Chapter 5
Theraphosinae

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Abstract Theraphosinae is the most diverse subfamily of tarantulas in the world, with more than 500 known species. The group is endemic to the New World and its geographic distribution ranges from Southern North America to temperate zones of South America. The largest and most long-lived spiders in the world belong to this subfamily. They inhabit almost all terrestrial environments from sea level up to 4500 m altitude. Beyond the morphological diagnostic characters of the subfamily, this group is also characterized by a singular mechanism of defense, employing abdominal urticating setae that they can release to the air when they are disturbed. For over a century, this subfamily remained poorly known from both biological and taxonomical aspects. In fact, most genera were established during the last few decades and several papers on behavior, ecology, and reproduction were published. Due to their size, longevity, sex dimorphism, relatively easy conditions for breeding, and other biological characteristics, this group constitutes an interesting model for studies on metabolism, thermoregulation, biomechanics, communication, reproduction, and development. This chapter will present an updated overview of the taxonomy and phylogeny of the group as well as a revision of recent scientific contributions in different fields of general biology.

5.1 Introduction

Theraphosinae is the most speciose subfamily of the spiders known in America as tarantulas or bird-eating spiders, with 67 genera and more than 500 species currently described (World Spider Catalog 2019; Kambas 2019), being highly diverse

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in the Neotropics. Theraphosinae is perhaps the Theraphosidae subfamily that least offers doubts about its monophyly, since Raven's formal proposal in 1985 and its subsequent internal phylogenetic analysis carried out by Pérez-Miles et al. in 1996. The monophyly is based on the combined presence of keels on the copulatory bulb, extended subtegulum, and abdominal urticating setae. The urticating setae are the most distinctive characteristic of the subfamily, and one of the most enigmatic of the tarantulas. These setae are an exclusive evolutionary novelty of New World tarantulas, shared only by Theraphosinae and some Aviculariinae (see Chap. 9).

Theraphosinae spiders are distributed in tropical regions of Central and South America, southern Mexico, and some Caribbean islands, even though some species inhabit temperate zones in the southwestern United States, northern Mexico, Chile, Argentina, and Uruguay (see Chap. 6). They inhabit a great diversity of environments, from tropical wet and montane forests, high Andean environments to sea coastlines, savannas, and deserts. Their retreats typically include cavities in the ground, crevices, and underneath rocks or fallen trunks. They mainly exhibit coloration between brown and black, although some species have patterns of other colors in the opisthosoma or prosoma and legs. The subfamily comprises species of a large variety of sizes, including the largest known spider, the Goliath tarantula *Theraphosa blondi* (Latreille 1804), which can measure up to 30 cm of legspan (Fig. 5.1).

The taxonomic history of the subfamily has been almost as extensive as the taxonomic history of the spiders, their numerous nomenclatural changes have affected the validity of their scientific names, but also several problems have been detected with vernacular names. The first spider species recognized as tarantula was the wolf spider (Lycosidae) *Lycosa tarantula* (Linnaeus 1758) from Tarento, Italy (hence the specific epithet), whereas in America the first known spiders of Theraphosidae were colloquially called by the European explorers bird-eating spiders or tarantulas.

Fig. 5.1 *Theraphosa blondi*, female habitus (Photo: R. West)

5.2 Taxonomic History

The spider group currently considered as Theraphosidae was initially placed in the Walckenaer's classification (1837) in "Theraphoses," and in the Lucas' (1840) approach within "Tetrapneumones." In 1870, Thorell established the family Theraphosidae (named Theraphosoidae), within the suborder Territelariae which was characterized by the "peculiar direction of the mandibular claw" oriented parallel to the body axis (paraxial), four book lungs, and "generally with two pairs of spinnerets and two tarsal claws." Thorell (1870) drew attention to the following nomenclature aspects: the first one, the synonymy of *Theraphosa* (Walckenaer) with *Mygale* (Walckenaer), and the second one, the differentiation between *Theraphosa* and *Avicularia* (Lamarck).

Thorell (1870) stressed Walckenaer's (1802) nomenclatural inaccuracies which included using the name *Mygale* (a taxonomic name for shrews initially proposed by Cuvier in 1800) to name a separate group of spiders with four book lungs of the "spiders properly so called" (*Aranea* Walckenaer), but also proposing a different genus called *Theraphosa* (Walckenaer), which "according to the original description is absolutely synonymous with *Mygale*" (Thorell 1870). Furthermore, Thorell (1870) emphasized that both Olivier (1811) and de Lamarck (1818) adopted the *Mygale* genus proposed by Walckenaer but restricted it to "*les Araignées mineuses*," excluding the other *Mygale* species (or "*les Araignées aviculaires*"). Nevertheless, de Lamarck (1818) postulated a new genus for the latter group called *Avicularia*. Consequently, Thorell (1870) proposed that *Theraphosa* should include the species "*les Araignées aviculaires*," which in Koch and Simon were named *Mygale* (Thorell 1870), partly because *Theraphosa* is the oldest denomination of the two, and also because according to Thorell the name *Avicularia* should be restricted to a group of species within "*les Mygales aviculaires*," which included *Aranea avicularia* (Lamarck). Thus, Thorell (1870) divided "*les Mygales aviculaires*" in four genera: *Theraphosa* (Walckenaer), *Avicularia* (Lamarck), *Trechona* (C. Koch), and *Diplura* C. Koch.

Ausserer (1871) kept Thorell's (1870) proposal and built a classification mainly based on characteristics of the chelicerae, maxillae, palps, and elevation of the cephalic area for the high ranks, and division of the tarsal scopulae, shape of the fovea, ocular arrangement, and others for the lower ranks. Ausserer (1871) recognized three subfamilies Atypinae (=Atypidae), Eriodontinae (=Actinopodidae), and Theraphosinae (composed by all the other known mygalomorphs). Almost two decades later, Simon (1889) performed the first general classification that included a representative sample of mygalomorphs taxa, with material from Venezuela and the Colombian west. Subsequently, Simon (1892, 1903) added and redescribed several taxa, and published his results in a memorable paper called "*Histoire naturelle des araignées*." In this work, Simon (1892) preserved the classification criterion proposed by Ausserer (1871), but added the character extension of the metatarsal scopulae, and recognized two families within mygalomorphs, Atypidae and Aviculariidae. Aviculariidae included diverse subfamilies (Aviculariinae, Barychelinae, Actinopodinae, Ctenizinae, Diplurinae, Miginae, and Paratropidinae) each one divided in groups (many of them now currently considered as subfamilies). Aviculariinae (Simon 1892) was divided into the following ten groups, by features related to the legs and fovea: Ischnocoleae, Chaetopelmateae, Crypsidromeae, Phlogieae, Selenocosmieae, Paecilotherieae, Avicularieae, Theraphoseae, Eurypelmateae, and Homoeommateae.

Pocock (1897, 1903) and F.O.P. Cambridge (1896) developed new proposals, reestablished new taxa and taxonomically upgraded some of the ranks proposed by Simon (1892, 1903) at the family and subfamily levels. Likewise, Pocock (1897, 1903) revised the stridulatory organs on the external faces of the chelicerae and maxillae, and the internal trochanters and coxae of the palp and first pair of legs. He also studied relationships between body measurements (patella + tibia/cephalothorax) and spination on the legs as taxonomic characters. Pocock (1897) argued that for practical purposes in the classification of theraphosid spiders it would be sufficient to refer to the classification proposed by Simon in 1892, which was an extension of Ausserer's (1871) proposal. Consequently, Pocock (1897) synonymized Aviculariinae (=Aviculariidae) (Simon 1892) with Theraphosidae (Thorell 1870), and discussed the validity of the scopulae condition as a taxonomic character, demonstrating ontogenetic differences within some species. Concurrently, he proposed the following subfamilies: Ornithoctoninae (Oriental Region), Harpactirinae (South and East Africa), Selenocosminae (Oriental Region and Australia), and Theraphosinae (Tropical and Subtropical America, Madagascar, Ethiopian Region, and the Mediterranean area of Paleartic); and strongly highlighted the imperious need to deeply examine South American species.

