

The copocrossean jumping spiders of Eugène Simon (Araneae: Salticidae: Salticinae: Ballini: *Copocrossa*, *Ligdus*, *Mantisatta*)

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More than a century ago Simon (1901a) proposed a *group* that he called the Copocrosseae, to include spiders that were closely related to his genus *Copocrossa*. Today we tend to follow the lead of Lucien Cuénot and, later, Will Hennig, in referring to a group like this as a *clade*, with the requirement that it includes a common ancestor and all of its descendants. Here is Simon's account of the Copocrosseae, followed by an English translation:

17, COPOCROSSEAE

Les deux genres *Mantisatta* et *Copocrossa*, pour lesquels je propose ce groupe, diffèrent des précédents par leur pièce labiale aussi large que longue, atténuée et obtuse, et par leurs filières infères, cachées en dessus par l'apex de l'abdomen; leur sternum est beaucoup moins atténué que celui des *Bavia* et tronqué en avant où il sépare les hanches, au moins de la largeur de la pièce labiale, sinon plus, mais ce dernier caractère est commun aux deux genres *Piranthus* et *Stagetillus*. Leur céphalotborax, très plat, ressemble à celui des *Piranthus*, mais il est au moins aussi étroit et aussi long que celui des *Goleta*. Leurs yeux ont aussi la disposition de ceux 'les *Piranthus*; les antérieurs sont très inégaux, les médians énormes, occupent presque toute la hauteur delà face, tandis que les latéraux, très petits, sont refoulés un peu en arrière, caractère surtout bien marqué dans le *Mantisatta trucidans* Warburton, et qui a pu faire comparer cette araignée aux *Lyssomanes* avec lesquels elle n'a aucune autre analogie (fig. 544A). Leur groupe oculaire est au moins deux fois plus court que la région thoracique. Leur abdomen est étroit, long, plat ou cylindrique, parfois recouvert chez le mâle (*C. politiventris* E. Sim.) d'un scutum glabre; celui du *Mantisatta* se termine en pointe conique et un peu relevée en forme de queue (fig. 546C); celui des *Copocrossa* est un peu saillant, mais très obtus, et son tubercule anal triangulaire et biarticulé est dirigé en basel un peu en arrière (fig. 552I); dans tous les cas les filières sont infères, insérées sur un plan oblique et cachées en dessus; les inférieures sont épaisses et contiguës, les supérieures plus grêles, un peu plus longues, un peu incurvées et terminées par un très petit article subaigu, infléchi en dedans (fig. 547D). Leurs pattes ont l'armature de celles des *Piranthus*, mais à la première paire la proportion des articles n'est pas la même, car le tibia est beaucoup plus long que le fémur, convexe en dessous au milieu, mais atténué aux extrémités et armé, dans la seconde moitié, de 3 paires de courtes épines couchées, presque dentiformes, tandis que le métatarse, grêle, un peu courbé et sinueux à la base, est armé de 2 paires d'épines encore plus petites, l'une médiane, l'autre apicale, dressées dans le genre *Copocrossa* (fig. 549F), dirigées en arrière en forme de harpons dans le genre *Mantisatta* (fig. 553J). Leurs chélicères, coniques et plus courtes que la face, ont le crochet assez long et très courbé; leur marge inférieure (*Copocrossa tenuilineata* E. Sim.) est pourvue de 3 ou 4 petites dents égales et isolées. Leur pièce labiale est au moins aussi large que longue et obtuse; leurs lames sont droites chez la femelle, divergentes mais obtuses et légèrement rebordées chez le mâle (fig. 551H). La patte-mâchoire du *Copocrossa politiventris* E. Sim. (fig. 550G) est petite; son tibia, cylindrique et plus court que la patella, est armé d'une petite apophyse supéro-externe aiguë; son tarse, beaucoup plus long mais à peine plus large que le tibia, recouvre un bulbe très convexe et débordant, pourvu d'un fort stylus apical roulé en cercle. Le genre *Ligdus* Thorell, qui m'est inconnu en nature, appartient probablement à ce groupe; on pourrait même le croire identique au genre *Copocrossa* si hauteur ne lui donnait un large bandeau incliné en arrière. Le groupe se compose de quelques petites espèces, étroites, longues et déprimées, garnies, au moins en partie, de pubescence blanche simple. Le *Mantisatta trucidans* Warburton, qui a

