

ARTÍCULO:

**Subfamily Lisposominae revisited  
(Scorpiones: Bothriuridae)**

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ARTÍCULO:

**SUBFAMILY LISPOSOMINAE REVISITED  
(SCORPIONES: BOTHRIURIDAE)**

**Victor Fet, Michael E. Soleglad  
& František Kovařík**

**Abstract:**

The cladistic analyses of Stockwell (1989) and Prendini (2000, 2003a) are reevaluated for the scorpionoid family Bothriuridae. The genus *Brandbergia* Prendini, 2003 is shown to be a synonym of *Lisposoma* Lawrence, 1928, its sole species forming a clade inside this genus with species *L. josehermana*, with *L. elegans* as a sister group to both. Based on the synonymy of *Brandbergia*, the subfamilies Lisposominae and Bothriurinae are reestablished, as originally suggested by Stockwell (1989). The monotypic subfamily Lisposominae, endemic to Namibia, comprises the most primitive scorpions in the family Bothriuridae.

**Key words:** Scorpiones, Bothriuridae, Bothriurinae, Lisposominae, *Lisposoma*, *Brandbergia*.

**Taxonomy:**

*Brandbergia* Prendini, 2003 = *Lisposoma* Lawrence, 1928 **syn. n.**

*Brandbergia haringtoni* Prendini, 2003 = *Lisposoma haringtoni* (Prendini, 2003) **comb. n.**  
subfamilies Bothriurinae Simon, 1880 and Lisposominae Lawrence, 1928 **restored  
from synonymy.**

**Reevaluación de la subfamilia Lisposominae (Scorpiones: Bothriuridae)**

**Resumen:**

Se reevalúan los análisis cladísticos de Stockwell (1989) y Prendini (2000, 2003a) en relación con la familia escorpionoide de los Bothriuridae. Se muestra que el género *Brandbergia* Prendini, 2003 es sinónimo de *Lisposoma* Lawrence, 1928 y su única especie forma un clado dentro de dicho género con *L. josehermana*, mientras que *L. elegans* es el grupo hermano de esa pareja de especies. Basándose en la sinonimia de *Brandbergia*, se restablecen las subfamilias Lisposominae y Bothriurinae, tal como sugería originalmente Stockwell (1989). La subfamilia Lisposominae, monotípica y endémica de Namibia, incluye los escorpiones más primitivos de la familia Bothriuridae.

**Palabras clave:** Scorpiones, Bothriuridae, Bothriurinae, Lisposominae, *Lisposoma*, *Brandbergia*.

**Taxonomía:**

*Brandbergia* Prendini, 2003 = *Lisposoma* Lawrence, 1928 **syn. n.**;

*Brandbergia haringtoni* Prendini, 2003 = *Lisposoma haringtoni* (Prendini, 2003) **comb. n.**  
subfamilias Bothriurinae Simon, 1880 y Lisposominae Lawrence, 1928 **revocación de  
sinonimia.**

**Introduction**

The phylogenetic position of the basal bothriurid genus *Lisposoma* Lawrence, 1928 has been a subject of controversy and recent reevaluation (Francke, 1982; Stockwell, 1989; Sissom, 1990; Lowe & Fet, 2000; Lourenço, 2000; Prendini, 2000, 2003a, 2003b). Francke (1982) demonstrated that *Lisposoma* was a bothriurid rather than a member of Scorpionidae as originally described. However, status of the monotypic subfamily Lisposominae Lawrence, 1928 within Bothriuridae Simon, 1880 remained unclear.

Stockwell (1989: Table 11) supported two subfamilies within the scorpionoid family Bothriuridae: the monotypic Lisposominae, containing the genus *Lisposoma*, and Bothriurinae, comprised of all remaining genera. Stockwell (1989: 168) considered subfamily Lisposominae a primitive member of Bothriuridae and thought its validity was well supported both from morphological and biogeographic reasons. He even discussed the possibility of establishing subfamilies for two other primitive clades, namely genera *Thestylus* and *Phoniocercus*; he thought this unwise, however, until the relationships of the other bothriurids were better understood. Since the monograph of Stockwell (1989) remained unpublished, his taxonomic changes were not implemented. Sissom (1990: 88) recognized three subfamilies within Bothriuridae (Bothriurinae, Brachistosterninae, and Vachonianinae) but listed *Lisposoma* as a genus *incertae sedis*. The subfamily Vachonianinae was previously synonymized with Bothriurinae by Acosta & Maury

(1998). Lowe & Fet (2000; published in May) listed only two valid subfamily names in Bothriuridae: Bothriurinae and Brachistosterninae. They listed Lisposominae explicitly as a synonym of both family Bothriuridae and subfamily Bothriurinae, indicating that it was synonymized by Sissom (1990); although Sissom did not publish any direct statement on synonymy, he indicated (p. 87) that *Lisposoma* “has no known characters that distinguish it from bothriurine genera”.

Prendini (2000; published in March), in his general revision of superfamily Scorpionoidea, was the first to formally synonymize Lisposominae and Brachistosterninae with Bothriuridae. Prendini (2000) chose not to retain any subfamilies in Bothriuridae, although in his cladistic analysis (Prendini, 2000, Fig. 2) two species of *Lisposoma* formed a monophyletic group, as in Stockwell's (1989) analysis. At the same time, Lourenço (2000; published in March) elevated Lisposominae to family status as Lisposomidae, without any reasonable justification.

Most recently, Prendini (2003a), in a cladistic analysis based almost entirely on his previous general revision of the superfamily Scorpionoidea (2000), described a new species and genus, *Brandbergia haringtoni*, from the Brandberg Massif in Namibia. Interestingly, this species, clearly quite closely related to *Lisposoma*, did not form a monophyletic group with *Lisposoma*, but instead was ladderized relatively to the two species of *Lisposoma* by Prendini (2003a). With the advent of this new genus, and the subsequent ladderized topology, the clear distinction between *Lisposoma* and the other bothriurid genera was blurred considerably. This also gave Prendini (2003a, 2003b) a reason to synonymize Lisposomidae back to Bothriuridae, and not to recognize Lisposominae. Further information on the genus *Lisposoma* appeared later same year in the revision of its two species by Prendini (2003b).

In this contribution, we investigate the relationship of *Brandbergia* and *Lisposoma* and show that, based on a combination of corrected representations in character coding and the reinterpretation of certain character modeling by Prendini (2003a), *Brandbergia* is not a valid genus but, instead, falls well inside the genus *Lisposoma*. The sole species of *Brandbergia* actually forms a sister group of *L. josehermana*, both species removed from *L. elegans*. With the establishment of three species of *Lisposoma*, we reinvestigate two subfamilies of Bothriuridae endorsed by Stockwell's (1989) original analysis.

## Methods and Material

### Conventions

Terminology describing chelal finger dentition and pedipalp chelal ornamentation follows that described and illustrated in Soleglad & Sissom (2001); sternum terminology follows that described and illustrated in Soleglad & Fet (2003a); and terminology of the chelicerae, and pedipalp patella and metasomal carinae follows that described in Soleglad & Fet (2003b).

### Cladistic analysis software packages

Software package PAUP\* Version 4 (beta) (Swofford, 1998) was used for Maximum Parsimony (MP) analysis of morphology based character codings. In all bootstrap and jackknife sequences, each was initiated three times for 1000 pseudoreplicates per sequence. Each support value reported is the mean of these three sequences, thus based on 3000 pseudoreplicates per algorithm.

### Material examined

**Bothriuridae:** *Bothriurus burmeisteri* Kraepelin, 1894, Chubut, Gobernador Costa, Argentina (VF); *Brachistosternus ehrenbergii* (Gervais, 1841), Valle de Azapa, Tarapaca Province, Chile ♂ (VF); *Brachistosternus* sp., Rio Loa, Antofagasta Province, Chile (VF); *Centromachetes pocockii* (Kraepelin, 1894), Lebu, Arauco Province, Chile (VF); *Cercophonius squama* (Gervais, 1843), Engadine, Sydney, New South Wales, Australia, ♀ (VF); *Lisposoma elegans* Lawrence, 1928, Königstein, Brandberg Massif, Omaruru District, Erongo Region, Namibia, subadult ♀ (FKCP), Farm Okosongomingo, Omaruru District, Erongo Region, Namibia, juvenile ♂ (FKCP); *Lisposoma josehermana*\* Lamoral, 1979, Waterberg, Namibia, subadult ♀ (CAS; det. L. Prendini); *Urophonius granulatus* Pocock, 1898, Laguna Amarga, Ultima Esperanza, Chile, ♂ (VF).

