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TARSAL SCOPULA SIGNIFICANCE IN ISCHNOCOLINAE PHYLOGENETICS (ARANEAE, MYGALOMORPHAE, THERAPHOSIDAE)

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ABSTRACT. Tarsal scopula condition and carapace length were studied for eighteen Ischnocolinae species. For cladistic analysis a matrix of 20 terminals and 30 characters of representatives of Ischnocolinae, Theraphosinae, Aviculariinae, Harpactirinae and Trichopelmatinae were analyzed using Nona 2.0 computer software. The matrix was analyzed in four different ways: 1. each tarsal scopula (legs I–IV) coded as separate characters; 2. one character with six ordered states; 3. one character with six independent states; 4. without tarsal scopula character. The first two matrices result in one tree with the same indices ($L = 72$; $CI = 0.54$; $RI = 0.74$) and topology: Part of Ischnocolinae is monophyletic (*H. rondoni*(*S. longibulbi*(*I. algericus*+*Catumiri*))) and the other representatives (*Oligoxystre* and *Genus* 1) form a distinct monophyletic group with Theraphosinae, Harpactirinae and Aviculariinae. There are no homoplasies in tarsal scopula evolution in the second cladogram. The other two cladograms show less resolution for the Ischnocolinae than the two first cladorams. The tarsal scopula condition appears to have no relation to spider size ($t = -0.80433$; $P = 0.438247$) and should be used in phylogenetic analysis of Ischnocolinae because it provides information on the character variability within the subfamily.

Keywords: Phylogeny, South America, cladistics

The condition of the tarsal scopula has had an important role in the systematics of the Ischnocolinae Simon 1892. The scopula shows ontogenetic differentiation, being divided in all juvenile Theraphosidae and becoming entire in adults of some groups (Pocock 1897; Gerschman de Pikelin & Schiapelli 1973; Pérez-Miles, 1994). The condition of the tarsal scopula has been considered a good taxonomic tool and has already been used to diagnose genera and species groups in Theraphosidae. Its use in phylogenetics is questionable since, within the Theraphosinae, the presence of a divided scopula is related to small sized species (Pérez-Miles 1994). Characterized as theraphosids with a divided tarsal scopula (plesiomorphic state), Ischnocolinae is considered a paraphyletic group. Ischnocolinae is the subfamily of Theraphosidae Thorell 1869 that shows the broadest geographic distribution, with species occurring in northern, central and eastern Africa, Seychelles, the Middle-East, the Mediterranean region, central and south Americas and the Antilles (Smith 1990; Rudloff 1997; Vol 2001). Considering that Ischnocolinae was proposed as a subfamily based on a plesiomorphic character state (divided tarsal scopula), the situation of the group's systematics is very confusing. Raven (1985) considered Ischnocolinae a paraphyletic group that should have been revised at the generic level and grouped into monophyletic units. However, since the description of the type-genus *Ischnocolus* Ausserer 1871, only a few genera have been revised. Gerschman de Pikelin & Schiapelli (1973) revised the subfamily as a whole but of the 42 genera included in this study, only 10 are in fact Ischnocolinae representatives. The remaining 12 were subsequently synonymyzed or transferred to other families and subfamilies. Rudloff (1997) revised the genus *Holothele* Karsch 1879 but did not present a diagnosis of the genus and its species; the identification key does not include all the species and the structures are poorly illustrated. Smith (1990) published a taxonomic revision of European and African Ischnocolinae and presented descriptions and diagnoses for all genera.

For over a century, the tarsal scopula state ‘‘divided by a longitudinal band of setae’’ was used in Theraphosidae taxonomy (Pérez-Miles

1994). Gerschman de Pikelin & Schiapelli (1973), following Ausserer (1871), considered the tarsal scopula condition an important taxonomic character and stated that the divided tarsal scopula is present in all juvenile theraphosids. Juvenile Theraphosinae Thorell 1870 have divided tarsal scopulae that become entire in the adult stage, in Ischnocolinae the scopulae remain divided into adulthood (Pocock 1897; Gerschman de Pikelin & Schiapelli 1973; Pérez-Miles 1994). Although this ontogenetic differentiation was detected, the divided condition continued to be used causing the inclusion of juvenile Theraphosinae within Ischnocolinae. This problem remained unresolved until Raven (1985) considered Ischnocolinae a paraphyletic group that presents poorly developed tarsal scopulae. The tarsal scopula as a phylogenetic character was used for the first time by Pérez-Miles (1992) in a preliminary cladistic analysis of the subfamily Theraphosinae. In this paper he shows that the entire tarsal scopula is synapomorphic for some genera of this subfamily. Later, Pérez-Miles (1994) discussed the value of the tarsal scopula in Theraphosinae systematics and concluded that the scopula condition is related to spider size, although some exceptions exist. Considering that the role of the tarsal scopula in Theraphosidae systematic remains obscure, the goal of this study is to vary the use of the character ‘‘tarsal scopula’’ in a phylogenetic analysis for Ischnocolinae and discuss the results.

