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SYSTEMATIC REVISION AND CLADISTIC ANALYSIS OF THERAPHOSINAE (ARANEAE: THERAPHOSIDAE)

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ABSTRACT. A systematic review and a phylogenetic analysis of the Theraphosinae is made. Most genera were represented by the type species and/or one or more species. As a result of this study, *Acanthopelma* and *Holothele* are transferred from Theraphosinae to Ischnocolinae *incertae sedis*; *Melloleitaoina, Metriopelma, Plesiopelma,* and *Tmesiphantes* are restored as valid genera; *Butantania* is removed from *Dryptopelma* and considered a junior synonym of *Homoeomma*; *Ceropelma* is designated a junior synonym of *Plesiopelma*; *Dryptopelma* is synonymized with *Cyclosternum*; *Crypsidromus* is synonymized with *Lasiodora,* and *Grammostola* is synonymized with *Phrixotrichus*. Apart from those new combinations created by the synonymy of genera, we established the following: *Plesiopelma rectimanus* (Mello-Leitão, 1923), from *Hapalopus*; *Cyclosternum macropus* (Ausserer, 1875), from *Schizopelma*; *Paraphysa scrofa* (Molina, 1788) from *Phrixotrichus,* and *Paraphysa phryxotrichoides* Strand, 1907 is placed as a junior synonym of *Euathlus truculentus* Ausserer, 1875. The 30 genera included in the Theraphosinae are diagnosed, figured, and a key is provided. The monophyly of Theraphosinae is supported and tested by additional characters. A data set of 30 taxa with 27 characters was analyzed. The most parsimonious tree was found and illustrated.

RESUMEN. Se realizó una revisión sistemática y análisis filogenético de la subfamilia Theraphosinae. Los géneros estuvieron representados por su especie tipo y/o una o más especies. Como resultado de este estudio los géneros *Acanthopelma* y *Holothele* son transferidos de Theraphosinae a Ischnocolinae *incertae sedis; Melloleitaoina, Metriopelma, Plesiopelma* y *Tmesiphantes* son restablecidos como géneros válidos; *Butantania* es transferida de *Dryptopelma* a *Homoeomma* considerándose sinónimo junior; *Ceropelma* es considerado sinónimo junior de *Plesiopelma*; *Dryptopelma* es sinonimizado con *Cyclosternum*; *Crypsidromus* es sinonimizado con *Lasiodora* y *Grammostola* es sinonimizada con *Phrixotrichus*. Ademas de las nuevas combinaciones creadas por la sinonimia de géneros establecemos las siguientes: *Plesiopelma rectimanus* (Mello-Leitão 1923), de *Hapalopus; Cyclosternum macropus* (Ausserer 1875) de *Schizopelma; Paraphysa scrofa* (Molina 1788) de *Phrixotrichus*; tambien *Paraphysa phryxotrichoides* Strand 1907 es considerada sinónimo junior de *Euathlus truculentus* Ausserer 1875. Se presenta una clave para los 30 géneros incluídos en Theraphosinae, así como sinonimias, diagnosis y figuras de sus caracteres sexuales. La monofilia de las Theraphosinae es argumentada con caracteres adicionales. Para el análisis filogenético se procesó una matriz de datos de 30 taxa por 27 caracteres. Se obtuvo un cladograma de máxima parsimonia.

INTRODUCTION

The first higher classification of Mygalomorphae based on an explicit phylogenetic analysis was proposed by Raven (1985). Coddington & Levi (1991) stressed the value of Raven's work. Goloboff (1993a) considered Raven (1985) as the starting point for higher systematics of Mygalomorphae, and reanalyzed the relationships among mygalomorph families using computer generated parsimony, contributing numerous new characters. Although Raven

(1985) proposed relationships among mygalomorph genera for most families, that was not the case for Theraphosidae. Raven's cladogram for Theraphosidae showed only subfamilial relationships and has several unresolved polytomies. Various authors agree about the difficulties and confusion of theraphosid systematics (Schiapelli & Gerschman 1979; Valerio 1980a; Minch 1989; Raven 1990), referred to as a "taxonomic and nomenclatural nightmare" by Raven (1990).

Theraphosinae is a speciose group from the New World showing high diversity in the southern region of North America, Central and South America. Major studies on Theraphosinae were done by Schiapelli & Gerschman (1979), Valerio (1980a; 1980b). The monophyly of Theraphosinae was argued by Raven (1985) on three synapomorphies; i) subtegulum large, extensive; ii) palpal bulb with keels; and iii) retrolateral femur IV with scopulae. He redefined Theraphosinae considering Grammostolinae as a junior synonym, and tentatively transferred some genera from Ischnocolinae to Theraphosinae. Pérez-Miles (1992a) in a concise revision of Theraphosinae relationships, removed certain genera. The monophyly of the Theraphosinae (Raven 1985) appears to be a good starting hypothesis, however, the generic relationships remain unresolved. This study tests the monophyly of the Theraphosinae and analyzes generic phylogenetic relationships.

METHODS

Taxa. -- Our analysis incorporates Theraphosinae genera used in Raven (1985), the systematic and nomenclatural changes produced up to 1993, and others that arose as a result of the present revision. Thirty genera were used as terminals in the analysis. Whenever possible, generic types of Theraphosinae were used. When generic types were not available (or presumed lost), congeners were studied. Types and congeners from Aviculariinae, Harpactirinae, and Ischnocolinae were also examined for outgroup selection. Biological material utilized is listed in Table 1.

Phylogenetic Analysis. -- A data matrix of 30 taxa and 27 characters (Table 2) was analyzed. Cladistic analysis was carried out using Pee-Wee 2.0, an MS-DOS computer program, developed by Goloboff (1993b). To find most parsimonious trees, the command "mult* 15" was used to randomize the order of the taxa, create a weighted Wagner tree, and submit the tree to branch-swapping using tree-bisection reconnection processes. Up to 20 trees are retained in the initial stage of the search. The process is repeated up to 15 times (the program abandons a replication if a tree with a superior fit is detected) (see Goloboff 1993b).

Abbreviations. -- Institutions. - BMNH, British Museum of Natural History, London; IB, Instituto Butantan, São Paulo; FNS, Forschunginstitut und Naturmuseum Senckenberg, Frankfurt; MACN, Museo Argentino de Ciencias Naturales, Buenos Aires; MHNM. Museo Nacional de Historia Natural, Montevideo; MHNP, Museum National d'Histoire Naturelle, Paris; MLP, Museo de Ciencias Naturales de La Plata, La Plata; MRJ, Museu Nacional de Rio de Janeiro, Rio de Janeiro; MZSP, Museu de Zoologia da Universidade de São Paulo, São Paulo; SI, Smithsonian Institution, Washington D. C.; SAM, South African Museum, Capetown; ZMB, Museum fur Naturkunde der Humboldt Universität zu Berlin, Berlin; NMV, Naturhistorisches Museum Wien, Wien.

Morphology and statistics. -- CL, carapace length; SD, standard deviation; T, Student's t test; P, probability.

Characters. -- The character distribution is shown in Table 2. Multistate characters were categorized as nonadditive.

Character 0: Apical region of bulb subcylindrical = 0; subconical = 1; concave/convex (spoon like) = 2.

Character 1: Relative width of sclerites II+III of the bulb (measured at 20% of its length, from the apex): narrow (less than 10% of the length of the bulb) = 0; wide

Table 1.--Species studied. Holotypes or paratypes of type species, of non type species (*) or congeners (**). Location abbreviations are listed in methods (page 34).

THERAPHOSINAE	
Acanthopelma rufescens F. O. P.-Cambridge, 1897	BMNH
Acanthoscurria geniculata (C. L. Koch, 1842)	BMNH
Acanthoscurria suina (Pocock, 1903)	BMNH*
Aphonopelma seemanni (F. O. P.-Cambridge, 1897)	BMNH
Aphonopelma texense (Simon, 1892)	SI*
Brachypelma emilia (White, 1856)	MHNP
Butantania hirsutum (Mello-Leitão, 1935)	IB
Ceropelma flavohirtum (Simon, 1889)	MHNP*
Ceropelma insulare Mello-Leitão, 1923	MZSP
Ceropelma longisternale Schiapelli & Gerschman, 1942	MACN*
Ceropelma semiaurantiecum (Simon, 1897)	MNHP*
Citharacanthus longipes (F. O. P.-Cambridge, 1897)	BMNH
Crypsidromus isabellinus Ausserer, 1871	NMV
Cyclosternum rufohirtum (Simon, 1889)	MHNP*
Cyclosternum schmardae Ausserer, 1871	MHNP
Cyriocosmus sellatus (Simon, 1889)	MHNP
Cyrtopholis cursor (Ausserer, 1875)	BMNH
Cyrtopholis palmarum Schiapelli & Gerschman, 1945	MACN*
Dryptopelma janthinum (Simon, 1888)	MHNP
Euathlus truculentus Ausserer, 1875	BMNH
Eupalaestrus campestratus (Simon, 1891)	MHNP
Eupalaestrus tarsicrassus Bücherl, 1947	IB*
Eupalaestrus weijenberghi (Thorell, 1894)	BMNH*
Grammostola actaeon (Pocock, 1903)	BMNH*
Grammostola alticeps (Pocock, 1903)	BMNH*
Grammostola australis Gerschman & Schiapelli, 1948	MACN*
Grammostola burzaquensis Ibarra-Grasso, 1946	MLP*
Grammostola cala Chamberlin, 1917	MCZH*
Grammostola chalcothrix Chamberlin, 1917	MCZH*
Grammostola fasciata Mello-Leitão, 1921	MZSP*
Grammostola ferruginea Mello-Leitão, 1921	MZSP*
Grammostola gigantea Mello-Leitão, 1921	MZSP*
Grammostola gossei (Pocock, 1899)	BMNH*
Grammostola grandicola Strand, 1908	FNS*
Grammostola iheringi (Keyserling, 1891)	BMNH*
Grammostola inermis Mello-Leitão, 1941	MLP*
Grammostola longimana Mello-Leitão, 1921	MRJ*
Grammostola mollicoma (Ausserer, 1875)	BMNH
Grammostola pulchra Mello-Leitão, 1921	MZSP*
Grammostola pulchripes (Simon ,1891)	MHNP*
Grammostola spatulata (F. O. P.-Cambridge, 1897)	BMNH*
Grammostola vachoni Gerschman & Schiapelli, 1960	MACN*
Hapalopus formosus Ausserer, 1875	NMV
Hapalotremus albipes Simon, 1903	MHNP
Holothele sericeus (Simon, 1903)	MHNP*
Homoeomma strandlingi (F. O. P.-Cambridge, 1887)	BMNH

Table 1.--Cont.

Homoeomma uruguayensie (Mello-Leitão, 1946)	MHNP*
Lasiodora klugi (C. L. Koch, 1842)	BMNH
Mygalarachne brevipes (Ausserer, 1871)	NMV
Pamphobeteus nigricolor (Ausserer, 1875)	BMNH
Paraphysa manicata Simon, 1892	MHNP
Phrixotrichus roseus (Walckenaer, 1837)	MHNP
Plesiopelma myodes Pocock, 1901	BMNH
Schizopelma bicarinatum F. O. P.-Cambridge, 1897	BMNH
Schizopelma macropus (Ausserer, 1875)	BMNH*
Sphaerobothria hoffmani Karsch, 1879	BMHN**
Theraphosa blondi (Latreille, 1804)	MHNP
Xenesthis immanis (Ausserer, 1875)	BMNH
AVICULARIINAE	
Avicularia sp.	MHNP**
Ephebopus murinus (Walckenaer, 1837)	BMNH
Iridopelma hirsuta Pocock, 1901	BMNH
Pachistopelma rufronigrum Pocock, 1901	BMNH
HARPACTIRINAE	
Ceratogyrus darlingi Pocock, 1897	BMNH
Coelogenium pillansi Purcell, 1902	SAM
Eucratoscelus longiceps Pocock, 1898	BMNH
Harpactirella treleaveni Purcell, 1902	SAM
ISCHNOCOLINAE	
Cratorrhagus concolor (Simon, 1873)	MHNP
Hemirrhagus cervinus (Simon, 1890)	MHNP

(equal or more than 10% of the length of the bulb) = 1.

