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A new genus and species of bothriurid scorpion from the Brandberg Massif, Namibia, with a reanalysis of bothriurid phylogeny and a discussion of the phylogenetic position of *Lisposoma* Lawrence

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Abstract. *Brandbergia haringtoni*, a new genus and species of bothriurid scorpion, is described from the Brandberg Massif, northwestern Namibia. A cladistic analysis, based on seventy-four morphological characters scored for thirty-one exemplar species representing all genera of Bothriuridae, and one genus from each of the six remaining families of Scorpionoidea, was conducted to test the phylogenetic placement of the new genus and whether it affects the internal relationships of Bothriuridae. The available data demonstrate, under a range of weighting regimes, that the new genus is the most basal bothriurid, and confirm the scheme of relationships among the remaining bothriurid genera that was recovered in a previous analysis: (*Brandbergia* (*Lisposoma* (*Thestylus* (*Phoniocercus* (*Tehuankea* (*Cercophonius* + *Urophonius*) (*Bothriurus* + *Brachistosternus* + *Orobothriurus* + *Centromachetes* (*Timogenes* + *Vachonia*)))))). On the basis of this evidence, Lourenço's recent proposal of family Lisposomidae for *Lisposoma* is rejected and Lisposomidae is synonymized with Bothriuridae. The implications of the phylogeny for understanding the biogeography of Bothriuridae are discussed.

Introduction

Namibia has the highest species richness and endemism of scorpions in southern Africa. All four families, seven genera (64%), and fifty-seven species (44%) of southern African scorpions occur within its borders, of which one genus (8%) and at least twenty-seven species (21%) are endemic (Lamoral, 1979; Prendini, 1995, 2000a,b, 2001a). Despite the fact that this country is relatively better sampled for scorpions than other southern African countries (including South Africa), new species continue to be discovered, partly due to the rugged and inhospitable desert terrain and partly due to the cryptic nature of most desert scorpion species that inhabit it. Many, for example, are fossorial and can only be collected nocturnally by means of ultraviolet detection.

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The mountainous northwestern Damaraland and Kaokoveld regions of Namibia are especially inaccessible and have remained more poorly sampled than other regions. The Brandberg Massif, recently brought to the attention of the global scientific community by the discovery of extant members of the newest order of insects, Mantophasmatodea (Klass *et al*., 2002; Picker *et al*., 2002), provides a striking example. The prominent, circular massif, covering an area of *c*. 650 km^2 in northwestern Namibia (Marais & Kirk-Spriggs, 2000), rises abruptly from the surrounding gravel plains of the central Namib Desert, and is geographically isolated from the discontinuous longitudinal escarpment further east. An extensive, undulating central plateau occurs at an altitude of about 2000 m, where many small peaks are evident, the highest of these being Königstein (2573 m), which is also the highest point in Namibia. Deep alluvial valleys and ravines, leading down to the surrounding pediplain, radially dissect the steep slopes of the periphery.

The Brandberg is an old feature of the Namibian landscape, predating the break-up of Gondwana and the

major changes in continental climate and environmental conditions that occurred during Plio-Pleistocene times (Marais & Kirk-Spriggs, 2000; Miller, 2000). Accordingly, although not particularly high compared with Mount Kilimanjaro, Tanzania (5896 m) and Mount Meru, Kenya (4567 m), a characteristic assemblage of species may have evolved on the massif over this protracted period, particularly in view of the geographical barriers imposed by its isolation from the main escarpment and its abrupt, steep periphery (Marais & Kirk-Spriggs, 2000). Similarly, at the higher altitudes, orographic amelioration of the prevailing hyperarid conditions around the base and lower slopes (Olszewski, 2000) may have provided a refugium for relict fauna (Irish, 1994; Craven & Craven, 2000; Marais & Kirk-Spriggs, 2000).

Given this background, it should come as no surprise that remarkable new taxa, e.g. extant members of insect lineages previously known only from Eocene-aged fossils (Klass *et al*., 2002), have been discovered on the massif. Namibian biologists justifiably regard the Brandberg as a national priority for biodiversity conservation (Barnard, 1998), but the logistical problems of sampling on the massif, notably the rugged terrain and absence of a reliable water supply, represent significant obstacles to documenting its unique biota (Marais & Kirk-Spriggs, 2000).

In the present contribution, *Brandbergia haringtoni*, a new genus and species of scorpion, is described from the higher altitudes of the Brandberg (Fig. 1). The type specimens of this new taxon were discovered among the contents of a large private collection of scorpions recently acquired by the American Museum of Natural History (AMNH), New York. Although 25 years old and severely damaged (they were evidently dried initially and later rehydrated), the specimens were immediately recognizable as a unique genus and species, closely related phylogenetically to the endemic Namibian genus *Lisposoma* Lawrence. Comprising two described species, *Lisposoma* represents the basal African lineage of the Gondwanan family Bothriuridae Simon, all other more derived genera of which occur in South America, India and Australia (Prendini, 2000c).

The phylogenetic position of *Lisposoma* has remained contentious. Originally placed in a separate subfamily, Lisposominae Lawrence, of Scorpionidae Latreille, the genus was later transferred to Bothriuridae (Francke, 1982), where its subfamilial status was not recognized (Francke, 1985; Sissom, 1990; Lowe & Fet, 2000). Lourenço (2000) elevated the taxon to family status as Lisposomidae Lawrence, despite cladistic evidence that it is a basal bothriurid (Stockwell, 1989; Prendini, 2000c). To test the phylogenetic placement of the new genus and whether it affects the relationships of *Lisposoma* and the remaining genera of Bothriuridae, a cladistic analysis was undertaken. The results of that analysis, based on morphological characters scored for exemplar species representing all bothriurid genera and one genus from each of the six remaining families of Scorpionoidea Latreille, are presented here.

Recognition of the new genus and species brings the total number of Namibian scorpion genera to eight, species to fifty-eight, and the number of Namibian endemic scorpion species to twenty-eight. Fifteen scorpion species, in six genera and four families, are now recorded from the Brandberg Massif and its immediate vicinity (Prendini, 2000b).

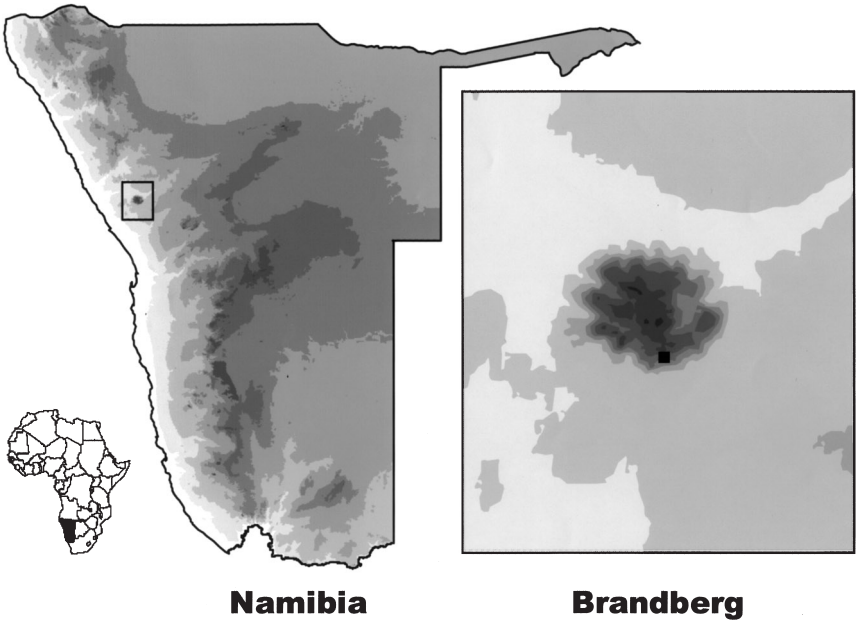

Fig. 1. The known distribution of *Brandbergia haringtoni* (square) on the Brandberg Massif, northwestern Namibia (contour interval 600 m).

Methods

Material, photography and terminology

The type specimens of *Brandbergia haringtoni* originate from the Alexis Harington Private Collection (AH), which is now deposited in the AMNH. Repositories of all other material examined for the cladistic analysis were provided by Prendini (2000c).

Photographs of the new species were taken under long wave ultraviolet light using a Microptics™ ML1000 digital imaging system. Measurements were made with Mitutoyo® digital callipers. Colour 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 (2000c) for remaining features.

Taxa

The present analysis was based on thirty-one terminal taxa (Appendix 1). The morphological data matrix provided here is a reduced version of the previously published matrix for relationships among the families and genera of Scorpionoidea (Prendini, 2000c), to which the new taxon has been added. All bothriurid terminals included in the previous analysis were retained to test the placement of the new taxon and determine whether it would affect the internal relationships of Bothriuridae (especially *Lisposoma*). Each bothriurid genus was represented by at least two exemplar species (unless monotypic), selected so as to reflect maximal morphological diversity within the genera, and thus provide the strongest test of monophyly for the genera they represented (Prendini, 2000c, 2001b). Type species were included as exemplars for all genera except *Timogenes* Simon. Specimens of the type species *Timogenes sumatranus* Simon could not be obtained for examination, but the exemplar species of *Timogenes* that were included are considered to be congeneric with it on the basis of available morphological evidence.

The sole Indian bothriurid, *Cercophonius himalayensis* Lourenço, was omitted from the analysis, as was the recently described *Brazilobothriurus pantanalensis* Lourenço & Monod, because the type specimens of these taxa could not be obtained for examination either. However, the omission of these taxa should have little impact on the present analyses for the following reasons. (1) According to the original description, the Indian *Cercophonius* Peters differs morphologically from most Australian species (revised by Acosta, 1990) only on the basis of a lower pectinal tooth count (Lourenço, 1996), on which basis it cannot be separated from *Cercophonius queenslandae* Acosta, already represented in the data matrix. (2) *Brazilobothriurus*, Lourenço & Monod's (2000) 'new' monotypic bothriurid genus, differs from the *araguayae* group of *Bothriurus* Peters solely on the presence of nine *V* trichobothria on the pedipalp chela, a character that is highly variable in many scorpion genera, including *Bothriurus*, most species of which have five or six *V* trichobothria (Stockwell, 1989; Prendini, 2000c). On the basis of cladistic evidence (C. Mattoni, personal communication), *Brazilobothriurus* is nested deep inside *Bothriurus*, a genus already represented by two species in the data matrix.

To confirm that the new taxon described in this paper is a bothriurid, a single exemplar species for each of the other scorpionoid families was also included. *Nebo hierichonticus* (Simon) represents Diplocentridae Pocock; *Hemiscorpius lepturus* Peters, Hemiscorpiidae Pocock; *Heteroscorpion opisthacanthoides* (Kraepelin), Heteroscorpionidae Kraepelin; *Opisthacanthus validus* (Thorell), Ischnuridae Simon; *Scorpio maurus mogadorensis* (Birula), Scorpionidae; and *Urodacus novaehollandiae* Peters, Urodacidae Pocock. All except *Nebo* Simon and *Opisthacanthus* Peters represent the type genera of their respective families. The latter were selected in favour of the type genera because they are more basal (Prendini, 2000c), and hence perhaps more representative of the ancestral condition for their respective families.

Trees were rooted using the outgroup method (Watrous & Wheeler, 1981; Farris, 1982; Nixon & Carpenter, 1993). As in the previous analysis, *Centruroides gracilis* (Latreille) and *Chaerilus granosus* Simon were chosen as exemplar species for the families Buthidae Simon and Chaerilidae Pocock, to be used as outgroup taxa to Scorpionoidea. The buthids and chaerilids are generally considered basal to all other Recent scorpions (Lamoral, 1980; Lourenço, 1985; Stockwell, 1989), although there is debate as to whether Chaerilidae is the sister taxon of the other Recent scorpions (Lamoral, 1980; Lourenço, 1985; Soleglad & Fet, 2001) or the sister taxon of Buthidae (Stockwell, 1989). Selection of a representative for the diverse family Buthidae was based on the criterion that the exemplar species should have distinct pedipalpal carinae (which are often obsolete in buthids) to facilitate homology assessment for the carinal characters, which would otherwise be scored with missing entries (Prendini, 2000c).