METHODS

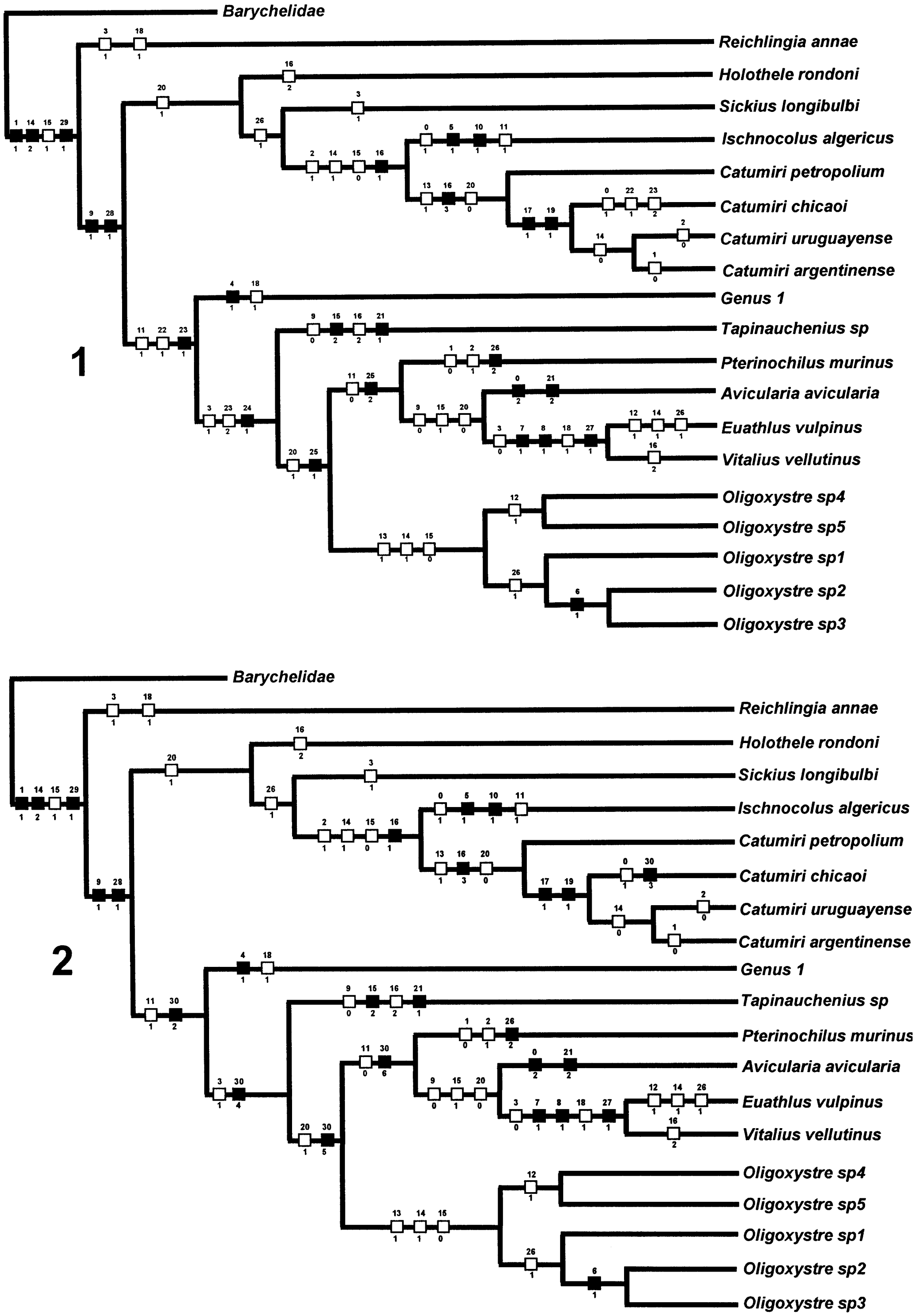
The material examined belongs to the following institutions: Instituto Butantan, São Paulo (IBSP); American Museum of Natural History, New York (AMNH); Museo Argentino de Ciencias Naturales Bernardino Rivadavia, Buenos Aires (MACN); Museo de la Plata, La Plata (MLP); Museu de Zoologia, Universidade de São Paulo, São Paulo (MZSP); Zoological Museum University of Copenhagen (ZMUC); Museu Paraense Emilio Goeldi, Belém (MPEG).

Tarsal scopula condition was observed under a stereomicroscope. Following Pérez-Miles (1994), a few isolated long and thin hairs in the tarsal scopula were not considered divided. Carapace length was used to estimate spider size. Below is a list of Ischnocolinae species used for tarsal scopulae condition and carapace length:

Holothele rondoni (Lucas & Bücherl 1972): 1 ♂, Apiácas, Mato Grosso, Brazil (MZSP 18046); 1 ♂, Apiácas, Mato Grosso, Brazil (MZSP 18038); 1 ♂, Manicoré, Amazonas, Brazil (MZSP 18990).
Sickius longibulbi Soares & Camargo 1948: 4 ♂, Itirapina, São Paulo, Brazil (MZSP 22756).
Genus 1: 3 ♂, Colinas do Sul, Serra da Mesa, Goiás, Brazil (MZSP 18992).
Catumiri petropolium Guadanucci 2004: 1 ♂, Petrópolis, Rio de Janeiro, Brazil (IBSP 8596).
Catumiri chicaoi Guadanucci 2004: 1 ♂, Una, Bahia, Brazil (IBSP 9514).
Catumiri uruguayense Guadanucci 2004: 1 ♂, Lavalleja, Águas Blancas, Uruguay (IBSP 9491).
Catumiri argentinenese (Mello-Leitão 1941): 1 ♂, Jujuy, Yuto, El Pantanoso, Argentina (MACN 6424).
Genus 2, sp. 1: 3 ♂, Jaraguá, Goiás, Brazil (MPEG 1677)
Genus 2, sp. 2: 1 ♂, Serra Norte, Pará, Brazil (MPEG 1678).
Genus 2, sp. 3: 1 ♂, Ilha Marajó Breves, Pará, Brazil (MPEG 1679).
Genus 2, sp. 4: 1 ♂ (IBSP 11083), 1 ♂ (IBSP 11086), 1 ♂ (IBSP 11087), Pimenta Bueno, Rondônia, Brazil; 1 ♂, Mineiros, Goiás, Brazil (IBSP 8070).
Genus 2, sp. 5: 1 ♂, Linhares, Espírito Santo, Brazil (IBSP 8654); 1 ♂, Linhares, Espírito Santo, Brazil (IBSP 7987); 1 ♂, Porto Seguro, Bahia, Brazil (IBSP 11084); 1 ♂, Ilhéus, Bahia, Brazil (IBSP 11085).
Oligoxystre new species 1: 1 ♂ (IBSP 9488), 1 ♂ (IBSP 9489), 1 ♂ (IBSP 9486), 1 ♂ (IBSP 9484), Central, Bahia, Brazil.

