



A reanalysis of *Parabuthus* (Scorpiones: Buthidae) phylogeny with descriptions of two new *Parabuthus* species endemic to the Central Namib gravel plains, Namibia

LORENZO PRENDINI^{1*} and LAUREN A. ESPOSITO^{1,2}

¹Division of Invertebrate Zoology, American Museum of Natural History, Central Park West at 79th Street, New York, NY 10024-5192, USA

²City University of New York, 365 Fifth Avenue, New York, NY 10016-4309, USA

Received 15 January 2009; accepted for publication 1 June 2009

Two new thick-tail scorpions in the genus *Parabuthus* Pocock, 1890 are described from the gravel plains of the Central Namib Desert, Namibia: *Parabuthus glabrimanus* sp. nov.; *Parabuthus setiventer* sp. nov. The two new species occupy discrete distributional ranges, allopatric with the closely related species *Parabuthus gracilis* Lamoral, 1979 and *Parabuthus nanus* Lamoral, 1979. The distributions of the four species are mapped and a key provided for their identification. Revised diagnoses are provided for *P. gracilis* and *P. nanus*. The two new species are added to a previously published morphological character matrix for *Parabuthus* species and their phylogenetic positions determined in a reanalysis of *Parabuthus* phylogeny. *Parabuthus setiventer* sp. nov. is found to be the sister species of *P. nanus*, whereas *P. glabrimanus* sp. nov. is sister to a monophyletic group comprising *P. gracilis*, *P. nanus*, and *P. setiventer* sp. nov. The discovery of two new scorpion species endemic to the Central Namib gravel plains contributes to a growing body of evidence that this barren and desolate region is a hotspot of arachnid species richness and endemism.

© 2010 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2010, 159, 673–710.
doi: 10.1111/j.1096-3642.2009.00608.x

ADDITIONAL KEYWORDS: Arachnida – dichotomous key – endemism – hotspot – morphology – Namib desert – systematics – taxonomy.

INTRODUCTION

The thick-tail scorpion genus *Parabuthus* Pocock, 1890, one of more than 80 genera in the diverse, cosmopolitan family Buthidae C.L. Koch, 1837 (Fet & Lowe, 2000; Kovařík, 2001, 2002, 2003a; Navidpour *et al.*, 2008), is near-endemic to the Afrotropical region. *Parabuthus* is of considerable interest to biologists for several reasons.

The genus includes the world's only diurnal buthid scorpion, *Parabuthus villosus* (Peters, 1862) (Newlands, 1974a; Harington, 1982) and the world's largest buthids, e.g. *Parabuthus granulatus*

(Ehrenberg, 1831), *Parabuthus schlechteri* Purcell 1899, *Parabuthus transvaalicus* Purcell, 1899, and *P. villosus*, which may reach a length of 140 mm and a mass of 14 g (Newlands, 1974a, 1978a).

Parabuthus species (with one exception) possess a stridulatory organ, composed of fine to coarse granules, sometimes forming transverse ridges, on the dorsal surfaces of mesosomal tergite VII, metasomal segments I, II, and, to a lesser extent, III (Newlands, 1974a, 1978a; Lamoral, 1977, 1979, 1980). The stridulatory organ is used to make an audible sound, known as 'stridulation', when the scorpion is alarmed, achieved by repeatedly scraping the aculeus (sting), across the granules or ridges (Hewitt, 1913, 1918; Lawrence, 1928; Alexander, 1958; Dumortier, 1964; Newlands, 1974a, 1978a; McCormick & Polis, 1990).

*Corresponding author. E-mail: lorenzo@amnh.org

Parabuthus displays an 'arid corridor' pattern of distribution (Balinsky, 1962). Twenty species occur in arid south-western Africa and eight species in arid north-eastern Africa and the Arabian Peninsula (Prendini, 2000, 2001a, 2004a, b, 2005; Kovařík, 2003b, 2004). During past periods of increased aridity, such as the Pliocene and the Upper Pleistocene (Tankard & Rogers, 1978; Lancaster, 1981, 1984; Ward, Seely & Lancaster, 1983), the two areas were contiguous, allowing dispersal or range expansion of arid-adapted taxa between them. As evidence for their arid requirements, the southern African species of *Parabuthus* are today restricted to areas receiving under 600 mm of rainfall per annum (Newlands, 1978a, b).

In addition to their dependence on aridity, *Parabuthus* species are specialized for life on particular substrata. Several species (e.g. *Parabuthus distridor* Lamoral, 1980, *Parabuthus kuanyamarum* Monard, 1937, and *Parabuthus kalaharicus* Lamoral, 1977) are restricted to the sand dune systems of the Namib and Kalahari deserts, and exhibit ecomorphological adaptations to facilitate locomotion and burrowing in the soft sand (Lamoral, 1977, 1979, 1980; Prendini, 2001b, 2004a). Others, e.g. *P. villosus*, are specialized for life in rocky areas (Prendini, 2001b, 2004a).

All species of *Parabuthus* are fossorial (Newlands, 1974b, 1978a, b). Burrows are constructed in open ground, at the base of shrubs or under stones (Newlands, 1974b, 1978a, b; Eastwood, 1977, 1978; Lamoral, 1979; Newlands & Martindale, 1980; Harington, 1984; Prendini, 2001a, b, 2004a, 2005). The evolution of burrowing behaviour, and the specialized ecomorphological adaptations associated with it, may explain the diversity and abundance of *Parabuthus* in the arid regions of sub-Saharan Africa. 'Adaptive radiation' in *Parabuthus* may be explained by the 'Effect Hypothesis of macroevolution' (Vrba, 1980), where repeated allopatric speciation is the predicted outcome of vicariance, promoted by stenotopic habitat requirements, i.e. 'substratum specialization' (Prendini, 2001a, b, 2005).

The dependence of *Parabuthus* species on aridity has fortunate implications for the geographical distribution of scorpionism in southern Africa. *Parabuthus* includes some of the world's most dangerously venomous scorpions, envenomation by which is a significant cause of morbidity and, occasionally, mortality, in the sparsely populated arid to semi-arid western regions of southern Africa (Müller, 1993; Bergman, 1997a, b). However, the more densely populated mesic eastern regions are devoid of *Parabuthus* (Prendini, 2001a, 2004a, 2005) and the incidence of scorpion envenomation in southern Africa is therefore lower than might be expected, given the abundance of medically important scorpion species in the region.

The medical importance of *Parabuthus* has received increasing attention during the past 25 years (Newlands, 1974a, 1978a; Newlands & Martindale, 1980; Petersen, 1987; Hill, 1990; Saunders & Morar, 1990; Lee, 1991). It was established that *P. granulatus* and, to a lesser extent, *P. transvaalicus* are responsible for the majority of serious envenomations, including all fatalities that could be unequivocally confirmed (Müller, 1993; Bergman, 1995, 1997a, b). Studies on venom composition showed that the venom of each species examined contains a unique mixture of toxins, which may explain clinical differences in the virulence of their venom (Swerts *et al.*, 1997; DeBont *et al.*, 1998; Tytgat *et al.*, 1998; Dyason *et al.*, 2002; Huys *et al.*, 2002). Studies on sting use and venom composition further demonstrated that *Parabuthus* species use venom conservatively and are able to differentially regulate venom secretion for use in offence or defence (Rein, 1993; Inceoglu *et al.*, 2003).

Several studies have addressed the systematics of *Parabuthus* in recent years (e.g. FitzPatrick, 1994; Prendini, 2000, 2001a, 2003, 2004a; Kovařík, 2003b). The genus currently includes 28 species and 14 subspecies, seven of which are nominotypic (Fet & Lowe, 2000; Kovařík, 2003b, 2004; Prendini, 2004a). Twenty species are endemic to southern Africa (Prendini, 2004a, 2005). Recent fieldwork in Namibia led to the discovery of two new species, described in the present contribution: *Parabuthus glabrimanus* sp. nov.; *Parabuthus setiventer* sp. nov. The two species are endemic to the gravel plains of the Central Namib Desert and occupy discrete distributional ranges, allopatric with the closely related species, *Parabuthus gracilis* Lamoral, 1979 and *Parabuthus nanus* Lamoral, 1979. The distributions of the four species are mapped and a key provided for their identification. Revised diagnoses are provided for *P. gracilis* and *P. nanus*. The two new species are added to a previously published morphological character matrix for *Parabuthus* species and their phylogenetic positions determined in a reanalysis of *Parabuthus* phylogeny. The discovery of two new scorpion species endemic to the Central Namib gravel plains contributes to a growing body of evidence that this barren and desolate region is a hotspot of arachnid species richness and endemism.

MATERIAL AND METHODS

MATERIAL, PHOTOGRAPHY, AND TERMINOLOGY

Specimens collected by the first author were located at night using a portable ultraviolet (UV) lamp, comprising two mercury-vapour tubes attached to a chromium parabolic reflector and powered by a rechargeable 7 Amp/hr, 12 V battery. A portable

Garmin global positioning system (GPS) V Plus device was used for recording the geographical coordinates of collection localities in the field.

Material examined is deposited in the following collections: American Museum of Natural History, New York (AMNH), some bearing numbers from the Alexis Harington Collection (AH); Natal Museum, Pietermaritzburg, South Africa (NM); National Museum of Namibia, Windhoek (SMN); Transvaal Museum, Pretoria, South Africa (TM). Tissue samples of the new species have been stored (in the vapour phase of liquid nitrogen at $-150\text{ }^{\circ}\text{C}$) in the Ambrose Monell Collection for Molecular and Microbial Research (AMCC) at the AMNH.

Photographs were taken in visible light as well as under long wave UV light using a Microptics ML1000 digital imaging system. Measurements were recorded with Mitutoyo digital callipers and counts taken using a Nikon SMZ-1500 stereomicroscope. Colour designation follows Smithe (1974, 1975, 1981). Morphological terminology and mensuration follow previous papers on *Parabuthus* by Prendini (2000, 2001a, 2003, 2004a).

A distribution map was produced using ArcView GIS Version 9.0 (Environmental Systems Research Institute, Redlands, CA, USA), by superimposing point locality records on spatial datasets depicting the topography (500 m contour interval) and political boundaries of southern Africa. A topographic contour coverage was created from the GTOPO30 raster grid coverage, obtained from the website of the US Government Public Information Exchange Resource (<http://edc.ugsgov/products/elevation/gtopo30.html>).

All records of sufficient accuracy were isolated from the material examined to create a point locality geographical dataset for mapping distributional ranges. Records for which geographical coordinates were previously entered by the collector were checked for accuracy and coordinates for the remaining records traced by reference to gazetteers, the official 1:250 000 and 1:500 000 topo-cadastral maps of South Africa published by the Government Printer, a 1:1 000 000 topo-cadastral map of Namibia published by the Surveyor-General (1994), the GEOnet Names Server (<http://earth-info.nga.mil/gns/html/index.html>), and the Fuzzy Gazetteer (<http://dmaweb2/jrc.it/services/fuzzyg/default.asp>). Names of provinces, regions, and magisterial districts of countries listed in the material examined follow the most recent systems (e.g. the post-1994 nine-province system in South Africa).

CLADISTIC ANALYSIS

The cladistic analysis presented is based on previously published morphological data matrices of

relationships amongst the species of *Parabuthus* (Prendini, 2001a, 2003), to which the two new species have been added (Table 1; Appendix). Fifteen new characters (4, 5, 15, 16, 18, 19, 21, 22, 32, 35, 36, 38, 39, 50, 52) were added, mostly to assist with clarifying the phylogenetic placement of the new species. The revised matrix comprises 68 characters, ten coded into multistates and 58 coded into binary states, scored for 29 species. Multistate characters were treated as unordered, i.e. non-additive (Fitch, 1971).

Trees were rooted using the outgroup method (Watrous & Wheeler, 1981; Farris, 1982; Nixon & Carpenter, 1993). As in previous analyses, an exemplar species from each of two Afrotropical buthid genera, *Grosphus* Simon, 1888, from Madagascar, and *Uroplectes* Peters, 1861, from southern and central Africa, were included as outgroup taxa on the basis of evidence that these genera are most closely related to *Parabuthus* (Pocock, 1890; Kraepelin, 1908; Werner, 1934; Prendini, 2004b). The outgroup taxa selected were *Grosphus flavopiceus* Kraepelin, 1900 and *Uroplectes triangulifer* (Thorell, 1876) (Table 1).

Character data were edited, cladograms prepared, and character optimizations conducted using WinClada, v. 1.00.08 (Nixon, 2002). Ambiguous optimizations were resolved using accelerated transformation (ACCTRAN) also known as Farris optimization, which favours reversals over parallelisms to explain homoplasy (Farris, 1970; Swofford & Maddison, 1987, 1992) and therefore maximizes homology (Griswold *et al.*, 1998). Eight uninformative characters (6, 21, 22, 29, 32, 35, 36, 65) were excluded from all analyses; tree statistics were calculated from phylogenetically informative characters only (Bryant, 1995).

Characters were not weighted a priori. Analyses with equal weighting were conducted using NONA v. 2.0 (Goloboff, 1999), according to the following command sequence: hold10000; hold/10; mult*100; [hold 10000 trees in memory; hold ten starting trees in memory; perform tree-bisection reconnection (TBR) branch-swapping on 100 random addition replicates]. Additional swapping on up to 1000 trees that were up to 5% longer than the shortest trees (command jump 50;) was performed to help the swapper move amongst multiple local optima ('islands' *sensu* Maddison, 1991). Finally, trees found with this command were again swapped with TBR, using the command max*; to retain only optimal trees.

Implied character weighting (Goloboff, 1993, 1995) was conducted to assess the effects of weighting against homoplasious characters, and the resultant topologies compared with the topology obtained by analysis with equal weights (see Prendini, 2001a, 2003, 2004b). Pee-Wee v. 3.0 (Goloboff, 1997) was used for analyses with implied weighting, applying the command sequence: hold1000; hold/10; mult*100;

Table 1. Distribution of 68 characters amongst 27 species of the genus *Parabuthus* Pocock, 1890

<i>G. flavopiceus</i>	01010	00100	01000	00000	00000	00000	00000	00000	00000	000--	---00	00000	00000	00000	000
<i>U. triangulifer</i>	10000	00000	00000	00000	01000	00000	00000	00000	00001	000--	---00	01000	00000	00100	000
<i>P. brevimanus</i>	10000	01001	10000	01011	01110	12100	00001	00011	00110	00001	01100	20001	10100	020	
<i>P. calvus</i>	00000	01100	00000	10010	01012	01010	00000	00000	00000	10111	00000	10101	20110	10100	1??
<i>P. capensis</i>	0AAAA	00000	10000	10010	01010	02000	00000	00001	11111	00010	00101	12210	10000	1B0	
<i>P. distridor</i>	10000	01001	10000	01011	01110	12101	00000	01001	000--	---00	1101-	20000	00100	020	
<i>P. glabrimanus</i>	10000	01001	10000	00011	01110	12100	00000	01101	00110	00000	0001-	20000	10100	020	
<i>P. gracilis</i>	10000	00011	10001	-0111	01110	12100	10100	01111	00110	00001	0001-	20000	00100	020	
<i>P. granimanus</i>	01111	00010	10010	10010	01010	02000	00010	00001	11200	00000	00000	12110	01000	1??	
<i>P. granulatus</i>	010AA	00100	11100	00010	01000	12100	00000	00000	10110	01000	00000	10010	10010	021	
<i>P. heterurus</i>	00100	00000	10000	10010	01010	02000	00010	00001	11200	00000	00000	12110	11000	1??	
<i>P. hunteri</i>	00100	00010	10010	10010	01010	02000	00010	00001	11200	00000	00000	12110	01000	1??	
<i>P. kalaharicus</i>	01010	00101	11100	00011	01100	12101	00000	00000	10110	01000	00000	10010	00110	021	
<i>P. kraepelini</i>	00000	00000	11000	10010	01010	02000	00000	00001	11110	10000	00100	12221	10000	120	
<i>P. kuanymarum</i>	10000	01001	11100	01011	01110	12101	00000	01000	00110	00000	1001-	20000	00100	020	
<i>P. laevifrons</i>	00100	01101	11100	00011	01110	12100	00000	00000	00211	00000	10000	11000	11000	021	
<i>P. leiosoma</i>	00100	00000	10000	10010	01010	02000	00010	00001	11100	00000	00000	12110	11000	1??	
<i>P. mossambicensis</i>	00000	00000	10000	10010	01010	02000	00000	00001	11111	10100	00100	12220	10000	120	
<i>P. muelleri</i>	00100	00001	01100	10010	01011	02000	00000	00001	10111	00010	00101	12210	10000	110	
<i>P. namibensis</i>	00100	01000	11100	01011	01010	12000	00000	00001	00211	00000	00000	11110	11000	021	
<i>P. nanus</i>	10000	00010	00001	-0111	11110	12100	10100	11121	00110	00001	0101-	20000	00100	020	
<i>P. pallidus</i>	00000	00000	00000	10010	01011	01000	00000	00001	11100	00000	00101	12110	10000	1??	
<i>P. planicauda</i>	00000	00000	00000	10010	01011	01000	00000	00001	10111	0A000	00101	12110	10000	110	
<i>P. raudus</i>	0AA00	00000	11000	10010	01010	02000	00000	00001	11110	11000	00101	12220	00000	120	
<i>P. schlechteri</i>	0A000	00000	11000	10010	01010	02000	00000	00001	11110	11000	00101	12221	00000	120	
<i>P. setiventer</i>	10000	00011	10001	-0111	01110	12100	10100	01121	00110	00002	0101-	20000	00100	021	
<i>P. stridulus</i>	00A00	01101	11100	00011	01010	12100	00000	00000	00211	00100	10000	11000	01001	021	
<i>P. transvaalicus</i>	01011	00000	11000	10010	01010	02000	00000	00001	11110	10000	00101	12221	00000	110	
<i>P. villosus</i>	010AA	10000	11000	10010	00010	02000	0A000	00002	10111	1A000	00101	12221	00000	111	

The first two taxa are outgroups. Refer to Appendix for character list. Character states are scored 0–2,? (unknown) and – (inapplicable). Characters that are polymorphic in particular taxa are indicated as follows: states [01] represented by ‘A’, and states [12] represented by ‘B’.

jump50; max*; Analyses with implied weighting investigated the use of six values for the concavity constant, k , spanning the input range permitted by Pee-Wee (command: conc N;).

The relative degree of support for each node in the tree obtained with equal weighting was assessed with branch support or decay indices (Bremer, 1988, 1994; Donoghue *et al.*, 1992). Branch support indices up to five extra steps (setting the maximum number of trees held in memory to 10000) were calculated with NONA, by means of the following command sequence: h10000; bsupport 5;

RESULTS

Analysis of the 60 informative characters with equal weights located two most parsimonious trees (MPTs) of 156 steps, consistency index (CI) of 45, and retention index (RI) of 75 (Table 2). The topology of one of these MPTs is portrayed in Figure 2. The other MPT differed with respect to the species comprising node ‘A’, for which the alternative arrangements are indicated in Figure 3.

A single MPT with the same topology as one of the two obtained with equal weights was retrieved in the analyses with implied weights when values for the concavity constant were moderate to mild, i.e. $k = 3–6$ (Table 2; Fig. 2).

Analyses with implied weights under strong concavity ($k = 1$ and 2), located two MPTs, each three steps longer, 4–9% less fit, and with a lower CI than the MPTs obtained by the analyses with equal weights or with implied weights under moderate to mild concavity (Table 2). The MPTs retrieved by these analyses differed from the topology in Figure 2 with respect to the species comprising node ‘B’, for which the alternative arrangements are indicated in Figure 4.

The MPTs obtained by analysis with implied weights under $k = 1$ and 2 are longer and less fit than the MPT obtained by the remaining analyses (Table 2), hence they are considered suboptimal. The single MPT obtained by the majority of analyses under weighting regimes that minimized length and those that maximized fit is regarded as optimal for the data matrix presented. Synapomorphies are indicated on this topology in Figure 2, which provides

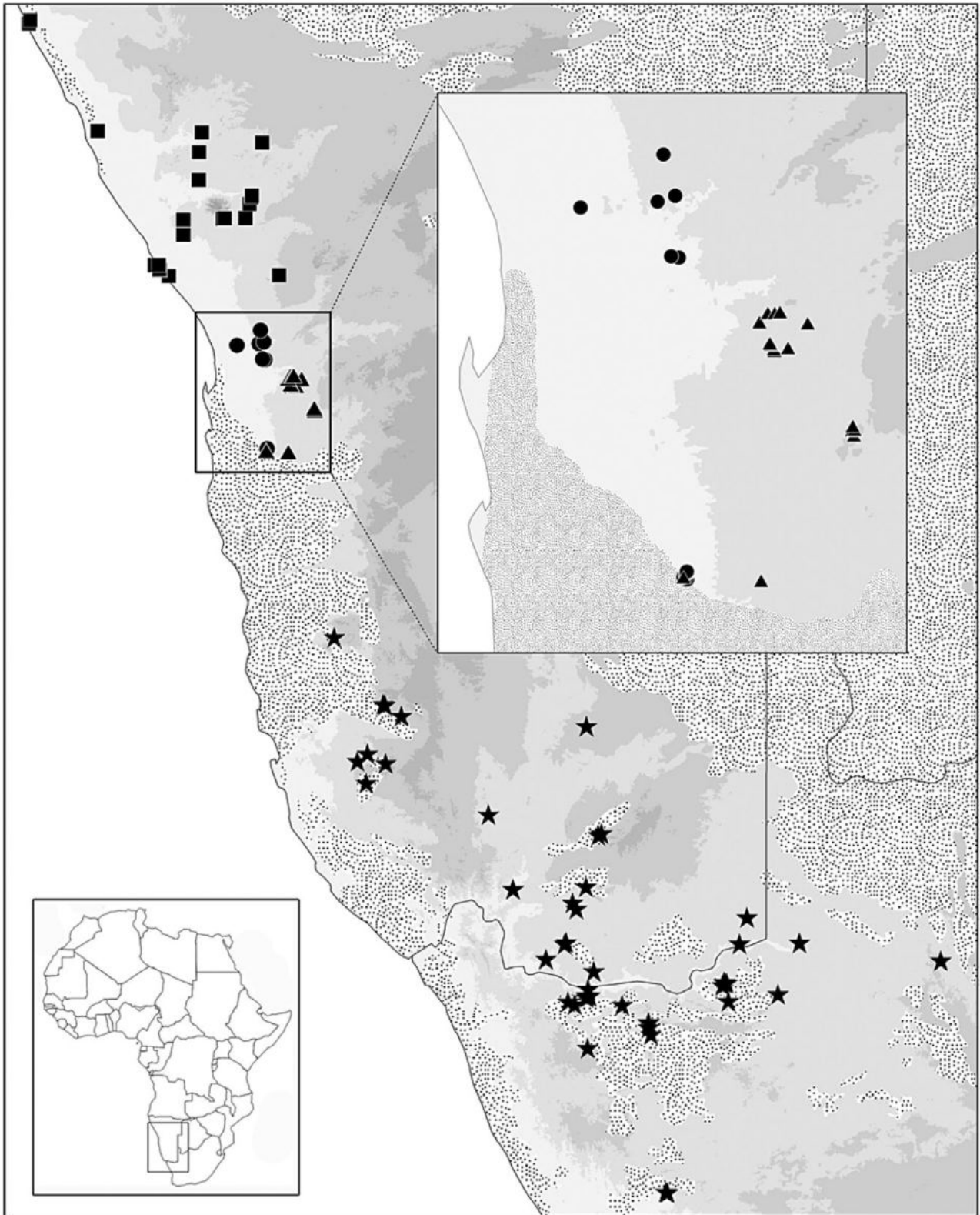


Figure 1. Map showing the known distributions of *Parabuthus glabrimanus* sp. nov. (triangles), *Parabuthus gracilis* Lamoral, 1979 (squares), *Parabuthus nanus* Lamoral, 1979 (stars) and *Parabuthus setiventer* sp. nov. (circles) in Namibia and South Africa. Contour interval, 500 m. Major sand systems stippled. Magnified inset shows distributions of *P. glabrimanus* and *P. setiventer* in finer detail.