In 1928, Petrunkevitch made his first classification based on external morphology following the bases of Simon (1892) and Pocock (1897), with some innovations, and discussed the taxonomic validity of the stridulatory setae proposed by Pocock (1897, 1903). Petrunkevitch (1928) proposed Barychelidae and Theraphosidae as related taxonomically, and the following theraphosid subfamilies: Ornithoctoninae (including Simon's Ornithoctoneae and Thrigmopoeae), Selenocosmiinae (including Simon's Selenocosmiae, Poecilotheriae, and Harpactireae), Eumenophorinae (Simon's Phoneyuseae), Aviculariinae, Ischnocolinae, Theraphosinae (including Simon's Theraphoseae and Lasiodoreae), and Grammostolinae (Simon's Eurypelmateae). Later, he performed a review using internal anatomic features (particularly cardiac ostia) (Petrunkevitch 1933), but proposed Paratropididae related with Theraphosidae, and both related with Ctenizidae and Dipluridae; all of them in a group named Octostiatae (four pairs of cardiac ostia).

One of the first classification works that included an important representation of Neotropical mygalomorph families was carried out by Mello-Leitão in 1923, which divided six Brazilian families based on presence/absence of claw tufts and rastellum, and labium condition (merged or free). According to Mello-Leitão (1923), the family Aviculariidae (Pocock 1897) would correspond to the true "caranguejeiras" (=tarantulas), represented in tropical America only by some Theraphosiinae, which he divided in four groups based on spination of the legs, scopulae condition, and presence/absence of retrolateral scopulae on femur IV: Ischnocoleas (= Ischnocolae) (Simon, 1903), Grammostoleas (= Eurypelmateae) (Simon, 1903), Theraphoseas (= Lasiodoreae + Theraphoseae) (Simon, 1903), and Avicularias (= Aviculariae + Phoneyuseae (only *Ephebopus*) (Simon, 1903). Grammostoleas and Theraphoseas were related by the presence of spines and entire scopulae in all legs, and differentiated from each other by the presence (Theraphoseas) or absence (Grammostoleas) of scopulae in retrolateral face of femur IV; contrary, Ischnocoleas have posterior tarsi with divided scopulae and Avicularias lack spines (Mello-Leitão 1923). The Mello-Leitão (1923) classification related Actinopodidae + Paratropididae as a sister group of Ctenizidae + Dipluridae and Theraphosidae + Barychelidae (Raven 1985).

By the middle of the twentieth century the research developed by Bucherl (e.g., 1947a, b, 1949a, b, 1951, 1957) on Brazilian taxa, and later by Schiapelli and G. de Pikelin (e.g., 1961, 1962, 1964, 1970, 1979) and G. de Pikelin and Schiapelli (e.g., 1970, 1972, 1973) on South America taxa was transcendental for Theraphosinae taxonomy and systematics. These authors revised several genera and established the morphology of reproductive organs as taxonomic characters that allowed the best “natural” systematic delimitation. Bücherl (1957) stressed the importance of comparing and describing the palpal bulb and tibial spur of the males, and judged that the use of spination legs, eye interdistances, and its disposition were subject to individual variations. Meanwhile, the Argentinean researchers Schiapelli and G. de Pikelin made valuable contributions such as detailed description and elaboration of drawings of the taxonomic characters, including palpal bulbs, and highlighted the importance of female genitalia in the mygalomorph system (Raven 1985).

Cooke et al. (1972) examined for the first time the morphology of the urticating setae in detail, comparing the abdominal setae of several theraphosid species. They recognized four urticating setae types (I–IV), studied the effects of these setae on a variety of animals and demonstrated the value of urticating setae in the systematics of Theraphosidae. Later, Marshall and Uetz (1990), Pérez-Miles (1998), and Perafán et al. (2016) discovered and described three other urticating setae types (V–VII). Urticating setae have been widely recognized as an important systematic character (e.g., Raven 1985; Pérez-Miles et al. 1996; Bertani and Guadanucci 2013; Turner et al. 2018; Kaderka et al. 2019). See detailed information in Chap. 9.

Raven’s masterpiece (1985) is considered as a starting point in the systematics of Mygalomorphae (Coddington and Levy 1991; Goloboff 1993; Pérez-Miles et al. 1996); admittedly, much of today’s classification scheme is still based on this work. Raven (1985) realized the first approach to a detailed examination of the phylogeny of Mygalomorphae, as well as the first revision of genera and species of the infraorder based on the type material comparison. Raven (1985) built phylogenetic trees by hand based on careful examination of morphological characters followed by logic-based arguments of primary and secondary homology. Regarding the family Theraphosidae, Raven (1985) advocated a close phylogenetic relationship between Paratropididae and Theraphosidae, supported by the presence of an anterior lobe on the maxillae and numerous labial cuspules. He considered both to also be related to Barychelidae with the combined three families constituting the Theraphosoidina: based on the shape of the male tibial spur, presence of claw tuft, absence of maxillary serrula, and female with few teeth on the tarsal claws. Raven's Theraphosidae cladogram showed only subfamilial relationships with several unresolved polytomies: Theraphosinae was related in a tetrachotomy with Harpactirinae, Aviculariinae, and Iscnocolinae (in part). These groups share the presence of tarsal scopulae in all legs, absence of inferior tarsal claw (Raven 1985), and only one row of few small teeth on the superior tarsal claw or alternatively, with such teeth absent (Goloboff 1993). Thereby, Theraphosinae was considered in a close phylogenetic relationship with Harpactirinae by sharing unilobed spermathecae or with Aviculariinae due to the presence of urticating setae in the abdomen (Lucas et al. 1991; Pérez-Miles 1992).

Raven (1985) synonimized Grammostoleae Mello-Leitão, 1923, Crypsidromeae Simon, 1889, and Homoeommeae, Simon 1892 with Theraphosinae Thorell, 1870, arguing that the conformation of the first groups was based upon artificial characters and/or characters of only tribal significance. He also expanded the subfamily by incorporating several genera previously located in Ischnocolinae. Thus, based on Schiapelli and Gerschman (1979), Valerio (1980) and the morphological review, Raven (1985) diagnosed the Theraphosinae subfamily as follows: male palpal bulb with modified embolus distally stout and broad or keeled; large subtegulum, extending down the bulb for half of the tegulum; and, additionally, femur IV sometimes with scopulae in retrolateral face. The resulting Theraphosinae group consisted of 31 genera distributed from southern North America to South America.

The first cladistic analysis of Theraphosinae was carried out by Pérez-Miles et al. (1996). They developed a data matrix with all genera known at the time (30) and 27 morphological characters, and analyzed the subfamily under a Maximum Parsimony approach. They suggested the monophyly of Theraphosinae and elucidated much of the phylogenetic relationships of the genera described up to that point (Fig. 5.2), but the phylogenetic relationships between Theraphosinae and other theraphosid subfamilies was not resolved. Pérez-Miles et al. (1996) discarded the presence of retrolateral scopulae of the femur IV as a synapomorphy for Theraphosinae and highlighted for the first time the importance of urticating setae within the systematics of the group. They proposed the presence of urticating setae type III as a new synapomorphy for the subfamily, with reversion in some genera (*Aphonopelma*, *Citharacantus*, *Cyrtopholis*, *Spaerobothria*, *Vitalus*, and *Xenesthis*) (Pérez-Miles et al. 1996). Additionally, their results indicated that types I and IV urticating setae were likely synapomorphies for two clades within Theraphosinae: type I present in most genera with a reasonable degree of phylogenetic resolution and on the contrary, type IV including only a small group of genera related within a large polytomy (Fig. 5.2).

Likewise, Pérez-Miles et al. (1996) emphasized that the unilobed receptacles of the spermathecae cannot be considered a synapomorphy of the group, because this interpretation would require three parallels for its explanation in some other subfamilies (Harpactirinae and some genera of Aviculariinae and Ischnocolinae). Thus,

