Discovery of the Male of *Parabuthus muelleri*, and Implications for the Phylogeny of *Parabuthus* (Scorpiones: Buthidae)

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ABSTRACT

The male of *Parabuthus muelleri* Prendini, 2000 is described, based on a specimen discovered in the Alexis Harington Scorpion Collection (recently acquired by the American Museum of Natural History). This is only the third known specimen of *P. muelleri*. The holotype and paratype are both female. The male presents several character states, including the lobate condition of the pectinal proximal median lamella and pedipalp chelae that are not incrassate, that are uncommon in male *Parabuthus* Pocock, 1890. These character states, previously scored with missing entries in a cladistic character matrix for *Parabuthus* species, are now added and a reanalysis of *Parabuthus* phylogeny, resulting in new insights about the phylogenetic position of *P. muelleri*, is presented. Lectotypes are designated for four northeastern African species of *Parabuthus*.

INTRODUCTION

Parabuthus Pocock, 1890 is an exclusively Old World genus of scorpions, 1 of 82 genera in the diverse, cosmopolitan family Buthidae (Fet and Lowe, 2000; Kovařík, 2001, 2002). The genus displays a classic "arid corridor" pattern of distribution (Balinsky, 1962), with 20 species occurring in southwestern Africa and 8 species occurring in northeast Africa and the Arabian Peninsula (Prendini, 2001a). All but six of the southern African species have been reported from Namibia (Lamoral, 1979), with four being endemic to that country, of which *P. muelleri* Prendini, 2000 is the most recent addition.

At the time of its description, *P. muelleri* was known from only two adult female spec-

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imens. A thorough search through the collections of the National Museum of Namibia (Windhoek), the South African Museum (Cape Town), the Transvaal Museum (Pretoria), and the Natal Museum (Pietermaritzburg), all with extensive holdings of sorted and unsorted *Parabuthus* material from southern Africa, revealed no additional specimens. The absence of adult male specimens prevented several important characters pertaining to sexual dimorphism and the male genitalia from being described for *P. muelleri*, and these characters also had to be scored with missing entries in a previously published cladistic character matrix for *Parabuthus* species (Prendini, 2001a).

A single adult male specimen has since been discovered in the Alexis Harington Scorpion Collection (recently acquired by the American Museum of Natural History). This is only the third known specimen of *P. muelleri*, but it is sufficient to update the diagnosis and description of the species, and provides additional diagnostic characters to distinguish it from the sister species, *P. capensis* (Ehrenberg, 1831). The male specimen presents several character states, including the lobate condition of the pectinal proximal median lamella and pedipalp chelae that are not incrassate, that are uncommon in male *Parabuthus*. These character states are now added to the cladistic character matrix for *Parabuthus* species (Prendini, 2001a), and a reanalysis of *Parabuthus* phylogeny, resulting in new insights about the phylogenetic position of *P. muelleri*, is presented.

MATERIALS AND METHODS

Material, Photography, and Terminology

The single adult male specimen of *P. muelleri* originates from the Alexis Harington Scorpion Collection (AH), which is now deposited in the American Museum of Natural History (AMNH). Consult appendix 1 for the repositories of other material examined for the cladistic analysis, where the full collection data (previously unpublished) are provided and lectotypes designated for four northeastern African species.

Photographs of *P. muelleri* were taken in visible light as well as under long-wave ultraviolet light using a Microptics ML1000 digital imaging system. Measurements were made with Mitutoyo digital calipers. Color designation follows Smithe (1974, 1975, 1981), trichobothrial notation follows Vachon (1974), and mensuration follows Stahnke (1970) and Lamoral (1979). Morphological terminology follows Couzijn (1976) for the segmentation of legs, Hjelle (1990) and Sissom (1990) for the segmentation of pedipalps, and Stahnke (1970), Lamoral (1979), Sissom (1990), and Prendini (2000a, 2001a) for remaining features.

As in previous papers (Prendini, 2000a, 2001a), the terms used by other authors on the southern African scorpion fauna (Eastwood, 1977; Lamoral, 1977, 1979; FitzPatrick, 1994) for certain metasomal carinae have been replaced with terms implying specific homology statements between carinae on segment V and those on the preceding segments. The term ''ventral'' (segments I–V) is replaced with ''ventrosubmedian'' (segments I–IV only) and ''ventromedian'' (segment V only) and the terms ''dorsal'' (segments I–IV only) and ''dorsal accessory'' (segment V only) are replaced with ''dorsosubmedian''.

Cladistic Analysis

The present analysis is based on the previously published morphological data matrix for relationships among the species of *Parabuthus* (Prendini, 2001a), to which the states of characters 9–12, 17, and 23, previously scored with missing entries for the male of *P. muelleri*, have now been added (table 1; appendix 2). The matrix comprises 51 characters, 9 coded into multistates and 44 coded into binary states, scored for 27 species. Multistate characters were treated as unordered, i.e., nonadditive (Fitch, 1971).

Trees were rooted using the outgroup method (Watrous and Wheeler, 1981; Farris, 1982; Nixon and Carpenter, 1993). As in the previous analysis, 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 morphological and molecular evidence that these genera are most closely related to *Parabuthus* (Pocock,

TABLE 1
Distribution of 53 Characters Among 25 Species of the Genus *Parabuthus* Pocock, 1890
The first two taxa are outgroups. Refer to appendix 1 for character list. Character states are scored 0 to 2, ? (unknown), – (inapplicable) or * (polymorphic).

G. madagascariensis	01000	10001	00000	00000	00000	00000	-----	00000	00000	00000	000
U. triangulifer	10000	00000	00000	00000	00000	01000	-----	00000	00000	00100	000
P. granimanus	01100	01010	01000	10020	00001	01112	00000	00000	12110	01000	1??
P. heterurus	00100	00010	00000	10020	00001	01112	00000	00000	12110	11000	1??
P. hunteri	00100	01010	01000	10020	00001	01112	00000	00000	12110	01000	1??
P. leiosoma	00100	00010	00000	10020	00001	01111	00000	00000	12110	11000	1??
P. pallidus	00000	00000	00000	11010	00000	01111	00000	00011	12110	10000	1??
P. brevimanus	10001	00110	00111	10121	00000	01001	10000	00001	20001	10100	020
P. calvus	00001	10000	00000	12010	10000	00101	11000	01011	20110	10100	1??
P. capensis	0**00	00010	00000	10020	00000	01111	11000	10011	12210	10000	1*0
P. distridor	10001	00110	00111	10121	01000	11000	-----	011--	20000	00100	020
P. gracilis	10000	01110	00011	10121	00110	11001	10000	001--	20000	00100	020
P. granulatus	01000	10011	10000	00121	00000	00101	10010	00000	10010	10010	021
P. kalaharicus	01000	10111	10011	00121	01000	00101	10010	00000	10010	00110	021
P. kraepelini	00000	00011	00000	10020	00000	01111	10100	00001	12221	10000	120
P. kuanyamarum	10001	00111	10111	10121	01000	10001	10000	011--	20000	00100	020
P. laevifrons	00101	10111	10011	10121	00000	00002	11000	01000	11000	11000	021
P. mossambicensis	00000	00010	00000	10020	00000	01111	11101	00001	12220	10000	120
P. muelleri	00100	00101	10000	11020	00000	01101	11000	10011	12210	10000	110
P. namibensis	00101	00011	10110	10120	00000	01002	11000	00000	11110	11000	021
P. nanus	10000	01000	00011	10121	00110	11001	10000	001--	20000	00100	020
P. planicauda	00000	00000	00000	11010	00000	01101	110*0	00011	12110	10000	110
P. raudus	0**00	00011	00000	10020	00000	01111	10110	00011	12220	00000	120
P. schlechteri	0*000	00011	00000	10020	00000	01111	10110	00011	12221	00000	120
P. stridulus	00*01	10111	10010	10121	00000	00002	11001	01000	11000	01001	021
P. transvaalicus	01000	00011	00000	10020	00000	01111	10100	00011	12221	00000	110
P. villosus	01010	00011	00000	10020	00000	02101	111*0	00011	12221	00000	111

1890; Kraepelin, 1908; Werner, 1934; Prendini and Wheeler, in prep.).

Character data were edited, cladograms prepared, and character optimizations conducted using WinClada, vers. 0.9.9+ (Nixon, 1999). Ambiguous optimizations were resolved using accelerated transformation (ACCTRAN) or Farris optimization, which favors reversals over parallelisms to explain homoplasy (Farris, 1970; Swofford and Maddison, 1987, 1992) and therefore maximizes homology (Griswold et al., 1998). Three autapomorphies (characters 4, 21, and 50) were excluded from all analyses; hence, tree statistics are calculated from phylogenetically informative characters only (Bryant, 1995).

Characters were not weighted a priori. Analyses with equal weighting were conducted using NONA vers. 2.0 (Goloboff, 1997a), according to the following command sequence: **hold10000; hold/10; mult*100;** (hold 10,000 trees in memory; hold 10 starting trees in memory; perform TBR branch-swapping on 100 random-addition replicates). Additional swapping on up to 1000 trees that are up to 5% longer than the shortest trees (command **jump 50;**) was performed to help the swapper move between 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.

Successive approximations character weighting (Farris, 1969) and implied character weighting (Goloboff, 1993, 1995) were conducted to assess the effects of weighting against homoplasious characters, and the resultant topologies were compared with the topology obtained by analysis with equal weights (see Prendini, 2000b, 2001a). Successive weighting, using the squared consis-

TABLE 2
Summary of Statistical and Topological Diferences Among the Most Parsimonious Trees (MPTs)
MPTs were obtained by analysis with equal weights (EW), successive weights (SW), and implied weights (IW) with six values for the concavity constant (k), arranged in order of decreasing fitness. Unweighted length is reported for the SW tree. Letters A and B refer to alternative topologies for node A (fig. 1).

