

Morphology of setae on the coxae and trochanters of theraphosine spiders (Mygalomorphae: Theraphosidae)

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Abstract. Mygalomorphae spiders have several cuticular structures, such as stridulating, sensory and urticating setae, which offer great potential for phylogenetic studies. Spiders of the subfamily Theraphosinae have stridulating setae that aid in group taxonomy, having been found in numerous genera including: *Acanthoscurria* Ausserer, 1871, *Aguapanela* Perafán, Cifuentes & Estrada-Gomez, 2015, *Citharacanthus* Pocock, 1901, *Cyrtopholis* Simon, 1892, *Grammostola* Simon, 1892, *Hemirrhagus* Simon, 1903, *Lasiadora* C. L. Koch, 1850, *Longilyra* Gabriel, 2014, *Pamphobeteus* Pocock, 1901, *Phormictopus* Pocock, 1901 and *Theraphosa* Thorell, 1870. Some distinct bristle-like setae were examined using scanning electron microscopy with the following objectives: (1) to sample and describe the diversity of setae on the coxae and trochanters of representatives of the subfamily Theraphosinae; and (2) to code morphological characters useful for phylogenetics. We used a previously published phylogenetic matrix, with modifications to those characters that scored stridulatory setae, and analyzed these data using parsimony with implied weighting. Setae of the same type were found in *Acanthoscurria*, *Brachypelma* Simon, 1891, *Cyrtopholis*, *Phormictopus* and *Theraphosa* (claviform stridulating setae). A second type, which we name velvet stridulating setae, emerged as an autapomorphy of the genus *Lasiadora*, and spiniform stridulating setae were recovered as an autapomorphy of the genus *Pamphobeteus*. Some other setae similar to those of *Lasiadora*, named plumose stridulating setae, were found in *Nhandu* Lucas, 1983, *Proshapalopus* Mello-Leitão, 1923, *Pterinopelma* Pocock, 1901 and *Vitalius* Lucas, Silva & Bertani, 1993.

Keywords: Theraphosinae, stridulating setae, phylogeny, cladistics

Mygalomorph spiders, as well as other arthropods, present cuticular structures with great morphological variation and phylogenetic information (Raven 1994; Ferretti et al. 2011; Guadanucci 2014; Bertani & Guadanucci 2013). Among these structures, we find different types of setae with different functions, such as chemosensory, mechanosensory and adhesive (Seyfarth 1985; Barth 2002). Many species of Mygalomorphae use sound production, presumably for sexual behavior or for protection against possible predators (Legendre 1963; Uetz & Stratton 1982; Marshall et al. 1995). Sounds are produced as a result of a phenomenon known as stridulation, and made by stridulatory organs that consist of specialized setae and antagonistic structures on the integument (Jocqué 2005). Other varieties of setae may also act in the stridulating process, such as the long spiniform setae of spiders of the genus *Grammostola* Simon, 1892 (Ferretti et al. 2011) and the spiniform setae found in *Acanthoscurria* *suina* Pocock, 1903 (Pérez-Miles et al. 2005). These organs are arranged on opposing surfaces and rub against each other, causing vibrations that are captured by trichobothria (Uetz & Stratton 1982).

The systematics and taxonomy of the family Theraphosidae have been heavily influenced by the presence and variations of stridulatory setae (Pocock 1895, 1897, 1899; Simon 1903; Pérez-Miles et al. 1996; Schmidt 1999). One of the earliest records of stridulatory setae in a theraphosid spider can be found in the work of Simon (1892), who cites a description made by Wood-Mason (1876) for some ‘Aviculariides’ spiders. Among representatives of the subfamily Selenocosmiinae, Raven (1985) recorded different stridulatory setae in the form of a lyra, on the retrolateral face of the chelicerae and the prolateral face of the maxillae.

Stridulatory organs are found in at least 22 families of spiders (Uetz & Stratton 1982). The taxonomy of spiders of

the subfamily Theraphosinae (family Theraphosidae) is largely based on the presence and distribution of stridulating organs (Pocock 1895, 1897, 1899; Simon 1903; Bücherl 1957; Pérez-Miles et al. 1996, Schmidt 1999, 2000), along with differences in the leg and body measurements, the disposition of eyes and scopulae, coloration (Simon 1892; Pocock 1903; Mello-Leitão 1923; Schiapelli & Gerschman de Pikelin 1979; Raven 1985; Smith 1995; Prentice 1997), the type of urticating setae (Cooke et al. 1972; Pérez-Miles et al. 1996), the morphology of the spermathecae (Schiapelli & Gerschman de Pikelin 1962), and the shape of the tibial apophysis and male palpal bulb (Raven 1985; Pérez-Miles et al. 1996; Guadanucci 2014). With respect to stridulating setae, the presence of such structures has hitherto been reported for 11 theraphosinae genera: *Acanthoscurria* Ausserer, 1871; *Aguapanela* Perafán, Cifuentes & Estrada-Gomez, 2015; *Citharacanthus* Pocock, 1901; *Cyrtopholis* Simon, 1892; *Grammostola*; *Hemirrhagus* Simon, 1903; *Lasiadora* C. L. Koch, 1850; *Longilyra* Gabriel, 2014; *Pamphobeteus* Pocock, 1901; *Phormictopus* Pocock, 1901; and *Theraphosa* Thorell, 1870.

Pocock (1901) noticed the presence of plumose setae, which he did not name or recognize as stridulatory, on the retrolateral face of the palpal trochanter and on the prolateral coxa I of spiders of the genus *Pterinopelma* Pocock, 1901 (similar to those of *Brachypelma* Simon, 1891). Bücherl (1957) also noticed varieties of these setae on some Theraphosinae. In *Acanthoscurria*, the setae were drawn by Bücherl (1957) as spear-shaped, with a smooth proximal portion and barbs covering the apical half, these barbs becoming denser at the apex. These stridulating setae are currently called claviform (Pérez-Miles et al. 2005). In the genus *Lasiadora*, Bücherl (1957) described the setae as having a velvet surface, and provided with many short barbs. Bertani (2001) also reported

the presence of distinct setae in *Lasiodora* on the upper prolateral faces of coxae I and II.