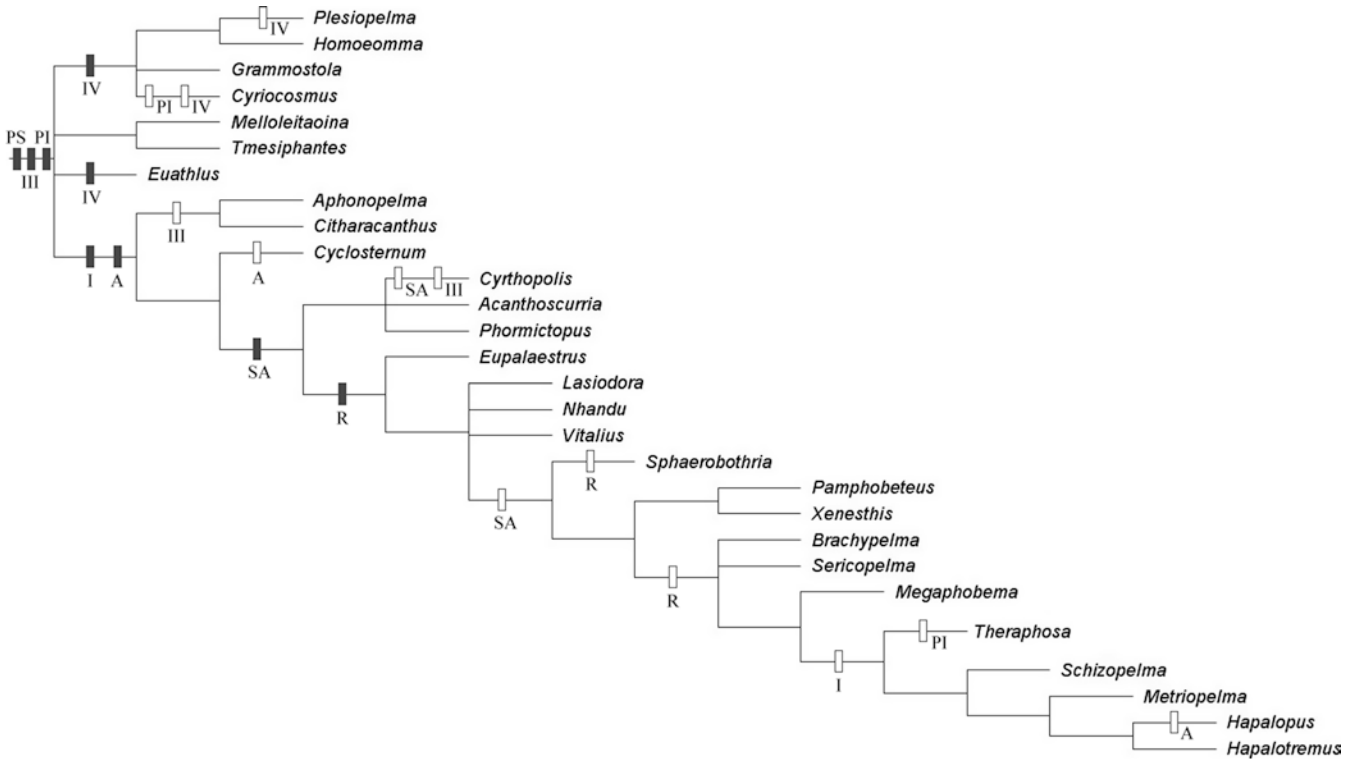

Fig. 5.2 Cladogram of Theraphosinae, modified from Pérez-Miles et al. (1996), keel indications modified from Bertani (2000) and urticating setae modified from Bertani and Guadanucci (2013). In black acquisitions, in white reversions. I = type I urticating setae, III = type III urticating setae, IV = type IV urticating setae, A = apical keel, PI = prolateral inferior keel, PS = prolateral superior keel, R = retrolateral keel, SA = sub-apical keel

the arboreal South American Aviculariinae (excluding Psalmopoeinae, formerly in Aviculariinae) was proposed as the preferred sister group to the Theraphosinae, since both subfamilies share the presence of abdominal urticating setae (Type II in Aviculariinae) and a defensive display with abdominal movements as synapomorphies (Pérez-Miles et al. 1996). Pérez-Miles et al. (1996) removed *Acanthopelma* and *Holothele* from Theraphosinae and transferred them to Ischnocolinae, because they lack urticating setae and keels on palpal bulb. Subsequently, Pérez-Miles (2000) increased taxon sampling in his morphological analysis with the addition of a newly described genus (recently renamed as *Bumba*), but his results remained similar as in previous data.

Bertani (2000) carried out an important contribution to the study of Theraphosinae cladistics and the description of new species. He performed the first approach to homologize male palpal bulb keels of Theraphosinae and proposed a new terminology to name the homologous keels. Thereby, his work increased the available number of characters for taxonomic studies and incorporated elements of the copulatory bulb in the phylogenetic analyzes. Furthermore, he studied the morphology and distribution of palpal bulb keels in over 60 species in 27 genera, resulting in four basic groups of keels (Fig. 5.3): prolateral inferior (PI) and prolateral superior (PS) keels, for the two more or less parallel keels found on the prolateral bulb face; apical (A) keel, for the ventral keel located just before the apex of the embolus; subapical (SA) keel, for a keel located just before the apical keel; and, retrolateral (R) keel, for the keel located in the retrolateral region, originating in the apical region and extending backward. Also, Bertani (2000) discussed that other palpal bulb keels, as well as other structures, were found in some genera and/or species constituting apomorphies for these groups. Bertani (2000) mapped the bulb characters in the cladogram proposed by Pérez-Miles et al. (1996) to explore the evolution of the male palpal keels in Theraphosinae, and as a result he found many concordances with the keel's evolution with few exceptions (Fig. 5.2). Later, Bertani (2001) focused on specific South American lineages (*Vitalius*, *Nhandu*, and *Proshapalopus*) and performed a phylogenetic analysis where he incorporated the recently proposed homology of the keels. In the last few decades, the description of genera and species with new keels is demanding a new revision of Bertani's proposal.

The phylogenies up to this point showed an acceptable resolution for most lineages except for the genera with type IV urticating setae (Pérez-Miles et al. 1996; Pérez-Miles 2000; Bertani 2001; Fukushima et al. 2008), of which the majority of workers previously defined in the Grammostolinae (Mello-Leitão 1923). Perafán (2010) in his master's thesis tested the monophyly of that group, where he constructed a data matrix with 40 species as terminals, belonging to 18 genera, and 78 morphological characters, gathering the characters proposed in previous works. Under Maximum Parsimony analysis, Perafán (2010) determined that genera with type IV urticating setae constitute a monophyletic group, additionally supported by the presence of metatarsal II scopulae occupying the distal half of the segment. In addition, he argued that this group is more closely related to the genera that possess both I + III urticating setae, than to those which possess only type I (Fig. 5.4).

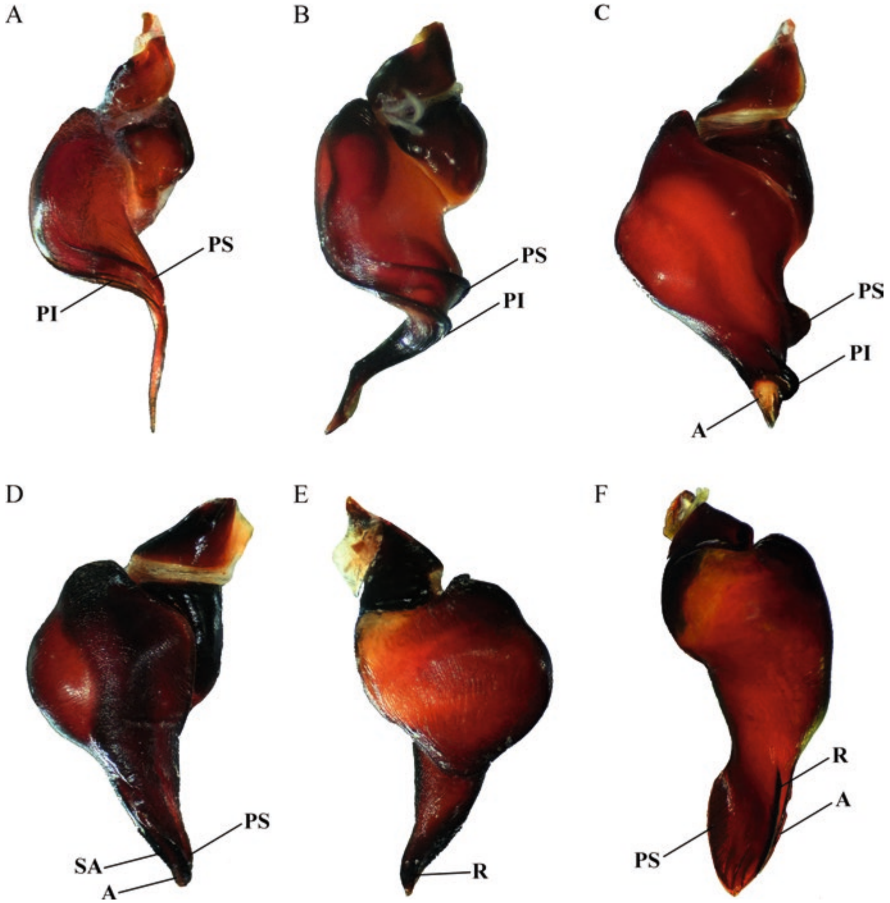

Fig. 5.3 Palpal bulb morphology and keels (**a**) *Plesiopelma longisternale*, (**b**) *Tmesiphantes nubilus*, (**c**) *Acanthoscurria cordubensis* (Ex *A. suina*) (**d**) *Eupalaestrus weijenberghi.* (**e**) Eupalaestrus weijenberghi, (**f**) *Pamphobeteus verdolaga.* (**a**–**d**) prolateral views, (**e**–**f**) retrolateral view. *A* apical keel, *PI* prolateral inferior keel, *PS* prolateral superior keel, *R* retrolateral keel, *SA* sub-apical keel