The use of an exemplar approach in my previous analysis (Prendini, 2000c) was recently questioned by Soleglad & Sissom (2001), who stated in their discussion on trichobothrial analysis that 'the exemplar approach employed in [Prendini's] analysis probably did not provide enough taxa to ascertain in detail the patterns and extent of neobothriotaxic conditions . . . less than 20% of scorpionoid species were actually evaluated'. Soleglad & Sissom (2001) stated that they studied thirty-three ingroup species ('over 60%' of ingroup species diversity) for their analysis of euscorpiid phylogeny, yet combined their observations into just eleven supraspecific terminal taxa (hypothetical placeholders for the eleven genera of Euscorpiidae Laurie), rather than presenting a matrix and analysis of the thirty-three species that they studied. As argued previously (Prendini, 2000c, 2001b), there are many theoretical and empirical disadvantages to using supraspecific terminal taxa instead of exemplars. The

most obvious that apply to the analysis by Soleglad & Sissom (2001) are (1) the loss of information resulting from the conversion of characters pertaining to thirty-three species into eleven supraspecific terminals, (2) the low potential for repeatability of this process (e.g. it is unclear from Soleglad & Sissom's methodological discussion how decisions regarding character polarity were made, and interspecific variation accommodated, a priori), (3) the fact that the monophyly of supraspecific taxa (genera) was assumed, rather than tested in the analysis, and (4) the implications that this could have for resolving (rather than assuming) the ancestral states of the supraspecific taxa (genera) in the course of a global analysis. The use of supraspecific terminal taxa by Soleglad & Sissom (2001) reduces the explanatory power, and consequently the general utility, of their proposed hypothesis and resultant classification. Their analysis, indeed, contradicts their criticism.

Characters

Of the 115 morphological characters used in the previous analysis of scorpionoid relationships (Prendini, 2000c), ninety-five were retained for the present analysis (Appendices 1 and 2). Twenty-one of these (characters 18, 22, 24, 29, 31, 32, 37–39, 44, 45, 51, 60, 61, 72, 75, 79, 86, 89, 94, 95), pertinent to scorpionoid relationships but uninformative in the present context, were retained in the matrix on the grounds that they contribute to its completeness and future utility, e.g. in diagnostic keys (Yeates, 1992; Prendini, 2000c), although they were excluded from all analyses. The present analyses were thus based on seventy-four characters. Twenty-one of these contain missing entries for the new taxon due to the fact that the adult male is presently unknown and characters of the male genitalia and secondary sexual dimorphism could not be scored.

Of the informative characters, fifty-three are binary and twenty-one are multistate (Appendix 2). Twelve multistate characters, for which transformation series could not be inferred, were treated as unordered, i.e. non-additive (Fitch, 1971). Nonadditive analysis of these characters is defended by invoking the principle of indifference, which asserts that if there is no apparent reason for considering one event to be more probable than its alternatives, then all should be considered equiprobable (Wilkinson, 1992). The remaining nine multistate characters were arranged in hypothesized transformation series, i.e. ordered (Farris, 1970). Arguments against the ordering of multistate characters have been proposed on the grounds that ordered (additive) characters represent hypotheses about character transformation that should be tested, rather than assumed, by cladistic analysis (Hauser & Presch, 1991; Wilkinson, 1992; Slowinski, 1993; Hormiga, 1994; Griswold *et al.*, 1998). Accordingly, the results of unordering these characters (non-additive analysis) are also presented. Following Prendini (2000c), this should not be taken to imply that unanimous unordering of characters is endorsed. Unordered multistate characters may appear superficially to avoid premises of transformation, but in reality merely provide a questionable alternative theory of transformation (Mickevich, 1982). Allowing any state to transform directly into any other amounts, in many cases, to nothing more than the 'common equals primitive' criterion: the most commonly occurring states will tend to be placed towards the base of the tree, with all other states being independently derived from them (Platnick, 1989). Furthermore, the denial of nested similarity is epistemologically equivalent to the omission of evidence and, hence, invalid for cladistic analysis (Pimentel & Riggins, 1987; Lipscomb, 1992).

Cladistic analysis

Character data were edited and cladograms prepared using WINCLADA, version 0.9.9+ (Nixon, 1999). The twenty-one uninformative characters noted above were excluded from all analyses. In addition, characters 33 and 67 were excluded from the analyses with unordered multistates, as they became uninformative when unordered. 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 version 2.0 (Goloboff, 1997a), according to the following command sequence: *hold10000*; *hold/10*; *mult*100*; (hold 10 000 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 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 compared with those obtained by analysis with equal weighting. In the present context, these methods of a posteriori weighting were investigated to provide a 'sensitivity analysis' (Wheeler, 1995), i.e. an assessment of the relative robustness of clades to different analytical parameters, in this case, method and intensity of character weighting (see Prendini, 2000c, 2001c). If a group is monophyletic only under a very specific combination of parameters, less confidence may be placed in the supposition that the data robustly support its monophyly than may be placed in a group that is monophyletic under a wider range and combination of parameters (for examples see Wheeler, 1995; Whiting *et al.*, 1997; Griswold *et al.*, 1998; Zrzavý *et al.*, 1998, 2001; Edgecombe *et al.*, 1999, 2000; Giribet & Wheeler, 1999; Giribet & Ribera, 2000; Giribet *et al.*, 2000; Prendini, 2000c).

As in other studies (e.g. Wheeler, 1995; Whiting *et al.*, 1997; Prendini, 2000c; Wheeler *et al.*, 2001), results of the

sensitivity analyses are summarized by means of 50% majority rule (Margush & McMorris, 1981), or 50% compromise (*sensu* Nixon & Carpenter, 1996), and strict consensus trees. The problems with using majority rule consensus trees as a means of resolving ambiguous strict consensus trees have been well elaborated by Nixon & Carpenter (1996) and Sharkey & Leathers (2001), among others. Their use in the present context is justified on the grounds that they serve a different purpose. Here, majority rule consensus trees are presented, alongside strict consensus trees, to provide a graphical representation of the results of the sensitivity analyses. Nodes that appear in the majority rule trees but are collapsed in the strict consensus trees were obtained under the majority of weighting regimes, hence more confidence may be placed in the supposition that they are robustly supported by the data than in the alternatives that were retrieved only under specific weighting regimes.

Successive weighting, using the squared consistency index 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 trees 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*. As there were more than 10 000 trees up to five extra steps, obtaining accurate branch support values required five successive searches to be conducted, starting with searching for trees only one step longer than the shortest, and continuing with searches for progressively longer trees until values had been obtained for nodes with the greatest support.

Results

Analysis of the seventy-four informative characters in NONA located a single most parsimonious tree (MPT) with equal weighting (Table 1, Fig. 2A). Three MPTs, each three steps shorter than the MPT obtained with the nine ordered multistate characters, were located when all multistate characters were unordered (Table 1, collapsed nodes indicated with squares in Fig. 2A). The topology of one of these MPTs was identical to that in Fig. 2A, except for a single node, which collapsed (indicated with a solid square).

The MPT located with equal weighting and nine ordered multistate characters (Fig. 2A) was also retrieved with successive weighting (Table 1). A single MPT, three steps shorter, was again obtained with successive weighting when all multistate characters were unordered, and differed from the MPT obtained in the successive weighting analysis with ordered multistates only in the collapse of a single node (indicated with a solid square in Fig. 2A). This topology was identical to one of the three MPTs obtained with equal weighting and multistate characters unordered.

When values for the concavity constant were mild to medium ($K = 3$–6), analyses with implied weighting and nine ordered multistate characters located a single MPT with the same topology as that obtained by the analyses with equal and successive weighting (Fig. 2A). However, under strong concavity ($K = 1$ and 2), analyses with implied weighting located a single MPT with a slightly different topology, four steps longer and 4–8% less fit, than the MPT obtained by the analysis with equal weighting (Table 1). The topology obtained by the analyses with implied weighting under $K = 1$ and 2 differed from those obtained with equal weighting, successive weighting and implied weighting under $K = 3$–6, only in the relative positions of the outgroup genera, *Heteroscorpion* Birula and *Urodacus* Peters (Fig. 2B). In the analyses under $K = 1$ and 2, *Heteroscorpion* grouped with (*Hemiscorpius* + *Opisthacanthus*), whereas *Urodacus* grouped with (*Nebo* + *Scorpio*), compared with the other analyses, where *Heteroscorpion* and *Urodacus* formed a monophyletic sister group of the larger group containing the other four genera.

Table 1. Summary of statistical and topological differences among the most parsimonious trees (MPTs) obtained by analysis under equal weighting (EW), successive weighting (SW), and implied weighting (IW) with six values for the concavity constant (K), arranged in order of decreasing fit. Analyses with multistates ordered and unordered are indicated, respectively, by subscripts 'O' and 'U'. Unweighted length is reported for SW trees. A, (*Heteroscorpion* + *Urodacus*) sister group; B, *Heteroscorpion* and *Urodacus* sister to (*Hemiscorpius* + *Opisthacanthus*) and (*Nebo* + *Scorpio*), respectively; C, position of *Centromachetes* unresolved; D, positions of *Bothriurus*, *Orobothriurus* and *Tehuankea* unresolved.

	MPTs	Steps	Fit (f_i)	Rescaled fit	CI	RI	A	B	C	D
IW_O: $K = 6$	1	156	666.6	75	63	84	×			
IW_O: $K = 5$	1	156	655.9	74	63	84	×			
IW_O: $K = 4$	1	156	641.7	72	63	84	×			
IW_O: $K = 3$	1	156	621.7	71	63	84	×			
SW_O	1	156	621.7	71	63	84	×			
EW_O	1	156	621.7	71	63	84	×			
IW_O: $K = 2$	1	160	588.5	67	62	83		×		
IW_O: $K = 1$	1	160	534.2	63	62	83		×		
IW_U: $K = 6$	1	153	649.7	75	64	84	×		×	
IW_U: $K = 5$	1	153	639.5	74	64	84	×		×	
IW_U: $K = 4$	1	153	625.8	73	64	84	×		×	
IW_U: $K = 3$	1	153	606.5	71	64	84	×		×	
SW_U	1	153	606.5	71	64	84	×		×	
EW_U	3	153	605.0	71	64	84	×		×	×
IW_U: $K = 2$	1	153	573.4	68	64	84	×		×	
IW_U: $K = 1$	1	157	517.2	63	63	84		×	×	

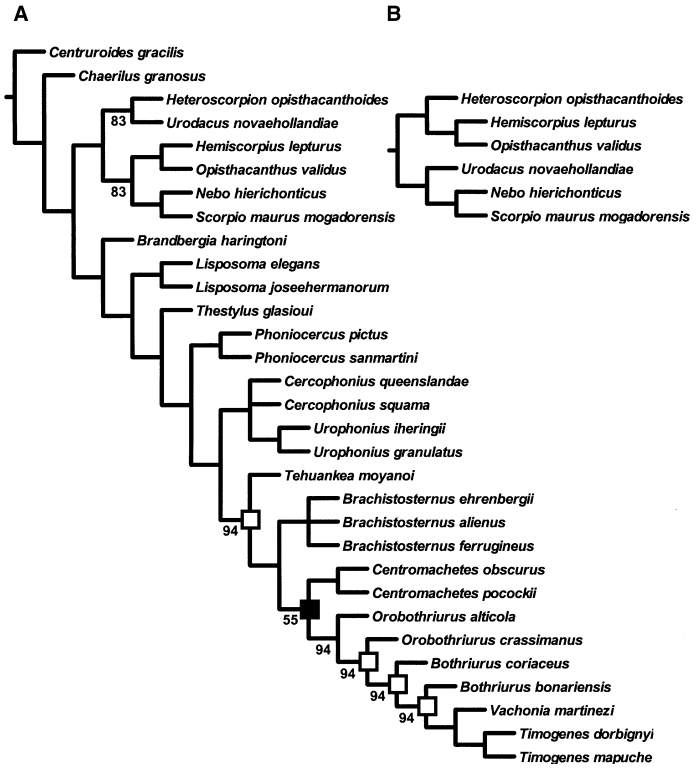

Fig. 2. A, The optimal tree obtained by analysis under weighting regimes that maximized fit and minimized length. This topology was retrieved by analyses with nine multistate characters ordered under equal weighting, successive weighting and implied weighting with $K = 3$–6, as well as by analyses with multistate characters unordered under equal weighting, successive weighting and implied weighting with $K = 2$–6 (Table 1). Zero-length branches are collapsed. Nodes that collapsed in the analysis with equal weighting when multistate characters were unordered are indicated with squares. The solid square indicates a node that also collapsed in the analyses with successive weighting and implied weighting, as a result of unordering. This topology also corresponds to the majority rule (>50%) consensus of most parsimonious trees obtained by the sixteen analyses in which weighting regime and multistate character transformation were varied (Table 1). The frequencies of nodes retrieved in >50% but <100% of the analyses are indicated below the branches. Nodes with frequencies <100% are collapsed in the strict consensus (Fig. 3). B, The alternative, suboptimal topology retrieved by analyses with nine multistate characters ordered under implied weighting with $K = 1$ and 2, as well as by analyses with multistate characters unordered under implied weighting with $K = 1$ (Table 1). Except for relationships among the outgroup taxa (shown here), this topology is identical to that retrieved by the analyses with nine multistate characters ordered under equal weighting, successive weighting and implied weighting with $K = 3$–6, as well as by analyses with multistate characters unordered under equal weighting, successive weighting and implied weighting with $K = 2$–6. The node indicated with a solid square in (A) collapsed in the analysis under implied weighting with $K = 1$, as a result of unordering.