	MPTs	Steps	Fit (fi)	Rescaled fit	CI	RI	A[a]	B[b]
IW (k=6)	1	133	410.4	61	44	74	+	
IW (k=5)	1	132	399.6	59	44	74	+	
IW (k=4)	1	133	382.9	57	44	74	+	
IW (k=3)	1	133	360.5	54	44	74	+	
EW	1	133	360.5	54	44	74	+	
SW	1	133	360.5	54	44	74	+	
IW (k=2)	2	136	325.4	49	43	73		+
IW (k=1)	2	136	267.9	42	43	73		+

[a]A: ((*P. capensis* (*P. muelleri* (*P. calvus* + *P. pallidus* + *P. planicauda*))) (*P. mossambicensis* (*P. kraepelini* ((*P. raudus* + *P. schlechteri*) (*P. transvaalicus* + *P. villosus*)))))

[b]B: (*P. mossambicensis* (*P. kraepelini* ((*P. raudus* + *P. schlechteri*) (*P. transvaalicus* P. villosus* (*P. capensis* (*P. muelleri* (*P. calvus* + *P. pallidus* + *P. planicauda*)))))))

tency index (CI) as a weighting function (Goloboff, 1991), was implemented with NONA by invoking the swt.run file (command sequence: **run swt.run hold10000; hold/10; mult*100; jump50; max*;**). Pee-Wee version 2.6 (Goloboff, 1997b) was used for analyses with implied weighting, applying the command sequence: **hold1000; hold/10; mult*100; 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 10,000) were calculated with NONA by means of the following command sequence: **h10000; bsupport 5;**.

RESULTS AND DISCUSSION

Analysis of the 50 informative characters in NONA located a single most parsimonious tree (MPT) with equal weights (table 2; fig. 1). The same topology was retrieved in the analysis with successive weights and also in the analyses with implied weights when val-

ues for the concavity constant were moderate to mild (i.e., k = 3–6; table 2). Although topologically identical, the MPTs obtained by the analyses with implied weights were 3–7% fitter than the MPTs obtained by analysis with equal weights, while the MPT retrieved under k = 5 was also one step shorter. In contrast, under strong concavity (k = 1–2), analyses with implied weights located two MPTs, each three steps longer and 5–12% less fit than the MPTs obtained by analysis with equal weights (table 2). These trees differed from the topology in figure 1 with respect to the species comprising node ''A'', for which the alternative arrangements were as follows: (*P. mossambicensis* (*P. kraepelini* ((*P. raudus* + *P. schlechteri*) ((*P. transvaalicus* + *P. villosus*) (*P. capensis* (*P. muelleri* (*P. calvus* + *P. pallidus* + *P. planicauda*))))))); (*P. mossambicensis* (*P. kraepelini* ((*P. raudus* + *P. schlechteri*) (*P. transvaalicus* (*P. villosus* (*P. capensis* (*P. muelleri* (*P. calvus* + *P. pallidus* + *P. planicauda*))))))).

The MPTs obtained by analysis with implied weights under k = 1–2 are longer and less fit than the MPTs obtained by the remaining analyses, and hence they are considered to be suboptimal. The alternative topology, obtained by weighting regimes that minimized length as well as those that maximized fit (table 2), is instead regarded as optimal.

Unambiguously optimized synapomorphies are indicated on this topology in figure 1, which also provides branch support values for nodes. The length, fit (f_i), consistency indices, retention indices, and final successive weights of informative characters on this topology are listed in table 3.

As might be expected, the arrangement of relationships among the species of *Parabuthus* retrieved in the present analyses is almost identical to that obtained previously (Prendini, 2001a), as are the major findings. Monophyly of the genus *Parabuthus* is again supported, but monophyly of the disjunct southern African versus northeastern African and Arabian species is not. The optimal topology presented here differs from that published previously only in relationships among the five species comprising node ''B'' (fig. 1): *P. calvus*, *P. capensis*, *P. muelleri*, *P. pallidus*, and *P. planicauda*. Previously, the relationships among these species were retrieved as follows by the majority of analyses, including those deemed optimal: ((*P. capensis* + *P. muelleri*) (*P. pallidus* (*P. calvus* + *P. planicauda*))). All previous analyses supported the (*P. capensis* + *P. muelleri*) group. In contrast, all present analyses retrieved the following arrangement of these species: (*P. capensis* (*P. muelleri* (*P. calvus* + *P. pallidus* + *P. planicauda*))). Thus, whereas a sister-group relationship between *P. capensis* and *P. muelleri* was identified by previous analyses, the addition of six character states for the male of *P. muelleri* indicates that this species actually shares a more recent common ancestor with *P. calvus*, *P. pallidus*, and *P. planicauda* than with *P. capensis*. The sister-group relationship between *P. calvus* and *P. planicauda*, retrieved by most, but not all previous analyses, is no longer supported either.

SYSTEMATICS

FAMILY BUTHIDAE C. L. KOCH, 1837
GENUS *PARABUTHUS* POCOCK, 1890

Parabuthus muelleri Prendini, 2000

Parabuthus muelleri Prendini, 2000a:
32–38,
figs. 1–9, table 2.

Parabuthus muelleri: Prendini, 2001a: 17; 2001b: 137.

TYPE MATERIAL: Holotype ♀ (NMNW 1854), Namibia: Hardap Region: Maltahöhe District: Farm Onis 8, 82 km from Sesriem to Naukluft, 24°22.46′S, 16°13.17′E, 1260 m, 7.i.1998, L. Prendini and E. Scott. Paratype ♀ (SAMC C4514), Namibia: Karas Region: Lüderitz District: Farm Plateau 38, near Aus, 26°40.62′S, 16°31.85′E, 1550 m, 30.xii.1997, L. Prendini and E. Scott.

DIAGNOSIS: *Parabuthus muelleri* falls in a group of species also including *P. calvus*, *P. capensis*, *P. pallidus*, and *P. planicauda*. This species is morphologically most easily confused with *P. capensis*, with which it shares the following combination of characters: metasomal segments I and II, stridulatory region extended anteriorly beyond anterodorsal edge of segment, giving a steplike appearance in lateral aspect; metasomal segments II–IV, dorsosubmedian carinae with distal spiniform granules more pronounced than preceding granules; metasomal segment IV, dorsosubmedian carinae medially discontinuous, median lateral carina continuous and distinct; metasomal segment V, dorsosubmedian carinae distinct with sharp, spiniform or subspiniform granules, and dorsolateral carinae distally obsolete. *Parabuthus muelleri* and *P. capensis* can be separated from all other *Parabuthus* on the basis of the following character: metasomal segment II, and to a lesser extent III, with posterodorsal edge elevated and slightly curved forward medially, forming a subtriangular V-shape.

Although morphologically similar, *P. muelleri* can be separated from *P. capensis* by several characters. The movable finger of the pedipalp chela (adult male and female) is curved ventrally in *P. muelleri*, such that the proximal dentate margin is distinctly emarginate when the fingers are closed (i.e., a proximal ''gap'' is evident). The emarginate condition occurs in the male of several *Parabuthus* species (e.g., *P. granulatus*, *P. kalaharicus*, and *P. laevifrons*), but it is uncommon in female *Parabuthus*, and does not occur in the male or female of *P. capensis*. In addition, *P. muelleri* has a more slender metasoma, in which the median width:length percentage for metasomal segments I–V (n = 3) is 80.5% (75–86%), 78% (75–81%), 76% (72–80%), 69.5% (65–74%), and 55% (53–57%), compared with the metasoma of

2 6 10
1 1 1
G. madagascariensis

1 48
1 1
U. triangulifer

27
1

45
1
P. brevimanus

1 13 15 40 41 44 48
1 1 1 1 2 0 1
3

30
0
P. distridor

22 37
1 1
2

10 11 27
1 1 0
P. kuanyamarum

26 38 46
1 1 0
1

5 7 13 23 24
0 1 0 1 1
3

P. gracilis

8 9
0 0
P. nanus

5 8 14 18 20
1 1 1 1 1
2

8 14
0 0
P. granulatus

2 5 16 28 34 49
1 0 0 1 1 1
5

15 22 46 48
1 1 0 1
P. kalaharicus

6 10 11 27 53
1 1 1 0 1
2

6 8 13 20 27 43
0 0 1 0 1 1
P. namibensis

3 30 32 42 47
1 2 1 1 1
3

15
1
P. laevifrons

37 44
1 0
1

35 46 50
1 0 1
P. stridulus

9 16 19 30 41 44 46 52
1 1 2 1 1 1 1 2
4

P. leiosoma

3 25 31 47
1 1 0 1
4

30
2
1
P. heterurus

7 12 46
1 1 0
3

2
1
P. granimanus

P. hunteri

28 29 42 43 51
1 1 2 1 1
4

36 39 52
1 1 1
1

B

P. capensis

3 8 10 11
1 1 1 1
P. muelleri

9 17 29
0 1 0
1

5 6 17 21 27 37 41 42 48
1 1 2 1 0 1 2 0 1
P. calvus

19 36 43
1 0 1
1

29 31 32
1 0 0
P. pallidus

P. planicauda

32 40 43
1 1 2
1

A

35
1
P. mossambicensis

33 44
1 2
1

P. kraepelini

10 32 45
1 0 1
2

2 39 46
1 1 0
2

45
0
P. raudus

34
1
P. schlechteri

52
1
P. transvaalicus

4 27 29 32 53
1 2 0 1 1
P. villosus

P. capensis, in which the median width: length percentage ($n = 6$) is 86% (77–95%), 73% (78–88%), 92% (79–105%), 73% (67–79%), and 58% (53–63%). Metasomal segment III is usually broader than segments I and II in *P. capensis*, but this is not the case in *P. muelleri*. *Parabuthus muelleri* is further distinguished by the unusual shape of the telson, which differs from all known *Parabuthus* species in the presence of a distal "bulge" and a very short, sharply curved aculeus. The median percentage of aculeus length:telson length in *P. muelleri* ($n = 3$) is 30% (26–34%), compared with 39% (36–42%) in *P. capensis* ($n = 6$). The two species may also usually be distinguished by the relative positions of the trichobothria on the fixed finger of the chela: *eb* and *esb* are located proximal to the basal dentate margin of the fixed finger in *P. muelleri*, whereas *eb* is located proximal to the basal dentate margin, and *esb* is located distal to it, in *P. capensis*. However, this character has been found to be polymorphic in *P. capensis*: in populations from the eastern part of the distributional range, *esb* is also located proximal to the basal dentate margin (Prendini, 2000a).

Two characters of the newly described male can also be used to separate *P. muelleri* from *P. capensis*, notably the lobate condition of the pectinal proximal median lamella and pedipalp chelae that are not incrassate (i.e., not sexually dimorphic). The absence of sexual dimorphism of the pedipalp chelae is a particularly obvious diagnostic difference between *P. muelleri* and *P. capensis*, in which the pedipalp chelae are markedly dimorphic (the pedipalp chela manus of the male is incrassate, whereas that of the female is slender). Both characters are discussed further in the description of sexual dimorphism, below.

