

## Review of the South American whip scorpions (Thelyphonida: Arachnida).

by

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### Abstract

The literature concerning South American thelyphonids presently supports recognition of about ten Recent species of thelyphonids representing two genera. Comparative and diagnostic features deduced from this literature and from study of some of these species are provided herein together with a discussion of the relevant morphological characters. A general review of the biology, distribution and diversity of the Thelyphonida is also provided. The genus *Amauromastigon* is synonymized with *Mastigoproctus* on subjective grounds. At least one species is known by fossils from the Lower Cretaceous of Brazil and is discussed relative to its possible relationships to Recent American taxa.

Keywords: **Thelyphonida, Neotropics, Mastigoproctus, Thelyphonellus, thelyphonid.**

### Resumo

Na literatura atual sobre Thelyphonida da América do Sul constam cerca de dez espécies recentes representando dois gêneros. Características comparativas e diagnósticas deduzidas desta literatura e de estudos de algumas destas espécies, são apresentados juntos com uma discussão sobre características morfológicas relevantes. Apresenta-se também uma revisão geral da biologia, distribuição e diversidade de Thelyphonida. Baseando-se em razões subjetivas, o gênero *Amauromastigon* é sinonimizado com *Mastigoproctus*. No mínimo uma espécie fóssil do cretáceo baixo brasileiro é conhecida, e suas possíveis relações com taxons recentes americanos é discutida.

### Introduction

About ten species representing two genera of Recent South American thelyphonids (whipscorpions) are presently recognized (ROWLAND & ADIS 2001). The relationships of the two South American genera are particularly interesting because these may be key to understanding the relationships of the family-group taxa in this order of arachnids. However, aside from bare taxonomic descriptions, almost all that has been written concerning South American thelyphonids is that in the last three decades by WEYGOLDT (1972, 1978, 1979), HÖFER & BECK (1974) and ADIS et al. (1997). The first work cited concerns the reproductive behavior of *Mastigoproctus brasilianus* and the other works concern the behavior, taxonomy and phenology of the only thelyphonid yet known from the central Amazon, *Thelyphonellus amazonicus*. The primary taxonomic literature concerning South American species is contained in 10 publications

(KOCH 1843; BUTLER 1872; TARNANI 1889; POCOCK 1894, 1899; HIRST 1912; WERNER 1916; MELLO-LEITÃO 1931, 1940; WEYGOLDT 1979). South American thelyphonids have also been treated within several, relatively comprehensive taxonomic reviews POCOCK 1894; KRAEPELIN 1897, 1899; MELLO-LEITÃO 1931; WERNER 1935; ROWLAND & COOKE 1973).

One of the principal original objectives of this study was to evaluate the enigmatic South American thelyphonid *Amauromastigon annectens* (WERNER) and to determine whether this species might shed some fresh light upon the phylogenetic relationships of *Mastigoproctus* and *Thelyphonellus*, and thus family-level relationships within the order (POCOCK 1894, 1899; ROWLAND & COOKE 1973). The descriptions of this species by WERNER (1916) and MELLO-LEITÃO (1931) suggested that it might possess character states intermediate between the latter genera. However, a re-examination of this species has revealed that critical characters were incorrectly reported by these authors and that it provides no such new information. Through examination of the above material it was hoped to test the family-level classification of the thelyphonid genera as proposed by POCOCK (1894, 1899) and largely followed in the revision by ROWLAND & COOKE (1973). Uncertainties concerning characters used to define the family-group taxa in the latter works have been acknowledged since an early date (GRAVELY 1916) and contested (WEYGOLDT 1979, 1988) according to phylogenetic considerations. While a comprehensive survey of taxonomic characters and possible classifications based upon these is beyond the scope of this study, such an analysis is under development and will be presented in a future report.

South American thelyphonids are scarcely represented in collections and only general inferences can be drawn regarding diversity and distribution of its taxa (Fig. 1). Nonetheless, this report reviews the current state of knowledge concerning this group in South America and hopes to provide a reliable starting point for the eventual improvement of that knowledge.

### Biology

Compared to many other orders of arthropods, the biology of thelyphonids has not been broadly investigated. However, since the thelyphonids appear to be a relatively homogeneous and adaptively conservative group, perhaps the observations on select species can be applied accurately to our understanding of the group in general. Thelyphonids are, moreover, pulmonate arachnids closest related to schizomids, amblypygids and spiders and share with them, besides morphological similarities, general aspects of their biology, from which useful inferences can be drawn.

Thelyphonids produce eggs, about twenty in *Mastigoproctus*, in a sac which is carried under the opisthosoma of the female. The eggs develop into an early nymphal stage, called by some a 'praenymph', which remains on the female's body. Four further nymphal stages, protonymph through tetranymph, precede development into the adult stage, which seems not to undergo further molting. YOSHIKURA (1965) and WEYGOLDT (1971) found this developmental pattern consistent between *Typopeltis stimpsonii* (WOOD) and *Mastigoproctus giganteus* (LUCAS). WEYGOLDT (1971) determined that *M. giganteus* passed through about one nymphal stage per year and developed to adulthood in about four years. Adults can live two or possibly several more years.

The fundamental pattern of mating behavior in thelyphonids consists of an intricate interactive ritual, which has been described for several species (e.g. GRAVELY 1915;

KAESTNER 1931; WEYGOLDT 1971, 1972). I have observed that upon meeting of receptive pairs of *Mastigoproctus giganteus* in New Mexico, the male may more or less aggressively pursue and grapple the female with its pedipalps, immediately beginning to grasp and secure with the chelicerae both of the female's leg I tarsi. An extended period then ensues in which the male holds the tarsi of the female in the above manner, and turns around to face the same directions as the female, whereupon the female grasps with the pedipalps the opisthosoma of the male from underneath. After a 'searching march' (WEYGOLDT 1978) and then a period of quiescence, a spermatophore packet is deposited on the substrate by the male. The male then moves forward, pulling and guiding the female to a position directly above the spermatophore, which the female then takes up into the genital operculum. In the final stage of mating the male faces the female again, reaches over and, with the pedipalps, grasps the female's opisthosoma from above, such that the distal elements of the pedipalps apparently move the spermatophore further into the genital operculum of the female. The entire process may require several to many hours (SCHMIDT 2000). WEYGOLDT (1971, 1978, 1988) has described comparative mating behavior of *Mastigoproctus*, *Thelyphonellus*, *Typopeltis* and *Thelyphonus*, which differ most significantly in the last stage of the mating process.