Analyses with implied weighting and multistate characters unordered each retrieved a single MPT, three steps shorter, but with the same topology as that obtained with nine ordered multistates under the corresponding concavity constant (Table 1), differing only in the collapse of a single node (indicated with a solid square in Fig. 2A). Another difference concerns the analysis under $K = 2$, which located the same topology as the analyses under $K = 3$–6, where *Heteroscorpion* and *Urodacus* formed a monophyletic sister group of the larger group containing *Hemiscorpius* Peters, *Opisthacanthus*, *Nebo* and *Scorpio* Linnaeus, rather than the topology located by the analysis under $K = 1$, where *Heteroscorpion* grouped with (*Hemiscorpius* + *Opisthacanthus*) and *Urodacus* grouped with (*Nebo* + *Scorpio*). In the analyses with multistates unordered, the MPT obtained by the analysis under $K = 1$ was four steps longer and 8% less fit than the MPT obtained by the analysis with equal weighting.

Topological results of the sensitivity analysis, in which sixteen combinations of weighting regime and character transformation (multistates ordered vs. unordered) were analysed, are summarized by means of a strict consensus (Fig. 3). Figure 2A represents the majority (>50%) rule consensus and provides the frequency percentiles for nodes that were retrieved by >50% but <100% of the analyses (nodes retrieved by <100% obviously collapsed in the strict consensus).

The optimal topology, here regarded as that with maximal explanatory power, i.e. with nine multistate characters ordered (Fig. 2A), was obtained by weighting regimes that

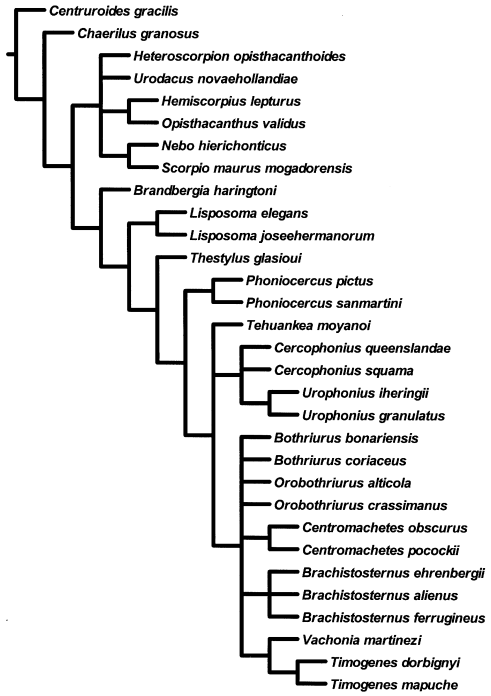

Fig. 3. Strict consensus of most parsimonious trees obtained by the sixteen analyses in which weighting regime and multistate character transformation were varied (Table 1).

minimized length as well as those that maximized fit (Table 1). This topology was obtained by the majority of analyses under an array of equal, moderate and mild weighting regimes. Unambiguously optimized synapomorphies are indicated on this topology in Fig. 4, which also provides branch support values for nodes and emphasizes major taxonomic groupings. The length, fit (f_i), consistency indices, retention indices and final successive weights of informative characters on this topology are listed in Table 2.

Discussion

Scorpionoid systematics

All MPTs produced in the present analyses were congruent with those obtained previously in a larger analysis of relationships among the families and genera of Scorpionoidea (Prendini, 2000c). Monophyly of Scorpionoidea was unanimously retrieved (Fig. 3) and supported by thirteen synapomorphies on the optimal topology (Fig. 4). The basal dichotomy between Bothriuridae and the remaining katoikogenic scorpionoid families (Diplocentridae, Hemiscorpiidae, Heteroscorpionidae, Ischnuridae, Scorpionidae and Urodacidae) was also unanimously retrieved (Fig. 3). Placement of Bothriuridae as sister taxon of the remaining Scorpionoidea differs from previously proposed topologies (Lamoral, 1980; Lourenço, 1985) and requires the hypothesis that characters 53, 57 and 65 (Appendix 2) are reversed in most bothriurids (Stockwell, 1989; Prendini, 2000c). The second monophyletic group of the basal scorpionoid dichotomy, comprising the remaining genera, conforms to the traditional superfamily Scorpionoidea (i.e. excluding Bothriuridae) and is supported by six synapomorphies on the optimal topology (Fig. 4). Some of the highest branch support values on the optimal topology were obtained for Scorpionoidea, Bothriuridae and the monophyletic group comprising the remaining katoikogenic scorpionoid families (Fig. 4). There appears to be no obvious rationale for Lourenço's (2000) recent proposal to place Bothriuridae in a separate superfamily Bothriuroidea Simon.

Apart from confirming the basal nodes retrieved in previous analyses (Stockwell, 1989; Prendini, 2000c), all analyses confirmed the following relationships among the katoikogenic families on the basis of the placements of their respective exemplars (Figs 3, 4): ((Hemiscorpiidae + Ischnuridae) (Diplocentridae + Scorpionidae)). The primary differences between the topologies obtained in the various analyses concern the placement of exemplars for the basal katoikogenic families Heteroscorpionidae and Urodacidae. Most analyses placed *Heteroscorpion* and *Urodacus* as a monophyletic sister group of the larger group containing *Hemiscorpius*, *Opisthacanthus*, *Nebo* and *Scorpio* (Figs 2A; 4). This arrangement recalls the early views of Laurie (1896a,b), who considered *Urodacus* to be the most basal of the katoikogenic scorpions. As demonstrated previously (Prendini, 2000c), five homoplasious synapomorphies optimize unambiguously at this node (Fig. 4). [Contrary to the opinion of Soleglad & Sissom (2001), homoplasious synapomorphies can indeed be optimized unambiguously (see also Soleglad & Sissom, 2001: Fig. 211).]

In three implied weighting analyses ($K = 1$ or 2 with multistates ordered, as well as $K = 1$ with multistates unordered), *Heteroscorpion* was placed basal to (*Hemiscorpius* + *Opisthacanthus*), whereas *Urodacus* was placed basal to (*Nebo* + *Scorpio*), in line with the analyses of Stockwell (1989). The two alternative hypotheses for the positions of *Heteroscorpion* and *Urodacus* were also retrieved in previous analyses under different weighting regimes (Prendini, 2000c) and it is clear that additional data from other sources (e.g. DNA sequences) are needed to discriminate between them. However, for the purposes of the present study, these alternative hypotheses have no effect on either the placement of the new taxon or the internal relationships of Bothriuridae.

Bothriurid systematics

The discovery of the new genus and its affinities with the enigmatic Namibian genus *Lisposoma* necessitated the

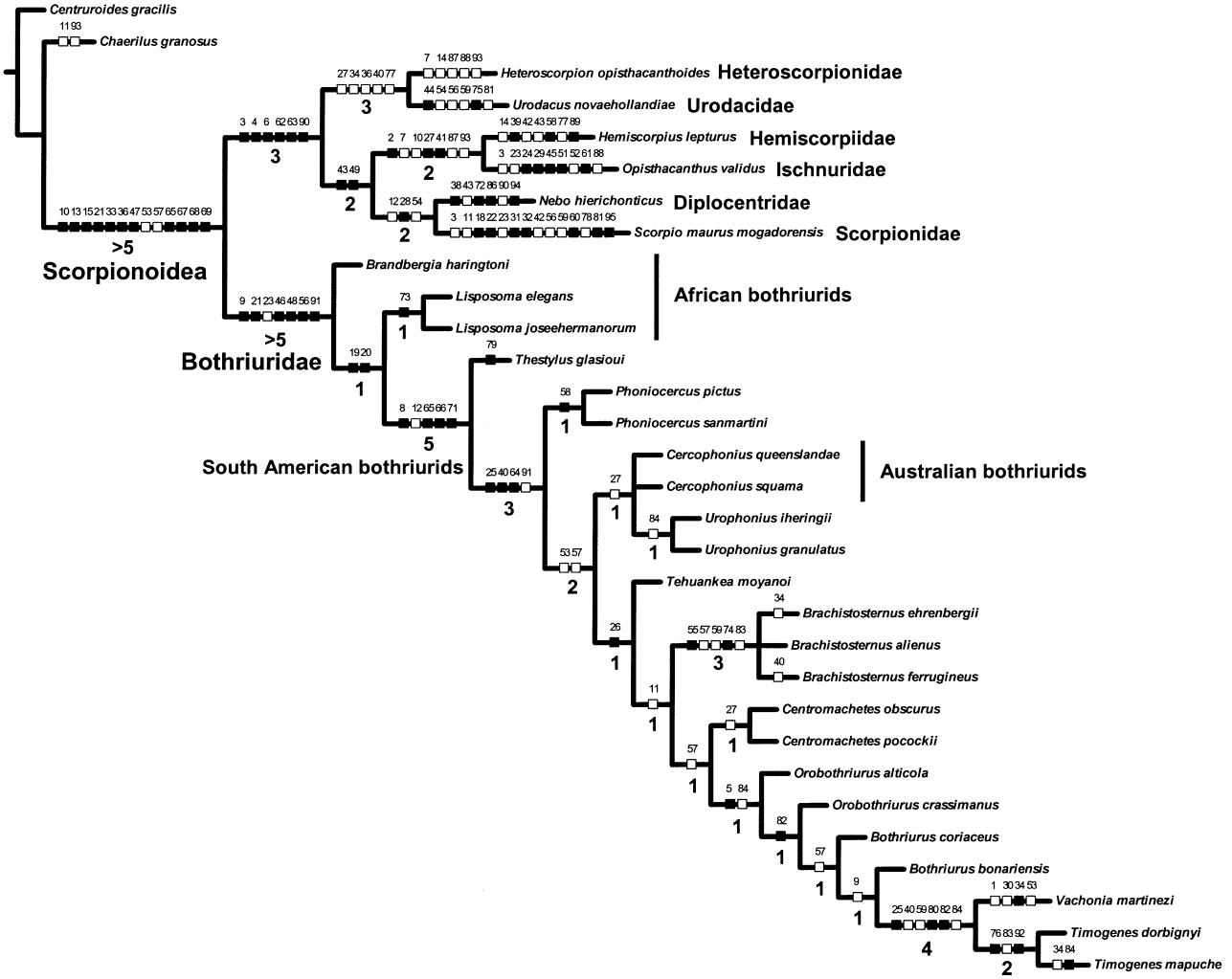

Fig. 4. The optimal tree obtained by the analysis with nine multistate characters ordered under weighting regimes that maximized fit and minimized length (Table 1). Unambiguously optimized synapomorphies are indicated with bars. Solid bars indicate uniquely derived apomorphic states, whereas empty bars indicate parallel derivations of apomorphic states. The number above each bar gives the character number. The numbers below the branches provide the branch support values for each node. Refer to Appendix 2 for character descriptions.

reanalysis of bothriurid relationships presented here and renewed attention on the phylogenetic position of *Lisposoma*. *Lisposoma* was originally placed in a separate subfamily, Lisposominae, of Scorpionidae by Lawrence (1928). Vachon (1974) discussed trichobothrial similarities between *Lisposoma* and Bothriuridae, but merely considered these to support Lawrence's (1928) placement of the genus in its unique subfamily. Francke (1982) realized that these, and other characters, were potentially synapomorphic and suggested that *Lisposoma* should be transferred to Bothriuridae, where it remained *incertae sedis* (Francke, 1985; Sissom, 1990; Lowe & Fet, 2000) until two cladistic analyses (Stockwell, 1989; Prendini, 2000c) confirmed that it is a basal bothriurid. Seven synapomorphies supported the grouping of *Lisposoma* with Bothriuridae in my previous analysis (Prendini, 2000c).