Character 2: Paraembolic apophysis present = 1; absent = 0.

Character 3: Bulbal keels smooth or absent = 0; serrated = 1.

Character 4: Bulbal keels absent = 0; two subequal keels (*Phrixotrichus* and related genera) = 1; two inequal keels (one clearly wider) = 2; peripheric keel = 3; peripheric keel + supernumerary keels = 4.

Character 5: Subtegulum large, extended (all genera of Theraphosinae) = 1; not = 0.

Character 6: Male tibial apophysis double = 0; one tibial apophysis = 1; absent = 2.

Character 7: Digitiform apophysis of bulb present = 1; absent = 0.

Character 8: Metatarsus I of male with basal process = 1; without = 0.

Character 9: Male palpal tibia with retrolateral process = 1; without = 0.

Character 10: Male palpal tibia with retrolateral cluster of spines = 1; without = 0.

Character 11: Male palpal tibia with prolateral process = 1; without = 0.

Character 12: Flexion of metatarsus I of males, outer side of the tibial spurs = 0; between tibial spurs = 1. Taxa with single or no spurs were scored as unknown (?).

Character 13: Spermathecae with two receptacles separated or only partly fused = 1; spermathecae widely fused (the fusion zone is half or more than spermathecal length) = 2; spermathecae with single semicircular receptacle = 3; spermathecae with single oval receptacle = 4.

Character 14: Spermathecae multilobular (part of outgroup) = 0; spermathecae unilobulated (all Theraphosinae genera) = 1.

Character 15: Femur III incrassate = 1; not incrassate = 0.

Character 16: Tibia IV incrassate = 1; not

Table 2.--Data matrix.

		Characters	
		1	2
Taxa	0123456789	0123456789	0123456
OUTGROUP	000000?000	0000000000	0000000
Acanthoscurria	1100211001	00?0100111	0100000
Aphonopelma	0000110000	0000100010	0001000
Brachypelma	2100410000	0002100011	0000000
Citharacanthus	0000110000	001??00010	0101000
Cyclosternum	110?110000	0000100?1	0000000
Cyriocosmus	0010110001	1000100000	1000000
Cyrtopholis	1100110001	0100100110	010?000
Euathlus	0000110000	000??00001	0000000
Eupalaestrus	1101110000	0000111111	0000000
Hapalopus	1100210000	1014100001	0000001
Hapalotremus	0000110000	0014100001	0000101
Homoeomma	0?01110110	0?10100001	100000?
Lasiodora	1101210000	0001100111	0010000
Megaphobema	2100410000	0003110111	0000000
Melloleitaoina	0000110000	0000110001	0000100
Metriopelma	1100212000	00?41?00??	?000000
Nhandu	1101212000	0001100111	0000000
Pamphobeteus	2100110000	0011100111	0000000
Paraphysa	0000110000	0000100001	1000?00
Phormictopus	2100?10001	0000100111	0110000
Phrixotrichus	0000110000	0000100001	1010000
Plesiopelma	0000110010	?010100001	1000000
Pseudotheraphosa	2100310000	0003100101	0010000
Schizopelma	11?0211000	?0???00101	0000000
Sericopelma	2100412000	00?2100111	0000000
Sphaerobothria	2101310000	0001?0010	0100010
Theraphosa	2100312000	00?3100101	0010000
Tmesiphanthes	0000110000	0000110001	0000000
Vitalius	1101210000	0001100110	0000000
Xenesthis	2100310000	0011100110	0000000

incrassate = 0.

Character 17: Femur IV with retrolateral scopula = 1; without = 0.

Character 18: Urticating hairs type I (of Cooke et al. 1972) present = 1; absent = 0.

Character 19: Urticating hairs type III (of Cooke et al. 1972) present = 1; absent = 0.

Character 20: Urticating hairs type IV (of Cooke et al. 1972) present = 1; absent = 0.

Character 21: Trochanteral stridulatory hairs present = 1; absent = 0.

Character 22: Coxal stridulatory hairs present = 1; absent = 0.

Character 23: Coxal spinules present = 1; absent = 0.

Character 24: Numerous labial cusps = 0; few or none = 1.

Character 25: Fovea normal = 0; with spherical process = 1.

Character 26: Metatarsus I of males strongly curved = 1; normal = 0.

CLADISTIC RELATIONSHIPS

Monophyly of Theraphosidae. -- The

monophyly of Theraphosidae was supported (Raven 1985) by the presence of dense tarsal scopulae in combination with claw tufts. The presence of dense tarsal scopulae was considered the most obvious synapomorphy for the family (Coddington & Levi 1991), but with a parallelism in Barychelidae (Raven 1985). Recently, Goloboff (1995) suggested that neither monophyly nor paraphyly of the Theraphosidae are strongly supported. Goloboff (1995) suggested that a group formed by the Paratropididae plus the Theraphosidae, but excluding Ischnocolinae is supported by the reduction of tooth rows of the male superior tarsal claws (STC).

Intra-Theraphosidae Relationships. -- The relationships within the Theraphosidae were resolved for only some groups (Fig. 1) by Raven (1985). The Theraphosinae were placed in a tetrachotomy with Aviculariinae, Harpactirinae, and part of the Ischnocolinae.

These four groups share the presence of dense tarsal scopulae, absence of third tarsal claw (indicated by Raven 1985), and the superior tarsal claws with teeth reduced or absent (Goloboff 1993a). Using these four taxa, attempts were made to find the sister group of the Theraphosinae. One way is to consider the Harpactirinae as the sister group of the Theraphosinae, taking into account that both subfamilies share unilobular (1 + 1) spermathecae (one receptacle in each side), suggested as apomorphic to Theraphosinae (Pérez-Miles 1992a). Most Ischnocolinae and Aviculariinae have bilobular (2 + 2) spermathecae, but there are some genera with unilobular spermathecae that contradict that hypothesis.

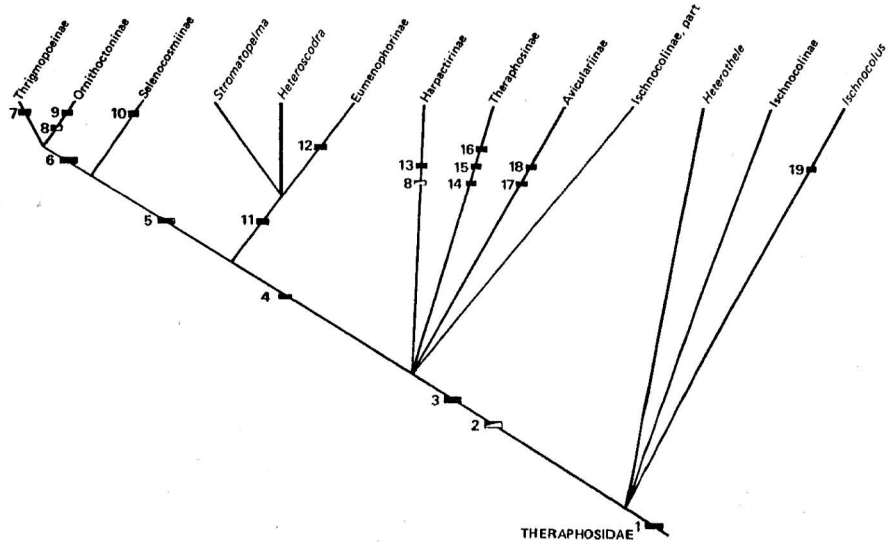


Figure 1.--Cladogram of the theraphosid subfamilies, from Raven (1985). Theraphosinae is placed in a tetrachotomy with Aviculariinae, Harpactirinae, and Ischnocolinae (in part).

Lucas et al. (1991) and Pérez-Miles (1992a) considered Avicullariinae and Theraphosinae as sister groups, based on the presence of urticating hair. However, Avicullariinae have type II urticating hair (Cooke et al. 1972), but Theraphosinae have only types I, III, and IV. There is no evidence of homology among these hairs, considering their structural differences and the presence of two hair types together in individuals of the same species. Despite this, a close relationship between Avicullariinae and Theraphosinae seems possible, since a defensive display with abdominal movements is known only for these two New World subfamilies, and could be regarded as a synapomorphy. The independent acquisition of different types of urticating hair could be a consequence of that visual display behavior. Type II hair still on the abdomen of Avicullariinae contact the aggressor directly (Bertani & Marques 1995). Other hair types are dislodged by friction from the hind legs striking against the abdomen (Gertsch 1949; Bücherl 1951; Cooke et al, 1972; Pérez-Miles & Prandi 1991).

The urticating hairs of *Ephebopus murinus* (Walckenaer) are located on the prolateral face of the palpal femur (Marshall & Uetz 1990). The hair could have evolved from an alternative defensive display; the elevation of the forelegs, palps, and cheliceral extension. This behavior is observed in most Theraphosidae and other spiders, and is plesiomorphic in the Theraphosinae.

The Ischnocolinae is a confused subfamily from a phylogenetic point of view. Raven (1985) considered it paraphyletic, recognizing a basal group with three tarsal claws and another group with two tarsal claws related to the Theraphosinae. Goloboff (1995) agrees with Raven (1985) in the paraphyly of Ischnocolinae.

Although the Avicullariinae are probably the sister group of the Theraphosinae, we more cautiously used the subfamilies Avicullariinae, Harpactirinae, and Ischnocolinae (in part) as the outgroup.

Monophyly of the Theraphosinae.-- The monophyly of the Theraphosinae was upheld by Raven (1985) by the following synapomorphies: i) extended subtegulum, ii) keels on palpal bulbs. The retrolateral scopulae of femur IV was used by Raven (1985) as a synapomorphy of the Theraphosinae, but only for the cladogram of the family. This character was discarded as a synapomorphy for the Theraphosinae, since it is present in only 14 of 30 genera (Pérez-Miles 1992a). Types I, III and IV urticating hair are found only in the Theraphosinae. Type III hairs are present in most Theraphosinae genera with some probable reversions in *Aphonopelma, Citharacanthus, Cyrtopholis, Spaerobothria, Vitalius,* and *Xenesthis.* Conversely, type IV urticating hairs are found in an important group of Theraphosinae (most genera of "Grammostolinae" previous to subfamilies, in Raven [1985]). Type I hairs are found in most "Theraphosinae" (previous to the concept of Theraphosinae in Raven [1985]). Consequently, type III urticating hair seems to be a synapomorphy of the Theraphosinae (with some generic reversions) and types I and IV are probably synapomorphic to some genera within the Theraphosinae.

Another character discussed by Pérez-Miles (1992a), the unilobular spermathecae, which was suggested as apomorphic in Theraphosinae. However, this interpretation would need at least three parallelisms in other subfamilies (Harpactirinae, part of Avicullariinae, and Ischnocolinae). For this reason, the character is not included to support the monophyly of Theraphosinae.

THERAPHOSINAE Thorell, 1870

Diagnosis. -- Differs from other Theraphosidae in the presence of urticating hair of types I and/or III and/or IV. The palpal bulb has a large subtegulum, extended, and with keels present.

