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All genera of the world: Order Thelyphonida (Animalia: Arthropoda: Arachnida)

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Abstract

Thirty-six genus-group names are available in the arachnid Order Thelyphonida Latreille, 1804 by the end of 2025. Thirty of these refer to currently accepted genera: 20 extant and ten extinct. Six genus-group names are in synonymy. Eighteen (60%) of the currently accepted genera were described since 1950. Thelyphonida includes 138 currently accepted species-group names (123 extant species, including three extant subspecies elevated to the rank of species herein, and 15 extinct species) and a *nomen dubium*. The phylogeny and suprageneric classification of the order remain poorly understood and several subfamilies appear to be paraphyletic. The systematics of Asian thelyphonids lags far behind that of New World thelyphonids.

Key words: Uropygi, Thelyphonidae, Hypoconinae, Mastigoproctinae, Thelyphoninae, Typopeltinae, generic names, synonyms, type species, thelyphonids, vinegaroons, whip scorpions

Introduction

Thelyphonids, also known as whip scorpions or vinegaroons (also spelled vinegarroons or vinegarones), are large (usually 25–30 mm in length, although some may reach 85 mm), impressive arachnids that superficially resemble true scorpions (*Scorpiones* C.L. Koch, 1850). They possess two body-segments, prosoma and segmented opisthosoma, connected by a narrow pedicel (the first opisthosomal segment). The prosoma comprises a carapace that is longer than wide, with one pair of eyes anteromedially and two smaller triads anterolaterally; two-segmented chelicerae; robust, spinose raptorial pedipalps; and a sensory, antenniform first pair of legs with a multisegmented tarsus (the ‘whips’) (Weygoldt & Paulus, 1979; Shultz, 1990, 2007; Coddington *et al.*, 2004). The opisthosoma possesses two pairs of book lungs and, unlike whip spiders (or tailless whip scorpions), the last three segments of the opisthosoma are constricted, forming a pygidium that terminates in a long, multisegmented flagellum (Harvey, 2003). Together with short-tailed whip scorpions (*Schizomida* Petrunkevitch, 1945), thelyphonids form the group Uropygi Thorell,

1883, united by the presence of pygidial glands, fused pedipalpal coxae, and elongated patellae of the first pair of legs (Weygoldt & Paulus, 1979; Shultz, 1990, 2007; Garwood & Dunlop, 2014; Ruiz & Valente, 2017). As the vernacular name suggests, vinegaroons produce noxious secretions, including acetic acid, capronic (hexanoic) acid, and caprylic (octanoic) acid, in abdominal glands, which can be sprayed from openings at the base of the pygidial flagellum, for chemical defense (Eisner *et al.*, 1961; Yogi & Haupt, 1977; Itokawa *et al.*, 1981, 1985; Haupt *et al.*, 1988, 1993; Schmidt *et al.*, 2000; Haupt & Müller, 2004). They lack venom and silk glands.

The presence of several fossil genera from the Late Carboniferous (Dunlop & Horrocks, 1996; Dunlop & Penney, 2012; Garwood & Dunlop, 2014) demonstrates the great antiquity of the whip scorpion lineage, over 300 Mya in which their body plan has barely changed. Living thelyphonids occur in the New World (on the Florida Peninsula, the Caribbean islands of Cuba and Hispaniola, and from the U.S. states of Arizona and Texas, southward through Mexico and Central America to Brazil), South Asia (India and Sri Lanka), East and Southeast Asia (including Japan and southern China, the islands of Hainan and Taiwan, across the Thai-Malay Peninsula, the Philippines and the Indonesian archipelago as far as Wallace’s Line) (Harvey, 2003). Various thelyphonid taxa are restricted to Asia, the New World, or the remnants of Gondwana. A single genus occurs on the African continent (Huff & Prendini, 2009), where it has been recorded from six countries. Whip scorpions are absent from many major landmasses, e.g., Antarctica, Australia, Europe, and islands, e.g., Greenland, Iceland, Madagascar, and New Zealand. Although most diverse in humid tropical or subtropical ecosystems, especially forests, some whip scorpions, e.g., *Mastigoproctus* Pocock, 1894, inhabit arid to semi-arid ecosystems like savannas and deserts (Haupt, 2000; McMonigle, 2013). Most are epigean, hiding by day in deep burrows in the soil, under stones or in rock crevices (Punzo, 2006; Hembree, 2013; McMonigle, 2013).

