MALE PALPAL BULBS AND HOMOLOGOUS FEATURES IN THERAPHOSINAE (ARANEAE, THERAPHOSIDAE)

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ABSTRACT.   A first attempt to homologize male palpal bulb structures of theraphosine spiders is made, with the aim of providing systematic characters. The morphology and distribution of palpal bulb keels of over 60 species in 27 genera of Theraphosinae is presented and discussed. Four basic groups of keels were recognized and a terminology was created to name them: prolateral inferior and prolateral superior keels, for the two more or less parallel keels found on the prolateral bulb face; apical keel, for the ventral keel located just before the apex of the embolus; subapical keel, for a keel located just before the apical keel; and, retrolateral keel, for the keel located on the retrolateral region, originating on the apical region and extending backwards. Other palpal bulb keels, apart from these four basic groups, as well as other structures, were found in some genera and/or species, constituting apomorphies for these groups.

Keywords: Theraphosidae, male palpal bulbs, morphology of genitalia, systematics, homology

Theraphosidae is a speciose group of mygalomorph spiders with about 800 described species (Coddington & Levi 1991). This group presents enormous morphological homogeneity and many taxonomic problems (Raven 1990). The classification and identification is based mainly on structures such as stridulatory organs, fovea shape, small differences in the proportions between leg articles and other body parts, size and disposition of the eyes and scopulae, color patterns (Simon 1892; Pocock 1903; Mello-Leitão 1923; Schiapelli & Gerschman de Pikelin 1979; Raven 1985; Smith 1995, Prentice 1997), spermathecae shape (Schiapelli & Gerschman de Pikelin 1962) and urticating hair type (Cooke et al. 1972; Pérez-Miles et al. 1996). Many of these characters are conservative; and new species, based either on plesiomorphies or slight morphological variations, are still being described.

Palpal bulb characters, important for the classification and identification of spiders, have been not satisfactorily explored in Theraphosidae, as well as in other mygalomorph families. There is an extensive terminology for the parts of the complex copulatory organs of the entelegyne araneomorph spiders (Comstock 1910; Coddington 1990; Sierwald 1990) that is constantly used to characterize the taxa and provide characters for phylogenetic analysis (Coddington 1990; Sierwald 1990). In the

haplogyne mygalomorphs, the male bulb shape, as well as other genitalic characters, are commonly used in species identification, but rarely in identification of higher groups (Goloboff 1995). One reason is that much of the variation in these character complexes comes in the form of slight shape differences that are difficult to homologize across a large number of species (Goloboff 1995).

However, many authors agree that the shape of the palpal bulbs in Theraphosidae is constant and useful to characterize the taxa. For example, Pocock (1903) distinguished between species of *Pamphobeteus* Pocock 1901 using male bulb characters such as embolus width and keel shape. Other authors emphasized that species with similar male bulb shapes were probably very closely related. Valerio (1980a) called attention to the resemblance of the male bulb shape of some species of *Brachypelma* Simon 1891 with *Sericopelma* Ausserer 1875. At that time, these genera were considered to belong to different subfamilies (Grammostolinae and Theraphosinae) with which Valerio did not agree. Raven (1985) synonymized Grammostolinae with Theraphosinae; and, after the theraphosine genera revision of Pérez-Miles et al. (1996), it was demonstrated that they were two related genera, confirming Valerio's initial proposition. Bücherl (1957) also perceived that the male bulb shape could be useful in taxonomy

and stressed the relation between the similarity found in the male bulb shape and relationship. However, he thought of the male bulb shape as being only of ''generic value,'' with which Schiapelli and Gerschman de Pikelin (1962) did not agree. These two authors consistently illustrated the male bulbs with high precision; and, in many cases, used their shape to separate species, as in the revision of *Acanthoscurria* Ausserer 1871 (Schiapelli & Gerschman de Pikelin 1964) and *Homoeomma* Ausserer 1871 (Gerschman de Pikelin & Schiapelli 1972).

Although the general resemblance of the palpal bulbs has been recognized as a relationship indicator, no attempt was made to homologize male bulb elements of theraphosid spiders. A first attempt is made here with species of Theraphosinae, a large New World subfamily with 36 genera and more than 300 described species that presents the male bulbs with a modified embolus, distally stout and broad or keeled (Raven 1985; Pérez-Miles et al. 1996). The aim of this paper is to homologize the theraphosine male bulb keels thus increasing the available number of characters for taxonomic work, particularly for cladistic analysis. Beside this, a terminology is proposed to name the homologous keels.

METHODS

The left male bulbs of 60 species belonging to 27 genera of Theraphosinae were analyzed and drawn with the aid of a stereomicroscope and a drawing tube. As the male bulb may rotate around its insertion in the palp, it was illustrated with the subtegulum pointing up, because the subtegulum, more constant in shape than the rest of the bulb, aids in positioning bulbs for comparison (Goloboff 1995). The classical homology criteria were used, i.e., (a) position criterion, (b) criterion of special, morphological similarity and (c) criterion of congruence with other characters (Remane 1956; Patterson 1982; Coddington 1990; Sierwald 1990). The last criterion is the most powerful way to test homology hypothesis, because it is the only test that discriminates useful comparisons from homoplasy (parallelism, convergence) and thus of value to the systematist (Patterson 1982).

Abbreviations.—*Institutions:* IBSP = Instituto Butantan, São Paulo; MCP = Museu de Ciência e Tecnologia da Pontifícia Universidade Católica, Porto Alegre; MHNM = Museo Nacional de Historia Natural, Montevideo; MNRJ = Museu Nacional do Rio de Janeiro; MZSP = Museu de Zoologia da Universidade de São Paulo, São Paulo; RCW = Richard C. West private collection, Victoria. *Morphology:* A = apical keel; AEE = anterior embolus edge; DR = denticulate row; PA = paraembolic apophysis; PAc = *Acanthoscurria juruenicola* prolateral accessory keel; PI = prolateral inferior keel; PS = prolateral superior keel; R = retrolateral keel; SGA = subapical granular area of *Acanthoscurria ferina* and *A. insubtilis*; TA = tegular apophysis of *Homoeomma*; VC = ventral crest.