Description. -- Eight eyes in a distinct tubercle, anterior row straight to procurved, posterior straight to recurved. ALE generally the largest, PME generally the smallest. Clypeus narrow or absent. Fovea slightly procurved to slightly recurved, closed, normal (most genera), or with a distinct sphe-

roid process (*Sphaerobothria*). Chelicerae without rastellum. Labium subrectangular, with numerous (most genera) or few cusps (*Hapalotremus, Melloleitaoina*). Palpal coxae with numerous cusps, prolateroventral angle pronounced. Plumose hairs ("stridulatory setae") in the prolateral face of coxae and/or trochanter I and retrolateral face of coxa and/or trochanter of palp in some genera, absent in most genera. Plumose hairs on coxae II (*Pseudotheraphosa*). Legs spinose, tarsi without spines, claviform setae on dorsal surface of tarsi. Tarsi densely scopulate; in large species, scopula is entire; in small species the scopula is divided by a longitudinal band of thicker and longer conical setae (mainly on hind legs). Metatarsal scopulae confined to distal region. Two tarsal claws monopectinate with few (if any) teeth. Retrolateral scopulae on femur IV present in some genera, absent in most. Femur III incrassate in *Megaphobema*, *Eupalaestrus* and *Melloleitaoina*; or not so (most genera). Tibia IV incrassate in *Eupalaestrus*, or not so (most genera). Dorsal surface of the abdomen with a patch of type III urticating hair (most genera), and/or types IV or I (some genera), or solely type I (*Aphonopelma, Citharacanthus,* and *Cyrtopholis)*. Short, strong spines on prolateral face of coxae present in *Citharacanthus,* and some species of *Aphonopelma*, or absent (most genera). Males with two tibial spurs (most genera), only one tibial spur (*Acanthoscurria* and *Schizopelma*), or without tibial spurs (*Metriopelma, Nhandu, Sericopelma,* and *Theraphosa*). Palpal bulb with subtegulum large, extended, and with keels. Distal embolus subcylindrical, subconical, or spoon-shaped (laminar, concave/convex). Paraembolic apophysis present (*Cyriocosmus*) or absent (other genera); digitiform apophysis present (*Homoeomma*) or absent (other genera). Males with basal process of metatarsus I (*Homoeomma, Plesiopelma*), or absent (other genera); retrolateral nodule in palpal tibia (*Acanthoscurria, Cyriocosmus, Cyrtopholis,* and *Phormictopus*), or prolateral (*Cyrtopholis,* and *Homoeomma* [in part]) or absent (other genera). Males with spiniform hairs in the retrolateral face of palpal tibia (*Cyriocosmus, Hapalopus,* and *Plesiopelma* [in part]) or absent (other genera). Males with metatarsus I normal (most genera) or strongly curved (*Hapalotremus, Hapalopus*). Females with seminal receptacles separate (most genera), fused at base (*Lasiodora, Nhandu, Pamphobeteus, Sphaerobothria, Vitalius,* and *Xenesthis*), or completely fused (*Brachypelma, Metriopelma, Hapalopus, Hapalotremus, Megaphobema, Pseudotheraphosa*, and *Theraphosa*).

Genera Included: *Acanthoscurria* Ausserer, *Aphonopelma* Pocock, *Brachypelma* Simon, *Citharacanthus* Pocock, *Cyclosternum* Ausserer, *Cyriocosmus* Simon, *Cyrtopholis* Simon, *Euathlus* Ausserer, *Eupalaestrus* Pocock, *Hapalopus* Ausserer, *Hapalotremus* Simon, *Homoeomma* Ausserer, *Lasiodora* C. L. Koch, *Megaphobema* Pocock, *Melloleitaoina* Gerschman & Schiapelli, *Metriopelma* Becker, *Nhandu* Lucas, *Pamphobeteus* Pocock, *Paraphysa* Simon, *Phormictopus* Pocock, *Phrixotrichus* Simon, *Plesiopelma* Pocock, *Pseudotheraphosa* Tinter, *Schizopelma* F. O. P.-Cambridge, *Sericopelma* Ausserer, *Sphaerobothria* Karsch, *Theraphosa* Thorell, *Tmesiphantes* Simon, *Vitalius* Lucas, da Silva & Bertani, *Xenesthis* Simon.

CLADISTIC ANALYSIS

The cladistic analysis assembled the most parsimonious tree of maximum fit 134.8 using 78 steps. Character steps and fits are given in Table 3. Synapomorphies are given in Table 4.

The group at node 47 showed high resolution, being dichotomous except for the trichotomy at node 45.

Eupalaestrus was the sister group of node 50. Node 51 was related with node 54 by a trichotomy (node 53) where *Phormictopus, Acanthoscurria,* and *Cyrtopholis* were placed. *Cyclosternum* was the sister group of node 54. *Aphonopelma* and *Citharacanthus* were sister genera (node 31) and both were the sister group of node 55.

Table 3.--Character steps and fit of the most parsimonious tree.

Character	Fit	Steps
0	5.0	5 (3)
1	7.5	2 (1)
2	-	-
3	6.0	3 (2)
4	3.3	10 (6)
5	-	-
6	2.7	10 (8)
7	-	-
8	10.0	1 (0)
9	7.5	2 (1)
10	7.5	2 (1)
11	-	-
12	5.0	4 (3)
13	10.0	4 (0)
14	-	-
15	6.0	3 (2)
16	-	-
17	5.0	4 (3)
18	7.5	2 (1)
19	3.3	7 (6)
20	10.0	1 (0)
21	6.0	3 (2)
22	5.0	4 (3)
23	10.0	1 (0)
24	7.5	2 (1)
25	-	-
26	10.0	1 (0)

Although the tetrachotomy of node 43 remained unresolved, the monophyly of the involved genera is strongly supported by the presence of type IV urticating hair; this character shows high consistency with the cladogram (Fig. 2). Within this group, *Plesiopelma* was placed as the sister group of *Homoeomma, Melloleitaoina,* and *Tmesphanthes* were resolved as sister groups (node 36).

GENERA OF THERAPHOSINAE

Acanthoscurria Ausserer

Mygale: Koch, 1842: 43.
Scurria Koch, 1850: 74.
Acanthoscurria Ausserer, 1871: 205.
Acanthopalpus Ausserer, 1871: 207.
Callyntropus Ausserer, 1875: 181.

Diagnosis. -- Differs from other Theraphosinae in the subspheric shape of the spermathecal receptacles in some species (Fig. 5) in combination with: i) few and distinct stridulatory setae on the retrolateral face of the palpal trochanter, ii) males with only one tibial apophysis (Fig. 4), and iii) retrolateral nodule on male palpal tibia (Fig. 6). Male palpal bulb (Fig. 3).

Types. -- *Acanthoscurria geniculata* (Koch, 1842), male in ZMB (2055) and females in BMNH (96-12-13), from Santarem, Brazil, examined.

Comments. -- The monophyly of *Acanthoscurria* is supported by the synapomorphic presence of only one tibial apophysis on leg I of males. The subspheric shape of spermathecal receptacles is only known from some species of this genus, and could be a synapomorphy.

Natural History. -- *Acanthoscurria suina* Pocock, 1903 a common species from Uruguay, lives in high meadows and hills. Females excavate tubular burrows that are generally vertical, but sometimes bent. On humid, warm, and cloudy or rainy days (with low atmospheric pressure) between March and April, as many as 20 wandering males have been observed in one hour (Pérez-Miles & Costa 1995). Probably, the atmospheric conditions synchronize male-female mating encounters. Postembryonic development of *Acanthoscurria sternalis* Pocock, 1903 was described by Galiano (1973, 1984, 1992). Natural history data for this species was briefly described by Brazil & Vellard (1926). Bücherl (1952) also noted maternal care for some species. The natural history of the Brazilian species, *Acanthoscurria atrox* (Vellard, 1924), was discussed by Lourenço (1978). This species incorporates urticating hair into the molting mat (Pérez-Miles & Costa 1994). Spermatogenesis of *Acanthoscurria* sp. was studied by Alberti et al. (1986).

Aphonopelma Pocock

Eurypelma: F. O. P.-Cambridge, 1897: 26.
Aphonopelma Pocock, 1901: 553.
Rhechostica: Raven, 1985: 149.

Table 4.--Synapomorphies, * = no synapomorph.

Taxon or Node	Changes
Acanthoscurria	6: 0 --> 1
Aphonopelma	*
Brachypelma	17: 1 --> 0
Citharacanthus	12: 0 --> 1
	21: 0 --> 1
Cyclosternum	*
Cyriocosmus	2: 0 --> 1
	9: 0 --> 1
	10: 0 --> 1
	19: 1 --> 0
Cyrtopholis	11: 0 --> 1
	19: 1 --> 0
Euathlus	*
Eupalaestrus	15: 0 --> 1
	16: 0 --> 1
Grammostola	22: 0 --> 1
Hapalopus	10: 0 --> 1
Hapalotremus	0: 1 --> 0
	1: 1 --> 0
	4: 2 --> 1
	24: 0 --> 1
Homoeomma	3: 0 --> 1
	7: 0 --> 1
Lasiodora	22: 0 --> 1
Megaphobema	15: 0 --> 1
Melloleitaoina	24: 0 --> 1
Metriopelma	6: 01 --> 2
Nhandu	6: 0 --> 2
Pamphobeteus	4: 3 --> 1
Paraphysa	*
Phormictopus	0: 1 --> 2
Phrixotrichus	22: 0 --> 1
Plesiopelma	*
Pseudotheraphosa	*
Schizopelma	*
Sericopelma	6: 0 --> 2
Sphaerobothria	17: 1 --> 0
	21: 0 --> 1
	25: 0 --> 1
Theraphosa	6: 01 --> 2
Tmesiphanthes	*
Vitalius	*
31	23: 0 --> 1
	19: 1 --> 0
32	8: 0 --> 1
	12: 0 --> 1
33	26: 0 --> 1
34	17: 1 --> 0
35	0: 2 --> 1
	4: 3 --> 2
36	15: 0 --> 1
37	12: 0 --> 1
38	22: 0 --> 1
39	18: 1 --> 0
40	13: 2 --> 3
43	20: 0 --> 1
45	13: 1 --> 2
46	3: 1 --> 0
47	0: 1 --> 2
	4: 2 --> 3
50	4: 1 --> 2
	13: 0 --> 1
51	3: 0 --> 1
53	9: 0 --> 1
	21: 0 --> 1
54	17: 0 --> 1
55	0: 0 --> 1
	1: 0 --> 1
56	18: 0 --> 1
59	4: 0 --> 1
	5: 0 --> 1
	14: 0 --> 1
	19: 0 --> 1

Diagnosis. -- Differs from the other Theraphosinae in the presence of only type I urticating hair in combination with the presence of spiniform hair on retrolateral face of coxae, the absence of stridulatory setae, and the morphology of palpal bulb and spermathecae (Figs. 7, 8).

Types. -- Female of *Aphonopelma seemanni* (F. O. P.-Cambridge) from Puerto Culebra, Costa Rica, in BMNH, examined. Male of *Aphonopelma texense* (Simon) from Texas, USA, in SI, examined. Congeners (five males in AMNH, one male in IB), examined.

Comments. -- Raven (1985) placed *Aphonopelma* Pocock, 1901 in the synonymy of *Rhechostica* Simon, 1892. Levi & Kraus (1989) proposed the conservation of *Aphonopelma* and its precedence over *Rhechostica* (ICZN Case 2662). *Aphonopelma* was a