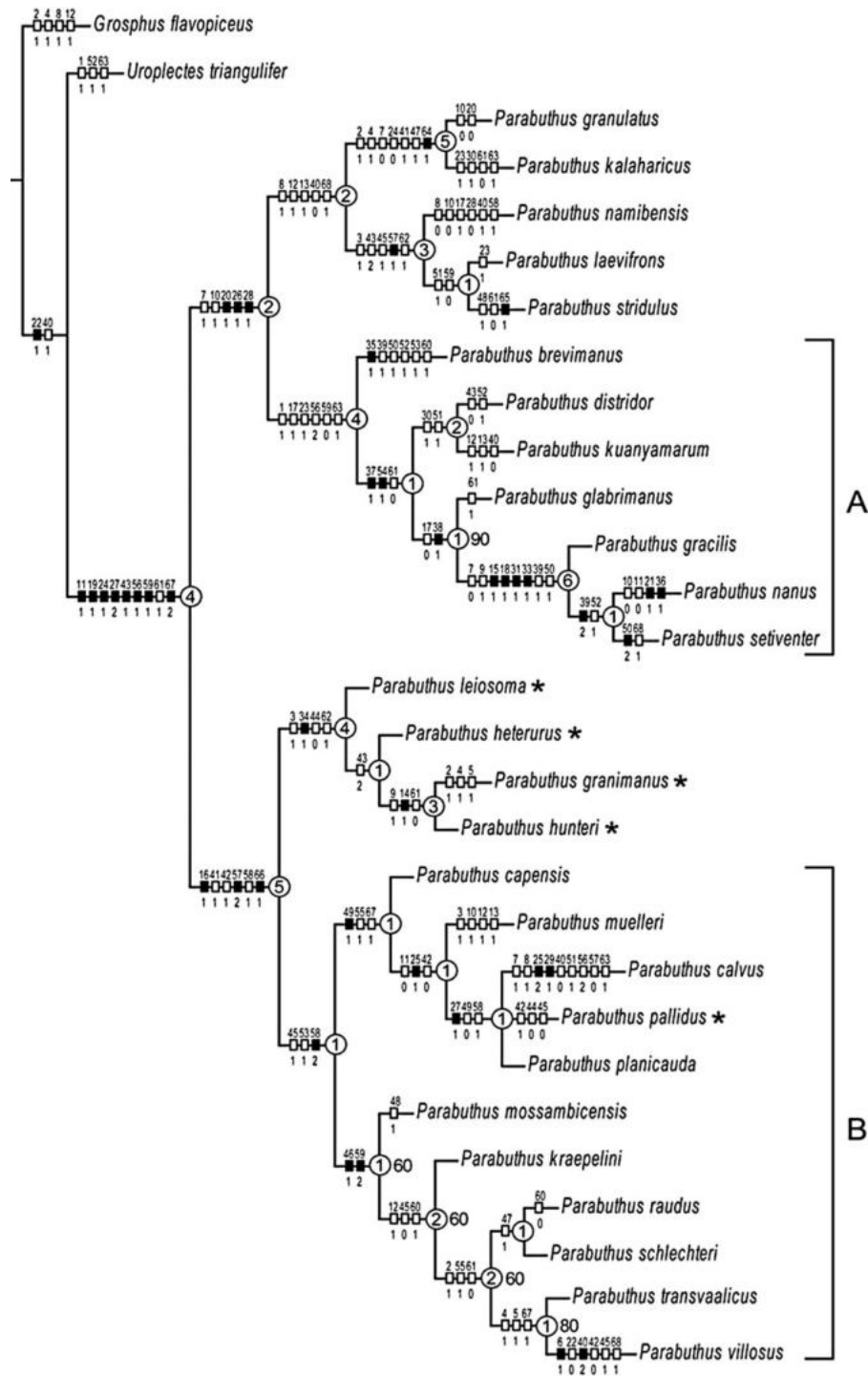


Figure 2. See Table 2 for details. The optimal tree retrieved by analyses with equal weights and implied weights under $k = 3-6$ (Table 2). This topology corresponds to the majority rule (> 50%) consensus of most parsimonious trees (MPTs) obtained by seven analyses in which weighting regime was varied; frequency percentages for nodes that collapsed in the strict consensus of the MPTs obtained by the seven analyses are indicated to the right of relevant nodes. Zero-length branches are collapsed. Solid bars indicate uniquely derived apomorphic character states, whereas empty bars indicate parallel derivations of apomorphic states under accelerated transformation (ACCTRAN) optimization. The number above each bar gives the character number, whereas the number below gives the character state. Branch support values are circled at nodes. Refer to Appendix for character descriptions. The East African species are indicated with asterisks. Alternative topologies for nodes A and B shown in Figures 3 and 4 respectively.

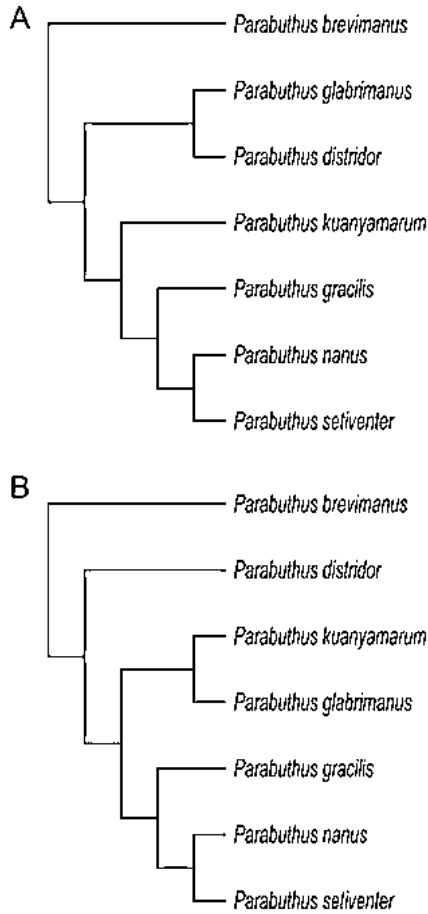


Figure 3. Alternative topologies for node A (Fig. 2) retrieved by analysis with equal weights. See Table 2 for details.

branch support values for nodes retrieved by the analysis with equal weights and frequency percentages for the nodes that collapsed in the strict consensus of the MPTs obtained by all seven analyses. The length, fit (f_i), CIs, and RIs of informative characters on this topology are listed in Table 3.

Phylogenetic relationships amongst the species of *Parabuthus* retrieved by the analyses presented are almost identical to those obtained previously (Pren dini, 2003), as are the major findings. Monophyly of the genus *Parabuthus* is supported, but monophyly of the disjunct southern African vs. north-eastern African and Arabian species is not (Fig. 2, marked with an asterisk). The optimal topology presented differs from that published previously only in the addition of the two new species described below. *Parabuthus setiventer* sp. nov. is found to be the sister species of *P. nanus*, whereas *P. glabrimanus* sp. nov. is sister to a monophyletic group comprising *P. gracilis*, *P. nanus*, and *P. setiventer* sp. nov.

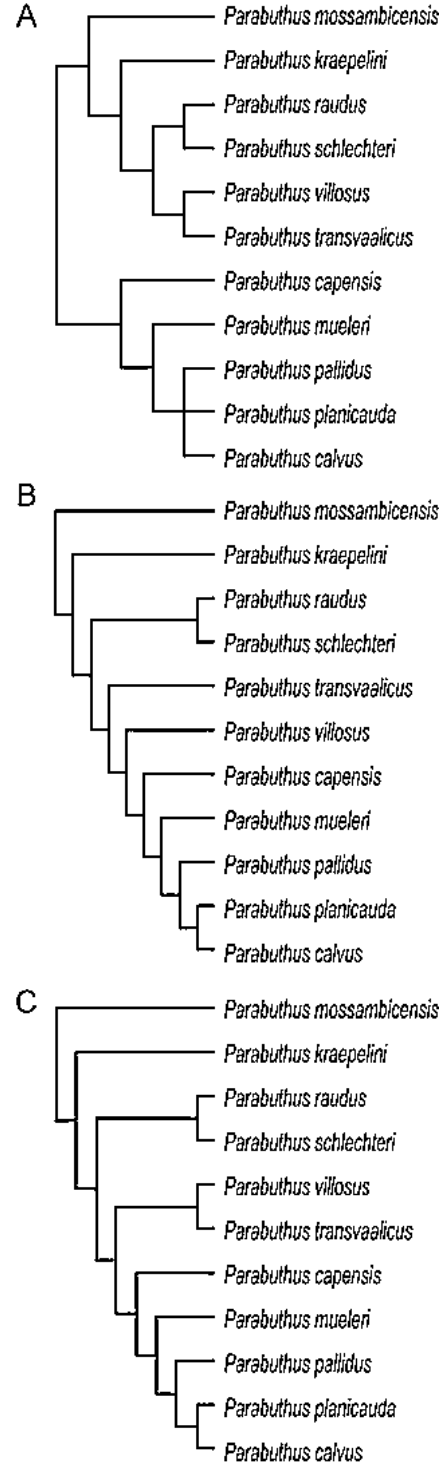


Figure 4. Alternative topologies for node B (Fig. 2) retrieved by analyses with equal weights and implied weights under $k = 3-6$ (A) and with implied weights under $k = 1$ and 2 (B, C). See Table 2 for details.

Table 2. Summary of statistical and topological differences amongst the most parsimonious trees (MPTs) obtained by analysis with equal weights (EW) and implied weights (IW) with six values for the concavity constant (k), arranged in order of decreasing fitness

	MPTs	Steps	Fit (F_i)	Rescaled fit	CI	RI	Node A	Node B
IW: $k = 6$	1	156	497.7	62%	45	75	Fig. 3A	Fig. 4A
IW: $k = 5$	1	156	484.0	61%	45	75	Fig. 3A	Fig. 4A
IW: $k = 4$	1	156	466.5	59%	45	75	Fig. 3A	Fig. 4A
IW: $k = 3$	1	156	441.1	56%	45	75	Fig. 3A	Fig. 4A
EW	2	156	441.1	56%	45	75	Fig. 3B	Fig. 4A
IW: $k = 2$	2	159	401.3	52%	44	75	Fig. 3A	Fig. 4B, C
IW: $k = 1$	2	159	336.0	45%	44	75	Fig. 3A	Fig. 4B, C

Alternative topologies for nodes A and B (Fig. 2) are provided in Figures 3 and 4.
CI, consistency index; RI, retention index.

Table 3. Length (steps), fit (f_i), consistency indices (CI), and retention indices (RI) of 68 informative characters on the most parsimonious tree obtained by the majority of analyses with weighting regimes that maximized fit and minimized length (Fig. 2)

Character	Steps	f_i	CI	RI	Character	Steps	f_i	CI	RI
1	2	5	50	85	38	1	10	100	100
2	4	2.5	25	40	39	3	5	66	50
3	3	3.3	33	66	40	6	2	33	33
4	4	2.5	25	0	41	2	5	50	90
5	2	5	50	0	42	4	2.5	25	70
7	4	2.5	25	57	43	4	3.3	50	71
8	4	2.5	25	40	44	2	5	50	75
9	2	5	50	75	45	5	2	20	50
10	5	2	20	55	46	1	5	100	100
11	3	3.3	33	66	47	2	5	50	66
12	5	1.6	20	66	48	2	5	50	0
13	3	3.3	33	66	49	2	5	50	0
14	1	10	100	100	50	3	5	66	50
15	1	10	100	100	51	3	3.3	33	50
16	1	10	100	100	52	4	2.5	25	25
17	3	3.3	33	33	53	2	5	50	90
18	1	10	100	100	54	1	10	100	100
19	1	10	100	100	55	2	10	50	87
20	2	5	50	90	56	3	5	66	87
23	3	3.3	33	75	57	3	5	66	92
24	2	5	50	66	58	4	3.3	50	85
25	2	10	100	100	59	4	2.5	50	86
26	1	10	100	100	60	3	2.5	33	50
27	2	10	100	100	61	7	1.2	14	53
28	2	5	50	90	62	2	5	50	83
30	2	5	50	50	63	4	2.5	25	66
31	1	10	100	100	64	1	10	100	100
33	1	10	100	100	66	1	10	100	100
34	1	10	100	100	67	3	10	66	75
37	1	10	100	100	68	3	3.3	33	66

DISCUSSION

The Central Namib is a barren, desolate region of the Namib Desert extending from the Kuiseb River northwards to the Huab River and inland from the coast, for about 450 km at the widest point (Giess, 1971; Burke, 1998; Mendelsohn *et al.*, 2002). The region is characterized by largely vegetationless, gravel and sand plains, scattered inselbergs, and numerous dry watercourses running from the escarpment to the sea. Isolated sand dunes occur in places, against the sides of inselbergs (e.g. the Amichab Mountains) and in dry watercourses (e.g. the Swakop River).

The gravel plains of the Central Namib were formed by erosion cutting back into higher ground and carving out the catchment areas of several major rivers, the Khan, Omaruru, Swakop, and Ugab rivers being the most prominent (Mendelsohn *et al.*, 2002). Much of the area lies between 500 and 1000 m above sea level and consists of metamorphic rocks that were forced up out of the sea during the formation of the Gondwana continent some 550 Mya.

The limited vegetation of the Central Namib was described by Giess (1971). A narrow strip of vegetation of varying width (up to 200 m) occurs along the coast north of the Swakop River. Small shrub-coppice or hummock dunes have formed over and around bushes of *Zygophyllum clavatum* Schlechter & Diels, 1907, *Psilocaulon salicomioides* (Schwantes, 1928), and *Salsola* Linnaeus, 1753 species in this area. The large gypsum and gravel plains, further inland, but still close to the coast, are in places densely covered by lichens such as *Teloschistes capensis* Müller Argau, 1911, and species of *Parmelia* Acharius, 1803 and *Usnea* Dillenius ex Adanson, 1763.

Although the bushes *Arthroa leubnitziae* Schinz, 1894 and *Tetraena stapfii* (Schinz) Beier & Thulin, 2003 sometimes occur widely spaced on the gravel plains, the vegetation of this area is dominated by annual white desert grasses. *Aristida parvula* (Nees) DeWinter, 1963, *Triraphis pumilio* Brown, 1826, and *Sporobolus nebulosus* Hackel, 1889 are found in addition to the conspicuous and common species of *Stipagrostis* Nees, 1832, including *Stipagrostis hirtigluma* (Steudel) DeWinter, 1963, *Stipagrostis namibensis* DeWinter, 1964, and *Stipagrostis uniplumis* (Licht) DeWinter, 1963. The grass plains between the true desert and the escarpment are covered mainly by *Stipagrostis obtusa* Nees, 1832 with *Stipagrostis ciliata* (Desfontaines) DeWinter, 1963 on the sandy parts and *Eragrostis nindensis* Ficalho & Hiern, 1881, a perennial grass, on the stony, gravelly, and limestone areas.

The vegetation of the dry watercourses and riverbeds of the Central Namib becomes progressively denser further inland. A shrub, *Acacia reficiens*

Wawra & Peyr, 1860, occurs 30 km from the coast near the Rössing Mountains. *Asclepias buchenaviana* Schinz, 1888 flowers and bears fruit almost throughout the year and the yellow fruits of the perennial *Citrullus ecirrhosus* Cogniaux, 1889 lie in clusters on the otherwise barren ground.

The !nara, *Acanthosicyos horrida* Welwitsch, 1886, is common at the mouth of the Kuiseb River and occurs along its bed to about 100 km inland, but is not widely distributed elsewhere in the Central Namib. It occurs mostly in or near riverbeds, each plant forming a shrub-coppice dune by continually growing through the sand that accumulates around it.

The southern limit of the distribution of *Welwitschia mirabilis* Hooker, 1863 occurs in the Central Namib, at a bend in the Kuiseb River near Natab. Populations of *Welwitschia* Reichenbach, 1837 occur near the Hope and Gorob mines, at the Haigamkab Vlake south of the Swakop River, and on the *Welwitschia* Vlake north of the Swakop River in the Khan-Swakop River triangle. Further north, the first population occurs east of the Strathford Mine, south of Cape Cross. It is found again at the Messum Mountains, north of Cape Cross, after which it occurs further to the west and the south of the Brandberg.

The Central Namib has long been recognized as a hotspot of endemism and species richness for tenebrionid beetles. Koch (1962: 82–85) reported 24 genera and 40 species of tenebrionid beetles from the region between the Kuiseb and the Huab rivers. Twenty-three of these were listed as endemic to the area. The famous ‘white’ tenebrionids of the Namib Desert (*Onymacris* Allard, 1885 and *Stenocara* Solier, 1835 of *Adesmiini* Lacordaire, 1859 and *Calosis* Deyrolle, 1867 of *Zophosini* Solier, 1834), characterized by a white to yellowish-white, more or less unpigmented elytral cuticle, are endemic to the Central and Northern Namib. Their range of distribution, like most Central Namib endemics, starts at the northern bank of the Kuiseb River and follows roughly the same distribution as *Welwitschia* (Koch, 1962). No ‘white’ tenebrionids occur south of the Kuiseb River.

The Central Namib is also known as a hotspot of endemism and species richness for reptiles (Griffin, 1998a; Mendelsohn *et al.*, 2002). Between 21 and 30 endemic Namibian lizards and nine or ten endemic Namibian snakes occur in the Central Namib (Griffin, 1998a). Between 25 and 28 endemic Namibian reptile species inhabit the gravel plains between the Kuiseb and Swakop rivers (Mendelsohn *et al.*, 2002: 113).

The high levels of endemism and species richness of non-acarine arachnids in the Central Namib are equally pronounced, although relatively less well known (Griffin, 1990, 1998b, c; Mendelsohn *et al.*, 2002). In Griffin’s (1998b: 128, table 2.23) assessment,

Table 4. Described spider, solifuge, and scorpion species endemic to the Central Namib Desert, Namibia

Order	Family	Species	Habitat
Araneae	Eresidae C.L. Koch, 1850	<i>Seothyra annettae</i> Dippenaar-Schoeman, 1991	Gravel plains
	Migidae Simon, 1889	<i>Moggridgea eremicola</i> Griswold, 1987	Inselbergs
	Zodaridae F.O.P. Cambridge, 1893	<i>Cyrioctea hirsuta</i> Platnick & Griffin, 1988	River mouth
		<i>Cyrioctea namibensis</i> Platnick & Griffin, 1988	Gravel plains
Scorpiones	Buthidae C.L. Koch, 1837	<i>Cyrioctea whartoni</i> Platnick & Griffin, 1988	Dry watercourse
		<i>Parabuthus glabrimanus</i> sp. nov.	Gravel plains
		<i>Parabuthus gracilis</i> Lamoral, 1979	Sand-dunes, dry watercourses
		<i>Parabuthus namibensis</i> Lamoral, 1979	Gravel plains
		<i>Parabuthus setiventer</i> sp. nov.	Gravel plains
		<i>Uroplectes pilosus</i> (Thorell, 1876)	Inselbergs
	Scorpionidae Latreille, 1802	<i>Opisthophthalmus jenseni</i> (Lamoral, 1972)	Sand-dunes, dry watercourses
		<i>Opisthophthalmus penrithorum</i> Lamoral, 1979	Gravel plains
		<i>Ceroma inerme</i> Purcell, 1899	Beach
		<i>Blossia planicursor</i> Wharton, 1981	Gravel plains
Solifugae	Ceromidae Roewer, 1933	<i>Blossia purpurea</i> Wharton, 1981	Gravel plains
		<i>Namibesia pallida</i> Lawrence, 1962	Inselbergs
	Gylippidae Roewer, 1933	<i>Trichotoma brunnea</i> Lawrence, 1968	Coast
		<i>Trichotoma michaelsoni</i> (Kraepelin, 1914)	Gravel plains
		<i>Hexisopus infuscatus</i> Kraepelin, 1899	Gravel plains
	Hexisopodidae Pocock, 1897	<i>Hexisopus moisei</i> Lamoral, 1972	Gravel plains
		<i>Hexisopus pusillus</i> Lawrence, 1962	Gravel plains
	Melanoblossiidae Roewer, 1933	<i>Lawrencega longitarsus</i> Lawrence, 1929	Gravel plains
		<i>Lawrencega procera</i> Wharton, 1981	Gravel plains

Data from Lamoral (1979), Wharton (1981), Griffin (1998), and unpublished sources.

the Central Namib ranked second amongst the 14 vegetation types of Giess (1971) in number of arachnid species per km². It ranked second (with 27 species), fourth (with 19 species), and fifth (with 45 species), respectively, in terms of solifuge, scorpion, and spider species richness. According to Mendelsohn *et al.* (2002: 111, 113), 18 to 21 scorpion species occur in the Central Namib, the greatest concentration of endemic Namibian scorpion species (nine to 11) occurring on the gravel plains to the east of Swakopmund. Based on our records, five spider species, seven scorpion species, and 11 solifuge species are endemic to the Central Namib (Table 4). Two spider species, four scorpion species, and eight solifuge species are endemic to the gravel plains. The discovery of two new scorpion species endemic to the gravel plains, described below, contributes to a growing body of evidence that this barren and desolate region is a hotspot of arachnid species richness and endemism. Future surveys and inventories of this part of the Namib Desert will undoubtedly reveal still further undescribed endemic arachnids. Indeed, Platnick's (1992) suggestion that the moist equatorial tropics are not inordinately rich, relative to the semi-arid

subtropics, is likely to be supported as arachnological research in arid regions progresses (Griffin, 1998b, c).

TAXONOMY

FAMILY BUTHIDAE C. L. KOCH, 1837

GENUS *PARABUTHUS* POCOCK, 1890

PARABUTHUS GLABRIMANUS SP. NOV.

(FIGS 1–4, 5A, B, 6A, 7A–C, 8, 9B–E, 10–12)

Holotype: Namibia: *Erongo Region*: Swakopmund District: Namib-Naukluft Park: Ganab, 23°08.71'S, 15°30.89'E, 26.i.1998, L. Prendini & E. Scott, soft sand in dry wash near Nature Conservation officers' houses, UV detection, 1 ♂ (SMN 2901).