DESCRIPTION: The following description of the male (AMNH [AH 3991]) supplements the previous descriptions (Prendini, 2000a) of the holotype female (NMNW 1854) and paratype female (SAMC C4514).

Color: Carapace, chelicerae, tergites, sternites, and metasomal segments I–III: Cinnamon no. 123A. Metasomal segments IV, V and telson: Burnt Sienna no. 132. Pedipalps and legs: Clay Color no. 123B. Pectines: Chamois no. 123D. Metasomal segments IV, V and telson are distinctly darker than segments I–III, whereas pedipalps and legs are distinctly paler than carapace, mesosoma, metasoma, and telson (figs. 2, 3).

Carapace: Carapace with sulci, without carinae, and covered entirely by uniform, coarse granulation, becoming coarser on interocular and posterolateral surfaces. Anterior margin of carapace procurved; posterior margin straight. Five pairs of lateral ocelli. Median ocelli considerably larger than lateral ocelli, situated anteromedially (fig. 4). Ocular tubercle with pair of smooth superciliary carinae, protruding slightly above median ocelli. Anteromedian furrow shallow; posteromedian furrow shallow anteriorly, becoming deeper posteriorly; posterolateral furrows shallow, wide, curved; posteromarginal furrow 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 a pair of denticles on the ventral surface.

Sternum: Subtriangular (fig. 3). Median longitudinal furrow Y-shaped, shallow anteriorly, deep and narrow posteriorly.

←

Fig. 1. The optimal tree obtained by analysis under weighting regimes that maximized fit and minimized length. This topology was retrieved by analyses with equal weights, successive weights, and implied weights under $k = 3$–6 (table 2). Zero-length branches are collapsed. This topology also corresponds to the majority rule (>50%) consensus of MPTs obtained by the eight analyses in which weighting regime and multistate character transformation were varied (table 2). Solid bars indicate uniquely derived apomorphic character states, whereas empty bars indicate parallel derivations of apomorphic states under ACCTRAN optimization. The number above each bar gives the character number, whereas the number below gives the character state. Branch-support values of nodes are provided below branches. Refer to appendix 2 for character descriptions.

TABLE 3
Length (steps), Fit (f_i), Consistency Indices (CIs), and Retention Indices (RIs) of 50 Informative Characters Scored Among 25 Species of the Genus *Parabuthus* Pocock, 1890
Final weights obtained with succesive weighting (SW) are also reported.

Char.	Steps	Fit	CI	RI	SW	Char.	Steps	Fit	CI	RI	SW
1	2	8.5	50	80	4	28	2	8.5	50	88	4
2	4	6.6	25	40	1	29	4	6.6	25	70	1
3	3	7.5	33	66	2	30	4	7.5	50	71	3
5	4	6.6	25	50	1	31	2	8.5	50	75	3
6	4	6.6	25	40	1	32	5	6.0	20	50	1
7	2	8.5	50	66	3	33	1	10.0	100	100	10
8	5	6.0	20	42	0	34	2	8.5	50	66	3
9	3	7.5	33	66	2	35	2	8.5	50	0	0
10	5	6.0	20	66	1	36	2	8.5	50	0	0
11	3	7.5	33	66	2	37	3	7.5	33	50	1
12	1	10.0	100	100	10	38	1	10.0	100	100	10
13	3	7.5	33	33	1	39	2	8.5	50	87	4
14	2	8.5	50	87	4	40	2	8.5	50	90	4
15	3	7.5	33	66	2	41	3	8.5	66	83	5
16	2	8.5	50	66	3	42	3	8.5	66	90	5
17	2	10.0	100	100	10	43	4	7.5	50	85	4
18	1	10.0	100	100	10	44	4	7.5	50	84	4
19	2	10.0	100	100	10	45	3	7.5	33	50	1
20	2	8.5	50	87	4	46	6	5.4	16	58	0
22	2	8.5	50	50	2	47	2	8.5	50	83	4
23	1	10.0	100	100	10	48	4	6.6	25	57	1
24	1	10.0	100	100	10	49	1	10.0	100	100	10
25	1	10.0	100	100	10	51	1	10.0	100	100	10
26	1	10.0	100	100	10	52	3	8.5	66	75	5
27	6	6.0	33	33	1	53	2	8.5	50	80	4

Pedipalps: Pedipalps covered in short macrosetae (figs. 7–9). Femur finely and uniformly granular; pentacarinate, all carinae distinct, granular, except for internomedian carina, comprising spiniform granules. Patella finely and uniformly granular; carinae absent or obsolete; dorsointernal and ventrointernal carinae each comprising a row of granules proximally; internomedian carina comprising a large spiniform granule, proximally, and a few smaller granules, distally. Chela smooth; carinae absent. Chela short, slender, length along ventroexternal carina 28% greater than chela width and 30% greater than chela height; length of movable finger 45% greater than length along ventroexternal carina. Chela fixed finger slightly curved dorsally and movable finger slightly curved ventrally, such that proximal dentate margin emarginate when fingers are closed (fig. 7). Dentate margins of chela fingers each with 11 oblique granular rows, each comprising 4–6 small granules and a large proximal granule, flanked by an inner and an outer accessory granule; chela fingers each with a terminal denticle.

Trichobothria: Orthobothriotaxic, type A, α configuration, with the following segment totals (figs. 7–12): femur, 11 (5 dorsal, 4 internal, 2 external), patella, 13 (5 dorsal, 1 internal, 7 external), and chela, 15 (8 manus, 7 fixed finger). Total number of trichobothria per pedipalp, 39. Chela with *eb* located proximal to basal dentate margin of fixed finger and *esb* located just distal; *dt* almost level with *et*; *db* equidistant between *est* and *esb*. Patella with esb_2 slightly distal to esb_1. Femur with d_2 on proximointernal side of dorsointernal carina; d_3 distal to d_2; d_4 equidistant between d_3 and d_5.

Mesosoma: Pre-tergites smooth and shiny, granular along posterior margins. Post-tergites entirely coarsely granular, granulation becoming coarser distally (fig. 2); I–VII each with a weakly developed, granular median
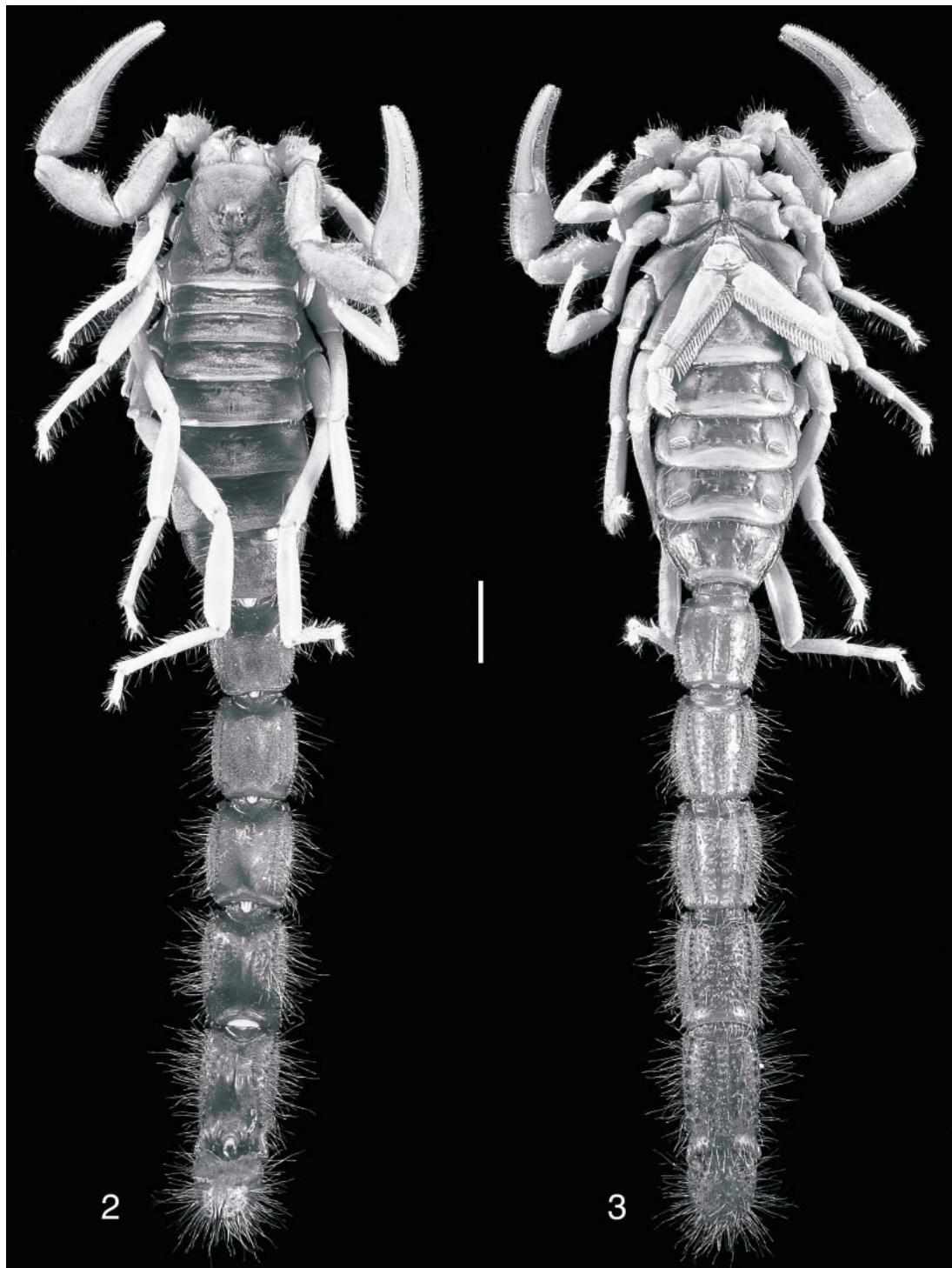
Figs. 2, 3. *Parabuthus muelleri* Prendini, 2000, male (AMNH [AH 3991]), habitus. **2.** Dorsal aspect. **3.** Ventral aspect. Scale bar = 5 mm.
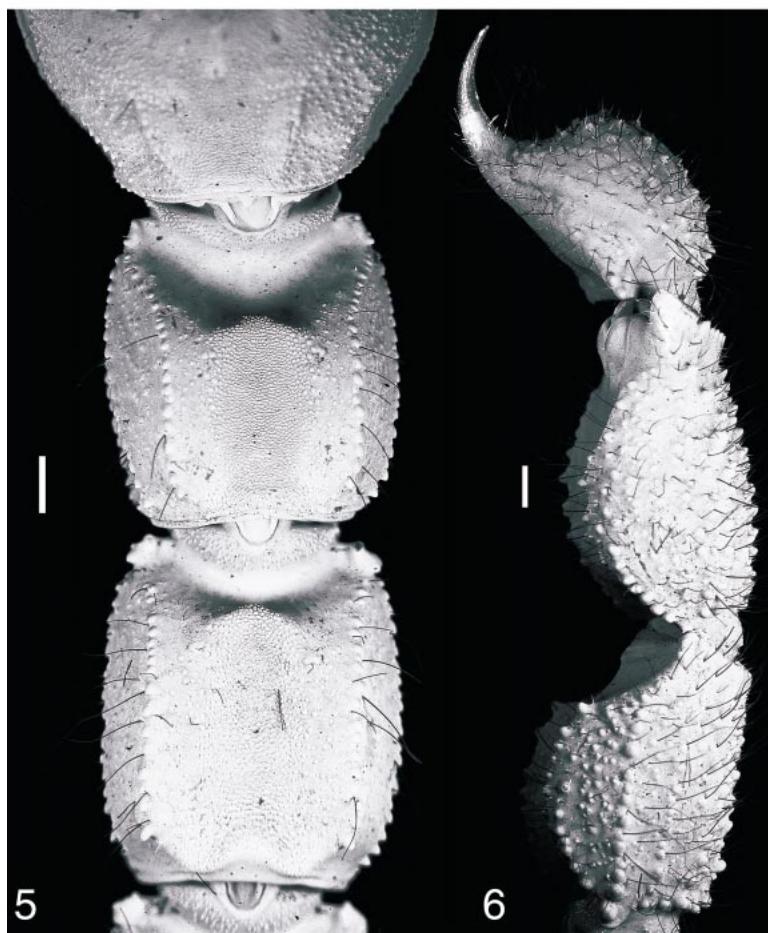
carina; VII additionally with distinct pairs of costate granular dorsosubmedian and dorsolateral carinae, and with well-developed stridulatory region between dorsosubmedian carinae, consisting of round to slightly crescent-shaped granules reaching the posterior margin. Sternites entirely smooth, except for posterolateral surfaces of sternite VII, which are sparsely granular; lateral and distal margins each with a row of sparsely distributed macrosetae; sternite VII with weakly developed pairs of costate ventrosubmedian and ventrolateral carinae.