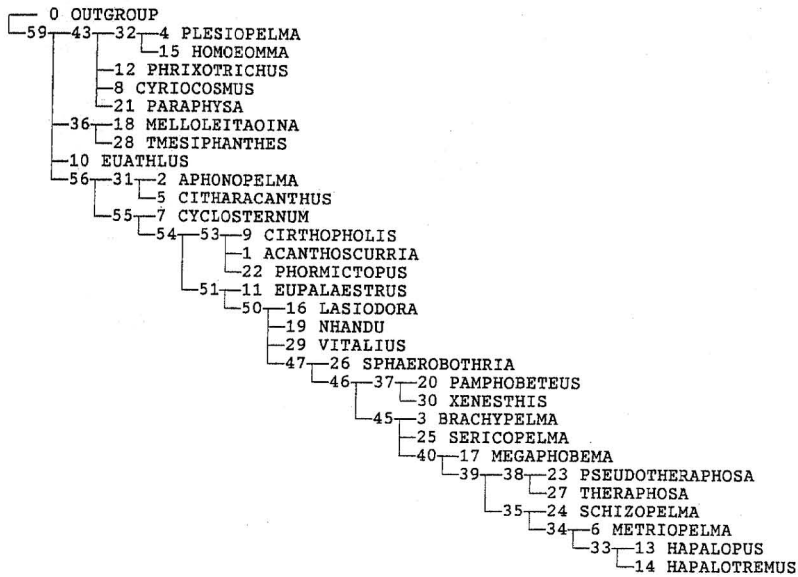
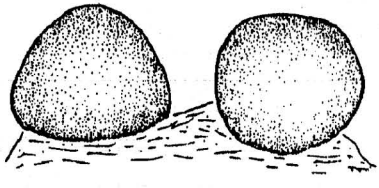
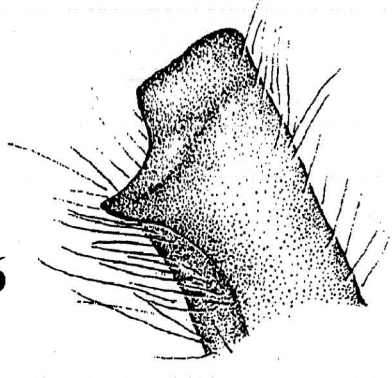
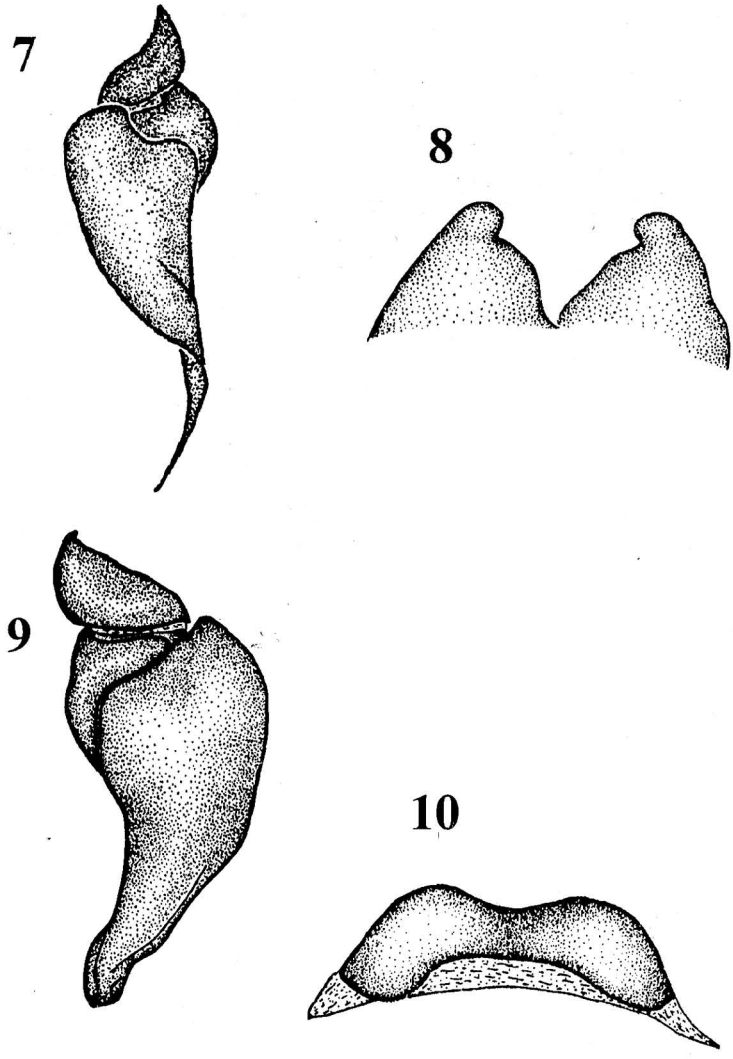


Figure 2.--Tree of genera of Theraphosinae, maximum fit (134.8, 78 steps).





Figures 3-6.--3, *Acanthoscruria geniculata* (C. L. Koch) holotype male, lateral view of palpal bulb; 4, *A. geniculata* tibial apophysis of leg I; 5, *Acanthoscurria suina* Pocock, holotype female spermathecae; 6, *A. geniculata* holotype male, prolateral nodule of palpal tibia.(Photographs: Vera Heinrich).



Figures 7-10.--7, *Aphonopelma texense* (Simon) holotype male, left palpal bulb, prolateral view; 8, *Aphonopelma seemanni* (F. O. P.-Cambridge) holotype female, spermathecae; 9, *Brachypelma emilia* (White) holotype male, right palpal bulb, prolateral view; 10, *B. emilia* holotype female, spermathecae.

widely used name and its conservation was finally established by the ICZN (1991, Opinion 1367).

Natural History. -- The natural history of some species of *Aphonopelma* was studied by Baerg (1928, 1958); Petrunkevitch (1911); Cazier & Mortenson (1964); Melchers (1964); Marer (1972); Minch (1978a; 1978b; 1978c; 1979a; 1979b); Whitcomb & Weems (1976); Herrero & Bolaños (1982); Herrero et al. (1982); Alberti et al. (1986); Herrero & Valerio (1986); Herrero & Odell (1988); Punzo (1989); Formanowicz & Ducey (1991), and others.

Brachypelma Simon

Brachypelma Simon, 1892: 168.
Euathlus: Raven, 1985: 150 (in part).

Diagnosis. -- Differs from the other Theraphosinae in the morphology of palpal bulb and spermathecae (Figs. 9, 10), in combination with two tibial aphophyses in males, and in lacking retrolateral scopulae on femur IV.

Types. -- *Brachypelma emilia* (White) male and female from Mazatlan, Mexico, in MHNP, examined.

Comments. -- *Brachypelma* was considered a junior synonym of *Euathlus* by Raven (1985). Schmidt (1992) restored it to validity. Our study of the types of both genera led us to agree with Schmidt's conclusions.

Natural History. -- Molting of *Brachypelma smithi* (F. O. P.-Cambridge) was described by Randall & Whitcomb (1976). This genus was recently placed in the Appendix II of CITES for protection (R. C. West pers. comm.) because of the increasing interest in some species as pets. Brief ecological data of *Brachypelma* spp. from Costa Rica were given by Valerio (1980a).

Citharacanthus Pocock

Eurypelma Koch, 1850: 73.
Citharacanthus Pocock, 1901: 551.

Diagnosis. -- Differs from other Theraphosinae in the morphology of the palpal bulb (Fig. 11) in combination with the following characters; claviform stridulatory setae on the prolateral face of trochanter, and coxae with spiniform hairs.

Types.--male of *Citharacanthus longipes* (F. O. P.-Cambridge) from Chicoyoito, Guatemala, in BMNH, examined.

Comments. -- *Plesiopelma* Pocock 1901 (type in BMNH, examined), is here removed from the synonymy of *Citharacanthus* Pocock, 1901 (type in BMNH, examined), from which it differs in the palpal bulb morphology (Figs. 11, 38) and other characters of generic significance.

Cyclosternum Ausserer

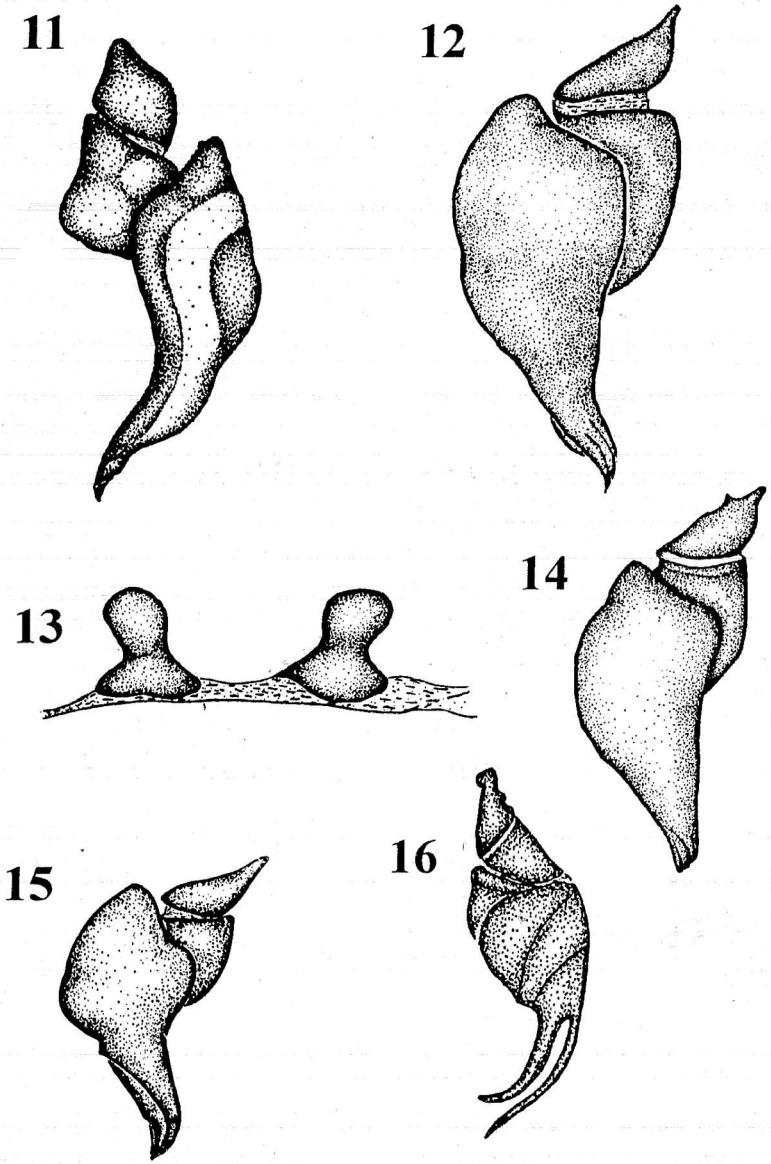
Cyclosternum Ausserer, 1871: 192.
Dryptopelma Simon, 1889a: 402 **NEW SYNONYMY.**

Diagnosis. -- Differs from most genera of Theraphosinae in the palpal bulb and spermathecal morphology (Figs. 12, 13). It differes from *Eupalaestrus* in having tibia IV not incrassate and tarsal scopulae divided.

Types. -- *Cyclosternum schmardae* Ausserer, 1871 male and female from Ecuador (in MHNP 9885), examined.

Comments. -- *Dryptopelma* Simon, 1889 (type in MHNP, examined) is placed in the synonymy of *Cyclosternum* Ausserer, 1871 (type in MHNP, examined). The width of femur IV is in itself considered insufficient to continue the separation of *Dryptopelma* from *Cyclosternum*. *Dryptopelma* shares the morphology of male palpal bulb with *Cyclosternum* (Fig. 14) as well as other characters of generic significance. *Schizopelma macropus* Ausserer, 1875 (type male in BMNH, examined) is here placed in *Cyclosternum*, with which it shares the morpholoy of male palpal bulb (Fig. 15) and other characters of generic significance. Consequently, we propose *Cyclosternum macropus* (Ausserer, 1875) **NEW COMBINATION** (see *Schizopelma*).

Natural History. -- Ecological data for some species were given by Valerio (1982). Magnusson (1985) reported a group of 89 male *Cyclosternum* moving through tropical rainforest in Manaus, Brazil.



Figures 11-16.--11, *Citharacanthus longipes* (F. O. P.-Cambridge) holotype male, right palpal bulb, prolateral view; 12, *Cyclosternum schmardae* Ausserer holotype male, left palpal bulb, prolateral view; 13, *C. schmardae* holotype female, spermathecae; 14, *Cyclosternum janthina* (Simon) type male, left palpal bulb, prolateral view; 15, *Schizopelma macropus* (Ausserer) type male, left palpal bulb, prolateral view; 16, *Cyriocosmus sellatus* (Simon) holotype male, right palpal bulb, prolateral view.

Cyriocosmus Simon

Hapalopus Simon, 1889b: 218
Cyriocosmus Simon, 1903: 929.
Pseudohomoeomma Mello-Leitão, 1930: 57.

Diagnosis. -- Differs from the other Theraphosinae genera in the presence of a paraembolic apophysis in the palpal bulb (Fig. 16).

Types. -- Male and female of *Cyriocosmus sellatus* (Simon, 1889a), from Upper Amazonas, in MHNP, examined.

Cyrtopholis Simon

Cyrtosternum Ausserer, 1875: 176.
Cyrtopholis Simon, 1892: 143.

Diagnosis. -- Differs from the other Theraphosinae in the presence of stridulatory setae on the retrolateral face of the palpal trochanter and prolateral face of trochanter I, in combination with prolateral and retrolateral nodules on the male palpal tibia. Spermathecae as in Fig. 17.

Types. -- Female of *Cyrtopholis cursor* (Ausserer, 1875), from Republica Dominicana, Santo Domingo, in BMNH, examined

Natural History. -- Aspects of molting and sexual behavior of *Cyrtopholis jamaicola* Strand were described by Petrunkevitch (1934).