\*We use Lamoral's original specific epithet *josehermana* rather than corrected name *josehermanorum* published by Lowe & Fet (2000: 34) and followed by Prendini (2003b); Acosta & Fet (in review) demonstrate that this correction is not valid.

**Liochelidae: Liochelinae:** *Hadogenes troglodytes* (Peters, 1861), Johannesburg, South Africa (MES); *Opisthacanthus lepturus* (Beauvois, 1805), Aguacate, Panama, ♀ (MES).

### Abbreviations

**List of depositories:** CAS, California Academy of Sciences, San Francisco, California, USA; FKCP, Personal collection of František Kovařík, Prague, Czech Republic; MES, Personal collection of Michael E. Soleglad, Borrego Springs, California, USA; VF, Personal collection of Victor Fet, Marshall University, Huntington, West Virginia, USA

### Brandbergia and Lisposoma

Prendini (2003a) established a new monotypic bothriurid genus *Brandbergia*, with the sole species *B. haringtoni* Prendini, 2003, found so far only on the Brandberg Massif in Namibia. The cladistic diagnostic characters used to separate *Brandbergia* from the most closely related genus *Lisposoma*, were the presence of the digital (*DI*) and ventroexternal (*VI*) carinae of pedipalp chela: in *Brandbergia* they are present, but are stated to be “absent” in the other bothriurid genera, including *Lisposoma*. In fact, if one views Prendini's (2003a: Fig. 4) resulting cladogram (labeled as the “optimal tree”),

Table I. Comparison of diagnostic characters of two species of *Lisposoma* (after Lamoral, 1979, and Prendini, 2003b, in part), and *Brandbergia haringtoni* (after Prendini, 2003a, in part). Shaded characters depict original diagnostic characters established by Lamoral (1979).

	<i>L. elegans</i>	<i>L. josehermana</i>	<i>B. haringtoni</i>
Chelal internal denticles ( <i>ID</i> and <i>IAD</i> ), movable finger	6 <i>ID</i> , large in size, <i>IAD</i> absent	12–16 <i>ID</i> and <i>IAD</i> , small to medium in size	18 (approx.) <i>ID</i> and <i>IAD</i> , small to medium in size (fixed finger)
Median projection of carapace anterior edge	Present	Absent	Absent
Metasomal (I–IV) dorsal and dorsolateral carinae	Absent	Present and granular	Present and granular
Metasomal (I–IV) ventro-lateral carinae	Absent	Present and smooth	Present, smooth I–III, granular IV
Metasomal (V) ventromedian carina	Absent	Serrate, irregular to bifurcated distally	Serrate, irregular to bifurcated distally
Cheliceral movable finger distal denticles ( <i>dd</i> and <i>vd</i> )	Not opposable, <i>vd</i> much longer than <i>dd</i>	Not opposable, <i>vd</i> much longer than <i>dd</i>	Not opposable, <i>vd</i> longer than <i>dd</i>
Chelal ventroexternal ( <i>V1</i> ) carina	Vestigial	Vestigial to weak, outlined with pigmentation	Strong and granular
Chelal digital ( <i>D1</i> ) carina	Vestigial	Vestigial to weak, outlined with pigmentation	Present, weakly granulate
Degree of vertical compression in sternum	Considerably shortened, lateral lobes exhibiting no separation	Considerably shortened, lateral lobes exhibiting minor separation	Considerably shortened, lateral lobes exhibiting some separation
Adult size	Male, 18 mm Female, 28 mm	Male, 27 mm Female, 32 mm	Male, unknown Female, 42 mm
Pectinal tooth counts	Male, 15–16 Female, 12–16	Male, 19–21 Female, 17–21	Male, unknown Female, 30–32

we see that *Brandbergia* is ladderized relative to other genera, thus the establishment of a separate genus is mandatory (i.e., “*Brandbergia* + *Lisposoma*” is not monophyletic). The distribution of the characters 19 and 20 in Prendini’s Fig. 4 shows the obsolescence of chelal carinae *D1* and *V1* as nonhomoplasious synapomorphies for the clade “Bothriuridae without *Brandbergia*” (i.e., their CI and RI = 1 (see his Table II)); hence the ladderization.

In his revision of genus *Lisposoma* published later the same year, Prendini (2003b) listed two additional characters as diagnostic between the two genera, although he did not incorporate them into his original cladistic analysis (Prendini, 2003a). All of these characters are discussed below.

#### Lamoral’s diagnostic characters

Before we analyze the validity of the characters proposed by Prendini (2003a, 2003b) to separate *Brandbergia* and *Lisposoma*, we need to examine the original diagnostic characters as defined by Lamoral (1979: 662 and 665) when he contrasted two species of *Lisposoma*, *L. elegans* Lawrence, 1928 and *L. josehermana* Lamoral, 1979. Three characters (see our Table I) were defined by Lamoral (1979) to distinguish the two species of *Lisposoma*: (1) the presence or absence of a median projection on the anterior edge of the carapace; (2) the number of internal denticles (*ID*) found on the chelal fingers; and (3) the presence or absence of the metasomal dorsal and dorsolateral carinae on segments I–IV.

The presence of a small median projection on the carapace anterior edge is unusual in scorpions in general and is uniquely present in *Lisposoma elegans* (Fig. 1), but is absent in both *L. josehermana* (Fig. 2) and *Brandbergia* (see Prendini, 2003a: Fig. 5B). This peculiar structure, to a lesser degree, is also found in the scorpion genera *Typhlochactas* and *Sotanochactas* (family Supersitioniidae, superfamily Chactoidea), both troglotic.

The number of internal denticles (*ID*) on the chelal fingers is an important character, and probably the most important of the three diagnostic characters proposed by Lamoral (1979). We can see in *L. elegans* (Fig. 3) that six well developed *ID*s are present on the movable finger, aligning up with the corresponding outer denticles (*OD*) at denticle groups 2–5 boundaries; the first two distal *ID*s are situated closer to each other at the distal aspect of denticle group-1. This is a typical configuration seen throughout Recent scorpions. In *L. josehermana*, we see several *ID*s mixed with smaller internal accessory denticles (*IAD*), positioned in a more irregular fashion (Fig. 4). The presence of *IAD* is unusual in scorpions in general; they are only found consistently in the chactoid family Euscorpidae, considered a primary diagnostic character of that family (see Soleglad & Sissom, 2001: 33–40). Interestingly, Prendini (2003a: 163) does not mention the composition of internal denticles (*ID*) in *Brandbergia*, but instead states: “... Dentate margins of the chela fingers linear (without lobe or notch), with a single row of denticles. ...”. We must presume that the internal denticles are absent in

*Brandbergia*, otherwise they would have been described. However, we find it curious that the absence of the *ID*s is not mentioned by Prendini, since it would be unprecedented in Recent scorpions, and, in addition, the number of *ID*s was used as an important diagnostic character for *Lisposoma* species by Lamoral (1979). Fortunately, we can solve this conundrum by closely inspecting the excellent photographs provided by Prendini (2003a: Fig. 6, A–D). In his Figs. 6C–D, we can see internal denticles do indeed exist: in Fig. 6C, which shows the ventral aspect of the left chela, we can see the distal one-fourth of the fixed finger denticle edge which exhibits the large distal denticle and four internal denticles; in Fig. 6D, which illustrates the internal view of the chela, showing the entire denticle edge, we can see an irregularly spaced row of internal denticles, numbering approximately 18 on the fixed finger. This configuration is identical to that exhibited in *L. josehermana* (see our Fig. 4). We can distinctly see the median denticle (*MD*) row of denticles in Prendini's (2003a) Fig. 6A, which number over 50; so the denticles visible in his Fig. 6D are definitely internal denticles (*ID*) rather than *MD*.

The third diagnostic character, the presence or absence of metasomal dorsal and dorsolateral carinae, is probably the least important of the three characters. *Lisposoma elegans* is generally a very smooth species, and its carination is minimal; *L. josehermana* is more granulate, thus showing more defined carinae. *Brandbergia haringtoni*, the most granulate of these three species, shows more pronounced overall carination on pedipalp as well as metasoma. We consider this distinction in carinal development to be a species-level character and not necessarily important in the delineation of genera.

