TWO NEW SPECIES OF *HADOGENES* (SCORPIONES, ISCHNURIDAE) FROM SOUTH AFRICA, WITH A REDESCRIPTION OF *HADOGENES BICOLOR* AND A DISCUSSION ON THE PHYLOGENETIC POSITION OF *HADOGENES*

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ABSTRACT. The taxonomic status of the endemic South African flat rock scorpion, *Hadogenes bicolor* Purcell 1899, is reassessed, based on a study of the types and a large series of newly-collected specimens. Specimens identified as *H. bicolor* by previous authors can be separated into at least three species on the basis of morphology, each of which occupies a discrete, allopatric distributional range. In light of this new evidence, *H. bicolor* is redescribed and two new species, *Hadogenes longimanus* and *Hadogenes newlandsi*, are described. A key is provided for the identification of the three allopatric species, and their ecology and conservation status are discussed. The phylogenetic position of *Hadogenes* is discussed in light of a recent cladistic analysis, and the monotypic family Hadogenidae Lourenço 2000 is synonymized with the family Ischnuridae Simon 1879.

Keywords: Scorpiones, Ischnuridae, *Hadogenes*

Scorpions of the genus *Hadogenes* Kraepelin 1894, commonly known as flat rock scorpions, are endemic to the Afrotropical region, where they are distributed from South Africa to Tanzania. Comprising 15 species, *Hadogenes* is the second most speciose genus in the family Ischnuridae Simon 1879, after *Opisthacanthus* Peters 1861.

With few exceptions, the distributional ranges of *Hadogenes* species are allopatric or parapatric (Newlands 1980; Prendini 1995), a tendency that appears to be related to the stenotopic ecological requirements of these scorpions. All of the currently recognized species are obligately lithophilous, inhabiting the narrow cracks, crevices and exfoliations of weathered rock outcrops. Ecomorphological adaptations that facilitate existence in this specialized habitat include extreme dorsoventral compression, elongation of the metasoma and pedipalps, greatly enlarged lateral ocelli relative to the median ocelli, presumably to aid in anterior light perception, and well-developed superciliary carinae to protect the median ocelli from abrasion (Newlands 1972a, b, 1978; Newlands & Prendini 1997). Species of *Hadogenes* are also characterized by stout, spiniform setae on the ventral surfaces of the

telotarsi and highly-curved telotarsal ungues, to provide a vice-like grip on rock surfaces. Such adaptations facilitate locomotion on rock but hinder locomotion across alternative substrata. Accordingly, these scorpions are restricted to regions of rugged, mountainous topography and readily subject to allopatric speciation when mountain ranges become separated through erosion.

As part of an ongoing revision of the taxonomy of *Hadogenes*, the status of the endemic South African flat rock scorpion, *Hadogenes bicolor* Purcell 1899, was reassessed. Purcell (1899: 437, 438) based his original description of *H. bicolor* on an adult female from ''twenty miles east of Pietersburg,'' although his syntype series contained ''several adult and young specimens.'' The description made no mention of the characters of the adult male *H. bicolor*. Hewitt (1918: 160, 161) subsequently described an adult male *Hadogenes* from Doornkop, near Belfast, *ca.* 200 km south of the type locality, noting ''I think [the male] is referable to the same species [*H. bicolor*].'' In his description of the male, Hewitt (1918) observed that the metasoma was unusually short for an adult male *Hadogenes* and that the lobe at the base of the movable finger

of the pedipalp was "larger, deeper and more acute" than in other species of the genus. Hewitt (1918) also listed two adult females from Woodbush (Pietersburg district), and described a "half-grown" male, in which the sides of the telson vesicle were finely granulated, from the same locality. The evidence supporting Hewitt's (1918) suggestion that the specimens from Woodbush and Doornkop were conspecific with each other, and with the syntypes of *H. bicolor*, was inconclusive. Nonetheless, this opinion was adopted by subsequent authors (Lawrence 1955; Lamoral & Reynders 1975).

Hadogenes bicolor was not reviewed until Newlands (1980) redescribed the species on the basis of newly-collected material (an adult male from Leopard's Crag and an adult female from Haffenden Heights), and again noted the large basal lobe of the movable finger and the short metasoma of the adult male as diagnostic characters. It is unclear whether Newlands (1980) actually examined the syntypes, for he listed the type specimens as "Female holotype and several nymphs housed in the Transvaal Museum (TMSA 4062) from 32 km east of Pietersburg." During the present investigation, the syntype series, deposited in the South African Museum, was found to comprise an adult male, two adult females, a subadult female, a juvenile male, and a juvenile female.

Newlands' (1980) redescription of *H. bicolor* was never published. However, Newlands & Cantrell (1985) published electrophoretic and cytogenetic data collected by Newlands (1980), as well as Newlands' (1980) key to the species of *Hadogenes*, in which the short metasoma of the adult male was yet again provided as a diagnostic character for *H. bicolor*. Following Newlands (1980), Newlands & Cantrell (1985) pointed out that the electrophoretic banding patterns of venom proteins from specimens of *H. bicolor* collected at two localities, *viz.* Haffenden Heights (Letaba district, Northern Province) and Zusterstroom (Bronkhorstspruit district, Gauteng Province), were distinctly different. Specimens from Zusterstroom displayed a protein component that was absent in specimens from Haffenden Heights, *ca.* 180 km northeast. Newlands & Cantrell (1985: 42) suggested that these differences might be indicative of a cryptic species complex (Paterson 1991), as "no morphological differences
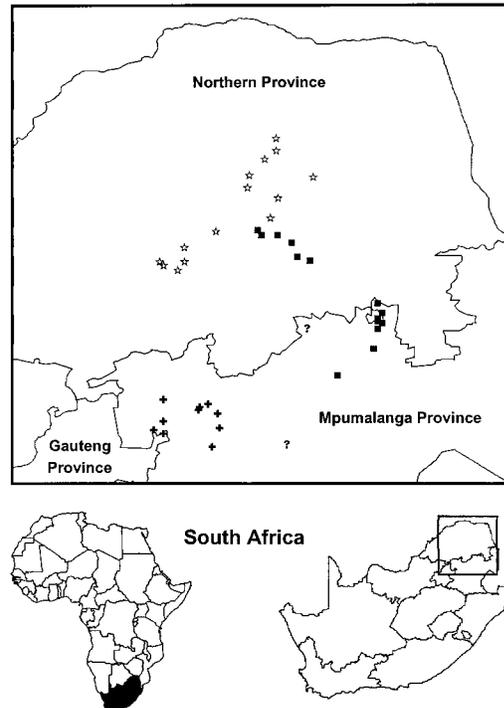
Figure 1.—Map showing the distribution of *Hadogenes bicolor* Purcell 1899 (■), *Hadogenes longimanus* new species (+), and *Hadogenes newlandsi* new species (★) in South Africa. The specimens from Doornkop and Steelpoort (?) have been provisionally identified as *H. longimanus*, but may comprise another undescribed species in this complex.

. . . could be detected" between specimens from the two localities.

In the present study, specimens from across the distributional range of *H. bicolor*, including the material examined by Hewitt and Newlands, and newly collected material, were compared with the syntypes. Since *Hadogenes* species are notoriously difficult to identify without examination of the adult male, new series of *H. bicolor*, including adults of both sexes, were collected from several localities in the same and neighboring districts as the type locality, and in the districts from which the other material, examined by Hewitt and Newlands, originated. Some of these localities are as much as 100 km north to 200 km south of the type locality of *H. bicolor*.

Examination of this new material has confirmed the suggestion of Newlands (1980) and Newlands & Cantrell (1985) that more than

Table 1.—The currently accepted species of *Hadogenes* Kraepelin 1894 (Scorpiones, Ischnuridae), with countries of distribution compiled from Prendini (1995). [1] Species of dubious validity. [2] Species complexes.

Hadogenes angolensis Lourenço 1999[1]	Angola
Hadogenes bicolor Purcell 1899	South Africa
Hadogenes gracilis Hewitt 1909	South Africa
Hadogenes granulatus Purcell 1901	Botswana, Mozambique, Zambia, Zimbabwe
Hadogenes gunningi Purcell 1899	South Africa
Hadogenes lawrencei Newlands 1972	Namibia
Hadogenes longimanus new species	South Africa
Hadogenes minor Purcell 1899	South Africa
Hadogenes newlandsi new species	South Africa
Hadogenes paucidens Pocock 1896[1]	Democratic Republic of Congo, ?Tanzania
Hadogenes phyllodes Thorell 1877[2]	Namibia, South Africa
Hadogenes taeniurus (Thorell 1877)	Angola, Namibia
Hadogenes tityrus (Simon 1888)[2]	Namibia, South Africa
Hadogenes trichiurus (Gervais 1843)[2]	South Africa
Hadogenes troglodytes (Peters 1861)	Botswana, Mozambique, South Africa, Zimbabwe
Hadogenes zuluanus Lawrence 1937	South Africa, Swaziland
Hadogenes zumpti Newlands & Cantrell 1985	?Namibia, South Africa

one species is involved. However, contrary to the view expressed by these authors, several consistent morphological differences could be identified between specimens from the localities at which samples, analyzed electrophoretically by Newlands (1980) and Newlands & Cantrell (1985), were found to differ in venom protein composition.

Specimens identified as *H. bicolor* by previous authors can be separated into at least three species on the basis of morphology, each of which occupies a discrete, allopatric distributional range (Fig. 1). In light of this new evidence, *H. bicolor* is redescribed and two new species, *Hadogenes longimanus* and *Hadogenes newlandsi*, are described. As in other closely related species of *Hadogenes*, adult female specimens of all three species are superficially similar morphologically, whereas adult male specimens differ markedly. However, adult females of all three species can also be reliably identified on the basis of several consistent diagnostic characters. These characters are summarized in a key to the identification of the three species. Recognition of the two new species raises the number of currently accepted species of *Hadogenes* to 17 (Table 1).

Lourenço's (1999, 2000) recent proposals to transfer *Hadogenes* to the Scorpionidae Latreille 1802, or provide a monotypic family Hadogenidae Lourenço 2000 are unsupported by cladistic analysis (Prendini 2000). This contribution concludes with a discussion of the phylogenetic position of *Hadogenes*, in which the Hadogenidae is synonymized with the Ischnuridae.

METHODS

Material examined, including the type specimens of *H. bicolor*, *H. longimanus* and *H. newlandsi*, is deposited in the following collections: South African Museum, Cape Town (SAMC); Transvaal Museum, Pretoria, South Africa (TMSA); Albany Museum, Grahamstown, South Africa (AMGS); Natal Museum, Pietermaritzburg, South Africa (NMSA); American Museum of Natural History, New York (AMNH); California Academy of Sciences, San Francisco (CASC). Tissue samples of the three species, stored in absolute ethanol at −20 °C, have been retained separately for DNA isolation and sequencing in the Ambrose Monell Collection for Molecular and Microbial Research at the American Museum of Natural History, New York (AMC).

Illustrations of *H. bicolor*, *H. longimanus* and *H. newlandsi* were produced using a Wild stereomicroscope and camera lucida. Measurements were made with Mitutoyo® digital calipers. Color designation follows Smithe (1974, 1975, 1981), trichobothrial notation follows Vachon (1974), and mensuration follows Stahnke (1970) and Lamoral (1979). Morphological terminology follows Couzijn

(1976) for the segmentation of legs, Hjelle (1990) and Sissom (1990) for the segmentation of pedipalps, and Stahnke (1970), Lamoral (1979), Newlands (1980), Sissom (1990) and Newlands & Prendini (1997) for remaining features.

Key to the identification of *Hadogenes bicolor* Purcell 1899, **Hadogenes longimanus** new species and **Hadogenes newlandsi** new species

1. Pedipalp chela with 5–8 trichobothria in the *i* series (Fig. 21) . . . .*Hadogenes longimanus*
   Pedipalp chela with two trichobothria in the *i* series (Figs. 10, 32). 2
2. Pedipalp chela of adult ♂ and ♀ with a pronounced lobe, distal to the notch in the fixed finger (Figs. 8, 9); metasoma of adult ♂ length *ca.* 55% of total length (Figs. 2, 3), with telson smooth and lateral surfaces of metasomal segment V sparsely granular (Fig. 33) . . . .*Hadogenes bicolor*
   Pedipalp chela of adult ♂ and ♀ without a pronounced lobe, distal to the notch in the fixed finger (Figs. 26, 30); metasoma of adult ♂ length *ca.* 60% of total length (Figs. 22, 23), with telson and lateral surfaces of metasomal segment V densely granular (Fig. 35). . . . .*Hadogenes newlandsi*

Hadogenes bicolor Purcell 1899
Figs. 1–10, 33, 36, Table 2

Hadogenes bicolor Purcell 1899: 437, 438.
Hadogenes bicolor: Lawrence 1955: 251 (part); Lamoral & Reynders 1975: 538 (part); Newlands 1980 (unpublished): 99–105 (part), figs. 48 (part), 49–53; Newlands & Cantrell 1985: 40, 42, 44 (part); Kovařík 1998: 132; Fet 2000: 387.

Types.—**SOUTH AFRICA:** *Northern Province:* Pietersburg district: Syntypes: ♂, 2♀, subadult ♀, juv ♂, juv ♀ (SAMC 4062), 20 miles east of Pietersburg [23°54′S, 29°47′E]. The ♂ is hereby designated as the lectotype of *H. bicolor* and the remaining specimens as paralectotypes.

Diagnosis.—*Hadogenes bicolor* is the sister species of *H. longimanus*. These two species are both characterized by a pronounced lobe, distal to the notch in the fixed finger of the pedipalp chela of adult ♂ and ♀, and a relatively short metasoma in the adult ♂, compared with *H. newlandsi* and other *Hadogenes* species. Accordingly, these characters are hypothesized to be synapomorphic for *H. bicolor* and *H. longimanus*.

Hadogenes bicolor can be separated from *H. longimanus* by the presence of two, rather than 5–8, trichobothria on the internal surface of the pedipalp chela. *Hadogenes bicolor* can be further distinguished from *H. newlandsi* by the smooth telson of the adult ♂, and the longer pedipalp segments of adult ♂ and ♀.