Euathlus Ausserer

Euathlus Ausserer, 1875: 188.
Paraphysa: Strand, 1907: 221 (not Simon 1892) **NEW SYNONYMY.**

Diagnosis. -- Differs from other the Theraphosinae in the palpal bulb morphology (Fig. 18) in combination with the characters given in Table 2.

Types. -- Male of *Euathlus truculentus* Ausserer, 1875, in BMNH, examined.

Comments. -- *Paraphysa phryxotrichoides* Strand, 1907 (type not located; male and female from Valparaíso, Chile, IB 3744 and 3720, examined) is here synonymized with *Euathlus truculentus* Ausserer (holotype male, examined) from which it does not differ. The characters and figures given by Legendre & Calderón-Gonzalez (1984) for *P. phryxotrichoides* agree with our observations on the type of *E. truculentus,* and the individuals in the IB. The morphology of spermathecae *E. truculentus* is shown (Fig. 19, see also *Brachypelma*).

Eupalaestrus Pocock

Eurypelma: Keyserling, 1891: 21 (in part).
Eupalaestrus Pocock 1901: 546.
Pterinopelma Pocock, 1901: 551.
Rhechostica: Raven, 1985: 158 (in part).

Diagnosis. -- Differs from the other genera of Theraphosinae in the incrassate tibiae IV (mainly in males). Palpal bulb and spermathecae are as in Figs. 20, 21.

Types. -- Female of *Eupalaestrus pugilator* Pocock, 1901, in BMNH, examined.

Comments. -- Pérez-Miles (1992b) removed this genus from the synonymy of *Rhechostica* established by Raven (1985) considering it a senior synonym of *Pterinopelma* Pocock, 1901.

Natural History. -- Females of *Eupalaestrus weijenberghi* (Thorell) live in meadow burrows. Males increase their locomotory activity during stormy days (85 males were observed in 86 km of highway in Flores, Uruguay, Pérez-Miles & Costa 1995). Maternal care was reported for two species in this genus by Bücherl (1952).

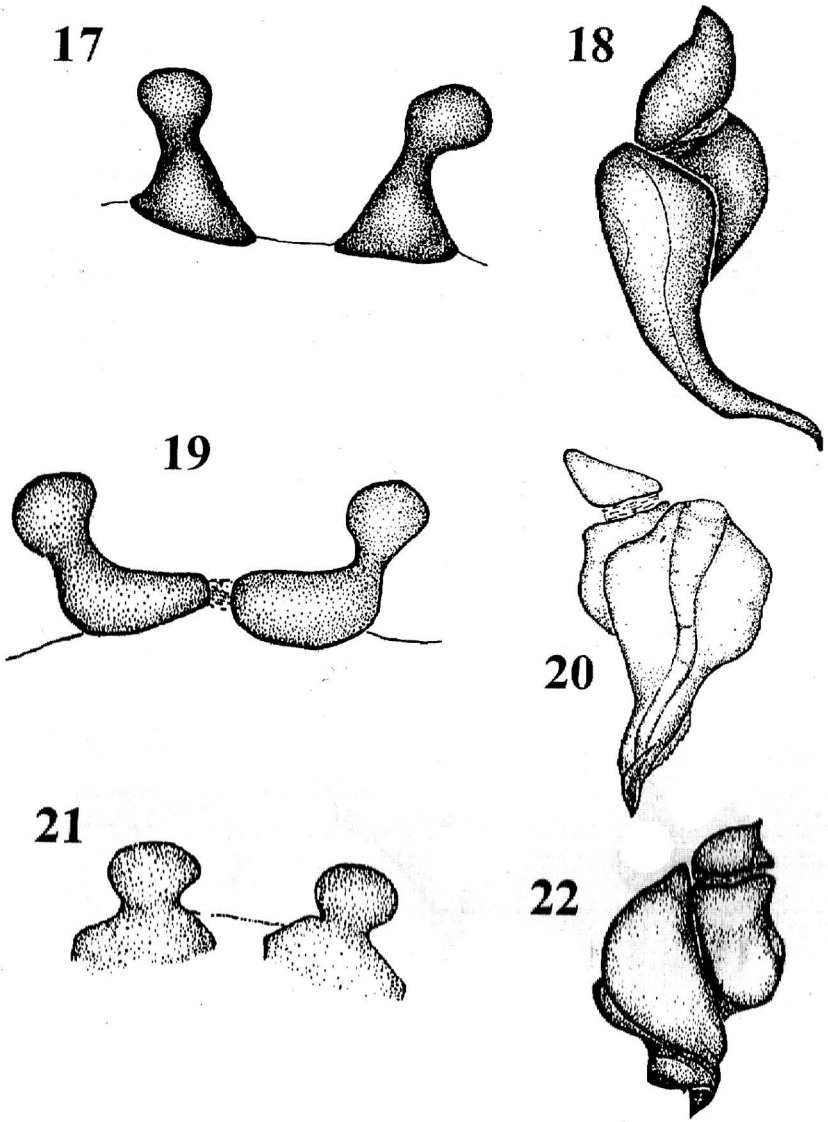
Hapalopus Ausserer

Hapalopus Ausserer, 1875: 175.

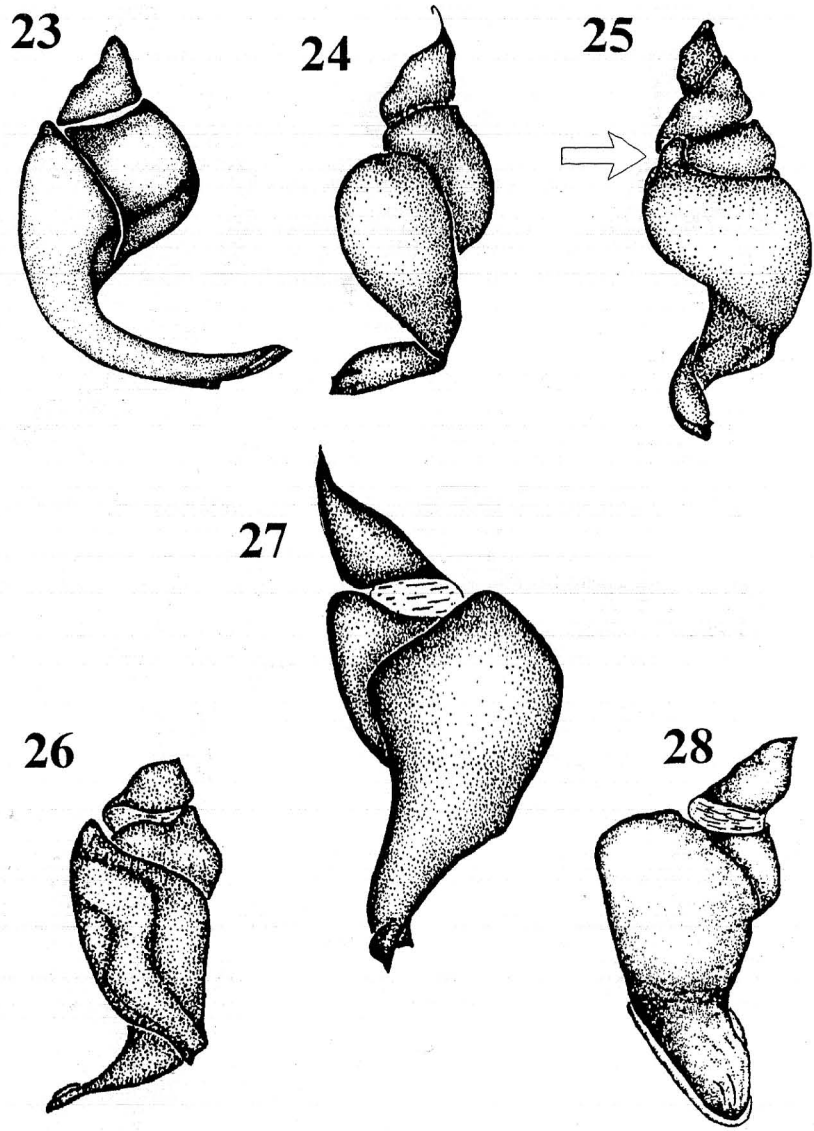
Diagnosis. -- Differs from other Theraphosinae in the palpal bulb morphology (Fig. 22), and the curved metatarsus I in males.

Types. -- Male of *Hapalopus formosus* (Ausserer, 1875) from Bogotá, Colombia, in NMV, examined.

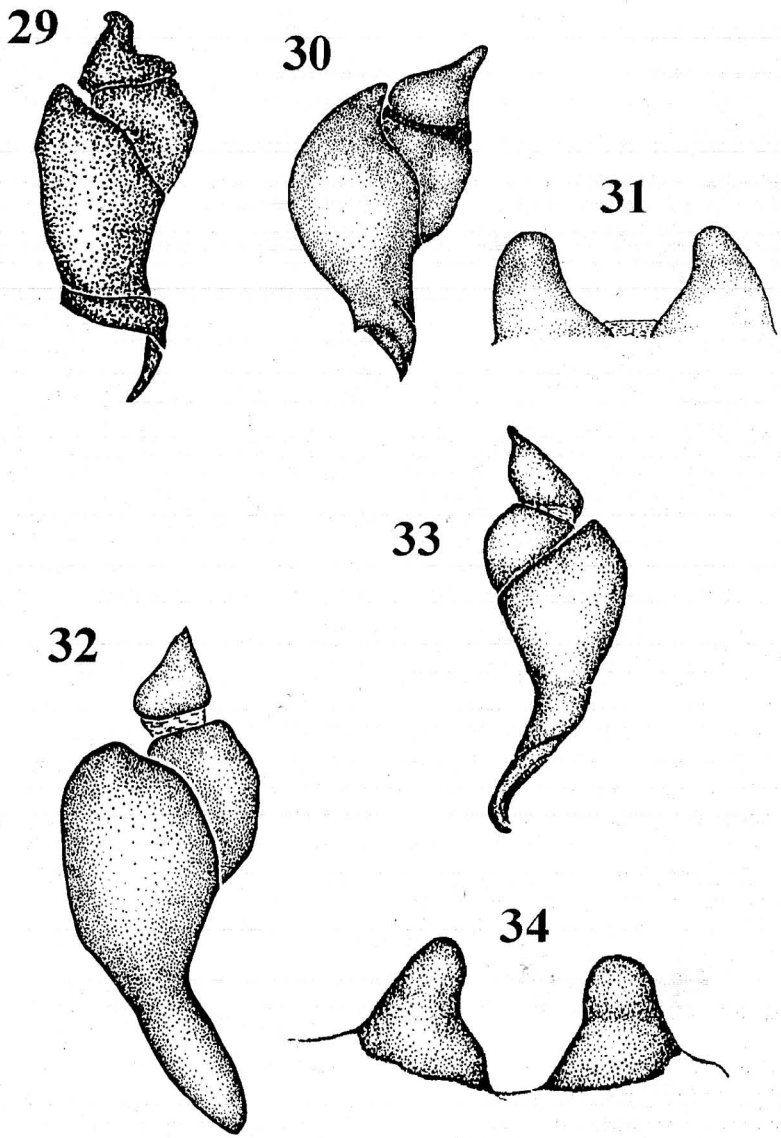
Comments. -- *Hapalopus rectimanus* Mello-Leitão 1923 (type in MZSP, examined) is transferred to *Plesiopelma* because it lacks the reduced number of labial cuspules of *Hapalopus,* and shares the palpal bulb morphology, the presence of a rastellum on the prolateral palpal tibia, and a retrolateral nodule on metatarsus I with *Plesiopelma*. As a consequence, *Plesiopelma rectimanus* (Mello-Leitão) **NEW COMBINATION** is established.



Figures 17-22.--17, *Cyrtopholis cursor* (Ausserer) holotype female, spermathecae; 18, *Euathlus truculentus* Ausserer holotype male, left palpal bulb, prolateral view; 19, female spermathecae of *E. truculentus* from Valparaiso, Chile; 20, *Eupalaestrus campestratus* (Simon) holotype male, left palpal bulb, prolateral view; 21, *E. campestratus* holotype female, spermathecae, dorsal view; 22, *Hapalopus formosus* (Ausserer) holotype male, left palpal bulb, prolateral view.