été découvert à Sarawak (Borneo), dans un nid de Termites, a la partie céphalique marquée de taches oculaires et médianes noires et l'abdomen de petites taches brunâtres quadriseriées dont les médianes sont linéaires; le *Copocrossa (Stenodina) tenuilineata* E. Sim., originaire du Nord-Est de l'Australie, est orné de 3 fines lignes noires et près l'extrémité de l'abdomen d'une ligne transverse; le *C. politiventris* E. Sim. est de teinte foncée, glabre en dessus, garni sur les flancs de pubescence blanche; son céphalothorax est finement ponctué; son abdomen est recouvert chez le mâle d'un scutum très lisse d'un noir irisé; ses longues pattes antérieures sont en partie noires, les autres jaune pâle; M. Warburton m'a communiqué un autre *Copocrossa* (inédit) de Malaisie qui est aussi d'un noir irisé; le *Marptusa tenerrima* L. Koch, appartient probablement aussi au même genre. Le *Ligdus chelififer* Thorell, est décrit de Birmanie.

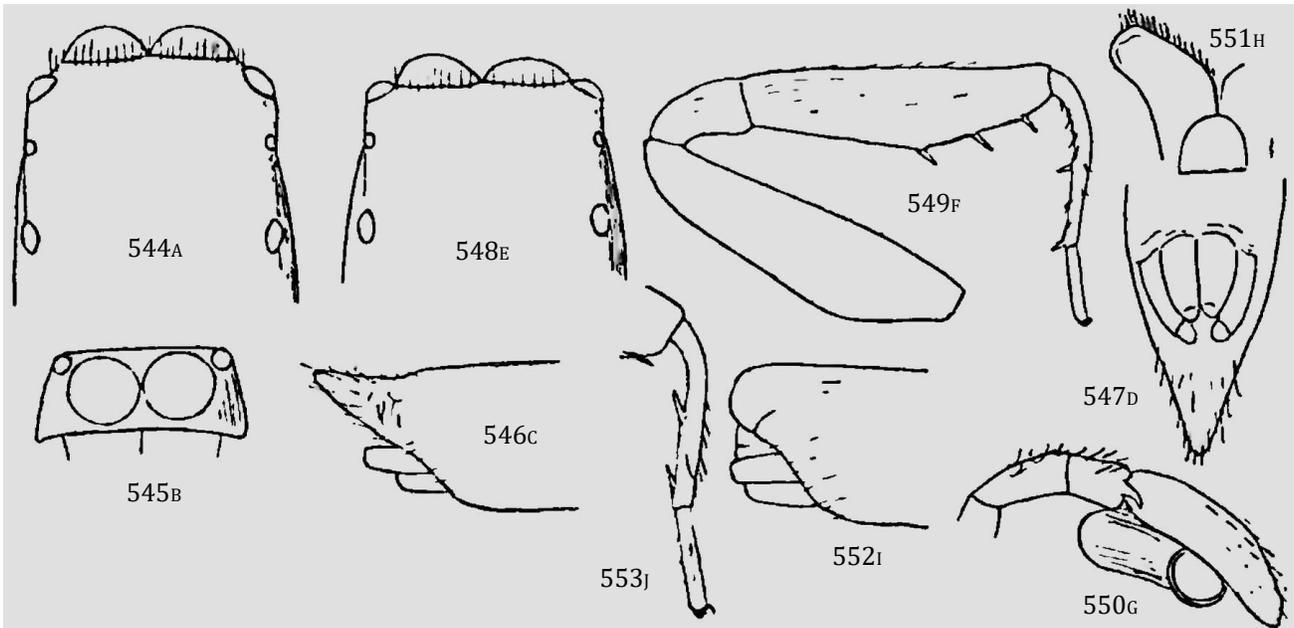


Fig. 544 à 553. A. *Mantisatta trucidans* Warburton, région céphalique en dessus. — B. *id.* face. — C. *id.* extrémité de l'abdomen et filières de profil. — D. *id.* en dessous. — E. *Copocrossa tenuilineata* E. Simon, région céphalique en dessus. — F. *id.* Patte de la 1^{re} paire. — G. *Copocrossa politiventris* E. Sim. patte-mâchoire du mâle. — H. *id.* pièces buccales. — I. *C. tenuilineata* E. Sim. extrémité de l'abdomen et filières de profil. — J. *Mantisatta*, métatarse de la 1^{re} paire.