Turner et al. (2018) highlighted that Theraphosidae‘s phylogenetic approaches are largely reliant of the attributes of a set of morphological characters many of which may be plesiomorphic and/or homoplastic, a problem commonly seen in all mygalomorph families. Also, these authors discussed that the majority studies with molecular data focused in the evolutionary history of Theraphosidae have little understanding beyond the generic limits (e.g., Hamilton et al. 2011, 2014, 2016; Hendrixson et al. 2013, 2015; Longhorn et al. 2007; Montes de Oca et al. 2016; Ortiz and Francke 2015, 2016; Petersen et al. 2007; Wilson et al. 2013), which have been historically inferred solely from morphological data (e.g., Pérez-Miles et al. 1996; Pérez-Miles 2000; Bertani 2001; Bertani 2012; Guadanucci 2014; Gabriel 2016). Turner et al. (2018) explored a mtDNA gene tree based on the

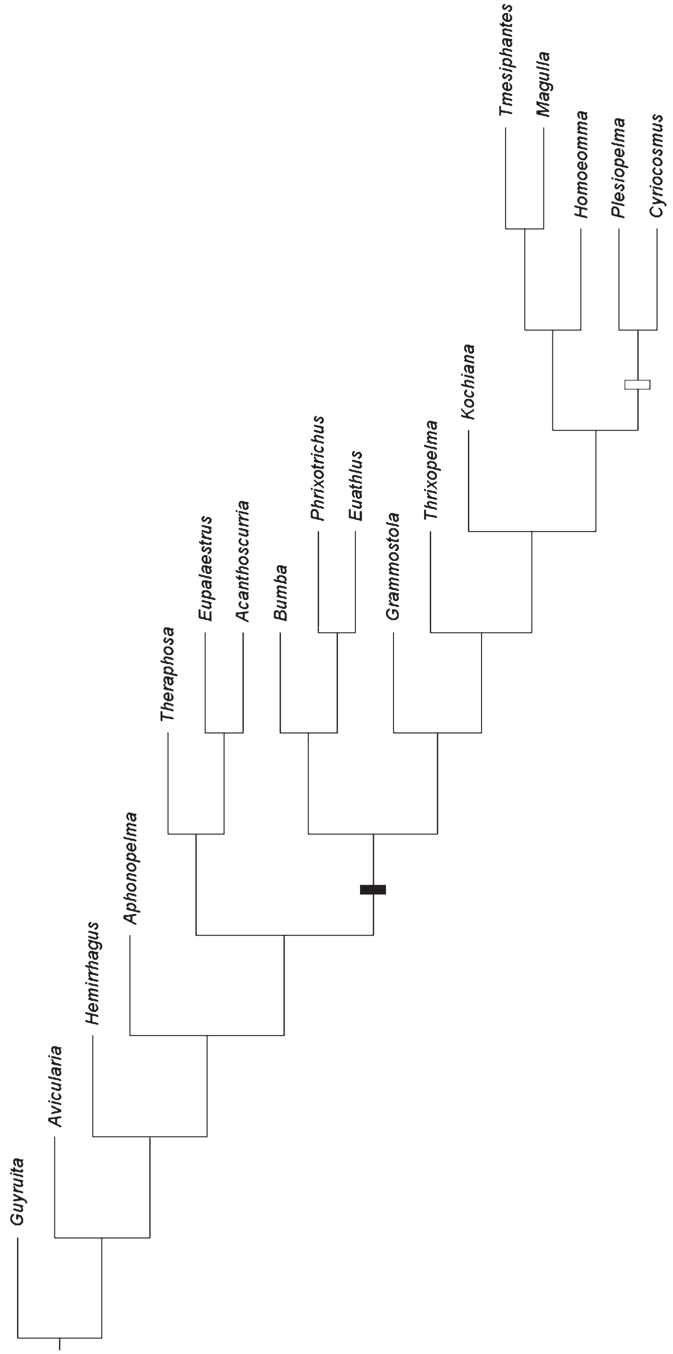

Fig. 5.4 Cladogram of "Grammostolinae" from Perafán (2010) (unpublished M.Sc. thesis). In black type IV urticating setae acquisition, in white reversions

mitochondrial 16S-tRNA (leu)-ND1 gene region, frequently used as a taxonomic "barcode" in spiders, to redefine the taxonomic limits and evolutionary relationships between some genera and species within the Theraphosinae subfamily.

Turner et al. (2018) confirmed the monophyly of Theraphosinae but uncertainty remains regarding relationships between subfamilies due to limited sampling of genes and phylogenetically informative characters, limited taxon sampling from Old World theraphosids, and few New World "Ischnocolinae." The hypotheses of Turner et al. (2018) supported in a single node the American theraphosids, related in two internal clades: one of them composed by Theraphosinae and the other composed by Aviculariinae as a sister group of the New World "Ischnocolinae," Schismatothelinae and Psalmopoeinae. However, according to Turner et al. (2018) the internal nodes relating to the subfamilies in the second node were weakly supported, and Aviculariinae (excluding Psalmopoeinae) may remain as the preferred sister-group of Theraphosinae. On the other hand, Turner et al. (2018) emphasized the presence of deep splits within the Theraphosinae, dividing the subfamily into three tribes within two supergroups (see Chap. 1, Fig. 1.11b). Furthermore, they stressed that the types of urticating setae seem especially congruent with the inferred groupings. One of the lineages named Grammostolini (with *Grammostola* as the type genus) includes several genera that ancestrally possess both type III and type IV urticating setae. The second major lineage was defined as the tribe Hapalopini, considered to contain multiple genera with only type III urticating setae ancestrally (with *Hapalopus* as the type genus). Finally, the major lineage defined as the tribe Theraphosini (with *Theraphosa* as the type genus, and as the sister genus to all others in this tribe), consists of the remaining genera that hypothetically possess urticating setae type I ancestrally.

Lüddecke et al. (2018) provided a preliminary molecular phylogenetic hypothesis of relationships among theraphosid subfamilies, based on 3.5 kbp of three nuclear and three mitochondrial markers. Like in previous morphological analysis, this study strongly validates the prevalent subfamily level classification within Theraphosidae. Besides the problems aroused from phylogenetic inferences obtained with morphological data, Foley et al. (2019) argued that traditional Sanger sequencing of preselected genes does not offer strong support for supra-generic clades. In this sense, they addressed the first robust phylogenetic hypothesis of theraphosid evolution inferred from transcriptome data, where they recovered a monophyletic group that comprises the vast majority of New World theraphosid subfamilies. As a result, the clade has been divided into the subfamily Theraphosinae and three other subfamilies Aviculariinae, Psalmopoeinae, and Schismatothelinae that together form another clade (Foley et al. 2019).

5.3 Taxonomy

5.3.1 Theraphosinae Thorell, 1870

Genera included: *Acanthoscurria*, *Acentropelma*, *Aenigmarachne*, *Agnostopelma*, *Aguapanela*, *Aphonopelma*, *Bistriopelma*, *Bonnetina*, *Brachypelma*, *Bumba*, *Proshapalopus*, *Cardiopelma*, *Catanduba*, *Chromatopelma*, *Citharacanthus*, *Clavopelma*, *Cotztetlana*, *Crassicrus*, *Cubanana*, *Cyclosternum*, *Cyriocosmus*, *Cyrtopholis*, *Davus*, *Euathlus*, *Eupalaestrus*, *Eurypelmella*, *Grammostola*, *Hapalopus*, *Hapalotremus*, *Hemirrhagus*, *Homoeomma*, *Kankuamo*, *Kochiana*, *Lasiodora*, *Lasiodorides*, *Magnacarina*, *Longilyra*, *Magulla*, *Megaphobema*, *Melloleitaoina*, *Metriopelma*, *Miaschistopus*, *Munduruku*, *Mygalarachne*, *Neischnocolus*, *Neostenotarsus*, *Nesipelma*, *Nhandu*, *Ozopactus*, *Pamphobeteus*, *Phormictopus*, *Phrixotrichus*, *Plesiopelma*, *Pseudhapalopus*, *Pterinopelma*, *Reversopelma*, *Sandinista*, *Schizopelma*, *Sericopelma*, *Sphaerobothria*, *Stichoplastoris*, *Theraphosa*, *Thrixopelma*, *Tliltocatl*, *Tmesiphantes*, *Umbyquyra*, *Vitalius*, *Xenesthis*.

