TARSAL SCOPULA DIVISION IN THERAPHOSINAE (ARANEAE, THERAPHOSIDAE): ITS SYSTEMATIC SIGNIFICANCE

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ABSTRACT. A study of entire/divided tarsal scopulae distribution was carried out on 28 genera of Theraphosinae. Although this character has been considered an important taxonomic tool for more than a century, present findings show that the scopula condition is related to spider size. These results call into question the systematic value of tarsal scopula division. Fine structure of theraphosid scopula is described, being different from that previously described for Araneomorphae. Function and phylogeny of scopula condition are discussed.

RESUMEN. Se realizó un estudio de la distribución del carácter escópulas tarsales enteras/divididas en 28 géneros de Theraphosinae. A pesar de que dicho carácter fue considerado importante en taxonomía durante más de un siglo, los resultados mostraron que la condición de la escópula está relacionada con el tamaño de la araña. Estos resultados permiten cuestionar el valor sistemático de la condición de las escópulas. Se describe la estructura de la escópula de las terafósidas, encontrándose diferencias con las escópulas descriptas previamente para las Araneomorphae. Se discute la función y filogenia de los tipos de escópula.

The structure and function of tarsal scopulae have been studied extensively in araneomorph spiders (Homann 1957; Foelix & Chu-Wang 1975; Rovner 1978; Miller et al. 1988; Roscoe & Walker, 1991), and less thoroughly in Mygalomorphae. The structure of tarsal scopulae in Theraphosidae was discussed by Foelix & Chu-Wang (1975) in *Dugesiella* Pocock 1901 and more recently studied by Roscoe & Walker (1991) in *Sericopelma rubronitens* Ausserer 1875 and by Prentice (1992) in *Aphonopelma paloma* Prentice 1992. Despite our limited knowledge, the tarsal scopulae condition has been used in Theraphosidae systematics for a long time.

For more than a century the character "tarsal scopulae entire or divided", has been widely used in taxonomy of Theraphosidae to diagnose genera and subfamilies. Entire tarsal scopulae have homogeneous adhesive hairs analogous to those described as Type A by Rovner (1978) in *Lycosa* spp. Divided scopulae have a longitudinal band of long thick setae similar to Type B of Rovner (1978). Beginning with Ausserer (1871), and Simon (1889, 1892) to the present, this character has been considered an important taxonomic tool. G. de Pikelin & Schiapelli (1973), following Ausserer (1871), considered it a key character of Ischnocolinae and pointed out that scopulae division is common in juveniles of all theraphosids,

becoming entire in adults of some subfamilies (such as Theraphosinae). Raven (1985) used entire/divided scopula to separate genera and groups in Theraphosidae and also studied anterior-posterior gradation of the character. Smith (1988) disregarded the scopula division, considering that in many theraphosids it only means immaturity, but later (Smith 1990) considered it an important taxonomic character for Ischnocolinae and Eumenophorinae. Pérez-Miles (1992) polarized this character on the basis of ontogeny, concluding that an entire scopula could be a synapomorphy of some genera of Theraphosinae.

A study of entire/divided scopula distribution was carried out on most (28) genera of Theraphosinae, four of Aviculariinae and four of Harpactirinae. Fine structure of tarsal scopula of five Uruguayan species from different genera is described and compared. The results of this study call into question the systematic and phylogenetic significance of the character. The function and phylogeny of tarsal scopulae in Theraphosinae are discussed.

