus* but present and distinct in *Heterometrus*. The chela manus dorsal surface is shallowly reticulate in *Sahyadrimetrus* but without reticulation in *Gigantometrus*, *Srilankametrus*, most species of *Chersonesometrus*, all except three species of *Heterometrus*, *H. glaucus*, *H. laevigatus*, and *H. thorellii*, and two species of *Deccanometrus*, *D. obscurus* and *D. phipsoni*; the dorsal surface is finely to coarsely granular in all except two species of *Sahyadrimetrus*, *S. kanarensis* and *S. tikaderi*, in which the dorsal surface is smooth, as in *Heterometrus*, *Javanimetrus*, and one species of *Dec-*

canometrus, *D. ubicki*. The chela manus ventral surface is flat, with the axes of the retroventral and ventromedian carinae in approximately the same plane in *Sahyadrimetrus* but angled, with the axis of the retroventral carina ventral to the axis of the ventromedian carina in *Javanimetrus*, four species of *Chersonesometrus*, *C. beccaloniae*, *C. hendersoni*, *C. pelekomanus*, and *C. tristis*, and two species of *Srilankametrus*, *S. indus* and *S. pococki*. The pro- and retrolateral surfaces of the tibiae of legs I and II each bear a row of two or three spiniform macrosetae in *Sahyadrimetrus* and scattered, setiform macrosetae, not arranged in a definite row, in *Heterometrus*. Macroseta *st* on the retroventral surface of the basitarsus of leg I is spiniform (figs. 54, 55) in *Sahyadrimetrus* but usually setiform in *Heterometrus*, and *sb* on the retroventral surface of the basitarsus of leg III is spiniform in *Sahyadrimetrus* but setiform in *Deccanometrus*, *Gigantometrus*, *Srilankametrus*, and most species of *Chersonesometrus* and *Heterometrus*. The pseudonychium (dactyl) of the telotarsi of legs I-IV is usually reduced and rounded in *Sahyadrimetrus* but prominent and acuminate in *Heterometrus*. The pectinal first proximal median lamella (scape) of the female is distinctly angular, $> 90^\circ$ but $< 180^\circ$ (figs. 39C-F, 40) in *Sahyadrimetrus* but straight or shallowly curved in *Srilankametrus*. The mesial surfaces of mesosomal tergites I-VI of the male are smooth in all except two species of *Sahyadrimetrus*, *S. mathewi* and *S. scaber*, but granular in *Gigantometrus*, one species of *Deccanometrus*, *D. xanthopus*, and some species of *Chersonesometrus*. The lengths of metasomal segments I and II are approximately equal to or less than their respective widths (figs. 73, 75) in *Sahyadrimetrus* but markedly greater than their respective widths in *Gigantometrus*. The ventrosubmedian and ventrolateral carinae are granular or costate-granular on metasomal segment IV only and costate on segments I-III (figs. 74, 75) in *Sahyadrimetrus* but granular on segments I-IV, II-IV (costate on I), or III and IV (costate on I and II) in *Gigantometrus*. The ventral intercarinal surfaces of metasomal segment IV are smooth in all except one species of *Sahyadrimetrus*, *S. tikaderi*, in which

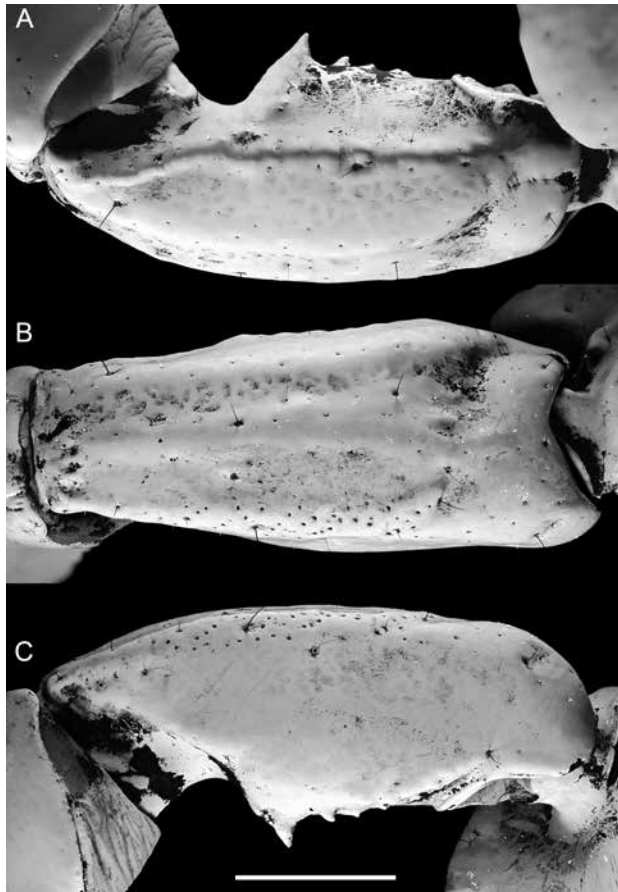


FIGURE 190. *Heterometrus thorellii* (Pocock, 1892), ♀ (AMNH), Pho Kyar Elephant Camp, Yedashe, Myanmar, pedipalp patella: A. dorsal, B. retrolateral, and C. ventral aspects. Scale bar = 5 mm.

the surfaces are sparsely granular, as in *Javanimetrus*. The dorsosubmedian carinae of metasomal segment V are vestigial (fig. 73) in *Sahyadrimetrus* but partial in *Gigantometrus* and absent in *Heterometrus*. The dorsal intercarinal surface of segment V is smooth in *Sahyadrimetrus* but granular in *Gigantometrus*, and some species of *Chersonesometrus* and *Srilankametrus*. The telson is paler than segment V in *Sahyadrimetrus* but as dark as segment V in most species of *Srilankametrus*, and some species of *Deccanometrus* and *Heterometrus*. The width of the telson vesicle is approximately equal to or less than the width of metasomal segment V in the female of *Sahyadrimetrus* but greater than the width of segment V in the female of *Gigantometrus* and the vesicle is elongate in

Sahyadrimetrus but globose in *Chersonesometrus*, *Deccanometrus*, *Gigantometrus*, and three species of *Srilankametrus*, *S. indus*, *S. pococki*, and *S. serratus*.

ETYMOLOGY: The generic name refers to the Western Ghats, also known as Sahyadri, a mountain range covering an area of 140,000 km² in a stretch of 1600 km parallel to the western coast of the Indian peninsula, traversing the states of Gujarat, Maharashtra, Goa, Karnataka, Kerala, and Tamil Nadu. Along with many other taxa, all species in the genus are endemic to the Sahyadri.

INCLUDED SPECIES: *Sahyadrimetrus*, gen. nov., is hereby created to accommodate four species, formerly assigned to subgenera *Chersonesometrus* and the nominotypical subgenus of *Heterometrus*



FIGURE 191. *Heterometrus thorellii* (Pocock, 1892), pedipalp chela, retrodorsal aspect. **A.** ♂ (AMNH), **B.** ♀ (AMNH), Pho Kyar Elephant Camp, Yedashe, Myanmar. Scale bar = 5 mm.



FIGURE 192. *Heterometrus thorellii* (Pocock, 1892), ♀ (AMNH), Pho Kyar Elephant Camp, Yedashe, Myanmar, pedipalp chela: **A**, ventral and **B**, prolateral aspects. Scale bar = 5 mm.

by various authors (Couzijn, 1981; Tikader and Bastawade, 1983; Fet, 2000), and two new species, recovered as a monophyletic group by phylogenetic analysis of morphological characters and DNA sequences from the nuclear and mitochondrial genomes (fig. 10): *Sahyadrimetrus barberi* (Pocock, 1900), comb. nov.; *Sahyadrimetrus kanarensis* (Pocock, 1900), comb. nov.; *Sahyadrimetrus mathewi*, gen. et sp. nov.; *Sahyadrimetrus rugosus* (Couzijn, 1981), comb. nov.; *Sahyadrimetrus scaber* (Thorell, 1876), comb. nov.; *Sahyadrimetrus tikaderi*, gen. et sp. nov.

DISTRIBUTION: This genus is endemic to the Konkan and Malabar Coast, and the Western Ghats of southern India and recorded from the states of Goa, Karnataka, Kerala and Tamil Nadu (figs. 4, 198, 199, table 1).

ECOLOGY: Species of *Sahyadrimetrus* inhabit scrub forest, deciduous forest, primary and secondary lowland rainforest, swamp forest and montane forest at elevations ranging from 10–1200 m above sea level. All species of the genus are pelophilous and fossorial, constructing shallow burrows (ca. 10–40 cm deep) or scrapes in clayey, sandy-clay, or sandy-loam soils under or at the base of stones and logs, in earthen banks, among the roots of trees, or in open ground. The species of *Sahyadrimetrus* are allopatric with each other and with the species of other Indian scorpionid genera.

CONSERVATION STATUS: *Sahyadrimetrus kanarensis* and *S. scaber* are occasionally harvested for the commercial trade in exotic pets.

Sahyadrimetrus barberi (Pocock, 1900),
comb. nov.

Figures 10, 25C, 39C, 54A–D, 73A, 74A, 75A,
198, 200–202, table 1

Palamnaeus barberi Pocock, 1900a: 85, 95, 96;

Couzijn, 1981: 150; Kovařík, 2004: 34.

Heterometrus barberi: Takashima, 1945: 94;

Kovařík, 2004: 4, 5, 51, 52, tables 2, 3, fig. 8;

2009: 34–36, 48, 73, tables 1, 2, figs. 1, 2;

Aswathi and Sureshan, 2017: 9847 (part).

Heterometrus (Chersonesometrus) phipsoni:

Couzijn, 1981: 153, 155, 157–159, 169, 171,
180, fig. 59 (misidentification, part);

Kovařík, 1998: 136 (part).

Heterometrus (Chersonesometrus) phipsoni phipsoni: Couzijn, 1981: 43, 87, 149–151, 153,
171, table 7, fig. 59 (misidentification, part).

Heterometrus (Chersonesometrus) barberi:

Tikader and Bastawade, 1983: 576, 614–619,
figs. 1625–1638; Fet, 2000: 441; Sureshan et
al., 2007a: 2903, 2906–2908, fig. 1 (part);

Indra, 2009: 142.

TYPE MATERIAL: INDIA: Tamil Nadu:

Tirunelveli Distr.: Palamnaeus barberi: Holotype
♀ (BMNH 1899.9.24.1), Kannikatti [ca. 08°40'N
77°17'E], Tinnevely, evergreen forest in Western
Ghats, 2500 ft., C.A. Barber [examined].

DIAGNOSIS: *Sahyadrimetrus barberi* may be separated from other species of *Sahyadrimetrus* as follows. The carapace is markedly dorsoventrally compressed, the lateral surfaces sloping gently (fig. 25C), in *S. barberi* but vaulted, the lateral surfaces sloping steeply in *S. scaber* to very steeply in *S. mathewi*. The carapace mediolateral margins diverge or converge slightly posteriorly (at the posterolateral sulci) in *S. barberi* but converge markedly posteriorly (at the posterolateral sulci) in *S. kanarensis*, *S. mathewi*, and *S. scaber*. The frontal lobes and medial region of the carapace interocular surface are granular with smooth areas in the female (fig. 25C) of *S. barberi*, whereas the interocular surface is entirely, uniformly granular in the female of *S. mathewi*. The carapace posterolateral surfaces of the female (fig. 25C) are smooth or nearly so in *S. barberi* but granular in *S. mathewi* and *S. scaber*. The pedipalp patella dorso-medial carina of the female (fig. 201) is absent or obsolete in *S. barberi* but entirely to predominantly granular in *S. rugosus*. The patella retrodorsal carina of the female is absent or obsolete, and the retromedian carinae present and granular in *S. barberi* whereas the retrodorsal carina is present, as strongly developed as or more strongly developed than the retromedian carinae, which are absent or obsolete in *S. kanarensis*, *S. mathewi*,

and *S. scaber*. The patella dorsal, retrodorsal, and retroventral intercarinal surfaces of the female (fig. 201) are smooth or nearly so in *S. barberi* but granular in *S. rugosus*. The pedipalp chela manus dorsal and retrolateral intercarinal surfaces are finely to coarsely granular or granulo-reticulate in the female (fig. 202) of *S. barberi*, whereas the dorsal surface is smooth in the female of *S. kanarensis* and *S. tikaderi*, and the retrolateral intercarinal surfaces are smooth or nearly so in the female of *S. kanarensis*, *S. mathewi*, and *S. scaber*. Macroseta *st* is spiniform on the retroventral surfaces of the basitarsi of legs I–III (fig. 54A–D) in *S. barberi* but setiform on the retroventral surfaces of the basitarsi of legs I–III in *S. kanarensis*, and legs I and II in *S. mathewi* and *S. scaber*; *st* on the proventral surface of the basitarsus of leg III is setiform in *S. barberi* but spiniform in *S. kanarensis*. The lateral surfaces of mesosomal tergites I–VI are smooth in the female of *S. barberi* but granular in the female of all other species except *S. rugosus*. The ventral intercarinal surfaces of metasomal segment IV are smooth (fig. 75A) in *S. barberi* but granular in *S. tikaderi*. The dorsolateral carinae of metasomal segment V are obsolete and discontinuous to absent (fig. 73A) in *S. barberi* but distinct and continuous in all other species.

DISTRIBUTION: This species is endemic to India and recorded only from the states of Kerala and Tamil Nadu (fig. 198, table 1). It appears to occur at higher elevations than *S. mathewi*, which inhabits the coastal plain, and is separated from *S. tikaderi*, occurring to the north, by the Shencottah Gap, a disjunction, 7.5 km at the narrowest point, in the southern part of the Western Ghats.

ECOLOGY: The type locality is situated in primary rainforest in the Western Ghats (Sahyadri). Although no data are available on the ecology of this species, the habitus of the holotype is consistent with the fossorial, pelophilous ecomorphotype (Prendini, 2001b). It probably constructs burrows under stones.

REMARKS: This species, previously placed in subgenus *Chersonesometrus* of *Heterometrus* by various authors (Couzijn, 1981; Tikader and Bastawade, 1983; Fet, 2000), is newly accommo-

dated in *Sahyadrimetrus*, gen. nov., based on a phylogenetic analysis (fig. 10).

Sahyadrimetrus kanarensis (Pocock, 1900),
comb. nov.

Figures 9G, 10, 26A, B, 40A, B, 55A–D, 73B,
74B, 75B, 198, 203–207, table 1

Palamnaeus scaber kanarensis Pocock, 1900a: 93.

Heterometrus (Chersonesometrus) phipsoni kanarensis: Couzijn, 1981: 43, 87, 133, 151–153, 171, 192, table 7, figs. 48, 59; Kovařík, 1998: 136.

Heterometrus (Chersonesometrus) kanaraensis:
Tikader and Bastawade, 1983: 577, 636–641 (part), figs. 1683–1695; Bastawade et al., 2004: 44, 48, 55, 56, 58 (part), figs. 71–74; Indra, 2006: 197, 199, 200 (part).

Heterometrus (Chersonesometrus) kanarensis:
Fet, 2000: 441, 442; Sureshan et al., 2007a: 2907, 2908 (part), fig. 2; 2007b: 52, 53, photo 5 (part).

Heterometrus kanaraensis: Kovařík, 2004: 1, 20, 51–53, tables 2, 3; 2009: 35, 36, 39, 48, 49, 81, 100, tables 1, 2, figs. 57–62, 213, 214; Aswathi and Sureshan, 2017: 9847 (part).

Heterometrus scaber: Kovařík, 2009: 43, 107, fig. 256 (misidentification).

Heterometrus (Chersonesometrus) wroughtoni:
Bastawade and Borkar, 2008: 212, 219, 220 (misidentification, part).

Heterometrus (Heterometrus) keralensis:
Bastawade and Borkar, 2008: 212, 218, 219 (misidentification, part).

TYPE MATERIAL: INDIA: Karnataka: *Palamnaeus scaber kanarensis*: Lectotype ♂, 2 ♀ paralectotypes (BMNH 1897.11.5.29–30 ex BNHS), Kanara, Bombay [Bombay Presidency], T.R.D. Bell [examined].

DIAGNOSIS: *Sahyadrimetrus kanarensis* may be separated from other species of *Sahyadrimetrus* as follows. The carapace is moderately dorsoventrally compressed, the lateral surfaces sloping gently (fig. 26A, B), in *S. kanarensis* but vaulted, the lateral sur-



FIGURE 193. *Javanimetrus cyaneus* (C.L. Koch, 1836), comb. nov., ♂ (AMNH), Ujung Kulon, Indonesia, habitus: A. dorsal and B. ventral aspects. Scale bar = 10 mm.

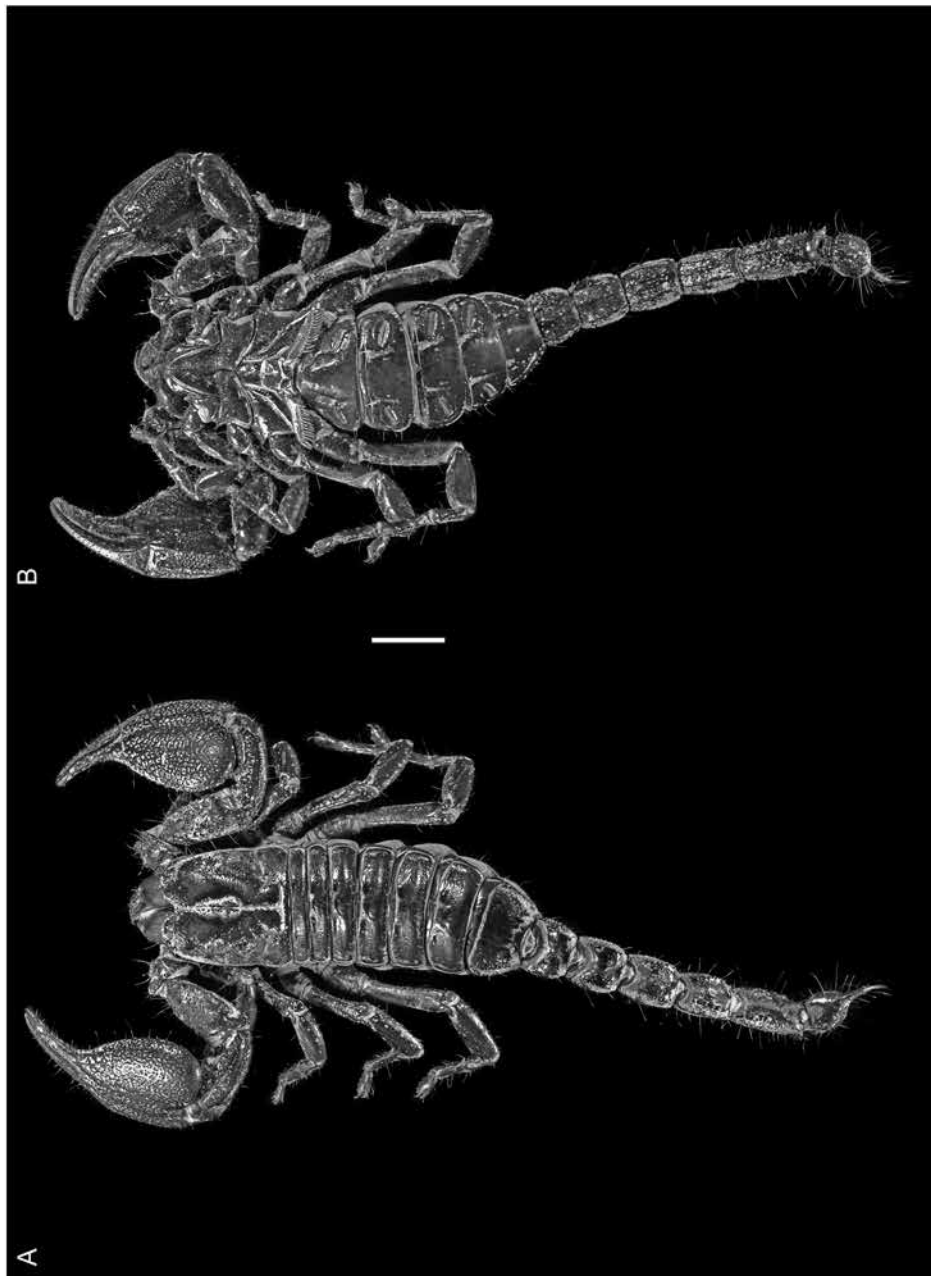


FIGURE 194. *Javanimetrus cyaneus* (C.L. Koch, 1836), comb. nov., ♀ (AMNH), Ujung Kulon, Indonesia, habitus: **A**, dorsal and **B**, ventral aspects. Scale bar = 10 mm.

faces sloping steeply in *S. scaber* to very steeply in *S. mathewi*. The carapace mediolateral margins converge markedly posteriorly (at the posterolateral sulci) in *S. kanarensis* but diverge or converge slightly posteriorly (at the posterolateral sulci) in *S. barberi*, *S. rugosus* and *S. tikaderi*. The frontal lobes and medial region of the carapace interocular surface are granular with smooth areas in the male and female (fig. 26A, B) of *S. kanarensis*, whereas the interocular surface is granular along the median longitudinal and anterior bifurcated sulci only in the male of *S. rugosus*, and the interocular surface is entirely, uniformly granular in the male and female of *S. mathewi*. The carapace posterolateral surfaces of the female (fig. 26B) are smooth or nearly so in *S. kanarensis* but granular in *S. mathewi* and *S. scaber*. The pedipalps of the adult male are short, with femur length : posterior carapace width ratio (FL:PCW) < 0.77 and femur length : carapace length ratio (FL:CL) < 0.74 (fig. 203) in *S. kanarensis* but long, with FL:PCW $\geq$ 0.80 and FL:CL $\geq$ 0.76 in *S. mathewi* and *S. rugosus*. The pedipalp patella dorsomedian carina of the female (fig. 205) is absent or obsolete in *S. kanarensis* but entirely to predominantly granular in *S. rugosus*. The patella retrodorsal carina of the female is present and as strongly developed as or more strongly developed than the retromedian carinae, which are absent or obsolete in *S. kanarensis*, whereas the retrodorsal carina of the female is absent or obsolete, and the retromedian carinae present and granular in *S. barberi*, *S. rugosus*, and *S. tikaderi*. The patella dorsal, retrodorsal, and retroventral intercarinal surfaces of the female (fig. 205) are smooth or nearly so in *S. kanarensis* but granular in *S. rugosus*. The maximum distance between the dorsomedian and dorsal secondary carinae (DMC–DSC) of the pedipalp chela manus is similar to the maximum distance between the dorsal secondary and digital carinae (DSC–DC) in the male (fig. 206) of *S. kanarensis* but less than the DSC–DC in the male of *S. mathewi*, *S. rugosus*, and *S. tikaderi*. The chela manus dorsal surface of the female (fig. 207) is smooth or nearly so in *S. kanarensis* but finely to coarsely granular or granulo-reticulate in all the other species except *S. tikaderi*. The chela manus

retrolateral intercarinal surfaces are smooth or nearly so in the male and female (figs. 206, 207) of *S. kanarensis*, but granular in the male of *S. mathewi* and *S. scaber*, and the female of *S. barberi*, *S. rugosus*, and *S. tikaderi*. Macroseta *st* is setiform on the retroventral surfaces of the basitarsi of legs I–III (fig. 55A–D) in *S. kanarensis* but spiniform on the retroventral surfaces of the basitarsi of legs I–III in *S. barberi*, *S. rugosus* and *S. tikaderi*, and leg III in *S. mathewi* and *S. scaber*; *st* on the proventral surface of the basitarsus of leg III is spiniform in *S. kanarensis* but setiform in the other species. The mesial surfaces of mesosomal tergites I–VI are smooth in the male and the lateral surfaces granular in the female of *S. kanarensis*, whereas the mesial surfaces are granular in the male of *S. mathewi* and *S. scaber*, and the lateral surfaces smooth in the female of *S. barberi* and *S. rugosus*. The ventral intercarinal surfaces of metasomal segment IV are smooth (fig. 75B) in *S. kanarensis* but granular in *S. tikaderi*. The dorsolateral carinae of metasomal segment V are distinct and continuous (fig. 73B) in *S. kanarensis* but obsolete and discontinuous to absent in *S. barberi*.

DISTRIBUTION: This species is endemic to the Indian states of Goa and Karnataka (fig. 198, table 1). Tikader and Bastawade (1983), Bastawade (2002) and Kovařík (2004) included Maharashtra in the distribution of this species. However, this refers to “Bombay” (presumably referring to the former Bombay Presidency) in the type locality and is erroneous. The distribution of *S. kanarensis* is parapatric with that of *S. scaber*.

ECOLOGY: *Sahyadrimetrus kanarensis* inhabits scrub forest and deciduous forest on the Konkan coast of central India. The locality records for which data are available range from 10–110 m above sea level. This species is fossorial and pelophilous, constructing shallow, single-occupant burrows or scrapes, ca. 10–20 cm long, in sandy-clay to sandy-loam soil, under stones (Bastawade and Borkar, 2008). This species occurs in sympatry with the buthids, *Buthoscorpio politus*, *Isometrus sankeriensis*, *Lychas tricarinatus*, *Reddyanus brachycentrus*, and *Thaicharmus lowei* Kovařík et al., 2007.

CONSERVATION STATUS: *Sahyadrimetrus kana-rensis* is occasionally available in the exotic pet trade.

REMARKS: This species, previously placed in subgenus *Chersonesometrus* of *Heterometrus* by various authors (e.g., Couzijn, 1981; Tikader and Bastawade, 1983; Fet, 2000), is newly accommodated in *Sahyadrimetrus*, gen. nov., based on a phylogenetic analysis (fig. 10).

A specimen illustrated as *S. scaber* by Kovařík (2009: 107, fig. 256) appears to be *S. kanarensis*.

MATERIAL EXAMINED: **INDIA: Goa: Canacona** Distr.: Fort Cabo de Rama [Cabo de Rama, 15°05'N 73°55'E], above coast line, ca. 30 m, 14.i.2003, S. Huber, under stones, 1 ♂ (AMCC [LP 2902]), 1 juv. ♂ (AMCC [LP 2289]). **South Goa Distr.:** Agonda, SE on Butterfly Beach Road, 15°02'N 74°00'E, 37 m, 25.xi.2009, R. Datta, secondary evergreen forest with scattered rock walls on coastal plain, in shallow burrows (ca. 10 cm deep) under stones or in open ground, sandy-clay, 1 subad. ♂, 1 juv. ♂ (AMNH), 1 juv. ♂ (AMCC [LP 16797]); Chaudi, hills N of, 15°01'N 74°03'E, 10 m, 28.xi.2006, P. Menon, coastal scrub forest with granite rocks along trail, many old rock/stone walls, hard clayey-loam soil, in shallow burrows/scrapes, ca. 10–20 cm long, under stones, 2 ♂, 1 ♀, 1 subad. ♂, 3 subad. ♀, 3 juv. ♂, 9 juv. ♀ (AMNH), 1 juv. ♂ (AMCC [LP 13960]), 24.xi.2009, R. Datta, coastal evergreen forest on low rocky hills, in shallow burrows (ca. 10–30 cm deep), under stones in hard clayey-loam soil, 7 ♂, 2 ♀, 10 subad. ♂, 4 subad. ♀, 8 juv. ♂, 10 juv. ♀, 1 ♂ sinistral pedipalp chela, 1 ♀ sinistral and dextral pedipalp chelae (AMNH), 3 juv. ♀ (AMCC [LP 16803]); Cortigão Canacona [15°01'N 74°01'E], 16.ii.1997, J. Nielsen, 1 juv. ♂ (NRS [JF 53]); Cotigão W.L.S., 14°59'N 74°07'E, 46 m, 25.xi.2009, R. Datta, dry evergreen forest on flat to gently rolling hills; at burrow entrances in open ground, at base of roots and stones, in sandy-clay soil, 2 ♀, 1 subad. ♀, 2 juv. ♂, 1 juv. ♀, 2 ♂ sinistral pedipalp chelae (AMNH), 2 juv. ♂, 1 juv. ♀ (AMCC [LP 16795]); Cotigão, near turnoff to Tirwal, 14°59'N 74°08'E, 98 m, 28.xi.2006, P. Menon, degraded dry forest with grassy areas and laterite ridge, gravelly-loam soil, excavated from shallow burrow (ca. 15 cm long) under stone on embankment, 1 subad. ♀ (AMCC [LP 14029]); Mangal roadside, 15°04'N 74°11'E, 108 m, 27.xi.2006, P. Menon, secondary dry forest with bamboo, earthen banks and leaf-litter slopes along road cuts, doorkeeping at burrow entrances in earthen banks and under stones, 1 ♀, 1 subad. ♂, 2 subad. ♀, 2 juv. ♂ (AMNH), 1 juv. ♀ (AMCC [LP 13963]); Mormugao [15°24'N 73°48'E], xii.1924, 1 juv.

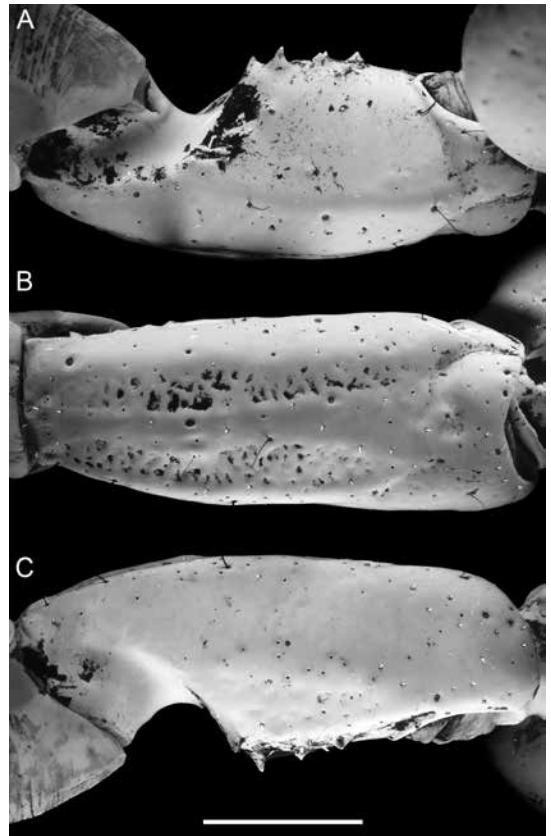


FIGURE 195. *Javanimetrus cyaneus* (C.L. Koch, 1836), comb. nov., ♂ (AMNH), Ujung Kulon, Indonesia, pedipalp patella: **A.** dorsal, **B.** retrolateral, and **C.** ventral aspects. Scale bar = 5 mm.

♂ (USNM 57-688); Molem [Mollem, 15°23'N 74°14'E], 25.iii.1993, P. Johansson, 1 juv. ♀ (NRS [JF 52]).

***Sahyadrimetrus mathewi*, gen. et sp. nov.**

Figures 10, 26C, D, 40C, D, 55E–H, 73C, 74C, 75C, 199, 208–212, tables 1, 3, 5

Palamnaeus scaber: Pocock, 1900a: 85, 93 (misidentification, part); Mathew, 1948: 111–117, table, figs. 1–6 (misidentification); Rosin and Shulov, 1963: 566 (misidentification); Warburg, 2010: 87 (misidentification).

Heterometrus liurus: Roewer, 1943: 228 (misidentification, part).



FIGURE 196. *Javanimetrus cyaneus* (C.L. Koch, 1836), comb. nov., ♂ (AMNH), Ujung Kulon, Indonesia, pedipalp chela: A. retrodorsal, B. ventral, and C. prolateral aspects. Scale bar = 5 mm.

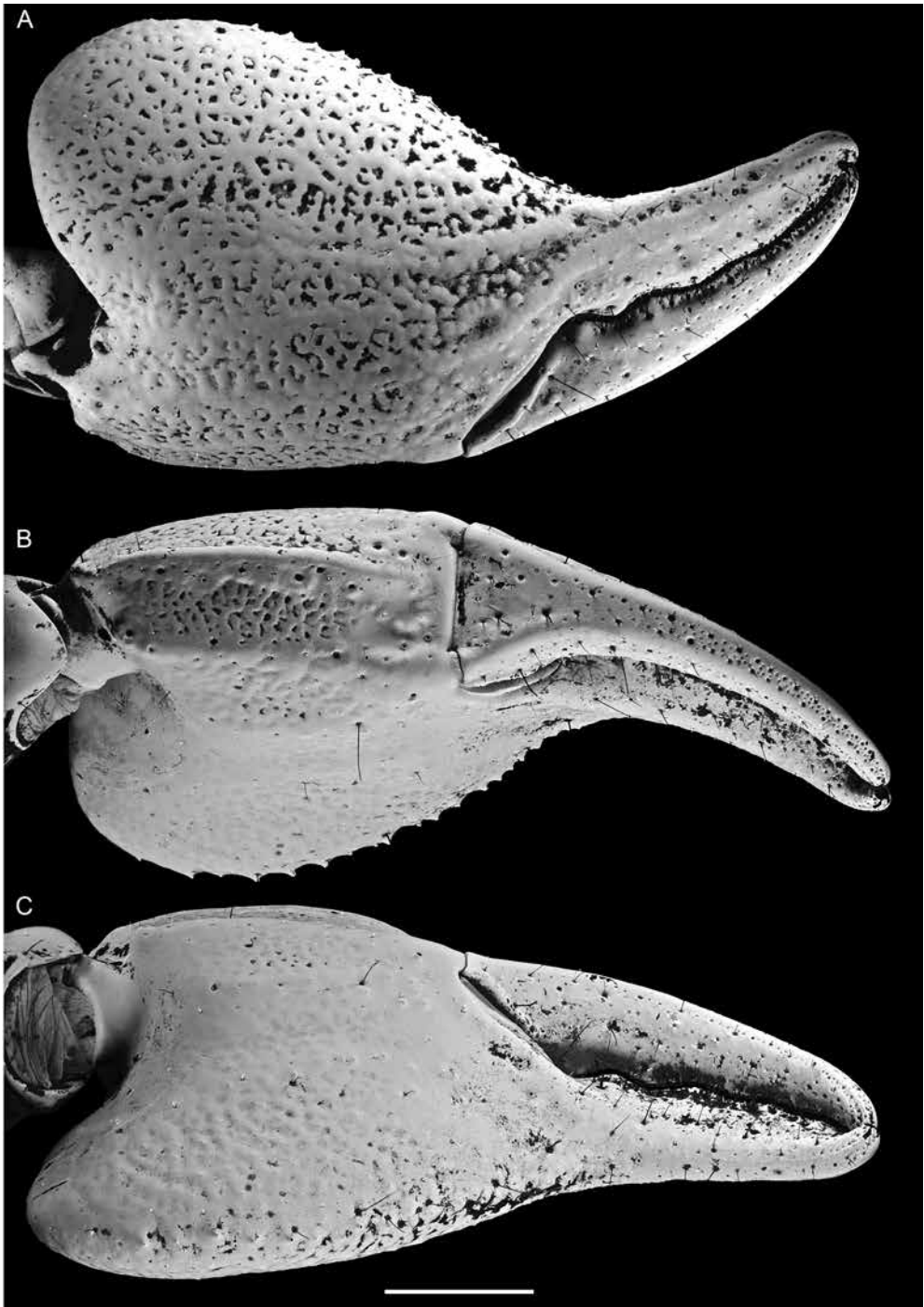


FIGURE 197. *Javanimetrus cyaneus* (C.L. Koch, 1836), comb. nov., ♀ (AMNH), Ujung Kulon, Indonesia, pedipalp chela: **A.** retrodorsal, **B.** ventral, and **C.** prolateral aspects. Scale bar = 5 mm.

Heterometrus scaber: Mathew, 1957: 853–857, figs. 1–3 (misidentification); 1962: 100–111, figs. 1–12 (misidentification); 1965: 272–275, fig. (misidentification); 1966: 411–414, figs. 2–4 (misidentification); Nayar, 1966: 173, 174 (misidentification); Garnier and Stockmann, 1971: 13 (misidentification); Govindarajan and Rajulu, 1974: 908 (misidentification); Nair and Kurup, 1975: 165–173, tables 1–4, figs. 1, 2 (misidentification); Vijayalakshmi and Kurup, 1976: 10–12, tables 1–4 (misidentification); Subburam and Gopalakrishna Reddy, 1989: 333 (misidentification); Cloudsley-Thompson, 1990: 484 (misidentification); Hjelle, 1990: 17, 54, 58 (misidentification, part); Polis and Sissom, 1990: 166, 179, 187, table 4.2 (misidentification); Simard and Watt, 1990: 419 (misidentification); Bastawade, 1992: 221 (misidentification); Makioka, 1992a: 213 (misidentification); 1992b: 165 (misidentification); Farley, 2005: 2 (misidentification); 2008: 1153 (misidentification); Volschenk et al., 2008: 652, 655, table 1 (misidentification); Kovařík, 2009: 35, 36, 43, 48, 90, tables 1, 2 (misidentification, part), figs. 118, 119, 122, 123; Mirza and Sanap, 2009: 488, 490, table 1 (misidentification); Warburg, 2010: 1749–1751, table 3 (misidentification); Farley, 2011: 2, 9, 10 (misidentification); Warburg, 2012a: 61, 63, 64 (misidentification); 2012b: 82, 87, table 1 (misidentification); Aswathi and Sureshan, 2017: 9847, 9849 (misidentification, part), image 19.

Heterometrus (Chersonesometrus) scaber: Couzijn, 1981: 170, fig. 58 (misidentification, part); Tikader and Bastawade, 1983: 576, 619, 620, 622, 624, 625 (misidentification, part); Fet, 2000: 440 (part); Sureshan et al., 2007a: 2907, 2908, fig. 2 (misidentification, part).

Heterometrus (Chersonesometrus) scaber scaber: Couzijn, 1981: 39, 87, 133, 144–147, 170, 192, table 7, fig. 58 (misidentification, part).

Heterometrus (Srilankametrus) indus: Kovařík, 2002: 17 (misidentification, part).

Heterometrus (Chersonesometrus) barberi: Sureshan et al., 2007a: 2903, 2906–2908, fig. 1 (misidentification, part).

Heterometrus (Chersonesometrus) kanarensis: Sureshan et al., 2007a: 2907, 2908, fig. 2 (misidentification, part).

Heterometrus (Heterometrus) keralaensis: Sureshan et al., 2007a: 2906–2908, fig. 1 (misidentification, part).

Heterometrus (Heterometrus) malapuramensis: Sureshan et al., 2007a: 2906–2908, fig. 2 (misidentification, part).

Heterometrus barberi: Aswathi and Sureshan, 2017: 9847 (part).

Heterometrus kanaraensis: Aswathi and Sureshan, 2017: 9847 (part).

Heterometrus keralaensis: Aswathi and Sureshan, 2017: 9847 (part).

TYPE MATERIAL: INDIA: Kerala: Thrissur
Distr.: Holotype ♂, paratypes: 2 ♂, 2 ♀, 3 subad. ♂, 1 subad. ♀, 2 juv. ♂, 1 juv. ♀ (AMNH), 1 subad. ♀ (AMCC [LP 13132]), Poomala, Pathazhakundu Dam Road, W side Pathazhakundu Dam, 10°37'N 76°14'E, 136 m, 25.xi.2004, S. Basi, coconut palm plantation on terraced slope, doorkeeping at burrow entrances mostly in rock walls; paratypes: 2 ♂, 2 ♀, 1 juv. ♂, 1 juv. ♀ (AMNH), 1 juv. ♀ (AMCC [LP 13131]), Attoor, Asurankundu Dam, 10°41'N 76°18'E, 118 m, 25.xi.2004, S. Basi, very humid, tropical lowland swamp forest with dense canopy on moist clayey-loam soil, many sandstone outcrops, moderate to sparse leaf-litter layer, in burrows (ca. 30–40 cm deep), under stones, at base of tree roots, or in open ground. *Ernakulam*
Distr.: Paratypes: 1 ♂, 1 ♀ (AMNH), 1 juv. ♀ (AMCC [LP 16752]), near Thattekad, 10°08'N 76°40'E, 39 m, 14.xi.2009, R. Datta, primary evergreen swamp forest on clayey-loam soil, dense canopy, sparse understorey with leaf-litter, doorkeeping at burrow entrances under stones; paratypes: 1 juv. ♂, 1 juv. ♀ (AMCC [LP 16759]), 1 ♂, 1 ♀, 1 subad. ♂, 1 juv. ♂, 1 ♀ sinistral and dextral pedipalp patella and chela (AMNH),

same data, except: 10°08'N 76°41'E, 22–40 m, 15.xi.2009. *Thiruvananthapuram Distr.*: Paratypes: 2 ♂, 5 ♀, 1 subad. ♂, 11 juv. ♂, 10 juv. ♀ (AMNH), 2 juv. ♂, 1 juv. ♀ (AMCC [LP 13130]), Kallar–Meenmutty Falls Road, SE of Kallar, 08°43'N 77°08'E, 157 m, 20.xi.2004, S. Basi, Vamanapuram River valley, tropical evergreen forest with short, open, canopy on gentle slope, many sandstone rocks and boulders on gravelly loam soil, in shallow burrows or scrapes under or at base of stones, logs, roots or in earthen banks; paratype ♂ (CAS [ASU 68-305]), paratype ♀ (CAS [ASU 68-303]), Trivandrum [Thiruvananthapuram, 08°31'N 76°56'E], 4.iv.1968, A.P. Mathew, ex Stahnke coll.

ETYMOLOGY: The specific epithet is a patronym honoring the Indian biologist, A.P. Mathew, formerly of University College, Trivandrum, for his pioneering contributions to the knowledge of embryology, parthenogenesis, courtship and mating behavior in scorpions, including the new species which bears his name.

DIAGNOSIS: *Sahyadrimetrus mathewi* may be separated from other species of *Sahyadrimetrus* as follows. The carapace is vaulted, the lateral surfaces sloping very steeply (fig. 26C, D), in *S. mathewi* but moderately to markedly dorsoventrally compressed, the lateral surfaces sloping gently, in *S. barberi*, *S. kanarensis*, *S. rugosus*, and *S. tikaderi*. The carapace mediolateral margins converge markedly posteriorly (at the posterolateral sulci) in *S. mathewi* but diverge or converge slightly posteriorly (at the posterolateral sulci) in *S. barberi*, *S. rugosus*, and *S. tikaderi*. The carapace interocular surface is entirely, uniformly granular in the male and female (fig. 26C, D) of *S. mathewi*, whereas the interocular surface is granular along the median longitudinal and anterior bifurcated sulci only in the male of *S. rugosus* and the frontal lobes and medial region of the interocular surface are granular with smooth areas in the female of *S. rugosus*, and the male and female of *S. kanarensis*, *S. tikaderi*, and *S. scaber*. The carapace posterolateral surfaces of the female (fig. 26D) are granular in *S. mathewi* but smooth or nearly so in all other

species except *S. scaber*. The pedipalps of the adult male are long, with femur length : posterior carapace width ratio (FL:PCW) ≥ 0.80 and femur length : carapace length ratio (FL:CL) ≥ 0.76 (fig. 208) in *S. mathewi* but short, with FL:PCW < 0.77 , FL:CL < 0.74 in *S. kanarensis*, *S. scaber*, and *S. tikaderi*. The pedipalp patella dorsomedian carina of the female is absent or obsolete in *S. mathewi* but entirely to predominantly granular in *S. rugosus*. The patella retrodorsal carina of the female is present and as strongly developed as or more strongly developed than, the retromedian carinae which are absent or obsolete in *S. mathewi*, whereas the retrodorsal carina of the female is absent or obsolete, and the retromedian carinae present and granular in *S. barberi*, *S. rugosus*, and *S. tikaderi*. The patella dorsal, retrodorsal, and retroventral intercarinal surfaces of the female are smooth or nearly so in *S. mathewi* but granular in *S. rugosus*. The maximum distance between the dorsomedian and dorsal secondary carinae (DMC–DSC) of the pedipalp chela manus is less than the maximum distance between the dorsal secondary and digital carinae (DSC–DC) in the male (fig. 211) of *S. mathewi* but similar to the DSC–DC in the male of *S. kanarensis* and *S. scaber*. The chela manus dorsal surface of the female (fig. 212) is smooth to finely granulo-reticulate in *S. mathewi* but smooth or nearly so in *S. kanarensis* and *S. tikaderi*. The chela manus retro-lateral intercarinal surfaces are granular in the male (fig. 211) and smooth or nearly so in the female (fig. 212) of *S. mathewi*, but smooth or nearly so in the male of *S. kanarensis*, and granular in the female of *S. barberi*, *S. rugosus*, and *S. tikaderi*. Macroseta *st* is setiform on the retroventral surfaces of the basitarsi of legs I and II and spiniform on leg III (fig. 55E–H) in *S. mathewi* but spiniform on the retroventral surfaces of the basitarsi of legs I–III in *S. barberi*, *S. rugosus*, and *S. tikaderi*, and setiform on legs I–III in *S. kanarensis*; *st* on the proventral surface of the basitarsus of leg III is setiform in *S. mathewi* but spiniform in *S. kanarensis*. The mesial surfaces of mesosomal tergites I–VI are granular in the male

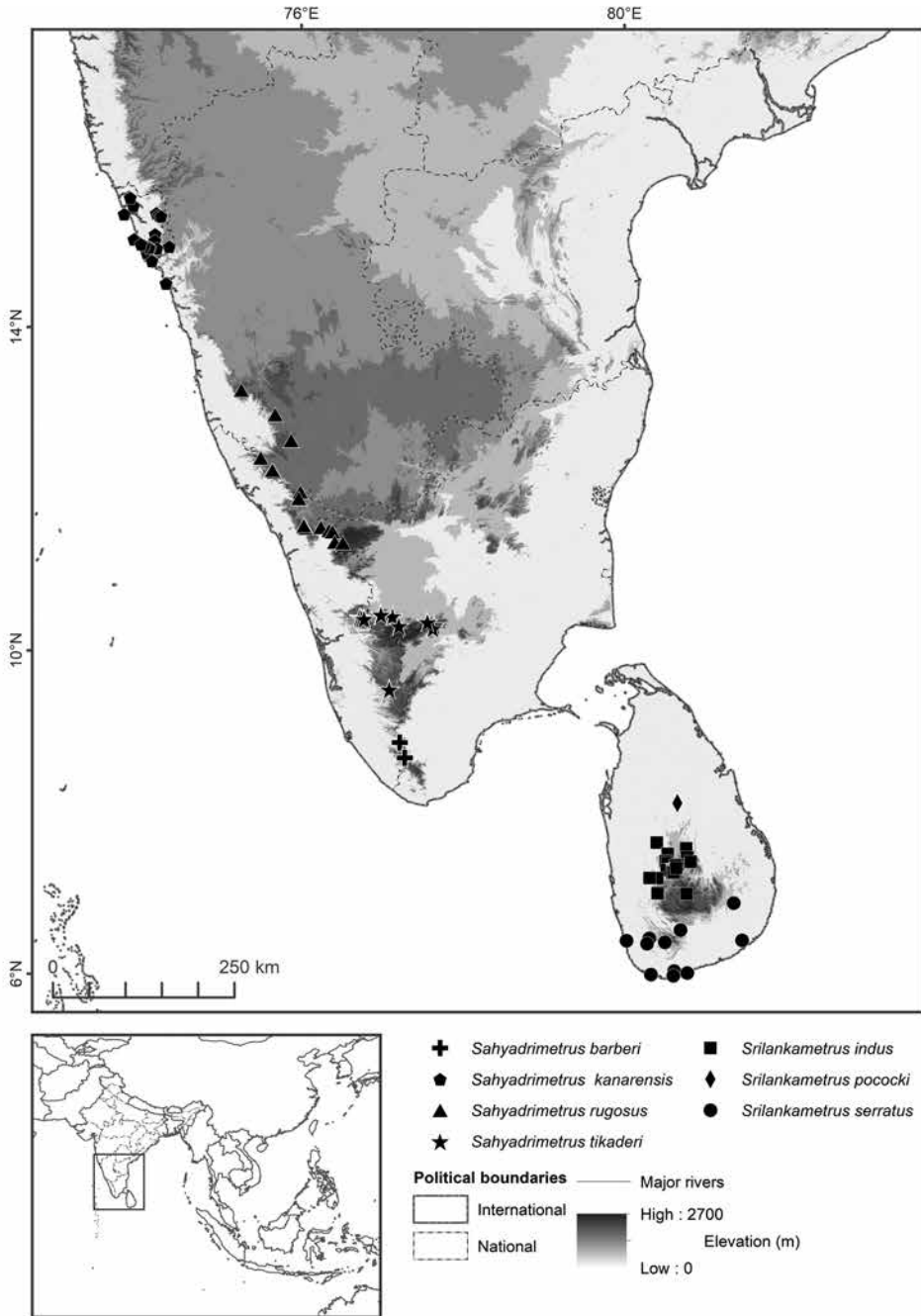


FIGURE 198. Map of South India and Sri Lanka, plotting known locality records of four species of *Sahyadrimetrus*, gen. nov., and three species of *Srilankametrus* Couzijn, 1981, stat. nov. et stat. rev., based on material examined, and verified records from virtual museums and the literature: *Sahyadrimetrus barberi* (Pocock, 1900), comb. nov.; *Sahyadrimetrus kanarensis* (Pocock, 1900), comb. nov.; *Sahyadrimetrus rugosus* (Couzijn, 1981), comb. et stat. nov.; *Sahyadrimetrus tikaderi*, gen. et sp. nov.; *Srilankametrus indus* (DeGeer, 1778), comb. nov.; *Srilankametrus pococki*, sp. nov.; *Srilankametrus serratus* (Pocock, 1900), comb. nov.

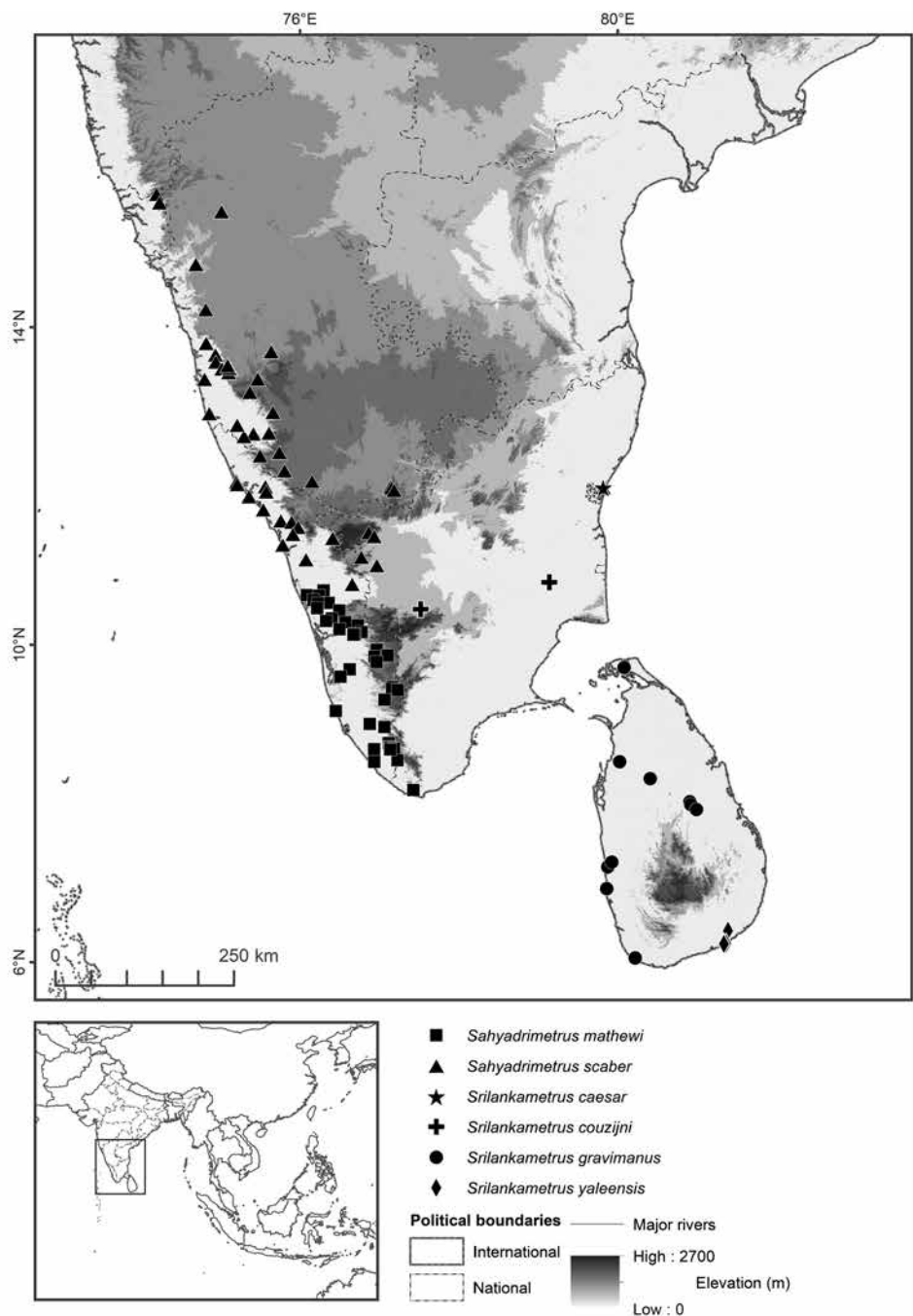


FIGURE 199. Map of South India and Sri Lanka, plotting known locality records of two species of *Sahyadrimetrus*, gen. nov., and four species of *Srilankametrus* Couzijn, 1981, stat. nov., based on material examined, and verified records from virtual museums and the literature: *Sahyadrimetrus mathewi*, sp. nov.; *Sahyadrimetrus scaber* (Thorell, 1876), comb. nov.; *Srilankametrus caesar* (C.L. Koch, 1841), comb. nov. et stat. rev.; *Srilankametrus couzijni*, sp. nov.; *Srilankametrus gravimanus* (Pocock, 1894), comb. nov.; *Srilankametrus yaleensis* (Kovářik et al., 2019), comb. nov.

and the lateral surfaces granular in the female of *S. mathewi*, whereas the mesial surfaces are smooth in the male of *S. kanarensis*, *S. rugosus*, and *S. tikaderi*, and the lateral surfaces smooth in the female of *S. rugosus*. The ventral intercarinal surfaces of metasomal segment IV are smooth (fig. 75C) in *S. mathewi* but granular in *S. tikaderi*. The dorsolateral carinae of metasomal segment V are distinct and continuous (fig. 73C) in *S. mathewi* but obsolete and discontinuous to absent in *S. barberi*.

DESCRIPTION: The following description is based on the holotype and paratypes. Meristic data are presented in table 3 and measurements in table 5.

Total length: Adult medium sized to large, maximum length, measured from anterior margin of carapace to tip of aculeus, 121 mm (117–123 mm, $n = 3$) (♂), 121 mm (114–127 mm, $n = 2$) (♀).

Color: Chelicerae, dorsal surfaces bicolored, lightly infusate prodorsal half of manus paler than densely infusate retrodorsal half of manus and fingers; manus slightly paler than carapace interocular surface. Carapace, pedipalps, tergites, sternites, and metasoma entirely infusate, uniformly black or greenish black. Coxosternal region infusate, brownish black, maxillary lobes darker. Legs infusate, uniformly black, similar to carapace, pedipalps, tergites, and metasoma (figs. 208, 209). Genital opercula slightly infusate, blackish brown; pectines uniformly pale cream. Metasomal segments I–V entirely infusate, similar to one another; carinae infusate, darker than intercarinal surfaces; dorsal intercarinal surfaces similar to tergites; ventral intercarinal surfaces similar to sternites. Telson vesicle immaculate, dark reddish, paler than metasomal segment V; aculeus black.

Chelicerae: Movable finger prodistal (DI) and retrodistal (DE) teeth unequal, with DE tooth considerably smaller than DI tooth, aligned longitudinally and not opposable. Fingers and manus, proventral surfaces with long, dense vestiture of macrosetae. Coxae, prodorsal surfaces

without stridulatory setae (scaphotrix); promedian surfaces without chemoreceptive lamelliform setae (trichocopae).

Carapace: Carapace vaulted, lateral surfaces sloping very steeply. Anterior margin concave, frontal lobes uneven, sloping medially toward deep median notch, without median projection or median depression (fig. 26C, D). Anterolateral margins converging gradually anteriorly, without distinct notch adjacent to posterior lateral ocelli; mediolateral margins converging markedly posteriorly (at posterolateral sulci). Anterior width of posterior width, 69% (68%–71%, $n = 3$) (♂), 70% (69%–70%, $n = 2$) (♀); posterior width of length, 85% (83%–87%, $n = 3$) (♂), 86% ($n = 2$) (♀). Three pairs of lateral ocelli (MLMa, PLMa, PDMi), all similar in size, two anterior pairs situated anteriorly, well separated from posterior pair, situated laterally. Median ocelli moderately larger than lateral ocelli, distance between ocelli less than or equal to width of ocellus; median ocular tubercle situated anteromedially, distance from anterior carapace margin, 51% (50%–53%, $n = 3$) (♂), 50% ($n = 2$) (♀). Median longitudinal sulcus narrow, suturiform; continuous from median notch to interocular sulcus; anteriorly furcated; without anterocular depression. Anterior furcated sulci diverging broadly from anterior edge of median longitudinal sulcus. Median ocular tubercle raised, superciliary carinae higher than ocelli, extended anteriorly, and slightly posteriorly, subparallel. Interocular sulcus present. Circumocular depressions completely encircling median ocular tubercle, converging anteriorly. Posteromedian and posteromarginal sulci deep. Paired mediolateral and posterolateral sulci shallow. Median longitudinal suture continuous from median notch to median ocular tubercle, equally strong along entire length; not extending to anterior margin of carapace, terminating at or posterior to median notch. Anterior furcated, anterocular, interocular, and posterior sutures absent. Interocular surface entirely coarsely granular (fig. 26C, D); anterolateral surfaces uniformly coarsely granular; mediolateral surfaces coarsely to finely gran-

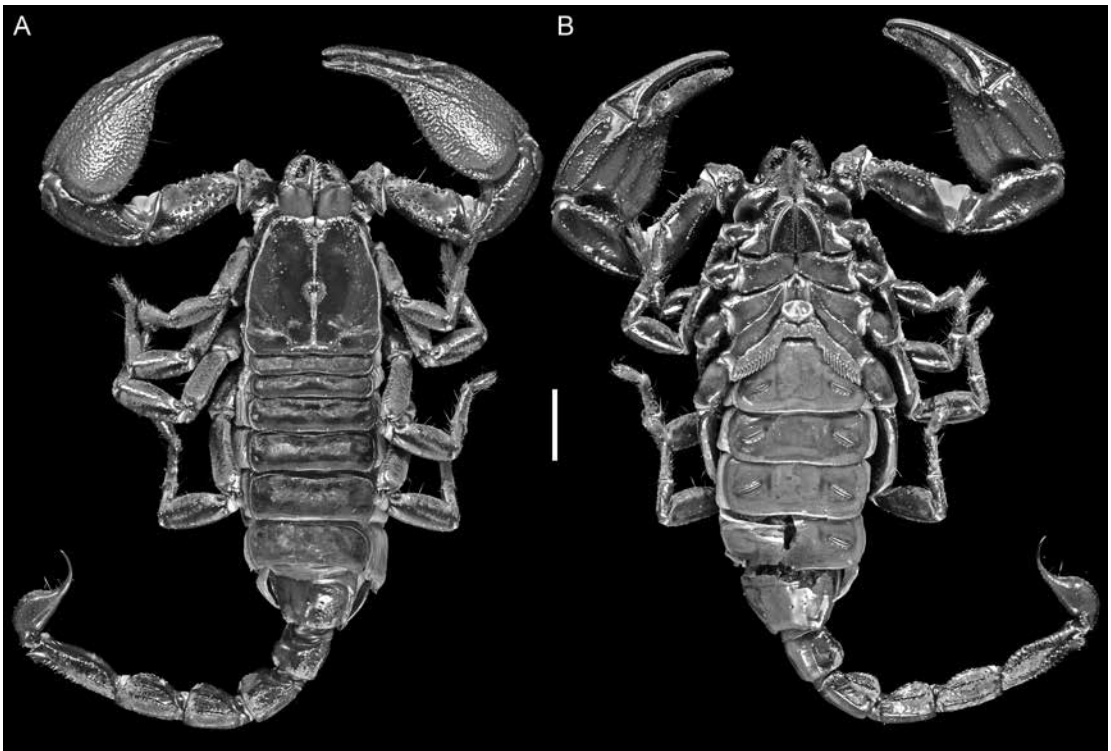


FIGURE 200. *Sahyadrimetrus barberi* (Pocock, 1900), comb. nov., holotype ♀ (BMNH 1899.9.24.1), habitus: A. dorsal and B. ventral aspects. Scale bar = 10 mm.

ular; posterolateral surfaces uniformly finely granular; posteromedian surface smooth.

Pedipalps: Pedipalp long (♂), pedipalp femur length : posterior carapace width ratio (FL:PCW) ≥ 0.80 , pedipalp femur length : carapace length ratio (FL:CL) ≥ 0.76 , or short (♀), FL:PCW < 0.77 , FL:CL < 0.74 . Femur width of length, 40% (37%–42%, $n = 3$) (♂), 45% (45%–46%, $n = 2$) (♀). Retrodorsal carina complete, granular, similar to or more strongly developed than prodorsal carina. Dorsal secondary carina obsolete, comprising few isolated granules. Dorsomedian carina vestigial, reduced to prominent granule demarcated by conspicuous macroseta. Prodorsal carina complete, granular. Promedian carina complete, comprising row of spiniform or subspiniform granules (several demarcated by conspicuous macrosetae), oriented diagonally between prodorsal and proventral carinae. Proventral carina complete, granular as strongly developed as or more strongly devel-

oped than retroventral carina. Ventromedian and secondary accessory carinae absent. Retroventral carina extending partly or entirely to distal edge of segment. Retromedian carinae absent, indicated only by macrosetal rows. Dorsal intercarinal surfaces finely granular; other surfaces smooth. Patella width of length, 41% (40%–41%, $n = 3$) (♂), 45% (43%–47%, $n = 2$) (♀). Dorsal surface convex, axis of dorsomedian carina dorsal to axis of retrodorsal carina. Dorsomedian carina obsolete, costate (fig. 210). Retrodorsal and retromedian carinae similarly developed, absent or obsolete. Retroventral carina obsolete, costate. Promedian carina vestigial, reduced to subspiniform granules, demarcated by conspicuous macroseta (♂) or absent (♀); promedian process absent. Other carinae absent. Intercarinal surfaces smooth. Chela long (♂) or short (♀), narrow (figs. 211, 212); manus height of width, 91% (84%–94%, $n = 3$) (♂), 92% (90%–93%, $n = 2$) (♀); manus length along retroventral carina

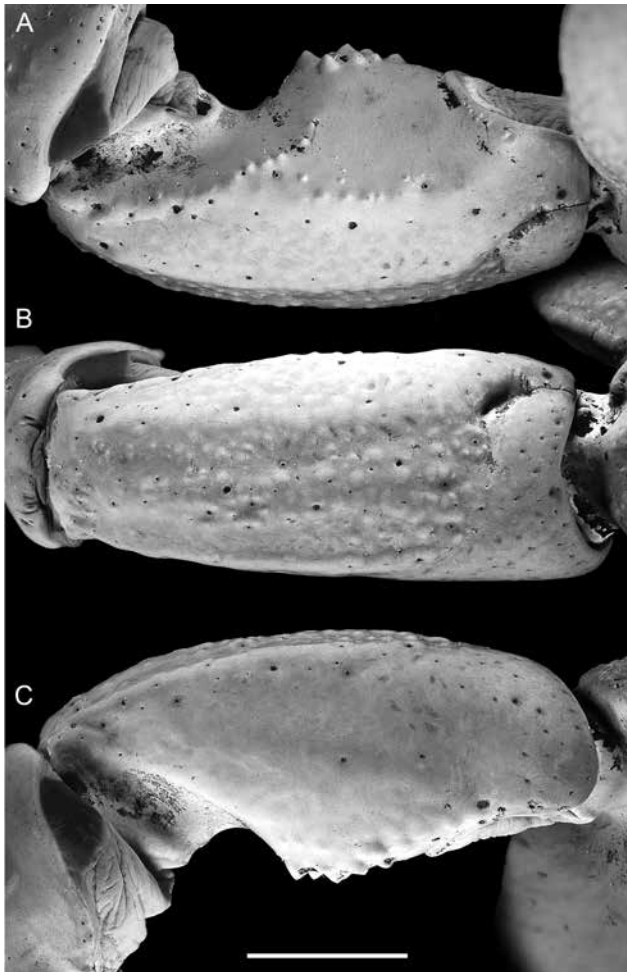


FIGURE 201. *Sahyadrimetrus barberi* (Pocock, 1900), comb. nov., holotype ♀ (BMNH 1899.9.24.1), pedipalp patella: A. dorsal, B. retrolateral, and C. ventral aspects. Scale bar = 5 mm.

of manus width, 106% (102%–111%, $n = 3$) (♂), 92% (90%–94%, $n = 2$) (♀); manus length along retroventral carina of movable finger length, 63% (59%–64%, $n = 3$) (♂), 64% ($n = 2$) (♀). Chela moderately (♂) to sparsely (♀) setose. Manus dorsal surface (between dorsomedian and digital carinae) curved, i.e., slightly to markedly convex; proximal margin (lobe) of dorsal surface moderately curved and aligned with (♂) or proximal to (♀) proximal margin of retrolateral surface. Dorsomedian carina obsolete, costate on fixed finger and comprising irregular row of spiniform granules on manus, becoming obsolete proximally. Dorsal sec-

ondary, subdigital, digital, and retromedian carinae absent. Maximum distance between dorsomedian carina and setal row demarcating dorsal secondary carina (DMC–DSC) less than (♂) or similar to (♀) maximum distance between setal rows demarcating dorsal secondary and digital carinae (DSC–DC). Retrolateral secondary and secondary accessory carinae vestigial, proximal to condyle of movable finger. Retroventral carina distinct, costate. Ventromedian carina obsolete, costate. Proventral and promedian carinae similarly developed, each comprising few spiniform granules and associated macrosetae. Prodorsal carina comprising



FIGURE 202. *Sahyadrimetrus barberi* (Pocock, 1900), comb. nov., holotype ♀ (BMNH 1899.9.24.1), pedipalp chela: A. retrodorsal, B. ventral, and C. prolateral aspects. Scale bar = 5 mm.

irregular row of spiniform granules and associated macrosetae. Distance between dorsomedian and promedian carinae (DMC–PMC) slightly to markedly greater than distance between promedian and proventral carinae (PMC–PVC). Manus, dorsal intercarinal surfaces smooth and shallowly reticulate to finely granulo-reticulate, except for smooth depression at base of fixed finger; retrolateral intercarinal surfaces weakly granular (δ) to smooth or nearly so ($\varnothing$); ventral intercarinal surface smooth; prolateral intercarinal surfaces smooth, except for few scattered spiniform granules dorsally and distally. Manus ventral surface flat, axes of retroventral and ventromedian carinae in approximately same plane. Fixed and movable fingers, intercarinal surfaces smooth; median denticle rows each with six enlarged retrolateral denticles (including terminal denticle), proximal three situated on lobes; first (proximal) lobe of fixed finger and second lobe of movable finger larger than others, with correspondingly deeper notches in movable and fixed fingers, respectively; terminal denticles of fingers interlocking unevenly when closed, movable finger displaced retrolaterally; distinct notch near tip of fixed finger to accommodate terminal denticle of movable finger.

Trichobothria: Orthobothriotaxic, Type C, with the following segment totals ($n = 16$): femur, 3 (1 d , 1 i , 1 e); patella, 19 (2 d , 1 i , 3 v , 13 e , comprising 3 et , 1 est , 2 em , 2 esb , 5 eb); chela, 26 (manus, 16, comprising 2 D , 10 E , 4 V ; fixed finger, 10, comprising 4 d , 4 e , 2 i). Total count of trichobothria per pedipalp: 48. Femur, i situated on dorsal surface. Patella, d_2 situated on internal surface, slightly closer to d_1 than to i ; distance v_2 – v_3 greater than half distance v_1 – v_2 . Chela, distance et – est ca. one-third distance est – esb ; distance est – esb greater than half distance esb – eb ; est distal to dst ; V_3 situated in proximal third of manus, closer to V_4 than V_2 .

Legs: First pair of maxillary lobes (coxapophyses) tapering anteriorly, longer than and encircling second pair. Stridulatory organs, comprising “rasp” (granular tubercles) and “scraper” (stridulatory setae or scaphotrix), present on opposing surfaces of coxae of first

pair of legs and pedipalps, respectively. Legs I–IV acarinate, except femora, with distinct pro- and retrolateral surfaces demarcated by partial to complete, costate proventral carinae. Femora, patellae, and tibiae, pro- and retrolateral surfaces each with scattered setiform macrosetae. Tibiae, prolateral surfaces, without spiniform macrosetae; I and II, retrolateral surfaces, each with two spiniform (t , st) macrosetae; III and IV, retrolateral surfaces, without spiniform macrosetae. Basitarsi I–IV, slightly dorsoventrally compressed; retrolateral margins similar, unmodified, rounded; prolateral pedal spurs present (fig. 55E–H); retrolateral pedal spurs absent. Basitarsi, pro- and retrolateral surfaces, each with scattered long and short setiform macrosetae, and spiniform macrosetae, more numerous on I and II than III and IV. Basitarsi, spiniform macrosetae, I, retrolateral: t , sb ; retroventral: t , sb ; proventral: t , st ; II, retrolateral: t , sb ; retroventral: t , sb ; proventral: t , st ; III, retrolateral: t , sb ; retroventral: t , st , sb ; proventral: t ; prolateral: t , st ; IV, retrolateral: t ; retroventral: t ; proventral: t , st ; prolateral: t , st . Telotarsi I–IV short, stout and distally broadened in dorsal and lateral views. Laterodistal lobes rounded. Dorsomedian lobes approximately equal to laterodistal lobes; each terminating in single setiform macroseta. Telotarsi, pro- and retrolateral surfaces, each with long and short, scattered macrosetae, not arranged in definite row. Telotarsi each with pro- and retroventral rows of spiniform macrosetae, two inserted on laterodistal lobes; counts in pro- and retroventral rows similar on I and II, and on III and IV ($n = 18$): I, proventral: 3, retroventral: 5 (4–6); II, 3 (3 or 4), 5 (5 or 6); III, 4 (3 or 4), 5 (4–6); IV, 4 (3 or 4), 5 (5 or 6). Telotarsal ungues short, curved, equal to subequal; pseudonychium (dactyl) reduced, rounded or acuminate.

Sternum: Shape subpentagonal (fig. 40C, D). Median longitudinal sulcus shallow anteriorly, deep and narrow posteriorly.

Genital operculum: Genital opercula suboval, completely divided longitudinally, partially overlapping, genital papillae present (δ) (fig. 40C);

subcordate, fused, genital papillae absent (♀) (fig. 40D).

Hemispermaphore: Lamelliform, with complex, folded capsule and accessory distal lobe protruding between articular suture and distal lobe (hook). Distal lamina with distal crest truncate, unfolded.

Pectines: Distal edge reaching distal edge of coxa IV (fig. 40C, D). First proximal median lamella (scape) of each pecten with mesial margin angular, approximately 90° (♂) or obtusely angular, greater than 90° but less than 180° (♀). Pectinal teeth straight and elongate (♂) or shorter and curved (♀), present along entire posterior margin; sinistral/dextral tooth count, 12/12 (11 or 12/9–12, $n = 5$) (♂), 11/10 (9–11/10–12, $n = 4$) (♀). Fulcra smooth proximally but densely setose (microsetae only) distally.