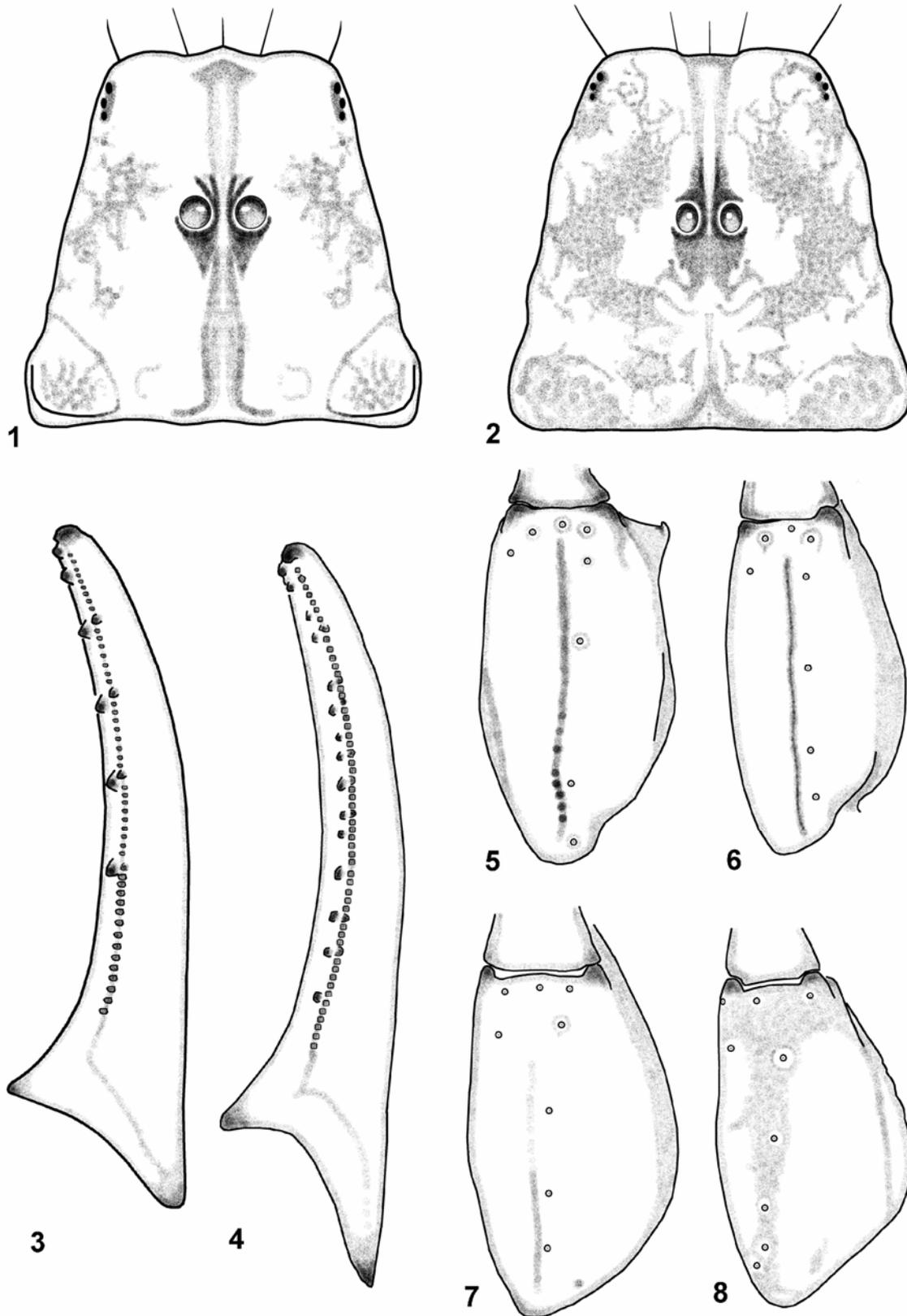
Therefore, if one used only Lamoral's (1979) original diagnostic characters, *Brandbergia* would key out to the species *Lisposoma josehermana*, since they match in *all three characters* (see Table I). Interestingly, Prendini (2003a) ignores *all three* of these characters in his cladistic analysis, using instead a subset of characters originally defined in his general systematic revision of superfamily Scorpionoidea (Prendini, 2000). Even more curious is the fact that Prendini (2003b), in his revision of *Lisposoma*, acknowledges all three of Lamoral's characters, but does not reevaluate his cladistic analysis, leaving it as originally presented in his *Brandbergia* paper (Prendini, 2003a). Although Lamoral's third character, the definition of metasomal carinal development, is a somewhat low species-level structure and its absence from Prendini's consideration is probably not crucial, the other two characters are important, especially the presence or absence of internal accessory denticles (*IAD*). We suggest here that, without inclusion of these two characters, Prendini's (2003a) analysis is inadequate for a proper evaluation of the generic delineation of these three closely related species. This suggestion becomes more apparent after one evaluates four diagnostic characters offered by Prendini (2003a, 2003b) to separate *Brandbergia* from the two species of *Lisposoma*.

### *Prendini's diagnostic characters*

In Prendini's (2000, 2003a) general cladistic modeling of the pedipalp chelal carina, he states that the digital (*DI*) and ventroexternal (*VI*) carinae are obsolete in all bothriurids except for the species *Brandbergia haringtoni*. Both carinae in *B. haringtoni* are indeed present and granular, especially *VI* (see Figs. 6A, 6C in Prendini, 2003a). The question arises whether these carinae are really absent in the other bothriurids. The answer to this question is no—especially the ventroexternal carina (*VI*), which is well developed in many species of the Bothriuridae.

Prendini (2003a) modeled the development of these two chelal carinae with his characters 19 (*DI* carina) and 20 (*VI* carina). These are the same characters defined in his general scorpionoid revision (Prendini, 2000), as characters 23 and 26, respectively. What is particularly interesting and somewhat puzzling is Prendini's (2003a) character 21 (character 27 in his scorpionoid revision): here he describes the orientation and distal termination of the *VI* carina, which vary from a straight carina connecting directly to the external condyle of the movable finger (as attributed to the primitive taxa, families Buthidae and Chaerilidae), to a carina that is oblique to the longitudinal axis of the palm terminating towards the internal condyle (attributed to *all* bothriurids). For this character, Prendini (2003a) attributes all bothriurids with the last state, an oblique oriented *VI* carina that terminates towards the internal condyle. Of course, what makes this character curious is the fact that in character 20 Prendini (2003a) stated that this carina is *absent* in the bothriurids (except *Brandbergia*). The immediate question arises—how can one characterize the position of a carina that is absent? As it turns out, this carina is visible and quite developed in several bothriurids, such as in genus *Brachistosternus* (Figs. 5–6), some *Bothriurus* species (Fig. 7), and *Timogenes* and *Vachonia* (see Vachon, 1974: Figs. 206–207). In *Brachistosternus*, *Timogenes* and *Vachonia*, *VI* is quite distinct and is visible the entire length of the palm (in our Fig. 5 one can see that the basal one-third of this carina is even granulate). In the *Bothriurus burmeisteri* (Fig. 7), the carina is visible and well developed on the basal one-third of the palm. In other species *VI* is more vestigial, *Cercophonius* for example, only outlined with pigmentation. We propose here that remnants of *VI* are even visible in species *Lisposoma josehermana* (Fig. 8). When a trichobothrium is located on a carina its follicle is usually situated inside a conspicuous *dimple* in the cuticle, as commonly seen, for example, in the chactoid genus *Euscorpium* where chelal trichobothrium *V*<sub>4</sub> or other ventral trichobothria are sometimes situated directly on the *VI* carina (see Gantenbein *et al.*, 2002: Figs. 3, 5, 7–8). In both species of *Lisposoma* trichobothrium *V*<sub>2</sub> is located inside a dimple, implying the vestigial existence of the *VI* carina (see our Fig. 8). In addition, all chelal carinae on *L. josehermana* are indicated by discrete contrasting pigmentation.

The digital carina (*DI*) is less developed in all bothriurids (including *Brandbergia haringtoni*) than it is



**Figs. 1–2:** Carapace of *Lisposoma* species showing the differences in the anterior edge. **1.** *Lisposoma elegans*, female; note the conspicuous median projection on anterior edge. **2.** *Lisposoma josehermana*, female. **Figs. 3–4:** Movable finger of pedipalp chela. **3.** *Lisposoma elegans*, female. **4.** *Lisposoma josehermana*, female. Note the presence of several internal accessory denticles (IAD) in *L. josehermana*. **Figs. 5–8:** Ventral view of pedipalp chela showing the development of the ventroexternal (VI) carina in bothriurid genera. **5.** *Brachistosternus ehrenbergii*, male. **6.** *Brachistosternus* sp., female. **7.** *Bothriurus burmeisteri*, female. **8.** *Lisposoma josehermana*, female. Trichobothria  $V_1$ – $V_3$ ,  $Et_1$ ,  $Et_2$ , and  $Est$  shown in *Brachistosternus* and *Bothriurus*;  $V_1$ – $V_4$ ,  $Et_1$ ,  $Et_2$ ,  $Est$ ,  $Eb_1$ , and  $Eb_2$  shown in *Lisposoma*.