Paratypes: Namibia: *Erongo Region*: Swakopmund District: Namib-Naukluft Park: Bloedkoppie, 500 m east, 22°50'36.1"S, 15°23'22.2"E, 31.vii–2.viii.2008, R.A. Wharton & T.L. Bird, 743 m, under stones, 1 ♀ (SMN 3391); North-east Range, Ganab flats, 23°08'S, 15°35'E, 8.xi.1974, S. Endrödy-Younga, 1 ♂ [TM 11332 (E-Y 483)]; Ganab Station, 200 m south of

KEY TO SOUTHERN AFRICAN SPECIES OF *PARABUTHUS* POCKOCK, 1890 WITHOUT VENTROSUBMEDIAN AND VENTROLATERAL CARINAE ON METASOMAL SEGMENT IV (COUPLET 2 IN THE KEY OF PRENDINI, 2004A)

1. Pedipalp chela asetose; trichobothrium *dt* in line with or distal to *et*.....*P. calvus* Purcell, 1898
Pedipalp chela covered in setae; trichobothrium *dt* proximal to *et*.....2
2. Metasomal segments I and II, dorsal stridulatory surface absent, ventrosulmedian and ventrolateral carinae absent.....*P. distridor* Lamoral, 1980
Metasomal segments I and II, dorsal stridulatory surface present, ventrosulmedian and ventrolateral carinae present.....3
3. Metasomal segments II and III, posterior section of ventrolateral carinae composed of strongly elevated, crescent-shaped tubercles, forming broad U-shaped pattern.....*P. brevimanus* (Thorell, 1876)
Metasomal segments II and III, posterior section of ventrolateral carinae costate or composed of isolated, round granules, not forming U-shaped pattern.....4
4. Carapace (female) with smooth areas; pedipalp chela smooth and shiny; sternite VII and metasomal segment I, ventral surface sparsely covered with acuminate setae.....5
Carapace (female) entirely granular; pedipalp chela granular; sternite VII and metasomal segment I, ventral surface moderately to densely covered with truncate setae.....6
5. Pedipalp chela fixed and movable fingers strongly curved, such that proximal dentate margin distinctly emarginate (i.e. proximal 'gap' evident) when fingers closed; metasomal segment V, ventrolateral carinae with spinose processes (narrow, conical or flattened, and tapering apically) posteriorly.....*P. kuanyamarum* Monard, 1937
Pedipalp chela fixed and movable fingers straight, such that proximal dentate margin linear (i.e. no proximal 'gap' evident) when fingers closed; metasomal segment V, ventrolateral carinae with lobate processes (broad and presenting a flat surface apically) posteriorly.....*P. glabrimanus* sp. nov.
6. Pedipalp chela movable finger long, compared with manus (measured along ventroexternal carina), length finger/length manus: 1.70–2.00; chela manus (adult male) slender.....*P. nanus* Lamoral, 1979
Pedipalp chela movable finger short, compared with manus (measured along ventroexternal carina), length finger/length manus: \pm 1.50; chela manus (adult male) incrassate (bulbous or swollen).....7
7. Sternite VII, metasomal segment I and, to a lesser extent, II–IV, ventral surfaces densely covered in short, truncate macrosetae; metasomal segment I, ventrosulmedian carinae absent.....*P. setiventer* sp. nov.
Sternite VII and metasomal segments I–IV, ventral surfaces moderately to sparsely covered in short, truncate macrosetae; metasomal segment I, ventrosulmedian carinae present.....*P. gracilis* Lamoral, 1979

turnoff from Ganab road, 23°08'41.9"S, 15°31'24.4"E, 20.i.2009, L. Prendini, T.L. Bird & J. Huff, 1053 m, Central Namib gravel plains on north side of Tumasberg, *Stipagrostis* grassland with few granite outcrops, sandy-loam soil, UV detection on cool, dark night, light breeze, specimens sitting on gravel plains, sympatric with *Parabuthus brevimanus*, *Uroplectes gracilior* Hewitt, 1914, and *Opisthophthamus jenseni* (Lamoral, 1972), 3 ♂ (AMNH); Ganab Station, 200 m east of Ganab road, 23°08'37.5"S, 15°31'17.2"E, 20.i.2009, L. Prendini, T.L. Bird & J. Huff, 1044 m, Central Namib gravel plains on north side of Tumasberg, *Stipagrostis* grassland with few granite outcrops, sandy-loam soil, UV detection on cool, dark night, light breeze, specimens sitting on gravel plains, sympatric with *P. brevimanus*, *P. granulatus*, *O. jenseni*, and *O. wahlbergii* (Thorell, 1876), 2 ♂ (AMNH), 1 juvenile ♂ [AMCC (LP 9413)]; Ganab Station, 800 m east of Ganab road, 23°08'42.7"S, 15°30'54.3"E, 20.i.2009, L. Prendini, T.L. Bird & J. Huff, 1035 m, Central Namib gravel plains on north side of Tumasberg, low granite outcrops, dry riverbed, sandy-loam soil, gritty in places, UV detection on cool, dark night, light breeze, specimens sitting on gravel

plains, sympatric with *P. brevimanus*, *U. gracilior*, *Opisthophthamus coetzeei* Lamoral, 1979 and *O. jenseni*, 1 juvenile ♀ (AMNH), 1 juvenile ♀ [AMCC (LP 9416)]; Ganab VIP campsite, turnoff on Ganab road, 23°09'35.6"S, 15°31'10.9"E, 20.i.2009, L. Prendini, T.L. Bird & J. Huff, 1048 m, Central Namib gravel plains on east side of Tumasberg, *Stipagrostis* grassland with few granite outcrops, sandy-loam soil, UV detection on cool, dark night, light breeze, specimens sitting on gravel plains, sympatric with *U. gracilior*, *O. jenseni*, and *O. wahlbergii*, 1 ♂, 1 juvenile ♂ (AMNH); Gobabeb, gravel plains around camp and immediately on north bank of Kuiseb River, 23°33'36.2"S, 15°02'23.45"E, 19.i.2009, L. Prendini, T.L. Bird & J. Huff, 405 m, central Namib gravel plains, UV detection on cool, moonless night, slight breeze, syntopic with *P. setiventer* sp. nov., 2 ♂ (AMNH); 22 km from Gobabeb to Mirabib, 23°30'S, 15°11'E, 28.ii.1975, S. Endrödy-Younga, 1 subadult ♂ (TM 11087), 1 subadult ♂ (TM 11096); 52 km from Gobabeb on Mirabib road, 23°23'S, 15°31'E, 26.i.1975, S. Endrödy-Younga, 1 juvenile ♂ (TM 11117); Gorob Mine, quartz hill c. 500 m east, 23°34'11.6"S, 15°15'29.1"E, 20.i.2009, L. Prendini, T.L. Bird & J.

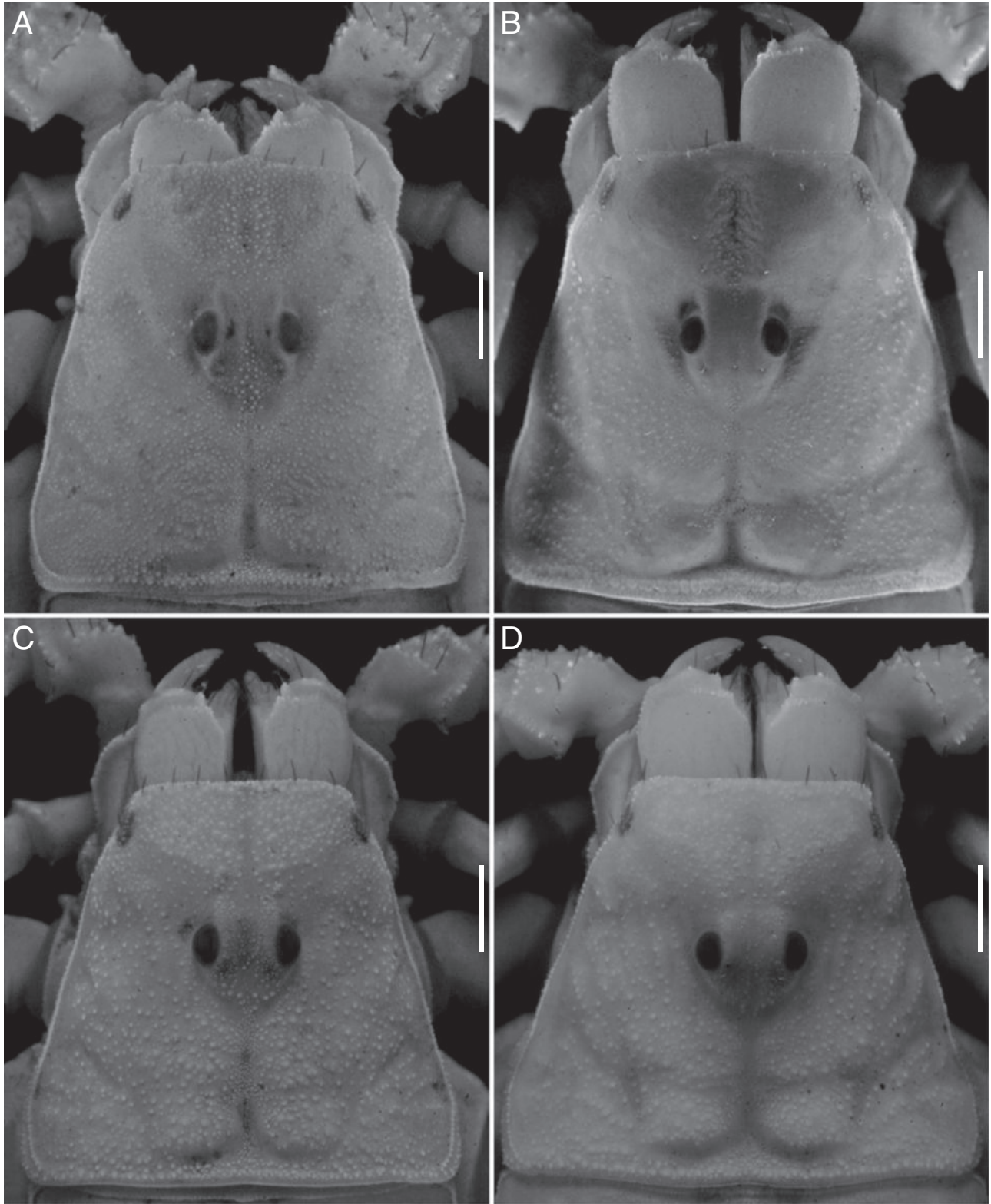


Figure 5. *Parabuthus glabrimanus* sp. nov. (A, B) and *Parabuthus setiventer* sp. nov. (C, D), carapace, dorsal aspect. A, holotype ♂ (SMN 2901). B, paratype ♀ (AMNH). C, holotype ♂ (SMN 2918). D, paratype ♀ (AMNH). Scale bars = 2 mm.

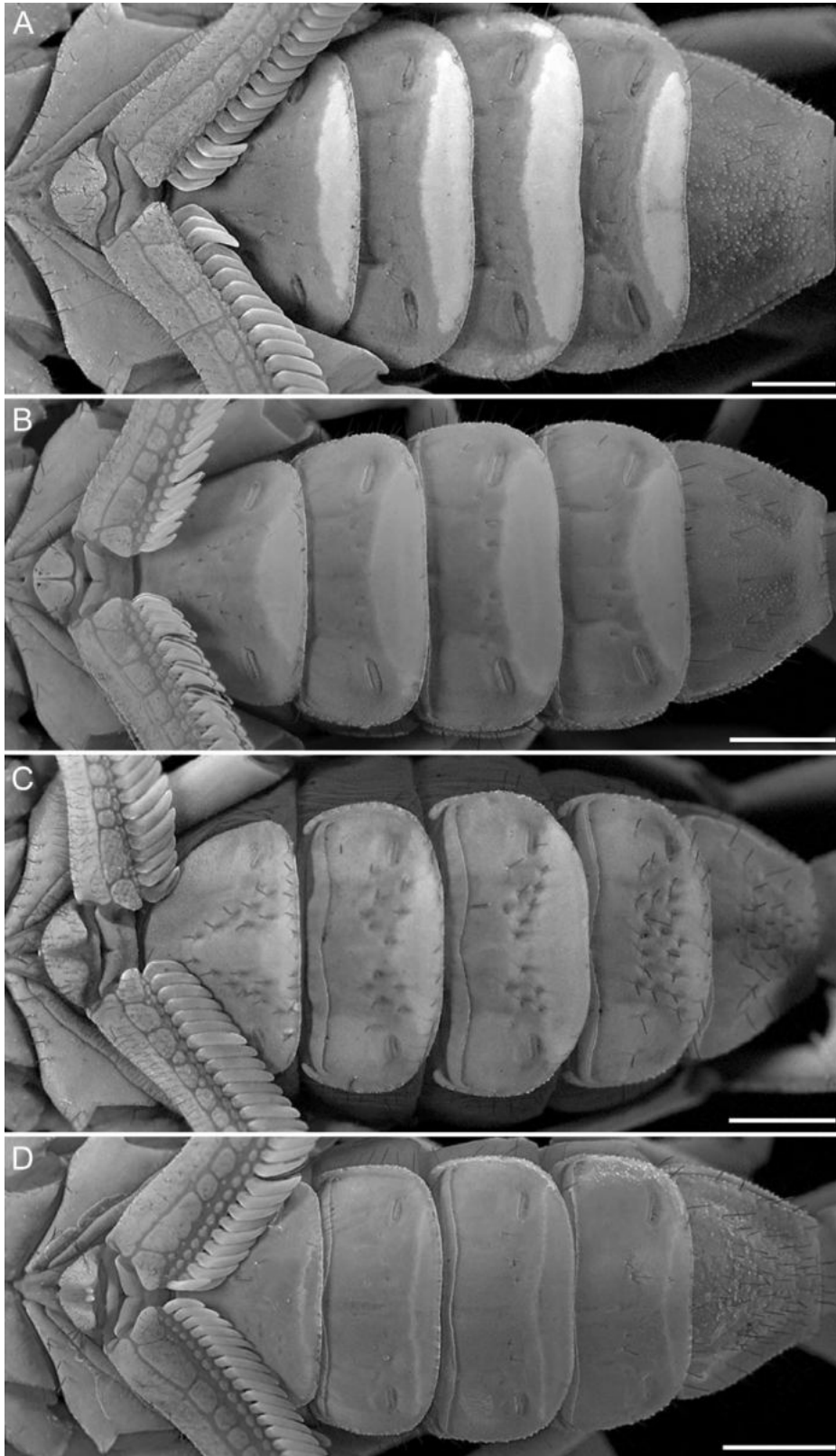


Figure 6. *Parabuthus glabrimanus* sp. nov. (A), *Parabuthus gracilis* Lamoral, 1979 (B), *Parabuthus nanus* Lamoral, 1979 (C) and *Parabuthus setiventer* sp. nov. (D), sternites III–VII, ventral aspect. A, ♂ [AMNH (AH 2164)]. B–D, ♂ (AMNH). Scale bars = 2 mm.

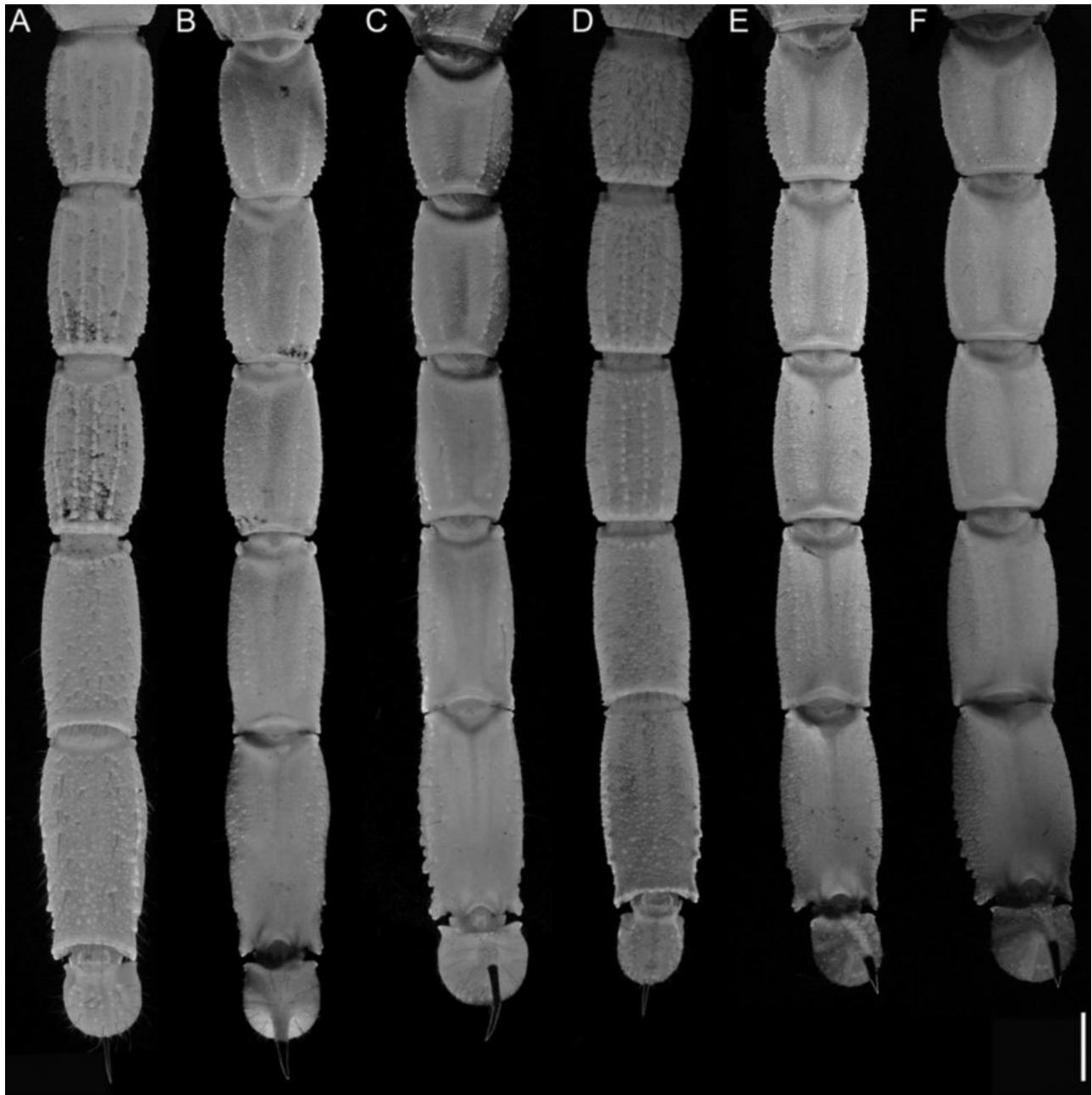


Figure 7. *Parabuthus glabrimanus* sp. nov. (A–C) and *Parabuthus setiventer* sp. nov. (D–F), metasoma and telson. A, D, ventral aspect. B, C, E, F, dorsal aspect. A, B, holotype ♂ (SMN 2901). C, paratype ♀ (AMNH). D, E, holotype ♂ (SMN 2918). F, paratype ♀ (AMNH). Scale bar = 2 mm.

Huff, 603 m, central Namib gravel plains with very sparse grass, Welwitschias in riverbed, soft, crumbly sandy-loam soil with high mica content, specimen taken from scrape under quartz stone on small rocky hill, syntopic with *O. jenseni*, 1 ♀ (AMNH); Langer Heinrich Mountain area, 22°48'40.9"S, 15°18'40.3"E, 27.ii.2006, Science EduVentures '06, 1 ♂ (SMN 2902 (EVS-1 P6-A)], 22°55'16.0"S, 15°17'44.7"E, 28.ii.2006,

Science EduVentures '06, 704 m, UV detection, syntopic with *Lisposoma elegans* Lawrence (1928) and *Uroplectes planimanus* (Karsch, 1879), 1 ♀, 1 subadult ♂, 2 subadult ♀, 2 juvenile ♂, 1 juvenile ♀ [SMN 2769 (SEV 06/03(a))], 22°48'49.2"S, 15°16'38.57"E, 1.iii.2006, Science EduVentures '06, 616 m, UV detection, syntopic with *Opisththalmus penrithorum* Lamoral, 1979 and *O. wahlbergii*, 1 ♂,



Figure 8. *Parabuthus glabrimanus* sp. nov., habitus. A, B, holotype ♂ (SMN 2918). C, D, paratype ♀ (AMNH). A, C, dorsal aspect. B, D, ventral aspect. Scale bar = 10 mm.

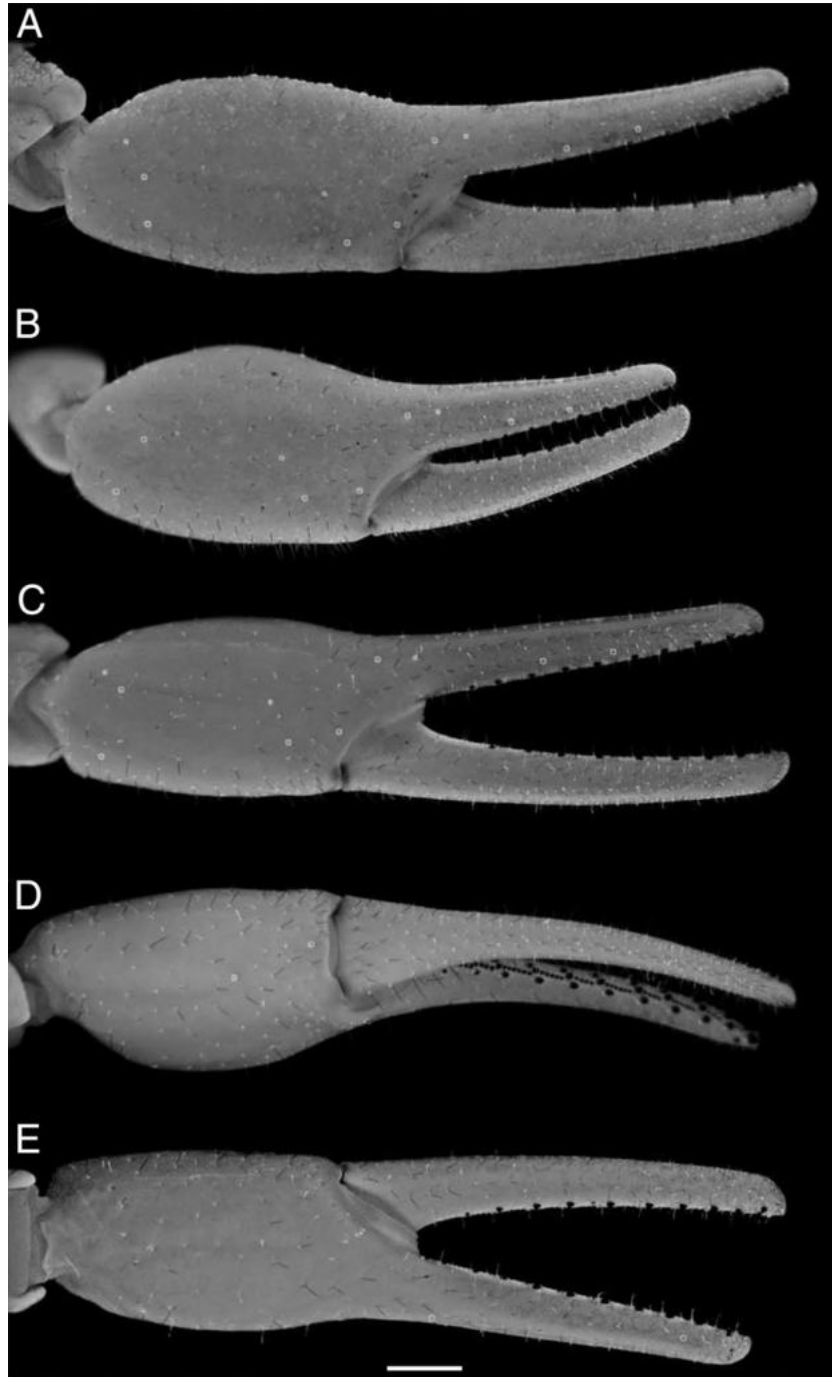


Figure 9. *Parabuthus gracilis* Lamoral, 1979 (A) and *Parabuthus glabrimanus* sp. nov. (B–E), dextral pedipalp chela, illustrating trichobothrial distribution. A, ♂ [AMNH (AH 4397)], external aspect. B, holotype ♂ (SMN 2901), external aspect. C–E, paratype ♀ (AMNH), external (C), ventral (D), and internal (E) aspects. Scale bar = 1 mm.