Species studied.—*Acanthoscurria atrox* Vellard 1924—IBSP 4247, Sacramento, Minas Gerais, Brazil; *A. chacoana* Brèthes 1909—IBSP 4727, Santo Antonio de Leverger, Mato Grosso, Brazil; *A. ferina* Simon 1892—IBSP 4742, Porto Velho, Rondônia, Brazil; *A. geniculata* (C.L. Koch 1842)—IBSP 7022, U.H.E. Tucuruí, Tucuruí, Pará, Brazil; *A. gomesiana* Mello-Leitão 1923—IBSP 4719, Itú, São Paulo, Brazil; *A. insubtilis* Simon 1892—IBSP 4713, Santo Antonio de Leverger, Mato Grosso, Brazil; *A. juruenicola* Mello-Leitão 1923—IBSP 4396, Alta Floresta, Mato Grosso, Brazil; *A. natalensis* Chamberlin 1917—IBSP 4204B, São Raimundo Nonato, Piauí, Brazil; *A. rondoniae* Mello-Leitão 1923—IBSP 2678, São Félix do Araguaia, Mato Grosso, Brazil; *A. sternalis* Pocock 1903—MNRJ, Jujuy, Argentina; *A. suina* Pocock 1903—MCP 2020, Vila Nova, Porto Alegre, Rio Grande do Sul, Brazil. *Aphonopelma seemani* (F.O. P.-Cambridge 1897)—IBSP 7019, Central América; *A. sp.*—IBSP 7047, Fresno County, California, U.S.A. *Brachypelma albopilosum* Valerio 1980—IBSP 7051, Guatemala; *B. boehmei* Schmidt & Klaas 1993—IBSP 7048, México; *B. emilia* (White 1856)—IBSP 7027, México; *B. klaasi* (Schmidt & Krause 1994)—IBSP 7050, México; *B. smithi* (F.O. P.-Cambridge 1897)—IBSP 4728, México. *Chromatopelma cyaneopubescens* (Strand 1907)—RCW, Punta Macolla, Panguana Península, Falcon State, Venezuela. *Crassicrus lamanai* Reichling & West 1996—RCW, N. Belmopan (Western Highway), Belize. *Cyclosternum symmetricum* (Bücherl 1946)—IBSP 3367, Ilha Bela, São Paulo, Brazil. *Cyriocosmus* cf. *elegans* (Simon 1889)—IBSP 4948, U.H.E. Balbina, Presidente Figueiredo, Amazonas, Brazil; *C.* cf. *sellatus* (Simon 1889)—IBSP 4947, U.H.E. Samuel, Porto Velho, Rondônia, Brazil. *Cyrtopholis portoricae* Chamberlin 1917—RCW, NW Guayama, Porto Rico; *C. palmarum* Schiapelli & Gerschman 1945—IBSP 4730, Paranaíba, Mato Grosso, Brazil. *Euathlus truculentus*

Table 1.—Homologous keels present, weakly developed (+), developed (++), well developed (+++), or absent (−) in representative taxa of Theraphosinae. A = apical; AEE = anterior embolus edge; DR = denticulate row; EPF = embolus prolateral face; PA = paraembolic apophysis; PI = prolateral inferior; PS = prolateral superior; R = retrolateral; SA = subapical; SGA = subapical granular area; TA = tegular apophysis; VC = ventral crest; cx = embolus prolateral face straight or convex; ec = embolus prolateral face extremely concave; sc = embolus prolateral face slightly concave above and under the prolateral keel.

	PS	PI	A	SA	R	EPF	Other structures
Euathlus truculentus	−	−	−	−	−	cx	VC
Cyriocosmus cf. *elegans*	+	−	−	−	−	cx	short PA
Cyriocosmus cf. *sellatus*	?	−	−	−	−	cx	long PA
Grammostola rosea	++	++	−	−	−	cx	none
Grammostola acteon	++	++	−	−	−	cx	none
Grammostola iheringi	++	++	−	−	−	cx	none
Grammostola longimana	++	++	−	−	−	cx	none
Grammostola pulchra	++	++	−	−	−	cx	none
Plesiopelma insulare	++	++	−	−	−	cx	none
Homoeomma montanum	++	++	−	−	−	cx	TA
Homoeomma stradlingi	++	++	−	−	−	cx	TA
Tmesiphantes nubilus	++	++	−	−	−	cx	none
Phrixotrichus scrofa	++	++	−	−	−	cx	none
Hapalopus sp.	+	+++	−	−	−	cx	PI split in two
Cyclosternum symmetricum	++	++	−	−	−	cx	none
Chromatopelma cyaneopubescens	++	+++	++	−	−	cx	crested triangular PI
Metriopelma sp.	++	+++	++	−	?	cx	two R keels ?; crested triangular PI
Aphonopelma seemani	+	++	++	−	−	cx	PI with a DR
Aphonopelma sp.	−	++	+	−	−	cx	none
Sphaerobothria hoffmani	+	++	++	−	−	cx	PI with a DR
Acanthoscurria atrox	+++	+++	+	−	−	cx	none
Acanthoscurria chacoana	+++	+++	+	−	−	cx	none
Acanthoscurria ferina	+	+	+++	?	−	cx	SGA
Acanthoscurria geniculata	+++	+++	+	−	−	cx	none
Acanthoscurria gomesiana	+++	+++	−	−	−	cx	none
Acanthoscurria insubtilis	++	++	+++	?	−	cx	SGA
Acanthoscurria juruenicola	+++	+++	+	−	−	cx	prolateral accessory keel
Acanthoscurria natalensis	+	++	+	−	−	cx	none
Acanthoscurria rondoniae	+	++	+	−	−	cx	none
Acanthoscurria sternalis	++	++	++	DR	−	cx	none
Acanthoscurria suina	+++	+++	−	−	−	cx	none
Phormictopus cancerides	++	++	++	DR	−	cx	none
Phormictopus cubensis	++	++	++	DR	−	cx	none
Cyrtopholis portoricae	+	+	−	−	−	cx	none
Cyrtopholis palmarum	++	++	++	−	−	cx	none
Eupalaestrus campestratus	++	++	++	DR	++	sc	none
Eupalaestrus weijenberghi	++	++	++	DR	++	sc	none
Eupalaestrus anomalus	++	++	++	++	++	sc	none
Lasiodora klugi	++	++	++	++	++	sc	none
Lasiodora mariannae	++	++	++	++	++	sc	none
Lasiodora subcanens	++	++	++	++	++	sc	none
Nhandu carapoensis	++	++	++	++	++	sc	none
Vitalius sorocabae	++	++	++	++	++	sc	none
Vitalius platyomma	++	++	++	++	++	sc	none
Vitalius roseus	++	++	++	+	++	sc	none
Vitalius cesteri	++	++	++	++	++	sc	none

Table 1.—Continued.

	PS	PI	A	SA	R	EPF	Other structures
Vitalius tetracanthus	++	++	++	++	++	sc	none
Crassicrus lamanai	++	++	++	−	++	sc	double A, one of them denticulate?
Pamphobeteus cf. *nigricolor*	++	+	+++	−	++	ec	long R
Pamphobeteus cf. *ornatus*	++	−	+++	−	++	ec	R half of the embolus long
Pamphobeteus sp.	++	−	+++	−	++	ec	R a third of the embolus long
Xenesthis immanis	++	++	+++	−	++	ec	none
Brachypelma albopilosum	++	++	+++	−	−	ec	none
Brachypelma boehemei	++	+	+++	−	−	ec	none
Brachypelma emilia	++	−	+++	−	−	ec	none
Brachypelma klaasi	++	−	+++	−	−	ec	AEE sinuous
Brachypelma smithi	++	+	+++	−	−	ec	none
Megaphobema sp.	++	++	+++	−	−	ec	prolateral accessory keels
Theraphosa blondi	++	−	+++	−	−	ec	AEE keels fused
Pseudotheraphosa apophysis	++	−	+++	−	−	ec	AEE keels fused