In the United States, *M. giganteus* is locally common in Florida and some southwestern states and is known as the vinegaroon. This name is derived from the ability of the thelyphonids to spray, as a defense, a caustic mixture of vinegar and other organic compounds from the apertures of the anal glands, which open on the last pygidial segment (EISNER et al. 1961; HAUPT et al. 1988; SCHMIDT et al. 2000). The spray can be accurately aimed and is an effective deterrent to both vertebrates and arthropods.

*M. giganteus* is most frequently encountered in New Mexico during the summer rainy season, inasmuch as they are, despite their occurrence in xeric environments, comparatively inefficient water conservators (CRAWFORD & CLOUDSLEY-THOMPSON 1971). During the day, they are to be found at rest under logs, rocks and other objects, under which, or against which, they have excavated burrows which open through a tunnel to the outside. They are generally only active above ground near dusk or at night. They emerge at the entrance of the burrow, and frequently assume a position with the opisthosoma and flagellum protruding out of the entrance, the anterior end of the body facing into the burrow, as if to aid rapid retreat into the burrow. When potential prey approaches their position, *M. giganteus* is able to quickly back out of its burrow and attempt to capture the prey. If this strategy is typical of other thelyphonids, then the group might well be characterized as 'sit-and-wait' predators. On the other hand, mature males of *M. giganteus* are frequently encountered at night after rains wandering about, possibly searching for females. In a tropical lowland forest in Malaysia, WEYGOLDT (1988) collected *Thelyphonus linganus* KOCH as they emerged at night and crawled slowly up large buttress trees. In tropical primary and secondary upland forest soils in Amazonia, ADIS et al. (1997) obtained *Thelyphonellus amazonicus* by a Kempson soil extraction methodology (ADIS 1987), along with palpigrades and schizomids.

### Distribution and diversity

Worldwide, there have been about one hundred Recent species described in about 16 genera, though the latter number probably deserves reduction. The latest inclusive treatment of the genera (ROWLAND & COOKE 1973) distinguished several family-

level taxa, in which the two South American genera, *Mastigoproctus* and *Thelyphonellus*, were classified in the families Thelyphonidae and Hypoconidae, respectively.

According to the system of POCOCK (1894, 1899), which was extended in ROWLAND & COOKE (1973), Thelyphonidae contains the Asian subfamily Thelyphoninae with about six genera and 40 species; the Asian and American Uroproctinae with two or three genera and 20 species, including the American genus *Mastigoproctus*; and the exclusively Asian Typopeltinae with one genus and about 10 species. The family Hypoconidae in ROWLAND & COOKE (1973), is recognized with three or four genera, including the South American genus *Thelyphonellus*.

The global distribution of thelyphonids finds by far the greatest diversity of genera and species in Southeast Asia and the Malay Archipelago. This fauna extends out into the Pacific at least as far as Samoa. A single species representing an endemic genus occurs in west Africa (HEURTAULT 1984). The Americas are represented by two Recent genera and about 15 described species. There are interesting species, however, from the Middle Americas and the West Indies that await description.

The fossil record of this group is quite uneven, but extends back to earliest Pennsylvanian times (BRAUCKMANN & KOCH 1983). Even the oldest of these fossils is strikingly modern in appearance, however, which suggest a very earlier divergence from the other pulmonate arachnids, certainly predating the Middle Devonian (SELDEN et al. 1991), and a very stable body plan. It is thus not surprising that the Lower Cretaceous thelyphonids recently discovered in Brazil (DUNLOP 1998; DUNLOP & MARTILL 2002) show no important differences when compared to Recent Brazilian forms.

### Systematics

It is presently common practice to recognize the thelyphonids as an independent order of arachnids, particularly as distinguished from schizomids. Others, however, treat thelyphonids and schizomids as suborders within a single order. This, in itself, presents little difficulty in the scientific discourse concerning these groups. However, along with the tendency to treat thelyphonids as an independent order, it has also become common practice to employ the order name Uropygi instead of Thelyphonida for the thelyphonids; that is, the order names Thelyphonida and Uropygi are sometimes treated as synonyms. It is the contrasting view and practice, however, of others (e.g. WEYGOLDT 1971-1988, WEYGOLDT & PAULUS 1979; SCHULTZ 1990; HAUPT 1996a, 1996b; ROWLAND in ROWLAND & ADIS 2001; DUNLOP & MARTILL 2002) that the order-level name Uropygi should be used only for that taxon which includes both thelyphonids and schizomids; and that the order-level name Thelyphonida should be used for that taxon which includes thelyphonids and excludes schizomids. Moreover, the order name Thelyphonida is unequivocal concerning its meaning and its use conveniently preserves the name Uropygi for that taxon within which thelyphonids and schizomids are contained, such as might be employed in a phylogenetic classification.

The long and somewhat difficult history of classification systems for the genera (e.g., POCOCK 1894, 1899; KRAEPELIN 1897, 1899; GRAVELY 1916; MELLO-LEITÃO 1931; WERNER 1935) was reviewed and expanded in ROWLAND & COOK (1973). The latter system is most frequently faulted for its use, first proposed by POCOCK (1894, 1899), of the lateral keels of the carapace as the principal character which unites the genera of the Thelyphonidae in its presence, and unites the genera of Hypoconidae in its absence. In relation to the South American fauna, for instance,

WEYGOLDT (1988) considered the lateral keels of the carapace to be a superficial character, and of insufficient value and stability upon which to base family-level taxa. He supported a view that primary sexual characters and courtship behaviors are better suited to this purpose. He suggested, for instance, that the similar and complex courtship and mating behaviors in *Mastigoproctus* and *Thelyphonellus* are synapomorphic relative to a simpler, more ancestral courtship behavior found in *Thelyphonus*. The merits of this argument and the counter-arguments, while interesting, are beyond the scope of this report, but will be addressed in a subsequent title.

