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Fernando Pérez-Miles *Editor*

New World Tarantulas

Taxonomy, Biogeography and
Evolutionary Biology of Theraphosidae

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Fernando Pérez-Miles
Editor

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Taxonomy, Biogeography and Evolutionary
Biology of Theraphosidae



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To tarantula taxonomists who bravely encouraged themselves to approach the study of a particularly difficult group.

To my colleagues, tarantula breeders and students for their multiple teachings and for encouraging me to face the challenge of this book.

To the loves of my life, especially to my children Lucia, Mateo, and Flavia.

Preface

Theraphosid tarantulas impressed naturalists since early times due to their large size, spectacular appearance, and extraordinary behaviors. However, the study of their taxonomy and especially their biology slowly increased until the second half of the twentieth century. The book of Baerg 1958 was one of the first contributions to the biology of North American theraphosids. Since the 1960s, starting with the papers of Argentinean arachnologists Gerschman de Pikelin and Schiapelli, the knowledge of the taxonomy of Neotropical tarantulas becomes more rigorous and some genera and subfamilies were seriously reviewed. The first cladistic analysis of Mygalomorphae done by Raven 1985 was a landmark in the taxonomy of the group and stimulated several colleagues to study the phylogeny of several mygalomorph families including Theraphosidae.

During the last few decades, many researchers interested in Theraphosidae from all over the world made relevant contributions in the study of tarantulas, mainly in taxonomical and phylogenetic aspects but also in biological aspects. The development of tarantula hobby also contributed to informal but valuable observations on breeding and other aspects of biology.

I prefer to use the name tarantula for the theraphosid spiders although it was originally used for lycosids because tarantula was widely extended in scientific and popular language for Theraphosidae, and I think the language is alive and dynamic.

I have been working on the taxonomy and biology of tarantulas for more than 40 years. This experience gave me the opportunity and privilege to know most specialists in the world, and I invited most of them to participate in this book. I trust their expertise and knowledge shared in this book could constitute a good motivation for students and researchers to continue developing studies in this fascinating group.

Montevideo, Uruguay

Fernando Pérez-Miles

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Chapter 1

Introduction to the Theraphosidae



Fernando Pérez-Miles

Abstract The mygalomorph spiders of the family Theraphosidae, commonly named as tarantulas, are one of the most famous and diverse groups of arachnids, which include the largest spider species in the world. Theraphosidae contains almost 1000 species from all continents, except Antarctica and includes burrowing, terrestrial and arboreal taxa with diverse ecological adaptations and natural histories. Since the description of the family in 1869 their systematics was largely based on the study of morphological characters, and many authors agreed in the chaotic situation of their taxonomy. First phylogenetic studies were also based on morphological characters and molecular studies only started in the twenty-first century. Most authors recognize 12–13 subfamilies in the world; 5 of them occur in the New World. The most diverse subfamily, Theraphosinae includes about a half of the known species of tarantulas. In this chapter we introduce the phylogenetic position of the Theraphosidae within the Araneae, the general characteristics of the tarantulas including taxonomical, evolutionary and biological aspects of the group. We analyze Theraphosidae diagnostic characters and the affinities with other families and discuss the intrafamilial relationships and subfamilial characteristics focusing in New World groups.

1.1 Introduction

Until now almost 50,000 species of spiders are described grouped into 128 families (World Spider Catalog 2020). All of them are carnivorous, some specialized as web builders, others live in burrows or are wandering species using circumstantial shelters. The order Araneae, which include the spiders, is divided into three suborders: the Mesothelae, the Araneomorphae, and the Mygalomorphae. The Mesothelae constitute a small group of spiders from Asia which exhibit segmented abdomen. The Araneomorphae constitute the largest group of spiders including about 90% of the species and characterized by the presence of vertical chelicerae opposing each other. Mygalomorphae is the sister group of the Araneomorphae and is

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characterized by the presence of the parallel alignment of the chelicerae; this group includes the tarantula family Theraphosidae.

Theraphosidae are mostly large, hairy spiders, that live more or less hidden in burrows, under stones or in silken retreats on the ground or on trees (Fig. 1.1). They occur mainly in tropical and subtropical regions and occupy habitats from sea level up to more than 4000 m (Ferretti et al. 2018) and are also found in caves at depths down to 800 m (Mendoza and Francke 2018). Theraphosidae are commonly called tarantulas although this common name was originally used also to name the wolf-spiders (Lycosidae). In several parts of Latin-America they are also called araña pollito (bird spider, chicken spider), araña mono (monkey spider); araña pica caballo (horse biting spider), and in Portuguese aranha caranguejeira or caragueijo (crabs-pider). Despite their large size and fearsome aspect, giving them a bad reputation, the great majority of tarantula species are not poisonous spiders. The bite can be painful due to the mechanic action of large chelicerae but the envenomation effect from the bite is usually similar to a wasp sting. In the last decades, the popularity of tarantulas as exotic pets increased considerably, mainly in developed countries.

Fig. 1.1 Habitus of Theraphosidae, (a) *Theraphosa blondi*, (b) *Psalmopoeus irminia* (Photos: R. West)



Consequently, the pet trade has exacerbated threats by overexploitation of natural populations (Costa and Pérez-Miles 2007; Aisenberg and Pérez-Miles 2016; Luddecke et al. 2018). In fact, several species from both the Old and New World were included in the IUCN red list as being in different status of risk; some of them protected by conservation actions as CITES (IUCN 2017) and national laws.

1.1.1 What Is a Theraphosidae?

Theraphosid tarantulas are usually large and hairy spiders. In fact, the type of setae that they have on their legs are fundamental for their classification as Theraphosidae. The diagnostic characters of the family are the presence of claw tufts together with dense tarsal scopulae (Fig. 1.2). Exceptionally, the genus *Agnostopelma* Pérez-Miles and Weinmann (2010) lacks the scopulae on posterior legs and an undescribed troglitic genus of Theraphosinae lacks scopulae on all legs (Perafán pers. comm.). Spiders of the family Barychelidae, closely related to the Theraphosidae, also have claw tufts and scopulae (usually less dense than Theraphosidae) and, in some genera, restricted to forelegs. According to Guadanucci (2014), Barychelidae has few clavate trichobothria in a group located on mid dorsal tarsi whereas in Theraphosidae the trichobothria are large and form lines or rows (Fig. 1.3). A typical barychelid has claw tufts, weak scopula, short apical segment of posterior lateral spinnerets (PLS), maxilla without projection and few trichobothria in a group; while a typical theraphosid presents claw tufts, dense scopula, apical segment of PLS digitiform, maxilla with anterior projection and trichobothria large and arranged in lines. Between both families there is a range of variation in morphology that makes difficult to clearly separate some barychelids from theraphosids. In this book we follow the most conservative criterion, using Theraphosidae *sensu stricto*, including only spiders that fit

