

Evidence for Eurogondwana: the roles of dispersal, extinction and vicariance in the evolution and biogeography of Indo-Pacific Hormuridae (Scorpiones: Scorpionoidea)

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Abstract

Scorpions previously assigned to the genus *Liocheles* Sundevall, 1883, of the family Hormuridae Laurie, 1896, are widely distributed in the tropical forests of the Indo-Pacific region. Revisionary systematics of these poorly known scorpions has revealed a tremendous diversity of species. As part of an ongoing investigation, the first analysis of Indo-Pacific hormurid scorpion phylogeny based on morphological data scored for all currently recognized species of *Hormiops* Fage, 1933, *Hormurus* Thorell, 1876, and *Liocheles*, is presented. The taxonomy of these scorpions is reassessed and their biogeography reinterpreted in the light of the phylogeny. Phylogenetic, morphological, and distributional data support the revalidation of *Hormiops* and *Hormurus*, previously synonymized with *Liocheles*. The phylogeny indicates that the Australasian hormurids are more closely related to the Afrotropical and Neotropical hormurids than to the Indian hormurids, as previously proposed, refuting the “out-of-India” origin of Asian hormurids. A recent paleogeographical hypothesis, the “Eurogondwana model”, is supported instead. According to this hypothesis, hormurid scorpions colonized Laurasia from Africa via the Apulia microplate (Europa terrane) in the Cretaceous, subsequently colonized the Australo-Papuan archipelago in the early-mid Cenozoic, and then went extinct in the Northern Hemisphere during the second half of the Cenozoic. These results suggest that, contrary to the traditional paradigm, dispersal and extinction may affect spatial and temporal biotic distributions as much as vicariance, even in animals with limited vagility, such as scorpions.

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Introduction

Scorpions previously assigned to the genus *Liocheles* Sundevall, 1883, of the family Hormuridae Laurie, 1896, are widely distributed in the tropical forests of the Indo-Pacific region, from India to the islands of the southwestern Pacific (Fig. 1). These unusual, dorsoventrally compressed scorpions (Fig. 2) inhabit the cracks and crevices of weathered rock outcrops, spaces under stones and the bark of trees, and, in a few cases, burrows excavated in the soil, habitats for which they exhibit an array of specialized ecomorphological adaptations.

Two species groups were recognized by Monod (2000) and Monod and Volschenk (2004), based on morphological differences. The *australasiae* species group contains the type species of *Liocheles* (Fig. 2d) and *Hormiops* Fage, 1933 (Fig. 2a) synonymized with *Liocheles* by Lourenço (1989), reinstated by Lourenço and Monod (1999), and returned to synonymy by Prendini (2000). The *waigiensis* species group corresponds to the genus *Hormurus* Thorell, 1876 (Fig. 2b, c) synonymized with *Liocheles* by Karsch (1880).

These taxa occupy distinct biogeographical regions, to the east and west of Huxley's (1868) modification of Wallace's (1859) Line. Species of *Hormurus* occur mostly east of the line (Fig. 1b), in Australia, the Molucas, New Guinea and surrounding islands, and the

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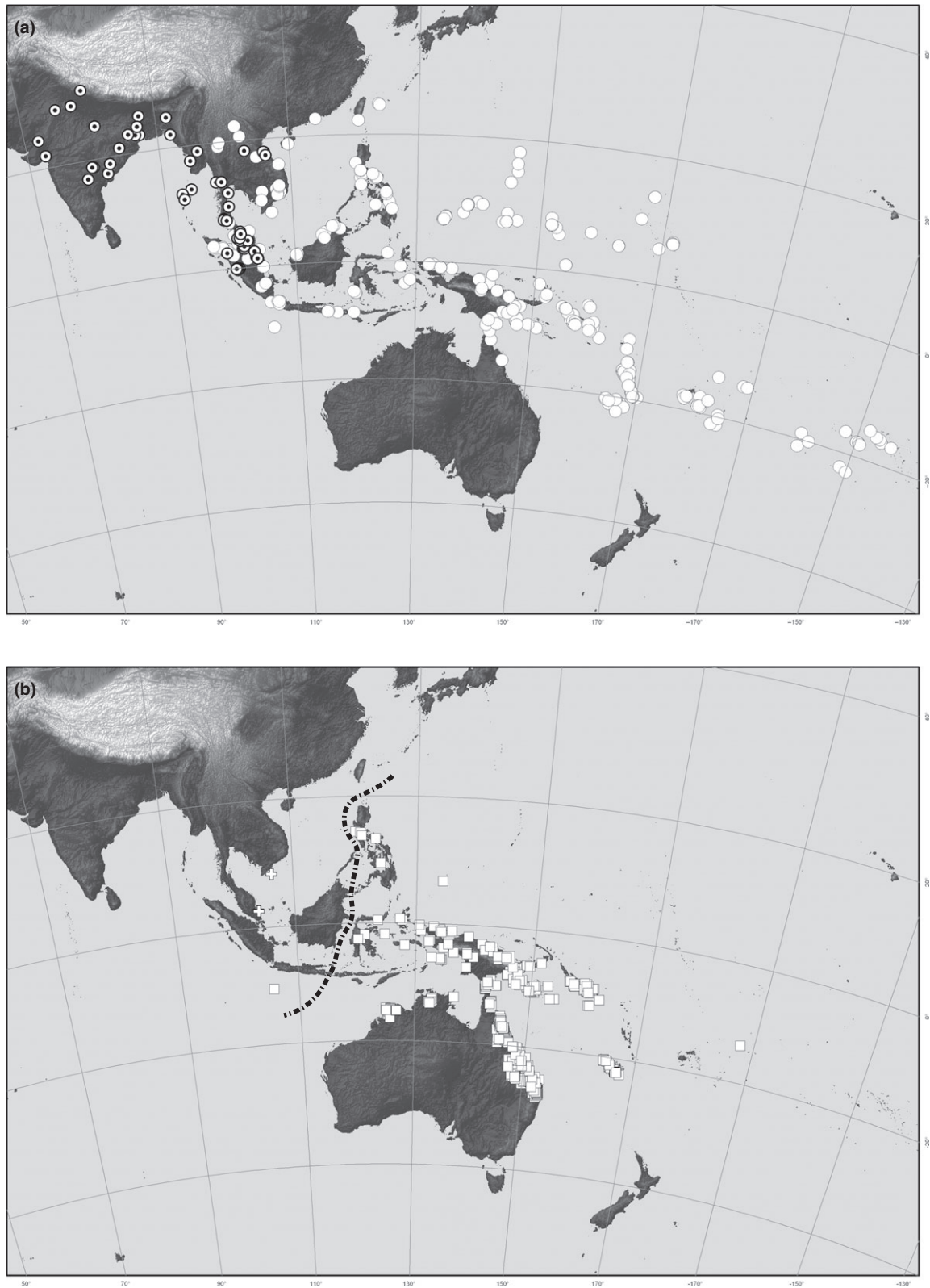


Fig. 1. Distributions of Indo-Pacific scorpion genera *Liocheles* Sundevall, 1883 (a); *Hormiops* Fage, 1933 and *Hormurus* Thorell, 1876 (b). Known locality records indicated by circles for *Liocheles* (records of *Liocheles australasiae* (Fabricius, 1775) indicated by circles without black dots), crosses for *Hormiops*, and squares for *Hormurus*. Huxley's (1868) line indicated by dashed line (b).



Fig. 2. Habitus of Indo-Pacific hormurid scorpion genera *Hormiops* Fage, 1933 (a); *Hormurus* Thorell, 1876 (b, c); and *Liocheles* Sundevall, 1883 (d). (a) *Hormiops davydovi* Fage, 1933; ♂, Con Dao Archipelago, Vietnam. (b) *Hormurus waigiensis* (Gervais, 1843), ♂, Queensland, Australia. (c) *Hormurus longimanus* (Locket, 1995), ♂, Northern Territory, Australia. (d) *Liocheles australasiae* (Fabricius, 1775), ♂, Trat Province, Thailand.

Philippines. Species of *Hormiops* and *Liocheles* (Fig. 2d) occur mostly west of the line, in India, mainland Southeast Asia, and western Indonesia. The only known exceptions are *Hormurus polisorum* Volschenk et al., 2001; endemic to Christmas Island in the Indian Ocean, south of Java, and the parthenogenetic supertramp (sensu Diamond, 1974) *Liocheles australasiae* (Fabricius, 1775), distributed from India to the western Pacific Islands and as far north as Japan. In contrast to the widespread distribution of *L. australasiae*, which crosses all biogeographical lines in the Indo-Pacific region, the distributions of most *Hormurus* and *Liocheles* species are very restricted (Monod and Volschenk, 2004; Monod, 2011a,b; Monod et al., 2013) like other scorpions with limited vagility (Birula, 1917b; Harington, 1984; Prendini, 2001a).

Colonization of Southeast Asia from India by the ancestors of *Hormiops*, *Hormurus*, and *Liocheles* during the early Paleocene is currently regarded as the most plausible explanation for the origin of these hormurid

scorpions in Asia (Stockwell, 1989; Sissom, 1990; Soleglad et al., 2005). The occurrence of *Hormurus* in Australia and Melanesia is considered to be the result of dispersal, presumably over land bridges, from Southeast Asia during the Cenozoic (Koch, 1977; Sissom, 1990). However, given the high proportion of endemic *Hormurus* species in Australia, and their relictual pattern of distribution in tropical forest and/or humid areas on the continent, Monod and Volschenk (2004) argued that these scorpions must have been present before the Neogene onset of aridification and contraction of ancestral forest habitats (Bowler, 1982; Kershaw et al., 1994; White, 1998; Morley, 2000). Monod and Volschenk (2004) further hypothesized that hormurid scorpions were present on the Australian plate before the fragmentation of Gondwana and dispersed in the opposite direction, from Australia to Southeast Asia.

None of these biogeographical hypotheses has been tested empirically, in part because the phylogenetic relationships of the Indo-Pacific hormurid taxa have

not been investigated in detail, beyond inclusion in analyses of scorpion higher phylogeny (Stockwell, 1989; Prendini, 2000).

Stockwell (1989) treated *Liocheles* as a supraspecific terminal, the monophyly of which was assumed rather than tested, whereas Prendini (2000) included a pair of exemplar species, the type species of *Liocheles* and a species of *Hormurus*. The derived position of the monophyletic group comprising these taxa within Hormuridae (as Ischnuridae Simon, 1879) was established by these analyses, but relationships among its component species remained unknown. A species-level phylogenetic analysis of the Indo-Pacific hormurid lineage was needed to test the monophyly and validity of *Hormurus*, *Liocheles*, and *Hormiops*, and to provide a framework with which to test hypotheses concerning their biogeographical origins.

The first analysis of Indo-Pacific hormurid phylogeny, based on morphological data scored for all currently recognized species of *Hormiops*, *Hormurus*, and *Liocheles*, is presented here. A monophyletic group comprising *Hormiops*, *Hormurus*, and *Liocheles* is recovered. The taxonomy of these scorpions is reassessed and their biogeography reinterpreted in light of the phylogeny. Phylogenetic, morphological, and distributional data support the revalidation of *Hormiops* and *Hormurus*.

The phylogeny indicates that the Australasian hormurids are more closely related to the Afrotropical and Neotropical hormurids than to the Indian hormurids, as previously proposed (Prendini, 2000). The “out-of-India” hypothesis, according to which India acted as a raft enabling Gondwanan hormurid lineages to colonize Southeast Asia (Stockwell, 1989; Sissom, 1990; Soleglad et al., 2005) and the “eastern Gondwana origin” hypothesis, according to which hormurid scorpions were present on the Australian plate before the fragmentation of Gondwana and dispersed in the opposite direction, from Australia to Southeast Asia (Monod and Volschenk, 2004), are refuted. Alternative hypotheses, involving dispersal and/or extinction rather than vicariance associated with the fragmentation of Gondwana, must be considered. A recent paleogeographical hypothesis, the “Eurogondwana model” (Ezcurra and Agnolín, 2012), is supported instead. According to this hypothesis, hormurid scorpions colonized Laurasia from Africa via the Apulia microplate (Europa terrane) in the Cretaceous, and subsequently went extinct in the Northern Hemisphere during the second half of the Cenozoic. Results also suggest that the Australo-Papuan archipelago was colonized from Asia by hormurid scorpions, probably before the Miocene, via translocation and dispersal associated with the emergence of subduction systems and concomitant volcanic island arcs between Asia and the Australian plate.

The results of this study suggest that dispersal and extinction may affect spatial and temporal biotic distributions as much as vicariance, even in animals with limited vagility, such as scorpions. Dispersal and extinction appear to have been preponderant in the development of the current distribution of Indo-Pacific hormurid scorpions.

Material and methods

Microscopy and nomenclature

Specimens were examined using Nikon SMZ 1500, Zeiss Stemi SV8, and Zeiss Stemi SV11 stereomicroscopes. Ultrasonic treatment (sonication) was used to clear soil particles adhering to the tegument of specimens (Nowak et al., 2008). Specimens were placed in a digital ultrasonic cleaner filled with soapy water for 15–90 s and then rinsed with distilled water. This procedure was repeated until satisfactory cleanliness was achieved. Shorter, more numerous rounds of sonication were conducted on smaller or older specimens to avoid damage.

Hemispermaphores were dissected from sexually mature male specimens using microsurgical scissors and forceps. Paraxial organ tissue was removed manually with forceps or chemically with Proteinase K (Qiagen, Venlo, the Netherlands) diluted to 50%. Hemispermaphores were placed in the Proteinase K solution in an oven at 45–50 °C for 15 min to 1 h, depending on their size and sclerotization. After the soft tissue of the paraxial organ was sufficiently digested, hemispermaphores were retrieved from the solution, rinsed with water, and the remaining digested tissues removed with forceps.

Morphological terminology follows Stahnke (1970) for pedipalp segmentation, Vachon (1974) for trichobothria, Couzijn (1976) for leg segmentation, Lamoral (1979) and Monod and Volschenk (2004) for hemispermaphore morphology, Prendini (2000) for pedipalp and metasomal carination, and Prendini et al. (2003) for carapace surfaces.

Taxon sampling

All currently recognized species of the ingroup were included in the analysis (Appendix 1): one species of *Hormiops*; 11 species of *Hormurus* (the former *waigiensis* species group of *Liocheles*); three species of *Liocheles* (the former *australasiae* species group). Outgroup selection was based on the phylogeny of Scorpionoidea Latreille, 1802 by Prendini (2000), in which the monophyletic group comprising exemplar species of *Hormurus* and *Liocheles* nested with *Iomachus* Pocock, 1893 and the nominate subgenus of *Opisthacanthus* Peters,

1861. Eight exemplar species representing the following hormurid taxa were thus included to polarize characters within the ingroup: four *Iomachus* species from India; the Afrotropical *Iomachus politus* Pocock, 1896; two Neotropical and one Afrotropical species of the nominate subgenus of *Opisthacanthus*. Additionally, *Chiromachus ochropus* (C. L. Koch, 1837) from the Seychelles islands and two Malagasy species, *Opisthacanthus* (*Monodopisthacanthus*) *madagascariensis* Kraepelin, 1894 and *Palaeocheloctonus pauliani* Lourenço, 1996; were included to represent all Gondwanan landmasses inhabited by hormurid scorpions in the biogeographical analysis. Trees were rooted on *Opisthacanthus* (*Nepabellus*) *laevipes* (Pocock, 1893) from South Africa, also following Prendini's (2000) phylogeny, which placed the African subgenus *Nepabellus* Francke, 1974 and the other two African hormurid genera, *Cheloctonus* Pocock, 1892 and *Hadogenes* Kraepelin, 1894, basal to all other hormurids.

Character matrix

External morphology and internal anatomy of specimens belonging to the 27 species included in the analysis were critically examined to score the morphological matrix (Table 1). A total of 139 discrete characters (Appendix 2) were scored for each species; 76 of these characters are new. The remaining 63 were compiled from 50 characters cited in previous works (Lamoral, 1979; Couzijn, 1981; Lourenço, 1985; Stockwell, 1989; Jeram, 1994; Prendini, 2000, 2001c, 2003; Soleglad and Sissom, 2001; Prendini et al., 2003; Soleglad and Fet, 2003; Soleglad et al., 2005; Volschenk and Prendini, 2008); 14 were modified, on the basis of new information, recognition of new states, or reinterpretation (four were split into two characters, one into three, one into four, and one into five); 47 remain unaltered. Missing entries are due to the absence of adult males for *Iomachus punctulatus* Pocock, 1897 or adult females for *Hormurus penta* (Francke and Lourenço, 1991) in the material examined.

Characters were edited with Delta version 1.04 (Dallwitz et al., 2000). A character matrix was generated in Nexus format from Delta and further edited in Mesquite version 2.75 (Maddison and Maddison, 2011).

Two characters (43, 88) were polymorphic in one taxon, and one character (71) in five taxa. Of the 139 discrete characters, 106 were coded into binary states and 33 were coded into multistates. Evolutionary transformation series could not be inferred for eight multistate characters (7, 48, 59, 76, 88, 117, 126, 132), which were treated as nonadditive (unordered) (Fitch, 1971) on the grounds that all character transformations should be considered equiprobable if there is no apparent reason for regarding one event more likely than its alternatives (Wilkinson, 1992). The remaining

25 multistate characters (4, 9, 10, 12, 23, 32, 33, 34, 41, 43, 46, 51, 52, 63, 67, 71, 81, 82, 104, 105, 115, 121, 124, 125, 130), discretized continuous variation reflecting a linear evolutionary transition, were treated as additive (ordered) (Farris, 1970). Characters were not weighted a priori.

Twenty-six uninformative characters (3, 6, 12, 19, 22, 42, 47, 50, 53, 56, 59, 61, 62, 65, 68, 72, 82, 85, 93, 94, 107, 110, 113, 116, 117, 139), detected with the “mop uninformative chars” function in Winclada version 1.00.08 (Nixon, 1999a), were excluded from the analysis. Although uninformative for phylogenetic reconstruction (Bryant, 1995), these characters were included in the matrix because they provide diagnostic information at the species level (e.g. autapomorphies). The analysis and tree statistics are thus based on 113 phylogenetically informative characters.

Cladistic analysis

Parsimony analysis was implemented in TNT version 1.1 (Goloboff et al., 2003b, 2008b). Heuristic search strategies were conducted using the new technology option, i.e. sectorial searches, tree drifting, and tree fusing (Goloboff, 1999). An equal weighting (EW) analysis was initially performed with 100 random taxon addition replicates as starting points. Each replication was initially auto-constrained with Wagner and previously inferred trees. Constrained and random sectorial searches with 200 parsimony ratchet (Nixon, 1999b) iterations, 50 iterations of tree drifting, and 10 rounds of tree fusing were performed at each replication. The maximum number of trees held in memory was initially set to 10 000. Cladograms presented here were generated as metafiles from TNT and Winclada version 1.00.08 (Nixon, 1999a), and subsequently edited in Illustrator CS3 (Adobe Systems, San Jose, CA, USA).

A sensitivity analysis (sensu Wheeler, 1995) was undertaken in order to assess the robustness of clade support and the stability of tree topologies under different weighting regimes. Implied weighting (IW) analyses (Goloboff, 1993, 1997) with concavity (*K*) values ranging from 1 to 10 were performed on the dataset. Topological results were presented by means of 50% majority-rule consensus trees (Margush and Mc Morris, 1981) of the most parsimonious trees (MPTs) generated from the separate analyses. Majority-rule consensus trees provide a graphical representation of the nodes most frequently retrieved under different weighting regimes (e.g. Prendini, 2000).

The relative degree of support for each node was assessed for each weighting scheme with symmetric resampling (SR) frequencies (Goloboff et al., 2003a). This metric is not impaired by the distortion of frequencies observed under other resampling metrics, e.g. bootstrap or jackknife (Goloboff et al., 2003a),

Morphological character matrix for cladistic analysis of Indo-Pacific hormurid scorpion phylogeny. Characters scored 0–3, polymorphic [*xy*], unknown (?), or inapplicable (–), with additive (+) and uninformative characters (U) indicated

[illegible]

Table 1
(Continued)

Character	<i>Opisthacanthus laevipes</i>	<i>Chiromachus ochropus</i>	<i>Tomachus laeviceps</i>	<i>Tomachus malabarensis</i>	<i>Tomachus nitidus</i>	<i>Tomachus politus</i>	<i>Tomachus punctulatus</i>	<i>Opisthacanthus cayaporum</i>	<i>Opisthacanthus elatus</i>	<i>Opisthacanthus lecontei</i>	<i>Opisthacanthus madagascariensis</i>	<i>Paiocheiloctonus pauliani</i>	<i>Hormiops davydovi</i>	<i>Liocheles australasiae</i>	<i>Liocheles longimanus</i>	<i>Liocheles nigripes</i>	<i>Hormurus bohliensis</i>	<i>Hormurus ischnoryctes</i>	<i>Hormurus karschii</i>	<i>Hormurus litodactylus</i>	<i>Hormurus longimanus</i>	<i>Hormurus macrocheila</i>	<i>Hormurus neocaledonicus</i>	<i>Hormurus ochyroscaptes</i>	<i>Hormurus penta</i>	<i>Hormurus polisorum</i>	<i>Hormurus waigiensis</i>
53	U	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
54		0	1	0	0	0	0	1	1	0	0	0	0	1	1	1	1	1	1	0	0	1	1	1	1	1	1
55		-	1	-	-	-	-	0	0	-	-	-	0	1	1	1	1	1	1	-	1	0	1	1	1	0	1
56	U	-	0	-	-	-	1	0	0	-	-	-	0	0	0	0	0	0	0	-	0	0	0	0	0	0	0
57		0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0
58		1	0	1	1	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
59	U	2	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
60		0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0
61		0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
62	U	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
63	+	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
64		1	1	1	1	1	1	0	0	0	-	-	1	0	0	0	0	0	1	0	0	1	0	1	0	1	1
65	U	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
66		0	0	0	0	0	1	0	0	1	0	0	1	1	0	0	1	1	1	1	1	1	1	1	1	1	1
67	+	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	3	3	3	2	2	3	2	2	2	3	2
68	U	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	
69		0	1	1	1	1	0	1	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
70		1	1	1	1	1	0	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
71	+	0	3	2	2	2	2	[12]	[02]	[02]	[13]	3	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
72	U	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
73		-	0	0	0	0	0	1	1	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1
74		0	1	0	0	0	0	0	1	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
75		0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
76		2	3	0	0	0	0	3	3	0	1	1	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3
77		0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	?	1	1	1
78		1	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	?	1	1	1
79		0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	?	1	1	1
80		0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	?	0	0	0
81	+	2	2	2	2	2	1	2	2	1	2	1	1	1	1	1	1	1	1	2	1	1	1	1	1	1	1
82	U	2	2	2	2	2	2	2	2	2	2	1	2	2	2	2	2	2	2	2	2	2	2	?	2	2	2
83		1	0	1	1	1	0	1	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0
84		0	0	0	0	0	1	0	1	1	0	0	0	1	1	1	1	1	1	1	1	1	1	0	0	1	1
85	U	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0
86		0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
87		0	1	0	0	0	0	1	1	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1
88		0	0	1	0	1	1	0	0	1	0	0	1	1	1	1	1	1	1	1	1	1	1	[12]	1	1	1
89		1	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
90		1	1	1	1	1	1	1	1	1	0	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1
91		1	1	0	0	0	0	0	0	0	1	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0
92		0	1	0	0	1	0	0	0	0	1	1	0	0	0	0	0	1	1	1	1	1	1	0	1	1	1
93	U	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
94	U	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
95		0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
96		0	1	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	1	0	1	0	1	0	0
97		1	1	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	1	0	1	0	1	0	0
98		0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0
99		0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	1	1	1	1	1	1	1	1	1	1
100		0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	1	0	1	0	0	0	0
101		0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0
102		0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0
103		0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0
104	+	0	0	0	0	0	0	0	0	0	0	0	2	2	2	2	2	1	1	1	1	2	1	2	0	0	1

Table 1
(Continued)