Cladistic analysis.—The cladistic analysis was carried out using Nona version 2.0 (Goloboff 1993). Search strategy was mult* with 100 replications. The data matrix included 20 terminal taxa and 30 characters and was constructed with NDE (Nexus Data Editor) version 0.5.0 (Page 2001). The out-group was chosen based on the phylogenetic relationships of Mygalomorphae presented by Goloboff (1993). In order to avoid an excess of missing entries, we preferred used a Barychelidae Simon 1889 rather than a Paratropididae Simon 1889 as the out group, since the last family presents some incomparable characters with Theraphosidae. Character polarity was read straight from the preferred cladogram following Nixon & Carpenter (1993).

Below is a list of species used in the cladistic analysis:



Figures 1–2.—Relationship hypothesis between Ischnocolinae and other Theraphosidae groups. 1. (L = 72; CI = 0.54; RI = 0.74). Tarsal scopula coded in four characters (22–25), one for each leg. 2. (L = 72; CI = 0.54; RI = 0.74). Tarsal scopula coded as one character with six ordered states.

Table 1.—Matrix composed of 20 terminals and 31 characters.

	Characters																													
	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
Barychelinae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	—	0	0	0	0	0	0	0	0	0	0	0	0	0
Reichlingia annae	0	1	0	1	0	0	0	0	0	0	0	0	0	0	2	1	0	—	1	0	0	0	0	0	0	0	0	0	0	1	0
Holothele rondoni	0	1	0	0	0	0	0	0	0	1	0	0	0	0	2	1	2	0	0	0	1	0	0	0	0	0	0	0	1	1	0
Sickius longibulbi	0	1	0	1	0	0	0	0	0	1	0	—	—	0	2	1	0	—	0	0	1	0	0	0	0	0	1	0	1	1	0
Ischnothele algericus	1	—	—	0	—	1	0	0	0	1	1	1	0	0	1	0	1	0	0	0	1	0	0	0	0	0	1	0	1	1	0
Catumiri petropolium	0	1	1	0	0	0	0	0	0	1	0	0	0	1	1	0	3	0	0	0	0	0	0	0	0	0	1	0	1	1	0
Catumiri chicaoi	1	—	—	0	—	0	0	0	0	1	0	?	?	1	1	0	3	1	0	1	0	0	1	2	0	0	1	0	1	1	3
Catumiri uruguayense	0	1	0	0	0	0	0	0	0	1	0	0	0	1	0	0	3	1	0	1	0	0	0	0	0	0	1	0	1	1	0
Catumiri argentinense	0	0	1	0	0	0	0	0	0	1	0	0	0	1	0	0	3	1	0	1	0	0	0	0	0	0	1	0	1	1	0
Genus 1	0	1	0	0	1	0	0	0	0	1	0	1	0	0	2	1	0	—	1	0	0	0	1	1	0	0	0	0	1	1	2
Tapinauch sp.	0	1	0	1	0	0	0	0	0	0	0	1	0	0	2	2	2	0	0	0	0	1	1	2	1	0	0	0	1	1	4
Pterinochilus murinus	0	0	1	1	0	0	0	0	0	1	0	0	0	0	2	1	0	—	0	0	1	0	1	2	1	2	2	0	1	1	6
Avicularia avicularia	2	—	0	1	0	0	0	0	0	0	0	0	0	0	2	1	0	—	0	0	0	2	1	2	1	2	0	0	1	1	6
Euathlus vulpinus	0	1	0	0	0	0	0	1	1	0	0	0	1	0	1	1	0	—	1	0	0	0	1	2	1	2	1	1	1	1	6
Vitalius vellutinus	0	1	0	0	0	0	0	1	1	0	0	0	0	0	2	1	2	0	1	0	0	0	1	2	1	2	0	1	1	1	6
Oligoxistre sp. 4	0	1	0	1	0	0	0	0	0	1	0	1	1	1	1	0	0	—	0	0	1	0	1	2	1	1	0	0	1	1	5
Oligoxistre sp. 5	0	1	0	1	0	0	0	0	0	1	0	1	1	1	1	0	0	—	0	0	1	0	1	2	1	1	0	0	1	1	5
Oligoxistre sp. 1	0	1	0	1	0	0	0	0	0	1	0	1	0	1	1	0	0	—	0	0	1	0	1	2	1	1	1	0	1	1	5
Oligoxistre sp. 2	0	1	0	1	0	0	1	0	0	1	0	1	0	1	1	0	0	—	0	0	1	0	1	2	1	1	1	0	1	1	5
Oligoxistre sp. 3	0	1	0	1	0	0	1	0	0	1	0	1	0	1	1	0	0	—	0	0	1	0	1	2	1	1	1	0	1	1	5

BARYCHELIDAE: *Reichlingia annae* (Reichling 1997): 1 ♂, 1 ♀, New River Lagoon, Orange Walk, Belize (AMNH).

THERAPHOSIDAE: *Avicularia avicularia* (Linnaeus 1758) (Aviculariinae): 1 ♂, Jacaré, Rio Trombetas, Oriximiná, Pará, Brazil (MZSP 5687); 1 ♀, Jacaré, Rio Trombetas, Oriximiná, Pará, Brazil (MZSP 5687).

Euathlus vulpinus (Karsch 1880) (Theraphosinae): 5 ♂, Osorno, Chile (IBSP 3817-A); 4 ♀, Osorno, Chile (IBSP 3817-B).

Catumiri petropolium Guadanucci 2004 (Ischnocolinae): 1 ♂, Petrópolis, Rio de Janeiro, Brazil (IBSP 8596); 1 ♂, Petrópolis, Rio de Janeiro, Brazil (IBSP 8606).

Catumiri chicaoi Guadanucci 2004 (Ischnocolinae): 1 ♂, Una, Bahia, Brazil (IBSP 9514); 1 ♀, Una, Bahia, Brazil (IBSP 9514).

Catumiri uruguayense Guadanucci 2004 (Ischnocolinae): 1 ♂, Lavalleja, Águas Blancas, Uruguay (IBSP 9491); 1 ♀, Lavalleja, Águas Blancas, Uruguay (IBSP 9507).