in most other scorpionoids. However, the *D1* carina is not completely absent in the bothriurids as stated by Prendini (2003a). In the species *Centromachetes pocockii* (Fig. 9) we can see a definite digital carina, especially on the basal two-thirds of the palm. This carina is in particular visible when the palm is viewed distally from the fingers, thus showing the diagrammatic outline of the cross section of the palm. In *Cercophonius squama* (Fig. 10) and *Lisposoma josehermana*, all carinae of the chela are outlined in a contrasting pigment, again implying the existence of all the carinae

Two new diagnostic characters were established by Prendini (2003b) in his revision of the genus *Lisposoma*: (1) the distal denticles of the cheliceral movable finger are subequal in *Brandbergia haringtoni*, while in two *Lisposoma* species they are not subequal; (2) metasomal carinae, ventrolateral (I–IV) and ventromedian (V), are well developed in *B. haringtoni*, while in two *Lisposoma* species they are obsolete. In the first character, Prendini is referring to the subequal opposable distal denticles as exhibited in the scorpionoid family Liochelidae—clearly, these denticles in *B. haringtoni* do not match this configuration (Fig. 12), since the dorsal distal tine is much shorter than its ventral counterpart. Compare Figure 12 with that of the liochelids *Hadogenes troglodytes* (Fig. 13) and *Opisthacanthus lepturus* (Fig. 14) which have the condition of subequal opposable distal denticles. The configuration of these two denticles found in *Brandbergia haringtoni* is quite close to that exhibited in *L. josehermana* (Fig. 11), though in the latter, as reported by Prendini (2003b), the denticles are less equal in length. The ventrolateral carinae of metasomal segments of *L. josehermana* as well as the ventromedian carina of segment V are well developed (see our Fig. 15 as well as Lamoral, 1979: Figs. 334). In *L. elegans*, they are vestigial due to this species overall smoothness. Consistent with this theme, we see a gradual increase in granulation, and therefore in carinae development as well, from *L. elegans* to *L. josehermana* to *B. haringtoni*, which clearly indicates a species-level character. This trend is present for both the pedipalp and metasoma. Therefore, we dismiss these two characters as diagnostic between the two genera (see section on cladistics).

#### Other characters

**Sternum.** In our continuing interest in the fundamental structure of the scorpion sternum (see Soleglad & Fet, 2003a), we have taken the opportunity to include illustrations of the sterna of *B. haringtoni* and both *Lisposoma* species (Figs. 17–19), one rendered from Prendini's (2003a: Fig. 5C) photograph. As established by Soleglad & Fet (2003a), the sternum in the bothriurids (Type 2) exhibits extreme vertical compression, causing a significant shortening of the sternum as well as conspicuous separation of its two lateral lobes. In Figures 17–19 we see all three sterna are definitely wider than long, but do not exhibit the extreme shortening of the sternum as seen in the other bothriurids. Interestingly, from these three figures we see that the lateral lobes exhibit subtle separation in *B. haringtoni* and *L. jose-*

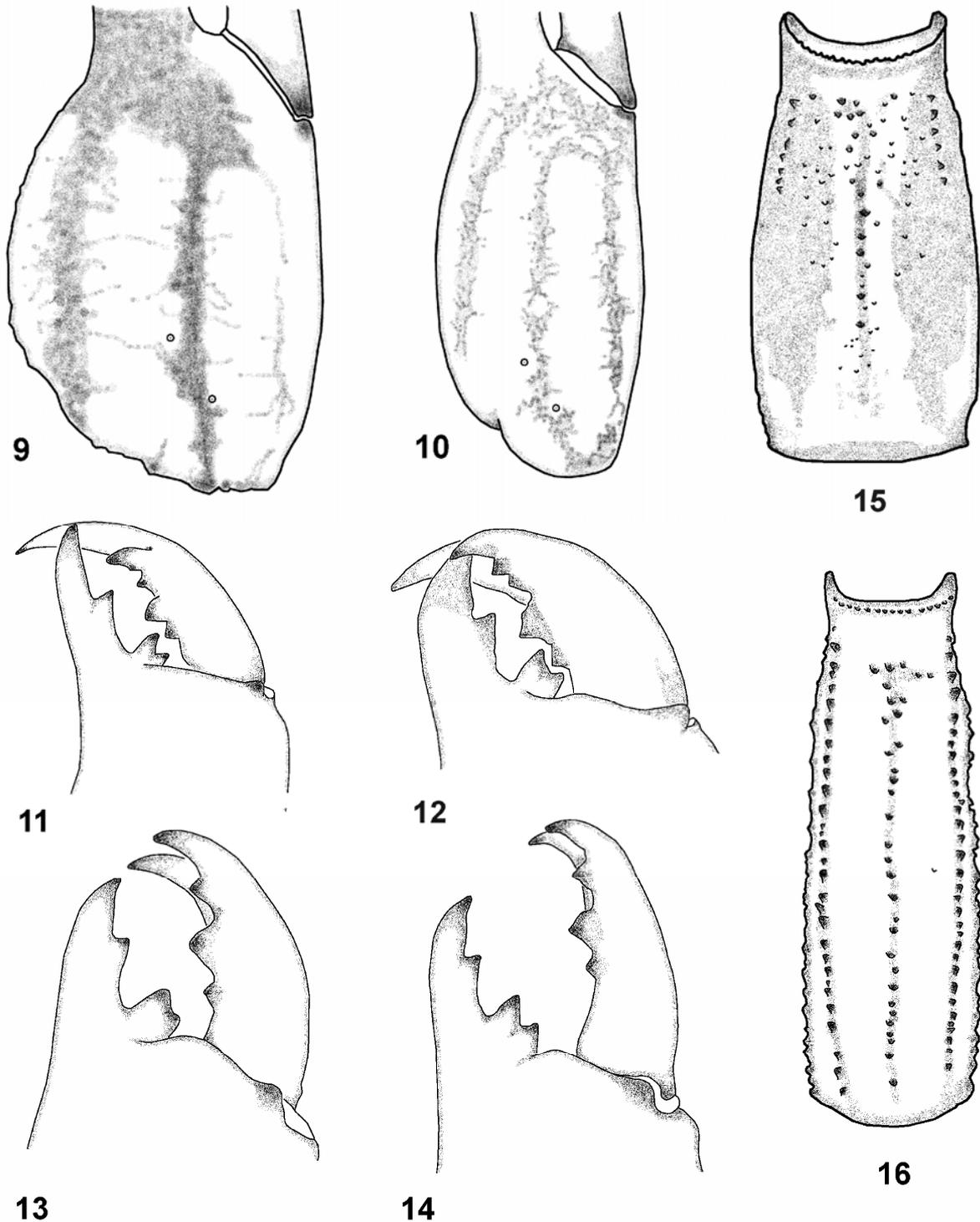
*hermana*, when contrasted with *L. elegans*, where the two lobes are touching. We consider the basic sternum exhibited in these three species to represent a primitive form of the bothriurid sternum, showing only traces of vertical compression.

**Trichobothria.** We compared the trichobothrial patterns of *B. haringtoni* with the two species of *Lisposoma*. These patterns, orthobothriotaxic, are identical as far as individual trichobothrium location, only subtle positional differences are detected in the trichobothria of chela fixed finger in *B. haringtoni* due to its overall slenderness as compared to the somewhat stocky pedipalps found in the other two species; this difference must be attributed to attenuation of the fingers in *B. haringtoni*.

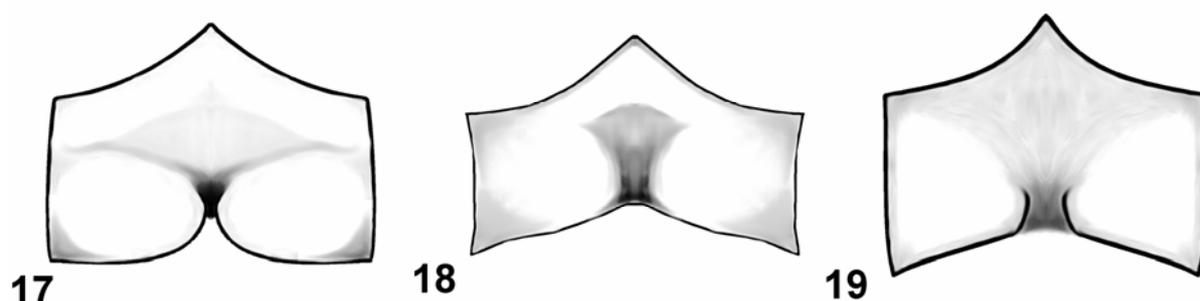
Common to all three species is the external position of patella  $v_3$  trichobothrium, unprecedented in the bothriurids; and the unusual location of the chelal  $Et_2$  trichobothrium on the external-ventral palm surface juncture. Although Prendini (2000, 2003a) states that this trichobothrium is located on the ventral surface of the palm, inside of the external condyle of the movable finger (a synapomorphy for family Bothriuridae), it is clear that it is in fact positioned on the external-ventral surface juncture, adjacent to the external condyle (compare Fig. 8 with Figs. 5–7). We propose that the position of  $Et_2$  found in *Lisposoma* and *Brandbergia* is a primitive stage compared to the relocation of  $Et_2$  to the ventral surface, commonly found in the other bothriurids.