After examining specimens of the genera *Nhandu* Lucas, 1983, *Proshapalopus* Mello-Leitão, 1923, *Pterinopelma* and *Vitalius* Lucas, Silva & Bertani, 1993, a conspicuous tuft of setae on the trochanters and coxae drew our attention. Thereafter, our objective was to examine the variations of stridulating setae of the coxae and trochanters of Theraphosinae using scanning electron microscopy. In this study, we present these data, and analyze and interpret our results in a phylogenetic context.

METHODS

Material was examined from the following scientific collections: IBSP, Instituto Butantan, São Paulo, Brazil (A. Brescovit); MCN, Museu de Ciências Naturais, Fundação Zoobotânica do Rio Grande do Sul, Porto Alegre, Brazil (R. Ott); CNAN, Colección Nacional de Arácnidos UNAM, México DF, México (O. F. Ballvé); CCEN, Centro de Ciências Exatas e da Natureza, Universidade Federal da Paraíba, João Pessoa, Paraíba, Brazil (M. B. da Silva); CAD, Coleção Aracnológica Diamantina, Diamantina, Minas Gerais, Brazil (J. P. L. Guadanucci).

Material examined.—*Acanthoscurria gomesiana* Mello-Leitão, 1923. BRAZIL: *Minas Gerais*: 1 ♂, Diamantina, November 2008 (CAD 021); 1 ♀, São Gonçalo do Rio Preto, 11 November 2009 (CAD 472).

Acanthoscurria juruenicola Mello-Leitão, 1923. BRAZIL: *Mato Grosso*: 1 ♂, Alta Floresta, 4 December 1979 (IBSP 4474).

Acanthoscurria natalensis Chamberlin, 1917. BRAZIL: *Mato Bahia*: 1 ♂, Riachão das Neves, 18 February 1974, A. Pereira Filho (IBSP 4234); 1 ♀, Irerê, September 1980, M. Guimarães (IBSP 4558).

Acanthoscurria paulensis Mello-Leitão, 1923. BRAZIL: *Minas Gerais*: 1 ♂, Alpinópolis, February 1983, J. Oliveira (IBSP 4759); 1 ♀, Campo Grande, 13 March 1972 (IBSP 2117).

Brachypelma smithi (F. O. Pickard-Cambridge, 1897). MEXICO: *Guerrero*: 2 ♂, Zihuatanejo, June 2015 (CNAN).

Cyrtopholis species. DOMINICAN REPUBLIC: *La Veja Contanza*: 1 ♂, La Piramide Paque Nacional Valle Nuevo, 18°42'27.7"N, 70°36'01.6"W, 19 October 2011, G. Santos (IBSP). *San Juan*: 1 ♀, Parque Nacional José del Carmen Pramiras, 14 November 2009 (IBSP).

Eupalaestrus species. BRAZIL: *São Paulo*: 1 ♂, Serra do Mar, 12 May 1976 (IBSP 4200).

Lasiodora parahybana Mello-Leitão, 1917. BRAZIL: *Parabá*: 1 ♂, João Pessoa, 22 April 2015 (CCEN 854). *Piauí*: 1 ♀, Oeiras, July 2008, T. Porto, H. Yamaguti & M. B. da Silva (CCEN 180).

Nhandu cerradensis Bertani, 2001. BRAZIL: *Piauí*: 1 ♂, Parque Nacional da Serra das Confusões, January 2002 (IBSP 11847); 1 ♀, 'Brazil', January 1994, A. P. da Silva (IBSP 13971).

Proshapalopus multicuspoidatus Mello-Leitão, 1929. BRAZIL: *Minas Gerais*: 1 ♂, Mendanha, P. S. Moreira (CAD 094).

Pterinopelma felipeleitei Bertani & Leal, 2016. BRAZIL: *Minas Gerais*: 1 ♂, Diamantina, 5 June 2011 (CAD 441); 1 ♀, Diamantina (CAD 584).

Pterinopelma sazimai Bertani, Nagahama & Fukushima, 2011. BRAZIL: *Minas Gerais*: 1 ♂, Diamantina, C. A. Bispo (CAD); 1 ♀, Diamantina (CAD).

Pterinopelma vitiosum Keyserling, 1891. BRAZIL: *Rio Grande do Sul*: 1 ♂, Encantado, 17 April 1992, L. Dacroce (MCN 22145); 1 ♀, Caxias do Sul, 18 December 1991, F. Becker (MCN 22102).

Theraphosa blondi Latreille, 1804. BRAZIL: *Pará*: 1 ♂, Caxiuanã-Melgaço, 17–30 March 2002 (MPEG 000176); 1 ♀, Almerim, 01°1'33.1"S, 52°34'2.8"W, 22 June 2005, T. Gardner & M. A. R. Junior (MPEG 007558).

Vitalius species. BRAZIL: *São Paulo*: 1 ♂, Jaú, R. Benetti (CAD).

Morphological methods.—The pro- and retrolateral faces of coxae and trochanters were surveyed in search of distinct types of setae. The articles were dissected and manually cleaned with thin brushes (synthetic fibers) towards the same direction of setal alignment to remove visible particles and debris. The articles were then cleaned in an ultrasonic vibrator after soaking for 12 hours in a water/detergent solution. Dehydration in ethanol series was done before critical-point drying. Each article was mounted on a separate aluminum stub with copper double-sided tape and finally sputter coated with gold. The preparations were examined under a Hitachi TM-1000 scanning electron microscope (SEM) at the Electronic Microscopy Laboratory of the Institute of Biosciences of São Paulo State University, campus Rio Claro, São Paulo, Brazil.

Cladistics.—To study the evolution of stridulating setae, we used the matrix assembled by Bertani et al. (2011) with the following changes regarding the terminal taxa: *Acanthoscurria geniculata* C. L. Koch, 1841 and *Acanthoscurria sternalis* Pocock, 1903 were replaced by *Acanthoscurria gomesiana*, *A. juruenicola*, *A. natalensis* and *A. paulensis*; and the terminal taxon *Pterinopelma felipeleitei* was added. The presence/absence of setae for species not examined under the SEM was checked under the stereomicroscope, with comparisons to the micrographs obtained. We treated the presence/absence of setae on the legs (coxae and trochanters) as a whole, without distinction between the legs or palps and the surfaces (prolateral and retrolateral), considering that the repetition of the structures (cuticular setae) is a case of serial homology, and that scoring the presence of such setae on different legs as distinct characters would be misleading.