Description.—The following description is based on the lectotype ♂ (SAMC 4062), a paralectotype ♀ (SAMC 4062), the ♂ from Leopard's Crag (TMSA 18004) and ♀ from Haffenden Heights (TMSA 18005) described by Newlands (1980), and a newly collected ♂

(Figs. 2, 3) and ♀ (Figs. 4, 5) from Jongmansspruit (SAMC C4585). It is intended to complement Purcell's (1899) original description and Newlands' (1980) unpublished redescription.

Color: (SAMC C4585). Pale chelicerae, legs, and telson contrasting markedly with darker carapace, pedipalps, tergites and metasomal segments I-V. Sternites also paler than tergites and metasomal segments. Pedipalps, Buff 24 on chela manus and intercarinal surfaces of patella and femur, Sepia 119 on carinae and chela fingers; cheliceral manus, legs (except prolateral surfaces of femora), telson, sternites, pectines, and genital operculum, Straw Yellow 36; cheliceral fingers, carapace, tergites (♂) and prolateral surfaces of leg femora, Sepia 119; tergites (♀) and metasomal segments I-V, Dark Brownish-olive 129.

Carapace: Three pairs of lateral ocelli, equal in size to median ocelli (Fig. 6). Median ocular tubercle with superciliary carinae well developed, protruding above ocelli, and interocular sulcus distinct. Anterior margin of carapace with median notch well developed, such that triangular inset is situated far back and frontal lobes protrude anteriorly. Anteromedian sulcus deep, suturiform, furcating anteriorly around triangular inset. Median longitudinal suture distinct, continuous from anterior furcated sutures, through ocular tubercle to posterior furcated sutures, which converge on ocular tubercle from posterior carapace margin. Posterior furcated sutures obsolete, discontinuous. Posteromedian and posteromarginal sulci distinct, but shallow. Paired median lateral and posterolateral sulci also distinct, shallow. Carapace entirely gran-
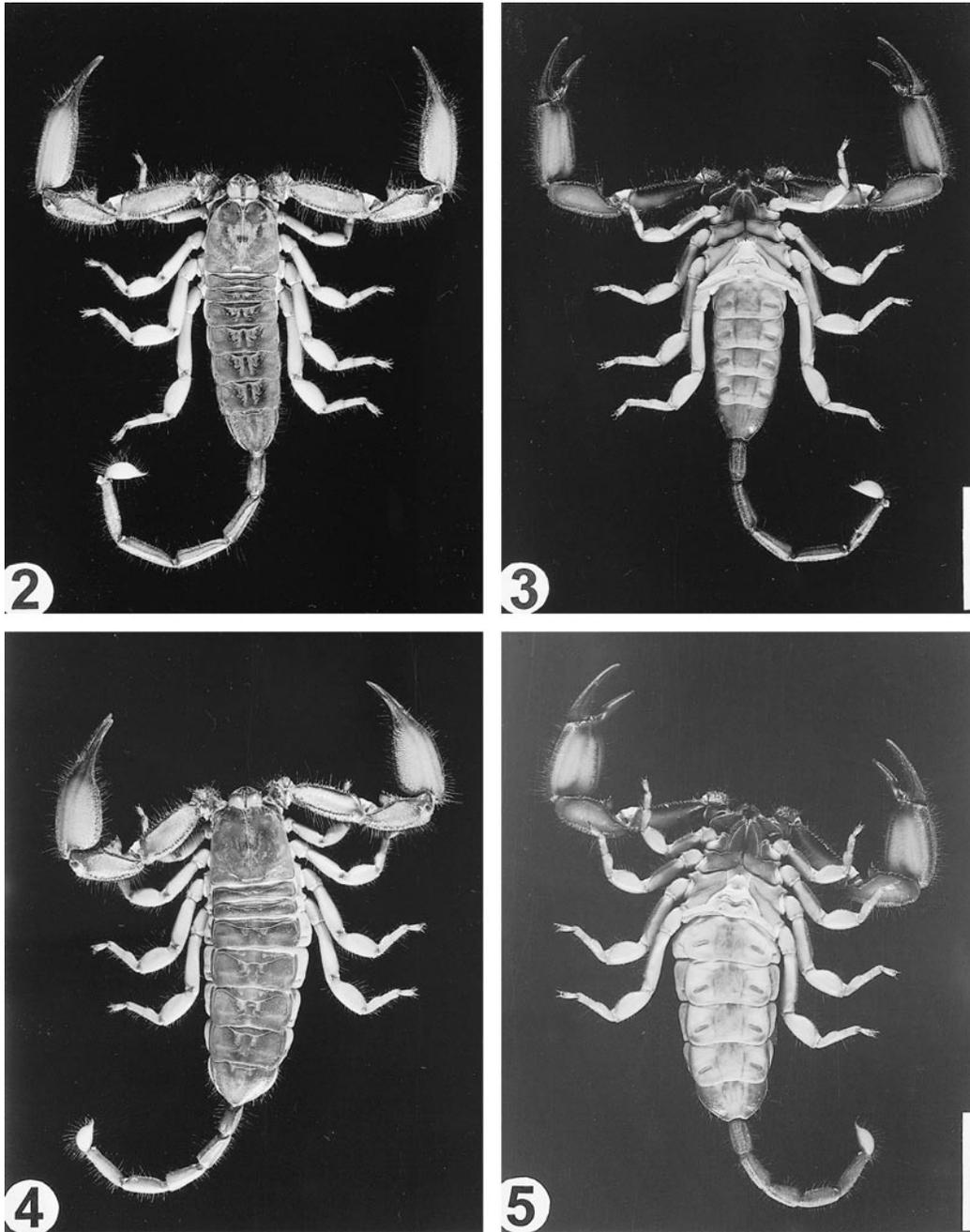
Figures 2–5.—*Hadogenes bicolor* Purcell 1899, habitus of ♂ and ♀ (SAMC C4585). 2. Dorsal aspect, ♂; 3. Ventral aspect, ♂; 4. Dorsal aspect, ♀; 5. Ventral aspect, ♀. Scale bars = 20 mm.

ular, except for surfaces of frontal lobes, median lateral, posterolateral and posteromarginal sulci, which are smooth. Granulation almost uniformly fine, becoming coarse on antero-ocular and anterolateral surfaces.

Chelicerae: Movable finger with distal internal tooth slightly smaller than distal external tooth, and apposable. Ventral aspect of fingers and manus with long, dense macrosetae.

Pedipalps: Femur pentacarinate, with four
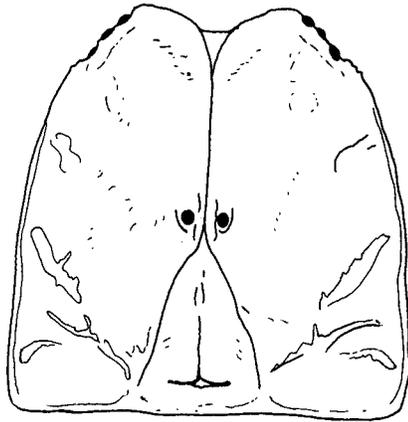
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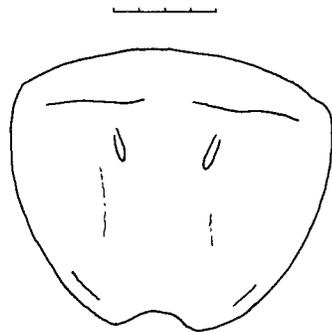
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Figures 6–7.—*Hadogenes bicolor* Purcell 1899, carapace and sternite VII of ♀ (SAMC C4585), showing carinae, depressions and sulci. 6. Carapace; 7. Sternite VII. Scale bar = 4 mm.

distinct carinae; ventroexternal carina obsolete, reduced to a few granules proximally; dorsoexternal and externomedian carinae granular, dorsointernal and ventrointernal carinae costate-granular, composed of very large heavily sclerotized granules; dorsoexternal and ventral intercarinal surfaces finely and uniformly granular; internal intercarinal surfaces smooth, except for a few scattered spiniform granules. Femur length 63% (62–64%) greater than width in ♂, 60.5% (58–63%) greater in ♀ (Table 2).

Patella with seven carinae, six of which are distinct, whereas the dorsoexternal carina is obsolete; dorsointernal and ventrointernal carinae costate to costate-granular; internomedian carina costate-granular, composed of

very large heavily sclerotized spiniform granules; externomedian and ventroexternal carinae granular; dorsoexternal and ventral intercarinal surfaces finely and uniformly granular, becoming granulo-reticulate on ventral surfaces; internal intercarinal surfaces smooth; anterior process strongly developed. Patella length 45% (44–46%) greater than width in ♂, 41% (40–42%) greater in ♀.

Chela pentacarinate, with three distinct carinae; dorsal secondary and digital carinae obsolete (Figs. 8, 9); external secondary carina strongly developed, costate to costate-granular; ventroexternal carina strongly developed, crenulate, aligned parallel to longitudinal axis of chela, with distal edge disconnected from external movable finger condyle and directed toward a point between external and internal movable finger condyles, but closer to external condyle (Fig. 10); ventromedian carina obsolete, reduced to a vestigial granule proximally; ventrointernal carina also obsolete; internomedian and dorsointernal carinae weakly developed, each comprising a series of isolated spiniform granules; dorsomedian carina strongly developed, composed of a continous double row of spiniform granules; dorsal and ventrointernal intercarinal surfaces smooth, reticulate; dorsointernal intercarinal surfaces with scattered spiniform granules, becoming finely granular on internal surface of fixed finger; external intercarinal surfaces coarsely granular. Chela with a pronounced, conical lobe on movable finger and corresponding notch in fixed finger; fixed finger additionally with a pronounced, conical lobe distal to the notch, and a smaller, rounded lobe proximally. Dentate margins of chela fingers with double row of denticles, which are fused at the lobe/notch. Chela length along ventroexternal carina 46.5% (44–49%) greater than chela width in ♂, and 36.5% (33–40%) greater in ♀; chela width 50.5% (44–57%) greater than chela height in ♂, and 52% (49–55%) greater in ♀; length of movable finger 9% (5–13%) less than length along ventroexternal carina in ♂, and 4% (1–7%) less in ♀.

Trichobothria: Neobothriotaxic major, type C (Figs. 8, 10), with the following segment totals (Table 2): femur 3 (1 *d*; 1 *i*; 1 *e*), patella 68–96 (2 *d*; 1 *i*; 27–34 *v*; 38–59 *e*) and chela 77–92 (67–82 manus; 10 fixed finger, including 2 *i*). Total number of *τ* per pedipalp, 148–191. Only femoral *τ*, *τ* in the *d* and *i* series of

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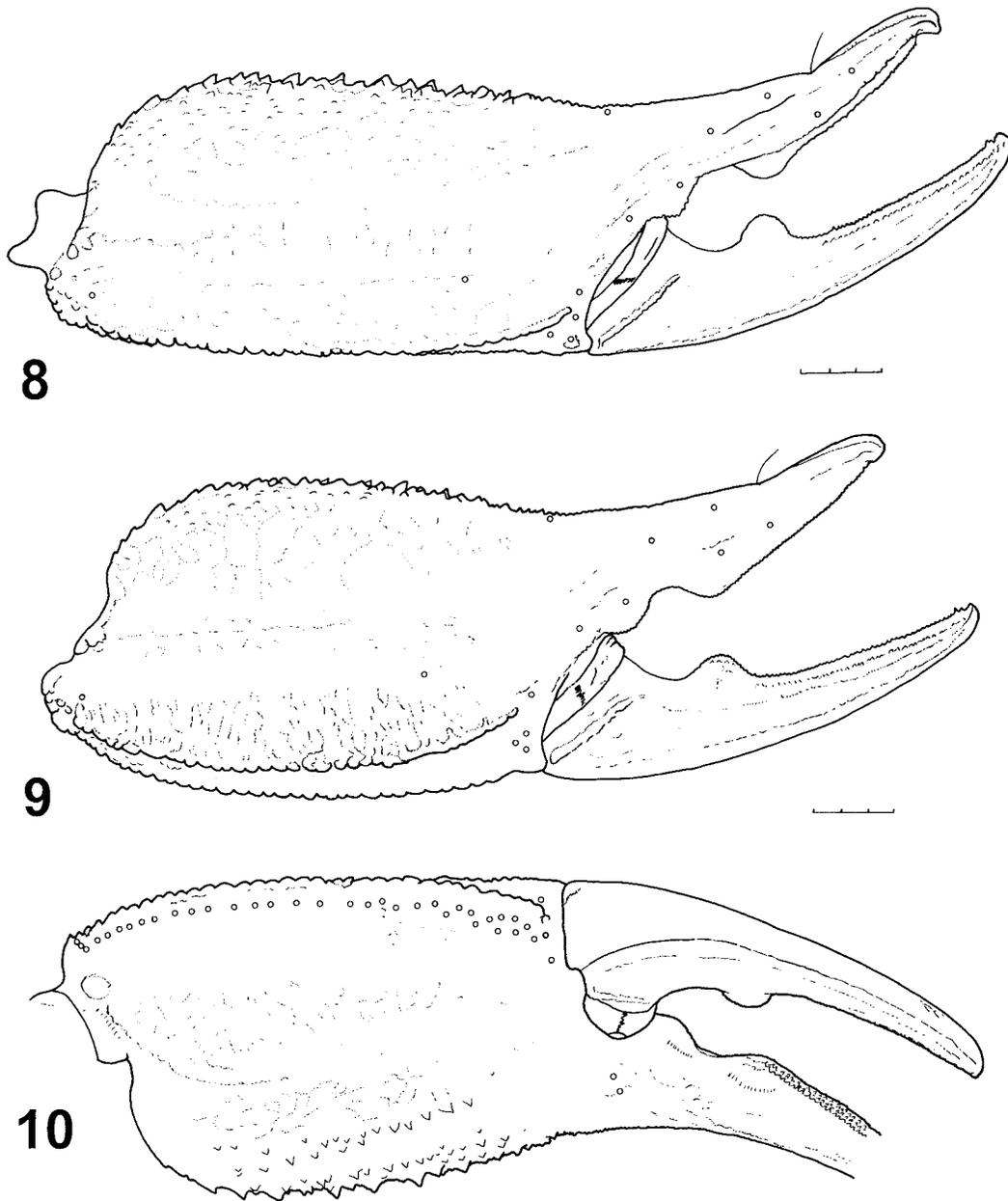
Figures 8–10.—*Hadogenes bicolor* Purcell 1899, dextral pedipalp chelae of ♂ and ♀ (SAMC C4585), showing trichobothrial distribution and shape of lobes on fixed and movable fingers. 8. Dorsal aspect, ♂; 9. Dorsal aspect, ♀; 10. Ventrointernal aspect, ♀. Scale bars = 3 mm.

the patella, and τ in the *D*, *d*, *e* and *i* series of the chela are stable in number and distribution. External and ventral τ of the chela and patella are numerically and distributionally too variable for diagnostic purposes.