Whip scorpions are carnivorous, nocturnal hunters which feed mostly on other terrestrial arthropods, as well as annelid worms and slugs (Carrel & Britt, 2009). Larger species occasionally prey on small vertebrates. Like the related amblypygids and schizomids, only six legs are

used for walking. Prey is detected by the antenniform first pair of legs, impaled by the chelicerae, and crushed by the powerful, grasping pedipalps with which it is held prior to mastication and ingestion. Whip scorpions can endure several months without food, especially prior to molting. They are important in ecological food webs, for controlling insect populations and as prey for various other predators, vertebrate and invertebrate (McMonigle, 2013).

What little is known about the biology and behavior of thelyphonids suggest that, in some respects, they are K-selected, resembling vertebrates in their life history traits (Haupt, 2000; McMonigle, 2013). Reproduction is indirect, intromission occurring via a spermatophore (Weygoldt, 1975, 1988, 1990). Some species are sexually dimorphic, the pedipalps more elongated and possessing prominent apophyses in the adult male (Huff *et al.*, 2008; McLean *et al.*, 2018). Courtship and mating involve ritualized behavior (Klingel, 1963a, 1963b; Weygoldt, 1970, 1971, 1972, 1978). The male grasps the first legs of the female with his pedipalps and moves to face her. After depositing a spermatophore on the substrate, the male pulls the female over it, and then turns around, embraces the opisthosoma of the female, and manipulates the spermatophore into her genital opening using the pedipalpal fingers. The sperm packet is stored in the female spermathecae until fertilization. After several months, the female digs a burrow and seals herself inside. Whip scorpions are oviparous, laying up to 40 eggs in a membranous broodsac that remains attached to the genital operculum and fifth sternite of the mother's opisthosoma (Weygoldt, 1971; Haupt, 2000; McMonigle, 2013). The female fasts and holds her opisthosoma upward above the substrate for the next few months, as the eggs develop into

postembryos. Protonymphs are large at birth and altricial, climbing atop the mother's opisthosoma and clinging there with suckers until the first molt (Weygoldt & Huber, 2013), dispersing thereafter. Thelyphonids take up to four years to reach sexual maturity but continue to molt after maturity (indeterminate growth). Larger species may live 8–10 years (Weygoldt, 1971; McMonigle, 2013).

Based on their absence from disturbed or degraded habitats, whip scorpions appear to be equilibrium species. These arachnids may therefore be bioindicators of environmental health and climate change. Fairly small litter sizes and low survivorship (Weygoldt, 1971) may contribute to a low rate of population increase for many species which are also habitat-specific, potentially exacerbating their risk of extinction due to human activities. Threatened by habitat destruction and harvesting for the souvenir and exotic pet trades, no thelyphonids receive formal protection. Although none are currently listed by the Convention on International Trade in Endangered Species of Wild Fauna and Flora, several North American and Asian species are harvested and sold commercially as exotic pets in Europe and the U.S.A. (Marshall *et al.*, 2022; Herzig *et al.*, 2023).

Kraepelin (1897, 1899) presented the first comprehensive taxonomic treatments of all extant thelyphonid taxa known at the time, updated thirty years later by Werner (1934) and again by Millot (1949). Almost half a century passed before Harvey (2003) presented the first catalog of the genera and species of the order. A list of suprageneric taxa with counts of genera and species was provided by Prendini (2011). The present contribution updates species counts from the World Uropygi Catalog (2025) through the end of 2025.