1 ♀, 5 subadult ♂, 1 subadult ♀ [SMN 2752 (SEV 06/08(a))], 1 ♂ [SMN 2898 (SEV 06/08(a))], 1 ♂, 3 ♀ [SMN 2899 (SEV 06/05(a))], 22°53'57.4"S, 15°16'58.4"E, 2.iii.2006, Science EduVentures '06, 638 m, UV detection, syntopic with *Hadogenes tityrus* (Simon, 1888), 1 ♂, 1 subadult ♂ [SMN 2897 (SEV

06/11)], 22°54'56.5"S, 15°17'40.2"E, 1.iii.2006, Science EduVentures '06, 701 m, UV detection, 1 subadult ♂ (SMN 2751), 2.iii.2006, Science EduVentures '06, 701 m, UV detection, 1 ♂, 1 subadult ♂ (SMN 2069); Langer Heinrich Mountain, gravel plains south, in Langer Heinrich Mining Lease area, 22°48'49.1"S,

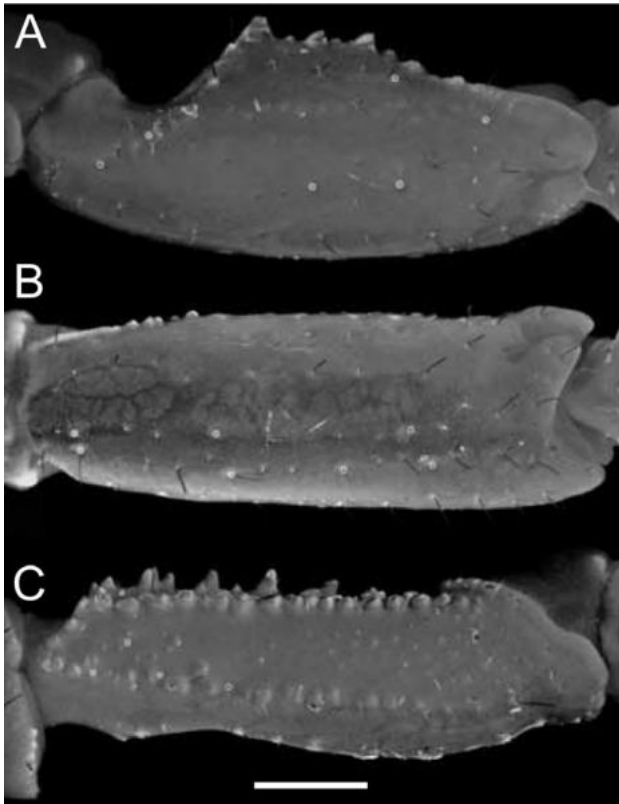


Figure 10. *Parabuthus glabrimanus* sp. nov., paratype ♀ (AMNH), dextral pedipalp patella and femur, illustrating trichobothrial distribution. A, patella, dorsal aspect. B, patella, external aspect. C, femur, dorsal aspect. Scale bar = 1 mm.

15°17'47.3"E, 29.iii.2006, L. Prendini, T.L. Bird & S.K. Uunona, 639 m, UV detection on warm, still, dark night on Central Namib gravel plains with sparse grass, 3 ♂ (AMNH); between Langer Heinrich Berge and Scheifferberge, 22°50'24.8"S, 15°15'12.7"E, 29.iii.2006, L. Prendini, T.L. Bird & S.K. Uunona, 614 m, UV detection on warm, still, dark night on Central Namib gravel plains with granite outcrops and sparse grass, 1 juvenile ♂ (SMN 2896); Scheiffer Mountains, south-east, 22°54'47.6"S, 15°20'03.2"E, 29.i.2007, T.L. Bird, A. Klann, P. Michalik & G. Talarico, 742 m, UV detection, 1 juvenile ♂ [SMN 3075 (TB 06/202)]; Scheiffer Mountains, south-west, 22°54'15.3"S, 15°17'16.6"E, 29.i.2007, A. Klann, G. Talarico, P. Michalik & T.L. Bird, 685 m, 1 ♀ (SMN 3099), 1 ♀ (SMN 3101); Scheifferberge, 1 km north-west, 22°54'07.7"S, 15°17'04.6"E, 29.iii.2006, L. Prendini, T.L. Bird & S.K. Uunona, 679 m, UV detection on warm, still, dark night on Central Namib gravel plains with granite boulders and outcrops, and sparse *Stipagrostis* grassland on sandy patches in between, specimens collected on open sandy flats, sympatric

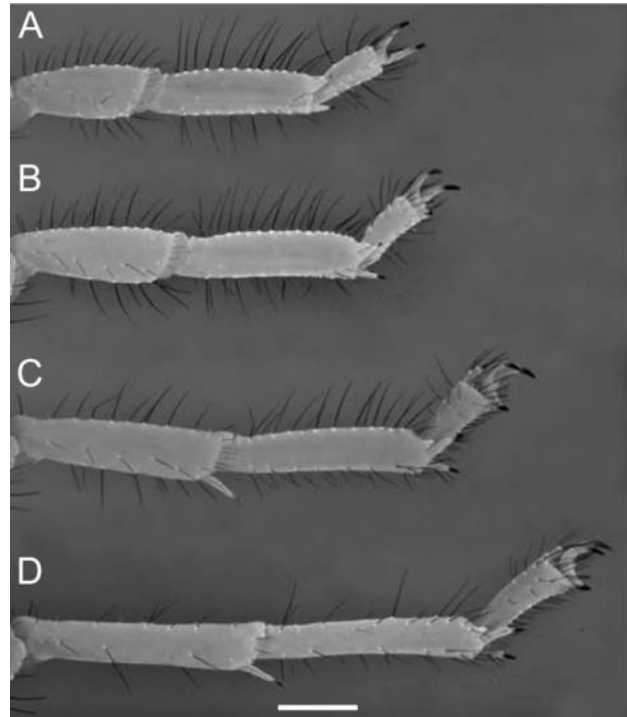


Figure 11. *Parabuthus glabrimanus* sp. nov., paratype ♀ (AMNH), dextral legs I–IV, tibia, basitarsus, and telotarsus, retrolateral aspect, illustrating setae, ungues, and spurs. A, leg I. B, leg II. C, leg III. D, leg IV. Scale bar = 1 mm.



Figure 12. *Parabuthus glabrimanus* sp. nov., paratype ♂ (AMNH), dextral hemispermatophore, ental (A) and ectal (B) aspects. Scale bar = 2 mm.

with *H. tityrus*, 20 ♂, 4 ♀ (AMNH), 1 subadult ♂, 9 subadult ♀, 3 juvenile ♂, 1 juvenile ♀ (SMN 2900).

Diagnosis: *Parabuthus glabrimanus* sp. nov. is sister to the monophyletic group comprising *P. gracilis*, *P. nanus*, and *P. setiventer* sp. nov. (Fig. 2). *Parabuthus glabrimanus* sp. nov. may be separated from these and all other species of *Parabuthus* by means of the following combination of characters: medium to small adult size, carapace length 5.0–6.5 mm; carapace, including median ocular tubercle (male, female), with smooth areas; pedipalp chela movable finger of female short, compared with manus (measured along ventro-external carina), length finger/length manus: ± 1.40 ; pedipalp chela manus of adult male, noticeably incrassate, compared with that of adult female, which is slender; pedipalp chela manus surfaces smooth; pedipalp chela trichobothrium *dt* situated proximal to *et*; pedipalp femur and patella trichobothria *d*₂ present; sternites III–VII and metasomal segment I, ventral surfaces smooth, sparsely setose; metasomal segments slender (length IV/width IV: 1.7–2.11); metasomal segment I, ventrosubmedian carinae absent; metasomal segments II and III, posteroventral margins demarcated by transverse row of lobate granules; metasomal segment IV, acarinate; metasomal segments IV and V, lateral intercarinal surfaces granular; metasomal segment V, dorsosubmedian, dorsolateral and ventromedian carinae absent, ventrolateral carinae present, subparallel to converging posteriorly, and with posterior spiniform granules enlarged into lobate processes.

Etymology: The species name refers to the smooth, shiny chela manus that is characteristic of this species.

Description: The following description is based on the holotype male, two paratype males, and three paratype females (Table 5).

Colour: Carapace, tergites and metasoma, base coloration: Buff-Yellow no. 53. Chelicerae, pedipalp chela, legs, sternites and telson slightly paler than carapace, pedipalp femur and patella, tergites and metasoma (Fig. 8). Chelicerae, pedipalp chela and telson, base coloration: Cream no. 54. Legs and sternites, base coloration: Sulfur Yellow no. 157. Pectines: Pale Horn Color no. 92. The following surfaces strongly to weakly infuscated (Chestnut no. 32): chelicera manus, dorsal surface, distal margin; carapace interocular surface; pedipalp femur and patella, dorsointernal and dorsoexternal surfaces; leg femur, dorsoexternal and dorsointernal surfaces, distal third; post-tergites, postermarginal surfaces; metasomal segments I and II, dorsal and dorsolateral surfaces,

III, dorsal surface, anterior two-thirds, IV, dorsal surface, anterior third, IV, V, and telson, ventrolateral and ventral surfaces. Pale pedipalp chela contrasting with darker patella and femur. Metasoma dorsal surfaces becoming paler posteriorly (IV, V, and telson paler than I–III), ventral surfaces becoming darker posteriorly (IV, V, and telson darker than I–III).

Carapace: Carapace uniformly finely granular, granulation becoming coarser on interocular and posterolateral surfaces (♂), anterolateral, posterolateral, and posteromedian surfaces finely to coarsely granulation, circumocular, interocular, and posteromedian surfaces finely granular, with smooth areas (♀); superciliary carinae smooth. Anterior and posterior margins of carapace slightly procurved (Fig. 5A, B). Five pairs of lateral ocelli. Median ocelli considerably larger than lateral ocelli, situated anteromedially. Ocular tubercle with pair of smooth superciliary carinae, protruding slightly above median ocelli. Anteromedian sulcus shallow; posteromedian sulcus shallow anteriorly, becoming deeper posteriorly; posterolateral sulci shallow, wide, and curved; postero-marginal sulcus narrow, deep.

Chelicerae: Movable finger with distal external and distal internal teeth equal, opposable. Ventral aspect of fingers and manus with long, dense macrosetae. Fixed finger with pair of denticles on ventral surface.

Sternum: Type I, subtriangular (Fig. 8B, D). Median longitudinal furrow Y-shaped, shallow anteriorly, deep, narrow posteriorly.

Pedipalps: Pedipalps covered in short macrosetae (Figs 9, 10). Femur dorsal, internal, and external intercarinal surfaces uniformly, finely granular, ventral surface smooth (♂) or dorsal surface uniformly, finely granular, other intercarinal surfaces smooth (♀) (Fig. 10C); dorsointernal, dorsoexternal, and ventrointernal carinae distinct, granular; internomedian carina comprising discontinuous row of spiniform granules; externomedian carina obsolete, smooth; other carinae absent. Patella intercarinal surfaces uniformly, finely granular (♂) or internal intercarinal surfaces uniformly, finely granular, other surfaces smooth (♀) (Fig. 10A, B); dorsointernal and ventrointernal carinae obsolete, each comprising few granules proximally and distally; internomedian carina comprising prominent spiniform granule, proximally, and few smaller granules, distally; other carinae absent. Chela smooth (Fig. 9B–E); acarinate. Chela short, slender (♀), or markedly incrassate (♂), length along ventroexternal carina 27–38% greater than chela width and 33–46% greater than chela height (Table 5); length of movable finger 14–20% (♂) or 34–40% (♀) greater than length along ventroexternal carina. Chela fixed and movable fingers straight, such that proximal dentate margin linear when fingers closed (Fig. 9B–E). Median denticle row of

chela fixed and movable fingers, respectively, comprising eight and nine oblique primary subrows; each subrow comprising three to six small denticles and large external denticle, flanked by internal and external accessory denticles; terminal subrow of fixed finger shorter than others; basal subrow of fixed and movable fingers longer, comprising fusion of basal and sub-basal subrows; each finger with enlarged terminal denticle.

Trichobothria: Orthobothriotaxic, Type A, α configuration (Figs 9B–E, 10), with following segment totals: femur, 11 (five dorsal, four internal, two external), patella, 13 (five dorsal, one internal, seven external) and chela, 15 (eight manus, seven fixed finger). Total number of trichobothria per pedipalp, 39. Femur d_2 present, situated on dorsal side of dorsointernal carina; e_1 situated level with or distal to d_5 . Patella d_2 present; esb_2 situated slightly distal to esb_1 . Chela Esb situated in line with or dorsal to Eb_2 – Et axis; eb situated proximal to basal dentate margin of fixed finger; dt situated proximal to et .

Mesosoma: Pre-tergites smooth, shiny, granular along posterior margins. Post-tergites entirely covered with uniform, fine granulation, becoming coarser posteriorly, especially along posterior margins (σ^7), anterolateral surfaces smooth, shiny, anteromedian surfaces uniformly, finely granular, posteromedian and posterolateral surfaces coarsely granular, especially along posterior margins (ϕ); I–VII each with weakly developed, costate dorsomedian carina; VII additionally with distinct pairs of costate-granular dorsosubmedian and dorsolateral carinae, and well-developed stridulatory surface between dorsosubmedian carinae, comprising rounded granules reaching posterior margin. Sternites III–VI, surfaces smooth, sparsely setose, lateral and posterior margins each with few macrosetae; VII acarinate, uniformly finely granular (σ^7) or smooth medially with sparse fine granules laterally (ϕ), sparsely setose, lateral and distal margins more densely so (Fig. 6A). Sternite VII, width 24–32% (σ^7) or 25–37% (ϕ) greater than length.

Pectines: First proximal median lamella of each pecten suboval, mesially enlarged, lobate in ϕ but not σ^7 (Fig. 8B, D). Pectinal teeth: 29–31/28–31 (σ^7), 24–26/25–26 (ϕ) (Table 5).

Genital operculum: Completely divided longitudinally. Genital papillae present (σ^7), absent (ϕ).

Legs: Tibiae III and IV with spurs; retrolateral margins with scattered macrosetae (Fig. 11C, D). Basitarsi I, II, and, to a lesser extent, III, dorsoventrally compressed, retrolateral margins each with dense row of long, fine macrosetae (Fig. 11A–C); III and IV, prolateral surfaces without dense tufts of macrosetae. Telotarsi each with paired ventrosubmedian rows of irregularly spaced macrosetae. Telotarsal

laterodistal lobes truncated; median dorsal lobes extending to unguis. Telotarsal unguis long, distinctly curved, equal in length.

Metasoma and telson: Metasomal segments I–V width/length ratio progressively decreasing (Table 5; Fig. 7A–C), width percentage of length 67–73% (σ^7) or 74–79% (ϕ) for I, 56–64% (σ^7) or 62–70% (ϕ) for II, 55–57% (σ^7) or 57–61% (ϕ) for III, 46–51% (σ^7) or 50–58% (ϕ) for IV, and 46–50% (σ^7) or 48–55% (ϕ) for V. Telson oval, globose, height 50–62% (σ^7) or 52–72% (ϕ) of length, with flattened dorsal surface, rounded ventral surface; vesicle not distinctly narrower than metasomal segment V, width 70–79% (σ^7) or 74–90% (ϕ) of metasomal segment V. Aculeus short, sharply curved, 57–92% of vesicle length (Table 5). Metasoma and telson 55–57% (σ^7) or 52–55% (ϕ) of total length. Metasoma intercarinal surfaces uniformly, finely granular, except segment V, dorsal surface, smooth and shiny (σ^7) or smooth and shiny, except segments I–V, dorsolateral and median lateral surfaces and segments IV and V, ventral and ventrolateral surfaces, finely granular, granulation becoming more pronounced posteriorly (ϕ); segments I–III, each with well-developed dorsal stridulatory surface, comprising fine rounded granules extending to posterior margin (Fig. 7B, C), less developed on segment III than I and II; II and III, posterodorsal edge sublinear. Metasoma sparsely to moderately covered with long acuminate macrosetae, especially on ventral surface of telson (Fig. 7A). Metasomal segments I–III each with ten carinae; IV acarinate; V with two carinae. Dorsosubmedian carinae distinct, converging posteriorly on segments I–III, absent on IV and V. Dorsolateral carinae distinct on segments I–III, absent on IV and V. Median lateral carinae distinct on segments I and II; obsolete on III; absent on IV and V. Ventrolateral carinae present, converging posteriorly on segments I–III, posterior section not forming U-shaped pattern on II and III; reduced to anterior row of isolated, rounded granules on IV; subparallel to converging posteriorly on V, with posterior spiniform granules enlarged into broad, lobate processes with flat surfaces apically (Fig. 7A). Ventrosubmedian carinae present on segments I–III; reduced to anterior row of isolated, rounded granules on IV; absent on V. All metasomal carinae costate-granular to granular, except for ventrosubmedian and ventrolateral carinae of segments I (σ^7 , ϕ) and II (ϕ), which are costate to costate-granular.

Hemispermaphore: Flagelliform, with *pars recta* parallel to axis of distal lamina (Fig. 12).

Geographical variation: There is little morphological variation amongst specimens from different localities. However, striking variation in coloration is observed amongst specimens from the same locality. Variation in the intensity of infuscation is most

obvious on the carapace, pedipalps, tergites, metasoma, and telson. Some specimens are darkly infuscated whereas others are pale. Pale specimens are not infuscated on the tergites and weakly so on the metasoma or devoid of infuscation altogether. Similar variation in coloration is observed in *P. gracilis* and *P. nanus* (Lamoral, 1979; this study). Specimens from the two southern- and western-most localities, Gobabeb and Gorob Mine, are devoid of infuscation and the base colour is yellow, unlike specimens from further east, which are buff-yellow.

Ontogenetic variation: As in other species of *Parabuthus*, male resembles female very closely until the final instar (Prendini, 2004a). Juveniles and subadults may be readily sexed by examination of the pectines and genital aperture.

Sexual dimorphism: *Parabuthus glabrimanus* sp. nov. is markedly dimorphic in several respects, most obviously in the shape of the pedipalp chela manus, and the structure of the pectines. As in most species of *Parabuthus* (Prendini, 2004a), the pedipalp chela manus of the adult male is markedly incrassate compared with that of adult female, which is more slender (Fig. 9B–E, Table 5), and the first proximal median lamella of each pecten is suboval, mesially enlarged, and lobate in the female but unmodified in the male. The male has a higher pectinal tooth count (28–31) than the female (24–26). In addition, the adult male is proportionally more slender, with a slightly longer metasoma, than the adult female (Fig. 8, Table 5). The granulation and carination are also more pronounced. For example, the carapace of the male is entirely granular, whereas there are smooth surfaces on the carapace of the female (Fig. 5A, B).

Distribution: Endemic to the gravel plains of the Central Namib, north of the Kuiseb River, in the Erongo Region (Swakopmund District) of western Namibia (Fig. 1). The known records fall within the range of 400–1100 m elevation. *Parabuthus setiventer* sp. nov. is more commonly found at lower elevations (300–450 m), further west. The known distribution of *P. glabrimanus* sp. nov. falls entirely within the boundaries of the Namib-Naukluft Park.

Ecology: *Parabuthus glabrimanus* sp. nov. is a psammophilous species, which displays several ecomorphological adaptations to its sandy habitat: elongated telotarsal ungues; basitarsi of legs I, II, and, to a lesser extent, III dorsoventrally compressed, with comb-like rows of long macrosetae ('sand combs') on the retrolateral margins (Fig. 11A–C); metasoma lacking carinae on segments III–V (Fig. 7A). Specimens of *P. glabrimanus* sp. nov. have been taken in pitfall traps and collected with UV light detection on

warm, dark, still nights, resting on the surface of sandy to gritty substrata, on open gravel plains between granite outcrops. One specimen was collected from under a stone during daytime.

Parabuthus glabrimanus sp. nov. has been collected in sympatry with the following scorpion species: Bothriuridae: *L. elegans*; Buthidae: *P. brevimanus*, *P. granulatus*, *P. setiventer* sp. nov., *U. gracilior*, and *U. planimanus*; Liochelidae: *H. tityrus*; Scorpionidae: *O. coetzeei*, *O. jenseni*, *O. penrithorum*, and *O. wahlbergii*. Its distribution is allopatric with those of the closely related species, *P. gracilis* and *P. nanus* (Fig. 1). *Parabuthus glabrimanus* sp. nov. inhabits softer substrata than *P. brevimanus*.

PARABUTHUS GRACILIS LAMORAL, 1979
(FIGS 1–4, 6B, 9A)

Parabuthus gracilis Lamoral, 1979: 566–571, figs 96, 103, 104, 107–116; Kovařík, 1998: 116; Fet & Lowe, 2000: 202; Prendini, 2001b: 136; Prendini, 2001a: 17; Prendini, 2003: 20; Prendini, 2004a: 116, 143, 144, figs 1, 11, 26, 43; Prendini, 2005: 66, appendix 1; Prendini and Bird, 2008: 79, 80, 87–90, 93, 100, 103, 104, table 1, figs 2, 11.

Holotype: Namibia: *Erongo Region:* Omaruru District: Messum Crater area, 21°16'S, 14°13'E, 26.iii.1976, B.H. Lamoral & L. Ferguson, on surface of sandy to gritty soil at night, 1 ♀ (NM 10925).

Paratypes: Namibia: *Erongo Region:* Omaruru District: Messum Crater area, 21°16'S, 14°13'E, 26.iii.1976, B.H. Lamoral & L. Ferguson, on surface of sandy to gritty soil at night, 8 ♂, 2 ♀, 4 juveniles (NM 10848), 1 ♂ [SMN 766 (ex NM 10848)], 1 ♂ (NM 10906). Swakopmund District: Cape Cross, 5 km north, 21°43'S, 13°56'E, 25.iii.1976, B.H. Lamoral & L. Ferguson, on surface of sandy to gritty soil at night, 2 ♂ (NM 10854). *Kunene Region:* Khorixas District: Skeleton Coast Park: Torra Bay, 30 km south-east, 20°23'S, 13°22'E, 30.iii.1976, B.H. Lamoral & L. Ferguson, on surface of dark brown gravel at night, 1 ♂, 1 juvenile ♂ (NM 10860). Opuwo District: Skeleton Coast Park: Möwe Bay, 8 km north, 19°17'S, 12°42'E, 28.iii.1976, B.H. Lamoral & L. Ferguson, on surface of sandy ground with scattered rocks near high white sand dunes, 1 subadult ♀, 1 juvenile ♀ (NM 10857); Möwe Bay, 4 km north, 19°19'S, 12°41'E, 29.iii.1976, B.H. Lamoral & L. Ferguson, on surface of rocky to gritty ground at night, 3 ♂, 1 ♀, 4 juveniles (NM 10859).