Regarding the characters, the following changes were applied to the original matrix of Bertani et al. (2011): characters 21 (presence of stridulating setae on the trochanters) and 22 (presence of stridulating setae on the coxae) were inactivated as they didn't distinguish different types of setae (see Results, below). Seven new characters referring to observed stridulating setae were added to the original matrix and numbered from the last character, as follows (all '0' absent and '1' present): (36) stridulating plumose setae on the coxae; (37) stridulating plumose setae on the trochanters; (38) stridulating claviform setae on the coxae; (39) stridulating claviform setae on the trochanters; (40) stridulating velvet setae on the coxae; (41) stridulating spiniform setae on the coxae; and (42) stridulating spiniform setae on the trochanters. The matrix for this revised and expanded dataset is shown in Table 1.

Table 2.—Results obtained from the trees found in the analyses.

K-Values	% of character weights	Nº of trees	Total fit
3.061	75	1	8.687
3.459	77.222	1	8.087
3.944	79.444	1	7.467
4.545	81.667	1	6.825
5.313	83.889	1	6.153
6.327	86.111	1	5.440
7.726	88.333	1	4.696
9.784	90.556	1	3.917
13.108	92.778	1	3.095
19.388	95	1	2.221

The most parsimonious trees were searched with heuristic methods and with implied weighting under different parameters (K-values), in order to perform a sensitivity analysis of the dataset. To decide upon which K-values to apply, we used TNT software 1.1 (Goloboff et al. 2008), with the script designed by Mirande (2009), which finds the K-values that divide the values of fit/distortion at regular intervals (script command line aaa 3 10 70 95 7). In order to avoid zero length branches (Coddington & Scharff 1995), nodes without support were collapsed (collapsing rule 1) and suboptimal trees were discarded. The K-values, percentages of the weights of the characters, number of trees and fit values are shown in Table 2. Character optimization and tree editing were done using Winclada 1.00.08 (Nixon 2002).

RESULTS

According to Pérez-Miles et al. (2005), a stridulatory seta needs to have a strong and rigid appearance, so that it can withstand the intense friction of stridulation. Studies such as those by Bücherl (1957), Pérez-Miles et al. (2005) and Bertani et al. (2008) show that stridulatory setae are always present on the coxae and trochanters. Genera examined and the types of stridulating setae they possess are shown in Table 3.

Setal morphology.—The types of stridulating setae found in our study are named and described below.

Claviform stridulating setae (Figs. 1–4, 15–18): The claviform stridulating setae have the appearance of a club, with the apical third slightly wider than the basal portion. The basal half is bare and the apical half is covered with coarse

barbs, which are directed towards the apical end, where there is a short area without barbs and with marked grooves. The claviform stridulating setae were first named by Pérez-Miles et al. (2005) for *Acanthoscurria suina*. The occurrence of these setae did not show any phylogenetic pattern in our study, however in all species analyzed they were found on the pro- and retrolateral faces of the trochanters of the palp and leg I in *Acanthoscurria*, *Cyrtopholis*, *Brachypelma*, *Theraphosa* and *Phormictopus*.

Plumose stridulating setae (Figs. 6–13, 19–22): The plumose stridulating setae were named by Perafán et al. (2015) for the genus *Aguapanela*. They are very slender, with the same width along their whole length, and the apical half is covered with many fine and long barbs, giving the appearance of a plume. Similar to the claviform setae, they have the apical end bare. In our dataset, the occurrence of this character did not show any phylogenetic pattern, however in all species analyzed they were found on the pro- and retrolateral faces of the frontal coxae and trochanters in *Lasiadora*, *Nhandu*, *Proshapalopus*, *Pterinopelma*, *Vitalius*, *Acanthoscurria juruenicola*, *A. natalensis* and *A. paulensis*.

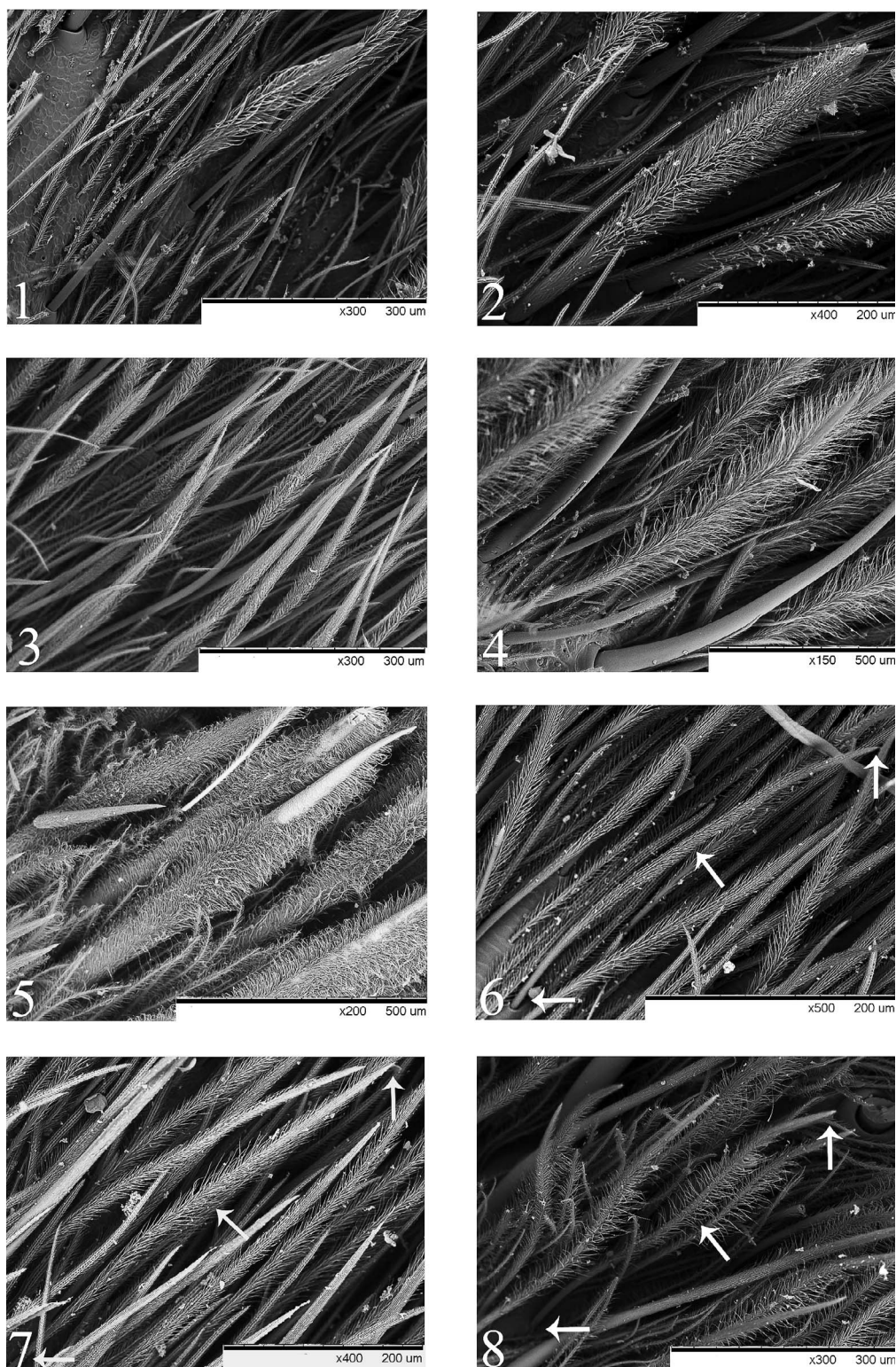
Velvet stridulating setae (Figs. 5, 23–26): The velvet stridulating setae are characterized by having a robust appearance, being thick and densely covered with fine and short barbs, giving them a velvety appearance. The apex is bare or partially covered by these fine barbs. These setae, named here as velvet stridulating setae (Figs. 23–26) in accordance with Bücherl (1957) (who also drew attention to their velvety morphology), are reported on the prolateral surfaces of coxae I and II in *Lasiadora*.