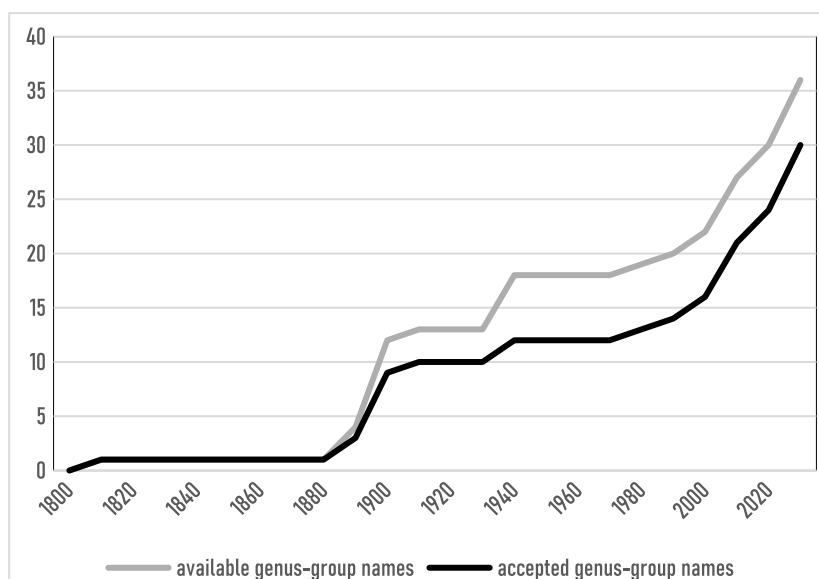


FIGURE 1. Cumulative number of available and accepted genus-group names in the arachnid Order Thelyphonida Latreille, 1804 by decade.

TABLE 1. Current classification of the Order Thelyphonida Latreille, 1804

Order Thelyphonida Latreille, 1804	
	† <i>Geralinura</i> Scudder, 1884
	† <i>Parageralinura</i> Tetlie & Dunlop, 2008
	† <i>Proschizomus</i> Dunlop & Horrocks, 1996
	† <i>Prothelyphonus</i> Frič, 1904
Superfamily Thelyphonoidea Lucas, 1835	
	† <i>Inmontibusichnus</i> Knecht, Benner, Dunlop & Renczkowski, 2023
	† <i>Parilisthelyphonus</i> Knecht, Benner, Dunlop & Renczkowski, 2023
Family Thelyphonidae Lucas, 1835	
	† <i>Burmathelyphonia</i> Wunderlich, 2015
	† <i>Mesoproctus</i> Dunlop, 1998
	† <i>Crethypoctonus</i> Zhou, Wang, Jarzembowski & Xiao, 2024
Subfamily Hypoctoninae Pocock, 1899	
	<i>Etiennus</i> Heurtault, 1984
	<i>Hypoctonus</i> Thorell, 1888
	<i>Labochirus</i> Pocock, 1894
	<i>Ravilops</i> Viquez & Armas, 2005
	<i>Thelyphonellus</i> Pocock, 1894
	<i>Wounaan</i> Botero-Trujillo, Moreno-González & Prendini, 2024
	<i>Yekuana</i> Botero-Trujillo, Moreno-González & Prendini, 2024
Subfamily Mastigoproctinae Speijer, 1933a	
	<i>Amauromastigon</i> Mello-Leitão, 1931
	<i>Heptatarsus</i> Castro-Pereira & Pinto-da-Rocha, 2025
	<i>Mastigoproctus</i> Pocock, 1894
	<i>Mayacentrum</i> Viquez & Armas, 2006
	<i>Mimoscorpis</i> Pocock, 1894
	<i>Sheylayongium</i> Teruel, 2018
	<i>Uroproctus</i> Pocock, 1894
	<i>Valeriphonus</i> Viquez & Armas, 2005
Subfamily Thelyphoninae Lucas, 1835	
	<i>Ginosigma</i> Speijer, 1933a
	<i>Glyptogluteus</i> Rowland, 1973
	† <i>Mesothelyphonus</i> Cai & Huang, 2017
	<i>Thelyphonoides</i> Krehenwinkel, Curio, Tacud & Haupt, 2009
	<i>Thelyphonus</i> Latreille, 1802
Subfamily Typopeltinae Rowland & Cooke, 1973	
	<i>Typopeltis</i> Pocock, 1894

The Order Thelyphonida Latreille, 1804¹ currently comprises a single superfamily, Thelyphonoidea Lucas, 1835 and four extinct genera *incertae sedis* (Table 1). Recent genera (20 extant, two extinct) are accommodated within a single family, Thelyphonidae Lucas, 1835, and two extinct genera *incertae sedis*. Thelyphonidae comprises four subfamilies, Hypoctoninae Pocock, 1899, with seven extant genera, Mastigoproctinae Speijer, 1933a, with eight extant genera, Thelyphoninae Lucas, 1835, with four extant genera and an extinct genus, and Typopeltinae Rowland & Cooke, 1973, with an extant genus; and three extinct genera *incertae sedis*.