Diagnosis: *Parabuthus gracilis* is sister to the monophyletic group comprising *P. nanus* and *P. setiventer* sp. nov. (Fig. 2). *Parabuthus gracilis* may be

separated from these and all other species of *Parabuthus* by means of the following combination of characters: small adult size, carapace length 2.5–5.0 mm; carapace, including median ocular tubercle (male, female), entirely granular; pedipalp chela movable finger of female short, compared with manus (measured along ventroexternal carina), length finger/length manus: ± 1.50 ; pedipalp chela manus of adult male noticeably incrassate (Fig. 9A) compared with that of adult female, which is slender; pedipalp chela manus surfaces granular; pedipalp chela trichobothrium *dt* situated proximal to *et*; pedipalp femur and patella trichobothria *d*₂ absent or very reduced; sternites punctate; sternites III–VII and metasomal segment I, ventral surfaces moderately to sparsely setose (Fig. 6B); metasomal segments slender (length IV/width IV: 1.7–2.11); metasomal segments II and III, posteroventral margins demarcated by transverse row of isolated, round granules; metasomal segment IV, acarinate; metasomal segments IV and V, lateral intercarinal surfaces granular; metasomal segment V, dorsosubmedian, dorsolateral, and ventromedian carinae absent, ventrolateral carinae present, converging posteriorly, and with posterior spiniform granules enlarged into spinose processes.

Remarks: Compared with specimens from typical populations along the coast (e.g. Cape Cross, Messum Crater), specimens from inland populations (e.g. Bethanis, Twyfelfontein) are paler, less granular, and exhibit morphometric differences in the pedipalp chela and metasoma. The differences observed are not presently considered sufficient to merit recognition of the inland populations as a different species, but the matter is under further investigation from a molecular perspective.

Distribution: Endemic to sandy areas in the Central and Northern Namib, north of the Swakop River, in north-western Namibia (Fig. 1). Recorded from the Erongo Region (Karibib, Omaruru, and Swakopmund districts) and the Kunene Region (Khorixas and Opuwo districts). The known records fall within the range of 0–600 m elevation. *Parabuthus gracilis* is protected in the Brandberg National Monument, the Cape Cross Seal Reserve, and the Skeleton Coast Park.

Ecology: *Parabuthus gracilis* is a psammophilous species, which displays several ecomorphological adaptations to its sandy habitat: elongated telotarsal unguis; basitarsi of legs I, II, and, to a lesser extent, III dorsoventrally compressed, with comb-like rows of long macrosetae ('sand combs') on the retrolateral margins; metasoma and telson lacking carinae on segments III–V. Specimens of *P. gracilis* have been

taken in pitfall traps, collected at night with UV light detection, resting on the surface of sandy to gritty substrata, as well as unconsolidated white sand dunes, and excavated from burrows in shrub-coppice dunes.

Parabuthus gracilis has been collected in sympatry with the following scorpion species: Bothriuridae: *L. elegans*; Buthidae: *P. brevimanus*, *P. granulatus*, *Parabuthus kraepelini* Werner, 1902, *P. namibensis* Lamoral, 1979, *P. stridulus* Hewitt, 1913, *U. gracilior*, *U. planimanus*; Uroplectes *teretipes* Lawrence, 1966; Scorpionidae: *O. jenseni*, *O. penrithorum*, and *O. wahlbergii*. *Parabuthus gracilis* is syntopic with *P. namibensis* and *P. stridulus* in the coastal part of its distributional range, and with *P. brevimanus* and *P. granulatus* inland (Lamoral, 1979; Prendini, 2004a; Prendini & Bird, 2008). *Parabuthus gracilis* generally inhabits softer substrata than *P. brevimanus* and *P. kraepelini*. The distribution of *P. gracilis* is allopatric with those of the closely related species, *P. glabri-manus* sp. nov., *P. nanus*, and *P. setiventer* sp. nov. (Fig. 1).

Additional material: Namibia: Erongo Region: Karibib District: Spitzkoppe, 21°49'S, 15°10'E, 18.xii.2000, Q. Martins, collected at night with UV light, sympatric with *P. brevimanus*, 1 ♂, 1 ♀ [AMNH (LP 1272)], 1 ♂ [AMCC 159716 (LP 1274)]. Omaruru District: Daweb (N Uis), 4 km south, 21°03'S, 14°54'E, 6.ii.1981, A. Harington, on sandy and rocky areas, sympatric with *L. elegans*, *P. granulatus*, *P. kraepelini*, *O. jenseni*, and *O. wahlbergii*, 1 subadult ♂ [AMNH (AH 3386)], 2 subadult ♀ [AMNH (AH 3387, 3388)]; Messum Crater area, 21°25'S, 14°13'E, 21.i.1981, A. Harington, syntopic with *P. brevimanus* and *U. gracilior*, 1 ♂ [AMNH (AH 2164)]; Nai-Gap riverbed at northern tip of Uis mountains, 21°07'S, 14°52'E, 6.ii.1981, A. Harington, syntopic with *P. brevimanus*, 2 subadult ♂ [AMNH (AH 1917, 1918)]; Uis townlands, 21°15'S, 14°50'E, 2.ii.1981, A. Harington, 1 subadult ♂ [AMNH (AH 2167)]; Uis, 20 km from turnoff to Khorixas, 21°02'S, 14°54'E, 6.ii.1981, A. Harington, drizzling, specimens abundant on sand and near rocky surfaces, syntopic with *P. granulatus*, *P. kraepelini*, *O. jenseni*, and *O. wahlbergii*, 1 ♂ [AMNH (AH 2089)], 2 subadult ♂, 3 subadult ♀ [AMNH (AH 2090)]; Brandberg National Monument: Brandberg, base of hill 282, opposite Orabeskopf, 21°15'S, 14°38'E, 1.ii.1981, A. Harington, night collecting (cloudy sky, warm, windless) on sand-dune (soft, white but sometimes gritty soil) near hill, syntopic with *P. granulatus*, *P. kraepelini*, *U. planimanus*, and *O. jenseni*, 2 ♂ [AMNH (AH 2067, 2068)], 3 ♀ [AMNH (AH 2059, 2060, 2069)], 1 subadult ♂ [AMNH (AH 2061)], 1 subadult ♀ [AMNH (AH 2062)], 1 juvenile ♀ [AMNH (AH 2063)]; Brandberg,

plains to south, opposite Orabeskopf, 21°15.48'S, 14°36.54'E, 16.i.1998, L. Prendini & E. Scott, collected at night with UV light, sympatric with *P. brevimanus*, 2 ♂ [AMCC 119231 (LP 1654)]. Swakopmund District: Cape Cross, 21°43'S, 13°58'E, 21.ii.1982, A. Harington, 2 ♂ [AMNH (AH 4397, 4404)], 1 ♀ [AMNH (AH 4398)]; Cape Cross, 21°45'53"S, 13°59'05.7"E, 18.i.2009, L. Prendini, T.L. Bird & J. Huff, 21 m, central Namib gravel plains, low rolling hills, and rock outcrops near Cape Cross seal colony, sandy-loam soil, UV detection on cool, moonless night, light breeze, specimens running on surface, syntopic with *Uroplectes pilosus* (Thorell, 1876), 1 ♀ (AMNH), 1 subadult ♂ [AMCC (LP 9367)]; Cape Cross, at entrance to seal colony, 21°45'40.7"S, 13°58'40.7"E, 18.i.2009, L. Prendini, T.L. Bird & J. Huff, 30 m, central Namib gravel plains, low rolling hills, and rock outcrops near Cape Cross seal colony, sandy-loam soil, UV detection on cool, moonless night, light breeze, specimens running on surface, syntopic with *P. namibensis*, *U. pilosus*, and *O. penrithorum*, 1 ♂, 1 ♀, 1 subadult ♂ (AMNH); Cape Cross, 12.2 km south of turnoff on C34, hills east of road, 21°49'34.4"S, 14°04'14.2"E, 18.i.2009, L. Prendini, T.L. Bird & J. Huff, 8 m, central Namib gravel plains, rocky hillslopes with no vegetation, sandy-loam to consolidated sand soil, UV detection on cool, moonless night, light breeze, syntopic with *U. pilosus*, 1 ♂ (AMNH). *Kunene Region*: Khorixas District: Farm Bethanis 514, 20°24'S, 14°24'E, 17.xii.1988, A. Harington, 1 ♂ [AMNH (AH 4051)], 1 ♀ [AMNH (AH 4052)]; Khorixas, 25 km towards Uis, 20°30'S, 15°00'E, A. Harington, 1 subadult ♂ [AMNH (AH 3719)]; Twyfelfontein, 20°35'51.4"S, 14°22'15.1"E, 17.xi–23.xii.2003, T.L. Bird, 591 m, preservative pitfall traps, sandy plain, 1 ♂ (SMN 2216), 20°35.729'S, 14°22.346'E, 21.i.2004, L. Prendini, E. Scott, T. & C. Bird, Q. & N. Martins, 592 m, 2 ♂, 2 ♀, 4 subadult ♂, 11 subadult ♀, 11 juvenile ♂, 8 juvenile ♀ (AMNH), 1 ♀ [AMCC 159717 (LP 2636)], 20°35'51.6"S, 14°22'08.4"E, 6.ii.2007, T.L. Bird, A. Klann, P. Michalik & G. Talarico, 593 m, in valley, UV detection, 1 ♀ [SMN 3094 (TB 07/08 (a))].

PARABUTHUS NANUS LAMORAL, 1979
(FIGS 1–4, 6C, 14A)

Parabuthus nanus Lamoral, 1979: 594–597, figs 100–102, 105, 106, 164–172; Kovařík, 1998: 117; Fet & Lowe, 2000: 208; Prendini, 2001b: 137; Prendini, 2001a: 17; Dyason *et al.*, 2002: 769; Prendini, 2003: 21; Prendini, 2004a: 116, 162, 163, figs 1, 13, 44, 45; Prendini, 2005: 66, appendix 1.

Holotype: Namibia: *Karas Region*: Keetmanshoop District: Farm Noachabeb 97, 27°22'S, 18°22'E, 6.ii.1973,

B.H. Lamoral, found on rocky gravel ground at night, 1 ♀ (NM 10926).

Paratypes: Namibia: *Karas Region*: Karasburg District: Farm Belda 361, east side of Haib River, 28°28'S, 18°00'E, 28.i.1973, B.H. Lamoral, night collecting on sand dune, 1 ♂, 1 ♀, 2 subadult ♂ (NM 10702), 28°27'S, 18°01'E, 1.ii.1973, B.H. Lamoral, 1 subadult ♂ [SMN 764 (ex NM 10701)]; Farm Loushoop 330, 28°07'S, 18°07'E, 3.ii.1973, B.H. Lamoral & K. Porter, night collecting on sand dunes, 1 ♀ (NM 10699). Keetmanshoop District: Farm Noachabeb 97, 27°22'S, 18°22'E, 6.ii.1973, B.H. Lamoral, night collecting with UV, found on rocky gravel ground, 1 ♂ (NM 10926), 2 ♂ (NM 10927); Farm Schwarzkuppen 104, Noachabeb, 27°23'S, 18°20'E, 8.ii.1973, B.H. Lamoral & K. Porter, night collecting on red sand dunes, 1 ♂, 1 subadult ♀, 1 juvenile ♂ (NM 10698). Lüderitz District: Diamond Area 1: Farm Tsirub 13, 26°52'S, 16°02'E, 3.iii.1976, B.H. Lamoral, on rocky to sandy surface, marginal zone on lower reaches of mountain, 1 ♂, 1 ♀ (NM 10772). South Africa: *North-eastern Cape Province*: Namaqualand District: Goodhouse, 10 km south, 29°00'S, 18°13'E, 30.i.1973, B.H. Lamoral, night collecting, 1 ♀ (NM 10700), 28°55'S, 18°14'E, 11.ii.1979, B.H. Lamoral, on northern margin of Koa valley, 2 ♀ (NM 11304); Goodhouse, 21 km south, 29°04'S, 18°06'E, 29–31.i.1973, B.H. Lamoral, night collecting near mountain in plain, 1 ♂ (NM 10703).

Diagnosis: *Parabuthus nanus* is most closely related to *P. setiventer* sp. nov., the two species forming a monophyletic sister group to *P. gracilis* (Fig. 2). *Parabuthus nanus* may be separated from *P. setiventer* sp. nov. and all other species of *Parabuthus* by means of the following combination of characters: small adult size, carapace length 2.5–5.0 mm; carapace, including median ocular tubercle (male, female), entirely granular; pedipalp chela movable finger of female long, compared with manus (measured along ventroexternal carina), length finger/length manus: 1.70–2.00; pedipalp chela manus of adult male, slender as in adult female (Fig. 14A); pedipalp chela manus surfaces granular; pedipalp chela with trichobothrium *dt* situated proximal to *et*; pedipalp femur and patella trichobothria *d*₂ absent or very reduced; sternites punctate; sternites III–VII, metasomal segment I and, to a lesser extent, II, ventral surfaces, densely covered in short, truncate macrosetae (Fig. 6C); metasomal segments slender (length IV/width IV: 1.7–2.11); metasomal segment I, ventro-submedian carinae absent; metasomal segments II and III, posteroventral margins demarcated by transverse row of isolated, round granules; metasomal segment IV, acarinate; metasomal segments IV and V,

lateral intercarinal surfaces granular; metasomal segment V, dorsosubmedian, dorsolateral, and ventromedian carinae absent, ventrolateral carinae present, converging distally, and with posterior spiniform granules enlarged into spinose processes.

Distribution: Endemic to sandy areas in the Karas Region (Bethanie, Karasburg, Keetmanshoop, and Lüderitz districts) of Namibia and the Northern Cape Province (Calvinia, Gordonina, Kenhardt, and Namaqualand districts) of South Africa (Fig. 1). The distribution of this species extends across the Orange River. The known records fall within the range of 350–1250 m elevation. *Parabuthus nanus* is protected in the Ai-Ais and Fish River Canyon National Park, the Namib-Naukluft Park and the Sperrgebiet National Park.

Ecology: *Parabuthus nanus* is a psammophilous species, which displays several ecomorphological adaptations to its sandy habitat: elongated telotarsal unguis; basitarsi of legs I, II, and, to a lesser extent, III dorsoventrally compressed, with comb-like rows of long macrosetae ('sand combs') on the retrolateral margins; metasoma and telson lacking carinae on segments III–V. Specimens of *P. nanus* have been taken in pitfall traps, collected at night with UV light detection, resting on the surface of sandy-loam gravel plains, dry riverbeds and semi-consolidated to unconsolidated sand dunes, and excavated from burrows at the base of shrubs.

Parabuthus nanus has been collected in sympatry with the following scorpion species: Buthidae: *Hottentotta arenaceus* (Purcell, 1901), *Karasbergia methueni* Hewitt, 1913, *P. brevimanus*, *P. capensis* (Ehrenberg, 1831), *P. granulatus*, *Parabuthus laevifrons* (Simon, 1888), *P. schlechteri*, *P. villosus*, *Uroplectes carinatus* (Pocock, 1890), *U. gracilior*; Liochelidae: *Hadogenes zumpti* Newlands & Cantrell, 1985; Scorpionidae: *Opisthophthalmus adustus* Kraepelin, 1908, *Opisthophthalmus carinatus* (Peters, 1861), *Opisthophthalmus haackei* Lawrence, 1966, and *Opisthophthalmus lornae* Lamoral, 1979 and other *Opisthophthalmus* species. *Parabuthus nanus* is syntopic with *P. granulatus*, *P. laevifrons*, and *P. schlechteri* throughout its distributional range. Where *P. nanus* and *P. brevimanus* are sympatric, the two species are not syntopic, however. *Parabuthus nanus* inhabits softer substrata than *P. brevimanus* (Prendini, 2004a). The distribution of *P. nanus* is allopatric with that of its sister species, *P. setiventer* sp. nov. (Fig. 1).

Additional material: Namibia: *Karas Region:* Bethanie District: Farm Geigoab 95, 0.5 km west of intersection with D459 on road to Farm Blouputs 158,

27°10'44.1"S, 17°14'44.8"E, 4.ii.2008, L. Prendini & T.L. Bird, 826 m, arid savannah with Acacia woodland on flat sandy plain intersected by dry watercourses (Nuichas riverbed) and large stable alluvial sand dunes near base Nuichas Mountain, UV detection on hot, still, dark night after brief shower, specimens running on ground surface, sympatric with *P. brevimanus*, *P. laevifrons*, and *P. schlechteri*, 1 ♂, 1 ♀ (AMNH). Karasburg District: Farm Haakiesdoorn 197, entrance gate, 28°44.306'S, 18°17.412'E, 18.i.2004, I. Engelbrecht & B. Watkins, 670 m, 1 ♀ (AMNH), 1 ♀ [AMCC 159719 (LP 2484)]; Farm Komsberg 158, c. 55 km south of Ariamsvlei, 28°27.862'S, 19°44.065'E, 12.i.2004, I. Engelbrecht & B. Watkins, 1 ♂ (AMNH); Farm Louwshoop 330, northern end, roadside next to main road, 28°03.379'S, 18°04.786'E, 16.i.2004, I. Engelbrecht & B. Watkins, 860 m, 1 ♂ (AMNH); Farm Naroep 45, where road to Beenbreekberg crosses powerlines, 29°04.500'S, 18°34.200'E, 21.i.2004, I. Engelbrecht & B. Watkins, 1 ♂, 2 ♀ (AMNH); Farm Witkop 36, 10 km south of Ariamsvlei, 28°12.034'S, 19°48.544'E, 11.i.2004, I. Engelbrecht & B. Watkins, 781 m, 6 ♂, 1 ♀ (AMNH), 1 ♂ [AMCC 159720 (LP 2662)]; Grünau, south, c. 3 km north of C10–B1 road intersection, 27°53.847'S, 18°12.758'E, 16.i.2004, I. Engelbrecht & B. Watkins, 899 m, 1 ♂ (AMNH); north of RTZ camp, 28°37'S, 17°49'E, 13–16.iv.1997, E. Griffin, gravel plains, preservative pitfall traps, 1 ♂ (SMN 1725); Ai-Ais and Fish River Canyon National Park: Fish River Canyon, 0.3 km east of Ai-Ais on C10 (Ai-Ais-Grünau), 27°55'09.5"S, 17°29'21.5"E, 5.ii.2008, L. Prendini & T.L. Bird, 502 m, alluvial sand dunes and flats on east bank of Fish River, tamarisk and *Euclea pseudebenus* Meyer, 1843 dominant trees, sparse grass and bushes, UV detection on hot, still, dark, humid night, specimens sitting/walking on open sand or small dunes, sympatric with *Hottentotta arenaceus* and *P. brevimanus*, 2 ♂, 6 ♀ (AMNH), 1 subadult ♂, 1 juvenile ♂, 3 juvenile ♀ (SMN 3304), 3 juvenile ♂ [AMCC (LP 8232)]. Keetmanshoop District: Farm Khabus 146, 26°18'S, 18°13'E, 14.iii–14.iv.1988, N. & P.G. Olivier, on sandy plain next to dry riverbed, preservative pitfall traps, 1 ex. (SMN 1388), 14.iv–30.vi.1988, N. & P.G. Olivier, on sandy plain next to dry riverbed, preservative pitfall traps, 1 ♀ (SMN 1415). Lüderitz District: Farm Gunsbewys 139, 26°11'56.16"S, 16°22'48.6"E, 5.i.2005, T.L. Bird, D. Kunz & B. Muramba, 1154 m, UV light, sand dunes, syntopic with *O. adustus*, 1 ♀ [SMN 2913 (TB 05/10)]; Farm Numis 89, 26°05'S, 16°12'E, 14.xii.2000, Q. Martins, collected at night with UV light, 1 ♂ [AMNH (LP 1269)]; Farm Numis 89, Tiras Mountains, 26°05'25.98"S, 16°13'02.46"E, 5.i.2005, T.L. Bird, D. Kunz, B. Muramba, 1128 m, UV light, 1 ♀ [SMN 2581 (TB 05/07)]; Farms Heinrichsfelde 10/Kubub 15

boundary, Geisterschlucht, 26°40.23'S, 16°13.47'E, 8.xii.2001, L. Prendini & C. Holmes, 1232 m, UV collecting, walking on sandy flats at night, 1 ♀ [AMNH (LP 1347)]; Diamond Area 2: Namib-Naukluft Park: Awasib plains, 25°25'S, 15°43'E, 26.ii.1981, G. Newlands, 1 ♂ [AMNH (AH 4345)]; Garub, 26°34'24"S, 16°02'37.2"E, 24–31.vii.2004, T. Greyling, pitfall trap BL2A, 1 subadult ♂ (SMN 2707), 26°38'57.6"S, 15°56'36.0"E, 12–19.viii.2004, T. Greyling, pitfall trap C1B, 1 ♂ (SMN 2688). South Africa: Northern Cape Province: Calvinia District: Farm Eselkopvlakte, west-north-west of Loeriesfontein, 30°56'13"S, 19°01'09"E, 29.x–7.xi.2005, M. Burger, T. Felmore, E. Campher & J.S. Makokho, caught in pitfall and funnel traps, at trap SARCA 1–3, 1 ♀ (AMNH), 1 juvenile ♂ [AMCC (LP 5806)]; Farm Ezelkopvlakte 333, near Kromrivier riverbed, plains near Sishen–Saldanha railway line, 30°55.948'S, 19°00.205'E, 26.ii.2009, L. Prendini & H. Bichard, 383 m, succulent karoo on Knersvlakte, flat undulating plain, cracked, clayey-loam soil with slightly reddish sandy surface covering, becoming much harder below surface, UV detection on cool, still, dark night, specimens sitting in open ground, syntopic with *P. capensis*, *P. laevifrons*, *P. schlechteri*, and *U. carinatus*, 1 ♂, 1 ♀ (AMNH). Gordonias District: Farm Arrebees, Kakamas, 28°58'S, 20°07'E, 11.i.1995, A. Harington, 1 ♂ [AMNH (AH 2562)]; Farm Boegoeberg 48, north section, c. 55 km due east-south-east of Upington, 5 km south-west of Grootdrink, 28°37'54.6"S, 21°43'46.2"E, 20.xii.2006, M. Burger, I. Engelbrecht & R. Mercurio, 879 m, UV lighting (21:40–21:54), collected on open soil surface, sandy soil, storms in distance, gentle breeze (east direction), 75–99% cloud cover, no moon, 1 ♀ [AMNH (IE06-358)]; Riemvasmaak area, at entrance gate to Augrabies Falls National Park, 28°27.337'S, 20°19.835'E, 9–10.i.2004, I. Engelbrecht & B. Watkins, 684 m, pitfall trapping and UV detection in red sandy flats, 1 ♂ (AMNH). Kenhardt District: Farm Oup 80, turnoff to Raap en Skraap from Kakamas–Onseepkans road, 28°50.699'S, 19°35'E, 26.i.2004, I. Engelbrecht & B. Watkins, 786 m, 1 ♂, 5 ♀ (AMNH); Farm Skuitklip 92, 0.8 km south-east of intersection with road Pofadder–Raap-en-Skraap on road Onseepkans–Kakamas, 28°51.117'S, 19°35.375'E, 1.i.2008, L. Prendini & M. Cooper, 803 m, rocky hill with soft, red sand accumulated around base, surrounded by flat gravel plain, vegetation *Stipagrostis* grass tussocks and scattered *Acacia mellifera* Bentham, 1842 trees/bushes, UV detection on cool, dark, windy night, sitting/walking on ground surface on plain, sympatric with *P. granulatus*, *P. laevifrons*, *U. gracilior*, *Uroplectes* sp., and *O. lornae*, 1 ♀ (AMNH); Farm Skuitklip 92, 2.5 km south-east of intersection with road Pofadder–Raap-en-Skraap on road Onseepkans–Kakamas,