Catumiri argentinenese (Mello-Leitão 1941) (Ischnocolinae): 1 ♂, Jujuy, Yuto, El Pantanoso, Argentina (MACN 6424); 1 ♀, Catamarca, Argentina (MLP 14608).

Genus 1 (Ischnocolinae): 1 ♂, Fazenda Sandoval, Porto Nacional, Tocantins, Brazil (IBSP 8585); 1 ♀, Fazenda Sandoval, Porto Nacional, Tocantins, Brazil (IBSP).

Holothele rondoni (Lucas & Bücherl 1972) (Ischnocolinae): 1 ♂, Apiácas, Mato Grosso, Brazil (MZSP 18046); 1 ♀, Tucuruí, Pará, Brazil (IBSP).

Ischnocolus algericus Thorell 1875 (Ischnocolinae): 1 ♂, 1 ♀, El Araish, Marocco (ZMUC 620, 628).

Oligoxystre new species 1 (Ischnocolinae): 1 ♂, Central, Bahia, Brazil (IBSP 9487); 1 ♀, Toca da Esperança, Jussara, Bahia, Brazil (IBSP 8549).

Oligoxystre new species 2 (Ischnocolinae): 1 ♂, Chapada dos Guimarães, Mato Grosso, Brazil (IBSP 9495); 1 ♀, Chapada dos Guimarães, Mato Grosso, Brazil (IBSP 9504).

Oligoxystre new species 3 (Ischnocolinae): 1 ♂, São Domingos, Goiás, Brazil (IBSP 8625); 1 ♀, Serra da Mesa, Minaçú, Goiás, Brazil (IBSP 9467).

Oligoxystre new species 4 (Ischnocolinae): 1 ♂, Tucuruí, Pará, Brazil (IBSP 9459); 1 ♀, Tucuruí, Pará, Brazil (IBSP 7936).

Oligoxystre new species 5 (Ischnocolinae): 1 ♀, Toca da Esperança, Central, Bahia, Brazil (IBSP 8553).

Pterinochilus murinus Pocock 1897 (Harpactirinae): 1 ♂, Africa (IBSP); 1 ♀, Kenya (IBSP).

Sickius longibulbi Soares & Camargo 1948 (Ischnocolinae): 1 ♂, Parnaíba, Mato Grosso do Sul, Brazil (IBSP 8019); 1 ♀, Votuporanga, São Paulo, Brazil (IBSP 8693).

Tapinauchenius sp. (Aviculariinae): 1 ♂, Tucuruí, Pará, Brazil (IBSP 4925-A); 1 ♀, Rio Marupí, Pará, Brazil (IBSP 4676).

Vitalius vellutinus (Mello-Leitão 1923) (Theraphosinae): 1 ♂, Porto Cabral, Rio Paraná, Teodoro Samapaio, São Paulo, Brazil (MZSP 14953); 1 ♀, Teodoro Samapaio, Porto Cabral, Rio Paraná, Teodoro Sampaio, São Paulo, Brazil (MZSP 3150).

CLADISTIC ANALYSIS

Below is a list of the characters used to construct the data matrix. The matrix was analyzed in four different ways: 1. tarsal scopula of each leg was coded as a separate character (characters 22–25) and these were treated as ordered; 2. the four tarsal scopula were coded as a single character with six ordered states (character 30); 3. the four tarsal scopula were coded as a single character with six independent states (character 30); 4. the character(s) of the tarsal scopula were deactivated in the matrix. The optimization option was ACCTRAN. Abbreviations: L = length of character; CI = consistency index; RI = retention index.

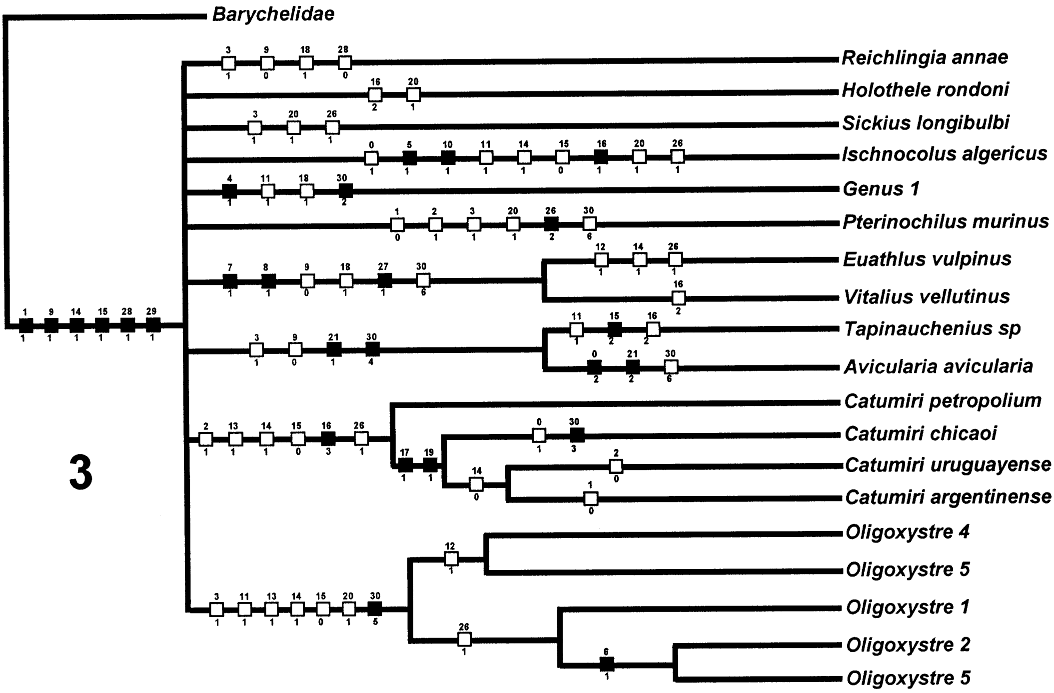
0. Male tibial spur (L = 3; CI = 0.66; RI = 0).–0, present; 1. absent; 2. present, formed by thick spines. The great diversity of male tibial spur morphology might be related to reproductive isolation. The tibial spur is the first structure that touches the female and could act as a mechanism for the female to recognize a conspecific male (Coyle 1985; Eberhard 1985; Jackson & Pollard 1990). Since the structures that compose the tibial spur are under independent evolution, the ‘‘tibial spur’’ is coded in three different characters.