Spiniform stridulating setae (Figs. 14, 27–30): Similar in shape to a leg spine, the spiniform stridulating setae are thick, with a typical surface marked with longitudinal striae. Spines are conspicuously present on theraphosid spider legs, mainly on the tibiae and metatarsi. The spiniform stridulating setae are short, present on the coxae and trochanters (which is unusual), and interspersed with many fine barbs. We found the spiniform setae on the coxae of *Theraphosa*, and this character was also previously reported by Bertani et al. (2008), who reported their presence in *Pamphobeteus crassifemur* Bertani, Fukushima & Silva, 2008.

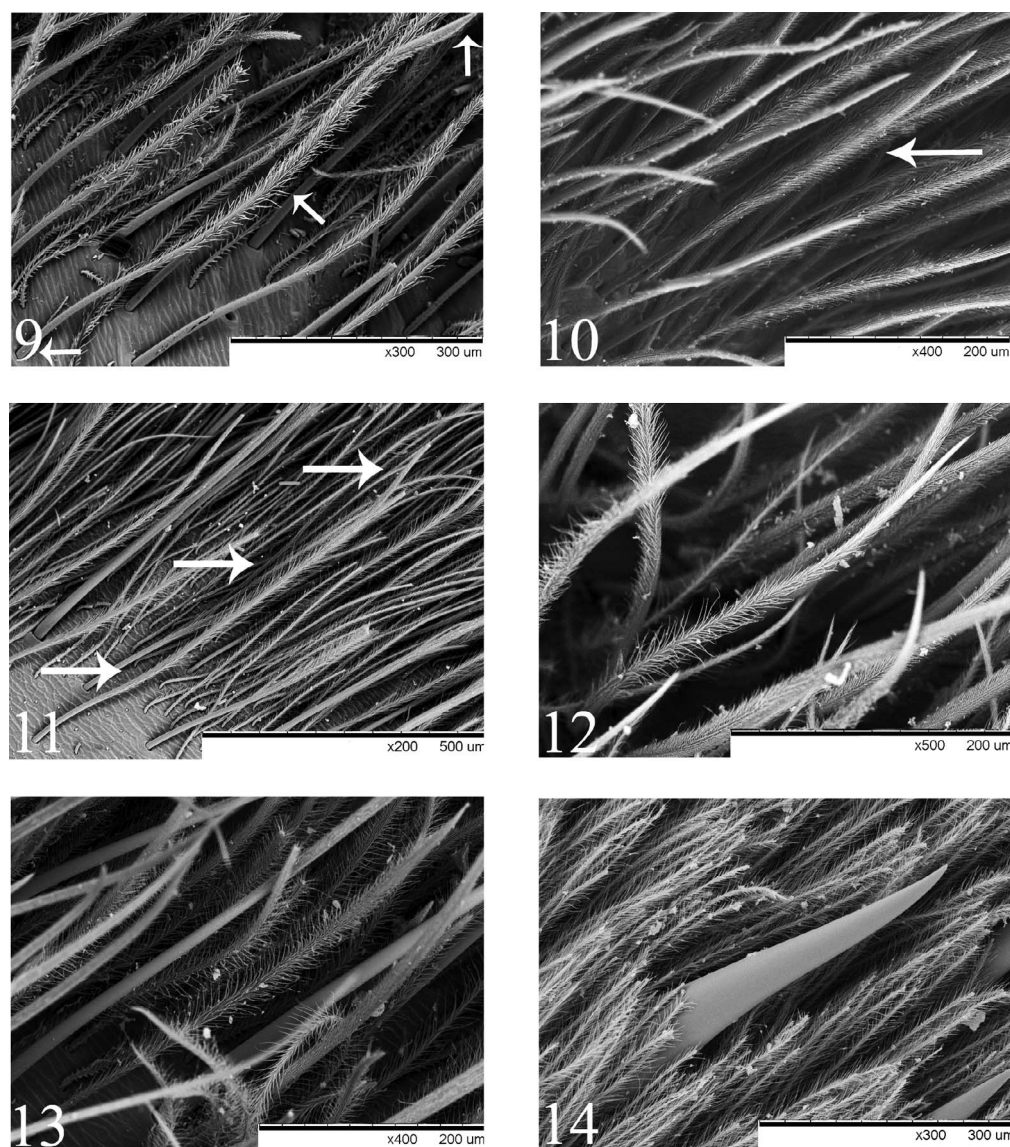
Cladistics.—The parsimony analyses resulted in a single tree of 103 steps (Fig. 31) with the same topology for all K-values (Table 2), and a consistency index of 0.49 and a retention index of 0.78. For the new characters added to the original

Table 3.—Genera examined and their types of stridulating setae.