Ausserer 1875—IBSP 3744, Valparaíso, Chile. *Eupalaestrus campestratus* (Simon 1891)—IBSP 4149, Coxim, Mato Grosso do Sul, Brazil; *E. weijenberghi* (Thorell 1894)—MHNM, Montevideo, Uruguay; *E. anomalus* (Mello-Leitão 1923)—IBSP 4747, Alta Floresta, Mato Grosso, Brazil. *Grammostola rosea* (Walckenaer 1837)—IBSP 7067, Chile; *G. acteon* (Pocock 1903)—IBSP 3876, Mallet, Paraná, Brazil; *G. iheringii* (Keyserling 1891)—IBSP 4498, Blumenau, Santa Catarina, Brazil; *G. longimana* Mello-Leitão 1921—IBSP 3754, Moreira, Paraná, Brazil ; *G. pulchra* Mello-Leitão 1921—IBSP 3519, Brazil. *Hapalopus* sp.—IBSP 7046, U.H.E. Tucuruí, Tucuruí, Pará, Brazil. *Homoeomma montanum* (Mello-Leitão 1923)—IBSP 7045, Paranapiacaba, São Paulo, Brazil; *H. stradlingi* O. P.-Cambridge 1881—IBSP 4683, Teresópolis, Rio de Janeiro, Brazil. *Lasiodora klugi* (C.L. Koch 1841)—IBSP 7013, Caruarú, Pernambuco, Brazil; *L. mariannae* Mello-Leitão 1921—IBSP 2525, Ouro Preto, Minas Gerais, Brazil; *L. subcanens* Mello-Leitão 1921—IBSP 6380, Iconha, Espírito Santo, Brazil. *Megaphobema* sp.—MNRJ 14002, Rio Purús, Brazil. *Metriopelma zebrata* Banks 1909—IBSP 7069, Central América. *Nhandu carapoensis* Lucas 1981—IBSP 6555, Piraputanga, Mato Grosso do Sul, Brazil. *Pamphobeteus* cf. *nigricolor* (Ausserer 1875)—IBSP 7024, Medellín, Colombia; *Pamphobeteus* cf. *ornatus* Pocock 1903—IBSP 7070, no locality; *Pamphobeteus* sp.—IBSP 4944, U.H.E. Samuel, Porto Velho, Rondônia, Brazil. *Phormictopus cancerides* (Latreille

1806)—RWC, Barahona, Dominican Republic; *P. cubensis* Chamberlin, 1917—MNRJ 13264, Cuba. *Phrixotrichus scrofa* (Molina 1788)—IBSP 3805, Chile. *Plesiopelma insulare* (Mello-Leitão 1923)—IBSP 4493, Tapiraí, São Paulo, Brazil. *Pseudotheraphosa apophysis* Tinter 1991—IBSP 7049, Brazil/Venezuela boundary. *Sphaerobothria hoffmani* Karsch 1879—RCW, Moraña, San Jose, Costa Rica. *Theraphosa blondi* (Latreille 1804)—IBSP 7029, U.H.E. Tucuruí, Tucuruí, Pará, Brazil. *Tmesiphantes nubilus* Simon 1892—IBSP 7068, Rio de Contas, Bahia, Brazil. *Vitalius sorocabae* (Mello-Leitão 1923)—IBSP 5073, Ibiúna, São Paulo, Brazil; *V. platyomma* (Mello-Leitão 1923)—IBSP 4812, São Sebastião, São Paulo, Brazil; *V. roseus* (Mello-Leitão 1923)—IBSP 6314, Assis, São Paulo, Brazil; *V. cesteri* (Mello-Leitão 1923)—IBSP 6585, Juquitiba, São Paulo, Brazil; *V. tetracanthus* (Mello-Leitão 1923)—IBSP 3203, Americana, São Paulo, Brazil. *Xenesthis immanis* (Ausserer 1875)—IBSP 7026, Venezuela.

RESULTS AND DISCUSSION

Theraphosine male bulb general morphology.—The theraphosine male bulb is pyriform and presents a distally stout and broad or keeled embolus and a large subtegulum, extending down the bulb for half the length of tegulum (Raven 1985). The presence of keels is considered one of the three synapomorphies

of Theraphosinae (Raven 1985; Pérez-Miles et al. 1996). Some groups present conspicuous and exclusive structures such as the paraembolic apophysis (PA) in *Cyriocosmus* Simon 1903 species (Figs. 17, 18) (Raven 1985; Pérez-Miles et al. 1996) or a digitiform tegular apophysis (TA) in *Homoeomma* species (Figs. 13, 14) (Gerschman de Pikelin & Schiapelli 1972; Pérez-Miles et al. 1996). In many species, the embolus is distally flattened, giving them a concave/convex, spoon-like appearance (Figs. 5, 6, 43, 44). I found this occurred to different degrees, from an almost circular to an extreme concave-retrolateral/convex-prolateral embolus shape (Figs. 1–6). Figs. 1, 2 show an almost circular embolus in which the retrolateral side is straight or slightly convex. The genera *Grammostola* Simon 1892, *Euathlus* Ausserer 1875, *Plesiopelma* Pocock 1901, *Homoeomma*, *Cyriocosmus*, *Tmesiphantes* Simon 1892, *Phrixotrichus* Simon 1892, *Hapalopus* Ausserer 1875, *Cyclosternum* Ausserer 1871, *Chromatopelma* Schmidt 1995, *Metriopelma* Becker 1878, *Aphonopelma* Pocock 1901, *Sphaerobothria* Karsch 1879, *Cyrtopholis* Simon 1892, *Phormictopus* Pocock 1901, and *Acanthoscurria* are included in this group. Other genera, such as *Crassicrus* Reichling & West 1996, *Eupalaestrus* Pocock 1901, *Lasiodora* C.L. Koch 1850, *Vitalius* Lucas, Silva Júnior & Bertani 1993, and *Nhandu* Lucas 1981 (Figs. 3, 4) have the embolus slightly distally concave in the areas above and under the retrolateral keel (see the next item for the keel terminology). In the genera *Pamphobeteus* Pocock 1901, *Xenesthis* Simon 1891, *Megaphobema* Pocock 1901, *Brachypelma*, *Pseudotheraphosa* Tinter 1991, and *Theraphosa* Thorell 1870 these areas are extremely concave, giving them the characteristic spoon-like appearance (Figs. 5, 6).

Theraphosine male bulb keels and homology.—The results of a comparative study carried out on the male bulb keels of 60 species of Theraphosinae is summarized in Figs. 1–44 and Table 1. Four main groups of homologous keels can be recognized and are described.

Prolateral keels: Comprises two parallel keels, superior (PS) and inferior (PI), present in the prolateral area of the embolus. These keels follow the twisted embolus shape of many species. The homology of the prolateral keels is evident in many genera. *Grammostola* (Figs. 9, 10), *Plesiopelma* (Figs. 11, 12), *Homoeomma* (Figs. 13, 14), *Tmesiphantes*, and *Phrixotrichus* have a tapering and twisted embolus with only the prolateral keels present, posing no difficulties in establishing the homology between them. The differences in these palpal bulbs concern the extension of the keels, the distance between them and their size.

In some taxa with a slender and more or less straight embolus, the prolateral keels are not so evident. That is what occurs in some species of *Cyrtopholis* and *Aphonopelma* (Figs. 19, 22). In *Aphonopelma* these keels are weakly developed and are confined to the distal tip of the embolus, and sometimes only one keel is visible (Figs. 21, 22). However, in other species, such as *A. seemani* (Figs. 19, 20), the two keels are evident, though the upper one is not well-developed. The *Aphonopelma seemani* and *Sphaerobothria hoffmani* bulbs are very similar, as pointed out by Valerio (1980b) (Figs. 19, 20, 23, 24). I found that the two species share a reduced PS and the well-developed PI keel, presenting a denticulate row backwards from its middle, that could constitute a synapomorphy of *Aphonopelma* + *Sphaerobothria*. This view differs from that of the cladogram from Pérez-Miles et al. 1996 (Fig. 45) and is discussed under ''conclusions.'' Other *Aphonopelma* species also possess this denticulate row, as can be seen in Pickard-Cambridge (1897), plate I, fig. 16, for *Aphonopelma serratum* (Simon 1890) and Smith (1995), fig. 261, for *Aphonopelma crinitum* (Pocock 1901). The absence of both the PS and the PI denticles could be seen as apomorphies to the group of *Aphonopelma* species found in the northernmost distribution of the genus (Smith 1995).