Mesosoma: Tergites each with paired sub-median depressions and obsolete median carina. Pre-tergites of ♂ and ♀ smooth and shiny. Post-tergites of ♂ covered with very fine and even granulation, imparting a matte appearance to all surfaces, except median carina and submedian depressions, which are

smooth; post-tergites of ♀ smooth and shiny. Sternites smooth and shiny, each with paired longitudinal depressions internal to spiracles. Sternite VII additionally with a pair of shallow posterolateral oval depressions (more prominent in ♂) and a pair of obsolete carinae, converging distally towards a shallow notch in distal apex (Fig. 7). Sternite VII 16.5% (9–24%) wider than long in ♂, 26% (19–33%) wider than long in ♀ (Table 2).

Pectines: ♂ with mesial margin of first proximal median lamella of each pecten angular, pectinal teeth present along entire posterior margin; ♀ with mesial margin of first proximal median lamella shallowly curved, proximal fifth of posterior margin devoid of teeth. Pectinal teeth: 19–20/18–20 (♂), 16–17/15–16 (♀).

Sternum: Subpentagonal. Median longitudinal furrow shallow anteriorly, deep and narrow posteriorly.

Genital operculum: Suboval, completely divided longitudinally, with genital papillae present (♂). Subcordate, partially connected by a membrane in anterior two-thirds, with distinct distal lobes in posterior third, and with genital papillae absent (♀).

Legs: Femora each with paired granular carinae on prolateral surface. Basitarsi each with a few spiniform setae on prolateral and retrolateral margins, decreasing in number from anterior to posterior legs. Telotarsi each with two rows of three ventrosubmedian spiniform setae and a basal row of 4–6 ventromedian spinules. Telotarsal laterodistal lobes truncated; median dorsal lobes extending to ungues. Telotarsal ungues short, distinctly curved, and equal in length. Retrolateral pedal spurs absent.

Metasoma and telson: Metasomal segment I 20% (10–30%) wider than high posteriorly (Table 2). Metasomal segments I-V progressively increasing in length, and decreasing in width, with segment V 36.5% (33–40%) narrower than segment I. Metasoma slender, width percentage of length for segment I, 40% (37–43%) in ♂, 53% (50–56%) in ♀; for II, 23.5% (23–24%) in ♂, 31.5% (31–32%) in ♀; for III, 21.5% (20–21%) in ♂, 28.5% (28–29%) in ♀; for IV, 18.5% (18–19%) in ♂, 26.5% (25–28%) in ♀; and for V, 17% (16–18%) in ♂, 23.5% (23–24%) in ♀. Telson vesicle 13% (9–17%) wider than metasomal segment V in ♂, 5% (2–8%) wider in ♀; oval in

shape, with flattened dorsal surface and rounded ventral surface (Fig. 33), height 36% (33–39%) of length. Aculeus short, 23% (21–25%) of vesicle length, and sharply curved. Total length of metasoma 17.5% (16–19%) longer than combined length of prosoma and mesosoma in ♂, but 14.5% (10–19%) shorter in ♀.

Eight carinae on segment I, six carinae on segments II-IV, and five carinae on segment V. Dorsosubmedian carinae of segment I becoming obsolete distally, but distinct throughout length of segments II-V. Median lateral carinae fully developed on segment I, but absent from segments II-V. Segments I-IV with closely paired ventrosubmedian carinae, fused into a single ventromedian carina on segment V. Ventrosubmedian and ventrolateral carinae costate on segment I, costate to costate-granular on segments II-IV. Ventrolateral and ventromedian carinae of segment V composed of spiniform granules. Median lateral and dorsosubmedian carinae costate on segment I, dorsosubmedian carinae costate to costate-granular on segments II-V (♀), or costate-granular on segment II, but composed of spiniform granules on segments III-V (♂). Dorsosubmedian carinae of metasomal segments II-III each terminating distally with an enlarged, spiniform granule; dorsosubmedian carinae of other metasomal segments without spiniform granules distally. Intercarinal surfaces smooth, except for lateral surfaces of segments II-V in ♀. Telson smooth, covered in long macrosetae.

Hemispermatophore: Doubled hook near the base of the distal lamella; distal crest truncate (Fig. 36).

Geographic variation: Specimens from lower elevation in the Phalaborwa and Pilgrim's Rest districts are larger, and lighter in color (especially the chelicerae, pedipalps, legs, and telson), than typical specimens from high elevation in the Letaba and Pietersburg districts.

Ontogenetic variation: The presence of a lobe on the movable finger of the pedipalp chela and a corresponding notch in the fixed finger is indicative of sexual maturity in all species of *Hadogenes*, except ♂ and ♀ *Hadogenes zumpti* Newlands & Cantrell 1985, and ♀ of certain species in the *Hadogenes tityus* (Simon 1888) complex (Newlands & Prendini 1997). The lobe and corresponding notch are absent from the fingers of the pedipalp chela

in subadults and juveniles, developing in the final instar of species, such as *H. bicolor*, in which these characters are present in the adults.

In the specimens of *Hadogenes* examined for this study, sexual maturity was assessed by the presence of the lobe and notch in ♂ and ♀, and by the presence of fully developed paraxial organs in ♂ or the gravid condition in ♀. The elongated metasoma (longer than the combined length of prosoma and metasoma), a secondary sexual characteristic only acquired in the final instar ♂ (Lamoral 1979; Newlands 1980), is a further indication that ♂ specimens are adult. In all species of *Hadogenes*, juvenile ♂ and ♀ resemble each other, and adult ♀, very closely in general morphological features (besides the absence of the lobe and notch on the pedipalp chela finger) until the final instar. The metasoma of the juvenile ♂ is also shorter than the combined length of the prosoma and mesosoma.

Sexual dimorphism: The characters of primary external sexual dimorphism are the undivided genital operculum of the ♀, which opens in a single flap, whereas in the ♂, the operculum consists of two unconnected sclerites which open independently and cover a pair of genital papillae. Secondary sexual characters observed in adult ♂, compared with adult ♀ and juveniles of both sexes, are as follows: more pronounced lobes on the fixed and movable fingers of the pedipalp chela, and a more pronounced notch in the fixed finger; longer, more slender pedipalps; more slender mesosoma; elongated metasoma (longer than the combined length of the prosoma and mesosoma); increased granulation of the carapace, tergites and metasoma; greater number of pectinal teeth.

Chromosome number: Newlands (1980) recorded a chromosome number of $2n = 96$, based on testicular and ovarian tissue, but noted that the quadruploid number ($2n = 192$) was also common.

Remarks: The ♂ specimen from Doornkop near Belfast, described by Hewitt (1918), is provisionally considered to be conspecific with *H. longimanus*, but may represent another undescribed species in this complex, whereas the three specimens from Woodbush, mentioned by Hewitt (1918), are conspecific with *H. newlandsi*. Newlands' (1980) material examined includes specimens of *H. bicolor*, *H.*

longimanus, and *H. newlandsi*; and his map of the distributional range of *H. bicolor* plots records for all three species. Electrophoretic data presented for *H. bicolor* from Zusterstroom (Bronkhorstpruit district, Gauteng Province) by Newlands (1980) and Newlands & Cantrell (1985) are applicable to *H. longimanus*.

Distribution.—*Hadogenes bicolor* is restricted to rocky outcrops along the Drakensberg escarpment in the Mpumalanga and Northern Provinces of South Africa (Fig. 1), at an elevation between 1000–2000 m. Most of the recorded localities fall in the square bounded by 24–25°S latitude and 30–31°E longitude, and occur at an elevation above 1200 m, which is generally higher than the elevation at which *H. longimanus* and *H. newlandsi* have been recorded.

In addition to the localities recorded in the material examined, Newlands' (1980: 100) records of *H. bicolor* from Boyne (Northern Province, Thabamoopo district) and Perkoe (Northern Province, Phalaborwa district [Farm Perkeo]) are probably referable to this species. However, Newlands' (1980: 100) records of *H. bicolor* from Lillie, Zeekoegat and Shaholle (Northern Province, Phalaborwa district) may be referable instead to *Hadogenes troglodytes* (Peters 1861).

Ecology.—*Hadogenes bicolor* is an obligately lithophilous scorpion, which inhabits the narrow cracks and crevices of weathered dolerite and granite rocks, but can also be found under large flat rocks resting on bedrock. Most of the distributional range of *H. bicolor* occurs in Northeastern Mountain Grassland (Bredenkamp et al. 1996), receiving an annual of rainfall of 700–1100 mm. However, on the lower eastern slopes and foothills of the Drakensberg escarpment (Northern Province, Phalaborwa district), the species occurs in Sour Lowveld Bushveld (Van Rooyen & Bredenkamp 1996b), which receives a rainfall of 600–1000 mm annually.

This species is sympatric with *Opistophthalmus glabrifrons* Peters 1861, *Pseudolychas pegleri* (Purcell 1901) and *Uroplectes triangulifer* (Thorell 1876) in most of its range. It has also been recorded in sympatry with *Opisthacanthus validus* Thorell 1876 at Bourke's Luck, Blyde River Canyon, and with *Parabuthus transvaalicus* Purcell 1899 and *Uroplectes olivaceus* Pocock 1896 at Jong-

mansspruit. Prey remains in the crevices inhabited by these scorpions commonly included the rings of spirobolid and harpagophorid millipedes (Myriapoda).

Conservation status.—As with other species of *Hadogenes* in southern Africa, *H. bicolor* is faced with two main threats: habitat destruction and collection for the international trade in exotic pets. *Hadogenes* species are especially vulnerable to the former because they commonly occur on granitic inselbergs, which are quarried in many parts of South Africa to provide gravestones, chipstone and other materials requiring fine-grained igneous rock. This is the case with *H. newlandsi* (see below), whose habitat has been extensively quarried in the Pietersburg and Soutpansberg districts. Fortunately, species inhabiting sedimentary geology are less vulnerable to this land use, but may still be eradicated by urbanization, as with *Hadogenes gunningi* Purcell 1899, a threatened species that inhabits sandstones and quartzites in the highly urbanized Gauteng Province of South Africa (including the cities of Johannesburg and Pretoria).

Hadogenes bicolor is less vulnerable to habitat destruction through industry or urbanization than many other species of *Hadogenes* because its distributional range coincides with areas of high ecotourism potential along the scenic Drakensberg escarpment. A large proportion of the known range of *H. bicolor* is already protected within existing parks, viable populations having been recorded from the Blyde River Canyon, Pilgrim's Rest and Lekgalameetse nature reserves. However, in unprotected areas throughout the region, the species faces the additional threat of habitat destruction through afforestation, a land-use practice that is not conducted in the regions of lower rainfall occupied by species such as *H. longimanus* and *H. newlandsi*.

In addition to habitat destruction, *Hadogenes* scorpions are extremely vulnerable to overharvesting for the international pet trade. They are much sought after as exotic pets because of their large size, unusual flattened appearance, generally docile temperament and mild venom. However, their specialized ecological requirements make them poor candidates for prolonged survival under captive conditions. Whereas these scorpions may live for more than 30 yr in the wild (Newlands 1980), captive specimens seldom survive more than a few years, even when apparently healthy. Moreover, unlike other common pet scorpion species, e.g., *Pandinus imperator* (C.L. Koch 1841), *Hadogenes* are notoriously difficult to breed in captivity, with the result that wild populations are placed under continued pressure from harvesting. Wild populations are expected to be slow to repopulate after harvesting for the following reasons. Females have gestation periods of up to 18 mo and produce small broods ($\bar{x} = 20$) compared with other scorpions (Williams 1971; Newlands 1980). Young are relatively altricial, spending several months on their mother's terga before their first ecdysis and subsequent departure (Williams 1971), thereby further protracting the period before a ♀ can give birth to her next brood. Age to sexual maturity is 8–10 yr in these scorpions (Newlands & Cantrell 1985), during which period juveniles must run the gauntlet of natural predation (including cannibalism).

Presently, the most commonly imported pet trade species appears to be *H. troglodytes*, usually mistakenly sold under the name *H. bicolor* (pers. obs.). Traders have been unwilling to divulge their sources, but wild-caught specimens are suspected to have originated in Mozambique, Zimbabwe and the Northern Province of South Africa.