Character		<i>Opisthacanthus laevipes</i>	<i>Chromacanthus ochropus</i>	<i>Iomachus laeviceps</i>	<i>Iomachus malabarensis</i>	<i>Iomachus nitidus</i>	<i>Iomachus politus</i>	<i>Iomachus punctulatus</i>	<i>Opisthacanthus cayaporum</i>	<i>Opisthacanthus elatus</i>	<i>Opisthacanthus lecontei</i>	<i>Opisthacanthus madagascariensis</i>	<i>Paleocheilopterus pauliani</i>	<i>Hormiops davydovi</i>	<i>Liocheiles australasiae</i>	<i>Liocheiles longimanus</i>	<i>Liocheiles nigripes</i>	<i>Hormurus boholiensis</i>	<i>Hormurus ischnoryctes</i>	<i>Hormurus karschii</i>	<i>Hormurus litodactylus</i>	<i>Hormurus longimanus</i>	<i>Hormurus macrocheila</i>	<i>Hormurus neocaledonicus</i>	<i>Hormurus ochyroscaptor</i>	<i>Hormurus penta</i>	<i>Hormurus polisorum</i>	<i>Hormurus waigiensis</i>
105	+	0	0	0	0	0	0	0	0	0	0	0	0	2	2	2	2	2	1	0	0	1	1	2	1	2	0	1
106		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0
107	u	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
108		0	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
109		0	0	1	1	1	1	1	1	1	1	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
110	u	1	0	-	-	-	-	0	-	-	-	0	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
111		1	0	-	-	-	-	0	-	-	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
112		0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0
113	u	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
114		0	0	0	0	0	-	0	0	0	0	0	1	0	0	0	0	1	0	1	0	0	0	1	0	0	1	0
115	+	1	1	1	1	2	-	1	1	1	1	1	-	0	0	0	0	-	1	-	2	1	1	-	1	1	-	1
116	u	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1
117	u	1	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
118		1	0	1	1	1	0	?	0	0	1	1	1	0	1	1	0	1	1	1	1	1	1	1	1	1	1	1
119		0	0	0	0	0	1	?	1	1	1	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
120		0	0	0	0	0	1	?	1	1	1	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1
121	+	0	0	0	0	0	2	?	2	2	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
122		0	1	1	1	1	0	?	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
123		0	1	1	1	1	0	?	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
124	+	0	-	-	-	-	0	?	0	0	0	-	-	1	2	2	2	2	2	2	2	2	2	2	2	2	2	2
125	+	2	-	-	-	-	0	?	0	0	0	-	-	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
126		0	0	1	1	1	2	?	2	2	2	3	3	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4
127		0	0	1	1	1	0	?	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
128		1	1	1	1	1	0	?	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
129		1	1	1	1	1	0	?	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
130	+	0	0	0	0	0	0	?	0	0	0	0	0	1	2	2	2	1	1	0	1	1	1	1	1	1	1	1
131		1	1	0	0	0	1	?	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
132		0	0	0	0	0	0	?	0	0	0	2	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
133		1	0	0	0	0	0	?	0	0	0	-	-	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
134		0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	1	0	0	0
135		1	1	1	1	1	1	?	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
136		-	-	-	-	-	-	?	-	-	-	-	-	0	0	0	0	1	0	1	1	1	1	1	1	1	1	1
137		0	1	1	1	1	0	?	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
138		1	1	0	0	0	1	?	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
139	u	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1

and shows lower error rates (Kopuchian and Ramírez, 2010). 10 000 pseudoreplicates were used to calculate the frequencies with the probability to increase and decrease character weight set to the default value ($P = 0.33$). Suboptimal trees were generated from 10 random addition sequences submitted to tree bisection–reconnection (TBR) branch swapping, and up to ten trees were kept per replication. Frequencies were reported on the trees as “group present/contradicted” (GC) scores, which represent the difference in frequency between a group and its most frequent contradictory group (Goloboff et al., 2003a). Nodes retrieved in fewer than 50% of the pseudoreplicates were collapsed.

A preferred hypothesis was selected from among the equally parsimonious alternatives as the basis for taxonomic emendations and biogeographical analysis, according to three criteria: maximum fit, minimum length, maximum congruence with the topological result of the sensitivity analysis. The tree was collapsed under “rule 1” (Swofford and Beagle, 1993; Coddington and Scharff, 1994).

Biogeographical optimization

Event-based biogeographical analysis or dispersal–vicariance analysis (DIVA; Ronquist, 1997) enables the reconstruction of ancestral areas of distribution for

each node on a phylogenetic tree based on a cost–benefit matrix that favours vicariance over dispersal and extinction events. A DIVA analysis implemented in RASP version 2.0 beta (Yu et al., 2011) was conducted to compute distributions for each ancestral node on the preferred phylogeny of Indo-Pacific hormurids, and to infer whether the distributional history retrieved was congruent with the biogeographical hypotheses proposed. The frequency of each possible area x at each node n was computed based on the total number of alternative optimal ancestral area reconstructions D , according to the formula $f(x_n) = i/D$ where i is the number of occurrences of x in D . An optimal sequence of events and its probability, given the total possible combinations, was also obtained for each node.

The geological criterion was used for area delimitation because it is less prone to interpretation and bias than using current species distributions and ecological tolerance (Buerki et al., 2011). It is also more appropriate in the present study, which aims to emphasize congruence and discrepancies between hormurid phylogeny and paleogeographical history.

In total, 11 areas were circumscribed (Fig. 3): Africa (A); Madagascar (B); Seychelles (C); India (D); Neotropics (E); Pre-Cretaceous Sundaland (mainland Southeast Asia and Sumatra), which has been stable since the Triassic (Metcalf, 1998, 2001, 2011; Hall, 2009, 2012; Hall et al., 2009) (F); Australasian islands of continental origin that compose the northern part of the Australian Craton (New Guinea except its northern rim, Maluku Province except Halmahera and southeast Sulawesi) (H); Australia (I); New Caledonia (J)—areas A, B, C, D, H, I, and J correspond to persistent fragments of continental shelves, i.e. Africa, Australia, India, and South America as fragments of Gondwana, and area F as part of Laurasia. An additional biogeographical area (G) was established for the Australasian islands (Bismarck Archipelago, Halmahera, Fiji, Philippines except Palawan, New Guinea northern rim, North Sulawesi, Solomon Islands) that originated from island arc volcanism in the Mid–Late Cenozoic (Hall, 1998, 2001; Hall, 2002; Schellart et al., 2006; Gaina and Müller, 2007) because their formation postdates Gondwanan fragmentation. Christmas Island was designated as an 11th distinct area (K) because it is part of a group of seamounts (the Christmas Island Seamount Province) that formed between 136 and 47 Ma from volcanism at the Australia/India mid-oceanic ridge (Hoernle et al., 2011).

Associations of some areas were excluded from the analysis based on particular criteria. Transoceanic dispersal representing a distance of 5000 km or more was deemed implausible, as was biotic connectivity between landmasses constantly separated by a third territory.

For example, colonization of Christmas Island from the Neotropics is unlikely to have occurred because Australia was situated between them at any given time. All other connections were considered plausible, allowing the evaluation of potential dispersal events between areas without a priori constraints. A maximum of four areas were considered per node.

Results

Cladistic analysis

Statistical differences among the MPTs obtained by analyses with different weighting regimes are summarized in Table 2. The topologies retrieved under the different IW regimes were more stable than the topology retrieved under EW. Thirty MPTs were located under EW. Analyses under IW with $K = 1$ –10 each located a single MPT. Tree length progressively decreased as the concavity constant increased. The MPTs obtained by analyses under IW with $K < 3$ were predictably longer than MPTs from analysis under EW, whereas those with $K \geq 3$ were the same length. As reported by Turner and Zandee (1995), MPTs obtained under IW with $K < 3$ (strong concavity) were less fit than those obtained under EW, whereas MPTs located under IW with $K \geq 3$ (moderate to mild concavity) were fitter. The average nodal support of MPTs was rather stable across the different weighting regimes, varying between 45.2 and 46.3%.

Most nodes were retrieved with high frequency (90% or more) in the 50% majority-rule consensus of the topological results of the sensitivity analysis (Fig. 3a). A few nodes were less stable. The monophyletic groupings of *C. ochropus* with Indian *Iomachus* and of Afro-Neotropical with Australasian hormurids were each recovered in 76% of the MPTs. *Hormiops* and *Liocheles* grouped together in only 66% of the MPTs. Relationships within *Liocheles* remained unresolved. Two nodes within *Hormurus* have low frequencies. The consistency indices (CI) measured for the MPTs recovered by the different analyses revealed a rather high level of homoplasy, but the retention indices (RI) suggested that grouping information (synapomorphies) was nonetheless reasonable (Table 2; Sanderson and Donoghue, 1989; Hauser and Boyajan, 1997). Analysis under IW with $K = 10$ retrieved two MPTs with minimum length (342 steps) and maximum fit ($F_i = 88.33\%$; adjusted homoplasy = 11.67%) (Table 2). The strict consensus of the two MPTs obtained under this weighting regime (Fig. 3b) and the MPT selected as the preferred hypothesis (Fig. 3c) are topologically congruent with the majority-rule consensus of the sensitivity analysis except within *Liocheles* (Fig. 3a).

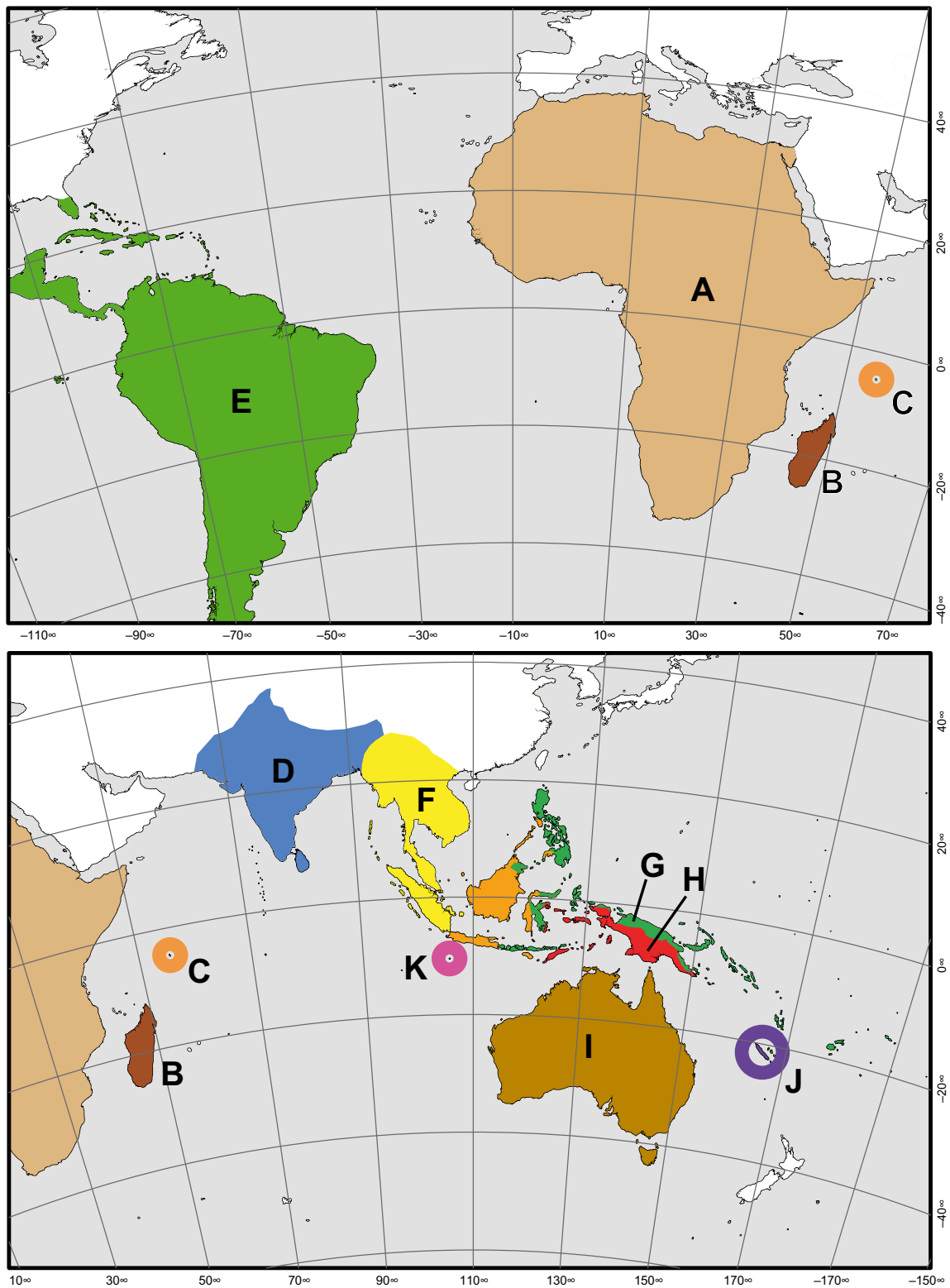


Fig. 3. Eleven biogeographical areas circumscribed for ancestral area reconstruction in analysis of Indo-Pacific hormurid biogeography: Africa (A); Madagascar (B); Seychelles (C); India (D); Neotropics (E); Pre-Cretaceous Sundaland (mainland Southeast Asia and Sumatra) (F); Australasian volcanic islands (Bismarck Archipelago, Halmahera, Fiji, Philippines except Palawan, New Guinea northern rim, North Sulawesi, Solomon Islands) (G); islands of the northern rim of the Australian Craton (New Guinea except its northern rim, Maluku Province except Halmahera and southeast Sulawesi) (H); Australia (I); New Caledonia (J); Christmas Island (K).

Table 2

Statistical differences in length (steps), fit (F_i), adjusted homoplasy (Hom), consistency index (CI), retention index (RI), and average group support (Sup) among most parsimonious trees (MPTs) obtained by cladistic analysis of Indo-Pacific hormurid scorpion phylogeny under equal weighting (EW) and implied weighting (IW) with 10 values for the concavity constant (K)

	MPTs	Length	F_i	Hom	CI	RI	Sup
EW	30	342	97.63–98.41 (72.32–72.90)	36.59–37.37 (27.10–27.68)	0.421	0.711	46.0
IW, $K = 1$	2	348	74.51 (55.19)	60.49 (44.81)	0.414	0.703	45.2
IW, $K = 2$	2	347	89.56 (66.34)	45.44 (33.66)	0.415	0.704	46.1
IW, $K = 3$	2	342	98.41 (72.90)	36.59 (27.10)	0.421	0.711	46.3
IW, $K = 4$	2	342	104.32 (77.27)	30.68 (22.73)	0.421	0.711	46.3
IW, $K = 5$	2	342	108.55 (80.41)	26.45 (19.59)	0.421	0.711	46.3
IW, $K = 6$	2	342	111.73 (82.76)	23.27 (17.24)	0.421	0.711	46.2
IW, $K = 7$	2	342	114.22 (84.61)	20.78 (15.39)	0.421	0.711	46.1
IW, $K = 8$	2	342	116.22 (86.09)	18.78 (13.91)	0.421	0.711	46.1
IW, $K = 9$	2	342	117.87 (87.31)	17.13 (12.69)	0.421	0.711	46.2
IW, $K = 10$	2	342	119.24 (88.33)	15.76 (11.67)	0.421	0.711	46.2

The length, F_i , CI and RI of informative characters on the preferred tree are provided in Appendix 4. Characters of the hemispermaphore (118–139) showed the least homoplasy ($F_i = 0.94$; CI = 0.74; RI = 0.86), confirming that genital structures are informative for inference of scorpion phylogenetic relationships as demonstrated by Mattoni et al. (2012). The metasoma (characters 90–115: $F_i = 0.87$, CI = 0.52, RI = 0.52) and pedipalp trichobothria (58–70: 0.84, 0.46, 0.51) were the second and third most informative character systems. Average statistics for other character systems are as follows: genital operculum and pectines (77–85: 0.86, 0.53, 0.68); pedipalp cuticle ornamentation (26–38: 0.81, 0.46, 0.57); pedipalp chela finger (39–57: 0.83, 0.46, 0.51); pedipalp carinae (9–25: 0.79, 0.37, 0.42).

The analyses consistently recovered a monophyletic group of Indian *Iomachus* species but falsified the monophyly of *Iomachus* as currently recognized, due to the placement of the eastern African *I. politus*, confirming an earlier finding by Prendini (2000). *Iomachus politus*, recovered as sister to the Indo-Pacific hormurid taxa by Prendini (2000), was consistently placed with the West African *Opisthacanthus lecomtei* (Lucas, 1858) in a relatively well supported group (six unambiguous synapomorphies, SR = 63%; Figs 4b,c and 5), sister to the Neotropical *Opisthacanthus*. The monophyletic group comprising *I. politus* and *Opisthacanthus* was also well supported (9, 88%; Figs 4b, c and 5) and, despite poor support (5, 14%; Figs 4b,c and 5), consistently placed sister to the monophyletic ingroup comprising *Hormiops*, *Hormurus*, and *Liocheles*. The Seychellian *C. ochropus*, Indian *Iomachus*, and Malagasy *O. madagascariensis* and *Palaeocheletoctonus* consistently grouped together with average support (4, 53%; Figs 4b,c and 5). *Chiromachus ochropus* and the Indian *Iomachus* species formed a subclade, sister to the Malagasy taxa, which was stable to parameter variation in the sensitivity analysis, but received little support (3, 0%; Figs 4b,c and 5).

The Indo-Pacific hormurid taxa, *Hormiops*, *Hormurus*, and *Liocheles*, consistently formed a monophyletic group with high support (15, 99%; Figs 4b,c and 5) under the optimal weighting regime. *Hormiops* was consistently placed sister to the three species of *Liocheles*, forming a monophyletic group to the exclusion of *Hormurus*, albeit with low support (3, 33%; Figs 4b,c and 5).

The monophyly of *Liocheles* and *Hormurus* was consistently recovered with relatively low support (4, 65% and 4, 40%, respectively; Figs 4b,c and 5). *Liocheles australasiae* was placed sister to *Liocheles longimanus* (Werner, 1939), to the exclusion of *Liocheles nigripes* (Pocock, 1897), in the majority of analyses.

Hormurus penta was placed sister to a monophyletic group comprising the remaining species of *Hormurus* in the majority of analyses. In this latter group, *Hormurus neocaledonicus* (Simon, 1877) and *Hormurus boholiensis* Kraepelin, 1914 consistently formed a basal clade, sister to the remaining species, albeit with relatively low support (2, 51%; Figs 4b,c and 5). The group comprising the remaining species of *Hormurus*, including all Australian taxa, received low support (4, 16%; Figs 4b,c and 5). Apart from the monophyletic grouping of *Hormurus ischnoryctes* Monod & Prendini, 2013 and *Hormurus ochyroscapter* Monod, 2013, all nodes among the remaining *Hormurus* received very low support.

Biogeographical optimization

Fourteen dispersal events and 11 vicariance events were identified by the RASP analysis, suggesting that dispersal and vicariance were equally important in shaping the current distribution patterns of hormurid scorpions in the Indo-Pacific region. The optimal ancestral area reconstruction is presented in Fig. 6. The distribution of optimal ancestral areas and the optimal sequence of events are summarized for each node in Appendix 5.

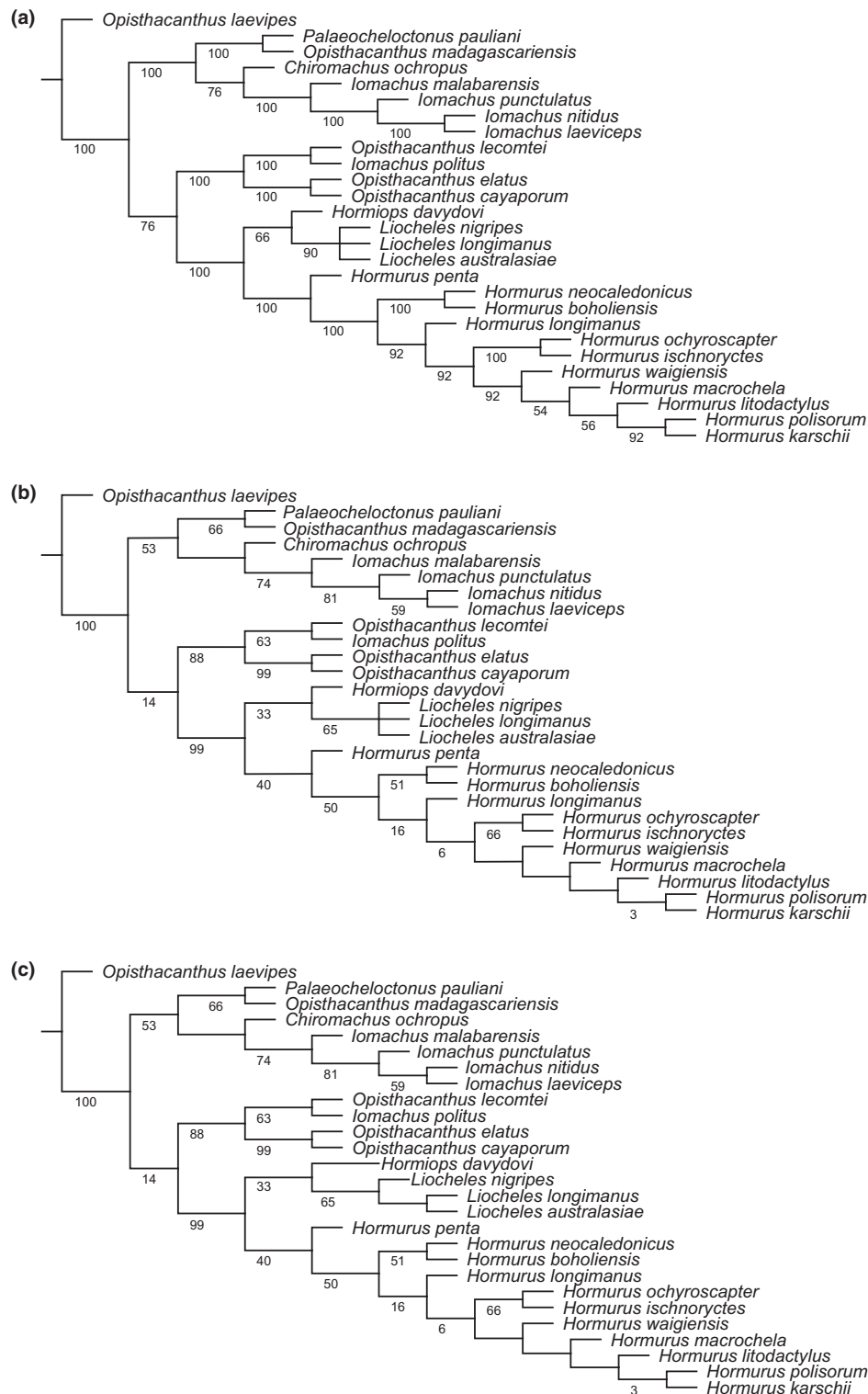


Fig. 4. Majority rule (> 50%) consensus of 50 most parsimonious trees (MPTs) generated from 10 cladistic analyses of Indo-Pacific hormurid scorpion phylogeny in which weighting regime was varied (a). Frequencies with which nodes were retrieved are indicated below corresponding branches. Nodes retrieved in fewer than 50% of the analyses are collapsed. Most parsimonious trees obtained by cladistic analysis of Indo-Pacific hormurid scorpion phylogeny under implied weighting regime ($K = 10$) that minimized length and maximized fit and branch support (b, c). (b) Strict consensus of two MPTs. (c) Preferred hypothesis, a single MPT with length, 342 steps, F_i , 88.33%; and average branch support, 46.2%. Zero-length branches are collapsed. Symmetric resampling frequencies (GC scores) of nodes are indicated below corresponding branches.