Lourenço (1996, 2000) chose to ignore the evidence that *Lisposoma* is a bothriurid. In Lourenço's (1996) opinion: 'This taxonomic position cannot be accepted as definitive, since *Lisposoma* presents characteristics of both Scorpionidae and of Bothriuridae. In fact, this genus should probably be assigned to a family, of its own. This has already been decided at the subfamilial by Lawrence in 1928 who erected the Lisposominae to accomodate it [*sic*]'. Lourenço (1996) did not address the possibility that the putatively scorpionid characteristics expressed by *Lisposoma* might be plesiomorphic in Bothriuridae.

Lourenço (2000) went on to place *Lisposoma* in its own family, Lisposomidae, citing only the opinions of Lawrence (1928) and Lamoral (1979), both of whom had maintained the genus in its unique subfamily of Scorpionidae, as evidence for the new rank: 'Les caractéristiques définissant ce

Table 2. Length (steps), fit (f_i), consistency indices (CI), retention indices (RI) and final successive weights of informative characters on the optimal tree obtained by analysis under weighting regimes that maximized fit and minimized length (Figs 2A, 4).

Character	Steps	f_i	CI	RI	Weight	Character	Steps	f_i	CI	RI	Weight
1	4	6	50	33	1	49	1	10	100	100	10
2	1	10	100	100	10	50	1	10	100	100	10
3	3	7.5	66	75	5	52	2	7.5	50	75	3
4	1	10	100	100	10	53	3	6	33	83	2
5	1	10	100	100	10	54	2	7.5	50	50	2
6	1	10	100	100	10	55	1	10	100	100	10
7	2	7.5	50	50	2	56	3	7.5	66	83	5
8	2	10	100	100	10	57	6	4.2	33	77	2
9	2	7.5	50	90	4	58	2	10	100	100	10
10	2	7.5	50	66	3	59	5	5	40	83	3
11	3	6	33	84	2	62	1	10	100	100	10
12	2	7.5	50	87	4	63	1	10	100	100	10
13	1	10	100	100	10	64	1	10	100	100	10
14	2	7.5	50	0	0	65	2	10	100	100	10
15	1	10	100	100	10	66	1	10	100	100	10
16	3	6	33	50	1	67	2	10	100	100	10
17	3	6	33	50	1	68	1	10	100	100	10
19	1	10	100	100	10	69	1	10	100	100	10
20	1	10	100	100	10	70	1	10	100	100	10
21	2	10	100	100	10	71	1	10	100	100	10
23	3	6	33	50	1	73	1	10	100	100	10
25	2	10	100	100	10	74	1	10	100	100	10
26	1	10	100	100	10	76	1	10	100	100	10
27	4	6	50	75	3	77	2	7.5	50	50	2
28	1	10	100	100	10	78	3	6	33	81	2
30	3	7.5	66	0	0	80	1	10	100	100	10
33	2	10	100	100	10	81	4	6	50	60	3
34	5	6	60	33	2	82	2	10	100	100	10
35	2	7.5	50	50	2	83	2	7.5	50	75	3
36	4	6	50	50	2	84	4	6	50	60	3
40	6	6	66	83	5	85	2	7.5	50	50	2
41	1	10	100	100	10	87	2	7.5	50	50	2
42	2	7.5	50	0	0	88	2	7.5	50	0	0
43	5	6	60	66	4	90	2	7.5	50	75	3
46	1	10	100	100	10	91	2	7.5	50	66	3
47	1	10	100	100	10	92	1	10	100	100	10
48	1	10	100	100	10	93	3	6	33	33	1

groupe familial sont celles déjà proposes par Lawrence (1928) por sa sous-famille, réitérées par Lamoral (1979). A noter qu'après le transfert de la sous-famille chez les Bothriuridae par Francke (1982), Sissom (1990) la maintien dans cette famille mais dans une position d'*incertae sedis*'.

On the basis of the reanalysis of bothriurid phylogeny presented here, recognition of Lisposomidae renders Bothriuridae paraphyletic. All analyses placed the new genus as the most basal of Bothriuridae, followed by *Lisposoma* as the next most basal (Fig. 3). To uphold Lisposomidae, yet another ad hoc monotypic family of scorpions would have to be erected to accommodate *Brandbergia*. This situation thus fully justifies the synonymy: Lisposomidae Lawrence, 1928 = Bothriuridae Simon, 1879, syn.n.

The pectinate arrangement of relationships among the remaining bothriurid genera retrieved in the present analyses is identical to that obtained previously (Prendini, 2000c), as are the major findings. As such, I shall only summarize the details here. The basal nodes of Bothriuridae are more strongly supported than the terminal nodes, which collapsed in the strict consensus of the analysis with equal weighting when multistates were unordered (collapsed nodes indicated in Fig. 2A). The node grouping *Centromachetes* Lönnberg with the remaining genera remained unsupported in all differentially weighted analyses with multistate characters unordered. As in previous analyses, the monophyly of three bothriurid genera, *Bothriurus*, *Orobothriurus* Maury and *Cercophonius* Peters, was not supported in the current analyses. *Orobothriurus* was rendered paraphyletic by *O. crassimanus* Maury, which formed a monophyletic group with (*Bothriurus* (*Timogenes* + *Vachonia*)), to the exclusion of *O. alticola* (Pocock),

and *Bothriurus* was similarly rendered paraphyletic by the grouping of *B. bonariensis* (C.L. Koch), with (*Timogenes* + *Vachonia*), to the exclusion of *B. coriaceus* Pocock (Fig. 4). *Bothriurus* is presently defined entirely by plesiomorphic states, relative to *Timogenes* Simon and *Vachonia* Abalos, which may have to be synonymized unless *Bothriurus* is split into more than one genus or synapomorphies for its component species are identified. However, it was not the purpose of this study to revise the status of the bothriurid genera. Revisions and cladistic analyses of several genera are in preparation (C. Mattoni, J. Ochoa & A. Ojanguren, personal communication), and a more comprehensive analysis of the relationships among them, incorporating a larger number of exemplar taxa and additional characters (including molecular data) is also underway (L. Prendini & W. Wheeler, unpublished). These investigations should assist in addressing the issues that remain unresolved.

Biogeographical implications

Scorpionoidea is a Gondwanan faunal element (Birula, 1917a,b; Lamoral, 1980; Stockwell, 1989; Prendini, 2001d). Bothriuridae exhibit a classic Gondwanan distribution pattern across South America, southern Africa and Australia (Sissom, 1990). As indicated by the present analyses, the most basal members of the family, *Brandbergia* and *Lisposoma*, occur in Africa, confirming a well known biogeographical pattern attributed to the earlier separation of Africa from the post-Gondwana landmass including South America and Australia (Brundin, 1965). However, the Australian genus *Cercophonius*, which forms a monophyletic group with the South American genus *Urophonius* Pocock, is nested within the larger monophyletic group of South American genera, suggesting that the common ancestor of this group was broadly distributed across southern Gondwana before the separation of South America and Australia in the Cretaceous (Stockwell, 1989). The recent discovery of a new species of *Cercophonius* from the Himalayas (Lourenço, 1996) suggests that Bothriuridae were also present on the Indian plate before its separation from Gondwana.

The main radiation of Bothriuridae, which resulted in the majority of extant bothriurid genera and species, including the most speciose genera (*Bothriurus*, *Brachistosternus* Pocock and *Orobothriurus*, collectively comprising more than sixty described species) evidently occurred after the separation of South America from Australia. Most extant South American bothriurids are fossorial and inhabit semiarid to hyperarid habitats (Lourenço, 1996). The derived genera (particularly, *Brachistosternus*, *Timogenes* and *Vachonia*) comprise mostly psammophilous and semipsammophilous species that probably evolved after the onset of aridity in the late Miocene (7–10 mya) resulted in the formation and distribution of the aeolian deposits they inhabit (Thomas & Goudie, 1984). The evolution of burrowing behaviour is a precursor for the evolution of psammophily and both are regarded as fundamental adaptations by scorpions to life in hot, arid, sandy environments (Fet *et al.*, 1998; Prendini, 2001d,e).

On the basis of the hypothesized recency of the evolution of derived, arid-adapted South American bothriurid genera, and the ubiquitous occurrence in mesic, usually forested (particularly *Nothofagus*) habitats of the basal South American, Indian and Australian bothriurid genera (*Thestylus* Simon, *Phoniocercus* Pocock, *Cercophonius* and *Urophonius*), the ancestral habitat of Bothriuridae is hypothesized to be mesic, and probably forested. Mesic habitats, especially tropical and temperate forests, are also regarded as ancestral in Scorpionoidea (Prendini, 2001e). Heteroscorpionidae, basal Urodacidae and Scorpionidae, most Ischnuridae and many Diplocentridae (including the most basal) inhabit forests, or mesic habitats (including caves), whereas arid habitats are inhabited, almost without exception, by derived members of these families.

The evolution of Bothriuridae in South America appears to be linked to the onset and intensification of aridity in the southwestern part of that continent. Arid conditions in South America, Australia and southwestern Africa (indeed, globally) developed around the same time (late Miocene), due to a common cause, global cooling and drying caused by the development of the Southern Ocean and swelling of the Antarctic ice cap (Mercer, 1973; van Zinderen Bakker, 1975; Bowler, 1976, 1978; Siesser, 1978, 1980; Tankard & Rogers, 1978; Wasson, 1983; Lancaster, 1984; Thomas & Goudie, 1984), which culminated in the end-Miocene Messinian Crisis 5–6 mya. Accordingly, it is interesting to compare diversity among African and Australian Bothriuridae with that among South American Bothriuridae. The diversity of bothriurids in South America (eleven genera and *c*. eighty-five species) provides a dramatic contrast to the two genera and three species of African bothriurids and the single genus and six species of Australian bothriurids. African and Australian bothriurids are generally regarded as palaeoendemics (Koch, 1977; Lamoral, 1979), relicts of a mesic scorpion fauna that existed before the advent of hyperarid conditions in the late Miocene and persisted after these conditions had developed to their fullest extent by the late Miocene–early Pliocene (van Zinderen Bakker, 1975; Bowler, 1976, 1978; Ward *et al.*, 1983; Wasson, 1983, 1984; Bowler & Wasson, 1984; Lancaster, 1984; Thomas & Goudie, 1984; Deacon & Lancaster, 1988; Ward & Corbett, 1990). The sole Indian bothriurid (Lourenço, 1996) may also be regarded as a palaeoendemic.

Why several lineages of South American bothriurids radiated in association with the onset of aridification, yet African and Australian bothriurids did not, is open to speculation. One possible clue is provided by the large diversity of derived fossorial species (including many psammophiles and semipsammophiles) of other scorpion genera inhabiting the arid regions of Australia and southwestern Africa. The arid regions of southwestern Africa are dominated by derived species of *Opistophthalmus* C.L. Koch (Scorpionidae) and *Parabuthus* Pocock (Buthidae), whereas the arid regions of Australia are dominated by derived species of *Urodacus* (Urodacidae). By contrast, the fossorial

scorpion fauna inhabiting the arid regions of South America is represented only by derived bothriurids. Altogether, these observations suggest that radiation by bothriurid lineages in the deserts and semideserts of South America may have occurred in the absence of competition or predation from other groups of scorpions, whereas this was not the case in Africa and Australia, where the other groups may have enjoyed a competitive advantage under the changing environmental conditions.