In some genera with short, stout and non spoon-like embolus, such as many species of *Acanthoscurria* (Figs. 25–30), *Hapalopus* (Figs. 15, 16), *Metriopelma*, and *Chromatopelma*, one or both of the prolateral keels are well-developed. In some *Acanthoscurria* species such as *A. atrox* (Figs. 25, 26), *A. geniculata* and *A. juruenicola* (Figs. 29, 30), these keels are so well-developed and twisted that the general shape of the organ is odd; and at first sight, it is difficult to recognize these keels as homologous to the anterior ones. The PS is very raised on its most proximal portion;
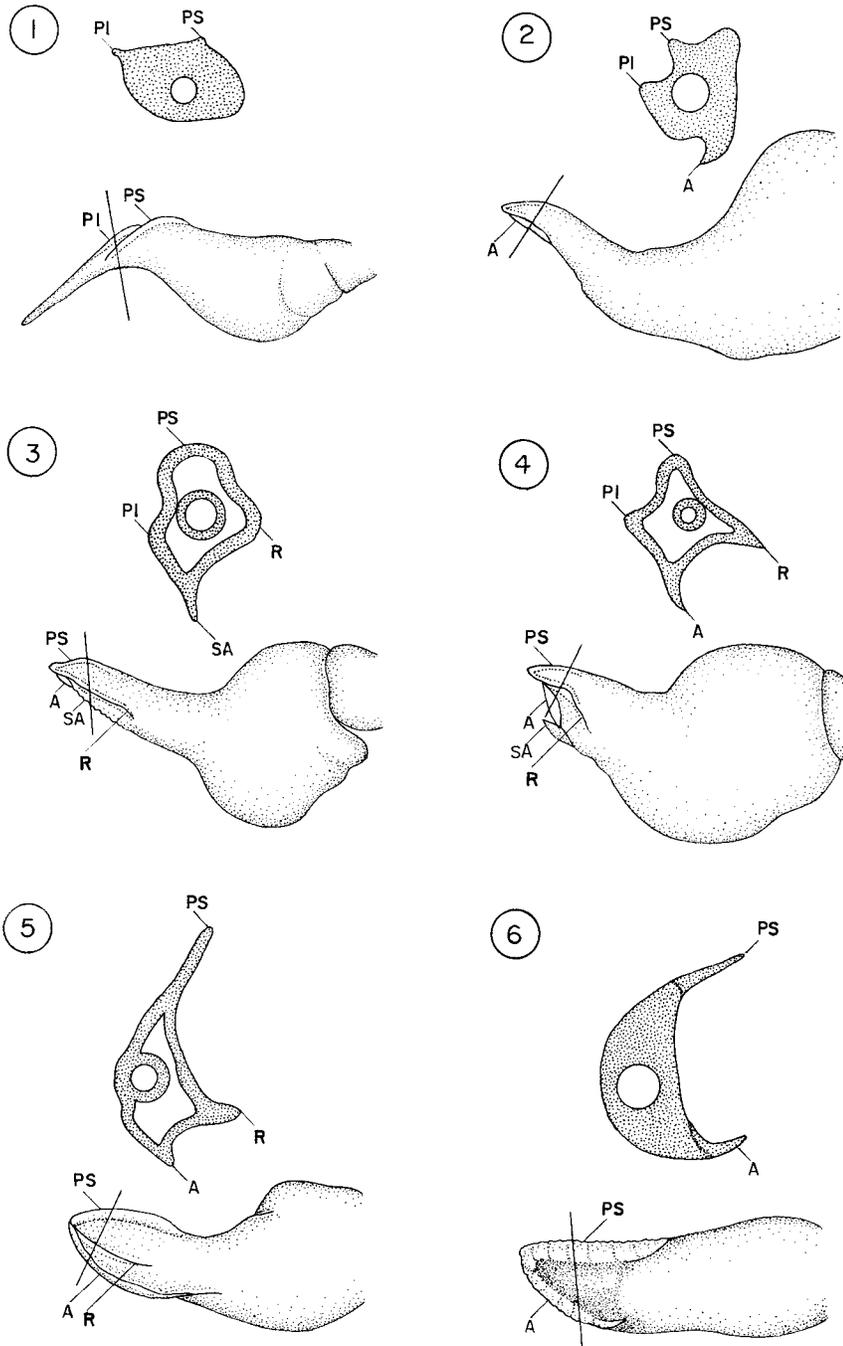
Figure 1–6.—Transverse view of the left embolus of some representative theraphosine species. 1, *Grammostola acteon* (Pocock 1903); 2, *Aphonopelma seemani* (F.O. P. -Cambridge 1897); 3, *Eupalaestrus campestratus* (Simon 1891); 4, *Vitalius tetracanthus* (Mello-Leitão 1923); 5, *Pamphobeteus* sp.; *Theraphosa blondi* (Latreille 1804). *Abbreviations:* A = apical keel; PI = prolateral inferior keel; PS = prolateral superior keel; R = retrolateral keel; SA = subapical keel.
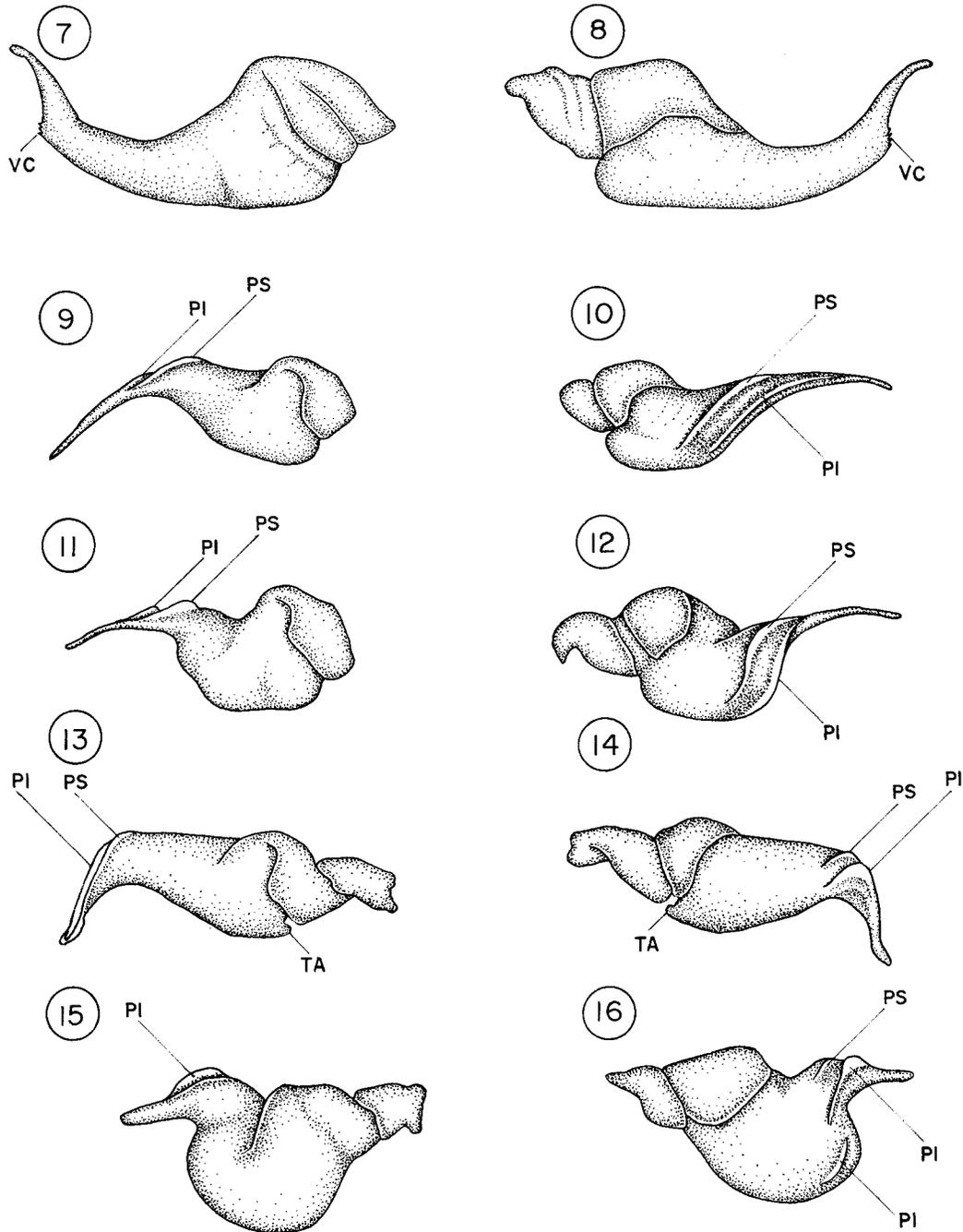