GENERA

1. Clypeus angustissimus vix ullus ... 2

— Clypeus latus valde reclinator (sec. Thorell) ... **Ligdus**.

2. Abdomen postice leviter prominulum sed obtusissimum ... **Copocrossa**.

— Abdomen postice acute productum et caudiforme ... **Mantisatta**.

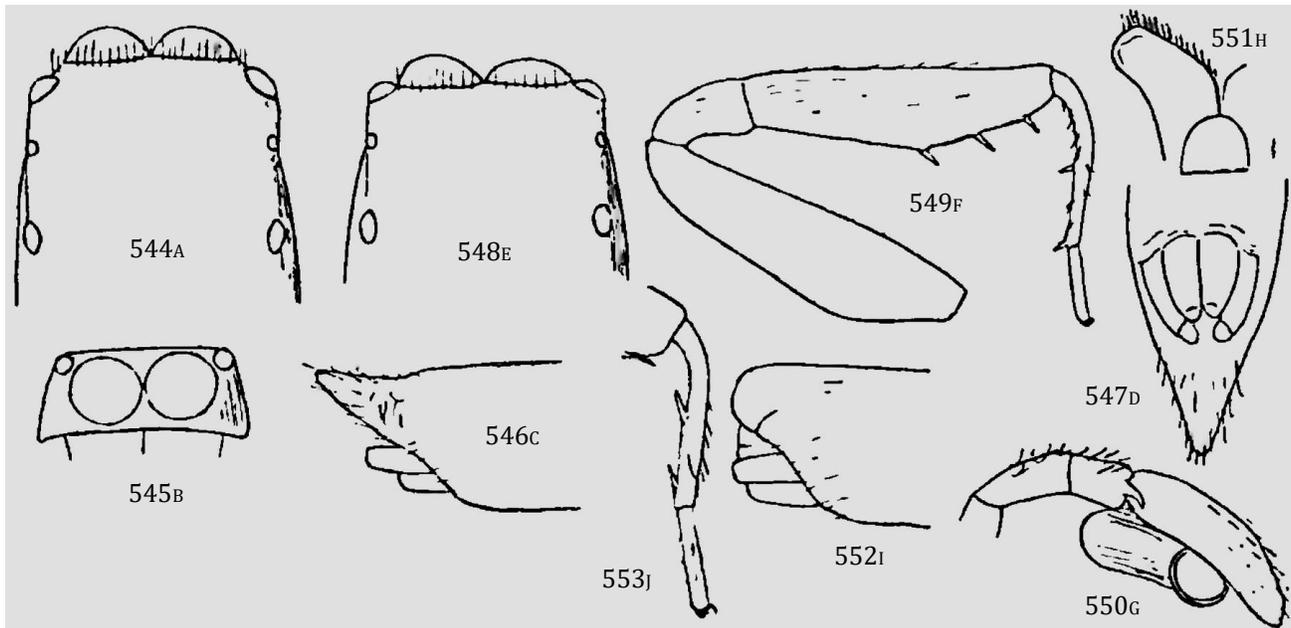
Copocrossa nom. nov. — ? *Marptusa* L. Koch, *Ar. Austr.* I, p. 1115 (ad. part. *M. tenerrima*). — *Stenodina* E. Simon, *Ann. Soc. ent. Belg.*, XLIV, 1900, p. 388. (nom. praeocc). A *Pirantho* differt parte labiali haud longiore quam ad basin latiore, apice attenuata atque obtusa, cephalothorace planissimo, multo longiore et angustiore, parte thoracica quadrangulo saltem duplo longiore, pedum 1ⁱ paris tibia longissima, subtus convexa et in parte apicali, aculeis robustis et brevibus 3-3 armata, metatarso gracili, leviter flexuoso, aculeis minutissimis et erecteis 2-2 munito, abdomine angusto et longo, apice leviter prominulo sed obtusissimo. Typus: *C. tenuilineata* E. Simon. Ar. geogr.: Nova Hollandia orient, et Malaisia.

Mantisatta Warburton, *Pr. Zool. Soc. Lond.*, 1000, p. 384. A *Copocrossa* differt abdomine apice acute producto et caudiformi atque aculeis brevibus metatarsorum anticorum valde reclinator. Typus: *M. trucidans* Warburton. Ar. geogr.: Borneo.