Figures 23-28.--23, *Hapalotremus albipes* Simon type male, left palpal bulb, prolateral view; 24, *Homoeomma stradlingi* (F.O.P.-Cambridge) type male, left palpal bulb, prolateral view; 25, retrolateral view of *H. stradlingi* palpal bulb, arrow shows the basal digitiform apophysis; 26, *Butantania hirsuta* (Mello-Leitão) type male, left palpal bulb, prolateral view; 27, *Lasiodora klugi* C. L. Koch type male, right palpal bulb, prolateral view; 28, *Megaphobema robustum* (Ausserer) type male, right palpal bulb, retrolateral view.



Figures 29-34.--29 *Melloleitaoina crassifemur* Gerschman & Schiapelli type male, left palpal bulb, prolateral view; 30, *Nhandu carapoensis* Lucas type male, left palpal bulb, prolateral view; 31, *N. carapoensis* female paratype, spermathecae, dorsal view; 32, *Pamphobeteus nigricolor* (Ausserer) male from Colombia, left palpal bulb, prolateral view; 33, *Paraphysa manicata* Simon type male, right palpal bulb, prolateral view; 34, *Phormictopus cancerides* (Latreille) type female, spermathecae, dorsal view.

Hapalotremus Simon

Hapalotremus Simon, 1903: 929.
Dolichothele Mello-Leitão, 1923: 120.
Goniodontium Mello-Leitão, 1923: 127.
Cyclothoracoides Strand, 1929: 17.
Sickius Soares & Camargo, 1948: 405.

Diagnosis. -- Differs from most Theraphosinae in the reduced labial cuspules. Differs from *Melloleitaoina*, *Phrixotrichus*, and *Hapalopus* in the palpal bulb morphology (Fig. 23).

Types. -- Male of *Hapalotremus albipes* Simon 1903, from Bolivia, in MHNP, examined; and male and female from Bolivia, in FNS, examined.

Comments. -- *Hapalotremus* Simon 1903, was placed in Ischnocolinae until 1985, when Raven tentatively transferred it to the Theraphosinae. Schmidt (1993) returned *Hapalotremus* to Ischnocolinae. *Hapalotremus* has a palpal bulb with extended subtegulum and conspicuous subapical keel in the embolus, synapomorphic for Theraphosinae, and the females have a single spermathecal receptaculum (Schmidt 1993), known in only some genera of Theraphosinae and in no Ischnocolinae. The single spermathecal receptaculum is here considered as synapomorphic for those Theraphosinae genera. Those characters and the presence of type III urticating hair support the placement of *Hapalotremus* in Theraphosinae, in agreement with Raven (1985).

Homoeomma Ausserer

Hommeocomma: Ausserer, 1871: 210.
Hapalopus: Keyserling, 1891: 7.
Agathostola Simon, 1892: 163.
Calopelma Chamberlin, 1917: 44.
Eurypelma: Chamberlin, 1917: 49.
Tmesiphantes: Mello-Leitão, 1923: 139.
Hapalotremus: Mello-Leitão, 1946: 7.
Butantania Mello-Leitão, 1935: 358 **NEW SYNONYMY.**

Diagnosis. -- Differs from the other Theraphosidae in the presence of a digitiform basal apophysis in male palpal bulbs (Figs. 24, 25). The males of some species, such as *Homoeomma uruguayense* (Mello-Leitão) have a retrolateral basal nodule in metatarsus I, similar to the one found in *Plesiopelma*.

Types. -- Male of *Homoeomma stradlingi* (F.O.P.-Cambridge, 1881) from Brazil, in BMNH, examined and type male of *H. uruguayense*, from Uruguay in MHNM, examined.

Comments. -- *Butantania* Mello-Leitão (type male in IB, examined) is removed from the synonymy of *Dryptopelma* Simon, 1889 (type male in MHNP, examined), where it was placed by Raven (1985), as it differs dramatically in palpal bulb morphology (Figs. 14, 26). *Butantania* is placed in the synonymy of *Homoeomma* Ausserer, 1871 (types in BMNH and others referred in Table 1, examined), with which it shares generic characters, mainly from palpal bulb morphology. The digitiform apophysis of the bulb, considered as an autopomorphy of *Homeomma*, is also present in the *Butantania* type.

Natural History. -- *Homoeomma uruguayense* is a small-sized species, common in hilly areas of Uruguay. It is usually found in burrows under stones. Other data about the ecology of this species were given in Pérez-Miles et al. (1993). Details concerning its bite were described in Ibarra-Grasso (1946), under the name *Crypsidromus moreni* (Holmberg).

Lasiodora C. L. Koch

Mygale: Koch, 1842: 25
Lasiodora C. L. Koch, 1850: 72.
Crypsidromus Ausserer, 1871: 193 **NEW SYNONYMY.**

Diagnosis. -- Differs from most genera of Theraphosinae in the presence of stridulatory setae on coxa I (prolateral face) and from *Aphonopelma*, *Phrixotrichus*, *Phormictopus*, *Pseudotheraphosa*, and *Theraphosa* in the morphology of the palpal bulb (Fig. 27).

Type. -- Male of *Lasiodora klugi* Koch 1850 from Iguarassu, Brazil, in BMNH, examined.

Comments. -- *Crypsidromus* Ausserer, 1871, type immature female in NMV, exam-

ined, is here removed from the synonymy of *Metriopelma* established by Raven (1985), from which it differs in characters of generic significance (see *Metriopelma*), and is considered a junior synonym of *Lasiodora*. The type of *Crypsidromus isabellinus* Ausserer is indistinguishable from immature specimens of *Lasiodora*, a very common genus in Rio de Janeiro, Brazil.

Natural History. -- A short description of the defensive behavior of *Lasiodora* spp. was given by Brazil & Vellard (1926). Maternal care in *L. klugi* and *Lasiodora curtior* Chamberlin was reported by Bücherl (1952).

Megaphobema Pocock

Lasiodora: Ausserer, 1875: 190 (in part).
Megaphobema Pocock, 1901: 546.

Diagnosis. -- Differs from the other Theraphosinae by the palpal bulb morphology (Fig. 28) in combination with the presence of two tibial apophyses, the femur III being incrassate, and females with a single spermathecal receptaculum.

Types. -- Male of *Megaphobema robustus* Pocock, 1901 from Bogotá, Colombia, in BMNH, examined.

Melloleitaoina Gerschman & Schiapelli

Melloleitaoina Gerschman & Schiapelli, 1960: 200.
Dryptopelma: Raven 1985: 156 (in part).

Diagnosis. -- Differs from most Theraphosinae in the reduced number of labial cuspules, and from *Hapalotremus* in the palpal bulb morphology (Fig. 29).

Types. -- Male of *Melloleitaoina crassifemur* Gerschman & Schiapelli, 1960 from Salta, Oran, Argentina, in MACN, examined.

Comments. -- *Melloleitaoina* Gerschman & Schiapelli, 1960 (type in MACN, examined) is removed from the synonymy of *Dryptopelma* (type in MHNP, examined) established by Raven (1985), from which it differs in the palpal bulb morphology (Figs. 14, 29) and the synapomorphically reduced number of labial cuspules.

Natural History. -- Data on the ecology of some species within this genus were given by Valerio (1982).

Metriopelma Becker

Metriopelma Becker 1878: 256.
Crypsidromus: Simon 1892: 143 (in part).

Diagnosis. -- Differs from most Theraphosinae in the absence of tibial spur in males and the presence of a single spermatheca in females; from *Theraphosa*, *Sericopelma*, and *Nhandu* in palpal bulb morphology (Valerio, 1982).

Types. -- *Metriopelma breyeri* Becker, 1878, male from Mexico, not located.

Comments. -- This genus is here removed from the synonymy of *Crypsidromus* Ausserer (1871) established by Raven (1985). The type of *Crypsidromus*, *Crypsidromus isabellinus* Ausserer, type examined, is here synonymized with *Lasiodora*, and is known only from an immature female that has two separate spermethecal receptacula. The female of the type species of *Metriopelma*, *Metriopelma breyeri* Becker, 1878 is unknown. Valerio (1982) placed within this genus, some species in which the females have a single spermatheca, including *Metriopelma zebrata* Banks, 1909, *Metriopelma drymusetes* Valerio, 1982, and *Metriopelma colorata* Valerio, 1982. Considering the single spermatheca as apomorphic within the Theraphosinae, and taking into account that this condition is not present in *Crypsidromus*, *Metriopelma* is restored as a valid genus. Returned to *Metriopelma* are the species previously attributed to *Crypsidromus*, where the females have a single spermatheca.

Nhandu Lucas

Nhandu Lucas, 1981: 153.

Diagnosis. -- Differs from most Theraphosinae in the absence of a male tibial apophysis, and from *Theraphosa* and *Sericopelma* in the palpal bulb morphology (Fig. 30). Spermathecae as in Fig. 31.

Types. -- Male and paratype female of *Nhandu carapoensis* Lucas, 1981 from Mato

Grosso do Sul, Carapo, Brazil, in IB, examined.

Comments. -- The genus *Nhandu* was considered by Raven (1985) as a junior synonym of *Mygalarachne*, but was removed from this synonymy by Schmidt (1989). Schmidt (1990a; 1990b) added some additional reasons to support the validity of *Nhandu*. The comparison of the types of *N. carapoensis* with *Mygalarchne brevipes* Ausserer showed differences mainly in the spermatheca morphology and tarsal condition, which led us to agree with Schmidt (1989) on the validity of *Nhandu*. Furthermore, *Mygalarachne* was recently considered as genus *incertae sedis* Lucas et al. (1991).

Pamphobeteus Pocock

Pamphobeteus Pocock, 1901: 545.

Diagnosis. -- Differs from most Theraphosinae in that the male metatarsus I closes between the two tibial apophyses, and from *Plesiopelma, Citharacanthus, Hapalopus, Homoeomma,* and *Xenesthis* in the palpal bulb morphology (Fig. 32).

Types. -- Male and female of *Pamphobeteus nigricolor* (Ausserer, 1875) from Bogotá, Colombia, in BMNH, examined.

Comments. -- Lucas et al. (1993) recently removed species from *Pamphobeteus* to *Vitalius*.

Natural History. -- Some aspects of the sexual biology of *P. nigricolor* were reported by Melchers (1964).

Paraphysa Simon

Paraphysa Simon, 1892: 166.

Diagnosis. -- Differs from *Phrixotrichus* in the absence of stridulatory setae, and the reduced cuspules on labium. Differs from *Plesiopelma, Homoeomma,* and *Cyriocosmus* in the morphology of the palpal bulb (Fig. 33). Differs from the other Theraphosinae in the presence of type IV urticating hair.

Types. -- Male of *Paraphysa manicata* Simon, 1892 from Chile, in MHNP, examined.

Comments. -- *Phrixotrichus scrofa* Molina, 1788 (type not examined) is here removed from *Phrixotrichus* and placed in *Paraphysa* with which it shares characters of generic significance, mainly the reduced cuspules on labium, the morphology of bulb, and the absence of stridulatory setae. A revision of the Chilean species of *Paraphysa* and *Phrixotrichus* can be found in Legendre & Calderón-Gonzalez (1984).

Phormictopus Pocock

Phormictopus Pocock, 1901: 545.

Diagnosis. -- Differs from the other Theraphosinae in the presence of stridulatory setae on the prolateral face of coxa and trochanter I, and spermathecae as in Fig. 34.

Types. -- Female of *Phormictopus cancerides* (Latreille, 1806), from Santo Domingo, Republica Dominicana, in BMNH, examined.

Natural History. -- Some aspects of the sexual biology were studied by Gerhardt (1929), and Petrunkevitch (1934).

Phrixotrichus Simon

Mygale: Walckenaer, 1837: 213.
Lasiodora: C. L. Koch, 1850: 73.
Phrixotrichus Simon, 1888: 222.
Eurypelma Keyserling, 1891: (in part).
Phryxotrichus (sic) Simon, 1892: 163.
Agathostola: Pocock, 1895: 227.
Citharoscelus Pocock, 1899: 347.
Grammostola Simon, 1892: 163 **NEW SYNONYMY**.

Diagnosis. -- Differs from most genera of Theraphosinae in the presence of type IV urticating hair, presence of stridulatory setae on the prolateral face of coxa I, palpal bulb morphology, and spermathecal morphology (Figs. 35-37).