For the present purpose of associating the South American taxa according to the system of POCOCK (1894, 1899) and ROWLAND & COOKE (1973), the South American Thelyphonidae can be characterized by the presence of a well-developed median ocular ridge somewhat separating and elevating the median pair of eyes and the presence of a keel on the lateral aspects of the carapace anterior to the lateral eyes and terminating proximal to the median eyes (Figs. 1, 2). The South American Hypoconidae, that is, the two species of *Thelyphonellus*, are thus diagnosed by the absence of a well-defined median ocular ridge and the absence of lateral keels on the carapace (Fig. 2).

The following taxonomical account presents all the described species of South American thelyphonids and provides a description of morphological characters that are useful in their recognition. Specimens of the following species were examined for this study: *Thelyphonellus amazonicus*; a species close to *T. amazonicus* and *T. ruschii*; *Mastigoproctus annectens*; *M. minensis*; a species close to *M. colombianus*; *M. brasilianus*; a species close to *M. maximus* and *Mesoproctus rowlandi*. The descriptions of all the South American species reported herein are based principally upon the original descriptions of type material, to which are added supplemental remarks based on other observations. The principal objective of providing these descriptive and diagnostic accounts is to aid the identification of these species and the detection of new taxa. However, it seems that the accuracy and consistency of some of the taxonomical information available in the literature is questionable, and is the product of independent work on different specimens. The work of MELLO-LEITÃO (1931) appears to have been based largely on descriptive accounts available in the literature and only three or four species were available to him for subjective and comparative studies. The latter and present reports should therefore be viewed as only generally indicative of the diversity of this group in South America. It is hoped, moreover, that this deficit will be addressed by a primary revision of the South American fauna, such as HAUPT (1996a, 1996b) has provided for the Asia fauna. The species of *Thelyphonellus*, the subject of a comparative review by WEYGOLDT (1979), are well described and illustrated, and are thus more readily recognizable from the available literature than are the other South American species.

### Key characters

**Integument.** The integument in *Mastigoproctus* is more or less granular in texture, more so dorsally than ventrally. In various species, however, the granularity is comparatively reduced or exaggerated generally, or in specific parts, particularly distinctively in the pedipalps. In *Thelyphonellus* the integument is smoother and less granular than in *Mastigoproctus*. The color in *Mastigoproctus* varies between red and brown and occurs in various values of these, especially according to the degree of maturity. The appenda-

ges often exhibit lighter values than the trunk. In *T. amazonicus* the integument is additionally somewhat greenish in appearance.

Carapace (Figs. 1, 2). The median eyes in *Mastigoproctus* are situated upon, and reside to either side of, a median ridge of variable development. In species where this ridge is highly developed, it has the effect of directing the visual field forward and laterally. In contrast, the median eyes of *Thelyphonellus* have a much lesser development of a median ridge and the eyes are thus directed more perpendicular to the plane of the carapace. The anterolateral margin of the carapace in *Mastigoproctus* bears a keel, which is essentially a narrow, linear crest-like production of the integument from the lateral eyes forward to near the median eyes. It is located at the edge of the carapace where its plane changes from generally horizontal to more or less vertical. On the other hand, there exists no evidence of a keel in *Thelyphonellus*.

Genital operculum. In the late instars of *Mastigoproctus*, the ventral plate of the second opisthosomal segment conceals the genital apparatus. In the adults of *Mastigoproctus* and *Thelyphonellus* the operculum is somewhat enlarged and extended outward compared to earlier nymphal stages and may develop subtle surface shapes that are unique.

10<sup>th</sup> opisthosomal pleuron. I have recently discovered this new character which may prove useful in helping decipher relationships among the Thelyphonida and in recognizing American species. In many American thelyphonids the 10<sup>th</sup> opisthosomal segment (the first pygidial segment) is divided mid-laterally by a pleuron into a tergum and sternum. The pleuron is present in *Mastigoproctus giganteus*; *M. tantalus* ROEWER; some specimens of *M. minensis* and *M. brasilianus*; the specimens tentatively referred to *M. colombianus* and *M. maximus* above; *M. pelegri* de Armas; and two undetermined species from Hispaniola, one of which might be referred to *M. proscorpio* (LATREILLE). In the Americas, the 10<sup>th</sup> opisthosomal segment lacks this pleuron in some specimens of *M. minensis*, *M. brasilianus*, *Thelyphonellus amazonicus*, and a single adult male from Purula, Guatemala which is possibly referable to *M. liochirus*. None of approximately twenty species representing eight genera of Asian and African Thelyphonida that I have examined possess the 10<sup>th</sup> opisthosomal pleuron.

Ommatidia. The last opisthosomal and pygidial segment often bears lateral translucent structures of a round or oval shape which are often superficially convex and lens-like. This appearance suggests that they might possess a light-receptive capacity, and are thus termed 'ommatidia'. HAUPT et al. (1980), however, found evidence contradictory to any such photoreceptive capacity. The ommatidia in *Thelyphonellus amazonicus* vary in size from well-developed to minute to absent, depending upon the locality. In *Mastigoproctus* the ommatidia are also highly variable among species. ROWLAND (1973) discussed the labile nature of this character in Pacific thelyphonines.

Pedipalps (Fig. 1). The pedipalps are sexually dimorphic, being slightly to much larger in males, and provide features for recognizing thelyphonid taxa at various taxonomic levels. The names of the segments used herein are coxa, trochanter, femur, patella, tibia, basitarsus and tarsus, the latter of which is the claw (SHEAR et al. 1987). In earlier works particularly, the patella of the pedipalps was not recognized, thus the article following the femur was called the tibia. Further, in many earlier publications the pedipalpal tibia was referred to as the hand, and the basitarsus and tarsus as the finger. The pedipalpal trochanter presents a number of cuticular armaments, however, there exists no systematic or established nomenclature to facilitate their description and

discussion. Most obvious of these are usually four to six large, horizontal teeth on its antero-dorsal margin which can vary distinctively between the sexes and among the species. The patella and the tibia both possess strong apophyses that also vary in morphology between the sexes and among the species.