Thirty-six genus-group names are available in Thelyphonida by the end of 2025. Thirty of these refer to currently accepted genera, 20 extant and ten extinct. Six genus-group names are in synonymy. Eighteen (60%) of the currently accepted genera were described since 1950 (Fig. 1). The order includes 138 currently accepted species-group names (123 extant species, including three extant subspecies elevated to the rank of species herein, and 15 extinct species), and a *nomen dubium*.

Despite considerable descriptive activity on Thelyphonida, as well as a preliminary molecular phylogenetic analysis (Clouse *et al.*, 2017), the suprageneric phylogeny and classification of the order remain poorly understood. Several subfamilies appear to be paraphyletic and many genera are monotypic or narrowly defined. The systematics of Asian thelyphonids lags far behind that of New World thelyphonids.

1 Following Prendini (2011), the earlier name, Thelyphonida Latreille, 1804, is applied to this order, rather than Uropygi Thorell, 1883, as recommended by CIDA (1996: 5):

During the general meeting was put forward by the Arachnology Nomenclature Committee under chairmanship of Norman Platnick to adopt a standardised list of arachnid ordinal names. The proposal was accepted. The recommended ordinal names are as pro[p]osed by Savory (1972): On the names of the orders of Arachnida. Systematics [*sic*] Zoology 21: 122–125 and would most closely conform to the principle of “current usage”. CIDA [Centre International de Documentation Arachnologique] therefore actively promotes the use of the following ordinal names: AMBLYPYGI, ARANEAE, OPILIONES, PALPIGRADI, PSEUDOSCORPIONES, RICINULEI, SCHIZOMIDA, SCORPIONES, SOLIFUGAE, UROPYGI.

Although adopted by Harvey (2003, 2013) and the World Uropygi Catalog (2025), CIDA’s (1996) recommendation to use Uropygi has not been universally accepted. In addition to the nomenclatural priority of Thelyphonida, Uropygi more precisely refers to the monophyletic group comprising Thelyphonida and Schizomida Petrunkevitch, 1945 (Weygoldt & Paulus, 1979; Shultz, 1990, 2007; Garwood & Dunlop, 2014; Ruiz & Valente, 2017) and, as noted by Harvey (2003: 60), use of the name Uropygi for the order “leaves the clade “Uropygi + Schizomida without a name”. The name Thelyphonida does not refer to Uropygi + Schizomida, as suggested by Clouse *et al.* (2017).

Acknowledgements

This list was developed from the World Uropygi Catalog (<https://wac.nmbe.ch/order/uropygi/7>), in turn based on the catalogs of Harvey (2003, 2013; <http://www.museum.wa.gov.au/catalogues/whip-scorpions>) and the list of fossil spiders and their relatives by Dunlop *et al.* (2023). The Biodiversity Heritage Library (<https://www.biodiversitylibrary.org>), the Global Biodiversity Information Facility (GBIF) (<https://www.gbif.org>), the Interim Register of Nonmarine and Marine Genera (<https://www.irmng.org>), and the Paleobiology Database (Uhen *et al.*, 2023; <https://paleobiodb.org>) were also consulted. The author's research on minor arachnid orders was supported by grants EAR 0228699, DEB 0640219, and DEB 2003382, from the National Science Foundation, U.S.A. The author thanks Zhi-Qiang Zhang for the invitation to submit this contribution, and Jairo Moreno-González, George Popovici and two anonymous reviewers for comments on earlier drafts of the manuscript.

Order **Thelyphonida** Latreille, 1804

(1 extant superfamily, 4 extinct genera *incertae sedis*)

Incertae sedis

- †**Geralinura** Scudder, 1884 [2 extinct species]. Type species: †*Geralinura carbonaria* Scudder, 1884, by monotypy.
- †**Parageralinura** Tetlie & Dunlop, 2008 [3 extinct species]. Type species: *Prothelyphonus naufragus* Brauckmann & Koch, 1983, by original designation.
- †**Proschizomus** Dunlop & Horrocks, 1996 [1 extinct species]. Type species: †*Proschizomus petrunkevitchi* Dunlop & Horrocks, 1996, by original designation.
- †**Prothelyphonus** Frič, 1904 [1 extinct species]. Type species: *Thelyphonus bohemicus* Kušta, 1884 = †*Prothelyphonus bohemicus* (Kušta, 1884), by subsequent designation (Pocock, 1911).