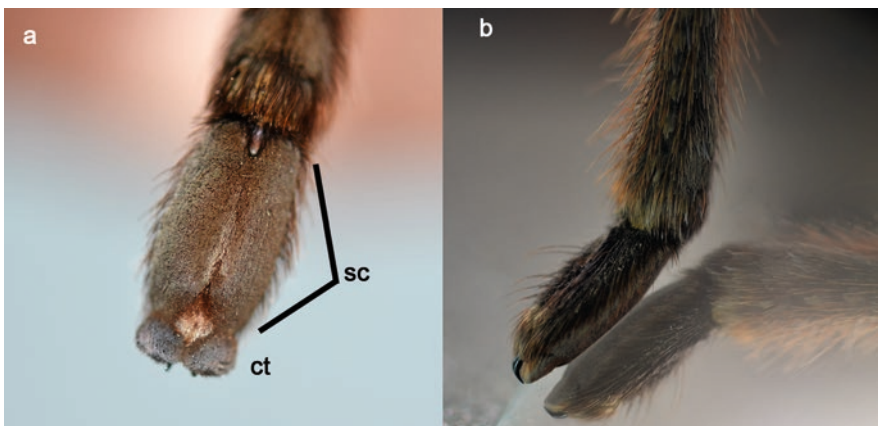


Fig. 1.2 Tarsal scopula (sc) and claw tufts (ct) of the tarantula *Grammostola anthracina*; (a) ventral view, (b) lateral view of tarsus on a glass surface

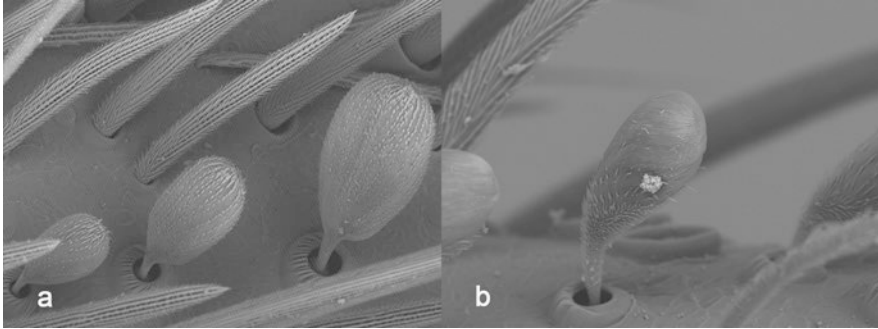


Fig. 1.3 Tarsal trichobotriae, (a) *Trichopelma* sp. (Theraphosidae), (b) *Neodiplothele martinsi* (Barychelidae) (Photos: JP Guadanucci)

with typical characters mentioned above. Most anatomical and morphological characteristics are similar to those found in other spiders. Characteristic morphological features consistent with other mygalomorphs are the parallel chelicerae (orthognath), two pairs of book lungs, absence of anterior spinnerets, palpal coxae similar to leg coxae, and presence of cuspules on labium and palpal coxae.

1.2 Morphology

Theraphosids are spiders with the carapace oval to subrectangular, of variable shape (Figs. 1.4 and 1.5). They usually have eight eyes in an elevated ocular tubercle; in some cave tarantulas (e.g., some species of *Hemirrhagus*) eyes can be reduced or absent, as well as the tubercle. As in other spiders, dorsally in the carapace, a transverse depression is present: the thoracic fovea. The tarantula fovea is usually procurved or straight. The spider fovea represents an internal invagination as an apodeme for the attachment of the sucking stomach muscle (dorsal dilator). The fovea presents a spherical process in the Central American genus *Sphaerobothria* and also could present a horn-like process as in some African baboon spiders as *Ceratogyrus* spp., in which the horn may provide an increased surface for muscle attachment (ring-shaped apodeme) as well as an increased area for midgut diverticula (West 1986).

Ventrally the mouth is surrounded by the labium behind and laterally by the palpal coxae, also named maxillae. Few to numerous cuspules can be present in the anterior edge or other position of the labium and in the prolatral proximal angle of maxillae (Fig. 1.6). These cuspules are considered as an apomorphy of the Mygalomorphae and their morphology seems to be homogeneous within the Theraphosidae and have limited systematic value (Pérez-Miles and Montes de Oca 2005). The probable functions proposed for the cuspules are mechanical, sensorial, and glandular. Cutler and Vuilliomenet (2001) proposed sensorial or glandular

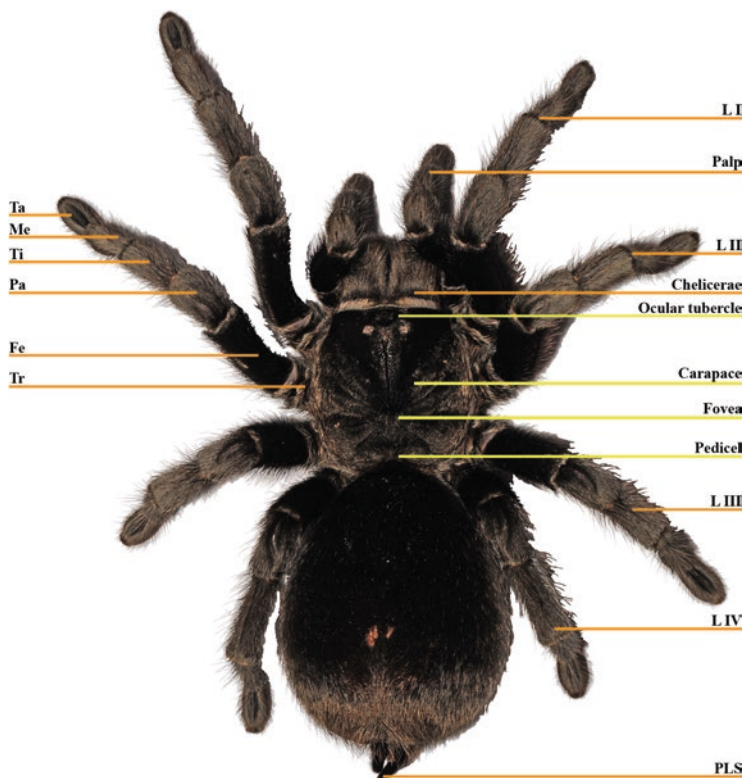


Fig. 1.4 Morphology of a Theraphosidae, dorsal view. *Fe* femur, *L* leg, *Me* metatarsus, *Ta* tarsus, *Ti* tibia, *Tr* trochanter, *Pa* patella, *PLS* posterior lateral spinnerets

function in *Aphonopelma seemani*, due to a pore observed in the apical region of the cuspule. Pérez-Miles and Montes de Oca (2005) proposed that cuspules could help in prey retention by opposing the backward force of the chelicerae. Posterior to the labium and separated by the labiosternal junction, there is the sternum with more or less conspicuous sigillae which represent apodemes. Sigillae are usually present in three pairs and could be marginal or submarginal.

Appendages In theraphosids the basal cheliceral segment usually has two rows of denticles on promargin and retromargin, respectively. The number and size of these denticles can vary in different species. Basal segments of chelicerae, palps and legs can present tegumentary modifications on prolateral and/or retrolateral faces; they are called stridulatory organs. Stridulatory organs are usually placed between the chelicerae on prolateral face, between chelicerae (retrolateral face) and palps (prolateral coxa); between basal segments of palps and legs I (retrolateral and prolateral faces, respectively) or between basal segments of legs. There are different types of stridulatory organs, that can be formed by bacilliform setae (most Selenocosmiinae), plumose setae (some Theraphosinae and most Harpactirinae), paddle- or spike-