Diagnosis: Differs from other Theraphosidae in the presence of urticating setae types I, III, IV, V, VI, or VII. Male palpal bulb with subtegulum extended and keels present along the embolus.

Distribution: Theraphosinae are mainly found in tropical regions of Central and South America, southern Mexico, and some Caribbean islands, but many species inhabit temperate climates in the southwestern United States, northern Mexico, Chile, Argentina, and Uruguay (see Chap. 6).

5.4 Taxonomic Key

We present a brief key and diagnosis of generic groups (tribes) inspired by the proposal of Turner et al. (2018), summarize a few characteristics of the genera and give an orientation to selected literature. The presently available information on several of these genera is not enough to recognize them easily, and some of them are monotypic; they are indicated here by an asterisk. The references given after the characteristics of the genera are the main source of information used here. The number of species and geographic distribution are taken from World Spider Catalog (2019).

Urticating setae types III and/or IV present; type I absent …....………… Group I
Urticating setae type III present, type I absent (Note: in a few genera the additional presence of type IV is questionable, but if present type III is nonetheless predominant) …..……...……...……...……...……...……...………… Group II
Urticating setae III and/or I present, type IV absent ……….....………… Group III
Urticating setae otherwise, types I, III, IV absent ……….....…….……. Group IV

Group I (Fig. 5.5)

Without prominent abdominal pattern in adults (patterning present faintly at rear in some *Euathlus*). Male tibial apophysis with two branches (lost in *Aguapanela*). No nodule on male metatarsi I. Femur IV without retrolateral scopulae. Presence of types III and IV urticating setae. Absence of coxal stridulatory setae (except *Aguapanela* and *Grammostola*). Absence of trochanter and femur stridulatory setae (except *Aguapanela*). Male palpal bulb piriform, usually with cylindrical filiform embolus. Presence of superior and inferior keels (PS and PI). Two spermathecal receptacles with separated bases.

Comprises: *Agnostopelma*, *Aguapanela*, *Bistriopelma*, *Bumba*, *Euathlus*, *Grammostola*, *Homoeomma*, *Magulla*, *Melloleitaoina*, *Phrixotrichus*, and *Tmesiphantes.*

Agnostopelma Pérez-Miles and Weinmann 2010. Differs from all other Theraphosinae in the absence of scopulae on leg tarsi IV. Two species from Colombia, Boyacá (Pérez-Miles and Weinmann 2010).

Aguapanela Perafán et al. 2015. Characterized by the presence of stridulatory plumose setae on coxae, trochantera, and femora of legs I and II. Males lack tibial

Fig. 5.5 Representatives of Theraphosinae Group I. (**a**) *Euathlus* sp. (**b**) *Bistriopelma matuskai*. (**c**) *Grammostola quirogai.* (**d**) *Aguapanela arvi.* (Photos **a**, **b**: R. Kaderka)

apophysis and females have two digitiform spermathecal receptacles. One species from Colombia, Medellin (Perafán et al. 2015).

Bistriopelma Kaderka 2015. Differs from all other Theraphosinae (except *Phrixotrichus* and *Tmesiphantes hypogeus*) by the presence of two patches of type III urticating setae. From *Phrixotrichus* and *Tmesiphantes* in the morphology of female of spemathecae and by the position of urticating patches, respectively. Three species from Peru (Kaderka 2015, 2017).

Bumba Pérez-Miles et al. 2014. Characterized by the presence of type IV urticating setae, a retrolateral process on male palpal tibiae, palpal bulb resting in a ventral distal excavation of the palpal tibia and spiniform setae on prolateral and retrolateral maxillae and coxae I–IV. Four species from Brazil, Ecuador, and Venezuela (Pérez-Miles 2000; Pérez-Miles et al. 2014; Perafán and Pérez-Miles 2014b).

Euathlus Ausserer 1875. Males have a palpal bulb with two prolateral keels and tip directed retrolaterally, the tibial apophyses with retrolateral spines, a subapical spine on retrolateral branch and a basal spine on prolateral branch. Females have two spermathecal receptacles with a lateral spheroid chamber. Differs from *Phrixotrichus* in the presence of only one central urticating setae patch. Ten species from Argentina and Chile (Perafán and Pérez-Miles 2014a, b; Ferretti 2015).

Grammostola Simon 1892. Stridulatory setae present on coxae of palp and leg I. Male palpal bulb with filiform embolus and prolateral superior and inferior keels subequal; tibial apophysis with two separated branches. Females with two spermathecal receptacles subconical with a spheroid chamber on apex (a subdistal constriction). Twenty-two species from Argentina, Brazil, Bolivia, Chile, Paraguay, and Uruguay (Schiapelli and Gerschman 1961; Ferretti et al. 2011, 2013; Montes de Oca et al. 2016).

Homoeomma Ausserer 1871. Both sexes small in size, males are characterized by palpal bulb with digitiform tegular apophysis and embolous twisted. In some species males present a baso-ventral nodule on metatarsus I. Females have two separated spermathecal sacular receptacles of variable morphology. Some species have only type IV urticating setae and lack type III. Fifteen species from Argentina, Brazil, Chile, Colombia, Peru, and Uruguay (Gerschman and Schiapelli 1972, 1973; Pérez-Miles et al. 1996; Montenegro et al. 2018; Sherwood et al. 2018).

Magulla Simon 1892. Both sexes small in size with comparatively short metatarsi. Male palpal bulb with embolous twisted; similar to *Homeomma* but differing by the lack of a digitiform tegular apophysis and differentiated from *Tmesiphantes* by the apex of the bulb not dilated. Female spermathecae formed by two receptacles with long neck, slightly dilated apex, which presents a ventral loop in lateral view. Four species from Brazil (Indicatti et al. 2008).

Melloleitaoina Gerschman and Schiapelli 1960. Extremely reduced number of labial cuspules (6–15) in both sexes. Males with thickened femur III and palpal bulb with long curved embolous (similar to *Tmesiphantes*). Females with two separated spermathecae with a slight subdistal constriction and spiniform setae on promargin of coxae III and IV. Four species from Argentina (Perafán and Pérez-Miles 2014a).

Phrixotrichus Simon 1889. Urticating setae type IV gathered in two dorso-lateral patches in both sexes. Male palpal bulb with two subequal prolateral superior and inferior keels, embolus tip directed retrolaterally. Female with two spermathecal receptacles with a lateral spheroid chamber. Five species from Argentina and Chile (Perafán and Pérez-Miles 2014b).

Tmesiphantes Simon 1892. Both sexes small in size with an absence of scopulae on metatarsi IV. Male with palpal bulb with conspicuous superior and inferior prolateral keels, and a long and curved embolus. Metatarsus I bends to the retrolateral side of the retrolateral tibial apophysis. Females with spermathecae slightly constricted near the apex. Nine species from Brazil (Yamamoto et al. 2007; Bertani et al. 2013; Fabiano-da-Silva et al. 2015).

Group II (Fig. 5.6)

Usually with an abdominal pattern in adults of both sexes (lateral banding and/or spots), reduced in some genera as *Thrixopelma*, *Plesiopelma*, *Schizopelma*, *Hapalopus*, and others. Some genera have species with abdominal patterning and others without it. Male tibial apophysis with two branches often fused at the bases; modified in *Schizopelma* (a megaspine) and in *Bonnetina* (accessory apophysis). Metatarsi I of adult males can have retrolateral nodule with spines (*Bonnetina*, *Magnacarina*) or basal process (*Plesiopelma*, *Catanduba*). Femur IV without retrolateral scopulae. Type III urticating setae present and predominant, type I absent. Stridulating setae absent. Male palpal bulb often short and strong (except *Plesiopelma* and *Catanduba*); can have very modified keels. Spermathecae usually single, fused, and sclerotized or, if separated, have sinuous or spiral morphology.