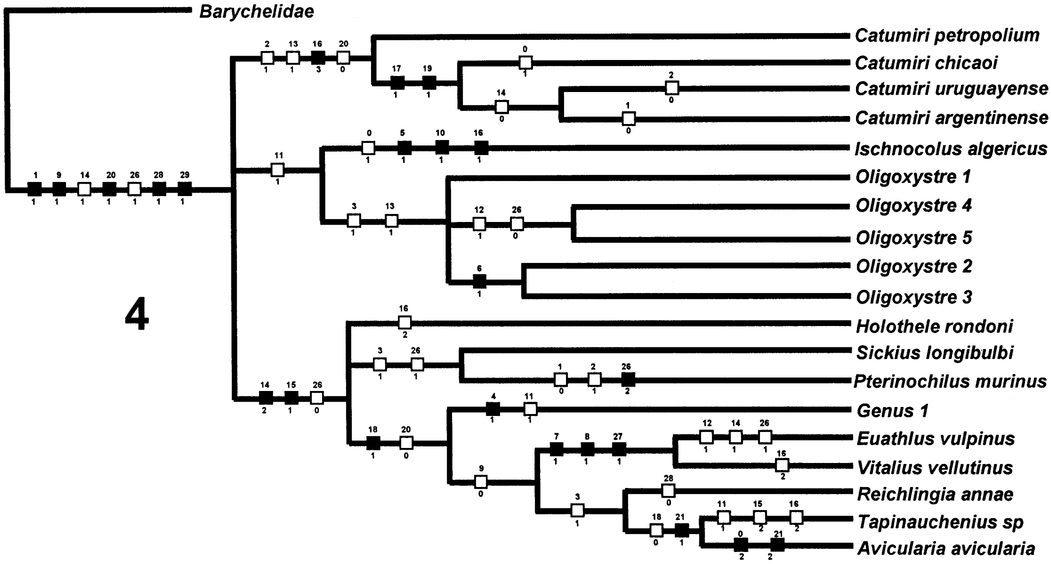
1. Apical megaspine in the tibial spur (L = 3; CI = 0.33; RI = 0).—0. present; 1. absent.

2. Prolateral branch of tibial spur (L = 3; CI = 0.33; RI = 0).—0. present; 1. absent.

3. Metatarsus I of males (L = 4; CI = 0.25; RI = 0.66).—0. straight; 1. dorsoventrally curved. This character shows great variation in the degree of curvature and in the taxa in which it is present.

4. Flexion of metatarsus I of males (L = 1; CI = 1; RI = 1).—0. flexes outside the prolateral branch of tibial spur; 1. flexes between the two branches of tibial spur. The way that the metatarsus flexes is related to the position of the tibial spur.





Figures 3–4.—Relationship hypothesis between Ischnocolinae and other Theraphosidae groups. 3. (L = 79; CI = 0.48; RI = 0.56). Tarsal scopula coded as one character with six unordered states. 4. (L = 57; CI = 0.57; RI = 0.72). Tarsal scopula deactivated.

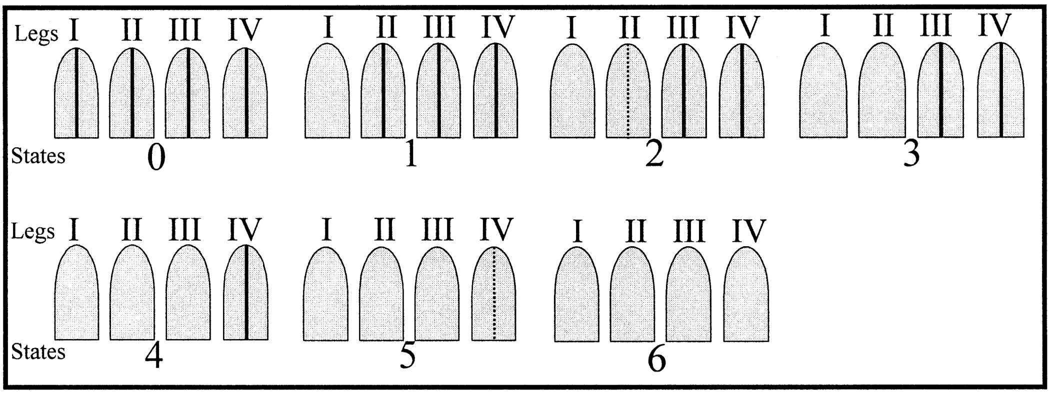


Figure 5.—Variation possibilities of Ischnocolinae tarsal scopulae. States correspond to character 30. Full line corresponds to divided scopulae with setae; dashed line corresponds to entire scopulae with band of setae.

5. Ventral depression of the palpal tibia of males (L = 1; CI = 1; RI = 1).—0. straight or slightly curved, occupying more than half of the article; 1. sigma-like, occupying half the article. Autapomorphic for *I. algericus*. Diagnostic for the genus *Ischnocolus* (Raven 1985).

6. Palpal bulb (L = 1; CI = 1; RI = 1).—0. apical keel absent; 1. apical keel present. The presence of keels on the bulb is a synapomorphy of Theraphosinae (Raven 1985; Perez-Miles *et al.* 1996; Bertani 2000). However, small keels were observed on the bulb of some *Oligoxystre* species. These are not considered homologous to the Theraphosinae bulb keels.

7. Prolateral keels on the palpal bulb (L = 1; CI = 1; RI = 1).—0. absent; 1. present. Synapomorphy of Theraphosinae (Raven 1985; Perez-Miles et al. 1996; Bertani 2000).

8. Subtegulum (L = 1; CI = 1; RI = 1).—0. narrow, not extending over the tegulum; 1. wide, extending over the tegulum. Synapomorphy of Theraphosinae (Raven 1985; Perez-Miles et al. 1996).