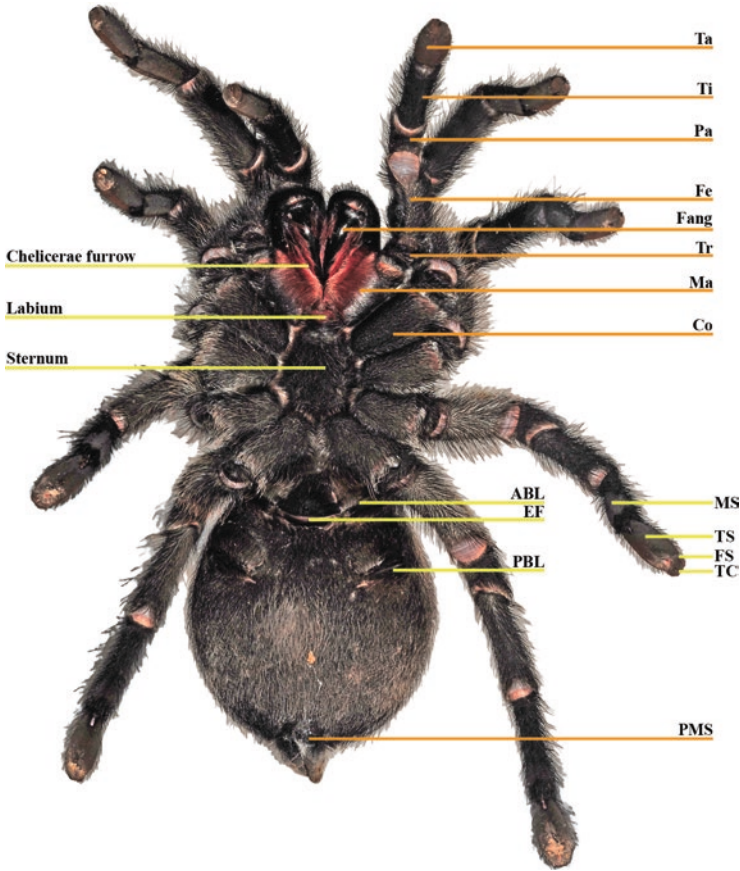


Fig. 1.5 Morphology of a Theraphosidae, ventral view. *ABL* anterior booklung, *Co* coxa, *EF* epigastric furrow, *FS* claw tufts, *Ma* maxilla, *Ms* metatarsal scopula, *PBL* posterior booklungs, *PMS* posterior median spinnerets, *Ts* tarsal scopula, *Tc* tarsal claw, other abbreviations as in Fig. 1.4

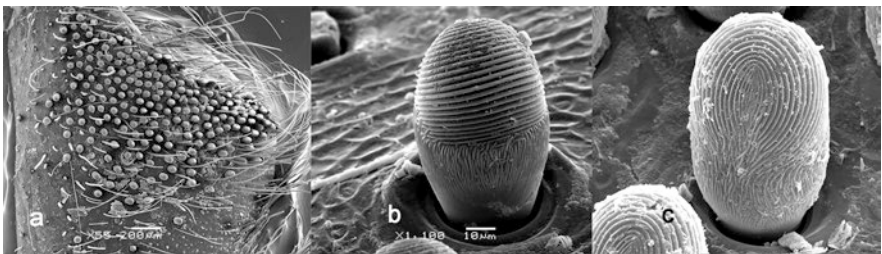


Fig. 1.6 Maxillary and labial cuspules of *Acanthoscurria cordubensis*. (a) Right maxillae (palpal coxa) showing cuspules, ventral view, (b) close-up of a labial cuspule (anterior view), (c) close-up of a labial cuspule (posterior view)

shaped setae (most Eumenophorinae), curved paddle setae (all Ornithoctoninae), and short modified setae (all Thrigmopoeinae) (Raven 1985; Gallon 2002; Bertani et al. 2008). Stridulatory setae present on New World genera of Theraphosinae were thoroughly studied in a recent article by Lima and Guadanucci (2019). These authors describe four different types of stridulatory setae present on coxae and/or trochantera and discuss function and evolution of such organs (See Chap. 11). In Old World tarantulas stridulatory organs can be more complex, involving diverse morphological types of setae, sometimes forming a lyra, and they are especially important to separate some subfamilies.

Palps are the second pair of appendages in spiders, they have one segment less than legs (lacking metatarsus) and have mainly sensitive functions. The palps are involved in prey capture and holding. In males, the apex of the palp is modified into sexual copulatory organs, the palpal bulbs. Theraphosid palpal bulbs are very sclerotized (not expandable) as in other mygalomorphs and in some subfamilies as Theraphosinae have conspicuous keels (Fig. 1.7). Because of the heavy sclerotization, the intake and expulsion of sperm is not activated by hydraulic forces but rather by glandular mechanisms (see Chap. 14). The morphology of male palpal bulb and nested morphology (keels, apophysis, etc.) are important sources of taxonomic characters to diagnose different categories such as subfamilies, genera, and species. The theraphosid palpal bulb is relatively simplified compared to other spiders (Kraus 1978, 1984) and two parts can be recognized: the proximal subtegulum and the distal part including the tegulum and embolous (Fig. 1.7). The subtegulum is extended in the subfamily Theraphosinae, which was considered as a synapomorphy of the group (Raven 1985). Although theraphosid bulbs are not as complex as those of most araneomorphs, the study of Bertani (2000) proposed many

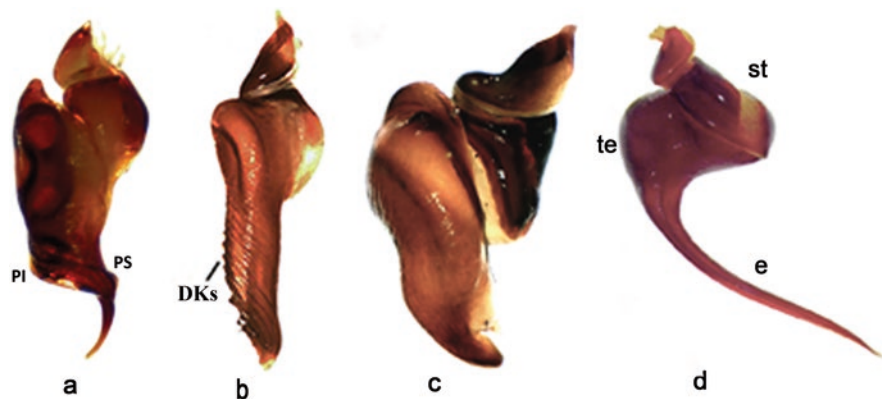


Fig. 1.7 Male palpal bulbs as examples of some New World Subfamilies (prolateral views). (a) *Tmesiphantes crassifemur* (Theraphosinae); (b) *Kankuamo marquezii* (Theraphosinae); (c) *Schismatothele weimanni* (Schismatothelinae); (d) *Avicularia merianae* (Aviculariinae). *DKs* dorsal supernumerary keels, *PI* prolateral superior keel, *PS* prolateral inferior keel, *st* subtegulum, *te* tegulum, *e* embolous. Photographs are not in scale. (c: after Valencia-Cuellar et al. (2019) and d: after Fukushima and Bertani (2017); with permission of the authors)

homologies among palpal bulb keels and main structures for Theraphosinae. The prolateral superior keel (PS) and prolateral inferior keel (PI) are widespread in most Theraphosinae genera whereas apical, subapical keels and other structures are present in some groups (Bertani 2000). Several other genera were described, and some of them with palpal bulb structures that obviously could not be considered in the homology hypothesis proposed by Bertani (2000). An extreme of these features are the supernumerary keels present in *Kankuamo* Perafán, Galvis and Pérez-Miles (Perafán et al. 2016). A new analysis of palpal feature homology seems to be necessary to include genera described in last decades.