Fig. 5.6 Representatives of Theraphosinae Group II. (**a**) *Cyriocosmus perezmilesi*. (**b**) *Chromatopelma cyaneopubescens*. (**c**) *Hapalotremus* sp. (**d**) *Hapalopus formosus*. (Photos **a**, **b**, **c**: R. West; **d**: R. Kaderka)

Comprises: *Aenigmarachne*, *Bonnetina*, *Cardiopelma*, *Catanduba*, *Chromatopelma*, *Cyriocosmus*, *Davus*, *Hapalopus*, *Hapalotremus*, *Kochiana*, *Magnacarina*, *Munduruku*, *Plesiopelma*, *Schizopelma*, and *Thrixopelma.*

Aenigmarachne Schmidt 2005. Characterized by the presence of type IV urticating setae distally bent; males lack tibial apophysis. One species from Costa Rica, female unknown (Schmidt 2005).*

Bonnetina Vol 2000. This genus differs from all other theraphosine because males have three tibial apohysis on leg I. Females with widely fused spermathecal receptacles, or if narrow, with wide bases. Seventeen species, endemic to Mexico (Ortiz and Francke 2017).

Cardiopelma Vol 1999. The genus was characterized by the spermathecae morphology, heart shaped with a wide basis. Male unknown. Locality unknown (Vol 1999). The validity of this genus offers serious doubts due to the absence of locality data and because is poorly diagnosed. Heart shaped spermathecae is also present in some *Hapalopus* species. One species without locality data (Vol 1999; Perdomo et al. 2009).*

Catanduba Yamamoto, Lucas and Brescovit 2012. Males of *Catanduba* are characterized by the presence of a prolateral inferior keel with a tooth in the middle of the embolus and a triangular basal nodule on metatarsus I (as in *Homoeomma*). Female spermathecae with a large number of spherical nodules. Seven species from Brazil (Yamamoto et al. 2012).

Chromatopelma Schmidt 1995. Similar to *Aphonopelma* but females differ by the abdominal pattern, presence of a single fused spermathecae, presence of type IV urticating setae, tarsal scopulae of leg III divided and larger posterior median eyes. Male palpal bulb with a triangular prolateral keel. Tibial apophysis with two separated and unequal branches. One species from Venezuela (Schmidt 1995; Schmidt and Herzig 1997).*

Cyriocosmus Simon 1903. Males are characterized by the presence of a paraembolic apophysis on palpal bulb, as in *Hapalopus*, but can be distinguished from *Hapalopus* by the divergent branches of tibial apophysis. Females have a sinuous or spiral spermathecae neck with a convex base and a caliciform fundus. Twenty-one species from Argentina, Bolivia, Brazil, Colombia, Paraguay, Trinidad and Tobago, Venezuela (Pérez-Miles 1998; Fukushima et al. 2005; Kaderka 2010, 2016).

Davus O. Pickard Cambridge 1892. Differ from most Theraphosinae in the laterally striped abdominal pattern. Males with palpal bulb with apical keel and embolus retrolaterally twisted. Palpal tibia with a retrolateral domed process, tibial apophysis with two convergent branches with bases fused. Female with single spermathecae with variable morphology; subquadrate, subtriangular, subspheric. Four species from Costa Rica, Guatemala, Nicaragua, Mexico, and Panama (Gabriel 2016).

Hapalopus Ausserer 1875. Most species have a dotted or striped abdominal pattern. Males with palpal bulb with prolateral inferior keel ring shaped, and retrolateral face of palpal tibia with a process or field of spines. Metatarsus I strongly curved. Females with single spermathecae usually very sclerotized or if two receptacles very fused at the bases. Nine species from Brazil, Bolivia, Colombia, Guyana, Panamá, and Venezuela (Fukushima et al. 2005; Perdomo et al. 2009; Gabriel 2011; Fonseca-Ferreira et al. 2017).

Hapalotremus Simon 1903. Male palpal bulb with embolus long, strongly curved, but not twisted, prolateral inferior keel curved, long, and not divided. Females with single spermathecae subrectangular, without membranose base. Nine species from Argentina, Bolivia, and Peru (Cavallo and Ferretti 2015; Ferretti et al. 2018).

Kochiana Koch 1842. Males with palpal bulb with long and narrow embolus twisted, pointing downward, prolateral accessory keel present. Females with horn shaped spermathecae with large granules. One species from Brazil (Fukushima et al. 2008)*.

Magnacarina Mendoza, Locht, Kaderka, Medina and Pérez-Miles 2016. Males with tri-branched tibial apophysis on leg I, bifid palpal bulb, and retrolateral nodule on metatarsus I with a field of megaspines. Females with low semicircular single spermathecae. Four species, endemic from Mexico (Mendoza et al. 2016).

Munduruku Miglio, Bonaldo and Pérez-Miles 2013. Abdomen laterally patterned with zig-zag light marks in both sexes. Male palpal bulb with prolateral superior, inferior, and subapical keels. Female spermathecae with two spheroid distal receptacles, with a straight funnel-shaped neck bearing a sclerotized area. One species from Brazil (Miglio et al. 2013)*.

Plesiopelma Pocock 1901. Males of most species have a small subapical tooth on the palpal bulb and a retrolateral basal nodule on metatarsus I. Females are characterized by the spiral-shaped spermathecae. Eleven species from Argentina, Brazil, Paraguay, Uruguay, and Venezuela (Ferretti and Barneche 2013).

Schizopelma F.O. Pickard Cambridge 1897. Males are characterized by the palpal bulb with bifid embolus and extended prolateral superior and subapical keels. Females with single semicircular spermathecae. Two species from Mexico and Central America (Gabriel 2016; Ortiz et al. 2018).

Thrixopelma Schmidt 1994. Teeth present on tarsal claws (usually seven large teeth). Males with palpal bulb subconical. Females with two sacular spermathecae. Some species have type IV urticating setae with few barbs. Five species from Chile and Peru (Schmidt 1994a, b; Peters 2005).

Group III (Fig. 5.7)

Without abdominal pattern in adults (except some *Neischnocolus* and *Neostenotarsus*). Male tibial apophysis variable: absent, with one branch or with two branches. Male metatarsi without retrolateral nodule, nor basal process. Femur IV usually with retrolateral scopulae. Type I urticating setae present (except *Theraphosa*); type III present (with some secondary losses). Type IV urticating setae absent. Some genera have coxal and trochanteral stridulating setae. Male palpal bulb highly variable, usually broad and/or spatulate with numerous keels. Spermathecae also variable, fused or twin receptacles with based fused or not.

Comprises: *Acanthoscurria*, *Acentropelma*, *Aphonopelma*, *Brachypelma*, *Citharacanthus*, *Clavopelma*, *Cotztetlana*, *Crassicrus*, *Cubanana*, *Cyclosternum*, *Cyrtopholis*, *Eupalaestrus*, *Eurypelmella*, *Lasiodora*, *Lasiodorides*, *Longilyra*,

Fig. 5.7 Representatives of Theraphosinae Group III. (**a**) *Aphonopelma mooreae*. (**b**) *Phormictopus* sp. (**c**) *Pamphobeteus* sp. (**d**) *Brachypelma albiceps*. (Photos **a**, **b**, **d**: R. West)

Megaphobema, *Mygalarachne*, *Metriopelma*, *Miaschistopus*, *Neischnocolus*, *Neostenotarsus*, *Nesipelma*, *Nhandu*, *Pamphobeteus*, *Phormictopus*, *Proshapalopus*, *Pseudhapalopus*, *Pterinopelma*, *Reversopelma*, *Sericopelma*, *Sphaerobothria*, *Stichoplastoris*, *Theraphosa*, *Tliltocatl*, *Vitalius*, and *Xenesthis*.

Acanthoscurria Ausserer, 1871. The genus is characterized by the presence of few stridulatory setae on retrolateral face of the palpal trochanter and prolateral face of trochanter I (except *A. sacsayhuaman*). Some species can reach a large size. Males have palpal bulb with wide embolus and in some species very developed keels (PI) and a nodule on retrolateral face of palpal tibia. Tibial apophysis constituted by one branch. Females have two sub-spherical or secular spermathecae. Twenty-seven species from Central and South-America (Schiapelli and G. de Pikelin 1964; Lucas et al. 2010; Rodríguez-Manzanilla and Bertani 2010; Gonzalez-Filho et al. 2012; Paula et al. 2014; Ferretti et al. 2016).

Acentropelma Pocock 1901. Stridulatory setae present on retrolateral face of palpal trochanter and in prolateral face of trochanter I and femur I. Males with palpal bulb not twisted with two prolateral keels. Females with two spermathecae with short neck and sub-spherical fundus. Four species from Belize, Guatemala, and Mexico (Gabriel 2016).