Figures 7–16.—Left male bulbs of some representative theraphosine species. 7, 8. *Euathlus truculentus* Ausserer 1875. 7, Retrolateral view; 8, Prolateral view. 9, 10. *Grammostola acteon* (Pocock 1903). 9, Retrolateral view; 10, Prolateral view; 11, 12. *Plesiopelma insulare* (Mello-Leitão 1923). 11, Retrolateral view; 12, Prolateral view; 13, 14. *Homoeomma montanum* (Mello-Leitão 1923). 13, Retrolateral view; 14, Prolateral view; 15, 16. *Hapalopus* sp. 15, Retrolateral view; 16, Prolateral view. *Abbreviations:* PI = prolateral inferior keel; PS = prolateral superior keel; TA = tegular apophysis; VC = ventral crest.
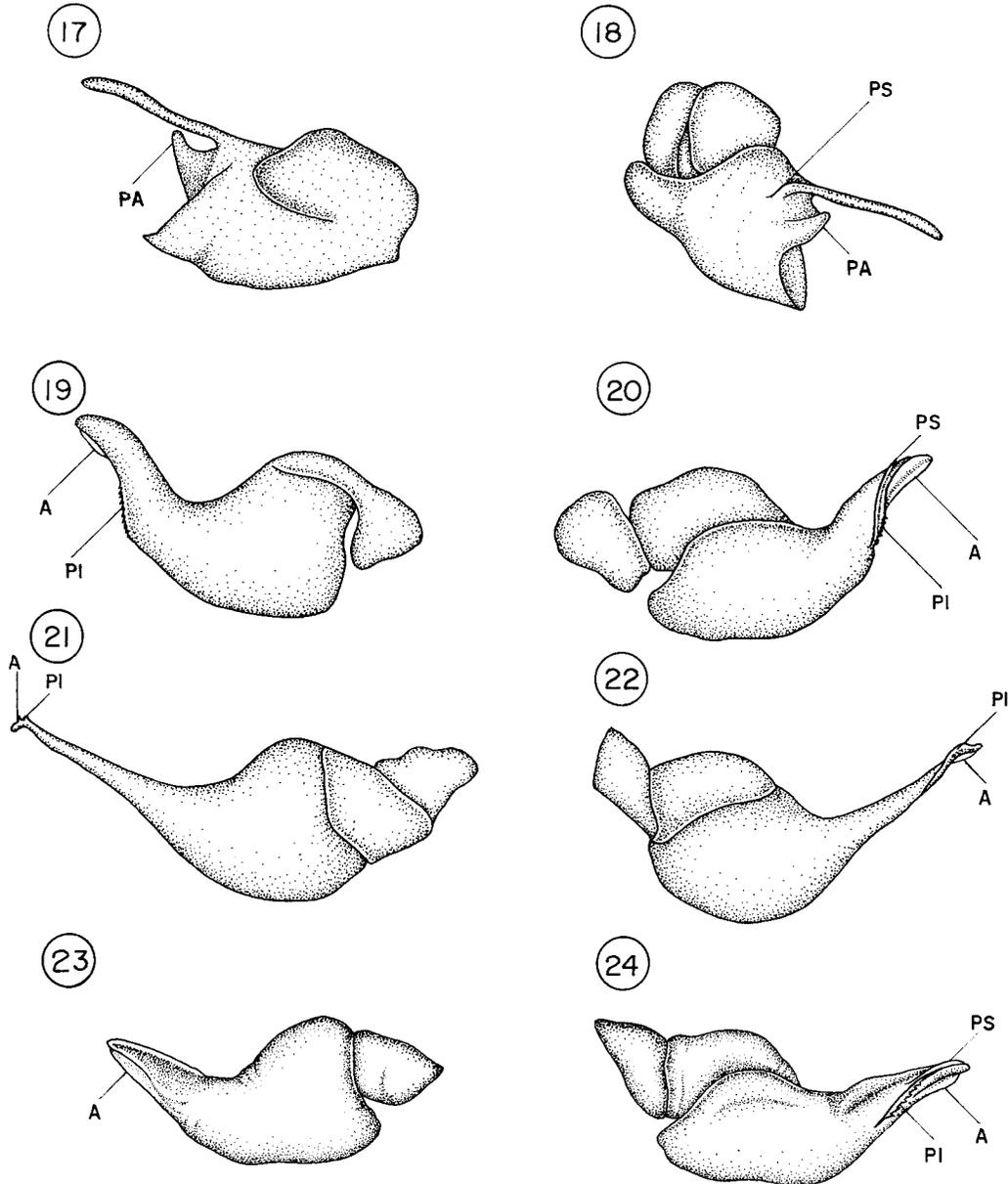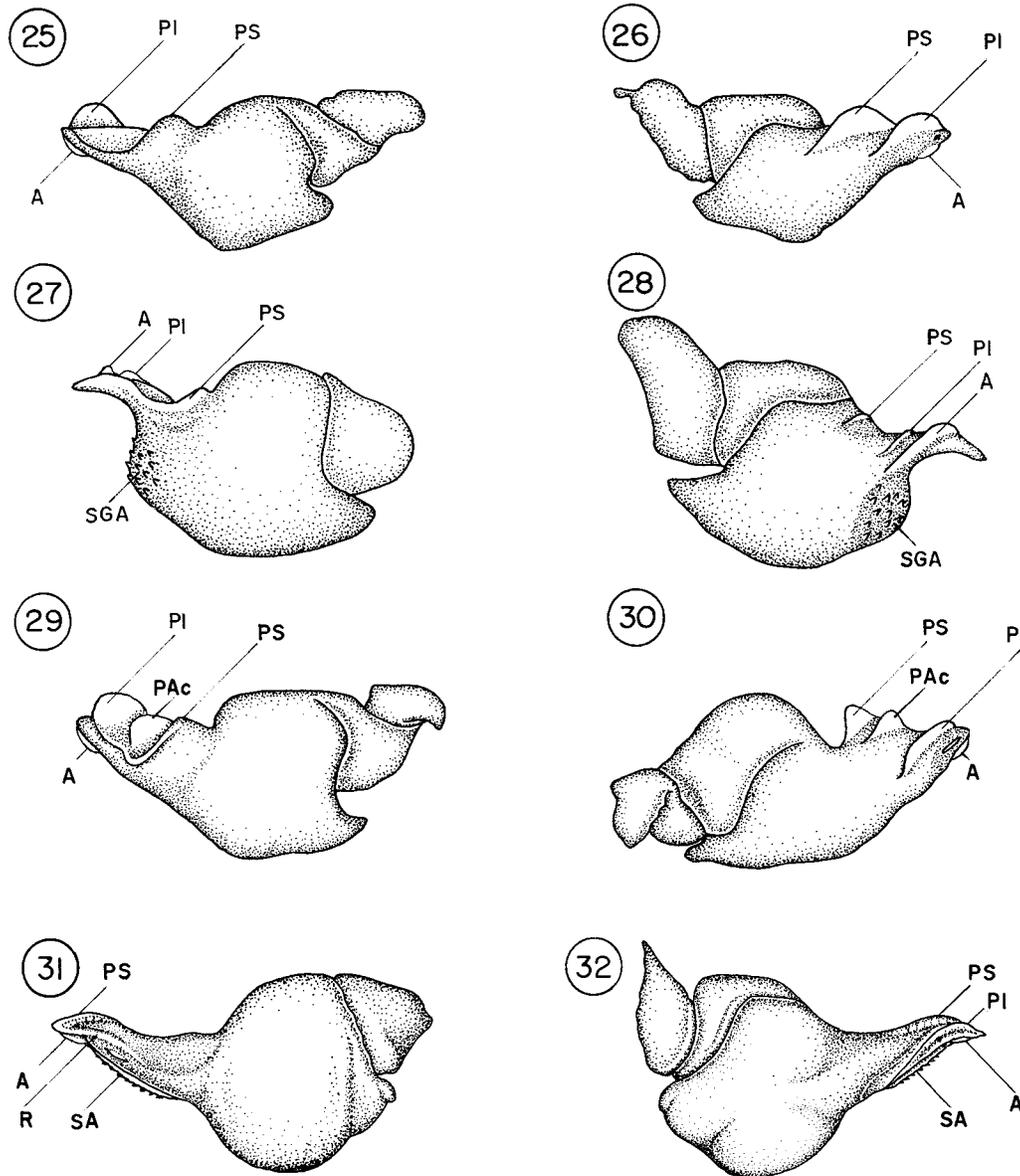
Figures 17–24.—Left male bulbs of some representative theraphosine species (continued). 17, 18. *Cyriocosmus* cf. *elegans* (Simon 1889). 17, Retrolateral view; 18, Prolateral view; 19, 20. *Aphonopelma seemani* (F.O. P.-Cambridge 1897). 19, Retrolateral view; 20, Prolateral view. 21, 22. *Aphonopelma* sp. 21, Retrolateral view; 22, Prolateral view; 23, 24. *Sphaerobothria hoffmani* Karsch 1879. 23, Retrolateral view; 24, Prolateral view. *Abbreviations:* A = apical keel; PA = paraembolic apophysis; PI = prolateral inferior keel; PS = prolateral superior keel.