Legs (Fig. 1). The basitarsus and tarsus of leg I in thelyphonids appears to form a single functional unit variously termed the basitarsus-tarsus. For convenience, the articles of this unit are herein informally called tarsomeres. The relative lengths of these tarsomeres in South American species of *Mastigoproctus* sometimes vary distinctively in certain species. It should be pointed out, however, that there exist variations among authors in interpreting the number of articles present in the basitarsus-tarsus, that is, some authors count eight articles, others nine articles. Those favoring the latter number count the minute first article as a distinct tarsomere, while the former believe that the minute first article is not a true tarsomere, and represents only the basal part of the first tarsomere. It is necessary to know how a particular author interprets this character, but it is frequently difficult to determine this. For convenience and to preserve utility of previously reported information, this report follows the interpretation of the basitarsus-tarsus as having nine articles as in KRAEPELIN (1897, 1899), POCOCK (1894) and MELLO-LEITÃO (1931); upon which model they have based their descriptions and diagnoses. The statement of MELLO-LEITÃO (1931, p. 26) that the relative lengths of the second and third tarsomeres of leg II differ between *M. formidabilis* and *M. perditus* is possibly a *lapsus* and refers rather to leg I. The presence or absence of tibial spurs on legs II-IV has long been employed to distinguish certain taxa, including some of those from South America. It is not uncommon, however, that these spurs are present on one side of a particular pair of legs, but absent from the other side, which limits its utility.

#### Taxonomic account

Genus *Thelyphonellus* POCOCK

POCOCK 1894: 133; KRAEPELIN 1897: 42; 1899: 226; WERNER 1916: 98; ROWLAND & COOKE 1973: 65; WEYGOLDT 1979: 110.

Description/Diagnosis: [from POCOCK (1894) and WEYGOLDT (1979)]. Carapace finely granulated; without lateral keels between medial and lateral eyes; median eyes more or less flat on surface of carapace, i.e., without well developed median ocular ridge; front third of carapace with three flat, longitudinal depressions. Opisthosomal tergites granulated, that of second and third segment completely, those following incompletely, divided; opisthosomal sternites smooth. Female genital operculum externally unmodified; receptaculum seminalis large, touching medially, its anterior-dorsal supporting plates forming an X-like figure; genital operculum in male distinctly larger than in female, swollen. Ommatidia small and oval or absent. Pedipalps shiny, not granular, and elongate in the males; a deep notch present at union of basitarsus and tarsus in the males.

Remarks: WEYGOLDT (1979) provides the most recent diagnosis of the genus *Thelyphonellus* which is based on his review of the type of the genus, *T. amazonicus*, and description of *T. ruschii*.

*Thelyphonellus amazonicus* (BUTLER)

BUTLER 1872: 201; POCOCK 1894: 133; KRAEPELIN 1897: 42; 1899: 226-227; WERNER 1916: 94; MELLO-LEITÃO 1931: 23; WEYGOLDT 1978: 147; 1979: 109-114.

Description/Diagnosis: [from WEYGOLDT (1979)]: Lateral keels absent; median ocular ridge weak; apex of carapace anteriorly rounded, indented or only weakly produced anteriorly, but not forming a pointed epistome. Inner sclerotization of receptaculum seminalis dorsally covered by tissue, only posterior

edge of this sclerotization visible. Ommatidia present or absent. Pedipalp of male slightly elongate compared to female, tibia shorter than patella. Second and third tarsomeres of leg I about equal in length. Tibial spurs present on legs IV only. Adult body length (apex of carapace to end of pygidium) less than 20 mm.

Remarks: WEYGOLDT (1979) pointed out that the holotype of *T. amazonicus* (Natural History Museum, London, NHM), as all other specimens known from Santarém, Obidos and Manaus, Brazil, lacks ommatidia. Newly studied specimens including those from Kamakusa, Guyana lack ommatidia, but those from Surinam and from Serra do Navio, Brazil possess ommatidia, although they are small. A female specimen in the Museum of Comparative Zoology (MCZ) from near Cali, Colombia that appears consistent with *T. amazonicus* possesses comparatively large ommatidia.

ADIS et al. (1997) reported a density of this species to be ca. 7/m<sup>2</sup> in primary forest near Manaus and ca. 6/m<sup>2</sup> in secondary forest. These specimens were present in 0-7 cm Kempson soil extractions during April and August in a primary forest site and January, March and August in a secondary forest site.

Localities: Specific details concerning collections of *T. amazonicus* from Brazil (Santarém, Obidos in Pará; Serra do Navio in Amapá; near Manaus in Amazonas) and Surinam can be found in WEYGOLDT (1979). To these are added the following localities: Brazil - two sites within 30 km of Manaus in Amazonas (ADIS 1997): Reserva Florestal A. Ducke, 2°55'S, 59°59'W, primary upland forest, two females and four juveniles (Instituto Nacional de Pesquisas da Amazonia, Manaus = INPA) and at Rio Tarumã Mirim, 3°2'S, 60°17'W, secondary upland forest, one female and three juveniles (INPA); Guiana: Kamakusa, Nov. 1922, Lange and La Varre, 1 male, 1 female, 1 juvenile (American Museum of Natural History, New York, AMNH); Surinam: Brownsberg Natr. Res. 5 Sep 1977, R.T. SAWYER, 1 juvenile (National Museum of Natural History, Washington, D.C., NMNH). Colombia: kilometer 74, cartera nueva, Cali - Buenaventura, 13 Feb. 1976, bajo piedra, 1 female (MCZ).

#### *Thelyphonellus ruschii* WEYGOLDT

WEYGOLDT, 1979: 109-114

Description/Diagnosis: [from WEYGOLDT (1979)] Lateral keels absent; median ocular ridge weak; apex of carapace produced as a pointed projection of the epistome. Inner sclerotization of receptaculum seminalis dorsally visible, each receptaculum forming a small comma-shaped structure. Ommatidia absent. Pedipalps strongly dimorphic in males and females, the males proportionally much larger than in *T. amazonicus*, tibia longer than patella. Adult body length greater than 20 mm.

Localities: The description of *T. ruschii* is based upon a series of specimens from Demerara, Guyana.

#### *Thelyphonellus* sp.

Remarks: A newly studied adult male *Thelyphonellus* in the MCZ from Surinam possesses an epistomal projection as in *T. ruschii*; has very small ommatidia as in some *T. amazonicus*; the dorsal spines of the pedipalpal trochanter are configured differently than those illustrated for either *T. amazonicus* or *T. ruschii* (WEYGOLDT 1979); the pedipalpal tibia is shorter than the patella as in *T. amazonicus*, and its body length is about 19 mm.