Legs Scopulae and claw tufts setae, present in all Theraphosidae spiders, are adhesive and are involved in prey capture and locomotion, mainly during climbing (see Chap. 12). In Aviculariinae the scopulae are laterally extended giving the appearance of wider tarsi than other leg segments; this feature is probably related with the arboreal habits of most species in the subfamily. In some species the scopula is entire, formed by more or less homogeneous setae or medially divided by a stripe of longer conical setae; such division is usually wider in hindlegs (see Chap. 12).

In most New World theraphosid genera, males have a specialized apophysis on distal ventral or proventral anterior tibiae (Fig. 1.8). This tibial apophysis clasps the female chelicerae during copulation and are variable in morphology; they can have one (e.g., *Acanthoscurria*, *Schizopelma*), two (most genera), or three branches (some *Bonnetina*) or can occasionally be absent (e.g., *Metriopelma*, *Theraphosa blondi*, *Nhandu carapoensis*, several Ischnocolinae and Old-world genera, among others). In those with paired branches they can be convergent, straight, or divergent and can have their bases more or less fused. In Aviculariinae tarantulas tibial apophyses can be formed by grouped megaspines and can be present only in first pair of legs or in first and second pair (e.g., *Iridopelma*).

Tarantula legs are covered by varied types of setae, tricothoria, and spines. In Aviculariinae spines are scarce or absent whereas they are usually present in the other subfamilies, and the pattern and disposition of spines can be useful for taxonomy. The tricothoria morphology and arrangement patterns were studied in

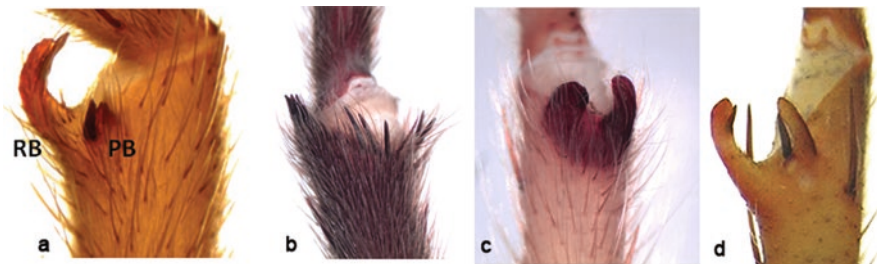


Fig. 1.8 Male tibial apophysis, (a) *Tmesiphantes uru*, two unequal branches, (b) *Acanthoscurria cordubensis* (ex *A. suina*), only one branch, (c) *Hapalopus formosus*, two branches fused at the bases, (d) *Schismatothele olsoni*, two separated branches (d: after Valencia-Cuellar et al. (2019), with permission of the author). RB retrolateral branch, PB prolateral branch

detail by Guadanucci et al. (2017) in Theraphosidae and Barychelidae spiders (see Chap. 11). The abundance of spines usually shows anterior posterior gradations, being more abundant in forelegs than in hindlegs.

Opisthosoma In theraphosids, the opisthosoma has a thinner cuticle in comparison with other body parts and similar to other spiders, this condition allows it to expand during prey ingestion and when females produce eggs. The opisthosoma is usually oval and can vary considerably in size and color pattern; most species have uniform dark coloration but several genera have conspicuous patterns and colorations as: *Avicularia*, *Antillena*, *Brachypelma*, *Caribena*, *Chromatopelma*, *Cyriocosmus*, *Davus*, *Hapalopus*, *Iridopelma*, *Megaphobema*, *Neoholothele*, *Pamphobeteus*, *Pachistopelma*, *Psalmopoeus*, *Typhochlaena*, *Xenesthis*, *Ybyrapora*.

A unique characteristic of the New World subfamilies Aviculariinae and Theraphosinae is the presence of urticating setae on the dorsal abdomen used for defense; also, the Aviculariinae *Ephobopus* has urticating setae on palps. Abdominal urticating setae can be transferred to the target by contact in some *Avicularia* or released to the air by the friction of hindlegs against the abdomen in other theraphosids. Urticating setae can be thrown as a reaction to the perturbing animal (active defense) or incorporated to egg-sac and/or molting mat (passive defense). There are several setae types described by Cooke et al. (1972), Marshall and Uetz (1990a, b), Pérez-Miles (1998), and Perafán et al. (2016). Detailed information on urticating setae morphology, biology, and evolution of tarantulas is given in Chap. 9.

Ventrally the opisthosoma shows two pairs of book-lungs; a transverse furrow can be seen between the anterior pair of lungs: the epigastric furrow. In the center of the epigastric furrow is located the genital opening, that in males serves to expel the sperm drop during the sperm induction maneuver (see Chap. 14). The epigastric furrow in males is also surrounded by a special type of spigots (epiandrous apparatus) that contribute to build a part of the sperm web. In adult females the epigastric furrow has a conspicuous darker and slightly raised crescent, that connects with the genitalia. Internally, female genitalia consist of seminal receptacles, the spermathecae (Fig. 1.9), that are connected with the external uterus.

The male palpal bulb delivers sperm into the spermathecae during copulation, which is defined as sperm transference. In tarantulas the copulatory duct is at the same time the fertilization duct, as in the Haplogynae. The shape, size, and characteristics of the spermathecae can vary, and are considered useful tools as taxonomic characters, since the contributions by Schiapelli and de Pikelin (1962). The receptacle wall is usually covered by glands that can be related with sperm nutrition (De Carlo 1973). The spermathecae is derived from the ectoderm, and thus the cuticular lining of spermathecae is shed with the exuvium.

Theraphosid spermathecae comprise one or two receptacles that can show different degrees of sclerotization. Exceptionally, *Sickius longibulbi* and *Encyocratella olivacea* are the only tarantula species in which females lack spermathecae (Bertani and Silva 2002; Gallon 2003, 2005); in the absence of spermathecae, sperm storage is undertaken by the oviducts and uterus and consequently a short interval between copulation and oviposition is expected.



Fig. 1.9 Female spermathecae as examples of some Theraphosidae. **(a)** *Schizopelma bicarinatum* (single, only one receptacle), **(b)** *Pamphobeteus* sp. (two receptacles, basally fused), **(c)** *Grammostola* sp. (two separated receptacles). **(a):** after Gabriel (2016), with permission of the author)

It is usually difficult or almost impossible to differentiate males from females in juvenile individuals, and it is also somehow difficult to distinguish adult females from all juveniles. Only adult males are clearly recognizable because of the presence of palpal organs, and in several species also by tibial spurs. Large juvenile males have on the anterior edge of the epigastric furrow a group of specialized spigots called epiandrous apparatus, which females lack. These spigots are involved in the production of additional silk for the sperm web (Costa and Pérez-Miles 2002). These structures can be used to distinguish between sexes in juveniles, but sometimes are not easy to see mainly in dark species; a good amount of light and high magnification is usually helpful. In some species it is possible to observe a different setae arrangement on the anterior edge of the epigastric furrow; males have a narrow semicircular darker area whereas females have a wider dark area and the epigastric furrow is more arched. Also the anterior pair of booklungs are more separated in females than in males.