Mesosoma: Tergites each with shallow pair of submedian depressions, without obsolete median carina. Pretergites smooth and glabrous. Posttergites finely granular (♂) or smooth and glabrous (♀) medially, coarsely granular laterally. Sternites IV–VI, each with paired longitudinal depressions prolateral to spiracles, absent on VII. Surface, sternites III–VII, smooth; VII with pair of weakly developed, costate ventrolateral carinae only, without posteromarginal carina. Sternite VII, length of width, 72% (66%–76%, $n = 3$) (♂), 68% (65%–71%, $n = 2$) (♀).

Metasoma and telson: Metasomal segments I–V progressively increasing in length, decreasing in width; segment V, width of segment I, width, 77% (72%–81%, $n = 3$) (♂), 72% ($n = 2$) (♀). Metasoma fairly robust, width of length, segment I, 86% (83%–89%, $n = 3$) (♂), 89% (86%–92%, $n = 2$) (♀); II, 74% (74%–75%) (♂), 75% (74%–75%) (♀); III, 64% (62%–66%) (♂), 68% (♀); IV, 51% (50%–53%) (♂), 56% (54%–58%) (♀); V, 37% (36%–37%) (♂), 37% (36%–38%) (♀). Telson vesicle, width of metasomal segment V, width, 105% (98%–109%, $n = 3$) (♂), 102% (101%–103%, $n = 2$) (♀); elongate, height of length, 50% (48%–53%, $n = 3$) (♂), 56% (53%–58%, $n = 2$) (♀); dorsal surface flat; ventral

surface evenly curved. Aculeus relatively long, gently curved, length of vesicle length, 50% (46%–54%, $n = 3$) (♂), 58% ($n = 2$) (♀). Length metasoma and telson, of total length, 59% (58%–59%, $n = 3$) (♂), 57% (56%–57%, $n = 2$) (♀). Dorsosubmedian carinae, segments I–IV, distinct, complete, granular or costate-granular, posterior spiniform granules obsolete (fig. 73C); V, vestigial. Dorsolateral carinae, segments I–V, distinct, complete, costate-granular on I–IV, costate-granular to granular on V. Median lateral carinae, segment I, incomplete, reduced to granular row in posterior half, diagonally oriented between dorsolateral and ventrolateral carinae (fig. 74C); II–IV, vestigial, each reduced to posterior granule; V, incomplete, granular row, restricted to anterior two-thirds. Ventrolateral and ventrosubmedian carinae, segments I–IV, distinct, complete, costate on I–III, granular or costate-granular on IV, more strongly developed on III and IV than on I and II (fig. 75C). Ventrolateral carinae, segment V, distinct, complete, comprising spiniform granules, diverging posteriorly, terminal granule slightly larger than preceding granules. Ventrosubmedian carinae, segment V, vestigial, each reduced to one or two isolated spiniform granules, demarcated by conspicuous macrosetae. Ventromedian carina, segment V comprising single row of spiniform granules, unmodified posteriorly. Anal arch, segment V, dorsal carina, costate; ventral carina comprising subspiniform granules. Dorsal intercarinal surfaces, segments I–IV, granular, V, smooth. Lateral and ventral intercarinal surfaces, segments I–V, smooth. Ventral surface, lateral aspect, segment IV, shallowly convex. Telson vesicle, dorsal and lateral surfaces smooth; ventral surface with four longitudinal carinae, each comprising spiniform granules.

DISTRIBUTION: This species is endemic to the Indian state of Kerala (fig. 199, table 1). All known records occur south of the Bharathappuzha River and the Palakkad (Palghat) Gap, a disjunction in the Western Ghats (Sahyadri) between the Nilgiri Hills to the north and Anaimalai Hills to the south, with an average eleva-

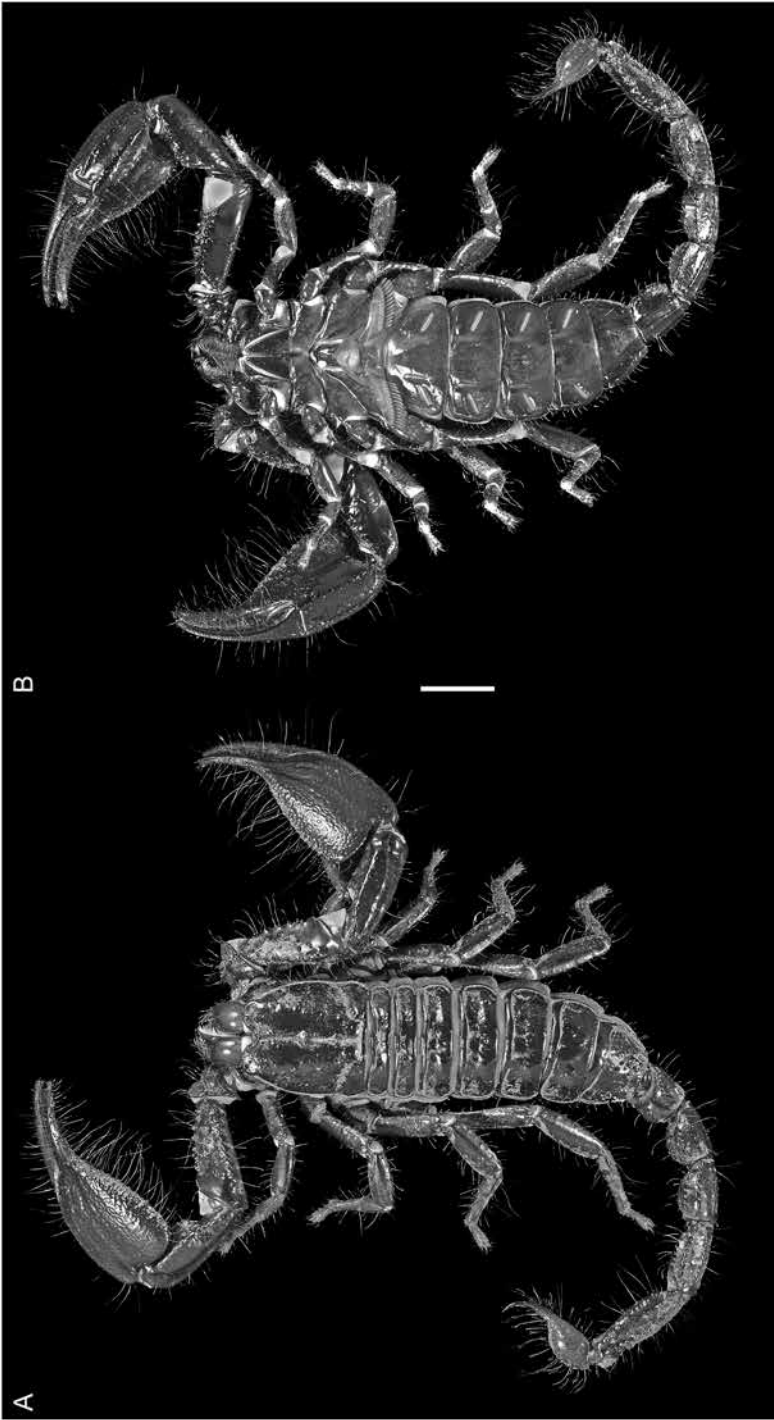


FIGURE 203. *Sahyadrimetrus kanarensis* (Pocock, 1900), comb. nov., ♂ (AMNH), Chaudi, India, habitus: **A**, dorsal and **B**, ventral aspects. Scale bar = 10 mm.

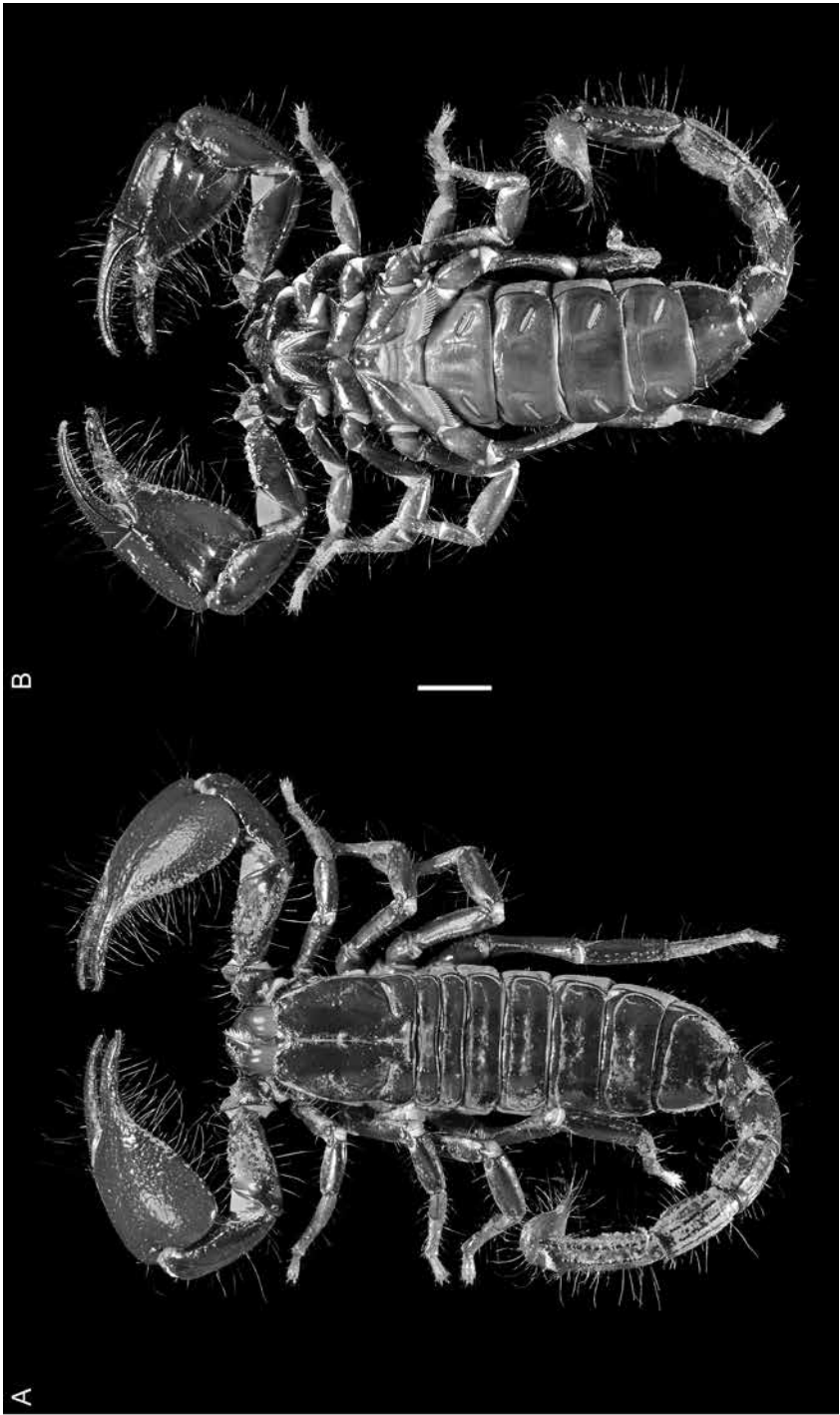


FIGURE 204. *Sahyadrimetrus kanarensis* (Pocock, 1900), comb. nov., ♀ (AMNH), Mangal, India, habitus: **A.** dorsal and **B.** ventral aspects. Scale bar = 10 mm.

tion of 140 m and a width of 24–30 km. The distribution of *S. mathewi* is parapatric with those of *S. barberi*, *S. scaber*, and *S. tikaderi*.

ECOLOGY: *Sahyadrimetrus mathewi* inhabits wet primary and secondary lowland rainforest, swamp forest and plantations on the Malabar Coast, and montane rainforest in the Western Ghats (Sahyadri) of southwestern India. The locality records for which data are available range from 20–160 m above sea level. This species is fossorial and pelophilous, excavating shallow burrows (ca. 30–40 cm deep) or scrapes in hard, clayey- or sandy-loam soils, under or at the base of stones and logs, in earthen banks, among the roots of trees, or in open ground. It occurs in sympatry with the buthids *Isometrus sankeriensis*, *Lychas tricarinatus*, *Reddyanus brachycentrus*, and an unidentified species of *Isometrus* Ehrenberg, 1828, the hormurids *Chiromachetes fergusonii* Pocock, 1899, and several species of *Iomachus* Pocock, 1893 (Sureshan et al., 2007a), and the rugodontid *Rugodontus keralaensis* (P. Jain, personal commun.).

Sahyadrimetrus rugosus (Couzijn, 1981),
comb. et stat. nov.

Figures 8D, 10, 25D, 39D, 54E–H, 73D, 74D,
75D, 198, 213–215, table 1

Heterometrus (Chersonesometrus) phipsoni:

Couzijn, 1981: 155, 157–159, 169, 171, 180,
fig. 59 (misidentification, part).

Heterometrus (Chersonesometrus) phipsoni phipsoni:

Couzijn, 1981: 43, 87, 149–151, 153,
170, 171, 192, table 7, fig. 59 (misidentification, part).

Heterometrus (Chersonesometrus) scaber rugosus

Couzijn, 1981: 40, 87, 133, 146, 147, 170,
192, table 7, figs. 45, 58; Kovařík, 1998: 137;
Fet, 2000: 441.

Heterometrus (Heterometrus) keralaensis Tikader

and Bastawade, 1983: 521, 528–533, figs.

1417–1430; Kovařík, 1998: 137; Fet, 2000:

432, 433; Bastawade et al., 2004: 47, 53, 57,

figs. 54–57; Sureshan et al., 2007a: 2906–
2908, fig. 1 (part); syn. nov.

Heterometrus (Heterometrus) keralaensis: Indra,

2001: 56, 57; Bastawade, 2006a: 131, 135,

136 (part); Bastawade and Borkar, 2008:

218, 219 (part); Bastawade, 2009: 212, 215,

220, 221 (part).

Heterometrus keralaensis: Kovařík, 2004: 20,

51–53, tables 2, 3 (part); 2009: 35, 36, 39,

48, tables 1, 2 (part); Aswathi and Sureshan,

2017: 9847.

Heterometrus phipsoni: Kovařík, 2004: 1, 4, 29,

34, 44, 49, 51, 52, tables 2, 3 (misidentifica-

tion, part); 2009: 35, 36, 42, 43, 48, tables 1,

2 (misidentification, part).

Heterometrus scaber: Kovařík, 2004: 1, 35, 38,

51–53, tables 2, 3 (misidentification, part);

2009: 35, 36, 43, 48, tables 1, 2 (misidentifi-

cation, part).

Heterometrus scaber rugosus: Kovařík, 2004: 38.

TYPE MATERIAL: INDIA: *Heterometrus (Chersonesometrus) scaber rugosus*: Holotype ♀ (MNHN RS 0082 [Simon coll. 17340]), Malabar Coast, E. Pougnet [examined]. **Kerala:** *Palghat Distr.:* *Heterometrus (H.) keralaensis*: Holotype ♂ (ZSI 5110/18), 1 imm. ♀ paratype (ZSI 5111/18), Meenmutty [Minmutty, 11°20'N 76°31'E], New Amaranbalan (R.F.) [New Amarambalam Reserved Forest], 21.ii.1979, T.S.N. Murthy.

DIAGNOSIS: *Sahyadrimetrus rugosus* may be separated from other species of *Sahyadrimetrus* as follows. The carapace is markedly dorsoventrally compressed, the lateral surfaces sloping gently (fig. 25D), in *S. rugosus* but vaulted, the lateral surfaces sloping steeply in *S. scaber* to very steeply in *S. mathewi*. The carapace mediolateral margins diverge or converge slightly posteriorly (at the posterolateral sulci) in *S. rugosus* but converge markedly posteriorly (at the posterolateral sulci) in *S. kanarensis*, *S. mathewi*, and *S. scaber*. The carapace interocular surface is granular along the median longitudinal and anterior bifurcated sulci only in the male, and the frontal lobes and medial region of the interocular surface are granular with

smooth areas in the female (fig. 25D) of *S. rugosus*, whereas the frontal lobes and medial region are granular with smooth areas in the male of *S. kanarensis*, *S. scaber*, and *S. tikaderi*, and the interocular surface is entirely, uniformly granular in the male and female of *S. mathewi*. The carapace posterolateral surfaces of the female (fig. 25D) are smooth or nearly so in *S. rugosus* but granular in *S. mathewi* and *S. scaber*. The pedipalps of the adult male are long, with femur length : posterior carapace width ratio (FL:PCW) ≥ 0.80 and femur length : carapace length ratio (FL:CL) ≥ 0.76 in *S. rugosus* but short, with FL:PCW < 0.77 , FL:CL < 0.74 in *S. kanarensis*, *S. scaber* and *S. tikaderi*. The pedipalp patella dorsomedian carina of the female (fig. 214) is present and entirely to predominantly granular in *S. rugosus* but absent or obsolete in all other species. The patella retrodorsal carina of the female (fig. 214) is absent or obsolete, and the retromedian carinae present and granular in *S. rugosus* whereas the retrodorsal carina is present, as strongly developed as or more strongly developed than the retromedian carinae, which are absent or obsolete in *S. kanarensis*, *S. mathewi*, and *S. scaber*. The patella dorsal, retrodorsal, and retroventral intercarinal surfaces of the female (fig. 214) are granular in *S. rugosus* but smooth or nearly so in the other species. The maximum distance between the dorsomedian and dorsal secondary carinae (DMC–DSC) of the pedipalp chela manus is less than the maximum distance between the dorsal secondary and digital carinae (DSC–DC) in the male of *S. rugosus* but similar to the DSC–DC in the male of *S. kanarensis* and *S. scaber*. The chela manus dorsal surface of the female (fig. 215) is coarsely granular to granulo-reticulate in *S. rugosus* but smooth or nearly so in *S. kanarensis* and *S. tikaderi*. The chela manus retrolateral intercarinal surfaces are smooth or nearly so in the male and granular in the female (fig. 215) of *S. rugosus*, but granular in the male of *S. mathewi* and *S. scaber*, and smooth or nearly so in the female of *S. kanarensis*, *S. mathewi*, and *S. scaber*. Macroseta *st* is spiniform on the retroventral surfaces of the

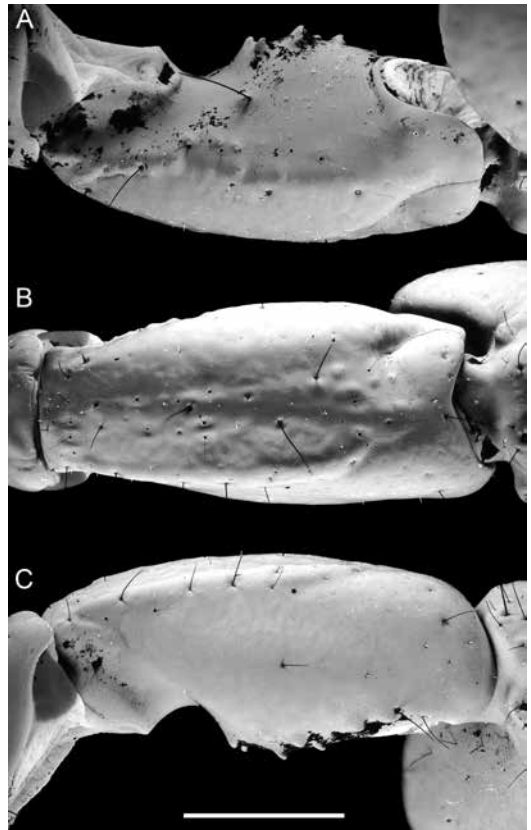


FIGURE 205. *Sahyadrimetrus kanarensis* (Pocock, 1900), comb. nov., ♀ (AMNH), Chaudi, India, pedipalp patella: A. dorsal, B. retrolateral, and C. ventral aspects. Scale bar = 5 mm.

basitarsi of legs I–III (fig. 54E–H) in *S. rugosus* but setiform on the retroventral surfaces of the basitarsi of legs I–III in *S. kanarensis*, and legs I and II in *S. mathewi* and *S. scaber*; *st* on the proventral surface of the basitarsus of leg III is setiform in *S. rugosus* but spiniform in *S. kanarensis*. The mesial surfaces of mesosomal tergites I–VI are smooth in the male and the lateral surfaces smooth in the female of *S. rugosus*, whereas the mesial surfaces are granular in the male of *S. mathewi* and *S. scaber* and the lateral surfaces granular in the female of all other species except *S. barberi*. The ventral intercarinal surfaces of metasomal segment IV are smooth (fig. 75D) in *S. rugosus* but granular in *S. tikaderi*. The dorsolat-

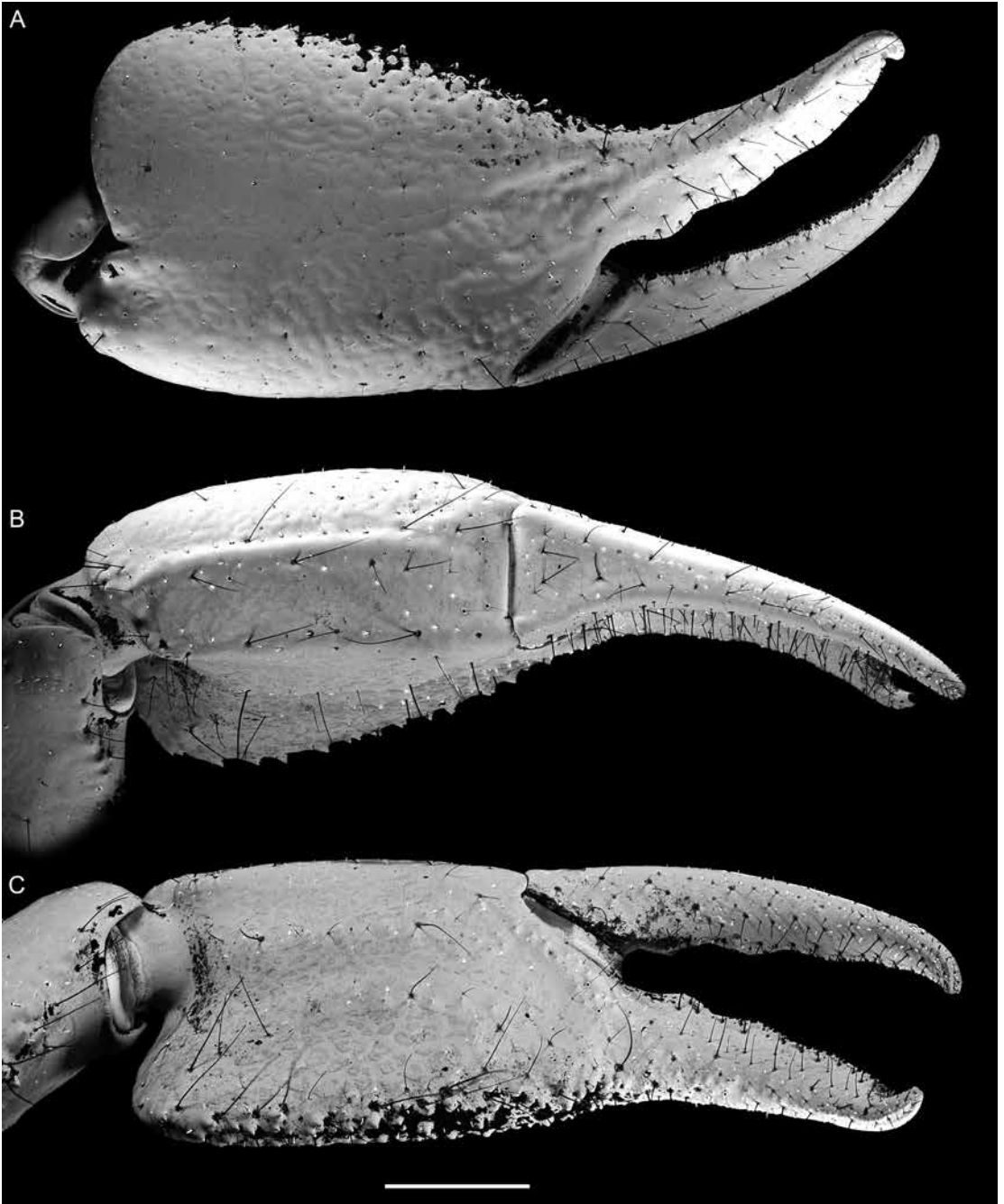


FIGURE 206. *Sahyadrimetrus kanarensis* (Pocock, 1900), comb. nov., ♂ (AMNH), Chaudi, India, pedipalp chela: **A.** retrodorsal, **B.** ventral, and **C.** prolateral aspects. Scale bar = 5 mm.



FIGURE 207. *Sahyadrimetrus kanarensis* (Pocock, 1900), comb. nov., ♀ (AMNH), Chaudi, India, pedipalp chela: A. retrodorsal, B. ventral, and C. prolateral aspects. Scale bar = 5 mm.

eral carinae of metasomal segment V are distinct and continuous (fig. 73D) in *S. rugosus* but obsolete and discontinuous to absent in *S. barberi*.

DISTRIBUTION: This species is endemic to the Indian states of Karnataka, Kerala, and Tamil Nadu (fig. 198, table 1). It appears to occur at higher elevations than *S. scaber* and is separated from *S. tikaderi*, occurring to the south, by the Palakkad (Palghat) Gap. Most records of this species (e.g., Sureshan et al., 2007a; Aswathi and Sureshan, 2017) remain unconfirmed and many are probably misidentifications of *S. mathewi*.

ECOLOGY: *Sahyadrimetrus rugosus* inhabits primary and secondary montane rainforest in the Western Ghats (Sahyadri) of southern India. The locality records for which data are available range from 750–1115 m above sea level. This species is fossorial and pelophilous, excavating single-occupant burrows (ca. 20–50 cm deep) in hard, moist, clayey-loam soils, under stones (fig. 8D) or in open ground on earthen banks. Burrow entrances are broad and flat (Indra, 2001). It occurs in sympatry with the buthid *Isometrus sankeriensis* and unidentified hor-murids of the genus *Iomachus* (Sureshan et al., 2007a).

REMARKS: Couzijn (1981) described *H. (C.) scaber rugosus* from the Malabar Coast of Kerala, India. The subspecies was not mentioned by Tikader and Bastawade (1983) but was listed by Fet (2000). Kovařík (2004: 35, 38; 2009: 43) listed the subspecies under *H. scaber* but did not formally synonymize it, being unable to examine the holotype. The holotype was examined during the present investigation but was not found to be conspecific with *S. scaber*. The diagnostic characters mentioned by Couzijn (1981: 146, 147), which include carination and surface macrosculpture of the carapace, described as “lateral and posterolateral areas and frontal margin granulated; remaining areas smooth though locally faint granules occur, and a few sparse and fine granules can be found near the superciliary crests,” are consistent with *H. keralaensis*, rather than *S. scaber*.

The status of *H. keralaensis*, previously known only from the type locality, Meenmutty, Kerala, also remained uncertain until now. Kovařík (2004: 20) “was unable to examine this species” and believed it “related to *H. thorellii* Pocock, 1892, from which it differs (apart from the characters given in the key) in having the dorsal surface of the chela reticulated.” Interestingly, Kovařík (2004: 20) examined and misidentified five females from Devala, Tamil Nadu (CAS 9070419 and 9070421) as *H. phipsoni*. Devala is close to the type locality of *H. keralaensis*.

This distinctive species, previously placed in the nominotypical subgenus of *Heterometrus* by various authors (Tikader and Bastawade, 1983; Fet, 2000), as *H. (H.) keralaensis*, is newly accommodated in *Sahyadrimetrus*, gen. nov., based on phylogenetic analysis (fig. 10). Contrary to the speculations of Kovařík (2004), it is not closely related to *H. thorellii* or other species of *Heterometrus*, despite the elongated pedipalps of the adult male. Among many other differences recounted in the key and diagnosis above, it lacks the prominent spiniform granule on the proventral carina of the pedipalp patella typical of all species of that genus. Among the species of *Sahyadrimetrus*, *S. rugosus* differs obviously from *S. scaber* in the smooth carapace interocular surface, and from *S. kanarensis* and *S. scaber* in the shape and elongation of the male pedipalps. It is most closely related to *S. barberi* and *S. tikaderi*, with which it shares similar counts of pro- and retroventral spiniform macrosetae on the telotarsi of legs I–IV (4/5, 4/5–6, 4/6, 4/6 in *S. rugosus* compared with 4/6, 4/6, 4/6, 4/6 in *S. barberi*) but differs from *S. barberi* in the more elongate chela manus, and from *S. barberi* and *S. tikaderi* in the more strongly developed dorsolateral carinae of metasomal segment V.

Based on these deductions, *Sahyadrimetrus rugosus* (Couzijn, 1981), comb. et stat. nov., is elevated from the rank of subspecies and the following new synonym presented: *Heterometrus (Heterometrus) keralaensis* Tikader and Bastawade, 1983 = *Sahyadrimetrus rugosus* (Couzijn, 1981), syn. nov.

MATERIAL EXAMINED: **Karnataka:** Kodagu Distr.: Nalknad Palace Rd, Yevakapadi, 12°14'N 75°38'E, 1115 m, 20.xi.2009, R. Datta, secondary evergreen forest/coffee plantations, in scrape under stone embedded in road cut, clayey loam, 1 ♀ (AMNH). **Kerala:** Wayanad Distr.: Chaliyar River, above Meenmutty Waterfalls, 11°32'N 76°14'E, 845 m, 24.xi.2006, P. Menon, secondary montane forest with bamboo thicket on banks of perennial river, sandy-clay soil, doorkeeping at burrow entrance below large rock, embedded in earthen bank, 1 ♀, 8 juv. ♀ (AMNH), 1 juv. ♀ (AMCC [LP 14007]); Kun-nathidavaka, 11°31'N 76°03'E, 838 m, 25.xi.2006, P. Menon, primary montane evergreen forest in steep ravine leading down to perennial rocky stream, granite outcrops and loose stones, many embedded in clayey-loam soil, fairly humid, in burrows (ca. 20 cm deep) under large stones or in open ground, 1 ♀, 1 subad. ♀ (AMNH), 1 subad. ♂ (AMCC [LP 14028]), 893 m, 18–19.xi.2009, R. Datta, 2 ♀, 1 subad. ♂, 3 juv. ♀ (AMNH), 1 juv. ♂ (AMCC [LP 16770]); Pookode Lake, Vythiri, 11°33'N 76°02'E, 748 m, 19.xi.2009, R. Datta, primary evergreen forest on low hills, excavated from 50 cm deep burrow in open, clayey ground with few stones, 1 subad. ♂ (AMCC [LP 16768]). **Tamil Nadu:** Nilgiris Distr.: Devala [11°28'N 76°23'E], S India, v.1961, P. Susai Nathan, ex Stahnke coll., 5 ♀ (CAS 9070419 [ASU 61-243], 9070421 [ASU 61-242, 244, 284, 286]).

Sahyadrimetrus scaber (Thorell, 1876),
comb. nov.

Figures 10, 26E, F, 40E, F, 55I–L, 73E, 74E, 75E,
199, 216–219, table 1

Buhus (*Heterometrus*) *spinifer*: Gervais, 1844a: 60, 61 (part).
Scorpio leioderma Dufour, 1856: 571, 586, 631, 632; Pocock, 1900a: 99; Couzijn, 1981: 58; Fet, 2000: 448; syn. nov.
Heterometrus afer (nec *Scorpio afer* Linnaeus, 1758): Simon, 1872b: 53, 59, 98–101, pl. VI, fig. 1 (part); Couzijn, 1981: 145.
Pandinus scaber Thorell, 1876b: 202; Simon, 1905: 161; Couzijn, 1981: 144.
Scorpio scaber: Pocock, 1893: 310, 311 (part); Kraepelin, 1894: 32, 58.

Heterometrus scaber: Kraepelin, 1899: 111, 116; 1913: 166 (part); Lampe, 1918: 198; Takashima, 1945: 93; Hjelle, 1990: 17, 54, 58 (part); Kovařík, 2004: 1, 35, 37, 38, 51–53, tables 2, 3 (part), fig. 25; 2009: 35, 36, 43, 48, 49, 90, 100, tables 1, 2 (part), figs. 120, 121, 212; Aswathi and Sureshan, 2017: 9847, 9848 (part), figs. 1–3, image 10.

Palamnaeus scaber: Pocock, 1900a: 85, 93 (part).

Heterometrus (*Scorpio*) *scaber*: Kraepelin, 1901: 271.

Heterometrus (*Chersonesometrus*) *scaber*:

Couzijn, 1981: 170, fig. 58 (part); Tikader and Bastawade, 1983: 576, 619–625 (part), figs. 1639–1652; Kovařík, 1998: 136; Fet, 2000: 440 (part); Bastawade et al., 2004: 48, 55, 58, figs. 69, 70; Sureshan et al., 2007a: 2907, 2908, fig. 2 (part).

Heterometrus (*Chersonesometrus*) *scaber scaber*:

Couzijn, 1981: 39, 87, 133, 144–147, 170, 192, table 7, figs. 44, 58 (part); Fet, 2000: 440.

Heterometrus (*Heterometrus*) *malapuramensis*

Tikader and Bastawade, 1983: 519, 522, 533–538, figs. 1431–1444 (synonymized by Kovařík, 2004: 1, 35, 38); Biswas, 1984: 320; Kovařík, 1998: 137; Fet, 2000: 436; Indra, 2001: 56, 57; Bastawade et al., 2004: 47, 48, 54, 57, figs. 58–62; Kovařík, 2004: 1, 38 (part); Sureshan et al., 2007a: 2906–2908, fig. 2 (part); Indra, 2009: 142.

Heterometrus (*Srilankametrus*) *indus*: Kovařík, 2002: 17 (misidentification, part).

Heterometrus rolciki Kovařík, 2004: 1, 7, 35, 36, 51–53, tables 1–3, fig. 24; 2009: 35, 36, 43, 48, 49, 89, 100, 111, tables 1, 2, figs. 111–117, 210, 211, 265; syn. nov.

Heterometrus (*Chersonesometrus*) *kanaraensis*:

Indra, 2006: 197, 199, 200 (misidentification, part).

TYPE MATERIAL: **INDIA:** *Scorpio leioderma*: Holotype [depository unknown], Malabar, India. *Pandinus scaber*: Holotype, “Bengale” [lost]. **Kerala:** Kozhikode Distr.: *Heterometrus* (*H.*) *mala-*

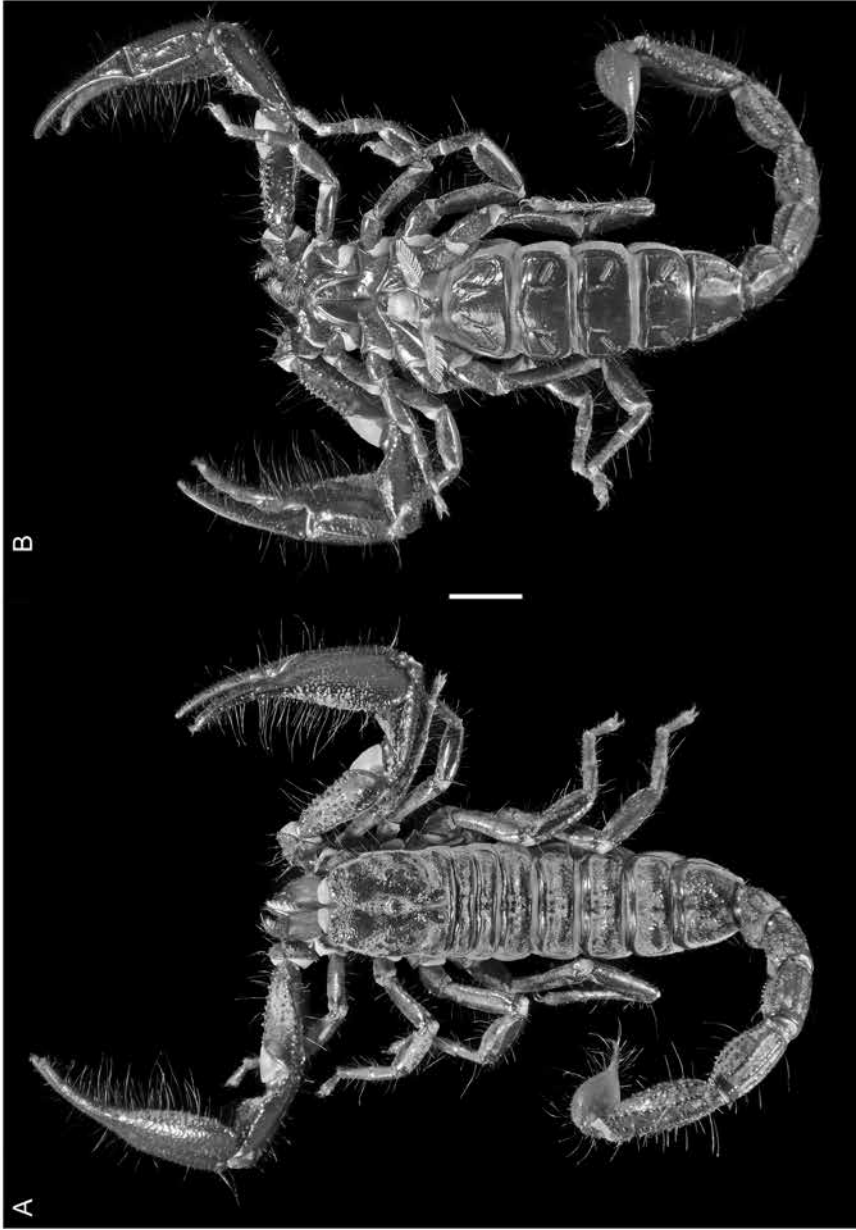


FIGURE 208. *Salhyadrimetrus mathewi*, gen. et sp. nov., holotype ♂ (AMNH), Poomala, India, habitus: A, dorsal and B, ventral aspects. Scale bar = 10 mm.

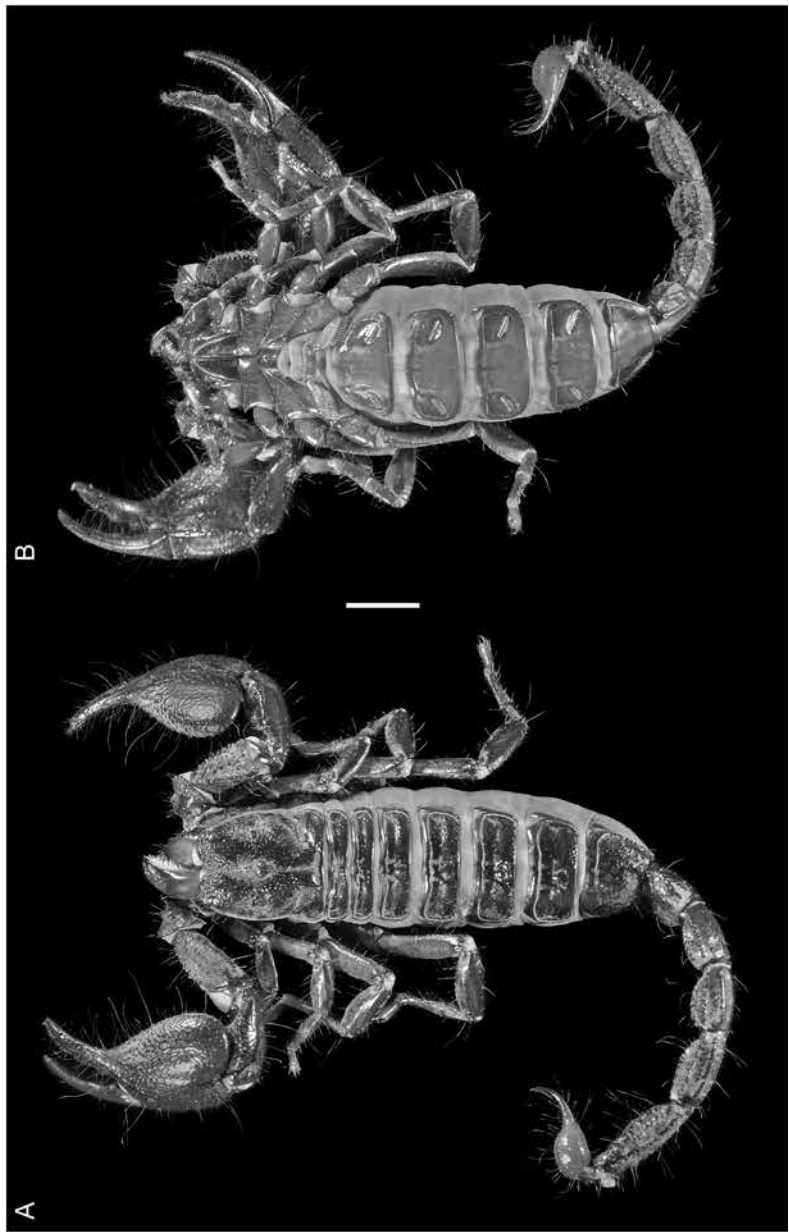


FIGURE 209. *Sahyadrimetrus mathewi*, gen. et sp. nov., paratype ♀ (AMNH), Poomala, India, habitus: **A**, dorsal and **B**, ventral aspects. Scale bar = 10 mm.

puramensis: Holotype ♂ (ZSI 5104/18), Malapuram [Malappuram, 11°04'N 76°04'E], Poonus estate, 16.vii.1981, K.N. Nair; paratypes: 2 ♂ (ZSI 5106/18–5108/18), same data except: 14.vii.1981; 3 imm. ♂ (ZSI 5106/18–5108/18), Perambra [11°34'N 75°45'E], Chermalai Hills, 18.vii.1981, K.N. Nair; 1 ♀, 29 imm. (ZSI 5109/18), Perumpally [09°10'E 76°27'E], 16.vii.1981, K.N. Nair; 3 imm. ♂ (ZSI 5106/18–5108/18), Puthupady [Puthuppady, 10°01'N 76°36'E], 14.vii.1981, K.N. Nair. **Puducherry:** *Mahé Distr.: Heterometrus (Chersonesometrus) s. scaber*: Neotype ♀ (MNHN RS 0098), Mahé [11°42'N 75°32'E], Deschamps [examined]. **Tamil Nadu:** *Nilgiris Distr.: Heterometrus rolciki*: Holotype ♂ (FKPC), Nilgiri Hills, 15 km SE of Kotagiri, Kunjappanai env., 11°22'N 76°56'E, ca. 900 m, 7–22.v.2000, J. Rolčík; paratypes: 1 ♂, 1 imm. (FKPC), same data, except: 23–30.v.1999, Z. Kejval and M. Trýzna; 1 ♀, 2 juvs. (FKPC), near Kotagiri [11°26'N 76°53'E], 27.x.1997, Werner.

As discussed by Couzijn (1981: 145, 146), Simon (1872b: 99) described an adult, the sex of which cannot be determined from the description, under the name *Heterometrus afer* (nec *Scorpio afer* Linnaeus, 1758). Simon (1872b: 99) noted “paraît commun au Bengale” and added a few measurements of the largest specimen. However, according to Couzijn (1981) none of the specimens of *H. scaber* (i.e., *H. afer* sensu Simon, 1872) that were once part of E. Simon's personal collection (now deposited in the MNHN) fit these measurements, no corresponding specimens from Bengal are present in the MNHN or other collections, and the type locality is probably erroneous (cf. Pocock, 1900a: 93, fn.). Couzijn (1981) therefore designated an adult female (MNHN RS 0098) from Mahé as neotype. A female was selected as neotype rather than a male, to facilitate comparison with the holotypes of *H. s. rugosus* and *H. s. obscurus* which are both female, no male being available at the time.

DIAGNOSIS: *Sahyadrimetrus scaber* may be separated from other species of *Sahyadrimetrus* as follows. The carapace is vaulted, the lateral sur-

faces sloping steeply (fig. 26E, F), in *S. scaber* but moderately to markedly dorsoventrally compressed, the lateral surfaces sloping gently, in *S. barberi*, *S. kanarensis*, *S. rugosus*, and *S. tikaderi*. The carapace mediolateral margins converge markedly posteriorly (at the posterolateral sulci) in *S. scaber* but diverge or converge slightly posteriorly (at the posterolateral sulci) in *S. barberi*, *S. rugosus*, and *S. tikaderi*. The frontal lobes and medial region of the carapace interocular surface are granular with smooth areas in the male and female (fig. 26E, F) of *S. scaber* whereas the interocular surface is granular along the median longitudinal and anterior bifurcated sulci only in the male of *S. rugosus*, and the interocular surface is entirely, uniformly granular in the male and female of *S. mathewi*. The carapace posterolateral surfaces of the female (fig. 26F) are granular in *S. scaber* but smooth or nearly so in all other species except *S. mathewi*. The pedipalps of the adult male are short, with femur length : posterior carapace width ratio (FL:PCW) < 0.77 and femur length : carapace length ratio (FL:CL) < 0.74 (fig. 216A, B) in *S. scaber* but long, with FL:PCW ≥ 0.80 and FL:CL ≥ 0.76 in *S. mathewi* and *S. rugosus*. The pedipalp patella dorsomedian carina of the female is absent or obsolete in *S. scaber* but entirely to predominantly granular in *S. rugosus*. The patella retrodorsal carina of the female is present and as strongly developed as or more strongly developed than the retromedian carinae, which are absent or obsolete in *S. scaber*, whereas the retrodorsal carina of the female is absent or obsolete, and the retromedian carinae present and granular in *S. barberi*, *S. rugosus*, and *S. tikaderi*. The patella dorsal, retrodorsal, and retroventral intercarinal surfaces of the female are smooth or nearly so in *S. scaber* but granular in *S. rugosus*. The maximum distance between the dorsomedian and dorsal secondary carinae (DMC–DSC) of the pedipalp chela manus is similar to the maximum distance between the dorsal secondary and digital carinae (DSC–DC) in the male (fig. 218) of *S. scaber* but less than the DSC–DC in the male of *S. mathewi*, *S. rugosus*, and *S. tikaderi*. The chela manus dorsal surface of the female (fig. 219) is smooth to finely

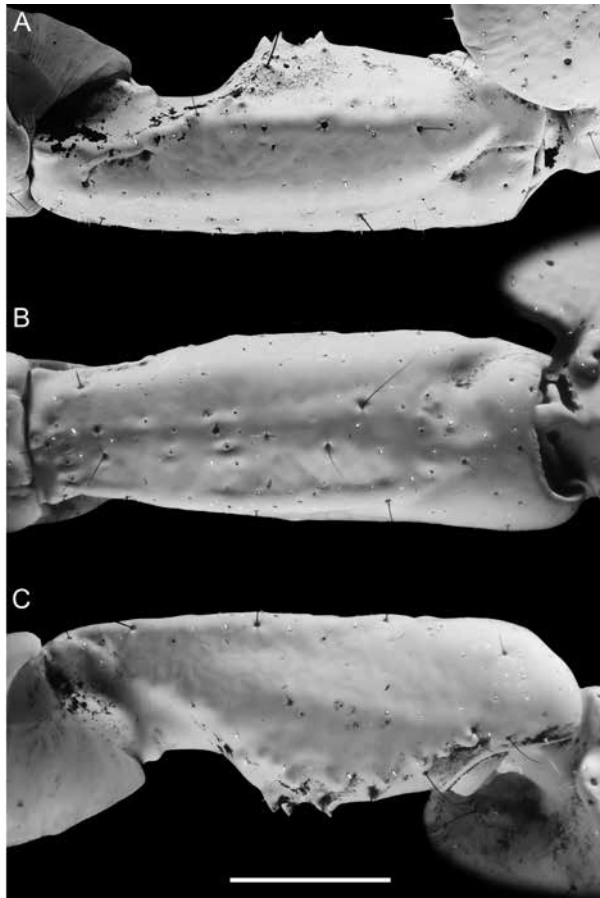


FIGURE 210. *Sahyadrimetrus mathewi*, gen. et sp. nov., holotype ♂ (AMNH), Poomala, India, pedipalp patella: **A.** dorsal, **B.** retrolateral, and **C.** ventral aspects. Scale bar = 5 mm.

granulo-reticulate in *S. scaber* but smooth or nearly so in *S. kanarensis* and *S. tikaderi*. The chela manus retrolateral intercarinal surfaces are granular in the male (fig. 218) and smooth or nearly so in the female (fig. 219) of *S. scaber*, but smooth or nearly so in the male of *S. kanarensis*, and granular in the female of *S. barberi*, *S. rugosus*, and *S. tikaderi*. Macroseta *st* is setiform on the retroventral surfaces of the basitarsi of legs I and II and spiniform on leg III (fig. 55I–L) in *S. scaber* but spiniform on the retroventral surfaces of the basitarsi of legs I–III in *S. barberi*, *S. rugosus*, and *S. tikaderi*, and setiform on legs I–III in *S. kanarensis*; *st* on the proventral surface of the basitarsus of leg III is setiform in *S. scaber* but spiniform

in *S. kanarensis*. The mesial surfaces of mesosomal tergites I–VI are granular in the male and the lateral surfaces granular in the female of *S. scaber*, whereas the mesial surfaces are smooth in the male of *S. kanarensis*, *S. rugosus*, and *S. tikaderi*, and the lateral surfaces smooth in the female of *S. rugosus*. The ventral intercarinal surfaces of metasomal segment IV are smooth (fig. 75E) in *S. scaber* but granular in *S. tikaderi*. The dorsolateral carinae of metasomal segment V are distinct and continuous (fig. 73E) in *S. scaber* but obsolete and discontinuous to absent in *S. barberi*.

DISTRIBUTION: This species is endemic to India (fig. 199, table 1), where it has been recorded in the states of Goa, Karnataka, Kerala,



FIGURE 211. *Sahyadrimetrus mathewi*, gen. et sp. nov., holotype ♂ (AMNH), Poomala, India, pedipalp chela: **A.** retrodorsal, **B.** ventral, and **C.** prolateral aspects. Scale bar = 5 mm.



FIGURE 212. *Sahyadrimetrus mathewi*, gen. et sp. nov., paratype ♀ (AMNH), Poomala, India, pedipalp chela: A. retrodorsal, B. ventral, and C. prolateral aspects. Scale bar = 5 mm.

TABLE 5

Measurement Data for Type Specimens of Two New Species of *Salvyadrimetrus*, gen. nov., and *Srilankametrus Couzijn*, 1981, stat. nov. et stat. rev.
Material deposited in the American Museum of Natural History (AMNH), New York; Natural History Museum (BMNH), London; Muséum National d'Histoire Naturelle (MNHN), Paris; and Forschungsinstitut und Naturmuseum Senckenberg (SMF), Frankfurt. Measurements (mm) follow Prendini (2000b): ¹sum of carapace, tergites I–V, and telson; ²distance from anterior carapace margin; ³sum of metasomal segments I–V and telson; ⁴distance from base of condyle to tip of fixed finger.

Species	<i>Salvyadrimetrus mathewi</i>				<i>Salvyadrimetrus tikaderi</i>				<i>Srilankametrus couzijn</i>			
Type	Holo.	Para.	Para.	Para.	Holo.	Para.	Para.	Para.	Holo.	Para.	Holo.	Para.
Sex	♂	♂	♀	♀	♂	♂	♀	♀	♂	♂	♀	♀
Collection	AMNH	AMNH	AMNH	AMNH	MNHN	MNHN	MNHN	MNHN	BMNH	SMF	AMNH	AMNH
Number					RS 3265	RS 3266	RS 3265	RS 3265	1896/7.30.121	5332/1		
Total length ¹	122.5	123.0	116.6	113.7	101.9	111.5	107.0	108.2	86.7	104.3		125.6
Carapace												
anterior width	9.7	9.3	9.1	9.7	8.2	10.0	10.2	10.0	8.5	9.9		10.6
posterior width	13.8	13.7	13.3	14.0	13.9	14.6	15.9	15.5	11.9	14.7		17.3
length	16.4	16.6	15.2	16.3	14.6	16.3	15.5	15.4	13.1	15.6		18.5
median ocelli ²	8.2	8.5	8.0	8.2	7.8	8.5	8.1	7.9	6.6	8.3		9.2
Tergite I	2.2	2.5	2.3	2.6	2.4	2.2	2.3	2.3	1.7	1.9		3.1
Tergite II	2.9	2.7	2.9	2.8	2.5	2.8	2.6	3.1	3.0	3.0		3.9
Tergite III	3.8	4.0	3.9	3.7	3.6	4.4	3.4	4.1	3.6	4.6		5.2
Tergite IV	4.6	4.7	5.0	4.7	4.3	5.2	5.2	4.9	4.5	5.1		6.5
Tergite V	5.0	5.3	5.4	5.1	4.8	6.0	5.8	5.3	4.7	6.0		7.8
Tergite VI	6.0	6.0	5.9	6.0	5.9	6.5	6.4	5.8	5.3	7.4		8.1
Tergite VII	8.8	8.5	8.0	8.6	7.0	8.5	8.0	7.4	6.2	7.8		8.6
Sternite VII	8.5	8.0	8.1	7.9	7.0	8.1	7.6	8.1	6.4	7.3		8.7
	11.5	12.2	10.7	12.2	11.1	13.1	12.9	13.0	10.3	11.1		13.3
Mesosoma	33.3	33.7	33.3	33.6	30.6	35.6	33.8	32.9	29.0	35.7		43.3
Metasoma I	9.1	8.5	8.4	8.0	6.9	7.5	7.1	7.5	6.2	7.0		8.1
	7.6	7.5	7.5	7.4	6.4	6.5	6.8	6.6	5.8	6.9		8.2
Metasoma II	10.0	9.5	9.3	8.9	7.6	8.3	7.4	8.2	6.3	6.9		8.4
	7.4	7.1	7.0	6.6	5.7	5.8	6.2	6.0	5.2	6.4		7.2

TABLE 5 continued

Species	Sahyadrimetrus mathewi				Sahyadrimetrus tikaderi				Srilankametrus couzjini				
	Holo.	Para.	Para.	Para.	Holo.	Para.	Para.	Para.	Holo.	Para.	Para.	Holo.	
Type	♂	♂	♀	♀	♂	♂	♀	♀	♂	♂	♂	♀	
Sex	AMNH	AMNH	AMNH	AMNH	MNHN	MNHN	MNHN	MNHN	BMNH	SMF	AMNH		
Collection Number					RS 3265	RS 3266	RS 3265	RS 3265	1896.7.30.121	5332/1			
Metasoma III	length	10.5	10.6	10.1	9.2	10.3	7.7	8.7	8.2	8.5	6.5	7.9	8.7
	width	6.9	6.6	6.6	6.2	7.0	5.4	5.5	5.8	5.6	4.8	5.6	6.8
Metasoma IV	length	12.5	12.3	11.3	10.3	11.1	9.3	9.3	9.1	9.8	7.2	8.7	10.2
	width	6.3	6.2	6.0	5.6	6.4	4.8	5.0	5.2	4.9	4.6	5.2	5.8
Metasoma V	length	15.6	16.3	14.9	14.0	15.8	12.4	12.7	13.3	12.7	9.7	11.3	14.7
	width	5.9	6.1	5.4	5.3	5.7	4.6	4.8	4.9	4.6	4.4	4.6	5.1
Telson	vesicle length	10.4	10.1	9.4	8.5	9.8	7.6	7.7	8.1	8.2	5.4	7.2	8.0
	vesicle width	6.4	6.6	5.3	5.3	5.9	4.7	5.0	4.6	4.5	3.8	4.8	4.9
	vesicle height	5.1	5.4	4.5	4.9	5.2	4.3	4.4	4.3	4.4	3.1	4.0	4.6
	aculeus length	4.8	5.5	4.7	5.0	5.7	5.3	5.5	4.6	5.0	3.4	4.0	5.8
	total length	15.2	15.6	14.1	13.4	15.5	12.9	13.1	12.7	13.2	8.8	11.2	13.7
Metasoma	total length ³	72.9	72.8	68.1	63.8	71.7	56.7	59.6	57.7	59.9	44.6	53.0	63.8
Femur	length	14.9	14.1	13.5	11.6	13.2	13.1	15.6	12.3	12.8	11.4	13.6	14.0
	width	5.5	6.0	5.6	5.2	6.1	5.3	5.7	5.6	5.8	4.4	4.9	6.8
Patella	length	14.9	15.1	14.0	12.4	13.8	14.2	15.7	12.7	12.8	11.8	15.1	15.2
	width	6.0	6.0	5.8	5.4	6.4	5.6	6.1	6.5	6.4	4.2	5.4	7.8
Chela	length ⁴	30.2	31.1	26.9	27.6	30.1	27.2	30.3	27.5	27.5	23.8	29.9	32.8
	width	10.4	10.1	10.1	11.2	12.9	8.3	8.5	12.3	10.7	8.8	10.4	10.2
	height	9.7	9.5	8.5	10.4	11.6	8.7	7.9	9.8	9.0	8.4	9.8	11.1
	length retroven. carina	11.5	10.7	10.3	10.5	11.5	11.2	14.2	11.6	11.7	10.2	13.5	13.3
	length mov. finger	17.7	18.3	16.1	16.3	18.1	14.6	16.0	15.3	15.3	13.1	16.1	19.3
Pecten	total length	6.6	7.6	6.3	5.9	7.1	6.5	6.7	7.1	6.9	9.1	9.5	8.5
	length dent. marg.	4.6	5.4	4.5	4.0	4.8	5.0	5.5	4.9	4.9	7.3	8.0	5.5

Tamil Nadu, and the union territory of Puducherry: Mahé District only; records from Pondicherry, e.g., Kovařík (2004: 38), are erroneous or misidentified. All known records occur north of the Bharathappuzha River and the Palakkad (Palghat) Gap. The distribution of *S. scaber* is parapatric with those of *S. kanarensis*, *S. mathewi*, and *S. rugosus*.

ECOLOGY: *Sahyadrimetrus scaber* inhabits wet primary and secondary lowland rainforest, swamp forest and plantations on the Malabar Coast, and montane rainforest in the Western Ghats (Sahyadri) of southwestern India. The locality records for which data are available range from 65–900 m above sea level. This species is fossorial and pelophilous, excavating shallow burrows (ca. 10–40 cm deep) or scrapes in hard, clayey- or sandy-loam soils, under or at the base of stones and logs, in earthen banks, among the roots of trees, or in open ground (P. Jain, personal commun.). It occurs in sympatry with the buthids *Isometrus sankeriensis*, *Lychas tricarinatus*, and *Reddyanus brachycentrus*, and the hor-
murid *Iomachus laeviceps* (Indra, 2006).

CONSERVATION STATUS: *Sahyadrimetrus scaber* is occasionally available in the exotic pet trade.

REMARKS: This species, previously placed in subgenus *Chersonesometrus* of *Heterometrus* by various authors (e.g., Couzijn, 1981; Tikader and Bastawade, 1983; Fet, 2000), is newly accommodated in *Sahyadrimetrus*, gen. nov., based on a phylogenetic analysis (fig. 10).

The following synonym is confirmed: *Heterometrus* (*H.*) *malapuramensis* Tikader and Bastawade, 1983 = *Sahyadrimetrus scaber* (Thorell, 1876), comb. nov., synonymized by Kovařík (2004). Although unable to examine the types, Kovařík (2004: 38) tentatively synonymized *H. (H.) malapuramensis* with *H. scaber* based on characters in the original description by Tikader and Bastawade (1983). Kovařík's (2004) decision is upheld in the present investigation, based on independent assessment of the illustrations and description of Tikader and Bastawade (1983: 533), citing char-

acters closely matching *S. scaber*, including "Male of large body, entirely granular. Carapace closely granular." The total length of *H. (H.) malapuramensis* is 101 mm compared with 100–130 mm in *S. scaber*; the pectinal tooth count is 11/11 in *H. (H.) malapuramensis* compared with 7–12 in *S. scaber*; and the counts of pro- and retroventral spiniform macrosetae on the telotarsi of legs I–IV are 3–4/5, 3–4/4–5, 4/5, 4/5 in *H. (H.) malapuramensis* compared with 3/5, 3/5–6, 4/6, 4/6 in *S. scaber*. Additionally, the type locality of *H. (H.) malapuramensis*, Malappuram on the Malabar Coast of Kerala, occurs in an area in which *S. scaber* is the only scorpionid species recorded (fig. 199).

Scorpio leioderma, described from Malabar, India, was deemed unrecognizable from the original description by Pocock (1900a: 99) and listed as incertae sedis by Fet (2000: 448). However, it appears most likely that *S. leioderma* is a senior synonym of *S. scaber*. Therefore, the following new synonym is proposed: *Scorpio leioderma* Dufour, 1856 = *S. scaber*, syn. nov. The name *Scorpio leioderma* Dufour, 1856, was published earlier than the name *Pandinus scaber* Thorell, 1876; however, Dufour's (1856) name was never used again, whereas the Thorell's (1876b) name won general acceptance and is the only name used since the 1880s.

Heterometrus rolciki was described from five specimens collected at two localities in the vicinity of Kotagiri, an area in which *S. scaber* is abundant at lower elevations (fig. 199). Kovařík (2004: 35) states that *H. rolciki* "is close to *H. scaber*, but its smaller size accounts for some morphological differences." The smaller size range of *H. rolciki*, cited as 80–100 mm (cf. 100–130 mm in *S. scaber*), and minor morphometric differences which are a function of the smaller size, are not uncommon in scorpionids, and could be explained by the higher elevations of the localities at which *H. rolciki* was collected, compared with populations of *S. scaber* at lower elevations. On the other hand, the specimens may be immature. *Heterometrus rolciki* is identical to *S. scaber* in other respects, notably the carapace shape, coarsely granular carapace sur-

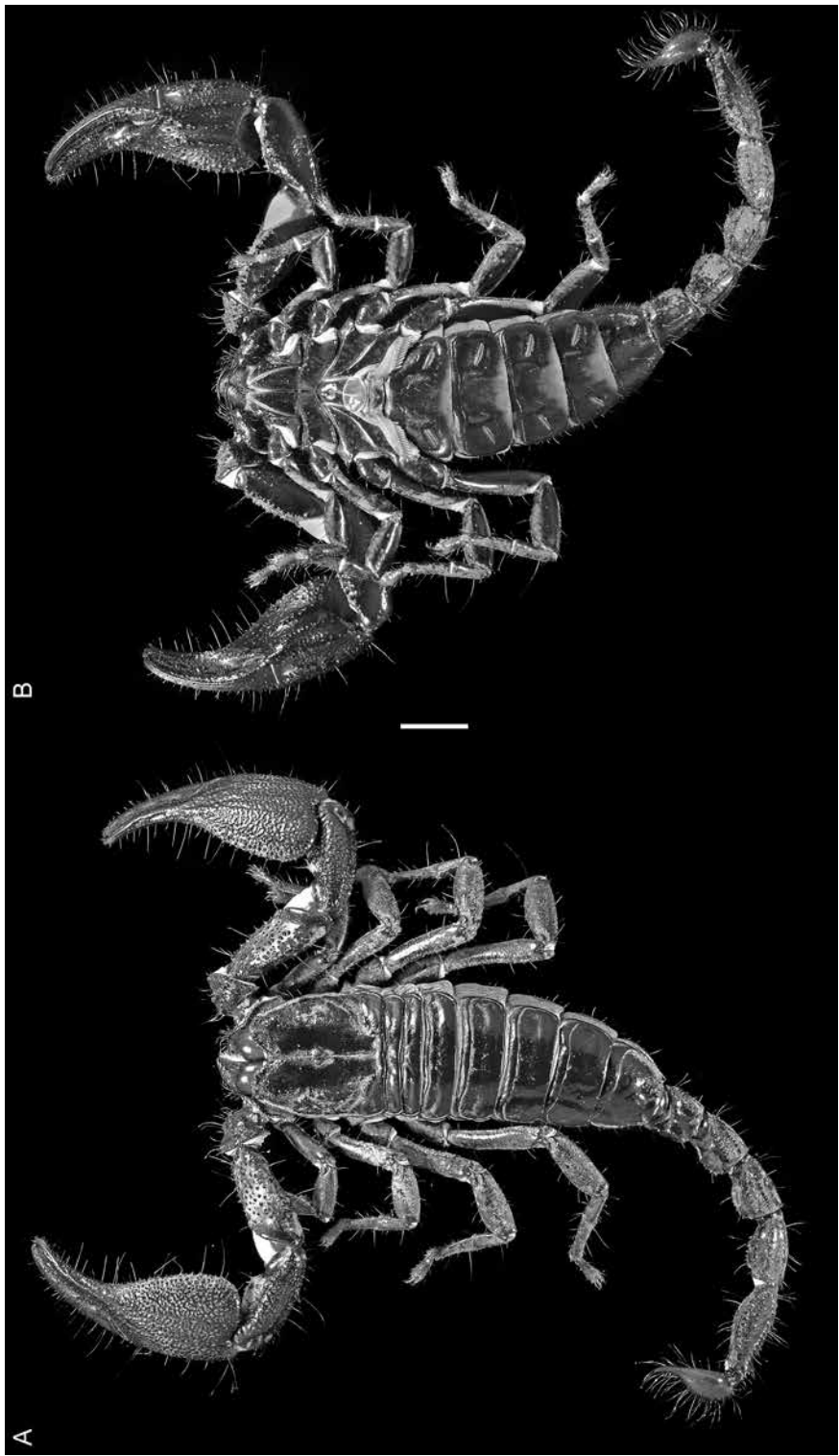


FIGURE 213. *Sahyadrimetrus rugosus* (Couzijn, 1981), comb. nov. et stat. nov., ♀ (AMNH), Chaliyar River, India, habitus: A. dorsal and B. ventral aspects. Scale bar = 10 mm.

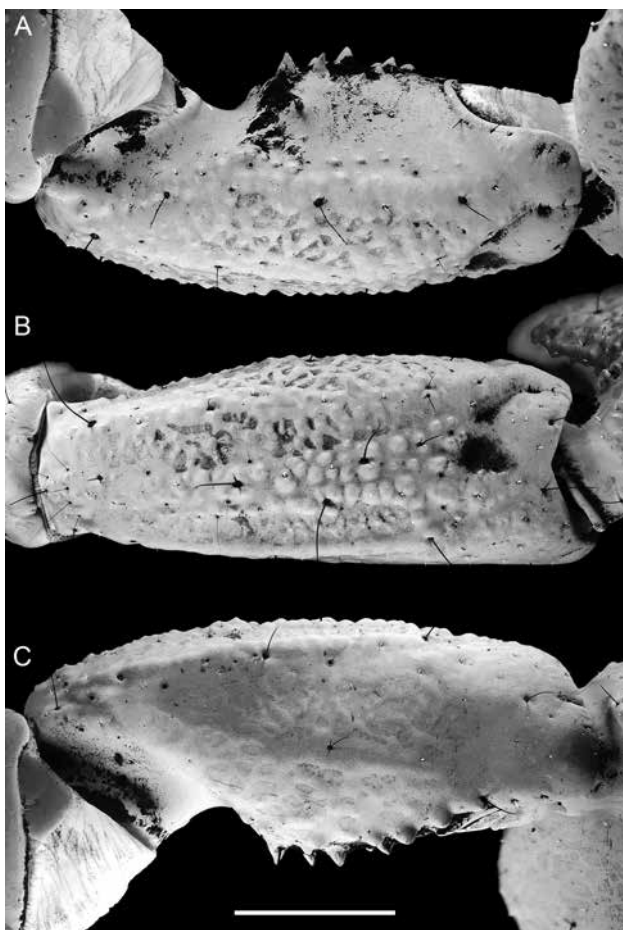


FIGURE 214. *Sahyadrimetrus rugosus* (Couzijn, 1981), comb. nov. et stat. nov., ♀ (AMNH), Chaliyar River, India, pedipalp patella: A. dorsal, B. retrolateral, and C. ventral aspects. Scale bar = 5 mm

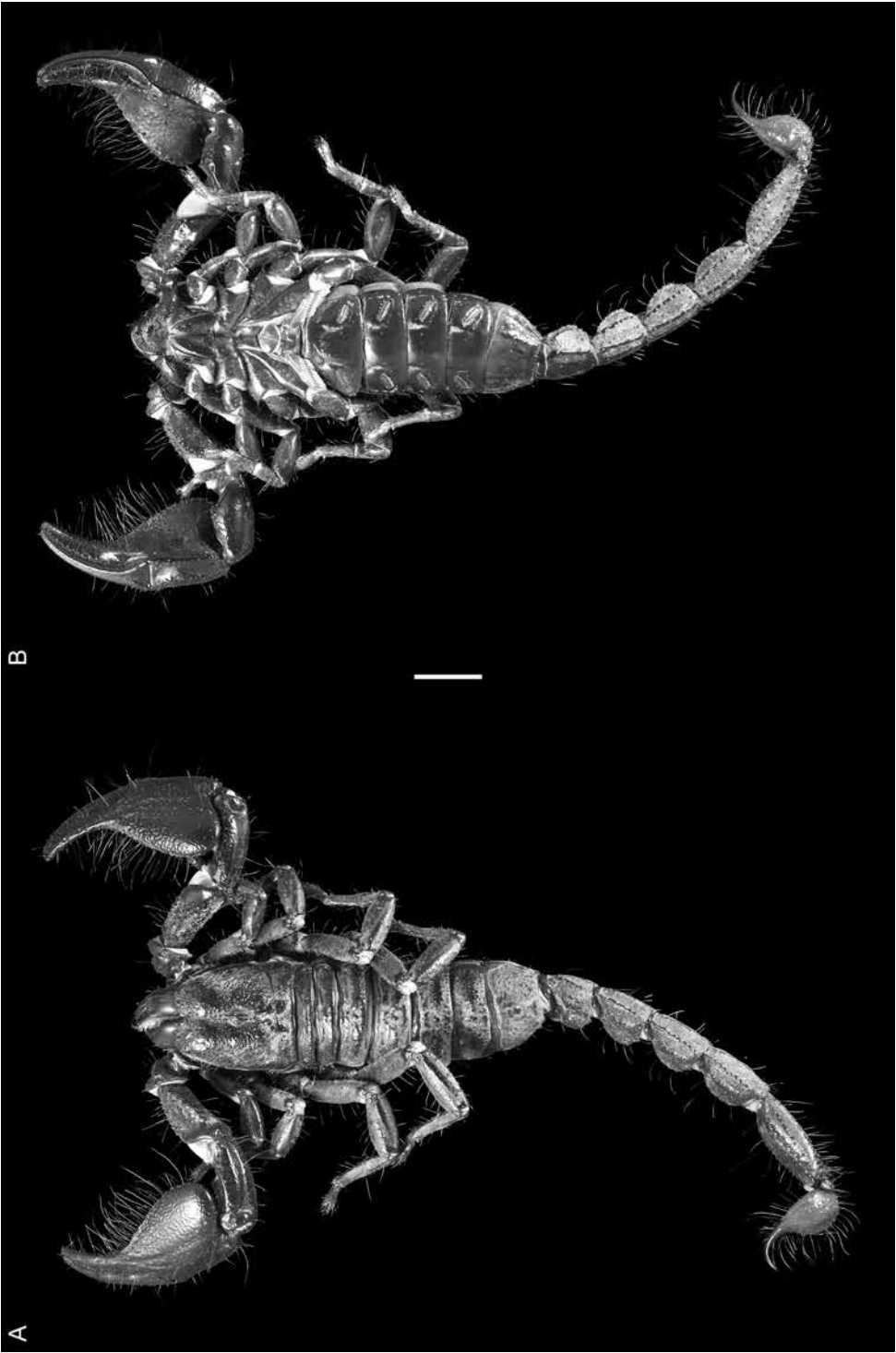
faces, and shape and relatively smooth surfaces of the pedipalp chela manus, pectinal tooth counts (10–12 in *H. rolciki* compared with 7–12 in *S. scaber*), and counts of pro- and retroventral spiniform macrosetae on the telotarsi of legs III and IV, 4/6 in *H. rolciki* and *S. scaber* (Tikader and Bastawade, 1983). Based on the abundant evidence that the types of *H. rolciki* are conspecific with *S. scaber*, the following new synonym is presented: *Heterometrus rolciki* Kovařík, 2004 = *S. scaber*, syn. nov.

Specimens illustrated as *S. scaber* by Tikader and Bastawade (1983: 576, 619–625, figs. 1639–1652) and Kovařík (2009: 107, fig. 256) are misidentifications of *S. kanarensis*.