and towards the apex it becomes lower, constituting the upper bulb edge.

The genera *Hapalopus*, *Metriopelma*, and *Chromatopelma* have the PI very well-developed, and in *Hapalopus* it is split in two (Figs.

15, 16). The genera *Metriopelma* and *Chromatopelma* have the PI presenting a triangular shape, with no such division.

In another group that includes *Eupalaestrus* (Figs. 31, 32), *Vitalius* (Figs. 33, 34)*, Lasio-*
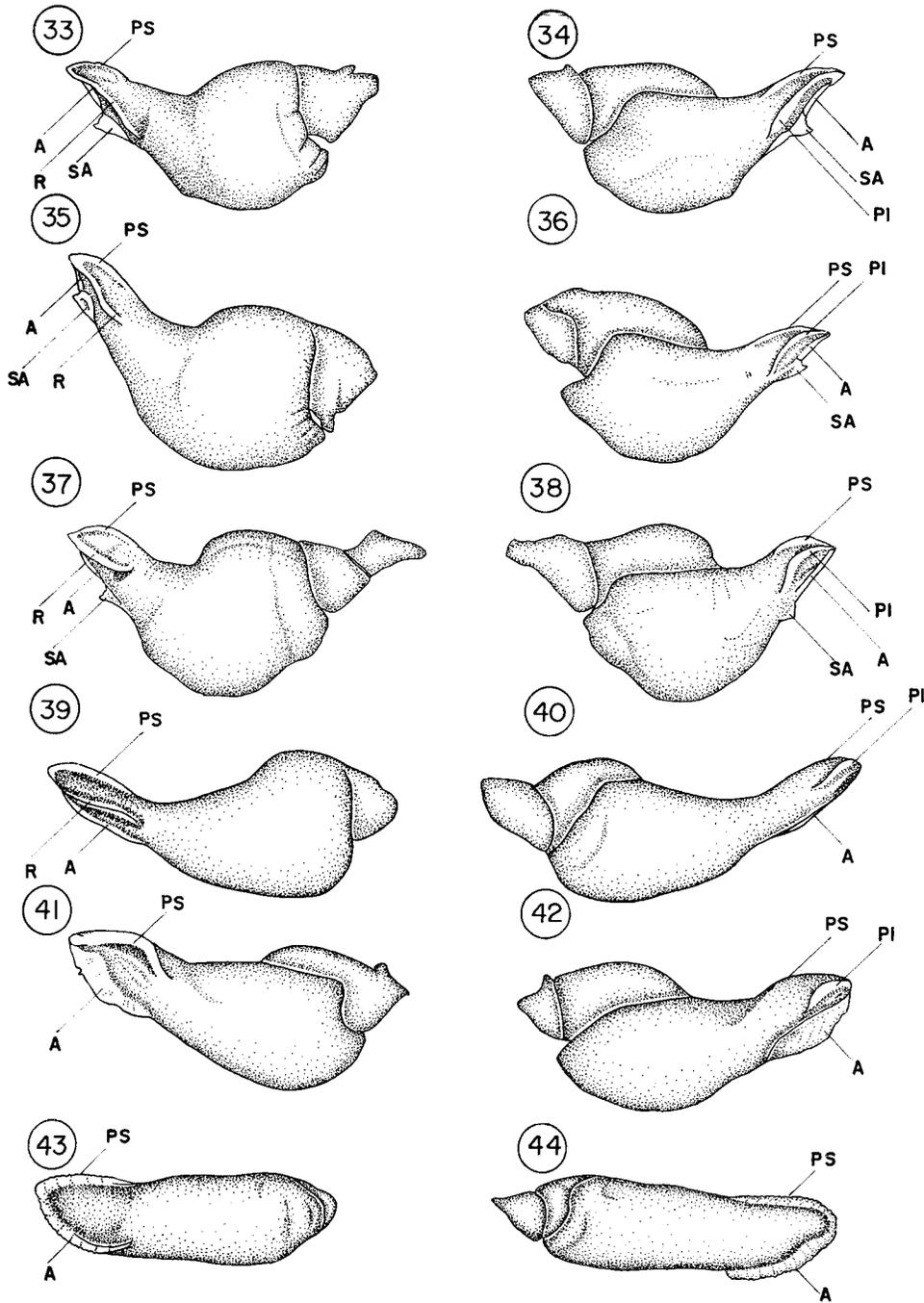
Figures 25–32.—Left male bulbs of some representative theraphosine species (continued). 25, 26. *Acanthoscurria atrox* Vellard 1924. 25, Retrolateral view; 26, Prolateral view. 27, 28. *Acanthoscurria insubtilis* Simon 1892. 27, Retrolateral view; 28, Prolateral view. 29, 30. *Acanthoscurria juruenicola* Mello-Leitão 1923. 29, Retrolateral view; 30, Prolateral view. 31, 32. *Eupalaestrus campestratus* (Simon 1891). 31, Retrolateral view; 32, Prolateral view. *Abbreviations:* A = apical keel; PAc = prolateral accessory keel; PI = prolateral inferior keel; PS = prolateral superior keel; R = retrolateral keel; SA = subapical keel; SGA = subapical granular area.