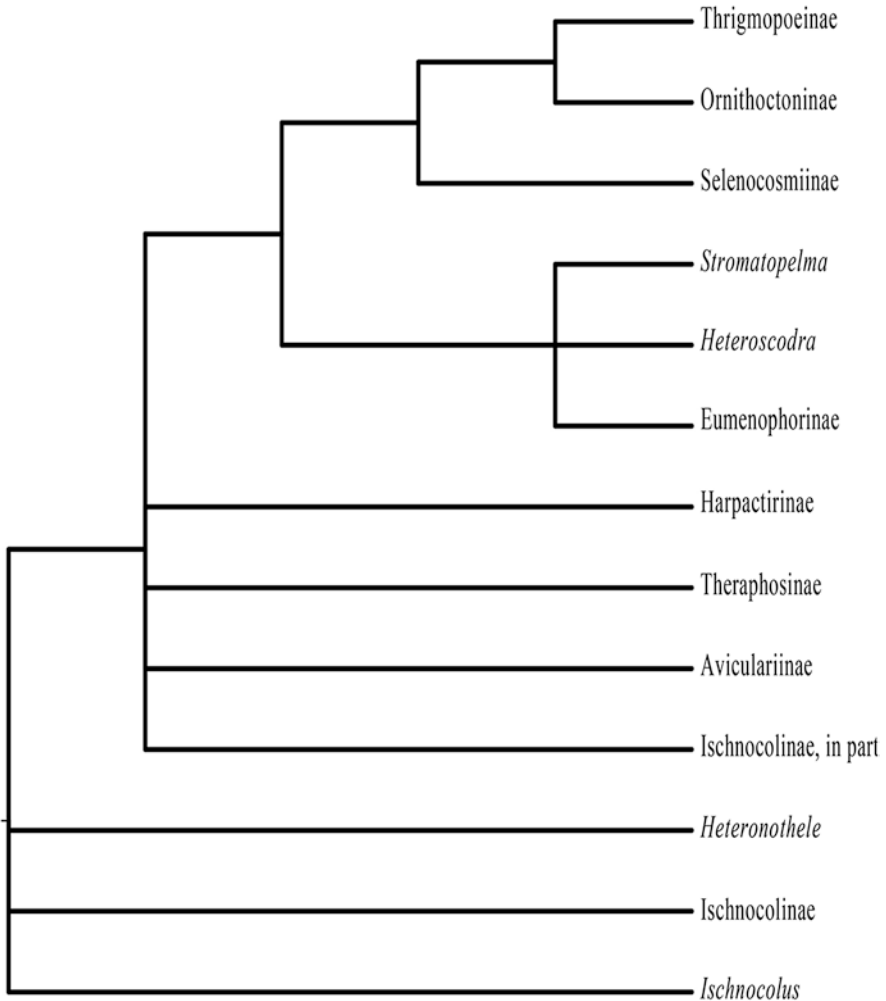
Another more accurate way to differentiate males from females is through the examination of the inner face of the exuviae, if available. Spermathecae cuticle remains attached to the females' molt and they can be observed inside the exuviae next to the epigastric furrow.

Tarantulas have two pairs of spinnerets on the posterior extreme of the opisthosoma; the posterior median spinnerets (PLS) have three segments, with the apical segment digitiform and longer than median; and the posterior median spinnerets (PMS), are short undivided.

1.3 Tarantulas: Numbers and Taxonomy

Theraphosidae is the largest family of the largest sized spiders among the infraorder Mygalomorphae. The family includes 985 species in 147 genera; they usually occur in tropical and subtropical regions, most of them in the Neotropics (World Spider Catalog 2020). Largest species of the family (*Theraphosa* spp.) reach about 30 cm of legspan and weight more than 100 g, but there are also small species in which adults measure only a few centimeters.

The arrangement of theraphosid tarantulas in subfamilies has been a matter of controversy (Figs. 1.10 and 1.11) but the latest classifications (Luddecke et al. 2018; Foley et al. 2019) include 12–13 subfamilies. Aviculariinae was considered endemic to the New World until West et al. (2008) analyzed the phylogeny of the group, and representatives of *Heteroscodra* and *Stromatopelma* from Africa that were previously classified in the subfamily Stromatopelminae, nested inside the clade Aviculariinae. Fukushima and Bertani (2017) exhaustively studied the Aviculariinae



a

Fig. 1.10 Phylogenetic proposals for the Theraphosidae. (a) Raven (1985), (b) Guadanucci (2014)

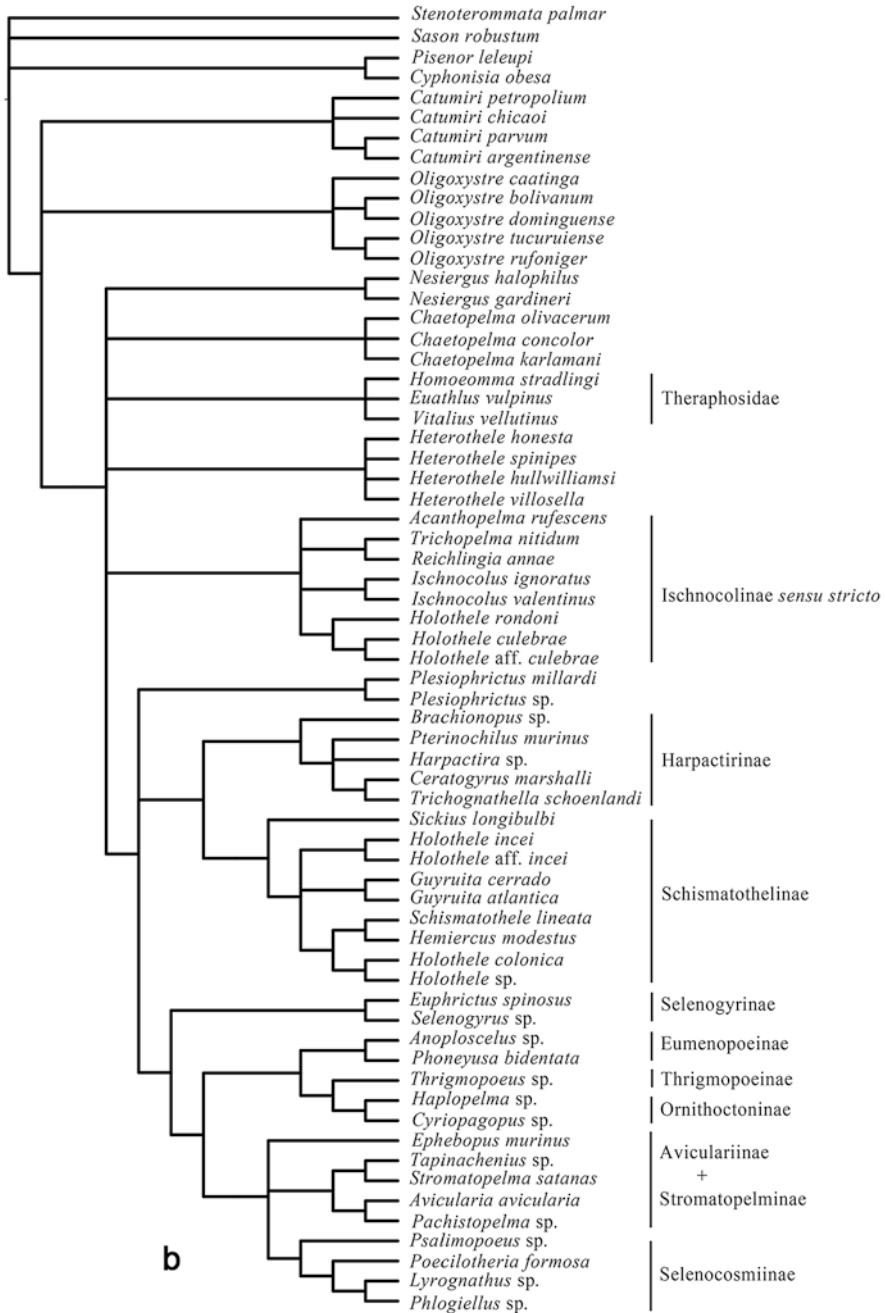


Fig. 1.10 (continued)