Genera	Claviform	Plumose	Velvet	Spiniform	Figures
<i>Acanthoscurria</i>	X	X	-	-	Figs. 1, 11–13
<i>Cyrtopholis</i>	X	-	-	-	Fig. 2
<i>Theraphosa</i>	X	-	-	X	Figs. 3, 14
<i>Brachypelma</i>	X	-	-	-	Fig. 4
<i>Phormictopus</i>	X	-	-	-	Ortiz & Bertani (2005)
<i>Pamphobeteus</i>	-	-	-	X	Bertani et al. (2008); Figs. 9–12
<i>Proshapalopus</i>	-	X	-	-	Fig. 6
<i>Pterinopelma</i>	-	X	-	-	Fig. 7
<i>Lasiadora</i>	-	X	X	-	Figs. 5, 8
<i>Nhandu</i>	-	X	-	-	Fig. 9
<i>Vitalius</i>	-	X	-	-	Fig. 10



Figures 1–8.—Variations of stridulating setae: (1) claviform stridulating setae of *Acanthoscurria*; (2) claviform stridulating setae of *Cyrtopholis*; (3) claviform stridulating setae of *Brachypelma*; (4) claviform stridulating setae of *Theraphosa*; (5) velvet stridulating setae of *Lasiadora*; (6) plumose stridulating setae of *Proshapalopus*; (7) plumose stridulating setae of *Pterinopelma*; (8) plumose stridulating setae of *Lasiadora*. Arrows show the stridulating setae. Images: A. Galleti-Lima.



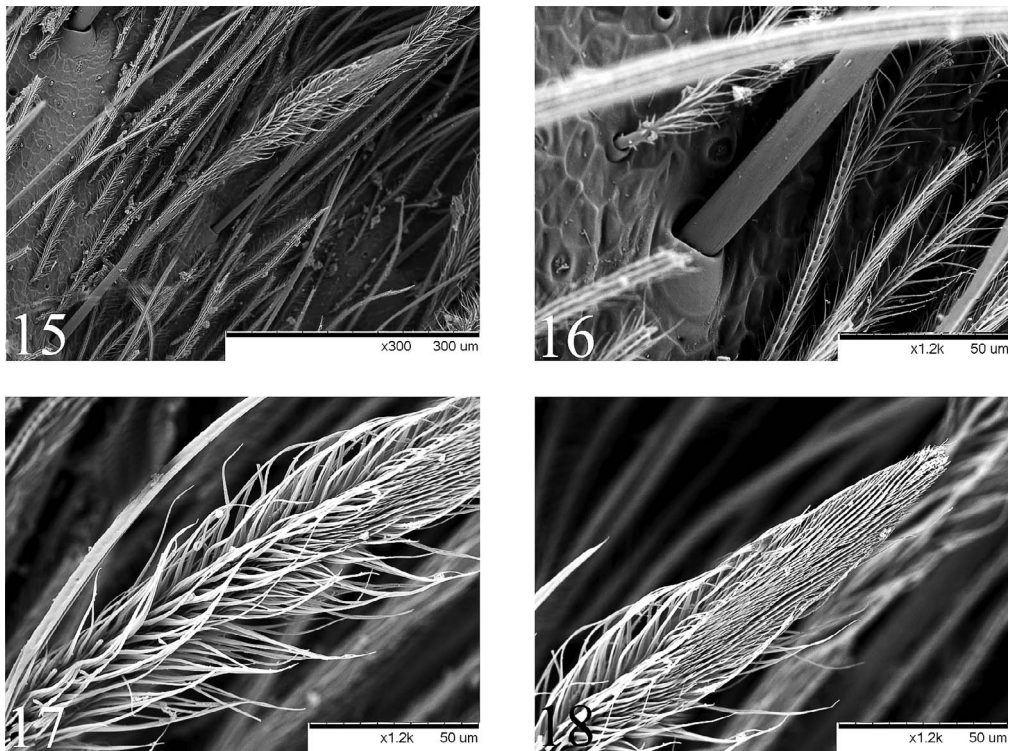
Figures 9–14.—Variations of stridulating setae: (9) plumose stridulating setae of *Nhandu*; (10) plumose stridulating setae of *Vitalius*; (11) plumose stridulating setae of *Acanthoscurria paulensis*; (12) plumose stridulating setae of *Acanthoscurria natalensis*; (13) plumose stridulating setae of *Acanthoscurria juruenicola*; (14) spiniform stridulating setae of *Theraphosa*; Arrows show the stridulating setae. Images: A. Galleti-Lima.

matrix of Bertani et al. (2011), optimizations are as follows: characters 36 (plumose setae on coxae) and 37 (plumose setae on trochanters) emerged as homoplastic synapomorphies that support the clades (*Lasiadora* + *Nhandu* + *Proshapalopus* + *Pterinopelma* + *Vitalius*) and (*Acanthoscurria juruenicola* + *A. natalensis* + *A. paulensis*). Character 38 (claviform setae on coxae) emerged as a homoplastic synapomorphy supporting the clades (*Acanthoscurria* + *Phormictopus cancerides* (Latreille, 1806)) and (*Brachypelma emilia* (White, 1856) + *Theraphosa*). Character 39 (claviform setae on trochanters) emerged as a homoplastic synapomorphy of the clades (*Acanthoscurria* + *Cyrtopholis portoricae* Chamberlin, 1917 + *Phormictopus cancerides*) and (*Brachypelma* + *Theraphosa*). Character 40 (velvet setae on coxae) emerged as an autapomorphy of the genus *Lasiadora*. Character 41 (spiniform setae on coxae) emerged as a homoplastic character, shared by the genera *Pamphobeteus* and *Theraphosa*, whereas character 42

(spiniform setae on trochanters) emerged as an autapomorphy of the genus *Pamphobeteus*.