MATERIAL EXAMINED: **INDIA: Goa:** M. Rousseau, 1 ♂ (MNHN RS 0100). **Karnataka:** *Belagavi Distr.:* Kalsa Waterfall, between Surla and Kankumbi, 15°41'N 74°11'E, 100 m, 28.xi.2006, P. Menon, riverine forest with open grassy patches along rocky gorge of perennial (Kalsa) river, many laterite stones, clayey-loam soil, in shallow burrows (ca. 10 c (*Sahyadri*) m long) under stones, 1 ♀, 5 juv. ♂, 1 juv. ♀ (AMNH), 1 juv. ♀ (AMCC [LP 14023]). *Dakshina Kannada Distr.:* Kalbale, Virajpet–Byndoor Rd, Guddadka, 12°38'N 75°18'E, 259 m, 20.xi.2009, R. Datta, secondary evergreen forest, surrounded by old plantations, on moderate slope, under stone on clayey loam beneath forest canopy, 1 juv. ♂ (AMCC [LP 16771]). *Shimoga Distr.:* Agumbe, 13°31'N 75°05'E, 629 m, 20.xi.2009, R. Datta, evergreen rainforest on plateau, doorkeeping at burrow



FIGURE 215. *Sahyadrimetrus rugosus* (Couzijn, 1981), comb. nov. et stat. nov., ♀ (AMNH), Chaliyar River, India, pedipalp chela: A. retrodorsal, B. ventral, and C. prolateral aspects. Scale bar = 5 mm.



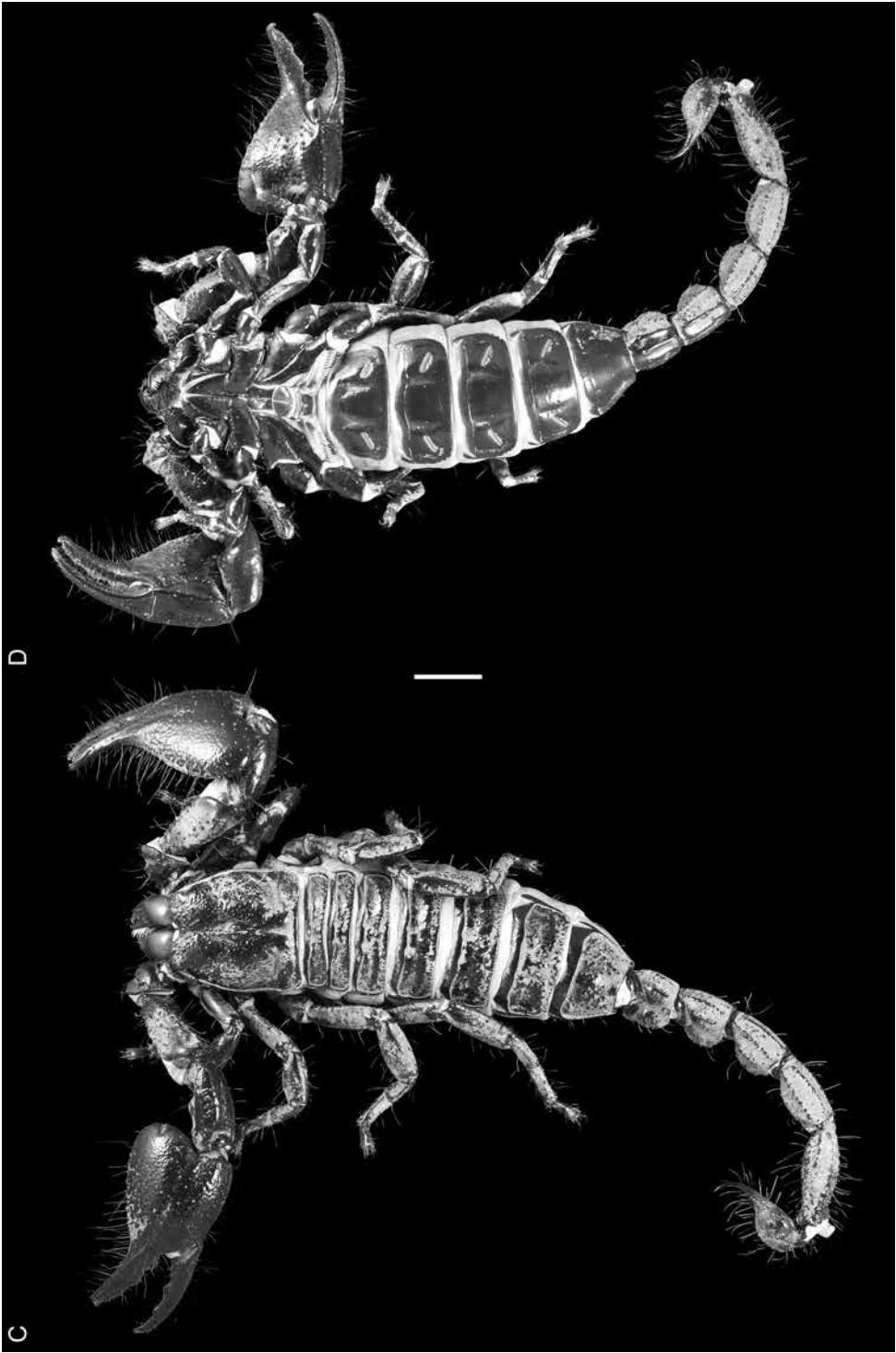


FIGURE 216. *Sahyadrimetrus scaber* (Thorell, 1876), comb. nov., habitus: A, C. dorsal and B, D. ventral aspects. A, B. ♂ (AMNH), Nadpalu, India. C, D. ♀ (AMNH), Agumbe, India. Scale bars = 10 mm.

entrances in clayey-loam soil, on forest floor and along road cuts, most observed in open ground, not under logs/stones, 2 ♀ (AMNH); Jogi Gundi Falls, 13°29'N 75°07'E, 662 m, 21.xi.2009, R. Datta, dense canopy, evergreen rainforest, on clayey loam with rock outcrops, loose and embedded stones, in scrape under stone, 1 juv. ♀ (AMCC [LP 16772]). *Udupi Distr.*: Someshwara, Nadpalu, intersection Sitha River with road to Koodlu Theertha Waterfalls, 13°26'N 75°06'E, 135 m, 27.xi.2006, P. Menon, riverine forest along rocky stream bed near perennial river, sandy-loam soil, in scrape under large stone on dry, rocky riverbed, 1 ♂ (AMNH); Someshwara, Sitha River, Seethanadi, 13°29'N 75°01'E, 68 m, 26.xi.2006, P. Menon, primary, lowland evergreen forest on flat plain near perennial river, forest dry but humid, damp, clayey-loam soil, moderate canopy, sparse understorey, female excavated from burrow, ca. 20 cm deep, in open ground, juv. in shallow burrow under small stone, 1 ♀ (AMNH), 1 juv. ♀ (AMCC [LP 13979]). **Puducherry: Mahé Distr.**: Malabar, Dussumier, 1 ♂ (MNHN RS 0095); Mahé, Malabar [11°42'N 75°32'E], 1903, M. Maindron, 1 ♀ (MNHN RS 3264).

ERRONEOUS RECORDS: INDIA: Puducherry: Puducherry Distr.: Pondichéry [Pondicherry/Puduchcheri/Puducherry, 11°59'N 79°49'E], 1883, Chaper, 1 ♂ (MNHN RS 0099). **Tamil Nadu:** Coimbatore, Pondichéry (Puttuchcheri), 2 ♂ (MNHN RS 0101 [Simon coll. 1647]).

Sahyadrimetrus tikaderi, gen. et sp. nov.

Figures 10, 25E, F, 39E, F, 54I–L, 73F, 74F, 75F, 198, 220–224, tables 1, 3, 5

Heterometrus (Chersonesometrus) kanaraensis:

Bastawade et al., 2004: 44, 48, 56, 58
(misidentification, part).

Heterometrus (Chersonesometrus) barberi:

Sureshan et al., 2007a: 2903, 2906–2908, fig. 1, image 2 (misidentification, part).

Heterometrus (Chersonesometrus) kanarensis:

Sureshan et al., 2007a: 2907, 2908, fig. 2 (misidentification, part); 2007b: 52, 53, photo 5 (misidentification, part).

Heterometrus barberi: Aswathi and Sureshan, 2017: 9847 (misidentification, part).

Heterometrus kanaraensis: Aswathi and Sureshan, 2017: 9847 (misidentification, part).

TYPE MATERIAL: INDIA: Tamil Nadu: Coimbatore Distr.: Holotype ♂, 2 ♀, 6 juv. ♂ paratypes (MNHN RS 3265), Attakatti [10°27'N 76°59'E], 9.vii.1945, Dr. K. Lindberg, sous pierres [under stones]; paratypes: 1 ♂, 1 ♀, 1 subad. ♂, 1 ♀ sinistral pedipalp chela (AMNH), 1 juv. ♀ (AMCC [LP 16766]), Attakatti, 10°27'N 76°59'E, 777–1012 m, 17.xi.2009, R. Datta, evergreen forest on moderate slope with granite outcrops, loose and embedded stones, excavated from burrows (10–40 cm deep) in sandy loam, two in rock crevice; paratypes: 3 ♂, 3 ♀, 2 juv. ♂, 2 juv. ♀ (AMNH), 2 juv. ♂ (AMCC [LP 16764]), 3 juv. ♂, 7 juv. ♀ (AMCC [LP 16767]), Attakatti, ca. 650 m S, 10°26'N 76°59'E, 962 m, 17–18.xi.2009, R. Datta, evergreen forest on steep slope near river with large, rocky granite outcrops, in scrapes or burrows (ca. 30–40 cm deep) beneath large, granite stones under canopy. **Dindigul Distr.**: 1 subad. ♂ paratype (AMCC [LP 16760]), MelPal-lam, ca. 9 km N on Palani Ghat/Perumal Malai/Palani–Kodaikanal Road, 10°21'N 77°34'E, 1133 m, 17.xi.2009, R. Datta, degraded secondary forest on moderate slope with granite outcrops and embedded stones, in scrape (ca. 15 cm long) under large stone, in sandy loam; 1 ♂, 1 subad. ♂ paratypes (MNHN RS 3266), Uslampatti (route a TandiKoudi, Mts. Palni) [Palni Mts., route from Usilampatti to Thandikudi, 10°19'N 77°39'E], 14.viii.1945, Dr. K. Lindberg, sous pierres; 3 juv. ♂ paratypes (MNHN RS 3142), Monts Palni, pente au dessus de la riviere Tanaikadu [Palni Mts., slope above Tanaikadu River, Pannaikadu, 10°17'N 77°38'E], 1200 m, viii.1943, Dr. K. Lindberg.

ETYMOLOGY: The specific epithet is a patronym honoring the Indian arachnologist Binoy Krishna Tikader (1928–1994), formerly of the Zoological Survey of India, Kolkata, and widely known as B.K. Tikader, who contributed significantly to the knowledge of Indian scorpions (e.g., Tikader and Bastawade, 1983) and other arachnids over the course of his career.

DIAGNOSIS: *Sahyadrimetrus tikaderi* may be separated from other species of *Sahyadrimetrus* as follows. The carapace is markedly dorsoventrally compressed, the lateral surfaces sloping gently (fig. 25E, F), in *S. tikaderi* but vaulted,

the lateral surfaces sloping steeply in *S. scaber* to very steeply in *S. mathewi*. The carapace mediolateral margins diverge or converge slightly posteriorly (at the posterolateral sulci) in *S. tikaderi* but converge markedly posteriorly (at the posterolateral sulci) in *S. kanarensis*, *S. mathewi*, and *S. scaber*. The frontal lobes and medial region of the carapace interocular surface are granular with smooth areas in the male and female (fig. 25E, F) of *S. tikaderi* whereas the interocular surface is granular along the median longitudinal and anterior bifurcated sulci in the male of *S. rugosus*, and the interocular surface is entirely, uniformly granular in the male and female of *S. mathewi*. The carapace posterolateral surfaces of the female (fig. 25F) are smooth or nearly so in *S. tikaderi* but granular in *S. mathewi* and *S. scaber*. The pedipalps of the adult male are short, with femur length : posterior carapace width ratio (FL:PCW) < 0.77 and femur length : carapace length ratio (FL:CL) < 0.74 (fig. 220) in *S. tikaderi* but long, with FL:PCW $\geq$ 0.80 and FL:CL $\geq$ 0.76 in *S. mathewi* and *S. rugosus*. The pedipalp patella dorsomedian carina of the female is absent or obsolete in *S. tikaderi* but entirely to predominantly granular in *S. rugosus*. The patella retrodorsal carina of the female is absent or obsolete, and the retromedian carinae present and granular in *S. tikaderi* whereas the retrodorsal carina is present, as strongly developed as or more strongly developed than the retromedian carinae, which are absent or obsolete in *S. kanarensis*, *S. mathewi*, and *S. scaber*. The patella dorsal, retrodorsal, and retroventral intercarinal surfaces of the female are smooth or nearly so in *S. tikaderi* but granular in *S. rugosus*. The maximum distance between the dorsomedian and dorsal secondary carinae (DMC–DSC) of the pedipalp chela manus is less than the maximum distance between the dorsal secondary and digital carinae (DSC–DC) in the male (fig. 223) of *S. tikaderi* but similar to the DSC–DC in the male of *S. kanarensis* and *S. scaber*. The chela manus dorsal surface of the female (fig. 224) is smooth or

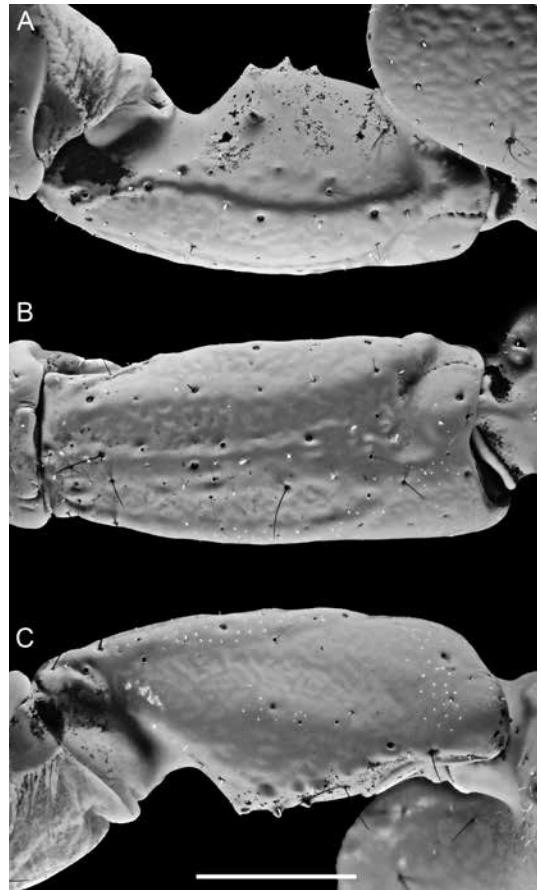


FIGURE 217. *Sahyadrimetrus scaber* (Thorell, 1876), comb. nov., ♂ (AMNH), Nadpalu, India, pedipalp patella: A. dorsal, B. retrolateral, and C. ventral aspects. Scale bar = 5 mm.

nearly so in *S. tikaderi* but finely to coarsely granular or granulo-reticulate in all the other species except *S. kanarensis*. The chela manus retrolateral intercarinal surfaces are smooth or nearly so in the male (fig. 223) and granular in the female (fig. 224) of *S. tikaderi*, but granular in the male of *S. mathewi* and *S. scaber*, and smooth or nearly so in the female of *S. kanarensis*, *S. mathewi*, and *S. scaber*. Macroseta *st* is spiniform on the retroventral surfaces of the basitarsi of legs I–III (fig. 54I–L) in *S. tikaderi* but setiform on the retroventral surfaces of the basitarsi of legs I–III in *S. kanarensis* and legs

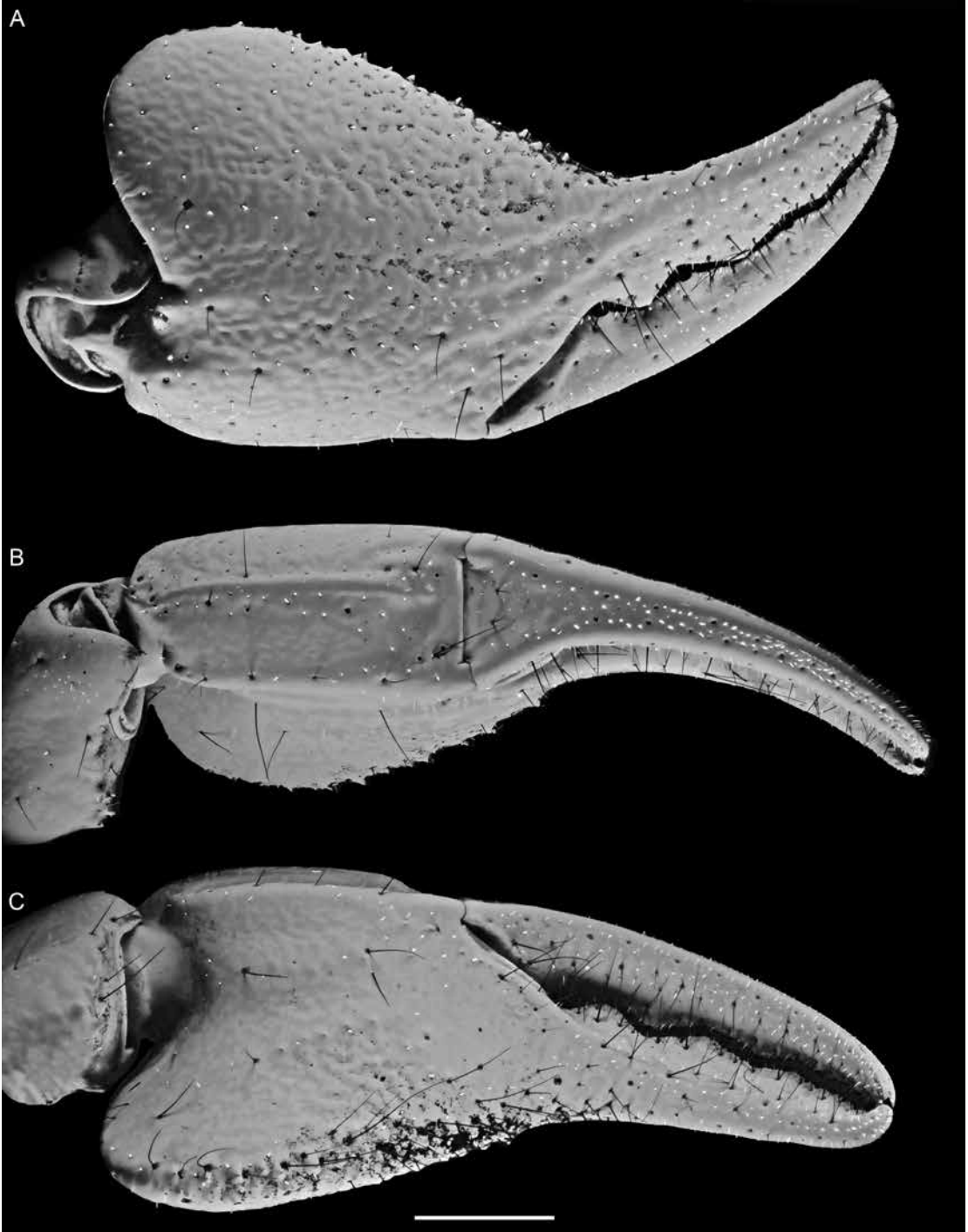


FIGURE 218. *Sahyadrimetrus scaber* (Thorell, 1876), comb. nov., ♂ (AMNH), Nadpalu, India, pedipalp chela: **A.** retrodorsal, **B.** ventral, and **C.** prolateral aspects. Scale bar = 5 mm.



FIGURE 219. *Sahyadrimetrus scaber* (Thorell, 1876), comb. nov., ♀ (AMNH), Agumbe, India, pedipalp chela: A. retrodorsal, B. ventral, and C. prolateral aspects. Scale bar = 5 mm.

I and II in *S. mathewi* and *S. scaber*; *st* on the proventral surface of the basitarsus of leg III is setiform in *S. tikaderi* but spiniform in *S. kana-rensensis*. The mesial surfaces of mesosomal tergites I–VI are smooth in the male and the lateral surfaces granular in the female of *S. tikaderi*, whereas the mesial surfaces are granular in the male of *S. mathewi* and *S. scaber*, and the lateral surfaces smooth in the female of *S. barberi* and *S. rugosus*. The ventral intercarinal surfaces of metasomal segment IV are granular (fig. 75F) in *S. tikaderi* but smooth in all other species. The dorsolateral carinae of metasomal segment V are distinct and continuous (fig. 73F) in *S. tikaderi* but obsolete and discontinuous to absent in *S. barberi*.

DESCRIPTION: The following description is based on the holotype and paratypes. Meristic data are presented in table 3 and measurements in table 5.

Total length: Adult medium sized, maximum length, measured from anterior margin of carapace to tip of aculeus, 107 mm (102–112 mm, $n = 2$) (♂), 108 mm (107–108 mm, $n = 2$) (♀).

Color: Chelicerae, dorsal surfaces bicolored, lightly infuscate prodorsal half of manus paler than densely infuscate retrodorsal half of manus and fingers; manus slightly paler than carapace interocular surface. Carapace, pedipalps, tergites, and metasoma entirely infuscate, uniformly black or greenish black. Sternites III–VII mostly or entirely infuscate, dark olive brown to black, becoming darker posteriorly. Coxosternal region infuscate, brownish black, maxillary lobes darker. Legs infuscate, uniformly black, similar to carapace, pedipalps, tergites, and metasoma (figs. 220, 221). Genital opercula and pectines uniformly pale cream. Metasomal segments I–V entirely infuscate, similar to one another; carinae infuscate, darker than intercarinal surfaces; dorsal intercarinal surfaces similar to tergites; ventral intercarinal surfaces similar to or darker than sternites. Telson vesicle immaculate, dark yellowish to reddish, paler than metasomal segment V; aculeus black.

Chelicerae: Movable finger prodistal (DI) and retrodistal (DE) teeth unequal, with DE tooth considerably smaller than DI tooth, aligned longitudinally and not opposable. Fingers and manus, proventral surfaces with long, dense vestiture of macrosetae. Coxae, prodorsal surfaces without stridulatory setae (scaphotrix); promedian surfaces without chemoreceptive lamelliform setae (trichocopae).

Carapace: Carapace markedly dorsoventrally compressed, lateral surfaces sloping gently. Anterior margin concave, frontal lobes uneven, sloping medially toward deep median notch, without median projection or median depression (fig. 25E, F). Anterolateral margins converging gradually anteriorly, without distinct notch adjacent to posterior lateral ocelli; mediolateral margins diverging or converging slightly posteriorly (at posterolateral sulci). Anterior width of posterior width, 64% (59%–69%, $n = 2$) (♂), 65% (64%–65%, $n = 2$) (♀); posterior width of length, 92% (89%–95%, $n = 2$) (♂), 102% (101%–102%, $n = 2$) (♀). Three pairs of lateral ocelli (MLMa, PLMa, PDMi), all similar in size, two anterior pairs situated anteriorly, well separated from posterior pair, situated laterally. Median ocelli slightly larger than lateral ocelli, distance between ocelli greater than or equal to width of ocellus; median ocular tubercle situated anteromedially, distance from anterior carapace margin, 53% (52%–53%, $n = 2$) (♂), 52% (51%–52%, $n = 2$) (♀). Median longitudinal sulcus narrow, suturiform; continuous from median notch to interocular sulcus; anteriorly furcated; without anterocular depression. Anterior furcated sulci diverging broadly from anterior edge of median longitudinal sulcus. Median ocular tubercle raised, superciliary carinae higher than ocelli, extended anteriorly, subparallel. Interocular sulcus present. Circumocular depressions completely encircling median ocular tubercle, converging anteriorly. Posteromedian and posteromarginal sulci deep. Paired mediolateral and posterolateral sulci shallow. Median longitudinal suture continuous from median notch to median ocular tubercle, equally strong along entire

length; not extending to anterior margin of carapace, terminating at or posterior to median notch. Anterior furcated, anterocular, interocular, and posterior sutures absent. Frontal lobes and medial region of interocular surface coarsely granular with smooth areas (fig. 25E, F); anterolateral surfaces uniformly coarsely granular; mediolateral surfaces uniformly finely granular; posterolateral surfaces uniformly finely granular (δ) or smooth (φ); posteromedian surface smooth.

Pedipalps: Pedipalp short, pedipalp femur length : posterior carapace width ratio (FL:PCW) < 0.77, femur length : carapace length ratio (FL:CL) < 0.74. Femur width of length, 39% (36%–41%, $n = 2$) (δ), 45% ($n = 2$) (φ). Retro-dorsal carina complete, granular, similar to or more strongly developed than prodorsal carina. Dorsal secondary carina obsolete, comprising few isolated granules. Dorsomedian carina vestigial, reduced to prominent granule demarcated by conspicuous macroseta. Prodorsal carina complete, granular. Promedian carina complete, comprising row of spiniform or subspiniform granules (several demarcated by conspicuous macrosetae), oriented diagonally between prodorsal and proventral carinae. Proventral carina complete, granular, as strongly developed as or more strongly developed than retroventral carina. Ventromedian and secondary accessory carinae absent. Retroventral carina extending partly or entirely to distal edge of segment. Retromedian carinae absent, indicated only by macrosetal rows. Dorsal intercarinal surfaces finely granular; other surfaces smooth. Patella width of length, 39% ($n = 2$) (δ), 51% (50%–51%, $n = 2$) (φ). Dorsal surface convex, axis of dorsomedian carina dorsal to axis of retrodorsal carina. Dorsomedian carina obsolete, costate (fig. 222). Retrodorsal carina obsolete, less strongly developed than granular retromedian carinae. Retroventral carina obsolete, costate. Promedian carina vestigial, reduced to subspiniform granules, demarcated by conspicuous macroseta (δ) or absent (φ); promedian process absent. Other carinae absent. Intercarinal sur-

faces smooth. Chela short, narrow (figs. 223, 224); manus height of width, 99% (93%–104%, $n = 2$) (δ), 82% (79%–84%, $n = 2$) (φ); manus length along retroventral carina of manus width, 151% (135%–166%, $n = 2$) (δ), 102% (94%–110%, $n = 2$) (φ); manus length along retroventral carina of movable finger length, 83% (77%–88%, $n = 2$) (δ), 76% ($n = 2$) (φ). Chela moderately (δ) to sparsely (φ) setose. Manus dorsal surface (between dorsomedian and digital carinae) curved, i.e., slightly to markedly convex; proximal margin (lobe) of dorsal surface moderately curved and aligned with proximal margin of retrolateral surface. Dorsomedian carina obsolete, costate on fixed finger and comprising irregular row of spiniform granules, becoming obsolete proximally, on manus. Dorsal secondary, subdigital, digital, and retromedian carinae absent. Maximum distance between dorsomedian carina and setal row demarcating dorsal secondary carina (DMC–DSC) less than (δ) or similar to (φ) maximum distance between setal rows demarcating dorsal secondary and digital carinae (DSC–DC). Retrolateral secondary and secondary accessory carinae vestigial, proximal to condyle of movable finger. Retroventral carina distinct, costate. Ventromedian carina obsolete, costate. Proventral and promedian carinae similarly developed, each comprising row of spiniform granules and associated macrosetae. Prodorsal carina comprising irregular row of spiniform granules and associated macrosetae. Distance between dorsomedian and promedian carinae (DMC–PMC) slightly to markedly greater than distance between promedian and proventral carinae (PMC–PVC). Manus, dorsal and retrolateral intercarinal surfaces finely and shallowly granulo-reticulate (δ), except for smooth depression at base of fixed finger, or nearly smooth (φ); ventral intercarinal surface smooth; prolateral intercarinal surfaces smooth, except for scattered spiniform granules dorsally and distally. Manus ventral surface flat, axes of retroventral and ventromedian carinae in approximately same plane. Fixed and movable fingers,

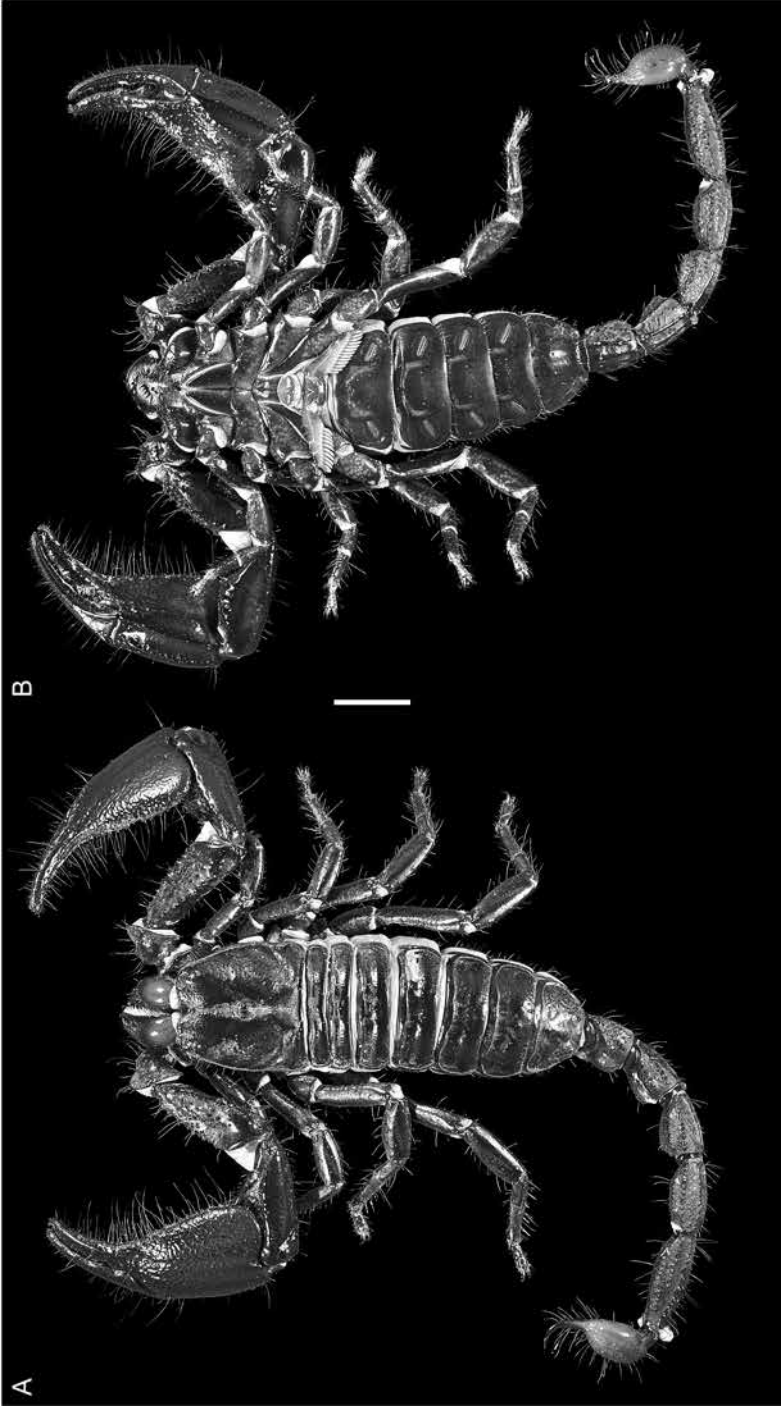


FIGURE 220. *Sahyadrimetrus tikaderi*, gen. et sp. nov., paratype ♂ (AMNH), Attakatti, India, habitus: **A**, dorsal and **B**, ventral aspects. Scale bar = 10 mm.

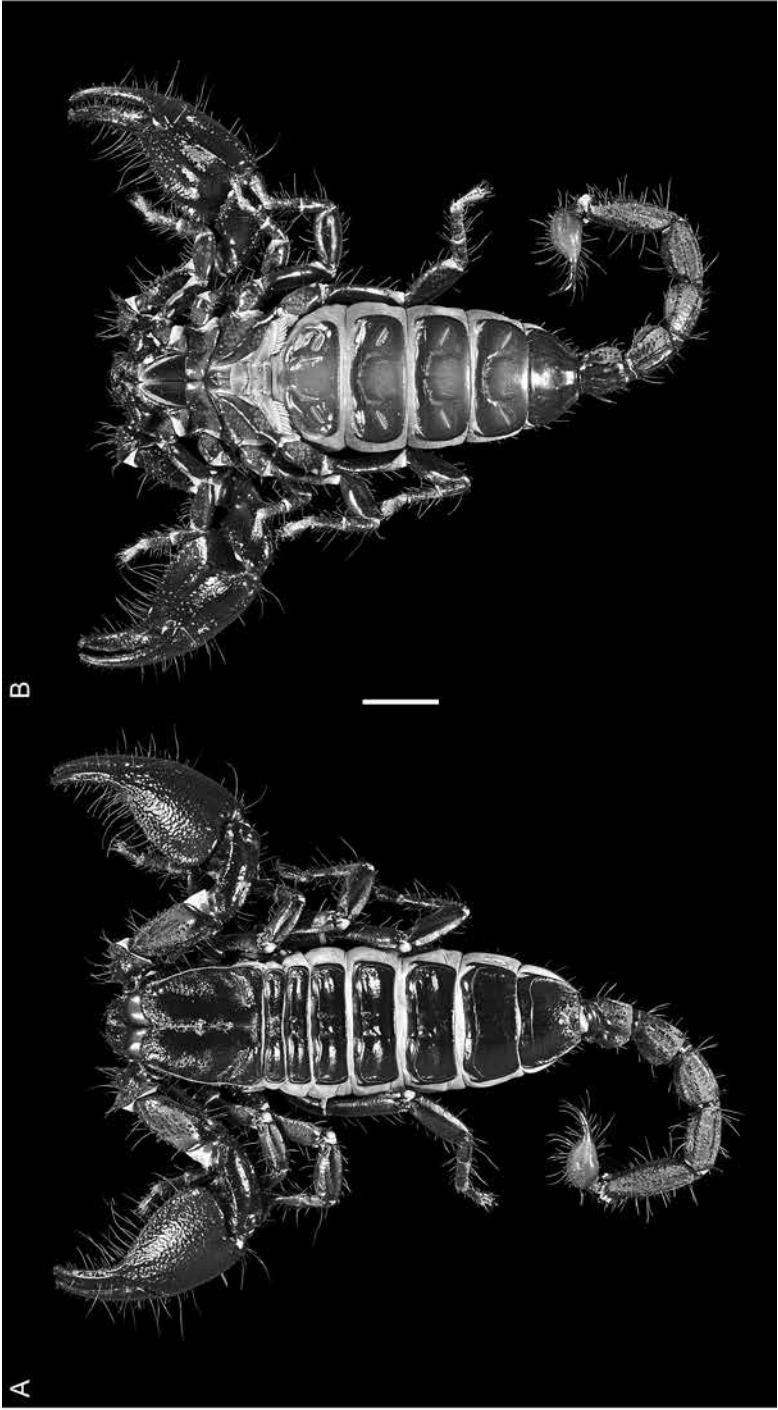


FIGURE 221. *Salyadrinetrus tikaderi*, gen. et sp. nov., paratype ♀ (AMNH), Attakatti, India, habitus: **A.** dorsal and **B.** ventral aspects. Scale bar = 10 mm.

intercarinal surfaces finely granular; median denticle rows each with six enlarged retrolateral denticles (including terminal denticle), proximal three situated on lobes; first (proximal) lobe of fixed finger and second lobe of movable finger larger than others, with correspondingly deeper notches in movable and fixed fingers, respectively; terminal denticles of fingers interlocking unevenly when closed, movable finger displaced retrolaterally; distinct notch near tip of fixed finger to accommodate terminal denticle of movable finger.

Trichobothria: Orthobothriotaxic, Type C, with the following segment totals ($n = 8$): femur, 3 (1 d , 1 i , 1 e); patella, 19 (2 d , 1 i , 3 v , 13 e , comprising 3 et , 1 est , 2 em , 2 esb , 5 eb); chela, 26 (manus, 16, comprising 2 D , 10 E , 4 V ; fixed finger, 10, comprising 4 d , 4 e , 2 i). Total count of trichobothria per pedipalp: 48. Femur, i situated on dorsal surface. Patella, d_2 situated on internal surface, slightly closer to d_1 than to i ; distance v_2-v_3 greater than half distance v_1-v_2 . Chela, distance $et-est$ ca. half distance $est-esb$; distance $est-esb$ ca. half distance $esb-eb$; est aligned with dst ; V_3 situated in proximal third of manus, closer to V_4 than V_2 .

Legs: First pair of maxillary lobes (coxapophyses) tapering anteriorly, longer than and encircling second pair. Stridulatory organs, comprising "rasp" (granular tubercles) and "scraper" (stridulatory setae or scaphotrix), present on opposing surfaces of coxae of first pair of legs and pedipalps, respectively. Legs I–IV acarinate, except femora, with distinct pro- and retrolateral surfaces demarcated by partial to complete, granular proventral carinae. Femora, patellae, and tibiae, pro- and retrolateral surfaces each with scattered setiform macrosetae. Tibiae, prolateral surfaces, without spiniform macrosetae; I and II, retrolateral surfaces, each with two spiniform (t , st) macrosetae; III and IV, retrolateral surfaces, without spiniform macrosetae. Basitarsi I–IV, slightly dorsoventrally compressed; retrolateral margins similar, unmodified, rounded; prolateral pedal spurs present (fig. 54I–L); retrolateral pedal spurs absent. Basitarsi, pro- and retrolat-

eral surfaces, each with scattered long and short setiform macrosetae, and spiniform macrosetae, more numerous on I and II than III and IV. Basitarsi, spiniform macrosetae, I, retrolateral: t , sb ; retroventral: t , st , sb ; proventral: t , st ; II, retrolateral: t , sb ; retroventral: t , st , sb ; proventral: t , st ; III, retrolateral: t , sb ; retroventral: t , st , sb ; proventral: t ; prolateral: t , st ; IV, retrolateral: t ; retroventral: t ; proventral: t , st ; prolateral: t , st . Telotarsi I–IV short, stout and distally broadened in dorsal and lateral views. Laterodistal lobes rounded. Dorsomedian lobes approximately equal to laterodistal lobes; each terminating in single setiform macroseta. Telotarsi, pro- and retrolateral surfaces, each with long and short, scattered macrosetae, not arranged in definite row. Telotarsi each with pro- and retroventral rows of spiniform macrosetae, two inserted on laterodistal lobes; counts in pro- and retroventral rows similar on I and II, and on III and IV ($n = 8$): I, proventral: 3 (3 or 4), retroventral: 6 (5 or 6); II, 4 (3 or 4), 6; III and IV, 4, 6. Telotarsal ungues short, curved, equal to subequal; pseudonychium (dactyl) reduced, rounded or acuminate.

Sternum: Shape subpentagonal (fig. 39E, F). Median longitudinal sulcus shallow anteriorly, deep and narrow posteriorly.

Genital operculum: Genital opercula suboval, completely divided longitudinally, partially overlapping, genital papillae present (σ) (fig. 39E); subcordate, fused, genital papillae absent (φ) (fig. 39F).

Hemispermaphore: Lamelliform, with complex, folded capsule and accessory distal lobe protruding between articular suture and distal lobe (hook). Distal lamina with distal crest truncate, unfolded.

Pectines: Distal edge reaching distal edge of coxa IV (fig. 39E, F). First proximal median lamella (scape) of each pecten with mesial margin angular, approximately 90° (σ) or obtusely angular, greater than 90° but less than 180° (φ). Pectinal teeth straight and elongate (σ) or shorter and curved (φ), present along entire posterior margin; sinistral/dextral tooth count,



FIGURE 222. *Sahyadrimetrus tikaderi*, gen. et sp. nov., paratype ♂ (MNHN RS 3266), pedipalp patella: A. dorsal, B. retrolateral, and C. ventral aspects. Scale bar = 5 mm.

11 or 12/11 or 12 ($n = 2$) (♂), 11/11 ($n = 2$) (♀). Fulcra smooth proximally but densely setose (microsetae only) distally.

Mesosoma: Tergites each with shallow pair of submedian depressions, without obsolete median carina. Pretergites smooth and glabrous. Posttergites smooth and glabrous medially, unevenly finely and coarsely granular to predominantly coarsely granular laterally. Sternites IV–VI, each with paired longitudinal depressions prolateral to spiracles, absent on VII. Surface, sternites III–VII, smooth; VII with pair of weakly developed, costate ventrolateral carinae only, without posteromarginal carina. Sternite VII, length of width, 63% (62%–64%, $n = 2$) (♂), 61% (59%–62%, $n = 2$) (♀).

Metasoma and telson: Metasomal segments I–V progressively increasing in length, decreasing in width; segment V, width of segment I, width, 72% (71%–73%, $n = 2$) (♂), 70% (69%–71%, $n = 2$) (♀). Metasoma fairly robust, width of length, segment I, 91% (87%–94%, $n = 2$) (♂), 92% (88%–96%, $n = 2$) (♀); II, 73% (70%–75%) (♂), 78% (73%–83%) (♀); III, 67% (63%–70%) (♂), 68% (65%–71%) (♀); IV, 53% (52%–54%) (♂), 54% (50%–58%) (♀); V, 38% (37%–38%) (♂), 37% (36%–37%) (♀). Telson vesicle, width of metasomal segment V, width, 104% (103%–105%, $n = 2$) (♂), 96% (94%–98%, $n = 2$) (♀); elongate, height of length, 57% ($n = 2$) (♂), 54% (53%–54%, $n = 2$) (♀); dorsal surface flat; ventral surface evenly curved. Aculeus relatively long, gently



FIGURE 223. *Sahyadrimetrus tikaderi*, gen. et sp. nov., paratype ♂ (MNHN RS 3266), pedipalp chela: A. retrodorsal, B. ventral, and C. prolateral aspects. Scale bar = 5 mm.



FIGURE 224. *Sahyadrimetrus tikaderi*, gen. et sp. nov., paratype ♀ (MNHN RS 3265), pedipalp chela: A. retrodorsal, B. ventral, and C. prolateral aspects. Scale bar = 5 mm.

curved, length of vesicle length, 70% (69%–71%, $n = 2$) (♂), 59% (57%–61%, $n = 2$) (♀). Length metasoma and telson, of total length, 55% (53%–56%, $n = 2$) (♂), 55% (54%–55%, $n = 2$) (♀). Dorsosubmedian carinae, segments I–IV, distinct, complete, granular or costate-granular, posterior spiniform granules obsolete (fig. 73F); V, vestigial. Dorsolateral carinae, segments I–V, distinct, complete, costate-granular on I–IV, costate-granular to granular on V. Median lateral carinae, segment I, incomplete, reduced to granular row in posterior half, diagonally oriented between dorsolateral and ventrolateral carinae (fig. 74F); II–IV, vestigial, each reduced to posterior granule; V, incomplete, granular row, restricted to anterior two-thirds. Ventrolateral and ventrosubmedian carinae, segments I–IV, distinct, complete, costate on I–III, granular or costate-granular on IV, more strongly developed on III and IV than on I and II (fig. 75F). Ventrolateral carinae, segment V, distinct, complete, comprising spiniform granules, diverging posteriorly, terminal granule slightly larger than preceding granules. Ventrosubmedian carinae, segment V, vestigial, each reduced to one or two isolated spiniform granules, demarcated by conspicuous macrosetae. Ventromedian carina, segment V comprising single row of spiniform granules, unmodified posteriorly. Anal arch, segment V, dorsal carina, costate; ventral carina comprising subspiniform granules. Dorsal intercarinal surfaces, segments I–IV, granular, V, smooth. Lateral intercarinal surfaces, segments I, smooth, II–V, granular. Ventral intercarinal surfaces, segments I–III, smooth, IV and V, granular. Ventral surface, lateral aspect, segment IV, shallowly convex. Telson vesicle, dorsal and lateral surfaces smooth; ventral surface with four longitudinal carinae, each comprising spiniform granules.

DISTRIBUTION: This species is endemic to India (fig. 198, table 1) and recorded only from the state of Tamil Nadu. It appears to occur at higher elevations than *S. mathewi*, which inhabits the coastal plain, and is separated from *S. rugosus*, occurring to the north, by the Palakkad (Palghat) Gap and from *S. barberi*, to the south, by the Shencottah Gap.

ECOLOGY: *Sahyadrimetrus tikaderi* inhabits primary montane rainforest in the Western Ghats (Sahyadri) of southern India, at elevations ranging from 775–1200 m above sea level. This species is fossorial and pelophilous, constructing shallow, single-occupant burrows or scrapes, ca. 10–40 cm deep, in sandy-loam soil, under stones, but also inhabits rock crevices (Bastawade et al., 2005; Sureshan et al., 2007b). This species occurs in sympatry with the buthids, *Isometrus sankeriensis*, *Lychas albimanus* Henderson, 1919, and *Iomachus punctulatus* Pocock, 1897.

Srilankametrus Couzijn, 1981,
stat. nov. et stat. rev.

Figures 4, 7H, 8B, G, I, 9H, 10, 27, 28, 41, 42, 56, 57, 76–78, 198, 199, 225–251, tables 1, 3, 5

Heterometrus (*Chersonesometrus*): Couzijn, 1981: 133, 170, 192, fig. 58 (part); Tikader and Bastawade, 1983: 573 (part); Bastawade, 2004: 290 (part); Bastawade et al., 2004: 48 (part).

Heterometrus (*Srilankametrus*) Couzijn, 1981: 80, 82, 120, 125, 170, 172, 174, 180, 181, 183, 184, 186–188, 191, table 14, figs. 21, 60, 66a, 68–70, type species by original designation: *Scorpio indus* DeGeer, 1778 [= *Srilankametrus indus* (DeGeer, 1778)]; Tikader and Bastawade, 1983: 519, 544; Biswas, 1984: 320; Francke, 1985: 8, 18; Fet, 2000: 446; Prendini, 2000a: 44; Prendini et al., 2003: 222, 252, appendix 1; Bastawade et al., 2004: 48; Kovařík, 2004: 1.

Heterometrus: Kovařík, 2004: 1, 2, 49, 51, table 2 (part); 2009: 34, 35, table 1 (part); Kovařík et al., 2016: 96, 100, 115 (part); Rossi, 2016a: 6–9, 15, 19, 20, 25 (part); Aswathi and Sureshan, 2017: 9847 (part); Kovařík et al., 2019a: 1, 9, 12, fig. 53 (part).

DIAGNOSIS: Species of *Srilankametrus* may be separated from other Asian scorpionid genera as follows. The carapace is vaulted, the lateral sur-

faces sloping steeply (fig. 27) in all except three species of *Srilankametrus*, *S. indus*, *S. pococki*, and *S. serratus*, in which the carapace is slightly to markedly dorsoventrally compressed, the lateral surfaces sloping gently (fig. 28), as in all except two species of *Deccanometrus*, *D. latimanus* and *D. xanthopus*, all except two species of *Sahyadrimetrus*, *S. mathewi* and *S. scaber*, and all except three species of *Chersonesometrus*, *C. fulvipes*, *C. madraspatensis*, and *C. shivashankari*. The carapace anterior margin is straight, with the frontal lobes evenly rounded or truncate (figs. 27, 28) in *Srilankametrus*, whereas the anterior margin is concave, with the frontal lobes uneven and sloping medially in *Heterometrus*, *Javanimetrus*, *Sahyadrimetrus*, all except two species of *Deccanometrus*, *D. latimanus* and *D. xanthopus*, and some species of *Chersonesometrus*. The carapace anterolateral margins are subparallel anteriorly in *Srilankametrus* but converge gradually anteriorly in all other genera except *Javanimetrus*; the mediolateral margins diverge or converge slightly posteriorly (at the posterolateral sulci) in *Srilankametrus*, but converge markedly posteriorly (at the posterolateral sulci) in *Gigantometrus*, *Heterometrus* and three species of *Sahyadrimetrus*, *S. kanarensis*, *S. mathewi*, and *S. scaber*. The carapace rostrolateral margin is entire in *Srilankametrus* but distinctly incised adjacent to the posterior lateral ocelli in *Heterometrus*. Anterocular extensions of the superciliary carinae are absent in *Srilankametrus* but present in the other genera. The median ocelli are relatively small, the distance between them equal to or greater than the width of an ocellus in *Srilankametrus* but relatively large, the distance between them less than the width of an ocellus in *Heterometrus*; the median ocular tubercle is situated anteromedially to medially, the distance from carapace anterior margin : carapace length (CAM:CL) 0.40–0.50 in *Srilankametrus*, but posteromedially, CAM:CL 0.51–0.62 in *Chersonesometrus*. The interocular suture is present in all species of *Srilankametrus* except *S. indus* and *S. pococki* but absent in *Heterometrus*, *Javanimetrus*, *Sahyadrimetrus*, and one species of *Deccanometrus*. The carapace posterior sutures are present,

extending past the median ocular tubercle, and connected anteriorly to the posterior bifurcations of the interocular suture, in all except two species of *Srilankametrus*, *S. indus* and *S. pococki*, in which the posterior sutures are absent, as in *Javanimetrus* and *Sahyadrimetrus*. The frontal lobes and medial region of the carapace interocular surface are entirely smooth (figs. 27C–F, 28) in all species of *Srilankametrus* except *S. caesar*, in which the interocular surface is mostly to entirely granular (fig. 27A, B), as in *Gigantometrus*, *Javanimetrus*, and *Sahyadrimetrus*. The cheliceral movable finger prodistal (DI) and retrodistal (DE) teeth are unequal, with the DE tooth considerably smaller than the DI tooth, aligned longitudinally and not opposable in *Srilankametrus*, but opposable, i.e., forming a bicuspid, in two species of *Deccanometrus*, *D. liurus* and *D. ubicki*, and subequal, with the DE tooth only slightly smaller than the DI tooth, and opposable in *Heterometrus* and some species of *Chersonesometrus*. The pedipalp patella dorsomedian carina of the female is absent or obsolete (fig. 245) in all species of *Srilankametrus* except *S. caesar*, in which the carina is predominantly granular or costate, as in *Chersonesometrus*, *Gigantometrus*, and all except three species of *Deccanometrus*, *D. latimanus*, *D. liurus*, and *D. ubicki*. The patella retromedian carinae of the female are absent or obsolete in all except two species of *Srilankametrus*, *S. gravimanus* and *S. yaleensis*, in which the carinae are granular or costate as in *Chersonesometrus*, three species of *Deccanometrus*, *D. bengalensis*, *D. obscurus*, and *D. phipsoni* and three species of *Sahyadrimetrus*, *S. barberi*, *S. rugosus*, and *S. tika-deri*. The prominent spiniform granule of the patella proventral carina is absent (figs. 227, 231, 235, 240, 245, 247, 249) in *Srilankametrus* but present in *Heterometrus*. The patella dorsal, retrodorsal, and retroventral intercarinal surfaces of the female are smooth or nearly so in *Srilankametrus* but granular in all species of *Chersonesometrus* except *C. nathanorum*. The pedipalp chela of the adult male is sparsely setose (figs. 228, 232, 233, 236, 248, 250) in all species of *Srilankametrus* except *S. indus*, in which the chela is moderately

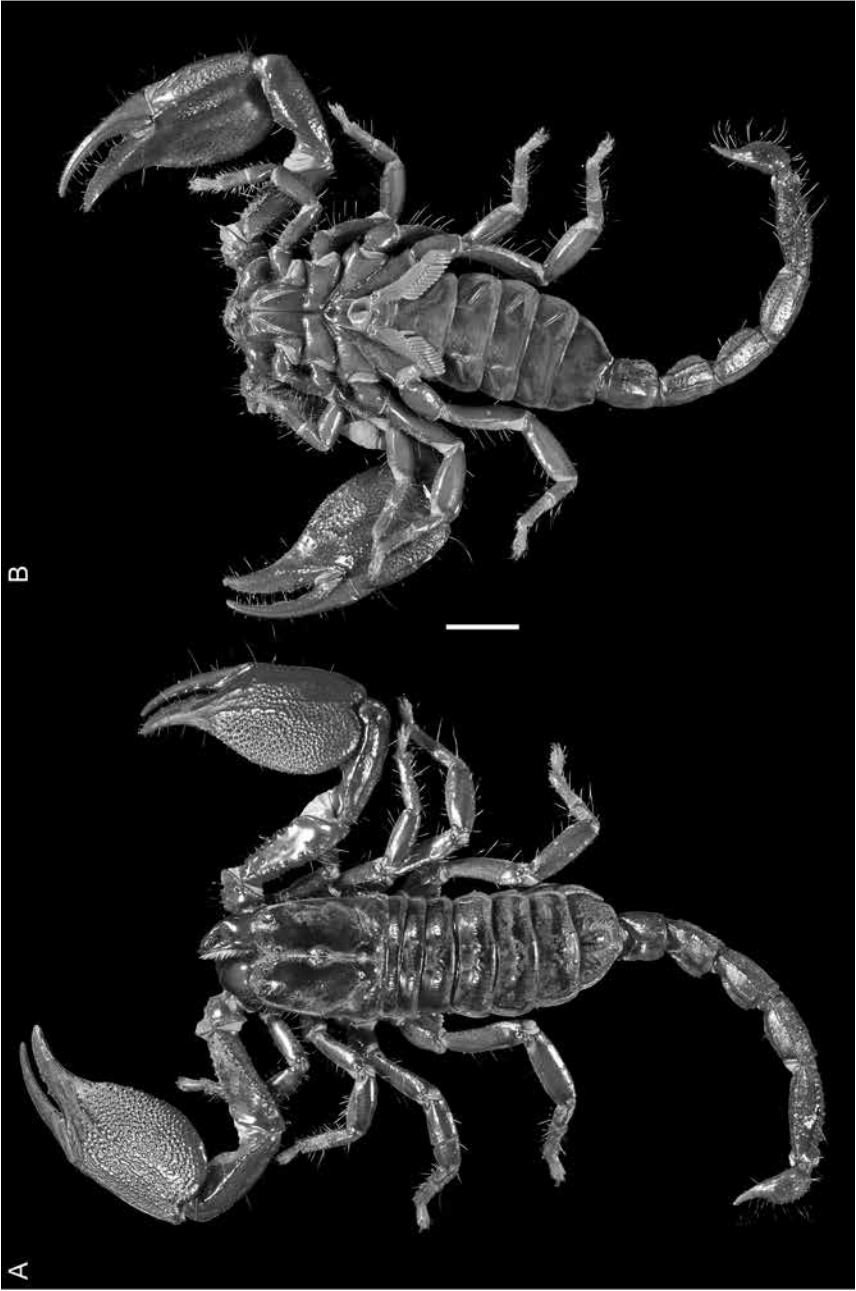


FIGURE 225. *Srilankametetrus caesar* (C.L. Koch, 1841), comb. nov. et stat. rev., ♂ (MNHN RS 0079), habitus: **A.** dorsal and **B.** ventral aspects. Scale bar = 10 mm.



FIGURE 226. *Srilankametrus caesar* (C.L. Koch, 1841), comb. nov. et stat. rev., ♀ (MNHN RS 0079), habitus: **A.** dorsal and **B.** ventral aspects. Scale bar = 10 mm.

to densely setose (fig. 241), as in *Sahyadrimetrus*, all species of *Deccanometrus* except *D. xanthopus*, and some species of *Chersonesometrus*. The distance between the chela manus dorsomedian and promedian carinae or setal rows (DMC-PMC) is slightly to markedly greater than the distance between the promedian and proventral carinae or setal rows (PMC-PVC) in *Srilankametrus* whereas the DMC-PMC is similar to the PMC-PVC in *Heterometrus*. The dorsomedian carina becomes obsolete proximally in *Srilankametrus* but is continuous to the proximal edge of the manus in *Chersonesometrus*, *Gigantometrus*, and two species of *Deccanometrus*, *D. obscurus* and *D. phipsoni*. The chela manus dorsal secondary, subdigital and digital carinae (or setal rows) are well separated along their entire length in *Srilankametrus* whereas the proximal half of the dorsal secondary carina, distal half of the subdigital carina and distal third of the digital carina are closely adjacent in *Chersonesometrus* and *Gigantometrus*. The dorsal secondary and subdigital carinae of the male are present and entirely to predominantly granular or costate in all species of *Srilankametrus* except *S. indus* and *S. pococki*, in which they are absent or obsolete as in *Deccanometrus*, *Heterometrus*, *Javanimetrus*, *Sahyadrimetrus*, and two species of *Chersonesometrus*, *C. bastawadei* and *C. fulvipes*. The chela manus digital and retromedian carinae are similarly developed (figs. 228, 229, 232, 233, 236, 237, 241, 242, 246, 248, 250, 251) in *Srilankametrus* whereas the retromedian carina is more pronounced than the digital carina in *Chersonesometrus*. The retromedian carina of the male is present and entirely to predominantly granular or costate in all species of *Srilankametrus* except *S. indus* and *S. pococki*, in which the carina is absent or obsolete, as in *Deccanometrus*, *Heterometrus*, *Javanimetrus*, and *Sahyadrimetrus*. The depression in the dorsal surface of the chela manus, proximal to the fixed finger of the adult male, is absent or obsolete (figs. 228, 232, 233, 236, 241, 248, 250) in *Srilankametrus* but present and distinct in *Heterometrus*. The chela manus dorsal surface is without reticulation in *Srilankametrus* but shallowly reticulate in *Javanimetrus*,

Sahyadrimetrus, all except two species of *Deccanometrus*, *D. obscurus* and *D. phipsoni*, and three species of *Heterometrus*, *H. glaucus*, *H. longimanus*, and *H. thorellii*; the dorsal surface is finely to coarsely granular in *Srilankametrus* but smooth in *Heterometrus*, *Javanimetrus*, two species of *Sahyadrimetrus*, *S. kanarensis* and *S. tika-deri*, and one species of *Deccanometrus*, *D. ubicki*. The chela manus retrolateral intercarinal surfaces are granular in *Srilankametrus* but smooth or nearly so in *Heterometrus*, *Javanimetrus*, and some species of *Sahyadrimetrus*. The chela manus ventral surface is flat, with the axes of the retroventral and ventromedian carinae in approximately the same plane in all except two species of *Srilankametrus*, *S. indus* and *S. pococki*, in which it is angled, with the axis of the retroventral carina ventral to the axis of the ventromedian carina, as in *Javanimetrus* and four species of *Chersonesometrus*, *C. beccaloniae*, *C. hendersoni*, *C. pelekomanus*, and *C. tristis*. The pro- and retrolateral surfaces of the tibiae of legs I and II each bear a row of two or three spiniform macrosetae in *Srilankametrus* and scattered, setiform macrosetae, not arranged in a definite row, in *Heterometrus*. Macroseta *sb* on the retroventral surface of the basitarsus of leg III is setiform (figs. 56, 57) in *Srilankametrus* but spiniform in *Javanimetrus* and *Sahyadrimetrus*. The pseudonychium (dactyl) of the telotarsi of legs I-IV is usually reduced and rounded in *Srilankametrus* but prominent and acuminate in *Heterometrus*. The pectinal first proximal median lamella (scape) of the female is straight or shallowly curved in *Srilankametrus* but distinctly angular, $\geq 90^\circ$ but $< 180^\circ$ (figs. 41, 42) in all the other genera. The mesial surfaces of mesosomal tergites I-VI of the male are smooth in *Srilankametrus*, but granular in *Gigantometrus*, one species of *Deccanometrus*, *D. xanthopus*, two species of *Sahyadrimetrus*, *S. mathewi* and *S. scaber*, and some species of *Chersonesometrus*. The lengths of metasomal segments I and II are approximately equal to or less than their respective widths (figs. 76, 78) in *Srilankametrus* but markedly greater than their respective widths in *Gigantometrus*. The ventrosubmedian and ventro-

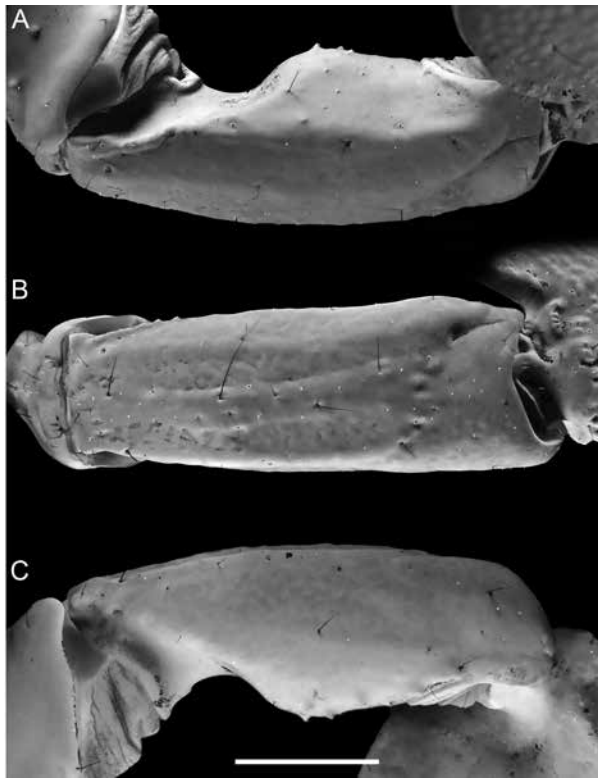


FIGURE 227. *Srilankametrus caesar* (C.L. Koch, 1841), comb. nov. et stat. rev., ♂ (MNHN RS 0079), pedipalp patella: **A.** dorsal, **B.** retrolateral, and **C.** ventral aspects. Scale bar = 5 mm.

lateral carinae are granular or costate-granular on metasomal segment IV only and costate on segments I–III (figs. 77, 78) in *Srilankametrus* but granular on segments I–IV, II–IV (costate on I), or III and IV (costate on I and II) in *Gigantometrus*. The ventral intercarinal surfaces of metasomal segment IV are smooth in all species of *Srilankametrus* except *S. caesar* and the males of *S. couzijni* and *S. gravimanus*, in which the surfaces are sparsely granular, as in *Javanimetrus*. The dorsosubmedian carinae of metasomal segment V are vestigial (fig. 76) in *Srilankametrus* but partial in *Gigantometrus* and absent in *Heterometrus*. The dorsal intercarinal surface of V is granular (fig. 76A–C, F) in all except two species of *Srilankametrus*, *S. indus* and *S. pococki*, in which it is smooth (fig. 76D, E), as in *Deccanometrus*, *Heterometrus*, *Javanimetrus*, *Sahyadrimetrus*, and some species of *Chersonesometrus*. The telson is as dark as meta-

somal segment V in most species of *Srilankametrus* but paler than segment V in *Chersonesometrus*, *Gigantometrus*, *Javanimetrus*, *Sahyadrimetrus*, and some species of *Deccanometrus* and *Heterometrus*. The width of the telson vesicle is approximately equal to or less than the width of metasomal segment V in the female of *Srilankametrus* but greater than the width of segment V in the female of *Gigantometrus* and the vesicle is globose (figs. 76A–C, 77A–C, 78A–C) in all except three species of *Srilankametrus*, *S. indus*, *S. pococki*, and *S. serratus*, in which the vesicle is elongate (figs. 76D–F, 77D–F, 78D–F) as in *Heterometrus*, *Javanimetrus*, and *Sahyadrimetrus*.

INCLUDED SPECIES: *Srilankametrus* accommodates seven species, three formerly assigned to subgenus *Srilankametrus* of *Heterometrus* by various authors (Couzijn, 1981; Tikader and Bastawade, 1983; Fet, 2000), one revalidated from synonymy,



FIGURE 228. *Srilankametrus caesar* (C.L. Koch, 1841), comb. nov. et stat. rev., ♂ (MNHN RS 0079), pedipalp chela: A. retrodorsal, B. ventral, and C. prolateral aspects. Scale bar = 5 mm.



FIGURE 229. *Srilankametrus caesar* (C.L. Koch, 1841), comb. nov. et stat. rev., ♀ (MNHN RS 0079), pedipalp chela: **A.** retrodorsal, **B.** ventral, and **C.** prolateral aspects. Scale bar = 5 mm.

another recently described (Kovářík et al., 2019), and two new, collectively recovered as a monophyletic group by phylogenetic analysis of morphological characters and DNA sequences from the nuclear and mitochondrial genomes (fig. 10): *Srilankametrus caesar* (C.L. Koch, 1841), comb. nov. et stat. rev.; *Srilankametrus couzijni*, sp. nov.; *Srilankametrus gravimanus* (Pocock, 1894), comb. nov.; *Srilankametrus indus* (DeGeer, 1778), comb. nov.; *Srilankametrus pococki*, sp. nov.; *Srilankametrus serratus* (Pocock, 1900), comb. nov.; *Srilankametrus yaleensis* (Kovářík et al., 2019), comb. nov.

DISTRIBUTION: The genus *Srilankametrus* is endemic to India, where it has been recorded only in the state of Tamil Nadu, and Sri Lanka, where it has been recorded across the island in the Central, North Central, North Western, Northern, Southern, Uva, and Western provinces (figs. 4, 198, 199, table 1).

ECOLOGY: Species of *Srilankametrus* inhabit primary forest at elevations of 20–765 m above sea level. They are fossorial and pelophilous, constructing single-occupant burrows 20–70 cm deep in clayey or sandy-loam soils. Burrows are usually constructed in open ground or in earthen banks but may also be constructed under logs or stones.

CONSERVATION STATUS: *Srilankametrus serratus* is occasionally harvested for the commercial trade in exotic pets.

REMARKS: *Srilankametrus* Couzijn, 1981, stat. nov., originally created as a subgenus of *Heterometrus*, and subsequently synonymized with the latter (Kovářík, 2004), is hereby revalidated and elevated to the rank of genus.

Srilankametrus caesar (C.L. Koch, 1841),
comb. nov. et stat. rev.

Figures 10, 27A, B, 41A, B, 56A–D, 76–78, 199,
225–229, table 1

Buthus caesar C.L. Koch, 1841b: 6–9, pl. CCXCI,
fig. 697; 1850: 87; Simon, 1872b: 101;
Thorell, 1876b: 202; Moritz and Fischer,
1980: 311; Couzijn, 1981: 123.

Heterometrus afer: Simon, 1872b: 53, 59, 98–101
(misidentification, part).

Pandinus caesar: Thorell, 1876b: 202, 205;
Karsch, 1884: 68.

Scorpio africanus: Pocock, 1893: 311
(misidentification).

Scorpio caesar: Pocock, 1893: 310, 311 (part).

Scorpio ceylonicus: Kraepelin, 1894: 31, 46–51,
54, 55, 57 (misidentification, part).

Heterometrus caesar: Kraepelin, 1899: 109, 114
(part); Roewer, 1943: 229 (part); Takashima,
1945: 92; Bücherl, 1964: 59; Brignoli, 1985:
415.

Palamnaeus caesar: Pocock, 1900a: 86, 97 (part).

Heterometrus (Scorpio) caesar: Kraepelin, 1901:
271.

Heterometrus (Scorpio) indus: Kraepelin, 1901:
271 (misidentification, part).

Pandinus gravimanus: Simon, 1905: 161
(misidentification, part).

Heterometrus (Chersonesometrus) fulvipes:
Couzijn, 1981: 40, 72, 88, 123, 133–136, 139,
140, 142, 192, table 7, fig. 16b (misidentifi-
cation, part); Fet, 2000: 439 (part).

Heterometrus (Chersonesometrus) granulomanus
Couzijn, 1981: 19, 22, 43, 87, 133, 141–143,
170, 192, table 7, figs. 2g, 4c, 43, 58; Tikader
and Bastawade, 1983: 573, 574, 577–582
(misidentification, part), figs. 1525–1538;
Kovářík, 1998: 136; Fet, 2000: 439 (part);
Bastawade, 2004: 286, 291, 292 (part);
Bastawade et al., 2004: 48, 54, 58, figs. 67,
68; Kovářík, 2004: 1, 29 (part); Thulsi Rao et
al., 2005: 3, 9 (misidentification, part); Sure-
shan et al., 2007a: 2906–2908 (misidentifica-
tion, part); Bastawade, 2008: 133, 136, 137
(part); Indra, 2009: 141; syn. nov.

Heterometrus (Srilankametrus) indus: Couzijn,
1981: 94, 121, 123 (misidentification, part);
Kovářík, 1998: 137 (part); Fet, 2000: 446,
447 (part).

Heterometrus (Srilankametrus) indus indus:
Couzijn, 1981: 82, 121–124, 129, 191
(misidentification, part).



FIGURE 230. *Srilankametrus couzijni*, sp. nov., habitus: **A, C.** dorsal and **B, D.** ventral aspects. **A, B.** Holotype ♂ (BMNH 1896.7.30.121), **C, D.** Paratype ♂ (SMF 5332/1). Scale bars = 10 mm.

Heterometrus indus: Kovařík, 2004: 2, 17, 20, 21, 32, 52 (misidentification, part); 2009: 38, 48 (misidentification, part).

Heterometrus latimanus: Kovařík, 2004: 21, 51, table 2 (misidentification, part); 2009: 35,

39, 47, 49, 73, 100 (misidentification, part), table 1, figs. 3, 4, 198 (misidentification).

Heterometrus madraspatensis: Kovařík, 2004: 1, 2, 27, 29, 51, 52, table 2 (misidentification,

part); 2009: 35, 41, 48, table 1 (misidentification, part).

TYPE MATERIAL: INDIA: *Buthus caesar*: Lectotype [here designated]: 1 subad. ♀ (ZMB 63), "India Orientalis" [East India] [examined]. **Puducherry:** *Puducherry Distr.: Heterometrus (Chersonesometrus) granulomanus*: Holotype ♂, paratype ♀ (MNHN RS 0087), Pondichéry [Pondicherry/Puduchcheri/Puducherry, 11°59'N 79°49'E], viii.1901, M. Maindron [examined].

Several syntypes were mentioned by Koch (1841b: 9), only one of which remains in the ZMB. As noted by Tahir and Prendini (2014: 6, 20), this single specimen precisely matches two females in a similar state of preservation, suggesting they are very old, and with the same locality data, i.e., "India," misidentified as *Heterometrus latimanus* by Kovařík (2004: 21, 51, table 2; 2009: 34, 35, 39, 47, 49, 73, 100, table 1, figs. 3, 4, 198).

In the description of *Heterometrus (Chersonesometrus) granulomanus*, Couzijn (1981: 142) specifically mentioned a male holotype and a female allotype (i.e., a designated paratype that is the opposite sex to the holotype) from the same locality but did not refer to other material examined as paratypes. Therefore, the other specimens listed in Couzijn's (1981) description are not paratypes of *H. (C.) granulomanus* contrary to Fet (2000: 439) and Kovařík (2004: 27).