28°51.324'S, 19°36.485'E, 1.i.2008, L. Prendini & M. Cooper, 821 m, steep rocky hills surrounded by grey sandy-loam gravel flats with grass tussocks and occasional bushes, dry riverbed and gravel plain with low rocky flats in places, UV detection on cool dark, windy night, sitting on gravel plain, sympatric with *Karabergia methueni*, *P. brevimanus*, *P. laevifrons*, *P. villosus*, *U. gracilior*, and *Opisthophthalmus carinatus*, 1 ♂, 1 juvenile ♀ (AMNH); Farm Skuitklip 92, Eskom substation/red sand dunes, 3.5 km south-west of intersection with road Kakamas–Onseepkans on road Raap-en-skraap–Pofadder, 28°52.686'S, 19°34.003'E, 1.i.2008, L. Prendini & M. Cooper, 813 m, *Stipagrostis* grassland on semi-consolidated red sand dunes surrounded by red gravel plains, UV detection on warm, dark, windy night, specimens sitting on sand or bushes, seldom moving, at base of dune and on gravel plains, sympatric with *Hottentotta arenaceus*, *P. granulatus*, *P. laevifrons*, *P. schlechteri*, *U. gracilior*, and *O. carinatus*, 6 ♂, 2 ♀, 1 juvenile ♂ (AMNH), 1 ♂, 1 juvenile ♂ [AMCC (LP 8231)]; Farm Skuitklip 92, hills and gravel flats at intersection of roads Kakamas–Onseepkans and Pofadder–Raap-en-Skraap, 28°50.831'S, 19°34.949'E, 1.i.2008, L. Prendini & M. Cooper, 784 m, grey sandy-loam gravel flats with grass tussocks and occasional bushes leading up to rocky hill where soil harder, more gritty, UV detection on warm, dark, windy night, specimen sitting on ground surface on gravel plain, sympatric with *Karabergia methueni*, *P. granulatus*, *P. laevifrons*, and *U. gracilior*, 1 ♂ (AMNH); Farm Skuitklip 92, red sandy flats at intersection with road Pofadder–Raap-en-Skraap on road Onseepkans–Kakamas, 28°50.966'S, 19°34.889'E, 1.i.2008, L. Prendini & M. Cooper, 791 m, flat gravel plain (grey to red sandy-loam soil) with *Stipagrostis* grass tussocks and scattered *Acacia mellifera* trees/bushes, UV detection on cool, dark, windy night, specimens walking on ground surface, sympatric with *P. laevifrons* and *Uroplectes gracilior*, 1 ♂, 1 ♀ (AMNH). Namaqualand District: Aggeneys, 29°15'S, 18°50'E, 30.xii.1988, A. Harington, sandy, grassy flats, red sand, sympatric with *P. granulatus* and *P. laevifrons*, 1 ♀ [AMNH (AH 3695)], 1 ex. [AMNH (AH 4180)], ii.1997, L. Prendini, G.J. Müller *et al.*, 2 ♂, 2 ♀ [AMNH (LP 820)], 3.xii.1997, L. Prendini & G.J. Müller, collected at night with UV light, 1 ♂, 2 ♀ [AMCC 159718 (LP 1653)], 6.xii.1997, L. Prendini, G.J. Müller *et al.*, 1 ♂ [AMNH (LP 824)], 12.i.1999, G.J. Müller, J.J. van der Walt, J. Tytgat, J. du Plessis *et al.*, 2 ♂ [AMNH (LP 471)]; Aggeneys, 10 km south, 29°18'S, 18°50'E, ii.1997, L. Prendini & G.J. Müller, 5 ♂, 2 ♀ [AMNH (LP 853)], ii.1997, L. Prendini, G.J. Müller *et al.*, 7 ♂, 3 ♀ [AMNH (LP 796)], 4.xii.1997, L. Prendini, G.J. Müller *et al.*, sympatric with *U. gracilior*, 1 ♂ [AMNH (LP 816)], 5.xii.1997, L. Prendini, G.J. Müller *et al.*, sympatric

with *P. brevimanus* 1 ♂, 2 ♀ [AMNH (LP 835)], 6.xii.1997, L. Prendini, G.J. Müller *et al.*, 2 ♂, 1 ♀ [AMNH (LP 859)], 7.xii.1997, L. Prendini, G.J. Müller *et al.*, 4 ♂ [AMNH (LP 823)]; Farm Aggeneys 56, Windpomp near Steneberg, south of R64, 29°21.959'S, 18°51.274'E, 20.ii.2003, L. Prendini & E. Scott, 853 m, UV detection in *Stipagrostis* grassland on red sandy flats at base of quartzite outcrop, 1 ♀ (AMNH); Farm Areb 75, west of Aggeneys, 29°30'04.6"S, 18°13'45.1"E, 12.ii.1995, A. Harington, 1 ♀ [AMNH (AH 2587)]; Farm Gemsbok Vlakke 140, c. 25 km north-east of Pofadder, 29°02.039'S, 19°37.423'E, 4.iii.2005, L. Prendini & E. Scott, 835 m, 8 ♂, 1 ♀ (AMNH), 1 ♀ [AMCC 159721 (LP 4063)] Farm Goodhouse 23, dunes 500 m south of Vuurdoodberg on Pella-Concordia road, 28°59.034'S, 18°14.949'E, 21.ii.2003, L. Prendini & E. Scott, 481 m, 1 ♂ (AMNH), 1 ♀ [AMCC 159722 (LP 4188)], 28°59.035'S, 18°14.597'E, 20.ii.2007, L. Prendini & J. Huff, 460 m, UV light detection in *Stipagrostis* grassland on semi-consolidated red sand dunes of Koa Valley system, sympatric with *Hottentotta arenaceus*, *P. laevifrons*, *P. schlechteri*, and *Opisthophthalmus* sp., 1 ♂ (AMNH); Farm Goodhouse 23, 1 km west of turnoff to Goodhouse, on Pella-Concordia road, 28°58.684'S, 18°13.337'E, 2-3.iii.2005, L. Prendini & E. Scott, 450 m, succulent karoo on granitic sandy loam along dry watercourse and gravel flats, with hard igneous rocks interspersed with quartzite at base of large hill, UV detection on hot, dark, windy nights, becoming still later, specimens collected on gravel flats and dry watercourse, 1 ♂ (AMNH), 28°58.904'S, 18°12.947'E, 20.ii.2007, L. Prendini & J. Huff, 479 m, UV light detection on warm, still, moonless night on sandy/gravel plains alongside rocky koppie, syntopic with *P. brevimanus*, *P. granulatus*, *P. laevifrons*, *P. schlechteri*, and *Opisthophthalmus* spp., 1 ♂ (AMNH); Farm Steinkopf 22, dunes 1-2 km east of road Steinkopf-Henkries, turnoff 12-12.5 km north of turnoff to Jakkalswater, 29°02.582'S, 18°02.073'E, 24.ii.2003, L. Prendini & E. Scott, 578 m, 1 ♀, 1 juvenile ♀ (AMNH), 1 ♂ [AMCC 159723 (LP 4191)].

PARABUTHUS SETIVENTER SP. NOV.

(FIGS 1-4, 5C, D, 6D, 7D-F, 13, 14B-E, 15-17)

Holotype: Namibia: *Erongo Region*: Swakopmund District: Namib-Naukluft Park: Gobabeb, pitfall site on gravel plains c. 1 km north, 23°32'39.6"S, 15°02'57.4"E, 27.iii.2006, L. Prendini, T.L. Bird & S.K. Uunona, 422 m, UV detection on cool, still, dark night, becoming windy and colder later, on Central Namib gravel plains with low granite outcrops north of Kuiseb River, very sparse *Stipagrostis* grass tussocks in places, 1 ♂ (SMN 2918).

Paratypes: Namibia: *Erongo Region*: Swakopmund District: Arandis Control Site, Rössing Mine Survey, 22°22'S, 14°59'E, 8.v-5.vi.1984, E. Griffin, preservative pitfall traps, 1 ♀ (SMN 841), 5.vi-3.vii.1984, J. Irish & H. Rust, preservative pitfall traps, 1 ♂ (SMN 854), 8.xii.1984-14.i.1985, J. Irish & H. Rust, preservative pitfall traps, 1 ♀ (SMN 879), 28.xii.1984-14.i.1985, J. Irish & H. Rust, preservative pitfall traps, 1 ♀ (SMN 875), 14.i-11.ii.1985, J. Irish & H. Rust, preservative pitfall traps, 1 ♂ (SMN 883), 11.ii-11.iii.1985, J. Irish & H. Rust, preservative pitfall traps, 2 ♂ (SMN 889), 11.iii-9.iv.1985, J. Irish & H. Rust, preservative pitfall traps, 1 ♀ (SMN 903), 5.iv-6.v.1985, E. Griffin, preservative pitfall traps, 1 ♂, 2 ♀ (SMN 924); Panner Gorge, Rössing Mine Survey, 22°29'S, 15°01'E, 13.iii-9.iv.1984, E. Griffin, preservative pitfall traps, 1 ♂ (SMN 853), 9.iv-8.v.1984, E. Griffin, preservative pitfall traps, 1 ♀ (SMN 836), 8.v-5.vi.1984, E. Griffin, preservative pitfall traps, 1 ♀ (SMN 843), 18.xii-14.i.1984, J. Irish & H. Rust, preservative pitfall traps, 1 ♂, 1 juvenile ♂ (SMN 880), 14.i-11.ii.1985, J. Irish & H. Rust, preservative pitfall traps, 1 ♂ (SMN 885); Lower Ostrich Gorge, Rössing Mine Survey, 22°30'S, 14°58'E, 8.v-5.vi.1984, E. Griffin, preservative pitfall traps, 1 ♂ (SMN 844), 27.ix-22.x.1984, J. Irish & H. Rust, preservative pitfall traps, 1 ♀ (SMN 868), 3.iii-9.iv.1984, E. Griffin, preservative pitfall traps, 1 ♂ (SMN 823), 9.iv-8.v.1984, E. Griffin, preservative pitfall traps, 2 ♀ (SMN 837); Upper Ostrich Gorge, Rössing Mine Survey, 22°30'S, 14°58'E, 13.iii-9.iv.1984, E. Griffin, preservative pitfall traps, 1 ♀, 1 juvenile ♂ (SMN 828), 9.iv-8.v.1984, E. Griffin, preservative pitfall traps, 1 juvenile ♀ (SMN 834), 20.xi-18.xii.1984, E. Griffin, preservative pitfall traps, 1 ♂, 1 subadult ♂ (SMN 876), 11.ii-11.iii.1985, E. Griffin, preservative pitfall traps, 1 ♂ (SMN 892), 5.iv-6.v.1985, E. Griffin, preservative pitfall traps, 2 ♂ (SMN 914); Deblin Mine (a few km south), east-north-east of Swakopmund, 22°31'S, 14°45'E, 20.ii.1982, A. Harington, 1 ♂ [AMNH (AH 3632)], 1 ♀ [AMNH (AH 3633)]; Namib-Naukluft Park: Gobabeb, gravel plains around camp and immediately on northern bank of Kuiseb River, 23°33'36.2"S, 15°02'23.45"E, 19.i.2009, L. Prendini, T.L. Bird & J. Huff, 405 m, Central Namib gravel plains, UV detection on cool, moonless night, slight breeze, syntopic with *P. glabrimanus* sp. nov., 1 ♂ (AMNH); Gobabeb, pitfall site on gravel plains c. 300 m north-east, 23°33'30"S, 15°02'50"E, 26.iii.2006, L. Prendini, T.L. Bird & S.K. Uunona, 300 m, 1 ♀ (AMNH), L. Prendini, C. Bird & T. Ipinge, 415 m, UV detection on warm, dark, windy night on Central Namib gravel plains with low granite outcrops north of Kuiseb River, very sparse *Stipagrostis* grass tussocks in places, 1 ♂ (AMNH); Gobabeb, pitfall site on gravel plains c. 600 m north, 23°33'05.8"S,



Figure 13. *Parabuthus setiventer* sp. nov., habitus. A, B, holotype ♂ (SMN 2918). C, D, paratype ♀ (AMNH). A, C, dorsal aspect. B, D, ventral aspect. Scale bar = 10 mm.

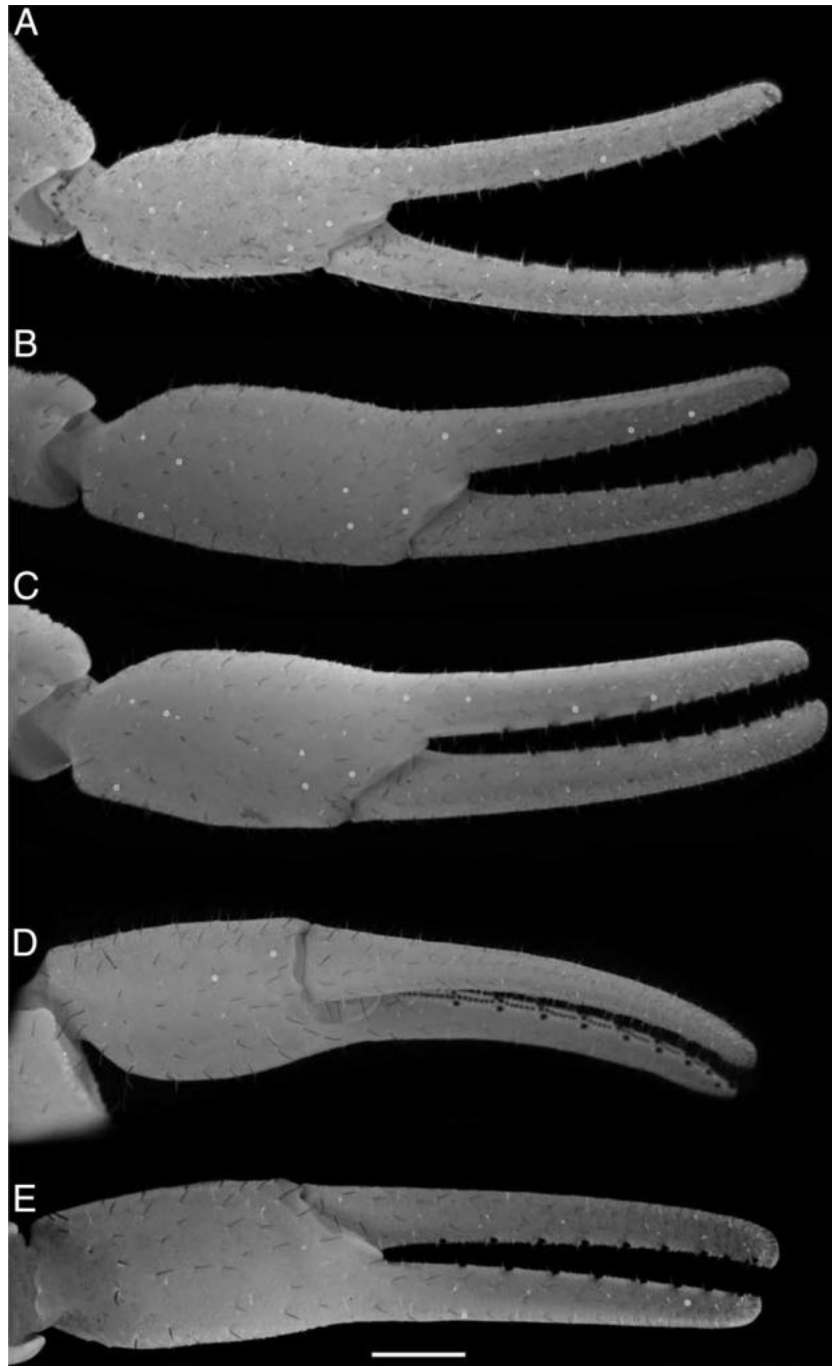


Figure 14. *Parabuthus nanus* Lamoral, 1979 (A) and *Parabuthus setiventer* sp. nov. (B–E), dextral pedipalp chela, showing trichobothrial distribution. A, ♂ [AMNH (LP 1269)], external aspect. B, holotype ♂ (SMN 2918), external aspect. C–E, paratype ♀ (AMNH), external (C), ventral (D), and internal (E) aspects. Scale bar = 1 mm.

15°02'47.9"E, 26.iii.2006, L. Prendini, C. Bird & T. Iipinge, 420 m, UV detection on warm, dark, windy night on Central Namib gravel plains with low granite outcrops north of Kuiseb River, very sparse *Stipagrostis* grass tussocks in places, 1 ♂ (AMNH), 23°33'06"S, 15°02'50"E, 27.iii.2006, L. Prendini, T.L.

Bird & S.K. Uunona, 395 m, UV detection on cool, still, dark night, becoming windy and colder later, on Central Namib gravel plains with low granite outcrops north of Kuiseb River, very sparse *Stipagrostis* grass tussocks in places, specimens collected moving about on surface, 1 ♂ (AMNH); Gobabeb, pitfall site

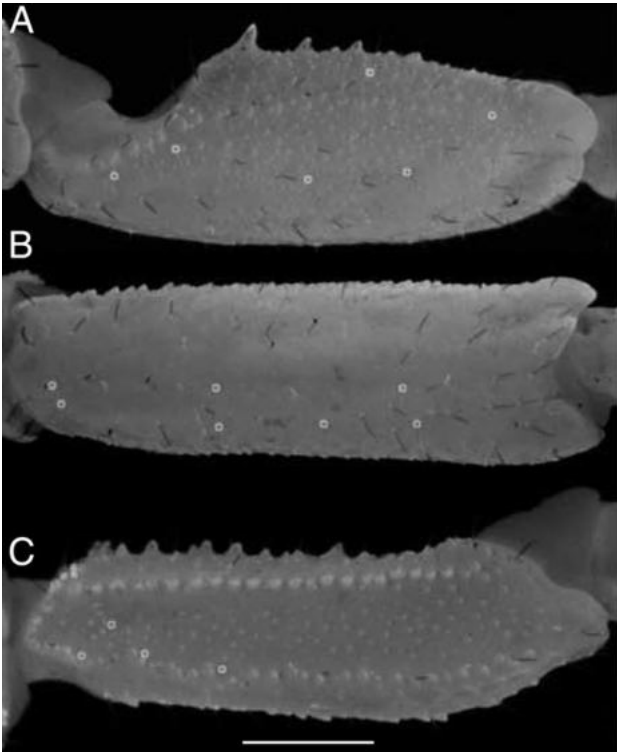


Figure 15. *Parabuthus setiventer* sp. nov., paratype ♀ (AMNH), dextral pedipalp patella and femur, illustrating trichobothrial distribution. A, patella, dorsal aspect. B, patella, external aspect. C, femur, dorsal aspect. Scale bar = 1 mm.

on gravel plains c. 700 m north, 23°32'54.4"S, 15°02'49.5"E, 27.iii.2006, L. Prendini, T.L. Bird & S.K. Uunona, 395 m, UV detection on cool, still, dark night, becoming windy and colder later, on Central Namib gravel plains with low granite outcrops north of Kuiseb River, very sparse *Stipagrostis* grass tussocks in places, specimens taken in open sandy ground, 3 ♂ (AMNH), 2 subadult ♂ (SMN 2919); Gobabeb, pitfall site on gravel plains c. 1 km north, 23°32'39.6"S, 15°02'57.4"E, 26.iii.2006, L. Prendini, C. Bird & T. Iippinge, 422 m, UV detection on warm, dark, windy night on Central Namib gravel plains with low granite outcrops north of Kuiseb River, very sparse *Stipagrostis* grass tussocks in places, 1 ♀ (AMNH), 27.iii.2006, L. Prendini, T.L. Bird & S.K. Uunona, 422 m, UV detection on cool, still, dark night, becoming windy and colder later, on Central Namib gravel plains with low granite outcrops north of Kuiseb River, very sparse *Stipagrostis* grass tussocks in places, 1 ♂, 2 ♀ (AMNH); Gobabeb, 3.1 km north, 23°32'55.5"S, 15°02'48.6"E, 19.i.2009, L. Prendini, T.L. Bird & J. Huff, 426 m, Central Namib gravel plains with low granite outcrops, little other vegetation, UV detection on cool, moonless night,

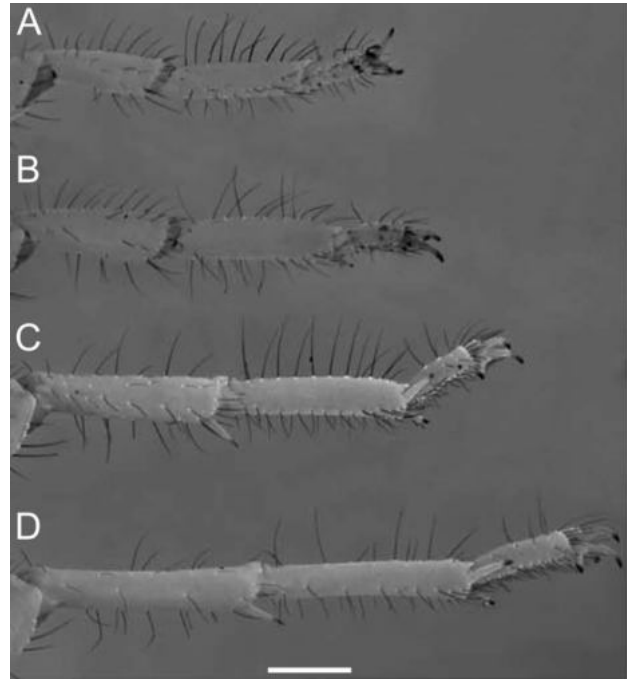


Figure 16. *Parabuthus setiventer* sp. nov., paratype ♀ (AMNH), dextral legs I–IV, tibia, basitarsus, and telotarsus, retrolateral aspect, illustrating setae, ungues, and spurs. A, leg I. B, leg II. C, leg III. D, leg IV. Scale bar = 1 mm.



Figure 17. *Parabuthus setiventer* sp. nov., paratype ♂ (AMNH), dextral hemispermatophore, ental (A) and ectal (B) aspects. Scale bar = 2 mm.

slight breeze, specimen walking on gravel plains, 1 ♀ (AMNH); Welwitschiavlake, c. 1 km north of turnoff to Giant Welwitschia, 22°39'30"S, 15°01'35.9"E, 30.iii.2006, L. Prendini, T.L. Bird & S.K. Uunona, 437 m, UV detection on cool, still, dark night on Central Namib gravel plains leading up to rocky schist slope, specimen collected on gravel plain, 1 ♂ (AMNH); Welwitschiavlake, mountain and gravel plain south of campsite, 22°39'15.6"S, 15°00'18.3"E, 30.iii.2006, L. Prendini, T.L. Bird & S.K. Uunona, 440 m, UV detection on cool, still, dark night on Central Namib gravel plains with sparse annual grasses leading up to schist mountain slope, specimens collected on gravel plain, 4 ♂ (AMNH).

Diagnosis: *Parabuthus setiventer* sp. nov. is most closely related to *P. nanus*, the two species forming a monophyletic sister group to *P. gracilis* (Fig. 2). *Parabuthus setiventer* sp. nov. may be separated from *P. nanus* and all other species of *Parabuthus* by means of the following combination of characters: small adult size, carapace length 2.5–5.0 mm; carapace, including median ocular tubercle (male, female), entirely granular; pedipalp chela movable finger of female moderate, compared with manus (measured along ventroexternal carina), length finger/length manus: ± 1.50 ; pedipalp chela manus of adult male, slightly incrassate, compared with that of adult female, which is slender; pedipalp chela manus granular; pedipalp chela with trichobothrium *dt* situated proximal to *et*; pedipalp femur and patella trichobothria *d*₂ absent or very reduced; sternites III–VI, punctate, moderately setose (Fig. 6D), VII, metasomal segments I and, to a lesser extent, II–IV, ventral surfaces densely covered in short, truncate macrosetae, becoming progressively less numerous, and acuminate from segments I–IV; metasomal segments slender (length IV/width IV: 1.7–2.11); metasomal segment I, ventrosulmedian carinae absent; metasomal segments II and III, posteroventral margins demarcated by transverse row of isolated, round granules; metasomal segment IV, acarinate; metasomal segments IV and V, lateral intercarinal surfaces granular; metasomal segment V, dorsosulmedian, dorsolateral, and ventromedian carinae absent, ventrolateral carinae present, converging distally, and with posterior spiniform granules enlarged into spinose processes.