9. Ventral region of the cymbium (L = 3; CI = 0.33; RI = 0.6).—0. as wide as long; 1. longer than wide. This character is very common among Ischnocolinae although it does not represent a synapomorphy for this group.

10. Size of the lobes of cymbium (L = 1; CI = 1; RI = 1).—0. similar; 1. different.

11. Lobular state of spermathecae (L = 3; CI = 0.33; RI = 0.71).—0. unilobular (Fig. 7); 1. multilobular (Fig. 8).

12. Lateral lobe of spermathecae (L = 2; CI = 0.5; RI = 0.5).—0. absent (Fig. 7); 1. present (Fig. 8).

13. Maxillae (L = 2; CI = 0.5; RI = 0.87).—0. many cuspules (more than 50); 1. few cuspules (less than 45).

14. Labium (L = 6; CI = 0.33; RI = 0.5) ordered.—0. cuspules absent; 1. few cuspules (less than10); 2. many cuspules (more than 15).

15. Labium shape (L = 5; CI = 0.4; RI = 0.57).—0. much wider than long (2.5–3 times wider); 1. almost as wide as long (less than 2 times wider); 2. longer than wide.

16. Tarsal claw (L = 5; CI = 0.6; RI = 0.6).—0. bare, without teeth; 1. two rows of teeth; 2. median row of teeth; 3. prolateral row of teeth; 4. single tooth.

17. Tarsal claw with teeth (L = 1; CI = 1; RI = 1).—0. present on all legs; 1. present on anterior legs (I–II).

18. Posterior sternal sigilla (L = 3; CI = 0.33; RI = 0.33).—0. marginal; 1. submarginal.

19. Metatarsus I (L = 1; CI = 1; RI = 1).—0. more than ¾ of the article scopulate; 1. less than half of the article scopulate.

20. Metatarsus IV (L = 4; CI = 0.25; RI = 0.62).—0. less than half of the article scopulate; 1. more than half of the article scopulate.

21. Legs spines (L = 3; CI = 0.66; RI = 0) ordered.—0. many spines, especially on tibia and metatarsus; 1. few reduced spines, on the apical region of tibia and metatarsus; 2. spines absent. The presence of several spines was considered plesiomorphic for Theraphosoidina (Raven 1985). Representatives of Aviculariinae Simon 1874 show a reduced number of leg spines. Bertani (2002) demonstrated that state 2 is a synapomorphy for Aviculariinae *sensu stricto*.

22. Tarsal scopula I (L = 2; CI = 0.5; RI = 0.85).—0. divided by a longitudinal band of setae; 1. entire.

23. Tarsal scopula II (L = 4; CI = 0.5; RI = 0.86) ordered.—0. divided by a longitudinal band of setae; 1. entire with a longitudinal band of setae; 2. entire. In the present study a third state was identified which differs from state 0 in having type A setae (Rovner 1978; Pérez-Miles 1994) mixed with type B setae (Rovner 1978; Pérez-Miles 1994). In this state the tarsal scopula is not divided but there are lined setae forming a longitudinal band.

24. Tarsal scopula III (L = 1; CI = 1; RI = 1).—0. divided by a longitudinal band of setae; 1. entire.

25. Tarsal scopula IV (L = 2; CI = 1; RI = 1) ordered.—0. divided by a longitudinal band of setae; 1, entire with a longitudinal band of setae; 2, entire.

26. Clypeus (L = 3; CI = 0.66; RI = 0.87).—0. absent; 1. present, narrower than the diameter of the anterior median eyes; 2. present, wider than the diameter of the anterior median eyes.

27. Urticating hair type III (L = 1; CI = 1; RI = 1).—0. absent; 1. present. Synapomorphy of Theraphosinae (Raven 1985; Perez-Miles et al. 1996).

28. Apical article of posterior lateral spinnerets (L = 1; CI = 1; RI = 1).—0. domed or rounded; 1, digitiform. This character is widely used to separate Barychelidae from Theraphosidae, the latter presenting the distal article of the PLS digitiform. However, among Barychelidae this character shows great variation making it impossible to place some representatives within either family.

29. Anterior maxillary projection (L = 1; CI = 1; RI = 1).—0. poorly developed; 1. developed.

30. Tarsal scopula I-IV (L = 9; CI = 0.66; RI = 0.92) (Fig. 5).—0. all scopula divided; 1. only tarsal scopula I entire; 2. only tarsal scopula I entire and scopula II entire with a longitudinal band of setae; 3. only tarsal scopula I and II entire; 4. tarsal scopula I–III entire; 5. tarsal scopula I–III entire and scopula IV entire with a longitudinal band of setae; 6. all tarsal scopula entire. Although state 1 was not observed in any of the specimens examined in this study, it was included in the matrix since it was observed in an ontogenetic series. The exuvia of a specimen of *Grammostola actaeon* (Pocock 1903) was observed and it demonstrated that from state 0 to 2, two steps must be counted since the tarsal scopula II does not turn into undivided with a band of setae unless the scopula I is undivided.

RESULTS

The first cladogram (Fig. 1) refers to the tarsal scopula character separated into four individual characters (characters 22–25). It resulted in a single tree (L = 72; CI = 0.54; RI = 0.74). It shows that part of Ischnocolinae, represented by the taxa (*Holothele rondoni*(*Sickius longibulbi*(*Ischnocolus algericus*+*Catumiri*))), is monophyletic. The remaining Ischnocolinae form a distinct group with Harpactirinae Pocock 1897, Theraphosinae and Aviculariinae. This hypothesis suggests that part of Ischnocolinae is the sister-group to the polytomy presented by Raven (1985) solving in part the cladogram presented in that study (Fig. 6).