DISCUSSION

According to Pérez-Miles et al. (2005), a stridulating seta needs to be strong enough to withstand the intense friction of stridulation. Despite their barbed morphology, these setae can be difficult to recognize under the stereomicroscope. We observed that all setae described here as stridulating present a rigid structure that is most noticeable when one attempts to bend them with fine forceps. Moreover, all stridulating setae documented in this study show a bare basal portion, a distal portion covered with numerous barbs, differing mainly in density among the distinct types, and an apex with a rough surface. However, distinguishing among the setal types is only possible when their ultrastructure has been previously well



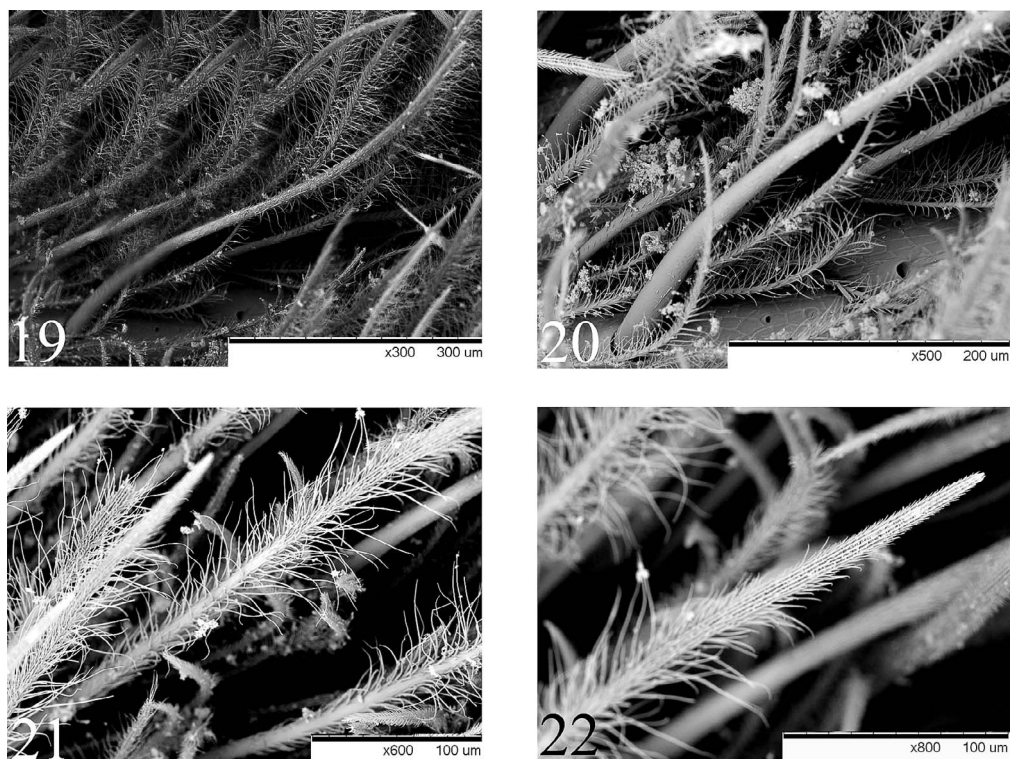
Figures 15–18.—Morphology of claviform stridulating setae; *Acanthoscurria* shown as an example. (15) Overview (arrows indicate a stridulating seta); (16) Base; (17) Middle region; (18) Apex. Photos: A. Galleti-Lima.

examined under the SEM for later comparison under the stereomicroscope. Since the first arachnologists started to notice the presence of distinct setae on the basal leg articles of Theraphosidae (Pocock 1901), there have been numerous proposals for naming these structures. Our study is the first

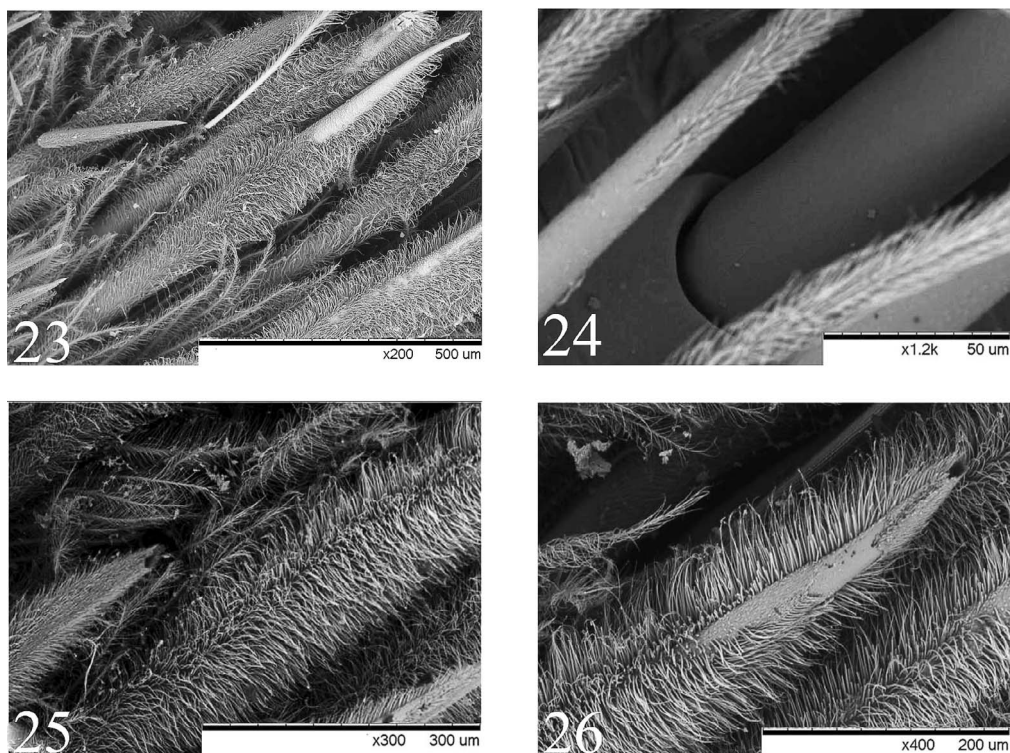
descriptive account that includes examinations under SEM. Therefore, the setal types described above are an attempt to formalize the classification of the distinct variations of these setae.

Table 4.—Changes in terminology of stridulating setae of some Theraphosinae.