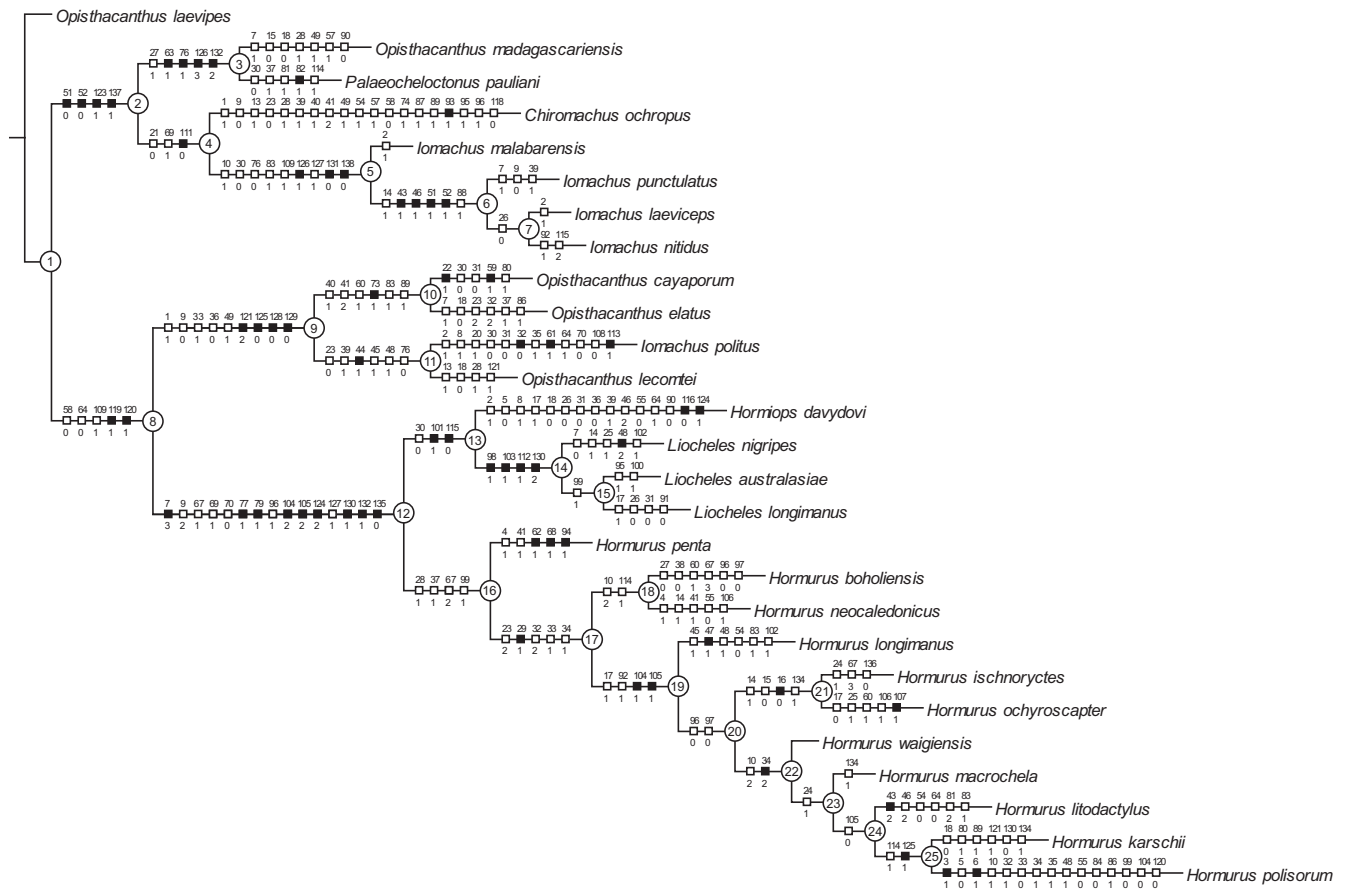


Fig. 5. Preferred hypothesis of Indo-Pacific hormurid scorpion phylogeny obtained by cladistic analysis under implied weighting with $K = 10$, indicating uniquely derived apomorphic states (closed squares) and parallel derivations of apomorphic states (open squares) for unambiguously optimized changes. Character numbers indicated above squares, character states indicated below (Appendix 2). Node numbers for synapomorphy list (Appendix 3) indicated at nodes.

The ancestral range retrieved for the root of the tree (node 0) and for node 1, ABCD, suggests that hormurid scorpions were absent from Southeast Asia prior to the fragmentation of Gondwana. At node 1, RASP postulated a combination of dispersal (ABCD to F) and vicariance (separation of AF and BCD) with a probability of 0.33. These events may be interpreted as, respectively, the colonization of Asia from Africa and the divergence of hormurids on India-Madagascar-Seychelles (BCD) as this terrane was splitting from West Gondwana.

The sequence of events postulated by DIVA at node 2 (vicariance between B and CD; $P = 0.3333$) and at node 4 (vicariance between C and D; $P = 1$) are congruent with the accepted Gondwanan fragmentation. The two vicariance events are interpreted, respectively, as the separation of Madagascar from India-Seychelles and the subsequent separation of India and Seychelles.

At node 8, the analysis recovered AF as the ancestral range, and a combination of dispersal (AF to E

and to G) and vicariance events (separation of AE and FG), with a probability of 1. The three events correspond, respectively, to the colonization of the nascent Melanesian archipelago from Southeast Asia, the colonization of the Neotropics from Africa, and the establishment of the Afro-Neotropical (*I. politus* + *Opisthacanthus*) and Australasian (*Hormurus* (*Hormiops* + *Liocheles*)) clades.

Vicariance was also inferred at node 9 between A and E ($P = 1$) and at node 12 between F and G ($P = 1$). The first event corresponds to the divergence of the Afrotropical (*I. politus* + *O. lecontei*) clade from the Neotropical *Opisthacanthus*, caused by the separation of Africa and South America, whereas the second coincides with the establishment of the Southeast Asian (*Liocheles* + *Hormiops*) and Australo-Papuan (*Hormurus*) clades.

The analysis also suggests that the Southeast Asian (*Liocheles* + *Hormiops*) clade colonized India after the subcontinent collided with Laurasia (dispersal from F to D at node 13; $P = 1$) and the Australo-Papuan

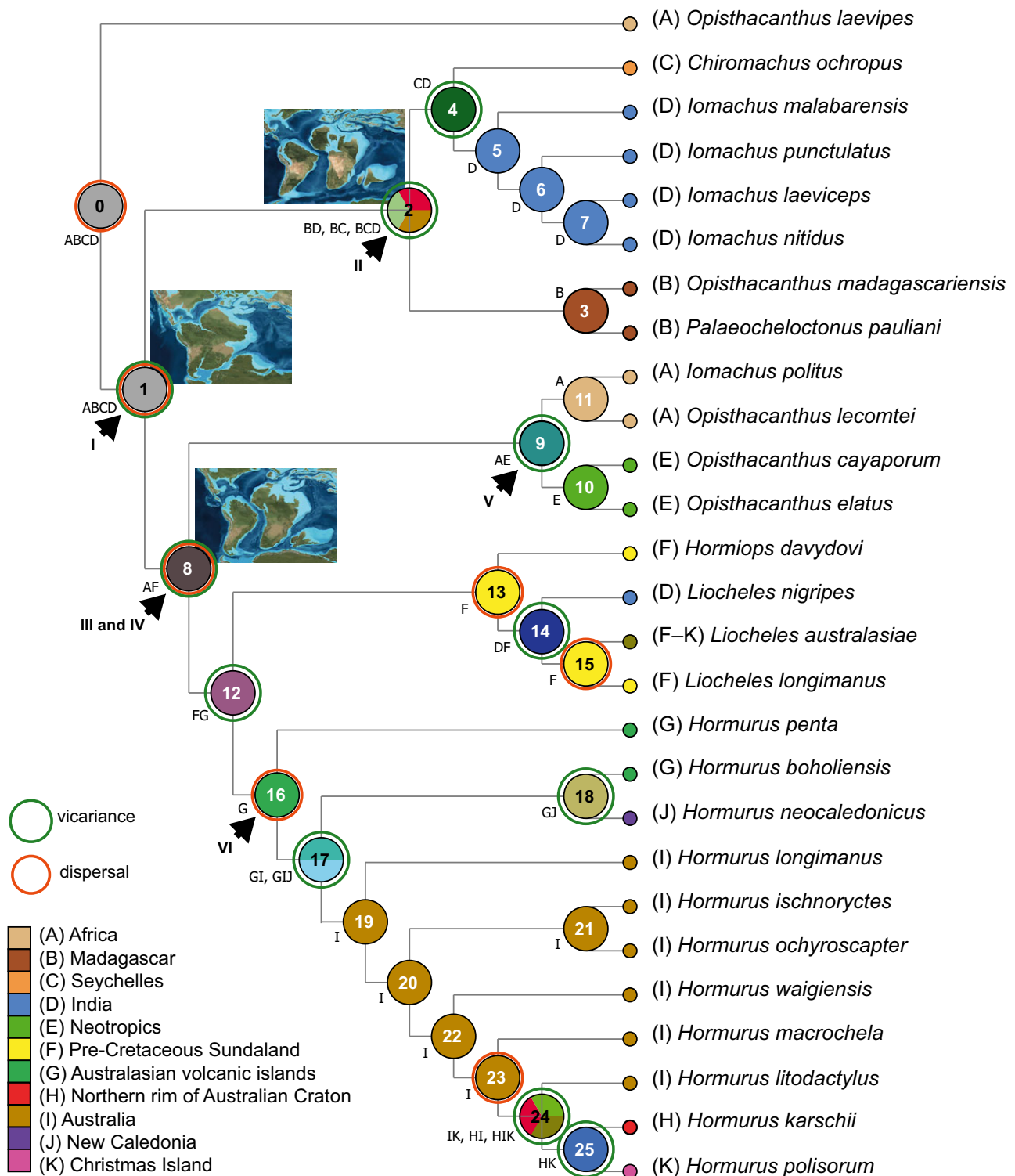


Fig. 6. Ancestral-area reconstruction on preferred hypothesis of Indo-Pacific hormurid scorpion phylogeny (Fig. 5). Geographical areas considered in the analysis are indicated at lower left. Current species distribution precedes species names. Pie charts at nodes indicate probabilities of alternative ancestral ranges. Major biogeographical events indicated by arrows: (Madagascar + Seychelles + India)/West Gondwanan separation (I); Madagascar/(Seychelles + India) separation (II); European terranes/West Gondwanan separation (III); Melanesian archipelago colonization from Sundaland (IV); Africa/South America separation (V); colonization of Australia and New Caledonia from Melanesia (VI). Node numbers for optimal ancestral areas (Appendix 5) are indicated at nodes. Paleogeographic maps from R. Blakey, N.A.U. Geology (<http://cpgeosystems.com/globaltext2.html>).

(*Hormurus*) clade evolved from Melanesian ancestors (dispersal from G to I at node 16; $P = 1$).

Discussion

Hormurus revalidated

Liocheles australasiae, the type species of *Liocheles*, was originally described as *Scorpio australasiae* Fabricius, 1775. Sundevall (1833) proposed the subgenus *Liocheles* for *Scorpio australasiae* in a footnote. Koch (1837a) subsequently established the genus *Ischnurus* C. L. Koch (1837) for *Ischnurus complanatus* C. L. Koch, 1837. Presumably unaware of Sundevall (1833), Koch (1837b) transferred *S. australasiae* to *Ischnurus*, inadvertently synonymizing *Ischnurus* with *Liocheles*, the older name. *Ischnurus* was nevertheless erroneously accepted as a valid name, instead of *Liocheles*, and several species were subsequently described thereunder. Thorell (1876a) mistakenly considered *Ischnurus trichiurus* (Gervais, 1843) (= *Hadogenes trichiurus*) to be the type species of *Ischnurus*. The substantial morphological differences between *I. trichiurus* and *Ischnurus caudicula* C. L. Koch, 1867 evidently prompted Thorell (1876a) to place both species in separate genera, and thus *Hormurus* was introduced in order to accommodate *I. caudicula*.

Karsch (1879) initially recognized *Hormurus* but later took note of Sundevall (1833) and synonymized *Hormurus* with *Liocheles* (Karsch, 1880). Simon (1887) initially followed Karsch (1880), but subsequently reverted to *Hormurus* (Simon, 1893, 1899, 1901). Other authors also neglected Karsch's (1880) synonymy and continued to use *Hormurus* incorrectly instead of the earlier name, *Liocheles*. Ten species and five subspecies were thus added to *Hormurus*. Kraepelin (1899) was aware of Sundevall (1833) but nonetheless listed the older name, *Liocheles*, in synonymy with *Hormurus*; the citation was preceded by a question mark without further justification.

As with Karsch (1879), Takashima (1941, 1942, 1945, 1948, 1949, 1950, 1952) noticed that *Liocheles* had nomenclatural priority over *Ischnurus* and *Hormurus* and should be used instead. However, Takashima's conclusions were also either disregarded or remained unknown (his publications were written and published in Japanese). The priority of Sundevall's (1833) genus *Liocheles* was finally endorsed and it was reinstated more than 20 years later by Koch (1977). Several taxa were subsequently added to *Liocheles*. Four new species were described (Francke and Lourenço, 1991; Locket, 1995, 1997; Volschenk et al., 2001; Monod and Volschenk, 2004), a subspecies was elevated to the rank of species, and two species were revalidated (Monod, 2011a).

The phylogenetic analysis presented here provides the first empirical evidence for the monophyly of *Hormurus* and *Liocheles*. Although the two genera received modest nodal support, including only four unambiguous synapomorphies each, they were both recovered under the majority of weighting regimes investigated. Such topological stability is probably more important than branch support when evaluating the phylogenetic validity of taxa (Giribet, 2003). More confidence may be placed in a clade retrieved under a wide range of parameter sets even if it is relatively weakly supported.

Hormurus can be consistently separated from *Liocheles* by seven diagnostic apomorphies. The two genera differ in pedipalp trichobothrial pattern (Fig. 7a–c; Monod, 2000; Monod and Volschenk, 2004), ornamentation of the pedipalps and metasoma (Fig. 7d), and hemispermaphore morphology. Additionally, *Hormurus* and *Liocheles* occupy distinct geographical areas separated by Huxley's (1868) line (Fig. 1). The consistent morphological differences and mostly non-overlapping distributions of *Hormurus* and *Liocheles*, together with the evidence of reciprocal monophyly, justify their separation. *Hormurus* is therefore removed from synonymy with *Liocheles*, and revalidated.

Hormiops revalidated

Fage (1933) established the monotypic genus *Hormiops* to accommodate *Hormiops davydovi* Fage, 1933 from the Con Dao archipelago, off the south coast of Vietnam. Lourenço (1989) synonymized *Hormiops* with *Liocheles*, but did not discuss the validity of the type species, *H. davydovi*. Fet (2000) doubted the validity of *H. davydovi* and suggested, given its geographical distribution, that it may be synonymous with *L. australasiae*. Lourenço and Monod (1999) revalidated *Hormiops* based on examination of the type material of *H. davydovi*, but in the absence of an empirical phylogenetic analysis to support their decision. Prendini (2000) considered the revalidation unjustified and synonymized *Hormiops* with *Liocheles* again. However, unlike Fet (2000), Prendini (2000) recognized *Liocheles davydovi* (Fage, 1933) as a valid species.

The generic validity of *Hormiops* has not been tested phylogenetically. Neither Lourenço and Monod (1999) who revalidated the genus, nor Prendini (2000) who subsequently returned it to synonymy with *Liocheles*, based their decisions on an empirical phylogenetic analysis. In the analysis presented here, *H. davydovi* was consistently retrieved as sister to *Liocheles*. Despite its close affinity to *Liocheles*, *H. davydovi* (Fig. 2a) is morphologically very distinct from the three species of *Liocheles* (Fig. 2d), including *L. longimanus* (see Monod, 2011a), males of which also possess elongated pedipalps. The habitus of *H. davydovi* is more similar to that of the Afrotropical *I. politus*,

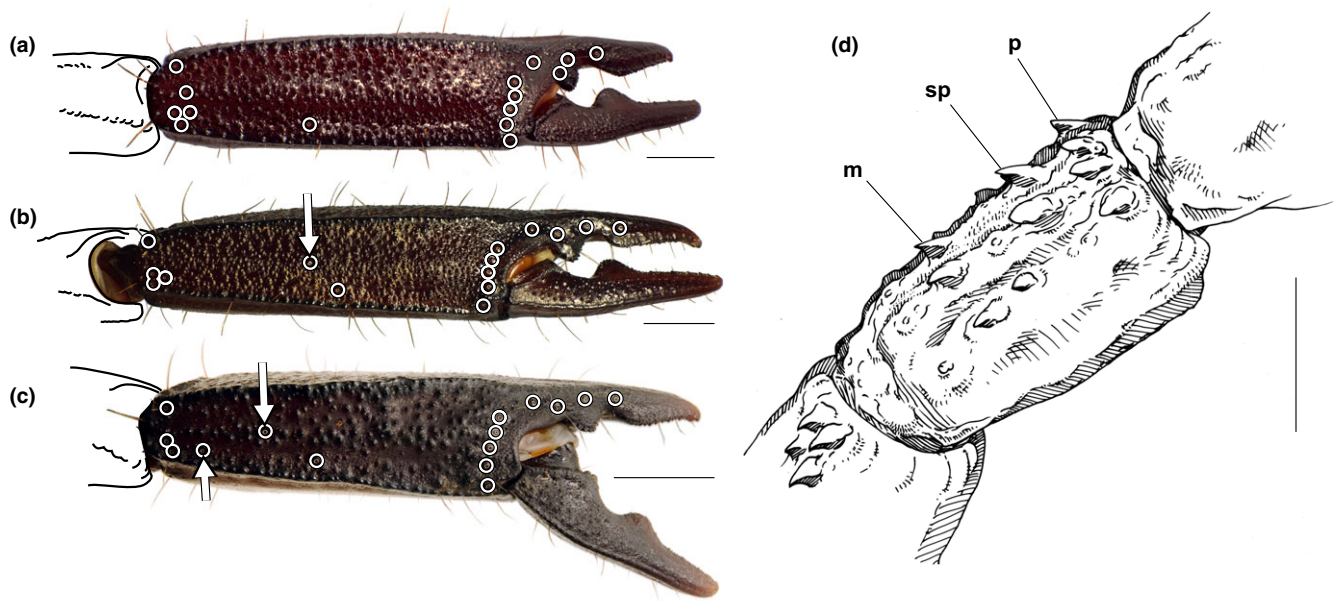


Fig. 7. Diagnostic characters of Indo-Pacific hormurid scorpion genera *Liocheles* Sundevall, 1883 (a, d) and *Hormurus* Thorell, 1976: trichobothrial patterns on external surfaces of pedipalp chela (a–c); spiniform granules on ventral surface of metasomal segment II (d). *Liocheles* sp., ♂ (MHNG), Perak, Malaysia (a). *Hormurus ischnoryctes* Monod and Prendini, 2013, ♂ (QM), Queensland, Australia (b). *Hormurus penta* Francke and Lourenco, 1991, ♂ (NHML), Guadalcanal Province, Solomon Islands (c). *Liocheles australasiae* (Fabricius, 1775), female (MHNG), Western Province, Solomon Islands (d). Arrows indicate trichobothria of *Hormurus* differing in position from putatively homologous trichobothria of *Liocheles*. Abbreviations: m, medial; p, posterior; sp, subposterior. Scale bars = 2 mm (a–c), 1 mm (d).

which may explain its relatively basal position in the Indo-Pacific hormurid clade.

Hormiops davydovi can be separated from *Liocheles* by 15 unambiguous apomorphies (Fig. 5; Appendix 3). Only the troglomorphic *H. polisorum* presents a similar level of morphological divergence (15 unambiguous apomorphies; Fig. 5; Appendix 3), which might be explained by its specialized ecology. Additionally, *H. davydovi* can be separated from *Liocheles* by 11 diagnostic apomorphies. *Hormiops* therefore differs from *Liocheles* in more diagnostic characters than *Liocheles* differs from *Hormurus*. The consistent morphological differences between *Hormiops* and *Liocheles* justify their separation. *Hormiops* is therefore removed from synonymy with *Liocheles*, and revalidated.

Indo-Pacific hormurid phylogeny

Stockwell (1989) and Prendini (2000) recovered *Liocheles* in a monophyletic group with *Iomachus*, together forming the most derived clade of Hormuridae. However, whereas generic monophyly was implicitly assumed in the supraspecific terminal taxa employed in Stockwell's (1989) analysis, the exemplar approach applied by Prendini (2000) demonstrated that *Iomachus*, among other genera, was paraphyletic. The Afrotropical exemplar species, *I. politus*, formed a monophyletic group with *Liocheles*, to the exclusion of

the Indian exemplar species, *Iomachus laeviceps* (Pocock, 1890). Prendini's (2000) phylogeny also consistently placed the Neotropical *Opisthacanthus elatus* (Gervais, 1844) as the sister taxon of the monophyletic group comprising *Iomachus* and *Liocheles*.

The phylogeny presented here confirmed the derived position within Hormuridae of the monophyletic group comprising the Indo-Pacific genera *Hormiops*, *Hormurus*, and *Liocheles*, as implied in the analyses by Stockwell (1989) and Prendini (2000), but contradicted these studies in the placement of *Iomachus*. The Indian species of *Iomachus* were not recovered as sister to *Hormiops*, *Hormurus*, and *Liocheles*. The sister group of the Indo-Pacific genera was instead recovered as a clade comprising the Afrotropical *I. politus* and *O. lecomtei*, together with two Neotropical exemplar species of *Opisthacanthus*. Although weakly supported, this grouping was stable to parameter variation in the sensitivity analysis. The biogeographical implications of the reconstruction of Indo-Pacific hormurid phylogeny presented here are incongruent with the current biogeographical model that places the origin of Asian Hormuridae on the Indian subcontinent. A reinterpretation of the biogeography is thus proposed below.

The origin of Asian Hormuridae

The “out-of-India” hypothesis is widely invoked to explain the distribution of plant and animal taxa in

tropical Asia and the Indian subcontinent (Bossuyt and Milinkovitch, 2001; Gower et al., 2002; Prendini et al., 2003; Sparks and Smith, 2004; Praveen Karanth, 2006; Azuma et al., 2008; Svenson and Whiting, 2009; Okajima and Kumazawa, 2010). This hypothesis implies survival of ancient Gondwanan lineages on the Indian plate during its rapid northward drift despite dramatic climatic changes and intense volcanism in the Late Cretaceous (Courillot et al., 1988; Cox, 1988; Duncan and Pyle, 1988). According to this hypothesis, a rich and diverse biota was carried on the so-called “Indian ark” and invaded Southeast Asia in the Early Eocene (about 57 Ma) when the northbound margin of the subcontinent collided with an intra-Tethyan island arc system, probably establishing a stepping-stone connection with Proto-Sumatra (Aitchison et al., 2007, 2008; Ali and Aitchison, 2008). The presence of *Liocheles* and related genera in Asia is generally considered to have resulted from colonization by Indian hormurid ancestors during the early Paleocene (Stockwell, 1989; Sissom, 1990; Soleglad et al., 2005).

Despite the prevailing dogma, the relationships between Afrotropical-Neotropical and Australasian hormurid taxa recovered in the analyses presented here refute the “out-of-India” hypothesis. The results of the present analysis are also incongruent with the “out-of-Sibumasu” hypothesis proposed by Clouse and Giribet (2010) for the Asian stylocellid opiliones. The Sibumasu terrane is part of the Cimmerian paleocontinent, a large fragment of continental shelf that rifted from Gondwana in the Late Permian (260–254 Ma) and drifted northward towards Eurasia (Metcalf, 1998, 2001, 2002, 2011), probably acting as a biotic raft in a manner similar to India. The phylogeny presented here implies that the hormurids on India-Madagascar-Seychelles diverged from their Gondwanan ancestors (Fig. 6; node 1; event I) prior to divergence of the Australasian and Afro-Neotropical hormurids (Fig. 6; node 12; event III). This, in turn, suggests that establishment of the (*Hormiops* + *Hormurus* + *Liocheles*) clade postdates the separation of India-Madagascar-Seychelles in the Late Jurassic (160–150 Ma), and thus also postdates the separation of the Cimmerian terrane 100 Myr earlier. The occurrence of hormurids in Asia therefore cannot be explained by the traditional Gondwanan vicariance paradigm alone. The evidence suggests that dispersal or extinction must have played a role in establishing the current distributions of these scorpions in Southeast Asia.