Material examined.—SOUTH AFRICA: *Mpumalanga Province:* Pilgrim's Rest district: ♂ (TMSA 10100), Blyde River, Lydenburg [24°38′S, 30°47′E], 14 January 1971, N.H.G. Jacobsen; juv ♂ (TMSA 12515), Blyde River Canyon Nature Reserve [24°35′S, 30°49′E], 8 May 1974, N.H.G. Jacobsen; ♀ (AMNH), 2 juv ♂, juv ♀ (AMC), Bourke's Luck Potholes, Blyde River Canyon Nature Reserve [24°40′S, 30°49′E], 12 July 2000, L. Prendini and M. MacFarlane, grassland, with mixed bushveld at edge of canyon, under sandstone; ♂ (AMGS), Dientje G.M., Vaalhoek, near Pilgrim's Rest [24°39′S, 30°47′E], Miss S. Preller; subadult ♀ (AMGS 4704), Dientje P.O., Vaalhoek [24°43′S, 30°47′E], S. Preller. *Northern Province:* Letaba district: ♀ (SAMC C1602), juv ♀ (SAMC C1613), Serala Wilderness Area, near Tzaneen, 24°00′S, 30°04′E, 30 August 1980, M. Stiller, under flat rocks on steep mountainside, grass, rocks; ♂ (TMSA 18004), 2♀ (TMSA 17449, 18005), Leopard's Crag, 50 km W of Haffenden Heights [Lekgalameetse Nature Reserve, 24°09′S, 30°13′E, I.H. Davidson; 6♀ (TMSA 17794, 17795, 17797—17800), Haffenden Heights, The Downs [Farm Haf-

fenden Heights 35, Lekgalameetse Nature Reserve], 24°07′S, 30°07′E, 26 June 1977, B.P.W. Fratscher. Pietersburg district: 2 juv ♂ (TMSA 17456, 17459), juv ♀ (TMSA 17457), 19 miles E of Pietersburg [23°54′S, 29°47′E], 26 December 1967, G. Newlands. Phalaborwa district: ♂, ♀ (SAMC C4585), Jongmansspruit, on Blyde River, near Swadini [24°30′S, 30°47′E], 3–8 January 1999, I. Engelbrecht & D. Eagan, in crevices in granite rocks; ♂, ♀, subadult ♂ (AMNH), juv ♀ (AMC), Peninsula trail, Blyderivierspoort Dam, Blyde River Canyon Nature Reserve [24°33′S, 30°48′E], 13 July 2000, L. Prendini, M. MacFarlane, and K.M.A. Prendini, mixed bushveld, crevice in quartz.

Hadogenes longimanus new species
Figs. 1, 11–21, 34, 37, Table 2

Hadogenes bicolor Purcell 1899: Hewitt 1918: 160, 161 (part), pl. 30, figs. 88, 89; Newlands 1980 (unpublished): 99–105 (part), fig. 48 (part); Newlands & Cantrell 1985: 40, 42, 44 (part).

Types.—SOUTH AFRICA: Holotype ♂ (SAMC C4602), *Mpumalanga Province:* Groblersdal district: 20 km S of Groblersdal on road to Middelburg, 25°20.30′S, 29°22.85′E, 13 January 2000, L. Prendini & I. Engelbrecht, mixed bushveld, crevices in granite rocks, 1077 m. Paratypes: *Gauteng Province:* Bronkhorstspruit district: ♂ (TMSA 17452), 2♀ (TMSA 17453, 17460), Farm Zusterstroom 447, 25°35′S, 29°01′E, 4 November 1977, G. Newlands. *Mpumalanga Province:* Bronkhorstspruit district: ♀ (SAMC C1600), Bundu Inn, Bronkhorstspruit to Groblersdal [25°29′S, 29°01′E], 20 December 1980, M. Stiller, on hill, under large granite rock lying on rock face, many millipede (Juliform) and beetle remains; ♀ (NMSA 13931), same data, except 18 December 1980; ♂ (TMSA 12507), Farm Boekenhoutskloofdrift 286 [25°18′S, 29°01′E], 20 September 1982, E. Voigt. Groblersdal district: 2♂, 2♀, 2 subadult ♀, juv ♂ (SAMC C4603), 20 km S of Groblersdal on road to Middelburg, 25°20.30′S, 29°22.85′E, 13 January 2000, L. Prendini & I. Engelbrecht, mixed bushveld, crevices in granite rocks, 1077 m. Middelburg district: 2♂ (TMSA 17458, 17513), Farm Noupoort 16, Selons River [25°25′S, 29°28′E], 1933; ♂, 5♀, juv ♂ (SAMC C4600), ♂, ♀ (CASC), 2 juv ♀ (AMC), 55 km S of Groblersdal on road to Middelburg, 25°32.27′S, 29°28.67′E, 13 January 2000, L. Prendini & I. Engelbrecht, grassland and mixed bushveld, crevices in sandstone, 1509

m; 2♂, 12♀ (SAMC C4601), ♂, ♀ (AMNH), Fort Merensky, Botshabelo Nature Reserve, 25°41.82′S, 29°24.87′E, 14 January 2000, L. Prendini & I. Engelbrecht, grassland, with mixed bushveld along banks of Olifants River, under flat stones and in crevices (sandstone), 1410 m. Witbank district: 2♀ (SAMC C4596), 2-D Ranch [Loskop Dam Nature Reserve], 25°22.101′S 29°18.409′E, October 1989, L. Prendini & M.R. Filmer, in crevices, 1070 m; ♀, juv ♀ (SAMC C4595), ♀ (SAMC C4598), 2-D Ranch [Loskop Dam Nature Reserve], 25°22.10′S, 29°18.41′E, October 1994, I. Engelbrecht, in crevices, 1070 m; ♀ (SAMC C4599), same data, except N. McLean; subadult ♂ (SAMC C4594), same data, except J. Laing; ♀, subadult ♂ (SAMC C4597), Amaphi Nature Reserve, on road from Loskop Dam to Verena, 25°21.66′S 29°18.69′E, 14 January 2000, L. Prendini & I. Engelbrecht, mixed bushveld, in crevices in granite, 1102 m.

Etymology.—The species name refers to the unusually long, slender pedipalps of the adult ♂.

Diagnosis.—*Hadogenes longimanus* is the sister species of *H. bicolor*. These two species are both characterized by a pronounced lobe, distal to the notch in the fixed finger of the pedipalp chela of adult ♂ and ♀, and a relatively short metasoma in the adult ♂, compared with *H. newlandsi* and other *Hadogenes* species. Accordingly, these characters are hypothesized to be synapomorphic for *H. bicolor* and *H. longimanus*.

Hadogenes longimanus can be distinguished from *H. bicolor*, and from *H. newlandsi*, by the presence of 5–8 trichobothria on the internal surface of the pedipalp chela. In both *H. bicolor* and *H. newlandsi*, there are only two *i* trichobothria on the chela.

Description.—The following description, which complements Hewitt's (1918) description of the ♂ from Doornkop, near Belfast, is based on the holotype ♂ (SAMC C4602; Figs. 11, 12), a paratype ♀ from 20 km S of Groblersdal (SAMC C4603; Figs. 13, 14), and a paratype ♂ and ♀ from Botshabelo (SAMC C4601), with differences between these specimens being noted.

Color: (SAMC C4602; SAMC C4603). Legs and tergites I-VI slightly paler, but not contrasting markedly with pedipalps, carapace, tergite VII and metasoma. Telson not distinctly paler than metasomal segments I-V.
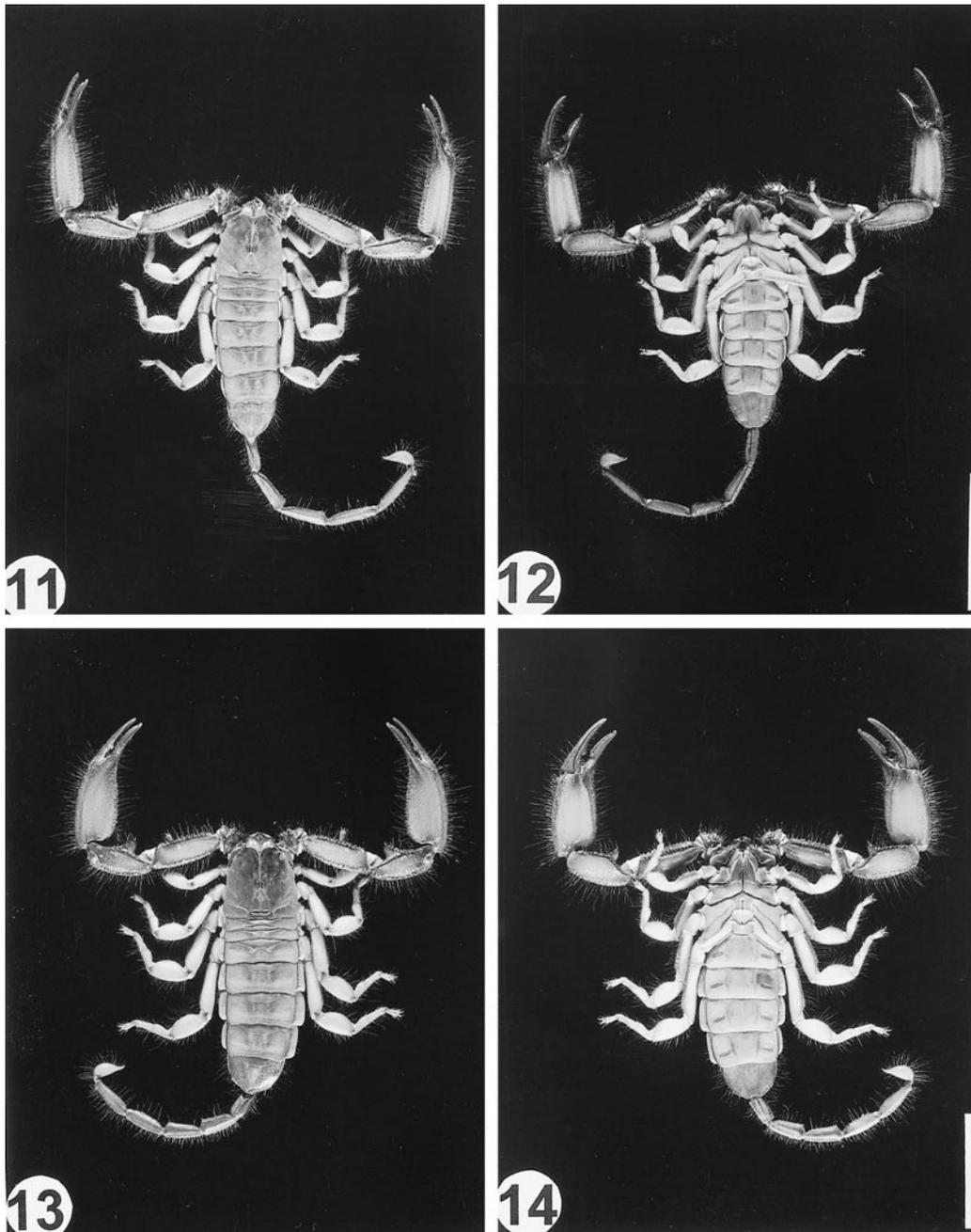
Figures 11–14.—**Hadogenes longimanus** new species, habitus of holotype ♂ (SAMC C4602) and paratype ♀ (SAMC C4603). 11. Dorsal aspect, ♂; 12. Ventral aspect, ♂; 13. Dorsal aspect, ♀; 14. Ventral aspect, ♀. Scale bars = 20 mm.

Sternites distinctly paler than tergites and metasoma. Carapace, Amber 36 (♂) to Burnt Sienna 132 (♀); pedipalps, Amber 36 (♂) to Burnt Sienna 132 (♀) on chela manus and in-

tercarinal surfaces of patella and femur, Sepia 119 on carinae and chela fingers; legs (except prolateral surfaces of femora) and tergites I-VI, Drab 27; cheliceral manus, tergite VII, and

metasoma, Fawn Color 25 (♂) to Burnt Sienna 132 (♀); cheliceral fingers and prolateral surfaces of leg femora, Sepia 119; sternites, pectines, and genital operculum, Sulphur Yellow 57.

Carapace: As for *H. bicolor*, with median notch in anterior margin slightly less pronounced.

Chelicerae: As for *H. bicolor*.

Pedipalps: As for *H. bicolor*, but differing in the following respects. Femur length 63.5% (60–67%) greater than width in ♂, 61.5% (61–62%) greater in ♀ (Table 2). Patella length 45% (42–48%) greater than width in ♂, 42.5% (42–43%) greater in ♀. Chela length along ventroexternal carina 49% (44–54%) greater than chela width in ♂, and 40.5% (40–41%) greater in ♀; chela width 47% (40–54%) greater than chela height in ♂, and 47.5% (46–49%) greater in ♀; length of movable finger 5% (2–8%) less than length along ventroexternal carina in ♂, and 4.5% (1–9%) less in ♀.

Trichobothria: Neobothriotaxic major, type C (Figs. 15–21), with the following segment totals (Table 2): femur 3 (1 *d*; 1 *i*; 1 *e*), patella 84–108 (2 *d*; 1 *i*; 28–43 *v*; 53–62 *e*) and chela 86–105 (73–89 manus; 13–16 fixed finger, including 5–8 *i*). Total number of τ per pedipalp, 173–216. Only femoral τ, τ in the *d* and *i* series of the patella, and τ in the *D*, *d*, and *e* series of the chela are stable in number and distribution. External and ventral τ of the chela and patella are numerically and distributionally too variable for diagnostic purposes. However, this species is characterized by the presence of accessory τ in the *i* series of the chela.

Mesosoma: Tergites each with paired submedian depressions and obsolete median carina. Pre-tergites of ♂ and ♀ smooth and shiny. Post-tergites I-VI smooth and shiny in ♂, except for very fine and even granulation on medial surfaces (excluding median carina and submedian depressions, which are smooth); post-tergite VII uniformly and finely granular in ♂; post-tergites of ♀ smooth and shiny. Sternites smooth and shiny, each with paired longitudinal depressions internal to spiracles. Sternite VII without posterolateral oval depressions, carinae, or notch in distal apex. Sternite VII 15.5% (13–18%) wider than long in ♂, 29.5% (29–30%) wider than long in ♀ (Table 2).

Pectines: As for *H. bicolor*, except pectinal teeth: 22–23/22–23 (♂), 16–19/15–19 (♀).

Sternum: As for *H. bicolor*.

Genital operculum: As for *H. bicolor*.

Legs: As for *H. bicolor*.

Metasoma and telson: As for *H. bicolor*, but metasomal segments shorter and more slender, with the following morphometric differences. Metasomal segment I 17% (10–24%) wider than high posteriorly (Table 2). Metasomal segments I-V progressively increasing in length, and decreasing in width, with segment V 30% (22–38%) narrower than segment I. Metasoma slender, width percentage of length for segment I, 45% (40–50%) in ♂, 47.5% (46–49%) in ♀; for II, 26% (23–29%) in ♂, 32% (30–34%) in ♀; for III, 23.5% (21–26%) in ♂, 29% (28–30%) in ♀; for IV, 20.5% (20–21%) in ♂, 26.5% (26–27%) in ♀; and for V, 17.5% (16–19%) in ♂, 24% (22–26%) in ♀. Telson vesicle 15% (14–16%) wider than metasomal segment V in ♂, 3.5% (2–5%) wider in ♀; oval in shape, with flattened dorsal surface and rounded ventral surface, height 37% (35–39%) of length. Aculeus short, 21.5% (19–24%) of vesicle length in ♂ and ♀, and sharply curved (Fig. 34). Total length of metasoma 9% (3–15%) longer than combined length of prosoma and mesosoma in ♂, but 13.5% (11–16%) shorter in ♀.