DIAGNOSIS: *Srilankametrus caesar* may be separated from other species of *Srilankametrus* as follows. The carapace is vaulted, the lateral surfaces sloping steeply (fig. 27A, B), in *S. caesar* but slightly to markedly dorsoventrally compressed, the lateral surfaces sloping moderately to gently, in *S. indus*, *S. pococki*, and *S. serratus*. The interocular and posterior sutures are present, the posterior sutures extending past the median ocular tubercle and connected anteriorly to the posterior bifurcations of the interocular suture, in *S. caesar* whereas the sutures are absent in *S. indus* and *S. pococki*. The frontal lobes and medial region of the carapace interocular surface are granular with

smooth areas (fig. 27A, B) in *S. caesar*, whereas the interocular surface is entirely smooth in the other species. The carapace anterolateral and mediolateral surfaces are granular in *S. caesar* but smooth or nearly so in *S. indus*. The carapace posterolateral surfaces of the female are granular in *S. caesar* but smooth or nearly so in *S. gravimanus* and *S. yaleensis*. The pedipalp patella dorsomedian carina of the female is entirely to predominantly costate in *S. caesar* but absent or obsolete in all other species. The patella retrodorsal carina of the female is absent or obsolete in *S. caesar* but as strongly developed as or more strongly developed than the retromedian carinae in *S. gravimanus*, *S. serratus*, and *S. yaleensis*. The retromedian carinae of the female are granular in *S. caesar* but absent or obsolete in *S. gravimanus* and *S. yaleensis*. The pedipalp chela of the adult male (fig. 228) is sparsely setose in *S. caesar* but moderately to densely setose in *S. indus* and *S. pococki*. The chela manus dorsal surface (between the dorsomedian and digital carinae) is curved and slightly to markedly convex in *S. caesar* but flat in *S. pococki*. The proximal margin (lobe) of the dorsal surface is moderately curved and proximal to the proximal margin of the retrolateral surface but distal to the proximal margin of the condyle (articulation with patella) in *S. caesar*, whereas it is markedly curved and proximal to the proximal margin of the condyle in *S. couzijnii*. The dorsomedian carina is pronounced and costate on the chela fixed finger and distally on the manus in *S. caesar*, pronounced and costate on the fixed finger and distal three-quarters of the manus in *S. yaleensis*, and obsolete on the fixed finger and manus in *S. indus*, *S. pococki*, and *S. serratus*. The maximum distance between the dorsomedian and dorsal secondary carinae (DMC–DSC) of the chela manus is greater than the maximum distance between the dorsal secondary and digital carinae (DSC–DC) in the male (fig. 228) of *S. caesar* but similar to the DSC–DC in the male of *S. gravimanus*. The dorsal secondary and subdigital carinae of the male (fig. 228) are entirely to predominantly

granular in *S. caesar* but entirely to predominantly costate in *S. gravimanus* and *S. yaleensis* and absent or obsolete in *S. indus* and *S. pococki*. The digital carina is entirely to predominantly granular (figs. 228, 229) in *S. caesar*, entirely to predominantly costate in *S. couzijni*, *S. gravimanus*, and *S. yaleensis*, and absent or obsolete in *S. indus* and *S. pococki*. The retromedian carina of the male is entirely to predominantly granular in *S. caesar*, entirely to predominantly costate in *S. couzijni*, *S. gravimanus*, and *S. yaleensis*, and absent or obsolete in *S. indus* and *S. pococki*. The manus ventral surface is flat, with the axes of the retroventral and ventromedian carinae in approximately the same plane in *S. caesar*, but angled, with the axis of the retroventral carina ventral to the axis of the ventromedian carina in *S. indus* and *S. pococki*. Macroseta *st* on the retroventral surfaces of the basitarsi of legs I and II is spiniform (fig. 56A–D) in *S. caesar* but setiform in all other species except *S. gravimanus* and *S. serratus*. The lateral surfaces of mesosomal tergites I–VI are granular in *S. caesar* but smooth in *S. indus*, *S. pococki*, and *S. yaleensis*. The dorsosubmedian carinae are granular or costate-granular on metasomal segments I–IV (fig. 76A) in *S. caesar*, costate on I–IV in *S. indus*, and costate on I and II or I–III and granular or costate-granular on III and IV or IV, in *S. yaleensis*. The ventral intercarinal surfaces of metasomal segment IV are granular in the male and female (fig. 78A) of *S. caesar*, but smooth in the male and female of *S. indus*, *S. pococki*, *S. serratus*, and *S. yaleensis*, and the female of *S. gravimanus*. The dorsolateral carinae of metasomal segment V are distinct and continuous (fig. 77A) in *S. caesar* but obsolete and discontinuous to absent in *S. indus* and *S. pococki*. The dorsal intercarinal surface of metasomal segment V is granular in the male and female (fig. 76A) of *S. caesar* but smooth in the male and female of *S. indus* and *S. pococki*, and the female of *S. serratus* and *S. yaleensis*. The telson is blackish, as dark as metasomal segment V, in *S. caesar* but dark reddish brown, paler than segment V, in *S. serratus*

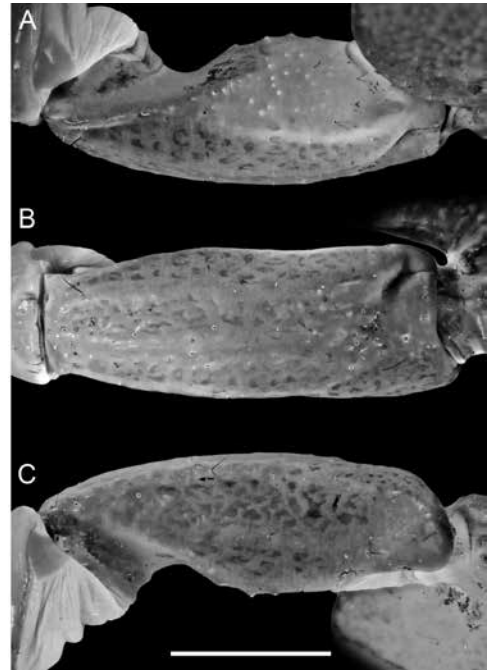


FIGURE 231. *Srilankametrus couzijni*, sp. nov., holotype ♂ (BMNH 1896.7.30.121), pedipalp patella: A. dorsal, B. retrolateral, and C. ventral aspects. Scale bar = 5 mm.

and *S. yaleensis*. The telson vesicle is elongate in *S. caesar* but globose in *S. indus*, *S. pococki*, and *S. serratus*.

DESCRIPTION: In addition to the original description of *Buthus caesar*, the holotype and paratype of *H. (C.) granulomanus* were described and illustrated by Couzijn (1981) and again by Tikader and Bastawade (1983).

DISTRIBUTION: This species is endemic to India. The only material with locality data is labelled as originating from the union territory of Puducherry (fig. 199, table 1). If accurate, this species would appear to be allopatric with all other species of *Srilankametrus*. Records from Ceylon (Sri Lanka) attributed to this species (Pocock, 1894a; Kraepelin, 1899) refer to *S. serratus*.

ECOLOGY: The only known locality record occurs in deciduous forest at low elevation. The habitus is consistent with the fossorial, pelophilous ecomorphotype (Prendini, 2001b). The spe-



FIGURE 232. *Srilankametrus couzijni*, sp. nov., holotype ♂ (BMNH 1896.7.30.121), pedipalp chela: **A.** retro-dorsal, **B.** ventral, and **C.** prolateral aspects. Scale bar = 5 mm.

cies probably excavates deep burrows in sandy-loam soil, in open ground.

CONSERVATION STATUS: This species has not been seen in over a century. Its habitat has been extensively modified and it may be extinct.

REMARKS: *Buthus caesar* was described from an unspecified number of syntypes from “India Orientalis” (Koch, 1841b). The identity of this

species has remained enigmatic since its description. According to Fet (2000: 445), Kraepelin (1894: 46) first synonymized *B. caesar* with *S. indus* whereas, according to Kovařík (2004, 2009), Simon (1872b: 99) was the first to do so. However, Simon (1872b: 99) synonymized *B. caesar* with specimens misidentified as *Heterometrus afer* (nec *Scorpio afer* Linnaeus, 1758)



FIGURE 233. *Srilankametrus couzijni*, sp. nov., paratype ♂ (SMF 5332/1), pedipalp chela: A. retrodorsal, B. ventral, and C. prolateral aspects. Scale bar = 5 mm.

that were conspecific with *Heterometrus* (*Chersonesometrus*) *scaber*, as discussed by Couzijn (1981: 145, 146). Kraepelin (1894: 46) synonymized *B. caesar* with *Scorpio ceylonicus*, which was synonymized with *S. indus*, notwithstanding that *S. indus* was the older name. Therefore, it appears Couzijn (1981: 123, 134) was the first to synonymize *B. caesar* with *H. indus* despite stating that a syntype of *B. caesar* in the ZMB “evidently belongs to *H. fulvipes* (Koch) and not to *H. indus* (de Geer), nor to *S. caesar* (Koch),” an opinion repeated by Fet (2000: 439, 447). Other authors confused *B. caesar* with *S. serratus* (Pocock, 1894a, 1900a; Kraepelin, 1899; Roewer, 1943; Takashima, 1945).

Despite immaturity, poor condition, and the absence of precise locality data, the sole remaining type (here designated as the lectotype) of *Buthus caesar* is clearly conspecific with type and nontype material of *H. (C.) granulomanus* (MNHN RS 0079, 0087, 3246) and several specimens, misidentified as *H. (C.) fulvipes* by Couzijn (1981: 134), with the same collection data (MNHN RS 6168) as well as material, in some cases identified as *Palamnaeus caesar*, from other collections (BMNH, ZMB 2282, 2283, 7244), based on the shape and macrosculpture of the carapace, pedipalp chela, metasoma, and telson. These specimens also match the original description and illustration of *B. caesar* in coloration, being completely black with pale tarsi (unlike *Chersonesometrus fulvipes*, in which the legs and telson are pale yellow); surface macrosculpture, differing from *S. indus* (and other species of *Srilankametrus*) in the granular frontal lobes of the carapace (“vorn an den zwei vorderrandslappen niedergedruckt und flach, auf dieser flache unordentlich zerstreute ungleichgrosse kleine kornchen”) and from *Sahyadrimetrus scaber* in the granular pedipalp chela manus; and the shape of the pedipalp chela with its bent, flat and broad fixed finger (“die finger etwas gebogen, sehr flach, breit”) (Koch, 1841b: 6–9, pl. CCXCI, fig. 697). Based on these differences, *S. caesar* is not synonymous with *S. scaber*, as proposed by Simon

(1872b) [misidentified as *H. afer*], *S. indus*, as proposed by Kraepelin (1894: 46) [as *S. ceylonicus*], or *C. fulvipes*, as proposed by Couzijn (1981). It is also distinct from *S. serratus*, for which it was mistaken by Pocock (1894a, 1900a), Kraepelin (1899), and others (Roewer, 1943; Takashima, 1945). *Srilankametrus caesar* (C.L. Koch, 1841), comb. nov. et stat. rev., is therefore revalidated, and the following new synonym presented: *Heterometrus* (*Chersonesometrus*) *granulomanus* Couzijn, 1981 = *Srilankametrus caesar* (C.L. Koch, 1841), syn. nov.

Couzijn (1981) based *H. (C.) granulomanus* on a holotype and paratype (MNHN RS 0087) that were subsequently redescribed and illustrated by Tikader and Bastawade (1983: 577–581). The species was listed as valid by subsequent authors (Fet, 2000; Kovařík, 1998, 2002) until synonymized with *H. madraspatensis* by Kovařík (2004: 29) based on an appeal to authority: “*Heterometrus* (*Chersonesometrus*) *granulomanus*...in my opinion is a synonym of *H. madraspatensis*.” Interestingly, two females in a similar state of preservation, with the same locality data as the holotype of *B. caesar*, and precisely matching the paratype and nontype females of *H. (C.) granulomanus* (MNHN RS 0079, 0087, 3246) were misidentified as *H. latimanus* by Kovařík (2004: 21, 51, table 2; 2009: 34, 35, 39, 47, 49, 73, 100, table 1, figs. 3, 4, 198), as noted by Tahir and Prendini (2014: 6, 20). Setting aside that Couzijn (1981: 142) synonymized *P. madraspatensis* with *H. (C.) fulvipes* and considered the latter closely related to *H. (C.) granulomanus*—even misidentifying as *H. (C.) fulvipes* several specimens with the same collection data as the types of *H. (C.) granulomanus* (MNHN RS 6168) (Couzijn, 1981: 134)—these species share little in common. *Srilankametrus caesar* differs from *C. fulvipes* and *C. madraspatensis* in coloration, carination of the retrolateral surface of the pedipalp chela manus, and macrosetae of the leg basitarsi. Accordingly, Kovařík’s (2004) synonymy of *H. (C.) granulomanus* with *H. madraspatensis* is rejected. Based on phylogenetic analysis (fig. 10), *S. caesar* is most closely related to *S.*

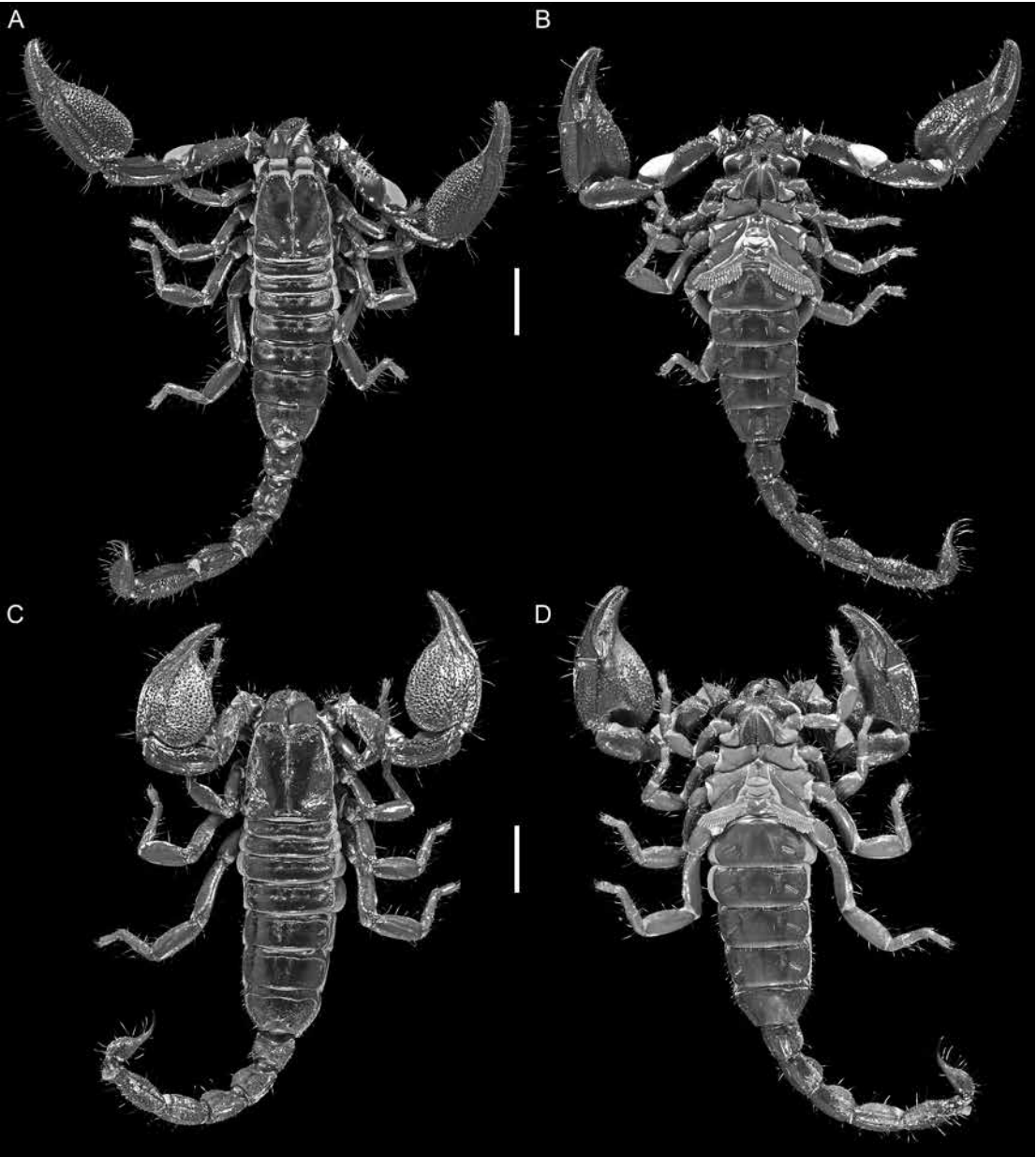


FIGURE 234. *Srilankametrus gravimanus* (Pocock, 1894), comb. nov., habitus: A, C. dorsal and B, D. ventral aspects. A, B. ♂ (AMNH), C, D. ♀ (AMNH), Kokmotte, Sri Lanka. Scale bars = 10 mm.

couzijni, *S. gravimanus*, and *S. yaleensis*, from which it differs in the surface macrosculpture of the carapace and pedipalp chela, shape of the pedipalp chela, and macrosetae of the leg basitarsi.

As discussed below, a nontype male from Palni Hills, India (SMF 5332/1), listed in the original description of *H. (C.) granulomanus*, and which closely matches an adult male from Tanjore, India (BMNH 1896.7.30.121), misidentified as *H. gravimanus* by Pocock (1900a), Tikader and Bastawade (1983) and Kovařík (2004), is newly described as the paratype of *S. couzijni*.

MATERIAL EXAMINED: 1 ♀, 1 subad. ♀, 2 ♂, 1 juv. ♀ (ZMB 7244). “Amerique?,” 1 ♀ (MNHN RS 0120). “India?,” 1 ♂ (ZMB 2283), 1 ♀ (MNHN RS 0149 [Simon coll. 8212]). **INDIA:** 1 ♀ (BMNH). “Ind. Or.” [India Orientalis], “Ostindien” [East India], 2 ♂ (ZMB 2282). **Puducherry:** *Puducherry Distr.:* Pondichéry [Pondicherry/Puduchcheri/Puducherry, 11°59'N 79°49'E], viii.1901, M. Maindron, 1 ♂, 1 ♀ (MNHN RS 0079), 1 ♀, 1 subad. ♂, 2 subad. ♀, 1 juv. ♀ (MNHN RS 0087), 5 ♂, 10 ♀, 3 subad. ♂, 7 subad. ♀, 3 juv. ♀ (MNHN RS 6168), 1902 [probably viii.1901], M. Maindron, 1 ♀ (MNHN RS 3246).

Srilankametrus couzijni, sp. nov.

Figures 10, 27C, D, 41C, D, 56E–H, 76B, 77B, 78B, 199, 230–233, tables 1, 3, 5

Palamnaeus gravimanus: Pocock, 1900a: 85, 90, 91 (misidentification. part), fig. 28.

Pandinus gravimanus: Simon, 1905: 161 (part).

Heterometrus gravimanus: Takashima, 1945: 94 (part); Kovařík, 2004: 1, 2, 15, 17, 18, 44, 51, 52, tables 2, 3 (misidentification, part), fig. 15 (misidentification); 2009: 35, 36, 38, 47, 49, 79, 100, tables 1, 2 (misidentification, part), figs. 40–42, 201 (misidentification); Kovařík et al., 2016: 96, 100, 103 (part); Aswathi and Sureshan, 2017: 9847 (misidentification).

Heterometrus (Chersonesometrus) granulomanus Couzijn, 1981: 43, 87, 133, 142, 143, 170, 192, table 7, fig. 58 (misidentification, part); Tikader and Bastawade, 1983: 573, 574, 577,

578, 580–582 (misidentification, part); Fet, 2000: 439 (part); Kovařík, 2002: 17 (misidentification); Bastawade, 2004: 286, 291, 292 (part); Kovařík, 2004: 1, 27, 29 (part); Thulsi Rao et al., 2005: 3, 9 (misidentification, part); Bastawade, 2008: 133, 136, 137 (part).

Scorpio gravimanus: Couzijn, 1981: 125.

Heterometrus (Srilankametrus) gravimanus:

Tikader and Bastawade, 1983: 545, 550–555 (misidentification, part), figs. 1469–1482 (misidentification); Fet, 2000: 446 (part); Indra, 2001: 56–58 (misidentification, part); Bastawade et al., 2004: 48, 54, 58, figs. 63–66 (misidentification); Sureshan et al., 2007a: 2906, 2907, fig. 2 (misidentification); Indra, 2009: 141 (misidentification, part).

Heterometrus madraspatensis: Kovařík, 2004: 1, 2, 27, 29, 51, 52, tables 2, 3 (misidentification, part); 2009: 35, 36, 41, 48, tables 1, 2 (part).

TYPE MATERIAL: INDIA: Tamil Nadu: Thanjavur Distr.: Holotype ♂ (BMNH 1896.7.30.121 [BNHS 317]), Tanjore [Thanjavur, 10°47'N 79°08'E], E.P. Popert. *Dindigul Distr.:* Paratype ♂ (SMF 5332/1), Palni Hills [Palani/Pullney/Pullnay Hills, 10°12'N 77°28'E], Kadai canal [Kodai kanal, 10°14'N 77°29'E], 1889, T.H. Kolb.

The paratype male was incorrectly indicated as a paratype of *Heterometrus (C.) granulomanus* by Fet (2000: 439) and Kovařík (2004: 27).

ETYMOLOGY: The specific epithet is a patronym honoring the Dutch arachnologist, Heinrich Wilhelm Cornelius Couzijn, formerly of the Rijksmuseum van Natuurlijke Historie, Leiden, and widely known as H.W.C. Couzijn, who contributed significantly to the knowledge of scorpions, especially Heterometrinae (e.g., Couzijn, 1978, 1981).

DIAGNOSIS: *Srilankametrus couzijni* may be separated from other species of *Srilankametrus* as follows. The carapace is vaulted, the lateral surfaces sloping steeply (fig. 27C, D), in *S. couzijni* but slightly to markedly dorsoventrally compressed, the lateral surfaces sloping moderately to gently, in *S. indus*, *S. pococki*, and *S. serratus*.

The interocular and posterior sutures are present, the posterior sutures extending past the median ocular tubercle and connected anteriorly to the posterior bifurcations of the interocular suture, in *S. couzijni* whereas the sutures are absent in *S. indus* and *S. pococki*. The carapace interocular surface is entirely smooth (fig. 27C, D) in *S. couzijni*, whereas the frontal lobes and medial region of the interocular surface are granular with smooth areas in *S. caesar*. The carapace anterolateral and mediolateral surfaces are granular in *S. couzijni* but smooth or nearly so in *S. indus*. The pedipalp chela of the adult male (figs. 232, 233) is sparsely setose in *S. couzijni* but moderately to densely setose in *S. indus* and *S. pococki*. The chela manus dorsal surface (between the dorsomedian and digital carinae) is curved and slightly to markedly convex in *S. couzijni* but flat in *S. pococki*. The proximal margin (lobe) of the dorsal surface is markedly curved and proximal to the proximal margin of the condyle (articulation with patella) in *S. couzijni* but moderately curved and proximal to the proximal margin of the retrolateral surface, or aligned with the proximal margin of the condyle in the other species. The dorsomedian carina is pronounced and costate on the chela fixed finger and distally on the manus in *S. couzijni*, pronounced and costate on the fixed finger and distal three-quarters of the manus in *S. yaleensis*, and obsolete on the fixed finger and manus in *S. indus*, *S. pococki*, and *S. serratus*. The maximum distance between the dorsomedian and dorsal secondary carinae (DMC–DSC) of the chela manus is greater than the maximum distance between the dorsal secondary and digital carinae (DSC–DC) in the male (figs. 232, 233) of *S. couzijni* but similar to the DSC–DC in the male of *S. gravimanus*. The dorsal secondary and subdigital carinae of the male (figs. 232, 233) are entirely to predominantly granular in *S. couzijni* but entirely to predominantly costate in *S. gravimanus* and *S. yaleensis*, and absent or obsolete in *S. indus* and *S. pococki*. The digital carina is entirely to predominantly costate (figs. 232, 233) in *S. couzijni*, entirely to predominantly granular in *S. caesar*

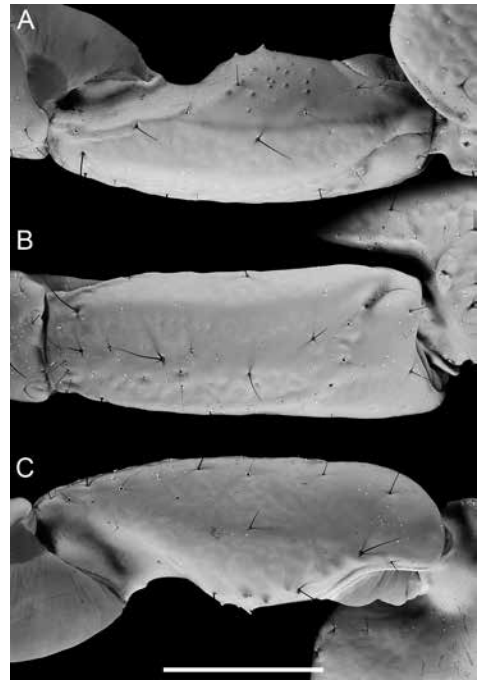


FIGURE 235. *Srilankametrus gravimanus* (Pocock, 1894), comb. nov., ♂ (AMNH), Kokmotte, Sri Lanka, pedipalp patella: A. dorsal, B. retrolateral, and C. ventral aspects. Scale bar = 5 mm.

and *S. serratus*, and absent or obsolete in *S. indus* and *S. pococki*. The retromedian carina of the male is entirely to predominantly costate in *S. couzijni*, entirely to predominantly granular in *S. caesar* and *S. serratus*, and absent or obsolete in *S. indus* and *S. pococki*. The manus ventral surface is flat, with the axes of the retroventral and ventromedian carinae in approximately the same plane in *S. couzijni*, but angled, with the axis of the retroventral carina ventral to the axis of the ventromedian carina in *S. indus* and *S. pococki*. Macroseta *st* on the retroventral surfaces of the basitarsi of legs I and II is setiform (fig. 56E–H) in *S. couzijni* but spiniform in *S. caesar*, *S. gravimanus*, and *S. serratus*. The lateral surfaces of mesosomal tergites I–VI are granular in the male of *S. couzijni* but smooth in the male of *S. indus*, *S. pococki*, and *S. yaleensis*. The dorsosubmedian carinae are granular or costate-granular on metasomal segments I–IV (fig. 76B) in *S.*



FIGURE 236. *Srilankametrus gravimanus* (Pocock, 1894), comb. nov., ♂ (AMNH), Kokmotte, Sri Lanka, pedipalp chela: **A.** retrodorsal, **B.** ventral, and **C.** prolateral aspects. Scale bar = 5 mm.

couzijni, costate on I–IV in *S. indus*, and costate on I and II or I–III and granular or costate-granular on III and IV or IV in *S. yaleensis*. The ventral intercarinal surfaces of metasomal segment IV are granular in the male (fig. 78B) of *S. couzijni* but smooth in the male of *S. indus*, *S. pococki*, *S. serratus*, and *S. yaleensis*. The dorsolateral carinae of metasomal segment V are distinct and continuous (fig. 77B) in *S. couzijni* but obsolete and discontinuous to absent in *S. indus* and *S. pococki*. The dorsal intercarinal surface of meta-

somal segment V is granular in the male (fig. 76B) of *S. couzijni* but smooth in the male of *S. indus* and *S. pococki*. The telson is blackish, as dark as metasomal segment V, in *S. couzijni* but dark reddish brown, paler than segment V, in *S. serratus* and *S. yaleensis*. The telson vesicle is elongate in *S. couzijni* but globose in *S. indus*, *S. pococki*, and *S. serratus*.

DESCRIPTION: The following description, based on the holotype and paratype, supplements previous descriptions of the holotype



FIGURE 237. *Srilankametrus gravimanus* (Pocock, 1894), comb. nov., ♀ (AMNH), Kokmotte, Sri Lanka, pedipalp chela: A. retrodorsal, B. ventral, and C. prolateral aspects. Scale bar = 5 mm.

(as *H. gravimanus*) by Pocock (1900a), Tikader and Bastawade (1981) and Kovařík (2004), and the paratype (as *H. granulomanus*) by Couzijn (1981). Meristic data are presented in table 3. The female is unknown hence measurements are presented only for the adult male (table 5).

Total length: Adult medium sized, maximum length, measured from anterior margin of carapace to tip of aculeus, 96 mm (87–104 mm, $n = 2$) (♂).

Color: Chelicerae, dorsal surfaces bicolored, mostly to entirely immaculate prodorsal half of manus paler than infuscate retrodorsal half of

manus and fingers; manus markedly paler than carapace interocular surface. Carapace, pedipalps, tergites, metasoma, and telson entirely infusate, uniformly dark reddish brown; pedipalp chela manus slightly paler than carapace, tergites, and pedipalp patella and femur, with darker fingers. Sternites III–VII infusate, dark olive to blackish brown, becoming darker posteriorly. Coxosternal region infusate, brownish, maxillary lobes darker. Legs infusate, dark brown but slightly paler than carapace, pedipalps, tergites, and metasoma (fig. 230), becoming paler distally, with basitarsi and telotarsi paler than preceding segments. Genital opercula and pectines uniformly pale cream. Metasomal segments I–V similar to one another; carinae infusate, darker than intercarinal surfaces; dorsal intercarinal surfaces similar to tergites; ventral intercarinal surfaces darker than sternites. Telson vesicle almost similar to but slightly paler than metasomal segment V; aculeus black.

Chelicerae: Movable finger prodistal (DI) and retrodistal (DE) teeth unequal, with DE tooth considerably smaller than DI tooth, aligned longitudinally and not opposable. Fingers and manus, proventral surfaces with long, dense vestiture of macrosetae. Coxae, prodorsal surfaces without stridulatory setae (scaphotrix); promedian surfaces without chemoreceptive lamelliform setae (trichocopae).

Carapace: Carapace vaulted, lateral surfaces sloping steeply. Anterior margin straight, frontal lobes evenly rounded or truncate, with deep median notch, without median projection or median depression (fig. 27C, D). Anterolateral margins subparallel anteriorly, without distinct notch adjacent to posterior lateral ocelli; mediolateral margins diverging or converging slightly posteriorly (at posterolateral sulci). Anterior width of posterior width, 69% (67%–71%, $n = 2$) (δ); posterior width of length, 93% (91%–94%, $n = 2$) (δ). Three pairs of lateral ocelli (MLMa, PLMa, PDMi), all similar in size, two anterior pairs situated anteriorly, well separated from posterior pair, situated laterally. Median ocelli moderately larger than lateral ocelli, distance

between ocelli less than or equal to width of ocellus; median ocular tubercle situated antero-medially, distance from anterior carapace margin, 52% (50%–53%, $n = 2$) (δ). Median longitudinal sulcus narrow, suturiform; continuous from median notch to interocular sulcus; anteriorly furcated; without anterocular depression. Anterior furcated sulci diverging broadly from anterior edge of median longitudinal sulcus. Median ocular tubercle raised, superciliary carinae higher than ocelli, not extended anteriorly or posteriorly. Interocular sulcus present. Circumocular depressions completely encircling median ocular tubercle, converging anteriorly. Posteromedian and posteromarginal sulci deep. Paired mediolateral and posterolateral sulci shallow. Median longitudinal suture continuous from median notch to median ocular tubercle, equally strong along entire length; not extending to anterior margin of carapace, terminating at or posterior to median notch. Anterior furcated sutures absent or obsolete. Anterocular furcated sutures absent. Interocular suture present, slender. Posterior sutures present but indistinct, converging on median ocular tubercle; connected anteriorly to posterior furcations of interocular suture and extending anteriorly beyond median ocular tubercle. Interocular surface entirely smooth (δ); anterolateral, mediolateral, and posterolateral surfaces uniformly finely granular (δ); posteromedian surface smooth.

Pedipalps: Pedipalp short, pedipalp femur length : posterior carapace width ratio (FL:PCW) < 0.77 , femur length : carapace length ratio (FL:CL) < 0.74 . Femur width of length, 37% (36%–38%, $n = 2$) (δ). Retrodorsal carina complete, granular, similar to or more strongly developed than prodorsal carina. Dorsal secondary carina obsolete, comprising few isolated granules. Dorsomedian carina vestigial, reduced to prominent granule demarcated by conspicuous macroseta. Prodorsal carina complete, granular. Promedian carina complete, comprising row of spiniform or subspiniform granules (several demarcated by conspicuous macrosetae), oriented diagonally between prodorsal and proven-

tral carinae. Proventral carina complete, granular, as strongly developed as or more strongly developed than retroventral carina. Ventromedian and secondary accessory carinae absent. Retroventral carina extending partly or entirely to distal edge of segment. Retromedian carinae absent, indicated only by macrosetal rows. Dorsal and prolateral intercarinal surfaces finely granular; ventral and retrolateral surfaces smooth. Patella width of length, 36% ($n = 2$) (δ). Dorsal surface convex, axis of dorsomedian carina dorsal to axis of retrodorsal carina. Dorsomedian carina absent or obsolete (fig. 231). Retrodorsal and retromedian carinae similarly developed, absent or obsolete (δ). Retroventral carina obsolete, costate. Promedian carina absent (δ); promedian process absent. Other carinae absent. Intercarinal surfaces smooth. Chela short, broad (figs. 232, 233); manus height of width, 95% ($n = 2$) (δ); manus length along retroventral carina of manus width, 123% (115%–130%, $n = 2$) (δ); manus length along retroventral carina of movable finger length, 81% (77%–84%, $n = 2$) (δ). Chela sparsely setose (δ). Manus dorsal surface (between dorsomedian and digital carinae) curved, i.e., slightly to markedly convex (δ); proximal margin (lobe) of dorsal surface markedly curved and proximal to proximal margin of condyle (articulation with patella) (δ). Dorsomedian carina pronounced, costate on fixed finger and distally on manus but comprising irregular row of spiniform granules medially, becoming obsolete proximally, on manus. Dorsal secondary and subdigital carinae incomplete, granular; digital carina complete, costate, similarly developed; dorsal secondary, subdigital and digital carinae well separated along entire length. Maximum distance between dorsomedian and dorsal secondary carinae (DMC–DSC) greater than maximum distance between dorsal secondary and digital carinae (DSC–DC). Retromedian carina complete, costate, similarly developed to digital carina. Retrolateral secondary and secondary accessory carinae vestigial, proximal to condyle of movable finger. Retroventral carina distinct, costate. Ventromedian carina obsolete,

costate. Proventral and promedian carinae similarly developed, each indicated by macrosetal row and few spiniform granules. Prodorsal carina comprising irregular row of spiniform granules and associated macrosetae. Distance between dorsomedian and promedian carinae (DMC–PMC) slightly to markedly greater than distance between promedian and proventral carinae (PMC–PVC). Manus, dorsal and retrolateral intercarinal surfaces densely and coarsely granular except for smooth depression at base of fixed finger; ventral intercarinal surface smooth; prolateral intercarinal surfaces smooth to reticulate, except for few scattered spiniform granules dorsally and distally. Manus ventral surface flat, axes of retroventral and ventromedian carinae in approximately same plane. Fixed and movable fingers, intercarinal surfaces smooth; median denticle rows each with six enlarged retrolateral denticles (including terminal denticle), proximal three situated on lobes; first (proximal) lobe of fixed finger and second lobe of movable finger larger than others, with correspondingly deeper notches in movable and fixed fingers, respectively; terminal denticles of fingers interlocking unevenly when closed, movable finger displaced retrolaterally; distinct notch near tip of fixed finger to accommodate terminal denticle of movable finger.

Trichobothria: Orthobothriotaxic, Type C, with the following segment totals ($n = 4$): femur, 3 (1 d , 1 i , 1 e); patella, 19 (2 d , 1 i , 3 v , 13 e , comprising 3 et , 1 est , 2 em , 2 esb , 5 eb); chela, 26 (manus, 16, comprising 2 D , 10 E , 4 V ; fixed finger, 10, comprising 4 d , 4 e , 2 i). Total count of trichobothria per pedipalp: 48. Femur, i situated on dorsal surface. Patella, d_2 situated on internal surface, slightly closer to d_1 than to i ; distance v_2 – v_3 ca. half distance v_1 – v_2 . Chela, distance et – est less than half distance est – esb ; distance est – esb greater than half distance esb – eb ; est aligned with dst ; V_3 situated in medial third of manus, closer to V_2 than V_4 .

Legs: First pair of maxillary lobes (coxa-physes) tapering anteriorly, longer than and encircling second pair. Stridulatory organs, comprising “rasp” (granular tubercles) and “scraper”

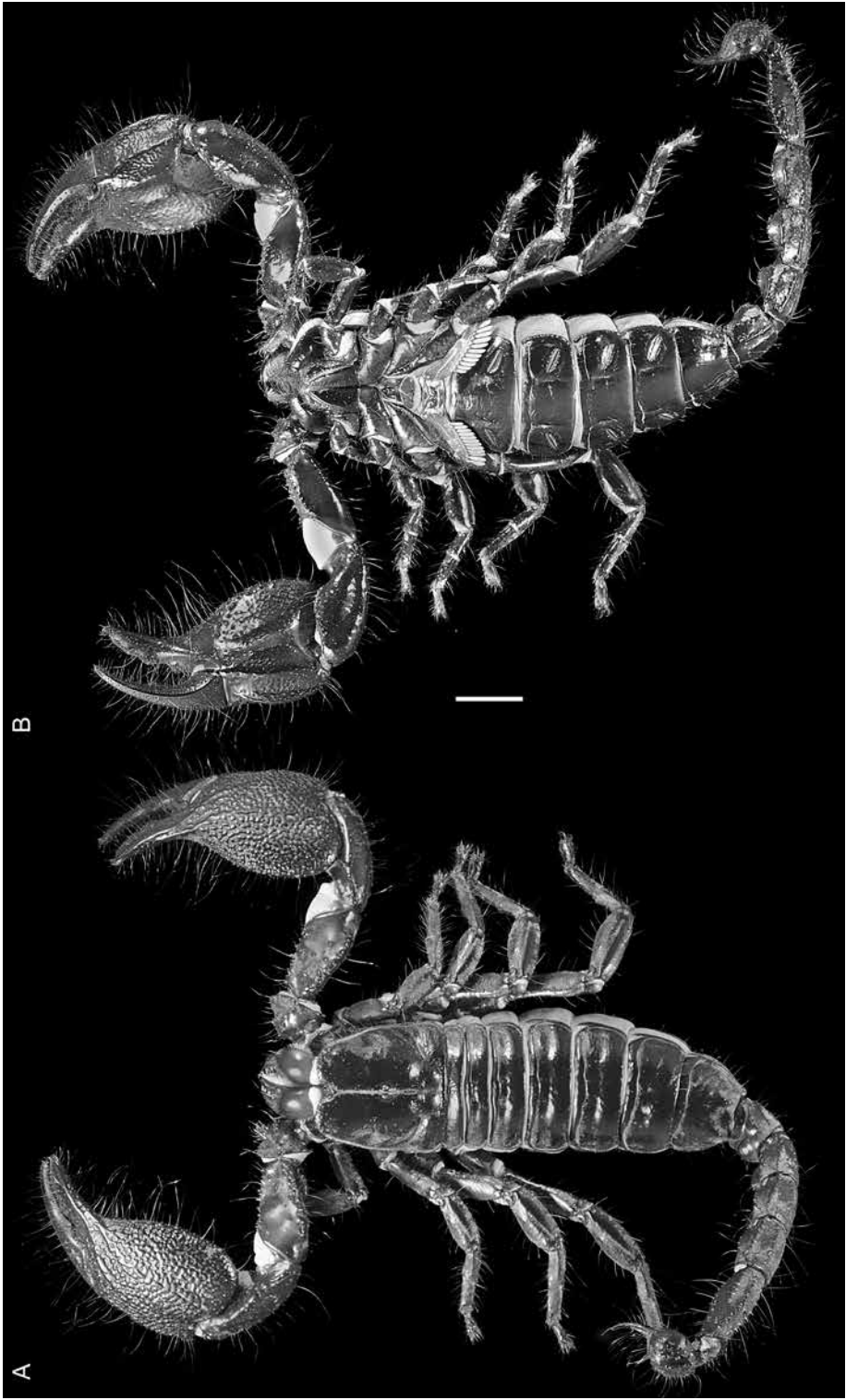


FIGURE 238. *Srilankametrus indus* (DeGeer, 1778), comb. nov., ♂ (AMNH), Kandy, Sri Lanka, habitus: A. dorsal and B. ventral aspects. Scale bar = 10 mm.

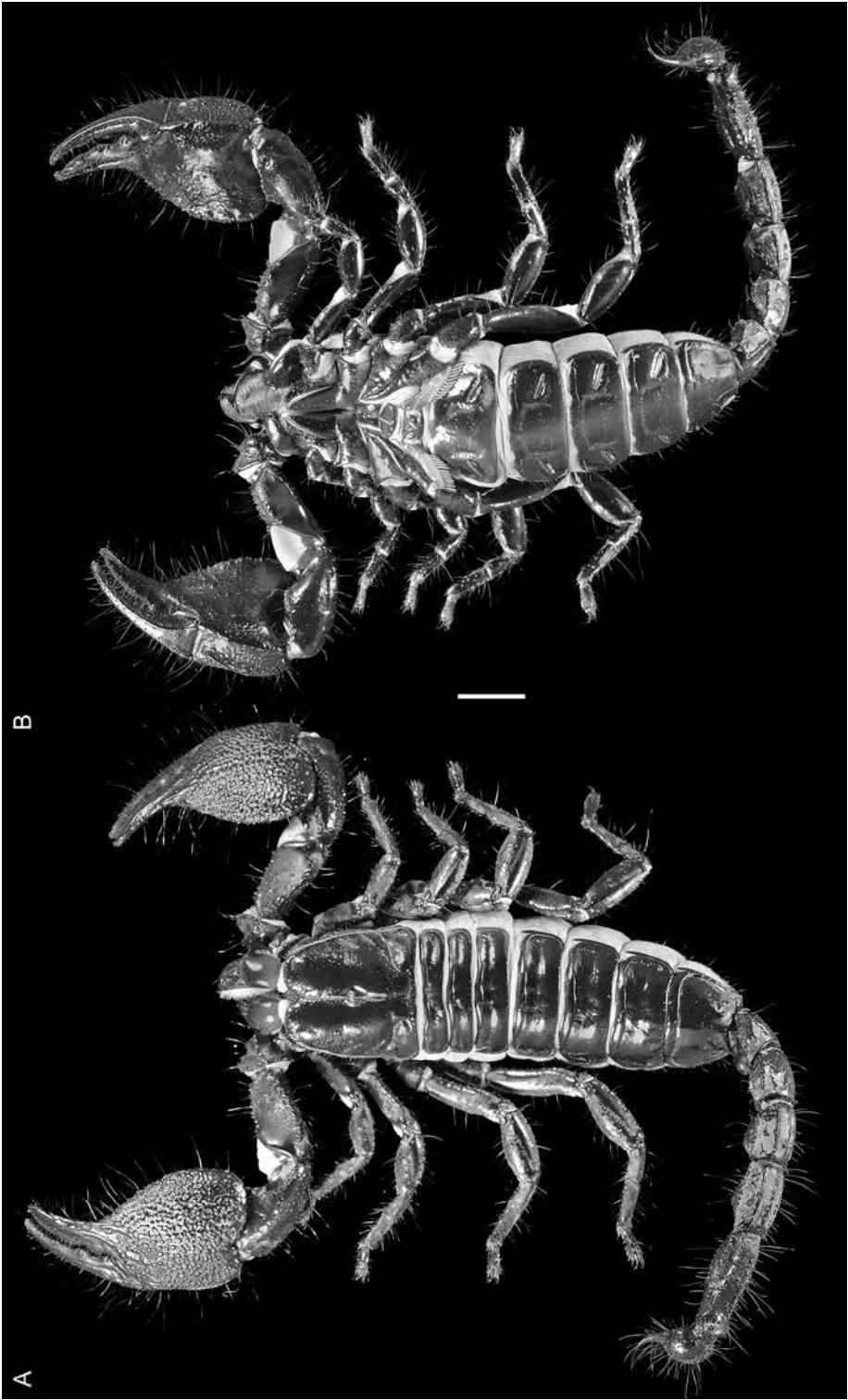


FIGURE 239. *Srilankametrus indus* (DeGeer, 1778), comb. nov., ♀ (AMNH), Kandy, Sri Lanka, habitus: **A**, dorsal and **B**, ventral aspects. Scale bar = 10 mm.

(stridulatory setae or scaphotrix), present on opposing surfaces of coxae of first pair of legs and pedipalps, respectively. Legs I–IV acarinate, except femora, with distinct pro- and retrolateral surfaces demarcated by partial to complete, granular proventral carinae. Femora, patellae, and tibiae, pro- and retrolateral surfaces each with scattered setiform macrosetae. Tibiae, prolateral surfaces, without spiniform macrosetae; I and II, retrolateral surfaces, each with two spiniform (*t*, *st*) macrosetae; III and IV, retrolateral surfaces, without spiniform macrosetae. Basitarsi I–IV, slightly dorsoventrally compressed; retrolateral margins similar, unmodified, rounded; prolateral pedal spurs present (fig. 56E–H); retrolateral pedal spurs absent. Basitarsi, pro- and retrolateral surfaces, each with scattered long and short setiform macrosetae, and spiniform macrosetae, more numerous on I and II than III and IV. Basitarsi, spiniform macrosetae, I, retrolateral: *t*, *sb*; retroventral: *t*, *sb*; proventral: *t*, *st*; II, retrolateral: *t*, *sb*; retroventral: *t*, *sb*; proventral: *t*, *st*; III, retrolateral: *t*, *sb*; retroventral: *t*, *st*; proventral: *t*, *st*; IV, retrolateral: *t*; retroventral: *t*; proventral: *t*, *st*; prolateral: *t*, *st*. Telotarsi I–IV short, stout and distally broadened in dorsal and lateral views. Laterodistal lobes rounded. Dorso-median lobes approximately equal to laterodistal lobes; each terminating in single setiform macroseta. Telotarsi, pro- and retrolateral surfaces, each with long and short, scattered macrosetae, not arranged in definite row. Telotarsi each with pro- and retroventral rows of spiniform macrosetae, two inserted on laterodistal lobes; counts in pro- and retroventral rows similar on I and II, and on III and IV ($n = 4$): I, proventral: 3, retroventral: 4; II, 2 or 3, 4; III, 3 (3 or 4), 5; IV, 4, 5. Telotarsal unguis short, curved, equal to subequal; pseudonychium (dactyl) reduced, rounded.

Sternum: Shape subpentagonal (fig. 41C, D). Median longitudinal sulcus shallow anteriorly, deep and narrow posteriorly.

Genital operculum: Genital opercula suboval, completely divided longitudinally, partially overlapping, genital papillae present (δ) (fig. 41C, D).

Hemispermaphore: Lamelliform, with complex, folded capsule and accessory distal lobe protruding between articular suture and distal lobe (hook). Distal lamina with distal crest truncate, unfolded.

Pectines: Distal edge extending past distal edge of coxa IV but not reaching distal edge of trochanter IV (δ) (fig. 41C, D). First proximal median lamella (scape) of each pecten with mesial margin angular, approximately 90° (δ). Pectinal teeth straight and elongate (δ), present along entire posterior margin; sinistral/dextral tooth count, 14/14 ($n = 2$) (δ). Fulcra smooth proximally but densely setose (microsetae only) distally.

Mesosoma: Tergites each with shallow pair of submedian depressions, without obsolete median carina. Pretergites smooth and glabrous. Posttergites smooth and glabrous medially, unevenly finely and coarsely granular to predominantly coarsely granular laterally (δ). Sternites IV–VI, each with paired longitudinal depressions prolateral to spiracles, absent on VII. Surface, sternites III–VII, smooth; VII with pair of weakly developed, costate ventrolateral carinae only, without posteromarginal carina. Sternite VII, length of width, 64% (62%–66%, $n = 2$) (δ).

Metasoma and telson: Metasomal segments I–V progressively increasing in length, decreasing in width; segment V, width of segment I, width, 72% (67%–76%, $n = 2$) (δ). Metasoma fairly robust, width of length, segment I, 98% (95%–100%, $n = 2$) (δ); II, 88% (83%–92%) (δ); III, 72% (70%–74%) (δ); IV, 62% (60%–63%) (δ); V, 44% (41%–46%) (δ). Telson vesicle, width of metasomal segment V, width, 95% (87%–103%, $n = 2$) (δ); elongate, height of length, 67% (64%–71%, $n = 2$) (δ); dorsal surface flat; ventral surface evenly curved. Aculeus relatively long, gently curved, length of vesicle length, 59% (56%–62%, $n = 2$) (δ). Length metasoma and telson, of total length, 51% ($n = 2$) (δ). Dorsosubmedian carinae, segments I–IV, distinct, complete, granular or costate-granular, posterior spiniform granules obsolete (fig. 76B); V, vestigial. Dorsolateral carinae, segments I–V, distinct, complete, costate-granular on

I–IV, costate-granular to granular on V. Median lateral carinae, segment I, incomplete, reduced to granular row in posterior half, diagonally oriented between dorsolateral and ventrolateral carinae (fig. 77B); II–IV, vestigial, each reduced to posterior granule, or absent; V, incomplete, granular row, restricted to anterior two-thirds. Ventrolateral and ventrosubmedian carinae, segments I–IV, distinct, complete, costate on I–III, granular or costate-granular on IV, more strongly developed on III and IV than on I and II (fig. 78B). Ventrolateral carinae, segment V, distinct, complete, comprising spiniform granules, diverging posteriorly, terminal granule slightly larger than preceding granules. Ventrosubmedian carinae, segment V, vestigial, each reduced to one or two isolated spiniform granules, demarcated by conspicuous macrosetae. Ventromedian carina, segment V comprising single row of spiniform granules, unmodified posteriorly. Anal arch, segment V, dorsal carina, costate; ventral carina comprising subspiniform granules. Dorsal intercarinal surfaces, segments I–V, granular (♂). Lateral intercarinal surfaces, segments I–IV, granular, V, smooth (♂). Ventral intercarinal surfaces, segments I–III, smooth, IV and V, granular (♂). Ventral surface, lateral aspect, segment IV, shallowly convex. Telson vesicle, dorsal and lateral surfaces smooth; ventral surface with four longitudinal carinae, each comprising spiniform granules.

DISTRIBUTION: This species, known from only two adult male specimens, is endemic to the southern Indian state of Tamil Nadu (fig. 199, table 1). Its distribution is allopatric with those of *Chersonesometrus*, *Deccanometrus*, *Sahyadrimetrus*, and all other species of *Srilankametrus* but appears to overlap that of *G. swammerdami*.

ECOLOGY: The known locality records are situated in region of deciduous forest at low elevation. Although no data are available on the ecology of this species, the habitus is consistent with the fossorial, pelophilous ecomorphotype (Prendini, 2001b). Like the closely related species *S. gravimanus* and *S. yaleensis*, this species probably excavates burrows in sandy-loam soils, in open ground.

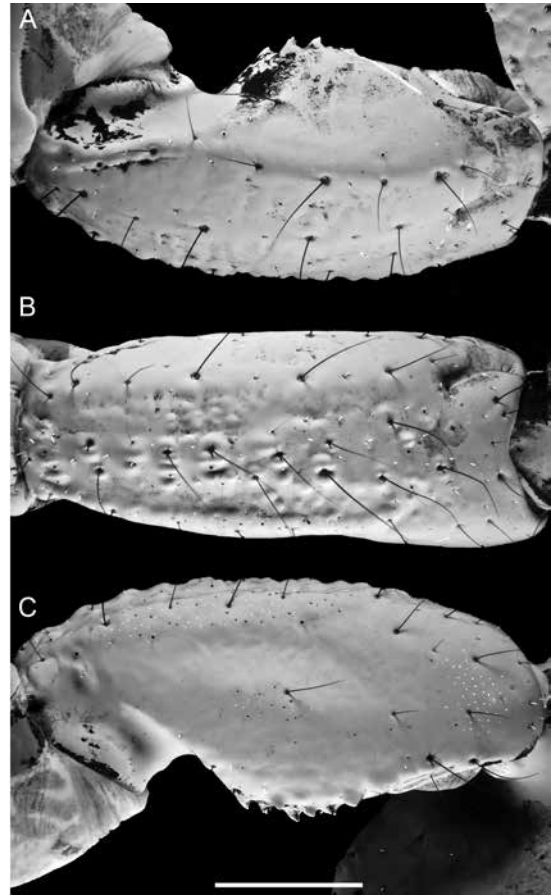


FIGURE 240. *Srilankametrus indus* (DeGeer, 1778), comb. nov., ♂ (AMNH), Kandy, Sri Lanka, pedipalp patella: A. dorsal, B. retrolateral, and C. ventral aspects. Scale bar = 5 mm.

CONSERVATION STATUS: This species has not been seen in over a century. Its habitat has been extensively modified and it may be extinct.

REMARKS: The holotype and paratype, the only known specimens of this unusual species, were repeatedly misidentified by previous workers. Pocock (1900a) initially assigned the male from Tanjore, southern India (BMNH 1896.7.30.121) to *Scorpio gravimanus*, originally described from Ceylon (Sri Lanka). Couzijn (1981) subsequently synonymized *Scorpio gravimanus* with *Heterometrus* (*Srilankametrus*) *indus*, described *Heterometrus* (*Srilankametrus*) *indus laevitensus*, allegedly from Madras, and



FIGURE 241. *Srilankametrus indus* (DeGeer, 1778), comb. nov., ♂ (AMNH), Kandy, Sri Lanka, pedipalp chela: A. retrodorsal, B. ventral, and C. prolateral aspects. Scale bar = 5 mm.

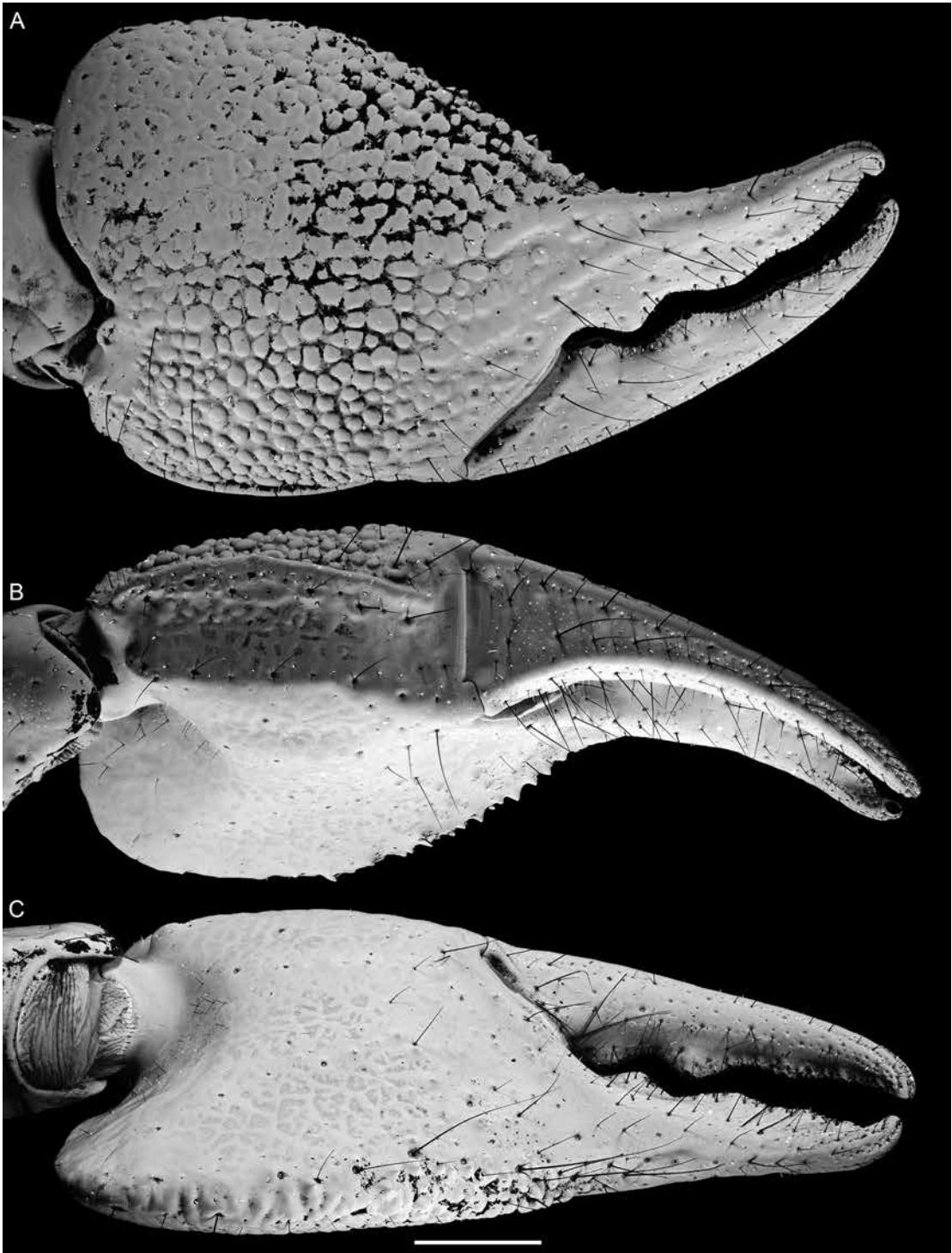


FIGURE 242. *Srilankametrus indus* (DeGeer, 1778), comb. nov., ♀ (AMNH), Kandy, Sri Lanka, pedipalp chela: A. retrodorsal, B. ventral, and C. prolateral aspects. Scale bar = 5 mm.

suggested that the male from Tanjore, mentioned by Pocock (1900a: 91) “probably refers to *H. indus laevitensus*” (Couzijn, 1981: 125). Tikader and Bastawade (1983: 550–555) redescribed and illustrated the Tanjore specimen as *H. gravimanus*, which they considered a valid species, but did not address *H. indus* or *H. (S.) indus laevitensus*. All three taxa were subsequently listed as valid (Kovařík, 1998: 137; Fet, 2000: 447) until Kovařík (2004: 17) synonymized *H. indus laevitensus* with *H. gravimanus* based on the following argument:

a male from Tanjore ... was assigned to this species [*H. gravimanus*] by its author (Pocock, 1900: 91) ... Like Pocock, I have had an opportunity to examine the specimen from Tanjore as well as ... one from Sri Lanka and am convinced that both populations belong to the same species, which differs from *H. indus* in smaller size, narrower chela of pedipalp and the presence of five carinae on the manus of pedipalp.

Kovařík’s (2004) synonymy of *H. indus laevitensus* with *H. gravimanus*, repeated by Kovařík (2009) and Kovařík et al. (2016), appears to rest on the mistaken assumption that the specimen from Tanjore, also examined by Pocock (1990b) and Tikader and Bastawade (1983), is conspecific with material of *S. gravimanus* from Sri Lanka. Curiously, despite identifying the Tanjore male as *H. gravimanus*, Kovařík (2004: 27) identified a male from Palni Hills, India (SMF 5332/1), originally assigned to *Heterometrus (C.) granulomanus* by Couzijn (1981: 142) as *H. madraspatensis*. This completely depigmented specimen (fig. 230C, D) has 14/14 pectinal teeth and counts of pro- and retroventral spiniform macrosetae on the telotarsi of legs I–IV (3/4, 3/4 3–4/5, 4/5) that compare favorably with counts on legs III and IV (4/5–6) cited by Kovařík (2004) for the male from Tanjore, which also matches closely in the shape and macrosculpture of the carapace, pedipalp chela, metasoma and telson, despite its smaller size (fig. 230).

Based on comparison of the two specimens from Tanjore and Palni Hills, India, the holotypes of *H. indus* and *H. indus laevitensus*, as well as additional material of *S. gravimanus* and

S. indus from Sri Lanka, the validity of *S. gravimanus* is upheld, and *H. indus laevitensus* is determined to be conspecific with *S. indus* rather than *S. gravimanus*. However, the markedly different shapes and macrosculpture of the male pedipalp chelae, including the much weaker carinae of the previously misidentified Indian specimens, compared with *S. gravimanus*, justify their recognition as a distinct species.

Srilankametrus gravimanus (Pocock, 1894),
comb. nov.

Figures 10, 27E, F, 41E, F, 56I–L, 76C, 77C,
78C, 199, 234–237, table 1

Scorpio gravimanus Pocock, 1894a: 75–77;

Kovařík, 2004: 17.

Heterometrus caesar?: Kraepelin, 1899: 109, 114
(misidentification, part).

Palamnaeus gravimanus: Pocock, 1900a: 85, 90,
91 (part); Henderson, 1919: 381.

Pandinus gravimanus: Simon, 1905: 161 (part).

Heterometrus gravimanus: Takashima, 1945: 94
(part); Geethabali and Pampathi Rao, 1973:
189, 191–196, figs. 3–5; Root, 1990: 354;
Kovařík, 2004: 1, 2, 15, 17, 44, 51, table 2
(part); 2009: 35, 38, 47, table 1 (part); War-
burg, 2013: 152, 155; Kovařík et al., 2016: 1,
5, 10, 91–96, 100, 103, 115, 117, 120, 122,
figs. 15, 458–481, 572, 579, 580, 586, 587
(part); 2019a: 8, 12, figs. 40–42, 53.

Heterometrus (Srilankametrus) indus indus:

Couzijn, 1981: 82, 119, 121–124, 129, fig. 35
(misidentification, part).

Heterometrus (Srilankametrus) indus: Couzijn,
1981: 82, 94, 121, 123 (misidentification,
part).

Heterometrus (Srilankametrus) gravimanus:

Tikader and Bastawade, 1983: 545, 550, 552,
554, 555 (part); Kovařík, 1998: 137; Fet,
2000: 446 (part); Indra, 2001: 56–58 (part).

Heterometrus indus: Root, 1990: 354.

Heterometrus (Srilankametrus) indus laevitensus:
Kovařík, 2004: 15, 17; 2009: 38.

TYPE MATERIAL: **INDIA**: *Scorpio gravimanus*: Syntype ♀ (BMNH), "India" [lost]. **SRI LANKA**: *S. gravimanus*: Syntype ♂ (BMNH), Ceylon, R. Templeton [lost].

The types of *Scorpio gravimanus* were not seen by previous revisers (Couzijn, 1981: 121, Tikader and Bastawade, 1983: 550; Kovařík, 2004: 17) and could not be located during the present investigation. They are presumed lost.

DIAGNOSIS: *Srilankametrus gravimanus* may be separated from other species of *Srilankametrus* as follows. The carapace is vaulted, the lateral surfaces sloping steeply (fig. 27E, F), in *S. gravimanus* but slightly to markedly dorsoventrally compressed, the lateral surfaces sloping moderately to gently, in *S. indus*, *S. pococki*, and *S. serratus*. The interocular and posterior sutures are present, the posterior sutures extending past the median ocular tubercle and connected anteriorly to the posterior bifurcations of the interocular suture, in *S. gravimanus*, whereas the sutures are absent in *S. indus* and *S. pococki*. The carapace interocular surface is entirely smooth (fig. 27E, F) in *S. gravimanus*, whereas the frontal lobes and medial region of the interocular surface are granular with smooth areas in *S. caesar*. The carapace anterolateral and mediolateral surfaces are granular in *S. gravimanus* but smooth or nearly so in *S. indus*. The carapace posterolateral surfaces of the female are smooth or nearly so in *S. gravimanus* but granular in all other species except *S. yaleensis*. The pedipalp patella dorsomedian carina of the female is absent or obsolete in *S. gravimanus* but entirely to predominantly costate in *S. caesar*. The patella retrodorsal carina of the female is as strongly developed as or more strongly developed than the retromedian carinae in *S. gravimanus*, but absent or obsolete in *S. caesar*, *S. indus*, and *S. pococki*. The retromedian carinae of the female are absent or obsolete in *S. gravimanus* but present and granular in the other species. The

pedipalp chela of the adult male (fig. 236) is sparsely setose in *S. gravimanus* but moderately to densely setose in *S. indus* and *S. pococki*. The chela manus dorsal surface (between the dorsomedian and digital carinae) is curved and slightly to markedly convex in *S. gravimanus* but flat in *S. pococki*. The proximal margin (lobe) of the dorsal surface is moderately curved and aligned with the proximal margin of the condyle (articulation with patella) in *S. gravimanus* but markedly curved and proximal to the proximal margin of the condyle in *S. couzijni*. The dorsomedian carina is pronounced and costate on the chela fixed finger and distally on the manus in *S. gravimanus*, pronounced and costate on the fixed finger and distal three-quarters of the manus in *S. yaleensis*, and obsolete on the fixed finger and manus in *S. indus*, *S. pococki*, and *S. serratus*. The maximum distance between the dorsomedian and dorsal secondary carinae (DMC–DSC) of the chela manus is similar to the maximum distance between the dorsal secondary and digital carinae (DSC–DC) in the male (fig. 236) of *S. gravimanus* but greater than the DSC–DC in the male of the other species. The dorsal secondary and subdigital carinae of the male (fig. 236) are entirely to predominantly costate in *S. gravimanus* but entirely to predominantly granular in *S. caesar*, *S. couzijni*, and *S. serratus*, and absent or obsolete in *S. indus* and *S. pococki*. The digital carina is entirely to predominantly costate (figs. 236, 237) in *S. gravimanus*, entirely to predominantly granular in *S. caesar* and *S. serratus*, and absent or obsolete in *S. indus* and *S. pococki*. The retromedian carina of the male is entirely to predominantly costate in *S. gravimanus*, entirely to predominantly granular in *S. caesar* and *S. serratus*, and absent or obsolete in *S. indus* and *S. pococki*. The manus ventral surface is flat, with the axes of the retroventral and ventromedian carinae in approximately the same plane in *S. gravimanus*, but angled, with the axis of the retroventral carina ventral to the axis of the ventromedian carina in *S. indus* and *S. pococki*. Macroseta *st* on the



FIGURE 243. *Srilankametrus pococki*, sp. nov., holotype ♀ (AMNH), Kodigala, Sri Lanka, habitus: A. dorsal and B. ventral aspects. Scale bar = 10 mm.

retroventral surfaces of the basitarsi of legs I and II is spiniform (fig. 56I–L) in *S. gravimanus* but setiform in all other species except *S. caesar* and *S. serratus*. The lateral surfaces of mesosomal tergites I–VI are granular in *S. gravimanus* but smooth in *S. indus*, *S. pococki*, and *S. yaleensis*. The dorsosubmedian carinae are granular or costate-granular on metasomal segments I–IV (fig. 76C) in *S. gravimanus*, costate on I–IV in *S. indus*, and costate on I and II or I–III and granular or costate-granular on III and IV or IV in *S. yaleensis*. The ventral intercarinal surfaces of metasomal segment IV are granular in the male (fig. 78C) and smooth in the female of *S. gravimanus* but smooth in the male of *S. indus*, *S. pococki*, *S. serratus*, and *S. yaleensis*, and granular in the female of *S. caesar*. The dorsolateral carinae of metasomal segment V are distinct and continuous (fig. 77C) in *S. gravimanus* but obsolete and discontinuous to absent in *S. indus* and *S. pococki*. The dorsal intercarinal surface of metasomal segment V is granular in the male and female (fig. 76C) of *S. gravimanus*, but smooth in the male and female of *S. indus* and *S. pococki*, and the female of *S. serratus* and *S. yaleensis*. The telson is blackish, as dark as metasomal segment V, in *S. gravimanus* but dark reddish brown, paler than segment V, in *S. serratus* and *S. yaleensis*. The telson vesicle is elongate in *S. gravimanus* but globose in *S. indus*, *S. pococki*, and *S. serratus*.

DISTRIBUTION: This species is endemic to Sri Lanka, where it has been recorded from the North, North Central, North Western, and Southern provinces (fig. 199, table 1). Indian records are misidentifications of *S. couzijni*. The distribution of *S. gravimanus* overlaps that of *G. titanicus* but is allopatric with all other species of *Srilankametrus*.

ECOLOGY: This species inhabits deciduous forest at elevations of 20–230 m above sea level. It is fossorial and pelophilous, excavating very deep (20–70 cm), usually single-occupant burrows in sandy-loam soils, in open ground. Burrow entrances are oval or semicircular, and the

burrows almost vertical, curving once or twice as they descend. According to Kovařík et al. (2016), more than one individual may be found within a burrow, usually juveniles with their own chambers separate from the mother. The following scorpions occur in sympatry: the buthids *Buthoscorpio sarasinorum* (Karsch, 1891), *Charmus laneus*, *Isometrus maculatus*, *Isometrus thwaitesi*, *Lychas srilankensis*, *Reddyanus besucheti*, *Reddyanus loebli*; and the scorpionid *G. titanicus* (Kovařík et al., 2016).

REMARKS: As noted above, based on examination of material from Sri Lanka, including a male (MNHN RS 7759) misidentified as *H. (S.) indus* by Couzijn (1981), the validity of *S. gravimanus* is upheld. However, neither the holotype of *H. indus laevitensus*, allegedly from Madras, nor the specimens from Tanjore (BMNH 1896.7.30.121) and Palni Hills (SMF 5332/1), were found to be conspecific with *S. gravimanus*. Whereas the holotype of *H. indus laevitensus* is conspecific with *S. indus*, the Indian specimens are newly described as *S. couzijni*.

MATERIAL EXAMINED: SRI LANKA: North Central Prov.: Polonnaruwa Distr.: Parakramabahu, S of Polonnaruwa, near Samudraya Dam, 07°56'N 81°00'E, 69 m, 27–30.i.2014, L. Prendini and P. Horsley, dry forest with moderate canopy cover, sparse understorey and moderate leaf-litter layer on low rocky hill with large granite outcrops, excavated from burrows ca. 40–70 cm deep in open ground under forest canopy, 5 ♀, 3 subad. ♂, 1 subad. ♀, 3 juv. ♀ (AMNH), 1 juv. ♂ (AMCC [LP 12279]). **North Western Prov.: Puttalam Distr.:** Wilpattu, Kokmotte on Modaragam Aru River, 08°32'N 80°01'E, 30 m, 24–25.i.2014, L. Prendini and P. Horsley, mesic savanna/thicket and riverine forest near perennial river, many villus (small lakes), *Ficus*, *Acacia*, among other trees, moderate canopy, sparse understorey with leaf litter in places, sandy-loam soil, doorkeeping at burrow entrances in open ground, excavated from almost vertical burrows ca. 20–35 cm deep, 1 ♂, 2 ♀, 1 subad. ♂, 2 subad. ♀, 3 juv. ♂, 1 juv. ♀ (AMNH), 1 juv. ♂ (AMCC [LP 12280]). **Western Prov.: Gampaha Distr.:** Negombo [07°12'N 79°52'E], west coast, N of Colombo, 1 ♂ (MNHN RS 7759).

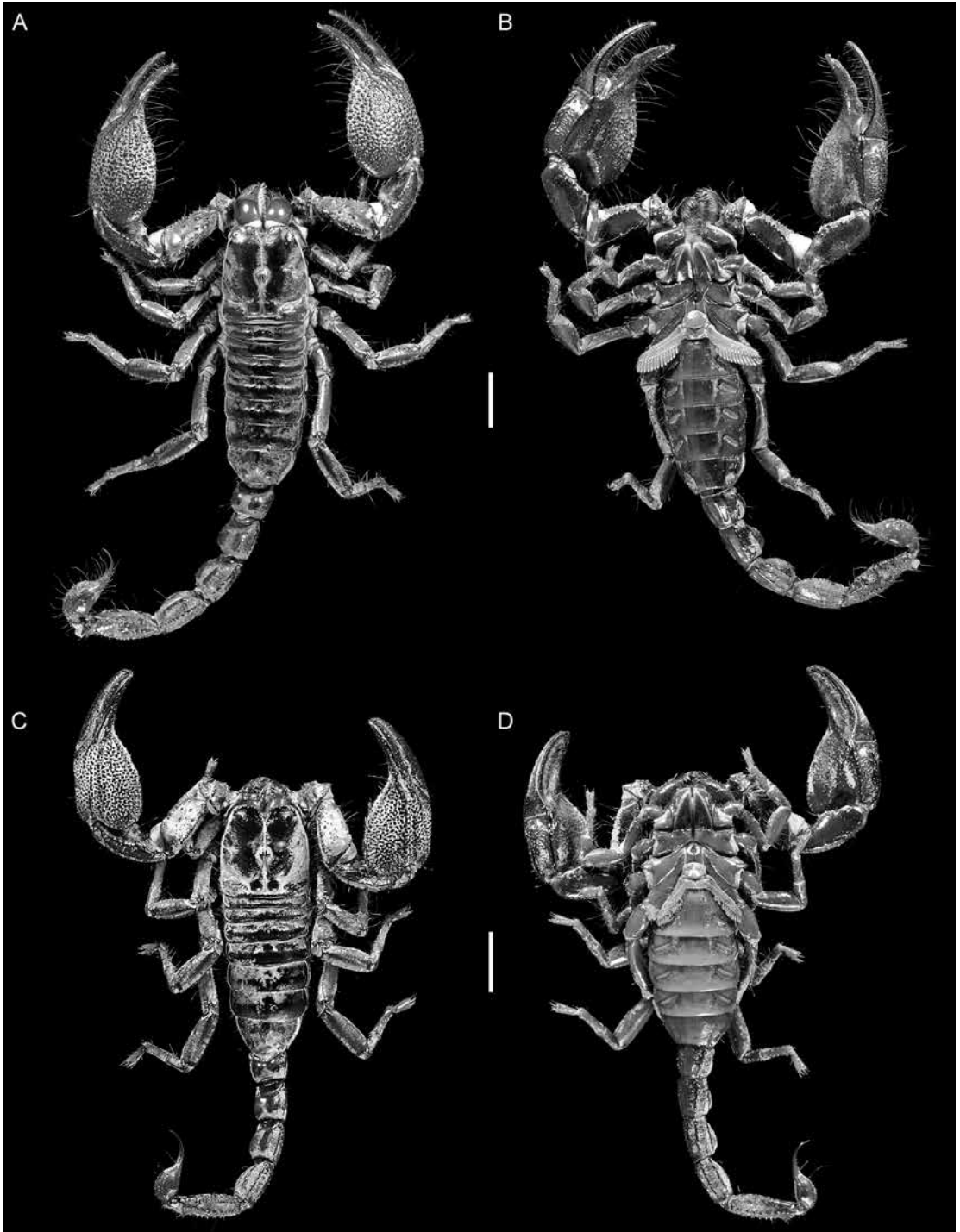


FIGURE 244. *Srilankametrus serratus* (Pocock, 1900), comb. nov., habitus: A, C. dorsal and B, D. ventral aspects. A, B. ♂ (ZMH), C, D. ♀ (ZMH), Ceylon [Sri Lanka]. Scale bars = 10 mm.