Results of the ancestral area reconstruction are also incongruent with the hypothesis that hormurids were cosmopolitan in Gondwana and Laurasia. The analysis suggests that these scorpions were absent from Asia prior to the major phase of Gondwanan fragmentation, and that their colonisation of the northern landmasses from Gondwana (Fig. 6; node 1) was

contemporaneous with the fragmentation of India-Madagascar-Seychelles in the Late Jurassic (Fig. 6; event I). A new hypothesis, involving biotic exchanges from the Afrotropics to Laurasia via European terranes in the Cretaceous, and subsequent extinction in the Northern Hemisphere during the second half of the Cenozoic, is proposed here to explain the close affinities between the Afro-Neotropical and Australasian hormurid taxa.

The geographical distributions and phylogenetic patterns of several invertebrate taxa restricted to tropical forests, mostly from the soil and leaf litter and with presumed poor dispersal ability (Monge-Najera, 1995; Boyer et al., 2007; Van Tol, 2009; Clouse and Giribet, 2010; Rasmussen and Cameron, 2010), closely resemble those of hormurid scorpions. The affinities observed between western Gondwanan and Laurasian elements strongly support the hypothesis of biotic connections between Africa/Meso-South America and Eurasia/North America in the Cretaceous and Early Cenozoic.

Boid and pythonid snakes, arguably more vagile than the above-mentioned invertebrates, show similar biogeographical patterns (Noonan and Chippindale, 2006; Noonan and Sites, 2010; Reynolds et al., 2014), providing further support for a Late Cretaceous connection between West Gondwana and Australasia and strengthening the common biogeographical pattern proposed.

Transoceanic dispersal from the Neotropics to the south-western Pacific was invoked to explain the disjunct trans-Pacific distributions of iguanas (Keogh et al., 2008). However, Noonan and Sites (2010) argued that rafting across 8000 km of open ocean is unlikely, and proposed an alternative hypothesis involving colonization of the Australo-Papuan Archipelago from Asia or Australia followed by extinction on the mainland and most of the islands. Evidence for sharp declines of species richness and/or extinction in the Afrotropics and Eurasia in several tropical forest invertebrate taxa (see below) raises the possibility that iguanas may have also once been present in these areas, and may have colonized the Australasian archipelago from Asia before disappearing from Africa and Laurasia.

The Eurogondwana model

The Cretaceous fossil record demonstrates that numerous supposedly endemic Gondwanan lineages were also present in Laurasia, whereas Laurasian biota were restricted to the Northern Hemisphere (see Ezcurra and Agnolín, 2012 for review). Transoceanic dispersal from the Neotropics to Asia across the Pacific Ocean, overland dispersal from the Neotropics to Asia through Laurentia and northern land bridges (Beringia or the Pacific Ring of Fire), or cosmopolitanism of Cretaceous biotas are usually invoked to explain these

faunal incongruences. However, these hypotheses imply an important bidirectional north–south biotic interchange that is unsupported by the absence of northern lineages in Gondwana. A new theory, referred to as the Eurogondwana model (Ezcurra and Agnolín, 2012), reconciles fossil evidence with paleogeology and paleobiogeography. Ezcurra and Agnolín (2012) proposed that most of the areas currently accreted to form the European region were probably connected to Africa during the Early Cretaceous through the Apulian microplate (Bosellini, 2002), and thus harboured a fauna with Gondwanan affinities. This biogeographical connection between Africa and Europe was severed around 130 Ma. Europe subsequently connected with western Asia, thus permitting the migration of Eurogondwana taxa into Asia and North America while preventing the migration of Laurasian taxa into Africa.

The Eurogondwana model is regarded here as the preferred hypothesis to account for the extant distribution and phylogenetic relationships of Indo-Pacific Hormuridae. West Gondwanan hormurids may have become isolated from the remaining African stock on the Apulia microplate in the early Cretaceous and diverged from the ancestors of *Iomachus* and *Opisthacanthus* (Fig. 6, event III; Fig. 8b), establishing the clade comprising *Hormiops*, *Hormurus*, and *Liocheles*. This clade may have subsequently colonized Laurasia after the European territories coalesced with the Asian plate. Hormurids are absent from the Holarctic region and fossils are thus far unknown from Laurasian territories. However, it is conceivable that the gradual decrease in global temperatures (Raven and Axelrod, 1974; Haq et al., 1987; Miller et al., 1999; Morley, 2000; Miller et al., 2005) and the recession of boreotropical habitats after the Paleocene–Eocene thermal maximum may have eradicated hormurids from northern latitudes.

The effect of extinction on hormurid diversity

Although not widely accepted, the extinction of lineages may be relatively common among tropical forest taxa. For example, the past and present distributions of three ancient groups of soil organisms, Onychophora Grube, 1853 (velvet worms), Ricinulei Thorell, 1876 (hooded tick-spiders), and Archaeidae C. L. Koch and Berendt, 1854 (assassin or pelican spiders), imply that several large-scale extinctions occurred (Selden, 1992; Poinar, 1996, 2000; Sena Oliveira et al., 2012; Muriénne et al., 2013). The patterns observed in Onychophora, Ricinulei, and archaeid spiders resemble those of hormurid scorpions, suggesting that they probably resulted, at least in part, from the same paleoclimatic and geological events.

Onychophora exhibit a circumtropical and circumaustral distribution (Sena Oliveira et al., 2012), like

hormurid scorpions. Although currently restricted to the tropics in the Northern Hemisphere (Greater Antilles, Mesoamerica, and South Asia), fossils in Baltic and Burmese amber (Poinar, 1996, 2000; Grimaldi et al., 2002; Sena Oliveira et al., 2012) confirm their occurrence in the Palearctic from at least the Cretaceous until the Eocene. Moreover, putative Onychophora fossils from Carboniferous deposits in France (Pacaud et al., 1981; Rolfe et al., 1982; Heyler and Poplin, 1988) and the USA (Thompson and Jones, 1980) suggest that the sub-phylum was present in northern Pangaea before the breakup of the super-continent, a hypothesis recently confirmed by a time-calibrated molecular phylogeny (Muriénne et al., 2014).

Extant ricinuleids are similarly restricted to the Afrotropics and the Neotropics, with a few species occurring in the caves of Mexico and southern Texas, but conspicuously absent from Eurasia (Selden, 1992; Muriénne et al., 2013). Ricinuleid fossils from North America, Burma, and Europe document the existence of an extinct Laurasian lineage until at least the Cretaceous (Selden, 1992; Wunderlich, 2012).

Archaeid spiders are presently found only in Australia, Madagascar, and South Africa (Forster and Platnick, 1984; Lotz, 1996, 2003, 2006; Wood, 2008; Rix and Harvey, 2011, 2012a,b). The extant species are remnants of a lineage widespread throughout Pangaea before the extinction of its northern members (Eskov, 1987, 1992; Selden et al., 2008; Wood et al., 2013). The family was originally described from several Baltic amber fossils (Koch and Berendt, 1854), indicating that it was present in the Northern Hemisphere in the mid-Eocene (Penney et al., 2011). Additional fossils from Burmese amber (Penney, 2003; Wunderlich, 2004, 2008) and from Jurassic strata in Mongolia (Selden et al., 2008) reveal that the occurrence of Archaeidae in Laurasia is older than previously thought, dating at least as far back as the mid-Jurassic (200–145 Ma).

Palearctic lineages of Archaeidae, Onychophora, and Ricinulei clearly went extinct relatively recently. Similarly, Nearctic and tropical Asian lineages were mostly or entirely eradicated in each group. Taxa that suffered complete or almost complete extinction of Laurasian lineages with survival of only relictual “Gondwanan” lineages are probably more common than currently acknowledged, and undoubtedly more groups exhibit a pattern similar to the three examples presented here.

Most of the diversity of Onychophora and Ricinulei occurs in the Neotropics. Only one tropical African and four tropical Asian species of Onychophora are known, compared with 68 Neotropical species (Sena Oliveira et al., 2012). Among the 72 extant species of Ricinulei, 61 occur in the Neotropics, compared with 11 in tropical Africa and none in tropical Asia (Muriénne et al., 2013). The low diversity of tropical African Ricinulei has been attributed to a sharp decline in

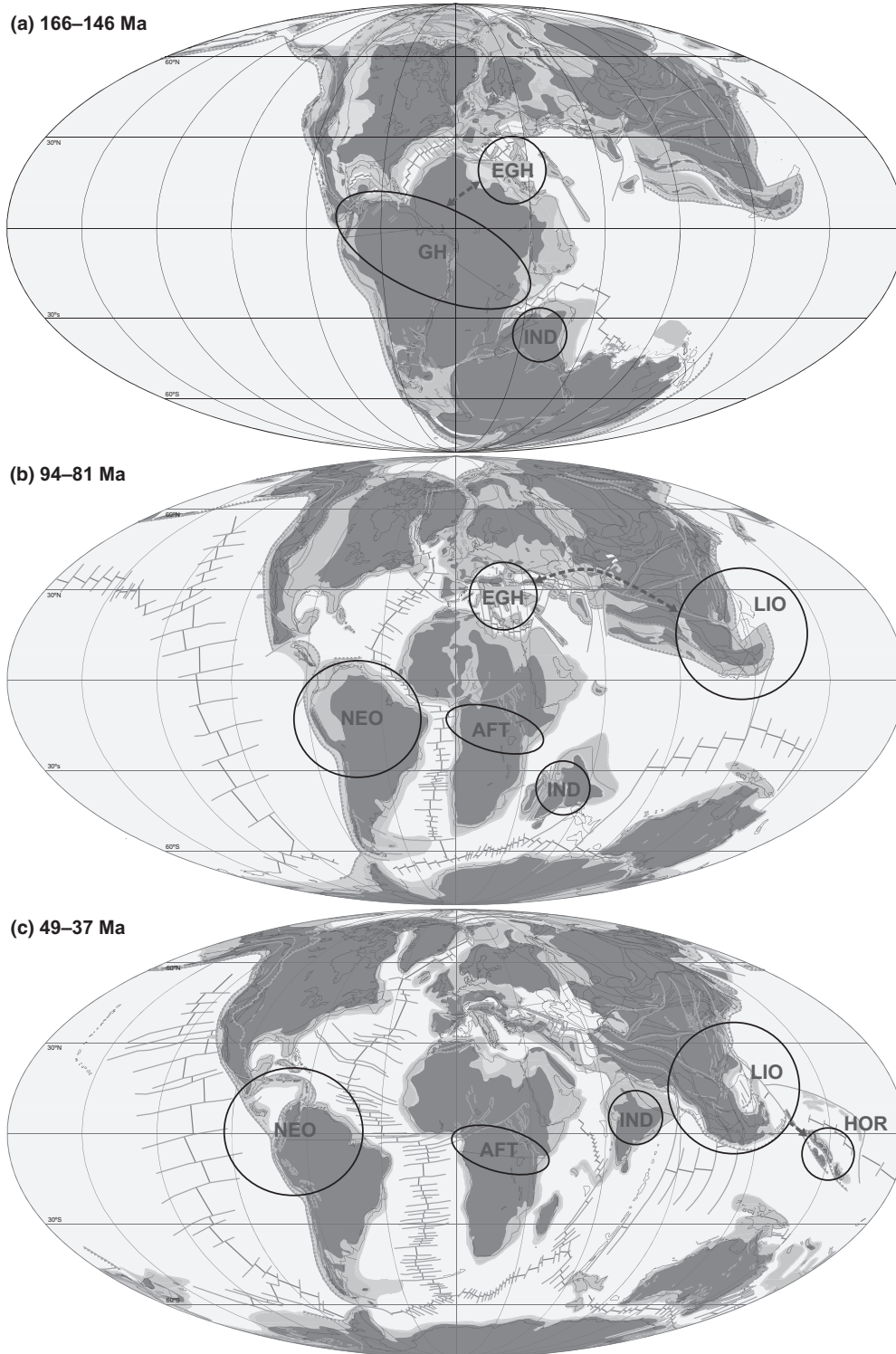


Fig. 8. Paleogeographical reconstruction of Earth after Golonka (2000). Late Jurassic (166–146 Ma): Gondwanan taxa present on Apulia microplate (a terrane of Europa). Indian *Iomachus* Pocock, 1893 isolated from GH by rifting of East Gondwana from eastern Africa (a). Late Cretaceous (94–81 Ma): Apulia microplate separates from Africa and subsequently merges with Asia allowing colonization of Laurasia by EGH and their divergence from GH. Africa separates from South America resulting in divergence of AFT and NEO (b). Eocene (49–37 Ma): LIO lineage colonizes nascent Australasian Archipelago, leading to evolution of *Hormurus* Thorell, 1876 (c). Abbreviations: EGH, Euro-Gondwanan hormurids ((*Hormiops* + *Hormurus* + *Liocheles*) ancestor); GH, West Gondwanan hormurids (*Iomachus politus* + *Opisthacanthus*); HOR, *Hormurus*; IND, Indian *Iomachus*; LIO, (*Hormiops* + *Hormurus* + *Liocheles*); NEO, Neotropical *Opisthacanthus*; AFT, Afrotropical hormurids (*Iomachus politus* + *Opisthacanthus lecomtei*).

species richness resulting from the reduction and loss of forest refugia during past phases of severe aridification (Axelrod, 1972; Raven and Axelrod, 1974; Hamilton, 1976; Axelrod and Raven, 1978; Whitmore, 1998; Muriene et al., 2013). The extant species are presumed to be relicts of a previously richer fauna. The disparate diversity of Onychophora in the Neotropics, tropical Africa, and Asia may result either from the same phenomenon or from an explosive radiation in the Neotropics, although current data do not support one hypothesis over the other.

The paleoclimatic changes putatively responsible for depletion of the tropical African Ricinulei probably had an impact on other sympatric organisms, and may offer an explanation for the disparate diversity between the clade of hormurids inhabiting the Neotropics and tropical Africa on one hand, and the Australasian clade on the other.

The paucity of hormurid species in the Neotropics (eight species of *Opisthacanthus*) and tropical Africa (*I. politus* and two species of *Opisthacanthus*) contrasts with the richness of the Australasian clade, currently comprising four Asian species (*H. davydovi* and *Liocheles*) plus 11 described and more than 40 undescribed Australo-Papuan (*Hormurus*) species. *Hormurus* mostly inhabit oceanic islands, whereas the other hormurid taxa mostly inhabit continental landmasses. The often severe climatic fluctuations experienced on continents over time are buffered on tropical and subtropical oceanic islands (Cronk, 1997; Sadler, 1999; Jansson, 2003). The resulting higher environmental stability, combined with lower levels of interspecific competition, on isolated islands often translates into the survival of paleoendemics and incipient neoendemics (Cronk, 1997). It is therefore hypothesized that the hormurid diversity of persistent continental landmasses (Africa, Eurasia, and the Americas) was decimated by the transition from “greenhouse” to “icehouse” climate in the Neogene (Zachos et al., 2001) and extreme global warming (“hothouse” climate) during the Late Paleocene–Early Eocene (Kennett and Stott, 1991; Zachos et al., 1993, 1994, 2001, 2008; Katz et al., 1999; Norris and Röhl, 1999; Peters and Sloan, 2000; Bralower et al., 2002; Huber and Caballero, 2003) and the Cretaceous (Jenkyns, 1980; Clarke and Jenkyns, 1999; Bralower et al., 2002; Huber et al., 2002) but remained relatively stable, or even increased, in the Australo-Papuan archipelago, and hence that continental extinction, at least in part, may account for the disparity in hormurid diversity between these areas.

Origin of Australo-Papuan Hormuridae

Koch (1977) rejected the hypothesis that *Hormurus* and *Liocheles* originated on the Australian plate because of their absence from the southern part of

the continent and their widespread distribution beyond the Australo-Papuan region, and instead proposed that they colonized Australia from Southeast Asia in the Cenozoic. Monod and Volschenk (2004) countered that, given the high proportion of endemic *Hormurus* species in Australia, and their relictual pattern of distribution in tropical forest and/or humid areas of the continent, the colonization of Southeast Asia by Australian hormurids in the Late Cenozoic was more plausible than the “out-of-Asia” hypothesis. Monod and Volschenk’s (2004) “eastern Gondwana origin” hypothesis was unsupported by the phylogeny recovered here, however. Australian *Hormurus* were more derived than Asian and Melanesian hormurids, confirming an “out-of-Asia” origin. Hormurid scorpions probably colonized the nascent Melanesian archipelago from Sundaland (Fig. 6, event IV; Fig. 8c), and subsequently invaded Australia (Fig. 6, event VI), in a manner similar to that proposed by Koch (1977).

Most Australian *Hormurus* species occur in tropical habitats of east Queensland, but relictual endemics also occur in distant remnant patches of monsoon forest in the Northern Territory Top End and northern Western Australia (Koch, 1977; Smith, 1991; Locket, 1995; Monod, 2000, 2011b; Volschenk et al., 2001; Monod and Volschenk, 2004; Monod et al., 2013). This disjunct distribution suggests that hormurid scorpions must have been present on the continent before the Miocene onset of aridification and contraction of ancestral rainforest habitats (Bowler, 1982; Kershaw et al., 1994; White, 1998; Morley, 2000). However, the occurrence of hormurid scorpions in Australia before the Miocene does not necessarily imply a Gondwanan origin as proposed by Monod and Volschenk (2004).

Although there are currently no absolute geological constraints on the timing of dispersal between Australasia and Sundaland, Metcalfe (2001) suggested that biotic exchanges between the Australo-Papuan Archipelago and Sundaland have occurred since at least the Mid-Oligocene (30 Ma), when the Australian Craton drifted into close proximity of the Asian continent (Hall, 1998, 2001, 2002). However, the two geological regions were probably connected before the Eocene by volcanic island arcs suitable for dispersal perhaps as early as the Lower Paleocene, when north–south sea floor spreading began in the rift between Australia and Antarctica (Kroenke, 1996; Hall, 1998; Müller et al., 2000). By then, subduction of the Australasian plate beneath the Asian and Pacific plates was initiated by its gradual northward drift, resulting in the emergence of oceanic island arc systems (Hamilton, 1988; Polhemus, 1996; Hall, 1998, 2001, 2002).

There is currently no geological evidence that the volcanic island arcs of the nascent Australo-Papuan Archipelago were emergent in the Early Cenozoic. However, the distribution of *Hormurus*, with its most

basal species endemic to New Caledonia, Papua New Guinea, the Philippines, and the Solomon Islands (*H. boholiensis*, *H. penta*, and *H. neocaledonicus*), suggests that these island chains constituted suitable dispersal corridors for hormurids. Similar scenarios, involving trans-Wallacean colonization of the Australo-Papuan archipelago by Asian ancestors followed by rapid diversification, were invoked to explain the extant distributions and high species diversity of *Livistona* R. Brown, 1810 palms (Crisp et al., 2009), *Lordomyrma* Emery, 1897 ants (Lucky and Sarnat, 2010), gecarcinuid freshwater crabs (Klaus et al., 2010), and several squamates (Reptilia), including agamid (Hugall and Lee, 2004; Hugall et al., 2008), gekkonid (Heinicke et al., 2011; Wood et al., 2012), and varanoid lizards (Fuller et al., 1998; Ast, 2001), and elapid (Keogh, 1998), pythonid (Rawlings et al., 2008; Reynolds et al., 2014), and typhlopod snakes (Vidal et al., 2010).

Adjacent islands of volcanic arcs in the Australasian Archipelago are usually separated only by small stretches of water that are easily crossed on rafting logs. The basal *H. penta* is arboreal and thus more likely to be carried away on uprooted trees or pieces of driftwood during storms and typhoons than species living on rocks (lithophilous) or underground (pelophilous). Arboreal species are eurytopic (substrate generalist) scorpions, capable of surviving on a wider range of substrates than stenotopic (substrate specialist) lithophilous and pelophilous taxa (Prendini, 2001a). The longevity of hormurids (3–30 years) (Newlands, 1980; Newlands and Cantrell, 1985; Polis and Sissom, 1990; Prendini, 2001b) increases the probability that potential mates arrive sufficiently close to one another temporally to reproduce. Repeated colonization from neighbouring islands may have enabled the establishment of durable breeding colonies. Moreover, the long gestation period of hormurid scorpions (1 or 2 years; L. Monod, pers. obs.) also increases the probability that females are gravid when dispersing, and reduces the need for two contemporaneous heterosexuals to establish a founder population. The greater dispersal ability and ecological plasticity of arboreal *Hormurus* may have facilitated the dispersal and expansion of the distribution of these scorpions across the Australasian archipelago. The absence of the stenotopic fossorial Asian scorpionid genus *Heterometrus* Ehrenberg, 1828 beyond Huxley's (1868) line (Stockwell, 1989; Prendini et al., 2003) may corroborate this hypothesis.

Explaining the distribution of Hormurus polisorum

All except one species of *Hormurus* occur east of Huxley's (1868) line. A troglomorphic species, *H. polisorum*, inhabits caves on Christmas Island (Volschenk et al., 2001), an uplifted limestone island isolated in the

eastern Indian Ocean south of Java (Grimes, 2001) and west of this biogeographical boundary. Recently published data on the geology of Christmas Island (Hoernle et al., 2011; Hall, 2012) provide insight into the mechanisms that may have resulted in the evolution and isolated distribution of this exceptional scorpion.

Christmas Island forms part of a large volcanic province that includes the Cocos/Keeling Islands and more than 50 large seamounts, 47–136 Myr old (Hoernle et al., 2011), created by mid-oceanic ridge vulcanism between Australia and East Java–West Sulawesi (Hall, 2012). The eastern seamounts were first formed in the Cretaceous whereas some of the western islands and mounts originated in the Paleogene. Christmas Island dates to 44–37 Ma. Most of the seamounts composing the Christmas Island Seamount Province (CHRISP) are guyots (flat-topped underwater mountains), suggesting that they were once emergent but have since eroded and subsided below sea level.

Due to the volcanic origin of Christmas Island, the ancestor of *H. polisorum* could only have reached it by oceanic dispersal. As it was not always a single isolated oceanic island, but was once part of a larger volcanic archipelago, the possibility of colonization from nearby landmasses is plausible. Although many seamounts of the CHRISP were below sea level after the Cretaceous, at least some were evidently emergent at any given time (Hoernle et al., 2011), providing an opportunity for colonization by hormurid scorpions, the descendants of which survive only in the caves of Christmas Island.

In the phylogeny, *H. polisorum* is placed sister to *Hormurus karschii* Keyserling, 1885; a species endemic to south-eastern New Guinea, suggesting that colonization of the paleo-islands of the CHRISP occurred from the northwestern Australian Craton. This is consistent with the surface paleocirculation patterns of the Indonesian Seaway. Although the collision between the Asian and Australian plates in the Miocene reduced its intensity, the throughflow from the Pacific Ocean to the Indian Ocean persisted during the late Cenozoic (Kuhnt et al., 2004; Fig. 9). During the last 25 Myr, the paleo-islands of the CHRISP were located sufficiently northward to lie in the pathway of the Indonesian throughflow (Fig. 9), allowing hormurid scorpions to colonize the archipelago by rafting on logs from the northwestern Australian Craton.