Types. -- Male of *Phrixotrichus roseus* (Walckenaer, 1837) in the MHNP, No. 258, examined.

Comments. -- *Grammostola* Simon, 1892 (types and additional material referred in Table 1, examined, Figs. 36, 37) is placed in the synonymy of *Phrixotrichus* with which it shares the presence of stridulatory

setae on the prolateral coxa I, and numerous labial cusps (also observed in the type of type species *P. roseus*). No other characters meriting the separation of *Grammostola* are known. *Phrixotrichus scrofa* (Molina, 1788) from Santiago, Chile, (not examined, a male from Valparaiso, Chile examined), is removed from here to *Paraphysa* Simon, 1892 with which it shares the absence of stridulatory setae on prolateral face of coxa I, and all other characters of generic significance (see *Paraphysa*).

Natural History. -- *Phrixotrichus mollicoma* (Ausserer) from Uruguay, lives in rocky hills, under large stones. Some characteristics of its ecology were described in Pérez-Miles et al. (1993). A brief description of its sexual behavior can be found in Pérez-Miles & Costa (1992), and of its defensive behavior in Pérez-Miles & Prandi (1991). Biological data of Brazilian species are detailed in Brazil & Vellard (1926), Bücherl (1951; 1952), and of the Argentinian species in Ibarra-Grasso (1961) and Galiano (1969). All these publications used the name *Grammostola*.

Plesiopelma Pocock

Plesiopelma Pocock, 1901: 553.
Ceropelma Mello-Leitão, 1923: 175 **NEW SYNONYMY.**

Diagnosis. -- Differs from the other genera of Theraphosinae in the presence of a small subapical tooth on the bulb (Fig. 38), in combination with a retrolateral basal nodule on the male metatarsus I (Fig. 39), and spiral-shaped spermathecae (Fig. 40).

Types. -- Male and female of *Plesiopelma myodes* Pocock, 1901 from Soriano, Uruguay, in BMNH, examined.

Comments. -- *Plesiopelma* Pocock, 1901 (types in BMNH, examined) is removed from the synonymy of *Citharacanthus* Pocock, 1901 (type in BMNH, examined), from which it differs in the palpal bulb morphology (Figs. 11, 38) and other characters of generic significance. *Ceropelma* Mello-Leitão, 1923; type male *Ceropelma insulare* Mello-Leitão, 1923 from Ilha dos Alcatrazes, São Paulo, Brazil, in MZSP (446), examined; and types of *Ceropelma longisternale* (Schiapelli & Gerschman) in MACN, *Ceropelma semiauranticum* (Simon, 1897) in MHNP and *Ceropelma flavohirtus* (Simon, 1889) in MHNP, examined; is placed in the synonymy of *Plesiopelma* Pocock, 1901 (type male from Uruguay, in BMNH, examined), because it shares characters of generic significance.

Natural History. -- *Plesiopelma longisternale* from Argentina and Uruguay, lives in hills, where it excavates burrows and covers the walls with a layer of silk. A brief description of sexual behavior and reproductive biology can be found in Costa & Pérez-Miles (1992). Additional aspects of its ecology are described in Pérez-Miles et al. (1993).

Pseudotheraphosa Tinter

Pseudotheraphosa Tinter, 1991: 6.

Diagnosis. -- Differs from other Theraphosinae, except *Theraphosa*, in the palpal bulb morphology (Fig. 41), and from *Theraphosa* in the presence of two male tibial apophyses and stridulatory setae in coxae II.

Types. -- Male of *Pseudotheraphosa apophysis* Tinter, 1991, not examined.

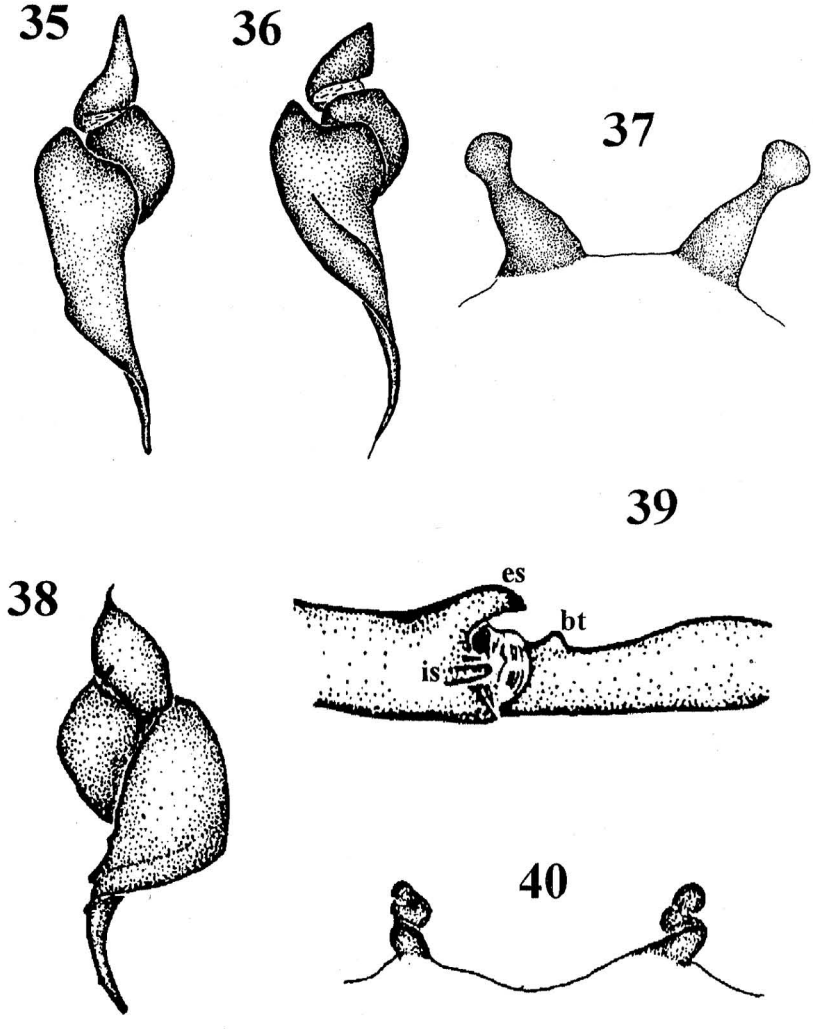
Schizopelma F. O. P.-Cambridge

Schizopelma F. O. P.-Cambridge, 1897: 28.

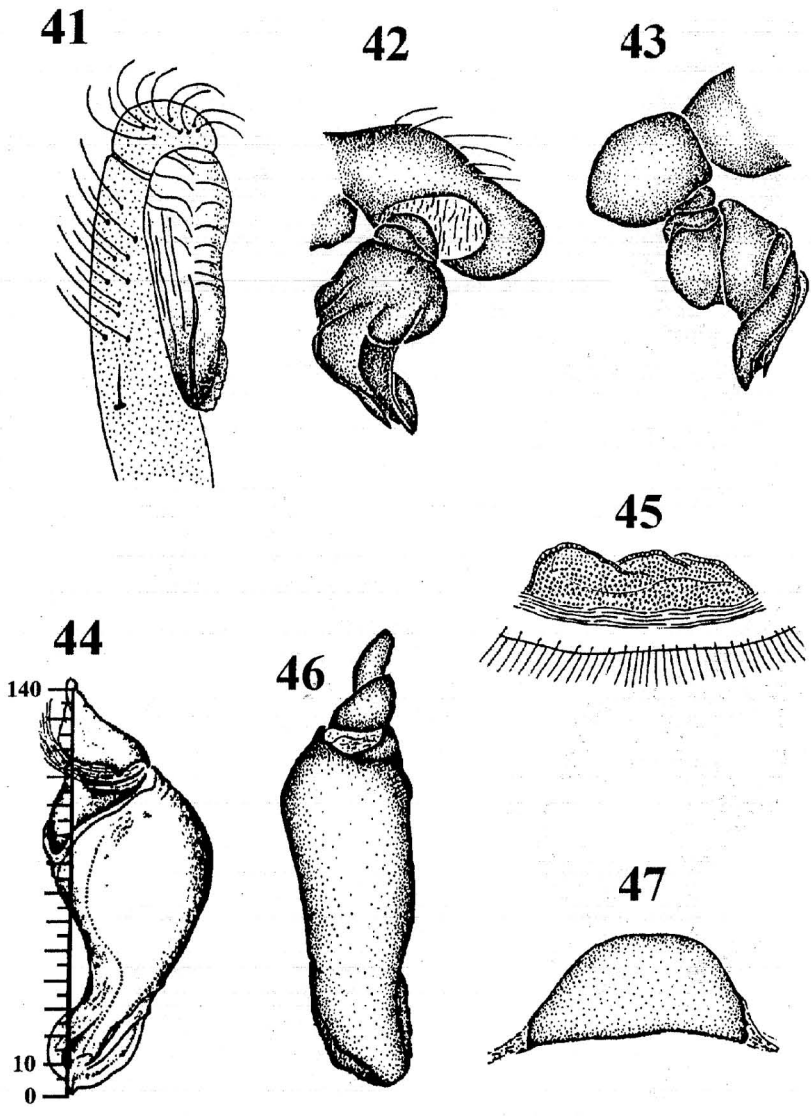
Diagnosis. -- Differs from the other Theraphosinae in the palpal bulb morphology, with a bifid apex present (Figs. 42, 43), and in the presence of a single male tibial apophysis.

Types. -- Male of *Schizopelma bicarinatum* F. O. P.-Cambridge, 1897 from Xantips, Mexico, in BMNH, examined.

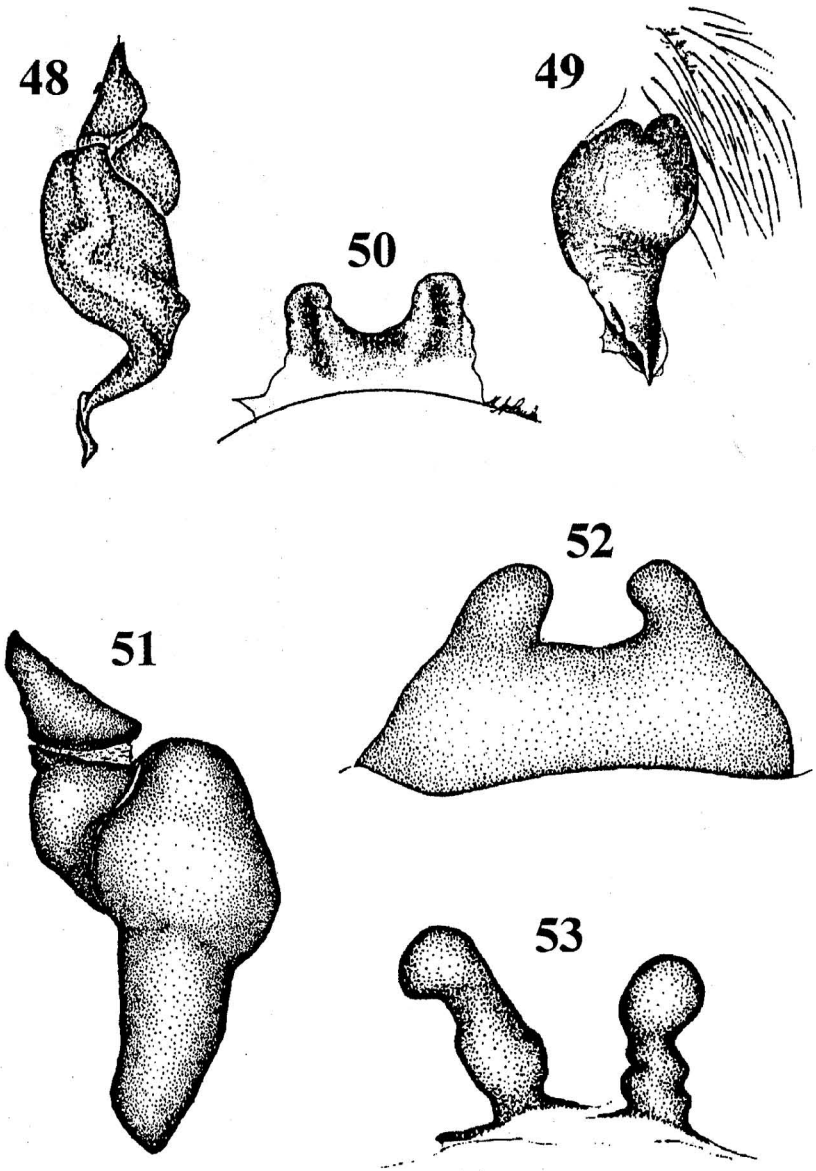
Comments. -- *Schizopelma* F. O. P.-Cambridge 1897 (type in BMNH, examined). Pickard-Cambridge (1897) moved *Schizopelma macropus* (Ausserer, 1875) (type in BMNH, examined) to this genus. The type species, *S. bicarinatum*, dramatically differs from *S. macropus* in the palpal bulb morphology (Figs. 15, 42, 43). *Schizopelma bicarinatum* has the palpal bulb with a bifid apex and a single tibial spur. *Schizopelma macropus* has the palpal