- Srilankametrus indus* (DeGeer, 1778),
comb. nov.
- Figures 7H, 9H, 8G, I, 10, 28A, B, 42A, B, 57A–D, 76D, 77D, 78D, 198, 238–242, table 1
- Scorpio afer* Linnaeus, 1758: 624 (part; synonymized by DeGeer, 1778: 341); 1767: 1038 (part); Fabricius, 1775: 399 (part); Linnaeus, 1775: 1091 (part); Fabricius, 1781: 550 (part); 1787: 348 (part); 1793: 434 (part); Herbst, 1800: 38–42 (part); Latreille, 1803: 267 (part); 1804: 120–122 (part); 1817: 106 (part); Dufour, 1856: 563, 571, 573, 574, 584, 590, 593, 614, 615, 622, 629, 631, 632, 641, 642, 644, 645, 648 (part).
- Scorpio indus* DeGeer, 1778: 341–343; 1783: 132–134; Kovařík, 2004: 2.
- Scorpio ceilonicus*: Herbst, 1800: pl. V, fig. 1.
- Scorpio ceylonicus* Herbst, 1800: 83, 84 (synonymized by Kraepelin, 1894: 46); Pocock, 1893: 308, 309; Kraepelin, 1894: 31, 46–51, 54, 55, 57, 240, 246, pl. I, fig. 29 (misidentification, part); Lönnberg, 1897b: 186 (misidentification); 1898a: 83; Couzijn, 1981: 129.
- Buthus afer* (nec *Scorpio afer* Linnaeus, 1758): C.L. Koch, 1836: 17–19 (misidentification, part); 1850: 87 (part).
- Buthus megacephalus* C.L. Koch, 1836: 73–75, pl. XCVII, fig. 224 (synonymized by Thorell, 1876b: 164, 168, 203, 204); Gervais, 1844a: 60; C.L. Koch, 1850: 88.
- Scorpio (Buthus) afer*: Gervais, 1844a: 60 (part).
- Scorpio (Buthus) ceylanicus*: Gervais, 1844a: 62.
- Heterometrus afer*: Simon, 1872b: 53, 59, 98–101 (misidentification, part).
- Pandinus megacephalus*: Thorell, 1876b: 164, 168, 203–205, 209–211 (misidentification); Karsch, 1884: 69; Thorell, 1893: 381, 382 (misidentification, part).
- Scorpio crassimanus* Becker, 1880: 140, 141, pl. III, fig. 1 (synonymized by Kraepelin, 1899: 113).
- Pandinus ceylonicus*: Karsch, 1884: 69.
- Scorpio megacephalus*: Pocock, 1893: 307, 309, 311.
- Palamnaeus ceylonicus*: Kraepelin, 1898: 439, 441.
- Heterometrus indus*: Kraepelin, 1899: 109, 113, 114 (part); Werner, 1902: 601; Lampe, 1918: 198; Roewer, 1929: 612 (part); Giltay, 1931: 8; Werner, 1934: 277 (part); Kästner, 1941: 233 (part), fig. 212; Roewer, 1943: 226 (misidentification, part); Takashima, 1945: 92; Bücherl, 1959: 269; Lourenço and Cloudsley-Thompson, 1996: 140, figs. 4, 5; Kovařík, 2004: 17, 20, 21, 32, 51, 52, table 2 (part); 2009: 35, 38, 47–49, 80, 100, 105, table 1 (part), figs. 50–56, 199, 200, 249–252; Javed et al., 2010a: 147; Tahir and Prendini, 2014: 11, 12; Kovařík et al., 2016: 1, 5, 10, 97–104, 106, 107, 110, 111, 115, 117–119 (part), figs. 15, 482–507, 573, 575, 577; 2019a: 12, fig. 53.
- Palamnaeus indus*: Pocock, 1900a: 96, 97, fig. 20A.
- Palamnaeus ndus*: Pocock, 1900a: 86.
- Heterometrus (Heterometrus) indus*: Couzijn, 1978: 330, table 1.
- Heterometrus (Srilankametrus) indus*: Couzijn, 1981: 80, 82, 94, 121, 123, 172, 181, figs. 21, 60, 66a (part); Tikader and Bastawade, 1983: 544; Kovařík, 1992: 185; 1998: 137, 138 (part); Fet, 2000: 446, 447 (part); Kovařík, 2002: 17 (part); 2004: 17.
- Heterometrus (Srilankametrus) indus indus*: Couzijn, 1981: 39, 82, 121–124, 129, 172, 191, table 7 (part), fig. 60; Vachon, 1982: 78, 79, 96, 101, 103–105, 110, figs. 50, 70–72, 75, 80, 81; Tikader and Bastawade, 1983: 550, 555, 561; Fet, 2000: 447.
- Heterometrus (Srilankametrus) indus laevitensus*: Couzijn, 1981: 39, 83, 124, 125, 172, 191, table 7, figs. 36, 60; Kovařík, 1998: 137; Fet, 2000: 447, 448; syn. nov.
- Heterometrus gravimanus*: Kovařík, 2004: 1, 2, 15, 17, 44, 51, table 2 (misidentification,

part); 2009: 35, 38, 47, table 1 (misidentification, part).

TYPE MATERIAL: *Buthus megacephalus*: 2 syntypes, probably East Indies [lost]. *Scorpio afer*: Syntypes [sex?], "Africa," [lost]. *Scorpio indus*: Holotype: 1 ♀ (NRS), "India" [examined]. *Heterometrus (Srilankametrus) indus laevitensus*: Holotype ♂ (MNHN RS 0089), Madras [examined]. **SRI LANKA:** *Scorpio ceylonicus*: Syntypes [sex?], Ceylon [lost]. *Scorpio crassimanus*: Holotype: 1 subad. ♀ (MRHNB [S.G. 38]), Netherlands Indies [examined; label in bottle: "Ceylan"].

According to the original description (Becker, 1880: 140), the holotype of *Scorpio crassimanus*, from "Indus néerlandaises," was deposited in the "Musée de Bruxelles." Kraepelin (1894) synonymized *S. crassimanus* with *H. indus*. A specimen from the MRHNB, previously examined by K. Kraepelin, and matching Becker's (1880) description and habitus illustration (pl. III, fig. 1) of *S. crassimanus*, e.g., in total length, carapace shape (including deep notch in anterior margin), granular pedipalp chela manus, and pectinal tooth counts, was examined during the present investigation. It was concluded to be the holotype of *S. crassimanus*, despite the absence of a label indicating the same, and the type locality given as "Ceylan" rather than "Indus néerlandaises." The Netherlands Indies is modern Indonesia. However, Ceylon (i.e., Sri Lanka) was also a Dutch colony until approximately 1800.

DIAGNOSIS: *Srilankametrus indus* may be separated from other species of *Srilankametrus* as follows. The carapace is markedly dorsoventrally compressed, the lateral surfaces sloping gently (fig. 28A, B), in *S. indus* but slightly dorsoventrally compressed, the lateral surfaces sloping moderately, in *S. serratus*, and vaulted, the lateral surfaces sloping steeply, in *S. caesar*, *S. couzijni*, *S. gravimanus*, and *S. yaleensis*. The interocular and posterior sutures are absent in *S. indus* but present, the posterior sutures extending past the median ocular tubercle and connected anteriorly to the posterior bifurcations of the interocular suture in all other species except *S. pococki*. The

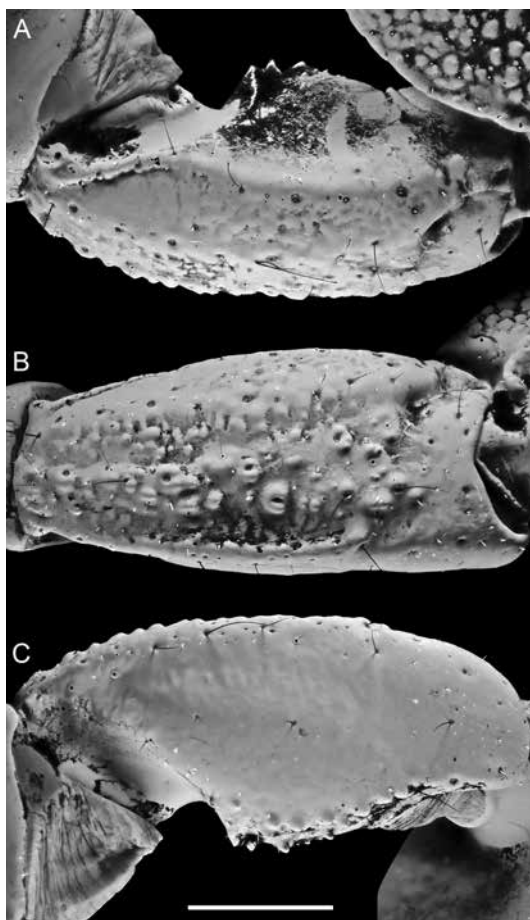


FIGURE 245. *Srilankametrus pococki*, sp. nov., holotype ♀ (AMNH), Kodigala, Sri Lanka, pedipalp patella: **A.** dorsal, **B.** retrolateral, and **C.** ventral aspects. Scale bar = 5 mm.

carapace interocular surface is entirely smooth (fig. 28A, B) in *S. indus* whereas the frontal lobes and medial region of the interocular surface are granular with smooth areas in *S. caesar*. The carapace anterolateral and mediolateral surfaces are smooth or nearly so in *S. indus* but granular in all other species. The carapace posterolateral surfaces of the female are granular in *S. indus* but smooth or nearly so in *S. gravimanus* and *S. yaleensis*. The pedipalp patella dorsomedian carina of the female is absent or obsolete in *S. indus* but entirely to predominantly costate in *S. caesar*. The patella retro-



FIGURE 246. *Srilankametrus pococki*, sp. nov., holotype ♀ (AMNH), Kodigala, Sri Lanka, pedipalp chela: A. retrodorsal, B. ventral, and C. prolateral aspects. Scale bar = 5 mm.

dorsal carina of the female is absent or obsolete in *S. indus* but as strongly developed as or more strongly developed than the retromedian carinae in *S. gravimanus*, *S. serratus*, and *S. yaleensis*. The retromedian carinae of the female are granular in *S. indus* but absent or obsolete in *S. gravimanus* and *S. yaleensis*. The pedipalp chela of the adult male (fig. 241) is moderately to densely setose in *S. indus* but sparsely setose in all other species except *S. pococki*. The chela manus dorsal surface (between the dorsomedian and digital carinae) is curved and slightly to markedly convex in *S. indus* but flat in *S. pococki*. The proximal margin (lobe) of the dorsal surface is moderately curved and aligned with the proximal margin of the condyle (articulation with patella) in *S. indus* but markedly curved and proximal to the proximal margin of the condyle in *S. couzijni*. The dorsomedian carina is obsolete on the chela fixed finger and manus in *S. indus*, pronounced and costate on the fixed finger and distally on the manus in *S. caesar*, *S. couzijni*, and *S. gravimanus*, and pronounced and costate on the fixed finger and distal three-quarters of the manus in *S. yaleensis*. The maximum distance between the dorsomedian and dorsal secondary carinae (DMC–DSC) of the chela manus is greater than the maximum distance between the dorsal secondary and digital carinae (DSC–DC) in the male (fig. 241) of *S. indus* but similar to the DSC–DC in the male of *S. gravimanus*. The dorsal secondary and subdigital carinae of the male (fig. 241) are absent or obsolete in *S. indus* but entirely to predominantly granular in *S. caesar*, *S. couzijni*, and *S. serratus*, and entirely to predominantly costate in *S. gravimanus* and *S. yaleensis*. The digital carina is absent or obsolete (figs. 241, 242) in *S. indus* but entirely to predominantly granular in *S. caesar* and *S. serratus*, and entirely to predominantly costate in *S. couzijni*, *S. gravimanus*, and *S. yaleensis*. The retromedian carina of the male is absent or obsolete in *S. indus* but entirely to predominantly granular in *S. caesar* and *S. serratus*, and entirely to predominantly costate in *S. couzijni*, *S. gravimanus*, and *S. yaleensis*. The manus ventral surface is angled, with the axis of the retroventral carina ventral to the axis of the ventro-

median carina in *S. indus*, but flat, with the axes of the retroventral and ventromedian carinae in approximately the same plane in all other species except *S. pococki*. Macroseta *st* on the retroventral surfaces of the basitarsi of legs I and II is setiform (fig. 57A–D) in *S. indus* but spiniform in *S. caesar*, *S. gravimanus*, and *S. serratus*. The lateral surfaces of mesosomal tergites I–VI are smooth in *S. indus* but granular in all other species except *S. pococki* and *S. yaleensis*. The dorsosubmedian carinae are costate on metasomal segments I–IV (fig. 76D) in *S. indus*, costate on I and II or I–III and granular or costate-granular on III and IV or IV, in *S. yaleensis*, and granular or costate-granular on I–IV in all other species. The ventral intercarinal surfaces of metasomal segment IV are smooth in the male and female (fig. 78D) of *S. indus* but granular in the male of *S. couzijni* and *S. gravimanus* and the male and female of *S. caesar*. The dorsolateral carinae of metasomal segment V are obsolete and discontinuous to absent (fig. 77D) in *S. indus* but distinct and continuous in all other species except *S. pococki*. The dorsal intercarinal surface of metasomal segment V is smooth in the male and female (fig. 76D) of *S. indus*, but granular in the male and female of *S. caesar* and *S. gravimanus*, and the male of *S. couzijni*, *S. serratus* and *S. yaleensis*. The telson is blackish, as dark as metasomal segment V, in *S. indus* but dark reddish brown, paler than segment V in *S. serratus* and *S. yaleensis*. The telson vesicle is globose in *S. indus* but elongate in *S. caesar*, *S. couzijni*, *S. gravimanus*, and *S. yaleensis*.

DISTRIBUTION: This species is endemic to Sri Lanka (fig. 198, table 1) and has been recorded only in the Central Province. The distribution of *S. indus* is allopatric with those of other species of *Srilankametrus*.

ECOLOGY: This species inhabits primary rainforest in the Knuckles Mountain Range in the central part of the island (fig. 7H). The locality records for which data are available vary from 220 m to 560 m above sea level. This species is fossorial and pelophilous, excavating moderately deep single-occupant burrows in hard, clayey soils, in earthen banks, under logs or stones

(Kovářík et al., 2016). Burrow entrances are characteristically broad and flat (fig. 8G, I). The following scorpions have been recorded in sympatry: the buthids *Buthoscorpio sarasinorum* and *Reddyanus ranawanai* Kovářík et al., 2016; and the scorpionid *G. titanicus* (Kovářík et al., 2016).

REMARKS: The following synonyms are recognized: *Scorpio afer* Linnaeus, 1758 (part) = *Srilankametrus indus* (DeGeer, 1778), comb. nov., synonymized by DeGeer (1778); *Scorpio ceylonicus* Herbst, 1800 = *S. indus*, synonymized by Kraepelin (1894); *Buthus megacephalus* C.L. Koch, 1836 = *S. indus*, first synonymized by Thorell (1876) not Kraepelin (1894) as stated by Fet (2000: 447); *Scorpio crassimanus* Becker, 1880 = *S. indus*, first synonymized by Kraepelin (1899) not Kraepelin (1894) as stated by Fet (2000: 447).

It is doubtful that *Buthus megacephalus* is synonymous with *S. indus*, based on characters in the original description and illustration, e.g., the narrower shape of the male pedipalp chela and reddish-brown coloration of the telson, compared with the black metasoma, consistent with several Indian species, but not *S. indus*. For example, Thorell (1893: 381) referred a specimen from Matheran, the type locality of *Deccanometrus obscurus*, to *Pandinus megacephalus*. In the absence of a type and a type locality, however, the true identity of *B. megacephalus* will never be verified. Additionally, *Buthus caesar* is not a synonym of *S. indus*, as proposed by Kraepelin (1894: 46) (as *Scorpio ceylonicus*) and Couzijn (1981: 123), nor is *Heterometrus* (*H.*) *spinifer solitarius* a synonym of *S. indus*, as proposed by Kovářík et al. (2016) (see above).

Fet (2000: 447) stated that Thorell (1893: 381) synonymized *Scorpio afer* with *S. indus*, but, as noted by Kovářík (2004), DeGeer (1778: 341) was the first to do so, and Thorell (1893) was followed by Kraepelin (1894: 53). Fet (2000: 447) also stated that Kraepelin (1894: 46) synonymized *B. megacephalus* and *S. crassimanus* with *S. indus*. However, Kraepelin (1894: 46) synonymized *B. megacephalus* and *S. crassimanus* with *S. ceylonicus*, not *S. indus*. As noted by Kovářík (2004, 2009), Thorell (1876b: 168) was the first to synonymize *B. megacephalus*

(as *Pandinus megacephalus* instead of *Buthus megacephalus*) with *S. indus* and Kraepelin (1899: 113) was the first to synonymize *S. crassimanus* with *S. indus*, followed by Couzijn (1981: 121). Kovářík (2004), also credited Lönnberg (1898a: 83) for synonymizing *B. megacephalus* with *S. indus* but, like Kraepelin (1894), Lönnberg (1898a) synonymized *B. megacephalus* with *S. ceylonicus*.

Kovářík (2004, 2009) stated that Kraepelin (1899: 113) and Pocock (1900a: 96) synonymized *S. ceylonicus* with *S. indus*, but Kraepelin (1894: 46) was the first to do so, as noted by Fet (2000: 447). Kraepelin (1894) recognized *S. ceylonicus* as a valid species and listed *S. indus* as a synonym thereof, despite being the older name.

As noted above, Kovářík (2004: 17) erroneously synonymized *H. indus laevitensus* with *H. gravimanus* based in part on the misidentification of a specimen from Tanjore, India, as *H. gravimanus*. Examination of the holotype of *H. indus laevitensus*, allegedly from Madras, revealed it to be conspecific with *S. indus*, rather than with the male from Tanjore, described above as the holotype of *S. couzijni*, or with Sri Lankan material of *S. gravimanus*. Kovářík's (2004) synonym is therefore rejected and the following new synonym presented: *Heterometrus* (*Srilankametrus*) *indus laevitensus* Couzijn, 1981 = *Srilankametrus indus* (DeGeer, 1778), syn. nov.

MATERIAL EXAMINED: **SRI LANKA:** i.1965, F. Layard, 2 ♂ (MCZ); Ceylan, 1 ♂ (MNHN RS 3245 [Simon coll. 5770]); Ceylan?, Dr. H. Mutvei, 1 ♀ (MNHN RS 8117). **Central Prov.:** *Kandy Distr.:* Kandy [07°17'N 80°38'E], 1902, Dr. Bedeker, 1 ♂ (MNHN RS 3263); Kandy, outskirts of Udawattakele, 07°18'N 80°38'E, 217 m, 30.i.2014, L. Prendini and P. Horsley, degraded tropical forest along roadcuts, UV light detection on warm, humid, moonless night, doorkeeping at burrow entrances in roadcuts and earthen banks, 3 ♀, 2 juv. ♂, 3 juv. ♀ (AMNH), 1 juv. ♀ (AMCC [LP 12282]); Kandy, Udawattakele, 07°18'N 80°38'E, 560 m, 31.i–4.ii.2014, L. Prendini and P. Horsley, primary tropical rainforest on steep hills, large trees with dense canopy and sparse understorey, moderate to thick leaf-litter layer, many rotten logs with rock outcrops and scattered stones in places, quartzite geology, coarse sandy-loam soil, in burrows in earthen banks, often at base of stones or under logs, some under large logs or

stones, 6 ♂, 9 ♀, 4 subad. ♂, 4 subad. ♀, 5 juv. ♂, 10 juv. ♀ (AMNH), 1 juv. ♀ (AMCC [LP 12283]); Paradeniya [Paradeniya, 07°16'N 80°36'E], vii.1914, B.H. Buxton, 2 ♂, 1 subad. ♂, 1 subad. ♀, 1 juv. ♀ (MNHN RS 0081).

Srilankametrus pococki, sp. nov.

Figures 8B, 10, 28D, 42D, 57E–H, 76E, 77E, 78E, 198, 243, 245, 246, tables 1, 3, 5

TYPE MATERIAL: **SRI LANKA:** **North Central Prov.:** *Anuradhapura Distr.:* Holotype ♀, paratypes: 3 subad. ♂, 2 subad. ♀, 3 juv. ♂, 3 juv. ♀ (AMNH), 1 juv. ♂, 1 juv. ♀ (IFS), 2 juv. ♀ (AMCC [LP 12281]), Ritigala, Kodigala Mountain, summit and rocky upper slopes, 08°07'N 80°39'E, 762 m, 6.ii.2014, L. Prendini and P. Horsley, many large granitic outcrops, moderate to thick leaf-litter layer, dense canopy cover with sparse understorey below summit, forest shorter and drier at summit, in burrows under stones, mostly on middle to upper slopes.

ETYMOLOGY: The specific epithet is a patronym honoring the English arachnologist, Reginald Innes Pocock (1863–1947), formerly of the British Museum of Natural History, London, for his many contributions to the knowledge of scorpions, including Heterometrinae (e.g., Pocock, 1900), and other arachnids.

DIAGNOSIS: *Srilankametrus pococki* may be separated from other species of *Srilankametrus* as follows. The carapace is markedly dorsoventrally compressed, the lateral surfaces sloping gently (fig. 28D) in *S. pococki* but slightly dorsoventrally compressed, the lateral surfaces sloping moderately in *S. serratus*, and vaulted, the lateral surfaces sloping steeply, in *S. caesar*, *S. couzijni*, *S. gravimanus*, and *S. yaleensis*. The interocular and posterior sutures are absent in *S. pococki* but present, the posterior sutures extending past the median ocular tubercle and connected anteriorly to the posterior bifurcations of the interocular suture in all other species except *S. indus*. The carapace interocular surface is entirely smooth (fig. 28D) in *S.*

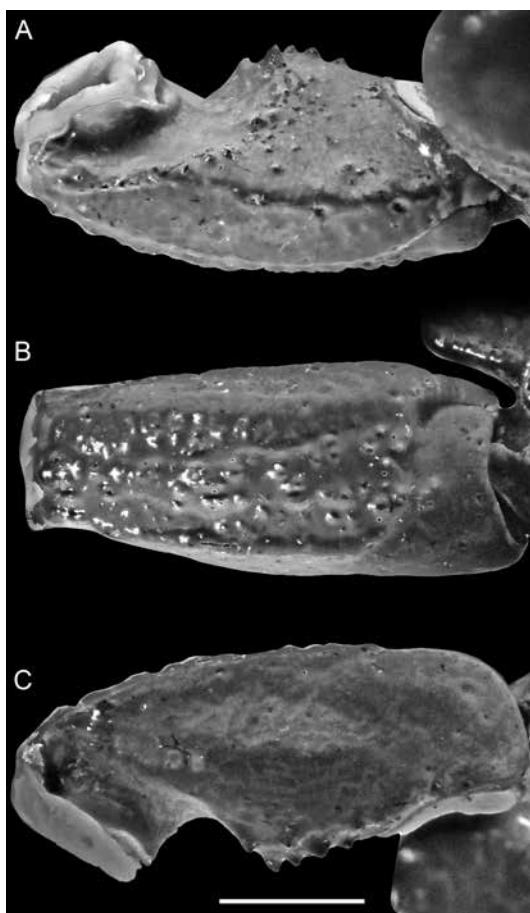


FIGURE 247. *Srilankametrus serratus* (Pocock, 1900), comb. nov., holotype ♂ (BMNH 1888.55), pedipalp patella: A. dorsal, B. retrolateral, and C. ventral aspects. Scale bar = 5 mm.

pococki whereas the frontal lobes and medial region of the interocular surface are granular with smooth areas in *S. caesar*. The carapace anterolateral and mediolateral surfaces are granular in *S. pococki* but smooth or nearly so in *S. indus*. The carapace posterolateral surfaces of the female are granular in *S. pococki* but smooth or nearly so in *S. gravimanus* and *S. yaleensis*. The pedipalp patella dorsomedian carina of the female (fig. 245) is absent or obsolete in *S. pococki* but entirely to predominantly costate in *S. caesar*. The patella retrodorsal carina of the female (fig. 245) is absent or obso-



FIGURE 248. *Srilankametrus serratus* (Pocock, 1900), comb. nov., holotype ♂ (BMNH 1888.55), pedipalp chela: **A.** retrodorsal, **B.** ventral, and **C.** prolateral aspects. Scale bar = 5 mm.

lete in *S. pococki* but as strongly developed as or more strongly developed than the retromedian carinae in *S. gravimanus*, *S. serratus*, and *S. yaleensis*. The retromedian carinae of the female are granular in *S. pococki* but absent or obsolete in *S. gravimanus* and *S. yaleensis*. The chela manus dorsal surface (between the dorsomedian and digital carinae) is flat (fig. 246) in *S. pococki* but curved and slightly to markedly convex in the other species. The proximal margin (lobe) of the dorsal surface is moderately curved and aligned with the proximal margin of the condyle (articulation with patella) in *S. pococki* but markedly curved and proximal to the proximal margin of the condyle in *S. couzijni*. The dorsomedian carina is obsolete on the chela fixed finger and manus in *S. pococki*, pronounced and costate on the fixed finger and distally on the manus in *S. caesar*, *S. couzijni*, and *S. gravimanus*, and pronounced and costate on the fixed finger and distal three-quarters of the manus in *S. yaleensis*. The maximum distance between the dorsomedian and dorsal secondary carinae (DMC–DSC) of the chela manus is greater than the maximum distance between the dorsal secondary and digital carinae (DSC–DC) in the male of *S. pococki* but similar to the DSC–DC in the male of *S. gravimanus*. The dorsal secondary and subdigital carinae of the male are absent or obsolete in *S. pococki* but entirely to predominantly granular in *S. caesar*, *S. couzijni*, and *S. serratus*, and entirely to predominantly costate in *S. gravimanus* and *S. yaleensis*. The digital carina is absent or obsolete (fig. 246) in *S. pococki* but entirely to predominantly granular in *S. caesar* and *S. serratus*, and entirely to predominantly costate in *S. couzijni*, *S. gravimanus*, and *S. yaleensis*. The retromedian carina of the male is absent or obsolete in *S. pococki* but entirely to predominantly granular in *S. caesar* and *S. serratus*, and entirely to predominantly costate in *S. couzijni*, *S. gravimanus*, and *S. yaleensis*. The manus ventral surface is angled, with the axis of the retroventral carina ventral to the axis of the ventromedian carina in *S. pococki*, but flat, with the axes of the retro-

ventral and ventromedian carinae in approximately the same plane in all other species except *S. indus*. Macroseta *st* on the retroventral surfaces of the basitarsi of legs I and II is setiform (fig. 57E–H) in *S. pococki* but spiniform in *S. caesar*, *S. gravimanus*, and *S. serratus*. The telotarsi are paler than the basitarsi in *S. pococki* but as dark as the basitarsi in *S. indus*. The lateral surfaces of mesosomal tergites I–VI are smooth in *S. pococki* but granular in all other species except *S. indus* and *S. yaleensis*. The dorsosubmedian carinae are granular or costate-granular on metasomal segments I–IV (fig. 76E) in *S. pococki*, costate on I–IV in *S. indus*, and costate on I and II or I–III and granular or costate-granular on III and IV or IV, in *S. yaleensis*. The ventral intercarinal surfaces of metasomal segment IV are smooth in the male and female (fig. 78E) of *S. pococki* but granular in the male of *S. couzijni* and *S. gravimanus* and the male and female of *S. caesar*. The dorsolateral carinae of metasomal segment V are obsolete and discontinuous to absent (fig. 77E) in *S. pococki* but distinct and continuous in all other species except *S. indus*. The dorsal intercarinal surface of segment V is smooth in the male and female (fig. 76E) of *S. pococki* but granular in the male and female of *S. caesar* and *S. gravimanus* and the male of *S. couzijni*, *S. serratus*, and *S. yaleensis*. The telson is blackish, as dark as metasomal segment V, in *S. pococki* but dark reddish brown, paler than metasomal segment V, in *S. serratus* and *S. yaleensis*. The telson vesicle is globose in *S. pococki* but elongate in *S. caesar*, *S. couzijni*, *S. gravimanus*, and *S. yaleensis*.

DESCRIPTION: The following description is based on the holotype and paratypes. Meristic data are presented in table 3. The adult male is unknown, hence, measurements are presented only for the adult female (table 5).

Total length: Adult large, maximum length, measured from anterior margin of carapace to tip of aculeus, 126 mm (♀).

Color: Chelicerae, dorsal surfaces bicolored, lightly infusate prodorsal half of manus paler than densely infusate retrodorsal half of manus

and fingers; manus slightly paler than carapace interocular surface. Carapace, pedipalps, tergites, metasoma, and telson entirely infusate, uniformly black to greenish black. Sternites III–VI, mostly or entirely infusate, dark brownish black; VII entirely infusate, black to greenish black. Coxosternal region infusate, brownish black, maxillary lobes darker. Legs infusate, black, similar to carapace, pedipalps, tergites, and metasoma (fig. 243), except telotarsi paler than preceding segments. Genital opercula and pectines uniformly pale olive-brown. Metasomal segments I–V similar to one another; carinae infusate, darker than intercarinal surfaces; dorsal intercarinal surfaces similar to tergites; ventral intercarinal surfaces similar to or darker than sternites. Telson vesicle as dark as metasomal segment V; aculeus black.

Chelicerae: Movable finger prodistal (DI) and retrodistal (DE) teeth unequal, with DE tooth considerably smaller than DI tooth, aligned longitudinally and not opposable. Fingers and manus, proventral surfaces with long, dense vestiture of macrosetae. Coxae, prodorsal surfaces without stridulatory setae (scaphotrix); promedian surfaces without chemoreceptive lamelliform setae (trichocopae).

Carapace: Carapace markedly dorsoventrally compressed, lateral surfaces sloping gently. Anterior margin straight, frontal lobes evenly rounded or truncate, with deep median notch, without median projection or median depression (fig. 28D). Anterolateral margins subparallel anteriorly, without distinct notch adjacent to posterior lateral ocelli; mediolateral margins diverging or converging slightly posteriorly (at posterolateral sulci). Anterior width of posterior width, 61% (♀); posterior width of length, 93% (♀). Three pairs of lateral ocelli (MLMa, PLMa, PDMi), all similar in size, two anterior pairs situated anteriorly, well separated from posterior pair, situated laterally. Median ocelli similar to lateral ocelli, distance between ocelli greater than or equal to width of ocellus; median ocular tubercle situated anteromedially, distance from anterior carapace margin, 50% (♀). Median longitudinal sulcus narrow,

suturiform; continuous from median notch to interocular sulcus; anteriorly furcated; without anterocular depression. Anterior furcated sulci diverging broadly from anterior edge of median longitudinal sulcus. Median ocular tubercle raised, superciliary carinae higher than ocelli, not extended anteriorly or posteriorly. Interocular sulcus present. Circumocular depressions completely encircling median ocular tubercle, converging anteriorly. Posteromedian and posteromarginal sulci deep. Paired mediolateral and posterolateral sulci shallow. Median longitudinal suture continuous from median notch to median ocular tubercle, equally strong along entire length; not extending to anterior margin of carapace, terminating at or posterior to median notch. Anterior furcated, anterocular, interocular, and posterior sutures absent. Interocular surface entirely smooth (fig. 28D); anterolateral, mediolateral, and posterolateral surfaces uniformly finely granular; postero-median surface smooth.

Pedipalps: Pedipalp short, pedipalp femur length : posterior carapace width ratio (FL:PCW) <0.77 , femur length : carapace length ratio (FL:CL) <0.74 . Femur width of length, 48% (♀). Retrodorsal carina complete, granular, similar to or more strongly developed than prodorsal carina. Dorsal secondary carina obsolete, comprising few isolated granules. Dorsomedian carina vestigial, reduced to prominent granule demarcated by conspicuous macroseta. Prodorsal carina complete, granular. Promedian carina complete, comprising row of spiniform or subspiniform granules (several demarcated by conspicuous macrosetae), oriented diagonally between prodorsal and proventral carinae. Proventral carina complete, granular, as strongly developed as or more strongly developed than retroventral carina. Ventromedian and secondary accessory carinae absent. Retroventral carina extending partly or entirely to distal edge of segment. Retromedian carinae absent, indicated only by macrosetal rows. Dorsal intercarinal surfaces finely granular; other surfaces smooth. Patella width of length, 51% (♀). Dorsal surface convex, axis of dorsomedian carina dorsal to

axis of retrodorsal carina. Dorsomedian carina obsolete (fig. 245). Retrodorsal carina obsolete, less strongly developed than granular retromedian carinae. Retroventral carina distinct, costate. Promedian carina vestigial, reduced to subspiniform granules, demarcated by conspicuous macroseta; promedian process absent. Other carinae absent. Intercarinal surfaces smooth. Chela short, broad (fig. 246); manus height of width, 109% (♀); manus length along retroventral carina of manus width, 130% (♀); manus length along retroventral carina of movable finger length, 69% (♀). Chela moderately to densely setose. Manus dorsal surface (between dorsomedian and digital carinae) flat; proximal margin (lobe) of dorsal surface moderately curved and aligned with proximal margin of condyle (articulation with patella). Dorsomedian carina obsolete, costate on fixed finger and comprising irregular row of spiniform granules, becoming obsolete proximally, on manus. Dorsal secondary, subdigital, digital, and retromedian carinae obsolete, granular, indistinguishable from granules of adjacent intercarinal surfaces. Maximum distance between dorsomedian carina and setal row demarcating dorsal secondary carina (DMC–DSC) greater than maximum distance between setal rows demarcating dorsal secondary and digital carinae (DSC–DC). Retrolateral secondary and secondary accessory carinae vestigial, proximal to condyle of movable finger. Retroventral carina distinct, costate. Ventromedian carina obsolete, costate. Proventral and promedian carinae similarly developed, each comprising row of spiniform granules and associated macrosetae. Prodorsal carina comprising irregular row of spiniform granules and associated macrosetae. Distance between dorsomedian and promedian carinae (DMC–PMC) slightly to markedly greater than distance between promedian and proventral carinae (PMC–PVC). Manus, dorsal and retrolateral intercarinal surfaces coarsely granular except for smooth depression at base of fixed finger; ventral intercarinal surface smooth; prolateral intercarinal surfaces smooth, except for few scattered

spiniform granules dorsodistally. Manus ventral surface angled, axis of retroventral carina ventral to axis of ventromedian carina. Fixed and movable fingers, intercarinal surfaces smooth; median denticle rows each with six enlarged retrolateral denticles (including terminal denticle), proximal three situated on lobes; first (proximal) lobe of fixed finger and second lobe of movable finger larger than others, with correspondingly deeper notches in movable and fixed fingers, respectively; terminal denticles of fingers interlocking unevenly when closed, movable finger displaced retrolaterally; distinct notch near tip of fixed finger to accommodate terminal denticle of movable finger.

Trichobothria: Orthobothriotaxic, Type C, with the following segment totals ($n = 12$): femur, 3 (1 d , 1 i , 1 e); patella, 19 (2 d , 1 i , 3 v , 13 e , comprising 3 et , 1 est , 2 em , 2 esb , 5 eb); chela, 26 (manus, 16, comprising 2 D , 10 E , 4 V ; fixed finger, 10, comprising 4 d , 4 e , 2 i). Total count of trichobothria per pedipalp: 48. Femur, i situated on dorsal surface. Patella, d_2 situated on internal surface, slightly closer to d_1 than to i ; distance v_2-v_3 less than half distance v_1-v_2 . Chela, distance $et-est$ ca. one-third distance $est-esb$; distance $est-esb$ greater than half distance $esb-eb$; est distal to d_{st} ; V_3 situated in medial third of manus, equidistant between V_2 than V_4 .

Legs: First pair of maxillary lobes (coxapophyses) tapering anteriorly, longer than and encircling second pair. Stridulatory organs, comprising “rasp” (granular tubercles) and “scraper” (stridulatory setae or scaphotrix), present on opposing surfaces of coxae of first pair of legs and pedipalps, respectively. Legs I–IV acarinate, except femora, with distinct pro- and retrolateral surfaces demarcated by partial to complete, granular proventral carinae. Femora, patellae, and tibiae, pro- and retrolateral surfaces each with scattered setiform macrosetae. Tibiae, prolateral surfaces, without spiniform macrosetae; I and II, retrolateral surfaces, each with two spiniform (t , st) macrosetae; III and IV, retrolateral surfaces, without spiniform macrosetae. Basitarsi I–IV, slightly dorsoventrally compressed; retrolateral

margins similar, unmodified, rounded; prolateral pedal spurs present (fig. 57E–H); retrolateral pedal spurs absent. Basitarsi, pro- and retrolateral surfaces, each with scattered long and short setiform macrosetae, and spiniform macrosetae, more numerous on I and II than III and IV. Basitarsi, spiniform macrosetae, I, retrolateral: *t, sb*; retroventral: *t, sb*; proventral: *t, st*; II, retrolateral: *t, sb*; retroventral: *t, sb*; proventral: *t, st*; III, retrolateral: *t, sb*; retroventral: *t, st*; proventral: *t*; prolateral: *t, st*; IV, retrolateral: *t*; retroventral: *t*; proventral: *t, st*; prolateral: *t, st*. Telotarsi I–IV short, stout, and distally broadened in dorsal and lateral views. Laterodistal lobes rounded. Dorsomedian lobes approximately equal to laterodistal lobes; each terminating in single setiform macroseta. Telotarsi, pro- and retrolateral surfaces, each with long and short, scattered macrosetae, not arranged in definite row. Telotarsi each with pro- and retroventral rows of spiniform macrosetae, two inserted on laterodistal lobes; counts in pro- and retroventral rows similar on I and II, and on III and IV ($n = 12$): I, proventral: 3, retroventral: 4; II, 3 (3 or 4), 4; III, 4 (3 or 4), 5; IV, 4, 5. Telotarsal ungues short, curved, equal to subequal; pseudonychium (dactyl) reduced, rounded or acuminate.

Sternum: Shape subpentagonal (fig. 42D). Median longitudinal sulcus shallow anteriorly, deep and narrow posteriorly.

Genital operculum: Genital opercula suboval, completely divided longitudinally, partially overlapping, genital papillae present (δ); subcordate, fused, genital papillae absent (φ) (fig. 42D).

Hemispermaphore: Unknown.

Pectines: Distal edge extending past distal edge of coxa IV but not reaching distal edge of trochanter IV (δ) or reaching to distal edge of coxa IV (φ) (fig. 42D). First proximal median lamella (scape) of each pecten with mesial margin angular, approximately 90° (δ) or straight to shallowly curved (φ). Pectinal teeth straight and elongate, present along entire posterior margin (δ) or shorter and curved, absent along proximal third (φ); sinistral/dextral tooth count, 12/12 (12 or 13/12 or 13, $n = 3$) (δ), 12/12 (12/11 or 12, $n = 3$)

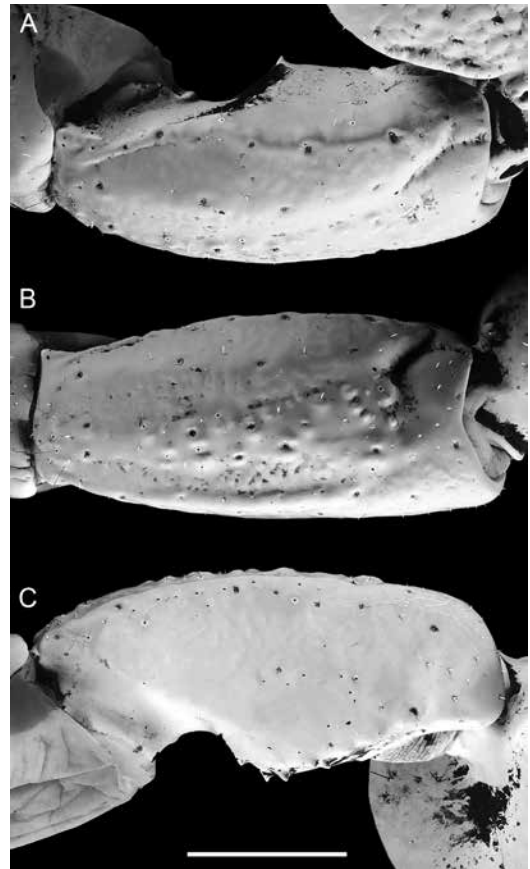


FIGURE 249. *Srilankametrus serratus* (Pocock, 1900), comb. nov., δ (FMNH 086 916), pedipalp patella: A. dorsal, B. retrolateral, and C. ventral aspects. Scale bar = 5 mm.

(φ). Fulcra smooth proximally but densely setose (microsetae only) distally.

Mesosoma: Tergites each with shallow pair of submedian depressions, without obsolete median carina. Pretergites and posttergites entirely smooth and glabrous. Sternites IV–VI, each with paired longitudinal depressions prolateral to spiracles, absent on VII. Surface, sternites III–VII, smooth; VII with pair of weakly developed, costate ventrolateral carinae only, without posteromarginal carina. Sternite VII, length of width, 66% (φ).

Metasoma and telson: Metasomal segments I–V progressively increasing in length, decreasing in width; segment V, width of segment I,



FIGURE 250. *Srilankametrus serratus* (Pocock, 1900), comb. nov., ♂ (FMNH 086 916), pedipalp chela: A. retrodorsal, B. ventral, and C. prolateral aspects. Scale bar = 5 mm.



FIGURE 251. *Srilankametrus serratus* (Pocock, 1900), comb. nov., ♀ (ZMH), Ceylon [Sri Lanka], pedipalp chela: A. retrodorsal, B. ventral, and C. prolateral aspects. Scale bar = 5 mm.

width, 62% (♀). Metasoma fairly robust, width of length, segment I, 102% (♀); II, 86% (♀); III, 78% (♀); IV, 57% (♀); V, 35% (♀). Telson vesicle, width of metasomal segment V, width, 96% (♀); vesicle globose, height of length, 57% (♀); dorsal surface flat; ventral surface evenly curved. Aculeus relatively long, gently curved, length of vesicle length, 72% (♀). Length metasoma and telson, of total length, 51% (♀). Dorsosubmedian carinae, segments I–IV, distinct, complete, granular or costate-granular, posterior spiniform granules obsolete (fig. 76E); V, vestigial. Dorsolateral carinae, segments I–V, distinct, complete, costate-granular on I–IV, costate-granular to granular on V. Median lateral carinae, segment I, incomplete, reduced to granular row in posterior half, diagonally oriented between dorsolateral and ventrolateral carinae (fig. 77E); II–IV, vestigial, each reduced to posterior granule, or absent; V, incomplete, granular row, restricted to anterior two-thirds. Ventrolateral and ventrosubmedian carinae, segments I–IV, distinct, complete, costate on I–III, granular or costate-granular on IV, more strongly developed on III and IV than on I and II (fig. 78E). Ventrolateral carinae, segment V, distinct, complete, comprising spiniform granules, diverging posteriorly, terminal granule slightly larger than preceding granules. Ventrosubmedian carinae, segment V, vestigial, each reduced to one or two isolated spiniform granules, demarcated by conspicuous macrosetae. Ventromedian carina, segment V comprising single row of spiniform granules, unmodified posteriorly. Anal arch, segment V, dorsal carina, costate; ventral carina comprising subspiniform granules. Intercarinal surfaces, segments I–V, smooth. Ventral surface, lateral aspect, segment IV, shallowly convex. Telson vesicle, dorsal and lateral surfaces smooth; ventral surface with four longitudinal carinae, each comprising spiniform granules.

DISTRIBUTION: This species is endemic to Sri Lanka and known only from the type locality in the North Central Province (fig. 198, table 1). The distribution of *S. pococki* is allopatric with those of the other species of *Srilankametrus*.

ECOLOGY: This species inhabits primary rain-forest on the Kodigala Mountain, at an elevation of 760 m above sea level, in the central part of the island. This species is fossorial and pelophilous, excavating moderately deep single-occupant burrows in hard, clayey soils under stones (fig. 8B). Burrow entrances are characteristically broad and flat. The following scorpions have been recorded in sympatry: the buthids *Isometrus maculatus*, *Isometrus thwaitesi*, *Reddyanus besucheti*, and *Reddyanus loebli*; and the chaerilid *Chaerilus ceylonensis*.

Srilankametrus serratus (Pocock, 1900),
comb. nov.

Figures 10, 28C, E, F, 42C, E, F, 57I–L, 76F, 77F, 78F, 198, 244, 247–251, table 1

Scorpio caesar: Pocock, 1894a: 73 (misidentification).

Heterometrus caesar: Kraepelin, 1899: 109, 114 (part); Roewer, 1943: 229 (part); Takashima, 1945: 92 (part).

Palamnaeus caesar: Pocock, 1900a: 86, 97 (part).

Palamnaeus serratus Pocock, 1900a: 86, 97;

Kovářík, 2004: 17, 19, 20, fig. 16.

Heterometrus serratus: Takashima, 1945: 94; Kovářík et al., 2016: 1, 5, 10, 103–108, 110, 111, 115, 117, 125, 126, figs. 15, 508–534, 571, 574, 593–595; 2019a: 12, fig. 53.

Heterometrus (Srilankametrus) indus: Couzijn, 1981: 82, 94, 121, 123 (misidentification, part); Kovářík, 1998: 137, 138 (part); Fet, 2000: 446, 447 (part).

Heterometrus (Srilankametrus) indus indus: Couzijn, 1981: 39, 82, 121–124, table 7 (misidentification, part); Fet, 2000: 447 (part).

Heterometrus (Srilankametrus) serratus: Tikader and Bastawade, 1983: 545, 555–561, figs. 1483–1496; Fet, 2000: 448.

Heterometrus indus: Kovářík, 2004: 17, 19, 20, 21, 32, 51, table 2 (misidentification, part),

fig. 16; 2009: 35, 38, 48, table 1 (misidentification, part).

Heterometrus (Srilankametrus) servatus: Majumder and Dey, 2005: 14 (misidentification).

TYPE MATERIAL: SRI LANKA: Holotype ♂ (BMNH 1888.55), Ceylon, Dr. Ondaatje [examined].

DIAGNOSIS: *Srilankametrus serratus* may be separated from other species of *Srilankametrus* as follows. The carapace is slightly dorsoventrally compressed, the lateral surfaces sloping moderately (fig. 28C, E, F) in *S. serratus*, but markedly dorsoventrally compressed, the lateral surfaces sloping gently, in *S. indus* and *S. pococki*, and vaulted, the lateral surfaces sloping steeply, in *S. caesar*, *S. couzijni*, *S. gravimanus*, and *S. yaleensis*. The interocular and posterior sutures are present, the posterior sutures extending past the median ocular tubercle and connected anteriorly to the posterior bifurcations of the interocular suture, in *S. serratus*, whereas the sutures are absent in *S. indus* and *S. pococki*. The carapace interocular surface is entirely smooth (fig. 28C, E, F) in *S. serratus* whereas the frontal lobes and medial region of the interocular surface are granular with smooth areas in *S. caesar*. The carapace antero-lateral and mediolateral surfaces are granular in *S. serratus* but smooth or nearly so in *S. indus*. The carapace posterolateral surfaces of the female are granular in *S. serratus* but smooth or nearly so in *S. gravimanus* and *S. yaleensis*. The pedipalp patella dorsomedian carina of the female is absent or obsolete in *S. serratus* but entirely to predominantly costate in *S. caesar*. The patella retrodorsal carina of the female is as strongly developed as or more strongly developed than the retromedian carinae in *S. serratus*, but absent or obsolete in *S. caesar*, *S. indus*, and *S. pococki*. The retromedian carinae of the female are granular in *S. serratus* but absent or obsolete in *S. gravimanus* and *S. yaleensis*. The pedipalp chela of the adult male (figs. 248, 250) is sparsely setose in *S. serratus* but moderately to densely setose in *S. indus* and *S. pococki*. The

chela manus dorsal surface (between the dorso-medial and digital carinae) is curved and slightly to markedly convex in *S. serratus* but flat in *S. pococki*. The proximal margin (lobe) of the dorsal surface is moderately curved and aligned with the proximal margin of the condyle (articulation with patella) (figs. 248, 250, 251) in *S. serratus* but markedly curved and proximal to the proximal margin of the condyle in *S. couzijni*. The dorsomedian carina is obsolete on the chela fixed finger and manus in *S. serratus*, pronounced and costate on the fixed finger and distally on the manus in *S. caesar*, *S. couzijni*, and *S. gravimanus*, and pronounced and costate on the fixed finger and distal three-quarters of the manus in *S. yaleensis*. The maximum distance between the dorsomedian and dorsal secondary carinae (DMC–DSC) of the chela manus is greater than the maximum distance between the dorsal secondary and digital carinae (DSC–DC) in the male (figs. 248, 250) of *S. serratus* but similar to the DSC–DC in the male of *S. gravimanus*. The dorsal secondary and subdigital carinae of the male (figs. 248, 250) are entirely to predominantly granular in *S. serratus* but entirely to predominantly costate in *S. gravimanus* and *S. yaleensis*, and absent or obsolete in *S. indus* and *S. pococki*. The digital carina is entirely to predominantly granular (figs. 248, 250, 251) in *S. serratus*, entirely to predominantly costate in *S. couzijni*, *S. gravimanus*, and *S. yaleensis*, and absent or obsolete in *S. indus* and *S. pococki*. The retromedian carina of the male is entirely to predominantly granular in *S. serratus*, entirely to predominantly costate in *S. couzijni*, *S. gravimanus*, and *S. yaleensis*, and absent or obsolete in *S. indus* and *S. pococki*. The manus ventral surface is flat, with the axes of the retroventral and ventromedian carinae in approximately the same plane in *S. serratus*, but angled, with the axis of the retroventral carina ventral to the axis of the ventromedian carina, in *S. indus* and *S. pococki*. Macroseta *st* on the retroventral surfaces of the basitarsi of legs I and II is spiniform (fig. 57I–L) in *S. serratus* but setiform in all other species

except *S. caesar* and *S. gravimanus*. The lateral surfaces of mesosomal tergites I–VI are granular in *S. serratus* but smooth in *S. indus*, *S. pococki*, and *S. yaleensis*. The dorsosubmedian carinae are granular or costate-granular on metasomal segments I–IV (fig. 76F) in *S. serratus*, costate on I–IV in *S. indus*, and costate on I and II or I–III and granular or costate-granular on III and IV or IV, in *S. yaleensis*. The ventral intercarinal surfaces of metasomal segment IV are smooth in the male and female (fig. 78F) of *S. serratus* but granular in the male of *S. couzijni* and *S. gravimanus*, and the male and female of *S. caesar*. The dorsolateral carinae of metasomal segment V are distinct and continuous (fig. 77F) in *S. serratus* but obsolete and discontinuous to absent in *S. indus* and *S. pococki*. The dorsal intercarinal surface of metasomal segment V is granular in the male (fig. 76F) but smooth in the female of *S. serratus*, smooth in the male of *S. indus* and *S. pococki*, and granular in the female of *S. caesar* and *S. gravimanus*. The telson is dark reddish brown, paler than metasomal segment V, in *S. serratus*, but blackish, as dark as segment V, in all other species except *S. yaleensis*. The telson vesicle is globose in *S. serratus* but elongate in *S. caesar*, *S. couzijni*, *S. gravimanus*, and *S. yaleensis*.

DISTRIBUTION: This species is endemic to Sri Lanka and has been recorded in the Southern and Uva provinces (fig. 198, table 1). Its distribution appears to overlap those of *G. titanicus*, *S. gravimanus*, and *S. yaleensis* and to be allopatric with the other two species of *Srilankametrus* occurring on the island.

ECOLOGY: *Srilankametrus serratus* inhabits deciduous forest on the coastal plains in the south of the island. The locality records for which data are available range from 40 m to 290 m above sea level (Kovářík et al., 2016). This species is fossorial and pelophilous, excavating single-occupant, straight, oblique burrows in hard, clayey soils, in earthen banks (Kovářík et al., 2016). The buthids *Isometrus maculatus* and *Reddyanus loebli* were recorded in sympatry.

CONSERVATION STATUS: *Srilankametrus serratus* is occasionally available in the exotic pet trade.

REMARKS: *Srilankametrus serratus* was synonymized with *S. indus* by Couzijn (1981) but revalidated and redescribed by Tikader and Bastawade (1983). Fet (2000) followed Tikader and Bastawade (1983) in regarding *S. serratus* as a valid species whereas Kovářík (1998, 2004, 2009) followed Couzijn (1981) in treating it as a synonym of *S. indus*. Recently, Kovářík et al. (2016: 110, 111) redescribed *S. serratus* based on new material from southern Sri Lanka and confirmed its validity as follows:

Pocock (1900: 86) differentiated *H. serratus* and *H. indus* as follows: 1) dorsal and dorsolateral carinae of metasomal segments granulated in *H. serratus*... smooth in *H. indus*.... We found other minor differences: 2) sexual dimorphism in proportions of pedipalps not noticeable in *H. indus*, male with slightly narrower chela than female in *H. serratus* (chela length to width ratio 1.79–1.94 in males, 1.69 in the females); 3) carapace smooth and glossy, only occasionally with granules at margins in *H. indus*; carapace smooth and glossy medially, always with more granules at margins in *H. serratus*... 4) spination formula of tarsomeres II of legs: 3/4 : 2–4/3–4 : 4/4–5 : 4/5 in *H. indus*; 3–4/4–6 : 4/4–5 : 4/5–6 : 4/5–7 in *H. serratus*.

Based on the present investigation, the species redescribed as *S. serratus* by Kovářík et al. (2016) is more closely related to *S. gravimanus* than to *S. indus* (fig. 10) but can be separated from both species by means of characters recounted in the key and diagnosis. These characters include Pocock's (1900a) original diagnostic difference in the macrosculpture of the metasomal carinae, as well as the difference in the distribution of carapace surface granulation, i.e., character 3, noted by Kovářík et al. (2016). The sexually dimorphic difference in proportions of the pedipalp chela of the male, i.e., character 2 of Kovářík et al. (2016), supports the closer relationship with *S. gravimanus*. On the other hand, the counts of telotarsal spiniform macrosetae (character 4) cannot be used to separate these species; the ranges given by Kovářík et al. (2016) for *S. indus* and *S. serratus*, as well as *S. gravimanus* (4/4–5, 4/5, 4/5–6, 4/5–6) overlap completely.

The adult male holotype of *S. serratus*, redescribed and illustrated by Tikader and Bastawade (1983) and again by Kovařík (2004, 2009), differs from the specimens from southern Sri Lanka, described by Kovařík et al. (2016), as well as material studied for the present investigation, in some respects. Firstly, the carapace shape of the holotype male of *S. serratus* more closely resembles *S. indus*, being broader and more markedly dorsoventrally compressed, than other *S. serratus* material from southern Sri Lanka examined in the present study, and cited by Kovařík et al. (2016), in which the carapace is longer and less dorsoventrally compressed. Secondly, the pedipalp chela manus of the holotype male of *S. serratus* is not noticeably narrower than the manus of an adult female, a character suggested by Kovařík et al. (2016); on the contrary, it is very broad, more closely resembling the adult male of *S. indus*. The spiniform macrosetal counts on the telotarsi of legs I–IV of the holotype, incorrectly cited as 5/6, 5/5–6, 5/6, 5/6 by Tikader and Bastawade (1983: 558), but verified as 4/5, 4/5, 4/5, 3–4/5 in the present study, fall within the range of the counts of *S. serratus* material from southern Sri Lanka cited by Kovařík et al. (2016), and four specimens from southern Sri Lanka in the FMNH examined during the present study (3 ♂: 4/4, 4/5, 4/5, 4/5; 4/5, 4/5, 4/5, 4/5; 3/4, 4/4, 4/5, 4/5; 1 subad. ♀: 3/4, 3–4/4, 4/5, 3–4/5) as well as within the range of counts for *S. gravimanus* and *S. indus* noted above. Therefore, although the species in southern Sri Lanka is clearly distinct from *S. gravimanus* and *S. indus*, it is unclear whether this species is, indeed, conspecific with the holotype of *S. serratus*, the precise type locality of which is unknown.

MATERIAL EXAMINED: **SRI LANKA:** Ceylon, E.C. Fernando, 1 ♂, 1 subad. ♀, 1 juv. ♂ (FMNH 086 264), 21.iv.1969, E.C. Fernando, 3 ♂ (FMNH 086 916), 1899, Dr. H. Driesch, 1 ♂, 1 juv. ♂, 1 juv. ♀ (ZMH), x.1912, 1 ♀, 1 juv. ♂ (ZMH ex Mus. Calcutta). **Southern Prov.: Galle Distr.:** between Bentota and Haburugala, 06°24'N 80°01'E, x.2016, A. Ullrich, 1 juv. ♀ (AMCC [LP 14058]). **Uva Prov.: Moneragala Distr.:** Warahana [06°27'N 81°27'E], Uva, Ceylon, xi.1962, E.C. Fernando, 1 subad. ♂, 1 subad. ♀ (FMNH 086 251).

Srilankametrus yaleensis (Kovařík et al., 2019),
comb. nov.

Figures 10, 199, table 1

Heterometrus yaleensis Kovařík et al., 2019a:

2–12, table 1, figs. 1–39, 43–53.

TYPE MATERIAL: SRI LANKA: Southern Province: Matara Distr.: Holotype ♂, paratype ♀ (FKPC), Yale National Park, 06°13'48.1"N 81°20'27.7"E, 7 m, 8–9.iii.2018, Kovařík et al. **Moneragala Distr.:** Paratype ♀ (FKPC), Yale National Park, 06°23'46.5"N 81°23'34.1"E, 40 m, 7–8.III.2018, Kovařík et al.

DIAGNOSIS: *Srilankametrus yaleensis* may be separated from other species of *Srilankametrus* as follows. The carapace is vaulted, the lateral surfaces sloping steeply, in *S. yaleensis* but slightly to markedly dorsoventrally compressed, the lateral surfaces sloping moderately to gently, in *S. indus*, *S. pococki*, and *S. serratus*. The interocular and posterior sutures are present, the posterior sutures extending past the median ocular tubercle and connected anteriorly to the posterior bifurcations of the interocular suture, in *S. yaleensis* whereas the sutures are absent in *S. indus* and *S. pococki*. The carapace interocular surface is entirely smooth in *S. yaleensis* whereas the frontal lobes and medial region of the interocular surface are granular with smooth areas in *S. caesar*. The carapace anterolateral and mediolateral surfaces are granular in *S. yaleensis* but smooth or nearly so in *S. indus*. The carapace posterolateral surfaces of the female are smooth or nearly so in *S. yaleensis* but granular in all other species except *S. gravimanus*. The pedipalp patella dorsomedian carina of the female is absent or obsolete in *S. yaleensis* but entirely to predominantly costate in *S. caesar*. The patella retrodorsal carina of the female is as strongly developed as or more strongly developed than the retromedian carinae in *S. yaleensis*, but absent or obsolete in *S. caesar*, *S. indus*, and *S. pococki*. The patella retromedian carinae of the female are absent or obsolete in *S. yaleensis* but granular in the other species. The pedipalp chela

of the adult male is sparsely setose in *S. yaleensis* but moderately to densely setose in *S. indus* and *S. pococki*. The chela manus dorsal surface (between the dorsomedian and digital carinae) is curved and slightly to markedly convex in *S. yaleensis* but flat in *S. pococki*. The proximal margin (lobe) of the dorsal surface is moderately curved and proximal to the proximal margin of the retrolateral surface but distal to the proximal margin of the condyle (articulation with patella) in *S. yaleensis*, whereas it is markedly curved and proximal to the proximal margin of the condyle in *S. couzijni*. The dorsomedian carina is pronounced and costate on the chela fixed finger and distal three-quarters of the manus in *S. yaleensis*, pronounced and costate on the fixed finger and distally on the manus in *S. caesar*, *S. couzijni*, and *S. gravimanus*, and obsolete on the fixed finger and manus in *S. indus*, *S. pococki*, and *S. serratus*. The maximum distance between the dorsomedian and dorsal secondary carinae (DMC–DSC) of the chela manus is greater than the maximum distance between the dorsal secondary and digital carinae (DSC–DC) in the male of *S. yaleensis* but similar to the DSC–DC in the male of *S. gravimanus*. The dorsal secondary and subdigital carinae of the male are entirely to predominantly costate in *S. yaleensis* but entirely to predominantly granular in *S. caesar*, *S. couzijni*, and *S. serratus*, and absent or obsolete in *S. indus* and *S. pococki*. The digital carina is entirely to predominantly costate in *S. yaleensis*, entirely to predominantly granular in *S. caesar* and *S. serratus*, and absent or obsolete in *S. indus* and *S. pococki*. The retromedian carina of the male is entirely to predominantly costate in *S. yaleensis*, entirely to predominantly granular in *S. caesar* and *S. serratus*, and absent or obsolete in *S. indus* and *S. pococki*. The manus ventral surface is flat, with the axes of the retroventral and ventromedian carinae in approximately the same plane in *S. yaleensis*, but angled, with the axis of the retroventral carina ventral to the axis of the ventromedian carina in *S. indus* and *S. pococki*. Macroseta *st* on the retroventral surfaces of the basitarsi of legs I and II is setiform in *S. yaleensis*

but spiniform in *S. caesar*, *S. gravimanus*, and *S. serratus*. The lateral surfaces of mesosomal tergites I–VI are smooth in *S. yaleensis* but granular in all other species except *S. indus* and *S. pococki*. The dorsosubmedian carinae are costate on metasomal segments I and II or I–III and granular or costate-granular on III and IV or IV, in *S. yaleensis*, costate on segments I–IV in *S. indus*, and granular or costate-granular on segments I–IV in all other species. The ventral intercarinal surfaces of metasomal segment IV are smooth in the male and female of *S. yaleensis* but granular in the male of *S. couzijni* and *S. gravimanus*, and the male and female of *S. caesar*. The dorsolateral carinae of metasomal segment V are distinct and continuous in *S. yaleensis* but obsolete and discontinuous to absent in *S. indus* and *S. pococki*. The dorsal intercarinal surface of metasomal segment V is granular in the male but smooth in the female of *S. yaleensis*, smooth in the male of *S. indus* and *S. pococki*, and granular in the female of *S. caesar* and *S. gravimanus*. The telson is dark reddish brown, paler than metasomal segment V, in *S. yaleensis* but blackish, as dark as segment V, in all other species except *S. serratus*. The telson vesicle is elongate in *S. yaleensis* but globose in *S. indus*, *S. pococki*, and *S. serratus*.

DISTRIBUTION: This species is endemic to Sri Lanka and presently known from only a few localities in the Southern Province (fig. 199, table 1). Its distribution appears to partially overlap those of *G. titanicus* and *S. serratus*, but is allopatric with the distributions of the other species of *Srilankametrus*.

ECOLOGY: This species is fossorial and pelophilous, excavating burrows in open terrain, 30–50 cm in length, curving once or twice (Kovářík et al., 2019a). The habitat illustrated (Kovářík et al., 2019a: 10, figs. 49, 50) is an open savanna formation with a sandy-loam substrate. Two other scorpion species were collected in sympatry: *Lychas srilankensis* and *Reddyanus basilicus* (Karsch, 1879).

REMARKS: This species is newly transferred to *Srilankametrus* based on phylogenetic analysis (fig. 10).

Subfamily Opisthophthalminae Rossi, 2016,
stat. nov.

Opisthophthalmini Rossi, 2016a: 20, 26, type
genus: *Opisthophthalmus* C.L. Koch, 1837.

Protophthalmini Rossi, 2016a: 20, 22, 26, type
genus: *Protophthalmus* Lawrence, 1969; syn.
nov.

DIAGNOSIS: Most species of Opisthophthalminae can be separated from the other subfamilies of Scorpionidae by means of the following characters (Prendini et al., 2003): cheliceral coxae with stridulatory setae (scaphotrix) on prodorsal surfaces and chemoreceptive lamelliform setae (trichocopae) on promedian surfaces. Opisthophthalminae can be further separated from Heterometrinae and Pandininae by means of the following characters: absence of a stridulatory organ, comprising a “rasp” (granular tubercles) and “scraper” (stridulatory setae or scaphotrix), on opposing surfaces of the coxae of the pedipalps and the first pair of legs; digital carina of pedipalp chela usually distinct; counts of pro- and retroventral spiniform macrosetae increasing from telotarsi I and II to III and IV. Opisthophthalminae can be further separated from Heterometrinae and Scorpioninae by means of the following character: pedipalps neobothriotaxic major, with more than 26 trichobothria (including more than 13 trichobothria in *e* series of patella).

INCLUDED TAXA: As redefined in the present contribution, a single genus, *Opisthophthalmus*, with 59 species (Prendini, 2001a), is currently recognized in Opisthophthalminae but the systematics of the subfamily is undergoing active revision by the first author. As discussed below, the synonymy of *Protophthalmus* by Newlands (1972a), confirmed by the phylogenetic analyses of Lamoral (1978a, 1979), Prendini (2000a) and Prendini et al. (2003), is upheld pending evidence to the contrary.

DISTRIBUTION: Africa: Angola, Botswana, Lesotho, Malawi, Mozambique, Namibia, South Africa, Swaziland, Tanzania, Zambia, Zimbabwe.

Opisthophthalminae are distributed from the Cape Peninsula of South Africa to Mount Kilimanjaro in Tanzania. The subfamily is absent from the tropical rainforests of the Congo basin and no records are known from north of the equator.

ECOLOGY: All species of Opisthophthalminae are obligate burrowers, constructing burrows under stones or in open ground (Purcell, 1899; Skaife, 1920; Lawrence, 1971, 1973; Newlands, 1972a, 1972b, 1978; Eastwood, 1978a, 1978b; Lamoral, 1978a, 1978b, 1979). As most are highly cannibalistic, cohabitation of multiple individuals within a single burrow (except during courtship or parental care) and/or the communal construction of burrows are absent (Eastwood, 1978a, 1978b). Burrows vary from shallow scrapes to elaborate, spiralling tunnels reaching depths of more than 1 m below the surface, depending on the species. Each species constructs burrows in substrata of specific hardness and composition, varying from unconsolidated sand dunes to compacted clayey soils, depending on the species (Newlands, 1972a, 1972b, 1978; Lamoral, 1978b, 1979). Several species have adapted to extremely rocky habitats (e.g., scree slopes) and virtually lost the ability to burrow, sheltering under stones instead (Purcell, 1899; Hewitt, 1925; Eastwood, 1978b). The ability of different species to burrow in substrata of specific hardness correlates closely with their morphology, such that a gradation of ecomorphotypes can be recognised, from lithophilous, through pelophilous, to psammophilous (Newlands, 1972a, 1972b, 1978; Eastwood, 1978b; Lamoral, 1979; Prendini, 2001d).

CONSERVATION STATUS: Habitat destruction through agriculture (ploughing), afforestation and urbanization poses the greatest threat to species of Opisthophthalminae, most of which are ecologically specialized (thus only occurring in pristine habitat), and range-restricted. Several are critically endangered, particularly in the Western Cape Province of South Africa.

The international trade in exotic pets poses a small, but ever-increasing threat to the future survival of Opisthophthalminae, given their increasing popularity as pets on the one hand,

and their often extremely restricted distributional ranges, together with the continued destruction of their habitat, on the other. Two species, *Opisthophthalmus glabrifrons* Peters, 1861 (the “Shiny burrowing scorpion”) and *Opisthophthalmus wahlbergii* (Thorell, 1876) (“Wahlberg’s Tri-colored scorpion”), allegedly imported from Mozambique, are commonly available in Europe, the United States, and Japan (Prendini et al., 2003). As the distribution of *O. wahlbergii* does not extend to Mozambique and the form offered occurs only in eastern Botswana and the Limpopo Province of South Africa, these scorpions are probably exported from one of the latter countries. A third species, *Opisthophthalmus boehmi* (Kraepelin, 1896), advertised as the “Tri-coloured scorpion” in the United States and as the “Kilimanjaro mustard scorpion” in Japan, is regularly imported from Tanzania (Dupré, 1992; Prendini et al., 2003).

REMARKS: Lawrence (1969) described *Protophthalmus* as a new genus with *Protophthalmus holmi* as type species. Newlands (1972a: 241) synonymized *Protophthalmus* with *Opisthophthalmus* while Lamoral (1972) described a second species, *Protophthalmus jenseni*. Lamoral and Reynders (1975) retained *P. holmi* and *P. jenseni* in *Protophthalmus* based on evidence available at the time. However, a phylogenetic analysis of morphological characters by Lamoral (1978a, 1979: 501) subsequently confirmed that *Protophthalmus* is congeneric with *Opisthophthalmus*:

In the distinctly tapered and fusiform distal crests of the distal lamina of their hemispermatophores, *Opisthophthalmus holmi* and *O. jenseni* share a character state uniquely derived in this genus. It was felt at some stage that such uniqueness provided sufficient distinctness to retain *holmi* and *jenseni* within Lawrence’s (1969: 105) genus *Protophthalmus*. The existence of several synapomorphies between the *holmi-jenseni* sister species and other species within the *wahlbergi* group has, however, prompted me not to reinstate the genus *Protophthalmus* as anticipated previously (Lamoral and Reynders, 1975: 569).

All subsequent phylogenetic analyses based on morphology and multilocus DNA sequences recovered the monophyly of *Opisthophthalmus*

and placed *Opisthophthalmus holmi* (Lawrence, 1969) in a distal position within it (Prendini, 2000a; Prendini et al., 2003), reinforcing the opinion of Lamoral (1979: 719) “that *Protophthalmus* is congeneric with *Opisthophthalmus* and that *holmi* and *jenseni* represent an extreme sister group separated from other species by a series of derived character states.”

Based solely on statements about “important characters,” and unsubstantiated by new evidence or analysis, Rossi (2016a: 18) revalidated *Protophthalmus* and erected two new tribes of Scorpioninae, in addition to the nominotypical tribe: Opisthophthalmini was created to accommodate *Opisthophthalmus* and Protophthalmini to accommodate *Protophthalmus*. Only three characters were offered to separate the putative tribes of Scorpioninae in Rossi’s (2016a: 26) key: total counts of pedipalp trichobothria (i.e., orthobothriotaxy vs. neobothriotaxy); counts of trichobothria on the ventral surface of the pedipalp chela manus; position of the median ocelli on the carapace.