Although no Hormuridae are currently recorded in the eastern Lesser Sunda Islands, they may have reached there from nearby emerged lands via the Indonesian throughflow. Whereas the CHRISP was emergent and in the path of currents for the past 25 Myr, the Lesser Sunda formed only 10–5 Ma (Hall, 1998, 2001, 2002, 2012), considerably reducing the window for potential colonization. Furthermore, the Lesser Sunda are markedly drier than the islands to the north and west

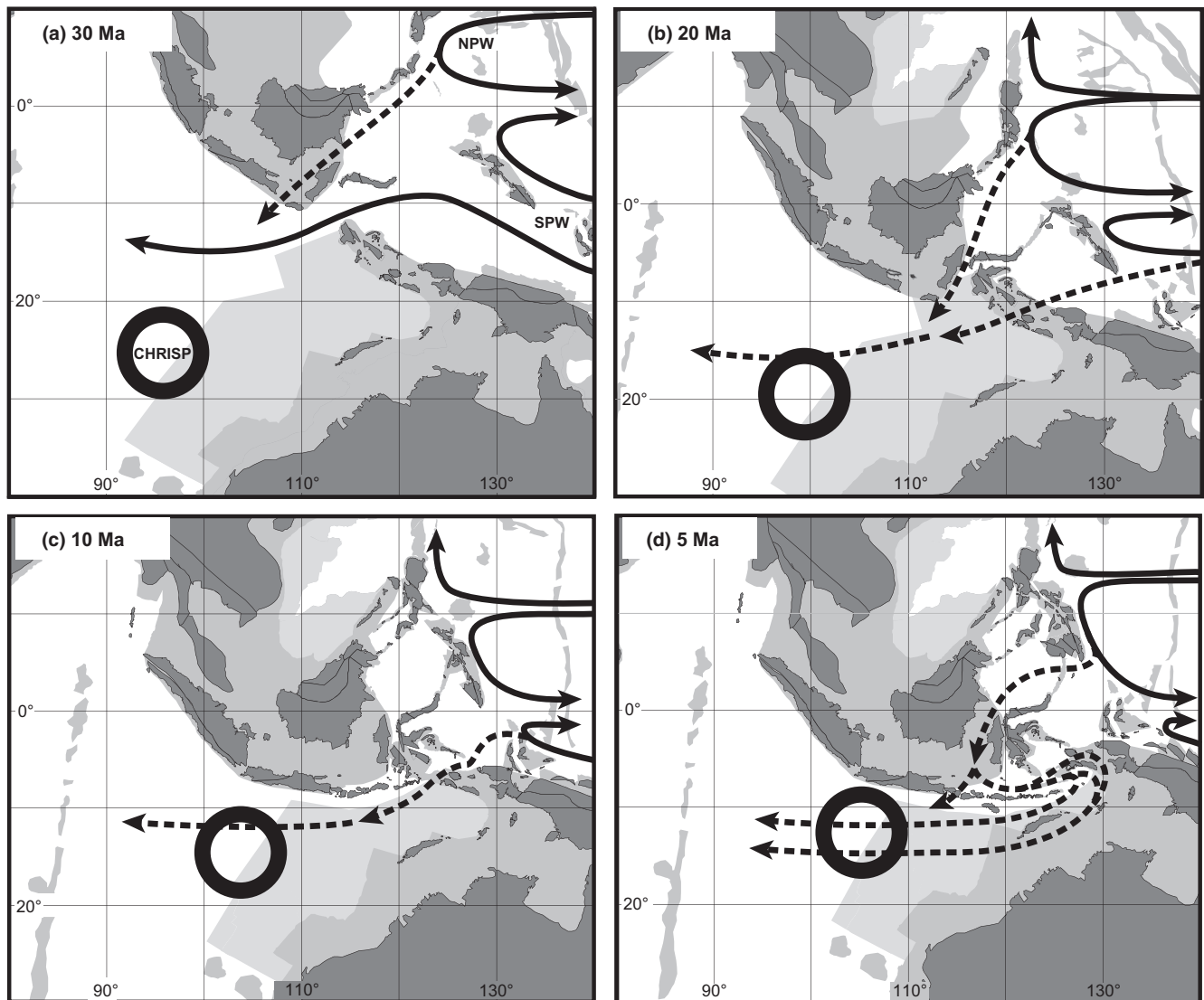


Fig. 9. Paleogeographical reconstructions of Australasian region showing major ocean currents postulated (modified from Kuhnt et al., 2004; Hall, 2012). Oligocene (30 Ma) (a); Early Miocene (20 Ma) (b); Late Miocene (10 Ma) (c); Pliocene (5 Ma) (d). Abbreviations: CHRISP, Christmas Island Seamount Province; NPW, North Pacific Water; SPW, South Pacific Water.

(Monk et al., 1997; Göltenboth and Erdelen, 2006), providing suboptimal habitat for these humidity-dependent scorpions, and a possible explanation for their absence.

Conclusions

Geological and climatic changes not only induce the formation of geographical barriers but can also remove such barriers, allowing taxa to expand their territory, a phenomenon referred to as “geo-dispersal” (Lieberman and Eldredge, 1996; Lieberman, 1997, 2000, 2005; Upchurch, 2008). Lieberman (2005) pointed out that the effects of geo-dispersal are overlooked by many

authors who regard vicariance as the only valid mechanism that affected biotic distributions, usually evoking limited vagility and dispersal ability of the organisms studied (Nelson and Platnick, 1981; Humphries and Parenti, 1986). However, the biogeographical importance of geo-dispersal and extinction has been confirmed in many organisms (McKenna, 1975; McKenna, 1983; Beard, 1998; Bossuyt and Milinkovitch, 2001; Sanmartín et al., 2001; Conti et al., 2002; Praveen Karanth, 2006), including some with putatively limited dispersal abilities (Gower et al., 2002; Wilkinson et al., 2002; Klaus et al., 2010). Likewise, the colonization of rafting microplates or emergent volcanic island arcs by plants and animals from nearby landmasses, followed by speciation of these biotas

through genetic isolation, founder effect, genetic drift, and ecological interaction, a process referred to as “pseudo-vicariance” (Van Welzen et al., 2003), is considered the main cause of current faunal and floral distributions in Australasia (Polhemus, 1996; Van Welzen et al., 2003). The phylogeny and resultant biogeographical hypotheses proposed here suggest that vicariance, geo-dispersal, and pseudo-vicariance are not mutually exclusive. All these mechanisms, as well as extinction, appear to have played a role in the development of the Indo-Pacific hormurid fauna, contrary to earlier models that consider Gondwanan vicariance to be the primary mechanism shaping their current patterns of distribution.

Future directions

The recognition of general patterns is essential for testing hypotheses of historical biogeography (Cracraft, 2001). In the present contribution, a biogeographical hypothesis consistent with the phylogeny and geographical distribution of Hormuridae and other sympatric taxa is proposed. An estimate of divergence times is required to validate this postulate, however. Ignoring the timing of lineage diversification may obscure the connection between biogeographical patterns and their underlying causes, i.e. dispersal and vicariance events (Posada et al., 2006). A molecular phylogenetic analysis of the Indo-Pacific Hormuridae (L. Monod and L. Prendini, in prep.) is underway, and will be used to test whether the temporal sequence of diversification is congruent with the biogeographical hypothesis presented here.

Hormurus species endemic to northern Australia and Wallacea are particularly important for reconstructing the historical biogeography of these scorpions, because they inhabit the interface between major biogeographical realms. For example, the Cape York, Torres Strait Islands, and eastern Northern Territory occur at the interface between the Australian and Papuan areas, whereas Wallacea and New Guinea is the interface between Asia and Melanesia. The inclusion of taxa from these areas, as well as many undescribed species, will permit a more precise assessment of the spatial and temporal sequence of colonization of the Australasian Archipelago.

Taxonomic emendations

The subfamily Hormurinae is hereby elevated to the rank of family, creating four new synonyms. The genera *Hormiops* and *Liocheles*, formerly placed in synonymy with *Liocheles*, are hereby reinstated, creating two new combinations.

Family Hormuridae Laurie, 1896, *new rank*

Type genus: *Hormurus* Thorell, 1876

Ischnuridae Simon, 1879 (unavailable name) (part): 92 [type genus: *Ischnurus* C. L. Koch, 1837 = *Liocheles* Sundevall, 1833], *new synonym*; Becker, 1880: 135; Pocock, 1900: 76 (part); Kraepelin, 1913: 162; Fage, 1933: 27; Tikader and Bastawade, 1983: 475, 477; Francke, 1985: 17 (part); Lourenço, 1985: 28–34, 47–49; tab. 1, pl. 12; Lourenço, 1989: 159–177 (part); Sissom, 1990: 121 (part); Locket, 1995: 192; Kovařík, 1997: 184; Fet, 2000: 381; Fet and Bechly, 2000: 27; Prendini, 2000: 33, 34; Prendini, 2001b: 170, 171; Volschenk et al., 2001: 162, 163.

Hormurini Laurie, 1896a (considered as subfamily): 128 [type genus: *Hormurus* Thorell, 1876].

Ischnurini: Pocock, 1893: 316–318 (considered as subfamily); Kraepelin, 1894: 108–110; Laurie, 1896a: 128; Lönnberg, 1897a: 187.

Ischnurinae: Kraepelin, 1899: 142, 1901: 271; Kraepelin, 1905: 345; Birula, 1917a: 162; Birula, 1917b: 58; Pavlovsky, 1924: 79; Pavlovsky, 1925: 192; Werner, 1934: 278; Kästner, 1941: 234; Takashima, 1945: 70, 72, 1948: 83; Millot and Vachon, 1949: 428; Takashima, 1949: 35; Bücherl, 1964: 59; Koch, 1977: 159, 1981: 876; Lourenço, 1989: 163; Stockwell, 1989: 211, 212; Nenilin and Fet, 1992: 5.

Hormurinae: Kraepelin, 1905: 343; Birula, 1917a: 162; Birula, 1917b: 58; Pavlovsky, 1925: 192, Sologlad et al., 2005: 31–35, tab. 6.

Opisthacanthinae: Kraepelin, 1905: 343 [type genus: *Opisthacanthus* Peters, 1861], *new synonym*.

Ischnuraria Birula, 1917a (“tribe”): 161, 162 (part); 1917b: 58, 59 (part).

Hadogenidae Lourenço, 2000: 26 [type genus: *Hadogenes* Kraepelin, 1894], *new synonym*.

Liochelidae: Fet and Bechly, 2001: 280 [type genus: *Liocheles* Sundevall, 1833], *new synonym*; ICZN, 2003: 159; Monod and Volschenk, 2004: 676, 677; Kamenz et al., 2005: 108; tab. 1; Prendini and Wheeler, 2005: 481, tab. 5, 10; Kamenz and Prendini, 2008: 30, 33, 43; Volschenk and Prendini, 2008: 239, 242, 249, tab. 1.

Liochelinae: Sologlad and Fet, 2003: 113.

Hormuridae: Monod, 2011b: 546; Monod et al., 2013: 286.

Remarks

Fet et al. (2000) recognized 16 families in their catalog of the scorpions of the world. The family Ischnuridae, first established by Simon (1879), was relegated to a subfamily of Scorpionidae Latreille, 1802 by Pocock (1893) and restored to family rank by Lourenço (1989). The subfamily Heteroscorpioninae Kraepelin, 1905, previously placed in Scorpionidae, was synonymized with Ischnuridae (Lourenço, 1989). Stockwell (1989) considered Ischnuridae a valid family, distinct

from Scorpionidae, and comprising three subfamilies: Ischnurinae Simon, 1879; Heteroscorpioninae Kraepelin, 1905, revalidated as a subfamily; Hemiscorpiinae Pocock, 1893, previously a subfamily of Scorpionidae. Lourenço (1996) elevated Heteroscorpionidae Kraepelin, 1905 to family rank based on Stockwell's (1989) phylogeny. The family Hemiscorpiidae Pocock, 1893 was recovered as the sister group of Liochelidae and elevated to family rank by Prendini (2000), along with Heteroscorpionidae. The name Liochelidae, proposed by Fet and Bechly (2001) to remove homonymy with Ischnurinae Fraser, 1957 (Insecta, Odonata), was approved by the International Commission on Zoological Nomenclature (ICZN) (2003). Soleglad and Fet (2003) relegated Heteroscorpionidae to a subfamily of Urodacidae Pocock, 1893 and Hemiscorpiidae to a subfamily of Liochelidae, although the name Hemiscorpiidae has priority over Liochelidae. Soleglad et al. (2005) subsequently proposed Hemiscorpiidae as a senior synonym of Liochelidae, and Hormurinae Laurie, 1896 as a senior synonym of Liochelinae Fet and Bechly, 2001. Prendini and Wheeler (2005) rejected these changes, and reinstated Hemiscorpiidae and Heteroscorpionidae as distinct from Liochelidae and Urodacidae, respectively. Hormurini, the oldest available name for the taxa assigned to Ischnurinae by Stockwell (1989), to Ischnuridae by Lourenço (1989), Prendini (2000), and Fet et al. (2000), and to Liochelidae by Fet and Bechly (2001) and Prendini and Wheeler (2005), is hereby reinstated as the valid name for the family, resulting in four new synonyms.

Included taxa

Ten genera: *Cheloctonus* Pocock, 1892; *Chiromachetes* Pocock, 1899; *Chiromachus* Pocock, 1893; *Hadogenes* Kraepelin, 1894; *Hormiops* Fage, 1933; *Hormurus* Thorell, 1876; *Iomachus* Pocock, 1893; *Liacheles* Sundevall, 1833; *Opisthacanthus* Peter, 1861; *Palaeocheloctonus* Lourenço, 1996.

Genus *Hormiops* Fage, 1933

Hormiops Fage, 1933: 30 [type species: *Hormiops davydovi* Fage, 1933]; Kästner, 1941: 234; Takashima, 1945: 71, 72, 94; Francke, 1985: 9, 17; Nenilin and Fet, 1992: 19, 20; Kovařík, 1998: 132; Lourenço and Monod, 1999: 338–343; Kovařík, 2000: 132; Monod, 2011b: 547.

Liacheles: Fet, 2000: 395; Lourenço, 1989: 170; Prendini, 2000: 72.

Diagnosis

Hormiops differs from *Hormurus* and *Liacheles* in the following combination of characters. The carapace is flat in *Hormiops*, whereas the median ocular tuber-

cle is at least slightly raised in *Hormurus* and *Liacheles*. The anterior furcated suture and sulci are vestigial or absent in *Hormiops* but present in *Hormurus* and *Liacheles*. Two pairs of lateral ocelli are present in *Hormiops*, whereas three pairs are present in *Liacheles* and *Hormurus* species except the troglobite, *H. polisorum*. The denticles of the median and inner accessory denticle rows of the pedipalp chela fingers are all similar in size in *Hormiops*, whereas several denticles are noticeably larger in *Hormurus* and *Liacheles*. Lateral transverse sulci are absent on the mesosomal tergites in *Hormiops* but present in *Hormurus* and *Liacheles*. Metasomal segments II–V are laterally compressed in *Hormiops*, whereas they are rounded in *Hormurus* and *Liacheles*. The telson is shorter than the metasomal segment V in *Hormiops*, whereas it is equal or slightly longer in *Hormurus* and *Liacheles*. The transverse ridge of the hemispermatophore distal lamina fuses with the ental edge near the base of the laminar hook in *Hormiops*, whereas it fuses with the ental edge, distal to the hook, in *Hormurus* and *Liacheles*.

Hormiops differs further from *Hormurus* in the following characters. The dorsal and retrolateral dorsal intercarinal surfaces of the pedipalp patella are smooth in *Hormiops*, but entirely granular or comprising at least a reticulated network of granules in *Hormurus*. The proximal part of the finger is smooth and trichobothria *db*, *dsb*, and *dst* are not surrounded by granules delimiting smooth depressions in *Hormiops*, whereas the surface of the finger is granular with *db*, *dsb*, and *dst* located in distinct, smooth depressions in *Hormurus*. Pedipalp chela trichobothrium *Esb* is proximal and in the same axis as the *Eb* series in *Hormiops*, whereas *Esb* is distal to the *Eb* series, usually situated midway between the *Eb* series and *Est* (Fig. 7c) or close to, and sometimes slightly distal to, *Est* (Fig. 7b) in *Hormurus*. Posterior spiniform granules on the ventrolateral carinae of metasomal segment II, present in *Hormiops*, are absent in *Hormurus*.

Hormiops differs further from *Liacheles* in the following characters. Pronounced posterior spiniform granules, absent on the ventrosubmedian carinae of metasomal segments I and II in *Hormiops*, are present in *Liacheles* (Fig. 7d). The posterior half of the ventral surface of metasomal segment V does not exhibit a smooth, shiny depression between the ventrolateral carinae in *Hormiops*, as in *Liacheles*. The apex of the capsular lamella of the hemispermatophore is aligned with, or proximal to, the base of the laminar hook in *Hormiops*, whereas it is aligned with, or slightly distal to, the apex of the hook in *Liacheles*.

Included taxa

One species: *Hormiops davydovi* Fage, 1933.

Distribution

Endemic to granitic islands of the South China Sea, off the southeastern coasts of Malaysia (Seribuat Archipelago) and Vietnam (Con Dao Archipelago).

Genus *Hormurus* Thorell, 1876

Hormurus Thorell, 1876a: 14 [type species by original designation: *Ischnurus caudicula* C. L. Koch, 1867 = *Hormurus waigiensis* (Gervais, 1843)]; 1876b: 249 (part); Karsch, 1879: 21; Keyserling, 1885: 21 (part); Thorell, 1888: 338, 419 (part); Pocock, 1893: 320; Kraepelin, 1894: 131–133 (part); Lönnberg, 1897b: 199; Kraepelin, 1899: 153 (part); Pocock, 1902: 364; Kraepelin, 1916: 42; Birula, 1917a: 162; Birula, 1917b: 58; Kopstein, 1921: 135 (part); Giltay, 1931: 13 (part); Werner, 1934: 280 (part); Kästner, 1941: 234 (part); Mello-Leitão, 1942: 125 (part); Roewer, 1943: 235 (part); Vachon, 1953: 8 (part); Chapin, 1957: 66, 67 (part); Pérez Minocci, 1974: 37; Tikader and Bastawade, 1983: 499, 500 (part); Monod, 2011b: 560; Monod et al., 2013: 286.

Liocheles: Karsch, 1880: 408 (part); Takashima, 1945: 71, 72, 95, 96 (part); Takashima, 1948: 73 (part), 83, 86; Takashima, 1949: 35 (part); Takashima, 1950: 20 (part); Takashima, 1952: 29 (part); Koch, 1977: 159, 160 (part); Takashima, 1981: 875, 876 (part); Lourenço, 1983: 404 (part); Francke, 1985: 9 (part); Lourenço, 1985: 35, 47 (part); Lourenço, 1989: 171 (part); Stockwell, 1989: 212 (part); Sissom, 1990: 126 (part); Nenilin and Fet, 1992: 19, 20 (part); Kovařík, 1995: 201 (part); Kovařík, 1998: 133 (part); Fet and Bechly, 2000: 26, 27 (part); Kovařík, 2000: 60 (part); Monod, 2000: 58–62 (part); Volschenk et al., 2001: 163 (part); Soleglad et al., 2003: 19, 57, 58, 67, 112, 113, 142, 146, tabs 3, 4, 9 (part); Monod and Volschenk, 2004: 677 (part); Soleglad et al., 2005: 32, 34; tab. 6 (part); Prendini and Wheeler, 2005: tabs 5, 10 (part); Kamenz and Prendini, 2008: 11, 30, 34, 35, 43 (part); Volschenk and Prendini, 2008: tab. 1; Monod, 2011a: 726 (part).

Diagnosis

Hormurus differs from *Hormiops* and *Liocheles* in the following combination of characters. The dorsal and retrolateral dorsal intercarinal surfaces of the pedipalp patella are entirely granular, comprising at least a reticulated network of granules in *Hormurus*, whereas these surfaces are smooth in the other two genera. The proximal part of the pedipalp chela finger is granular with trichobothria *db*, *dsb*, and *dst* located in distinct, smooth depressions in *Hormurus*, whereas the surface of the finger is smooth and *db*, *dsb*, and *dst* are not surrounded by granules delimiting smooth depressions in *Hormiops* and *Liocheles*. Pedipalp chela

trichobothrium *Esb* is distal to the *Eb* series, and usually situated midway between the *Eb* series and *Est* (Fig. 7c) or close to, and sometimes slightly distal to, *Est* (Fig. 7b) in *Hormurus*, whereas *Esb* is proximal and in the same axis as the *Eb* series in *Hormiops* and *Liocheles* (Fig. 7a). Posterior spiniform granules, absent on the ventral surface of metasomal segments I and II in *Hormurus*, are present on the ventrolateral carinae of segment II in *Hormiops* and on the ventrolateral and ventrosulmedian carinae of segments I and II in *Liocheles*.

Included taxa

Eleven species: *Hormurus boholiensis* Kraepelin, 1914; *Hormurus ischnoryctes* Monod and Prendini, 2013; *Hormurus karschii* Keyserling, 1885; *Hormurus litodactylus* (Monod and Volschenk, 2004), new combination; *Hormurus longimanus* (Locket, 1995); *Hormurus macrochela* Monod, 2013; *Hormurus neocaledonicus* (Simon, 1877); *Hormurus ochyroscapter* Monod, 2013; *Hormurus penta* (Francke and Lourenço, 1991); *Hormurus polisorum* (Volschenk, Locket and Harvey, 2001), new combination; *Hormurus waigiensis* (Gervais, 1943).

Distribution

All except one species of *Hormurus* occur east of Huxley's (1868) line (Fig. 1b) in Australia, the Moluccas, New Caledonia, New Guinea and surrounding islands, and the Philippines. *Hormurus polisorum* is endemic to Christmas Island (Australia) in the Indian Ocean, south of the Indonesian island of Java.

Genus *Liocheles* Sundevall, 1833

Scorpio (*Liocheles*) Sundevall, 1833: 31 [type species by monotypy: *Scorpio australasiae* Fabricius, 1775 = *Liocheles australasiae* (Fabricius, 1775)].

Ischnurus C. L. Koch, 1837a (part): 37, pl. VI, fig. 69 [type species by subsequent designation (Pocock, 1902: 364): *Ischnurus complanatus* C. L. Koch, 1937 = *Liocheles complanatus* (C. L. Koch, 1837), synonymized with *Hormurus* by Pocock, 1902: 364]; C. L. Koch, 1837b: 71–73; Birula, 1917b: 162.

Sisyphus: C. L. Koch, 1837a; pl. VI, fig. 69 (*lapsus calami*; name created in legend to fig. 69; see Remarks).

Hormurus: Thorell, 1876b: 249 (part); Keyserling, 1885: 21 (part); Thorell, 1888: 338, 419 (part); Kraepelin, 1894: 131–133 (part); Laurie, 1896b: 193; Laurie, 1896a: 128; Kraepelin, 1899: 153 (part); Pocock, 1900: 78, 79, 1902: 364; Kulczyński, 1910: 411; Kopstein, 1921: 135 (part); Giltay, 1931: 13 (part); Werner, 1934: 280 (part); Wu, 1936: 121; Kästner, 1941: 234 (part); Mello-Leitão, 1942: 125 (part); Roewer, 1943: 235

(part); Vachon, 1953: 8 (part); Chapin, 1957: 66, 67 (part); Pérez Minocci, 1974: 37 (part); Tikader and Bastawade, 1983: 499, 500 (part).

Liocheles: Karsch, 1880: 408; Takashima, 1945: 71, 72, 95 (part); Takashima, 1948: 73, 83; Takashima, 1949: 35; Takashima, 1950: 20 (part); Takashima, 1952: 29 (part); Koch, 1977: 159, 160 (part); Koch, 1981: 875, 876 (part); Lourenço, 1983: 404 (part); Francke, 1985: 9, 17 (part); Lourenço, 1985: 35, 47 (part); Lourenço, 1989: 171 (part); Stockwell, 1989: 212 (part); Sissom, 1990: 126 (part); Nenilin and Fet, 1992: 19, 20 (part); Lourenço, 1996: 40; Kovařík, 1995: 201 (part); Kovařík, 1998: 133 (part); Kovařík, 2000: 60 (part); Fet and Bechly, 2000: 26, 27 (part); Monod, 2000: 58–62 (part); Volschenk et al., 2001: 163 (part); Soleglad et al., 2003: 19, 57, 58, 67, 112, 113, 142, 146, tabs. 3/4/9 (part); Monod and Volschenk, 2004: 677 (part); Kamenz et al., 2005: 107, 108; Prendini and Wheeler, 2005: tab. 5/10 (part); Soleglad et al., 2005: 32, 34; tab. 6 (part); Kamenz and Prendini, 2008: 11, 30, 34, 35, 43 (part); Monod, 2011a: 726 (part); Monod, 2011b: 733.

Idocheles: Nenilin and Fet, 1992: 20.