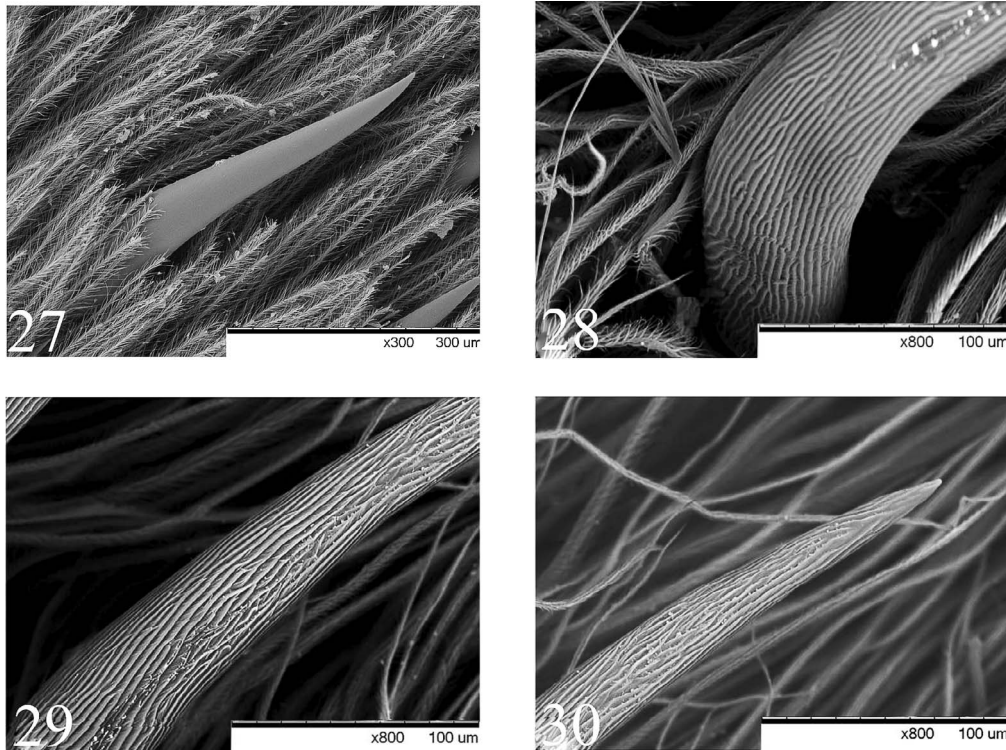
Genera	Name of stridulating setae (literature)	Name of stridulating setae (named in this work)
<i>Lasiodora</i> C. L. Koch, 1850	Plumose	Velvet
<i>Acanthoscurria</i> Ausserer, 1871	Mello-Leitão 1921, Bertani 2001, Perez-Miles et al. 1996 Clavate Pocock 1903; Claviform Pérez-Miles et al. 2005	Claviform
<i>Theraphosa</i> Thorell, 1870	Black spine and plumose setae Gerschman & Schiapelli 1966, Marshall et al. 1995, Tinter 1991, Perez-Miles et al. 1996, Rudloff & Weinmann 2010	Spiniform and Claviform
<i>Pamphobeteus</i> Pocock, 1901	Spiniform Bertani et al. 2008	Spiniform
<i>Phormictopus</i> Pocock, 1901	Plumose Perez-Miles et al. 1996, Ortiz & Bertani 2005	Claviform
<i>Cyrtopholis</i> Simon, 1892	Clavate Pocock 1903; Plumose Rudloff 1994, Perez-Miles et al. 1996	Claviform
<i>Aguapanela</i> Perafán, Cifuentes & Estrada-Gomez 2015	Plumose Perafán et al. 2015	Plumose



Figures 19–22.—Morphology of plumose stridulating setae; *Lasiodora* shown as an example. (19) Overview (arrows indicate a stridulating seta); (20) Base; (21) Middle region; (22) Apex. Photos: A. Galleti-Lima.



Figures 23–26.—Morphology of velvet stridulating setae; *Lasiodora* shown as an example. (23) Overview (arrows indicate stridulating setae); (24) Base; (25) Middle region; (26) Apex. Photos: A. Galleti-Lima.



Figures 27–30.—Morphology of spiniform stridulating seta; *Theraphosa* shown as an example. (27) Overview; (28) Base; (29) Middle region; (30) Apex. Photos: A. Galletti-Lima.

The variation known as claviform stridulating setae (Figures 15–18) was described by Pérez-Miles et al. (2005) for *Acanthoscurria suina*, on the retrolateral palpal trochanter and on the prolateral trochanter I, and they were also found on other species of *Acanthoscurria*, *Cyrtopholis* and *Phormictopus*, corroborating their close relationships (Pérez-Miles et al. 1996; Bertani 2000; Perafán et al. 2015). The homoplastic presence of claviform setae in *Brachypelma* and *Theraphosa* was unexpected, as representatives of these two genera have already been reported as possessing a stridulatory apparatus (Pocock 1901; Gerschman & Schiapelli 1966), but were never previously examined under SEM. Ortiz & Bertani (2005) and Rudloff (1994), when describing new species of *Cyrtopholis* and *Phormictopus*, respectively, used the term plumose to refer to the claviform setae, which according to our characterization should be referred to with the latter name.

The plumose setae, considered here, are hardly noticeable in some spiders as they are very thin and may be interspersed with other body and stridulating setae. First reported in the genus *Aguapanela* (Perafán et al. 2015), we also found these setae in *A. juruenicola*, *A. natalensis*, *Acanthoscurria paulensis*, *Lasiadora*, *Nhandu*, *Proshapalpus*, *Pterinopelma* and *Vitalius*. Other types of setae, such as the velvet setae of *Lasiadora*, were also previously called plumose by Bertani (2001).

The velvet setae are clearly visible on all representatives of the genus *Lasiadora*, being restricted to the upper portion of the prolateral coxae I and II, and characterized mainly by their thick morphology. The velvet setae were resolved as autapomorphic for *Lasiadora*, which are known to produce an audible sound (pers. obs.). Interestingly, velvet setae, along with plumose setae, had not been noticed before in

Theraphosinae, and spiders of the genera *Nhandu*, *Proshapalopus*, *Pterinopelma* and *Vitalius* bear only the plumose type, which are rather delicate compared to the velvet type; these genera are not yet known to produce an audible stridulating sound. According to Bücherl et al. (1971) and Bertani et al. (2008), there are other cases of theraphosine spiders producing audible stridulating sounds, and they all bear two distinct types of stridulating setae: *Theraphosa blondi*, which has claviform and spiniform types; some species of *Acanthoscurria*, with plumose and claviform types; and *Pamphobeteus* species, with the spiniform type and possibly also the plumose type. Although we did not have any specimens of *Pamphobeteus* available to scan, the illustrations in Bertani et al. (2008) show some setae very similar to the spiniform type that we describe herein. It is important to note that different stridulating setae may be present on the same individual, as in representatives of *Acanthoscurria juruenicola*, *A. natalensis* and *A. paulensis* (claviform setae and plumose setae), *Theraphosa blondi* (claviform setae and spiniform setae), and *Lasiadora* species (velvet setae and plumose setae).