Brandbergia, gen.n.

Type species. *Brandbergia haringtoni*, sp.n.

Etymology. The generic name is derived from the Brandberg Massif, where the type species is probably endemic. It is feminine in gender.

Diagnosis. The new genus is placed unequivocally in Bothriuridae on the basis of the following combination of characters: carapace without median notch in anterior margin; cheliceral movable finger with 2 subdistal teeth; pedipalp chela ventroexternal carina oblique to longitudinal axis of chela, distal edge disconnected from external movable finger condyle and directed towards (almost connecting) internal movable finger condyle; pedipalp chela with trichobothrium *db* located on dorsal surface of manus and trichobothrium Et_2 located on ventral surface of manus; sternum width greater than twice its length; ovariuterine follicles sessile, without diverticula. It differs from all other bothriurid genera, except *Lisposoma*, on the basis of the following characters: pedipalp patella with distal *v* trichobothrium located on external surface; sternum subpentagonal; genital opercula (female) fused. It can be separated from all other bothriurid genera, including *Lisposoma*, on the basis of the following characters: pedipalp chela digital and ventroexternal carinae distinct.

Description. Only characters relevant to Scorpionoidea (Bothriuridae in particular) are described. *Chelicerae*: Cheliceral movable finger with 2 subdistal teeth; distal external and distal internal teeth subequal, distal external tooth smaller than distal internal tooth, but opposable. *Carapace*: Anterior margin without median notch; median longitudinal furrow broad and shallow, without suture; posterior carapacial sutures absent. Three pairs of lateral ocelli. Median ocular tubercle raised. Nongranular surfaces of prosoma, mesosoma, metasoma and legs smooth to weakly punctate. *Pedipalps*: Patella with anterior process obsolete but with dorsoexternal carina distinct. Chela with dorsal secondary and subdigital carinae obsolete, but with digital and ventroexternal carinae distinct; ventroexternal carina oblique to longitudinal axis of chela, with distal edge directed towards and almost connecting with internal movable finger condyle; ventrointernal and internomedian carinae equally, but weakly developed to obsolete. Chela fingers with a single primary row of denticles. *Trichobothria*: Orthobothriotaxic, type C. Pedipalp patella with trichobothrium d_2 located on dorsal surface and distal *v* trichobothrium located on external surface. Pedipalp chela with trichobothria *ib* and *it* located basally on fixed finger; *db* located on dorsal surface of manus; *eb* and *esb* located proximally on fixed finger, *esb* below the *eb–est–et* axis and near articulation of fixed and movable fingers; *Db* located on external surface of manus; *Dt* located proximally on manus; *Est* located distally on manus; Et_2 located on ventral surface of manus; V_2 and V_3 not widely separated. *Sternum*: Subpentagonal, width greater than twice its length. *Genital operculum*: Opercula (female) fused. *Legs*: Basitarsi each with a few scattered spiniform setae on prolateral and retrolateral margins, decreasing in number from anterior to posterior legs. Telotarsi I–IV each with paired ventrosubmedian rows of spiniform setae, increasing in number from anterior to posterior legs, and a ventromedian row of setiform setae; laterodistal lobes truncated, flush with base of median dorsal lobe; retrolateral pedal spurs absent. *Metasoma and telson*: Metasomal segments I–IV with paired ventrosubmedian carinae obsolete, ventrolateral carinae distinct and more strongly developed on segments III and IV than I and II; segment V without transverse carina, and with distal portion of ventromedian carina bifurcating; telson vesicle not laterally compressed, anterodorsal lateral lobes present but weakly developed; aculeus long, shallowly curved, without subaculear tubercle. Venom glands complex. *Reproductive anatomy*: Ovariuterine follicles sessile, without diverticula. Embryonic development presumed to be apoikogenic.

Included taxa. A single species, *Brandbergia haringtoni*, sp.n.

Distribution. Known only from a single locality on the Brandberg Massif, in the Omaruru District (Erongo Region) of northwestern Namibia (Fig. 1).

Brandbergia haringtoni, sp.n.

Type specimens. Holotype ♀ and paratype ♀, NAMIBIA: Goaseb [21°14′S 14°35′E], 1650 m, Brandberg (Omaruru District, Erongo Region), 1 March 1978, H. Pager (AH 1029, deposited in AMNH).

Etymology. The specific name is a patronym, honouring the late Dr Alexis Harington (formerly of the University of the Witwatersrand, Johannesburg, and the Institut Pasteur, Paris), whose vast private collection of scorpions, of which the type specimens of this new genus and species form part, is now deposited in the AMNH.

Diagnosis. As for genus.

Description. The following description is based on the holotype and paratype, both of which are adult females. Males, subadults and juveniles are unknown. *Colour*: Carapace, chelicerae, legs, pedipalp patellae and femora, Buff 124; pedipalp chelae and telson, Buff-Yellow 54; tergites, sternites, metasoma, pectines and genital operculum, Straw Yellow 56. *Chelicerae*: Movable finger with 2 subdistal teeth

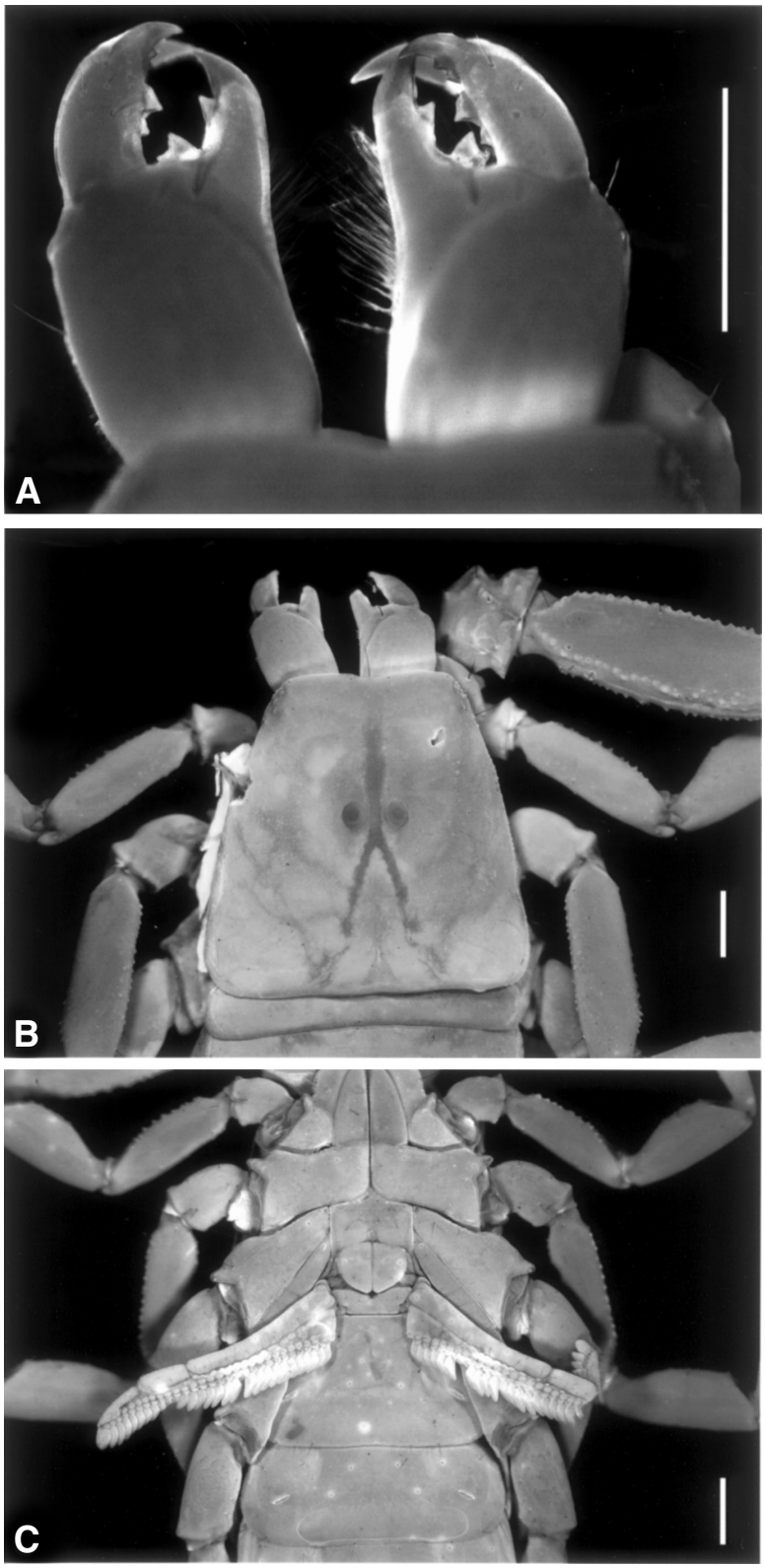

Fig. 5. *Brandbergia haringtoni*, holotype. A, Chelicerae; B, carapace; C, sternum, pectines and genital operculum. Scale bars = 1 mm.

Table 3. Meristic data for holotype and paratype of *Brandbergia haringtoni*. Measurements (mm) following Stahnke (1970) and Lamoral (1979).

		Holotype	Paratype
Carapace	anterior width	2.27	2.47
	posterior width	5.04	4.73
	length	4.89	4.52
Chela	maximum width	2.89	2.76
	maximum height	2.46	2.40
	length[a]	9.08	8.00
	length of ventroexternal carina	4.35	3.98
	length of movable finger	5.13	4.52
Patella	maximum width	2.02	1.91
	maximum height	1.68	1.45
	length	4.57	4.47
Femur	maximum width	1.60	1.56
	maximum height	1.54	1.21
	length	4.44	4.03
Pedipalp	total length (including trochanter)	19.91	18.20
Mesosoma	total length (tergites)	12.03	12.08
Sternite VII	width	4.41	3.73
	length	2.93	2.63
Metasoma I	maximum width	2.41	2.10
	maximum height	1.96	1.78
	length	2.83	2.82
Metasoma II	maximum width	2.23	1.90
	maximum height	1.85	1.76
	length	3.01	2.99
Metasoma III	maximum width	2.02	1.80
	maximum height	1.80	1.70
	length	3.23	3.31
Metasoma IV	maximum width	2.01	1.79
	maximum height	1.64	1.57
	length	4.15	3.91
Metasoma V	maximum width	1.97	1.75
	maximum height	1.59	1.46
	length	6.33	5.90
Telson	maximum width	1.94	1.90
	maximum height	1.92	1.88
	aculeus length	2.20	2.01
	total length	5.67	5.61
Metasoma	total length[b]	25.22	24.54
Total length	prosoma + mesosoma + metasoma	42.14	41.14
Pectines	total length	5.54	4.19
	length along dentate margin	4.70	3.96
	tooth count (left/right)	30/30	31/32
Telotarsi I	spiniform setal count prolateral row (left/right)	2/2	2/2
	spiniform setal count retrolateral row (left/right)	1/1	1/1
Telotarsi II	spiniform setal count prolateral row (left/right)	3/3	3/3
	spiniform setal count retrolateral row (left/right)	2/2	2/2
Telotarsi III	spiniform setal count prolateral row (left/right)[c]	3/3	3/–
	spiniform setal count retrolateral row (left/right)	3/3	3/–
Telotarsi IV	spiniform setal count prolateral row (left/right)	3/3	3/–
	spiniform setal count retrolateral row (left/right)	3/3	3/–

[a]Measured from the base of the condyle to the tip of the fixed finger.
[b]Sum of metasomal segments I–V and telson.
[c]Dextral telotarsi III and IV missing in paratype.