The second cladogram (Fig. 2) refers to the tarsal scopula coded as a single character with six ordered states (character 30). It resulted in a single tree with the same topology and indices of the first cladogram but with different optimizations in the following nodes: *Catumiri petropolium*; ((*Genus* 1((*Tapinauchenius* sp.((*Pterinochilus murinus*(*Avicularia avicularia*(*Euathlus vulpinus*+*Vitalius vellutinus*)(*Oligoxystre* spp.)))); ((*Tapinauchenius* sp.((*Pterinochilus murinus*(*Avicularia avicularia*(*Euathlus vulpinus*+*Vitalius vellutinus*)(*Oligoxystre* spp.))); (*Pterinochilus murinus*(*Avicularia avicularia*(*Euathlus vulpinus*+*Vitalius vellutinus*)(*Oligoxystre* spp.)) and ((*Pterinochilus murinus*(*Avicularia avicularia*(*Euathlus vulpinus*+*Vitalius vellutinus*)). Moreover it showed no homoplasies for the tarsal scopula character.

The third cladogram (Fig. 3), which is a consensus of 16 trees, refers to the tarsal scopula coded as a single character with six independent states. The only monophyletic groups in this tree are (*Euathlus vulpi-*

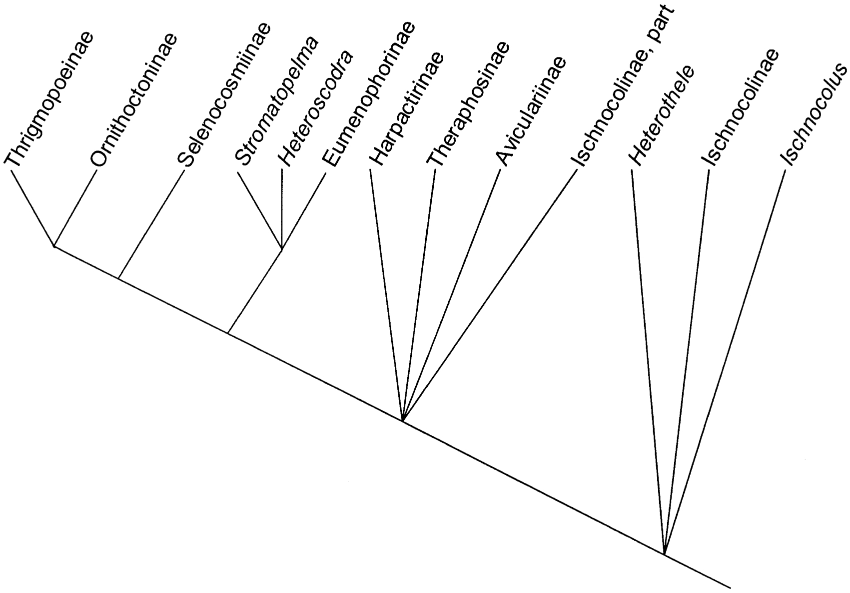


Figure 6.—Relationship hypothesis among Theraphosidae subfamilies (Raven 1985).

nus+*Vitalius vellutinus*); (*Tapinauchenius* sp.+*Avicularia avicularia*); *Catumiri* spp. and *Oligoxystre* spp.

The fourth cladogram (Fig. 4), which is a consensus of two trees, refers to the tarsal scopula character deactivated in the matrix. The only Ischnocolinae representatives that formed a monophyletic group are (*Oligoxystre* spp.+*Ischnocolus algericus*).

The tarsal scopula I condition did not show any relation to spider size (t = −0.80433; P = 0.438247) (graphic 1). Divided tarsal scopula I is present in large species (*H. rondoni*) and entire scopula I in small (Genus 2 spp.).

DISCUSSION

Anterior-posterior gradation.—Some characters (e.g. number of spines, development of teeth on the paired tarsal claws) show an anterior-posterior gradation that was described by Raven (1985). Concerning the tarsal scopula, many species of Ischnocolinae present different states on legs I–IV, where there is a tendency towards the anterior legs

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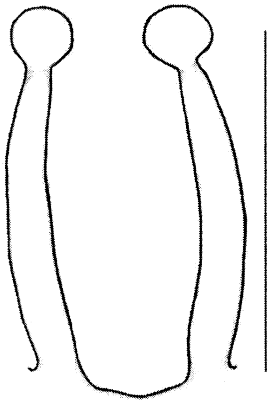

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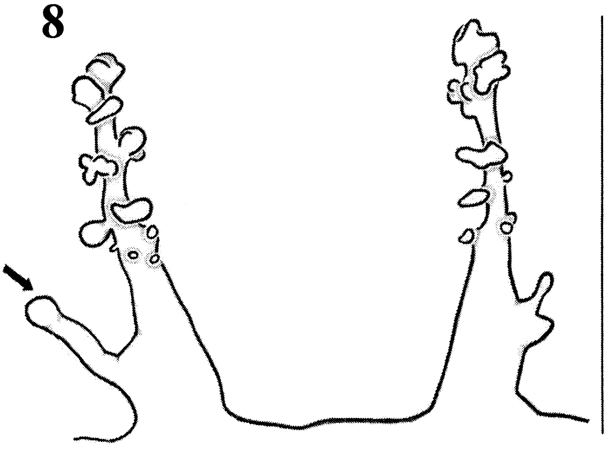

Figures 7–8.—7. Unilobular spermathecae (*Catumiri argentinense*). 8. Multilobular spermathecae, arrow showing the lateral lobe (*Oligoxystre* sp4).

presenting the apomorphic state. If the plesiomorphic state (divided scopula) is present on leg I, then legs II–IV always show the same state. If the apomorphic state (entire scopula) is present on leg I, legs II–IV may or may not have the scopulae entire. The opposite happens if we observe the state of the tarsal scopula on leg IV: if scopula IV is divided, it can be entire or divided on the anterior legs. If scopula IV is entire, all the anterior legs will present the apomorphic entire state. Moreover, if all the tarsal scopulae are divided on all legs, then leg IV will present the widest band of setae dividing the scopula.

Character dependency.—Considering the ontogenetic differentiation (Gerschman de Pikelin & Schiapelli 1973), the anterior-posterior gradation (Raven 1985) and the variability of states (described above) of the tarsal scopula in the Theraphosidae it is reasonable to conclude that there is a dependency of this character between the legs. As such, a posterior tarsal scopula will not become entire unless the anterior one is entire during the ontogenesis and an anterior tarsal scopula will not be divided if the posterior one is entire. An ontogenetic series composed of the exuviae of a specimen of *G. actaeon* showing this sequenced transformation and all the combinations found within the Ischnocolinae (Fig. 5) confirms this character dependency.