The lack of a comparative study including both distinct types of stridulating setae and descriptions of their ultrastructure, and the recognition of these setae by many authors, has resulted in a confusing terminology. As discussed above, the terminology we use for each seta is a proposal to formalize the terminology for similar structures. Table 4 shows the changes in the nomenclature of stridulating setae and the genera in which they occur, according to the literature.

The character coding that we adopt for stridulating setae (i.e., without appendage and surface discrimination) is justified

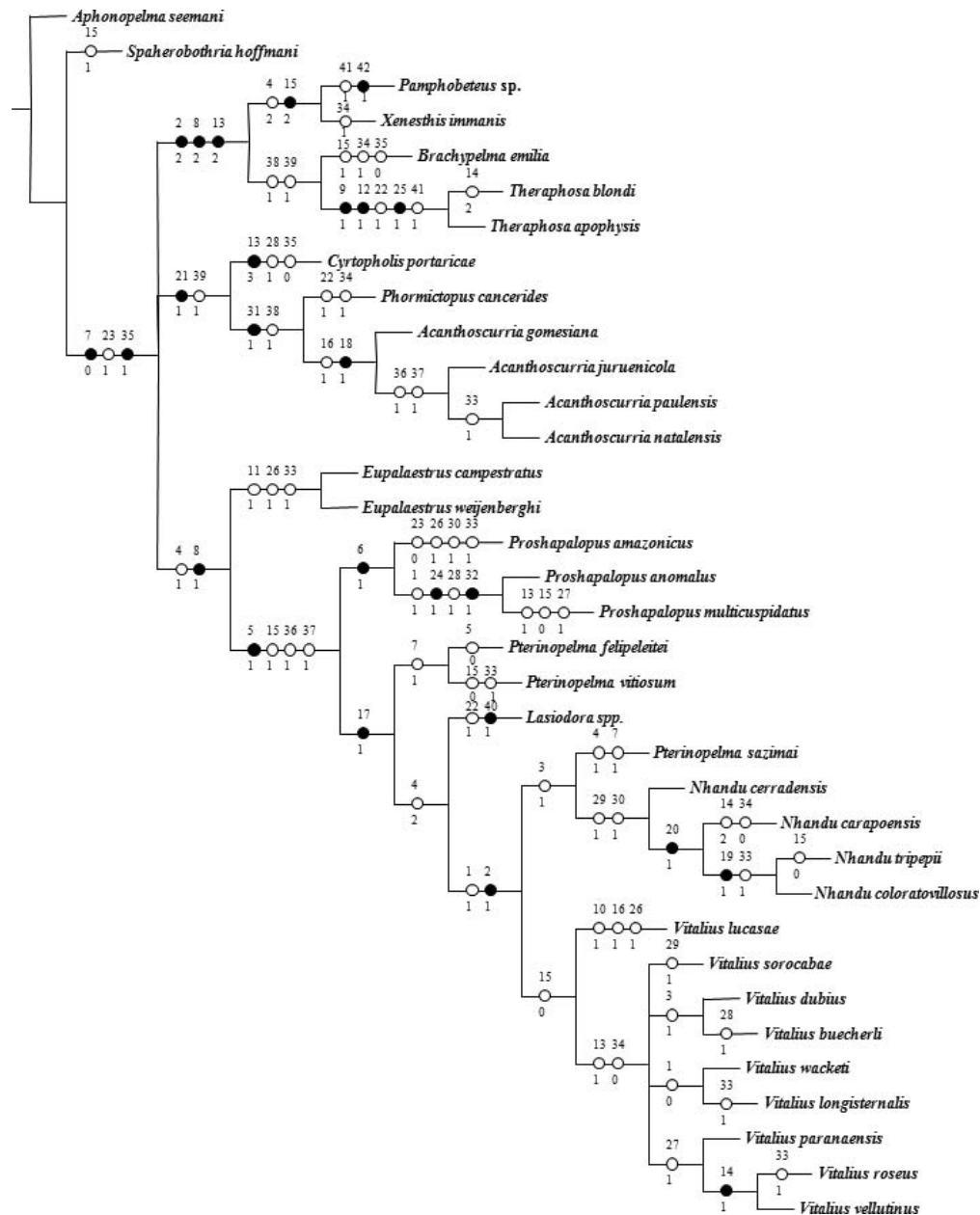


Figure 31.—Cladogram for some species of Theraphosinae, following re-analysis of Bertani et al. (2011). White circles indicate homoplastic character states, and black circles indicate synapomorphies.

by the likely evolution of these structures under serial or iterative homology (Wagner 1989). According to Van Valen (1993), the repetition of homologous structures is, in many cases, guided by copies of the structure on which they originate. Starck (1985) observed that stridulating setae are morphologically different and found in distinct positions, and suggested that these organs aren't homologous, having developed independently within Theraphosinae. However, Haszprunar (1992) explains that during evolution, localized copies of these setae may undergo changes into more specialized structures, as also suggested by Van Valen (1994) based on studies by de Beer (1971) and Roth (1988). Wagner (1989) recognized two types of homology: (1) serial homology, whereby shared similar structures are present on the same

organism; and (2) evolutionary homology, whereby shared similar structures are present on different taxa. In the case of evolutionary homology, we should consider the possibility that stridulating setae are modifications of the covering setae, as proposed for the origin and evolution of urticating setae in Theraphosinae (Bertani & Guadanucci 2013).

A more extensive survey with a comparative approach including other representatives of Theraphosinae and Theraphosidae may reveal additional variation among these setae. Moreover, behavioral and functional morphology studies would clarify whether these setae are in fact stridulating and whether distinct setae produce different vibrating sound wave frequencies. Such a study would require specific and precise equipment for soundwave recording.

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