METHODS

Taking into account that width of tarsal scopula division increases in hind legs (Raven 1985), legs IV were studied to avoid ambiguity with respect to entire or divided condition. Few iso-
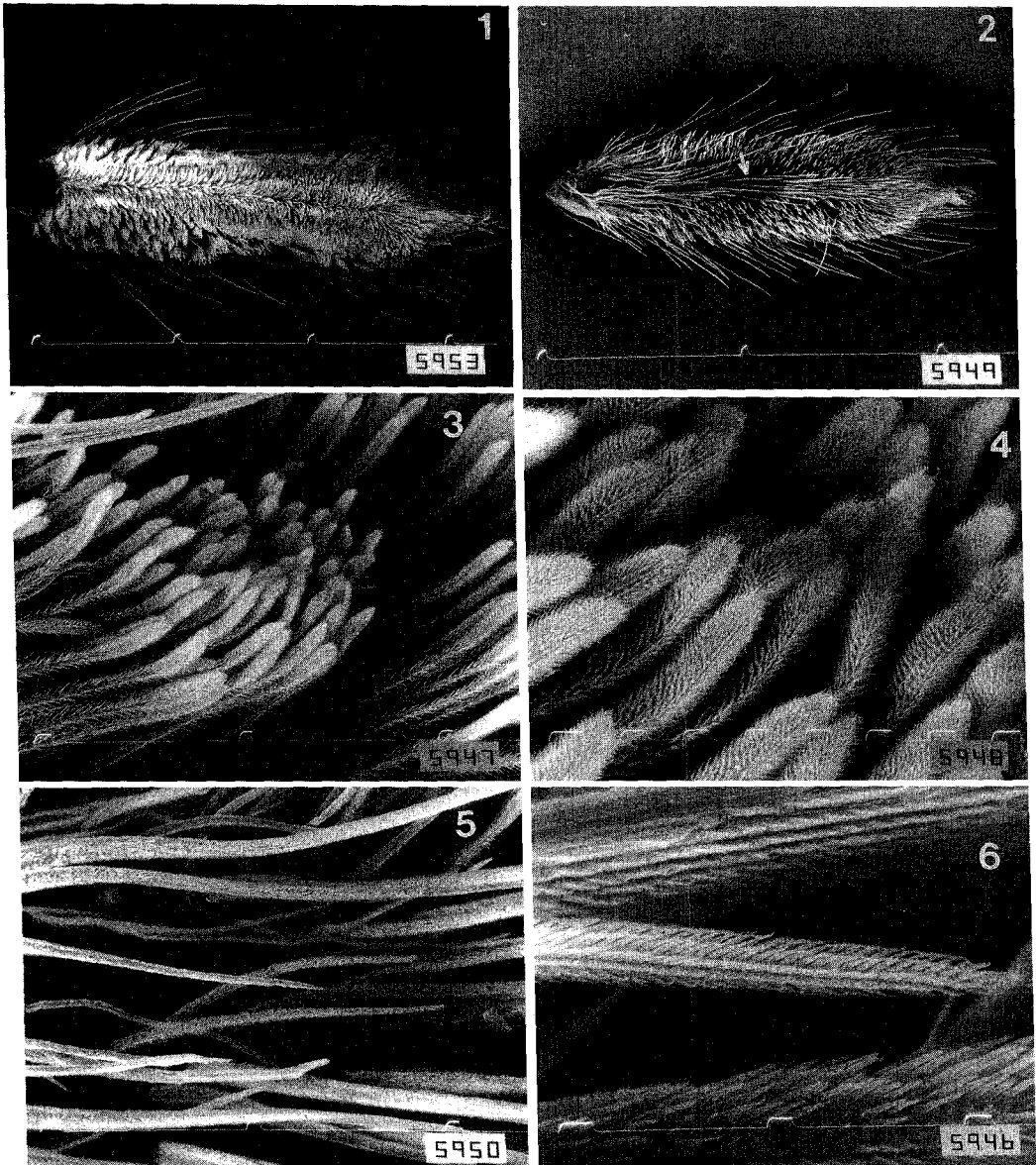
Figures 1–6.—Structures of the tarsal scopula. 1. *Acanthoscurria suina*, tarsus IV, ventral view, showing entire scopula, Type A hairs; 2. *Homoeomma uruguayense*, tarsus IV, ventral view, showing divided scopulae. Arrow shows the band of Type B scopula hairs, with Type A hairs laterally; 3. Type A hairs on tarsus IV of *Ceropelma longisternale*, showing the cylindrical stalk and the club-shaped distal zone. The entire hair is covered by small spines which are denser in the distal portion; 4. Tips of Type A hairs of *Ceropelma longisternale*, showing the small spines covering the hairs; 5. Type B hairs on tarsus IV of *Homoeomma uruguayense*, showing their subconical shape; 6. Type B hair tip on tarsus IV of *Ceropelma longisternale*, showing the small spines covering it. Scales: Figs. 1, 2 = 2 mm; Figs. 3, 5 = 0.2 mm; Figs. 4, 6 = 0.02 mm.