Pectines: First proximal median lamella of each pecten suboval, mesially enlarged and lobate (fig. 3). Pectinal teeth: 36/36.

Genital operculum: Completely divided longitudinally. Genital papillae present.

Legs: Tibia III and IV with spurs; retrolateral margins with scattered macrosetae. Basitarsi I and II only slightly compressed dorsoventrally, retrolateral margins each with dense row of long, fine macrosetae. Telotarsi each with paired ventrosubmedian rows of fine macrosetae. Telotarsal laterodistal lobes truncated; median dorsal lobes extending to ungues. Telotarsal ungues short, distinctly curved, and equal in length.

Metasoma and telson: Metasomal segments I–V width/length ratio progressively decreasing, width percentage of length 86% for I, 81% for II, 80% for III, 68% for IV, and 53% for V (table 4). Telson oval, globose (fig. 6), height 66% of length, with flattened dorsal surface and rounded ventral surface; vesicle not significantly narrower than metasomal segment V, width 90% of metasomal segment V. Metasoma entirely granular, except for ventromedian surfaces of segments I and II, and dorsomedian surfaces of segments IV, V and telson. Metasomal segments I and II each with a well-developed stridulatory region on the dorsomedian surface, consisting of round to slightly crescent-shaped fine granules extending to the posterior margin (fig. 5); stridulatory region of

segment III narrow, virtually obsolete, consisting of a few granules in the proximal third of the segment; segment II, and to a lesser extent III, with posterodorsal edge elevated and slightly curved forward medially, forming a subtriangular V-shape (fig. 5). Metasoma densely covered with long macrosetae, especially on the ventral surface of the telson. Metasomal segments I–IV each with 10 carinae, but segment IV with ventrosubmedian and median lateral carinae distinct only in the proximal half of the segment; segment V with seven carinae, including a single, obsolete granular ventromedian carina, a pair of distinct ventrolateral carinae, a pair of dorsolateral carinae, distinct only in the proximal half of the segment, and a pair of dorsosubmedian carinae reduced to a few prominent rounded or subspiniform granules medially. Metasomal segments I–V with dorsosubmedian carinae converging distally in segment I, subparallel in segments II–V; ventrolateral carinae converging distally in segments I–III, subparallel in segment IV, diverging in segment V. All metasomal carinae costate granular to granular, except for ventrosubmedian and ventrolateral carinae of segment I, which are costate to costate granular. Metasomal segments II–IV with distal granules of dorsosubmedian carinae very slightly enlarged, rounded; segments II and III with distal granules of ventrosubmedian carinae and, to much a lesser extent, ventrolateral carinae, enlarged, obtuse, and elevated; segment V with subdistal granules of ventrolateral carinae enlarged into laterally compressed, lobate processes. Telson with a distal "bulge" and a very short, sharply curved aculeus (fig. 6); aculeus length percentage of vesicle length, 35%.

Hemispermatophore: A hemispermatophore was dissected from the male, confirming that it is adult. The hemispermatophore is typical of other species of *Parabuthus*, characteristically flagelliform, with *pars recta* parallel to axis of distal lamina (fig. 13).


←

Figs. 4–6.   *Parabuthus muelleri* Prendini, 2000, male (AMNH [AH 3991]), diagnostic characters. **4.** Carapace. **5.** Dorsal aspect of segments I and II, showing dorsomedian stridulatory region and subtriangular V-shape curvature at posterodorsal edge. **6.** Lateral aspect of segments IV, V and telson. Scale bars = 1 mm.
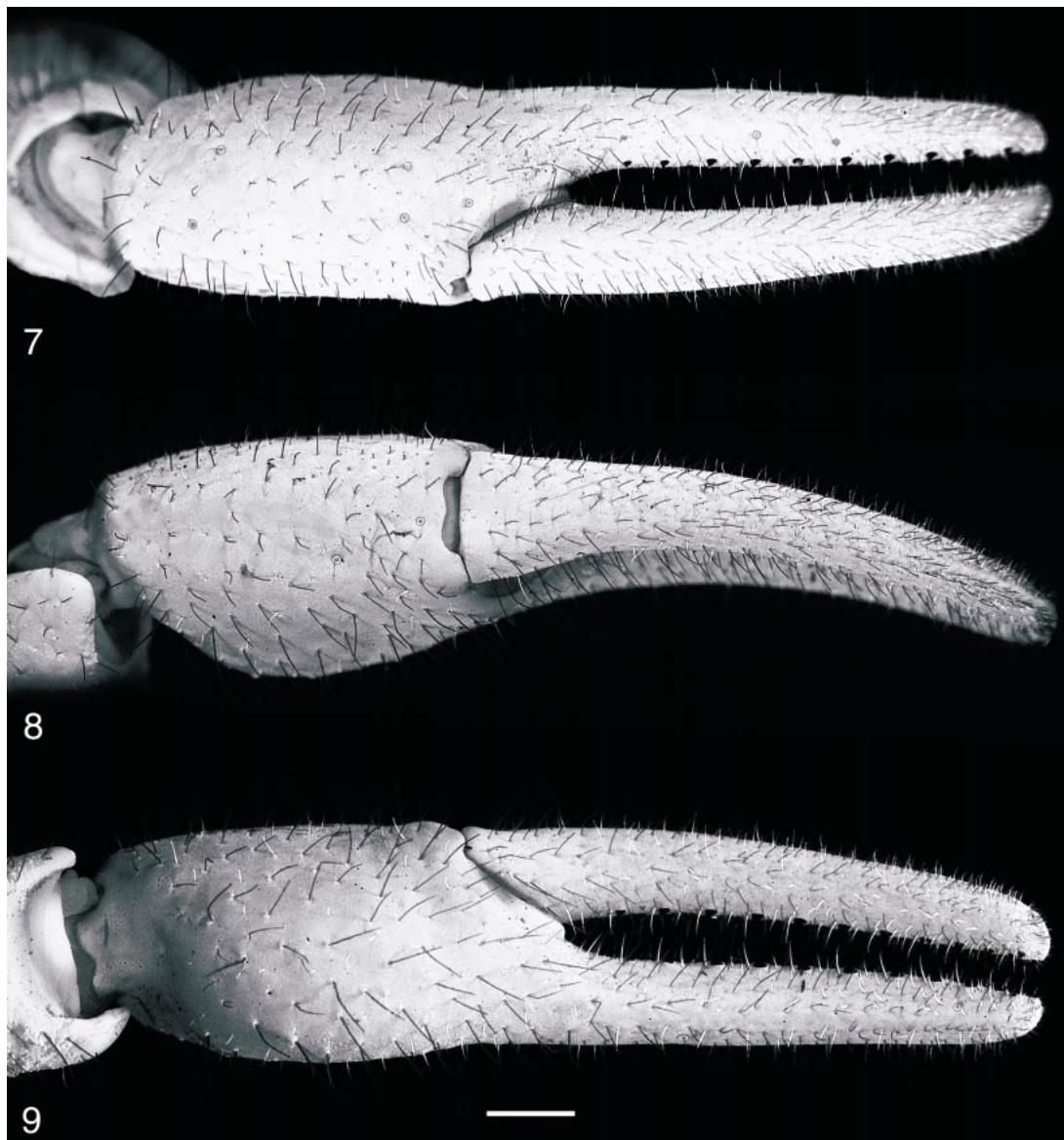
Figs. 7–9. *Parabuthus muelleri* Prendini, 2000, male (AMNH [AH 3991]), distribution of trichobothria and macrosetae on the dextral pedipalpal chela. **7.** Dorsal aspect. **8.** Ventral aspect. **9.** Internal aspect. Scale bar = 1 mm.