Hemispermatophore: Similar to that of *H. bicolor*, but teeth of doubled hook noticeably shorter (Fig. 37).

Geographic variation: Specimens from the Olifants River system (Bronkhorstspruit, Groblersdal, Middelburg and Witbank districts) are all very similar morphologically, although a general decrease in size occurs with increase in elevation from north to south in the distributional range. However, four specimens from Steelpoort (Lydenburg district), *ca.* 100 km northeast of the northernmost locality record in the Groblersdal district (Fig. 1), and the ♂ specimen from Doornkop (Carolina district), described by Hewitt (1918), differ from the typical form in several respects. The pedipalps, especially of the ♂, are proportionally shorter and broader, the carapace, post-tergites and metasoma are slightly more granular, and the trichobothrial counts are higher (total number of τ per pedipalp, 201–225).

Morphometric ratios of the pedipalps of a ♂ and ♀ from Steelpoort (Table 2) that differ from typical specimens are as follows: femur

length 57% greater than width in ♂, 55% greater in ♀; patella length 41% greater than width in ♂ and ♀; chela length along ventroexternal carina 39% greater than chela width in ♂, and 35% greater in ♀; length of movable finger 1% greater than length along ventroexternal carina in ♂, and 2% greater in ♀.

Unfortunately, the absence of any specimens from the area between these localities prevented an assessment of whether this variation is continuous or discrete. Further investigation, including the collection of additional material, will be required to determine if this variation has an ecological basis, or if these specimens represent yet another cryptic species in this complex. In light of this possibility, these five specimens have not been designated as paratypes of *H. longimanus*, and are thus listed below as "Material examined."

Ontogenetic variation: As for *H. bicolor*.

Sexual dimorphism: As for *H. bicolor*, except in this species the lobe distal to the notch in the fixed finger of the pedipalp chela is more pronounced in adult ♀ (Fig. 19), compared with adult ♀ *H. bicolor* (Fig. 9).

Chromosome number: Unknown.

Remarks: Electrophoretic data presented for *H. bicolor* from Zusterstroom (Bronkhorstspruit district, Gauteng Province) by Newlands (1980) and Newlands & Cantrell (1985) was derived from specimens that are conspecific with *H. longimanus* (e.g., TMSA 17452, 17453, 17460).

Distribution.—*Hadogenes longimanus* is endemic to a series of rocky outcrops and mountain ranges in the Gauteng and Mpumalanga provinces of South Africa (Fig. 1). Most of the known localities fall within the square bounded by 25–26°S latitude and 29–30°E longitude, and occur at an elevation between 1100–1500 m. However, *H. longimanus* has been collected below 1100 m in the Groblersdal district (Mpumalanga Province). The distributional range of this species coincides roughly with the upper reaches of the Olifants River and its tributaries, and is bounded by the Springbokvlakte plain (below 1000 m) to the north and west, and the Drakensberg escarpment (above 1500 m) to the south and east. The Springbokvlakte provides a natural barrier between *H. longimanus* and *H. newlandsi*, which occurs at lower elevation to the north of this plain. *Hadogenes bicolor* occurs at higher elevation than *H. longimanus* in the Drakensberg escarpment to the northeast.

Ecology.—In common with all other species of *Hadogenes*, *H. longimanus* is an obligately lithophilous scorpion. It inhabits the narrow cracks and crevices of weathered sandstone and granite rocks, and has also been collected from under large flat rocks resting on bedrock.

Below 1100 m, *H. longimanus* occurs in Mixed Bushveld (Van Rooyen & Bredenkamp 1996a), receiving a rainfall of 350–650 mm annually. However, above 1100 m, the species occurs in Rocky Highveld Grassland, receiving an annual rainfall of 650–750 mm (Bredenkamp & Van Rooyen 1996).

This species is sympatric with *Opistophthalmus glabrifrons* and *Uroplectes triangulifer* throughout most of its range. Prey remains in the crevices inhabited by these scorpions commonly included the rings of spirobolid and harpagophorid millipedes (Myriapoda), and the elytra of tenebrionid beetles (Coleoptera).

Conservation status.—*Hadogenes longimanus* is faced with the same threats as other *Hadogenes* species but, like *H. bicolor*, is comparatively less vulnerable for the following reasons. Firstly, it occurs mainly in regions of sedimentary geology, and less commonly on granite outcrops, and is thus less vulnerable to habitat destruction by the quarry-stone industry. Secondly, the distributional range of this species coincides with areas of high ecotourism potential in the Mpumalanga Province, and a considerable portion is already protected within existing parks. Viable populations have been recorded from the Loskop Dam and Botshabelo nature reserves, but additional populations probably exist within other reserves in the region.

Material examined.—SOUTH AFRICA: *Mpumalanga Province:* Carolina district: ♂ (AMGS), Doornkop, near Belfast, 25°55′S, 30°16′E, R. Gerhardt. Lydenburg district: 2♂ (SAMC C4275, 4276), ♀ (SAMC C4281), juv ♂ (SAMC C3901), Steelpoort, 24°43′S, 30°12′E, J. Visser.

Hadogenes newlandsi new species
Figs. 1, 22–32, 35, 38, Table 2

Hadogenes bicolor Purcell 1899: Hewitt 1918: 160, 161 (part); Lamoral & Reynders 1975: 538 (part); Newlands 1980 (unpublished): 99–105 (part), fig.

Table 2.—Meristic data for adult ♂ and ♀ *Hadogenes bicolor* Purcell 1899, **Hadogenes longimanus** new species and **Hadogenes newlandsi** new species. Measurements following Stahnke (1970), Lamoral (1979) and Newlands & Prendini (1997). [1] Measured from base of condyle to tip of fixed finger. [2] Sum of metasomal segments I-V and telson.

Specimen:		*Hadogenes bicolor* Purcell					
	Sex	♂	♀	♂	♀	♂	♀
	Collection	SAMC	SAMC	TMSA	TMSA	SAMC	SAMC
	Number	4062	4062	18004	18005	C4585	C4585
	Type	lecto	paralecto				
Carapace:	anterior width	7.54	8.28	8.12	8.82	9.22	10.49
	posterior width	12.78	13.67	13.85	14.08	16.12	17.02
	length	12.70	13.37	13.33	14.20	16.10	16.59
Chela:	maximum width	7.59	8.55	7.78	9.90	9.73	11.00
	maximum height	3.29	4.28	3.76	4.56	5.47	5.66
	length[1]	25.86	27.30	27.99	29.18	34.12	31.69
	length of ventroexternal carina	13.61	14.14	15.28	15.77	18.22	16.36
	length of movable finger	12.84	13.65	13.29	14.72	16.24	16.26
	i trichobothria (left/right)	2/2	2/2	2/2	2/2	2/2	2/2
	E trichobothria (left/right)	39/40	36/39	35/35	34/35	37/38	34/39
	V trichobothria (left/right)	34/33	42/36	37/37	34/39	35/38	37/35
Patella:	maximum width	7.28	7.85	7.75	8.28	9.22	9.17
	maximum height	3.86	4.06	3.89	4.19	5.34	5.12
	length	13.28	13.15	13.92	14.23	16.97	15.24
	e trichobothria (left/right)	57/57	59/56	42/38	53/54	53/54	56/55
	v trichobothria (left/right)	34/31	31/30	31/30	29/29	27/28	30/31
Femur:	maximum width	5.28	5.64	5.64	5.59	6.98	6.83
	maximum height	2.99	3.39	3.28	3.27	4.45	4.13
	length	14.50	14.14	15.82	14.97	18.55	16.23
Pedipalp:	total length (including trochanter)	58.34	60.00	63.61	64.45	76.23	70.41
Mesosoma:	total length (tergites)	34.28	36.11	33.97	38.86	43.19	47.10
Sternite VII:	width	8.63	10.76	9.66	10.63	11.54	14.07
	length	7.87	8.11	7.37	8.51	9.94	9.46
Metasoma I:	maximum width	3.21	3.28	2.73	3.24	4.14	3.96
	maximum height	2.48	2.28	2.45	2.68	3.27	3.13
	length	7.49	6.11	7.46	6.43	9.83	7.05
Metasoma II:	maximum width	2.27	2.23	2.16	2.28	3.01	2.83
	maximum height	3.38	2.80	2.99	3.24	4.03	4.12
	length	9.52	7.27	9.56	7.10	12.60	9.02
Metasoma III:	maximum width	2.09	2.10	2.10	2.14	2.61	2.72
	maximum height	3.36	2.84	2.88	3.11	4.08	3.86
	length	9.96	7.33	9.98	7.53	12.92	9.38
Metasoma IV:	maximum width	1.96	2.04	1.91	2.12	2.52	2.51
	maximum height	2.84	2.72	2.80	2.93	3.67	3.63
	length	10.55	8.02	10.57	7.57	13.92	9.76
Metasoma V:	maximum width	2.06	2.02	1.82	2.03	2.50	2.54
	maximum height	2.79	2.48	2.68	2.65	3.39	3.24
	length	11.18	8.81	11.09	8.41	14.51	10.76
Telson:	maximum width	2.31	2.20	2.18	2.13	2.75	2.60
	maximum height	2.57	2.61	2.79	2.81	3.42	3.41
	aculeus length	1.84	1.61	1.68	1.86	2.38	2.13
	total length	7.77	7.52	7.98	7.59	9.34	8.78
Metasoma:	total length[2]	56.47	45.06	56.64	44.63	73.12	54.75
Total length:	prosoma + mesosoma + metasoma	103.45	94.54	103.94	97.69	132.41	118.44
Pectines:	total length	8.29	7.20	8.72	7.36	9.68	8.34
	length along dentate margin	7.53	6.03	8.13	6.21	8.30	6.61
	tooth count (left/right)	19/18	16/15	20/20	16/16	19/18	17/16

Table 2.—Extended.