Superfamily **Thelyphonoidea** Lucas, 1835
(1 extant family, 2 extinct genera *incertae sedis*)

Incertae sedis

- †**Inmontibusichnus** Knecht, Benner, Dunlop & Renczkowski, 2023 [1 extinct species]. Type species: *Inmontibusichnus charleshenryturneri* Knecht, Benner, Dunlop & Renczkowski, 2023, by monotypy.
- †**Parilisthelyphonus** Knecht, Benner, Dunlop & Renczkowski, 2023 [1 extinct species]. Type species: *Parilisthelyphonus bryantae* Knecht, Benner, Dunlop & Renczkowski, 2023, by monotypy.

Family **Thelyphonidae** Lucas, 1835
(4 extant subfamilies, 3 extinct genera *incertae sedis*)

Incertae sedis

- †**Burmathelyphonia** Wunderlich, 2015 [1 extinct species]. Type species: *Burmathelyphonia prima* Wunderlich, 2015, by original designation.
- †**Mesoproctus** Dunlop, 1998 [2 extinct species]. Type species: †*Mesoproctus rowlandi* Dunlop, 1998, by original designation.
- †**Crethypoctonus** Zhou, Wang, Jarzembowski & Xiao, 2024 [1 extinct species]. Type species: †*Crethypoctonus kachinus* Zhou, Wang, Jarzembowski & Xiao, 2024, by original designation.

Subfamily **Hypoctoninae** Pocock, 1899
(7 extant genera)

- Etiennus** Heurtault, 1984 [1 extant species]. Type species: *Hypoctonus africanus* Hentschel, 1899 = *Etiennus africanus* (Hentschel, 1899), by original designation.
- Hypoctonus** Thorell, 1888 [20 extant species]. Type species: *Thelyphonus formosus* Butler, 1872 = *Hypoctonus formosus* (Butler, 1872), by original designation. [One subspecies is hereby returned to its former rank of species (Appendix 1).]
- Labochirus** Pocock, 1894 [3 extant species, 1 *nomen nudum*]. Type species: *Thelyphonus proboscideus* Butler, 1872 = *Labochirus proboscideus* (Butler, 1872), by original designation.
- Ravilops** Viquez & Armas, 2005 [2 extant species]. Type species: *Thelyphonellus wetherbeeii* Armas, 2002 = *Ravilops wetherbeeii* (Armas, 2002), by original designation.

Thelyphonellus Pocock, 1894 [3 extant species]. Type species: *Thelyphonus amazonicus* Butler, 1872, by original designation.

Wounaan Botero-Trujillo, Moreno-González & Prendini, 2024 [2 extant species]. Type species: *Thelyphonellus vanegasae* Giupponi & Vasconcelos, 2008 = *Wounaan vanegasae* (Giupponi and Vasconcelos, 2008), by original designation.

Yekuana Botero-Trujillo, Moreno-González & Prendini, 2024 [1 extant species]. Type species: *Yekuana wanadi* Botero-Trujillo, Moreno-González & Prendini, 2024, by monotypy.

Subfamily **Mastigoproctinae** Speijer, 1933a
(8 extant genera)

Amauromastigon Mello-Leitão, 1931 [1 extant species].

Type species: *Mastigoproctus annectens* Werner, 1916 = *Auromastigon maximus* (Tarnani, 1889), by monotypy.

Heptatarsus Castro-Pereira & Pinto-da-Rocha, 2025 [2 extant species]. Type species: *Thelyphonus brasiliensis* C.L. Koch, 1843 = *Heptatarsus brasiliensis* (C.L. Koch, 1843), by original designation.

Mastigoproctus Pocock, 1894 [17 extant species]. Type species: *Thelyphonus giganteus* Lucas, 1835 = *Mastigoproctus giganteus* (Lucas, 1835), by original designation.

Mayacentrum Viquez & Armas, 2006 [3 extant species]. Type species: *Mastigoproctus tantalus* Roewer, 1954 = *Mayacentrum tantalus* (Roewer, 1954), by original designation.

Mimoscorpis Pocock, 1894 [1 extant species]. Type species: *Thelyphonus pugnator* Butler, 1872 = *Mimoscorpis pugnator* (Butler, 1872), by original designation.