Whereas total counts of the pedipalp trichobothria were correctly applied for the separation of *Scorpio* from the other scorpionid taxa, it was erroneously suggested that *Opisthophthalmus* usually possess more than three trichobothria on the ventral surface of patella. The high counts of trichobothria on the ventral surface of the pedipalp chela manus, cited as diagnostic for *Protophthalmus*, are autapomorphic and therefore phylogenetically uninformative (Prendini, 2000a; Prendini et al., 2003). Additionally, as noted by Lamoral (1979: 519, 658) and Prendini (2016: 52), it is inadvisable to use neobothriotaxic patterns as diagnostic characters for genera and species, in the absence of other characters, especially when trichobothrial counts are high, due to the greater instability of the patterns. With specific reference to neobothriotaxy in *O. holmi*, Lamoral (1979: 519) noted:

The frequency of...variations is higher in cases of marked (+) neobothriotaxies reaching levels where the trichobothriotaxies of certain segmental surfaces cease to be of interspecific value, e.g., the external trichobothria of the tibia [patella] in *Opisthophthalmus holmi* and

the ventral trichobothria of the tibia in species of *Hadogenes*.... While trichobothria have proved to be of diagnostic value in many taxa, trichobothriotaxy must be used with caution. Its value varies from group to group and both intra- and interspecific variation needs to be studied.

Finally, it was erroneously suggested that the position of the median ocelli is usually closer to the posterior border in *Opisthophthalmus*. On the contrary, the position of the median ocelli varies tremendously among the species of *Opisthophthalmus* and was disregarded as a diagnostic character for *Protophthalmus* by previous authors for that very reason (Newlands, 1972a; Lamoral, 1979, 1980; Prendini, 2000a, 2001a; Prendini et al., 2003).

The inclusion of *Opisthophthalmus* and *Protophthalmus* in Scorpioninae by Rossi (2016a) implies that these taxa form a monophyletic group with *Scorpio*, a relationship confirmed in only one phylogenetic analysis to date (Prendini, 2000a). However, that analysis formed part of a larger analysis of relationships within superfamily Scorpionoidea, based on exemplar species, and did not include molecular data. Analyses based on multilocus DNA sequence data and morphology, including more extensive sampling of scorpionid exemplars, failed to recover a monophyletic group comprising the type species of *Opisthophthalmus*, *Protophthalmus*, and *Scorpio* (Prendini et al., 2003). The evidence overwhelmingly suggests that Scorpioninae, as defined by Rossi (2016a), is paraphyletic, justifying the removal of Opisthophthalmini and its elevation to the rank of subfamily, i.e., Opisthophthalminae Rossi, 2016, stat. nov. Furthermore, pending evidence to the contrary, both *Opisthophthalmus* and Opisthophthalminae are rendered paraphyletic by *Protophthalmus* and Protophthalmini, justifying their synonymy as follows: *Protophthalmus* Lawrence, 1969 = *Opisthophthalmus* C.L. Koch, 1837, syn. nov.; Protophthalmini Rossi, 2016 = Opisthophthalminae Rossi, 2016, syn. nov.

Opisthophthalminae is the largest and most morphologically diverse subfamily of Scorpionidae (Prendini et al., 2003). Compared with the

other scorpionid subfamilies, Opisthophthalminae are characterised by numerous morphological apomorphies, many of which are also unique among scorpions. For example, most species of Opisthophthalminae possess organs for chemoreception and stridulation on the chelicerae that are absent in other scorpions (Pocock, 1896b; Purcell, 1899; Hewitt, 1915, 1918, 1925, 1931; Pavlovsky, 1924b; Skaife, 1920; Lawrence, 1928, 1971, 1973; Werner, 1934; Millot and Vachon, 1949; Alexander and Ewer, 1957; Alexander, 1958, 1959; Vachon et al., 1958, 1960; Dumortier, 1964; Sissom, 1990; Prendini, 2000a). A unique proximal displacement of the median ocelli on the carapace (Hewitt, 1925; Lawrence, 1969; Newlands, 1972a, 1978), from which the genus derives its Latin name (Skaife, 1920, 1954), is exhibited by many species of Opisthophthalminae. Most species also display peculiar, segmentally variable surface macrosculpture of the mesosomal sternites and ventral side of the first four metasomal segments, often associated with loss or reduction of the ventrosubmedian and ventrolateral metasomal carinae (Hewitt, 1918, 1925; Prendini, 2000b).

Among other characters, some species of Opisthophthalminae display exceptionally high pedipalp trichobothrial counts among scorpions, whereas others display exceptionally low pectinal tooth counts. The subfamily is further characterized by marked extremes in adult size, varying from among the largest known scorpion species such as *Opisthophthalmus gigas* Purcell, 1898, which commonly reaches 160 mm in length, to dwarves (including the smallest scorpionid species) such as *Opisthophthalmus pygmaeus* Lamoral, 1979, a mere 40 mm in length. Finally, many species in the subfamily display exaggerated sexual dimorphism in the shape of the pedipalp chelae (Purcell, 1899; Hewitt, 1918, 1925; Newlands, 1972a; Eastwood, 1978b; Prendini, 2000b), surface macrosculpture of the pedipalps, mesosoma, and metasoma, and the pectinal tooth counts (Hewitt, 1925; Lawrence, 1969; Newlands, 1972a; Lamoral, 1979).

Given the tremendous morphological diversity within Opisthophthalminae, attempts to parti-

tion the variation into subunits without the application of modern analytical methods and genomic sources of data (work that is actively underway) are even less likely to be successful than past attempts to do so among the taxa presently accommodated within Heterometrinae and Pandininae.

Subfamily Pandininae Thorell, 1876

Pandinini Thorell, 1876a: 11 (subfamily, part), type genus: *Pandinus* Thorell, 1876; 1876b: 84 (subfamily, part); Karsch, 1879a: 19 (subfamily, part); Thorell and Lindström, 1885: 25 (subfamily, part); Rossi, 2016a: 19, 20, 22, 26, 27.

Pandininae: Rossi, 2016a: 19, 20, 22, 26.

Pandinopsini Rossi, 2016a: 19, 20, 24, 26; syn. nov.

DIAGNOSIS: Pandininae are the sister group of Heterometrinae (Prendini, 2000a; Prendini et al., 2003). Both subfamilies share the following characters, by means of which they can be separated from Opisthophthalminae and Scorpioninae: presence of a stridulatory organ, comprising a “rasp” (granular tubercles) and “scraper” (stridulatory setae or scaphotrix), on opposing surfaces of the coxae of the pedipalps and the first pair of legs; similar counts of pro- and retroventral spiniform macrosetae on telotarsi I and II and III and IV. Pandininae can be separated from Heterometrinae by means of the following characters: pedipalps neobothriotaxic major, with more than 26 trichobothria (patella with more than 13 trichobothria in *e* series and more than 3 trichobothria in *v* series; chela usually with more than 4 trichobothria in *V* series and often with more than 2 trichobothria in *i* series); granular tubercles of “rasp” and stridulatory setae (scaphotrix) of “scraper” situated on coxae of pedipalp and first leg, respectively. Pandininae can be further separated from Opisthophthalminae by means of the following characters: cheliceral coxae without stridulatory setae (scaphotrix) on prodorsal surfaces and chemoreceptive lamelli-

form setae (trichocopae) on promedian surfaces. Pandininae can be further separated from Scorpioninae by means of the following characters: digital carina of pedipalp chela obsolete; pedipalps neobothriotaxic major, with more than 26 trichobothria.

INCLUDED TAXA: As redefined in the present contribution, Pandininae includes 44 species in seven genera (Prendini, 2001a, 2016; Kovařík et al., 2016, 2017b, 2017c, 2019b): *Pandiborellius* Rossi, 2015; *Pandinoides* Fet, 1997; *Pandinops* Birula, 1913; *Pandinopsis* Vachon, 1974, stat. nov.; *Pandipalpus* Rossi, 2015, stat. nov.; *Pandinurus* Fet, 1997; *Pandinus* Thorell, 1876.

DISTRIBUTION: Africa: Benin, Burkina Faso, Cameroon, Central African Republic, Chad, Congo, Côte d’Ivoire, Democratic Republic of Congo, Djibouti, Equatorial Guinea (including Bioko Island), Eritrea (including Daisei Island), Ethiopia, Gabon, the Gambia, Ghana, Guinea, Guinea-Bissau, Kenya, Liberia, Malawi, Mali, Mozambique, Nigeria, Niger, Senegal, Sierra Leone, Somalia, Sudan, Tanzania, Togo, Uganda, Zambia. Asia: Saudi Arabia, Yemen.

Pandininae are distributed from the tropical rainforest and mesic savanna of western and central Africa to the arid savanna and semidesert of eastern Africa and the southwestern Arabian Peninsula. Species of Pandininae have not been recorded from Burundi or Rwanda but may also occur in those countries.

Several authors (Lamoral and Reynders, 1975; Fet, 2000) cited the presence of *Pandipalpus viatoris* (Pocock, 1890) (as *Pandinus viatoris*) in Zimbabwe, apparently based on Hirst’s (1911) records from Petauke and Broken Hill [Kabwe]. Hewitt (1918: 152) also mentioned these records but noted that *P. viatoris* “is not known to the Rhodesian Museum from South Rhodesia [Zimbabwe].” Prendini et al. (2003: 234) discussed the putative records of *P. viatoris* from Zimbabwe, demonstrated that these records occur in Zambia (formerly Northern Rhodesia), and noted that there are no credible records of *Pandinus* south of the Zambezi River. Kovařík (2012: 19, fig. 64) did not cite Prendini et al. (2003) and erroneously plotted

three points for *P. viatoris* south of the Zambezi River, one in the extreme north of Zimbabwe (presumably, the specimen erroneously labelled “Mashonaland” [ZMB 35310]) and two in Mozambique, corresponding to the approximate locations of Tete and Beira, where this species does not appear to occur based on surveys by the first author. Rossi (2015a: 20, 21, 29) discussed the reliability of Kovařík’s (2012) Zimbabwean record, but apparently missed the point about the Zambezi River, as he did not mention the other two localities, and went on to describe *Pandinurus* (*P. prendinii* Rossi, 2015, from a single female, allegedly from Messina in the Limpopo Province of South Africa. Prendini (2016: 57) synonymized *P. prendinii* with *Pandinurus* (*P.*) *sudanicus* (Hirst, 1911) on the grounds that the meristic data listed as diagnostic for *P. prendinii* fall entirely within the ranges given for *P. sudanicus*. Additionally, Prendini (2016) noted that the suggestion that *P. prendinii* may represent a relictual population of Pandininae in southern Africa, and that, because the putative type locality is 5000 km from the known localities of *P. sudanicus*, this could justify its recognition as distinct from the latter, rests entirely on the grossly mistaken assumption that the locality data are trustworthy, an assumption doubted by others (Kovařík, 1997). Despite extensive surveys of scorpions throughout southern Africa by the first author, there are no credible records of Pandininae from south of the Limpopo River, let alone south of the Zambezi River (Prendini et al., 2003; Prendini, 2005, 2016).

ECOLOGY: Pandininae includes some of the largest extant scorpions, e.g., *Pandinopsis dictator* (Pocock, 1888) and *Pandinus imperator* (C.L. Koch, 1841), which can reach 170–200 mm in length (Vachon, 1952b; Newlands, 1987; Sissom, 1990). The ecology, behaviour and ecophysiology of *P. imperator* have been extensively studied (e.g., Toye, 1970; Garnier and Stockmann, 1973; Casper, 1985; Mahsberg, 1990). Burrows are preferentially constructed in termitaria and under stones or logs, and may contain up to 20 individuals, with the largest nearest the entrance (Toye, 1970; Polis and Lourenço, 1986; Mahsberg, 1990). Mixed age

groups of related and unrelated individuals cohabit with minimal aggression or cannibalism in laboratory terraria, and group living has been demonstrated to contribute significantly to post-embryonic growth rate and survival probability, especially among kin (Mahsberg, 1990; Kriesch, 1994). *Pandinus imperator* (C.L. Koch, 1841) is known for its unusual activity rhythms. Diurnal activity has frequently been observed in this species, which may appear on the surface in large numbers, especially after rains (Toye, 1970; Newlands, 1987).

Ecological data are unavailable for many species of Pandininae. However, the thickened metasoma, short, robust legs with stout, spini-form macrosetae distributed retrolaterally and distally on the basitarsi, and curved telotarsal ungues of most species are consistent with the fossorial, pelophilous ecomorphotype (Prendini, 2001b), as in *Pandinoides*, *Pandinops*, *Pandipalpus*, and, to a lesser extent, *Pandinopsis* and *Pandinus* (Newlands, 1987; Prendini et al., 2003; Kovařík, 2016; Prendini, 2016; personal obs.).

Pandinoides and *Pandipalpus viatoris* construct very deep burrows (up to 1 m) in hard, compacted clayey to sandy-clay soils using the chelicerae, first two pairs of legs, and metasoma. Burrow entrances are situated in open ground, often at the base of small bushes or shrubs. Burrows may be single entrance, occupied by a single individual, or composite and multientrance, containing multiple related individuals of overlapping generations which cohabit with minimal aggression or cannibalism (Newlands, 1987; Prendini, 2016; personal obs.). Burrows of the smaller *Pandinops*, usually constructed in sandy or clayey loam are usually shallower (40–50 cm deep), spiralling, and always with a single entrance and occupied by a single individual (Kovařík, 2016; L. Prendini, personal obs.). Some species of *Pandinops* approach the semipsammophilous ecomorphotype observed among some Opisthophthalminae, with the macrosetae on the basitarsi usually longer and more numerous than in *Pandinoides* and *Pandipalpus*.

Unlike *Pandinoides*, *Pandinops*, and *Pandipalpus*, species of *Pandiborellius* and *Pandinurus* appear to be lapidicolous, corticolous, or semilithophilous (Prendini, 2001b). Species of both genera for which data are available, e.g., *Pandiborellius awashensis* (Kovářík, 2012), *Pandiborellius insularis* Kovářík et al., 2017, *Pandiborellius magrettii* (Borelli, 1901), *Pandiborellius nistriae* (Rossi, 2014), *Pandinurus afar* Kovářík et al., 2017, *Pandinurus citernii* (Borelli, 1919), *Pandinurus platycheles* (Werner, 1916), and *Pandinurus trailini* (Kovářík, 2013), construct shallow burrows or scrapes under large stones (Kovářík, 2011, 2013; L. Prendini, personal obs.). Some species of *Pandinurus*, e.g., *Pandinurus exitialis* (Pocock, 1888), *Pandinurus fulvipes* Kovářík et al., 2019, *Pandinurus gregoryi* (Pocock, 1896), *P. trailini*, *Pandinurus phillipsii* (Pocock, 1896), and *Pandinurus smithi* (Pocock, 1899), also inhabit the cracks and crevices of rock outcrops, spaces under the peeling bark of fallen or standing trees, or the holes of tree trunks, up to 2 m above ground (Kovářík, 2011, 2013; Kovářík et al., 2019b; L. Prendini, personal obs.). Some of these species, especially *Pandinurus*, are partially dorsoventrally compressed, and exhibit elongation of the legs, reduction of the retrolateral row of spiniform macrosetae on the leg tibia, strongly curved ungues and, in some species, an enlarged, curved pseudonychium (dactyl) on the telotarsi. Similar characters occur in some Heterometrinae (notably *Heterometrus* and some *Chersonesometrus* and *Deccanometrus*) as well as arboreal chactids and hormurids, and are regarded as semilithophilous, corticolous and lapidicolous adaptations (Prendini 2001b).

CONSERVATION STATUS: *Pandinus imperator* (the “Emperor scorpion”), three species of *Pandinoides* (the “Red-claw scorpion”), i.e., *Pandinoides cavimanus* (Pocock, 1888), *Pandinoides duffmackayi* Prendini, 2016, *Pandinoides militaris* (Pocock, 1900), and, to a lesser extent, *Pandipalpus viatoris*, are readily available in Europe, the United States, and Japan for the international

trade in exotic pets. Most of these appear to originate from Ghana, Côte d’Ivoire, and Togo (*P. imperator*) and Tanzania (*P. cavimanus* and *P. duffmackayi*). *Pandiborellius awashensis* and *Pandinops hawkeri* (Pocock, 1900), from Ethiopia, have occasionally been offered for sale in the United States, and *Pandinus ugandaensis* Kovářík, 2011, from Uganda, has been offered in Germany (Prendini et al., 2003; L. Prendini, personal obs.). Dupré (1992) records the importation of *P. dictator* into France from Cameroon and that of *P. militaris* (as *P. cavimanus*) from Kenya. *Pandinus imperator* is the most common species of scorpion in the exotic pet trade, for which an extensive literature on captive husbandry and breeding exists (e.g., Larrouy et al., 1973; Garnier, 1974; Hull-Williams, 1986; Krapf, 1988; Copeland, 1990; Dupré, 1990; Montambaux, 1996; Schiejok, 1997; Mahsberg et al., 1999; Rubio, 2000).

As with Heterometrinae, wild populations of Pandininae are vulnerable to overharvesting for the exotic pet trade due to their long gestation period (at least 7 mo.), small brood sizes (30–35), and longevity (4–7 yr to sexual maturity) (Vachon et al., 1970; Larrouy et al., 1973; Polis and Lourenço, 1986; Mahsberg, 1990; Polis and Sissom, 1990). Furthermore, wild populations are threatened not only by overexploitation but by continuing destruction of their habitat through deforestation and agriculture.

The decline in *P. imperator* may be partially alleviated by its CITES status (IUCN 1994; Lourenço and Cloudsley-Thompson, 1996), which has led to the issuing of export quotas in several West African countries (e.g., Benin, Chad, Niger, and Togo), and the ease with which this species may be bred in captivity. However, it is unclear whether the CITES status has had any real impact in protecting the remaining wild populations, because wild-caught specimens continue to be advertised alongside captive-bred specimens by major dealers. Moreover, although two other closely related species, *P. dictator* and *P. gambiensis*, were also provided CITES status, these are seldom available in the pet trade

whereas others that are (especially species of *Pandinoides*) have no CITES status. The conservation status of most species of Pandininae is presently unknown, but the restricted ranges of most are cause for concern. Species of *Pandinoides*, in particular, should be CITES listed (Prendini, 2016).

REMARKS: Extensive work on the systematics of the taxa presently assigned to Pandininae was conducted by several authors during the past two decades (Kovářík, 2000, 2003, 2009, 2011, 2012, 2013, 2016, 2017; Prendini, 2000b, 2004, 2016; Prendini et al., 2003; Lourenço, 2014; Rossi, 2014a, 2014b, 2014c, 2014d, 2015a, 2015b, 2015c, 2016a, 2016b; Kovářík et al., 2017b, 2017c, 2019b). A history and critique of the taxonomy of the group, summarizing all developments to that point and providing several amendments to the classification, was presented by Prendini (2016). Rossi (2016a, 2016b) meanwhile presented another revised classification, followed by an attempted rebuttal of Prendini's (2016) critique. Kovářík et al. (2017b) followed with yet another revised classification and critique of Rossi's (2016a) classification. Whereas Rossi (2016a) recognized seven genera and six subgenera (three nominotypical), arranged into three tribes (one nominotypical) of subfamily Pandininae, Kovářík et al. (2017b) recognized five genera and three subgenera (one nominotypical), without tribes, in subfamily Scorpioninae, following the long-discredited classification of Sölgård and Fet (2003a), according to which Diplocentridae and Urodacidae are treated as subfamilies of Scorpionidae despite overwhelming evidence dating back three decades (Stockwell, 1989; Prendini, 2000a) that Scorpionidae, so construed, is a paraphyletic assemblage. Aside from disagreements in the suprageneric ranks, the primary differences between the classifications of Pandininae by Rossi (2016a) and Kovářík et al. (2017b) boil down to the recognition of three genera, *Pandicaporiaccous* Rossi, 2015, *Pandinopsis* and *Pandipalpus*, and three subgenera, *Pandinurus* (*Pandipavesius*) Rossi, 2015, and *Pandinus*

(*Pandinoriens*) Rossi, 2015, and *Pandinoides* (*Dunlopandinoides*) Rossi, 2016, by Rossi (2016a) but not by Kovářík et al. (2017b).

Prendini (2016) previously synonymized *Pandinurus* (*Pandicaporiaccous*) Rossi, 2015, with *Pandinurus* (*Pandiborellius*) Rossi, 2015, and both Rossi (2016a) and Kovářík et al. (2017b) elevated *Pandiborellius* to the rank of genus, hence *Pandinurus* (*Pandicaporiaccous*) Rossi, 2015 = *Pandiborellius* Rossi, 2015, syn. nov. Additionally, Kovářík et al. (2017b) synonymized *Pandinurus* (*Pandipavesius*) with *Pandiborellius* and *Pandinus* (*Pandinoriens*) Rossi, 2015, with *Pandinurus*, decisions that appear well justified. Kovářík et al. (2017b) did not address *Pandinoides* (*Dunlopandinoides*), but it is evident from both the diagnosis and examination of the type material (2 ♂, ZMB 15009) that this subgenus, justified solely on the slightly shallower concavity in the male pedipalp chela manus in its type species, cannot be upheld. Accordingly, *Pandinoides* (*Dunlopandinoides*) Rossi, 2016 = *Pandinoides* Fet, 2000, syn. nov.

The decision by Kovářík et al. (2017b) to recognize *Pandinopsis* and *Pandipalpus* as subgenera of *Pandinus* in the face of evidence to the contrary is unjustifiable, however; their recognition as subgenera of *Pandinus* became untenable with the removal and elevation to the equivalent rank of genus of other former subgenera, i.e., *Pandinoides*, *Pandinops*, and *Pandinurus*. The inclusion of *P. dictator* and the two species of *Pandipalpus* within *Pandinus* renders the latter paraphyletic, as demonstrated in phylogenetic analyses based on morphology and multilocus DNA sequence data, which recovered *P. viatoris* monophyletic with *P. cavimanus* to the exclusion of *P. imperator*, and *P. imperator* monophyletic with *P. cavimanus* and *P. viatoris* to the exclusion of *P. dictator* (Prendini, 2000a; Prendini et al., 2003; unpublished data). In order to restore the monophyly of *Pandinus*, these taxa are hereby elevated to the rank of genus, *Pandinopsis* Vachon, 1974, stat. nov., and *Pandipalpus* Rossi, 2015, stat. nov., resulting in two new combinations: *Pandinopsis dictator* (Pocock, 1888), comb. nov., and *Pandipalpus viatoris* (Pocock,

1890), comb. nov. Any other course would obviously require all currently recognized genera of Pandininae to be relegated to subgenera of *Pandinus*, as originally proposed by Vachon (1974), with some adjustments.

Unpublished data, indicating that *Pandipalpus*, *Pandinoides*, and *Pandinops* form a monophyletic group, to the exclusion of other genera of Pandininae, imply that Pandinini, as defined by Rossi (2016a), is also paraphyletic, justifying the following synonymy: Pandinopsini Rossi, 2016 = Pandininae Thorell, 1876, syn. nov. It is also evident, based firstly on the absence of consistent morphological differences, and secondly on low genetic divergence between samples collected at the type locality of *Pandinus lowei* Kovařík, 2012, and across the distribution of *P. viatoris* (unpublished data), that these taxa are conspecific, justifying the following synonymy: *Pandinus lowei* Kovařík, 2012 = *Pandipalpus viatoris* (Pocock, 1890), syn. nov. Consequently, *Pandinurus* (*Pandipalpus*) *pygmaeus* Rossi, 2015 = *Pandipalpus viatoris* (Pocock, 1890), syn. nov., as originally proposed by Prendini (2016). The same is true for two Ethiopian species of *Pandinurus*, described from the same type locality, which are synonymized accordingly: *Pandinus intermedius* Borelli, 1919 = *Pandinurus citernii* (Borelli, 1919), syn. nov.

Subfamily Scorpioninae Latreille, 1802

Scorpionides Latreille, 1802: 46, 47 (part), type genus: *Scorpio* Linnaeus, 1758; 1804: 110 (part); 1806: 130 (part); 1810: 116, 118 (part); Leach, 1814: 412; 1815: 390; Latreille, 1817: 310 (“tribe,” i.e., part); 1825: 310 (“tribe”; part); Sundevall, 1833: 29 (part).
Scorpionini: Peters, 1861: 510 (part); Lankester, 1885: 379 (subfamily, part); Pocock, 1893: 305 (subfamily); Kraepelin, 1894: 24 (subfamily); Laurie, 1896b: 128 (subfamily); Pocock, 1900a: 84; Rossi, 2016a: 20, 26.
Scorpioninae: Kraepelin, 1899: 106; 1901: 270; 1905: 344; Birula, 1917a: 161; 1917b: 59;

Kopstein, 1921: 128; 1926: 111; Pavlovsky, 1924a: 78, 79; 1925: 192; Werner, 1934: 277; Kästner, 1941: 233; Millot and Vachon, 1949: 428; Bücherl, 1964: 59; Lamoral, 1979: 668; Levy and Amitai, 1980: 102; Tikader and Bastawade, 1983: 518; Lourenço, 1989: 174; Sissom, 1990: 131; Fet, 2000: 430, 431; Indra, 2001: 56; Bastawade, 2002: 295; Soleglad and Fet, 2003a: 56, 86, 88, 112–115, 117, 120, 140, tables 9, 11, appendix A; Prendini et al., 2003: 185, 186, 212, table 1; Bastawade, 2004: 290; Bastawade et al., 2004: 47, 57; Bastawade, 2005: 417; Bastawade et al., 2005: 72, 82; Fet and Soleglad, 2005: 9, 13; Soleglad et al., 2005: 1, 2, 3, 5, 6, 8, 20, 21, 26, 28–30, 33–35, tables 1, 6, figs. 72–74; Thulsi Rao et al., 2005: 3, 8; Sureshan et al., 2007a: 2906; 2007b: 52; Bastawade and Borkar, 2008: 218; Indra, 2009: 141; Kovařík, 2009: 1, 2, 5, 17; Prendini, 2009: 17, 32, 34, 40, tables 1, 3, fig. 6; Veronika et al., 2013: 72; Rossi, 2016a: 18, 20, 22, 26; Kovařík et al., 2017b: 1, 6; Esposito et al., 2018: 115, appendix 1.
Scorpionaria: Birula, 1917a: 161 (“tribus”).

DIAGNOSIS: Scorpioninae can be separated from Heterometrinae and Pandininae by means of the following characters (Prendini et al., 2003): absence of a stridulatory organ, comprising a “rasp” (granular tubercles) and “scraper” (stridulatory setae or scaphotrix), on opposing surfaces of the coxae of the pedipalps and the first pair of legs; digital carina of pedipalp chela usually distinct; counts of pro- and retroventral spiniform macrosetae increasing from telotarsi I and II to III and IV. Scorpioninae can usually be further separated from Heterometrinae by means of the following character: sternite VII with paired ventrosubmedian and ventrolateral carinae. Scorpioninae can be further separated from Pandininae by means of the following character: pedipalps orthobothriotaxic, with 26 trichobothria (patella with 13 trichobothria in *e* series and 3 trichobothria in *v* series; chela with 4 trichobothria in *V*

series and 2 trichobothria in *i* series). Scorpioninae can be separated from Opisthophthalminae by means of the following characters: pedipalps orthobothriotaxic, with 26 trichobothria (including 13 trichobothria in *e* series of patella); cheliceral coxae without stridulatory setae (scaphotrix) on prodorsal surfaces and chemoreceptive lamelliform setae (trichocopae) on promedian surfaces.

INCLUDED TAXA: As redefined in the present contribution, Scorpioninae comprises a single genus, *Scorpio* Linnaeus, 1758, with 17 species and at least four subspecies (Fet, 2000; Kovařík, 2009; Lourenço, 2009; Lourenço and Cloudsley-Thompson, 2009, 2012; Lourenço et al., 2012; Talal et al., 2015; Lourenço and Rossi, 2016).

DISTRIBUTION: Africa: Algeria, Benin, Cameroon, Chad, Egypt (including Sinai), Eritrea, Ethiopia, Libya, Mauritania, Morocco, Niger, Senegal, Sudan, Tunisia. Asia: Iraq, Iran, Israel and the Palestinian territories, Jordan, Kuwait, Lebanon, Qatar, Saudi Arabia, Syria, Turkey, Yemen.

The broad distribution of *Scorpio* extends across the Sahel from Senegal, Niger and Benin in West Africa, through northern Cameroon, to Sudan and northern Ethiopia, and from Morocco, along the Mediterranean to Egypt, the northern part of the Arabian Peninsula, and the Middle East as far north as southern Turkey and as far east as central Iran. Although the full extent of the distributional range has yet to be accurately mapped, it appears to be discontinuous, as evidenced by the occurrence of isolated populations in the Hoggar, Tassili n'Ajjer and Ennedi mountain ranges of the Sahara (Vachon, 1952a; Kanter, 1971; Lourenço et al., 2012; Lourenço and Rossi, 2016). This disjunction is interpreted as relictual and attributed to range contraction associated with the onset of aridification in northern Africa (Niethammer, 1971; Dumont, 1982).

As noted by Prendini et al. (2003), the distributions of the species of *Scorpio* conform to the typical pattern of localized endemics exhibited among species of the other African scorpionid genera, suggesting that similar mechanisms of speciation have operated in all. The only differ-

ence is that the species of *Scorpio* have not diverged to the same extent as the species of the other genera, which may reflect the relatively recent onset of aridification in northern Africa in the late Miocene–early Pliocene (< 8 Ma; Axelrod and Raven, 1978; Van Zinderen Bakker, 1978, 1980; Pickford and Senut, 2000). Less time for morphological divergence may explain why the species of *Scorpio* are more similar morphologically than the species of Opisthophthalminae and Pandininae.

Scorpio has not been recorded from Burkina Faso, the Gambia, Mali, or Mauritania but may occur in some or all of those countries. Vachon (1950) rejected Pallary's (1938) record from the central Congo, but Levy and Amitai (1980) suggested that the genus could occur there. As with records from Tanzania (e.g., Lamoral and Reynnders, 1975; Fet, 2000), this record is probably attributable to a misidentification. *Scorpio* does not occur in India as suggested by some authors (Birula, 1925; Levy and Amitai, 1980).

ECOLOGY: All subspecies of *Scorpio* appear to be obligate burrowers, constructing burrows under stones and/or in open ground by means of their chelicerae, short, robust legs with stout, spiniform macrosetae distributed laterally and distally on the basitarsi, curved telotarsal unguis, and thickened metasoma. In contrast with *Opisthophthalmus*, no species of *Scorpio* exhibits psammophilous or lithophilous adaptations, although different species exhibit specific substratum preferences. High densities of burrows occur in suitable habitat but, unlike some Heterometrinae and Pandininae, cohabitation of multiple individuals within a single burrow (except during courtship or parental care) and/or the communal construction of burrows are absent (Levy and Amitai, 1980; Shachak and Brand, 1983).

Although ecological data are unavailable for most species, *S. fuscus* (Ehrenberg, 1829) and *S. palmatus* (Ehrenberg, 1828), occurring parapatrically in Israel, have been extensively studied (Levy and Amitai, 1980; Shachak and Brand, 1983; Kotzman et al., 1989; Danin, 1994; Rutin, 1996; Talal et al., 2015), while ecological studies on *S.*

kruglovi Birula, 1910 (as *S. maurus fuscus*) have also been conducted in neighbouring Jordan and Turkey (Amr and El-Oran, 1994; Crucitti, 1999). These species differ markedly in their substratum requirements, *S. fuscus* preferring harder soils, e.g., terra rossa, basalt, and rendzina, than *S. palmatus*, which inhabits brown-red sandy soils, loess and alluvium (Levy and Amitai, 1980). They also differ in their burrow structure. The burrows of *S. palmatus* are always constructed in open ground and run parallel to the ground surface for approximately 10 cm, before turning downward for 20–70 cm and ending in an enlarged chamber. The burrows of *S. fuscus* are often constructed under stones and usually run vertically, without turns, to a depth of approximately 40 cm, where they end in an enlarged chamber. Mesosomal percussion, involving rapid drumming of the posterior sternites against the ground, has been observed in males of both species (Rosin and Shulov, 1961).

CONSERVATION STATUS: Perhaps due to smaller size and more specialized ecological requirements (necessitating more elaborate methods for successful captive husbandry), *Scorpio* appears to be less popular in the exotic pet trade and thus more seldom offered. Nonetheless, at least one species, *S. palmatus* (imported from Egypt), is available almost year-round in Europe, the United States, and Japan (Hull-Williams, 1986; Mahsberg et al., 1999; Rubio, 2000). Another, *S. fuscus* (imported from Israel) is rarely available. Similar life history parameters to *Heterometrus*, *Opisthophthalmus*, and *Pandinus*, including long gestation period (14–15 mo.), small brood sizes (8–25), age to sexual maturity (3–4 yr) and parental care (Birula, 1917b; Levy and Amitai, 1980; Shachak and Brand, 1983; Polis and Lourenço, 1986; Crucitti, 1999), together with restricted distributional ranges, render species of *Scorpio* vulnerable to overharvesting. Fortunately, the reduced demand for *Scorpio* in the pet trade, together with their occurrence in many countries from which exportation of wildlife is strictly prohibited and in arid to semiarid habitats that are less vulnerable to

destruction than the rainforests inhabited by many species of Heterometrinae and Pandininae, suggests that they are somewhat less vulnerable.

REMARKS: Rossi (2016a) created two new tribes of Scorpioninae, in addition to the nominotypical tribe: Opisthophthalmini accommodated *Opisthophthalmus* and Protophthalmini accommodated *Protophthalmus*, revalidated from synonymy with *Opisthophthalmus*. As noted above, the evidence overwhelmingly suggests that Scorpioninae, as defined by Rossi (2016a), is paraphyletic, justifying the removal of Opisthophthalmini and its elevation to the rank of subfamily, thereby restricting the nominotypical subfamily Scorpioninae to the genus *Scorpio*.

Although *Scorpio* originally accommodated several species (e.g., Simon, 1872a; Pocock, 1900b), only a single, widespread species, *S. maurus* Linnaeus, 1758, with 19 official subspecies (Fet, 2000), was recognized by 1910, a status quo that persisted for almost a century. *Scorpio* remained monotypic on the grounds that no reliable characters could distinguish its subspecies and circumstantial evidence of hybridization between two subspecies occurring in the eastern Mediterranean region (Vachon, 1950; Levy and Amitai, 1980). The fact that the subspecies of *S. maurus* could be diagnosed on the basis of somatic characters presented in several keys (Birula, 1910; Vachon, 1950, 1952a; Levy and Amitai, 1980), however, prompted the suggestion that most if not all should be recognized as phylogenetic species (Prendini et al., 2003; Froufe et al., 2008), a move partially implemented without rigorous reanalysis of the variation by Lourenço (2009). Analyses of multilocus DNA sequence data, morphology and burrowing behavior among two putative subspecies from the eastern Mediterranean region (Talal et al., 2015) confirmed earlier suggestions that *S. maurus* is a species complex, rather than a single widespread polymorphic species, with many subspecies, as portrayed by earlier literature. A thorough systematic revision of *Scorpio*, applying modern concepts and techniques, including a phylogenetic analysis based on morphological and

molecular data for a comprehensive taxon sample, remains to be presented, however.

ACKNOWLEDGMENTS

S.F.L. was financially supported by a fellowship from the AMNH Richard Gilder Graduate School, a National Science Foundation (NSF) Graduate Research Fellowship, and a Postdoctoral Research Fellowship from NSF grant DEB 1655050. Aspects of this research were funded by the following awards: NSF Doctoral Dissertation Improvement grant DEC 1310855 to L.P. and S.F.L.; NSF grants EAR 0228699, DEB 0413453 and DEB 1655050 to L.P.; U.S.-Israel Binational Science Foundation grant 2014046 to L.P.; a grant from the Richard Lounsbery Foundation to L.P.; two Constantine S. Niarchos Expedition grants from the Stavros Niarchos Foundation to L.P.; a grant from the Exploration Fund of the Explorer's Club to S.F.L.; Young Explorers Grant 9816-15 from the National Geographic Society to S.F.L. Travel by L.P. to Israel was funded by the Israel Taxonomy Initiative; to Pakistan by the Visiting Scholar's Program of the Higher Education Commission, Pakistan; to collections in South Africa by a grant from the JRS Biodiversity Foundation; and to collections in the U.K. by the Systematics Association and Oxford University. The Habitat Foundation funded S.F.L. to participate in a BioBlitz on Penang Island, Malaysia. We acknowledge the following friends and colleagues for assistance with fieldwork and/or donations of material used in the study: M. Ahsan, A. Ang, S.M. Aye, M. Ayyub, M. Azhar, S. Basi, S.P. Benjamin, T.L. Bird, B.T. Chin, S.H. Chit, R. Datta, L.A. Esposito, E. Gefen, A. Goncharov, C.E. Griswold, M.S. Harvey, P. Horsley, S. Huber, J. Huff, M. Hussain, M. Irfan, P. Jäger, A. Khan, S. Kangnavong, P. Kanyavong, T. Kroes, E. Leong, M. Locke, Y. Lubin, P. Menon, L. Ngo, J. Ove Rein, F. Paul, C. Rahmadi, M. Roppo, P. Schwendinger, M. Seiter, M. Shahid, F. Somma, H.M. Tahir, M. Teo, A. Tietz, A. Ullrich, C.K. Wee, R.C. West, R. Wickramarachchi, and the late J. Visser; the following colleagues and agencies for facilitating permissions to collect and export material: V. Khem and T. Chea (Cambodia), C. Rahmadi (Indonesia), B.T. Chin, P.C. Ee, C. Lee, and N.A.B. Umar (Malaysia), T. Win and officials at Hlawga National Park (Myanmar), H.M. Tahir (Pakistan), S. Lai (Singapore), S.P. Benjamin (Sri Lanka), N. Warrit (Thailand), P.D. Sac (Vietnam); the following curators and collections managers for loaning material from the collections in their care and/or assistance during our visits: J. Becaloni and E. McAlister (BMNH), L.A. Esposito, C.E. Griswold, and D. Ubick (CAS), P. Sierwald and C. Maier (FMNH), W. Wang (LKC), M. Tavano (MCSNG), G. Giribet and L. Leibesperger (MCZ), M. Judson, C. Rollard, and E.-A. Leguin (MNHN), W. Dekoninck (MRHNB), C. Hörweg, and M. Seiter (NHMW), D. Herbert, B. Muller, and C. Stoffels (NM), C. Jonsson (NMG), T. Kronstedt, J. Ferrer, and G. Lindberg (NRS), M. Rafique and M. Ullah (PMNH), J. Goud (RMNH), S. van Noort, M. Cochrane, D. Larsen, and A. Mayekiso (SAM), P. Jäger and J. Altmann (SMF), M. Krüger and A. Ndaba (TM), J. Coddington, H. Wood, and D. DeRoche (USNM), M.S. Harvey (WAM), Jason Dunlop (ZMB), D. Harms and N. Dupérré (ZMH), N. Scharff and J. Pedersen (ZMUC); P. Colmenares, O. Delgado, P. Horsley, J. Huff, M.M. Locke, and L. Sorkin for logistical support with collections at AMNH; D. Sherwood and R. Botero-Trujillo for assistance locating type material at BMNH; the following for generating DNA sequence data used in the study: D. Casellato (funded by the Brazil Scientific Mobility Program of the Institute for International Education), D. Chin (funded by NSF grant DEB 1655050), O. Delgado, E. Goetz, and S. Reiter (funded by the AMNH Science Research Mentoring Program), V. Ehrenthal, P. Rubi, and T. Sharma; the following for field data, habitat and/or live habitus photos: S. Basi, R. Datta, K. Febriyanto, P. Horsley, P. Jain, S. Khunte, M.M. Locke, P. Menon, R. Mercurio, Z. Mirza, R. Naidu, J. Ove Rein, D. Renoult, J. Sullivan; P. Bradshaw for preparing the maps for this contribution; S. Thurston for imaging and preparing the plates; S. Perkins, D. Grimaldi, and

S. Ceccarelli for assistance with analyses and/or comments on preliminary results of the project; L. Herman for advice on nomenclatural issues; O.F. Francke and J.A. Ochoa for constructive comments on a previous draft of the manuscript.

REFERENCES

- Adams, A., E. Marais, S. Turner, L. Prendini, and B. Pinshow. 2016. Similar burrow architecture of three arid-zone scorpion species implies similar ecological function. *Natuurwissenschaften (Science of Nature)* 103: 56 (11 pp.).
- Alexander, A.J. 1958. On the stridulation of scorpions. *Behaviour* 12: 339–352.
- Alexander, A.J. 1959. A note on the evolution of stridulation within the family Scorpionidae. *Proceedings of the Zoological Society of London* 133: 391–399.
- Alexander, A.J., and D.W. Ewer. 1957. A chemo-receptor in the scorpion *Opisthophthalmus*. *South African Journal of Science* 53: 421–422.
- Amr, Z., O.A. Abed, T. Al Share, N. Hamidan, and L. Prendini. 2015. New records of Jordanian scorpions. *Jordan Journal of Natural History* 2: 30–38.
- Amr, Z.S., and R. El-Oran. 1994. Systematics and distribution of scorpions (Arachnida, Scorpionida) in Jordan. *Bolletino di Zoologia* 61: 185–190.
- Aswathi, K., and P.M. Sureshan. 2017. Additions to the scorpion fauna (Arachnida: Scorpiones) of Kerala, India, with an illustrated key to the genera. *Journal of Threatened Taxa* 9: 9844–9850.
- Auber, M. 1963. Reproduction et croissance de *Buthus occitanus* Amx. *Annales des Sciences Naturelles, Zoologie, Paris* 5: 273–286.
- Ausserer, A. 1880. Arachnida. *Zoologischer Jahresbericht* 1879: 430–470.
- Axelrod, D.I., and P.H. Raven. 1978. Late Cretaceous and Tertiary vegetation history of Africa. In M.J.A. Werger (editor), *Biogeography and ecology of southern Africa* 1: 77–130. The Hague: W. Junk.
- Banks, N. 1928. Scorpiones and Pedipalpi collected by Dr. E. Mjöberg in Borneo. *Journal of Sarawak Museum* 3: 505–506.
- Bardi, J.K., and C.J. George. 1943. Digestive glands of the scorpion. A physiological study. *Journal of the University of Bombay n.s. B* 11: 91–115.
- Bastawade, D.B. 1992. Morphological study of spermatophore of a common Indian scorpion *Mesobuthus tamulus tamulus* (Fabr.). *Records of the Zoological Survey of India* 91: 221–225.
- Bastawade, D.B. 2002. Scorpion diversity. In A.P. Jagtap and N.P. Singh (editors), *Biodiversity of the Western Ghats of Maharashtra*. Current Knowledge: 94, 95, 294–296. Dehra Dun: Bishen Singh Mahendra Pal Singh.
- Bastawade, D.B. 2004. Scorpionida, Araneae and Solifugae. In *Fauna of Pench National Park*. Zoological Survey of India, Conservation Area Series 20: 285–312.
- Bastawade, D.B. 2005. Arachnida: Scorpionida and Solifugae. In *Fauna of Melghat Tiger Reserve*. Zoological Survey of India, Conservation Area Series 24: 411–419.
- Bastawade, D.B. 2006a. Arachnida: Scorpionida and Amblypygi. In *Fauna of Sanjay Gandhi National Park (Invertebrates)*. Zoological Survey of India, Conservation Area Series 26: 131–138.
- Bastawade, D.B. 2006b. Arachnida: Scorpionida and Solifugi. In *Fauna of Tadoba Andhari Tiger Reserve*. Zoological Survey of India, Conservation Area Series 25: 283–309.
- Bastawade, D.B. 2008. Arachnida: Scorpionida, Araneae and Opiliones. In *Fauna of Lonar Wildlife Sanctuary*. Zoological Survey of India, Conservation Area Series 37: 133–153.
- Bastawade, D.B. 2009. Arachnida: Scorpiones. In *Fauna of Bhimashankar Wildlife Sanctuary*. Zoological Survey of India, Conservation Area Series 42: 215–222.
- Bastawade, D.B., and M. Borkar. 2008. Arachnida (Orders Scorpiones, Uropygi, Amblypygi, Araneae and Phalangida). In *Fauna of Goa*. Zoological Survey of India, State Fauna Series 16: 211–242.
- Bastawade, D.B., P.M. Sureshan, and C. Radhakrishnan. 2004. An illustrated key to the identification of scorpions (Scorpionida: Arachnida) of Kerala and notes on some interesting new records. *Records of the Zoological Survey of India* 103: 43–58.
- Bastawade, D.B., P.M. Sureshan, and C. Radhakrishnan. 2005. A new subfamily, genus and species of scorpion (Arachnida: Scorpionida) from India. *Records of the Zoological Survey of India* 104: 77–82.
- Becker, L. 1880. Études sur les scorpions. *Annales de la Société Entomologique de Belgique* 25: 134–145.
- Bellevoye, A. 1870. Dons divers faits au Cabinet d'Histoire Naturelle de Metz et description des espèces nouvelles qu'ils contiennent. *Bulletin de la Société d'Histoire Naturelle du Département de la Moselle (Metz)* 12: 105–114.
- Birula, A.A. 1898. Ein Beitrag zur Kenntniss der Skorpionenfauna Kleinasiens. *Horae Societatis Entomologicae Rossicae* 33: 132–140. [preprint: October 1898; collated issue: 1901]

- Birula, A.A. 1910. Über *Scorpio maurus* Linné und seine Unterarten. *Horae Societatis Entomologicae Rossicae* 35: 115–192.
- Birula, A.A. 1917a. Arachnoidea Arthrogastra Caucásica. Pars I. Scorpiones. *Zapiski Kavkazskogo Muzeya* [Mémoires du Musée du Caucase]. Tiflis: Imprimerie de la Chancellerie du Comité pour la Transcaucasie A (5): 1–253. [in Russian; English translation: A.A. Byalynitskii-Birulya. 1964. Arthrogastric arachnids of Caucasia. 1. Scorpions. Jerusalem: Israel Program for Scientific Translations, 170 pp.]
- Birula, A.A. 1917b. Faune de la Russie et des pays limitrophes fondée principalement sur les collections du Musée Zoologique de l'Académie des Sciences de Russie. *Arachnides* (Arachnoidea). Petrograd 1 (1): xx, 1–227. [in Russian; English translation: A.A. Byalynitskii-Birulya. 1965. Fauna of Russia and Adjacent Countries. Arachnoidea. Vol. I. Scorpions. Jerusalem: Israel Program for Scientific Translations, xix, 154 pp.]
- Birula, A.A. 1925. Skorpiologische Beiträge. 10. Zur geographischen Verbreitung zweier weitverbreiteter Skorpionen-Arten Palaearcticums. *Zoologischer Anzeiger* 63: 93–96.
- Biswas, A.T. 1984. Scorpions (Scorpiones). In *Fauna of Rajaji National Park. Zoological Survey of India, Fauna of Conservation Areas* 5: 317–323.
- Booncham, U., D. Sitthicharoenchai, A.O. Pradatsundarasar, S. Prasarnpun, and K. Thirakhupt. 2007. Sexual dimorphism in the Asian giant forest scorpion, *Heterometrus laoticus* Couzijn, 1981. *NU International Journal of Science* 4: 42–52.
- Borelli, A. 1915. Gli scorpioni del Museo Civico di Storia Naturale di Milano. *Atti della Società Italiana di Scienze Naturali* 53: 456–464.
- Braunwalder, M.E., and V. Fet. 1998. On publications about scorpions (Arachnida, Scorpiones) by Hemprich and Ehrenberg (1828–1831). *Bulletin of the British Arachnological Society* 11: 29–35.
- Brignoli, P.M. 1985. On the correct dates of publication of the arachnid taxa described in some works by C.W. Hahn and C.L. Koch (Arachnida). *Bulletin of the British Arachnological Society* 6: 414–416.
- Brindle, A. 1965. A revision of the subfamily Allostethinae (Dermaptera, Labiduridae). *Annals and Magazine of Natural History* 13: 575–596.
- Bücherl, W. 1959. Escorpiões e escorpionismo no Brasil. X. Catálogo da coleção escorpionica do Instituto Butantan. *Memórias do Instituto de Butantan* 29: 255–275.
- Bücherl, W. 1964. Distribuição geográfica dos aracnóides peçonhentos temíveis. *Memórias do Instituto de Butantan* 31: 55–66.
- Bücherl, W. 1967. Escorpiões, aranhas e escolopendromorfos da Amazônia. In H. Lent (editor), *Atas do simposio sobre a biota amazônica* 5 (Zoologia): 111–125.
- Casper, G.S. 1985. Prey capture and stinging behavior in the emperor scorpion, *Pandinus imperator* (Koch) (Scorpiones, Scorpionidae). *Journal of Arachnology* 13: 277–283.
- Cekalovic, T.K. 1982. Estado actual de la colección aracnológica del Museo de Zoología de la Universidad de Concepción (M.Z.U.C.), parte Scorpiones. *Memórias do Instituto de Butantan* 46: 187–192.
- Chandrasekara Reddy, D., and B. Padmanabhanaidu. 1977. Diurnal rhythmicity of alkaline and acid phosphatases in the scorpion, *Heterometrus fulvipes* C. Koch. *Comparative Physiology and Ecology* 2: 217–219.
- Chengal Raju, D., M.D. Bashamohideen, and C. Narasimham. 1973. Circadian rhythm in blood glucose and liver glycogen levels of scorpion, *Heterometrus fulvipes*. *Experientia* 29: 964–965.
- Chengal Raju, D., S. Govindappa, and K.S. Swami. 1978. Influence of sex on hepatopancreatic glycogenolysis of scorpion *Heterometrus fulvipes* (C. Koch). *Current Science* 47: 111–113.
- Cloudsley-Thompson, J.L. 1981. A comparison of rhythmic locomotory activity in tropical forest Arthropoda with that in desert species. *Journal of arid environments* 4: 327–334.
- Cloudsley-Thompson, J.L. 1990. Scorpions in mythology, folklore and history. In G.A. Polis (editor), *The biology of scorpions*: 462–485. Stanford, CA: Stanford University Press.
- Condevaux-Lanloy, C. 1996. Notes sur la parturition d'*Heterometrus spinifer* (H. & E., 1898) (Scorpiones, Scorpionidae). *Arachnides* 30: 5–6.
- Copeland, R.J.N. 1990. Notes on the breeding of imperial scorpions (*Pandinus imperator*). Browse Press.
- Couzijn, H.W.C. 1978. The method of polythetic analysis applied to a source of taxonomic difficulty: the genus *Heterometrus* H. and E., 1828 (Scorpionidae). *Symposium of the Zoological Society of London* 42: 327–333.
- Couzijn, H.W.C. 1981. Revision of the genus *Heterometrus*. *Zoologische Verhandelingen* 184: 1–196.
- Crucitti, P. 1998 ("1999"). Ricerche bio-ecologiche su *Scorpio maurus fuscus* (Hemprich and Ehrenberg, 1829) nell'Atay, Turchia meridionale (Scorpiones, Scorpionidae). *Atti della Società Italiana di Scienze Naturali* (Museo Civico di Storia Naturale di Milano) 139: 203–211.
- Dalingwater, J.E. 1980. SEM observations of the cuticles of some chelicerates. In *Proceedings of the 8th Inter-*

- national Congress of Arachnology, Vienna, 1980: 285–289.
- Danin, A. 1994. Association of *Salsola inermis* and scorpion burrows in leached soils in the Judean desert, Israel. *Israel Journal of Plant Sciences* 42: 37–40.
- Darriba, D., G.L. Taboada, R. Doallo, and D. Posada. 2012. jModelTest 2: more models, new heuristics and parallel computing. *Nature Methods* 9: 772.
- Davydov, K.N. 1898. [Notes on some scorpion species of the Palestinian fauna.] *Annuaire du Musée Zoologique de l'Académie Impériale des Sciences de St.-Petersbourg* 3: 39–51. [in Russian]
- DeGeer, C. (K. DeGeer). 1778. *Mémoires pour servir à l'histoire des insectes*. Stockholm: Imprimerie Pierre Hesselberg 7: 1–950.
- DeGeer, C. (K. DeGeer). 1783. *Abhandlungen zur Geschichte der Insekten, aus dem Französischen uebersetzt und mit Anmerkungen herausgegeben von J.A.E. Goeze*. Nürnberg: Gabriel Nikolaus Raspe. Nürnberg 7: 1–275, pl. 4. [translation of DeGeer, 1778]
- Delfosse, E. 1998. *Essais de nourriture pour les arachnides*. Première partie: les scorpions (Arachnida, Scorpiones). *Arachnides* 37: 28–32.
- Devarajulu Naidu, V. 1969. Some studies on the heart beat of scorpion, *Heterometrus fulvipes*. *Experientia* 25: 1274.
- Devarajulu Naidu, V., and B. Padmanabhanaidu. 1976. Diurnal rhythmic activity in the heart-beat of the scorpion *Heterometrus fulvipes* C. Koch. *Indian Journal of Experimental Biology* 14: 1–5.
- Devarajulu Naidu, V., and S.A.T. Venkatachari. 1974. Succinate dehydrogenase activity in the heart muscles of the scorpion, *Heterometrus fulvipes* C. Koch. *Indian Journal of Experimental Biology* 12: 539–542.
- Di, Z., X. Xu, Z. Cao, Y. Wu, and W. Li. 2013. Notes on the scorpions (Arachnida, Scorpiones) from Xizang with the redescription of *Scorpiops jendeki* Kovařík, 2000 (Scorpiones, Euscorpiidae) from Yunnan (China). *ZooKeys* 301: 51–99.
- Dimitrov, D., et al. 2012. Tangled in a sparse spider web: single origin of orb weavers and their spinning work unravelled by denser taxonomic sampling. *Proceedings of the Royal Society B, Biological Sciences* 279: 1341–1350.
- Dimitrov, D., J.J. Astrin, and B.A. Huber. 2013. Pholcid spider molecular systematics revisited, with new insights into the biogeography and the evolution of the group. *Cladistics* 29: 132–146.
- Domaniewski, M.J. 1913. *Spostrzeżenia nad zjawiskami zmiennosci i korrelacyi u niedzwiedka jawanskiego (Heterometrus cyaneus C.L. Koch)* (Beiträge zur Kenntnis der Variabilität und Korrelationserscheinungen bei dem javanischen Skorpion). *Bulletin de l'Académie des Sciences de Cracovie (ser. B)* 1913: 251–271.
- Dubale, M.S., and A.B. Vyas. 1968. The structure of the chela of *Heterometrus* sp. and its mode of operation. *Bulletin of the Southern California Academy of Sciences* 67: 240–244.
- Dufour, L. 1856. *Histoire anatomique et physiologique des scorpions*. Mémoires Présentés par Divers Savants a l'Académie des Sciences de l'Institut Impérial de France 14: 561–653.
- Dumont, H.J. 1982. Relict distribution patterns of aquatic animals: another tool in evaluating Late Pleistocene climate changes in the Sahara and Sahel. *Palaeoecology of Africa* 14: 1–24.
- Dumortier, B. 1964. Morphology of sound emission apparatus in Arthropoda. In R.-G. Busnel (editor), *Acoustic behaviour of animals*: 277–345. Amsterdam: Elsevier.
- Dupré, G. 1989. Esquisse de détermination du genre *Heterometrus* H. & E. (Scorpionida: Scorpionidae) d'après son lieu de capture. *Arachnides* 3: 4–6.
- Dupré, G. 1990. Le point sur l'élevage de *Pandinus (Pandinus) imperator* (C.L. Koch 1842) (Scorpionida, Scorpionidae). *Arachnides* 7: 9–13.
- Dupré, G. 1992. Evolution des importations de scorpions exotiques en France. *Arachnides* 12: 14–16.
- Dupré, G. 1993. Fiche d'élevage *Heterometrus* sp. et ssp. *Arachnides* 16: 13.
- Dupré, G., N. Lambert, and P. Gérard. 1998. *Les scorpions: biologie, élevage*. Paris: P. Gérard. 82 pp.
- Eastwood, E.B. 1978a. Notes on the scorpion fauna of the Cape. Part 3. Some observations on the distribution and biology of scorpions on Table Mountain. *Annals of the South African Museum* 74: 229–248.
- Eastwood, E.B. 1978b. Notes on the scorpion fauna of the Cape. Part 4. The burrowing activities of some scorpionids and buthids (Arachnida, Scorpionida). *Annals of the South African Museum* 74: 249–255.
- Esposito, L.A., H.Y. Yamaguti, C.A. Souza, R. Pinto-da-Rocha, and L. Prendini. 2017. Systematic revision of the Neotropical club-tailed scorpions, *Physoctonus*, *Rhopalurus*, and *Troglophopalus*, revalidation of *Heteroctenus*, and descriptions of two new genera and three new species (Buthidae: Rhopalurusinae). *Bulletin of the American Museum of Natural History* 415: 1–136.
- Esposito, L.A., H.Y. Yamaguti, R. Pinto-da-Rocha, and L. Prendini. 2018. Plucking with the plectrum: phylogeny of the New World buthid scorpion subfamily

- Centruroidinae Kraus, 1955 (Scorpiones: Buthidae) reveals evolution of three pecten-sternite stridulation organs. *Arthropod Systematics and Phylogeny* 76: 87–122.
- Fabricius, J.C. 1775. *Systema entomologiae*. Flensburg et Leipzig: Officina Libraria Kortii. 832 pp.
- Fabricius, J.C. 1781. *Species insectorum exhibentes eorum differentias specificas, synonyma autorum, loca natalia, metamorphosin adjectis observationibus, descriptionibus* 1: 550–552. Bohnii: Impensis Carol. Ernest.
- Fabricius, J.C. 1787. *Mantissa insectorum sistens eorum species nuper detectas adjectis characteribus genericis, differentiis, specificis, emendationibus, observationibus, descriptionibus, emendationibus* 1. [Scorpiones: p. 348.] Hafniae: Impensis Christ. Gottl. Proft.
- Fabricius, J.C. 1793. *Entomologica systematica emendata et aucta, secundum classes, ordines, genera, species adjectis synonymis, locis, observationibus, descriptionibus* 2: 1–519. Hafniae: Impensis Christ. Gottl. Proft.
- Fage, L. 1933. Les scorpions de l'Indochine française, leurs affinités, leurs distribution géographique. *Annales de la Société Entomologique de France* 102: 25–34.
- Fage, L. 1936. Nouvelle contribution à l'étude des scorpions de l'Indochine française. *Bulletin de la Société Entomologique de France* 41: 179–181.
- Fage, L. 1946. Scorpions et pédipalpes de l'Indochine française. *Annales de la Société Entomologique de France* 113: 71–81.
- Farley, R.D. 2005. Developmental changes in the embryo, pronymph, and first molt of the scorpion *Centruroides vittatus* (Scorpiones: Buthidae). *Journal of Morphology* 265: 1–27.
- Farley, R.D. 2008. Development of respiratory structures in embryos and first and second instars of the bark scorpion, *Centruroides gracilis* (Scorpiones: Buthidae). *Journal of Morphology* 269: 1134–1156.
- Farley, R.D. 2011. Pectine development in scorpion embryos and first and second instars. *Euscorpius* 120: 1–47.
- Fet, V. 2000. Family Scorpionidae Latreille, 1802. In V. Fet, W.D. Sissom, G. Lowe, and M.E. Braunwalder, *Catalog of the scorpions of the World (1758–1998)*: 427–486. New York: New York Entomological Society.
- Fet, V., and M.E. Sologlad. 2005. Contributions to scorpion systematics. I. On recent changes in high level taxonomy. *Euscorpius* 3: 1–13.
- Fitch, W.M. 1971. Toward defining the course of evolution: minimum change for a specific tree topology. *Systematic Zoology* 20: 406–416.
- Flower, S.S. 1901. Notes on millipedes, centipedes, scorpions, etc. of the Malay Peninsula and Siam. *Journal of the Straits Branch of the Royal Asiatic Society* 36: 1–48.
- Francke, O.F. 1982. Order Scorpiones. In S.P. Parker (editor), *Synopsis and classification of living organisms*: 73–75. New York: McGraw Hill.
- Francke, O.F. 1985. *Conspectus genericus scorpionorum 1758–1982* (Arachnida: Scorpiones). Occasional Papers of the Museum, Texas Tech University 98: 1–32.
- Francke, O.F., and W.D. Sissom. 1984. Comparative review of the methods used to determine the number of molts to maturity in scorpions (Arachnida), with analysis of the post-birth development of *Vaejovis coahuilae* Williams (Vaejovidae). *Journal of Arachnology* 12: 1–20.
- Froufe, E., P. Sousa, P.C. Alves, and D.J. Harris. 2008. Genetic diversity within *Scorpio maurus* (Scorpiones: Scorpionidae) from Morocco: preliminary evidence based on CO1 mitochondrial DNA sequences. *Biologia* 63: 1157–1160.
- Garnier, G. 1974. Élevage en laboratoire de *Pandinus imperator* (C.L. Koch, 1842) (Scorpionidae – Scorpioninae). *Bulletin de la Société Zoologique de France* 99: 693–699.
- Garnier, G., and R. Stockmann. 1973 (“1971”). Comportement de la reproduction chez le scorpion *Pandinus imperator*. In *Proceedings of the 5th International Congress of Arachnology, Brno, 1971*: 13–22.
- Geethabali. 1976. Central course of photic input in the ventral nerve cord of scorpion (*Heterometrus fulvipes*). *Experientia* 32: 345–347.
- Geethabali, and K. Pampathi Rao. 1973. A metasomatic neural photoreceptor in the scorpion. *Journal of Experimental Biology* 58: 189–196.
- Gervais, P.M. 1844a. Scorpions. In C.A. Walckenaer (editor), *Histoire naturelle des insectes. Apètres*. 3: 14–74. Paris: Librairie Encyclopédique de Roret.
- Gervais, P.M. 1844b. Remarques sur la famille des scorpions et description de plusieurs espèces nouvelles de la collection du Muséum. *Archives du Muséum d'Histoire Naturelle* 4: 201–240.
- Giltay, M.L. 1931. Scorpions et pédipalpes. Résultats scientifiques du voyage aux Indes Orientales Néerlandaises de LL. AA. RR. le Prince et la Princesse Léopold de Belgique. *Mémoires du Musée Royal d'Histoire Naturelle de Belgique* 3: 1–28.
- Giltay, M.L. 1935. Liste des arachnides d'Extrême-Orient et des Indes Orientales recueillis, en 1932, par S.A.R. le Prince Léopold de Belgique. *Bulletin du Musée Royal d'Histoire Naturelle de Belgique* 11: 1–3.

- Goloboff, P.A. 1993. Estimating character weights during tree search. *Cladistics* 9: 83–91.
- Goloboff, P.A., J.S. Farris, and K.C. Nixon. 2003. TNT: tree analysis using new technology. Computer software and documentation. Online resource (<https://cladistics.org/tnt>).
- Goloboff, P.A., J.S. Farris, and K.C. Nixon. 2008. TNT, a free program for phylogenetic analysis. *Cladistics* 24: 774–786.
- Gopalakrishnakone, P., J. Cheah, and M.C.E. Gwee. 1995. Black scorpion (*Heterometrus longimanus*) as a laboratory animal: maintenance of a colony of scorpion for milking of venom for research, using a restraining device. *Laboratory Animals* 29: 456–458.
- Gough, L.H., and S. Hirst. 1927. Key to the identification of Egyptian scorpions. A method of identifying Egyptian scorpions from the fifth caudal segment and stings. *Bulletin of the Ministry of Agriculture of Egypt, Technical Scientific Service* 76: 1–7.
- Govindarajan, S., and G.S. Rajulu. 1974. Presence of resilin in a scorpion *Palamnaeus swammerdami* and its role in the food-capturing and sound-producing mechanisms. *Experientia* 30: 908–909.
- Guindon, S., and O. Gascuel. 2003. A simple, fast, and accurate algorithm to estimate large phylogenies by maximum likelihood. *Systematic Biology* 52: 696–704.
- Harrison, J.L. 1954. A family of the great black scorpion (*Heterometrus longimanus*). *Malayan Nature Journal* 9: 31–32.
- Hemprich, F.G., and C.G. Ehrenberg. 1828. *Zoologica II. Arachnoidea*. Plate I: *Buthus*; plate II: *Androctonus*. In *Symbolae physicae seu icones et descriptiones animalium evertibratorum sepositis insectis quae ex itinere per Africam borealem et Asiam occidentalem*. Decas Prima, Plates IX et X. Berolini: Officina Academica.
- Hemprich, F.G., and C.G. Ehrenberg. 1829. Vorläufige Uebersicht der in Nord-Afrika und West-Asien einheimischen Scorpione und deren geographischen Verbreitung, nach den eigenen Beobachtungen. *Verhandlungen der Gesellschaft Naturforschende Freunde in Berlin* 1: 348–362.
- Hemprich, F.G., and C.G. Ehrenberg. 1831. *Animalia articulata, Arachnoidea. Scorpiones africani et asiatici*. In *Symbolae physicae. Animalia evertabrata, exclusis insectis*. Series prima, tabularum decade prima. Berolini: Officina Academica, 12 pp.
- Henderson, J.R. 1919. Two new scorpions from southern India. *Records of the Indian Museum* 16: 378–381.
- Herbst, J.F.W. 1800. *Naturgeschichte der Skorpionen*. In *Natursystem der Ungeflügelten Insekten* 4: 1–86. Berlin: Gottlieb August Lange.
- Hewitt, J. 1915. New South African Arachnida. *Annals of the Natal Museum* 3: 289–327.
- Hewitt, J. 1918. A survey of the scorpion fauna of South Africa. *Transactions of the Royal Society of South Africa* 6: 89–192.
- Hewitt, J. 1925. Facts and theories on the distribution of scorpions in South Africa. *Transactions of the Royal Society of South Africa* 12: 249–276.
- Hewitt, J. 1931. A new solifuge and scorpion from South-West Africa. *Annals of the South African Museum* 30: 93–99.
- Hincks, W.D. 1960. Indian Dermaptera of the genus *Diplatys* Serville (Pygidicranidae), with the description of a new species. *Bulletin of Entomology* 1: 14–15.
- Hirst, S. 1911. On a collection of Arachnida and Chilopoda made by Mr. S.A. Neave in Rhodesia, north of the Zambezi. *Memoirs of the Linnean Philosophical Society* 56: 1–11.
- Hjelle, J.T. 1990. Anatomy and morphology. In G.A. Polis (editor), *The biology of scorpions*: 9–63. Stanford, CA: Stanford University Press.
- Hosoi, F. 1990. [Breeding and display of a scorpion *Heterometrus cyaneus*.] *Insectarium* 27: 164–167. [in Japanese]
- Hue, L.-X., Q.-M. Pham, D.-S. Pham, and T.-C. Ngo. 1998. [Scorpions (Scorpionoides) in Vietnam.] *Tap Chi Sinh Hoc* 20: 7–9. [in Vietnamese]
- Hull-Williams, V. 1986. *How to keep scorpions*. Fitzgerald Entomological Series 2. London: Fitzgerald Publishing.
- Hull-Williams, V. 1989. A brief description of the collection and appearance of *Heterometrus gigantometrus swammerdami titanicus* in Sri Lanka. *Journal of the British Tarantula Society* 5: 12–14.
- Indra, T.J. 2001. Scorpion. In *Fauna of Nilgiri Biosphere Reserve*. Zoological Survey of India, Fauna of Conservation Area Series II: 55–58.
- Indra, T.J. 2006. Scorpion. In *Fauna of Bilgiri Rangaswamy Temple Wildlife Sanctuary*. Zoological Survey of India, Conservation Area Series 27: 197–200.
- Indra, T.J. 2009. Scorpionida. In *Fauna of Tamil Nadu*. Zoological Survey of India, Fauna Series 17: 141–143.
- IUCN (International Union for the Conservation of Nature). 1994. Analyses of proposals to amend the CITES appendices. Inclusion of Emperor Scorpions *Pandinus dictator*, *P. gambiensis* and *P. imperator* in appendix II. Ghana. IUCN Document 9.47.63–65: 186–188.
- Janion-Scheepers, C., et al. 2016. Soil biota in a megadiverse country: current knowledge and future directions in South Africa. *Pedobiologia – Journal of Soil Ecology* 59: 129–174.

- Javed, S.M.M., Z.A. Mirza, F. Tampal, and W.R. Lourenço. 2010a. A new species of the genus *Heterometrus* Ehrenberg, 1828 (Scorpiones: Scorpionidae) from India with notes on its natural history. *Boletín de la Sociedad Entomológica Aragonesa* 47: 143–148.
- Javed, S.M.M., Z.A. Mirza, R.V. Sanap, and F. Tampal. 2010b. First record of *Liocheles nigripes* Pocock, 1897 (Scorpiones: Hemiscorpidae) from Andhra Pradesh with a checklist of scorpions of the state. *Journal of Threatened Taxa* 2: 783–785.
- Jayaram, V., and B. Padmanabhanaidu. 1979. Carbohydrate metabolism in the heart of the scorpion, *Heterometrus fulvipes* (C.L. Koch) with reference to sex. *Current Science* 48: 6–8.
- Jayaram, V., and B. Padmanabhanaidu. 1980. Utilisation of carbohydrates in the heart of the scorpion *Heterometrus fulvipes* (C.L. Koch). *Proceedings: Animal Sciences* 89: 109–112.
- Jayaram, V., D. Chandrasekara Reddy, and B. Padmanabhanaidu. 1978. Circadian rhythmicity in phosphorylase activity and glycogen content in the heart muscle of the scorpion, *Heterometrus fulvipes*, C. L. Koch. *Experientia* 34: 1184–1185.
- Kalarani, V., P. Murali Mohan, and R.W. Davies. 1992. Thermal acclimation and metabolism of the hepatopancreas in the tropical scorpion, *Heterometrus fulvipes*. *Journal of Thermal Biology* 17: 141–146.
- Kamenz, C., and L. Prendini. 2008. An atlas of book lung ultrastructure in the order Scorpiones (Arachnida). *Bulletin of the American Museum of Natural History* 316: 1–259.
- Kanter, H. 1971. Giftschlangen und Skorpione Nordafrikas. In H. Schiffers (editor), *Die Sahara und ihre Randgebiete*: 587–603. Munich: Weltforum Verlag.
- Kanungo, M.S. 1954. The ecology and behaviour of the scorpion *Palamnaeus bengalensis* C. Koch. *Journal of the Bombay Natural History Society* 52: 536–539.
- Karsch, F. 1879a. Skorpionologische Beiträge. Part I. *Mitteilungen des Münchener Entomologischen Vereins* 3: 6–22.
- Karsch, F. 1879b. Skorpionologische Beiträge. Part II. *Mitteilungen des Münchener Entomologischen Vereins* 3: 97–136.
- Karsch, F. 1884. Ueber einige neue und minder bekannte Arthropoden des Bremer Museums. *Abhandlungen, Herausgegeben vom Naturwissenschaftlichen Verein zu Bremen* 9: 65–71.
- Karsch, F. 1892. Arachniden von Ceylon und von Minikoy, gesammelt von den Herren Doctoren P. und F. Sarasin. *Berliner Entomologische Zeitschrift* 36: 267–310.
- Kästner, A. 1931. Die Hüfte und ihre Umformung zu Mundwerkzeugen bei den Arachniden. *Zeitschrift für Morphologie und Ökologie der Tiere* 22: 721–758.
- Kästner, A. 1941. 1. Ordnung der Arachnida: Scorpiones. In T. Krumbach (editor), *Handbuch der Zoologie* 3: 117–240. Berlin: Walter de Gruyter Verlag.
- Katoh, K., and D.M. Standley. 2013. MAFFT multiple sequence alignment software version 7: improvements in performance and usability. *Molecular Biology and Evolution* 30: 772–780.
- Katoh, K., K. Misawa, K.I. Kuma, and T. Miyata. 2002. MAFFT: a novel method for rapid multiple sequence alignment based on fast Fourier transform. *Nucleic Acids Research* 30: 3059–3066.
- Keyserling, E. 1885. Die Arachniden Australiens. Ordo Scorpiones. In *Die Arachniden Australiens nach der Natur beschrieben und abgebildet* begonnen von Dr. L. Koch 2: 1–86, tab. I–VI. Nürnberg: Bauer and Raspe.
- Khatavkar, R.S., and N.K. More. 1990. A note on the burrow and burrowing activity of *Heterometrus xanthopus* Pocock (Arachnida: Scorpionidae). *Journal Soil Biology and Ecology* 10: 79–81.
- Khatoon, S. 1999. Scorpions of Pakistan (Arachnida: Scorpionida). *Proceedings of the Pakistan Congress of Zoology* 19: 207–225.
- Kishida, K. 1939. Arachnida of Jehol. Order Scorpiones. Report of the first scientific expedition to Manchoukuo under the leadership of Shigeyasu Tokunaga, June–October, 1933, Sect. 5, 1(4) 10: 1–67.
- Klußmann-Fricke, B.-J., L. Prendini, and C.S. Wirkner. 2012. Evolutionary morphology of the hemolymph vascular system in scorpions: a character analysis. *Arthropod Structure and Development* 41: 545–560.
- Koch, C.L. 1836. Die Arachniden. Nürnberg: C.H. Zeh'sche Buchhandlung 3 (1–5): 1–104, pl. 73–105 (figs. 164–245).
- Koch, C.L. 1837. Die Arachniden. Nürnberg: C.H. Zeh'sche Buchhandlung 4 (1–5): 1–108, pl. 119–138 (figs. 253–318).
- Koch, C.L. 1838. Die Arachniden. Nürnberg: C.H. Zeh'sche Buchhandlung 4 (6): 109–144, pl. 139–144 (figs. 319–339).
- Koch, C.L. 1840. Die Arachniden. Nürnberg: C.H. Zeh'sche Buchhandlung 8 (1, 2): 1–40, pl. 248–264 (figs. 595–620).
- Koch, C.L. 1841a. Die Arachniden. Nürnberg: C.H. Zeh'sche Buchhandlung 8 (3–6): 41–131, pl. 265–288 (figs. 621–694).
- Koch, C.L. 1841b. Die Arachniden. Nürnberg: C.H. Zeh'sche Buchhandlung 9 (1): 1–56, pl. 289–306 (figs. 695–726).