Hadogenes longimanus new species						*Hadogenes newlandsi* new species			
♂ SAMC C4602 holo	♀ SAMC C4603 para	♂ AMNH para	♀ AMNH para	♂ SAMC C4275	♀ SAMC C4281	♂ SAMC C4589 holo	♀ SAMC C4593 para	♂ SAMC C4586 para	♀ SAMC C4586 para
9.97	9.48	7.76	8.01	9.89	11.64	9.40	10.00	8.92	9.47
15.80	15.51	12.49	12.83	16.04	18.58	15.43	16.81	14.43	15.63
15.57	15.34	12.36	12.74	16.07	19.11	16.13	16.60	14.87	15.53
8.62	9.76	7.63	8.03	10.13	12.11	10.22	11.26	9.25	10.46
5.17	5.00	3.49	4.30	5.35	6.47	5.13	5.72	4.39	4.82
34.49	31.63	25.94	25.00	32.07	36.52	31.25	32.89	26.66	28.42
18.71	16.30	13.82	13.50	16.57	18.68	16.95	17.69	13.59	15.26
18.15	16.28	12.77	12.34	16.75	19.01	16.03	17.60	13.52	14.50
6/5	5/5	7/6	6/5	6/6	7/8	2/2	2/2	2/2	2/2
37/39	40/43	39/39	39/38	39/36	41/44	30/34	32/30	30/29	33/34
34/36	42/38	44/46	38/38	47/45	46/49	33/35	33/34	34/37	33/36
9.06	8.80	7.19	7.08	8.96	10.36	8.70	9.72	8.17	8.64
4.57	4.66	3.58	3.80	5.37	5.79	4.78	5.23	4.35	4.58
17.56	15.52	12.34	12.27	15.12	17.64	15.15	15.54	13.06	13.51
56/55	62/60	54/53	54/57	73/70	69/70	41/49	52/48	48/50	52/51
28/32	33/33	34/33	43/39	37/36	33/31	29/28	29/31	29/31	30/32
6.56	6.35	5.50	5.04	6.68	8.03	6.78	7.31	6.58	6.41
4.15	4.04	3.13	3.18	4.02	5.19	4.24	4.38	3.50	3.72
20.10	16.55	13.87	13.02	15.64	18.00	15.76	16.04	13.60	14.19
79.36	70.56	58.11	56.00	68.83	80.76	68.92	71.51	59.41	62.75
44.35	42.20	37.67	36.17	46.84	55.17	50.68	47.58	41.27	44.25
12.10	12.26	9.67	10.88	11.77	13.86	12.26	13.88	10.56	12.17
9.90	8.61	8.40	7.75	10.00	11.05	10.83	10.38	10.08	9.48
3.46	3.04	3.19	2.79	3.43	3.96	4.11	3.95	4.08	3.68
3.11	2.99	2.43	2.42	3.14	3.30	3.66	3.24	2.81	2.84
8.58	6.58	6.38	5.66	9.77	8.58	12.24	7.86	10.25	7.26
2.87	2.57	2.44	2.43	2.73	2.84	3.02	2.84	2.84	2.90
3.73	3.41	3.13	3.21	3.75	4.06	4.83	4.00	3.95	3.42
12.24	8.44	8.54	7.16	12.34	10.85	16.22	10.10	13.88	9.32
2.69	2.44	2.37	2.15	2.48	2.88	2.92	2.69	2.71	2.63
3.58	3.42	3.09	3.00	3.72	4.16	4.53	4.03	3.85	3.52
12.69	8.73	9.20	7.28	12.64	11.17	16.29	10.09	14.63	9.35
2.66	2.43	2.12	2.03	2.48	2.69	2.73	2.57	2.33	2.24
3.15	2.98	2.68	2.72	3.10	3.54	3.88	3.73	3.23	2.99
13.41	9.27	9.95	7.59	13.15	12.08	17.43	11.05	15.46	10.38
2.42	2.37	1.97	1.97	2.31	2.63	2.52	2.67	2.28	2.17
3.19	2.81	2.51	2.35	3.03	3.38	3.76	3.63	2.92	2.67
14.69	10.57	10.61	7.61	13.49	12.53	17.29	11.60	15.81	10.54
2.89	2.50	2.30	2.01	2.47	3.16	2.95	2.90	2.47	2.23
3.37	2.82	2.82	2.55	3.08	3.48	3.68	3.57	3.26	2.71
2.17	1.96	1.37	1.44	2.12	2.92	1.73	2.32	1.79	1.94
9.17	8.12	7.14	6.74	8.71	10.33	10.01	9.22	8.63	8.10
70.78	51.71	51.82	42.04	70.10	65.54	89.48	59.92	78.66	54.95
130.70	109.25	101.85	90.95	133.01	139.82	156.29	124.10	134.80	114.71
11.10	8.49	9.38	6.84	12.23	9.50	10.77	8.62	8.48	7.62
10.29	7.34	8.47	5.59	11.84	7.84	10.25	6.98	8.11	5.80
23/23	19/19	22/22	16/15	24/23	18/18	21/22	17/16	23/21	18/16
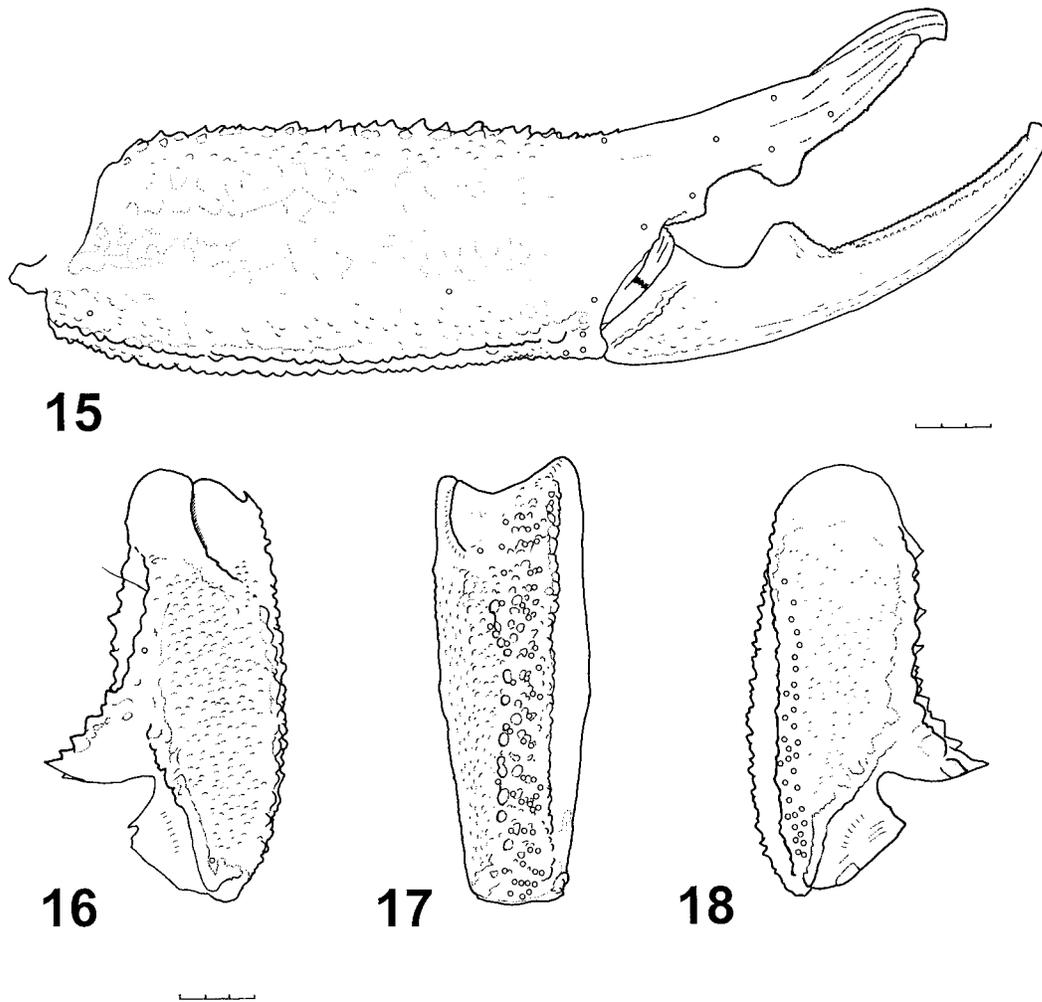
Figures 15–18.—***Hadogenes longimanus*** new species, dextral pedipalp segments of holotype ♂ (SAMC C4602) and paratype ♀ (SAMC C4603), showing trichobothrial distribution and shape of lobes on fixed and movable fingers of the chela. 15. Dorsal aspect of chela, ♂; 16. Dorsal aspect of patella, ♀; 17. External aspect of patella, ♀; 18. Ventral aspect of patella, ♀. Scale bars = 3 mm.

48 (part); Newlands & Cantrell 1985: 40, 42, 44 (part).

Types.—SOUTH AFRICA: *Northern Province:* Holotype ♂ (SAMC C4589), Soutpansberg district: Ben Lavin Nature Reserve, 23°07.544′S, 29°56.573′E, 31 December 1999, L. Prendini & E. Scott, in crevices in granite rocks, mixed bushveld, 850 m. Paratypes: Letaba district: subadult ♂ (TMSA 12565), Letsitele, Tzaneen [23°53′S, 30°24′E], 21 September 1964, R.D. Faul; 2♂ (TMSA 114, 117), 10♀ (TMSA 112, 113, 115, 116, 118–122, 125), 2 juv ♀ (TMSA 127, 128), Mooketsi [23°35′S, 30°03′E], April 1924, G.P.F. van Dam. Pietersburg district: subadult ♂ (TMSA 1057), Clearwaters, Haenertsburg [23°51′S, 29°57′E], 4 February 1916, G.A. Thompson; subadult ♀ (TMSA 1058), Farm Munniks [23°37′S, 29°57′E], 16 January 1914, Pienaar; ♀ (AMNH), Pietersburg area [23°54′S, 29°27′E]; ♀ (TMSA 1055), Woodbush [23°47′S, 29°54′E], December 1907, D. Gough; subadult ♂ (AMGS 3990), The Woodbush. Potgietersrus district: juv ♀ (TMSA 2184), Potgietersrus [24°11′S, 29°01′E], 27 March 1919, H.B. Pretorius; juv
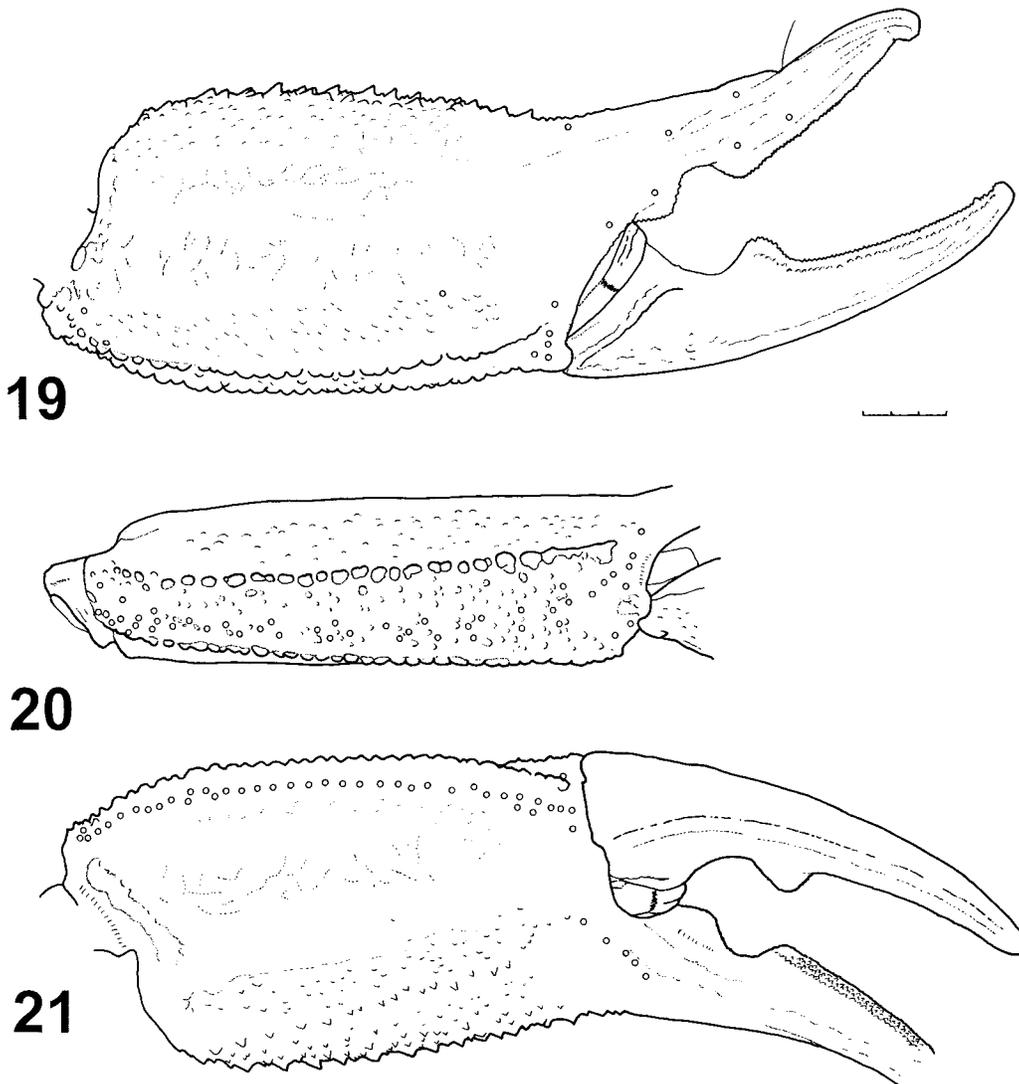
Figures 19–21.—***Hadogenes longimanus*** new species, dextral pedipalp chela of paratype ♀ (SAMC C4603), showing trichobothrial distribution and shape of lobes on fixed and movable fingers. 19. Dorsal aspect; 20. External aspect; 21. Ventrointernal aspect. Scale bar = 3 mm.

♀ (TMSA 6108), Maribashoek [24°13′S, 29°08′E], December 1924, G.P.F. van Dam; ♂ (TMSA 10484), 3♀ (TMSA 10481–10483), juv ♂ (TMSA 10485), Percy Fife Nature Reserve [24°02′S, 29°11′E], 11 May 1972, N.H.G. Jacobsen; subadult ♀ (TMSA 20393), Potgietersrus Nature Reserve [24°09′S, 28°59′S], 11 May 1972, N.H.G. Jacobsen; juv ♀ (TMSA 708), Makapan Caves [24°09′S, 29°11′E], 4 February 1911, A. Roberts; juv ♂ (TMSA 10781), Makapansgat, 31 August 1973, R. Clark; ♀ (TMSA 17451), juv ♀ (TMSA 17450), Makapansgat, I.H. Davidson; ♀ (AMC), Makapansgat World Heritage Site, April 2000, I. Engelbrecht. Sekgosese district: 2♂, 9♀, juv ♂, juv ♀ (SAMC C4592), ♂, ♀ (CASC), juv ♂, juv ♀ (AMC), St. Brendan's Catholic School (Mission Matok), 23°25.63′S, 29°43.28′E, 29 December 1999, L. Prendini & E. Scott, mixed bushveld, granite outcrops, in crevices, 980 m; ♀, juv ♀ (SAMC C4591), Mphakane, south, granite koppies 1 km from turnoff to Munnik, 23°32.20′S, 29°42.42′E, 29 December 1999, L. Prendini & E. Scott, in

Figures 22–25.—***Hadogenes newlandsi*** new species. habitus of holotype ♂ (SAMC C4589) and paratype ♀ (CASC). 22. Dorsal aspect, ♂; 23. Ventral aspect, ♂; 24. Dorsal aspect, ♀; 25. Ventral aspect, ♀. Scale bars = 20 mm.