dora (Figs. 35, 36) and *Nhandu* (Figs. 37, 38), the prolateral keels are confined to the distal part of the embolus and, as observed in some *Acanthoscurria* species, the PS forms the upper edge of the distal embolus. These keels are rounded in this group, differing from sharp keels present in other genera.

In the group with a spoon-like embolus (*Pamphobeteus* (Figs. 39, 40), *Xenesthis, Megaphobema, Brachypelma* (Figs. 41, 42),

Figures 33–44.—Left male bulbs of some representative theraphosine species (continued). 33, 34. *Vitalius sorocabae* (Mello-Leitão 1923). 33, Retrolateral view; 34, Prolateral view. 35, 36. *Lasiodora klugi* (C.L. Koch 1841). 35, Retrolateral view; 36, Prolateral view; 37, 38. *Nhandu carapoensis* Lucas 1981. 37, Retrolateral view; 38, Prolateral view; 39, 40. *Pamphobeteus* cf. *nigricolor* (Ausserer 1875). 39, Retrolateral view; 40, Prolateral view. 41, 42. *Brachypelma boehemei* Schmidt & Klaas 1993. 41, Retrolateral view; 42, Prolateral view. 43, 44. *Theraphosa blondi* (Latreille 1804). 43, Retrolateral view; 44, Prolateral view. *Abbreviations:* A = apical keel; PI = prolateral inferior keel; PS = prolateral superior keel; R = retrolateral keel; SA = subapical keel.

Theraphosa (Figs. 43, 44), and *Pseudotheraphosa*) the PS also constitutes the upper edge of the embolus, but it is thinner and retrolaterally directed. The PI is weakly developed or absent in some species of the genera *Pamphobeteus* (Figs. 39, 40), *Xenesthis*, *Megaphobema*, and *Brachypelma* (Figs. 41, 42). In *Theraphosa* (Figs. 43, 44) and *Pseudoteraphosa* there is no vestige of the PI.

Apical keel (A): A small, slightly transparent keel located just below the apex of the embolus. It is highly developed in some groups and usually presents a fissure delimiting its area. The apical keel is absent in the genera *Grammostola*, *Euathlus*, *Cyriocosmus*, *Plesiopelma*, *Homoeomma*, *Tmesiphantes*, *Phrixotrichus*, *Hapalopus* and *Cyclosternum*. In the genus *Acanthoscurria* (Figs. 25, 26, 29, 30) and *Aphonopelma* (Figs. 19–22) it is very small in some species and seems to be absent in others (see Table 1). In the genera *Eupalaestrus* (Figs. 31, 32), *Vitalius* (Figs. 33, 34), *Lasiodora* (Figs. 35, 36), and *Nhandu* (Figs. 37, 38) it is always present, but it is small and confined to the distal part of the embolus. In the group with spoon-like embolus, however, it has a great backward development, extending for almost all the inferior embolus edge. Thus, the two keels on the edges of these characteristic male bulbs derived independently. The superior keel is derived from the PS and the lower keel from the A. In the male bulbs of *Pamphobeteus* (Figs. 39, 40), *Xenesthis*, *Brachypelma* (Figs. 41, 42) and *Megaphobema* species, these two keels are not anteriorly fused and are positioned at different levels. In *Theraphosa* (Figs. 6, 43, 44) and *Pseudotheraphosa* the PS and the A keels are anteriorly completely fused, constituting a unique piece surrounding the entire embolus edge. It is possible to recognize this as being the result of such a fusion only through the comparison with species of the other genera previously cited that do not have this fusion but have a very similar spoon-like embolus. Furthermore, in many species, as in *Brachypelma boehemei* (Figs. 41, 42) there is a fissure which delimits the apical keel boundary from the remaining part of the embolus. This does not occur with the PS, where no delimitation is visible, suggesting they had distinct origins.

Subapical keel (SA): A keel located just below the apical keel. It assumes a triangular shape in the genera *Vitalius* (Figs. 33, 34), *Lasiodora* (Figs. 35, 36), and *Nhandu* (Figs. 37, 38). In *Eupalaestrus campestratus* (Figs. 31, 32), *E. weijenberghi*, *Phormictopus*, and *A. sternalis* it is constituted by a denticulate row (DR) which is a primary homologue to the triangular keel present in the other genera above.

Retrolateral keel (R): A keel developed retrolaterally from the apex of the embolus to the rear. This keel is shared by species of *Crassicrus*, *Eupalaestrus* (Figs. 31, 32), *Vitalius* (Figs. 33, 34), *Lasiodora* (Figs. 35, 36), *Nhandu* (Figs. 37, 38), *Pamphobeteus* (Figs. 39, 40), and *Xenesthis*. It seems to be lost in the genera *Brachypelma* (Figs. 41, 42), *Megaphobema*, *Theraphosa* (Figs. 43, 44), and *Pseudotheraphosa*, constituting possibly a synapomorphy (Fig. 45). This option seems to be more parsimonious, because the genera *Pamphobeteus* and *Xenesthis* share other characters with these genera, such as the spermathecae shape, the spoon-like embolus and the well-developed apical keel. Additional steps are required if they are considered as independently acquired, whereas if the absence of the R is considered a reversal, only one step is required.

Other keel groups: Apart from these four basic groups of keels, there are others not so widespread and such are sometimes confined to only one species. An example is a small keel found between the prolateral keels in *Acanthoscurria juruenicola* (PAc, Figs. 29, 30). The general shape of the male bulb is the same as the related species *A. atrox* (Figs. 25, 26) and *A. gomesiana* due to the well-developed PS and PI, but only *A. juruenicola* and perhaps *A. geniculata* have this keel, which is smaller and isolated from the PS and PI. Thus, this structure is called ''*Acanthoscurria juruenicola* prolateral accessory keel (PAc),'' following Coddington 1990, as a way of avoiding confusion with the terminology among other similar but non-homologous keels.