Ligdus Thorell, *Descr. Catal. Spid. Burma*, 1895, p. 336. Gen. invisum a *Copocrossa*, cui verisimiliter valde affine est, differt, sec. Thorell, clypeo valde reclinato, dimidium oculi maximi diametrum altitudine superanti. Typus: *L. chelififer* Thorell. Ar. geogr.: Birmania

17. COPOCROSSEAE

The two genera *Mantisatta* and *Copocrossa*, for which I propose this group, differ from the preceding ones by their labial plate, which is as wide as it is long, tapered and blunt, and by their lower spinnerets, which are hidden from above by the apex of the abdomen. Their sternum is much less tapered than that of *Bavia*, and it is truncated at the front, where it separates the coxae (hip joints) by at least the width of the labial plate, if not more — although this last feature is also shared by the genera *Piranthus* and *Stagetillus*. Their cephalothorax, very flat, resembles that of *Piranthus*, but it is at least as narrow and as long as that of *Goleta*. Their eyes are also arranged similarly to those of *Piranthus*: the front eyes are very unequal, with the median ones enormous — occupying nearly the entire height of the face — while the lateral eyes, very small, are pushed slightly backward. This feature is especially prominent in *Mantisatta trucidans* Warburton, which has led to comparisons with the *Lyssomanes*, despite there being no real affinity between them (fig. 544A).



Figs. 544 to 553. A. *Mantisatta trucidans* Warburton, cephalic region from above. — B. same, face. — C. same, tip of the abdomen and spinnerets in profile. — D. same, from below. — E. *Copocrossa tenuilineata* E. Simon, cephalic region from above. — F. same, leg of the 1st pair. — G. *Copocrossa politiventris* E. Sim., male palpal organ. — H. same, mouthparts. — I. *C. tenuilineata* E. Sim., tip of the abdomen and spinnerets in profile. — J. *Mantisatta*, metatarsus of the 1st pair.

Their eye group is at least twice as short as the thoracic region. Their abdomen is narrow, long, flat or cylindrical, and in males (e.g., *C. politiventris* E. Simon), sometimes covered by a smooth scutum. That of *Mantisatta* ends in a pointed, slightly raised cone-shaped tip resembling a tail (fig. 546C). That of *Copocrossa* is slightly projecting but very blunt, with a triangular, two-segmented anal tubercle directed downward and slightly backward (fig. 552I). In all cases, the spinnerets are lower, inserted at an oblique angle and hidden from above. The lower spinnerets are thick and close together; the upper ones are thinner, slightly longer, somewhat curved, and end in a very small, somewhat sharp segment that is bent inward (fig. 547D). Their legs have an armature like those of *Piranthus*, but in the first pair the proportions of the segments differ: the tibia is much longer than the femur, convex underneath in the middle, but tapered at both ends and armed in the second half with 3 pairs of short, flattened, almost tooth-like spines. The metatarsus is slender, slightly curved and sinuous at the base, and bears 2 pairs of even smaller spines — one median and one apical. These spines are upright in *Copocrossa* (fig. 549F) and point backward like barbs in *Mantisatta* (fig. 553J). Their chelicerae are conical and shorter than the face, with a fairly long, strongly curved fang. The lower margin (in *Copocrossa tenuilineata* E. Simon) bears 3 or 4 small, equal, and isolated teeth. The labial plate is at least as wide as it is long, and blunt. The endites (maxillary lobes) are straight in the female; in the male, they are divergent but blunt and slightly edged (fig. 551H). The palpal organ of *Copocrossa politiventris* E. Simon (fig. 550G) is small. Its tibia is cylindrical and shorter than the patella, bearing a small, sharp, upper-external apophysis. The tarsus, much longer but only slightly wider than the tibia, covers a very convex and protruding bulb, which has a strong apical stylus coiled in a circle. The genus *Ligus* Thorell, which I have not seen in nature, likely belongs to this group. One might even think it identical to the genus *Copocrossa*,

except that *Ligdus* has a broad band across the head slanting backward. The group is composed of a few small species — narrow, long, and flattened — covered, at least in part, with simple white pubescence. *Mantisatta trucidans* Warburton, which was discovered in Sarawak (Borneo), in a termite nest, has a cephalic part marked with black eye and median spots, and an abdomen with small brownish spots in four rows, the median ones being linear. *Copocrossa (Stenodina) tenuilineata* E. Simon, from northeastern Australia, is decorated with three fine black lines and a transverse line near the end of the abdomen. *C. politiventris* E. Simon is dark-colored, glabrous above, and bears white pubescence on the sides. Its cephalothorax is finely punctured; its abdomen in the male is covered by a very smooth, iridescent black scutum. Its long front legs are partly black, while the others are pale yellow. Mr. Warburton also sent me another (yet unpublished) *Copocrossa* species from Malaysia, which is also iridescent black. *Marptusa tenerrima* L. Koch probably also belongs to the same genus. *Ligdus chelififer* Thorell is described from Burma (Myanmar).