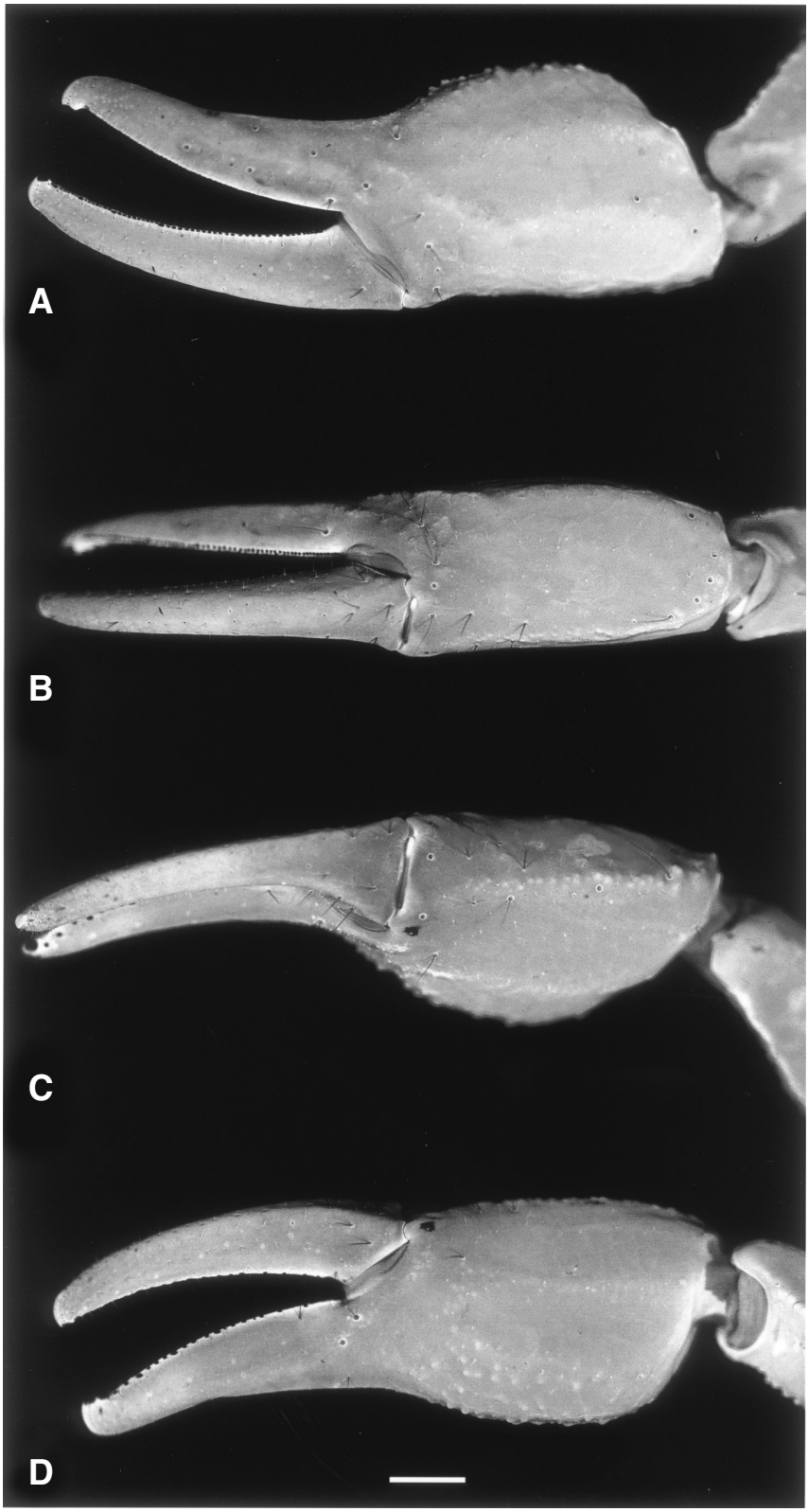

Fig. 6. *Brandbergia haringtoni*, holotype. Sinstral pedipalp chela, showing trichobothrial distribution. A, Dorsal aspect; B, external aspect; C, ventral aspect; D, internal aspect. Scale bar = 1 mm.

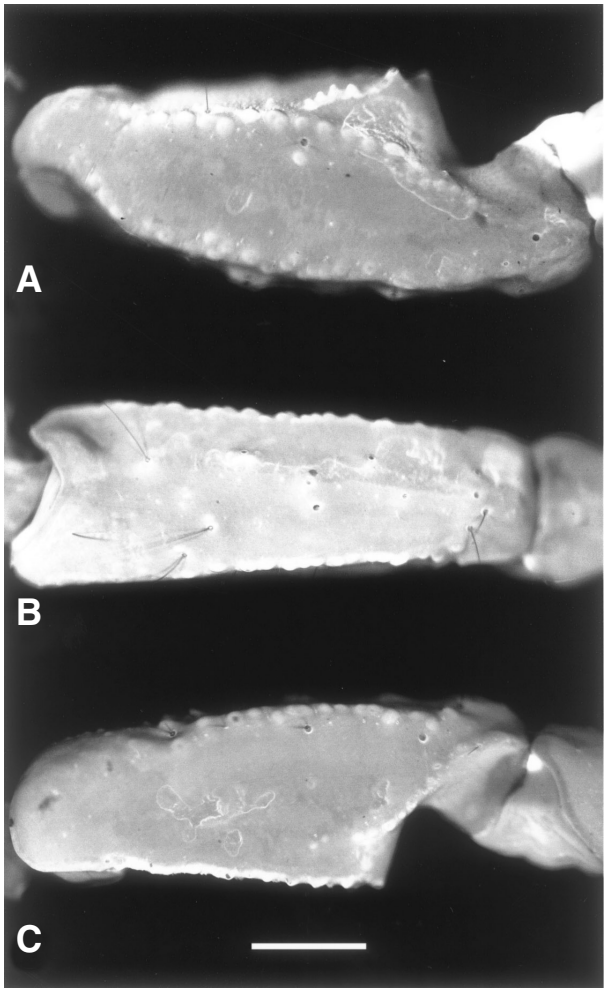

Fig. 7. *Brandbergia haringtoni*, holotype. Sinstral pedipalp patella, showing trichobothrial distribution. A, Dorsal aspect; B, external aspect; C, ventral aspect. Scale bar = 1 mm.

(Fig. 5A); distal external and distal internal teeth subequal, distal external tooth smaller than distal internal tooth, but opposable. Ventral aspect of fingers and manus with long, dense macrosetae. *Carapace*: 3 pairs of lateral ocelli, considerably smaller than median ocelli (Fig. 5B). Median ocular tubercle raised, with distinct interocular sulcus, but superciliary carinae obsolete. Anterior margin of carapace without median notch. Anteromedian sulcus broad and shallow, without suture; posterior furcated sutures absent. Posteromedian and posteromarginal sulci distinct, but shallow. Carapace uniformly finely granular, with a few coarse granules on anterolateral surfaces. *Pedipalps*: Femur pentacarinate, ventroexternal carina obsolete, reduced to a few granules proximally; dorsoexternal, externomedian and internomedian carinae granular; dorso-internal and ventro-internal carinae costate granular, composed of large, heavily sclerotized granules; dorsal surface finely granular, all other intercarinal surfaces smooth. Femur length 62.5% (61–64%) greater than width (Table 3). Patella pentacarinate, externomedian carinae obsolete; dorso-internal and ventro-internal carinae costate to costate granular; internomedian carina costate granular, composed of several large, heavily sclerotized spiniform granules; dorso-external and ventro-external carinae granular; all intercarinal surfaces smooth; anterior process obsolete. Patella length 56.5% (56–57%) greater than width (Table 3). Chela pentacarinate; dorsal secondary, subdigital and external secondary carinae obsolete (Fig. 6A); digital carina weakly developed, costate to costate granular; ventro-external carina strongly developed, costate to costate granular (Fig. 6B), aligned obliquely to longitudinal axis of chela, with distal edge directed towards and almost connecting with internal movable finger condyle (Fig. 6C); ventromedian carina obsolete, reduced to a vestigial granule proximally; ventro-internal carina also obsolete (Fig. 6D); dorsomedian, internomedian and dorso-internal carinae weakly developed, each comprising a series of isolated spiniform granules; all intercarinal surfaces smooth, except for distal region of dorso-external surface and base of fixed finger, which are finely granular. Dentate margins of chela fingers linear (without lobe or notch), with a single row of denticles. Chela length along ventro-external carina 32.5% (31–34%) greater than chela width (Table 3); chela width 14% (13–15%) greater than chela height; length of movable finger 13.5% (12–15%) greater than length along ventro-external carina. *Trichobothria*: Orthobothriotaxic, type C (Figs 6, 7), with the following segment totals: femur 3 (1 *d*; 1 *i*; 1 *e*), patella 19 (2 *d*; 1 *i*; 3 *v*; 13 *e*) and chela 26 (16 manus, including 4 *V*; 10 fixed finger). Total number of trichobothria per pedipalp 48. Pedipalp patella with trichobothrium d_2 located on dorsal surface and distal *v* trichobothrium located on external surface. Pedipalp chela with trichobothria *ib* and *it* located basally on fixed finger; *db* located on dorsal surface of manus; *eb* and *esb* located proximally on fixed finger, *esb* below the *eb–est–et* axis and near articulation of fixed and movable fingers; *Db* located on external surface of manus; *Dt* located proximally on manus; *Est* located distally on manus; Et_2 located on ventral surface of manus; V_2 and V_3 not widely separated. *Mesosoma*: Tergites each with paired submedian depressions and obsolete median carina. Pretergites smooth and shiny. Postergites covered with very fine and even granulation, imparting a matt appearance to all surfaces, except submedian depressions, which are smooth. Sternites smooth to faintly punctate and shiny, each with paired longitudinal depressions internal to spiracles. Sternite VII acarinate, with a shallow notch in distal apex. Sternite VII 31.5% (29–34%) wider than long (Table 3). *Pectines*: First proximal median lamella of each pecten with mesial margin angular, pectinal teeth present along entire posterior margin (Fig. 5C). Pectinal teeth 30–31/30–32. *Sternum*: Subpentagonal, width greater than twice its length. *Genital operculum*: Subcordate, opercula (female) fused. *Legs*: Femora each with paired granular carinae on prolateral surface. Basitarsi each with a few scattered spiniform setae on prolateral and retrolateral margins, decreasing in number from anterior to posterior legs.