crevices in rock, 1000 m. Soutpansberg district: subadult ♂ (CASC), 10 mi S of Louis Trichardt, 25 March 1958, E.S. Ross & R.E. Leech, 1000 m; ♀, 3 juv ♂, juv ♀ (CASC), same data, except 18 mi S of Louis Trichardt; 2 juv ♀ (CASC), same data, except 35 mi S of Louis Trichardt, 26 March 1958; 2 ♀ (SAMC C4587), Bandelierkop, 23°18′S,
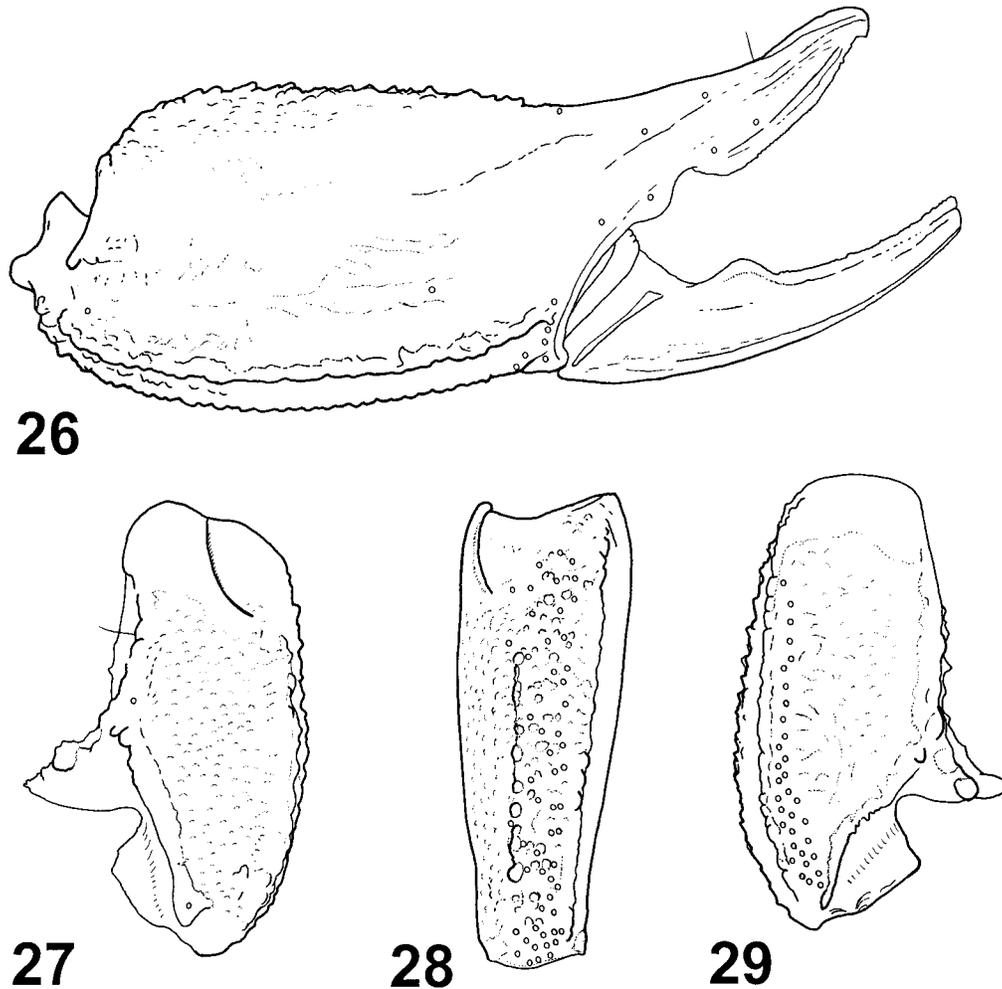
Figures 26–29.—***Hadogenes newlandsi*** new species, dextral pedipalp segments of ♂ and ♀ paratypes (SAMC C4586), showing trichobothrial distribution and shape of lobes on fixed and movable fingers of the chela. 26. Dorsal aspect of chela, ♂; 27. Dorsal aspect of patella, ♀; 28. External aspect of patella, ♀; 29. Ventral aspect of patella, ♀. Scale bar = 3 mm.

29°51′E, April 1988, L. Prendini, M.R. Filmer, A.M. Smith & V. Hull-Williams, in crevices in granite koppie; ♂, ♀, juv ♂ (SAMC C4586), Bandelierkop, 1995, I. Engelbrecht; ♀, 2 juv ♀ (SAMC C4590), Mailaskop, 23°13.43′S, 29°56.63′S, 30 December 1999, L. Prendini & E. Scott, in crevices in dolerite rocks on koppie, 1124 m; ♂, ♀ (SAMC C4588), Tabajwane Koppie, Ben Lavin Nature Reserve, December 1990, L. Prendini & K.M.A. Prendini, in crevices in granite rocks, 970 m; 3♂, 5♀, subadult ♀ (SAMC C4593), ♂, ♀ (AMNH), Ben Lavin Nature Reserve, 23°07.544′S, 29°56.573′E, 31 December 1999, L. Prendini & E. Scott, in crevices in granite rocks, mixed bushveld, 850 m.

Etymology.—The new species is named in honor of Dr. Gerald Newlands for his contributions to the ecology and systematics of southern African scorpions in general and *Hadogenes* in particular.

Diagnosis.—*Hadogenes newlandsi* is most closely related to the group comprising *H. bicolor* and *H. longimanus*. In all three species, the distal width of metasomal segment I is greater than its height. *Hadogenes newlandsi* can be distinguished from the latter species by the absence of a pronounced lobe, distal to the

notch in the fixed finger of the pedipalp chela of adult ♂ and ♀, and by the longer metasoma of the adult ♂ (which is approximately the same length as the metasoma of certain other *Hadogenes* species, e.g., *H. gunningi*). *Hadogenes newlandsi* is further characterized by the presence, in adult ♂, of dense granulation on the telson and lateral surfaces of metasomal segment V. The latter character has proved consistent in separating *Hadogenes granulatus* Purcell 1901 from the morphologically similar *H. troglodytes*, which occur sympatrically in parts of Zimbabwe (Bergman 1995).

Description.—The following description is based on the holotype ♂ (SAMC C4589; Figs. 22, 23), two paratype ♀ from Ben Lavin (SAMC C4593, CASC; Figs. 24, 25), and a paratype ♂ and ♀ from Bandelierkop (SAMC C4586).

Color: (SAMC C4589; SAMC C4593). Pale legs contrasting markedly with darker pedipalps, carapace, tergites and metasoma. Telson not distinctly paler than metasomal segments I-V. Sternites distinctly paler than tergites and metasoma. Pedipalps, Tawny 38 on chela manus and intercarinal surfaces of patella and femur, Sepia 119 on carinae and chela fingers; cheliceral manus, carapace, tergites (♂) and metasoma, Hooker's Green 162; tergites (♀), Grayish Olive 43; legs (except prolateral surfaces of femora) of ♂, sternites, pectines and genital operculum, Straw Yellow 36; legs (♀), Tawny 38; cheliceral fingers and prolateral surfaces of leg femora, Sepia 119.

Carapace: As for *H. bicolor*, except median notch in anterior margin very weakly developed, and frontal lobes of ♂ almost entirely granular.

Chelicerae: As for *H. bicolor*.

Pedipalps: As for *H. bicolor*, but differing in the following respects. Femur length 54.5% (52–57%) greater than width in ♂ and ♀ (Table 2). Patella length 40% (37–43%) greater than width in ♂, 36.5% (36–37%) greater in ♀. Chela with a pronounced, conical lobe on movable finger and corresponding notch in fixed finger; fixed finger additionally with a small, rounded lobe proximal to the notch, but without a pronounced, conical lobe distally (Figs. 26, 30). Chela length along ventroexternal carina 35.5% (32–39%) greater than chela width in ♂, and 33.5% (31–36%) greater in ♀; chela width 51.5% (49–54%) greater

than chela height in ♂ and ♀; length of movable finger 3% (1–5%) less than length along ventroexternal carina in ♂ and ♀.

Trichobothria: Neobothriotaxic major, type C (Figs. 26–32), with the following segment totals (Table 2): femur 3 (1 *d*; 1 *i*; 1 *e*), patella 72–87 (2 *d*; 1 *i*; 28–32 *v*; 41–52 *e*) and chela 72–81 (62–71 manus; 10 fixed finger, including 2 *i*). Total number of τ per pedipalp, 147–171. Only femoral τ, τ in the *d* and *i* series of the patella, and τ in the *D*, *d*, *e* and *i* series of the chela are stable in number and distribution. External and ventral τ of the chela and patella are numerically and distributionally too variable for diagnostic purposes.

Mesosoma: Tergites each with paired submedian depressions and obsolete median carina. Pre-tergites of ♂ and ♀ smooth and shiny. Post-tergites of ♂ covered with very fine and even granulation, imparting a matte appearance to all surfaces, except median carina and submedian depressions, which are smooth; post-tergites of ♀ smooth and shiny. Sternites smooth and shiny, each with paired longitudinal depressions internal to spiracles. Sternite VII additionally with a pair of shallow posterolateral oval depressions (more prominent in ♂), and a pair of obsolete carinae, converging distally towards a shallow notch in distal apex. Sternite VII 8.5% (5–12%) wider than long in ♂, 23.5% (22–25%) wider than long in ♀ (Table 2).

Pectines: As for *H. bicolor*, except pectinal teeth: 21–23/21–22 (♂), 17–18/16 (♀).

Sternum: As for *H. bicolor*.

Genital operculum: As for *H. bicolor*.

Legs: As for *H. bicolor*.

Metasoma and telson: As for *H. bicolor*, except for the presence, in adult ♂, of more pronounced spiniform granules on metasomal segments II-V, and dense granulation on the lateral surfaces of segment V and telson (Fig. 35). In addition, metasomal segments of adult ♂ longer than in *H. bicolor*, with morphometric differences as follows. Metasomal segment I 21% (11–31%) wider than high posteriorly (Table 2). Metasomal segments I-V progressively increasing in length, and decreasing in width, with segment V 35% (29–41%) narrower than segment I. Metasoma slender, width percentage of length for segment I, 36.5% (34–39%) in ♂, 50.5% (50–51%) in ♀; for II, 19.5% (19–20%) in ♂, 29.5% (28–31%) in ♀; for III, 18.5% (18–
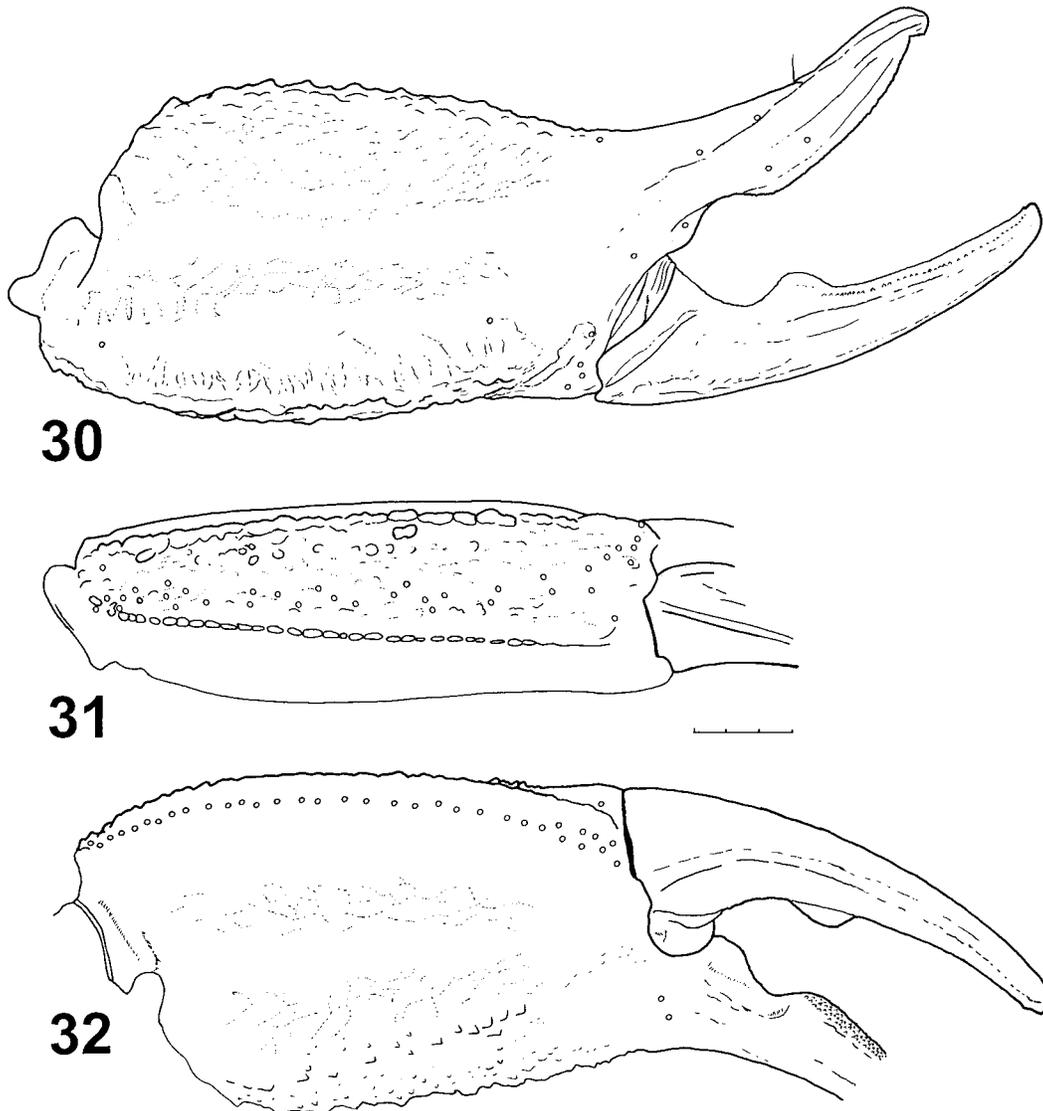
Figures 30–32.—**Hadogenes newlandsi** new species, dextral pedipalp chela of paratype ♀ (SAMC C4586), showing trichobothrial distribution and shape of lobes on fixed and movable fingers. 30. Dorsal aspect; 31. External aspect; 32. Ventrointernal aspect. Scale bar = 3 mm.

19%) in ♂, 27.5% (27–28%) in ♀; for IV, 15.5% (15–16%) in ♂, 22.5% (22–23%) in ♀; and for V, 14.5% (14–15%) in ♂, 22.5% (22–23%) in ♀. Telson vesicle 11.5% (8–15%) wider than metasomal segment V in ♂, 5.5% (3–8%) wider in ♀; distinctly elongated in ♂, oval in ♀, with flattened dorsal surface and rounded ventral surface, height 36% (33–39%) of length. Aculeus short, 19% (17–21%) of vesicle length in ♂, 24.5% (24–25%) in ♀, and sharply curved. Total length of metasoma

27% (25–29%) longer than combined length of prosoma and mesosoma in ♂, but 8% (7–9%) shorter in ♀.

Hemispermatophore: Similar to that of *H. bicolor*, but teeth of doubled hook noticeably longer (Fig. 38).