Sexual dimorphism: Unlike most species of *Parabuthus*, in which the pedipalp chela manus of the adult male is noticeably incrassate (bulbous or swollen), compared with the more slender manus of the adult female (Pocock, 1889, 1890, 1902; Kraepelin, 1899, 1908; Purcell, 1898, 1899, 1901; Werner, 1916; Hewitt, 1913, 1915, 1918; Eastwood, 1977; Lamoral, 1977, 1979, 1980; Newlands and Martindale, 1980; Prendini, 2001a), the adult male of *P. muelleri* is not sexually dimorphic in this respect. The chela width: length and height:length ratios of 72% and 70%, respectively, in the male do not differ significantly from the equivalent ratios of 74% and 69%, respectively, in the female.
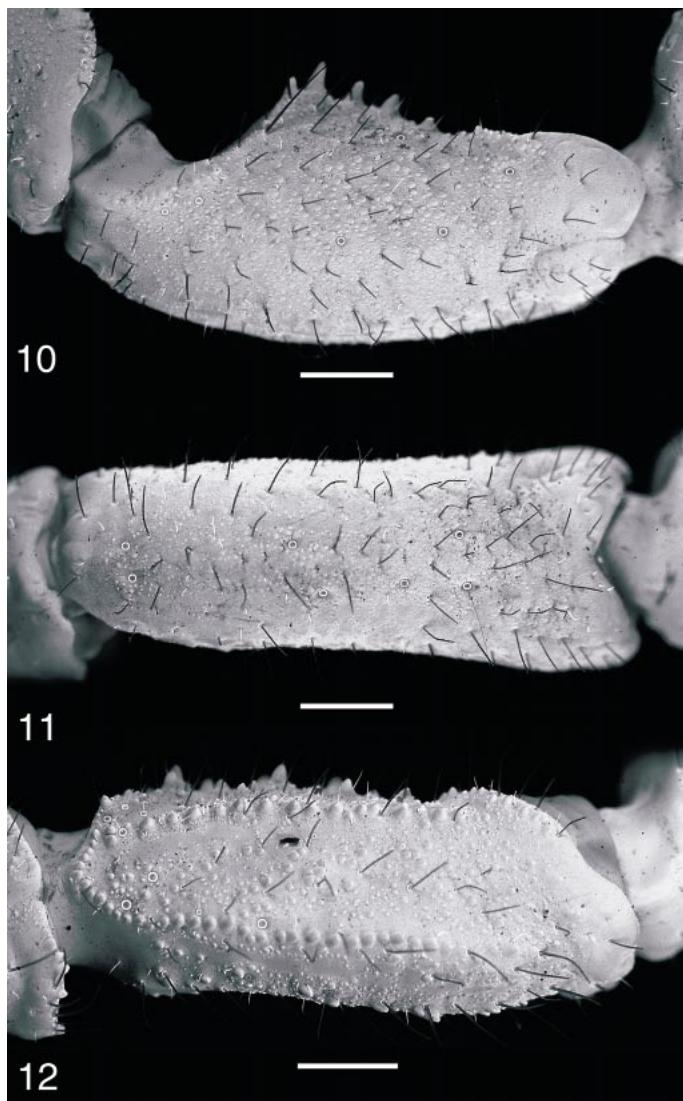
Figs. 10–12. *Parabuthus muelleri* Prendini, 2000, male (AMNH [AH 3991]), distribution of trichobothria and macrosetae on the dextral pedipalpal patella and femur. **10.** Dorsal aspect of patella. **11.** External aspect of patella. **12.** Dorsal aspect of femur. Scale bars = 1 mm.

Parabuthus calvus, *P. nanus*, *P. pallidus*, and *P. planicauda* are the only other species of the genus in which the pedipalp chelae of the adult male are not sexually dimorphic. The absence of sexual dimorphism of the pedipalp chelae provides an additional obvious diagnostic character for separating *P. muelleri* from the closely related and morphologically similar *P. capensis*. The male of *P. muelleri* also displays weakly lobate prox-imal median lamellae of the pectines, a char-acter observed in the female of most *Parabuthus* species—*P. granulatus* and *P. kalaharicus* are exceptions—but otherwise only in the male of *P. calvus* and *P. planicauda* (Purcell, 1898, 1901; Pocock, 1902; Krae-pelin, 1908; Hewitt, 1918; Werner, 1934; Lawrence, 1955; Eastwood, 1977; Lamoral, 1979; Sissom, 1994; Prendini, 2001a). In other respects, the differences between the

TABLE 4

Meristic Data for Holotype Female (NMNW 1854), Paratype Female (SAMC C4514), and Newly Discovered Male (AMNH [AH 3991]) of *Parabuthus muelleri* Prendini, 2000

Male *Parabuthus capensis* (Ehrenberg, 1831) from Vanrhynsdorp, Western Cape Province, South Africa (SAMC C4565) included for comparison. Measurements follow Stahnke (1970), Lamoral (1979), and Prendini (2000a).

	♀NMNW 1854	♀SAMC C4514	♂AH 3991	♂SAMC C4565
Total length[a]	69.96	61.82	70.71	75.28
Carapace				
length	7.41	6.76	7.25	8.66
anterior width	4.48	4.35	4.38	5.20
posterior width	8.22	7.03	7.83	8.90
Mesosoma				
total length[b]	20.73	16.26	18.46	19.95
Sternite VII				
length	4.79	4.31	4.71	5.73
width	7.36	6.39	7.41	8.32
Metasoma				
total length[c]	41.82	38.80	45.00	46.67
Metasoma I				
length	6.19	5.74	6.12	7.62
width	4.88	4.30	5.26	6.18
Metasoma II				
length	6.38	5.98	6.66	8.12
width	4.90	4.46	5.4	6.46
Metasoma III				
length	6.75	6.06	6.82	7.75
width	5.02	4.36	5.43	8.16
Metasoma IV				
length	6.77	6.47	7.96	9.02
width	5.04	4.22	5.38	6.04
Metasoma V				
length	7.90	7.35	9.11	10.40
width	4.51	3.97	4.80	5.51
Telson				
total length[d]	7.83	7.20	8.33	11.22
aculeus length	2.05	2.04	2.82	4.71
vesicle length	5.78	5.16	5.51	6.51
vesicle width	3.92	3.62	4.34	4.42
vesicle height	3.50	3.01	3.64	3.97
Pedipalp				
total length[e]	22.20	21.64	27.51	31.60
Femur				
length	4.74	4.64	5.79	6.75
width	2.30	1.86	2.59	2.41
Patella				
length	5.40	5.40	6.36	7.77
width	2.69	2.44	3.09	3.67
Chela				
length	9.68	9.22	11.86	13.38
width	2.62	2.26	2.72	3.86
height	2.45	2.29	2.62	3.52
length of ventroexternal carina	3.55	3.54	3.76	5.41
length of movable finger	6.03	6.08	6.78	7.97
Pectines				
total length	7.31	7.12	8.86	10.36
length along dentate margin	6.62	6.51	8.98	9.98
tooth count (left/right)	31/32	31/31	36/36	41/41

[a]Sum of carapace, tergites I–VII, metasomal segments I–V, and telson.
[b]Sum of tergites I–VII.
[c]Sum of metasomal segments I–V and telson.
[d]Measured along an axis parallel to the dorsal surface.
[e]Measured from base of condyle to tip of fixed finger.

Fig. 13. *Parabuthus muelleri* Prendini, 2000, male (AMNH [AH 3991]), hemispermatophore, ental aspect. Scale bar = 1 mm.

male and female of *P. muelleri* are typical of other species of *Parabuthus*. The male exhibits genital papillae, a greater pectinal tooth count, increased granulation and setation (particularly of the pedipalps, metasoma, and telson), and is proportionally more slender than the female.

DISTRIBUTION: *Parabuthus muelleri* is endemic to Namibia (fig. 14) and presently recorded from two neighboring localities in the Lüderitz District (Karas Region) and a third locality, ca. 260 km north, in the Maltahöhe District (Hardap Region). Despite the large distance between the first two localities and the third, the habitat in which the specimens were collected (at the two localities for which habitat data are available) was remarkably similar (Prendini, 2000a). The specimens were each found in an area of level ground, with chalky soil, calcrete nodes, and dolomitic rocks. The localities at which they were collected both occur along an extensive ridge of dolomite, extending from the Huib-Hoch Plateau in the south (Plateau is situated at the northern end) to the Naukluft mountains in the north (Onis is ca. 20 km south of the Naukluft). Thus, the two localities are fairly close to the northern and southern edges of this geological formation. It is not known whether *P. muelleri* is restricted to this formation, but the occurrence of two of the three known specimens in such similar, albeit distantly located habitats suggests that the species may occur in similar habitats throughout the intervening areas (Prendini, 2000a).

ECOLOGY: The holotype and paratype of *P. muelleri* were collected in a region of compacted, chalky soil, calcrete nodes, and dolomite rocks. The holotype was excavated from the burrow of a scorpionid, *Opistophthalmus opinatus* (Simon, 1888), which it had preyed on, and was also syntopic with *O. scabrifrons* Hewitt, 1918. The paratype was found sitting motionless on a stone at night and was syntopic with the ischnurid *Hadogenes tityrus* (Simon, 1888), the scorpionids *Opistophthalmus gigas* Purcell, 1898 and *O. scabrifrons*, and also with *Parabuthus granulatus* and *P. villosus*. According to A. Harington's collecting notes, the newly described male specimen was collected in an area with *P. villosus* and *P. laevifrons*, with the latter probably being a misidentification of *P. stridulus*.