Figures 35-40.--35, *Phrixotrichus roseus* (Walckenaer) type male, left palpal bulb, prolateral view; 36, *Phrixotrichus mollicoma* (Ausserer) (=*Grammostola pulchripes*, male type), left palpal bulb, prolateral view; 37, *P. mollicoma* female from Uruguay, spermathecae, dorsal view; 38, *Plesiopelma insulare* (Mello-Leitão) holotype male, right palpal bulb, prolateral view; 39, *Plesiopelma longisternale* (Schiapelli & Gerschman) male from Uruguay, ventral view (slightly prolateral) of tibial metatarsus joint showing external (es) and internal (is) tibial spurs, and metatarsal basal tubercle (bt) (from Costa & Pérez-Miles 1992); 40, *Plesiopelma myodes* Pocock paratype female, spermathecae, dorsal view.



Figures 41-47.--41, *Pseudotheraphosa apophysis* Tinter holotype male, palpal bulb (from Tinter 1991); 42, 43, *Schizopelma bicarinatum* F. O. P.-Cambridge; 42, type male, right palpal bulb, retrolateral view; 43, prolateral view; 44, 45, *Sericopelma* sp. 44, male from Nicaragua, palpal bulb; 45, female from Nicaragua, spermathecae (from Schiapelli & Gerschman 1979). 46, 47, *Theraphosa blondi* (Latreille); 46, type male, left palpal bulb, prolateral view; 47, type female, spermathecae, dorsal view.



Figures 48-53.--48, *Tmesiphanthes nubilus* Simon type male, left palpal bulb, prolateral view; 49, 50, *Vitalius sorocabae* (Mello-Leitão); 49, male, right palpal bulb, retrolateral view; 50, female, spermathecae (from Lucas et al. 1993); 51, 52, *Xenesthis immanis* (Ausserer); 51, type male, left palpal bulb; 52, female, spermathecae; 53, *Holothele sericeous* (Simon), type female, spermathecae, dorsal view.

bulb with simple apex and two tibial spurs. *Schizopelma macropus* is moved to the genus *Cyclosternum*.

Sericopelma Ausserer

Sericopelma Ausserer, 1875: 195.
Theraphosa: Karsch, 1880: 844.
Mygalarachne: Raven, 1985: 158.

Diagnosis. -- Differs from the other Theraphosinae in the palpal bulb morphology (Fig. 44), in combination with the absence of a tibial apophysis and a single spermethecal receptaculum with a median notch (Fig. 45).

Types. -- Male of *Sericopelma rubronitens* Ausserer, 1875 from Panama, in NMV, not examined.

Comments. -- Recently Lucas et al. (1991) removed *Mygalarachne* (type in NMV, examined) from the synonymy of *Sericopelma* where it had been placed by Raven (1985). Lucas et al. (1991) considered *Mygalarachne* as a genus *incertae sedis*.

Natural History. -- Data about the species from Costa Rica can be found in Valerio (1980a). Prey detection of *S. rubronitens* was studied by Den Otter (1974).

Sphaerobothria Karsch

Sphaerobothria Karsch, 1879: 534.

Diagnosis. -- Differs from the other Theraphosinae in the presence of a spheroid foveal process.

Types. -- Congener female from *Sphaerobothria hoffmani* Karsch, 1879 in BMNH, examined.

Natural History. -- Ecology of *S. hoffmani* was studied by Herrero & Bolaños (1982), and its venom components by Herrero & Odell (1988).

Theraphosa Thorell

Mygale Latreille, 1804: 159.
Theraphosa Thorell, 1870: 161.

Diagnosis. -- Differs from the other Theraphosinae, except *Pseudotheraphosa*, in the morphology of the palpal bulb and spermathecae (Figs. 46, 47), and from *Pseudotheraphosa* in the absence of a tibial apophysis.

Types. -- Male and female of *Theraphosa blondi* (Latreille, 1804) from Guyana, in MHNP (233, 235), examined.

Natural History. -- The ecology and post-embryonic development of *T. blondi* were described in Marshall & Uetz (1993).

Tmesiphanthes Simon

Tmesiphanthes Simon, 1892: 138.
Dryptopelma: Raven, 1985: 159.

Diagnosis. -- Differs from most Theraphosinae in the incrassate femur III, from *Eupalaestrus* and *Megaphobema* in the palpal bulb morphology (Fig. 48), and from *Melloleitaoina* in the presence of numerous cuspules on the labium.

Types. -- Male of *Tmesiphanthes nubilus* Simon, 1892 in MHNP, examined.

Comments. -- It is here removed from the synonymy of *Dryptopelma*, where it had been placed by Raven (1985), from which *Tmesiphanthes* differs in the palpal bulb morphology.

Vitalius Lucas, da Silva & Bertani

Pamphobeteus Pocock, 1901: 545 (in part).
Vitalius Lucas, da Silva & Bertani, 1993: 234.

Diagnosis. -- Differs from the other Theraphosinae in the morphology of palpal bulb and spermathecae (Figs. 49, 50).

Types. -- Paratype male of *Vitalius sorocabae* (Mello-Leitão, 1923) from Sorocaba, São Paulo, Brazil, in IB, examined.

Comments. -- Lucas et al. (1993) concluded that this species, formerly attributed to *Pamphobeteus*, should be divided into two groups on the basis of differences of palpal bulb morphology and the mode of closing of metatarsus I, with respect to the tibial spurs. The first main group, with species from Ecuador, Bolivia, and Colombia, was maintained in *Pamphobeteus*. The second group includes Brazilian species, which were placed in the new genus, *Vitalius*.

Natural History. -- Maternal care of some species was described in Bücherl (1952). Some aspects of sexual biology were

reported in Bauab-Vianna et al. (1985), Valente et al. (1985a; 1985b), and Bergo & Abe (1985). Spermatogenesis was described in Alberti et al. (1986).

Xenesthis Simon

Xenesthis Simon, 1891: 324.

Diagnosis. -- Differs from other Theraphosinae in the palpal bulb morphology (Fig. 51) in combination with spermathecae morphology (Fig. 52), and in the metatarsus I closing between the tibial apophyses.

Types. -- Male of *Xenesthis immanis* (Ausserer, 1875) from Bogotá, Colombia, in BMNH, examined. Female from Caracas, Venezuela, in IB, examined.

GENERA REMOVED FROM THERAPHOSINAE

Acanthopelma F. O. P.-Cambridge, 1897 (type male in BMNH, examined) is transferred from Theraphosinae to Ischnocolinae (*incertae sedis*) because it lacks urticating hair, bulbal keels, and other synapomorphies of the subfamily.

Holothele Karsch, 1879 (type in ZMB, not examined) was considered by Raven (1985) as a synonym of *Scopelobates* Simon, 1903 (type in MHNP, examined, Fig. 53). On the assumption that this synonymy is correct, *Holothele* is transferred to Ischnocolinae *incertae sedis* because *Scopelobates* lacks the synapomorphies of Theraphosinae.

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KEY TO THE GENERA OF THERAPHOSINAE

1. Type IV urticating hair present 2
   Type IV urticating hair absent 6

2. Coxa I with stridulatory setae. . . . . *Phrixotrichus*
   Coxa I without stridulatory setae.. 3

3. Digitiform apophysis on base of tegulum (Fig. 25) . . . . . *Homoeomma*
   Palpal bulb without digitiform aphophysis 4

4. Retrolateral basal nodule on metatarsus I in males (Fig. 39), metatarsus I closing between the tibial apophysis, females with spiral spermathecae (Fig. 40) . . . . . *Plesiopelma*
   Metatarsus I without nodule 5

5. Paraembolic apophysis present . . . . . *Cyriocosmus*
   Paraembolic apophysis absent, spermathecae as in Fig. 33 . . . . . *Paraphysa*

6. Labium with few cuspules (less than 15) 7
   Numerous labial cuspules (more than 20) 8

7. Palpal bulb with embolus subcylindrical (Fig. 29), spiral, females with two separated spermathecal receptacles . . . . . *Melloleitaoina*
   Palpal bulb with embolus subcylindrical, curved (Fig. 23), metatarsus I strongly curved, single spermathecal receptaculum . . . . . *Hapalotremus*

8. Palpal bulb as in Fig. 18 . . . . . *Euathlus*
   Palpal bulb not as above 9

9. Palpal bulb as in Fig. 48 . . . . . *Tmesiphantes*
   Palpal bulb not as above 10

10. Spiniform hairs on the retrolateral face of coxae, type I urticating hair present 11
    Without such spiniform hairs. 12

11. Stridulatory setae on the prolateral face of trochanter I . . . . . *Citharacanthus*
    Stridulatory setae absent . . . . . *Aphonopelma*

12. Palpal bulb with one keel wider than the others 13
    Palpal bulb with subequal keels 14

13. Males without tibial apophyses, females with one fused spermathecae. . . . . *Metriopelma*
Males with two tibial apophyses and metatarsus I strongly curved . . . *Hapalopus*

14. Palpal bulb and spermathecae as in Figs. 12, 13 . . . . . *Cyclosternum*
Palpal bulb and spermathecae not as above. 15

15. Embolus with bifid apex . . . . . *Schizopelma*
Embolus apex not bifid. 16

16. Type I urticating hair present. 17
Type I urticating hair absent 29

17. Only one tibial apophysis, embolus corkscrew shaped (Figs. 3, 4), two subspherical spermathecae (Fig. 5). . . . . *Acanthoscurria*
Two or no tibial apophyses 18

18. Male without tibial apophyses, female with two spermathecae (Figs. 30, 31). . . . . *Nhandu*
Female with single, or two spermathecal receptaculum 19

19. Female with notched spermatheca (Fig. 44, 45), males without tibial apophyses . . . . . *Sericopelma*
Males with two tibial apophyses 20

20. Tibia IV of males highly incrassate, palpal bulb and spermathecae as in Figs. 20, 21 . . . . . *Eupalaestrus*
Tibia IV not so 21

21. Palpal bulb and spermathecae as in Figs. 49, 50 . . . . . *Vitalius*
Palpal bulb and spermathecae not as above. 22

22. Stridulatory setae on the trochanter and coxa of leg I . . . . . *Phormictopus*
Stridulatory setae on trochanter or coxa of leg I, or absent 23

23. Stridulatory setae only on trochanter 24
Stridulatory setae only on coxa, or absent 25

24. With spherical foveal process . . . . . *Sphaerobothria*
Without such a process. . . . . *Cyrtopholis*

25. Palpal bulb as in Fig. 27 . . . . . *Lasiodora*
Palpal bulb different, no stridulatory setae 26

26. Femur III incrassate, palpal bulb as in Fig. 28 . . . . . *Megaphobema*
Femur III not so 27

27. Palpal bulb as in Fig. 32 . . . . . *Pamphobeteus*
Palpal bulb not as above 28

28. Palpal bulb and spermathecae as in Figs. 51, 52 . . . . . *Xenesthis*
Palpal bulb and spermathecae as in Figs. 9, 10 . . . . . *Brachypelma*

29. Males without tibial apophyses, stridulatory setae absent. . . . . *Theraphosa*
Males with two tibial apophyses, stridulatory setae on coxa II . . *Pseudotheraphosa*