Aphonopelma Pocock 1901. Only type I urticating setae present in both sexes. Hair-like, spiniform, or plumose setae on retrolateral face of palpal trochanter and prolateral face of trochanter I. Absence of stridulatory setae. Setae on the prolateral surface of coxa I hair-like and not basally swollen, spiniform and basally swollen, or distinctly stout and thorn-like. Scopulae divided on tarsi IV. Males with lower process of tibial apophysis curving prolaterodistally and widening apically, with apical or subapical megaspine; upper branch stout and shorter, with an inner megaspine. Fifty-nine species from Mexico, United States, and Central America (Hamilton et al. 2016; Hendrixson 2019; Sherwood 2019). Turner et al. (2018) proposed that *Aphonopelma* is polyphyletic and includes four different lineages.

Brachypelma Simon 1891. Differs from all other known Theraphosinae genera (except the genus *Tliltocatl*) having just claviform stridulating setae on the prolateral face of leg I trochanter/femur and on the retrolateral face trochanter of the palp. Male palpal bulb distally wide and flattened (spoon-shaped) and presents prolateral superior and apical keels and can have a small or reduced prolateral inferior keel. Females can have a divided spermatheca with each lobe as large as wide or a simple undivided/fused spermatheca; spermatheca baseplate divided and sclerotized. Absence of plumose pad of setae on leg IV femur in both sexes. *Brachypelma* differs from *Tliltocatl* by the red/orange coloration pattern on legs and/or carapace (except *B. albiceps*) and in the morphology of genitalia in both sexes. Eight species endemics from Mexico (Longhorn 2001; Mendoza and Francke 2017, 2019; Turner et al. 2018).

Citharacanthus Pocock 1901. Urticating setae I and III (see Chap. 9), type I simple or with longer area b (similar to *Neischnocolus*) in both sexes. Spiniform or clavated setae on palpal and leg coxae. Male palpal bulb piriform with apically serrated prolateral inferior keel, tibial apophysis with two branches. Female with two subspherical spermathecae. Nine species from Mexico and Central America (Reichling and West 2000; Estrada-Alvarez et al. 2013).

Clavopelma Chamberlin 1940. Spatulate lanciform setae on retrolateral face of palpal trochanter and prolateral face of trochanter I. Male palpal bulb with straight narrow embolus. Females have twin spermathecae with wide basis, narrow neck, and subspherical fundus. One species from Mexico (Prentice 1997; Schmidt 1998).*

Cotztetlana Mendoza 2012. The genus is characterized by the incrassate barrel-shaped tibia IV. Type I urticating setae present. Absence of scopulae on metatarsus IV. Metatarsus and tarsus IV wide and strong. Females with two spermathecae with lobular receptacles a constriction at the neck and separated basis. Two species endemic from Mexico (Mendoza 2012; Estrada-Alvarez 2014).

Crassicrus Reichling and West 1996. Only type I urticating setae. Presence of cuneiform thorn-like setae on prolateral face of leg coxae, thicker near the ventral region. Male palpal bulb with proventral face of subapical region of embolus convex. Several keels present: prolateral superior, prolateral inferior, subapical (serrated), apical, retrolateral superior, retrolateral median, and retrolateral inferior. Females have spiniform setae on the ventral and proventral surfaces of leg femora II–IV and two spermathecae partially fused by a heavily sclerotized median region. Tibia IV can be slightly or very incrassate. Five species from Belize and Mexico (Candia-Ramírez and Francke 2017).

Cubanana Ortíz 2008. Retrolateral face of femora IV covered by a pad of ciliate hairs. Absence of stridulatory setae. Male palpal bulb with smooth apical and prolateral inferior keels and serrated subapical keel. Male palpal tibiae with retrolateral nodule. Tibial apophysis with two branches on a common base. Females with twin spermathecae with fundus subspherical, neck marked, and wide separated basis. One species endemic from Cuba (Ortiz 2008)*.

Cyclosternum Ausserer 1871. Tarsal scopulae divided in both sexes. Male palpal bulb not twisted with prolateral superior and inferior keels slightly developed. Female with two spermathecae with a short neck and sub-spherical fundus. Eleven species from Bolivia, Brazil, Colombia, Costa Rica, Ecuador, Mexico, Paraguay, and Venezuela (Pérez-Miles et al. 1996; Gabriel 2016). This genus is probably not monophyletic.*

Cyrtopholis Simon, 1892. Stridulatory setae on retrolateral trochanter of palp and prolateral trochanter of leg I in combination with the presence of retrolateral nodule on male palpal tibia. Female with two spermathecae with base wider than sub-spherical fundus, median-sized neck narrowing apically. Twenty-four species from Antilles and South America (Pérez-Miles et al. 1996).

Eupalaestrus Pocock, 1901. Tibia IV thickened. Male palpal bulb with retrolateral serrated keel and an embolus slightly flattened. Females with two spermathecae, receptacles low, with base and fundus of similar size, fundus sub-spheric. Five species from Argentina, Brazil, Guyana, Paraguay, and Uruguay (Pérez-Miles 1992; Pérez-Miles et al. 1996, Bertani 2001; Ferretti and Barneche 2012).

Eurypelmella Strand 1907. Male palpal bulb piriform with a strongly curved at the subapical region, two tibial apophysis. Female unknown. One species from Guatemala (Gabriel 2016). This genus was restored by Gabriel (2016) based on the differences with *Schizopelma* found in the original description of Strand (1907) but the types were destroyed in the Second World War.*

Lasiodora Koch 1850. Stridulatory setae on prolateral face of coxae I and II. Male palpal bulb with a subapical triangular keel. Female with two sub-spheric spermathecae separated by a weakly sclerotized area. Thirty-three species from Argentina, Bolivia, Brazil, Costa Rica, and Uruguay. Localities out of Brazil are doubtful (Bertani 2001).

Lasiodorides Schmidt and Bischoff 1997. Resembles *Lasiodora* but differs from it in the absence of stridulatory setae and of retrolateral scopulae on femur IV. Four species from Ecuador and Peru (Schmidt and Bischoff 1997; Peters 2000).*

Longilyra Gabriel 2014. Small tarantulas characterized by the presence of few long club-shaped stridulatory setae on retrolateral face of palpal trochanter and prolateral face of trochanter I. Female spermathecae with a sub-rectangular fused base and two apical lateral sub-spherical receptacula (fundus). Male unknown. One species from El Salvador (Gabriel 2014)*.

Megaphobema Pocock 1901. Large-sized tarantulas. Males palpal bulb with very wide concave–convex embolus with prolateral superior and inferior keels, and apical and prolateral accessory keels. Females have one spermathecal receptacle transversely striated. Five species from Brazil, Ecuador, Colombia, and Costa Rica (Pérez-Miles et al. 2006).

Mygalarachne Ausserer 1871. Females with a single sub-rectangular spermathecae medially notched. Types I and III urticating setae present. Absence of stridulatory setae. Male unknown. One species from Honduras (Gabriel and Longhorn 2011).*

Metriopelma Becker 1878. Absence of tibial apophysis. Palpal bulb lacking a tegular heel. Prolateral superior, prolateral inferior, apical, subapical, retrolateral superior, retrolateral inferior and retrolateral accesory keels present and weakly developed. Subapical keel serrate. Female unknown. One species from Mexico (Gabriel 2016)*.

Miachistopus Pocock 1897. Male palpal bulb strongly subquadrate with a very well developed subapical keel placed from the base of the bulb to the apical keel. Female unknown. One species from Venezuela (Gabriel 2016)*.

Neischnocolus Petrunkevitch 1925. The genus is characterized by the presence of modified urticating setae type I with long area b (median zone without barbs, see Chap. 9). Males with one or two conical processes on retrolateral palpal tibia. Females differ from those of all other theraphosines by their spermathecae with paired ventral receptacles attached to a semicircular, sclerotized back-plate or a single notched receptaculum. Eight species from Brazil, Colombia, Costa Rica, Ecuador, Panama, Peru, and Venezuela (Pérez-Miles et al. 2008, 2019; Kaderka 2014; Lapinski et al. 2018).