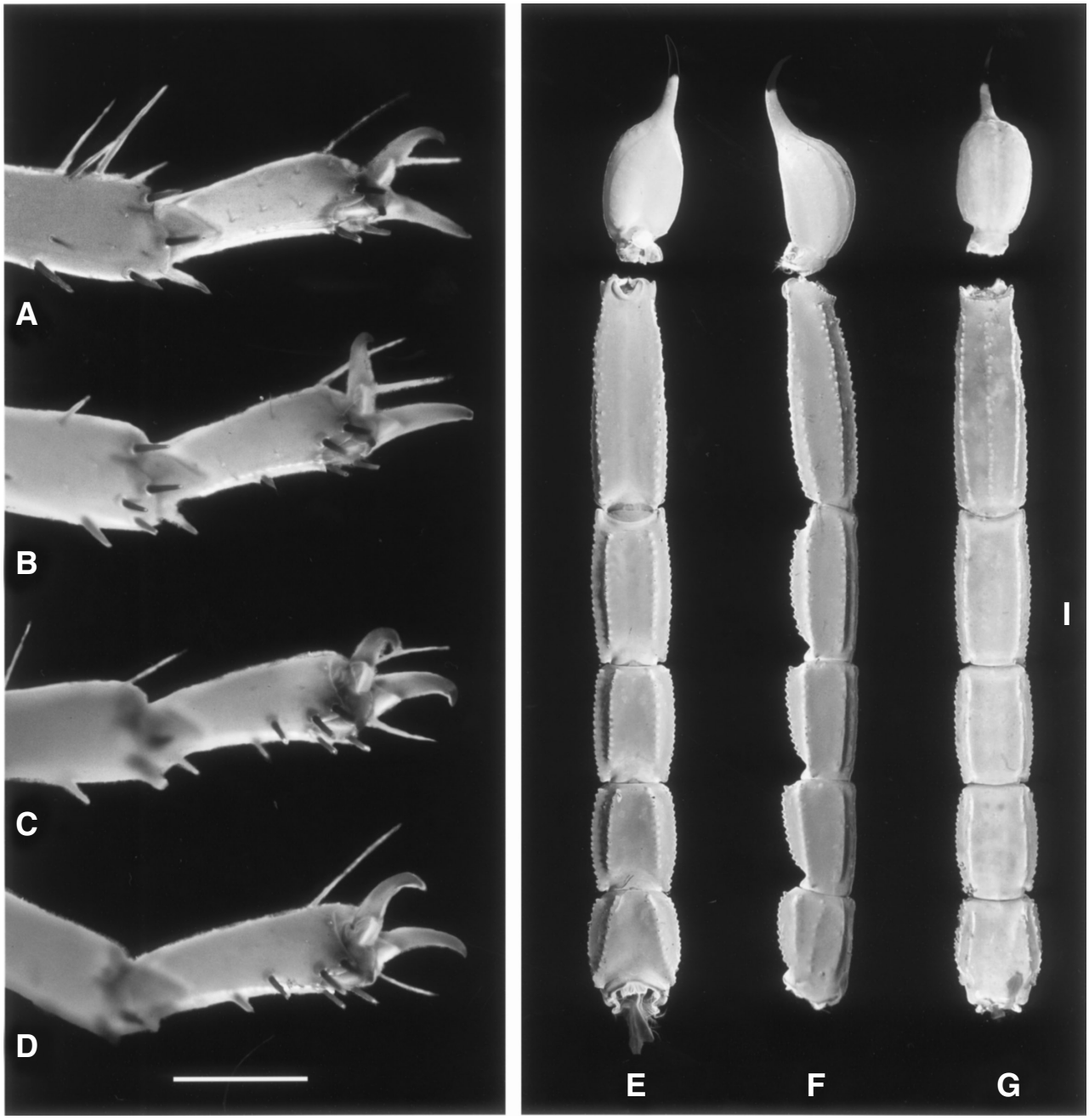

Fig. 8. *Brandbergia haringtoni*, holotype. A–D, Dextral telotarsi I–IV, ventrolateral aspect: (A) telotarsus I, (B) telotarsus II, (C) telotarsus III, (D) telotarsus IV. E–G, Metasomal segments I–V and telson: (E) dorsal aspect, (F) lateral aspect, (G) ventral aspect. Scale bars = 1 mm.

Telotarsi I–IV each with paired ventrosubmedian rows of spiniform macrosetae and a ventromedian row of setiform macrosetae (Fig. 8A–D); counts of spiniform macrosetae in pro- and retrolateral rows, 2/1 for telotarsi I, 3/2 for II and 3/3 for III and IV. Telotarsal laterodistal lobes truncated, flush with base of median dorsal lobe. Telotarsal ungues short, distinctly curved, and of equal length. Retrolateral pedal spurs absent. *Metasoma and telson*: Metasomal segments I–V progressively increasing in length, and decreasing in width, segment V 17.5% (17–18%) narrower than segment I (Table 3). Metasoma slender, width percentage of length for segment I 79.5% (74–85%), II 69% (64–74%), III 58% (54–62%), IV 47% (46–48%) and V 30.5% (30–31%). Telson vesicle oval in shape, height 25% of length, with

flattened dorsal surface and rounded ventral surface, and not laterally compressed; anterodorsal lateral lobes present but weakly developed. Aculeus long, 37.5% (36–39%) of vesicle length, shallowly curved, and without subaculear tubercle. Total length of metasoma 32% greater than combined length of prosoma and mesosoma. Eight carinae on segment I, 6 on II–IV, and 7 on V (Fig. 8E–G). Dorsosubmedian carinae distinct throughout length of segments I–V. Dorsolateral carinae becoming obsolete distally on segment V. Median lateral carinae fully developed on segment I, but absent from II–V. Ventrolateral carinae distinct and more strongly developed on segments III and IV than I and II. Ventrosubmedian carinae obsolete on segments I–IV, fused into a single distinct, distally bifurcating ventromedian carina on V. Transverse carina absent on segment V. Ventrolateral carinae costate on segments I and II, costate to costate granular on III, and costate granular to granular on IV and V; dorsosubmedian and dorsolateral carinae of segment V, granular; all other carinae costate granular. Dorsosubmedian carinae of metasomal segments II–IV each terminating distally with a slightly enlarged, spiniform granule; dorsosubmedian carinae of other metasomal segments without enlarged spiniform granules distally. Dorsal surfaces of segments III–V, lateral surfaces of I–V and ventral surfaces of V finely granular; all other intercarinal surfaces smooth. Telson smooth dorsally, very weakly granular laterally and ventrally; sparsely covered in macrosetae. Venom glands complex. *Reproductive anatomy*: Ovariuterine follicles sessile, without diverticula. Embryonic development presumed to be apoikogenic.

Distribution. The holotype and paratype were collected along the Goaseb gorge on the southern side of the Brandberg Massif (Fig. 1), at an altitude of 1650 m. According to the vegetation map of Namibia (Giess, 1971), the Brandberg lies in the semidesert and savannah transitional zone, whereas the Namibian biomes, as defined by Irish (1994), place the massif in the desert biome. The base and lower slopes of the Brandberg receive a mean annual rainfall of 100 mm, falling entirely in the months January to March (Olszewski, 2000). However, the extreme aridity at the base and lower slopes is offset at higher altitudes on the massif, which receive a mean annual rainfall of 200 mm, falling during a greater range of months, November to April (Breunig, 1990; Olszewski, 2000). The plant community on the upper Brandberg is therefore more characteristic of the highland or bergthorn savannah vegetation type (Giess, 1971; Craven & Craven, 2000). Consequently, Irish (1994) considered the upper Brandberg to constitute a high altitude savannah biome outlier.

Ecology. Nothing is known about the ecology of the new species. However, on the basis of tarsal morphology, elongation of the legs and pedipalps, as well as some degree of dorsoventral compression, it appears that the species would be lapidicolous, sheltering under stones. Indeed, this would be expected given the rocky habitat on the slopes of the Brandberg.

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Appendix 1. Distribution of ninety-five characters among the exemplar taxa chosen for the cladistic analysis of Bothriuridae. Character states are scored 0–4, ? (unknown) or – (inapplicable). Twenty-one characters, pertinent to scorpionoid relationships but uninformative in the present analysis (and hence excluded), are indicated with an asterisk below.

Centruroides gracilis	0000000000000000000---0-00010000000--1---000000---00000-00000000000000000000000000000000000
Chaerilus granosus	2000000100100000000000-000-000200110010000---000000---00000-00000000100000000000000000000000100
Nebo hierichonticus	1021010101011011100010000-0100002101110200300010110111002000011020211001-00000000000110000000010
Hemiscorpius lepturus	1121011100001110000010000-1000002101101211300010110110002100011020211000000010000000101011001000
Heteroscorpion opisthacanthoides	2021011101001110000010000-2000002202100 4-0000010010110002000011020211000000010000000001101001000
Opisthacanthus validus	1111011100001011100010110-1010002101100210101010111010002000111020211000000000000000101101001000
Scorpio maurus mogadorensis	1011010101111101111001100-0100112101100201200010110111022011011020211000000001002000000001000001
Urodacus novaehollandiae	2021010101001010000010000-2000002202100 4-001-0100101110220100110202110000010100010000000001000000
Bothriurus bonariensis	1000100201111011101120101100000021011003-0000111000000011010000111211110000001000101000000000000
Bothriurus coriaceus	1000100211111011101120101100000021011003-0000111000000011010000111211110000001000101000000000000
Brachistosternus ehrenbergii	1000000211111011101120101100000022011003-0000111000000110-2000011121111001000-0000100000000000000
Brachistosternus alienus	1000000211111011101120101100000021011003-0000111000000110-2000011121111001000-0000100000000000000
Brachistosternus ferrugineus	1000000211111011101120101100000021011004-0000111000000110-2000011121111001000-0000100000000000000
Brandbergia haringtoni	1000000111001017100020107?00?0002111100200000111000010012000070?2?????????????0000010??00?0?0100?0
Centromachetes obscurus	1000000211111011101120101120000021011003-0000111000000001201000011121111000000100000000000000000
Centromachetes pocockii	1000000211111011101120101120000021011003-0000111000000001201000011121111000000100000000000000000
Cercophonius queenslandae	1000000211011011101120101020000021011003-0000111000000001100000011121111000000100100000000000000
Cercophonius squama	1000000211011011101120101020000021011003-0000111000000001100000011121111000000100100000000000000
Lisposoma elegans	1000000111001011101120100-0000002111100200000111000010012000000020211100100000000-000000000010000
Lisposoma joseehermanorum	1000000111001011101120100-0000002111100200000111000010012000000020211100100000000-000000000010000
Orobothriurus alticola	1000100211111011101120101100000021011003-0000111000000001201000011121111000000100000100000000000
Orobothriurus crassimanus	1000100211111011101120101100000021011003-0000111000000001201000011121111000000100010100000000000
Phoniocercus pictus	1000000211011011101120101000000021011003-0000111000010012200000111211110000000000-000000000000000
Phoniocercus sanmartini	1000000211011011101120101000000021011003-0000111000010012200000111211110000000000-000000000000000
Tehuankea moyanoi	1000000211011011101120101100000021011003-0000111000000000110?0000?112111100000-000000000000000000
Thestylus glasioui	1000000211011011101120100-0000002101100200000111000010012000000001121111000000110-000000000010000
Timogenes dorbignyi	1000100201111011101120102-0000002101100 4-0000111000000001102000011121111000010-01-210000000001000
Timogenes mapuche	1000100201111011101120102-0000002202100 4-0000111000000001102000011121111000010-01-212000000001000
Urophonius iheringii	1000000211011011101120101020000021011003-0000111000000001100000011121111000000100100100000000000
Urophonius granulatus	1000000211011011101120101020000021011003-0000111000000001100000011121111000000100100100000000000
Vachonia martinezi	2000100201111011101120102-0001002302100 4-0000111000010011020000?112111100000-01-200000000000000
	* * * * ** *** ** * ** * * * * **

Appendix 2.

Characters and character states employed in the cladistic analysis of Bothriuridae. Character states were scored 0–4, ? (unknown) or – (inapplicable). Multistate characters were treated non-additively, except where indicated otherwise. Character numbers corresponding to the previous analysis of scorpionoid relationships (Prendini, 2000c: appendix 3) are denoted by LP numbers. Twenty-one characters, pertinent to scorpionoid relationships, but uninformative in the present analysis (and hence excluded) are indicated with an asterisk.