Tarsal scopula as a character.—Pérez-Miles (1992) used the tarsal scopula as a character on a preliminary cladistic analysis for Theraphosinae. In this analysis the plesiomorphic state was ‘‘at least one of the tarsal scopula divided’’. It means that if a certain species has the tarsal scopula IV divided, it would be coded as plesiomorphic and the state of scopula I would be ignored. It would be interesting to study the condition of the anterior tarsal scopulae in the species that have the scopula IV divided.

The use of the tarsal scopula in phylogenetics was discussed by Pérez-Miles (1994). According to him, results presented in that paper questioned the use of this character in cladistic analysis since a close relation between body size and scopula condition (small sized species tend to possess divided scopula), in Theraphosinae and Harpactirinae adults, could suggest a functional adaptation or a developmental effect. However it is admitted that the role of this character in theraphosid evolution remains obscure. Pérez-Miles (1994) explained that the scopula of tarsus IV was the only one used in order to avoid ambiguity, since scopula division width increases on the hind legs (Raven 1985). It can be supposed that the tarsal scopula condition within Theraphosinae is either all legs with scopula divided or entire. Species of the genera *Hapalopus* Ausserer 1875 and *Homoeomma* Ausserer 1871 have all tarsal scopula divided (pers. obs.).

Ischnocolinae is a very problematic group that lacks synapomorphies (Raven 1985) and its genera and species are mostly recognized by sexual characters (e.g. spermatheca and bulb morphology; presence, absence and morphology of structures of the tibial apophysis). So far, Ischnocolinae is considered a paraphyletic subfamily and the results presented in this paper show that at least part of this group is supported by having more than half of the metatarsus IV occupied by scopula. The main difficulty to infer phylogenetic hypotheses for Ischnocolinae is the reduced number of characters that can be defined, since these spiders have a very homogeneous morphology. Different from Theraphosinae, Ischnocolinae shows a great diversity of tarsal scopula states. If the divided scopula is related to small sized species, the large ones would be more likely to present the scopula I entire, which does not happen in Ischnocolinae (Fig. 9). Since the tarsal scopula condition is not related to spider size in Ischnocolinae ($t = -0.80433$; $P = 0.438247$), this character might have an important role in ischnocoline phylogenetics. This importance is evident when cladogram 4 is analyzed: monophyletic groups like (*S. longibulbi*+*Pterinochilus murinus*) are based on characters that are very variable (clypeus and curvature of metatarsus I of males); the monophyletic group ((*E. vulpinus*+*V. vellutinus*)(*R. annae*(*Tapinauchenius* sp.+*A. avicularia*)) has *R. annae* (Trichopelmatinae) as the sister-group of Aviculariinae. This does not agree with the basal position of Trichopelmatinae within Theraphosidae proposed by Raven (1994). Furthermore, the position of *R. annae* within this group does not agree with the monophyly of Theraphosinae + Aviculariinae proposed by Lucas (et al. 1991) and Pérez-Miles (1992).

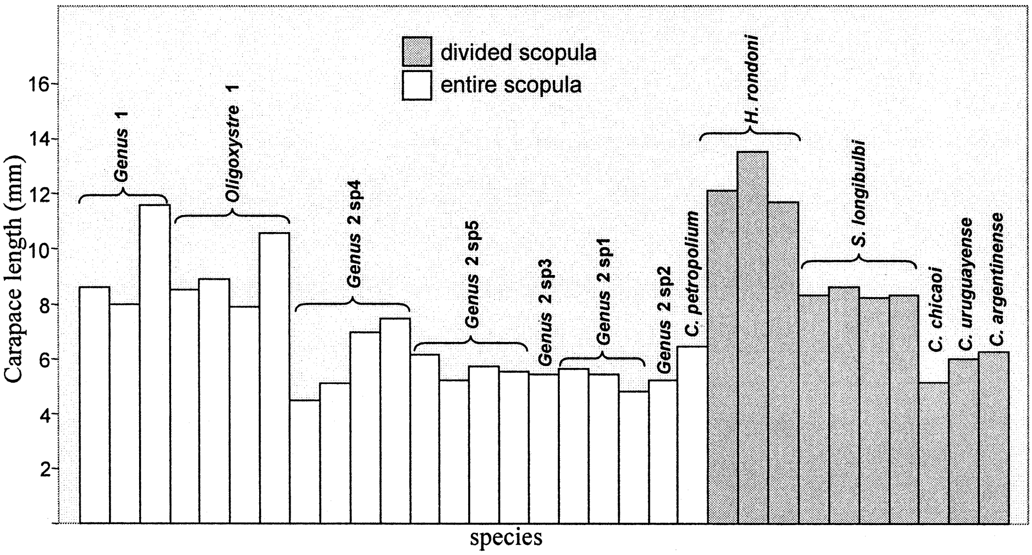

Figure 9.—Carapace length and tarsal scopula I condition for some Ischnocolinae species.

It was possible to show all the variability of the tarsal scopula condition with the six state character. There was no mask on the variation of a character using the synthetic code, contrary to Pogue & Mickevich (1990). The difference between cladograms 1 and 2 is that the second one provided no homoplasies for the tarsal scopula character. Another difference between the two optimizations is that the first cladogram has more synapomorphies on the nodes mentioned above. Since the character dependency is admitted, these synapomophies (characters 22, 23, 24) might be false. The use of the tarsal scopula condition as six unordered states of only one character admits that the transformation from divided to entire scopula is independent in all pairs of legs. If this is true, we could find a spider with divided anterior scopula and entire posterior scopula, or even scopula I and II entire, scopula III divided and scopula IV entire. The dependency of tarsal scopula condition between the legs means that the more entire the scopula the more apomorphic conditions (states) it will show. From these results it is possible to conclude that since there is relation between tarsal scopula condition and spider size, this character should be used in cladistic analysis. Additional Ischnocolinae taxa must be included in this analysis in order to provide a better knowledge of this character.

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