Etymology: The species name refers to the densely setose sternite VII that is characteristic of the species (Fig. 6D).

Description: The following description is based on the holotype male, two paratype males, and three paratype females (Table 6).

Colour: Carapace, tergites, and metasomal segments I–IV, segment V, anterior third: Buff-Yellow no. 53. Metasomal segment V, posterior two-thirds and telson infuscated: Dark Brownish Olive no. 129. Chelicerae, pedipalps, legs, pectines, and sternites slightly paler than carapace, tergites, and metasoma (Fig. 13). Chelicerae, pedipalps, legs, and sternites: Sulfur Yellow no. 157. Pectines: Pale Horn Color no. 92.

Carapace: As for *P. glabrimanus* sp. nov., except as follows. Carapace covered entirely by uniform, coarse granulation, becoming coarser on interocular and posterolateral surfaces. Anterior and posterior margins of carapace sublinear (Fig. 5C, D).

Chelicerae: As for *P. glabrimanus* sp. nov.

Sternum: As for *P. glabrimanus* sp. nov. (Fig. 13B, D).

Pedipalps: As for *P. glabrimanus* sp. nov., except as follows. Pedipalps covered in short macrosetae (Figs 13B–E, 14). Femur surfaces uniformly, finely granular (♂), external and ventral intercarinal surfaces with smooth areas (♀) (Fig. 15C); dorsoexternal, and ventrointernal carinae distinct, granular; internomedian carina comprising discontinuous row of spiniform granules; externomedian carina obsolete, granular; other carinae absent. Patella intercarinal surfaces uniformly, finely granular (♂), external intercarinal surfaces with smooth areas (♀) (Fig. 15A, B); dorsointernal carina obsolete, reduced to few granules proximally and distally; ventrointernal carina vestigial, reduced to single spiniform granule, proximally; internomedian carina comprising prominent spiniform granule, proximally, and few smaller granules, distally; other carinae absent. Chela finely granular (Fig. 14B–E); acarinate. Chela long, slender (♀) or slightly incrassate (♂), length along ventroexternal carina 29–51% greater than chela width and 42–54% greater than chela height (Table 6); length of movable finger 13–29% (♂) or 40–47% (♀) greater than length along ventroexternal carina. Chela fixed and movable fingers straight, such that proximal dentate margin linear when fingers closed (Fig. 14B–E). Median denticle row of chela fixed and movable fingers each comprising eight or nine oblique primary subrows; each subrow comprising three to six small denticles and large external denticle, flanked by internal and external accessory denticles; terminal subrow of fixed finger usually shorter than others; basal subrow of fixed and movable fingers longer, comprising fusion of basal and sub-basal subrows; each finger with enlarged terminal denticle.

Trichobothria: Neobothriotaxic minor, Type A, α configuration (Figs 14B–E, 15), with following segment totals: femur, ten (four dorsal, four internal, two external), patella, 12 (four dorsal, one internal,

Table 6. Meristic data for holotype and paratypes of *Parabuthus setiventer* sp. nov. Measurements (mm) follow Prendini (2000, 2003, 2004a)

Specimen	♂		♂		♂		♀		♀		♀	
	SMN	AMNH	SMN	AMNH	SMN	AMNH	SMN	AMNH	SMN	AMNH	SMN	AMNH
Sex												
Collection	SMN	AMNH	SMN	AMNH	SMN	AMNH	SMN	AMNH	SMN	AMNH	SMN	AMNH
Number	2918	889	924				879				924	
Type	Holo.	Para.	Para.	Para.	Para.	Para.	Para.	Para.	Para.	Para.	Para.	Para.
Total length*	50.1	50.7	45.2	46.5	49.3	56.7	46.5	53.8	50.3	53.8	50.3	53.8
Carapace												
Length	4.7	5.0	4.4	4.2	5.0	5.3	4.5	5.2	5.0	5.2	5.0	5.2
Anterior width	2.6	2.6	2.4	2.3	2.8	2.8	2.9	2.8	2.8	2.8	2.8	3.1
Posterior width	5.0	5.3	4.4	4.6	5.4	6.2	5.2	6.1	6.1	5.9	6.1	5.9
Length	0.9	1.1	0.9	0.8	1.0	1.3	1.0	1.0	1.0	1.2	1.0	1.2
Tergite I	1.1	1.1	1.0	1.0	1.1	1.4	1.1	1.4	1.4	1.3	1.4	1.3
Tergite III	1.2	1.2	1.3	1.3	1.4	1.8	1.4	1.5	1.5	1.5	1.5	1.5
Tergite IV	1.7	1.7	1.7	1.8	1.8	2.2	1.7	2.1	2.1	2.0	2.0	2.0
Tergite V	1.9	2.0	1.8	1.8	2.0	2.1	2.3	2.2	2.4	2.5	2.5	2.5
Tergite VI	2.2	2.3	2.0	2.0	2.2	2.6	2.2	2.4	2.4	2.6	2.4	2.6
Tergite VII	3.5	3.5	3.2	3.0	3.4	3.4	2.7	3.0	3.0	2.7	3.0	3.7
Mesosoma	12.5	12.9	11.4	11.8	13.0	14.9	12.3	14.7	13.8	14.7	13.8	14.7
Sternite VII	3.1	3.1	2.6	2.9	3.1	3.5	3.1	3.5	3.1	3.4	3.4	3.4
Length	4.3	4.4	4.2	3.9	4.1	5.6	4.9	5.7	5.7	5.1	5.7	5.1
Width	3.8	3.4	3.4	3.5	3.8	3.4	3.3	3.6	3.6	3.7	3.6	3.7
Length	2.6	2.9	2.6	2.5	3.1	3.3	2.6	3.0	3.0	2.9	3.0	2.9
Width	4.3	4.1	3.7	3.9	4.4	4.8	3.5	3.8	4.0	4.0	3.8	4.0
Length	2.5	2.7	2.3	2.5	2.8	3.1	2.5	2.8	2.8	2.8	2.8	2.8
Width	4.2	4.2	4.2	4.1	4.3	4.1	4.1	4.5	4.0	4.5	4.0	4.5
Length	2.5	2.7	2.5	2.4	2.9	2.7	2.7	2.5	2.8	2.7	2.8	2.7
Width	4.8	4.9	4.3	4.4	4.6	5.3	4.2	4.5	4.5	5.1	4.5	5.1
Length	2.5	2.7	2.2	2.4	2.9	3.1	2.6	2.6	2.5	2.8	2.8	2.8
Width	5.4	5.7	4.7	5.0	5.6	6.0	4.9	5.8	5.3	5.8	5.3	5.8
Length	2.6	2.7	2.4	2.5	3.1	3.3	2.6	2.9	2.9	2.9	2.9	2.9
Width	27.7	27.6	24.6	26.0	25.7	30.8	26.1	28.5	26.3	28.5	26.3	28.5
Total length†	5.3	5.3	4.8	4.7	5.2	5.6	5.0	5.4	5.2	5.4	5.2	5.4
Length	2.4	2.5	2.1	2.3	2.4	2.4	2.6	2.3	2.3	2.8	2.3	2.8
Aculeus length	2.8	3.8	3.0	2.9	3.3	3.8	2.9	3.5	3.2	3.5	3.2	3.5
Vesicle length	1.8	2.0	1.6	1.7	2.2	2.4	2.1	2.2	2.2	2.2	2.2	2.2
Vesicle width	1.7	1.9	1.5	1.6	1.7	2.0	1.8	2.0	1.7	2.0	1.9	1.9
Vesicle height	15.7	16.8	14.6	15.3	15.0	14.8	15.2	15.2	15.2	15.2	15.2	15.2
Total length	4.4	4.4	4.0	4.2	4.4	4.7	4.1	4.3	4.1	4.3	4.1	4.3
Length	0.9	1.3	1.0	1.1	1.2	1.3	1.1	1.3	1.1	1.3	1.1	1.3
Width	4.5	4.8	4.2	4.2	4.4	4.6	4.2	4.4	4.2	4.4	4.2	4.4
Length	1.2	1.3	1.2	1.3	1.4	1.5	1.5	1.4	1.4	1.6	1.4	1.6
Width	6.8	7.6	6.4	6.9	6.6	7.5	6.9	6.8	6.5	6.8	6.5	6.8
Length‡	1.7	2.0	1.5	1.4	1.4	1.7	1.4	1.5	1.5	1.8	1.5	1.7
Width	1.5	1.7	1.3	1.3	1.3	1.4	1.4	1.2	1.4	1.4	1.2	1.4
Height	3.0	3.2	2.7	2.9	2.6	2.6	2.3	2.6	2.3	2.6	2.3	2.7
Manus length along ventroexternal carina	4.2	3.7	3.9	4.0	4.0	4.8	4.3	4.8	4.0	4.4	4.4	4.6
Length of movable finger	7.6	6.6	7.2	7.8	7.3	7.4	7.0	7.3	7.4	5.4	5.7	5.6
Total length	7.6	6.5	7.1	7.7	7.6	7.6	7.2	7.1	7.1	4.9	5.2	5.3
Length along dentate margin	30/30	25/26	32/32	30/30	27/28	31/31	28/28	30/31	29/25	29/24	22/24	23/23
Tooth count (left/right)												

Holo., holotype; Para., paratype.
 *Sum of carapace, tergites I–VII, metasomal segments I–V, and telson.
 †Sum of metasomal segments I–V and telson.
 ‡Measured from base of condyle to tip of fixed finger.
 §Sinistral pecten damaged.

seven external) and chela, 15 (eight manus, seven fixed finger). Total number of trichobothria per pedipalp, 37. Femur d_2 absent or very reduced; e_1 situated level with or distal to d_5 . Patella d_2 absent or very reduced; esb_2 situated level with esb_1 . Chela Esb situated in line with or dorsal to Eb_2 – Et axis; eb situated proximal to basal dentate margin of fixed finger; dt situated proximal to et .

Mesosoma: Pre-tergites smooth, matt (♂), smooth, shiny (♀), granular along posterior margins. Post-tergites entirely covered with uniform, fine granulation, becoming coarser posteriorly, especially along posterior margins; I–VII each with weakly developed, costate-granular dorsomedian carina; VII additionally with distinct pairs of costate-granular dorsosubmedian and dorsolateral carinae, and well-developed stridulatory surface between dorsosubmedian carinae, comprising rounded granules reaching posterior margin. Sternites III–VI surfaces smooth, punctate, moderately setose, lateral and posterior margins each with few macrosetae; VII acarinate, punctate, uniformly finely granular (♂) or smooth medially with sparse fine granules laterally (♀), densely covered in short, truncate macrosetae (Fig. 6D). Sternite VII, width 24–38% (♂) or 33–40% (♀) greater than length.

Pectines: As for *P. glabrimanus* sp. nov., except as follows (Fig. 13B, D). Pectinal teeth: 25–32/26–32 (♂), 22–30/23–31 (♀) (Table 6).

Genital operculum: Completely divided longitudinally. Genital papillae present (♂), absent (♀).

Legs: As for *P. glabrimanus* sp. nov. (Fig. 16).

Metasoma and telson: Metasomal segments I–V width/length ratio progressively decreasing (Table 6), width percentage of length 69–85% (♂) or 76–85% (♀) for I, 60–66% (♂) or 65–75% (♀) for II, 57–63% (♂) or 61–69% (♀) for III, 52–56% (♂) or 54–62% (♀) for IV, and 48–51% (♂) or 50–56% (♀) for V. Telson oval, globose, height 51–61% (♂) or 54–62% (♀) of length, with flattened dorsal surface, rounded ventral surface; vesicle not distinctly narrower than metasomal segment V, width 66–74% (♂) or 70–79% (♀) of metasomal segment V. Aculeus short, sharply curved, 65–85% (♂) or 71–89% (♀) of vesicle length (Table 6). Metasoma and telson 54–57% (♂) or 52–55% (♀) of total length. Intercarinal surfaces entirely granular, except for posterodorsal surfaces, which are smooth and matt (♂) or shiny (♀); segments I–III, each with well-developed dorsal stridulatory surface, comprising fine rounded granules extending to posterior margin (Fig. 7E, F); segments II and III, posterodorsal edge sublinear. Metasomal segments I–V, dorsal and lateral surfaces and V, ventral surface, moderately to densely covered with long, acuminate macrosetae, especially on ventral surface of telson; I and, to a lesser extent, II–IV, ventral surfaces densely

covered in short, truncate macrosetae, becoming progressively less numerous, and acuminate from segments I–IV (Fig. 7D). Metasomal segments I–III each with eight carinae; IV acarinate; V with two carinae. Dorsosubmedian carinae present, converging posteriorly on segments I–III, absent on IV and V. Dorsolateral carinae present on segments I–III, absent on IV and V. Median lateral carinae present on segment I only. Ventrolateral carinae present, converging posteriorly on segments I–III; posterior section not forming U-shaped pattern on II and III; reduced to anterior row of isolated, rounded granules on IV; subparallel to converging posteriorly on V, with posterior spiniform granules enlarged into spinose processes (Fig. 7D). Ventrosubmedian carinae absent on segment I, present on II and III; reduced to anterior row of isolated, rounded granules on IV; absent on V. All metasomal carinae costate-granular to granular.

Hemispermatochore: Flagelliform, with *pars recta* S-shaped (Fig. 17).

Geographical variation: There is little variation amongst specimens from different localities.

Ontogenetic variation: As in other species of *Parabuthus*, male resembles female very closely until the final instar (Prendini, 2004a). Juveniles and subadults may be readily sexed by examination of the pectines and genital aperture.

Sexual dimorphism: Unlike most species of *Parabuthus*, *P. setiventer* sp. nov. is not markedly dimorphic in the shape of the pedipalp chela manus or the structure of the pectines. The manus of adult male is only slightly incrassate, compared with that of adult female (Fig. 14B–E, Table 6). As in most species of *Parabuthus*, the first proximal median lamella of each pecten is suboval, mesially enlarged, and lobate in the female, but unmodified in the male (Prendini, 2004a). However, the pectinal tooth counts of the male (25–32) and female (22–31) are similar (Table 6). The adult male is proportionally more slender, with a longer metasoma and more pronounced granulation and carination, than the adult female (Figs 5C, D, 13, Table 6).

Distribution: Endemic to the gravel plains of the Central Namib, north of the Kuiseb River, in the Erongo Region (Swakopmund District) of western Namibia (Fig. 1). The known records fall within the range of 300–450 m elevation. *Parabuthus glabrimanus* sp. nov. is more commonly found at higher elevation (400–1100 m), further east. *Parabuthus setiventer* sp. nov. is protected in the Namib-Naukluft Park.

Ecology: *Parabuthus setiventer* sp. nov. is a semi-sammophilous species, which displays several ecomorphological adaptations to its sandy habitat:

basitarsi of legs I, II, and, to a lesser extent, III dorsoventrally compressed, with comb-like rows of long macrosetae ('sand combs') on the retrolateral margins (Fig. 16A–C); metasoma lacking carinae on segments III–V (Fig. 7D). Specimens of *P. setiventer* sp. nov. have been taken in pitfall traps and collected with UV light detection on cool or warm, dark, still, or windy nights, moving about on the surface of gritty gravel plains between low granite outcrops.

Parabuthus setiventer sp. nov. has been collected in sympatry with the following scorpion species: Bothriuridae: *L. elegans*; Buthidae: *P. glabrimanus* sp. nov.; Scorpionidae: *O. penrithorum*. Its distribution is allopatric with that of its sister species, *P. nanus* (Fig. 1).

ACKNOWLEDGEMENTS

We wish to express our gratitude to the following organizations, institutions, and individuals for their assistance during the course of this investigation. For financial support towards the costs of expeditions during which specimens were collected by the first author: University of Stellenbosch, Department of Pharmacology, kindly arranged by Gerbus Müller (Namibia, 1997–1998); U.S. National Science Foundation, grants EAR 0228699 (South Africa, 2003, 2005, 2005–2006, 2007; Namibia/South Africa, 2003–2004; Namibia, 2006) and DEB 0228699 (South Africa, 2007–2008); Stavros Niarchos Foundation, with appreciation to Maria Niarchos (Namibia, 2003–2004; South Africa, 2007–2008; Namibia and South Africa, 2009); Division of Invertebrate Zoology, American Museum of Natural History (South Africa, 2003–2004). For permission to collect and export scorpions from the Northern Cape Province, South Africa in 1997, 1998, 2003–2009: Northern Cape Nature Conservation Service. For permission to collect and export scorpions from Namibia in 1997, 1998, 2001, 2003–2004, 2006, and 2009 (including special exemption to collect in the restricted Diamond Area I, the Ai-Ais and Fish River Canyon Park, the Brandberg National Monument, and the Namib-Naukluft Park): the Ministry of Environment and Tourism, Government of Namibia (permit application process kindly facilitated by Eryn Griffin and Tharina Bird; permits issued by Colin Craig, Mike Griffin, Holger Kolberg, and Toivo Uahengo); NAMDEB Diamond Corporation. For permission to visit and collect scorpions on their property: the owners or managers of mines or private farms, local police commissioners of municipal lands, tribal authorities of communal grazing lands, and wardens or rangers of parks and reserves, listed under material examined, with special appreciation to Berry van Biljon, Manager, Black Mountain Mineral Development Co., Aggeneys. For congenial

company and participation in fieldwork: Gerbus Müller, Raad de Waal, Johan du Plessis, Karin Dyason, Feff le Roux, and Piet Riedeman (South Africa, 1997); Elizabeth Scott (Namibia, 1997–1998; South Africa, 2003, 2005); Elizabeth Scott, Jane Scott, and Charles Holmes (Namibia, 2001); Chris and Tharina Bird, Quinton and Nicole Martins, and Elizabeth Scott (Namibia, 2003–2004); Chris and Tharina Bird, Tauno Ipinge and Sylvanis Uunona (Namibia, 2006); Jeremy Huff (South Africa, 2007); Mark Cooper (South Africa, 2007–2008); Tharina Bird and Jeremy Huff (Namibia, 2009); Howard Bichard (South Africa, 2009). For leading additional trips to collect material: Ian Engelbrecht, accompanied by Bronwyn Watkins (Namibia, South Africa, 2003–2004) and Randy Mercurio (South Africa, 2005–2006). For donating further specimens for study: Quinton Martins, Gerbus Müller, Jurg van der Walt, Ian Engelbrecht. For transferring the Alexis Harington Scorpion Collection to the American Museum of Natural History: Jack Harington, Lucian Harington, and Eone de Wet; for accommodation and assistance while sorting and packing the collection in Johannesburg: the Scott family; for expediting the financial aspects of bringing the collection to New York: Randall T. Schuh. For facilitating the transfer of scorpions collected as by-catch of the South African Reptile Conservation Assessment (SARCA) to the American Museum of Natural History: Ansie Dippenaar-Schoeman; James Harrison; Randall T. Schuh; Les Underhill. For loaning and assisting in transportation of specimens and providing data from the collections of their institutions: Eryn Griffin and Tharina Bird (National Museum of Namibia, Windhoek); Michelle Hamer, Allison Ruiters, Guy Redman, Debbie Jennings, Mike Mostovski, and Juthika Baijoo (Natal Museum, Pietermaritzburg, South Africa); Martin Filmer, Paul Bayliss, Rob Toms, Klaas Manamela, Barbara Dombrowsky, Martin Krüger, and Ruth Müller (Transvaal Museum, Pretoria, South Africa). For assistance with the illustrations: Steve Thurston. For comments on an earlier draft of the manuscript: three anonymous reviewers.

REFERENCES

- Alexander AJ.** 1958. On the stridulation of scorpions. *Behaviour* **12**: 339–352.
- Balinsky BI.** 1962. Patterns of animal distribution on the African continent. *Annals of the Cape Provincial Museums* **2**: 299–309.
- Bergman NJ.** 1995. Scorpionism in Zimbabwe. An epidemiological and clinical investigation into scorpionism in the Gwanda District of Zimbabwe, with particular reference to *Parabuthus transvaalicus* (Purcell). M.D. Thesis, University of Zimbabwe, Harare.