**Chela ventroexternal (V1) carina.** Prendini (2003a) makes the important observation that the *V1* carina of the chela is aligned obliquely to the horizontal plane of the chelal palm in the bothriurids, considered a synapomorphy for this family. We find this distinction of alignment interesting, and important, because we believe it may, in part, explain why trichobothrium  $Et_2$  is located on the ventral surface of the palm, considered a synapomorphy for Bothriuridae as well. We do take exception to this depiction across the family, however: this description of oblique alignment should be limited to *Lisposoma* and *Brandbergia* only, and possibly also to *Thestylus*. It is clear that the *V1* carina is parallel to the chelal palm axis in the other bothriurids, as seen in Figs. 5–7. As with trichobothrium  $Et_2$  position, we consider the alignment of *V1* carina as exhibited in *Brandbergia* and the two *Lisposoma* species as a primitive stage of this characteristic of the family Bothriuridae.

**Pedipalp and metasoma carinal granulation.** We compared the development of the metasomal and pedipalpal carinae of *Brandbergia haringtoni* and two species of *Lisposoma*. Without any exceptions, we noted that *L. elegans* was the smoothest of all species, the metasomal carinae were in general essentially obsolete. The pedipalpal carinae were either vestigial, or smooth in nature. *L. josehermana* and *B. haringtoni* exhibit more carinal development and granulation, *B. haringtoni* being much more granulated and carinated than *L. josehermana*. Prendini (2003a), in his depiction of these carinae in *L. elegans* and *L. josehermana*, as contrasted to *B. haringtoni*, has either ignored the development of carinae in *L.*



**Figs. 9–10:** External view of pedipalp chela showing the development of the digital (*DI*) carina in bothriurid genera. **9.** *Centromachetes pocockii*, male. **10.** *Cercophonius squama*. Only trichobothria *Db* and *Dt*, which straddle the *DI* carina, are shown. **Figs. 11–14:** Dorsal view of chelicerae contrasting relative development of the dorsal distal (*dd*) and ventral distal (*vd*) denticles of the movable finger for *Lisposoma*, and *Brandbergia*, and selected liochelids. **11.** *Lisposoma josehermana*, female. **12.** *Brandbergia haringtoni*, female (after Prendini, 2003a: Fig. 5A, in part). **13.** *Hadogenes troglodytes*, female. **14.** *Opisthacanthus lepturus*, female. **Figs. 15–16:** Metasomal segment V, ventral view, showing development of the ventromedian carina. Note the irregular composition of carina on distal aspect. **15.** *Lisposoma josehermana*. **16.** *Brandbergia haringtoni* (after Prendini, 2003a: Fig. 8G, in part).



**Figs. 17–19:** Sternum. **17.** *Lisposoma elegans*, subadult female. **18.** *Lisposoma josehermana*, subadult female. **19.** *Brandbergia haringtoni*, adult female holotype (after Prendini, 2003a: Fig. 5C, in part).

*josehermana*, or misrepresented it in part. Of particular importance here is the ventral median (*VM*) carina of metasomal segment V, which is modeled in Prendini's cladistic analysis. For this carina, Prendini (2003a) states that it is developed and bifurcated distally in *B. haringtoni*, whereas in the two *Lisposoma* species it is obsolete. For *L. elegans*, Prendini is correct, but for *L. josehermana* he is incorrect, since it exhibits a serrate carina (Fig. 15). In addition, the distal termination of this carina is irregular, similar to that found in *B. haringtoni* (compare Figs. 15 and 16).

#### Cladistic considerations

As discussed above, we believe Prendini's (2003a) exclusion of two of the original diagnostic characters established by Lamoral (1979) in his cladistic analysis places his result of *Brandbergia*'s legitimacy in question. In addition, we take strong exception to his hypothesis that the chelal digital (*DI*) and ventroexternal (*VI*) carinae are obsolete in all bothriurids other than *Brandbergia* (Prendini, 2003a). Consequently, we conducted our own cladistic analysis using Prendini's (2003a: Appendix 1) original matrix and assumptions (i.e., nine ordered ("additive") characters) as a basis, and added the two Lamoral's (1979) characters, as well as altered five other characters. We first discuss the new and changed characters, and then present the results of this analysis.

**Character changes.** Based on the discussion above involving Lamoral's (1979) original diagnosis of *Lisposoma*, Prendini's (2003a, 2003b) diagnoses of *Brandbergia* and *Lisposoma*, and the analysis conducted in this study, we have found it necessary to create or change seven characters in Prendini's (2003a: Appendix 1) data matrix as follows (see Table II).

#### Character 8 – Sternum shape (Ordered)

**0:** Type 1 (*Centruroides* and *Chaerilus*)

**1:** Type 2, no vertical compression (Scorpionidae, Liochelidae, Urodacidae)

**2:** Type 2, vertical compression minor, sternum considerably shortened (*Brandbergia*, *Lisposoma*)

**3:** Type 2, vertical compression conspicuous, sternum considerably shortened, lateral lobes noticeably separated (other bothriurids)

Soleglad and Fet (2003a) defined two fundamental sternum types, which replaces the previous characterizations based on shape, "subpentagonal", "subtriangular", and "transverse" (these conventions were used by Prendini, 2003a). Type 1 sterna are quite primitive being found in the Paleozoic fossil family Palaeopisthacanthidae, as well as in the three primitive Recent scorpion parvorders Pseudochactida, Buthida, and Chaerilida (Soleglad & Fet, 2003b). Type 2 sterna are found in parvorder Iurida, where Bothriuridae resides. The two "forms" of "subtriangular" and "transverse" were explained by Soleglad & Fet (2003a) with notions of horizontal and vertical compression, respectively. As discussed elsewhere in this paper, in *Lisposoma* and *Brandbergia* (Figs. 17–19) we see a considerably shortened sternum, evidently the beginnings of vertical compression, with subtle separation between the convex lateral lobes seen in *B. haringtoni* and *L. josehermana*. We consider this a primitive form of the complete compressed sternum as exhibited in the other bothriurid genera (see Soleglad and Fet, 2003a: Fig. 5).

Although this character is changed considerably from Prendini's (2003a) original modeling, both versions exhibited the same support, CI/RI = 1.

#### Character 10 – Cheliceral movable finger, dorsal distal (*dd*) and ventral distal (*vd*) denticles

**0:** *dd* and *vd* subequal, opposable (*Centruroides*, *Chaerilus*, *Hemiscorpius*, *Opisthacanthus*)

**1:** *dd* and *vd* not subequal, *dd* much shorter than *vd* (*Nebo*, *Heteroscorpion* (incorrect coding), *Scorpio*, *Urodacus*, other bothriurids)

**2:** *dd* and *vd* not subequal, *dd* shorter than *vd* (*Brandbergia*)

Character state 2 has been added in order to accommodate Prendini's (2003b) additional diagnostic character separating his *Brandbergia* from the *Lisposoma* species (Figs. 11–14). As discussed above, the original intent of this character was to contrast the drastic differences between these two distal tines for families Scorpionidae + *Urodacus* vs. Liochelidae. The distal denticles in the genus *Heteroscorpion* are also opposable as in the liochelids, but we leave this error in the matrix for this study. Issues involving the taxonomic position of *Heteroscorpion* in the Scorpionoidea were discussed in detail in Soleglad & Fet (2003b: 115–117)



and are being addressed further by Soleglad *et al.* (in press).

The addition of this new state had no effect on the resulting topology since it is autapomorphic for *B. haringtoni*. The character support of this character was slightly improved from that reported by Prendini (2003a: Table 2), CI/RI = 0.667/0.667 vs. 0.500/0.667.

**Characters 19–20** – Development of the chelal digital (*DI*) and ventroexternal (*VI*) carinae. (Character states as in Prendini's (2003a) original matrix)

As discussed in detail above, we strongly disagree with Prendini's (2003a) hypothesis that these two carinae are absent in all bothriurids except *Brandbergia haringtoni*. In particular, the *VI* carina is well developed in several bothriurid genera (e.g., Figs. 5–7). We experimented with these two characters alone by changing one and/or both to stating that all bothriurids have these carinae. Of course, by making this change the character(s) became constant and therefore had no effect on the result except removing the ladderization of *B. haringtoni* from Prendini's (2003a: Fig. 4) original result (i.e., the original impetus for creating *Brandbergia* in the first place). Incorporating these changes (one change, two changes, or no change) with the other character changes proposed herein, we obtained no difference in the final topology. Therefore, although we strongly disagree with these two characters as presently modeled, we have left them as originally proposed by Prendini (2000, 2003a), in order to minimize the number of changes to his data matrix.