ADDITIONAL MATERIAL EXAMINED: ♂ (AMNH [AH 3991]), Namibia: Karas Region: Lüderitz District: locality uncertain, probably Aus [26°41′S, 16°15′E], A. Harington. Unfortunately, the collection locality data for this specimen are ambiguous. Harington suggests two possible localities, the other being Wortel (Khomas Region: Windhoek District: 23°08′S, 17°10′E). Aus is clearly the more plausible of the two alternatives, given its close proximity to Plateau, the collection locality of the paratype female. Indeed, it is quite possible that the male specimen also originated from Plateau, where Harington collected extensively and also received material donated by the owners of the property, H. and W. Erni. The possibility that the male specimen was collected at Plateau also seems more likely in view of the considerably different habitats at Aus and Plateau, which have few scorpion species in common, de-
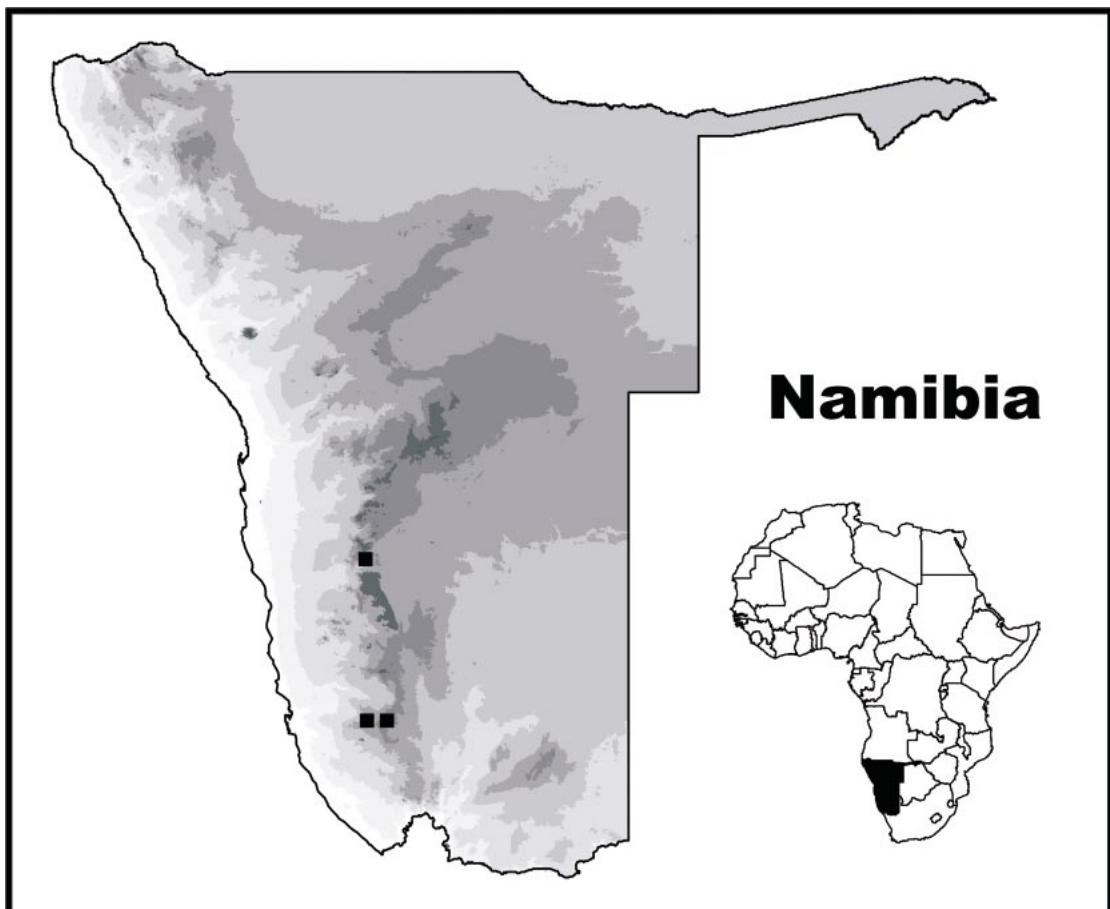
Fig. 14. The known distribution of *Parabuthus muelleri* Prendini, 2000 (■), which is endemic to Namibia. Contour interval = 600 m.

spite their proximity. The Aus Mountains are part of a granitic formation completely separated from the dolomitic Huib-Hoch Plateau by a sandy plain approximately 10 km across at the narrowest point. No scorpions associated with rocky habitats in either the Aus Mountains or the Huib-Hoch Plateau have been collected on this plain, which probably represents a significant barrier to their dispersal, as has been demonstrated elsewhere for lithophilous and lapidicolous scorpion species (Newlands, 1972; Prendini, 2001b).

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APPENDIX 1

TAXA EXAMINED FOR CLADISTIC ANALYSIS OF *PARABUTHUS* POCOCK, 1890

Depositories for specimens examined are abbreviated as follows: AMNH, American Museum of Natural History (New York, NY); AH, Alexis Harington Collection (lodged at AMNH); BMNH, The Natural History Museum (London, UK); NMSA, Natal Museum (Pietermaritzburg, South Africa); NMNW, National Museum of Namibia (Windhoek, Namibia); SAMC, South African Museum (Cape Town, South Africa); TMSA, Transvaal Museum (Pretoria, South Africa); USNM, US National Museum of Natural History, Smithsonian Institution (Washington, DC). Taxonomic notes are provided and lectotypes designated for the northeastern African and Arabian species of which type material was examined.

OUTGROUPS

1. *Grosphus madagascariensis* (Gervais, 1843): 10 ♂, 3 ♀, MADAGASCAR, Nosy Lava (AMNH).

2. *Uroplectes triangulifer* (Thorell, 1876): ♂, ♀, SOUTH AFRICA, Northern Prov., Potgietersrus, 24°11′S, 29°01′E, iv.1934, R.F. Lawrence (SAMC B8227); ♂, SOUTH AFRICA, Eastern Cape Prov., Karoo Nature Reserve, Graaff-Reinet, 32°12′S, 24°28′E, 8–9.ix.1987, S. van Noort (SAMC C3754); 2 ♀, SOUTH AFRICA, Eastern Cape Prov., Alicedale, 25.i.1979, A. Harington (AMNH); 2 ♀, SOUTH AFRICA, North West Prov., Lichtenburg, 27.vii.1975, A. Harington (AMNH).

NORTHEASTERN AFRICAN AND ARABIAN *PARABUTHUS*

3. *Parabuthus granimanus* Pocock, 1895: Lectotype ♂, paralectotype ♀, SOMALIA, Zaila [Zeyla], E.W. Oates (BMNH 1893.1.11.48–54); juv ♀, same data (BMNH 1893.1.11.48–54); 2 ♀, SOMALIA, Somali Coast, Berbera, H.M. Phipson (BMNH 1895.6.1.45). This species, with two subspecies (one nominotypical), has not been revised since the original description, and the status of the subspecies, *Parabuthus granimanus fuscicauda* Caporiacco, 1947, is unknown. The two specimens referred to by Pocock (1895: 312) as "types of ♂ and ♀" are hereby designated as lectotype and paralectotype. Based on a comparison of Pocock's type specimens, the nominotypical subspecies is suspected to be conspecific with *P. hunteri*. The types of *P. granimanus* and *P. hunteri* share the apomorphic state of characters 7 and 12 and differ only in the darker coloration, and reduced granulation and setation of the metasoma, of *P. granimanus*. The two specimens of *P. granimanus* from "Somali Coast" (also discussed in Pocock's description) are indistinguishable from the types of *Parabuthus hunteri* Pocock, 1895. Nonetheless, I have refrained from providing a formal synonymy, pending a more detailed revision of the *Parabuthus* species from northeastern Africa and Arabia.

4. *Parabuthus heterurus* Pocock, 1899: Lectotype ♀, paralectotype ♂, SOMALIA, Schebegh River [Shebeli River], Dr A. Donaldson-Smith (BMNH 1897.11.10.9–10); ♀, SOMALIA, Burao, 2.v.1938, E.F. Peck (BMNH 1939.3.16.17–18); ♂, SOMALIA, Burao, 8.v.1947, W.A. Macfadyeu (BMNH 1949.12.19.5). This species, with two subspecies (one nominotypical), has not been revised since its description but can be separated from the closely related *P. granimanus* and *P. hunteri* on the basis of characters 7, 12, and 46. The taxonomic status of the subspecies, *Parabuthus heterurus stefaninii* Caporiacco, 1927, is presently unknown. Pocock's (1899) two syntypes were examined and are hereby designated as lectotype and paralectotype.

5. *Parabuthus hunteri* Pocock, 1895: Lectotype ♀, paralectotype ♂, SUDAN, Duroor, 60 mi N of Suakin, D. Anderson (BMNH 1894.11.2.52–60); paralectotype ♂, same data (BMNH 1894.11.2.41–50); paralectotype ♂, SUDAN, Suakin, 7.ix1892, Dr B. Penton to D. Anderson (BMNH 1892.12.22.1). This species, which has not been revised since the original description, is suspected to be conspecific with the nominotypical subspecies of *P. granimanus* (see above). One of Pocock's (1895) 38 syntypes has been selected as the lectotype of *P. hunteri*. The remaining specimens, referred to in Pocock's (1895) description, are hereby designated as paralectotypes.

6. *Parabuthus leiosoma* (Ehrenberg, 1828): ♂, ♀, KENYA, Sabuk Retreat, Rift Valley, 2.vi.1999, H. Herren (AMNH); subadult ♀, 3 juv ♂, 6 juv ♀, KENYA, Nguruman, Rift Valley, vi–vii.1998, J. Lazell (USNM); ♂, ♀, juv ♂, SOMALIA (SAMC 409.60); ♂, ♀, SOMALIA, 1899, ex Hamburg Mus. (SAMC 4060); ♀, juv ♂, juv ♀, YEMEN, Aden, 1899, Oates and Shopland (SAMC 6343). Three subspecies (one nominotypical) are currently recognized, of which *P. leiosoma leiosoma* was reviewed by Vachon (1979) and subsequently redescribed by Sissom (1994). The taxonomic validity of *Parabuthus leiosoma abyssinicus* Pocock, 1901 and *P. leiosoma dmitrievi* Birula, 1903, both from Ethiopia, is dubious. Neither has been reviewed since Birula (1915). Probst (1973) neglected to mention subspecies in his brief treatment of *P. leiosoma* from East Africa.

7. *Parabuthus pallidus* Pocock, 1895: Lectotype ♂, paralectotype ♀, KENYA, Mombasa, Mr Last, purchased of H. Grose-Smith (BMNH 1890.3.15.10–11); 2 ♀, KENYA, N Turkana, Lake Rudolf Rift Valley Exped., 1934, N. Fuchs (BMNH); 3 ♀, KENYA, Sabuk Retreat, Rift Valley, 2.vi.1999, H. Herren (AMNH). This species was briefly reviewed by Probst (1973). Pocock's (1895) two syntypes were examined and are hereby designated as the lectotype and paralectotype.