GENERA

1. Clypeus very narrow, hardly present ... 2
— Clypeus broad, strongly reclined (according to Thorell) ... *Ligdus*.
2. Abdomen slightly protruding at the rear but very blunt ... *Copocrossa*.
— Abdomen sharply produced at the rear and tail-like ... *Mantisatta*.

Copocrossa, new name. — ? *Marptusa* L. Koch, *Arachn. Austral.* I, p. 1115 (in part: *M. tenerrima*). — *Stenodina* E. Simon, *Ann. Soc. ent. Belg.*, XLIV, 1900, p. 388. (preoccupied name). Differs from *Piranthus* in the labial part, which is not longer than its basal width, with a tapered and blunt apex; in the cephalothorax, which is very flat, much longer and narrower; the thoracic part at least twice as long as wide; the tibia of the first pair of legs is very long, convex underneath and, in the apical part, armed with three pairs of robust and short spines (3–3); the metatarsus is slender, slightly sinuous, and provided with two pairs of very small, erect spines (2–2); the abdomen is narrow and long, slightly protruding at the tip, but very blunt. Type: *C. tenuilineata* E. Simon. Geographical distribution: Eastern Australia and Malaysia.

Mantisatta Warburton, *Proc. Zool. Soc. Lond.*, 1900, p. 384. Differs from *Copocrossa* in having the abdomen sharply produced at the apex and tail-like, and in the short spines of the front metatarsi being strongly reclined. Type: *M. trucidans* Warburton. Geographical distribution: Borneo.

Ligdus Thorell, *Descriptive Catalogue of the Spiders of Burma*, 1895, p. 336. A genus unseen by the author; likely very closely related to *Copocrossa*, but differs, according to Thorell, by the clypeus being strongly reclined and exceeding the height of half the diameter of the largest eye. Type: *L. chelififer* Thorell. Geographical distribution: Burma (Myanmar).

To date, seven species (and now, six) have been described in the three genera of this group, ranging from southern India to the eastern coast of Australia (Table 1, Figure 1).

Table 1. Species of Copocrosseae (after WSC 2025). As noted here, we recognize the ♀ *Copocrossa harpina* as a junior synonym of the ♂ *C. politiventris*. Species 1-6 have been described but there are few published records; species 7-9 are not described but can be associated with records posted in *iNaturalist*. Reference numbers (#) are also used in Figure 1.

| # | species | ♂♀ | reference | locality | notes |
|---|---------------------------------|----|------------------------------------|-------------------------------|----------------------------------|
| 1 | <i>Copocrossa politiventris</i> | ♂ | Simon 1901b | Gunung Inas, Perak, Malaysia | |
| | <i>Copocrossa politiventris</i> | ♀ | (<i>C. harpina</i>) Simon 1903 | Nirou Forest, Sumatra | ♀ <i>politiventris</i> , n. syn. |
| 2 | <i>Copocrossa tenuilineata</i> | i♂ | (<i>Stenodina t.</i>) Simon 1900 | Cooktown, Queensland | immature |
| | <i>Copocrossa tenuilineata</i> | ♀ | Davies & Žabka 1989 | Mission Beach, Queensland | similar to immature ♂ |
| 3 | <i>Ligdus chelififer</i> | i♀ | Thorell 1895 | Myanmar | immature |
| 4 | <i>Ligdus garvale</i> | ♂ | Caleb, in Caleb et al. 2024 | 12.5658N, 75.7819E, Karnataka | |
| 5 | <i>Mantisatta longicauda</i> | ♂♀ | Cutler & Wanless 1973 | Lingayen, Luzon, Philippines | ♂ holotype |
| 6 | <i>Mantisatta trucidans</i> | ♀ | Warburton 1900 | Sarawak | |
| 7 | <i>Copocrossa</i> sp. A | ♂ | | Andaman Islands | |
| 8 | <i>Copocrossa</i> sp. B | ♂ | | southern Queensland coast | |
| 9 | <i>Ligdus</i> sp. A | ♀ | | southeastern Australian coast | nests like <i>Ligdus</i> spp. |