With the addition of the new characters and changes to existing characters, the support of these two characters is reduced from Prendini's (2003a: Table 2) original result, CI/RI = 0.500/0.875 vs. 1/1.

**Character 21** – Chelal ventroexternal (*VI*) carina alignment (*Ordered*)

**0:** parallel to longitudinal axis of palm, terminates at external condyle of movable finger (*Centruroides*, *Chaerilus*)

**1:** parallel to longitudinal axis of palm, terminates internal to external condyle (Scorpionidae, Liochelidae, Urodacidae)

**2:** oblique to longitudinal axis of palm, terminates internal to external condyle, closer to internal condyle (*Brandbergia*, *Lisposoma*, *Thestylus*)

**3:** parallel to longitudinal axis of palm, but torqued internally, terminates between the external and internal condyles (other bothriurids)

Prendini's (2000, 2003a) observation about the alignment of the *VI* carina in the bothriurids is important, because, in our opinion, it explains, in part, the ventral disposition of the chelal trichobothrium *Et*<sub>2</sub> on the ventral aspect of the palm (see character 46 below). As this carina's position relocated more onto the ventral surface of the palm, trichobothrium *Et*<sub>2</sub> moved as well. We disagree, however, that the oblique alignment is found throughout the Bothriuridae, since this carina is

clearly parallel to the palm's longitudinal axis in *Brachistosternus* and *Bothriurus* (Figs. 5–7) as well in other bothriurids (see Vachon, 1974: Figs. 203, 206–207) that exhibit five or more ventral trichobothria on the palm. For these cases, trichobothrium *Et*<sub>2</sub> is definitely located well on the ventral surface. We agree that the oblique alignment is indeed present in *Lisposoma* and *Brandbergia*, as well as, to lesser degree, in the presumably primitive bothriurid genus *Thestylus* (see Vachon, 1974: Fig. 205). In the case of *Lisposoma* and *Brandbergia*, we see that trichobothrium *Et*<sub>2</sub> (Fig. 8) is on the external-ventral surface boundary, external to the external condyle, not ventrally located as in the other bothriurids. We consider this a primitive stage in the position of the ventroexternal (*VI*) carina for the bothriurids, endorsed as well by the position of *Et*<sub>2</sub>.

The support for this character did not change from Prendini's (2003a: Table 1) original result, CI/RI = 1/1.

**Character 46** – Chela, position of trichobothrium *Et*<sub>2</sub> (*Ordered*)

**0:** external surface of palm (*Centruroides*, *Chaerilus*, Scorpionidae, Liochelidae, Urodacidae)

**1:** external-ventral surface juncture of palm (*Brandbergia*, *Lisposoma*)

**2:** ventral surface of palm (other bothriurids)

As discussed above for character 21, we consider the condition found in genera *Lisposoma* and *Brandbergia* to represent a primitive stage of the movement of the ventroexternal (*VI*) carina to the ventral surface of the chelal palm in the bothriurids. And, also as discussed above, we believe that the position of trichobothrium *Et*<sub>2</sub> is, in part, dependent on the relocation of this carina. Consequently we established another state to represent this intermediate condition for *Lisposoma* and *Brandbergia* which is clearly a more accurate description of *Et*<sub>2</sub> position (see our Fig. 8 for *L. josehermana*; Fig. 320–321 in Lamoral (1979), for *L. elegans*; and Fig. 6A–C in Prendini (2003a) for *B. haringtoni*). This character was ordered to reflect this hypothesized character evolution and also to maintain consistency with character 21, which was originally ordered by Prendini (2000, 2003a).

The support for this character did not change from Prendini's (2003a: Table 1) original result, CI/RI = 1/1.

**Character 81** – Metasomal segment V, ventromedian (*VM*) carina distal portion

**0:** straight (see data matrix in Table II)

**1:** bifurcating (*Brandbergia haringtoni*, *Lisposoma josehermana*, plus others)

**2:** breaking up into numerous granules (see data matrix in table II)

**(-):** (*Lisposoma elegans*, plus others)

Prendini (2003a) depicted the ventromedian (*VM*) carina of metasomal segment V as obsolete in *Lisposoma elegans* and *L. josehermana*, and therefore coded an inapplicable state for these two species. We disagree with this assignment for *L. josehermana*, which has a definite serrated *VM* carina (compare Figs. 15 and 16).

Although it is not clear whether *B. haringtoni* has a truly bifurcated *VM* carina as proposed by Prendini (2003a), such as, for example, exhibited in the genera *Uroctonus* and *Anuroctonus* (family Chactidae; see Soleglad & Fet, 2004: Figs. 14–15, published in this volume), it certainly is not any different distally from that found in *L. josehermana*, and consequently we make this state change in the data matrix.

The support for this character differed slightly from that obtained by Prendini (2003a: Table 1), CI/RI = 0.429/0.667 vs. 0.500/0.600.

**Character 96 (NEW)** – Chelal internal denticles (*ID*) and internal accessory denticles (*IAD*)

**0:** ID present, IAD absent (*Lisposoma elegans*)

**1:** ID and IAD present (*Brandbergia haringtoni*, *Lisposoma josehermana*)

**(-):** inapplicable (others)

This new character is based on the original diagnoses of *Lisposoma* species provided by Lamoral (1979) as well as on the detailed analysis of specimens studied in this paper and the chela photographs of *Brandbergia haringtoni* contained in Prendini (2003a: Figs. 6A–D). As stated elsewhere in this paper, we believe Prendini (2003a) was remiss in ignoring Lamoral's original diagnostic characters (see our Table I), which provided the proper perspective and level for the taxonomic analysis of these three closely related species. Prendini, instead, relied on a subset of his original characters established in his general cladistic analysis of the superfamily Scorpionoidea (Prendini, 2000). The presence of internal accessory denticles (*IAD*), in our opinion, is an important character and therefore cannot be ignored. We assigned inapplicable states to all other taxa in the analysis since the presence of *IAD* is clearly a derived state (i.e., it is rare in Recent scorpions, only found consistently in the chactoid family Euscorpiidae (Soleglad & Sissom, 2001)). Of course, *IAD* are also found in the outgroup taxon *Centruroides gracilis* (a synapomorphy for this bothrid genus), but clearly it is not the same derivation, in our opinion, as seen in *Brandbergia haringtoni* and *Lisposoma josehermana*. Therefore to assign a separate state to this taxon would have no effect on the results of this study (i.e., it would be autapomorphic).

The support for this new character is CI/RI = 1/1.

**Character 97 (NEW)** – Median protuberance on carapace anterior edge

**0:** absent (*Brandbergia haringtoni*, *Lisposoma josehermana*)

**1:** present (*Lisposoma elegans*)

**(-):** inapplicable (others)

For the same reasons stated for character 96 above, we believe this character should not be ignored in the cladistic analysis of *Lisposoma* and *Brandbergia*. Again, this character was emphasized by Lamoral (1979) and ignored by Prendini (2003a). Interestingly, Prendini (2003b) illustrates and discusses the protuberance found on the carapace of *L. elegans* but excludes it from his key (2003b: 262). We illustrate the carapace of *L. elegans*, which shows the median protuberance, and of *L. josehermana*, which is lacking this peculiar structure, in

Figs. 1–2. As for the same reasons discussed in character 96, we map the other taxa with inapplicable states.

The support for this new character is CI/RI = 1/1.

**Results.** As established elsewhere in this paper, *Brandbergia haringtoni* and *Lisposoma josehermana* agree in two new characters, whereas *L. elegans* stands alone in both cases. Although we disagree with Prendini's (2003a) hypothesis that the *D1* and *V1* chelal carinae are absent in all bothriurids except *Brandbergia*, we left these characters unaltered for reasons discussed above. The result of this analysis differs dramatically from that shown in Prendini's (2003a: Fig. 4) cladogram: (1) the ladderization of *Brandbergia haringtoni* from the other bothriurids is removed; (2) the two species of *Lisposoma* and *Brandbergia haringtoni* form a monophyletic group; and (3) *Brandbergia haringtoni* combines with *L. josehermana*, while *L. elegans* is isolated in a separate clade (see Fig. 20). If we invoke the character changes to *D1* and *V1*, we obtain the same topology but the bootstrap/jackknife support of these results increases considerably.