Geographic variation: Little geographic variation besides a general decrease in size, associated with increase in elevation from north to south in the distributional range. Specimens from the southern part of the range
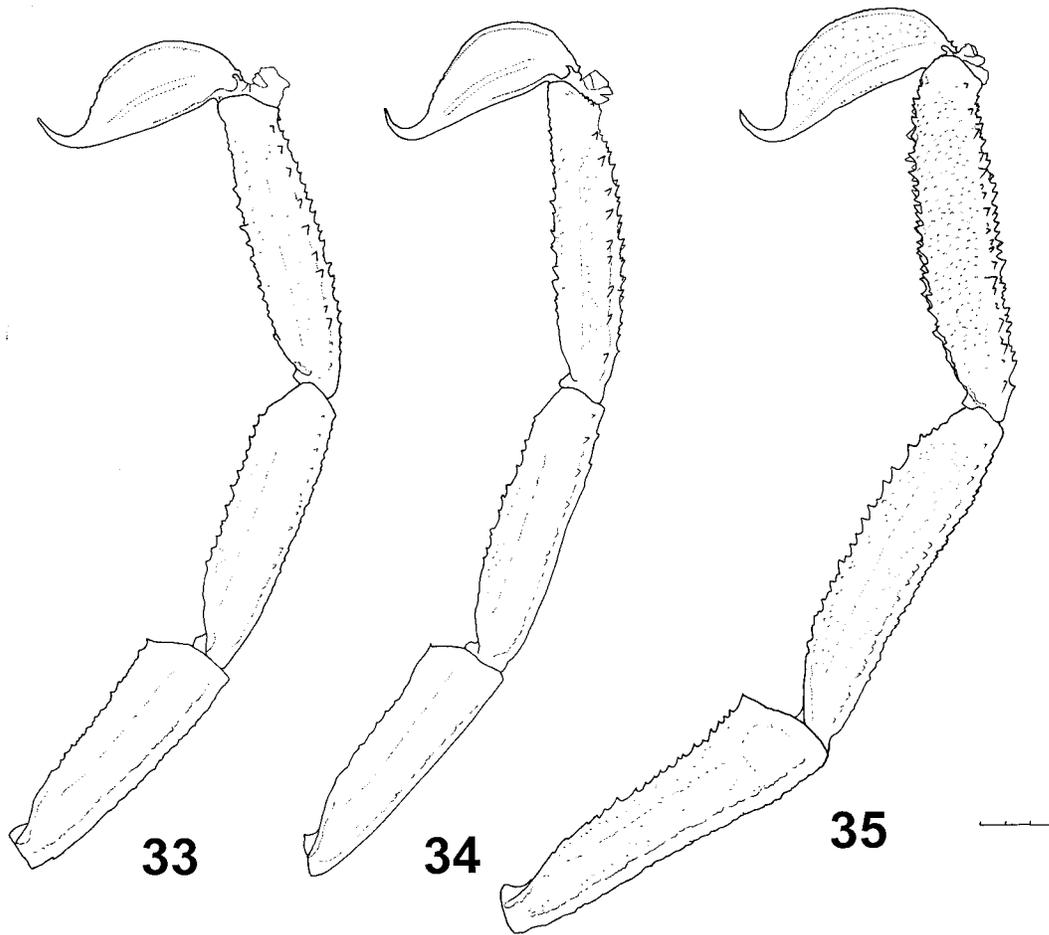
Figures 33–35.—Lateral aspect of metasomal segments III-V and telson, showing diagnostic differences in shape and granulation. 33. *Hadogenes bicolor* Purcell 1899 (♂, SAMC C4585); 34. **Hadogenes longimanus** new species (holotype ♂, SAMC C4602); 35. **Hadogenes newlandsi** new species (holotype ♂, SAMC C4589). Scale bar = 3 mm.

(e.g., Makapansgat) are also lighter in color, and have longer metasomal segments, than those from further north (e.g., Ben Lavin).

Ontogenetic variation: As for *H. bicolor*.

Sexual dimorphism: As for *H. bicolor*, except in this species the lobe on the movable finger of the pedipalp chela and notch in the fixed finger (no lobe is present distal to the notch), are equally pronounced in adult ♂ and ♀ (Figs. 26, 27), compared with adult ♂ and ♀ *H. bicolor* (Figs. 8, 9), and the metasoma of adult ♂ is considerably more elongated, with segment V and telson densely granular (Fig. 35).

Chromosome number: Unknown.

Remarks: The three specimens of *H. bicol-or* from Woodbush, mentioned by Hewitt (1918), are conspecific with *H. newlandsi* (e.g., TMSA 1055, AMGS 3990).

Distribution.—*Hadogenes newlandsi* is restricted to inselbergs and mountain ranges in the Northern Province of South Africa (Fig. 1). Most locality records fall in the square bounded by 23–24°S latitude and 29–30°E longitude. Although specimens have been collected at an elevation between 800–1100 m in the northern part of the distributional range, locality records from the southern part of the distribution occur at an elevation between 1200–1500 m. The area of distribution is delimited by the Soutpansberg mountain range (above 1300 m) to the north, the Drakensberg

escarpment (above 1500 m) to the east, the Mogalakwena River Valley (below 900 m) to the west, and the Springbokvlakte plain (below 1000 m) to the south. The Springbokvlakte provides a natural barrier between *H. newlandsi* and *H. longimanus*, which occurs at higher elevation to the south of this plain. *Hadogenes bicolor* occurs at higher elevation than *H. newlandsi* in the Drakensberg escarpment to the southeast.

Ecology.—*Hadogenes newlandsi* is obligately lithophilous, inhabiting the narrow cracks, crevices and exfoliations of weathered granite and dolerite outcrops. It is restricted to Mixed Bushveld, receiving a rainfall of 350–650 mm annually (Van Rooyen & Bredenkamp 1996a).

In the rocky inselbergs that it inhabits, *H. newlandsi* is sympatric with *Parabuthus transvaalicus* and *Uroplectes olivaceus*. This species has also been collected in sympatry with *Cheloctonus jonesii* Pocock 1892 and *Opistophthalmus glabrifrons* at Bandelierkop and Ben Lavin. Prey remains in the crevices occupied by these scorpions included the rings of spirobolid millipedes (Myriapoda) and the elytra of carabid and tenebrionid beetles (Coleoptera).

Conservation status.—*Hadogenes newlandsi* is heavily threatened by habitat destruction for the quarry-stone industry. Many of the granite inselbergs inhabited by this species have been extensively quarried in the Pietersburg and Soutpansberg districts. Fortunately, the conservation status of *H. newlandsi* is assured by the existence of viable populations in the Percy Fife, Potgietersrus and Ben Lavin Nature Reserves, as well as at the Makapansgat World Heritage Site. The occurrence of the species in the Happy Rest, Kuschke and Pietersburg nature reserves, which also fall within its known distributional range, has not been verified, but seems probable.

DISCUSSION

The phylogenetic position of *Hadogenes* within the Ischnuridae was recently questioned by Lourenço (1999, 2000). Lourenço (1985, 1989, 1999) has consistently maintained that *Hadogenes* is the sister genus of *Heteroscorpion* Kraepelin 1905, the endemic Malagasy genus for which Lourenço (1996) erected the monotypic family Heteroscorpionidae Kraepelin 1905. Although it has never

been explicitly stated by Lourenço, the hypothesized relationship between *Hadogenes* and *Heteroscorpion* has presumably been adopted from Kraepelin (1896, 1899, 1901) and inferred from the following characters: the presence of accessory trichobothria in the *v* and *e* series of the pedipalp patella and in the *V* series of the pedipalp chela; the presence of an elongated, laterally compressed metasoma, particularly conspicuous in the adult male. These characters provided the primary justification for Kraepelin's (1896) original placement of the type species, *Heteroscorpion opisthacanthoides* (Kraepelin 1896), in the genus *Hadogenes*.

According to Kraepelin (1896: 137):

"Die cauda [of *H. opisthacanthoides*] ist weniger zusammengedrückt als bei der typischen Art [*Hadogenes*] *trichiurus*, zeigt aber noch die concaven Begrenzungslinien des Oberrandes der Segmente (Fig. 16 [illustrating lateral aspect of metasomal segments I-II]), welche für *Hadogenes* so charackterisch sind. Noch mehr endlich entfernt sich die Art von *Opisthacanthus* durch den Besitz einer Reihe von etwa zehn sehr deutlichen Haargruben am unteren Hinterrande des Unterarms (Fig. 18 [illustrating ventral aspect of right pedipalp patella]), denen eine ebenfalls scharf ausgeprägte dichte Reihe von Haargrübchen am Außenrande der Unterhand entspricht. Diese Bildungen schließen sich eng an die Vorkommnisse bei [*Hadogenes*] *tityrus* an, und da die stärkere oder schwächere Ausrandung der Stirn ebensowenig wie die stärkere oder schwächere Compression der Cauda oder die Abplattung des Körpers als generische Merkwale verwerthet werden können, so glaube ich die neue Art [*H. opisthacanthoides*] auf Grund eben jener Haargrübchenreihen der Gattung *Hadogenes* einreihen zu sollen."

In addition, all species of *Hadogenes* are characterized by the presence of a doubled hook on the hemispermatophore (Lamoral 1979). Lourenço (1999: 930) considered these characters to provide justification for the creation of a new subfamily Hadogeninae, which he transferred to the Scorpionidae:

"Lamoral (1979) dresse une liste des car-
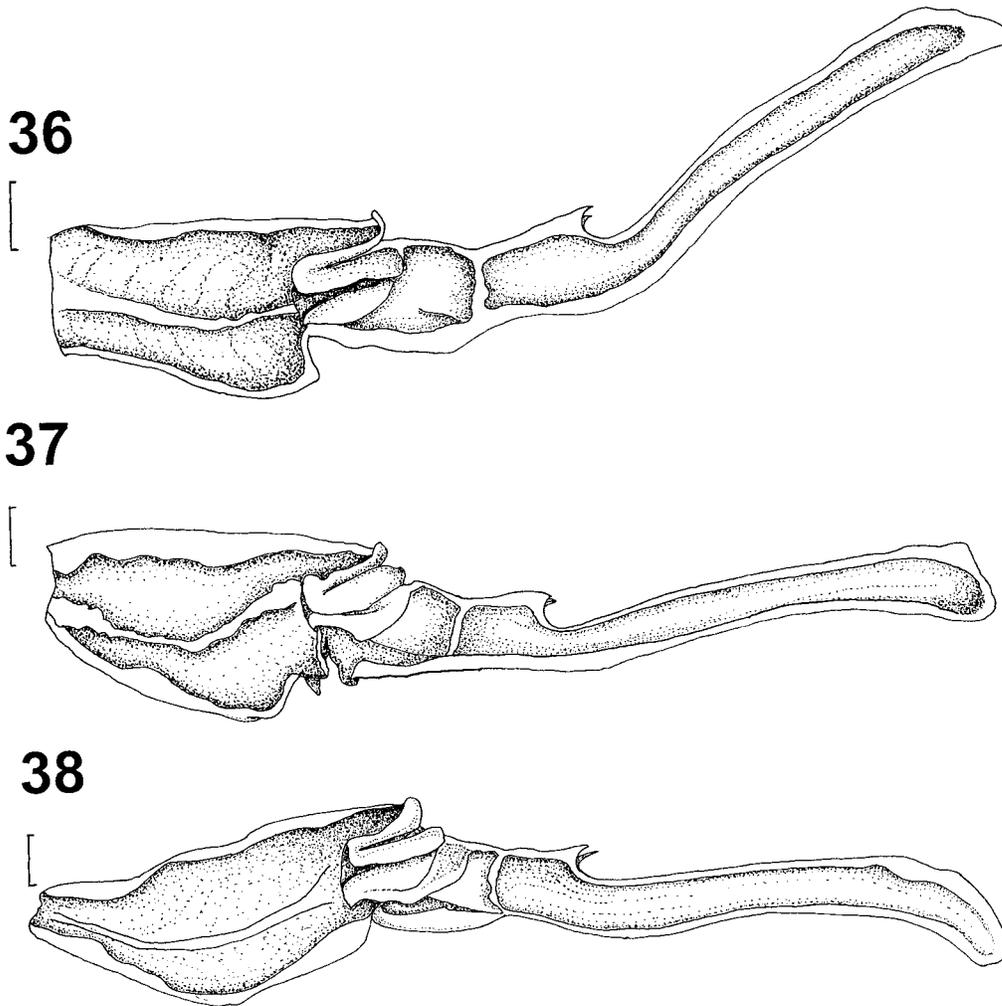
Figures 36–38. Left hemispermatophores. 36. *Hadogenes bicolor* Purcell 1899 (♂, TMSA 18004); 37. **Hadogenes longimanus** new species (paratype ♂, TMSA 17513); 38. **Hadogenes newlandsi** new species (paratype ♂, SAMC C4588). Scale bars = 1 mm.

actères différentiels entre le genre *Hadogenes* et les autres genres appartenant aux Ischnuridae, en particulier ceux tirés de la structure des hémispermatophores et du modèle trichobothriotaxique, caractères globalement négligés par les auteurs précédents déjà cités. Ces caractères sont réanalysés lors de l'étude réaliseé par Lourenço (1985, 1989), sans pour autant aboutir a une décision sur la position systématique des *Hadogenes*. A présent, un ensemble de caractères m'amène à proposer une nouvelle sous-famille monotypique avec genre-type *Hadogenes*. Cette

sous-famille est placée, par prudence, au sein de la famille des Scorpionidae.''

Lourenço (2000: 26) subsequently elevated the Hadogeninae to Hadogenidae in a footnote, which states: ''Les caractéristiques définissant les Hadogeninae sont exposées dans ma note de 1999.''

Prendini (2000) falsified the hypothesis that *Hadogenes* is the sister genus of *Heteroscorpion* in a cladistic analysis that consistently placed *Hadogenes* within the Ischnuridae. Fourteen extra steps (17.5 decrease in fitness) were required to constrain (*Hadogenes + Het-*

eroscorpion) to be the monophyletic sister-group of the remaining ischnurid genera, as proposed by Lourenço (1985, 1989). Similarly, there was no evidence for a relationship between *Hadogenes* and the Scorpionidae. Optimization of the characters proposed for the Hadogenidae revealed that dorsoventral and lateral compression are plesiomorphic, the doubled hook of the hemispermatophore is autapomorphic, and both the elongated metasoma and the accessory trichobothria have been independently derived on numerous occasions within the Hemiscorpiidae Pocock 1893, Heteroscorpionidae, Ischnuridae and Scorpionidae (Prendini 2000). Provision of familial status for *Hadogenes* renders the Ischnuridae paraphyletic and is unjustified by the evidence. Accordingly, I hereby propose the new synonymy: Hadogenidae Lourenço 2000 = Ischnuridae Simon 1879.

ACKNOWLEDGMENTS

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