Neostenotarsus Pribik and Weinmann 2004. Resembles *Aphonopelma* but differs by the presence of types I and III urticating setae, procurved fovea and male palpal bulb distally widened. Basal-ventral nodule on metatarsus I. Female with single spermathecae, widely fused at the base with two sub-spherical lateral apical cameras (fundi). One species from French Guiana (Tesmoingt and Schmidt 2002).*

Nesipelma Schmidt and Kovarik 1996. Resembles *Acanthoscurria* by the presence of stridulatory setae on retrolateral face of palpal trochanter and prolateral trochanter I. Male differs from this genus by the palpal bulb with embolus narrower and acuminate, and tibial apophysis with two branches. Female with two separated sacular spermathecae. One species from St. Kitts and Nevis (Schmidt and Kovařík 1996).*

Nhandu Lucas 1983. Male palpal bulb with triangular subapical keel and absence of accessory keel. Tibial apophysis absent or if present two parallel branches on a common base, the retrolateral branch constricted in the middle. Females with retrolateral scopulae on femur IV, two spermathecal receptacles separated by a hard sclerotized short area. Long curly hairs over the carapace. Five species from Brazil and Paraguay (Bertani 2001).

Pamphobeteus Pocock, 1901. Male palpal bulb with broad embolus and slightly developed apical keel, prolateral inferior keel and retrolateral keel of similar length to apical, and usually a prolateral accessory keel present. Prolateral superior and retrolateral keels well developed. Females have spermathecae with a wide base and very short seminal oval receptacles, usually curved toward the center. Thirteen species from Bolivia, Brazil, Colombia, Ecuador, Panama, and Peru (Bertani et al. 2008; Cifuentes et al. 2016).

Phormictopus Pocock 1901. Plumose bristles on coxae and trochanters in both sexes. Male palpal tibiae with a retrolateral nodule, a tegumentary prominence and ventral subapical zone of tibiae of legs I with two branched spurs. Retrolateral face of legs IV covered by a scopulae of plumose setae. Fifteen species from Argentina, Brazil, Cuba, Hispaniola, Caribbean region (Ortiz and Bertani 2005).

Proshapalopus Mello-Leitao 1923. Male palpal bulb with an accessory keel present under the prolateral inferior keel. Females can be distinguished by having a thickened tibia IV together with absence of type III urticating setae (*Proshapalopus amazonicus* Bertani, 2001); or type I urticating setae with the region "a" shorter than the region "b." Four species from Brazil and Colombia (Bertani 2001; Perafán and Valencia-Cuéllar 2018).

Pseudhapalopus Strand 1907. Male palpal tibia very spinose on prolateral and dorsal faces. Palpal bulb short and wide, subconical, with prolateral superior and inferior keels present. Females with two separated spermathecal receptacles, tubular, sinuous and divergent or sacular. Type I urticating setae present. Five species from Bolivia, Colombia, Ecuador, and Trinidad (Schmidt and Weinmann 1997; Gabriel 2016).

Pterinopelma Pocock 1901. Resembles *Lasiodora*, *Vitalius*, and *Nhandu*, by the absence of accessory prolateral keels and presence of prolateral superior, prolateral inferior, retrolateral and apical keels in palpal bulb. Prolateral inferior keel with denticles and subapical keel weak or absent. Females differ from those genera by the spermathecae short, separated by a heavily sclerotized short area and absence of long setae on carapace. Both sexes are distinguished from those of *Lasiodora* by the absence of stridulatory setae on the prolateral coxae. Three species from Brazil (Bertani et al. 2011).

Reversopelma Schmidt 2001. Differs from other genera in the modification of type I urticating setae having barbs apically directed on the base of the setae, basally directed in the median region and apically directed in the subapically zone. One species from Ecuador or Peru (Schmidt 2001)*.

Sericopelma Ausserer, 1875. Absence of stridulatory setae on trochanter I. Male without tibial apophysis, palpal bulb with spoon shaped distal region, prolateral superior and apical keels fused in the apex of the embolus. Female with single spermathecae swollen at the apex forming a P-shaped cross-section. Dense scopulae of plumose setae present on retrolateral femur of leg IV. Fourteen species from Brazil, Central America (Costa Rica, Panama), and Mexico (Gabriel and Longhorn 2015; Andre and Esche 2011; Gabriel 2016).

Sphaerobothria Karsch 1879. Differs from other genera in the presence of a prominent spheroid tegumentary protuberanceon the fovea. One species from Costa Rica and Panama (Valerio 1980)*.

Stichoplastoris Rudloff 1997. Male palpal bulb with tegulum and subtegulum wide, embolus short, prolateral superior, and inferior keels presents, two tibial apophysis convergent and fused in the base. Female with two sacular/tubular spermathecae weakly fused at their base. Eight species from Costa Rica, El Salvador, and Panama (Rudloff 1997; Valerio 1980).*

Theraphosa Thorell 1870. Very large tarantulas characterized by the presence of stridulatory setae on prolateral coxae I and II. Type III urticating setae short and type I absent. Males with or without tibial apophysis, palpal bulb sub-cylindrical, concave–convex with apical keel completely fused with prolateral superior keel. Females with fused sclerotized spermathecae. Three species from Brazil, Colombia, Guyana, and Venezuela (Bertani 2001; Almeida et al. 2018).

Tliltocatl Mendoza and Francke 2019. Differs from all other Theraphosinae genera (except *Brachypelma*) having claviform stridulating setae on the prolateral face of trochanter/femur I and retrolateral face trochanter of the palp. Male palpal bulb distally wide and flattened (spoon-shaped) with prolateral superior and apical keels united at the apex, prolateral superior, and prolateral inferior keels are joined at their distal end and widely separating toward the embolus base, the apical keel can extend widely to backward just as the prolateral inferior keel. Females have a single fused spermatheca, apically narrowed, spermathecal baseplate absent or slightly developed. Plumose pad of setae on femur of legs IV absent. Differs from *Brachypelma* by the coloration of legs, which are black or have long, whitish setae and by the morphology of genitalia. Seven species from Mexico, Guatemala, Belize, Honduras, El Salvador, Nicaragua, and Costa Rica (Mendoza and Francke 2019).

Vitalius Lucas, Silva and Bertani 1993. Characterized by the absence of stridulatory setae on the superior region of coxae I and II in both sexes. Many long curly scattered setae on carapace. Male palpal bulb with triangular subapical keel present, accessory keel absent. Two tibial apophysis present, metatarsus closing over the tibial apophysis, between the branches. Females with two spermathecae separated by a heavily sclerotized short area. Ten species from Argentina and Brazil (Bertani 2001; Ferretti et al. 2015).

Xenesthis Simon 1891. Large tarantulas without stridulatory setae. Male palpal bulb spoon shaped with prolateral superior and apical keels fused at the apex of the embolus. Two unequal tibial apophysis and metatarsus closing between branches. Females with two spermathecae widely fused in the base with spheric apical cameras. Metatarsal scopulae on leg IV entire. Three species from Colombia, Panama, and Venezuela (Schiapelli and Gerschman 1979; Pérez-Miles et al. 1996).

Group IV: Incertae Sedis (Fig. 5.8)

Hemirrhagus Simon 1903. Characterized by retrolateral projections (heels) on ventral face of coxae of all legs. Type VI urticating setae arranged in one dorsomedian patch, two dorsal paramedian or lateral patches, or two lateral patches (excepting the troglobite species). Male palpal bulb with a slender embolus (except *H. embolulatus*). Subapical keel extended posteriorly and retrolaterally, a ventral grove presents between the tegulum and the embolus. Females with spermathecae paired, unilobular, which can be completely separated (most of the troglobitic species) or fused at their base (epigean species). Twenty-seven species endemic from Mexico (Mendoza 2014; Mendoza and Francke 2018).

Kankuamo Perafán, Galvis and Pérez-Miles 2016. The genus is characterized by having a distinct type of urticating setae type (VII), similar to type II but having a small distal patch of lanceolated barbs arranged in reversed direction, regarding the main barbs, oriented with their tips toward the penetration tip. Males have a curved sub-conical palpal bulb with many conspicuous keels distributed throughout the majority of the subtegulum and embolus, especially developed on the dorsal and

Fig. 5.8 Representatives of Theraphosinae Group IV. (**a**) *Hemirrhagus benzaa*. (**b**) *Kankuamo marquezi*. (Photo **a**: J. Mendoza)

prolateral faces, most of them with serrated edges. Tibial apophysis absent. Females have a spermathecae with a single notched receptacle, with two granulated lobes, and several irregular sclerotized longitudinal striations. One species from Colombia (Perafán et al. 2016)*.

Ozopactus Simon 1889. Resembles *Crypsidromus* but differs by the sternum convex and more spinose legs. Anterior and posterior lateral eyes subequal. One species from Venezuela (Simon 1889, 1892).*

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