lated long and fine hairs (not line ordered) in tarsal scopulae were not considered the divided condition.

Observations were made with a stereoscopic microscope submersing the specimens in 80% alcohol. Light microscope studies were carried out to observe and measure scopula hairs. To estimate spider size, carapace length (CL) was

Table 1.—Tarsal scopula condition (TS) and carapace length (CL) of holotypes of type species, of non type species (*) or congeners (**) of Theraphosinae and some Aviculariinae and Harpactirinae. Abb = abbreviatures; LOC = location of examined material: BMNH = British Museum of Natural History, London; IB = Instituto Butantan, Sao Paulo; MACN = Museo Argentino de Ciencias Naturales, Buenos Aires; MHNP = Muséum National d'Histoire Naturelle, Paris; MHNM = Museo Nacional de Historia Natural, Montevideo; MZSP = Museu de Zoologia, Sao Paulo; NMV = Naturhistorisches Museum, Vienna; SI = Smithsonian Institution, Washington; SAM = South African Museum, Capetown; ZMB = Zoologisches Museum, Berlin; NE = not examined, data from literature. Eighteen types of *Grammostola* spp. (all with entire scopulae) are omitted due to space reasons.

	Abb	CL	TS	LOC
Theraphosinae				
Acanthoscurria geniculata (Koch 1842)	Ag	25.5	E	BMNH
Acanthoscurria suina (Pocock 1903)	As	18.5	E	BMNH*
Aphonopelma seemani (Cambridge 1897)	Ase	20.0	E	NE
Aphonopelma crinita (Pocock 1901)	—	13.0	D	BMNH*
Aphonopelma paloma Prentice 1992	—	5.7	D	NE*
Brachypelma emilia (White 1856)	Be	21.5	E	MHNP
Ceropelma insulare Mello-Leitao 1923	Ci	7.8	D	MZSP
Ceropelma flavohirtus (Simon 1889)	—	6.0	D	MHNP*
Ceropelma longisternale Sch. & Ger. 1942	—	7.5	D	MACN*
Ceropelma semiauranticum (Simon 1897)	—	6.2	D	MHNP*
Crypsidromus isabellinus Ausserer 1871	Cis	12.0	D	NMV
Citharacanthus longipes (Cambridge 1897)	Cl	26.0	E	BMNH
Cyriocosmus sellatus (Simon 1889)	Cs	4.3	D	MHNP
Cyrtopholis cursor (Ausserer 1875)	Cc	13.0	E	BMNH
Cyclosternum schmardae Ausserer 1871	Csc	17.8	D	MHNP
Cyclosternum rufohirta (Simon 1889)	Cr	14.0	D	MHNP*
Dryptopelma janthina (Simon 1888)	Dj	14.4	D	MHNP
Eupalaestrus campestratus Simon 1891	Ec	20.0	E	MHNP
Eupalaestrus weijenberghi (Thorell 1894)	Ew	14.6	E	BMNH*
Eupalaestrus tarsicrassus Bucherl 1947	—	17.6	E	IB*
Euathlus truculentus (Ausserer 1875)	Et	20.0	E	BMNH
Grammostola mollicoma (Ausserer 1875)	Gm	19.0	E	BMNH*
Hapalotremus albipes Simon 1903	Ha	9.7	D	MHNP
Hapalopus formosus Ausserer 1875	Hf	9.0	D	NMV
Holothele sericeus (Simon 1903)	Hs	7.2	D	MHNP*
Homoeomma stradlingi Cambridge 1881	Hs	17.5	E	BMNH
Homoeomma uruguayense (Mello-Leitao 1946)	Hu	7.0	D	MHNM*
Lasiodora klugii (Koch 1842)	Lk	27.0	E	BMNH
Mygalarachne brevipes Ausserer 1871	Mb	17.0	E	NMV
Megaphobema robusta (Ausserer 1875)	Mr	28.0	E	BMNH
Phormictopus cancerides (Latreille 1806)	Pc	20.7	E	MHNP
Paraphysa manicata Simon 1892	Pm	20.7	E	MHNP
Pamphobeteus nigricolor (Ausserer 1875)	Pn	26.5	E	BMNH
Phrixotrichus roseus (Guerin 1838)	Pr	28.2	E	MHNP
Sphaerobothria hoffmani Karsch 1879	Sh	17.5	E	BMHN**
Schizopelma macropus (Ausserer 1875)	Sm	12.0	D	BMNH*
Theraphosa blondi (Latreille 1804)	Tb	34.2	E	MHNP
Xenesthis immanis (Ausserer 1875)	Xi	29.0	E	BMNH
Aviculariinae				
Avicularia sp.	—	22.0	E	MHNM**
Ephebopus murinus (Walckenaer, 1837)	—	15.3	D	BMNH
Iridopelma hirsutum Pocock 1901	—	16.5	D	BMNH
Pachistopelma rufronigrum Pocock 1901	—	12.5	D	BMNH