Diagnosis

Liocheles differs from *Hormiops* and *Hormurus* in the following combination of characters. The ventral surfaces of metasomal segments I and II possess 1 or 2 pairs and 1–3 pairs of pronounced posterior spiniform granules, respectively, in *Liocheles* (Fig. 7d), whereas these granules are absent in *Hormurus*, and are present only on the ventrolateral carinae of segment II in *Hormiops*. A smooth, shiny depression, present between the posterior half of the ventrolateral carinae of the metasomal segment V in *Liocheles*, is absent in *Hormiops* and *Hormurus*. The apex of the hemispermatophore capsular lamella is aligned with, or slightly distal to, the apex of the laminar hook in *Liocheles*, whereas it is aligned with, or proximal to, the base of the hook in *Hormiops* and *Hormurus*.

Liocheles differs further from *Hormurus* in the following characters. The dorsal and retrolateral dorsal intercarinal surfaces of the pedipalp patella are smooth in *Liocheles*, but entirely granular, or comprising at least a reticulated network of granules, in *Hormurus*. The proximal surface of the pedipalp chela finger is smooth and trichobothria *db*, *dsb*, and *dst* are not surrounded by granules delimiting smooth depressions in *Liocheles*, whereas the surface of the finger is granular with *db*, *dsb*, and *dst* located in distinct, smooth depressions in *Hormurus*. Pedipalp chela trichobothrium *Esb* is proximal to, and in the same axis as, the *Eb* series in *Liocheles*, whereas *Esb* is distal to the *Eb* series, and usually situated midway between the *Eb* series and *Est* (Fig. 7c) or close and sometimes slightly distal to *Est* (Fig. 7b) in *Hormurus*.

Included taxa

Three species: *Liocheles australasiae* (Fabricius, 1775); *Liocheles longimanus* (Werner, 1939); *Liocheles nigripes* (Pocock, 1897).

Distribution

Species of *Liocheles* are distributed from eastern India to the islands of French Polynesia.

Remarks

C. L. Koch (1837a) used the name *Sisyphus* C. L. Koch, 1837 instead of *Ischnurus* in the legend to figure 69; the genus is called *Ischnurus* in the rest of the paper. Fet (2000) considered this name a *lapsus calami*.

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Appendix 1

Material examined for cladistic analysis of Indo-Pacific hormurid scorpion phylogeny. Depositories abbreviated as follows: AMNH, American Museum of Natural History, New York, USA, including tissue samples stored in the Ambrose Monell Cryocollection (AMCC); AM, Australian Museum, Sydney, Australia; BMNH, Natural History Museum, London, UK; BPBM, Bernice P. Bishop Museum, Honolulu, Hawaii, USA; CAS, California Academy of Sciences, San Francisco, USA; ESV, Erich S. Volschenk Private Collection, Perth, Australia; MHNG, Muséum d'histoire naturelle, Geneva, Switzerland; MNHN, Muséum National d'Histoire Naturelle, Paris, France; NHMW, Naturhistorisches Museum, Vienna, Austria; NNHM, Naturalis Biodiversity Center, Nationaal Natuurhistorisch Museum, Leiden, The Netherlands; NTM, Northern Territory Museum of Arts and Sciences, Darwin, Australia; QM, Queensland Museum, Brisbane, Australia; USNM, United States National Museum of Natural History, Smithsonian Institution, Washington, DC, USA; WAM, Western Australian Museum, Perth, Australia; ZFMK, Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn, Germany; ZMB, Museum für Naturkunde, Berlin, Germany.

Outgroup

Genus *Chiromachus* Pocock, 1893

Chiromachus ochropus (C.L.Koch, 1837). MAURITIUS: Île de France [=Mauritius], Dröger, 1 ♂ (ZMB 46). SEYCHELLES: S.M.S. Planet, 1904 (1053/08), 1 ♂ (ZMB 15167); S.M.S. Silhouette, Brauer, 1 ♂ (ZMB 15168), 1 ♀ (ZMB 15169); 1 ♀, (Koebel's Nachlap, Acquis. No. 1896.VIII.613) (NHMW 1731). Frigate Island, 10.VII.1967, under stones, J. F. G. Lionette, 2 ♂, 2 ♀ (USNM, jar 101); 1.X.2002, J. Gerlach, 1 juv. ♀ (AMCC [LP 2189]); palm forest (seasonally dry) near Grande Anse, 93 m, 16.VII.2008, under logs and rocks partially buried in the ground, L. Monod, 1 ♂, 2 ♀, (MHNG); 1 juv. ♀ (AMCC [LP 9069]). Mahé, 10–18.II.1885, Frundsberg Expedition, 1 ♀, juv. (NHMW 1732). Praslin, 1 juv. (ZMB 15185); 1.2006, W. R. Lourenço, 1 juv. (AMCC [LP 6894]).

Genus *Iomachus* Pocock, 1893

Iomachus laeviceps (Pocock, 1890). INDIA: Tamil Nadu: Nilgiris, 1000 ft, J. R. Henderson, 1 ♂, 1 ♀, 4 juv. (BMNH 1891.11.20.9.15). Madras [=Chennai], E. Thurston, 4 ♂, 3 ♀, 3 juv. (BMNH).

Iomachus malabarensis Pocock, 1900, **new rank**. INDIA: South India, Carl & Escher, no 6811, 1 ♀, 2 juv. (MHNG); no 6813, 5 juv. (MHNG). Karnataka: Mangalore, R. C. Wroughton (p.), Battie (c.), 3 ♂, 3 ♀ syntypes (BMNH 1896.7.30.75–80).

Remark: The subspecies *Iomachus laeviceps malabarensis* Pocock, 1900 is hereby elevated to the rank of species. It is consistently diagnosable from *I. laeviceps* by the sculpturing on the denticle margins of the pedipalp chela fingers. Male and female *I. malabarensis* possess a pronounced supra-basal lobe on the movable finger and corresponding notch in the fixed finger that are absent in *I. laeviceps*.

Iomachus nitidus Pocock, 1900. INDIA: Andhra Pradesh: Tirupati, 50 km SW, dry deciduous forest, on slope of hill, under medium-sized stones, 2009, 1 pedipalp (AMCC [LP 9827]). Karnataka: Biligiri Rangan Hills, NE Nilgiri, 10 km NE Dhimbam, 1200 m, sifting, 29.XI.1972, C. Besuchet & I. Löbl, 2 juv. (MHNG). Tamil Nadu: Nilgiris, Hill-Grove, Carl & Escher, 1 juv. (MHNG).

Iomachus politus Pocock, 1896. KENYA: British East Africa, Woi, P. Oberlaender, 1 ♀ (NHMW 1735). MOZAMBIQUE: Pflanzung Nangoro near Porto Amelia, 1928/29, M. Zitzmann, 1 ♂ (NHMW 1736). TANZANIA: 4.VI.1999, T. Gearheart, 1 ♂, 1 juv. ♀ (AMCC [LP 1514]); VII.2004, R. MacInnes, 1 ♀ (AMCC [LP 3256]). German East Africa, 1905, Steindachner, 6 ♂, 9 ♀, 1 juv. (NHMW 1733). Tanganyika, W. V. Harris, J. Omer Gosper, 1 juv. (BMNH). Morogoro Region: 20 miles SW of Morogoro, 15.XI.1957, 450 m, E. S. Ross & R. E. Leech, 1 ♂, 1 juv. (CAS). Mtwara Region: Mikindani, 1897.XXI, Reimer, 4 ♀ (NHMW 1734). Pwani Region: Bagamoyo District: Kiono Forest, Makange Forest Reserve, 1.1990, forest proper, collected by participants in frontier, 2 juv. (MHNG); Frontier Tanzania, Kiono Forest Reserve, VIII.1989, J. Bryant, 1 ♀ (MHNG [KMH 6612]); Kiono Forest Reserve, Coast Region, 1050 ft, coastal forest, under bark of rotting/fallen tree, 29–30.III.1986, K. M. Howell, 1 ♀ (MHNG [KMH 3311]); 1 ♂ (MHNG [KMH 3312]); 18.I.1986, J. Kiellmann, 1 juv. (MHNG [KMH 3348]); 19.I.1986, J. Kiellmann, 1 ♂ (MHNG [KMH 3347]). Rufiji District: Kiwengoma Forest Reserve, near Utete, 1000–1750 ft, J. Kingdon, 1 juv. (CAS). Tanga Region: Handeni District: Handeni, IX.2006, J. Beraducci, 2 ♂, 4 ♀, 4 juv. (AMNH); 15 miles S of Handeni, 13.XI.1957, 630 m, E. S. Ross & R. E. Leech, 1 ♂ (CAS).

Iomachus punctulatus Pocock, 1897. INDIA: South India, Pa. Bris...?, Kukkal, Carl & Escher (no 6815), 1 ♀, 2 juv. (MHNG). Palnis inf, Tan Dikuli, Carl & Escher (no 6814), 1 ♀, 1 juv. (MHNG). Kerala/Tamil Nadu: Anamalai Hills, Attakatti, Carl & Escher, 1 ♀ (MHNG); Kadamparai (3500 ft), 5.VIII.1963, P. Susai Nathan, 1 juv. (CAS [CASENT 9026735]). H. L. Stahnke coll. [ASU 63-1160], 1 juv. (CAS [CASENT 9026734]). H. L. Stahnke coll. [ASU 63-1161]. Tamil Nadu: Coimbatore [=Coimbatore], W. Davidson Esq., 1 ♂, 1 ♀ syntypes (NHML 1888.16.TYPE).

Genus *Opisthacanthus* Peters, 1861

Subgenus *Monodopisthacanthus* Lourenço, 2001

Opisthacanthus (Monodopisthacanthus) madagascariensis Kraepelin, 1894. MADAGASCAR: Fianarantsoa Province: Forêt d'Analava, 29.6 km 280° W Ranohira, 700 m, general collecting, tropical dry forest, 1–5.II.2003, B. L. Fisher, C. E. Griswold et al., BLF 7386, 2 ♂ (CAS [CASENT 90185207]/AMCC [LP 2800]). Parc National d'Isalo, Ambovo Springs, 29.3 km 4° N Ranohira, 990 m, pitfall trap in Uapaca woodland, 9–14.II.2003, B. L. Fisher, C. E. Griswold et al., BLF 7649, 1 juv. (CAS [CASENT 9018526]/AMCC [LP 2812]). Mahajanga Province: Parc National de Namoroka: 9.8 km 300° WNW Vilanandro, 140 m, general collecting, tropical dry forest, 4–8.XI.2002, B. L. Fisher, C. E. Griswold et al., BLF 6452, 1 ♂ (CAS [CASENT 9018471]/AMCC [LP 2803]); 16.9 km 317° NW Vilanandro, 100 m, general collecting, tropical dry forest, 12–16.XII.2002, B. L. Fisher, C. E. Griswold et al., BLF 6585, 2 ♂ (CAS [CASENT 9018473]/AMCC [LP 2801]); 17.8 km 329° WNW Vilanandro, 100 m, general collecting, tropical dry forest, 8–12.XI.2002, B. L. Fisher, C. E. Griswold et al., BLF 6509, 1 ♂, 1 ♀ (CAS [CASENT 9018472]/AMCC [LP 2802]). Parc National Tsingy de Bemaraha: 2.5 km 62° ENE Bekopaka, Ankidrodra River, 100 m, tropical dry forest on Tsingy, 11–15.XI.2001, B. L. Fisher, C. E. Griswold et al., BLF 4342, 1 ♂, 1 ♀ (CAS [CASENT 9018515]/AMCC [LP 2805]); 3.4 km 93° E Bekopaka, Tombeau Vazimba, 50 m, tropical dry forest, 6–10.XI.2001, B. L. Fisher, C. E. Griswold et al., BLF 4231, 3 ♂, 1 ♀, 1 juv. (CAS [CASENT 9018524]/AMCC [LP 2806]), 1 ♂ (CAS [CASENT 9018468]/AMCC

[LP 2808]; 10.6 km 123° ESE Antsalova, 150 m, tropical dry forest on Tsingy, 16–20.XI.2001, B. L. Fisher, C. E. Griswold et al., BLF 4435, 1 ♀ (CAS [CASENT 9018516]/AMCC [LP 2807]). Toliara Province: Lake Ranobe, 30 m, 1.II.2003–8.II.2003, pitfall trap, spiny forest/tamarinds, 50 m from lake edge, Frontier Wilderness Project, C. E. Griswold, MGF 060, 1 ♂ (CAS [CASENT 9018506]/AMCC [LP 2811]).

Subgenus *Nepabellus* Francke, 1974

Opisthacanthus (Nepabellus) laevipes (Pocock, 1893). SOUTH AFRICA: Mpumalanga Province: Bushbuckridge Municipality, Bushbuckridge communal lands, ca. 7 km NNW Bushbuckridge town, 551 m, plains with ridges, broadleaf savanna, moderate S slope, 2.VII.2004, I. Engelbrecht, 1 ♂, 1 ♀ (AMCC [LP 3973]); 2 ♀ (AMCC [LP 3974]). Lowveld Botanical Garden, Nelspruit, 14.VII.2000, mixed bushveld, crevice in quartz, L. Prendini, M. MacFarlane, & K. M. A. Prendini, 1 ♀ (AMCC [LP 1835]).

Subgenus *Opisthacanthus* Peters, 1861

Opisthacanthus (Opisthacanthus) cayaporum Vellard, 1932. BRAZIL: Para: Campos de Cayapos, savannahs, in termite mounds, 10.VI.1979, W. R. Lourenço, 3 ♂, 1 ♀, 19 juv. (MHNG); II.1979, II.1987, W. R. Lourenço, 2 ♂, 1 ♀ (MHNG).

Opisthacanthus (Opisthacanthus) elatus (Gervais, 1844). COLOMBIA: Boyaca: Otanche-Muzo, 100 km W Tunja, IV–VI.1986, Indian from Muzo Mine, 2 ♂, 1 ♀, 3 juv. (MHNG). PANAMA: Soberalie National Park, 15.X.2000, M. Makovec, 1 ♀ (AMCC [LP 1837]).

Opisthacanthus (Opisthacanthus) lecomtei (Lucas, 1858). CAMEROON: 1 ♂ (MNHN RS 0308). Foullassi, Sangmelima, J. L. Perret, 1953–1955, 1 ♀ (MHNG); forêt primaire, XII.1959, J. L. Perret, 1 juv. (MNHN RS 3602). Foullassi, Lobe River, 1960, J. L. Perret, 1 juv. (MNHN RS 3603). Mengalé, 616 m, 12.X.2002, under tree bark on fallen log, R. C. West, 1 ♀ (AMCC [LP 2194A]). GABON: Ogooue-Ivindo Province: Belinga, 12.II.1963, H. Coiffait, 1 ♂ (MNHN RS 6264). Ogooue-Maritime Province: Aire d'Exploitation Rationnelle de Faune des Monts Doudou, 630 m, 18.III.2000, rainforest, sifted litter, B. L. Fisher, BF 2276 (2), 1 ♂ (AMCC [LP 1608]).

Genus *Palaeocheiloctonus* Lourenço, 1996

Palaeocheiloctonus pauliani Lourenço, 1996. MADAGASCAR: SW Madagascar, SE Ampanihy, Plateau Mahafaly, near Behahitso (after Ankalinaro), 90 m, sinkholes area, high shrubby thicket with Euphorbiaceae and Didiereaceae, hand collecting, under logs and rocks, I.1966, P. Griveaud, 1 ♂ holotype, 4 ♂, 6 ♀♀, 2 juv. paratypes (MNHN RS 4451). SW, Plateau Mahafaly, near Bihahitso, I.1966, P. Griveaud, 1 ♂, 1 juv. paratypes (MHNG).

Ingroup

Genus *Hormiops* Fage, 1933

Hormiops davydovi Fage, 1933. VIETNAM: Con Dao Archipelago, Poulo-Condor Island [Con Son Island], M. Germain, 1 ♀, 11 juv. (MNHN RS 0499); forest, under stones, II.1930/IV.1931, Davidoff 1932, 1 ♂ holotype (MNHN RS 0562), 2 ♀ paratypes (MNHN RS 0562). Con Dao National Park, Con Son Island, track to Dat Tham Beach, 10.I.2012, rainforest, in rock crevices (granitic boulders), L. Monod, 2 ♂, 2 ♀, 1 juv. (MHNG); track to Dam Tre Bay, 11.I.2012, rainforest, in rock crevices (granitic boulders), L. Monod, 1 ♂, 4 ♀, 1 juv. (MHNG); track to Ong Dung Beach, 8.I.2012, rainforest, in rock crevices (granitic boulders), L. Monod, 2 ♀ (MHNG); Soy Ray plantation track, 9.I.2012, rainforest, in rock crevices (granitic boulders), L. Monod, 2 ♂, 4 ♀, 2 juv. (MHNG).

Genus *Hormurus* Thorell, 1876

Hormurus boholiensis Kraepelin, 1914. PHILIPPINES: Luzon: Manila, Mr. Cuming, 1 ♀ (BMNH). Mount Makiling, Baker, 1 ♀ (AMNH). Subig Bay, II.1907, S. C. Thompson, 1 juv. (CAS). Panay: Aklan Province: Caticlan, J. L. Gonzales, 6 ♂ (MHNG).

Hormurus ischnoryctes Monod and Prendini, 2013. AUSTRALIA: Queensland: Mount Mulligan cattle station, 340 m, 16–17.VII.2006, open woodland savanna, in vertical burrows 15–30 cm deep, with terminal chambers, G. Romand & L. Monod, 1 ♂ holotype (QM), 1 ♂, 4 ♀♀, 5 juv. paratypes (AMNH), 3 ♀♀, 4 juv. paratypes (QM), 1 juv. paratype (AMCC [LP 6639]); 10.IX.1983, A. Williamson, 1 ♂ paratype (QM-S17140). Ravenshoe, ca. 600 m, VIII.1963, H. St Girons, open Eucalyptus forest, marked cold season, low rainfall, 1 ♂, 1 ♀ (MNHN RS 4209).

Hormurus karschii Keyserling, 1885. INDONESIA: West Papua: Segaa Bay, Gazelle, 1875, 2 ♂ syntypes [dried] (ZMB 3016). Sekroe, Maarx, 1897, S. Schädler, 1 juv. (NNHM 253); 1 ♂, 2 ♀, 2 juv. (NNHM 254).

Hormurus litodactylus Monod and Volschenk, 2004. AUSTRALIA: Queensland: Daintree National Park, Mount Sorrow ridge walk, 7.XII.2006, highland rainforest (very humid, misty, cool), under stones, in between roots of trees, L. Monod, 6 ♂, 5 ♀ (MHNG), 1 juv. (AMCC [LP 5559]).

Hormurus longimanus (Locket, 1995). AUSTRALIA: Northern Territory: Arnhem Land, Oenpelli area, 21–22.VII.1992, A. Wells & J. Webber, 1 ♂ holotype (NTM A000196). Kakadu National Park: 20.II.1994, under decaying bark in monsoon vine forest, G. Wallis, 1 ♂ paratype (NTM A000197). Gorge NE of Mount Gilruth, 10–13.VII.1979, rainforest, G. B. Monteith & D. J. Cook, 1 ♀, 1 juv. (QM-S23252). Jim Jim Falls, 31.V.1992, under rocks, M. S. Harvey & J. M. Waldo, 4 juv. (WAM 98/1852–5); 64–129 m, 21–22.VIII.2009, monsoon forest, in rock crevices, G. Brown & L. Monod, 1 ♂, 4 ♀, 2 juv. (WAM), 1 ♂, 1 ♀ (AMNH), 1 ♂, 1 ♀ (MHNG), ♂ [leg], 1 juv. (AMCC [LP 10319]). Koolpin Creek, 107 m, 24.VIII.2009, vine thicket beside creek, in rock crevices, G. Brown & L. Monod, 1 ♀ (WAM), 1 ♀ (AMNH); 1 ♀ (MHNG), ♀ [leg] (AMCC [LP 10317]). Maguk, 98 m, 23.VIII.2009, monsoon forest beside pools, in rock crevices, G. Brown & L. Monod, 2 ♂, 3 ♀, 2 juv. (WAM), 1 ♂, 1 ♀ (AMNH), 1 ♂, 1 ♀ (MHNG), ♀ [2 legs] (AMCC [LP 10314]).

Hormurus macrochela Monod, 2013. AUSTRALIA: Keyserling, 1 ♂ (BMNH 1890.7.1.216–221). Queensland: Magnetic Island, G. F. Hill, 1 ♂, 1 ♀, 2 juv. (BMNH 1925.IX.12.1–4); VI.1992, vine forest, E. S. Volschenk, 1 ♂ (ESV 3370); 41 m, 28–29.XI.2004, vine thicket along dry creek, in rock crevices (very narrow or in between stones), R. Wyss & L. Monod, 4 ♂♂, 7 ♀♀, 2 juv. (MHNG), 1 ♂, 1 ♀ (QM), 1 juv. (AMCC [LP 5555]). Orpheus Island, XI.1982, R. Tiesley, 1 ♀ (NTM). Palm Island, L. Bancroft, 1 ♀, 3 juv. paratypes (QM-S17042); IX.1923, H. A. Longman, 1 juv. (QM-S17088). Palm Island, site 1, 450 m, 20–21.II.2001, rainforest, G. B. Monteith (8323), 1 ♂, 1 ♀ paratypes (QM-S59206). Palm Island, site 4, 100 m, 22.II.2001, rainforest, G. B. Monteith (8325), ♂ holotype (QM-S59212).

Hormurus neocaledonicus (Simon, 1877). NEW CALEDONIA: 20.VIII.1900, Bougier, 1 ♀ paratype (ZMH). Col des Roussettes, 11.II.1993, rainforest, M. S. Harvey, N. I. Platnick & R. J. Raven, 1 ♀ (WAM 98/1892); 427 m, 21.IX.2004, small patch of rainforest in between niaoulis savannah, in between stones in a scree covered by litter and tree roots, D. Gaillard & L. Monod, 2 ♂♂, 3 ♀♀, 7 juv. (MHNG), 1 juv. (AMCC [LP 5544]). Dothio, Col de Pétchékara, Station 287, 340 m, 27.X.1986, mesic forest, A. & S. Tillier, 2 ♀♀, 13 juv. (MNHN RS 8537). Farino, Louis Barbou forest exploitation, 7.X.2004, C. Mille, S. Cazerès & T. Nuques (I.A.C. Pocqueureux), L. Monod, 383 m, degraded humid forest, near dry creek, under stones, 3 ♂♂, 4 ♀♀ (MHNG), 1 juv. (AMCC [LP 5547]); 477 m, degraded humid forest, under stones, 2 ♂♂, 3 ♀♀ (MHNG), 1 juv.

(AMCC [LP 5548]). S of Grand Lac, Station 235, 280 m, 26.XI.84, mesic forest on peridotites, A. & S. Tillier & P. Bouchet, 1 ♂, 1 juv. (MNHN RS 8537). Koya Boa Forest (Poindimié), NE central coast, 16/22.X.1983 / Saint Louis (Noumea), 16.XI.1979, on the banks of a creek, A. Renévier, 3 ♂♂, 17 ♀♀, 2 juv. (AMNH [AH 4622–4643]). Ile des Pins, near Grotte de la 3ème, 19.III.1993, rainforest, M. S. Harvey, N. I. Platnick & R. J. Raven, 1 ♂, 1 juv. (WAM 98/1887–8). Mt Arago, P. D. Montague, 4 ♀♀ (NHML 1927.II.1.2–5). Mt Humboldt, near mine, 505 m, 4.X.2004, degraded primary forest, vine thicket, in between stones in a scree covered by leaves litter and humus, and under larger stones, L. Monod, 3 ♂♂, 2 ♀♀ (MHNG), 1 juv. (AMCC [LP 5546]). Mt Koghis, 500 m, 2–3.XI.2002, rainforest, night collecting, Burwell, Monteith & Wright (11088), 1 ♀ (QM); 440 m, 26.IX.2004, rainforest, under rocks, D. Gaillard & L. Monod, 3 ♂♂, 3 ♀♀ (MHNG), 1 juv. (AMCC [LP 5545]). Road Nouméa–Rivière Bleue Forest Reserve, 177 m, 17.IX.2004, vine thicket, in rock crevices, D. Gaillard & L. Monod, 1 ♀ (AMCC [LP 5542]). Plaine des Lacs, 23.II.1914, forest, under bark, D. Montague, 1 ♂, 1 ♀ (NHML 1924.II.1.6–7). Rivière Blanche, Parc Cagous, Station 256, 160/170 m, 1.IX.1986, mesic forest, A. & S. Tillier, 1 ♂, 1 ♀, 2 juv. (MNHN RS 8537). Rivière Bleue Forest Reserve, 240 m, 9.III.1993, rainforest, M. S. Harvey, N. I. Platnick & R. J. Raven, 1 ♂, 1 ♀ (WAM 98/1885–6); Kaori geant, 11–12.XI.2000, P. Bouchard, C. Burwell & G. Monteith (9957), 1 ♂, 2 juv. (QM-S 39696); trail between Pont Pérignon and Kaori geant, 116–169 m, 18.IX.2004, rainforest, under stones and in rock crevices, D. Gaillard & L. Monod, 3 ♂♂, 3 ♀♀ (MHNG), 1 juv. (AMCC [LP 5543]); Pic du Grand Kaori, 250 m, 16–18.XI.2002, S. Wright (11198), 1 ♂ (QM). Thi Forest Reserve, 150 m, 21.V.1984, G. Monteith & D. Cook, 1 ♀ (QM-S 23330). Touaourou, 25.XII.1960, J. P. E. Morrison (3927, gto VI), 1 ♀ (USNM 00753).