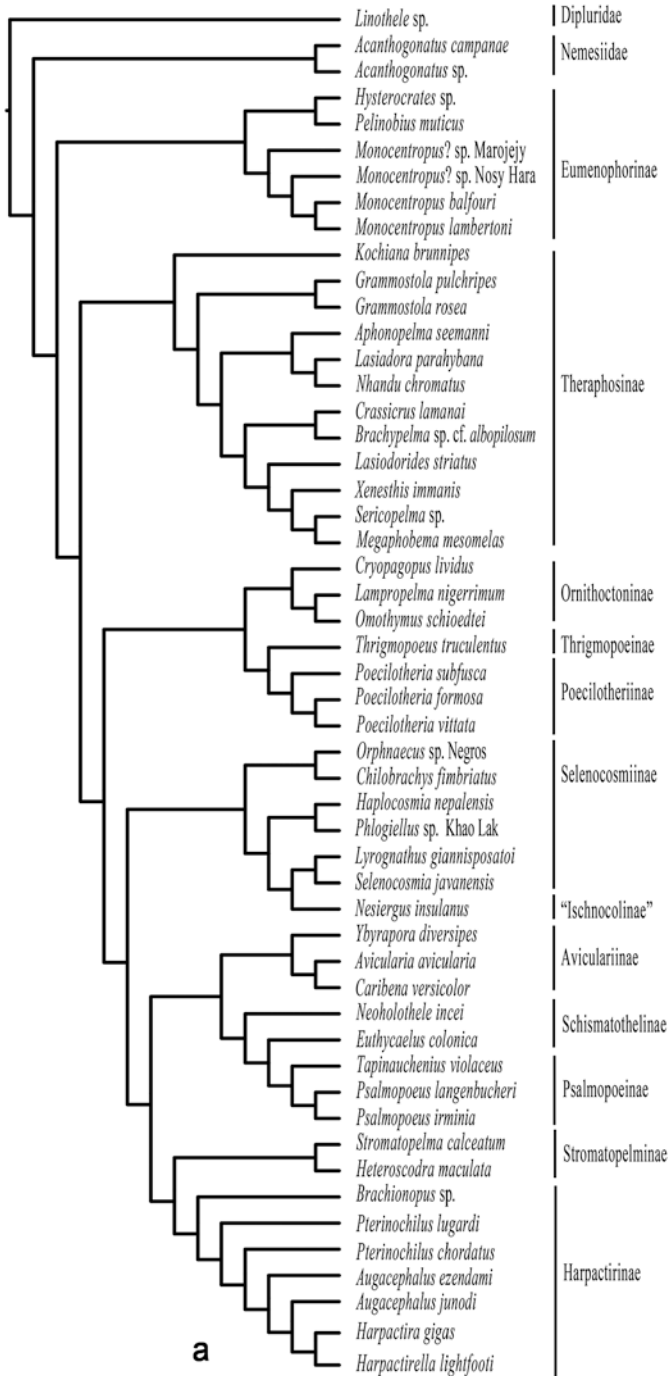


Fig. 1.11 Phylogenetic proposals for the Theraphosidae. **(a)** Luddecke et al. (2018), **(b)** Turner et al. (2018), **(c)** Foley et al. (2019)

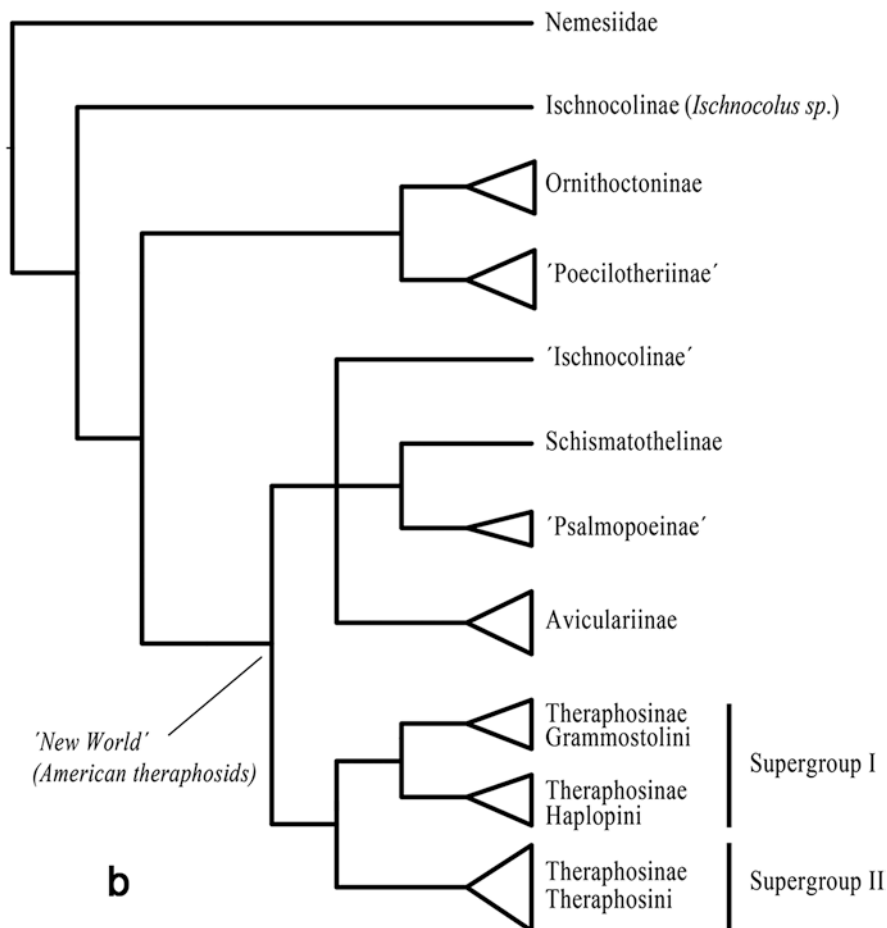


Fig. 1.11 (continued)

and in their morphologically based cladogram the subfamily also included *Heteroscodra* and *Stromatopelma*, as well as *Psalmopoeus*, *Tapinauchenius*, and *Ephebopus*. In the study of Guadanucci (2014) *Stromatopelma satan* was recovered in the same clade with the aviculariines with *Avicularia* and *Ephebopus*. In that study, Guadanucci (2014) revised intrafamilial relationships, and as a consequence, established Schismatothelinae including some genera previously considered as Ischnocolinae.