SOUTHERN AFRICAN *PARABUTHUS*

8. *Parabuthus brevimanus* (Thorell, 1876): 20 ♂, 5 ♀, 2 subadult ♂, 2 juv ♂, 8 juv ♀, NAMIBIA, Erongo Region, Farm Kranzberg 59, 21°58′S, 15°39′E, 23.iii.1976, B. Lamoral and L. Ferguson (NMSA 10819); 3 ♂, ♀, juv ♀, SOUTH AFRICA, Northern Cape Prov., Richtersveld, Springbokvlakte, 28°23′S, 17°04′E, 20–21.ii.1973, B. Lamoral (NMSA 10442).

9. *Parabuthus calvus* Purcell, 1898: Holotype ♂, SOUTH AFRICA, Northern Cape Prov., Onder Bokkeveld, Bokkeveld Mountains, 31°20′S, 19°04′E, Calvinia, 1897, M. Schlechter (SAMC

1201); ♀, SOUTH AFRICA, Western Cape Prov., Betjesfontein [Biesjesfontein], 31°10′S, 17°53′E, 1898, M. Bergh (SAMC 2228); ♀, SOUTH AFRICA, Western Cape Prov., Knersvlakte, N of Vanrhynsdorp, 31°37′S, 18°44′E, 1999, M. de Jager (SAMC C4615); ♀, SOUTH AFRICA, Northern Cape Prov., Paulshoek, E of Garies, 30°22′S 18°16′E, i.1997, S. Todd (AMNH).

10. *Parabuthus capensis* (Ehrenberg, 1831): ♂, NAMIBIA, Karas Region, Boomrivier [Fish River Canyon National Park], 28°01′S, 17°04′E, 13–26.ix.1992, E. Marais (NMNW 1509); 5 ♂, 2 ♀, 2 juv ♀, SOUTH AFRICA, Eastern Cape Prov., Graaff-Reinet and Kruidfontein, 8 mi from Graaff Reinet, 32°22′S, 24°36′E, ix.1902, J. Paynter (SAMC 12010); ♀, juv ♂, SOUTH AFRICA, Western Cape Prov., Table View, Cape Town, 33°49′S, 18°29′E, 29.iv.1986, Louw (SAMC C1618); 2 ♂, 3 ♀, 4 subadult ♂, 2 subadult ♀, 3 juv ♂, 2 juv ♀, SOUTH AFRICA, Western Cape Prov., Port Nolloth, 29°17′S, 16°51′E, iv.1972, J. Visser (NMSA 10358); ♂, 2 subadult ♀, subadult ♂ [black form], SOUTH AFRICA, Western Cape Prov., Laaiplek, 32°46′S, 18°10′E, ix.1976, G. McLachlin (SAMC C74).

11. *Parabuthus distridor* Lamoral, 1980: Paratypes 12 ♂, 2 ♀, juv ♂, juv ♀, SOUTH AFRICA, Northern Cape Prov., Richtersveld, sandy ridge, 8 km S Springklipberg, 28°40′S, 16°53′E, 21.ii.1979, B. Lamoral (NMSA 11305); paratype ♂, same data (NMSA 11436); paratype ♀, same data (NMSA 11435); 2 ♂, ♀, SOUTH AFRICA, Northern Cape Prov., 25 km E of Port Nolloth at turnoff to Wolfberg, iii.1997, L. Prendini and E. Scott (SAMC C4604).

12. *Parabuthus gracilis* Lamoral, 1979: Paratypes 5 ♂, 2 ♀, 5 juv, NAMIBIA, Erongo Region, Messum Crater area, 21°16′S, 14°13′E, 26.iii.1976, B. Lamoral (NMSA 10848); paratypes 3 ♂, ♀, 4 juv ♂, NAMIBIA, Kunene Region, Möwebaai, 4 km N, 19°19′S, 12°40′E, 29.iii.1976, B. Lamoral and L. Ferguson (NMSA 10859).

13. *Parabuthus granulatus* (Ehrenberg, 1831): 9 ♂, 2 ♀, juv ♂, juv ♀, NAMIBIA, Karas Region, Berseba, 10 km S, 26°07′S, 17°46′E, 27.ii.1976, B. Lamoral (NMSA 10731); 4 ♂, 2 ♀, 3 subadult ♀, 9 juv, NAMIBIA, Kunene Region, Farm Vrede 719, 20°23′S, 14°14′E, 31.iii.1976, B. Lamoral and L. Ferguson (NMSA 10836).

14. *Parabuthus kalaharicus* Lamoral, 1977: Paratypes 9 ♂, NAMIBIA, Karas Region, Farm Sterkstroom 320, 25°43′S, 19°19′E, 19.iii.1969, B. Lamoral (NMSA 10947); paratypes 2 ♀, SOUTH AFRICA, Northern Cape Prov., Kalahari Gemsbok National Park, Twee Rivieren, 26°30′S, 20°35′E, iii.1970, B. Lamoral (NMSA 10946);

paratypes 3 ♂ (SAMC C213), Twee Rivieren, 1960–1970, le Riche family and staff.

15. *Parabuthus kraepelini* Werner, 1902: ♀, NAMIBIA, Kunene Region, Etosha National Park, Aus, 2–6.iii.1969, B. Lamoral and R. Day (NMSA 10022); 2 ♀, NAMIBIA, Kunene Region, Etosha National Park, Gemsbokvlakte, 4.iii.1969, B. Lamoral and R. Day (NMSA 10019); subadult ♂, NAMIBIA, Hardap Region, Farm Kangas 371, 23°36′S, 17°03′E, 14.iii.1976, B. Lamoral (NMSA 10850); 2 ♂, 2 ♀, NAMIBIA, Otjozondjupa Region, Okahandja, 24.ix.1994, I. Engelbrecht (SAMC C4605).

16. *Parabuthus kuanyamarum* Monard, 1937: 3 ♀, BOTSWANA, N Khwaai and Lechwee camps, 18°40′S–19°00′S, 23°00′E–23°45′E, 16–20.xi.1979, B. Lamoral (NMSA 13972); 13 ♂, ♀, 7 juveniles, NAMIBIA, Hardap Region, Farm Ghobab 381, 23°26′S, 17°21′E, 12.iii.1976, B. Lamoral (NMSA 10813).

17. *Parabuthus laevifrons* (Simon, 1888): 2 ♂, ♀, juv ♀, NAMIBIA, Karas Region, Farm Ortmansbaum 120, 28°19′S, 18°43′E, 26–28.i.1973, B. Lamoral and L. Ferguson (NMSA 10509); ♂, 4 ♀, 2 subadult ♀, 3 juv ♂, 3 juv ♀, NAMIBIA, Karas Region, Tses, dune strip SE, 25°53′S, 18°10′E, 23–24.ii.1973, B. Lamoral and K. Porter (NMSA 10521).

18. *Parabuthus mossambicensis* (Peters, 1861): ♂, MOZAMBIQUE, Gorongoza, 22.ii.1971, G. Vasse (NMSA 10088); ♂, SOUTH AFRICA, Northern Prov., Messina Nature Reserve, xii.1993, L. Prendini and K.M.A. Prendini (SAMC C4606); 3 ♂, SOUTH AFRICA, Northern Prov., Farm Rochdale 700, i.1996, L. Prendini and J. Laing (SAMC C4607); 3 ♀, SOUTH AFRICA, Northern Prov., Waterpoort, i.1996, L. Prendini and J. Laing (SAMC C4608).

19. *Parabuthus muelleri* Prendini, 2000: Holotype ♀, NAMIBIA, Hardap Region, Farm Onis 8, 82 km from Sesriem to Naukluft, 24°22.46′S, 16°13.17′E, 1260 m, 7.i.1998, L. Prendini and E. Scott (NMNW 1854); paratype ♀, NAMIBIA, Karas Region, Farm Plateau 38, near Aus, 26°40.62′S, 16°31.85′E, 1550 m, 30.xii.1997, L. Prendini and E. Scott (SAMC C4514); ♂, NAMIBIA, Karas Region, locality uncertain, probably Aus, 26°41′S, 16°15′E, A. Harington (AMNH [AH 3991]).

20. *Parabuthus namibensis* Lamoral, 1979: Holotype ♀, paratype ♂, NAMIBIA, Erongo Region, Cape Cross, 5 km N, 21°43′S, 13°56′E, 25.iii.1976, B. Lamoral and L. Ferguson (NMSA 2184); ♂, NAMIBIA, Erongo Region, Rössing, Lower Ostrich Gorge, 22°30′S, 14°58′E, 2–3.xi.1985, Irish and Rust (NMNW 896); ♀, juv ♂, same data, except 8.v–5.vi.1984, E. Griffin (NMNW 845).

21. *Parabuthus nanus* Lamoral, 1979: Paratypes ♂, ♀, NAMIBIA, Karas Region, Farm Tsirub 13, 26°52′S, 16°02′E, 3.iii.1976, B. Lamoral (NMSA 10772); paratype ♂, SOUTH AFRICA, Northern Cape Prov., Goodhouse, 21 km S, 29°04′S, 18°06′E, 29–31.i.1973, B. Lamoral (NMSA 10703); paratypes ♂, ♀, SOUTH AFRICA, Northern Cape Prov., Goodhouse, 10 km S, 28°55′S, 18°14′E, 11.ii.1979, B. Lamoral (NMSA 11304).

22. *Parabuthus planicauda* (Pocock, 1889): Lectotype ♀, SOUTH AFRICA, Dr Quain (BMNH 1870.26); 6 ♀, SOUTH AFRICA, Western Cape Prov., Ashton, 33°49′S, 20°03′E, i.1914, W.F. Purcell (SAMC B1748); 4 ♂, 6 ♀, 2 subadult ♂, juv ♀, SOUTH AFRICA, Eastern Cape Prov., Brakkloof, Grahamstown, 33°14′S, 26°23′E, 1897, J. White (SAMC 1734); 15 ♂, 28 ♀, SOUTH AFRICA, Eastern Cape Prov., Graaff-Reinet and Kruidfontein, 8 mi from Graaff-Reinet, 32°22′S, 24°36′E, ix.1902, J. Paynter (SAMC 12008); ♂, ♀, SOUTH AFRICA, Western Cape Prov., Stilbaai, 8–12.xi.1940, V. Fitzsimons (TMSA 8520).

23. *Parabuthus raudus* (Simon, 1888): 8 ♂, 5 ♀, subadult ♀, 3 juv ♂, juv ♀, NAMIBIA, Khomas Region, Farm Frischgewaagd 289, 22°32′S, 17°50′E, 20.iii.1976, B. Lamoral (NMSA 10817); ♀, 2 subadult ♂, SOUTH AFRICA, Northern Cape Prov., Kalahari Gemsbok National Park, Mata Mata, 3 miles N, 24.iv.1970, B. Lamoral (NMSA 10931); 3 ♂, 2 ♀, SOUTH AFRICA, Northern Cape Prov., Richtersveld, Swaartpoort near Ochta Diamond Mine, 28°07′S, 16°56′E, ii.1974, R. Faber (NMSA 10924).