Locality: An adult male, Surinam, Sipaliwini, Feb. 1942, L. SCHMIDT (MCZ).

#### *Mastigoproctus* POCOCK

POCOCK 1894: 129-131; KRAEPELIN 1897: 36-37; 1899: 223-224; ROWLAND & COOKE 1973: 68; LAZELL 2000. *Amauromastigon* MELLO-LEITÃO, NEW SYNONYMY WERNER 1916: 94; MELLO-LEITÃO 1931: 23; ROWLAND & COOKE 1973: 62.

Description/Diagnosis: American thelyphonids in which the median ocular ridge and lateral keels of the carapace are well developed. The male genital operculum lacks a median furrow, and the posterior operculum lacks a sharp medial acumination. The female genital operculum is not strongly sclerotized. The 10<sup>th</sup> opisthosomal segment is divided by a pleuron in some or all species and all species possess omma-

toids. The pedipalpal patellar apophysis in the male is elongate compared to the females, but lacks terminal enlargement. The tarsomeres of leg I of the females are not modified, and are relatively elongate as in the males.

Remarks: KRAEPELIN (1897, 1899) and MELLO-LEITÃO (1931, 1940) distinguished the South American species of *Mastigoproctus* principally upon the basis of the following characters: texture of the pedipalpal femur and patella; relative lengths of the proximal tarsomeres of leg I; number and occurrence of tibial spurs of the walking legs; size and shape of the ommatidia; and body size of the adults. LAZELL (2000) reports that various species of *Mastigoproctus* can be distinguished on the basis of other pedipalpal characters.

The holotype of *Amauromastigon annectens* (WERNER) has recently been found in the Landesmuseum Darmstadt, Germany. Prof. Dr. P. WEYGOLDT examined this specimen and found that it is consistent with *Mastigoproctus* and keys to *M. maximus*, in the key below. Thus the genus *Amauromastigon* MELLO-LEITÃO is herein designated a synonym of *Mastigoproctus*. See further remarks under *M. annectens*, below.

#### *Mastigoproctus annectens* WERNER 1916

WERNER 1916: 92, 94; MELLO-LEITÃO: 23-24.

Description/Diagnosis: [from WERNER (1916) and MELLO-LEITÃO (1931)] Carapace finely granular, shiny dark golden red, with two rounded elevations separated by a longitudinal median sulcus originating between the median eyes. The original description indicated that the median ocular ridge was relatively indistinct, however, re-examination of the specimen shows the ridge to be as in other *Mastigoproctus*. The lateral keels of carapace were reported in the above publications to be 'little accentuated, but well pronounced'; re-examination of the type specimen found the keels to be normal for *Mastigoproctus*. The above publications indicate that the female genital operculum possesses two smooth lateral depressions or pits. Re-examination of the type indicates that the specimen is an early nymph, not identifiable to sex. The ommatidia were reported by WERNER (1916) and MELLO-LEITÃO (1931) to be absent, however, re-examination of the type by P. WEYGOLDT revealed large, circular ommatidia. Flagellum yellowish, entirely without setae. Trochanter of the pedipalps with five robust dorsal teeth, those of the anterior angle larger; trochanter and femur granular, patella and tibia smooth, with scattered small depressions; tibial apophysis serrate at top and with two inferior teeth. Second tarsomere of leg I as long as the third tarsomere. Body length 18 mm, flagellum length 23 mm and carapace length 8 mm.

Remarks: WERNER (1916) originally described and placed this species in the genus *Mastigoproctus*, but also remarked that its small size, and the absence of ommatidia suggested a possible close relationship to *Thelyphonellus*. MELLO-LEITÃO (1931) created the genus *Amauromastigon* for this species based on the characters that WERNER noted and apparently his own observations that the primary opisthosomal sternite did not have a median sulcus; that the median ocular ridge and the lateral keels of the carapace were little developed; and that the tibial apophysis of the pedipalp and the basitarsus-tarsus of leg I were similar in the two sexes. WERNER's description was based upon a single specimen, which he considered to be a subadult female (Catalog # 1115, originally deposited in the Naturhistorischen Museum Wiesbaden, now repositied in the Hessisches Landesmuseum Darmstadt). The remarks of MELLO-LEITÃO (1931) concerning the similarity in the two sexes of pedipalpal and leg I anatomy suggests that he had obtained specimens additional to the type.

Examination of the holotype by WEYGOLDT revealed that it is an early nymphal stage and thus it might be difficult to determine the relationship of this specimen to other species of *Mastigoproctus*, but that the specimen keys to *M. maximus* in the key below. The statement in ROWLAND & COOKE (1973) that the posterior opisthosomal tergites are undivided in *Amauromastigon annectens* is a *lapsus* because the state of that character had not been reported.

Locality: The type and only reported locality is Santa Catarina, Brazil.

*Mastigoproctus brasiliensis* (KOCH)

KOCH 1843: 24; POCOCK 1894: 134; KRAEPELIN 1897: 36-37, 39-40; 1899: 223-224, 225; MELLO-LEITÃO 1931: 26-28; WEYGOLDT 1972: 24, 44-46.

Description/Diagnosis: [from KRAEPELIN (1897, 1899) and MELLO-LEITÃO (1931, 1940)] Color brown to light red, the legs red-brown. Carapace granular and rugose, the medial ocular ridge much punctured. Lateral keel not extending posterior to lateral eyes. Posterior prosomal sternites smooth. Ommatidia large, round. Pedipalpal coxa granulose, the internal apophysis with fine teeth; trochanter with six to eight comparatively small spines on the anterior border, in the female larger on the anterior border, in the male all about equal in size; femur in the females very rugose, in male densely granulose; tibia of the female with numerous depressions, in the male granulose. Second tarsomere of leg I nearly the same length as third, both two and one-half to three times longer than wide. Tibial spurs of the posterior legs present on fourth pair, and sometimes only on one side on the third pair. Body length 46 mm.

Remarks: WEYGOLDT (1972) studied the comparative mating behavior and spermatophores in *M. brasiliensis* and *M. giganteus*. He determined that these species were incapable of reproduction due to differences in behavior and functional morphology of the spermatophores.