Carapace

1. *Lateral ocelli*, *number of pairs*: (0) more than 3; (1) 3; (2) 2. [LP 1]
2. *Median ocular tubercle*: (0) raised; (1) shallow. [LP 2]
3. *Median notch*: (0) absent; (1) shallow; (2) strongly excavated. [LP 3]
4. *Median longitudinal furrow*: (0) broad, shallow, without suture; (1) narrow, suturiform. [LP 4]
5. *Median longitudinal furrow*: (0) well developed; (1) obsolete. [LP 5]
6. *Posterior sutures*: (0) absent; (1) present. [LP 7]
7. *Nongranular surfaces of prosoma, mesosoma, metasoma and legs*: (0) smooth; (1) distinctly punctate. [LP 8]

Sternum

8. *Sternum shape*: (0) subtriangular; (1) subpentagonal; (2) transverse. [LP 9]

Chelicerae

9. *Cheliceral movable finger, number of subdistal teeth*: (0) 1; (1) 2. [LP 10]
10. *Cheliceral movable finger, distal external and distal internal teeth*: (0) subequal, with distal external tooth only slightly smaller than distal internal tooth, and opposable, i.e. forming a bicusp; (1) unequal, with distal external tooth considerably smaller than distal internal tooth, aligned longitudinally and usually not opposable or, at most, moderately opposable. [LP 11]

Pedipalp ornamentation

11. *Patella*, *dorsal surface*: (0) flat, dorsomedian and dorsoexternal carinae in same axis; (1) convex, dorsomedian carina raised above horizontal axis of dorsoexternal carina. [LP 15]
12. *Patella*, *dorsoexternal carina*: (0) distinct; (1) obsolete. [LP 16]
13. *Patella*, *externomedian carina*: (0) continuous from proximal to distal edges; (1) discontinuous, interrupted two-thirds along. [LP 17]
14. *Patella*, *anterior process*: (0) absent; (1) present. [LP 18]
15. *Chela*, *number of carinae*: (0) 8; (1) 10. [LP 19]
16. *Chela* (♂), *dorsal secondary carina*: (0) distinct; (1) obsolete; (?) unknown. [LP 20]
17. *Chela* (♀), *dorsal secondary carina*: (0) distinct; (1) obsolete. [LP 21]
18. *Chela*, *dorsal secondary carina*: (0) extending full way across dorsal surface, subdigital carina vestigial; (1) extending part way across dorsal surface, subdigital carina extending part way across in opposite direction. [LP 22]*
19. *Chela*, *digital carina*: (0) distinct; (1) obsolete. [LP 23]
20. *Chela*, *ventroexternal carina*: (0) distinct; (1) obsolete. [LP 26]
21. *Chela*, *ventroexternal carina*: (0) parallel to longitudinal axis of chela, distal edge connected to external movable finger condyle; (1) parallel to longitudinal axis of chela, distal edge disconnected from external movable finger condyle and directed towards a point between external and internal movable finger condyles, but closer to external condyle; (2) oblique to longitudinal axis of chela, distal edge disconnected from external movable finger condyle and directed towards (almost connecting) internal movable finger condyle. Additive. [LP 27]
22. *Chela*, *ventromedian carina*: (0) vestigial or obsolete; (1) distinct; (–) inapplicable. [LP 28]*
23. *Chela*, *ventrointernal carina*: (0) more strongly developed than internomedian carina, which may be obsolete; (1) equally or less strongly developed than internomedian carina; (–) inapplicable. [LP 29]
24. *Chela*, *ventrointernal carina*: (0) equally or more strongly developed than internomedian carina, which may be obsolete; (1) less strongly developed than internomedian carina, often obsolete; (–) inapplicable. [LP 30]*
25. *Chela* (♂), *secondary sexual structure*: (0) absent; (1) hooklike apophysis; (2) semicircular, rimmed depression; (?) unknown. Additive. [LP 31]
26. *Chela* (♂), *hooklike secondary sexual structure with granular ridge at base of fixed finger*: (0) present; (1) absent; (?) unknown; (–) inapplicable. [LP 32]
27. *Chela fingers*, *number of rows of primary denticles*: (0) single; (1) double, often fused at the base; (2) multiple. [LP 33]
28. *Chela fingers*, *dentate margin*: (0) entire; (1) markedly scalloped. [LP 34]
29. *Chela* (♂), *lobe of movable finger*: (0) absent or at most weakly developed, close to base movable finger and lacking an obvious notch in fixed finger; (1) well developed, almost midway along movable finger (if dentate margin markedly scalloped, first lobe disproportionately developed), with a distinct notch in fixed finger, lobe rounded dorsally and lacking a sharp conical tooth; (?) unknown. [LP 35]*

Trichobothria

30. *Femur, number of e trichobothria*: (0) 1; (1) 2; (2) 4. [LP 39]
31. *Femur, position of trichobothrium i*: (0) internal; (1) dorsal. [LP 40]*
32. *Patella, position of trichobothrium* d_2: (0) dorsal; (1) internal. [LP 41]*
33. *Patella, v trichobothria*: (0) absent; (1) 3 prolaterals; (2) 3 or more retrolaterals. Additive. [LP 42]
34. *Patella, number of v trichobothria*: (0) absent; (1) single row of 3; (2) single row of 4–20; (3) 2 or more rows, with more than 30. [LP 43]
35. *Patella, position of distal v trichobothrium*: (0) ventral; (1) external. [LP 44]
36. *Patella, number of e trichobothria*: (0) 7; (1) 13, rarely 12; (2) 14 or more. Additive. [LP 45]
37. *Chela, number of i trichobothria*: (0) 1; (1) 2. [LP 46]*
38. *Chela, position of trichobothrium it*: (0) basal or midfinger; (1) distal; (–) inapplicable. [LP 47]*
39. *Chela, position of trichobothria ib and it*: (0) basal; (1) midfinger; (–) inapplicable. [LP 48]*
40. *Chela, number of V trichobothria*: (0) 1; (1) 2; (2) 4; (3) 5; (4) 6 or more. [LP 49]
41. *Chela, distance between trichobothria* V_2 *and* V_3: (0) normal; (1) widely separated; (–) inapplicable. [LP 50]
42. *Chela, position of trichobothrium Db*: (0) external surface; (1) dorsal surface; (–) inapplicable. [LP 51]
43. *Chela, position of trichobothrium Dt*: (0) manus, at proximal end; (1) manus, midlength or slightly less than midlength; (2) manus, distal half, near base of fixed finger; (3) proximal end of fixed finger; (–) inapplicable. Additive. [LP 52]
44. *Chela, external surface with accessory trichobothria*: (0) absent; (1) 10–15. [LP 53]*
45. *Chela, position of trichobothrium Est*: (0) distal; (1) midpalm; (–) inapplicable. [LP 55]*
46. *Chela, position of trichobothrium* Et_2: (0) external surface; (1) ventral surface. [LP 56]
47. *Chela, number of d trichobothria*: (0) 2; (1) 4. [LP 57]
48. *Chela, position of trichobothrium db*: (0) fixed finger; (1) manus. [LP 58]
49. *Chela, position of trichobothrium db*: (0) dorsal; (1) internal. [LP 59]
50. *Chela, position of trichobothrium dsb*: (0) below *db–dst* axis; (1) in line with *db–dst* axis; (–) inapplicable. [LP 60]
51. *Chela, position of trichobothrium eb*: (0) proximal region of fixed finger; (1) manus, behind point of articulation between fixed and movable fingers; (–) inapplicable. [LP 61]*
52. *Chela, position of trichobothrium esb*: (0) manus, behind point of articulation between fixed and movable fingers and below *eb–est–et* axis; (1) midway along fixed finger, in line with *eb–est–et* axis; (–) inapplicable. [LP 62]

Legs

53. *Retrolateral pedal spurs*: (0) present; (1) absent. [LP 63]
54. *Telotarsi*, *laterodistal lobes*: (0) truncated, base of median dorsal lobe flush; (1) rounded, notches at base of median dorsal lobe. [LP 65]
55. *Telotarsi*, *laterally compressed*: (0) absent; (1) present. [LP 66]
56. *Telotarsi*, *well developed ventromedian row of setae*: (0) spiniform; (1) setiform; (2) absent. [LP 68]
57. *Telotarsi I–IV*, *ventrosubmedian setae distribution*: (0) setiform on I–IV; (1) setiform on I or I and II, spiniform on III and IV; (2) spiniform (or secondarily setiform) on I–IV. Additive. [LP 69]
58. *Telotarsi*, *ventrosubmedian setae type*: (0) stout spiniform; (1) slender spiniform; (2) few secondarily setiform; (–) inapplicable. [LP 70]
59. *Basitarsi I and II*, *retrolateral row of macrosetae*: (0) absent; (1) spiniform; (2) setiform, sand comb; (?) unknown. Additive. [LP 72]
60. *Stridulatory surface on opposing surfaces of coxae of pedipalps and first walking legs*: (0) absent; (1) present, partially developed. [LP 74]*
61. *Maxillary lobes*, *shape of first pair*: (0) rounded-truncate anteriorly; (1) tapering anteriorly. [LP 76]*

Reproductive anatomy

62. *Embryonic development*: (0) apoikogenic; (1) katoikogenic; (?) unknown. [LP 77]
63. *Ovariuterine follicles*: (0) sessile; (1) stalked. [LP 78]
64. *Testis*: (0) straight; (1) coiled; (?) unknown. [LP 79]
65. *Genital opercula* (♀): (0) separated; (1) loosely joined; (2) fused. [LP 80]
66. *Genital opercula* (♂): (0) separated; (1) loosely joined; (?) unknown. [LP 81]

Hemispermatophore and paraxial organ

67. *Hemispermatophore*: (0) flagelliform; (1) fusiform; (2) lamelliform; (?) unknown. Additive. [LP 82]
68. *Hemispermatophore*, *truncal flexure*: (0) absent; (1) present; (?) unknown. [LP 83]
69. *Paraxial organ*, *internobasal reflection of sperm duct*: (0) absent; (1) present; (?) unknown. [LP 84]
70. *Paraxial organ*, *internal wall of sperm duct*: (0) simple; (1) with semilunar shelf; (?) unknown. [LP 85]
71. *Hemispermatophore*, *distal lamina*: (0) smooth; (1) with prominent crest; (?) unknown. [LP 86]
72. *Hemispermatophore*, *lamellar hook and median lobe*: (0) separate; (1) fused; (?) unknown. [LP 88]*
73. *Hemispermatophore*, *position of lamellar hook*: (0) basal; (1) distal; (?) unknown; (–) inapplicable. [LP 89]
74. *Hemispermatophore*, *spines in capsular region*: (0) absent; (1) present; (?) unknown. [LP 91]

75. *Hemispermatophore*, *sclerotized mating plug*: (0) absent; (1) present; (?) unknown. [LP 92]*

Mesosoma

76. *Pretergites III and VI with stridulatory granules*: (0) absent; (1) present. [LP 93]

Metasoma

77. *Metasomal segments I–IV*, *carinae*: (0) paired ventrosubmedian carinae; (1) single ventromedian carina. [LP 95]
78. *Metasomal segments I–IV*, *carinae*: (0) more strongly developed on III and IV than I and II; (1) more strongly developed on I and II than III and IV; (–) inapplicable. [LP 96]
79. *Metasomal segment I, ventromedian carinae with circular configuration*: (0) absent; (1) present. [LP 97]*
80. *Metasomal segment V*, *ventrolateral carinae*: (0) continuous from proximal to distal edges; (1) discontinuous, interrupted in distal region. [LP 98]
81. *Metasomal segment V*, *ventromedian carina distal portion*: (0) straight; (1) bifurcating; (2) breaking up into numerous granules; (–) inapplicable. [LP 99]
82. *Metasomal segment V*, *transverse carina*: (0) absent; (1) type I, discontinuous and merging proximally with ventrolateral carinae; (2) type II, continuous, not merging proximally with ventrolateral carinae. Additive. [LP 100]
83. *Metasomal segment V (♂), dorsal surface with paired androvestigia (metasomal glands)*: (0) absent; (1) present; (?) unknown. [LP 103]

Telson

84. *Vesicle (♂)*, *dorsal surface with androvestigia* (*metasomal glands*): (0) absent; (1) single; (2) paired; (?) unknown. [LP 104]
85. *Aculeus*: (0) long, shallowly curved; (1) very short, sharply curved. [LP 105]
86. *Subaculear tubercle*: (0) absent; (1) distinct. [LP 106]*
87. *Vesicle (♂), laterally compressed*: (0) absent; (1) present; (?) unknown. [LP 107]
88. *Vesicle (♀), laterally compressed*: (0) absent; (1) present. [LP 108]
89. *Vesicle (♂), elongated with pair of distal lobes*: (0) absent; (1) present; (?) unknown. [LP 109]*
90. *Vesicle*, *anterodorsal lateral lobes*: (0) present; (1) absent. [LP 110]
91. *Vesicle*, *ventral surface*: (0) with 2 or more longitudinal granular carinae extending towards aculeus; (1) without granules. [LP 111]
92. *Vesicle, ventral surface with semicircular carina*: (0) absent; (1) present. [LP 112]
93. *Venom glands*: (0) complex; (1) simple. [LP 113]
94. *Venom pigment*: (0) opalescent; (1) reddish; unknown. [LP 114]*

Behaviour

95. *Mesosomal percussion*: (0) absent; (1) present. [LP 115]*