Hormurus ochyroscaptes Monod, 2013. AUSTRALIA: Queensland: Almaden, Chillagoe District, XI–XII.1925, W. D. Campbell, 1 juv. (AM KS 94922). Reedybrook, 2.VIII.1967, excavated from hole 6" deep, J. D. Brown, 1 ♂ holotype (QM-S17072), 1 ♀, 2 juv. paratypes (QM-S17072).

Hormurus penta (Lourenço and Francke, 1991). PAPUA NEW GUINEA: SE Papua New Guinea, 10.X.1914, 1 ♂ (QM-S 23254). Samarai, 5.VII.1937, S. Bemrose, 1 ♂ (WAM 37-2542). SOLOMON ISLANDS: Guadalcanal: Chocho, ca. Tamba, 200 m, 27.I.1999, J. Lattke 2354, 1 ♂ (AMCC [LP 1817]). Mt Austen, 20.XII.1963, P. Greenslade, Royal Society B.S.I.P. 1965, 1446, Acc. No. 2182, 1 ♂, (BMNH). San Jorge, IX.1965, Casuarina forest and fringing semb. (Royal Society Expedition 23/27), 1 juv. (BMNH). Russell Islands, XII.1944, Lt. R. B. Eads, Navy #60, 1 juv. (AMNH).

Hormurus polisorum (Volschenk, Locket and Harvey, 2001). AUSTRALIA: Christmas Island, Bishop's Cave, 120 m from light, 11.VIII.1987, N. Plumley, top of rockpile, first main chamber, 1 ♂ holotype (WAM 97/2938). 19th Hole, cave CI-19, 30.III.1998, wall, dark zone (BES 5782), S. M. Eberhard, 1 ♀ paratype (WAM 98/1624), leg (AMCC [LP 1614]);

Hormurus waigiensis (Gervais, 1843). AUSTRALIA: Queensland: Buhot Creek, Burbank, V.2003–VI.2003, riparian forest, 1 ♂, 1 ♀ (AMCC [LP 2339]). Cameron Scrub, knoll top, 11.XI.1998–13.I.1999, 90 m, vine scrub, pitfall 7557, G. B. Monteith, D. J. Cook & Thompson, 8 ♂, 1 ♀ (QM-S 73960). Carnarvon National Park, Mt Moffatt section, 13.XII.2002, pitfall trap, upper slope of steep-sided ridge, brown heavy clay, C. Eddie, R. Perry & D. Harboe, 1 ♀ (AMCC [LP 2340]). Connondale National Park, 17.III.1999, black-lighting amongst boulders, E. S. Volschenk & P. A. Aitken, 1 ♀ (AMCC [LP 1502]).

Genus *Liocheles* Sundevall, 1833

Liocheles australasiae (Fabricius, 1775). FIJI: Vanua Levu Island, 2.VII.2008, 402 m, under bark fallen logs, D. Grimaldi, 2 ♀ (AMCC [LP 8676]). Viti Levu Island, Nakobaleva Mountain Road,

10.VII.2008, 300 m, under bark, D. Grimaldi, 2 ♀, 13 juv. (AMCC [LP 8677]). INDONESIA: West Papua: Sansapor, XII.1944, A.P.O. 159, R. B. Burrows, 1 ♂, 1 ♀, 3 juv. (AMNH). MALAYSIA: Pahang: Pulau Tioman, foothills of Gunung Kajang, track from Kampung Paya to Gunung Kajang Summit, 59 m, 1.X.2001, rainforest, in crevices of boulders along the stream, L. Monod, 4 ♀ (MHNG), 1 ♀ (AMCC [LP 2183]). SELANGOR: Batu Caves area, 200 m, 19.V.2005, W. Maddison, D. Li, I. Agnarsson & J. X. Zhang, 1 ♀ (AMCC [LP 4764]). TERENGGANU: Pulau Perhentian Kecil, above Rock Garden Resthouse, 77 m, 18.IX.2001, seasonally dry tropical forest, rocky outcrop, in crevices, L. Monod, 5 ♀, (MHNG), 1 juv. (AMCC [LP 2181]). PAPUA NEW GUINEA: Central Province: Dorobisoro, J. D. Slapcinsky & F. Kraus, 1 ♀, 2 juv. (AMCC [LP 2729]). Laronu, 880 m, 25.I.2004, F. Kraus & J. D. Slapcinsky, 2 juv. (AMCC [LP 2996]). Morobe Province, Mt. Shungol, Teron's House, 15.X.2003, F. Kraus, 25 ex. (AMCC [LP 2733]). SOLOMON ISLANDS: Western Province: Tetepare Island, N of WWF research station, around creeks, 10 m, 7.XI.2004, rainforest, in rock crevices, near a creek, R. Suka & L. Monod, 9 ♀, 18 juv. (MHNG), 1 juv. (AMCC [LP 5553]). VANUATU: Tanna Island, 2 km S Ipeukeul, 25 m, 23.VIII.1979, W. C. Gagne, 1 ♂, 1 ♀ (BPBM 1979.380).

Liocheles longimanus (Werner, 1939). INDONESIA: Sumatra: Kenandam?, III.1913, Buxton, 1 ♀ (MNHN RS 3477). Kenandam?, Kanamelean?, 1913, Buxton, 2 ♂♂, 4 ♀♀, 4 juv. (MNHN RS 3471). Sumatera Barat Province: Harau Canyon, N of Payakumbuh, 750 m, 7.VI.2006, old secondary forest, P. Schwendinger, 1 ♂ (AMCC [LP 6388]). Lubuk Sikaping (Sumatra's Westkust), 450 m, 1926, E. Jacobson, 1 ♂ (NNHM). Mangani, mine near Kota Tinggi, 700 m, 21.VII.1983, E. S. Ross, 1 ♂, 1 ♀, 1 juv. (CAS). Ngalau Kamang Cave, near Bukittinggi (Central Sumatra), 20.VII.1979, J. Balazuc, 1 ♀, 1 juv. (MNHN RS 7417). Sumatera Utara Province: Montes Battak, H. Fruhstorfer, ♂ lectotype (ZFMK, alte Trockenpräparate 111), 1 ♀ paralectotype (ZFMK, alte Trockenpräparate 110).

Liocheles nigripes (Pocock, 1897). INDIA: West Bengal: Janida, Jhargram, Midnapore, 30.VIII.1965, C. L. Kau, 1 ♂ (CAS, H. L. Stahnke coll. [ASU 65-0345 #1]); 17.VIII.1965, C. L. Kau, 1 ♀ (CAS, H. L. Stahnke coll. [ASU 65-0331 #1]).

Appendix 2

Morphological character descriptions for cladistic analysis of Indo-Pacific hormurid scorpion phylogeny. Character states scored 0–3, – (inapplicable) or ? (unknown). Twenty-six uninformative characters are indicated by U. Corresponding characters from previous works abbreviated as follows (author date/number): C81 (Couzijn, 1981); G02 (Giribet et al., 2002); J94 (Jeram, 1994); L79 (Lamoral, 1979); L85 (Lourenço, 1985); P00 (Prendini, 2000); P01 (Prendini, 2001c); P03 (Prendini, 2003); PCW03 (Prendini et al., 2003); SFK05 (Soleglad et al., 2005); S&F03 (Soleglad and Fet, 2003); S&S01 (Soleglad and Sissom, 2001); S89 (Stockwell, 1989); V&P08 (Volschenk and Prendini, 2008).

Cuticle ornamentation

1 Non-granular cuticular surfaces of prosoma, mesosoma, metasoma, legs, and pedipalp, punctation: present (0); absent (1). (P00/8).

Carapace

2 Anterior furcated suture/sulci: present, distinct (0); vestigial or absent (1). (P01/9).

3 Median ocelli: present (0); absent (1) [U].

4 Median ocular tubercle, width relative to carapace width: small (ca. 1/9) (0); intermediate (ca. 1/7) (1); large (ca. 1/5) (2) [additive].

5 Lateral ocelli, number of pairs: two (0); three (1). (S89/21, 25, J94/14, P00/1 [part], G02/5, S&F03/102, P03/1, V&P08/5).

6 Lateral ocelli, development: well developed (0); extremely reduced, vestigial (1) [U].

7 Lateral ocelli, interocular distance: second ocellus adjacent to first ocellus, separated from third ocellus (0); second ocellus adjacent to third ocellus, separated from first ocellus (1); ocelli equidistant and separated from one another (2); ocelli equidistant and adjacent to one another (3); inapplicable (–).

8 Median ocular tubercle, elevation: at least slightly elevated (0); flat (1). (P00/2, P03/2, V&P08/7).

Pedipalp carinae

9 Femur, internodorsal carina: vestigial, comprising three or four large spiniform granules (0); vestigial, comprising two large spiniform granules (1); absent, without granules or comprising single spiniform granule proximally (2) [additive].

10 Femur, internomedian carina: vestigial, comprising three or four large spiniform granules (0); vestigial, comprising large spiniform granules proximally and medially (1); absent, without spiniform granules or vestigial, comprising a single spiniform granule proximally (2) [additive].

11 Femur, internomedian carinae: oriented parallel to dorsointernal and ventrointernal carinae (0); oriented diagonally across from ventrointernal carinae to dorsointernal carina (1). (PCW03/46).

12 Femur, ventroexternal carina: absent or obsolete (0); partial, only expressed proximally (1); present (2) [U, additive]. (LP01/75; PCW03/47 [part, state 1 added]).

13 Patella, prolateral process: prolateral dorsal and prolateral ventral spiniform processes equally developed and fused medially (0); prolateral dorsal spiniform process reduced, prolateral ventral spiniform process reduced to absent, processes not fused medially (1). (L85/5, P00/18, P03/14, V&P08/17 [part, state 1 added]).

14 Patella, prolateral process, development: strong (0); weak (1).

15 Patella, prolateral process, angle of proximal margin relative to longitudinal axis of patella (♂): less than 90°, usually about 45° (0); 90° or more (1).

16 Patella, prolateral process, angle of proximal margin relative to longitudinal axis of patella (♀): less than 90°, usually about 45° (0); perpendicular or nearly so (1).

17 Patella, prolateral process, prolateral dorsal and prolateral ventral spiniform processes: distinct, not forming a large spiniform granule medially (0); forming a single large spiniform granule (1).

18 Patella, dorsoexternal carina: distinct, comprising at least a low ridge or granular row (0); absent or obsolete (1). (P00/16, P03/12).

19 Patella, dorsoexternal carina: smooth or nearly so (0); co-state-granular or granular (1) [U]. (LP01/68).

20 Patella, externomedian carina: granular or costate (0); absent or obsolete (1). (PCW03/43).

21 Patella, ventroexternal carina: absent, vestigial or expressed in distal half only (0); present and distinct along most of length (may not be expressed at proximal and distal extremities) (1).

22 Chela manus, digital carina: distinct (0); absent or obsolete (1) [U]. (P00/23, PCW03/31 [part], P03/19).

23 Chela manus, ventroexternal carina: costate (0); costate-granular (1); granular or crenulate (2) [additive]. (L79/21, P01/58).

24 Chela manus, ventrointernal carina: absent or obsolete (0); present, at least as a low ridge or granular row (1).

25 Chela manus, internomedian carina: present, granular (at least sparsely) (0); absent or obsolete (1). (PCW03/35).

Pedipalp cuticle ornamentation

26 Femur, dorsal intercarinal surface, macrosculpture: entirely smooth or granular along proximal and retrolateral edges only (0); entirely granular except distally (1).

27 Femur, ventral intercarinal surface, macrosculpture: entirely smooth or granular at retrolateral edge only (0); granular proximally, smooth distally or at distal extremity only (1).

28 Patella, dorsal intercarinal surface, macrosculpture: entirely smooth or weakly granular along prolateral and proximal edges only (0); entirely granular, or at least comprising a reticulated network of granules (1). (P01/66, PCW03/40).

29 Patella, ventral intercarinal surface, macrosculpture: entirely smooth (0); entirely granular, or at least comprising a reticulated network of granules (1).

30 Patella, retrolateral dorsal intercarinal surface, macrosculpture: entirely smooth (0); at least sparsely granular (1). (L79/32, C81/37, P01/67, PCW03/40 [split into characters 30 and 31]).

31 Patella, retrolateral ventral intercarinal surface, macrosculpture: entirely smooth (0); at least sparsely granular (1). (L79/32, C81/37, P01/67, PCW03/40 [split into characters 30 and 31]).

32 Chela, dorsal intercarinal surface, macrosculpture: entirely smooth (0); granular along prolateral and retrolateral edges only, smooth medially (1); entirely granular (2) [additive].

33 Chela, dorsal intercarinal surface, macrosculpture: granulation vestigial, comprising at most low granules (0); distinct spiniform granules (1); network of ridges and dimples (reticulation) (2) [additive]. (L17, 18, C81/61, P01/51, 52, PCW03/29, 30 [added states 0 and 1]).

34 Chela, ventral intercarinal surface, macrosculpture: entirely smooth (0); granular along prolateral and retrolateral edges only, smooth medially (1); entirely granular (2) [additive].

35 Chela, retrolateral intercarinal surface, macrosculpture: entirely granular (0); entirely smooth or with only a few scattered granules (1). (P01/55, 56, PCW03/33, 34).

36 Chela, prolateral ventral intercarinal surface, macrosculpture: entirely smooth (0); granular at least along prolateral edge (1).

37 Chela, fixed finger, dorsal surface, circumtrichobothrial depressions, trichobothria *db*, *dsb*, and *dst*: indistinct, adjacent surfaces smooth (0); distinct, adjacent surfaces granular (at least proximally) (1).

38 Chela, fixed finger, dorsal surface, circumtrichobothrial depressions, trichobothria *dst*, *dsb*, and *db*: a single confluent depression around all three trichobothria (0); three separate depressions, one around each trichobothrium (1).

Pedipalp chela fingers

39 Chela, movable finger, dentition, median denticle row with several larger denticles: present (0); absent (1). (L85).

40 Chela, fixed and movable fingers, denticle row: even distally, without enlarged granules (0); uneven, with additional enlarged granules (lobes) distally (1). (P01/43).

41 Chela, movable finger, basal lobe and corresponding notch in fixed finger (♂): absent or at most comprising two or three small spiniform granules (0); low hump comprising two or three larger conical teeth (1); pronounced (2) [additive].

42 Chela, movable finger, basal lobe, shape (♂): gently rounded dorsally and without sharp conical tooth (0); unevenly pointed dorsally, due to a sharp conical tooth (1) [U].

43 Chela, movable finger, suprabasal lobe (δ): well developed (if dentate margin markedly scalloped, first lobe disproportionately developed) (0); weakly developed, broad low hump extending from base to mid-finger (1); absent, margin straight or nearly so, at most comprising a low hump at base of finger (2) [additive]. (P00/35, P01/45, PCW03/25, P03/29, V&P08/13 [split into characters 43, 44 and 46; state 1 added]).

44 Chela, movable finger, suprabasal lobe, shape (δ): gently rounded dorsally, without sharp conical tooth (0); unevenly pointed dorsally, due to sharp conical tooth, or at least with larger tooth (1). (P00/35, P01/45, PCW03/25, P03/29, V&P08/13 [split into characters 43, 44, and 46]).

45 Chela, movable finger, suprabasal lobe, shape (δ): rounded, wider than high (0); conical, as high as or higher than wide (1).

46 Chela, fixed finger, suprabasal notch (δ): distinct, deep (0); distinct, shallow (1); absent (2) [additive]. (P00/35, P01/45, PCW03/25, P03/29, V&P08/13 [split into characters 43, 44 and 46; state 1 added]).

47 Chela, movable finger, suprabasal lobe, alignment relative to fixed finger retrolateral surface when fingers closed (δ): aligned, not overlapping retrolateral surface (0); overlapping retrolateral surface, distal to notch (1) [U].

48 Chela, fixed and movable fingers, suprabasal notch and lobe connectivity when fingers closed (δ): contiguous or at most with a small gap, distal to lobe (0); discontinuous, with distinct gap, proximal to lobe (1); discontinuous, with distinct gap, distal and dorsal to lobe (2).

49 Chela, movable finger, basal lobe and corresponding notch in fixed finger (δ): absent (0); present (1). (P00/38 [split into characters 49 and 50]).

50 Chela, movable finger, basal lobe, shape (δ): gently rounded dorsally and without sharp conical tooth (0); unevenly pointed dorsally, due to a sharp conical tooth (1) [U]. (P00/38 [split into characters 49 and 50]).

51 Chela, movable finger, suprabasal lobe (δ): well developed, situated almost midway along finger (0); weakly developed, long low hump in proximal half of finger (1); absent or at most weakly developed, situated close to base of finger (2) [additive]. (P00/37 [split into characters 51 and 52; state 1 added]).

52 Chela, fixed finger, suprabasal notch (δ): deep (0); shallow (1); absent (2) [additive]. (P00/37 [split into characters 51 and 52; state 1 added]).

53 Chela, fixed finger, small basal process extending from base of fixed finger onto distal part of retrolateral surface of manus, partially covering membrane between manus and movable finger (δ): present (0); absent (1) [U].

54 Chela, fixed finger, basal lobe (δ): absent or weakly developed (0); present and pronounced (1). (P00/36).

55 Chela, fixed finger, basal lobe, shape (δ): low, reduced (0); conical, pronounced (1).

56 Chela, fixed finger, basal lobe, with three or four conical teeth (δ): absent (0); present (1) [U].

57 Chela, fixed finger, basal lobe (δ): absent (0); present, at least weakly developed (1).

Pedipalp trichobothria

58 Patella, dorsal surface, d_2 position: distal to patellar process (0); in proximal half of segment (aligned with patellar process) (1).

59 Patella, retrolateral surface, *esb* series, number of trichobothria: two (no accessory) (0); three (one accessory, between *esb* and *em* series) (1); three (one accessory, between *eb* and *esb* series) (1) [U]. (L80/17, S89/60–68, P00/45, S&S01/51, 54–56, 59–65, S&F03/30, 36 [split into several characters]).

60 Patella, retrolateral surface, *em-esb* series, arrangement: *esb*_{1–2} separated from *em*_{1–2} (0); *esb*_{1–2} adjacent to *em*_{1–2} or *esb*₂ separated from *em*_{1–2}/*esb*₁ (1).

61 Patella, retrolateral surface, *eb* series, arrangement: *eb*₁ separated from *eb*_{2–5} or *eb*₁/*eb*_{4–5} separated from *eb*_{2–3} (0); *eb*₁ and *eb*₃ separated from each other and from *eb*₂/*eb*_{4–5} (1) [U].

62 Patella, ventral surface, *v* series, number of trichobothria: three (no accessory) (0); five (two accessory) (1) [U]. (L80/1, L80/17 [part], S89/52, 56–59, P00/42, 43, S&S01/52, 53, S&F03/35, P03/34, PCW03/55, V&P08/30).

63 Chela manus, dorsal surface, *Dt* position: proximal half of manus (0); distal half of manus (1); proximal on fixed finger (2) [additive]. (S89/81, S89/83–85, P00/52, S&F03/19, P03/43, V&P08/24).

64 Chela manus, dorsal surface, *Dt* position: at or slightly proximal to midsegment (0); in proximal third (1).

65 Chela manus, ventral surface, *V* series, number of trichobothria: four (0); five (three distal, two proximal) (1) [U]. (P00/49, LP01/80, PCW03/51, P03/40, V&P08/26).

66 Chela manus, ventral surface, *V*₃ position: close to *V*₄, in proximal part of manus (0); separated from *V*₄ ca. 1/3 length of manus to midsegment (1). (C81/52, P01/81; PCW03/52).

67 Chela manus, retrolateral surface, *Esb* position: proximal to *Eb* series (0); proximal, aligned with *Eb* series (1); distal to *Eb* series, midway between *Eb* series and *Est* (2); distal to *Eb* series, close, and sometimes slightly distal to *Est* (3) [additive].

68 Chela manus, retrolateral surface, *Eb*₃ position: close to *Eb*_{1–2} (0); distal to *Eb*_{1–2} (1) [U]. (S89/88, P00/54).

69 Chela manus, retrolateral surface, *Est* position: distal (0); at or near midsegment (1). (S89/86, P00/55, P03/45).

70 Chela, fixed finger, *db* position: dorsal surface (0); prolateral surface (1). (P00/59, P03/49, V&P08/21).

Legs

71 Telotarsi, pro- and retrolateral rows of macrosetae (excluding distal pair), type: stout spiniform (0); slender spiniform (1); sparse secondarily setiform (2); dense secondarily setiform (3) [additive, U]. (L80/9, S89/93, 94, 97, P00/68, 70, S&S01/83, 84, 88, 89, S&F03/57, 58, P03/58, V&P08/32).

72 Telotarsi I–IV, distal macrosetae of pro- and retrolateral rows, type: spiniform (0); setiform (1) [U].

73 Telotarsi I–IV, distal setiform macrosetae of pro- and retrolateral rows, number of pairs: one (0); two (1).

74 Telotarsi, well developed ventromedian row of spinules: present (0); absent or vestigial (1). (L80/9, S89/97[part], P00/68, P03/56).

75 Telotarsi, basal spinules: present (at least one, usually a short row) (0); absent (1).

76 Telotarsi, terminal ventromedian spinules: present, single median spinule (0); present, pair of submedian spinules (1); present, bundle of several spinules (2); absent (3).

Genital operculum

77 Genital opercular sclerites, median suture (δ): sclerites completely fused, suture absent (0); sclerites partly fused, suture present (1). (L80/12 [part], S89/105, S89/107, P00/80 [split into characters 77 and 78]).

78 Genital operculum, posterior notch (δ): absent (0); present, at least weakly developed (1). (L80/12 [part], S89/105, S89/107, P00/80 [split into characters 77 and 78]).

79 Genital operculum, shape (δ): subpentagonal to pentagonal (0); oval to semi-oval (1). (L85/11).

80 Genital operculum, shape (♀): as wide as or wider than long (0); longer than wide (1).

Pectines

81 Pecten length, expressed relative to length of leg IV coxa (♂): long, distal edge reaching beyond distal edge of coxa (0); moderate, distal edge reaching to, but not beyond, distal edge of coxa (1); short, distal edge not reaching to distal edge of coxa (2) [additive]. (PCW03/60).

82 Pecten length, expressed relative to length of leg IV coxa (♀): long, distal edge reaching beyond distal edge of coxa (0); moderate, distal edge reaching to, but not beyond, distal edge of coxa (1); short, distal edge not reaching to distal edge of coxa (2) [U, additive].

83 Pectines, number of marginal lamellae: three (0); two (1).

84 Pectinal teeth, shape and distribution of peg sensillae on ventral surface (♂): short, sensillae covering distal portion of surface only (0); long, sensillae covering entire surface (1). (L85/8, PCW03/63).