- Koch, C.L. 1850. Scorpiones. In *Übersicht des Arachnidensystems*. Nürnberg: C.H. Zehsche Buchhandlung 5: 86–92.
- Koch, L.E. 1977. The taxonomy, geographic distribution and evolutionary radiation of Australo-Papuan scorpions. *Records of the Western Australian Museum* 5: 83–367.
- Kopstein, F. 1921. Die Skorpione des Indo-Australischen Archipels. Mit Grundlage der in holländischen Sammlungen, vornähmlich des Rijks-Museums in Leiden, vorhandenen Arten. *Zoologische Mededeelingen* 6: 115–144.
- Kopstein, F. 1923. Liste der Skorpione des Indo-Australischen Archipels im Museum zu Buitenzorg. *Treubia* 3: 184–187.
- Kopstein, F. 1926. De Schorpioenen van Java. *De Troopischer Natuur* 15: 109–118.
- Kopstein, F. 1927. Der javanische Reiskorpion. *Der Zoologische Reisdor Tropen* 1927: 102–108.
- Kopstein, F. 1929. *Spolia Mentawiensia*. Scorpiones. *Bulletin of the Raffles Museum* 2: 124.
- Kotzman, M., Y. Lubin, and M. Goldberg. 1989. The activities of a burrow-dwelling scorpion revealed at the surface. *Acta Zoologica Fennica* 190: 205–208.
- Kovářík, F. 1992. A check list of scorpions (Arachnida: Scorpiones) in the collections of the Zoological Department, National Museum in Prague. *Acta Societatis Zoologicae Bohemicae* 56: 181–186.
- Kovářík, F. 1994. *Isometrus zideki* sp. n. from Malaysia and Indonesia, and a taxonomic position of *Isometrus formosus*, *I. thurstoni* and *I. sankariensis* (Arachnida: Scorpionida: Buthidae). *Acta Societatis Zoologicae Bohemicae* 58: 195–203.
- Kovářík, F. 1995. Review of Scorpionida from Thailand with descriptions of *Thaicharmus mahunkai* gen. et sp. n. and *Lychas krali* sp. n. (Buthidae). *Acta Societatis Zoologicae Bohemicae* 59: 187–207.
- Kovářík, F. 1997. A check-list of scorpions (Arachnida) in the collections of the Hungarian Natural History Museum, Budapest. *Annales Historico-Naturales Musei Nationalis Hungarici* 89: 177–185.
- Kovářík, F. 1998. Štíři [Scorpions]. Jihlava, Czech Republic: Madagaskar, 176 pp. [in Czech]
- Kovářík, F. 2000. *Pandinus (Pandinops) pococki* sp. n. from Somalia, and *Pandinus pugilator*, a junior synonym of *Pandinus (Pandinops) bellicosus* comb. n. (Scorpiones, Scorpionidae). *Serket* 7: 1–7.
- Kovářík, F. 2002. A checklist of scorpions (Arachnida) in the collection of the Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt am Main, Germany. *Serket* 8: 1–23.
- Kovářík, F. 2003. Scorpions of Djibouti, Eritrea, Ethiopia, and Somalia (Arachnida: Scorpiones), with a key and descriptions of three new species. *Acta Societatis Zoologicae Bohemicae* 67: 133–159.
- Kovářík, F. 2004. A review of the genus *Heterometrus* Ehrenberg, 1828, with descriptions of seven new species (Scorpiones, Scorpionidae). *Euscorpius* 15: 1–60.
- Kovářík, F. 2009. Illustrated catalog of scorpions. Part 1. Introductory remarks; keys to families and genera; subfamily Scorpioninae with keys to *Heterometrus* and *Pandinus* species. Prague: Clarion Production. 170 pp.
- Kovářík, F. 2011. A review of the subgenus *Pandinus* Thorell, 1876 with descriptions of two new species from Uganda and Ethiopia (Scorpiones: Scorpionidae). *Euscorpius* 129: 1–18.
- Kovářík, F. 2012. Review of the subgenus *Pandinurus* Fet, 1997 with descriptions of three new species (Scorpiones, Scorpionidae, *Pandinus*). *Euscorpius* 141: 1–22.
- Kovářík, F. 2013. *Pandinus (Pandinus) trailini* sp. n. from Ethiopia (Scorpiones: Scorpionidae), with data on localities and life strategy. *Euscorpius* 163: 1–14.
- Kovářík, F. 2016. Scorpions of the Horn of Africa (Arachnida: Scorpiones). Part VIII. *Pandinops* Birula, 1913 (Scorpionidae), with description of two new species. *Euscorpius* 229: 1–20.
- Kovářík, F. 2017. Scorpions of the Horn of Africa (Arachnida, Scorpiones). Part XI. *Pandinurus kmoniceki* sp. n. (Scorpionidae) from Somaliland. *Euscorpius* 243: 1–14.
- Kovářík, F., et al. 2016. Scorpions of Sri Lanka (Scorpiones: Buthidae, Chaerilidae, Scorpionidae) with description of four new species of the genera *Charmus* Karsch, 1879 and *Reddyanus* Vachon, 1972, stat. n. *Euscorpius* 220: 1–133.
- Kovářík, F., S. Navidpour, and M.E. Söleglad. 2017a. *Hemiscorpius shahii* sp. n. from Iran (Scorpiones: Hemiscorpiidae). *Euscorpius* 249: 1–9.
- Kovářík, F., G. Lowe, M.E. Söleglad, and J. Plíšková. 2017b. Scorpions of the Horn of Africa (Arachnida: Scorpiones). Part X. *Pandiborellius* stat. n. and *Pandinurus* (Scorpionidae) with description of four new species from Eritrea and Ethiopia, and review of *Pandinus* sensu lato taxonomy. *Euscorpius* 238: 1–103.
- Kovářík, F., et al. 2017c. Scorpions of the Horn of Africa (Arachnida: Scorpiones). Part XII. *Pandinurus hangarale* sp. n. (Scorpionidae) from Somaliland and a review of type locality and true distribution of *Pandinurus smithi* (Pocock, 1897). *Euscorpius* 253: 1–18.

- Kovářík, F., et al. 2019a. Scorpions of Sri Lanka (Arachnida: Scorpiones). Part III. *Heterometrus yaleensis* sp. n. (Scorpionidae). *Euscorpius* 283: 1–13.
- Kovářík, F., G. Lowe, and T. Mazuch. 2019b. Scorpions of the Horn of Africa (Arachnida: Scorpiones). Part XIX. *Pandiborellius meidensis* (Karsch, 1879) and *Pandinurus fulvipes* sp. n. (Scorpionidae) from Somaliland. *Euscorpius* 275: 1–18.
- Kraepelin, K. 1894. Revision der Skorpione. II. Scorpionidae und Bothriuridae. Beiheft zum Jahrbuch der Hamburgischen Wissenschaftlichen Anstalten 11: 1–248.
- Kraepelin, K. 1897. Scorpione und Thelyphoniden. In *Ergebnisse einer zoologischen Forschungsreise in den Molukken und Borneo, im Auftrage der Senckenbergischen naturforschenden Gesellschaft ausgeführt von Dr. Willy Kükenenthal. Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft* 23: 537.
- Kraepelin, K. 1898. Über die Linnéschen Arten der Gattung *Scorpio*. *Zoologischer Anzeiger* 564–565: 438–447.
- Kraepelin, K. 1899. Scorpiones und Pedipalpi. In F. Dahl (editor), *Das Tierreich*, 8 (Arachnoidea): 1–265. Herausgegeben von der Deutschen Zoologischen Gesellschaft. Berlin: R. Friedländer und Sohn Verlag.
- Kraepelin, K. 1901. Catalogue des scorpions des collections du Muséum d'Histoire Naturelle de Paris. *Bulletin du Muséum National d'Histoire Naturelle*, Paris 7: 265–274.
- Kraepelin, K. 1904. Zur Nomenklatur der Skorpione und Pedipalpen. *Zoologischer Anzeiger* 28: 195–204.
- Kraepelin, K. 1905. Die geographische Verbreitung der Skorpione. *Zoologische Jahrbücher, Abtheilung für Systematik* 22: 321–364.
- Kraepelin, K. 1908 (“1907”). Die sekundären Geschlechtscharaktere der Skorpione, Pedipalpen und Solifugen. *Mitteilungen aus dem Naturhistorischen Museum*. (2. Beiheft zum Jahrbuch der Hamburgischen Wissenschaftlichen Anstalten) 25: 181–225.
- Kraepelin, K. 1913 (“1912”). Neue Beiträge zur Systematik der Gliederspinnen. III. A. Bemerkungen zur Skorpionenfauna Indiens. B. Die Skorpione, Pedipalpen und Solifugen Deutsch-Ostafrikas. *Mitteilungen aus dem Naturhistorischen Museum*. (2. Beiheft zum Jahrbuch der Hamburgischen Wissenschaftlichen Anstalten) 30: 123–196.
- Krapf, D. 1988. Skorpione II. Fortpflanzung, Wachstum und Haltung. *Herpetofauna* (Weinstadt) 56: 24–33.
- Kriesch, M. 1994. Note sur la sociabilité du scorpion *Pandinus imperator* (C.L. Koch, 1842). *Arachnides* 21: 9.
- Lamoral, B.H. 1972. New and little known scorpions, solifuges and spiders from the Namib Desert, S.W.A. *Madoqua* (II) 1: 117–131.
- Lamoral, B.H. 1978a. Systematics and bionomics of the scorpions of South West Africa (Arachnida: Scorpionida). Ph.D. dissertation, University of Natal, Pietermaritzburg, South Africa.
- Lamoral, B.H. 1978b. Soil hardness, an important and limiting factor in burrowing scorpions of the genus *Opisthophthalmus* C.L. Koch, 1837 (Scorpionidae, Scorpionida). *Symposium of the Zoological Society of London* 42: 171–181.
- Lamoral, B.H. 1979. The scorpions of Namibia (Arachnida: Scorpionida). *Annals of the Natal Museum* 23: 497–784.
- Lamoral, B.H. 1980. A reappraisal of the suprageneric classification of Recent scorpions and their zoogeography. In J. Grube (editor), *Verhandlungen. 8. Internationaler Arachnologen-Kongress abgehalten an der Universität für Bodenkultur Wien, 7–12 Juli, 1980*: 439–444. Vienna: H. Egermann.
- Lamoral, B.H., and S.C. Reynders. 1975. A catalogue of the scorpions described from the Ethiopian faunal region up to December 1973. *Annals of the Natal Museum* 22: 489–576.
- Lampe, E. 1918. Katalog der Skorpione, Pedipalpen und Solifugen des Naturhistorischen Museums der Residenzstadt Wiesbaden. *Jahrbücher des Nassauischen Vereins für Naturkunde* 70: 185–203.
- Lankester, E.R. 1885. Notes on certain points of the anatomy of generic characters of scorpions. *Transactions of the Zoological Society, London* 11: 372–384.
- Larrouy, G., M.C. Signorel, and Y. Cambefort. 1973. Comportement en captivité de *Pandinus imperator* C.L. Koch et connaissance des jeunes. *Bulletin de la Société d'Histoire Naturelle de Toulouse* 109: 346–350.
- Latreille, P.A. 1802 (“An X”). *Histoire naturelle, generale et particuliere, des crustaces et des insectes*. 3. (Ouvrage faisant suite à l'histoire naturelle générale et particulière, composée par Leclerc de Buffon, et redigée par C.S. Sonnini.) Paris: F. Dufart.
- Latreille, P.A. 1803. Scorpion. In *Nouveau dictionnaire d'histoire naturelle, appliquée aux arts* 20: 264–268.
- Latreille, P.A. 1804. Histoire des scorpions. In *Histoire naturelle, générale et particulière, des crustacés et des insectes. Ouvrage faisant suite aux Oeuvres de Leclerc de Buffon, et partie de cours complet d'histoire naturelle rédigée par C.S. Sonnini*, 7: 111–129. Paris: F. Dufart.
- Latreille, P.A. 1806. *Genera crustaceorum et insectorum secundum ordinem naturalem in familias dis-*

- posita, iconibus exemplisque plurimis explicata. Tome 1. Paris: Amand Koenig, 302 pp. [Scorpiones: pp. 130–132.]
- Latreille, P.A. 1810. Considérations générales sur l'ordre naturel des animaux composant les classes des crustacés, des arachnides et des insectes. Paris: F. Schoell, 444 pp. [Scorpiones: pp. 116, 118.]
- Latreille, P.A. 1817. Les crustacés, les arachnides et les insectes. In [G.G.L.C.F.D.] Cuvier (editor), *Le règne animal distribué d'après son organisation, pour servir de base à l'histoire naturelle des animaux et d'introduction à l'anatomie comparée*. 3. Paris: Deterville.
- Latreille, P.A. 1825. Familles naturelles du règne animal, exposées succinctement et dans un ordre analytique, avec l'indication de leurs genres. Paris: J.B. Baillière.
- Laurie, M. 1890. The embryology of the scorpion (*Euscorpius italicus*). Quarterly Journal of Microscopical Science, New Ser. 31: 105–141, pl. XIII–XVIII.
- Laurie, M. 1891. Some points in the development of *Scorpio fulvipes*. Quarterly Journal of Microscopical Science, New Ser. 32: 587–597, pl. XL.
- Laurie, M. 1896a. Notes on the anatomy of some scorpions, and its bearing on the classification of the order. Annals and Magazine of Natural History (Ser. 6) 17: 185–193.
- Laurie, M. 1896b. Further notes on the anatomy and development of scorpions, and their bearing on the classification of the order. Annals and Magazine of Natural History (Ser. 6) 17: 121–133.
- Laverack, M.S. 1966. Observations on a proprioceptive system in the legs of the scorpion *Hadrurus hirsutus*. Comparative Biochemistry and Physiology 19: 241–251.
- Lawrence, R.F. 1928. Contributions to a knowledge of the fauna of South-West Africa. VII. Arachnida (Part 2). Annals of the South African Museum 25: 217–312.
- Lawrence, R.F. 1969. A new genus of psammophile scorpion and new species of *Opisthophthalmus* from the Namib Desert. Scientific Papers of the Namib Desert Research Station 48: 105–116.
- Lawrence, R.F. 1971. Spiders and other Arachnida. In D.J. Potgieter, P.C. du Plessis, and S.H. Skaife. Animal life in southern Africa: 210–217. Cape Town: NASOU Ltd.
- Lawrence, R.F. 1973. Scorpions. In J.J. Spies and P.C. du Plessis (editors), Standard encyclopaedia of southern Africa: 543–544. Cape Town: NASOU Ltd.
- [Leach, W.E.] 1814. Scorpionides. In D. Brewster (editor), Edinburgh encyclopaedia 7: 412. Edinburgh: William Blackwoods and Sons. [anonymous article]
- Levy, G., and P. Amitai. 1980. Fauna Palaestina. Arachnida. I. Scorpiones. Jerusalem: Israel Academy of Sciences and Humanities.
- Lewis, P.O. 2001. A likelihood approach to estimating phylogeny from discrete morphological character data. Systematic Biology 50: 913–925.
- Linnaeus, C. (C. von Linné). 1746. Museum Adolpho-Fridericianum, dissertatio, respondens Laur. Balk. 4–48 pp. Holmiae (Stockholm).
- Linnaeus, C. (C. von Linné). 1748. Systema naturae sistens regna tria naturae, in classes et ordines, genera et species redacta tabulisque aeneis illustrata. Ed. 6, emendata et aucta. 1: 1–224. [Scorpiones: p. 68.] Holmiae (Stockholm): Gododfr. Kiesewetteri.
- Linnaeus, C. (C. von Linné). 1758. Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, loci. Ed. 10. 1: 1–821. [Scorpiones: pp. 624, 625.] Holmiae (Stockholm): Laurentii Salvii.
- Linnaeus, C. (C. von Linné). 1767. Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Ed. 12. 1: 533–1327. Holmiae (Stockholm): Laurentii Salvii.
- Linnaeus, C. (C. von Linné). 1775. Scorpionen. In Natursystem, tab. 33: 1088–1092.
- Lönnberg, E. 1897a. Om skorpionernas och pedipalpernas geografiska utbredning. Entomologisk Tidskrift 18: 193–211.
- Lönnberg, E. 1897b. Scorpioner och pedipalper i Upsala Universitets Zoologiska Museum. Entomologisk Tidskrift 18: 175–192.
- Lönnberg, E. 1898a. A revision of the Linnean type specimens of scorpions and pedipalps in the Zoological Museum of the Royal University of Upsala. Annals and Magazine of Natural History 7: 82–89.
- Lönnberg, E. 1898b. Noch einmal über die Linnéschen Arten der Gattung *Scorpio*. Zoologischer Anzeiger 21: 549–552.
- Loria, S.F., and L. Prendini. 2014. Homology of the lateral eyes of Scorpiones: a six-ocellus model. PLoS One 9: e112913. [doi: 10.1371/journal.pone.0112913]
- Loria, S.F., and Prendini, L. (in press). Burrowing into the forest: phylogeny of the Asian forest scorpions (Scorpionidae: Heterometrinae) and the evolution of ecomorphotypes. Cladistics.
- Lourenço, W.R. 1989. Rétablissement de la famille des Ischnuridae, distincte des Scorpionidae Pocock, 1893, à partir de la sous-famille des Ischnurinae, Pocock, 1893. Revue Arachnologique 8: 159–177.
- Lourenço, W.R. 1999. Considérations taxonomiques sur le genre *Hadogenes* Kraepelin, 1894; création de la

- sous-famille des Hadogeninae n. subfam., et description d'une espèce nouvelle pour l'Angola (Scorpiones, Scorpionidae, Hadogeninae). *Revue Suisse de Zoologie* 106: 929–938.
- Lourenço, W.R. 2000. Panbiogeographie, les familles des scorpions et leur repartition géographique. *Biogeographica* 76: 21–39.
- Lourenço, W.R. 2002. Reproduction in scorpions, with special reference to parthenogenesis. In S. Toft and N. Scharff (editors), *European Arachnology 2000*: 71–85. Aarhus: Aarhus University Press.
- Lourenço, W.R. 2009. Reanalysis of the genus *Scorpio* Linnaeus 1758 in sub-Saharan Africa and description of one new species from Cameroon (Scorpiones, Scorpionidae). *Entomologische Mitteilungen aus dem Zoologischen Museum Hamburg* 15: 99–113.
- Lourenço, W.R. 2014. Further considerations on the identity and distribution of *Pandinus imperator* (C.L. Koch, 1841) and description of a new species from Cameroon (Scorpiones: Scorpionidae). *Entomologische Mitteilungen aus dem Zoologischen Museum Hamburg* 17: 139–151.
- Lourenço, W.R., and J.L. Cloudsley-Thompson. 1996. Recognition and distribution of the scorpions of the genus *Pandinus* Thorell, 1876 accorded protection by the Washington Convention. *Biogeographica* 72: 133–143.
- Lourenço, W.R., and J.L. Cloudsley Thompson. 2009. A new species of the genus *Scorpio* Linnaeus 1758 from Sudan (Scorpiones, Scorpionidae). *Boletín de la Sociedad Entomológica Aragonesa* 45: 123–126.
- Lourenço, W.R., and J.L. Cloudsley Thompson. 2012. About the enigmatic presence of the genus *Scorpio* Linnaeus, 1758 in Congo with the description of a new species from Niger (Scorpiones, Scorpionidae). *Serket* 13: 1–7.
- Lourenço, W.R., and D. Huber. 2002. New addition to the scorpion fauna (Arachnida: Scorpiones) of Sri Lanka. *Revue Suisse de Zoologie* 109: 265–275.
- Lourenço, W.R., and A. Rossi. 2016. Confirmation of a new species of *Scorpio* Linnaeus, 1758 in the Tassili n'Ajjer Mountains, south Algeria (Scorpiones: Scorpionidae). *Onychium* 12: 11–18.
- Lourenço, W.R., J.-X. Qi, and M.-S. Zhu. 2005. Description of two new species of scorpions from China (Tibet) belonging to the genera *Mesobuthus* Vachon (Buthidae) and *Heterometrus* Ehrenberg (Scorpionidae) *Zootaxa* 985: 1–16.
- Lourenço, W.R., B. Duhem, and J.L. Cloudsley Thompson. 2012. Scorpions from Ennedi, Kapka and Tibesti, the mountains of Chad, with descriptions of nine new species (Scorpiones: Buthidae, Scorpionidae). *Arthropoda Selecta* 21: 307–338.
- Mahsberg, D. 1990. Brood care and family cohesion in the tropical scorpion *Pandinus imperator* (Koch) (Scorpiones: Scorpionidae). *Acta Zoologica Fennica* 190: 267–272.
- Mahsberg, D., R. Lippe, and S. Kallas. 1999. *Skorpione*. Münster: Natur und Tier Verlag.
- Majumder, S.C., and A. Dey. 2005. Studies on some enthnomedicinal arachnids and insects in relation to their usage as drugs among the tribals of Sundarbans, West Bengal, India. *Records of Zoological Survey of India, Occasional Paper* 236: 1–38.
- Makioka, T. 1992a. Reproductive biology of the viviparous scorpion, *Liocheles australasiae* (Fabricius) (Arachnida, Scorpiones, Ischnuridae) III. Structural types and functional phases of the adult ovary. *Invertebrate Reproduction and Development* 21: 207–214.
- Makioka, T. 1992b. Reproductive biology of the viviparous scorpion, *Liocheles australasiae* (Fabricius) (Arachnida, Scorpiones, Ischnuridae) II. Repeated pregnancies in virgins. *Invertebrate Reproduction and Development* 21: 161–167.
- Marx, G. 1890 ("1889"). Arachnida. In L.O. Howard (editor), *Scientific results of the explorations by the U.S. Fish Commission Steamer Albatross. No. V. – Annotated catalogue of the insects collected in 1887–'88. Proceedings of the United States National Museum* 12: 207–211.
- Masi, L. 1912. Note sugli scorpioni appartenenti al R. Museo Zoologico di Roma. *Bollettino Società Zoologica Italiana* 1: 88–108, 120–144.
- Mastanaiah, S., D. Chengul Raju, and K.S. Swami. 1977. Rhythmic variation in the isocitrate dehydrogenase activity in the scorpion *Heterometrus fulvipes* (C. Koch). *Experientia* 33: 1051–1052.
- Mastanaiah, S., V. Doraswamy Reddy, D. Chengul Raju, and K.S. Swami. 1978. Circadian rhythmic activity of lipase in the scorpion, *Heterometrus fulvipes* (C. Koch). *Current Science* 47: 130–132.
- Mastanaiah, S., D. Chengul Raju, D. Ravi Varma, and K.S. Swami. 1979. Rhythmic variations in the activities of aldolase and isocitrate dehydrogenase in the heart muscle of the scorpion, *Heterometrus fulvipes* (C. Koch). *Experientia* 35: 69–70.
- Mathew, A.P. 1948. Nutrition in the advanced scorpion embryos: *Palamnaeus scaber* Thorell. *Proceedings of Indian Academy of Sciences, Section B* 27: 111–118.
- Mathew, A.P. 1956. Embryology of *Heterometrus scaber*. *Bulletin of the Central Research Institute (University of Travancore, India)* 1: 1–96.

- Mathew, A.P. 1957. Mating in scorpions. *Journal of the Bombay Natural History Society* 54: 853–857.
- Mathew, A.P. 1962. Changes in the structure of the ovarian and diverticular mucosa in *Heterometrus scaber* (Thorell) during a reproductive cycle. In R.V. Seshaiya and B.S. Chauhan (editors), *Proceedings of the First All-India Congress of Zoology*, 24–28 October 1959, University of Jabalpur, Part 2, pp. 100–111. Calcutta: Zoological Society of India.
- Mathew, A.P. 1965. On the movable claw of the pedipalp in the scorpion *Heterometrus scaber*. *Journal of Animal Morphology and Physiology* 12: 271–275.
- Mathew, A.P. 1966. The movable claw of the pedipalp of the scorpion, *Heterometrus scaber*. In G.S. Thapar (editor), *Proceedings of the Second All-India Congress of Zoology*, October 1962, Banaras Hindu University, Varanasi, Part 2, pp. 411–414. Calcutta: Zoological Society of India.
- Mathew, A.P. 1968. Embryonic nutrition in *Urodacus abruptus* Pocock. *Journal of Animal Morphology and Physiology* 15: 162–167.
- McCormick, S.J., and G.A. Polis. 1990. Prey, predators and parasites. In G.A. Polis (editor), *The biology of scorpions*: 294–320. Stanford, CA: Stanford University Press.
- Meise, W. 1932. Fehlender und extrem entwickelter Sexualdimorphismus im Formenkreis *Heterometrus longimanus* (Scorpion). *Archiv für Naturgeschichte, Neue Folge* 1: 660–671.
- Menzel, P., and F. D'Aluisio. 1998. Man eating bugs: the art and science of eating insects. Berkeley, CA: Material World Books/Ten Speed Press.
- Michalik, P., and D. Mercati. 2010. First investigation of the spermatozoa of a species of the superfamily Scorpionoidea (*Opisthophthalmus penrithorum*, Scorpioniidae) with a revision of the evolutionary and phylogenetic implications of sperm structures in scorpions (Chelicerata, Scorpiones). *Journal of Zoological Systematics and Evolutionary Research* 48: 89–101.
- Miles, C. 2015. The earwig collection (Dermaptera) of the Manchester Museum, U.K., with a complete type catalogue. *European Journal of Taxonomy* 141: 1–138.
- Millot, J., and M. Vachon. 1949. Ordre des scorpions. In P.-P. Grassé (editor), *Traité de zoologie*, vol. 6: 386–436. Paris: Masson et Cie.
- Mirza, Z.A., and R. Sanap. 2009. Notes on the reproductive biology of *Heterometrus phipsoni* Pocock, 1893 (Scorpiones, Scorpionidae). *Journal of Threatened Taxa* 1: 488–490.
- Mirza, Z.A., D. Joshi, G. Desouza, and R.V. Sanap. 2012. Description of a new species of scorpion of the genus *Heterometrus* Ehrenberg, 1828 (Scorpiones, Scorpionidae) from the Western Ghats, India. *Indian Journal of Arachnology* 1: 1–8.
- Monod, L., and W.R. Lourenço. 2005. Hemiscorpiidae (Scorpiones) from Iran, with descriptions of two new species and notes on biogeography and phylogenetic relationships. *Revue Suisse de Zoologie* 112: 869–942.
- Monod, L., and L. Prendini. 2014. Evidence for Eurogondwana: the roles of dispersal, extinction and vicariance in the evolution and biogeography of Indo-Pacific Hormuridae (Scorpiones: Scorpionoidea). *Cladistics* 31: 71–111.
- Montambaux, P. 1996. Maintenance en captivité de *Pandinus imperator*. *Reptile Magazine* 5: 15–16.
- Moritz, M., and S.C. Fischer. 1980. Die Typen der Arachniden-Sammlung des Zoologischen Museums Berlin. III. Scorpiones. *Mitteilungen aus dem Zoologischen Museum in Berlin* 56: 309–326.
- Nagaraj, S.K., P. Dattatreya, and T.N. Boramuthi. 2015. Indian scorpions collected in Karnataka: maintenance in captivity, venom extraction and toxicity studies. *Journal of Venomous Animals and Toxins including Tropical Diseases* 21: 51. [doi: 10.1186/s40409-015-0053-4]
- Nair, B., and P.A. Kurup. 1975. Investigations on the venom of the Indian scorpion *Heterometrus scaber*. *Biochimica et Biophysica Acta* 381: 165–174.
- Nayar, K.K. 1966. Endocrine nature of the lymphoid organs of the scorpion, *Heterometrus scaber* Thor. In G.S. Thapar (editor), *Proceedings of the Second All-India Congress of Zoology*, October 1962, Banaras Hindu University, Varanasi, Part 2, pp. 173–174.
- Nemenz, H., and J. Gruber. 1967. Experimente und Beobachtungen an *Heterometrus longimanus petersii* (Thorell) (Scorpiones). *Verhandlungen der Zoologisch-Botanischen Gesellschaft in Wien* 107: 5–24.
- Nenilin, A.B., and V. Fet. 1992. Zoogeographical analysis of the world scorpion fauna (Arachnida: Scorpiones). *Arthropoda Selecta* 1: 3–31. [in Russian; extended English summary]
- Newlands, G. 1972a. Notes on psammophilous scorpions and a description of a new species (Arachnida: Scorpionida). *Annals of the Transvaal Museum* 27: 241–257.
- Newlands, G. 1972b. Ecological adaptations of Kruger National Park scorpionids (Arachnida: Scorpiones). *Koedoe* 15: 37–48.
- Newlands, G. 1978. Arachnida (except Acari). In M.J.A. Werger (editor), *Biogeography and ecology of southern Africa* 2: 677–684. The Hague: W. Junk.
- Newlands, G. 1987. Scorpions. Pretoria: De Jager-HAUM.

- Newport, G. 1843. On the structure, relations, and development of the nervous and circulatory systems, and on the existence of a complete circulation of the blood in vessels, in Myriapoda and macrourous Arachnida. *Philosophical Transactions of the Royal Society of London* 133: 243–302.
- Niethammer, G. 1971. Die Fauna der Sahara. In H. Schiffers (editor), *Die Sahara und ihre Randgebiete*: 499–587. Munich: Weltforum Verlag.
- Nixon, K.C. 2002. WinClada, ver. 1.00.08. Computer software and documentation. Online resource (<http://www.diversityoflife.org/winclada>).
- Pallary, P. 1929. Les scorpions du Sahara central. *Bulletin de la Société d'Histoire Naturelle de l'Afrique du Nord* 20: 133–141.
- Pallary, P. 1934. Scorpions du Sahara central. Mission du Hoggar III (février à mai 1928). *Mémoires de la Société d'Histoire Naturelle de l'Afrique du Nord* 4: 90–100.
- Pallary, P. 1938. Sur les scorpions de la Berbérie, de la Syrie et du Congo. *Archives de l'Institut Pasteur d'Algérie* 16: 279–282.
- Pampapathi Rao, K. 1964. Neurophysiological studies of an arachnid, the scorpion *Heterometrus fulvipes*. *Journal of Animal Morphology and Physiology* 11: 133–142.
- Pampapathi Rao, K., and M. Habibulla. 1973. Correlation between neurosecretion and some physiological functions of the scorpion *Heterometrus swammerdami*. *Proceedings of the Indian Academy of Sciences, Section B* 77: 148–155.
- Pampapathi Rao, K., and V.S.R. Murthy. 1966. Oscillographic analysis of some proprioceptors in the scorpion *Heterometrus fulvipes*. *Nature* 212: 520–521.
- Pande, S., D. Bastawade, A. Padhye, and A. Pawashe. 2012. Diversity of scorpion fauna of Saswad-Jejuri, Pune District, Maharashtra, western India. *Journal of Threatened Taxa* 4: 2381–2389.
- Patil, A.E., and U.H. Shah. 2012a. Hemocytes in scorpion – *Heterometrus xanthopus*. *Bioscan* 7: 139–141.
- Patil, A.E., and U.H. Shah. 2012b. Ultrastructure studies of hemocytes in scorpion *Heterometrus xanthopus*. *Bioscan* 7: 491–493.
- Patil, A.E., and U.H. Shah. 2013. Hemocytes in scorpion – *Heterometrus phipsoni*. *Bioscan* 8: 33–35.
- Pavesi, P. 1880. Studi sugli aracnidi africani. I. Aracnidi di Tunisia. *Annali del Museo Civico di Storia Naturale di Genova* 15: 283–388.
- Pavesi, P. 1884. Materiali per lo studio della fauna Tunisina raccolta da G. e L. Doria: aracnidi. *Annali del Museo Civico di Storia Naturale di Genova* 20: 446–486.
- Pavesi, P. 1895a. Viaggio del Dott. E. Festa in Palestina, nel Libano e regioni vicine. XIV. Aracnidi. *Bollettino dei Musei di Zoologia ed Anatomia Comparata* 10: 1–11.
- Pavesi, P. 1895b. Aracnidi raccolti ne paese dei Somali dall'ing L. Bricchetti-Robecchi. *Bollettino Scientifico*, Pavia 17: 37–46.
- Pavesi, P. 1898. Sugli aracnidi raccolti a Giava dal dott. Penzig nel 1895–96. *Bollettino Scientifico*, Pavia 20: 93–96.
- Pavlovsky, E.N. 1924a. On the morphology of the male genital apparatus in scorpions. *Trudy Leningradskogo Obshchestva Yestestvoispytatelei* [Transactions of the Leningrad Society of Naturalists] 53: 17–86.
- Pavlovsky, E.N. 1924b. Studies on the organization and development of scorpions. (Introduction. 1: On the external morphology of the scorpions. 2: The integument and its processes. 3: The circulatory system. 4: The system of lymphatic/phagocytic organs). *Quarterly Journal of Microscopical Science* 68: 615–640.
- Pavlovsky, E.N. 1925. Zur Morphologie des weiblichen Genitalapparatus und zur Embryologie der Skorpione. *Annuaire du Musée Zoologique de l'Académie des Sciences d'URSS* 26: 137–205.
- Pérez Minnocci, S. 1974. Un inventario preliminar de los escorpiones de la región Paleártica y claves para la identificación de los géneros de la región Paleártica Occidental. Madrid: Universidad Complutense de Madrid, Facultad de Ciencias, Departamento de Zoología, Cátedra de Artrópodos 7: 1–45.
- Peters, W. 1861. [Ueber eine neue Eintheilung der Skorpione und ueber die von ihm in Mossambique gesammelten Arten von Skorpionen.] *Monatsberichte der Königlichen Preussischen Akademie der Wissenschaften zu Berlin* 1861: 507–516.
- Petrunkévitch, A. 1955. Arachnida. In R.C. Moore (editor), *Treatise on invertebrate paleontology*. Part P. Arthropoda. 2. Chelicerata with sections on Pycnogonida and *Palaeoisopus*: 42–162. Lawrence, KS: Geological Society of America and University of Kansas Press.
- Pham, D.S., T.H. Tran, and W.R. Lourenço. 2017. Diversity and endemism in the scorpion fauna of Vietnam. A preliminary synopsis. *Comptes Rendus Biologies* 340: 132–137.
- Pickford, M., and B. Senut. 2000. Geology and palaeobiology of the central and southern Namib Desert, southwestern Africa. Vol. 1: Geology and history of study. Geological Survey of Namibia, Memoir 18: 1–155. Windhoek: Ministry of Mines and Energy.
- Plíšková, J., F. Kovařík, O. Košulič, and F. Štáhlavský. 2016. Description of a new species of *Heterometrus*

- Ehrenberg, 1828 (Scorpiones: Scorpionidae) from Thailand with remarks about the utilization of cyto-genetic data in taxonomy of the genus. *Annales Zoologici* (Warszawa) 66: 467–476.
- Pocock, R.I. 1888. On the African specimens of the genus *Scorpio* (Linn.), contained in the collection of the British Museum. *Annals and Magazine of Natural History* (Ser. 6) 2: 245–255.
- Pocock, R.I. 1890. Report upon a small collection of scorpions and centipedes sent from Madras by Mr. Edgar Thurston, of the Government Central Museum. *Annals and Magazine of Natural History* (Ser. 6) 5: 236–259.
- Pocock, R.I. 1892. Descriptions of two new genera of scorpions, with notes upon some species of *Palamnaeus*. *Annals and Magazine of Natural History* (Ser. 6) 9: 38–49.
- Pocock, R.I. 1893. Report upon a small collection of scorpions sent to the British Museum by Mr. Edgar Thurston, of the Government Central Museum, Madras. *Journal of the Bombay Branch of the Royal Asiatic Society* 7: 295–312.
- Pocock, R.I. 1894a. A small contribution to our knowledge of the scorpions of India. *Annals and Magazine of Natural History* (Ser. 6) 13: 72–84.
- Pocock, R.I. 1894b. Supplementary note on the Arachnida and Myriapoda of the Mergui Archipelago: with descriptions of some new species from Siam and Malaysia. *Journal of the Linnean Society* 24: 316–318.
- Pocock, R.I. 1894c. Scorpions from the Malay Archipelago. In M. Weber (editor), *Zoologische Ergebnisse einer Reise in Niederländisch Ost-Indien* 3: 84–99. Leiden: E.J. Brill Verlag.
- Pocock, R.I. 1896a. On a new generic distinction between the scorpions of the genera *Scorpio* and *Palamnaeus*. *Annals and Magazine of Natural History* (Ser. 6) 18: 75–77.
- Pocock, R.I. 1896b. How and why scorpions hiss. *Natural Science* 9: 17–25.
- Pocock, R.I. 1896c. On the scorpions, centipedes and millipedes obtained by Dr. Gregory on his expedition to Mount Kenia, East Africa. *Annals and Magazine of Natural History* (Ser. 6) 17: 425–444.
- Pocock, R.I. 1897. Descriptions of some new species of scorpions from India. *Journal of the Bombay Natural History Society* 11: 102–117.
- Pocock, R.I. 1899. Diagnoses of some new Indian Arachnida. *Journal of the Bombay Natural History Society* 12: 744–753.
- Pocock, R.I. 1900a. Arachnida. In W.T. Blandford (editor), *The fauna of British India, including Ceylon and Burma*. London: Taylor and Francis, 279 pp.
- Pocock, R.I. 1900b. The scorpions of the genus *Heterometrus*. *Annals and Magazine of Natural History* (Ser. 7) 5: 362–365.
- Pocock, R.I. 1902. A contribution to the systematics of scorpions. I. Some corrections in nomenclature. II. Notes on some species of *Parabuthus* contained in the British Museum. III. Descriptions of some new and old species. *Annals and Magazine of Natural History* (Ser. 7) 10: 364–380.
- Pointer, M. 1991. The genus *Heterometrus* and the family Scorpionidae. *Journal of the British Tarantula Society* 7: 23–25.
- Polis, G.A. 1990. Ecology. In G.A. Polis (editor), *The biology of scorpions*: 247–340. Stanford, CA: Stanford University Press.
- Polis, G.A., and W.R. Lourenço. 1986. Sociality among scorpions. In J.A. Barrientos (editor), *Actas X Congreso de Aracnología, Jaca (España), Septiembre 1986*, 1: 111–115. Barcelona: Instituto Pirenaico de Ecología (C.S.I.C.) Grupo de Aracnología (Asoc. Esp. Entomol.)
- Polis, G.A., and W.D. Sissom. 1990. Life history. In G.A. Polis (editor), *The biology of scorpions*: 161–223. Stanford, CA: Stanford University Press.
- Poljansky, I. 1903. Wissenschaftliche Mitteilungen. 1. Zur Embryologie des Skorpions. *Zoologischer Anzeiger* 27: 49–58.
- Prendini, L. 2000a. Phylogeny and classification of the superfamily Scorpionioidea Latreille 1802 (Chelicerata, Scorpiones): an exemplar approach. *Cladistics* 16: 1–78.
- Prendini, L. 2000b. Chelicerata (Scorpiones). In A.H. Kirk-Spriggs and E. Marais (editors), *Dâures – Biodiversity of the Brandberg Massif, Namibia*. *Cimbebasia Memoir* 9: 109–120.
- Prendini, L. 2001a. A review of synonyms and subspecies in the genus *Opisthophthalmus* C.L. Koch (Scorpiones: Scorpionidae). *African Entomology* 9: 17–48.
- Prendini, L. 2001b. Substratum specialization and speciation in southern African scorpions: the Effect Hypothesis revisited. In V. Fet and P.A. Selden (editors), *Scorpions 2001: In memoriam Gary A. Polis*: 113–138. Burnham Beeches, Bucks, U.K.: British Arachnological Society.
- Prendini, L. 2003. A new genus and species of bothriurid scorpion from the Brandberg Massif, Namibia, with a reanalysis of bothriurid phylogeny and a discussion of the phylogenetic position of *Lisposoma* Lawrence. *Systematic Entomology* 28: 1–24.

- Prendini, L. 2004. On the scorpions of Gabon and neighbouring countries, with a reassessment of the synonyms attributed to *Babycurus buettneri* Karsch and a redescription of *Babycurus melanicus* Kovařík. In B.L. Fisher (editor), Monts Doudou, Gabon. A floral and faunal inventory with reference to elevational variation. Memoirs of the California Academy of Sciences 28: 235–267.
- Prendini, L. 2005. Scorpion diversity and distribution in southern Africa: pattern and process. In B.A. Huber, B.J. Sinclair, and K.-H. Lampe (editors), African biodiversity: molecules, organisms, ecosystems. Proceedings of the 5th International Symposium on Tropical Biology, Museum Alexander Koenig, Bonn: 25–68. New York: Springer Verlag.
- Prendini, L. 2009. Assembling the scorpion Tree of Life: ‘High-level systematics and phylogeny of the extant scorpions (Scorpiones: Orthosterni)’ reanalysed. In J. Arrivillaga, M. El Souki, and B. Herrera, B. (editors), Monografía digital sociedad venezolana de entomología 2: 1–41. Caracas: Sociedad Venezolana de Entomología.
- Prendini, L. 2011. Order Scorpiones C.L. Koch, 1850. In Z.-Q. Zhang (editor), Animal biodiversity: an outline of higher-level classification and survey of taxonomic richness. Zootaxa 3148: 115–117.
- Prendini, L. 2016. Redefinition and systematic revision of the East African scorpion genus *Pandinoidea* (Scorpiones: Scorpionidae) with critique of the taxonomy of *Pandinus*, sensu lato. Bulletin of the American Museum of Natural History 407: 1–66.
- Prendini, L. and T.L. Bird. 2008. Scorpions of the Brandberg Massif, Namibia: species richness inversely correlated with altitude. African Invertebrates 49: 77–107.
- Prendini, L., and W.C. Wheeler. 2005. Scorpion higher phylogeny and classification, taxonomic anarchy, and standards for peer review in online publishing. Cladistics 21: 446–494.
- Prendini, L., T.M. Crowe, and W.C. Wheeler. 2003. Systematics and biogeography of the family Scorpionidae Latreille, with a discussion of phylogenetic methods. Invertebrate Systematics 17: 185–259.
- Pringle, J.W.S. 1955. The function of the lyriform organs of arachnids. Journal of Experimental Biology 32: 270–278.
- Purcell, W.F. 1899. On the species of *Opisthophthalmus* in the collection of the South African Museum, with descriptions of some new forms. Annals of the South African Museum 1: 131–180.
- Rajyalakshmi, A., P. Umamaheshwara Reddy, B. Narasimha Rao, and T. Gopalakrishna Reddy. 1991. The disposition of carbaryl in the hepatopancreas, haemolymph and embryos of the viviparous scorpion, *Heterometrus fulvipes* (Koch) during gestation. Xenobiotica 21: 429–432.
- Ravindranath, M.H. 1974. The hemocytes of a scorpion *Palamnaeus swammerdami*. Journal of Morphology 144: 1–10.
- Robert, J.-Y. 1999. Reproduction et croissance en captivité d'*Heterometrus spinifer* (Scorpiones, Scorpionidae). Arachnides 41: 19–27.
- Roewer, C.F. 1929. Süd-indische Skorpione, Chelonethi und Opilioniden. Revue Suisse de Zoologie 36: 609–613.
- Roewer, C.F. 1943. Über eine neuerworbene Sammlung von Skorpionen des Natur-Museums Senckenberg. Senckenbergiana 26: 205–244.
- Ronquist, F., and J.P. Huelsenbeck. 2003. MrBayes 3: Bayesian phylogenetic inference under mixed models. Bioinformatics 19: 1572–1574.
- Root, T.M. 1990. Neurobiology. In G.A. Polis (editor), The biology of scorpions: 341–413. Stanford, CA: Stanford University Press.
- Rosin, R., and A. Shulov. 1961. Sound production in scorpions. Science 133: 1918–1919.
- Rosin, R., and A. Shulov. 1963. Studies of the scorpion *Nebo hierichonticus*. Proceedings of the Zoological Society of London 140: 547–575.
- Rossi, A. 2014a. Notes on the distribution of *Pandinus* (Pandinus) Thorell, 1876 and *Pandinus* (Pandinurus) Fet, 1997 with the descriptions of two new species from Central African Republic and Djibouti (Scorpiones: Scorpionidae). Onychium 10: 10–31.
- Rossi, A. 2014b. The fragmented peri-Saharan distribution of the subgenus *Pandinurus* Fet, 1997 with the description of a new species from Chad (Scorpiones, Scorpionidae, *Pandinus*). Serket 14: 6–14.
- Rossi, A. 2014c. New data on the rare species *Pandinus nistrii* Rossi, 2014 (Scorpiones: Scorpionidae). Arachnides 72: 3–12.
- Rossi, A. 2014d. Clarification of the type locality of *Pandinus ulderigoi* Rossi, 2014 with notes on the scorpions protected by CITES (Scorpiones: Scorpionidae). Arachnologische Mitteilungen 49: 47–54.
- Rossi, A. 2015a. Sui sottogeneri di *Pandinus* Thorell, 1876 con revisione del genere *Pandinurus* Fet, 1997 stat. n. e descrizione di sette nuove specie e tre nuovi sottogeneri (Scorpiones: Scorpionidae). Onychium 11: 10–66.
- Rossi, A. 2015b. Due ulteriori nuove specie del sottogenero *Pandiborellius* Rossi, 2015 dal Corno d’Africa (Scorpiones, Scorpionidae). Arachnida 1: 2–36.
- Rossi, A. 2015c. Una revisione preliminare del genere *Pandinus* Thorell, 1876 con la descrizione di un

- nuovo sottogenere e due nuove specie dall'Etiopia (Scorpiones, Scorpionidae). *Arachnida* 3: 37–52.
- Rossi, A. 2016a. Atlas of scorpions. Volume 1. (Scorpionidae: Pandininae: *Pandinoides*). *Rivista Aracnologica Italiana* 8 (Suppl.): 1–148.
- Rossi, A. 2016b. On *Pandinus duffmackayi* Prendini, 2016, a junior synonym of *Pandinoides* (*Pandinoides*) *mariachiarae* Rossi, 2016, with comments on the recent revisions of the genus *Pandinoides* Fet, 2000 proposed independently by Rossi and Prendini. *Rivista Aracnologica Italiana* 10: 45–48.
- Rubio, M. 2000. Scorpions. A complete pet owner's manual. Barrons Educational Series.
- Rutin, J. 1996. The burrowing activity of scorpions (*Scorpio maurus palmatus*) and their potential contribution to the erosion of hamra soils in Karkur, central Israel. *Geomorphology* 15: 159–168.
- Santibáñez-López, C.E., O.F. Francke, and L. Prendini. 2014a. Phylogeny of the North American scorpion genus *Diplocentrus* Peters, 1861 (Scorpiones: Diplocentridae) based on morphology, nuclear and mitochondrial DNA. *Arthropod Systematics and Phylogeny* 72: 257–279.
- Santibáñez-López, C.E., O.F. Francke, and L. Prendini. 2014b. *Koloth*, n. gen. (Scorpiones: Diplocentridae), a new scorpion genus from Mexico. *American Museum Novitates* 3815: 1–28.
- Sareen, M.L., and D. Monga. Size relationship of oocytes and their nuclei in three species of scorpions. *Current Science* 42: 281–282.
- Sasirababu, K. 1961. "Giant" fibres in the central nervous system of scorpion. *Journal of Animal Morphology and Physiology* 8: 11–18.
- Sasirababu, K., and S.A.T. Venkatachari. 1966. Certain anatomical features of the ventral nerve cord of the scorpion, *Heterometrus fulvipes*. *Journal of Animal Morphology and Physiology* 13: 22–33.
- Scheuring, L. 1912. Über ein neues Sinnesorgan bei *Heterometrus longimanus* Hbst. *Zoologischer Anzeiger* 40: 370–374.
- Schiejok, H. 1997. Einige Gedanken zur Haltung von *Pandinus imperator* (C.L. Koch, 1842). *Skorpion-News* 2: 39–43.
- Schultze, W. 1927. Biology of the large Philippine forest scorpion. *Philippine Journal of Science* 32: 375–388.
- Sergeant, E. 1938. Iconographie des scorpions de l'Afrique du Nord. *Archives de l'Institut Pasteur d'Algérie* 16: 513–522.
- Sergeant, E. 1941. Sur le postabdomen (queue) del quelques scorpions de l'Afrique du Nord. *Archives de l'Institut Pasteur d'Algérie* 19: 353–357.
- Shachak, M., and S. Brand. 1983. The relationship between sit-and-wait foraging strategy and dispersal in the desert scorpion *Scorpio maurus palmatus*. *Oecologia* 60: 371–377.
- Sharma, P.P., R. Fernández, L.A. Esposito, E. González-Santillán, and L. Monod. 2015. Phylogenomic resolution of scorpions reveals multilevel discordance with morphological phylogenetic signal. *Proceedings of the Royal Society B, Biological Sciences* 282: 1–10.
- Shivashankar, T. 1992. The importance of burrowing for the scorpion *Heterometrus fulvipes* Koch (Arachnida). *Journal of Soil Biology and Ecology* 12: 134–138.
- Shivashankar, T. 1994. Advanced subsocial behaviour in the scorpion *Heterometrus fulvipes* Koch (Arachnida). *Journal of Bioscience* 19: 81–90.
- Shivashankar, T., and G.K. Veeresh. 1991. Advantages of burrowing by a tropical scorpion, *Heterometrus fulvipes* (Arachnida: Scorpionidae). In G.K. Veeresh, D. Rajagopal and C.A. Viraktamath (editors), *Advances in management and conservation of soil fauna*: 697–702. New Delhi: Oxford.
- Shultz, J.W. 2007. Morphology of the prosomal endoskeleton of Scorpiones (Arachnida) and a new hypothesis for the evolution of cuticular cephalic endoskeletons in arthropods. *Arthropod Structure and Development* 36: 77–102.
- Simard, J.M., and D.D. Watt. 1990. Venoms and toxins. In G.A. Polis (editor), *The biology of scorpions*: 414–444. Stanford, CA: Stanford University Press.
- Simon, E. 1872a. Arachnides de Syrie rapportés par M. Charles Piochard de la Brulerie (scorpions et *Galeodes*). *Annales de la Société Entomologique de France* 2: 247–264.
- Simon, E. 1872b. Études sur les scorpions. Révision des *Heterometrus* du groupe de l'*H. afer*, L. *Revue et Magasin de Zoologie Pure et Appliquée* 23: 51–59; 97–101.
- Simon, E. 1879. 3^e Ordre. Scorpiones. In *Les arachnides de France*. VII. Contenant les ordres des Chernetes, Scorpiones et Opiliones: 79–115. Paris: Rôret.
- Simon, E. 1880. [Scorpions du Mossoul (ancienne Ninive), sur le Tigre, en Mésopotamie.] *Bulletin de la Société Entomologique de France* 10: 29.
- Simon, E. 1884a. Arachnides recueillis en Birmanie par M. le Chevalier J.B. Comotto et appartenent au Musée Civique d'Histoire Naturelle de Gènes. *Annali del Museo Civico di Storia Naturale di Genova* 20: 37–48 (361–372).
- Simon, E. 1884b. Études arachnologiques. 15^e Mémoire. XXII. Arachnides recueillis par M. l'abbé A.

- David à Smyrne, à Beirout et à Akbès en 1883. *Annales de la Société Entomologique de France* 4: 181–196.
- Simon, E. 1885. Matériaux pour servir à la faune arachnologique de l'Asie méridionale. *Annales de la Société Entomologique de France* 7: 22–39.
- Simon, E. 1887. Étude sur les arachnides de l'Asie méridionale faisant partie des collections de l'Indian Museum (Calcutta). I. Arachnides recueillis à Tavoy (Tenasserim) par Moti Ram. *Journal of the Asiatic Society of Bengal* 56: 101–117.
- Simon, E. 1892. Liste des arachnides recueillis en Syrie par M. le docteur Théod. Barrois. *Revue Biologique du Nord de la France* 5: 80–84.
- Simon, E. 1893. Arachnides de l'Archipel Malais recueillis par MM. M. Bedot et C. Pictet. *Revue Suisse de Zoologie* 1: 319–328.
- Simon, E. 1899. Contributions à la faune de Sumatra. Arachnides recueillis par M.J.L. Weyers, à Sumatra (2^e mémoire). *Annales de la Société Entomologique de Belgique* 43: 78–125.
- Simon, E. 1901. On the arachnids collected during the “Skeat Expedition” to the Malay Peninsula, 1899–1900. *Proceedings of the Zoological Society of London* 2: 45–84.
- Simon, E. 1904. Arachnides recueillis par M.A. Pavie en Indo-Chine. In *Mission Pavie en Indo-Chine 1879–1895. Etudes diverses III. Recherches sur l'histoire naturelle de l'Indochine orientale*: 270–295. Paris: Ernest Leroux.
- Simon, E. 1905. Voyage de M. Maurice Maindron dans l'Inde méridionale. Arachnides. *Annales de la Société Entomologique de France* 74: 160–180.
- Simon, E. 1910. Révision des scorpions d'Égypte. *Bulletin de la Société Entomologique d'Égypte (Cairo)* 1910: 57–87.
- Sinha, R.C. 1966. Effect of starvation on the concentration of ascorbic acid in the pedipalp muscle of the scorpion (*P. bengalensis*). *Experientia* 22: 221–222.
- Sinha, R.C., and M.S. Kanungo. 1967. Effects of starvation on the scorpion *Palamnaeus bengalensis*. *Physiological Zoology* 40: 386–390.
- Sissom, W.D. 1990. Systematics, biogeography and paleontology. In G.A. Polis (editor), *The biology of scorpions*: 64–160. Stanford, CA: Stanford University Press.
- Skaife, S.H. 1920. *Animal life in South Africa*. Cape Town: Maskew Miller.
- Skaife, S.H. 1954. *South African nature notes*. 2nd ed. Cape Town: Maskew Miller.
- Soleglad, M.E., and V. Fet. 2003a. High-level systematics and phylogeny of the extant scorpions (Scorpiones: Orthosterni). *Euscorpius* 11: ii+1–175.
- Soleglad, M.E., and V. Fet. 2003b. The scorpion sternum: structure and phylogeny (Scorpiones: Orthosterni). *Euscorpius* 5: 1–34.
- Soleglad, M.E., V. Fet, and F. Kovařík. 2005. The systematic position of the scorpion genera *Heteroscorpion* Birula, 1903 and *Urodacus* Peters, 1861 (Scorpiones: Scorpionioidea). *Euscorpius* 20: 1–38.
- Sreenivasa-Reddy, R.P. 1968. Contribution à la connaissance des scorpions de l'Inde. 5. Le genre *Iomachus* Pocock, 1893 (Scorpionidae, Ischnurinae). *Bulletin du Muséum National d'Histoire Naturelle, Paris* 40: 759–767.
- Srivastava, D.S. 1955. Maxillary processes and mechanism of feeding in scorpions. *Sugar University Journal* 2: 85–91.
- Srivastava, D.S., and M.S. Kanungo. 1966. Metabolism of the liver of the scorpion, *Palamnaeus bengalensis*. *Comparative Biochemistry and Physiology* 19: 629–632.
- Stahnke, H.L. 1974. An estimate of the number of taxa in the order Scorpionida. *BioScience* 24: 339.
- Stamatakis, A. 2006. RAXML-VI-HPG: maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics* 22: 2688–2690.
- Stamatakis, A. 2014. RAXML version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics* 30: 1312–1313.
- Stockmann, R. 1979. Développement postembryonnaire et cycle d'intermue chez un scorpion Buthidae – *Buthotus minax occidentalis*. *Bulletin du Muséum National d'Histoire Naturelle, Paris* 4: 405–420.
- Stockwell, S.A. 1989. Revision of the phylogeny and high classification of scorpions (Chelicerata). Ph.D. dissertation, University of California, Berkeley.
- Subburam, V., and T. Gopalakrishna Reddy. 1978a. Breeding season and gestation period of the scorpion *Heterometrus fulvipes*. *Journal of the Bombay Natural History Society* 75: 513–514.
- Subburam, V., and T. Gopalakrishna Reddy. 1978b. Changes of glucose and glycogen content in the maternal and embryonic tissues of the viviparous scorpion *Heterometrus fulvipes* during gestation period. *Current Science* 47: 665–667.
- Subburam, V., and T. Gopalakrishna Reddy. 1979. Changes in the protein content of the maternal and embryonic tissues of the viviparous scorpion *Heterometrus fulvipes* during gestation period. *Current Science* 48: 853–856.

- Subburam, V., and T. Gopalakrishna Reddy. 1980a. Changes in the lipid content of the maternal and embryonic tissues and variations in the maternal hepatosomatic index during the gestation period of the viviparous scorpion, *Heterometrus fulvipes*. *Current Science* 49: 658–661.
- Subburam, V., and T. Gopalakrishna Reddy. 1980b. Changes in the oxygen consumption of the maternal animal, and maternal and embryonic tissues during the gestation period of the viviparous scorpion, *Heterometrus fulvipes*. *Current Science* 49: 138–140.
- Subburam, V., and T. Gopalakrishna Reddy. 1981. Morphology of the embryonic stages of the viviparous scorpion, *Heterometrus fulvipes*: a photographic study. *Journal of Morphology* 169: 275–281.
- Subburam, V., and T. Gopalakrishna Reddy. 1989. Functional morphology of the appendix of the viviparous scorpion, *Heterometrus fulvipes* (Koch) (Arachnida: Scorpionidae). *International Journal of Insect Morphology and Embryology* 18: 329–333.
- Sundevall, C.J. 1833. *Conspectus arachnidum*. Londoni Gothorum: C.F. Berling. 39 pp.
- Sureshan, P.M., D.B. Bastawade, and C. Radhakrishnan. 2007a. Taxonomic studies on a collection of scorpions (Scorpiones: Arachnida) from Western Ghats in Kerala, India with two new distribution records. *Zoos' Print Journal* 22: 2903–2908.
- Sureshan, P.M., D.B. Bastawade, and C. Radhakrishnan. 2007b. Scorpion fauna (Arachnida: Scorpionida) of Parambikulam Wild Life Sanctuary, Kerala, India. *Records of the Zoological Survey of India* 107: 49–54.
- Tahir, H.M., and L. Prendini. 2014. Redescription of *Heterometrus latimanus* and confirmation of the genus *Heterometrus* (Scorpiones: Scorpionidae) in Pakistan. *American Museum Novitates* 3805: 1–23.
- Takashima, H. 1941. [Scorpiones and Pedipalpi from the islands of Riu-Kiu.] *Biogeographica* (Tokyo) 3: 273–285. [in Japanese]
- Takashima, H. 1945. [Scorpions of eastern Asia.] *Acta Arachnologica* 9: 68–106. [in Japanese]
- Takashima, H. 1952. [Miscellaneous notes on scorpions.] *Acta Arachnologica* 13: 26–36. [in Japanese]
- Talal, S., et al. 2015. Scorpion speciation in the Holy Land: multilocus phylogeography corroborates diagnostic differences in morphology and burrowing behavior among *Scorpio* subspecies and justifies recognition as phylogenetic, ecological and biological species. *Molecular Phylogenetics and Evolution* 91: 226–237.
- Tare, T.G., N.E. Vad, and D.M. Renapurkar. 1993. Burrow patterns of the scorpion *Heterometrus indus*. *Medical and Veterinary Entomology* 7: 102–104.
- Thorell, T. 1876a. On the classification of scorpions. *Annals and Magazine of Natural History* (Ser. 4) 17: 1–15.
- Thorell, T. 1876b. Études Scorpiologiques. *Atti della Società Italiana di Scienze Naturali* 19: 75–272.
- Thorell, T. 1888. Pedipalpi e scorpioni dell'Archipelago Malesi conservati nel Museo Civico di Storia Naturale di Genova. *Annali del Museo Civico di Storia Naturale di Genova* "Giacomo Doria" 26: 327–428.
- Thorell, T. 1890. Aracnidi di Nias e di Sumatra raccolti nel 1886 dal Sign. E. Modigliani. *Annali del Museo Civico di Storia Naturale di Genova* "Giacomo Doria" 30: 5–106.
- Thorell, T. 1893. Scorpiones exotici R. *Musei Historiae Naturalis Florentini*. *Bolletino della Società Entomologica Italiana* 25: 356–387.
- Thorell, T., and G. Lindström. 1885. On a Silurian scorpion from Gotland. *Bihang till Kungliga Svenska Vetenskapsakademiens Handlingar* 21: 1–33.
- Thulsi Rao, K., D.B. Bastawade, M. Sudhakar, S.M.M. Javed, and I.S.R. Krishna. 2005. Arachnid fauna of Nallamalai Region Eastern Ghats, Andhra Pradesh, India. *Records of the Zoological Survey of India, Occasional Paper* 239: 1–42.
- Tikader, B.K. 1973. Arachnida of the Deccan area. *Bulletin of the Indian National Science Academy* 45: 260–276.
- Tikader, B.K. 1987. The scorpions. *In Handbook Indian spiders*: 20–38. Calcutta: Zoological Survey of India.
- Tikader, B.K., and D.B. Bastawade. 1983. Fauna of India, vol. 3. Scorpions (Scorpionida: Arachnida). *Zoological Survey of India*. Pune: Sangam Press. 671 pp.
- Toye, S.A. 1970. Some aspects of the biology of two common species of Nigerian scorpions. *Journal of Zoology, London* 162: 1–9.
- Uthaman, M., and Y. Srinivasa Reddy. 1979. Bimodal oscillation in the oxygen consumption of the isolated tissues of the scorpion *Heterometrus fulvipes*. *Journal of Arid Environments* 2: 347–353.
- Vachon, M. 1950. Études sur les scorpions. III (suite). Description des scorpions du nord de l'Afrique. *Archives de l'Institut Pasteur d'Algérie* 28: 152–216.
- Vachon, M. 1952a. Études sur les scorpions. *Alger: Institut Pasteur d'Algérie*, 482 pp.
- Vachon, M. 1952b. La Réserve Naturelle Intégrale du Mt. Nimba I. Scorpions. *Mission M. Lamotte en Guinée (1942). Mémoires de l'Institut Français de Afrique Noire* 19: 9–15.
- Vachon, M. 1953. Quelques remarques sur les frontières en biogéographie à propos de la Ligne Wallace et des scorpions indonésiens. *Comptes Rendus des Séances de la Société de Biogéographie* 30: 6–12.

- Vachon, M. 1963. De l'utilité, en systématique, d'une nomenclature des dents de chélicères chez les scorpions. *Bulletin du Muséum National d'Histoire Naturelle*, Paris 35: 161–166.
- Vachon, M. 1974 ("1973"). Étude des caractères utilisés pour classer les familles et les genres de scorpions (arachnides). 1. La trichobothriotaxie en arachnologie. Sigles trichobothriaux et types de trichobothriotaxie chez les scorpions. *Bulletin du Muséum National d'Histoire Naturelle*, Paris 140: 857–958.
- Vachon, M. 1982. Les scorpions de Sri Lanka (Recherches sur les scorpions appartenant ou déposés au Muséum d'Histoire naturelle de Genève III.). *Revue Suisse de Zoologie* 89: 77–114.
- Vachon, M., and T. Abe. 1988. Colonization of the Krakatau Islands (Indonesia) by scorpions. *Acta Arachnologica* 37: 23–33.
- Vachon, M., and W.R. Lourenço. 1985. Scorpions cavernicoles du Sarawak (Borneo). *Chaerilus chapmani* n. sp. (Chaerilidae) et *Lychas hosei* (Pocock, 1890) (Buthidae). *Mémoires Biospéologiques* 12: 9–18.
- Vachon, M., B. Dumortier, and R.-G. Busnel. 1958. Enregistrement de stridulations d'un scorpion sud-africain. *Bulletin de la Société Zoologique de France* 83: 253–254.
- Vachon, M., R.-G. Busnel, and B. Dumortier. 1960. Production de sons par un scorpion sud-africain (*Opisthophthalmus latimanus*). *Bulletin de la Société Zoologique de France* 85: 79.
- Vachon, M., R. Roy, and M. Condamin. 1970. Le développement post-embryonnaire du scorpion *Pandinus gambiensis* Pocock. *Bulletin de l'Institut Français de Afrique Noire (A)* 32: 414–432.
- Van Zinderen Bakker, E.M. 1978. Late-Mesozoic and Tertiary palaeoenvironments of the Sahara region. In E.M. van Zinderen Bakker (editor), *Antarctic glacial history and world palaeoenvironments*: 129–135. Rotterdam: A.A. Balkema.
- Van Zinderen Bakker, E.M. 1980. Comparison of late-Quaternary climatic evolutions in the Sahara and the Namib-Kalahari region. *Palaeoecology of Africa* 12: 381–394.
- Venkatachari, S.A.T., and P. Muralikrishna Dass. 1968. Choline esterase activity rhythm in the ventral nerve cord of scorpion. *Life Sciences* 7: 617–621.
- Venkateswara Rao, P., and S. Govindappa. 1967. Dehydrogenase activity and its diurnal variations in different muscles of the scorpion *Heterometrus fulvipes*. *Proceedings of the Indian Academy of Sciences*, B 66: 243–249.
- Veronika, K., K. Akilan, T. Eswaramohan, and A. Muruganathan. 2013. Diversity and identification key to the species of scorpions (Scorpiones: Arachnida) from Jaffna Peninsula, Sri Lanka. *Journal of Entomology and Zoology Studies* 1: 70–77.
- Vijayalakshmi, N.R., and P.A. Kurup. 1976. Metabolism of glycosaminoglycans in *Heterometrus scaber*. *Indian Journal of Experimental Biology* 14: 10–13.
- Volschenk, E.S., and L. Prendini. 2008. *Aops oncodactylus* gen. et sp. nov., the first troglobitic urodacid (Chelicerata: Scorpiones), with a re-assessment of cavernicolous, troglobitic and troglomorphic scorpions. *Invertebrate Systematics* 22: 235–257.
- Volschenk, E.S., C.I. Mattoni, and L. Prendini. 2008. Comparative anatomy of the mesosomal organs of scorpions (Chelicerata, Scorpiones), with implications for the phylogeny of the order. *Zoological Journal of the Linnean Society* 154: 651–675.
- Vyas, A.B. 1971. Adaptive diversification of the prosomatic appendages in the scorpion *Heterometrus fulvipes*. *Annals of Zoology* 7: 65–80.
- Vyas, A.B. 1974. The cheliceral muscles of the scorpion *Heterometrus fulvipes*. *Bulletin of the Southern California Academy of Sciences* 73: 9–14.
- Vyas, A.B., and S.M. Laliwala. 1972. Certain noteworthy features of the circulatory system of *Heterometrus fulvipes*. *Proceedings of the National Academy of Sciences (India) Sect. B*, 42: 267–271.
- Wallin, L. 1994. Uppsala University Zoological Museum. Catalog of type specimens (Version 4). 4. Linnean specimens. Uppsala. [Scorpiones: p. 13.]
- Wang, K., et al. 2019. Vibrational receptor of scorpion (*Heterometrus petersii*): the basitarsal compound slit sensilla. *Journal of Bionic Engineering* 16: 76–87.
- Warburg, M.R. 2010. Reproductive system of female scorpion: a partial review. *Anatomical Record* 293: 1738–1754.
- Warburg, M.R. 2012a. Reviewing the structure and function of the scorpion's hepatopancreas. *Arthropods* 1: 79–93.
- Warburg, M.R. 2012b. Ovulation, fertilization and embryonic development in scorpions: a partial review. *African Entomology* 20: 60–68.
- Warburg, M.R. 2013. The circadian rhythm and visual elements in scorpions: a review. *Arthropods* 2: 150–158.
- Warburg, M.R., and G.A. Polis. 1990. Behavioral responses, rhythms and activity patterns. In G.A. Polis (editor), *The biology of scorpions*: 224–246. Stanford, CA: Stanford University Press.

- Weidner, H. 1959. Die entomologischen Sammlungen des Zoologischen Staatsinstituts und Zoologischen Museums Hamburg, I. Teil, Pararthropoda und Chelicerata I. Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut 57: 89–142.
- Werner, F. 1902. Die Skorpione, Pedipalpen und Solifugen in der zoologisch-vergleichend-anatomischen Sammlung der Universität Wien. Verhandlungen der Kaiserlich-Königlichen Zoologisch-Botanischen Gesellschaft in Wien 52: 595–608.
- Werner, F. 1916. Über einige Skorpione und Gliederspinnen des Naturhistorischen Museum in Wiesbaden. Jahrbücher des Nassauischen Verein für Naturkunde 69: 79–97.
- Werner, F. 1932. Die Skorpione und Pedipalpen der Deutschen Limnologischen Sunda-Expedition. Archiv für Hydrobiologie 3: 575–576.
- Werner, F. 1934. Scorpiones, Pedipalpi. In H.G. Bronn (editor), Klassen und Ordnungen des Tierreichs: 5, IV, 8, Lief. 1, 2 (Scorpiones): 1–316. Leipzig: Akademische Verlagsgesellschaft.
- Werner, F. 1936. Neu-Eingänge von Skorpionen im Zoologischen Museum in Hamburg. Festschrift zum 60. Geburtstag von Professor Dr. Embrik Strand 2: 171–193.
- Wirkner, C.S., and L. Prendini. 2007. Comparative morphology of the hemolymph vascular system in scorpions – a survey using corrosion casting, MicroCT and 3D-reconstruction. Journal of Morphology 268: 401–413.
- Yellamma, K., M. Mohan, and K. Sasirababu. 1980. Morphology and physiology of the giant fibres of the seventh abdominal ganglion of the scorpion *Heterometrus fulvipes*. Proceedings of the Indian Academy of Sciences 89: 29–38.
- Yellamma, K., K. Subhashini, M. Mohan, and K. Sasirababu. 1982. Microanatomy of the 7th abdominal ganglion and its peripheral nerves in the scorpion *Heterometrus fulvipes*. Proceedings of the Indian Academy of Sciences 91: 225–234.
- Zhu, M., and X. Yang. 2007. Two species of the genus *Heterometrus* Ehrenberg, 1828 (Scorpionidae) from south Vietnam sold in pet shoppes in China. Acta Arachnologica Sinica 16: 92–103.

APPENDIX 1

DISTRIBUTION OF MORPHOLOGICAL CHARACTERS USED FOR PHYLOGENETIC ANALYSIS OF THE
ASIAN FOREST SCORPIONS (SCORPIONIDAE: HETEROMETRINAE SIMON, 1879, STAT. NOV.)
Character states scored 0–4, inapplicable (-) or unknown (?). Character descriptions in appendix 2.