**Bootstrap/jackknife analysis.** We analyzed three data matrix configurations with bootstrap/jackknife analysis (three sequences of 1000 pseudoreplicates per algorithm, 6000 pseudoreplicates in all): (1) the original Prendini (2003a: Appendix 1) data matrix; (2) an altered data matrix with the two new characters and the alterations to existing characters as described above; and (3) an altered data matrix as described in (2) with changes to characters 19 (*D1* carina) and 20 (*V1*). For the original Prendini (2003a) data matrix, we obtained modest support for two clades of interest: (*B. haringtoni* + (*L. elegans* + *L. josehermana*) + (other bothriurid genera)) = 64.67/59% (read bootstrap/jackknife), and (*L. elegans* + *L. josehermana*) = 64/52.67%. For the modified data matrix (2), we obtained 72.33/68.33% for the monophyletic clade (*L. elegans* + (*B. haringtoni* + *L. josehermana*)) and 58.67/51.67% for clade (*B. haringtoni* + *L. josehermana*). In the second modified data matrix which included changes to characters 19 and 20 as well, the two clades of (2) above were significantly supported by 92.33/87% and 77.67/67%, respectively.

**Unknown characters.** Another interesting aspect of Prendini's (2003a) analysis is the large number of "unknown" characters assigned to *Brandbergia* (due, in large part, to the absence of a male specimen for the coding of the hemispermaphore structure, sexual dimorphic differences in the pedipalp chelae, metasoma, and telson, and other related data). In all these characters (21 in all, over 20% of all characters) we see that species *Lisposoma elegans* and *L. josehermana* agree in all cases, whereas *Brandbergia haringtoni* is assigned "unknown". This, of course, causes an unnatural coupling of the former two species as it relates to *B. haringtoni* (i.e., we believe *B. haringtoni* in all likelihood would agree in most of these characters as well). As an exercise, we set all 21 unknown characters for *B. haringtoni* to the same value assigned to the other two *Lisposoma* species, but otherwise left Prendini's (2003a: Appendix 1) data matrix intact. The ladderized topology reported

in Prendini's (2003a: Fig. 4) cladogram was not supported by any of the four consensus algorithms available in PAUP (i.e., strict, semistrict, majority rule, and Adams). Instead, three species formed a polytomy with a branch leading to all other bothriurid genera, or a reduced polytomy where *L. elegans* and *L. josehermana* were combined. In addition, bootstrap/jackknife analysis of this modified data matrix resulted in support for a monophyletic clade combining all three *Lisposoma* species as a polytomy, weakly supported with 53.5/53%. Clearly, the unknown character assignments to *B. haringtoni* by themselves could have caused the ladderized topology reported by Prendini (2003a), which was the impetus for the creation of genus *Brandbergia*. We are not faulting Prendini (2003a) for coding *B. haringtoni* with the unknown state values, as he had no other choice; however, it is also clear this coding affected, in part, his results and therefore he should have considered it as well before creating a new genus. Of course, if all alterations are taken into effect, i.e., new characters, characters changes, including characters 19 and 20, and the removal of unknown codes for *B. haringtoni*, we obtain the highest bootstrap/jackknife support, 92.67/87% and 80.33/69.33%, for the two clades discussed above in analysis (2).

### Conclusions

**Synonymy of *Brandbergia*.** We analyzed Prendini's (2003a) result from several directions, from a modest change of the unknown character assignments in *Brandbergia haringtoni*, to a more substantial change, incorporating new characters that supported Lamoral's (1979) original diagnoses of *Lisposoma* species, and changes to characters that were deemed incorrect by us. Even the most modest change to Prendini's (2003a: Appendix 1) data matrix, the removal of the unknown character states, nullified his ladderized result. More importantly, when considering the two characters that Prendini (2003a) used to cladistically contrast *Brandbergia* with all other bothriurids (including *Lisposoma*), the development of the *DI* and *VI* chelal carinae, we see that the proposition that these carinae are absent in non-*Brandbergia* bothriurids is patently false. Although the interpretation of relative carinal development can be subjective, it is clear that there was no significant evolutionary event where the *DI* and *VI* carinae disappeared in the other bothriurid genera—instead, they are present to one degree or another, and in some cases quite distinct, as, for example, *VI* is in genus *Brachistoternus*.

Therefore, based on all this evidence, we refute *Brandbergia* as a valid genus and place it in synonymy with *Lisposoma*: *Brandbergia* Prendini, 2003 = *Lisposoma* Lawrence, 1928, **syn. n.**; *Brandbergia haringtoni* Prendini, 2003 = *Lisposoma haringtoni* (Prendini, 2003), **comb. n.**

***Lisposoma* taxonomy.** In Fig. 20, we see that species *Lisposoma josehermana* and *L. haringtoni* form a monophyletic clade with their sister species being *L. elegans*. We strongly suggest here, based on the sternum as well as the characters involving the carapace anterior

edge and the presence/absence of internal accessory denticles (*IAD*), that the grouping of *L. haringtoni* and *L. josehermana* is a legitimate relationship. We propose here that the differences in chelal carinae *DI* and *VI* development are a byproduct of the differences in overall granulation seen in the three species of *Lisposoma*, *L. haringtoni* the most granulated and *L. elegans* the least granulated. Based on the lack of compression in the sternum and the lack of *IAD*, we suggest here that *L. elegans* is the least derived and therefore the most primitive species among the bothriurids.

### Bothriuridae: Subfamilies

Based on the analysis presented above, we see that the three species of *Lisposoma* not only form a monophyletic group but also are well separated from all other bothriurids. The ladderized clade comprising the remaining genera is highly supported (over 93%) with both bootstrap and jackknife tests. This strong support is exhibited in all of our analyses presented in this paper as well as in Prendini's (2003a) original result.

We concur with Stockwell's (1989) endorsement of two bothriurid subfamilies based on the character analysis he described (see our Fig. 20). In addition, based on analysis conducted for this paper, we ramify Stockwell's result further with additional refinement to his character analysis. Below, we give amended diagnoses of both valid bothriurid subfamilies.

While we support status of *Lisposominae* as a subfamily, we do not go as far as Lourenço (2000) to establish a separate family *Lisposomidae*. While family-group ranks are somewhat arbitrary, the taxonomic balance within three superfamilies of the scorpion parvorder Iurida (Iuroidea, Chactoidea, and Scorpionoidea) is best achieved by assigning family level only to primary clades. It is tempting to separate family-level taxa on biogeographic grounds, and the spectacular, textbook Gondwanaland disjunction of the endemic Namibian *Lisposoma* is surely worth attention. However, as we explained earlier (Soleglad & Fet, 2003b), the family-group ranks have to be approached with a degree of proportionality for cladistically defined family-level distinctions. For instances, while we accepted topology of Scorpionoidea by Prendini (2000), we downgraded three of his families (Diplocentridae, Hemiscorpiidae, and Heteroscorpionidae) to subfamily rank (Soleglad & Fet, 2003b). The same reasoning applies to the status of *Lisposominae*.