Localities: The type locality is Brazil. MELLO-LEITÃO (1931) mentions specimens from Pará and from Rio Doce, Espírito Santo. WEYGOLDT (1972) collected specimens in the Reserva Docemada, a coastal forest north of Rio Doce and from Linares in Espírito Santo.

*Mastigoproctus butleri* POCOCK

POCOCK 1894: 130-132; KRAEPELIN 1897: 38-39; 1899: 224; MELLO-LEITÃO 1931: 26-29; 1940: 53.

Description/Diagnosis: [from POCOCK (1894) and MELLO-LEITÃO (1931, 1940)] Color blackish red. Rather coarsely granular throughout, the ocular keel complete and finely serrate, the area below it vertical; median ocular ridge well developed. Genital operculum large, smooth, strongly impressed just above the stigma and laterally in front of the midline; a shallow median groove in the posterior half, and behind this a shallow transverse impression. Ommatidia very small, punctiform. Pedipalpal trochanter with three blunt tuberculiform teeth on the inner edge and a small tooth at the base of the larger angular tooth on its outer side, its lower edge armed with one strong, tooth-like spine; femur with only one small inferior tubercle, tibia with a conspicuous, blunt, cylindrical tooth at the base of the apophysis; tarsus-basitarsus internally conspicuously emarginate. Third tarsomere of leg I longest, the second and ninth about equal, fourth to eighth becoming gradually shorter. Tibial spurs absent from the legs II. Total length 39mm, carapace 16mm.

Localities: The type and only known specimen, probably a female, was collected in Brazil.

Comments: This species was treated as a synonym of *M. proscorpio* by KRAEPELIN (1897, 1899). As KRAEPELIN pointed out, the single, strong, tooth-like spine on the lower edge of pedipalpal trochanter described in the type of *M. butleri* is reminiscent of certain male thelyphonids from Haiti, which he identified as *M. proscorpio*. There are, however, at least two distinct species of thelyphonids identifiable in MCZ collections from Haiti and San Domingo, and the identity of *M. proscorpio* is uncertain.

*Mastigoproctus colombianus* MELLO-LEITÃO

MELLO-LEITÃO 1940: 51-53.

Description/Diagnosis: [from MELLO-LEITÃO (1940)] Color dark red. Carapace and opisthosomal tergites densely granular. Median ocular ridge united with the lateral eyes by the serrate keel. Carapace sulcus conspicuous, reaching to the posterior border of the medial ocular ridge. Ommatidia small, transversely elliptical. Pedipalpal trochanter with three equal, robust internal teeth, and five dorsal teeth that are equal in size, the ventral face with two teeth, femur with three pointed teeth, one dorsal, one ventral and one internal; patella smooth, with two or three denticles and robust apophysis directed straight forward; teeth of the tibia rounded. Second tarsomere of leg I much smaller than third. Tibial spurs of legs II absent, but present on legs III and IV. Body length 50 mm.

Remarks: MELLO-LEITÃO (1940) distinguished this species from all but *M. perditus* and *M. butleri* by its lack of tibial spines on leg II and because the second tarsomere of leg I is smaller than the third. He distinguished *M. colombianus* from *M. perditus* by the former having tibial spurs on leg III but only on the posterior legs in *M. perditus* and from *M. butleri* by the larger ommatidia in *M. colombianus* and its two inferior spines of the pedipalpal trochanter.

Localities: The type locality is Villavicencio, Colombia. A male in the MCZ from 'Carimagua, Meta, Colombia, 370 meters' bears a label identifying it as *M. colombianus*. The MCZ specimen deviates from the description of the type, however, in the following aspects: The median ocular ridge is not united with the lateral eyes by the keel; the median sulcus of the carapace is not particularly conspicuous and does not reach the posterior border of the median ocular ridge; the pedipalpal femur has only two teeth, one dorsal and one ventral; the patella is not less granular than the other pedipalpal articles; and a tibial spur is present on leg II. More notably, however, the pedipalpal patella is conspicuously laterally compressed such that the dorsal margin is developed into a sharp ridge that runs from the femoral condyle to near the base of the patellar apophysis. The patella is generally more-or-less dorsally rounded in other species of *Mastigoproctus*. Also, the pedipalpal tibia is distinctly spherical in shape. Neither of these peculiar modifications of the pedipalps present in the Carimagua specimen were noted by MELLO-LEITÃO (1940) in his description of *M. colombianus* from Villavicencio. Thus, the former specimen warrants careful comparison to the latter. Unfortunately, the location of the type of *M. colombianus*, originally deposited by MELLO-LEITÃO "... em minha coleção particular" is uncertain, and the paratypes have probably been destroyed in a fire at the Instituto de La Salle de Bogota (pers. com. C. VISQUEZ).

*Mastigoproctus formidabilis* HIRST

HIRST 1912: 235-237; MELLO-LEITÃO 1931: 26-27.

Description/Diagnosis: [from HIRST (1912) and MELLO-LEITÃO (1931)] Trunk dark brown, distal segments of appendages reddish. Lateral keels present; median ocular ridge well developed. Genital operculum in male marked with a pair of very shallow impressions and with a little median impression near the posterior margin; it has transverse ridges and granules at the sides and is striate in the middle, except posteriorly, where it is finely punctured. Ommatidia minute, elliptical, transverse, like those in *M. giganteus*. Upper surface of femur and tibia of pedipalps smooth and shiny, with sparse punctures. Pedipalp much more slender than in *M. maximus*, especially the patella and tibia, the latter being about twice as long as wide; trochanter with five spines above, the outermost much the longest; patellar apophysis very long and slender; a rather large and sharply pointed tooth present on the ventral surface of the tibia near the point of attachment of the basitarsus; pedipalp in female with segments less elongate and more distinctly punctured than in the male; trochanter with six spines above, but the outer spine is minute. Second tarsomere of leg I longer than third. Tibial spines are present on legs III and IV. Second tarsomeres of walking legs longer than third. Body length 55.5 mm, carapace 22.5 mm.

Locality: The type and only reported locality is La Polonia, Venezuela.