Sheylayongium Teruel, 2018 [1 extant species]. Type species: *Mastigoproctus pelegri* Armas, 2000 = *Sheylayongium pelegri* (Armas, 2000), by monotypy.

Uroproctus Pocock, 1894 [1 extant species]. Type species: *Thelyphonus assamensis* Stoliczka, 1869 = *Uroproctus assamensis* (Stoliczka, 1869), by original designation.

Valeriophonus Viquez & Armas, 2005 [1 extant species]. Type species: *Mastigoproctus nara* Valerio, 1981 = *Valeriophonus nara* (Valerio, 1981), by original designation.

Subfamily **Thelyphoninae** Lucas, 1835
(4 extant genera, 1 extinct genus)

Ginosigma Speijer, 1933a [*nomen nudum*]; Speijer, 1936 [2 extant species]. Type species: *Thelyphonus schimkewitschi* Tarnani, 1894 = *Ginosigma schimkewitschi* (Tarnani, 1894), by subsequent designation (Rowland & Cooke, 1973).

Glyptogluteus Rowland, 1973 [1 extant species]. Type species: *Glyptogluteus augustus* Rowland, 1973, by original designation.

†**Mesothelyphonus** Cai & Huang, 2017 [2 extinct species]. Type species: †*Mesothelyphonus parvus* Cai & Huang, 2017, by monotypy.

Thelyphonoides Krehenwinkel, Curio, Tacud & Haupt, 2009 [1 extant species]. Type species: *Thelyphonoides panayensis* Krehenwinkel, Curio, Tacud & Haupt, 2009, by original designation.

Thelyphonus Latreille, 1802 [47 extant species]. Type species: *Phalangium caudatum* Linnaeus, 1758 = *Thelyphonus caudatus* (Linnaeus, 1758), by subsequent designation (Latreille, 1810). [One subspecies is hereby returned to its former rank of species and another subspecies is newly elevated to the rank of species (Appendix 1).]

Tetrabalius Thorell, 1888. Type species: *Thelyphonus seticauda* Doleschall, 1857, by original designation. Synonymized by Haupt (2009).

Abalius Kraepelin, 1897. Type species: *Abalius rohdei* Kraepelin, 1897 = *Thelyphonus rohdei* (Kraepelin, 1897), by subsequent designation (Mello-Leitão, 1931). [Junior homonym of *Abalius* Cabanis, 1861 (Aves).]

Abaliella Strand, 1928. Type species: *Abalius rohdei* Kraepelin, 1897 = *Thelyphonus rohdei* (Kraepelin, 1897), by subsequent designation (Mello-Leitão, 1931). [Replacement name for *Abalius* Kraepelin, 1897.] Synonymized by Haupt (2009).

Minbosius Speijer, 1933a [*nomen nudum*]; Speijer, 1933b [no description, but with single included species]. Type species: *Minbosius kopsteini* Speijer, 1933b, by monotypy. Synonymized by Haupt (2009).

Chajnus Speijer, 1936. Type species: *Chajnus renschi* Speijer, 1936, by monotypy. Apparently synonymized by Haupt (2009).

Subfamily **Typopeltinae** Rowland & Cooke, 1973
(1 extant genus)

Typopeltis Pocock, 1894 [13 extant species, 1 *nomen dubium*]. Type species: *Typopeltis crucifer* Pocock, 1894, by original designation.

Gipopeltis Speijer, 1934. Type species: *Typopeltis harmandi* Kraepelin, 1900, by original designation. Synonymized by Speijer (1936).

Teltus Speijer, 1936. Type species: *Teltus vanoorti* Speijer, 1936 = *Typopeltis vanoorti* (Speijer, 1936), by monotypy. Synonymized by Haupt & Song (1996).

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APPENDIX 1. New taxonomic changes in the Order Thelyphonida Latreille, 1804

Order **Thelyphonida** Latreille, 1804
Superfamily **Thelyphonoidea** Lucas, 1835
Family **Thelyphonidae** Lucas, 1835
Subfamily **Hypoctoninae** Pocock, 1899

Hypoctonus insularis (Oates, 1889), stat. rev.

Subfamily **Thelyphoninae** Lucas, 1835

Thelyphonus hosei Pocock, 1894, stat. rev.

Thelyphonus halmaheirae Kraepelin, 1897, stat. nov.