Outgroup***Nebo hierichonticus***

0000020000	0000000100	0000000000	
0000000000	0000000010	0010000011	
0011000000	0000001000	0000000000	
0000000000	0000000001	0100101100	
1011000000	000-000100	0001000000	
0000000000	0000000110	0000000001	000000

Opisthophthalmus capensis

0211240020	1101111111	1113010011	
1010012000	1000111101	0100100012	
0111100001	1000000001	1122011110	
0100111001	1200013101	0111101111	
0011101111	0011010120	1102112221	
2100101101	1101111111	1001110001	002100

Ingroup***Chersonesometrus bastawadei***

0100210000	0000100220	0002000000	
0001102220	1100101100	1010000023	
0122020110	0110122202	1021111100	
0101120001	0122002011	1100111001	
1001010000	0110111111	0101110101	
0000010000	1100000011	0011100000	001000

Chersonesometrus beccaloniae

0100010001	0000100210	0002000000	
0101102221	1100101000	1010000012	
0112010111	0111112212	1022111100	
0101120011	0122002011	1100111001	
1001010000	0110111111	0111100001	
0001011100	1100000101	0011100000	001000

Chersonesometrus fulvipes

0100210010	0000100210	0002000000	
0001102220	1100101100	1010000023	
0122020110	0110122202	1021111100	
0101120101	0122002011	1100111001	
1001010000	0110111111	0101110101	
0000011101	1100000011	0011100000	001000

Chersonesometrus hendersoni

1100010001	0000100210	0002000000	
0101102220	1100101000	1010000044	
0022020110	0111112212	1022111100	
0101120001	0122002011	1100111001	
1001010000	0110111111	0111100001	
0000010000	1100000111	0011100000	001000

Chersonesometrus madraspatensis

0100210010	0000100220	0002000000	
0001102221	1100101100	1010000023	
1112020110	0111122202	1021111100	
0101120101	0122002010	1100011001	
1001010000	0110111111	0101110101	
0000011101	1100000111	0011100000	001000

Pandinus imperator

1100000011	0000100320	0102000000	
0001002210	1101100121	1120111133	
1122000001	1000020102	1022111100	
1-11020011	0122002010	1100011001	
0111010000	0110011111	0101110101	
0000001101	1100000111	0011100001	001100

Scorpio fuscus

0100210010	1000000300	0112000000	
0000002110	1010100101	0110000033	
1122000001	1001000001	1021011100	
0100110001	0111111110	1110011101	
0011100000	0010011120	0101101011	
1000000001	1101111111	0100001110	000101

Chersonesometrus nathanorum

?100010001	0000100210	0002000000	
010110222?	?100101101	0100000011	
0112010110	0112102202	1022?01100	
0101120011	0122002011	1100111001	
1101010000	01???11111	0100100101	
0000011110	1100000101	0011100000	00100?

Chersonesometrus pelekomanus

0100010001	0000100220	0002000000	
0101102220	1100101000	1010000044	
0022020110	0111112212	1022111100	
0101120011	0122002011	1100111001	
1001010000	0110111111	0111100001	
0000010000	1100000111	0011100000	001000

Chersonesometrus shivashankari

0100210010	0000100220	0002000000	
0101101220	1100101100	1010000023	
1122020110	0111122202	1021111100	
0101120101	0122002011	1100011001	
1001010000	0110111111	0101110101	
0000011101	1100000011	0011100000	001?00

Chersonesometrus tristis

0100010001	0000100210	0002000000	
0101102221	1100101000	1010000023	
0012020111	0111112212	1022111100	
0101120011	0111112202	1100111001	
1001010000	0110111111	0110100101	
0011011100	1100000111	0011100000	001000

Chersonesometrus wroughtoni

0100210000	0000100210	0002000000	
0101102220	1100101100	1010000023	
0122020110	0111112202	1021111100	
0101120011	0122002011	1100111001	
1001010000	01???11111	0111100101	
0000010100	1100000001	0011100000	00100?

APPENDIX 1 *continued****Deccanometrus bengalensis***

01002[01]0001 0000100120 0001000000
 0001102221 1100101111 0110000011
 1100100001 0010120102 1022100100
 0101120011 0122002011 1100111001
 0011010000 0110111111 0111110101
 0000011101 1100000001 00111000[01]0 001000

Deccanometrus latimanus

0100220010 0000100110 0011000000
 0001101220 1100100121 0120000033
 1122100001 1010020102 1122100100
 0101120101 0122002010 0100001000
 0011000000 0110110111 0110110001
 0022011111 1110000001 0111100011 001110

Deccanometrus liurus

0100130001 1000100110 0011020000
 0001121221 1101101121 0120000012
 1100100001 1000020102 1022100100
 0101120101 0122002010 1100011001
 0011010000 01???10111 0110110001
 0033011110 1210000001 0111100001 001?0?

Deccanometrus obscurus

0100200001 0000100110 0001000000
 0101102221 1100101110 1010000012
 1101000001 0010120102 1022111100
 0101120011 0122002011 1100111001
 1001010000 0110111111 0111110101
 0000011101 1100000001 00111000[01]0 001000

Deccanometrus phipsoni

0100210001 0000100110 0001000000
 0101102221 1100101110 1010000012
 [01]100000001 0010120102 1022111100
 0101120011 0122002011 1100111001
 1001010000 0110111111 011[01]100101
 0000011101 1100000001 00111000[01]0 001000

Deccanometrus ubicki

0100110001 0000100220 0011000000
 0101102221 1100101121 0120000012
 1100100001 1000020102 1022100011
 0101120101 0122002011 1100111001
 1011010000 0110111011 0110110001
 0000011100 1210000001 0111100001 001?0?

Deccanometrus xanthopus

0100231010 0000100[23]20 0001000000
 0101101221 1101101111 0120000022
 1111100000 0110120102 1121100100
 0101120101 0122002010 01000[01]1001
 0011010000 0110110[01]11 0100100001
 0000011110 1100000001 0111100001 001110

Gigantometrus swammerdami

1100220110 0000100220 0001000000
 0001101220 1100101101 1120000044
 1122010110 0111111102 1021111100
 01011200[01]1 0122002011 1100111001
 1001010000 0110111111 0101110100
 0000020000 1100000001 0001100000 101100

Gigantometrus titanicus

1100210110 0000100220 0001000000
 0001102220 1100101101 1120000044
 1122010110 0111111102 1021111100
 0101120011 0122002011 1100111001
 1001010000 0110111111 0101110100
 0000020000 1100000001 0001100000 101100

Heterometrus glaucus

1100000111 0010100220 0001120000
 0001012221 1100101121 1121000001
 1101100001 1000020102 1011000011
 0101120011 0000002011 1000111001
 1101010000 1110111111 0111110101
 0000011101 1100000001 0011100001 021100

Heterometrus laevigatus

0100000111 0010100010 0001120000
 0001012221 1100101121 1121000012
 1101100001 1000020102 1111000011
 0101020011 0000002011 1100111001
 1001010000 1110111111 0110110101
 0000001101 1100000001 0011100010 021100

Heterometrus laoticus

0100000111 0010100000 0001121100
 0101012220 1100101121 1121000021
 1111100001 1000020102 1011011011
 0101020011 0000002011 1000110001
 1001010000 1110111111 0110110101
 0000001101 1100001011 0001100010 021100

Heterometrus longimanus

0100000111 0010100[12][12]0 0001120000
 0101012221 1100101121 1121000000
 1100100001 1000020102 1011011011
 0101120011 0000002011 1000110001
 1001010000 1110111111 0111110101
 0000001100 1100000001 0011100001 021100

Heterometrus petersii

[01]100000111 0010100110 0001120000
 0001012220 1100101121 1121000022
 1111100001 1000020102 1011011011
 0101020011 0000002011 1000110001
 1101010000 1110111111 0111110101
 0000001101 1100000001 0011100000 021100

Heterometrus silenus

0100000111 0010100110 0001120000
 0001012220 1100101121 1121000032
 1121100001 1000020102 1011011011
 0101020011 0000002011 1000110001
 1001010000 1110111111 0111110101
 0000001101 1100000001 0001100010 021100

Heterometrus spinifer

1100000111 0010100110 0001120000
 0001012220 1100101121 1121000022
 1111100001 1000020102 1011011011
 0101020011 0000002011 1000110001
 1101010000 1110111111 0111110101
 0000001101 1100000001 0011100000 021100

APPENDIX 1 *continued****Heterometrus thorellii***

0100000111 0010100220 0001120000
 0001012221 1100101121 1121000001
 1101100001 1000020102 1011011011
 0101120011 0000002011 1100111001
 1001010000 1110111111 0110110101
 0000001101 1100000001 0011100010 021100

Javanimetrus cyaneus

0100201011 0000100220 0001020000
 00012-2220 1100101121 1120000023
 1122100001 1000120112 1021100011
 0101120011 0122002010 1100011001
 1101010000 0110111111 0111110101
 0000011101 1100000111 0011100000 011100

Sahyadrimetrus barberi

0100200001 0000100?20 0001020000
 010?2-222? 110010?121 01100000?1
 11?110000? 0?1?12?102 102?1?01?0
 0101?20011 0122002011 1100111001
 1101010000 0???11? 01?0?1?101
 000001?111 110?0?0?01 0011100000 011???

Sahyadrimetrus kanarensis

0100200101 0000100220 0001020000
 01012-2220 1100101121 1120000012
 1111100001 1000120102 1022100011
 0101120011 0122002010 1100011001
 0111010000 0110111111 0111110101
 0000011101 1100000001 0011100000 011100

Sahyadrimetrus mathewi

0100200121 0000100330 0001020000
 00012-2221 1100101121 1120000012
 1101100001 1000120102 1022100101
 0101120011 0122002010 1100011001
 1101010000 0110111111 0101110101
 0000011101 1100000001 0011100000 011100

Sahyadrimetrus rugosus

0100200001 0000100120 0001020000
 01012-2221 1100101110 0010000011
 1101100000 0110120102 1022100110
 0101120011 0122002011 1100111001
 1101010000 0110111111 0110110101
 0000011101 1100000001 0011100000 011000

Sahyadrimetrus scaber

0100200111 0000100220 0001020000
 00012-2220 1100101121 1120000022
 1111100001 1000120102 1022100101
 0101120011 0122002010 1100011001
 1101010000 0110111111 0101110101
 0000011101 1100000001 0011100000 011100

Sahyadrimetrus tikaderi

0100200001 0000100220 0001020000
 01012-2220 1100101121 0110000011
 1101100000 0110120102 1022100010
 0101120011 0122002011 1100111001
 1101010000 0110111111 0111110101
 0000011101 1100000111 0011100000 011000

Srilankametrus caesar

0100211010 0000100220 0101000000
 0001102220 1100101101 0110000023
 1122101001 1111121102 1021111100
 01011200[01]1 0122002011 1100111001
 1001010000 0110111211 0111110101
 0000010001 1100000111 0011100010 021110

Srilankametrus couzjini

0100211010 00001000?0 0101000?00
 0?01102220 ?1001011?? ???000004?
 112?101001 ?1?1102102 ??2111?0?
 0101120011 0122002010 1100011001
 1001010000 0110111?11 011?1101?1
 0000010?01 1100?0?1?1 0011100010 021110

Srilankametrus gravimanus

0100211010 0000100000 0101000000
 0101102220 1100101121 1120000033
 1112101001 1112102102 1021111100
 0101120011 0122002011 1100111001
 1001010000 0110111211 0111110101
 0000010001 1100000101 0011100010 021110

Srilankametrus indus

0100201000 0000100000 0101021100
 00012-2220 1100101121 0110000033
 1122100001 1000120112 1022111100
 0101120011 0122002010 1100011001
 1001010000 0110111211 0120-10101
 0022011111 1100000001 0011100010 001100

Srilankametrus pococki

0100201000 0000100000 0101020000
 00012-2220 1100101121 0110000033
 0022100001 1000120112 1022111100
 0101120011 0122002010 1100011001
 1001010000 0110111211 0120-10101
 0000011111 1100000001 0011100010 001100

Srilankametrus serratus

0100211010 0000100000 0101000000
 0001102220 1100101121 1110000033
 1122100001 1001111102 1021111100
 0101120011 0122002011 1100111001
 1001010000 0110111211 0111110101
 0000010101 1100000001 0011100000 001110

Srilankametrus yaleensis

0100211010 0000100000 0101000000
 0101102220 1100101121 1120000022
 1122102001 1112102102 1021111100
 0101120011 0122002010 1100011001
 1001010000 0110111211 0120-10101
 0011010101 1100000001 0011100000 021110

APPENDIX 2

MORPHOLOGICAL CHARACTERS AND CHARACTER STATES USED FOR PHYLOGENETIC ANALYSIS OF THE ASIAN FOREST SCORPIONS (SCORPIONIDAE: HETEROMETRINAE SIMON, 1879, STAT. NOV.)

Terminology follows previous papers on Scorpionidae Latreille, 1802, by the first author (e.g., Prendini 2000b, 2001a; Prendini et al., 2003; Tahir and Prendini, 2014; Prendini, 2016). Characters corresponding to the lists of Lamoral (1979: table 6), Couzijn (1981: tables 2 and 9), and Prendini (2000a: appendix 3) and Prendini et al. (2003: appendix 2) are denoted, respectively, by the abbreviations BHL, HWC, LP, and PEA, followed by the corresponding number. Character matrix in appendix 1. Fifty-two uninformative characters are indicated by †.

Total Length

1. Adult length, measured from anterior margin of carapace to tip of aculeus: **0**, medium, minimum length of 50 mm to maximum length of 120 mm; **1**, extremely large, minimum length > 120 mm. [PEA 1]

Chelicerae

2. Chelicerae dorsal surfaces, infuscation: **0**, entirely pale or nearly so, fingers may be very slightly infuscate (cheliceral manus similar to, or paler than carapace interocular surface); **1**, bicolored, prodorsal half of cheliceral manus paler than retrodorsal half and fingers (manus similar to or paler than carapace interocular surface); **2**, entirely dark (cheliceral manus darker than carapace interocular surface). [PEA 90]
- †3. Cheliceral coxae prodorsal surfaces, scaphotrix (stridulatory setae): **0**, absent; **1**, present. [LP 13, PEA 3]
- †4. Cheliceral coxae promedian surfaces, trichocopae (chemoreceptive lamelliform setae): **0**, absent; **1**, present. [LP 14, PEA 4]
5. Cheliceral movable finger, prodistal (DI) and retrodistal (DE) teeth: **0**, subequal, DE tooth only slightly smaller than DI tooth, and opposable, i.e., forming a bicuspid; **1**, unequal, DE tooth considerably smaller than DI tooth, and opposable, i.e., forming a bicuspid; **2**, unequal, DE tooth considerably smaller than DI tooth, aligned longitudinally and not opposable. [LP 11, PEA 2]

General Color

6. Carapace, pedipalps, tergites and metasoma, base coloration: **0**, black; **1**, very dark reddish or brownish black; **2**, dark reddish brown; **3**, light yellowish brown; **4**, light yellowish.

Carapace

7. Carapace shape, anterolateral margins, dorsal aspect: **0**, converging gradually anteriorly; **1**, converging slightly to subparallel anteriorly.
8. Carapace shape, mediolateral margins, dorsal aspect: **0**, diverging or converging slightly posteriorly (at posterolateral sulci); **1**, converging markedly posteriorly (at posterolateral sulci).

9. Carapace shape, lateral aspect: **0**, slightly to markedly dorsoventrally compressed, lateral surfaces sloping gently; **1**, vaulted, lateral surfaces sloping steeply; **2**, vaulted, lateral surfaces sloping very steeply.
10. Carapace, anterior margin/frontal lobes, shape: **0**, anterior margin straight, frontal lobes evenly rounded or truncate; **1**, anterior margin concave, frontal lobes uneven, sloping medially (toward notch/midline).
11. Carapace anterior margin, median notch: **0**, deeply excavated; **1**, shallow. [LP 3, PEA 5]
- †12. Carapace anterior margin, median projection: **0**, absent; **1**, present. [PEA 6]
13. Carapace rostrrolateral margin: **0**, entire; **1**, distinct incision adjacent to posterior lateral ocelli. [PEA 13]
- †14. Carapace anterior median depression: **0**, absent; **1**, present. [PEA 7]
15. Carapace median longitudinal sulcus, infuscation: **0**, bordered by infuscation from anterior median depression to anterocular depression; **1**, immaculate.
- †16. Carapace interocular surface, base coloration: **0**, similar to, or darker than lateral and posterior surfaces; **1**, noticeably paler than lateral and posterior surfaces. [PEA 91]
- †17. Carapace interocular surface, infuscation: **0**, infuscate; **1**, immaculate.
18. Carapace interocular surface, macrosculpture distribution (♂): **0**, entirely smooth; **1**, granular along median longitudinal and anterior furcated sulci only; **2**, frontal lobes and medial region granular, with smooth areas; **3**, entire surface uniformly granular; **?**, unknown. [modified BHL 4 by adding two states to account for variation in the distribution of granulation, PEA 17]
19. Carapace interocular surface, macrosculpture distribution (♀): **0**, entirely smooth; **1**, granular along median longitudinal and anterior furcated sulci only; **2**, frontal lobes and medial region granular, with smooth areas; **3**, entire surface uniformly granular. [modified BHL 5 by adding two states to account for variation in the distribution of granulation, PEA 18]
- †20. Carapace anterocular depression: **0**, absent, anterior portions of superciliary carinae parallel; **1**, present, anterior portions of superciliary carinae subparallel or diverging. [PEA 8]
- †21. Carapace circumocular depressions: **0**, converging anteriorly; **1**, diverging anteriorly. [PEA 9]
22. Carapace superciliary carinae, anterocular extensions: **0**, present; **1**, absent. [incorporates HWC 7, PEA 11]
23. Carapace superciliary carinae: **0**, higher than median ocelli; **1**, lower than median ocelli. [merged BHL 9 and 10, PEA 12]
24. Carapace median ocular tubercle position, expressed as ratio of distance from carapace anterior margin : carapace length (CAM:CL): **0**, distinctly anterior, CAM:CL < 0.40; **1**, anteromedial to medial, CAM:CL 0.40–0.50; **2**, postero-medial, CAM:CL 0.51–0.62; **3**, distinctly posterior, CAM:CL 0.63–0.78. [modified BHL 3, PEA 10]
25. Carapace median ocelli size relative to ocellus width: **0**, small, distance between ocelli equal to or greater than an

ocellus width; **1**, large, distance between ocelli less than an ocellus width.

26. Carapace interocular suture, presence and breadth: **0**, slender; **1**, broad; **2**, absent. [PEA 14]
27. Carapace anterolateral and mediolateral surfaces, macrosculpture (δ): **0**, granular; **1**, smooth or nearly so. [part of BHL 5: separated into two characters for antero- and posterolateral surfaces]
28. Carapace anterolateral and mediolateral surfaces, macrosculpture (φ): **0**, granular; **1**, smooth or nearly so. [part of BHL 6: separated into two characters for antero- and posterolateral surfaces, PEA 19]
- †29. Carapace mediolateral surfaces, infuscation: **0**, infuscate; **1**, immaculate.
- †30. Carapace posterolateral and, often, posteromedian surfaces, base coloration: **0**, as dark as or darker than tergites; **1**, as pale as tergites, if tergites immaculate, or paler than tergites, if tergites infuscate. [PEA 92]
- †31. Carapace posterolateral surfaces, infuscation: **0**, infuscate; **1**, immaculate.
32. Carapace posterolateral surfaces, macrosculpture (φ): **0**, granular; **1**, smooth or nearly so. [part of BHL 6: separated into two characters for antero- and posterolateral surfaces]
- †33. Carapace posteromedian surface, infuscation: **0**, infuscate; **1**, immaculate.
34. Carapace posteromedian surface, macrosculpture (δ): **0**, granular; **1**, smooth or nearly so; **?**, unknown. [BHL 7, PEA 20]
35. Carapace posterior sutures, presence and length relative to median ocular tubercle: **0**, present, extending to tubercle; **1**, present, extending past tubercle; **2**, absent. [PEA 15]
36. Carapace posterior sutures, connection: **0**, connected anteriorly to posterior furcations of interocular suture; **1**, connected by short cross-suture anterior to postocular depression, regardless of presence or absence of interocular suture; **2**, disconnected; **-**, absent. [PEA 16]

Pedipalps

37. Pedipalps infuscation: **0**, immaculate; **1**, femur and patella infuscate only; **2**, femur, patella, and chela infuscate. [PEA 93]
38. Pedipalps and first walking legs, opposing surfaces of coxae, stridulatory surface, presence and development: **0**, absent; **1**, weakly developed; **2**, well developed. [LP 74, PEA 48]
39. Pedipalps and first walking legs, opposing surfaces of coxae, stridulatory surface, granular tubercles of “rasp” and stridulatory setae (scaphotrix) of “scraper” relative positions: **0**, absent; **1**, “rasp” and “scraper” situated on coxae of pedipalp and first leg, respectively; **2**, “rasp” and “scraper” situated on coxae of first leg and pedipalp, respectively. [LP 75, PEA 49]
40. Pedipalps length (δ), expressed as ratios of pedipalp femur length : posterior carapace width (FL:PCW) and pedipalp femur length : carapace length (FL:CL): **0**, short, FL:PCW

< 0.77, FL:CL < 0.74; **1**, long, FL:PCW $\geq$ 0.80, FL:CL $\geq$ 0.76; **?**, unknown. [replaces BHL 16, PEA 21]

- †41. Pedipalps length (φ), expressed as ratios of femur length : posterior carapace width (FL:PCW) and femur length : carapace length (FL:CL): **0**, long, FL:PCW $\geq$ 0.80, FL:CL $\geq$ 0.76; **1**, short, FL:PCW < 0.77, FL:CL < 0.74. [replaces BHL 16, PEA 21]
42. Pedipalp femur retrodorsal carina, development relative to prodorsal carina: **0**, less developed; **1**, similar or more strongly developed. [modified HWC 28: corrected entry for *Opisthophthalmus*, PEA 44]
- †43. Pedipalp femur trichobothrium *i*, position: **0**, prolateral surface; **1**, dorsal surface. [LP 40, PEA 56]
44. Pedipalp femur prodorsal carina, vertical development: **0**, present and distinct; **1**, absent or obsolete. [PEA 45]
- †45. Pedipalp femur prodorsal and promedian carinae, orientation relative to dorsal secondary and proventral carinae: **0**, parallel to dorsal secondary and proventral carinae; **1**, diagonally from proventral carina to dorsal secondary carina. [PEA 46]
- †46. Pedipalp femur secondary accessory carina, macrosculpture: **0**, absent; **1**, present, comprising weakly developed granular row.
47. Pedipalp femur retroventral carina, longitudinal development (δ): **0**, absent or obsolete; **1**, present, extending partly or entirely to distal edge of segment; **?**, unknown. [PEA 47]
- †48. Pedipalp patella dorsal surface, shape: **0**, flat (or nearly so), axes of dorsomedian and retrodorsal carinae in same plane; **1**, convex, axis of dorsomedian carina dorsal to axis of retrodorsal carina. [LP 15, PEA 38]
49. Pedipalp patella dorsomedian carina, macrosculpture (φ): **0**, entirely to predominantly costate; **1**, entirely to predominantly granular; **2**, absent or obsolete. [PEA 39]
50. Pedipalp patella dorsal intercarinal surfaces, macrosculpture (φ): **0**, granular; **1**, smooth or nearly so. [HWC 37, PEA 40]
51. Pedipalp patella retrodorsal carina, development relative to retromedian carinae (φ): **0**, absent or obsolete; **1**, as strongly developed as or more strongly developed than retromedian carinae. [PEA 42]
52. Pedipalp patella retrodorsal and retroventral intercarinal surfaces, macrosculpture (φ): **0**, granular; **1**, smooth or nearly so. [merged BHL 32 and 33; incorporates HWC 37, PEA 41]
53. Pedipalp patella retromedian carinae, macrosculpture (φ): **0**, costate; **1**, granular; **2**, absent or obsolete. [PEA 43]
54. Pedipalp patella proventral carina, prominent spiniform granule: **0**, absent; **1**, present.
55. Pedipalp patella *est* trichobothria, count: **0**, 1; **1**, 2 (one accessory). [split PEA 54 into three characters]
- †56. Pedipalp patella *em* trichobothria, count: **0**, 2; **1**, 3 (one accessory). [split PEA 54 into three characters]
- †57. Pedipalp patella *esb* trichobothria, count: **0**, 2; **1**, 3 (one accessory). [split PEA 54 into three characters]

- †58. Pedipalp patella *v* trichobothria, count: **0**, single row of 3; **1**, two or more rows of > 25. [modified BHL 28 and LP 43 with extra states, PEA 55]
59. Pedipalp chela manus dorsal surface, proximal margin (lobe), curvature (δ): **0**, dorsal surface, proximal margin distal to retrolateral surface, proximal margin; **1**, dorsal surface, proximal margin aligned with retrolateral surface, proximal margin; **2**, dorsal surface, proximal margin proximal to retrolateral surface, proximal margin but distal to manus condyle (articulation with patella), proximal margin; **3**, dorsal surface, proximal margin aligned with manus condyle, proximal margin; **4**, dorsal surface, proximal margin proximal to manus condyle, proximal margin.
60. Pedipalp chela manus dorsal surface, proximal margin (lobe), curvature (φ): **0**, dorsal surface, proximal margin distal to retrolateral surface, proximal margin; **1**, dorsal surface, proximal margin aligned with retrolateral surface, proximal margin; **2**, dorsal surface, proximal margin proximal to retrolateral surface, proximal margin but distal to manus condyle (articulation with patella), proximal margin; **3**, dorsal surface, proximal margin aligned with manus condyle, proximal margin; **4**, dorsal surface, proximal margin proximal to manus condyle, proximal margin.
61. Pedipalp chela manus dorsal surface (between dorsomedian and digital carinae), curvature (δ): **0**, flat; **1**, curved, slightly to markedly convex.
62. Pedipalp chela manus dorsal surface (between dorsomedian and digital carinae), curvature (φ): **0**, flat; **1**, curved, slightly to markedly convex.
63. Pedipalp chela manus dorsal intercarinal surface, maximum distance between dorsomedian and dorsal secondary carinae (DMC–DSC) relative to maximum distance between dorsal secondary and digital carinae (DSC–DC) or rows of setae demarcating carinae (δ): **0**, DMC–DSC less than DSC–DC; **1**, DMC–DSC similar to DSC–DC; **2**, DMC–DSC greater than DSC–DC.
64. Pedipalp chela manus dorsal intercarinal surface, maximum distance between dorsomedian and dorsal secondary carinae (DMC–DSC) relative to maximum distance between dorsal secondary and digital carinae (DSC–DC) or rows of setae demarcating carinae (φ): **0**, DMC–DSC less than DSC–DC; **1**, DMC–DSC similar to DSC–DC; **2**, DMC–DSC greater than DSC–DC.
65. Pedipalp chela manus dorsomedian carina, longitudinal development: **0**, continuous to proximal edge of manus; **1**, becoming obsolete proximally. [PEA 27]
66. Pedipalp chela manus dorsomedian carina, macrosculpture: **0**, obsolete proximally with irregular spiniform granules distally, or irregular spiniform granules along entire length; **1**, costate to costate-granular proximally, becoming irregular row of spiniform granules distally; **2**, costate to costate-granular proximally, becoming regular row of spiniform granules along entire length.
67. Pedipalp chela manus, distal half, and fixed finger, dorsomedian carina, vertical development: **0**, obsolete; **1**, pronounced, costate on fixed finger and distally on manus; **2**, pronounced, costate on fixed finger and distal three-quarters of manus.
68. Pedipalp chela manus dorsal secondary, subdigital and digital carinae, relative orientation of ridges or setal rows: **0**, dorsal secondary, subdigital and digital carinae well separated along entire length; **1**, proximal half of dorsal secondary carina, distal half of subdigital carina and distal third of digital carina closely adjacent.
69. Pedipalp chela manus dorsal secondary carina, macrosculpture: **0**, single row; **1**, double row.
70. Pedipalp chela manus dorsal secondary carina, sulcus accommodating macrosetae (regardless of presence or absence of carina) (δ): **0**, present; **1**, absent or obsolete.
71. Pedipalp chela manus dorsal secondary carina, sulcus accommodating macrosetae (regardless of presence or absence of carina) (φ): **0**, present; **1**, absent or obsolete.
72. Pedipalp chela manus, sulcus between dorsal secondary and subdigital carinae or rows of setae demarcating carinae (δ): **0**, absent or obsolete; **1**, present.
73. Pedipalp chela manus, sulcus between dorsal secondary and subdigital carinae or rows of setae demarcating carinae (φ): **0**, absent or obsolete; **1**, present.
74. Pedipalp chela manus dorsal secondary and subdigital carinae, macrosculpture (δ): **0**, absent or obsolete; **1**, entirely to predominantly granular; **2**, entirely to predominantly costate; **?**, unknown (?). [incorporates HWC 61, PEA 31]
75. Pedipalp chela manus, sulcus between subdigital and digital carinae or rows of setae demarcating carinae: **0**, absent or obsolete; **1**, partial; **2**, complete.
76. Pedipalp chela manus digital carina, macrosculpture: **0**, entirely to predominantly costate; **1**, entirely to predominantly granular; **2**, absent or obsolete. [merged BHL 19 and 20, PEA 32]
77. Pedipalp chela manus retromedian carina, macrosculpture (δ): **0**, absent or obsolete; **1**, entirely to predominantly granular; **2**, entirely to predominantly costate; **?**, unknown.
78. Pedipalp chela manus retromedian carina, development relative to digital carina (δ , φ): **0**, less developed; **1**, similar; **2**, more developed.
79. Pedipalp chela manus ventral surface, shape: **0**, flat, axes of retroventral and ventromedian carinae in approximately same plane; **1**, angular, axis of retroventral carina ventral to axis of ventromedian carina.
80. Pedipalp chela manus ventromedian carina, macrosculpture: **0**, absent or reduced to few proximal granules; **1**, present and strongly sclerotized; **2**, present and weakly sclerotized. [modified LP 28 with new state to distinguish between weak and strong sclerotization, PEA 37]
81. Pedipalp chela manus proventral carina, development relative to promedian carina (φ): **0**, more strongly developed than promedian carina, which may be obsolete; **1**, similarly developed. [LP 29, PEA 36]
82. Pedipalp chela manus promedian carina, macrosculpture (φ): **0**, present, granular; **1**, absent or obsolete. [PEA 35]

83. Pedipalp chela manus prolateral surface, distance between dorsomedian and promedian carinae (DMC–PMC) relative to distance between promedian and proventral carinae (PMC–PVC) or rows of setae demarcating carinae: **0**, DMC–PMC less than PMC–PVC; DMC–PMC similar to PMC–PVC; **1**, DMC–PMC slightly to markedly greater than PMC–PVC.
84. Pedipalp chela setation (δ): **0**, virtually asetose; **1**, sparsely setose; **2**, moderately to densely setose. [PEA 22]
85. Pedipalp chela manus dorsal surface, depression proximal to fixed finger (δ , sometimes evident in φ): **0**, present and distinct; **1**, absent or obsolete.
86. Pedipalp chela manus dorsal intercarinal surface, macrosculpture (δ): **0**, shallowly reticulate; **1**, reticulation absent; **?**, unknown. [state 0 of BHL 17; incorporates HWC 61, PEA 29]
87. Pedipalp chela manus dorsal surface, macrosculpture (φ): **0**, shallowly reticulate; **1**, reticulation absent. [state 0 of BHL 18; incorporates HWC 61, PEA 30]
88. Pedipalp chela manus dorsal intercarinal surface, macrosculpture (φ): **0**, smooth; **1**, finely to coarsely granular. [state 1 of BHL 17 and 18; incorporates HWC 60 and 61, PEA 28]
89. Pedipalp chela manus retrolateral intercarinal surfaces, macrosculpture (δ): **0**, granular; **1**, smooth or nearly so; **?**, unknown. [PEA 33]
90. Pedipalp chela manus retrolateral intercarinal surfaces, macrosculpture (φ): **0**, granular; **1**, smooth or nearly so. [PEA 34]
- †91. Pedipalp chela manus *V* trichobothria, count: **0**, 4; **1**, 8–10. [modified BHL 26 and LP 49 with extra states, PEA 51]
- †92. Pedipalp chela manus *V* trichobothria, longitudinal position of trichobothrium *V*₃ if only four *V* trichobothria: **0**, distal third; **1**, proximal third; **-**, inapplicable if more than four *V* trichobothria. [BHL 25 with extra state for *Nebo*, PEA 52]
- †93. Pedipalp chela *i* trichobothria, count: **0**, two; **1**, three. [LP 46, PEA 53]
94. Pedipalp chela fingers retrolateral intercarinal surface, macrosculpture: **0**, smooth; **1**, granular. [PEA 26]
95. Pedipalp chela movable finger second lobe, development relative to other lobes on finger (δ): **0**, more strongly developed than other lobes, with correspondingly well-developed notch in fixed finger; **1**, not noticeably larger or only slightly larger than other lobes; **?**, unknown. [modified LP 35; also recognized in *Nebo*, PEA 25]
96. Pedipalp chela fingers terminal teeth, interlocking when closed: **0**, evenly, fixed and movable fingers aligned; **1**, unevenly, movable finger displaced retrolaterally, with weakly developed notch near tip of fixed finger; **2**, unevenly, movable finger displaced retrolaterally, with strongly developed notch near tip of fixed finger. [PEA 23]
- †97. Pedipalp chela fixed finger trichobothria *est*–*esb*, distance relative to trichobothria *esb*–*eb*, distance: **0**, *est*–*esb* greater than half *esb*–*eb*; **1**, *est*–*esb* ca. half *esb*–*eb* [merged BHL 23 and 24 because these have the same distribution, PEA 50]

Coxosternum

98. Coxosternal region, infuscation: **0**, maxillary lobes darker than rest; **1**, uniformly pale, immaculate.

Legs

99. Legs, color: **0**, pale (though perhaps very lightly infuscate); **1**, very dark or heavily infuscate. [PEA 99]
- †100. Legs I–IV femora, ventromedian surfaces, macrosculpture: **0**, acarinate, little or no discernable carina demarcating pro- and retrolateral surfaces; **1**, uncarinate, distinct pro- and retrolateral surfaces demarcated by macrosetae and, usually, granules. [PEA 63]
- †101. Legs I and II patellae, pro- and retrolateral surfaces, setation: **0**, scattered macrosetae, not arranged in definite row; **1**, comb-like row of more than three long to very long macrosetae.
102. Legs I and II tibiae, pro- and retrolateral surfaces, setation: **0**, scattered macrosetae, not arranged in definite row; **1**, row of spiniform macrosetae only; **2**, comblike row of more than three long to very long macrosetae. [PEA 66]
103. Leg I tibia, retrolateral surface, spiniform macrosetae: **0**, absent; **1**, one; **2**, two or three.
104. Leg II tibia, retrolateral surface, spiniform macrosetae: **0**, absent; **1**, one; **2**, two or three.
- †105. Legs I–IV basitarsi, shape in cross section: **0**, I–IV dorsoventrally compressed; **1**, I and II dorsoventrally compressed, III and IV terete.
106. Legs I–IV basitarsi, retrolateral margins: **0**, unmodified, rounded, similar on I–IV; **1**, produced into blade-like edge on I and II, unmodified, rounded on III and IV.
107. Legs I and II basitarsi, pro- and retrolateral surfaces, setation: **0**, scattered macrosetae, not arranged in definite row; **1**, row of three or more spiniform macrosetae; **2**, only two spiniform macrosetae; **3**, comblike row of more than three setiform macrosetae with or without elongated spiniform macrosetae [modified BHL 76 and merged LP 72 and 73, PEA 67]
108. Leg I basitarsus, retrolateral surface, macroseta *st*: **0**, setiform; **1**, spiniform.
109. Leg I basitarsus, retrolateral surface, macroseta *sb*: **0**, setiform; **1**, spiniform.
110. Leg I basitarsus, retroventral surface, macroseta *st*: **0**, setiform; **1**, spiniform.
111. Leg I basitarsus, retroventral surface, macroseta *sb*: **0**, setiform; **1**, spiniform.
112. Leg I basitarsus, proventral surface, macroseta *st*: **0**, setiform; **1**, spiniform.
113. Leg II basitarsus, retrolateral surface, macroseta *st*: **0**, setiform; **1**, spiniform.
- †114. Leg II basitarsus, retrolateral surface, macroseta *m*: **0**, setiform; **1**, spiniform.
115. Leg II basitarsus, retroventral surface, macroseta *st*: **0**, setiform; **1**, spiniform.
116. Leg II basitarsus, retroventral surface, macroseta *sb*: **0**, setiform; **1**, spiniform.
117. Leg II basitarsus, proventral surface, macroseta *st*: **0**, setiform; **1**, spiniform.

118. Leg II basitarsus, prolateral surface, macroseta *t*: **0**, setiform; **1**, spiniform.
- †119. Leg III basitarsus, retrolateral surface, macroseta *st*: **0**, setiform; **1**, spiniform.
120. Leg III basitarsus, retrolateral surface, macroseta *sb*: **0**, setiform; **1**, spiniform.
121. Leg III basitarsus, retroventral surface, macroseta *st*: **0**, setiform; **1**, spiniform.
122. Leg III basitarsus, retroventral surface, macroseta *sb*: **0**, setiform; **1**, spiniform.
123. Leg III basitarsus, proventral surface, macroseta *st*: **0**, setiform; **1**, spiniform.
- †124. Leg IV basitarsus, retrolateral surface, macroseta *t*: **0**, setiform; **1**, spiniform.
125. Legs I and II telotarsi, pro- and retrolateral surfaces, setation: **0**, long and short, densely scattered macrosetae, not arranged in definite row; **1**, two or more, dense brushlike rows of long to very long setiform macrosetae.
126. Legs I–IV telotarsi, laterodistal lobes, setation: **0**, three or more spiniform macrosetae on each laterodistal lobe; **1**, two spiniform macrosetae on each laterodistal lobe. [PEA 69]
- †127. Legs I–IV telotarsi, number of spiniform macrosetae in proventral rows: **0**, constant or increasing from I–IV; **1**, constant or increasing from I–III but decreasing on IV. [PEA 70]
- †128. Legs I–IV telotarsi, proventral row of spiniform macrosetae (excluding macrosetae on laterodistal lobes): **0**, present on I–IV; **1**, present on I–III, absent on IV. [incorporates BHL 77 and 79, LP 71, PEA 71]
- †129. Legs I–IV telotarsi, unguis, shape: **0**, short and distinctly curved; **1**, elongated and curved (proximally or distally) to sublinear. [modified BHL 82 with extra states, PEA 72]
- †130. Legs I–IV telotarsi, unguis, relative length within each pair: **0**, equal to subequal on I–IV; **1**, unequal on I and II, equal to subequal on III and IV. [merged BHL 83 and 84, PEA 73]
131. Legs I–IV telotarsi, pseudonygium: **0**, reduced, rounded; **1**, prominent, acuminate.

Genital Operculum

132. Genital opercula (δ): **0**, not overlapping; **1**, overlapping; **?**, unknown. [PEA 57]

Hemispermaphore

- †133. Distal lamina, distal crest: **0**, tapering; **1**, truncate; **?**, unknown. [PEA 58]
- †134. Hook notch, position on distal lamina: **0**, basal; **1**, medial; **?**, unknown; **-**, inapplicable (no hook notch in *Nebo*).
135. Accessory distal lobe protruding between articular suture and distal lobe (hook): **0**, absent; **1**, present; **?**, unknown. [PEA 59]

Pectines

- †136. Pecten length, expressed relative to length of leg IV coxa and trochanter (δ): **0**, distal edge extending past distal edge of coxa but not extending to distal edge of trochanter; **1**, distal edge extending to distal edge of coxa; **?**, unknown. [PEA 60]

137. First proximal median lamella (scape), angle (δ): **0**, approximately 90°; **1**, obtuse, > 90° but < 180°; **?**, unknown. [PEA 61]
138. First proximal median lamella (scape), angle (φ): **0**, distinctly angular, approximately 90°; **1**, distinctly angular, > 90° but < 180°; **2**, straight or shallowly curved. [PEA 62]
139. Internal fulcral plates, setation: **0**, smooth to sparsely setose (3–4 microsetae distally); **1**, smooth proximally but densely setose (microsetae only) distally; **2**, sparsely setose (scattered macrosetae) across entire surface. [modified HWC 86: redefined states, PEA 64]
140. Pectinal teeth, shape (δ): **0**, short, curved; **1**, long, straight; **?**, unknown. [PEA 63]

Tergites

- †141. Tergites I–VII, base coloration: **0**, uniform; **1**, posterior third noticeably paler. [PEA 94]
- †142. Tergites I–VII, infuscation: **0**, entirely or mostly (more than two-thirds) immaculate; **1**, entirely or mostly (more than two-thirds) infuscate. [PEA 95]
143. Tergites I–VI, macrosculpture distribution (δ): **0**, mesial and lateral surfaces granular; **1**, mesial surfaces smooth, lateral surfaces granular (rarely smooth); **2**, mesial and lateral surfaces smooth; **?**, unknown. [modified BHL 34 states 0, 1, and 2; incorporates HWC 91, PEA 74]
144. Tergites I–VI, macrosculpture distribution (φ): **0**, mesial and lateral surfaces smooth; **1**, mesial surfaces smooth, lateral surfaces granular; **2**, mesial and lateral surfaces granular. [HWC 91, PEA 75]
- †145. Tergites I–VI, macrosculpture (δ): **0**, uniformly finely granular; **1**, unevenly finely and coarsely granular to predominantly coarsely granular; **?**, unknown; **-**, inapplicable. [BHL 34 states 1 and 2, with state 0 transferred to another character, PEA 76]

Sternites

146. Sternites III–VII, infuscation: **0**, III–VI immaculate, VII occasionally infuscate; **1**, III–VII infuscate. [PEA 98]
- †147. Sternites III–VII surfaces, macrosculpture (δ): **0**, smooth; **1**, III–VI, finely rugose, VII, scattered granules; **2**, III–VII, tuberculate; **?**, unknown. [PEA 101]
148. Sternite VII surface, ventrosubmedian and ventrolateral carinae: **0**, two pairs of moderately to strongly developed ventrosubmedian and ventrolateral carinae; **1**, pair of weakly developed ventrolateral carinae only; **2**, acarinate. [PEA 100]
- †149. Sternite VII surface, and metasomal segment I ventral intercarinal surface, macrosculpture (φ): **0**, smooth; **1**, scattered granules; **2**, tuberculate. [modified BHL 36, PEA 101]

Metasoma

150. Metasomal segments I and II, length relative to width: **0**, markedly greater than; **1**, approximately equal to or less than.
- †151. Metasomal segments I–V, color: **0**, segments similar, dark; **1**, posterior segments darker than anterior segments; **2**, segments similar, pale.
- †152. Metasomal segments I–V, dorsal intercarinal surfaces, color (δ , φ): **0**, as dark as tergites, if pigmented; **1**, at least

- segments I and II or I–III as pale as tergites, if tergites immaculate or paler than if tergites infusate. [PEA 96]
153. Metasomal segments I–IV dorsosubmedian carinae, macrosculpture (δ): **0**, distinct, granular or costate-granular on segments I–IV; **1**, distinct, granular or costate-granular on segments III–IV or IV, costate on I and II or I–III; **2**, distinct, costate on segments I–IV; **3**, obsolete.
154. Metasomal segments I–IV dorsosubmedian carinae, macrosculpture (φ): **0**, distinct, granular or costate-granular on segments I–IV; **1**, distinct, granular or costate-granular on segments III–IV or IV, costate on I and II or I–III; **2**, distinct, costate on segments I–IV; **3**, obsolete.
- †155. Metasomal segments II–IV dorsosubmedian carinae, posterior spiniform granules, development: **0**, weak (not noticeably larger than preceding granules); **1**, moderate to strong (distinctly larger than preceding granules). [modified BHL 58: merged states 1 and 2, PEA 78]
156. Metasomal segment V dorsosubmedian carinae, longitudinal development: **0**, absent; **1**, vestigial; **2**, partial.
157. Metasomal segment V dorsal intercarinal surface, macrosculpture (δ): **0**, granular; **1**, smooth; **2**, unknown (?). [BHL 64, PEA 79]
158. Metasomal segment V dorsal intercarinal surface, macrosculpture (φ): **0**, granular; **1**, smooth. [BHL 65, PEA 80]
159. Metasomal segment V dorsolateral carinae, development: **0**, strong, continuous; **1**, weak, discontinuous to absent. [merged BHL 66 and 67, PEA 77]
160. Metasomal segments I–IV lateral surfaces, curvature, dorsal and ventral aspect: **0**, straight, subparallel; **1**, convex.
- †161. Metasomal segments I and II lateral carinae, orientation relative to dorsolateral and ventrolateral carinae (inferred from carina or setal row if carina absent): **0**, parallel to carinae; **1**, diagonal between carinae.
162. Metasomal segment I lateral carinae, longitudinal development: **0**, complete; **1**, partial; **2**, vestigial.
163. Metasomal segment V lateral carinae, longitudinal development: **0**, partial; **1**, absent or obsolete.
164. Metasomal segment II ventral surface, macrosculpture (δ): **0**, smooth; **1**, scattered granules; **?**, unknown. [components of BHL 35, 42, 48, 55, and 61, PEA 102]
165. Metasomal segment II ventral surface, macrosculpture (φ): **0**, smooth; **1**, scattered granules. [modified BHL 36, PEA 102]
166. Metasomal segment III ventral surface, macrosculpture (δ): **0**, smooth; **1**, scattered granules; **?**, unknown. [components of BHL 35, 42, 48, 55, and 61, PEA 103]
167. Metasomal segment III ventral surface, macrosculpture (φ): **0**, smooth; **1**, scattered granules. [modified BHL 36, PEA 103]
168. Metasomal segment IV ventral surface, macrosculpture (δ): **0**, smooth; **1**, scattered granules; **?**, unknown. [components of BHL 35, 42, 48, 55, and 61]
169. Metasomal segment IV ventral surface, macrosculpture (φ): **0**, smooth; **1**, scattered granules. [components of BHL 35, 42, 48, 55, and 61]
- †170. Metasomal segments I–V ventrosobmedian and/or ventrolateral carinae, infuscation (may be present even if carinae obsolete or absent) (δ): **0**, immaculate; **1**, infusate. [PEA 97]
- †171. Metasoma segments I–IV ventrosobmedian carinae, development: **0**, present and distinct on segments I–IV; **1**, absent or obsolete on segments I, I and II, or I–IV. [merged BHL 40, 45, 50, 51, and 59 and modified, by merging states 1, 2 and 3, PEA 81]
172. Metasomal segments I–IV ventrosobmedian and ventrolateral carinae, development on segments I and II relative to III and IV: **0**, more strongly developed on segments III and IV than on I and II; **1**, more strongly developed on segments I and II than on III and IV; **-**, inapplicable. [LP 96, PEA 82]
173. Metasomal segments I–IV, ventrosobmedian and ventrolateral carinae: **0**, granular on segments I–IV, II–IV (costate on I), or III and IV (costate on I and II); **1**, granular or costate-granular on segment IV only, costate on segments I–III. [merged states 1–3 from BHL 40, 41, 45, 46, 50–53, 59 and 60]
174. Metasomal segment V ventrolateral carinae, macrosculpture: **0**, rounded granules; **1**, spiniform or denticulate granules. [BHL 69, PEA 84]
175. Metasomal segment V ventrolateral carinae, posterior spiniform granules, development: **0**, obsolete (not noticeably larger than preceding granules); **1**, weak (slightly larger than preceding granules). [incorporates HWC 113, PEA 85]
- †176. Metasomal segment V ventrolateral carinae, posterior orientation: **0**, divergent; **1**, subparallel to convergent. [BHL 70, PEA 83]
- †177. Metasomal segment V ventromedian carina, posterior macrosculpture: **0**, unmodified moniliform row; **1**, breaking into numerous granules; **-**, inapplicable. [part of LP 99, PEA 86]
- †178. Metasomal segment V anal arch, anterior carina, macrosculpture: **0**, costate; **1**, serrate. [PEA 87]

Telson

179. Telson color relative to metasomal segment V: **0**, paler than segment V; **1**, as dark as segment V.
180. Telson vesicle, width relative to metasomal segment V, width (δ): **0**, approximately equal to or less than; **1**, greater than.
181. Telson vesicle, width relative to metasomal segment V, width (φ): **0**, approximately equal to or less than; **1**, greater than.
182. Telson vesicle shape: **0**, globose; intermediate; **1**, elongate. [PEA 88]
183. Telson vesicle surfaces, macrosculpture: **0**, longitudinal rows of granules on lateral and ventral surfaces; **1**, longitudinal rows of granules on all or part of ventral surface only; **2**, entirely smooth. [merged BHL 73 and 74, PEA 89]

Ecology and Behavior

184. Burrows constructed in the open: **0**, absent; **1**, present; **?**, unknown. [PEA 104]
185. Burrows constructed under stones: **0**, present; **1**, absent; **?**, unknown. [PEA 105]
- †186. Mesosomal percussion (δ): **0**, absent; **1**, present; **?**, unknown. [LP 115, PEA 106]

APPENDIX 3

TISSUE SAMPLES AND GENBANK ACCESSION CODES FOR DNA SEQUENCES USED FOR PHYLOGENETIC ANALYSIS
OF THE ASIAN FOREST SCORPIONS (SCORPIONIDAE: HETEROMETRINAE SIMON, 1879, STAT. NOV.)

Sequences of the 18S rDNA (18S), 28S rDNA (28S), 12S rDNA (12S), 16S rDNA (16S), and cytochrome *c* oxidase subunit I (COI) loci. Tissue samples deposited in the Ambrose Monell Collection for Molecular and Microbial Research (AMCC) at the American Museum of Natural History, New York.

Family	Species	AMCC	Country	18S	28S	12S	16S	COI
Diplocentridae	<i>Nebo hierichonticus</i> (Simon, 1872)	LP 11138	Israel	MT417898	MT418125	MT417773	MT418351	MT418015
	<i>Opisthophthalmus capensis</i> (Herbst, 1800)	LP 1046	South Africa	MT417899	AY156532	AY156547	AY156562	AY156577
Scorpionidae	<i>Pandinus imperator</i> (C.L. Koch, 1841)	LP 1601	Ghana	MT417900	AY156537	AY156552	AY156567	AY156582
	<i>Scorpio fuscus</i> (Ehrenberg, 1829)	LP 1556	Israel	MT417901	AY156539	AY156554	AY156569	AY156584
	<i>Chersonesometrus bastawadei</i> , sp. nov.	LP 16785	India	MT417902	MT418126	MT417774	MT418352	MT418016
		LP 16787		MT417903	MT418127	MT417775	MT418353	MT418017
	<i>Chersonesometrus beccaloninae</i> (Kovářík, 2004)	LP 13133		MT417904	MT418128	MT417776	MT418354	MT418018
		LP 13134		MT417905	MT418129	MT417777	MT418355	MT418019
	<i>Chersonesometrus fulvipes</i> (C.L. Koch, 1837)	LP 8268		MT417911	MT418135	MT417783	MT418361	MT418025
		LP 13125		MT417906	MT418130	MT417778	MT418356	MT418020
		LP 13981		MT417907	MT418131	MT417779	MT418357	MT418021
		LP 13990		MT417908	MT418132	MT417780	MT418358	MT418022
		LP 13997		MT417909	MT418133	MT417781	MT418359	MT418023
		LP 14031		MT417910	MT418134	MT417782	MT418360	MT418024
	<i>Chersonesometrus hendersoni</i> , sp. nov.	LP 16776		MT417912	MT418136	MT417784	MT418362	MT418026
		LP 16782		MT417913	MT418137	MT417785	MT418363	MT418027
	<i>Chersonesometrus madraspatensis</i> (Pocock, 1900)	LP 1533		MT417915	AY156527	AY156542	AY156557	AY156572
		LP 4324		MT417916	MT418139	MT417787	MT418365	MT418029
		LP 13127		MT417914	MT418138	MT417786	MT418364	MT418028
	<i>Chersonesometrus pelekomanus</i> (Coutzjin, 1981)	LP 16773		MT417917	MT418140	MT417788	MT418366	MT418030
		LP 16774		MT417918	MT418141	MT417789	MT418367	MT418031

APPENDIX 3 continued

Family	Species	AMCC	Country	18S	28S	12S	16S	COI
Scorpionidae	<i>Chersonomesometrus tristis</i> (Henderson, 1919)	LP 2276	India	MT417921	MT418144	MT417792	MT418370	MT418034
		LP 13135		MT417919	MT418142	MT417790	MT418368	MT418032
		LP 13136		MT417920	MT418143	MT417791	MT418369	MT418033
	<i>Deccanometrus bengalensis</i> (C.L. Koch, 1841)	LP 14238	Pakistan	MT417922	MT418145	MT417793	MT418371	MT418035
	<i>Deccanometrus latimanus</i> (Pocock, 1894)	LP 11568		MT417923	MT418146	MT417794	MT418372	MT418036
		LP 11569		MT417924	MT418147	MT417795	MT418373	MT418037
	<i>Deccanometrus obscurus</i> (Couzijn, 1981)	LP 11601	India	MT417925	MT418148	MT417796	MT418374	MT418038
		LP 6225		MT417929	MT418152	MT417800	MT418378	MT418042
		LP 13974		MT417926	MT418149	MT417797	MT418375	MT418039
		LP 16800		MT417927	MT418150	MT417798	MT418376	MT418040
		LP 16817		MT417928	MT418151	MT417799	MT418377	MT418041
	<i>Deccanometrus xanthopus</i> (Pocock, 1897)	LP 13126		MT417930	MT418153	MT417801	MT418379	MT418043
		LP 13971		MT417931	MT418154	MT417802	MT418380	MT418044
		LP 16814		MT417932	MT418155	MT417803	MT418381	MT418045
		LP 1607		MT417935	AY156530	AY156545	AY156560	AY156575
		LP 13128		MT417933	MT418156	MT417804	MT418382	MT418046
	<i>Gigantometrus swammerdami</i> (Simon, 1872)	LP 13129	Sri Lanka	MT417934	MT418157	MT417805	MT418383	MT418047
	<i>Gigantometrus titanicus</i> (Couzijn, 1981)	LP 12287		MT417936	MT418158	MT417806	MT418384	MT418048
		LP 12288		MT417937	MT418159	MT417807	MT418385	MT418049
	<i>Heterometrus glaucus</i> (Thorell, 1876)	LP 13922	Indonesia	MT417938	MT418160	MT417808	MT418386	MT418050
		LP 13928		MT417939	MT418161	MT417809	MT418387	MT418051
	<i>Heterometrus laevigatus</i> (Thorell, 1876)	LP 1789		MT417945	MT418167	MT417815	MT418393	MT418057
		LP 12335	Thailand	MT417940	MT418162	MT417810	MT418388	MT418052
		LP 12337		MT417941	MT418163	MT417811	MT418389	MT418053
		LP 13045		MT417942	MT418164	MT417812	MT418390	MT418054

APPENDIX 3 continued

Family	Species	AMCC	Country	18S	28S	12S	16S	COI
Scorpionidae	<i>Heterometrus laevigatus</i> (Thorell, 1876)	LP 13047	Thailand	MT417943	MT418165	MT417813	MT418391	MT418055
		LP 13048		MT417944	MT418166	MT417814	MT418392	MT418056
	<i>Heterometrus laoticus</i> Couzijn, 1981	LP 11330	Laos	MT417946	MT418168	MT417816	MT418394	MT418058
		LP 11331		MT417947	MT418169	MT417817	MT418395	MT418059
		LP 11352		MT417948	MT418170	MT417818	MT418396	MT418060
		LP 12336	Thailand	MT417949	MT418171	MT417819	MT418397	MT418061
		LP 13046		MT417950	MT418172	MT417820	MT418398	MT418062
		LP 15584	Laos	MT417951	MT418173	MT417821	MT418399	MT418063
		LP 16489	Thailand	MT417952	MT418174	MT417822	MT418400	MT418064
<i>Heterometrus longimanus</i> (Herbst, 1800)		LP 11948	Malaysia	MT417953	MT418175	MT417823	MT418401	MT418065
		LP 12114		MT417954	MT418176	MT417824	MT418402	MT418066
		LP 12115		MT417955	MT418177	MT417825	MT418403	MT418067
		LP 12116		MT417956	MT418178	MT417826	MT418404	MT418068
		LP 12139		MT417957	MT418179	MT417827	MT418405	MT418069
<i>Heterometrus petersii</i> (Thorell, 1876)		LP 1604	Singapore	MT417958	AY156529	AY156544	AY156559	AY156574
		LP 8269		MT417960	MT418181	MT417829	MT418407	MT418071
		LP 16458	Malaysia	MT417959	MT418180	MT417828	MT418406	MT418070
<i>Heterometrus silenus</i> (Simon, 1884)		LP 1603	Vietnam	MT417965	AY156528	AY156543	AY156558	AY156573
		LP 1888		MT417966	MT418186	MT417834	MT418412	MT418076
		LP 11248		MT417961	MT418182	MT417830	MT418408	MT418072
		LP 11252		MT417962	MT418183	MT417831	MT418409	MT418073
		LP 11353		MT417963	MT418184	MT417832	MT418410	MT418074
<i>Heterometrus spinifer</i> (Ehrenberg, 1828)		LP 15590	Cambodia	MT417964	MT418185	MT417833	MT418411	MT418075
		LP 1906	Malaysia	MT417972	MT418192	MT417840	MT418418	MT418082
		LP 10581		MT417967	MT418187	MT417835	MT418413	MT418077

APPENDIX 3 continued

Family	Species	AMCC	Country	18S	28S	12S	16S	COI
Scorpionidae	<i>Heterometrus spinifer</i> (Ehrenberg, 1828)	LP 11920	Malaysia	MT417968	MT418188	MT417836	MT418414	MT418078
		LP 11949		MT417969	MT418189	MT417837	MT418415	MT418079
		LP 11950		MT417970	MT418190	MT417838	MT418416	MT418080
		LP 11974		MT417971	MT418191	MT417839	MT418417	MT418081
	<i>Heterometrus thorellii</i> (Pocock, 1892)	LP 2704	Myanmar	MT417980	MT418200	MT417848	MT418426	MT418090
		LP 13049		MT417973	MT418193	MT417841	MT418419	MT418083
		LP 13050		MT417974	MT418194	MT417842	MT418420	MT418084
		LP 13051		MT417975	MT418195	MT417843	MT418421	MT418085
		LP 13052		MT417976	MT418196	MT417844	MT418422	MT418086
		LP 13153		MT417977	MT418197	MT417845	MT418423	MT418087
		LP 13155		MT417978	MT418198	MT417846	MT418424	MT418088
		LP 15604		MT417979	MT418199	MT417847	MT418425	MT418089
	<i>Javanimetrus cyaneus</i> (C.L. Koch, 1836)	LP 2309	Indonesia	MT417984	MT418204	MT417852	MT418430	MT418094
		LP 8270		MT417985	MT418205	MT417853	MT418431	MT418095
		LP 12112		MT417981	MT418201	MT417849	MT418427	MT418091
		LP 12113		MT417982	MT418202	MT417850	MT418428	MT418092
	<i>Sahyadrimetrus kanarensis</i> (Pocock, 1900)	LP 12117	India	MT417983	MT418203	MT417851	MT418429	MT418093
		LP 2289		MT417991	MT418211	MT417859	MT418437	MT418101
		LP 2902		MT417992	MT418212	MT417860	MT418438	MT418102
		LP 13960		MT417986	MT418206	MT417854	MT418432	MT418096
		LP 13963		MT417987	MT418207	MT417855	MT418433	MT418097
		LP 14029		MT417988	MT418208	MT417856	MT418434	MT418098
		LP 16795		MT417989	MT418209	MT417857	MT418435	MT418099
		LP 16797		MT417990	MT418210	MT417858	MT418436	MT418100

APPENDIX 3 continued

Family	Species	AMCC	Country	18S	28S	12S	16S	COI
Scorpionidae	<i>Sahyadrimetrus mathewi</i> , gen. et sp. nov.	LP 13130	India	MT417993	MT418213	MT417861	MT418439	MT418103
		LP 13131		MT417994	MT418214	MT417862	MT418440	MT418104
		LP 13132		MT417995	MT418215	MT417863	MT418441	MT418105
		LP 16752		MT417996	MT418216	MT417864	MT418442	MT418106
		LP 16759		MT417997	MT418217	MT417865	MT418443	MT418107
	<i>Sahyadrimetrus rugosus</i> (Coutzin, 1981)	LP 14007		MT417998	MT418218	MT417866	MT418444	MT418108
		LP 14028		MT417999	MT418219	MT417867	MT418445	MT418109
		LP 16768		MT418000	MT418220	MT417868	MT418446	MT418110
		LP 13979		MT418001	MT418221	MT417869	MT418447	MT418111
		LP 14023		MT418002	MT418222	MT417870	MT418448	MT418112
<i>Sahyadrimetrus scaber</i> (Thorell, 1876)	<i>Sahyadrimetrus tikaderi</i> , gen. et sp. nov.	LP 16771		MT418003	MT418223	MT417871	MT418449	MT418113
		LP 16772		MT418004	MT418224	MT417872	MT418450	MT418114
		LP 16760		MT418005	MT418225	MT417873	MT418451	MT418115
		LP 16764		MT418006	MT418226	MT417874	MT418452	MT418116
		LP 16766		MT418007	MT418227	MT417875	MT418453	MT418117
	<i>Srilankametrus gravimanus</i> (Pocock, 1894)	LP 16767	Sri Lanka	MT418008	MT418228	MT417876	MT418454	MT418118
		LP 12279		MT418009	MT418229	MT417877	MT418455	MT418119
		LP 12280		MT418010	MT418230	MT417878	MT418456	MT418120
		LP 12282		MT418012	MT418232	MT417880	MT418458	MT418122
		LP 12283		MT418013	MT418233	MT417881	MT418459	MT418123
<i>Srilankametrus pococki</i> , sp. nov.	<i>Srilankametrus serratus</i> (Pocock, 1900)	LP 12281		MT418011	MT418231	MT417879	MT418457	MT418121
		LP 14058		MT418014	MT418234	MT417882	MT418460	MT418124

APPENDIX 4

CHECKLIST OF CURRENTLY RECOGNIZED GENERA,
SPECIES AND SYNONYMS OF ASIAN FOREST SCORPIONS
(SCORPIONIDAE: HETEROMETRINAE SIMON, 1879,
STAT. NOV.)

Chersonesometrus Couzijn, 1978, stat. nov. et stat. rev.

Type species: *Chersonesometrus fulvipes* (C.L. Koch, 1837),
comb. nov.

Chersonesometrus bastawadei, sp. nov.

Chersonesometrus beccaloniae (Kovářík, 2004), comb. nov.
= *Heterometrus atrascorpius* Mirza et al., 2012, syn. nov.

Chersonesometrus fulvipes (C.L. Koch, 1837), comb. nov.
= *Palamnaeus fulvipes bombayensis* Pocock, 1900
(synonymized by Couzijn, 1981: 133–136).

Chersonesometrus hendersoni, sp. nov.

Chersonesometrus madraspatensis (Pocock, 1900), comb. nov.
Chersonesometrus nathanorum, sp. nov.

Chersonesometrus pelekomanus (Couzijn, 1981), comb. nov. et
stat. rev.

Chersonesometrus shivashankari, sp. nov.

Chersonesometrus tristis (Henderson, 1919), comb. nov.

= *Heterometrus mysorensis* Kovářík, 2004, syn. nov.

Chersonesometrus wroughtoni (Pocock, 1899), comb. nov.

Deccanometrus, gen. nov.

Type species: *Deccanometrus obscurus* (Couzijn, 1981), comb.
et stat. nov.

Deccanometrus bengalensis (C.L. Koch, 1841), comb. nov.

= *Heterometrus* (*Chersonesometrus*) *fastidiosus* Couzijn,
1981 (synonymized by Kovářík, 2004: 1, 7, 9, 44).

= *Heterometrus nepalensis* Kovářík, 2004, syn. nov.

= *Heterometrus tibetanus* Lourenço et al., 2005, syn. nov.

Deccanometrus latimanus (Pocock, 1894), comb. nov.

Deccanometrus liurus (Pocock, 1897), comb. nov.

Deccanometrus obscurus (Couzijn, 1981), comb. et stat. nov.

Deccanometrus phipsoni (Pocock, 1893), comb. nov.

= *Palamnaeus phipsoni collinus* Pocock, 1900

(synonymized by Kovářík, 2004: 1, 34).

Deccanometrus ubicki (Kovářík, 2004), comb. nov.

Deccanometrus xanthopus (Pocock, 1897), comb. nov.

= *Heterometrus telanganaensis* Javed et al., 2010, syn. nov.

Gigantometrus Couzijn, 1978, stat. nov.

Type species: *Gigantometrus swammerdami* (Simon, 1872),
comb. nov.

Gigantometrus swammerdami (Simon, 1872), comb. nov.

= *Pandinus asper* Thorell, 1876 (synonymized by Pocock,
1890: 237–239).

= *Pandinus kochii* Karsch, 1879 (synonymized by Pocock,
1890: 237, 239).

= *Scorpio lucidipes* Simon, 1885 (synonymized by Pocock,
1890: 237, 239, 240).

= *Palamnaeus swammerdami flavimanus* Pocock, 1900,
syn. nov.

Gigantometrus titanicus (Couzijn, 1981), comb. nov. et stat. rev.

Heterometrus Ehrenberg, 1828

Type species: *Heterometrus spinifer* (Ehrenberg, 1828).

Heterometrus glaucus (Thorell, 1876), comb. nov. et stat. rev.

= *Heterometrus liophysa* var. *madoerensis* Kopstein, 1921,
syn. nov.

= *Heterometrus laevifrons* Roewer, 1943, syn. nov.

= *Heterometrus* (*Heterometrus*) *liophysa separatus* Couzijn,
1981, syn. nov.

= *Heterometrus* (*Heterometrus*) *liophysa spartanicus*

Couzijn, 1981, syn. nov.

Heterometrus laevigatus (Thorell, 1876), comb. nov. et stat. rev.

= *Heterometrus cimrmani* Kovářík, 2004, syn. nov.

= *Heterometrus minotaurus* Plíšková et al., 2016, syn. nov.

Heterometrus laoticus Couzijn, 1981

Heterometrus longimanus (Herbst, 1800)

= *Buthus costimanus* C.L. Koch, 1837 (synonymized by
Kraepelin, 1894: 34).

= *Centrurus galbivus* C.L. Koch, 1838 (synonymized by
Kraepelin, 1894: 34).

= *Palamnaeus angustimanus* Thorell, 1876 (synonymized
by Kraepelin, 1894: 34).

= *Palamnaeus costimanus* var. *borneensis* Thorell, 1876,
syn. nov.

= *Pandinus humilis* Simon, 1877 (synonymized by
Kraepelin, 1894: 34).

= *Palamnaeus liophysa* Thorell, 1888, syn. nov.

= *Heterometrus* (*Heterometrus*) *longimanus belitungensis*
Couzijn, 1981 (synonymized by Kovářík, 2004: 1, 25, 27).

= *Heterometrus* (*Heterometrus*) *longimanus bengkalitensis*
Couzijn, 1981, syn. nov.

= *Heterometrus* (*Heterometrus*) *longimanus marmoratus*
Couzijn, 1981, syn. nov.

= *Heterometrus* (*Heterometrus*) *longimanus paris* Couzijn,
1981 (synonymized by Kovářík, 2009: 40, 41).

= *Heterometrus* (*Heterometrus*) *longimanus tarawakanensis*
Couzijn, 1981 (synonymized by Kovářík, 2004: 1, 25, 27).

Heterometrus petersii (Thorell, 1876)

= *Palamnaeus oatesii* Pocock, 1900, syn. nov.

Heterometrus silenus (Simon, 1884), comb. nov. et stat. rev.

= *Heterometrus* (*Heterometrus*) *petersii mindanaensis*
Couzijn, 1981, syn. nov.

= *Heterometrus liangi* Zhu and Yang, 2007, syn. nov.

Heterometrus spinifer (Ehrenberg, 1828)

= *Heterometrus* (*Heterometrus*) *spinifer solitarius* Couzijn,
1981, syn. nov.

Heterometrus thorellii (Pocock, 1892)

Javanimetrus Couzijn, 1981, stat. nov. et stat. rev.

Type species: *Javanimetrus cyaneus* (C.L. Koch, 1836), comb. nov.

Javanimetrus cyaneus (C.L. Koch, 1836), comb. nov.

= *Scorpio afer* Linnaeus, 1758 (part) (synonymized by
Thorell, 1876b: 205–211).

= *Buthus reticulatus* C.L. Koch, 1837 (synonymized by
Simon, 1872b: 98).

- = *Buthus setosus* C.L. Koch, 1841 (synonymized by Kraepelin, 1899: 115).
- = *Pandinus indicus* Karsch, 1884 (synonymized by Couzijn, 1981: 126).
- = *Heterometrus (Heterometrus) petersii luzonensis* Couzijn, 1981 (synonymized by Kovařík, 2002: 3, 17).
- Couzijn, 1981: 126).
- = *Heterometrus (Javanimetrus) cyaneus insulanus* Couzijn, 1981 (synonymized by Kovařík, 2009: 36).
- = *Heterometrus (Javanimetrus) cyaneus sumatrensis* Couzijn, 1981 (synonymized by Kovařík, 2009: 36).
- = *Heterometrus sejnai* Kovařík, 2004, syn. nov.

***Sahyadrimetrus*, gen. nov.**

Type species: *Sahyadrimetrus scaber* (Thorell, 1876), comb. nov.

- Sahyadrimetrus barberi* (Pocock, 1900), comb. nov.
- Sahyadrimetrus kanarensis* (Pocock, 1900), comb. nov.
- Sahyadrimetrus mathewi*, gen. et sp. nov.
- Sahyadrimetrus rugosus* (Couzijn, 1981), comb. et stat. nov.
 - = *Heterometrus (Heterometrus) keralaensis* Tikader and Bastawade, 1983, syn. nov.
- Sahyadrimetrus scaber* (Thorell, 1876), comb. nov.
 - = *Scorpio leioderma* Dufour, 1856: 571, syn. nov.
 - = *Heterometrus (Heterometrus) malapuramensis* Tikader and Bastawade, 1983 (synonymized by Kovařík, 2004: 1, 35, 38).
 - = *Heterometrus rolciki* Kovařík, 2004, syn. nov.
- Sahyadrimetrus tikaderi*, gen. et sp. nov.

***Srilankametrus* Couzijn, 1981, stat. nov. et stat. rev.**

Type species: *Srilankametrus indus* (DeGeer, 1778), comb. nov.

- Srilankametrus caesar* (C.L. Koch, 1841), comb. nov. et stat. rev.
 - = *Heterometrus (Chersonesometrus) granulomanus* Couzijn, 1981, syn. nov.
- Srilankametrus couzijni*, sp. nov.
- Srilankametrus gravimanus* (Pocock, 1894), comb. nov.
- Srilankametrus indus* (DeGeer, 1778), comb. nov.
 - = *Scorpio afer* Linnaeus, 1758 (part) (synonymized by DeGeer, 1778: 341).
 - = *Scorpio ceylonicus* Herbst, 1800 (synonymized by Kraepelin, 1894: 46).
 - = *Buthus megacephalus* C.L. Koch, 1836 (synonymized by Thorell, 1876b: 164, 168, 203, 204).
 - = *Scorpio crassimanus* Becker, 1880 (synonymized by Kraepelin, 1899: 113).
 - = *Heterometrus (Srilankametrus) indus laevitensus* Couzijn, 1981, syn. nov.
- Srilankametrus pococki*, sp. nov.
- Srilankametrus serratus* (Pocock, 1900), comb. nov.
- Srilankametrus yaleensis* (Kovařík et al., 2019), comb. nov.

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