*Mastigoproctus maximus* (TARNANI)

TARNANI 1889: 121; KRAEPELIN 1897: 36-37, 39; 1899: 223-224, 225; MELLO-LEITÃO 1931: 26-27, 30.

Description/Diagnosis: [from MELLO-LEITÃO (1931) and KRAEPELIN (1897, 1899)] Color brown, legs reddish-brown. Carapace densely granular in form with a deep median sulcus; the medial ocular ridge elevated and pointed, the distance from the border about one diameter. Lateral keels running continuously to the median ocular ridge. Opisthosoma less granular than carapace. Female genital operculum with two shallow depressions lateral to a small median depression at the posterior border, the third segment grossly granular, except on the median part. Ommatidia medium sized, conspicuously transversely elliptical. Pedipalps very granular; coxa with two files of internal teeth; trochanter with six superior spines, the three internal ones small and the three anterior ones clearly more conspicuous, approximately equal with the two small spines on the ventral face; femur less granular, with two small spines in the middle of the internal

face, obliquely directed to the front; patellar apophysis similar in the two sexes; tibia large, less than one and one half times longer than wide. Third tarsomere of tarsus I two and one-half times longer than wide, shorter than second, the five apical segments short and equal, the first segment a little bigger than second. Tibial spurs present on legs IV, and sometimes on one of leg III, absent from legs II. Body length 65 mm, carapace 28 mm, flagellum 50 mm.

Locality: The type and only reported locality is Mato Grosso, Brazil.

Comments: KRAEPELIN (1897, 1899) described only females, however the remarks of MELLO-LEITÃO (1931) concerning the similarity in the two sexes of pedipalpal anatomy suggests that he had obtained more specimens besides the type.

*Mastigoproctus minensis* MELLO-LEITÃO  
MELLO-LEITÃO 1931: 26-27, 29-30.

Description/Diagnosis: [from MELLO-LEITÃO (1931)] Carapace slightly granular. Opisthosoma sparsely granular except for the last four segments; all with a posterior file of granulations. Lateral opisthosomal borders and pleura very granular, granules deposited in oblique series. Anterior border of the carapace very narrow. Medial ocular ridge high. Lateral keels forming a clear arch, starting from the middle of the median ocular ridge and extending over the lateral eyes. Ommatidia very large, circular. Flagellum smaller than body. Pedipalps very granular: coxa with apical apophysis, wider than long, curved, relatively distant from the opposite coxa; trochanter with two inferior spines, and six anterior spines, the fourth from the top the largest, then diminishing regularly on both sides; apophysis of femur almost obsolete; patellar apophysis armed apically with two inferior teeth and eight superior teeth; internal border of tibia denticulate; basitarsus with dentate inner margin. Second tarsomere of leg I longer than third, thereafter tarsomeres diminishing regularly in length. Tibial spurs present on legs II - IV. Male body length 34 mm, carapace 12 mm.

Remarks: A series of four subadult specimens in the MCZ from Minas Gerais conform closely to the above description except that there is no variation in granularity among opisthosomal tergites as described in the type. Additionally, the MCZ specimens are the only example of the genus *Mastigoproctus* that I have examined in which the 10<sup>th</sup> opisthosomal segment lacks a pleuron separating the tergum and sternum in some specimens. Two specimens, possibly tetranymphs, lack any evidence of a 10<sup>th</sup> opisthosomal pleuron, while in the other two specimens, possible deutonymphs, the pleuron is present.

Locality: The type and only reported locality is Minas Gerais, Brazil.

*Mastigoproctus perditus* MELLO-LEITÃO  
MELLO-LEITÃO 1931: 26-27, 31; 1940: 53.

Description/Diagnosis: [from MELLO-LEITÃO (1931, 1940)] Carapace densely granular, the median sulcus flat. Median ocular ridge well developed but low, contiguous with the anterior border, which is vertical. Lateral keels originating from median eyes. Opisthosoma with granulations in regular transverse rows. Genital operculum with two lateral and one median depressions. Ommatidia circular, conspicuous. Pedipalps small, granular; coxal gnathobase with two rows of internal denticles, one basal-inferior and two apical-superior; trochanter with six very robust superior spines, more robust than in any other species, and with two spines on the inferior face, slightly excavated; femur nearly smooth, with a small spine median inferior; patellar apophysis very robust, bigger than the basitarsus; tibia wide, a little longer than wide, with small spine at the base of the basitarsus. First tarsomere of leg I smaller than second, the second smaller than third, all others clearly shorter, and of about equal size. Tibial spurs absent from legs II, but present on legs IV. Adults 45 mm or smaller.

Locality: The type and only reported locality is Mato Grosso, Brazil.

*Mesoproctus rowlandi* DUNLOP  
DUNLOP 1998: 294; DUNLOP & MARTILL: 2002: 331.

Remarks: Six thelyphonid specimens of Lower Cretaceous age have recently been discovered in the

richly fossiliferous Santana Formation of Brazil (DUNLOP 1998; DUNLOP & MARTILL 2002). Collectively, these specimens seem indistinguishable from the genus *Mastigoproctus* and probably could as easily be treated as such. The general habitus and the size of the pedipalps relative to the other anatomical features of the holotype, especially the femur, suggests that this specimen might be a mature male identifiable with, or closely related to, *Mastigoproctus*. A better preserved specimen of about the same size as the holotype, also consistent with *Mastigoproctus*, has much smaller pedipalps relative to the rest of the body, and could be a female or subadult. Another specimen is a 32-mm carapace and thus represents a thelyphonid much larger than the holotype. Moreover, if the holotype is, in fact, a mature male, then the latter specimen is probably a different species. The large size of the latter specimen might suggest a close relationship to some Recent species such as *M. giganteus* and *M. maximus* that attain a similar size.

**Key to South American Thelyphonida**

The utility of the following key is constrained principally by two circumstances. First, it seems that South American thelyphonids are not well represented in major academic collections and consequently the number of taxa thus far described is probably small relative to the numbers that might be described in the future. Therefore, there is a relatively high likelihood that undescribed forms will be found and which will resolve improperly in the key. Second, this key is based largely upon published descriptions by several independent authors. Their various interpretations and lack of uniformity limits the number of contrasting character states that can be employed in this key. These deficits are likely to yield errors in use of the key. To minimize these limiting effects, compare specimens also to the descriptions above as an adjunct to the key. The holotype and presently the only known specimen of *M. annectens* is an early nymphal instar and keys to the *M. maximus* couplet below (WEYGOLDT, pers. com).