85 Pectinal teeth, shape and distribution of peg sensillae on ventral surface (♀): short, sensillae covering distal portion of surface only (0); long, sensillae covering entire surface (1) [U].

Mesosomal tergites

86 Tergites I–VII, pretergites, posterior margin, macrosculpture (♂): smooth (0); crenulate or with small spiniform granules (1).

87 Tergites I–VI, lateral transverse sulcus: absent or vestigial (extremely shallow) (0); present (1).

Stigmata

88 Stigma (spiracle), shape: slit-like (straight) (0); crescentic (distinctly curved on one side only) (1); round or oval (2). (L80/20 [part], S&F03/101 [part, state 1 added]).

89 Stigma (spiracle), length: short, less than third of sternite width (0); long, at least third of sternite width (1).

Metasoma

90 Segments I–IV, lateral compression: present, height greater than length (0); absent, height similar to or slightly greater than length (1).

91 Anal arch, anterior carina: crenulate, comprising at least several reduced teeth (0); comprising several large conical teeth (1). (PCW03/87 [two new states]).

92 Segments I–IV, median furrow: shallow, weak to absent or visible on segments I–III only (0); deep, distinct on at least segments I–IV, sometimes on V (1).

93 Segment I, dorsosubmedian carinae, posterior spiniform granules: weak to absent, not noticeably larger than preceding granules (0); moderate to strong, distinctly larger than preceding granules (1) [U]. (PCW03/78 [split into characters 93, 95–97]).

94 Segment I, dorsomedian posterior spiniform granules: small to absent, not noticeably larger than preceding granules (0); present, strongly developed (1) [U].

95 Segment II, dorsosubmedian carinae, posterior spiniform granules: small to absent, not noticeably larger than preceding granules (0); moderate to pronounced, distinctly larger than preceding granules (1). (PCW03/78 [split into characters 93, 95–97]).

96 Segment III, dorsosubmedian carinae, posterior spiniform granules: small to absent, not noticeably larger than preceding granules (0); moderate to pronounced, distinctly larger than preceding granules (1). (PCW03/78 [split into characters 93, 95–97]).

97 Segment IV, dorsosubmedian carinae, posterior spiniform granules: small to absent, not noticeably larger than preceding granules (0); moderate to pronounced, distinctly larger than preceding granules (1). (PCW03/78 [split into characters 93, 95–97]).

98 Segment I, ventral surface, posterior spiniform granules: absent (0); one or two pairs, well developed (1).

99 Segment I, ventrosubmedian carinae, subposterior spiniform granules: small to absent (0); one or two pairs, moderate to pronounced (1).

100 Segment I, ventrosubmedian carinae, medial granules: small to absent (0); 1–3 pairs, pronounced (1).

101 Segment II, ventrolateral carinae, posterior spiniform granules: absent (0); pronounced (1). (P00/102 [split into characters 101–105]).

102 Segment II, ventrolateral carinae, subposterior granules: absent (0); small (1). (P00/102 [split into characters 101–105]).

103 Segment II, ventrosubmedian carinae, posterior spiniform granules: absent (0); 1–3 pairs, pronounced (1). (P00/102 [split into characters, 101–105]).

104 Segment II, ventrosubmedian carinae, subposterior spiniform granules: absent (0); 1–3 pairs, small (1); 1 pair, pronounced (2) [additive]. (P00/102 [split into characters 101–105]).

105 Segment II, ventrosubmedian carinae, medial spiniform granules: absent (0); one or two pairs, small (1); 1–3 pairs, pronounced (2) [additive]. (P00/102 [split into characters 101–105]).

106 Segment III, ventrosubmedian carinae, subposterior spiniform granules: absent (0); one pair, pronounced (1).

107 Segment III, ventrosubmedian carinae, medial spiniform granules: absent (0); one pair, small (1) [U].

108 Segment V, dorsolateral carinae: present, distinct (0); absent or obsolete (1). (PCW03/77, V&P08/40).

109 Segment V, ventromedian carina: present, distinct (0); absent or obsolete (1).

110 Segment V, ventromedian carina: single (0); double (1) [U]. (L79/68; P01/132).

111 Segment V, ventromedian carina, distal portion: straight (0); bifurcating (1). (P00/99, P03/81, PCW03/86, SFK05/81).

112 Segment V, ventral surface, smooth, shiny depression in posterior half between ventrolateral carinae: absent (0); present (1).

113 Segment V, ventrolateral carinae: present, distinct (0); absent or obsolete (1) [U].

114 Segment V, ventrolateral carinae, posterior half: at least comprising small spiniform granules (0); smooth, rarely with one pair of vestigial granules posteriorly (1). (L79/52, PCW03/84).

115 Segment V, ventrolateral carinae, posterior half, spiniform granules: strong conical tooth-like granules (0); medium spiniform granules more pronounced than granules in anterior half (1); small spiniform granules, not noticeably larger than granules in anterior half (2) [additive]. (C81/113, PCW03/85).

Telson

116 Telson, length compared to metasomal segment V, length: less than (0); similar to or slightly greater than (1) [U].

117 Telson, vesicle, surface macrosculpture: two or more longitudinal rows of granules on all or part of ventral surface only (0); smooth, without granules (1) [U]. (P00/111 [modified], P03/91, PCW03/89, V&P08/53).

Hemispermaphore

118 Distal lamina, shape: straight or nearly so (0); at least slightly curved (1). (L85/3).

119 Distal lamina, ental edge, distal crest: present (0); absent (1). (L85/2, P00/86).

120 Distal lamina, distal and basal parts, relative lengths: distal part distinctly longer than basal part (0); distal part similar to or slightly longer than basal part (1).

121 Laminar hook, position on distal lamina: proximal third of distal lamina (0); subdistal, approximately midway or slightly less than midway along lamina (1); midway to distal third of lamina (2) [additive]. (P00/89 [state 1 added]).

122 Distal lamina, ental edge, basal extrusion: present (0); absent (1).

123 Transverse ridge: present and distinct (0); weak or absent (1).

124 Transverse ridge, fusion point with ental edge, relative to base of laminar hook: fusion proximal to base of hook (0); fusion with base of hook (1); fusion distal to base of hook (2) [additive].

125 Transverse ridge, position relative to laminar hook: ridge markedly proximal to base of hook (0); ridge slightly proximal to base of hook (1); ridge approximately aligned with base of hook (2) [additive].

126 Capsule, lamella, shape: narrow, elongated and pointed, apex narrower than base, folded longitudinally on both sides, forming narrow groove (0); broad, only folded proximally, forming wide groove, and unfolded into broad lobe distally (1); broad, apex not markedly narrower than base, folded longitudinally on both sides forming groove (2); broad basally, forming wide groove, ental edge folded distally, tip much narrower than base (3); narrow, only folded proximally and unfolded to flattened distal extremity, with apex and base similar in width (4).

127 Capsule, lamella, longitudinal carina on dorsal surface: present (0); absent to weak (1).

128 Capsule, lamella, accessory hook on distal part of dorsal surface, oriented toward basal part: present (0); absent (simple lamella) (1).

129 Capsule, accessory lobe on basal part of ectal surface of lamella: present (0); absent (simple lamella) (1).

130 Capsule, apex of lamella, position relative to laminar hook: proximal to base of hook (0); aligned with base of hook (1); aligned with apex of hook (2) [additive].

131 Capsule, apex of lamella, position relative to apex of distal lobe: proximal to or aligned with apex of distal lobe (0); distal to apex of distal lobe (1).

132 Capsule, distal lobe: well developed, finger-like projection (0); moderately developed hump (1); absent or weakly developed hump (2).

133 Capsule, distal lobe, shape: hook-like (0); dome-shaped (1).

134 Capsule, distal lobe, accessory hook on ental surface: absent (0); present (1).

135 Capsule, basal lobe: well developed, spoon-shaped, merging with ental accessory lobe (0); weak to absent (1).

136 Capsule, ectal edge of basal lobe, angle formed with lamella: 90° (0); 135–150° (1).

137 Capsule, ental edge of basal lobe, angle formed with lamella: 90° (0); in same plane as lamella (1).

138 Capsule, ental edge of basal lobe, accessory fold toward ectal part: present (0); absent (1).

139 Capsule, ectal edge of basal lobe, accessory distal fold, forming a median groove: present (0); absent (1) [U].

Appendix 3

Unambiguous synapomorphies optimized on preferred hypothesis of Indo-Pacific hormurid scorpion phylogeny. Node numbers refer to Fig. 5. Character numbers refer to Appendix 2. Character transformations denoted by listing ancestral and derived states separated by >.

Chiromachus ochropus: 1: 0 > 1; 9: 1 > 0; 13: 0 > 1; 23: 1 > 0; 28: 0 > 1; 39: 0 > 1; 40: 0 > 1; 41: 0 > 2; 49: 0 > 1; 54: 0 > 1; 57: 0 > 1; 58: 1 > 0; 74: 0 > 1; 87: 0 > 1; 89: 0 > 1; 93: 0 > 1; 95: 0 > 1; 96: 0 > 1; 118: 1 > 0.

Iomachus laeviceps: 2: 0 > 1.

Iomachus malabarensis: 2: 0 > 1.

Iomachus nitidus: 92: 0 > 1; 115: 1 > 2.

Iomachus politus: 2: 0 > 1; 8: 0 > 1; 20: 0 > 1; 30: 1 > 0; 31: 1 > 0; 32: 1 > 0; 35: 0 > 1; 61: 0 > 1; 64: 0 > 1; 70: 1 > 0; 108: 1 > 0; 113: 0 > 1.

Iomachus punctulatus: 7: 2 > 1; 9: 1 > 0; 39: 0 > 1.

Opisthacanthus cayaporum: 22: 0 > 1; 30: 1 > 0; 31: 1 > 0; 59: 0 > 1; 80: 0 > 1.

Opisthacanthus elatus: 7: 2 > 1; 18: 1 > 0; 23: 1 > 2; 32: 1 > 2; 37: 0 > 1; 86: 0 > 1.

Opisthacanthus lecomtei: 13: 0 > 1; 18: 1 > 0; 28: 0 > 1.

Opisthacanthus madagascariensis: 7: 2 > 1; 15: 1 > 0; 18: 1 > 0; 28: 0 > 1; 49: 0 > 1; 57: 0 > 1; 90: 1 > 0.

Palaeocheilopterus pauliani: 30: 1 > 0; 37: 0 > 1; 81: 2 > 1; 82: 2 > 1; 114: 0 > 1.

Hormiops davydovi: 2: 0 > 1; 5: 1 > 0; 8: 0 > 1; 17: 0 > 1; 18: 1 > 0; 26: 1 > 0; 31: 1 > 0; 36: 1 > 0; 39: 0 > 1; 46: 0 > 2; 55: 1 > 0; 64: 0 > 1; 90: 1 > 0; 116: 1 > 0.

Hormurus boholiensis: 27: 1 > 0; 38: 1 > 0; 60: 0 > 1; 67: 2 > 3; 96: 1 > 0; 97: 1 > 0.

Hormurus ischnoryctes: 24: 0 > 1; 67: 2 > 3; 136: 1 > 0.

Hormurus karschii: 18: 1 > 0; 80: 0 > 1; 89: 0 > 1; 121: 0 > 1; 130: 1 > 0; 134: 0 > 1.

Hormurus litodactylus: 43: 0 > 2; 46: 0 > 2; 54: 1 > 0; 64: 1 > 0; 81: 1 > 2; 83: 0 > 1.

Hormurus longimanus: 45: 0 > 1; 47: 0 > 1; 48: 0 > 1; 54: 1 > 0; 83: 0 > 1; 102: 0 > 1.

Hormurus macrochela: 134: 0 > 1.

Hormurus neocaledonicus: 4: 0 > 1; 14: 0 > 1; 41: 0 > 1; 55: 1 > 0; 106: 0 > 1.

Hormurus ochyroscapter: 17: 1 > 0; 25: 0 > 1; 60: 0 > 1; 106: 0 > 1; 107: 0 > 1.

Hormurus penta: 4: 0 > 1; 41: 0 > 1; 62: 0 > 1; 68: 0 > 1; 94: 0 > 1.

Hormurus polisorum: 3: 0 > 1; 5: 1 > 0; 6: 0 > 1; 10: 2 > 1; 32: 2 > 1; 33: 1 > 0; 34: 2 > 1; 35: 0 > 1; 48: 0 > 1; 55: 1 > 0; 84: 1 > 0; 86: 0 > 1; 99: 1 > 0; 104: 1 > 0; 120: 1 > 0.

Liocheles australasiae: 95: 0 > 1; 100: 0 > 1.

Liocheles longimanus: 17: 0 > 1; 26: 1 > 0; 31: 1 > 0; 91: 1 > 0.

Liocheles nigripes: 7: 3 > 0; 14: 0 > 1; 25: 0 > 1; 48: 0 > 2; 102: 0 > 1.

Node 2: 51: 2 > 0; 52: 2 > 0; 123: 0 > 1; 137: 0 > 1.

Node 3: 27: 0 > 1; 63: 0 > 1; 76: 3 > 1; 126: 0 > 3; 132: 0 > 2.

Node 4: 21: 1 > 0; 69: 0 > 1; 111: 1 > 0.

Node 5: 10: 0 > 1; 30: 1 > 0; 76: 3 > 0; 83: 0 > 1; 109: 0 > 1; 126: 0 > 1; 127: 0 > 1; 131: 1 > 0; 138: 1 > 0.

Node 6: 14: 0 > 1; 43: 0 > 1; 46: 0 > 1; 51: 0 > 1; 52: 0 > 1; 88: 0 > 1.

Node 7: 26: 1 > 0.

Node 8: 58: 1 > 0; 64: 1 > 0; 109: 0 > 1; 119: 0 > 1; 120: 0 > 1.
 Node 9: 1: 0 > 1; 9: 1 > 0; 33: 0 > 1; 36: 1 > 0; 49: 0 > 1; 121: 0 > 12; 125: 2 > 0; 128: 1 > 0; 129: 1 > 0.
 Node 10: 40: 0 > 1; 41: 0 > 2; 60: 0 > 1; 73: 0 > 1; 83: 0 > 1; 89: 0 > 1.
 Node 11: 23: 1 > 0; 39: 0 > 1; 44: 0 > 1; 45: 0 > 1; 48: 0 > 1; 76: 3 > 0.
 Node 12: 7: 2 > 3; 9: 1 > 2; 67: 0 > 1; 69: 0 > 1; 70: 1 > 0; 77: 0 > 1; 79: 0 > 1; 96: 0 > 1; 104: 0 > 2; 105: 0 > 2; 124: 0 > 12; 127: 0 > 1; 130: 0 > 1; 132: 0 > 1; 135: 1 > 0.
 Node 13: 30: 1 > 0; 101: 0 > 1; 115: 1 > 0.
 Node 14: 98: 0 > 1; 103: 0 > 1; 112: 0 > 1; 130: 1 > 2.

Node 15: 99: 0 > 1.
 Node 16: 28: 0 > 1; 37: 0 > 1; 67: 1 > 2; 99: 0 > 1.
 Node 17: 23: 1 > 2; 29: 0 > 1; 32: 1 > 2; 33: 0 > 1; 34: 0 > 1.
 Node 18: 10: 1 > 2; 114: 0 > 1.
 Node 19: 17: 0 > 1; 92: 0 > 1; 104: 2 > 1; 105: 2 > 1.
 Node 20: 96: 1 > 0; 97: 1 > 0.
 Node 21: 14: 0 > 1; 15: 1 > 0; 16: 1 > 0; 134: 0 > 1.
 Node 22: 10: 1 > 2; 34: 1 > 2.
 Node 23: 24: 0 > 1.
 Node 24: 105: 1 > 0.
 Node 25: 114: 0 > 1; 125: 2 > 1.

Appendix 4

Length (steps), Fit (F_i), adjusted homoplasy (Hom), consistency index (CI), and retention index (RI) of informative characters (Char) on preferred hypothesis of Indo-Pacific hormurid scorpion phylogeny (Fig. 5).

Char	Steps	Hom	Fi	CI	RI	Char	Steps	Hom	Fi	CI	RI
1	1	0.09	0.91	50	75	51	1	0.09	0.91	67	89
2	3	0.23	0.77	25	1	52	1	0.09	0.91	67	89
4	3	0.23	0.77	25	25	54	5	0.33	0.67	17	55
5	1	0.09	0.91	50	1	55	3	0.23	0.77	25	25
7	3	0.23	0.77	50	70	57	1	0.09	0.91	50	1
8	4	0.29	0.71	20	33	58	1	0.09	0.91	50	83
9	2	0.17	0.83	50	88	60	2	0.17	0.83	33	33
10	5	0.4	0.6	29	50	63	0	0	1	100	100
11	2	0.17	0.83	33	33	64	5	0.33	0.67	17	55
13	2	0.17	0.83	33	1	66	2	0.17	0.83	33	82
14	3	0.23	0.77	25	50	67	3	0.23	0.77	50	88
15	4	0.29	0.71	20	20	69	2	0.17	0.83	33	67
16	0	0	1	100	100	70	1	0.09	0.91	50	90
17	4	0.29	0.71	20	56	71	0	0	1	100	100
18	5	0.33	0.67	17	1	73	0	0	1	100	100
20	2	0.17	0.83	33	1	74	2	0.17	0.83	33	75
21	3	0.23	0.77	25	57	75	1	0.09	0.91	50	50
23	2	0.18	0.82	50	83	76	1	0.09	0.91	75	83
24	2	0.17	0.83	33	50	77	0	0	1	100	100
25	1	0.09	0.91	50	1	78	1	0.09	0.91	50	90
26	4	0.29	0.71	20	33	79	0	0	1	100	100
27	3	0.23	0.77	25	75	80	1	0.09	0.91	50	1
28	3	0.23	0.77	25	75	81	3	0.23	0.77	25	67
29	0	0	1	100	100	83	4	0.29	0.71	20	50
30	4	0.29	0.71	20	60	84	3	0.23	0.77	25	70
31	3	0.23	0.77	25	1	86	1	0.09	0.91	50	1
32	2	0.17	0.83	50	78	87	3	0.23	0.77	25	67
33	2	0.17	0.83	50	82	88	2	0.17	0.83	33	67
34	2	0.17	0.83	50	83	89	3	0.23	0.77	25	25
35	1	0.09	0.91	50	1	90	1	0.09	0.91	50	1
36	1	0.09	0.91	50	75	91	4	0.29	0.71	20	20
37	2	0.17	0.83	33	83	92	2	0.17	0.83	33	82
38	4	0.29	0.71	20	1	95	1	0.09	0.91	50	1
39	3	0.23	0.77	25	25	96	3	0.23	0.77	25	57
40	1	0.09	0.91	50	50	97	4	0.29	0.71	20	50
41	4	0.32	0.68	33	33	98	0	0	1	100	100
43	1	0.09	0.91	67	67	99	3	0.23	0.77	25	73
44	0	0	1	100	100	100	2	0.17	0.83	33	33
45	2	0.17	0.83	33	50	101	0	0	1	100	100
46	3	0.26	0.74	40	40	102	1	0.09	0.91	50	1
48	3	0.23	0.77	40	25	103	0	0	1	100	100
49	2	0.17	0.83	33	60	104	2	0.18	0.82	50	89

Appendix 4
(Continued)

Char	Steps	Hom	Fi	CI	RI	Char	Steps	Hom	Fi	CI	RI
105	3	0.26	0.74	40	82	125	1	0.09	0.91	67	88
106	1	0.09	0.91	50	1	126	0	0	1	100	100
108	1	0.09	0.91	50	1	127	1	0.09	0.91	50	86
109	1	0.09	0.91	50	67	128	0	0	1	100	100
111	1	0.09	0.91	50	1	129	0	0	1	100	100
112	0	0	1	100	100	130	1	0.09	0.91	67	92
114	2	0.17	0.83	33	50	131	0	0	1	100	100
115	1	0.09	0.91	67	75	132	0	0	1	100	100
118	4	0.29	0.71	20	20	133	1	0.09	0.91	50	86
119	0	0	1	100	100	134	2	0.17	0.83	33	33
120	1	0.09	0.91	50	86	135	0	0	1	100	100
121	2	0.18	0.82	50	67	136	1	0.09	0.91	50	75
122	1	0.09	0.91	50	75	137	0	0	1	100	100
123	0	0	1	100	100	138	0	0	1	100	100
124	1	0.09	0.91	67	89						

Appendix 5

Distribution of ancestral areas and event sequence retrieved in ancestral area reconstruction optimized on preferred hypothesis of Indo-Pacific horned scorpion phylogeny. Geographical areas considered in analysis (Figs 3 and 6): Africa (A); Madagascar (B); Seychelles (C); India (D); Neotropics (E); Pre-Cretaceous Sundaland (F); Australasian volcanic islands (G); Islands of the northern rim of the Australian Craton (H); Australia (I); New Caledonia (J); Christmas Island (K). Events in event matrix and event route denoted as follows: dispersal (Dis); vicariance (Vic, |); *in situ* diversification (*).

Node 0: Matrix: Dis: 1; Vic: 0. Route: ABCD > ABCD^A > A|ABCD. Probability: 1.0.
Node 1: Matrix: Dis: 1; Vic: 1. Route: ABCD > AFBCD > AF|BCD. Probability: 0.3333.
Node 2: Matrix: Dis: 0; Vic: 1. Route: BCD > B|CD. Probability: 0.3333.
Node 3: Matrix: Dis: 0; Vic: 0. Route: B > B^B > B|B. Probability: 1.0.
Node 4: Matrix: Dis: 0; Vic: 1. Route: CD > C|D. Probability: 1.0.
Node 5: Matrix: Dis: 0; Vic: 0. Route: D > D^D > D|D. Probability: 1.0.
Node 6: Matrix: Dis: 0; Vic: 0. Route: D > D^D > D|D. Probability: 1.0.
Node 7: Matrix: Dis: 0; Vic: 0. Route: D > D^D > D|D. Probability: 1.0.
Node 8: Matrix: Dis: 2; Vic: 1. Route: AF > FGAE > FG|AE. Probability: 1.0.
Node 9: Matrix: Dis: 0; Vic: 1. Route: AE > E|A. Probability: 1.0.

Node 10: Matrix: Dis: 0; Vic: 0. Route: E > E^E > E|E. Probability: 1.0.
Node 11: Matrix: Dis: 0; Vic: 0. Route: A > A^A > A|A. Probability: 1.0.
Node 12: Matrix: Dis: 0; Vic: 1. Route: FG > G|F. Probability: 1.0.
Node 13: Matrix: Dis: 1; Vic: 0. Route: F > F^F > FD^F > F|DF. Probability: 1.0.
Node 14: Matrix: Dis: 0; Vic: 1. Route: DF > D|F. Probability: 1.0.
Node 15: Matrix: Dis: 5; Vic: 0. Route: F > F^F > FGHIJK^F > FGHIJK|F. Probability: 1.0.
Node 16: Matrix: Dis: 2; Vic: 0. Route: G > G^G > GIJ^G > G|GIJ. Probability: 0.5.
Node 17: Matrix: Dis: 0; Vic: 1. Route: GIJ > I|GJ. Probability: 0.5.
Node 18: Matrix: Dis: 0; Vic: 1. Route: GJ > G|J. Probability: 1.0.
Node 19: Matrix: Dis: 0; Vic: 0. Route: I > I^I > I|I. Probability: 1.0.
Node 20: Matrix: Dis: 0; Vic: 0. Route: I > I^I > I|I. Probability: 1.0.
Node 21: Matrix: Dis: 0; Vic: 0. Route: I > I^I > I|I. Probability: 1.0.
Node 22: Matrix: Dis: 0; Vic: 0. Route: I > I^I > I|I. Probability: 1.0.
Node 23: Matrix: Dis: 2; Vic: 0. Route: I > I^I > IHK^I > I|HIK. Probability: 0.3333.
Node 24: Matrix: Dis: 0; Vic: 1. Route: I HIK > I|HK. Probability: 0.3333.
Node 25: Matrix: Dis: 0; Vic: 1. Route: HK > H|K. Probability: 1.0.
Global Matrix: Global Dis: 14; Global Vic: 11.