Table 1.—Continued.

	Abb	CL	TS	LOC
Harpactirinae				
Ceratogryus darlingii Pocock 1897	—	23.5	E	BMNH
Coelogenium pillansi Purcell 1902	—	24.0	E	SAM
Eucratoscelus longipes Pocock 1898	—	17.0	E	BMNH
Harpactirella treleaveni Purcell 1902	—	6.8	D	SAM

measured with an ocular micrometer. Fine structure of scopulae was documented using a scanning electronic microscope.

Holotypes and additional material examined are referenced in Table 1. In *Aphonopelma seemanni* (Cambridge 1897), CL and scopula condition were taken from Valerio (1980) and in *A. paloma* from Prentice (1992).

I followed Raven (1985) in classification and nomenclatural aspects, with the following exceptions: a) *Aphonopelma* Pocock 1901 precedence over *Rhechostica* Simon 1892 (ICZN 1991, Opinion 1637); b) *Pterinopelma* Pocock 1901 transferred to *Eupalaestrus* Pocock 1901 (Pérez-Miles 1992); c) *Brachypelma* Simon 1891 restored (Schmidt 1991); d) *Oligoxystre* Vellard 1924 and *Stichoplastus* Simon 1889 removed from Theraphosinae (Pérez-Miles 1992); e) *Ephebopus* Simon 1892 transferred from Theraphosinae to Aviculariinae (Lucas et al. 1991).

Statistical analyses were carried out with the Presta P-C, V1.1, package developed at the Centro Ramón y Cajal, Spain. Mean comparisons were done by Student *t*-test, with restrictions to variance (Snedecor's *F*).

RESULTS

Structure of scopulae.—Two types of tarsal scopulae were found within the Theraphosinae: entire and divided. A third type of scopula (divided by strong spines) was present in *Acanthopelma* Cambridge 1897 but is not considered here. The entire scopula (Fig. 1) has homogeneous adhesive hairs on the ventral surface of the tarsus. Following Rovner's (1978) nomenclature on lycosids, and without establishing any homology (only positional criteria), I call them Type A hairs.

Divided scopula (Fig. 2) has another type of hairs (called Type B) arranged on a medial longitudinal band which lies between the two ventro-lateral bands of Type A hairs.