Recently, Turner et al. (2018) analyzed intrafamilial and generic relationships focussing on Theraphosinae using mitochondrial DNA and accepted, at least as informal groups, "Poecilotheriinae" and "Psalmopoeinae." Luddecke et al. (2018) reanalyzed the intrafamilial phylogeny using nuclear and mitochondrial sequences and gave important insights to the taxonomy of theraphosid subfamilies. The

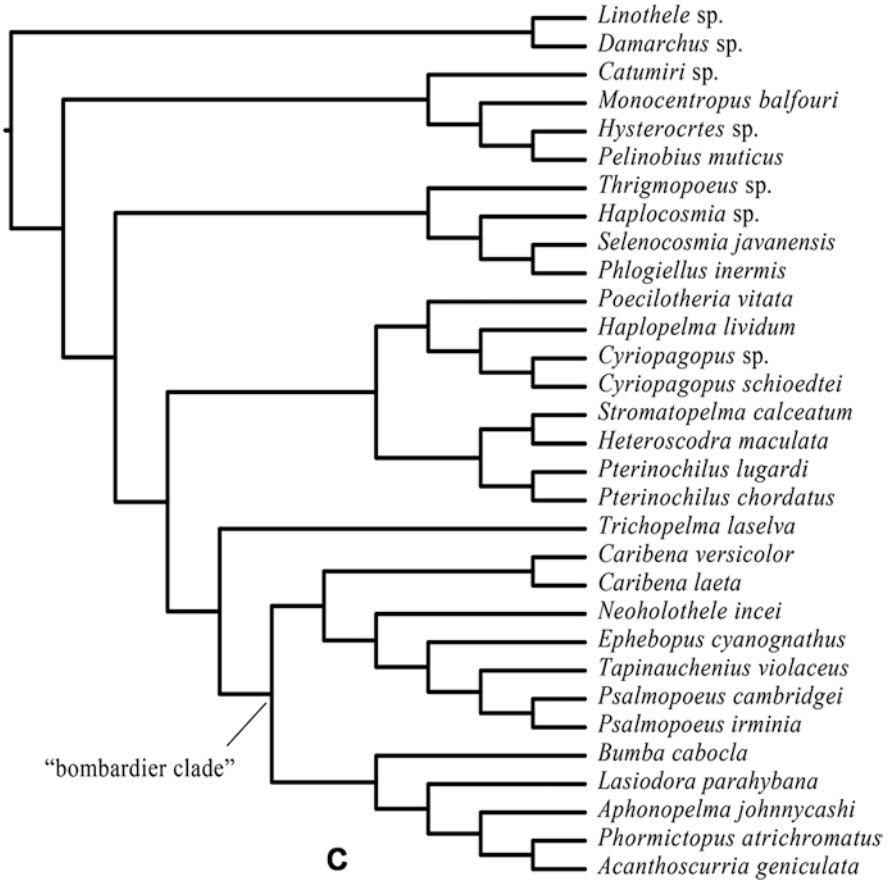


Fig. 1.11 (continued)

analysis of Luddecke et al. (2018) supports the monophyly of Poecilotheriinae, Psalmopoeinae, and Stromatopelminae. As *Stromatopelma* and *Heteroscodra* from Africa were transferred back from Aviculariinae to Stromatopelminae, then Aviculariinae remains endemic to the New World. In the analysis of Luddecke et al. (2018) Schismatothelinae was rendered paraphyletic and related to Psalmopoeinae whereas the "Ischnocolinae" *Nesiergus* was nested in Selenocosmiinae, but the authors said "...a more comprehensive sampling is necessary to confirm these results." The study of Guadanucci (2014) had an exhaustive sampling of Ischnocolinae sensu lato; for this reason I prefer to maintain Schismatothelinae as valid until new studies are performed (see Chap. 3 for further information).

More recently Foley et al. (2019) performed the first phylogenomic multigene study with representatives of several theraphosid subfamilies. Besides Old-World tarantulas, they concluded that Ischnocolinae, as suggested by Guadanucci (2014) represent multiple independent theraphosid taxa. Considering Ischnocolinae sensu

lato, Foley et al. (2019) found at least three lineages: *Catumiri* as one of the earliest branching of Theraphosidae; *Trichopelma laselva* considered as Ischnocolinae sensu stricto and *Neoholothele incei*, formerly in Ischnocolinae and now in Schismatotherlinae. These authors proposed the “bombardier clade” (in reference to their ability of throwing urticating setae) for the group which comprises: ((Aviculariinae) (*Neoholothele incei* (Psalmopoeinae)) (Theraphosinae)). Foley et al. (2019) also agree with the monophyly and validity of Psalmopoeinae supported in Luddecke et al. (2018) and in Turner et al. (2018), including the genus *Ephebopus* in this subfamily, as proposed by Hüsler (2018). A relationship between Aviculariinae (sensu lato) and Theraphosinae, was earlier suggested by Pérez-Miles et al. (1996) based on behavioral evidence, and never followed until now; the “bombardier clade” is somehow reminiscent of that proposal. Furthermore, Foley et al. (2019) found that with the exception of *Catumiri* all Neotropical representatives included in their study resulted in a monophyletic clade.

Although the molecular studies cited above greatly increased the evidences about the phylogeny of Theraphosidae and important limitation is the fragmentary taxonomic sampling of each study. The development of integrative studies including an exhaustive taxonomic sampling throughout the diversity of tarantulas, is fundamentally important.

Summarizing, five subfamilies are currently considered as present in the New World: Aviculariinae, Ischnocolinae, Psalmopoeinae, Schismatotherlinae, and Theraphosinae.

1.3.1 Key to New World Theraphosidae Subfamilies

- 1.- Abdominal urticating setae present (See Chap. 9).....2
 - Abdominal urticating setae absent.....3
- 2.- One or two types of urticating setae, types: I, III, IV, VI, VII (except some cave dwelling species), male palpal bulb with keels and subtegulum extendedTheraphosinae (Chap. 5)
 - Type II urticating setae, tarsal scopula laterally extended, male palpal bulb without conspicuous keels and subtegulum not extended; most species arboreal, legs with few or no spines.....Aviculariinae (Chap. 4)
- 3.- Tarsal scopula extended in combination with the absence of abdominal urticating hairs. Lyriform stridulatory organs on prolateral face of palpal coxa (*Psalmopoeus*, *Pseudoclamoris*), reduced or absent (*Tapinauchenius*) or type V urticating setae present on prolateral palpal femur (*Ephebopus*); males always with double tibial apophysis, legs with few spines.....Psalmopoeinae (Chap. 4)
 - Tarsal scopula not extended, urticating setae absent, legs usually spinose..... Ischnocolinae and Schismatotherlinae (Chap. 3)

1.4 Biology

Most tarantula species live in burrows or crevices on the ground but others are arboreal and live in silken retreats on trees. They are usually sit-and-wait predators with nocturnal habits but during reproductive periods it is possible to observe wandering males during daylight searching for females (Costa and Pérez-Miles 2002). Adult females remain inside their retreats most of the time, leaving the burrow only for prey capturing and to discard remains of cocoons or food (or etc.). They usually do not move very far away from the burrow entrance (Alvarez et al. 2016). Detailed information about tarantula ecology is given in Chaps. 7, 8 and 10.

1.4.1 Life Cycles, Lifespan

Theraphosid tarantulas are among the longest-lived spiders; females can reach an age of 30 years in captivity (Costa and Pérez-Miles 2002). Although the mygalomorph *Gaius villosus* (Idiopidae) was recently reported as a record reaching 43 years old in the wild (Mason et al. 2018), the lifespan of Theraphosidae is high as compared to most araneomorphs which usually live 1 or 2 years. Particularly long lifespans are restricted to female tarantulas because males usually die after their first reproductive season (Costa and Pérez-Miles 2002; Klaas 2007). This sexual difference in lifespan could be explained because males have higher metabolic rates at resting and during locomotion, as reported for *Aphonopelma anax*, in which males weigh half as much as females (Shillington and Peterson 2002; Shillington 2005).