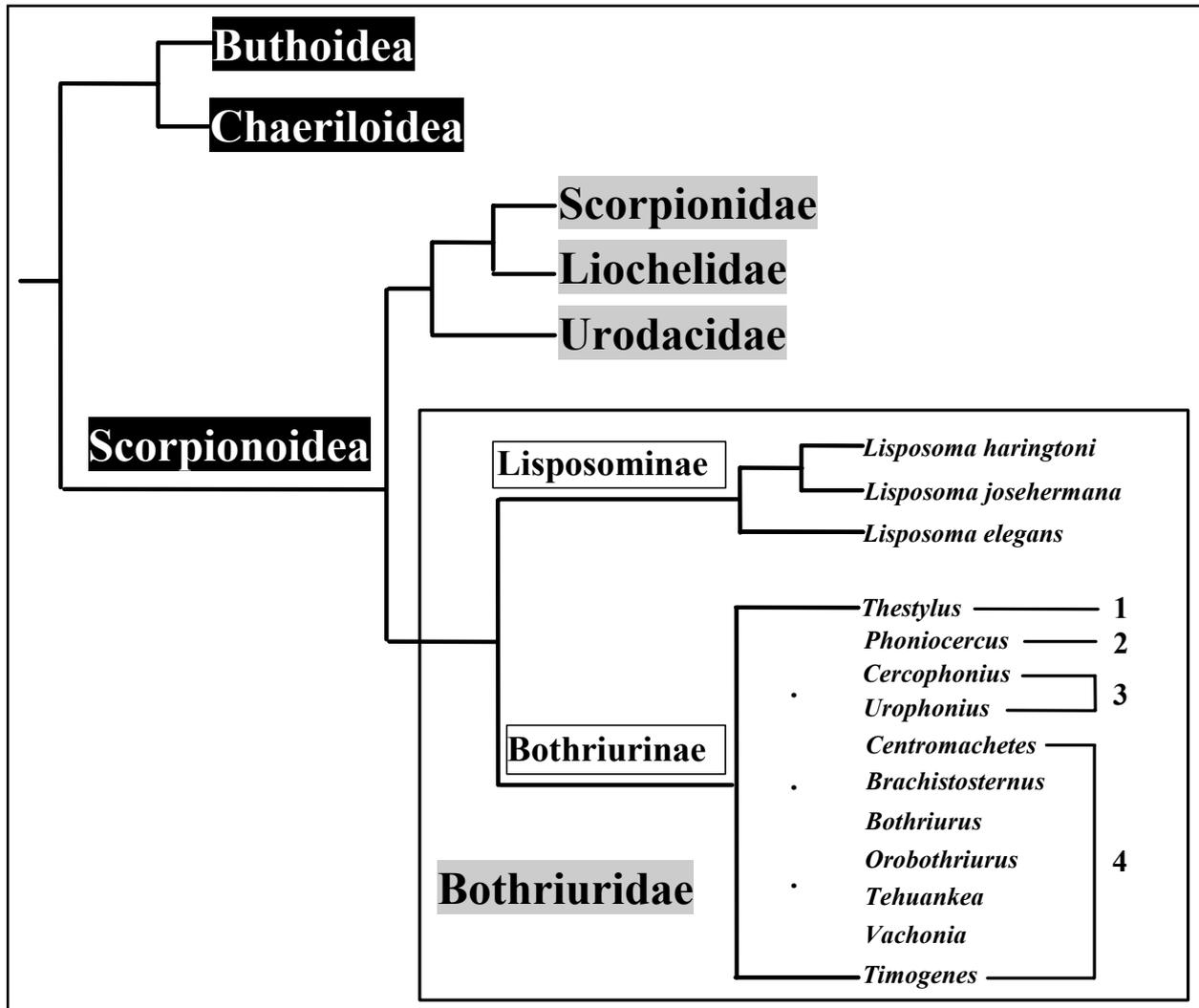
#### *Subfamily Lisposominae* Lawrence, 1928

**TYPE GENUS.** *Lisposoma* Lawrence, 1928.

**SYNONYMS.** *Lisposomidae* (as family): Lourenço, 2000.

**COMPOSITION.** The subfamily is monotypic, with a single genus *Lisposoma* from Namibia (three species).

**DIAGNOSIS. *Synapomorphies.*** Pedipalp patella trichobothrium  $v_3$  located on external surface of segment; lamellar hook of hemispermatophore located distally on lamina (not verified in *L. haringtoni*). **Important *Synplesiomorphies.*** Sternum, type 2, exhibits rudimentary



**Fig. 20:** Generalized cladogram based on modified dataset of Prendini (2003a: Appendix 1) showing taxonomy of family Bothriuridae broken down into two basic subfamilies, the primitive South African subfamily Lisposominae and the South American-Australian-Indian subfamily Bothriurinae. Topology of genus *Lisposoma* also depicted, showing *Lisposoma haringtoni* binding with *L. josehermana*. Numbered grouped genera depict a ladderized topology inside subfamily Bothriurinae, group 1 on the outside and group 4 the most inner clade. Family-group names are given after Soleglad & Fet (2003b: Table 9). Selection of outgroup taxa based on Prendini (2003a); thus, Recent scorpion superfamilies Pseudochactoidea, Iuroidea, and Chactoidea (the sister superfamily of Scorpionoidea), are absent from Prendini's analysis and therefore omitted here. *White text on black background* depicts superfamilies, *black text on grey background* depicts scorpionoid families, and *black text inside rectangles* depicts bothriurid subfamilies.

ventral compression, sternum considerably shortened; dorsal edge of cheliceral movable finger with two subdistal (*sd*) denticles; chelal ventroexternal (*VI*) carina oblique to longitudinal axis of palm, terminates internal to external condyle, closer to internal condyle; chelal trichobothrium *Et*<sub>2</sub> found on external-ventral surface juncture of palm, external to external condyle of movable finger; chelal finger trichobothrium *db* located on distal aspect of palm; internal wall of sperm duct of paraxial organ with semilunar shelf.

**DISCUSSION.** Many of the symplesiomorphies stated above represent early primitive stages of well known bothriurid characteristics: the shortened sternum, exhibiting, in some cases, slight separation between the lateral lobes; the partial torquing of the chelal *VI* carina, ori-

ented obliquely on the palm; the partial relocation of chelal trichobothrium *Et*<sub>2</sub> to the ventral surface of the palm. All three of these characters (with one exception for the *VI* carina, see below) derive to their full state in Bothriurinae, the sister subfamily of Lisposominae. Clearly, all three species of genus *Lisposoma* exhibit primitive stages of these characters. The derivation from one subdistal (*sd*) denticle on the chelicerae to two *sd* is also seen in subfamily Lisposominae.

Subfamily Lisposominae shares several presumably primitive characters with the South American genus *Thestylus*: the lack of secondary sexual structures (i.e., processes on the inner aspect of the chelal palm), whereas they are commonly found in other bothriurid genera (Stockwell, 1989: 94); having only one pedal spur on legs (i.e., the retrolateral spur is absent, as it is

in the other scorpionoid families); the partially torqued *VI* carina of the chela; heavy spinoid setae on the ventral aspect of the leg tarsus (Stockwell, 1989: 116).

### **Subfamily Bothriurinae Simon, 1880**

**TYPE GENUS.** *Bothriurus* Peters, 1861.

#### **SYNONYMS.**

Brachistosterninae Maury, 1973; type genus *Brachistosternus* Pocock, 1893 (synonymized by Prendini, 2000).

Vachoniinae Maury, 1973; type genus *Vachonia* Abalos, 1954 (synonymized as Vachonianinae by Acosta & Maury, 1998; see Fet & Braunwalder (2000) for correction of the name from incorrect original spelling Vachonianinae).

**COMPOSITION.** The subfamily includes 12 genera (*Bothriurus*, *Brachistosternus*, *Brazilbothriurus*, *Centromachetes*, *Orobothriurus*, *Phoniocercus*, *Tehuanka*, *Thestylus*, *Timogenes*, *Urophonius* and *Vachonia* from South America, and *Cercophonius* from Australia and India). Details for separate genera see Lowe & Fet (2000).

**DIAGNOSIS. Synapomorphies.** Sternum, type 2, vertical compression conspicuous, sternum considerably shortened, lateral lobes noticeably separated; chelal trichobothrium *Et*<sub>2</sub> located on ventral surface of palm, internal of external condyle of movable finger; distal aspect of hemispermatophore lamina with conspicuous crest. **Important Sympleiomorphies.** Sternum, type 2, exhibits rudimentary ventral compression, sternum considerably shortened; dorsal edge of cheliceral movable finger with two subdistal (*sd*) denticles; chelal ventroexternal (*VI*) carina oblique to longitudinal axis of palm, terminates internal to external condyle, closer to internal

condyle; chelal trichobothrium *Et*<sub>2</sub> found on external-ventral surface juncture of palm, external to external condyle of movable finger; chelal finger trichobothrium *db* located on distal aspect of palm; internal wall of sperm duct of paraxial organ with semilunar shelf.

**DISCUSSION.** This subfamily is composed of four well defined clades, ladderized as follows (see Fig. 20): (1) *Thestylus*; (2) *Phoniocercus*; (3) *Cercophonius* + *Urophonius*; and (4) the remaining genera (i.e., *Bothriurus*, *Brachistosternus*, *Centromachetes*, *Orobothriurus*, *Tehuanka*, *Timogenes*, and *Vachonia*). The recently described genus *Brazilbothriurus* Lourenço & Monod, 2000 is not evaluated or included in this analysis, but we assume it belongs to clade (4); Prendini (2003a: 151) indicates that this genus might not be valid as it is “nested deep within *Bothriurus*”, but it was not yet formally synonymized. Agreeing with Stockwell (1989), we note that genus *Thestylus* is certainly the most primitive of the genera comprising Bothriurinae, sharing many plesiomorphic characters with the subfamily Lisposominae (discussed above). For the clade “((2) + ((3) + ((4))))” we see that the chelal ventroexternal (*VI*) carina is located on the ventral surface, parallel to the longitudinal axis of the palm; neobothriotaxy is exhibited on the chelal ventral surface of the palm; and the secondary sexual structures are present on the chela. For the clade “((3) + ((4)))” we see two pedal spurs of the leg are present (in clade (4) *Vachonia* is lacking the retrolateral spur).

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