- 1a. Lateral keels of carapace well-developed; median eyes separated by a well-developed medial ridge; median eyes directed anterolaterally ..... *Mastigoproctus* (3)
- 1b. Carapace without lateral keels; median eyes separated by, at most, a slightly developed medial ridge; median eyes directed more or less vertically ..... *Thelyphonellus* (2)
- 2a. Apex of carapace anteriorly rounded, indented or only weakly produced anteriorly, but not forming a pointed epistome; pedipalp of male slightly elongate compared to female, tibia shorter than patella; inner sclerotization of receptaculum seminalis in female dorsally covered by tissue, only posterior edge of sclerotization visible; adult body length less than 20 mm ..... *T. amazonicus*
- 2b. Apex of carapace produced as a pointed projection of the epistome; pedipalps strongly dimorphic in males and females, the males proportionally much larger than in *T. amazonicus*, tibia longer than patella; inner sclerotization of receptaculum seminalis dorsally visible, each receptaculum forming a small comma-shaped structure; ommatidia absent; adult body length greater than 20 mm ..... *T. ruschii*
- 3a. Superior surface of the pedipalpal femur and patella smooth and shining, sparsely punctate ..... *M. formidabilis*
- 3b. Superior surface of the pedipalps granulose, rugose and densely punctate ..... (4)
- 4a. Tibial spurs present on legs II ..... *M. minensis*
- 4b. Tibial spurs not present on legs II ..... (5)
- 5a. Ommatidia conspicuous ..... (6)
- 5b. Ommatidia very small, punctiform ..... *M. butleri*
- 6a. Second tarsomere of leg I equal to or longer than third tarsomere ..... (7)
- 6b. Second tarsomere of leg I shorter than third tarsomere ..... (8)
- 7a. Second tarsomere of leg I longer than third tarsomere; ommatidia transverse, elliptical; adults about 65 mm ..... *M. maximus*
- 7b. Second tarsomere of leg I equal in length to third tarsomere; ommatidia circular; adults about 39 mm ..... *M. brasilianus*
- 8a. Tibial spurs present on legs III and IV; ommatidia small, transversely elliptical; adults about 50 mm ..... *M. colombianus*

8b. Tibial spurs present on legs IV only; ommatidia circular, conspicuous; adults less than 45 mm . . .  
..... *M. perditus*

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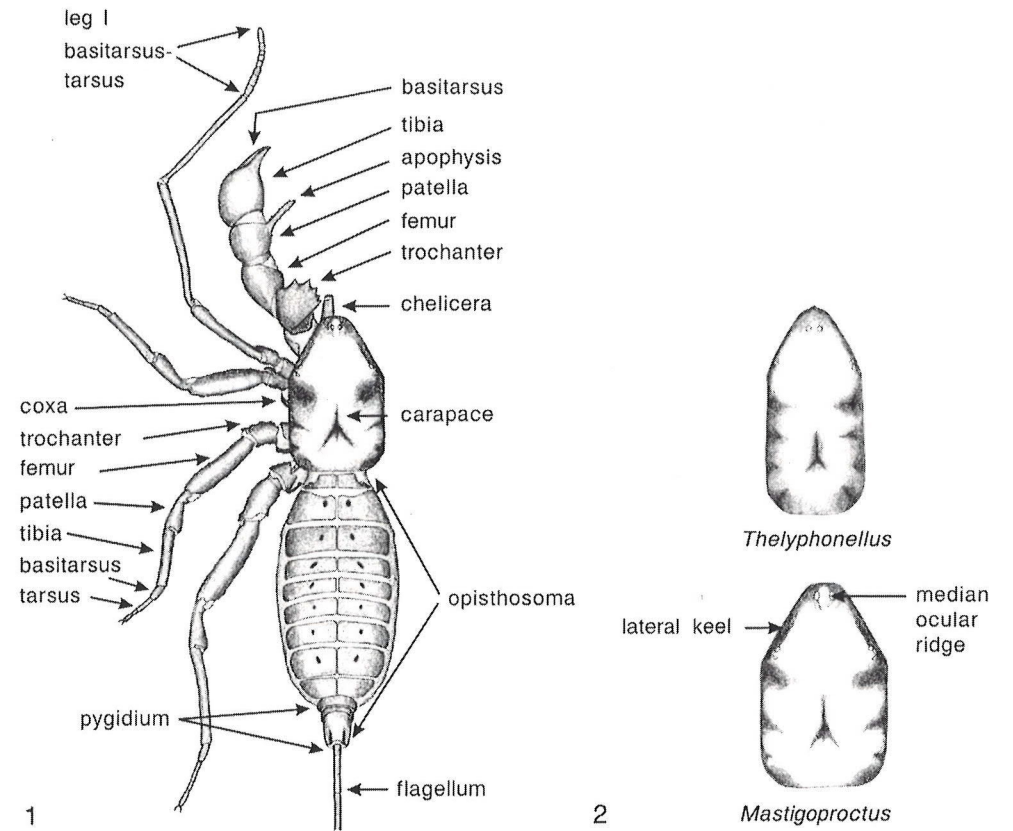


Fig. 1:

Dorsal view of a thelyphonid. Names of several anatomical structures, useful in recognizing taxa, are identified (from ROWLAND & ADIS 2002).

Fig. 2:

Dorsal view of the carapace in *Thelyphonellus* and *Mastigoproctus*. Indicated are location and approximate appearance of the lateral keels and distinct median ocular ridge in *Mastigoproctus* and the absence of the lateral keels and much less distinct median ocular ridge in *Thelyphonellus* (from ROWLAND & ADIS 2002).



Map:

Localities reported for species of South American thelyphonids. 1: *Mastigoproctus formidabilis*; 2: *M. colombianus*; 3-8, (9): *Thelyphonellus amazonicus*; (10): *T. ruschii*; (11): *M. maximus*; (12): *M. perditus*; (13): *M. minensis*; (14): *M. brasiliensis*; (15): *M. butleri*; (16): *M. annectens*. ( ) = only the state or country is known.