Ibler et al. (2013) compiled lifespan data for 85 theraphosid species held in captivity; they also studied patterns of correlation between lifespan and other variables taken from literature and found several interesting relations. These authors suggest that species inhabiting more predictable environments such as humid tropics or low altitudes have longer lifespans. Also large body size, low abundance, fossorial lifestyle, and aggressive behavior are associated with longer lifespans. However, some reasons underlying these relations are unclear. The mean lifespan reported by Ibler et al. (2013) is relatively shorter than that of other studies; the authors explain such differences because they raised their animals at relatively high temperatures and provided ad libitum feeding. Also this difference could be influenced because they averaged male and female lifespans together, whereas several data from the literature correspond to longer-lived females.

We observed that males of some species as *Eupalaestrus weijenberghi* and *Acanthoscurria cordubensis* (ex *A. suina*) that live about 2 months as adults in the wild, could reach almost a year in captivity (pers. obs.). This could be explained because they feed less and have a lower metabolic cost than in nature, due to limited movements and other activities.

1.4.2 *Cocoons and Development*

Three types of Theraphosidae cocoons or egg-sacs have been described (Gallon and Gabriel 2006): (1) mobile cocoon, (2) fixed hammock, and (3) fixed flat. A mobile cocoon is a fully detached sac, usually a subspherical or ovoid loose sac, of which the female takes care during incubation, and is present in most Theraphosidae. A fixed hammock is a sac forming a hammock-like structure, permanently attached to the female's retreat by distinct silk bands. This kind of egg-sac is found in some Eumenophorinae, Harpactirinae, Stromatopelminae, and Thrigmopoeinae. A fixed flat is a sac permanently attached to the female's retreat, which is usually discoidal, flat, and secured against a surface. A fixed flat egg-sac is only present in some Ischnocolinae and Stromatopelminae. Gallon (2003) considered the mobile egg-sac to be plesiomorphic while fixed egg-sacs evolved independently in several groups. In several theraphosids studied egg-sacs can contain between 12 and 2000 eggs (Punzo and Henderson 1999); usually clutch size is correlated with adult body size in spiders (Simpson 1995).

In the temperate region, spiderlings emerge between 30 and 75 days after oviposition (Célérier 1992; Costa and Pérez-Miles 2002) but this period should vary with temperature and probably other environmental conditions. Studies of post-embryonic development show that tarantulas have 3–4 larval stages inside the cocoon, the first of them intrachorionic (Galiano 1969, 1973a, b). It is interesting to remark that the urticating setae occur in the first stage free of the cocoon (stages 4 or 5). The occurrence of different types of urticating setae during the development was studied in some species (Pérez-Miles 2002). Type III urticating setae are related with active defense, usually occurring later than other types.

Theraphosid species usually take 3–6 years to reach adulthood in humid tropical and temperate conditions, while they can take longer (up to 10 years in *Aphonopelma hentzi*) in arid zones (Baerg 1958; Stradling 1978; Trabalon and Blais 2012). As in all arthropods, spiders have to molt in order to grow in body size. In contrast with other spiders, tarantula females continue molting after maturation whereas males cease molting after reaching adulthood. During female post-mature molting spermathecae dimensions increase allometrically more than body size, which was interpreted to increase fecundity (Pérez-Miles 1989). Males are prevented from molting after adulthood due to anatomical limitations such as the basal constriction at palpal bulb. Some males that exceptionally molted after adulthood by hormonal disorders showed male palpal organ aberrations (pers. obs.).

In males, the juvenile period is shorter than in females, undergoing from 8 to 12 molts, while females usually have more than 9 juvenile molts (Trabalon and Blais 2012). Shortest male juvenile periods were found in the African species *Pterinochilus* sp. and *Stromatopelma grisepis*, lasting about 500–600 days to adulthood (Perret 1974; Célérier 1981). Several environmental factors such as temperature, food availability and photoperiod can produce variation in size increasing and instar duration (Turnbull 1962, 1965; Peck and Whitcomb 1970; Kotzman 1990).

1.5 Venom

Due to their body size and fearsome appearance, tarantulas usually have a bad reputation as being poisonous. However, this is far from true because most species' venom is not dangerous to humans. The bite could be painful due to the size of chelicerae that can penetrate deeply, but toxicity effects can be compared with a wasp sting. Most tarantulas are not aggressive and they usually try to escape rather than trying to bite. Old-world tarantulas are not so quiet, and more reactive than their New-World relatives; and their bites can be more severe. In effect species of *Pterinochilus*, *Poecilotheria*, and *Hysteroocrates* can produce painful muscle cramps that can last approximately for a month (Ezendam 2007; Fuchs et al. 2014; Hoffer 1996 and pers. observ.). Toxicologists have paid significant attention to tarantula venom because of the high quantities that can be extracted from large-size individuals. The venom of about 60 species of tarantula was studied (Bode et al. 2001; Escoubas and Rash 2004); some peptides found in tarantula venom seem to have potential application in medicine and industry. For example, venom of *Theraphosa blondi* is a source of curaremimetic toxins and ω -toxins of possible interest as tools in bioscientific research (Fontana et al. 2002). Spider venoms are complex mixtures of substances such as inorganic salts, small molecules such as amino acids, neurotransmitters and larger polyamines, peptides, and proteins, which work synergistically, improving venom efficiency (Santana et al. 2017). Tarantula venoms contain adenosine, histamine, and serotonin (Krug and Elston 2011). The purpose and function of spider venom is prey capture and digestion; secondarily venom could be used against predators as a deterrence tactic. A very interesting discovery demonstrates changes in venom composition during development in *Selenocosmia crassipes*. This modification in venom composition could be associated with change in the prey the spiders encounter at different life stages or to defend themselves from different predators along their lifespans (Santana et al. 2017).

1.6 Origin and Paleontology

Several authors suggested that Mygalomorphae radiated in major lineages during the Mesozoic (Dunlop et al. 2008). Eskov and Zhonshtein (1990) called the Cretaceous as the “age of the mygalomorphs” suggesting that in the Cenozoic the araneomorphs dominated the araneofauna until more recent times. Recent phylogenomic studies estimated the origin of the Theraphosidae between 34 and 71 Mya (Bond et al. 2014) and between 2 and 125 Mya (Garrison et al. 2016). Very recently Opatova et al. (2019) suggested the split between Barychelids and Theraphosidae around 106 Mya.

In fact, the geographic distribution of tarantulas with gondwanic preponderance suggests the origin of the family prior to the division of the continental plate, near to higher age estimations. However, the theraphosid fossil record is scarce and came

entirely from Neogene-Recent (Dunlop et al. 2018); in their list three fossil species are recognized as Theraphosidae. The first described was found in Dominican amber and assigned to the subfamily Ischnocolinae: *Ischnocolinopsis acutus* Wunderlich 1988 (Dunlop et al. 2018). Two other species came from Chiapas amber in Mexico, an undetermined genus and species described by Dunlop et al. (2008) and *Hemirrhagus* sp. described by García-Villafuerte (2008). Probably the environmental conditions prior to the Neogene were not favorable for fossilization of tarantulas, which could explain the absence of theraphosid fossils in earlier times. Recently, Hembree (2017) developed a neoichnological study of tarantula burrows presenting criteria to recognize these spider burrows in the fossil record. This study has potential application for continental ischnofossil assemblages in order to improve paleoecological interpretations of ancient soil ecosystems and to improve the knowledge of tarantula biochron.

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