Type A hairs are cylindrical in their proximal portion (stalk) and club-shaped in their distal portion (Fig. 3). No differences in hair morphology among genera were detected but the length varies relative with spider size. Total length of Type A hairs is 0.49 mm ($\pm$ 0.023) in *Acanthoscurria suina* (Pocock 1903); 0.66 mm ($\pm$0.027) in *Grammostola mollicoma* (Ausserer 1875); 0.43 mm ($\pm$0.044) in *Eupalaestrus weijenberghi* (Thorell 1894); 0.35 mm ($\pm$ 0.032) in *Ceropelma longisternale* Schiapelli y Gerschman 1942; and 0.30 mm ($\pm$0.029) in *Homoeomma uruguayense* (Mello-Leitão 1946). All possible mean comparisons among hair length of these five Uruguayan species resulted in significant differences ($P < 0.00001$). However, distal zone length (approx. 0.096 mm) did not show significant differences in most comparisons, except between *A. suina* with *C. longisternale* and with *H. uruguayense*. Hairs are covered by small spines oriented at an angle of 30° with the axis of the hair and with tips oriented toward the apical region (Fig. 4); no triangular end feet were observed in such spines. These spines are distributed in an orderly fashion and are more dense in the distal region (Figs. 3, 4). Type A hairs are more or less vertical or slightly inclined (80° with respect to the surface of tarsus) with tips orientated distally.

Type B hairs are subconical (Fig. 5). They are longer (0.607 mm in *H. uruguayense* and 0.596 mm in *C. longisternale*) and thicker than Type A; no significant differences in hair mean length were found between these two species ($P = 0.866$). The surface is also covered by small spines, resembling those of Type A, but less dense (Fig. 6). Type B hairs have angles of approximately 30° with respect to the ventral surface of the tarsus with their tips orientated distally.

Character distribution.—A close relation between size and tarsal scopula condition was found (Fig. 7, Table 1). Tarsal scopulae are divided in the small species of Theraphosinae and entire in large ones. Size/scopular condition relationship was observed between adults of different species of differing sizes and between adults (or large
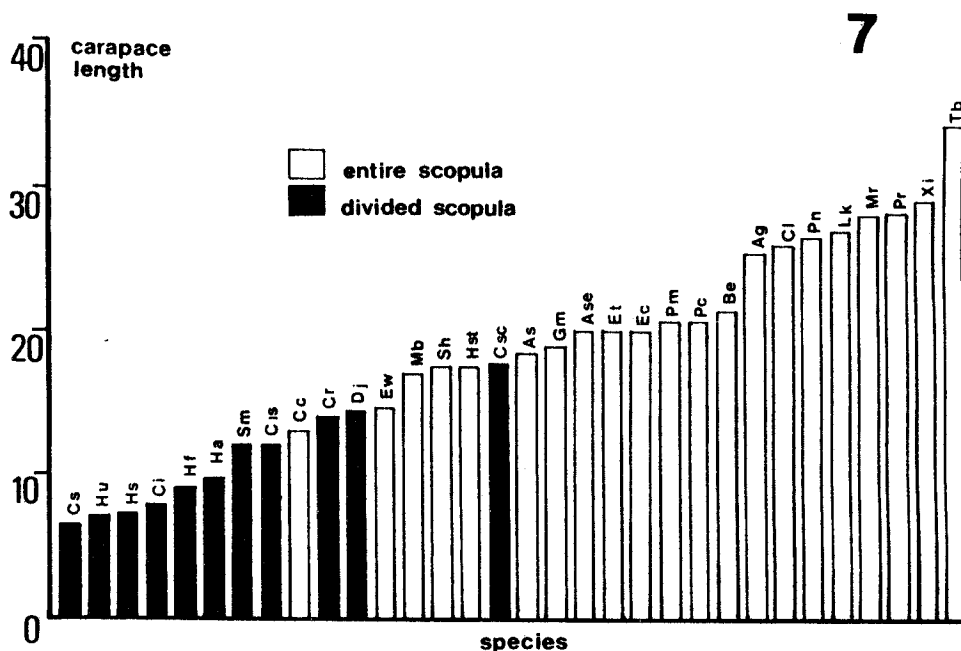
Figure 7.—Tarsal scopula condition and carapace length (in mm) in Theraphosinae species (abbreviations as in Table 1).

juveniles) and small juveniles of the same species (which have entire scopula as adults).