- Bergman NJ. 1997a.** Scorpion sting in Zimbabwe. *South African Medical Journal* **87**: 163–167.
- Bergman NJ. 1997b.** Clinical description of *Parabuthus transvaalicus* scorpionism in Zimbabwe. *Toxicon* **35**: 759–771.
- Bremer K. 1988.** The limits of amino acid sequence data in angiosperm phylogenetic reconstruction. *Evolution* **42**: 795–803.
- Bremer K. 1994.** Branch support and tree stability. *Cladistics* **10**: 295–304.
- Bryant HN. 1995.** Why autapomorphies should be removed: a reply to Yeates. *Cladistics* **11**: 381–384.
- Burke A. 1998.** Vegetation zones. In: Barnard P, ed. *Biological diversity in Namibia: a country study*. Windhoek: Namibian National Biodiversity Task Force, 26–28.
- DeBont T, Swerts A, Van der Walt JJ, Müller GJ, Verdonck F, Daenens P, Tytgat J. 1998.** Comparison and characterization of the venoms of three *Parabuthus* scorpion species occurring in southern Africa. *Toxicon* **36**: 341–352.
- Donoghue MJ, Olmstead RG, Smith JF, Palmer JD. 1992.** Phylogenetic relationships of Dipsacales based on *rbcL* sequence data. *Annals of the Missouri Botanical Garden* **79**: 333–345.
- Dumortier B. 1964.** Morphology of sound emission apparatus in Arthropoda. In: Busnel RG, ed. *Acoustic behaviour of animals*. Amsterdam: Elsevier, 277–345.
- Dyason K, Brandt W, Prendini L, Verdonck F, Tytgat J, du Plessis J, Müller G, Van der Walt J. 2002.** Determination of species-specific components in the venom of *Parabuthus* scorpions from southern Africa using matrix-assisted laser desorption time-of-flight mass spectrometry. *Rapid Communications in Mass Spectrometry* **16**: 768–773.
- Eastwood EB. 1977.** Notes on the scorpion fauna of the Cape. Part 2. The *Parabuthus capensis* (Ehrenberg) species-group; remarks on taxonomy and bionomics (Arachnida, Scorpionida, Buthidae). *Annals of the South African Museum* **73**: 199–214.
- Eastwood EB. 1978.** Notes on the scorpion fauna of the Cape. Part 4. The burrowing activities of some scorpionids and buthids (Arachnida, Scorpionida). *Annals of South African Museum* **74**: 249–255.
- Farris JS. 1970.** Methods for computing Wagner trees. *Systematic Zoology* **19**: 83–92.
- Farris JS. 1982.** Outgroups and parsimony. *Systematic Zoology* **31**: 328–334.
- Fet V, Lowe G. 2000.** Family Buthidae C.L. Koch, 1837. In: Fet V, Sissom WD, Lowe G, Braunwalder ME, eds. *Catalog of the scorpions of the world (1758–1998)*. New York: The New York Entomological Society, 54–286.
- Fitch WM. 1971.** Toward defining the course of evolution: minimum change for a specific tree topology. *Systematic Zoology* **20**: 406–416.
- FitzPatrick MJ. 1994.** A checklist of the *Parabuthus* Pocock species of Zimbabwe with a re-description of *P. mossambicensis* (Peters, 1861) (Arachnida: Scorpionida). *Transactions of the Zimbabwe Scientific Association* **68**: 7–14.
- Giess W. 1971.** A preliminary vegetation map of South West Africa. *Dinteria* **4**: 5–114.
- Goloboff PA. 1993.** Estimating character weights during tree search. *Cladistics* **9**: 83–91.
- Goloboff PA. 1995.** Parsimony and weighting: a reply to Turner and Zandee. *Cladistics* **11**: 91–104.
- Goloboff PA. 1997.** *Pee-Wee, Version 3.0. Computer software and documentation*. New York: The American Museum of Natural History.
- Goloboff PA. 1999.** *NONA, Version 2.0. Computer software and documentation*. New York: The American Museum of Natural History.
- Griffin E. 1990.** Seasonal activity, habitat selection and species richness of Solifugae (Arachnida) on the gravel plains of the central Namib Desert. In: Seely MK, ed. *Namib ecology: 25 years of Namib research. Transvaal Museum Monograph No. 7*. Pretoria: Transvaal Museum, 77–82.
- Griffin E. 1998a.** Arachnid diversity. In: Barnard P, ed. *Biological diversity in Namibia: a country study*. Windhoek: Namibian National Biodiversity Task Force, 126–129.
- Griffin M. 1998b.** Reptile diversity. In: Barnard P, ed. *Biological diversity in Namibia: a country study*. Windhoek: Namibian National Biodiversity Task Force, 148–154.
- Griffin RE. 1998c.** Species richness and biogeography of non-acarine arachnids in Namibia. *Biodiversity and Conservation* **7**: 467–481.
- Griswold CE, Coddington JA, Hormiga G, Scharff N. 1998.** Phylogeny of the orb-web building spiders (Araneae, Orbicularia: Deinopoidea, Araneoidea). *Zoological Journal of the Linnean Society* **123**: 1–99.
- Harington A. 1982.** Diurnalism in *Parabuthus villosus* (Peters) (Scorpiones, Buthidae). *Journal of Arachnology* **10**: 85–86.
- Harington A. 1984.** Character variation in the scorpion *Parabuthus villosus* (Peters) (Scorpiones, Buthidae): a case of intermediate zones. *Journal of Arachnology* **11**: 393–406.
- Hewitt J. 1913.** The Percy Sladen Memorial Expedition to Great Namaqualand, 1912–1913. Records and descriptions of the Arachnida of the collection. *Annals of the Transvaal Museum* **4**: 146–159.
- Hewitt J. 1918.** A survey of the scorpion fauna of South Africa. *Transactions of the Royal Society of South Africa* **6**: 89–192.
- Hill G. 1990.** A tale with a sting. *Journal of the Medical Defence Union* **6**: 69.
- Huys I, Dyason K, Waelkens E, Verdonck F, Van Zyl J, du Plessis J, Müller GJ, Van der Walt J, Clynen E, Schoofs L, Tytgat J. 2002.** Purification, characterization and biosynthesis of parabutotoxin 3, a component of *Parabuthus transvaalicus* venom. *European Journal of Biochemistry* **269**: 1854–1865.
- Inceoglu B, Lango J, Jing J, Chen L, Doymaz F, Pessah IN, Hammock BD. 2003.** One scorpion, two venoms: pre-venom of *Parabuthus transvaalicus* acts as an alternative type of venom with distinct mechanism of action. *Proceedings of the National Academy of Sciences of the United States of America* **100**: 122–126.
- Koch C. 1962.** The Tenebrionidae of southern Africa. XXXI. Comprehensive notes on the tenebrionid fauna of the Namib

- desert. *Annals of the Transvaal Museum* **24**: 9–15 [plates] and 61–106.
- Kovařík F. 1998.** *Štíři (Scorpions)*. Madagaskar: Jihlava.
- Kovařík F. 2001.** Catalog of the scorpions of the world (1758–1998) by V. Fet, W.D. Sissom, G. Lowe, and M. Braunwalder (New York Entomological Society, 2000:690 pp.). Discussion and supplement for 1999 and part of 2000. *Serket* **7**: 78–93.
- Kovařík F. 2002.** Co nového u štírů v roce 2000 (Novelties in scorpions in the year 2000). *Akvárium Terárium* **45**: 55–61.
- Kovařík F. 2003a.** Co nového u štírů v roce 2001 (Novelties in scorpions in the year 2001). *Akvárium Terárium* **46**: 56–61.
- Kovařík F. 2003b.** Scorpions of Djibouti, Eritrea, Ethiopia, and Somalia (Arachnida: Scorpiones), with a key and descriptions of three new species. *Acta Societatis Zoologicae Bohemoslovenicae* **67**: 133–159.
- Kovařík F. 2004.** *Parabuthus cimrmani* sp. nov. from Somalia (Scorpiones: Buthidae). *Acta Societatis Zoologicae Bohemoslovenicae* **68**: 15–19.
- Kraepelin K. 1908.** Skorpione und Solifugen. In: Schultze LG, ed. *Forschungsreise im Westlichen und Zentralen Südafrika, Ausgeführt in den Jahren 1903–1905*. Jena: Fischer, 1: 247–282.
- Lamoral BH. 1977.** *Parabuthus kalaharicus*, a new species of scorpion from the Kalahari Gemsbok National Park in the Republic of South Africa (Buthidae, Scorpionida). *Koedoe* **20**: 101–107.
- Lamoral BH. 1978.** Systematics and bionomics of the scorpions of South West Africa (Arachnida, Scorpionida). Ph.D. Thesis, University of Natal, Pietermaritzburg.
- Lamoral BH. 1979.** The scorpions of Namibia (Arachnida: Scorpionida). *Annals of the Natal Museum* **23**: 498–783.
- Lamoral BH. 1980.** Two new psammophile species and new records of scorpions from the northern Cape Province of South Africa (Arachnida: Scorpionida). *Annals of the Natal Museum* **24**: 201–210.
- Lancaster N. 1981.** Paleoenvironmental implications of fixed dune systems in southern Africa. *Palaeogeography, Palaeoclimatology, Palaeoecology* **33**: 327–346.
- Lancaster N. 1984.** Aridity in southern Africa: age, origins and expression in landforms and sediments. In: Vogel JC, ed. *Late Cainozoic palaeoclimates of the Southern Hemisphere. Proceedings of an International Symposium held by the South African Society for Quaternary Research, Swaziland, 29 August–2 September 1983*. Rotterdam: A.A. Balkema, 433–444.
- Lawrence RF. 1928.** Contributions to a knowledge of the fauna of South-West Africa. VII. Arachnida (Part 2). *Annals of the South African Museum* **25**: 217–312.
- Lee NC. 1991.** Scorpion stings. *South African Medical Journal* **79**: 120.
- McCormick SJ, Polis GA. 1990.** Prey, predators, parasites. In: Polis GA, ed. *The biology of scorpions*. Stanford, CA: Stanford University Press, 294–320.
- Maddison D. 1991.** The discovery and importance of multiple islands of most parsimonious trees. *Systematic Zoology* **40**: 315–328.
- Mendelsohn J, Jarvis A, Roberts C, Robertson T. 2002.** *Atlas of Namibia. A portrait of the land and its people*. Cape Town: David Philip.
- Müller GJ. 1993.** Scorpionism in South Africa. A report of 42 serious scorpion envenomations. *South African Medical Journal* **83**: 405–411.
- Navidpour S, Kovařík F, Soleglad ME, Fet V. 2008.** Scorpions of Iran (Arachnida, Scorpiones). Part I. Khoozestan Province. *Euscorpius* **65**: 1–41.
- Newlands G. 1974a.** The venom-squirting ability of *Parabuthus* scorpions (Arachnida: Buthidae). *South African Journal of Medical Science* **39**: 175–178.
- Newlands G. 1974b.** Transvaal scorpions. *Fauna and Flora* **25**: 3–7.
- Newlands G. 1978a.** Review of southern African scorpions and scorpionism. *South African Medical Journal* **54**: 613–615.
- Newlands G. 1978b.** Arachnida (except Acari). In: Werger MJA, ed. *Biogeography and ecology of Southern Africa*. Vol. 2, The Hague: W. Junk, 687–702.
- Newlands G, Martindale CB. 1980.** The buthid scorpion fauna of Zimbabwe-Rhodesia with checklists and keys to the genera and species, distribution and medical importance (Arachnida: Scorpiones). *Zeitschrift für angewandte Zoologie* **67**: 51–77.
- Nixon KC. 2002.** *WinClada. Version 1.00.08. Computer software and documentation*. Available at <http://www.cladistics.com/wincDownload.htm>
- Nixon KC, Carpenter JM. 1993.** On outgroups. *Cladistics* **9**: 413–426.
- Petersen J. 1987.** Death due to a scorpion sting. *South African Medical Journal* **71**: 406.
- Platnick NI. 1992.** Patterns of biodiversity. In: Eldredge N, ed. *Systematics, ecology, and the biodiversity crisis*. New York: Columbia University Press, 15–24.
- Pocock RI. 1890.** A revision of the genera of scorpions of the family Buthidae, with descriptions of some South-African species. *Proceedings of the Zoological Society* **1890**: 114–141.
- Prendini L. 2000.** A new species of *Parabuthus* Pocock (Scorpiones: Buthidae), and new records of *Parabuthus capensis* (Ehrenberg), from Namibia and South Africa. *Cimbebasia* **16**: 31–45.
- Prendini L. 2001a.** Phylogeny of *Parabuthus* (Scorpiones, Buthidae). *Zoologica Scripta* **30**: 13–35.
- Prendini L. 2001b.** Substratum specialization and speciation in southern African scorpions: the Effect Hypothesis revisited. In: Fet V, Selden PA, eds. *Scorpions 2001*. In Memoriam Gary A. Polis. Burnham Beeches, Buckinghamshire: British Arachnological Society, 113–138.
- Prendini L. 2003.** Discovery of the male of *Parabuthus muelleri*, and implications for the phylogeny of *Parabuthus* (Scorpiones: Buthidae). *American Museum Novitates* **3408**: 1–24.
- Prendini L. 2004a.** The systematics of southern African *Parabuthus* Pocock (Scorpiones, Buthidae): revisions to the taxonomy and key to the species. *Journal of Arachnology* **32**: 109–186.
- Prendini L. 2004b.** Systematics of the genus *Pseudolychas*

- Kraepelin (Scorpiones: Buthidae). *Annals of the Entomological Society of America* **97**: 37–63.
- Prendini L. 2005.** Scorpion diversity and distribution in southern Africa: Pattern and process. In: Huber BA, Sinclair BJ, Lampe, KH, eds. *African biodiversity: molecules, organisms, ecosystems. Proceedings of the 5th International Symposium on Tropical Biology, Museum Alexander Koenig, Bonn*. New York: Springer Verlag, 25–68.
- Prendini L, Bird TL. 2008.** Scorpions of the Brandberg Massif, Namibia: species richness inversely correlated with altitude. *African Invertebrates* **49**: 77–107.
- Rein JO. 1993.** Sting use in two species of *Parabuthus* scorpions (Buthidae). *Journal of Arachnology* **21**: 60–63.
- Saunders CR, Morar AB. 1990.** Beware the scorpion *Parabuthus*. *Central African Journal of Medicine* **36**: 114–115.
- Smithe FB. 1974.** *Naturalist's color guide supplement*. New York: The American Museum of Natural History.
- Smithe FB. 1975.** *Naturalist's color guide*. New York: The American Museum of Natural History.
- Smithe FB. 1981.** *Naturalist's color guide. Part III*. New York: The American Museum of Natural History.
- Swerts A, Debont T, Verdonck F, Van der Walt JJ, Daenens P, Tytgat J. 1997.** Development and optimization of a purification strategy for the venom of the scorpion *Parabuthus transvaalicus*. *Journal de Pharmacie de Belgique* **52**: 194–195.
- Swofford DL, Maddison WP. 1987.** Reconstructing ancestral character states under Wagner parsimony. *Mathematical Biosciences* **87**: 199–229.
- Swofford DL, Maddison WP. 1992.** Parsimony, character-state reconstructions, and evolutionary inferences. In: Mayden RL, ed. *Systematics, historical ecology, and North American freshwater fishes*. Stanford, CA: Stanford University Press, 186–283.
- Tankard AJ, Rogers J. 1978.** Late Cenozoic palaeoenvironments on the west coast of southern Africa. *Journal of Biogeography* **5**: 319–337.
- Tytgat J, DeBont T, Rostoll K, Müller GJ, Verdonck F, Daenens P, Van der Walt JJ, Possani LD. 1998.** Purification and partial characterization of a 'short' insectotoxin-like peptide from the venom of the scorpion *Parabuthus schlecteri*. *FEBS Letters* **441**: 387–391.
- Vrba ES. 1980.** Evolution, species and fossils: how does life evolve? *South African Journal of Science* **76**: 61–84.
- Ward JD, Seely MK, Lancaster N. 1983.** On the antiquity of the Namib. *South African Journal of Science* **79**: 175–183.
- Watrous LE, Wheeler QD. 1981.** The out-group comparison method of character analysis. *Systematic Zoology* **30**: 1–11.
- Werner F. 1934.** Scorpiones, Pedipalpi. In: Bronn HG, ed. *Klassen und Ordnungen des Tierreichs*. Leipzig: Akademische Verlagsgesellschaft, 5, IV, 8, Lief. 1–2 [Scorpiones, 1–316].

APPENDIX

List of 68 characters for 27 species in the genus *Parabuthus* Pocock, 1890 and two outgroup taxa.

Character states were scored 0–2, ? (unknown), – (inapplicable) or polymorphic. Multistate characters were treated as unordered (non-additive). Eight uninformative characters, indicated by †, were excluded from all analyses. Characters from previous analyses that correspond partially or entirely to those in present matrix are as follows (author/number): L78 = Lamoral (1978); P0103 = Prendini (2001a, 2003). Refer to Table 1 for character matrix.

SIZE

1. Adult general size: large, carapace length 6.5–17.0 mm (0); small, carapace length 2.5–5.0 mm (1). [L78/2, P0103/1].

COLOUR

2. Colour of carapace, mesosoma, and metasoma: pale yellow to light brown (0); dark brown to black (pedipalps and legs may be dark or pale) (1); polymorphic (0 1). [P0103/2]
3. Colour pattern of metasoma: metasomal segments I–V and telson uniformly coloured (0); metasomal segments III–V and telson infuscated (i.e. darker than segments I and II) (1); polymorphic (0 1). [P0103/3]
4. Pedipalps, colour: pale (though perhaps very lightly infuscated) (0); very dark or heavily infuscated (1).
5. Legs, colour: pale (though perhaps very lightly infuscated) (0); very dark or heavily infuscated (1).

CARAPACE

6. †Carapace dorsoventrally compressed: absent (0); present (1). [P0103/4]
7. Granulation of median ocular tubercle (male, female) and surrounding surfaces (female): entire (0); smooth areas (1). [P0103/5]

PEDIPALPS

8. Pedipalps, setation: setose (0); smooth (1). [P0103/6]
9. Chela manus, surface: smooth (0); granular (1). [P0103/7]
10. Chela movable finger, length compared with length of manus (measured along ventroexternal carina), in female: long (length finger/length manus: 1.70–2.00) (0); short (length finger/length manus: ± 1.50) (1). [L78/15, P0103/8]
11. Chela manus, shape in adult male, compared with adult female: similar (0); sexually dimorphic (1). [P0103/9]

12. Chela fixed finger, shape in adult male: straight or slightly curved dorsally, such that proximal dentate margin linear when fingers are closed (0); strongly curved dorsally, proximal dentate margin distinctly emarginate when fingers are closed (1). [P0103/10]
13. Chela movable finger, shape in adult male: straight, proximal dentate margin linear when fingers are closed (0); curved ventrally, proximal dentate margin distinctly emarginate when fingers are closed (1). [P0103/11]
14. Chela fixed and movable fingers with basal lobe in adult male: absent (0); present (1). [P0103/12]

TRICHOBOTHRIA

15. Pedipalp femur, d_2 : present, unmodified (0); very reduced or absent (1).
16. Pedipalp femur, position of d_2 : dorsal side of dorsointernal carina (0); internal side of dorsointernal carina (1).
17. Pedipalp femur, position of e_1 : level with or distal to d_5 (0); proximal to d_5 , almost halfway between d_4 and d_5 (1). [L78/13, P0103/13]
18. Pedipalp patella, d_2 : present, unmodified (0); very reduced or absent (1).
19. Pedipalp patella, position of em : very close to et (0); medial between est and esb_2 or slightly closer to et (1).
20. Pedipalp patella, position of esb_2 : distinctly distal to esb_1 (0); level with or slightly distal to esb_1 (1). [L78/10, P0103/14]
21. †Chela manus, position of Esb : in line with or dorsal to Eb_2-Et axis (0); ventral to Eb_2-Et axis (1).
22. †Chela fixed finger, position of eb : proximal to basal dentate margin (0); distal to basal dentate margin (1).
23. Chela fixed finger, position of dt : in line with or distal to et (0); proximal to et (1). [P0103/15]

PECTINES

24. Proximal median lamella of pectines, in female: arcuate (0); enlarged and lobate (dilate) (1). [L78/3, P0103/16]
25. Proximal median lamella of pectines, in male: subrectangular (0); weakly lobate (dilate) (1); strongly lobate (dilate) (2). [P0103/17]

LEGS

26. Legs IV, length: moderately long, not reaching to posterior edge of metasomal segment III (0); very long, reaching past posterior edge of metasomal segment III (1). [L78/19, P0103/18]

27. Basitarsi of legs I and II, macrosetal combs: absent (0); weakly developed (1); strongly developed (2). [P0103/19]
28. Basitarsi of legs I and II, laterally expanded: absent (0); present (1). [P0103/20]
29. †Basitarsi of legs III and IV, prolateral surfaces with dense tufts of macrosetae: absent (0); present (1). [P0103/21]
30. Telotarsal ungues, relative length: equal (0); subequal (1). [P0103/22]

HEMISPERMATOPHORE

31. Hemispermatophore, *pars recta*: parallel to axis (0); S-shaped (1). [P0103/23]

MESOSOMA

32. †Tergites, posterior margins: sparsely setose (0); densely setose (1).
33. Sternites, surface: smooth (0); punctate (1). [L78/12, P0103/24]
34. Sternite III, 'pit' organ at proximal apex: absent (0); present (1). [P0103/25]
35. †Sternites III and VI, with pale raised surface posteromedially: absent or very weakly developed (0); prominent (1).
36. †Sternites III and VI, short, truncate setae: absent or sparse (0); very dense (1).
37. Sternite VII, carinae: present (0); absent (1). [P0103/26]
38. Sternite VII, median surface: smooth (0); granular (1).
39. Sternite VII and metasomal segment I, ventral surface, short, truncate setae: absent (0); sparse (1); very dense (2).

METASOMA

40. Metasomal segments I–V and telson, setation: absent (0); sparse (1); very dense (2). [L78/9, P0103/27]
41. Metasomal segments, width relative to length: much narrower (length IV/width IV: 1.7–2.11) (0); slightly narrower (length IV/width IV: 1.2–1.5) (1). [P0103/28]
42. Metasomal segments, width from I–IV: becoming narrower distally, metasomal segment I wider than segment IV (0); becoming wider distally, metasomal segment I narrower than segment IV (1). [L78/8, P0103/29]
43. Metasomal segments I–III, stridulatory region on dorsal surface: absent on I–III (0); strongly developed on I–III (1); strongly developed on I and II, weakly developed to absent on III (2). [P0103/30]

44. Metasomal segment I, shape of stridulatory region (if present) in dorsal aspect: narrow, parallel-sided (0); broad, rounded anteriorly, with posterior constriction (1); inapplicable (-). [P0103/31]
45. Metasomal segments I, and to a lesser extent II, shape of stridulatory region (if present) in lateral aspect: truncated at anterodorsal edge of segment (0); rounded, extended beyond anterodorsal edge of segment (1); inapplicable (-). [P0103/32]
46. Metasomal segment I, extent of stridulatory region (if present) in dorsal aspect: terminating at anterodorsal edge of segment (0); extended forwards in V-shape onto anterior surface (1); inapplicable (-). [P0103/33]
47. Metasomal segment II, extent of stridulatory region (if present) in dorsal aspect: reaching posterodorsal margin (0); not reaching posterodorsal margin (1); inapplicable (-); polymorphic (0 1). [L78/7, P0103/34]
48. Metasomal segment II, nature of stridulatory region (if present): fine to coarse granules (0); horizontal ridges (1); inapplicable (-). [P0103/35]
49. Metasomal segments II and III, posterodorsal edge: sublinear (0); anteromedially curved in a V-shape (1). [P0103/36]
50. Metasomal segments II–IV, ventral surface, short, truncate setae: absent (0); sparse (1); very dense (2).
51. Metasomal segments IV and V, lateral intercarnal surfaces: granular (0); smooth (1). [L78/11, P0103/37]
52. Metasomal segment I, ventrosubmedian carinae: present (0); absent (1)
53. Metasomal segments II and III or II–IV, distal spiniform granules of dorsosubmedian carinae (if present), size relative to preceding granules: equally developed (0); noticeably more pronounced (1); inapplicable (-). [P0103/40]
54. Metasomal segment IV, dorsosubmedian carinae: present (0); absent (1). [P0103/38]
55. Metasomal segment IV, dorsosubmedian carinae (if present): continuous (0); discontinuous (1); inapplicable (-). [P0103/39]
56. Metasomal segment IV, ventrosubmedian and ventrolateral carinae: present and continuous to edge of segment (0); present but ventrosubmedian carinae becoming obsolete distally (1); absent (2). [L78/1, P0103/41]
57. Metasomal segment IV, median lateral carina: absent to obsolete anteriorly (0); continuous but poorly developed (1); continuous and distinct (2). [L78/4, P0103/42]
58. Metasomal segment V, dorsosubmedian carinae: absent (0); present, poorly developed with blunt, rounded granules (1); present, distinct with sharp, spiniform granules (2). [L78/6, P0103/43]
59. Metasomal segment V, dorsolateral carinae: absent, except for a few proximal granules (0); posteriorly obsolete (1); continuous to distal edge of segment (2). [P0103/44]
60. Metasomal segment V, ventrolateral carinae: converging posteriorly (0); subparallel to diverging posteriorly (1). [L78/17, P0103/45]
61. Metasomal segment V, posterior half of ventrolateral carinae: with spinose processes (0); with lobate processes (1). [L78/14, P0103/46]
62. Metasomal segment V, ventrosubmedian carinae: absent or indistinct from surrounding granules (0); distinct (1). [P0103/47]
63. Metasomal segment V, ventromedian carina: present (may be indistinct) (0); absent (1). [P0103/48]

TELSON

64. Telson vesicle, width relative to width of metasomal segment V: approximately equal (0); considerably narrower (1). [L78/5, P0103/49]
65. †Telson vesicle, dorsoproximal surface: very shallowly excavated along longitudinal half (0); deeply excavated (1). [L78/18, P0103/50]
66. Telson aculeus, shape: gently curved (0); abruptly bent (1). [P0103/51]

BEHAVIOUR

67. Diurnal retreat: hides under rocks (0); burrows under rocks (1); burrows in open ground (2); unknown (?) polymorphic (1 2). [P0103/52]
68. Foraging strategy: sit-and-wait (0); errant (1); unknown (?) [P0103/53]