In a similar way, the *Megaphobema* species examined has, in the prolateral area, some keels other than the prolateral keels, and, if they are present in the other species of *Megaphobema*, they are called ''*Megaphobema* prolateral accessory keels.'' Also, in the species *Acanthoscurria ferina* and *Acanthoscurria insubtilis* there is a granular area in the
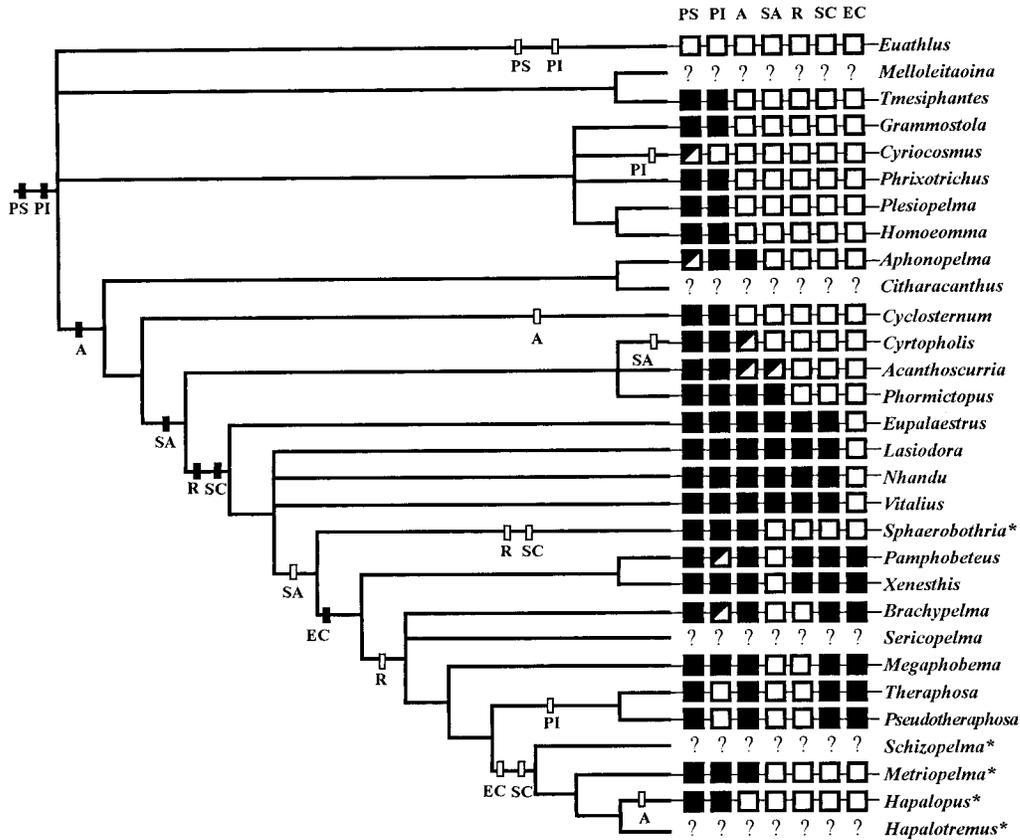
Figure 45.—Probable evolution of male palpal bulb keels in Theraphosinae. Bulb characters were mapped on the cladogram of Pérez-Miles et al. (1996). Taxa which show incongruence between the character evolution proposed here and in the cladogram of Pérez-Miles et al. (1996) are indicated by an asterisk. See text for further discussions. *Abbreviations:* ? = information absent, refers to genera which did not have specimens examined in this work. A = apical keel; EC = embolus prolateral face extremely concave; PI = prolateral inferior keel; PS = prolateral superior keel; R = retrolateral keel; SA = subapical keel; SC = embolus prolateral face slightly concave above and under the prolateral keel. SC and EC were treated as additive multistate characters. Black rectangle = synapomorphy; white rectangle = reversal. Black square = present; white square = absent; upper black triangle in a square = character exhibiting interspecific variation.

ventral subapical region (SGA) that seems to be a synapomorphy of these species and is called *Acanthoscurria ferina* and *A. insubtilis* subapical granular area.

The opposite occurs in some species of the genera *Cyriocosmus* and *Euathlus*, where the four basic groups of keels are absent. The palpal bulb of *Cyriocosmus* (Figs. 17, 18) is highly modified and the species possess from short to large paraembolic apophysis (PA) (see Schiapelli & Gerschman de Pikelin 1973). In some species studied I have found some vestiges of the superior prolateral keel and I believe that, with an increased knowl-

edge of the genus, there is the possibility that some basal species with a less modified embolus can be found, which still retain these keels plesiomorphically.

In *Euathlus truculentus*, however, the only keel present is one ventral medial crest (VC, Figs. 7, 8) not found in other theraphosine species. There is no vestige of the prolateral keels that, as shown above, are the most plesiomorphic ones in Theraphosinae. Because of the basal position in a politomy occupied by *Euathlus* in the cladistic analysis of Theraphosinae by Pérez-Miles et al. (1996) (Fig. 45), there are two possibilities: (1). The pro-

lateral keels are a synapomorphy of all theraphosine except *Euathlus*; in this case *Euathlus* is the most basal taxon of all Theraphosinae. (2). The prolateral keels were lost in *Euathlus truculentus*. The two possibilities seem equally parsimonious.

CONCLUSIONS

As shown above, the theraphosine palpal bulbs present some basic groups of keels which are widespread among almost all theraphosine species. These five keels were homologized through the classical criteria of homology, i.e., they presented the same relative position in the bulbs; they presented morphological similarity, considering that no extreme and improbable changes were seen; and they were in accordance with the other characters, in this case the other keels. The last one is the most powerful test of homology and the most important to systematics (Patterson 1982). Also, the co-occurence of the five proposed keels in some species is in accordance with the conjunction test of Patterson (1982), i.e., they constitute five homologous keels. Keels other than these basic ones were found and some morphological modifications were seen. I consider this only one more argument to justify that these structures, overlooked for so long, could be valuable for taxonomy and systematic work due to their great morphological interspecific variability. Of course, this work must be seen as an initial approach and surely many alterations will take place when more information on theraphosine morphology and hypothesis of relationship become available, a reason why no phylogenetic analysis was carried out here. However, when considering the cladogram of theraphosine genera proposed by Pérez-Miles et al. 1996, I found concordance with the keels evolution proposed here, with two exceptions (Fig. 45). The first one is the genus *Sphaerobothria* which, as discussed earlier, has a very similar bulb when compared with some *Aphonopelma* species. The second is the branch including *Schizopelma*, *Metriopelma*, *Hapalopus*, and *Hapalotremus*. The position of these branches in this cladogram is due in part to a distinct interpetration of male palpal bulb characters carried out in Pérez-Miles et al. (1996) cladistic analysis. For example, in this paper the character ''bulbal keels smooth or absent'' is considered primitive, while ''bulbal keels serrated'' is

considered derived for *Eupalaestrus*, *Nhandu*, *Vitalius*, *Lasiodora* and *Sphaerobothria*. However, in *Sphaerobothria* the serrated (denticulated) keel is the PI (Fig. 24), while in the other four genera, the serrated keel is the SA (Fig. 32); thus these characters are non-homologous and should be recoded. The reinterpretation of these characters surely will cause some changes to this cladogram topology.

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