Divided tarsal scopulae were found in type species of seven genera of Theraphosinae, plus *Holothele* and *Schizopelma* (non type species); entire tarsal scopulae were found in type species of 19 genera of Theraphosinae (Table 1).

Size/scopular condition relationship was also found between species within same genus. For

Figure 8.—*Homoeomma stradingli* (Holotype male), ventral view of tarsus IV, showing entire scopula (Type A hairs).

example, in *Homoeomma* (described by Simon 1892 as having entire scopula but diagnosed by Gerschman & Schiapelli 1972 as having divided scopulae), large species (*H. stradlingi* (Cambridge 1881), carapace length 17.5 mm) have entire scopulae (Fig. 8) whereas small ones (*H. uruguayense*, CL = 7 mm) have divided scopulae (Fig. 2). A similar phenomenon was observed in *Aphonopelma*: *A. crinita* (CL = 13 mm) and *A. paloma* (CL = 5.7 mm) have divided scopula while *A. seemanni* (Cambridge 1897) (CL = 20 mm) has entire scopulae. Only two species contradicting the size/scopular condition relation were found: *Cyrthopholis cursor* (Ausserer 1875) and *Cyclosternum schmardae* Ausserer 1871.

Examined theraphosid species with divided scopula have a mean CL = 10.66 mm (SD = 3.50), while species with entire scopula present a mean CL = 22.11 mm (SD = 5.27). A comparison of CL means showed highly significant differences between spiders with entire or divided scopulae ($t = 6.285$, $P = 0.0000014$). As shown in Fig. 7, Theraphosinae species up to 12 mm of carapace length exhibited divided scopulae only; species between 12 and 18 mm had either entire or divided scopulae, and species larger than 18 mm exhibited entire scopulae only. This trend

was also observed in type species of some genera of Aviculariinae and Harpactirinae (Table 1).

Size/scopular division relationship is also hold between small juveniles and large ones or adults of the same species (which have entire scopulae as adults). Some evidence of a shift in this character condition related to the individual's growth was found. A study of juveniles of *G. mollicoma* showed divided scopulae when CL is 10.40 mm, scopulae proximally divided and distally entire when CL is 15.60, and entire scopulae when CL is 16.00 mm (clearly before maturity molt when CL is more than 19.00 mm).

DISCUSSION

Character distribution and phylogenetic significance.—Since Ausserer (1871), "entire/divided scopula" has been extensively considered as an important taxonomic tool in Theraphosidae. Recently Pérez-Miles (1992) polarized this character by ontogeny, to apply it in a preliminary phylogenetic analysis of Theraphosinae; concluding that entire is apomorphic. Present results, however, question the use of this character in phylogenetic systematics. At least *Aphonopelma* and *Homoeomma* are polythetic for this character, although there would be several synapomorphies supporting the monophyly of each genus (e. g., the digitiform apophysis of the bulb in *Homoeomma*). Both states are present within the Theraphosinae and its sister group, (*sensu* Lucas et al. 1991, the Aviculariinae) and in the Harpactirinae. A close relation between body size and scopula condition in these taxa and also within *Aphonopelma* and *Homoeomma* suggests a functional adaptation or a developmental effect. Influence of environment and interaction with phylogeny in this character remains obscure. Considering character distribution and since size could change independently in diverse taxa, similarity in scopulae condition will not clearly reveal phylogenetic relationship in Theraphosinae. *Acanthoscurria suina* and *Eupalaestrus weijenberghi*, both with entire scopulae and large CL, live in similar environments (holes in meadows), which would be interpreted as convergence. However, *Grammostola mollicoma* and *Avicularia* sp., also with entire scopula and large CL, live in different environments (the former under stones in hills and the latter arboreal). Similarly Miller et al. (1988) observed that lycosid groups with different tendencies or