24. *Parabuthus schlechteri* Purcell, 1899: ♀, subadult ♂, subadult ♀, NAMIBIA, Karas Region, Farm Tsirub 13, 26°52′S, 16°02′E, 3.iii.1976, B. Lamoral (NMSA 10730); ♂, ♀, NAMIBIA, Karas Region, Keetmanshoop, Farm Noachabeb, 7–12.i.1972, (NMSA 11406); ♂, ♀, SOUTH AFRICA, Northern Cape Prov., Aggeneys, 6–8.xii.1997, L. Prendini, G.J. Müller, K. Rostoll, and J. du Plessis (SAMC C4609); ♂, SOUTH AFRICA, Western Cape Prov., Gamkaskloof Nature Reserve, 33°31′S, 21°37′E, 21.ii.1997, M. de Jager (SAMC C4610).

25. *Parabuthus stridulus* Hewitt, 1913: Holotype ♂, NAMIBIA, Lüderitzbucht, South West Africa [Karas Region, 26°35′S, 15°10′E], 26.xi.1912 (TMSA 1868); ♂, 2 ♀, NAMIBIA, Karas Region, Agate Beach, Lüderitz, ii.1973, B. Lamoral (NMSA 10573); ♀, NAMIBIA, Erongo Region, Cape Cross, 5 km N, 21°43′S, 13°56′E, 25.iii.1976, B. Lamoral and L. Ferguson (NMSA 10907); ♂, NAMIBIA, Erongo Region, Cape Cross, 5 km N, 21°43′S, 13°56′E, 25.iii.1976, B. Lamoral and L. Ferguson (NMSA 10904); ♂, sub-

adult ♂, NAMIBIA, Karas Region, Kolmanskop, 12 km E Lüderitz, 26°43′S, 15°17′E, iii.1973, C.J. Coetzee (NMSA 10501); ♂, ♀, NAMIBIA, Karas Region, Farm Plateau 38, near Aus, 26°38.63′S, 16°30.77′E, 30.xii.1997, L. Prendini and E. Scott (SAMC C4611).

26. *Parabuthus transvaalicus* Purcell, 1899: Lectotype ♀, paralectotype ♀, SOUTH AFRICA, "Transvaal" (SAMC 3003); ♀, SOUTH AFRICA, Northern Prov., Dendron, Soutpansberg, 18.iii.1970, (NMSA 11449); ♀, SOUTH AFRICA, Northern Prov., Kruger National Park, Pafuri, 22°27′S, 31°17′E, 18.x.1980, L. Braack (NMSA 13899); ♂, ♀, SOUTH AFRICA, Northern Prov., Mphakane, S, granite koppies 1 km from turnoff to Munnik, 23°32.20′S, 29°42.42′E, 29.xii.1999, L. Prendini and E. Scott (SAMC 4612); ♂,

SOUTH AFRICA, Northern Prov., Langjan Nature Reserve, i.2000, L. Prendini and E. Scott (SAMC C4613).

27. *Parabuthus villosus* (Peters, 1862): subadult ♂, NAMIBIA, Kunene Region, Farm Grootberg 191, 19°46′S, 14°15′E, 2.iv.1976, B. Lamoral and L. Ferguson (NMSA 10913); ♂, 3 ♀, NAMIBIA, Karas Region, Farm Plateau 38, 26°40′S, 16°30′E, 29.ii.1976, B. Lamoral (NMSA 10805); ♀, NAMIBIA, Kunene Region, Kamanjab, 3 km W, 19°37′S, 14°48′E, 5.iv.1976, B. Lamoral and L. Ferguson (NMSA 10833); ♀, NAMIBIA, Kunene Region, Sesfontein, 3 km N clinic, 19°07′S, 13°36′E, 3.iv.1976, B. Lamoral (NMSA 10738); 2 ♂, SOUTH AFRICA, Northern Cape Prov., Pella pumpstation, iii.1997, L. Prendini and G.J. Müller (SAMC C4614).

APPENDIX 2

CHARACTERS AND CHARACTER STATES USED FOR CLADISTIC ANALYSIS OF *PARABUTHUS* POCOCK, 1890

Character states were scored 0–2, ? (unknown), – (inapplicable), or * (polymorphic). Multistate characters were treated as unordered (nonadditive). Three autapomorphies, indicated by †, were excluded from all analyses. Refer to table 1 for data matrix.

GENERAL

1. Adult general size: large, carapace length 6.5–17.0 mm (0); small, carapace length 2.5–5.0 mm (1).

2. Color 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 (*).

3. Color pattern of metasoma: metasomal segments I–V and telson uniformly colored (0); metasomal segments III–V and telson infuscated (i.e., darker than segments I and II) (1); polymorphic (*).

CARAPACE

4. †Carapace dorsoventrally compressed: absent (0); present (1).

5. Granulation of median ocular tubercle (♂, ♀) and surrounding surfaces (♀): entire (0); smooth areas (1).

PEDIPALPS

6. Pedipalps, setation: setose (0); smooth (1).

7. Chela manus, surface: smooth (0); granular (1).

8. Chela movable finger, length compared with length of manus (measured along ventroexternal carina), in ♀: long (length finger/length carina: 1.70–2.00) (0); short (length finger/length carina: ±1.50) (1).

9. Chela manus, shape in adult ♂, compared with adult ♀: similar (0); sexually dimorphic (1); unknown (?).

10. Chela fixed finger, shape in adult ♂: 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); unknown (?).

11. Chela movable finger, shape in adult ♂: straight, proximal dentate margin linear when fingers are closed (0); curved ventrally, proximal dentate margin distinctly emarginate when fingers are closed (1); unknown (?).

12. Chela fixed and movable fingers with basal lobe in adult ♂: absent (0); present (1); unknown (?).

TRICHOBOTHRIA

13. Pedipalp femur, position of e_1: level with or distal to d_5 (0); almost halfway between d_4 and d_5 (1).

14. Pedipalp patella, position of esb_2: distinctly distal to esb_1 (0); level with or slightly distal to esb_1 (1).

15. Chela fixed finger, position of dt: in line with or distal to et (0); proximal to et (1).

PECTINES

16. Proximal median lamella of pectines, in ♀: arcuate (0); enlarged and lobate (dilate) (1).

17. Proximal median lamella of pectines, in ♂: subrectangular (0); weakly lobate (dilate) (1); strongly lobate (dilate) (2); unknown (?).

LEGS

18. 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).

19. Basitarsi of legs I and II, macrosetal combs: absent (0); weakly developed (1); strongly developed (2).

20. Basitarsi of legs I and II, laterally expanded: absent (0); present (1).

21. †Basitarsi of legs III and IV, prolateral surfaces with dense tufts of macrosetae: absent (0); present (1).

22. Telotarsal ungues, relative length: equal (0); subequal (1).

HEMISPERMATOPHORE

23. Hemispermatophore, *pars recta*: parallel to axis (0); S-shaped (1); unknown (?).

MESOSOMA

24. Sternites, surface: smooth (0); punctate (1).

25. Sternite III, "pit" organ at proximal apex: absent (0); present (1).

26. Sternite VII, carinae: present (0); absent (1).

METASOMA

27. Metasomal segments I–V and telson, setation: virtually asetose (0); sparsely to moderately setose (1); very densely setose (2).

28. 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).

29. 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).

30. Metasomal segments I–III, stridulatory region on dorsal surface: absent from I–III (0); strongly developed on I–III (1); strongly developed on I and II, weakly developed to absent on III (2).

31. Metasomal segment I, shape of stridulatory region (if present) in dorsal aspect: narrow, parallel-sided (0); broad, rounded anteriorly, with posterior constriction (1); inapplicable (–).

32. 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 (–).

33. 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 (–).

34. Metasomal segment II, extent of stridulatory region (if present) in dorsal aspect: reaching posterodorsal margin (0); not reaching posterodorsal margin (1); inapplicable (–); polymorphic (*).

35. Metasomal segment II, nature of stridulatory region (if present): fine to coarse granules (0); horizontal ridges (1); inapplicable (–).

36. Metasomal segments II and III, posterodorsal edge: straight (0); anteromedially curved in a V-shape (1).

37. Metasomal segments IV and V, lateral intercarinal surfaces: granular (0); smooth (1).

38. Metasomal segments I–IV, dorsosubmedian carinae: present (0); absent (1).

39. Metasomal segment IV, dorsosubmedian carinae (if present): continuous (0); discontinuous (1); inapplicable (–).

40. Metasomal segments II–IV, distal spiniform granules of dorsosubmedian carinae (if present), size relative to preceding granules: equally developed (0); noticeably more pronounced (1); inapplicable (–).

41. 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).

42. Metasomal segment IV, median lateral carina: absent to proximally obsolete (0); continuous but poorly developed (1); continuous and distinct (2).

43. Metasomal segment V, dorsosubmedian carinae: absent (0); present, poorly developed with blunt, rounded granules (1); present, distinct with sharp, spiniform granules (2).

44. Metasomal segment V, dorsolateral carinae: absent, except for a few proximal granules (0); distally obsolete (1); continuous to distal edge of segment (2).

45. Metasomal segment V, ventrolateral carinae: converging distally (0); subparallel to diverging distally (1).

46. Metasomal segment V, distal half of ventrolateral carinae: with spinose processes (0); with lobate processes (1).

47. Metasomal segment V, ventrosubmedian carinae: absent or indistinct from surrounding granules (0); distinct (1).

48. Metasomal segment V, ventromedian carina: present (may be indistinct) (0); absent (1).

TELSON

49. Telson vesicle, width relative to width of metasomal segment V: approximately equal (0); considerably narrower (1).

50. †Telson vesicle, dorsoproximal surface: very shallowly excavated along longitudinal half (0); deeply excavated (1).

51. Telson aculeus, shape: gently curved (0); abruptly bent (1).

BEHAVIOR

52. Diurnal retreat: hides under rocks (0); burrows under rocks (1); burrows in open ground (2); unknown (?); polymorphic (*).

53. Foraging strategy: sit-and-wait (0); errant (1); unknown (?).