abilities to move (burrowers and non burrowers) did not show differences in scopulae morphology, which was conflicting with the incidence of adaptive pressures on locomotion. It also seems possible that theraphosids with different scopula condition and CL live in similar habitats. Field observations in Uruguay showed that theraphosids of similar adult sizes do not occur in the same habitat, with the exception of *A. suina* and *E. weijenberghi*.

The exceptions observed in *C. cursor* and *C. schmardae* could reveal possible phylogenetic constrains to the character.

Ontogeny and scopula condition.—All Theraphosidae have divided scopulae in juvenile states, but they become entire (Type B hairs absent) in adults of several species (Gerschman & Schiapelli 1973). Present findings in *G. mollicoma* showed that the entire scopula condition is reached much before the adult state. This suggests that scopular condition is more related to size and weight than to maturity. On the other hand, small species retain divided scopulae throughout their lives.

Structure and function.—Tarsal scopulae hairs (Type A) observed here in theraphosid spiders have different morphology from those described for *Philodromus aureolus* (Foelix & Chu-Wang 1975; Foelix 1982) and from those of Lycosidae (Rovner 1978; Miller et al. 1988). The main difference is that triangular end-feet were not found in spines of Type A hairs of Theraphosidae, which agrees with the observation of Roscoe & Walker (1991) in *Sericopelma rubronitens*. Differences in Type A hair size were found with *Philodromus* and within some genera of Theraphosinae, probably due to a correlation with spider size. In Theraphosinae, this correlation is associated mainly with hair stalk (with high variability) but not with distal zone (less variable). Type B hairs were similar to those described by Rovner (1978) and Miller et al. (1988) in Lycosidae; but judging from their photographs, those of theraphosids have a more spine-like appearance.

Differences in hair fine structure between Theraphosidae and Philodromidae may relate to differences in adhesive requirements between both taxa: Philodromidae are small sized, light weight (with trachea); whereas Theraphosidae are large and heavy (with booklungs instead of trachea). Also differences in hair structure would be related to differences in hair distribution, which is restricted to claw tufts in *Philodromus*. The resemblance between Type B hairs of *Lycosa* spp.

and Theraphosinae would be a case of functional convergence: the traction role during locomotion established by Rovner (1978) in the former and here suggested for Theraphosidae. This is also supported by the wandering behavior of both taxa.

Functionally, Type A hairs could be more adhesive than Type B which are related to traction on smooth surfaces in *Lycosa* spp. (Rovner 1978). Type B hair morphology (similar to *Lycosa* spp.) along with the increase of band width in posterior legs, support their traction role during locomotion. In large, heavy theraphosids (some of them arboreal) adhesive requirements probably predominated, favoring Type A hairs, but this was not the case for small and light species. Consequently, functional arguments also support the influence of size and weight in determining scopula condition. Mechanisms of adhesion attributed by Roscoe & Walker (1991) to scopulae hairs (molecular adhesion and surface tension effect) would be both related to spider weight.

In lycosid spiders, which do not climb on smooth surfaces, the main role attributed to scopular hairs (mainly Type A) is prey capture (Rovner 1978; Miller et al. 1988). In theraphosids it could also serve in prey capture, mainly in crevices. However, considering that theraphosids can climb on more or less smooth surfaces, the scopulae seem to play a more important adhesive role in locomotion.

Scopula condition would not only reflect adaptive pressures related with locomotion, prey capture or other environmental factors, but also their interaction with spider size and weight.

ACKNOWLEDGMENTS

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