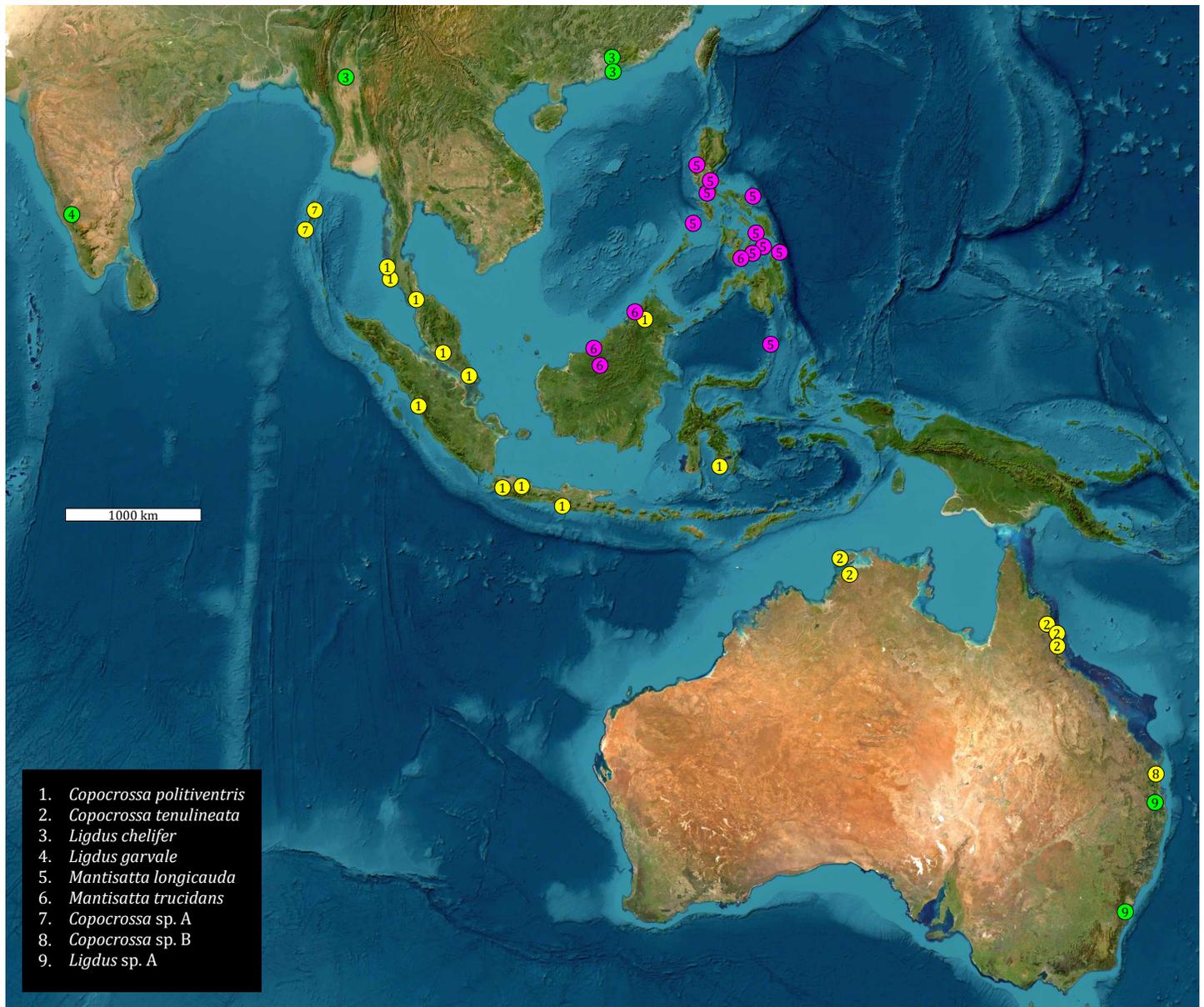


Figure 1. Distribution of the Copocrosseae, from South Asia to Australasia. 1-6, Described species. 7-12, Undescribed forms or species. This includes both published records (Table 1: #1-6), and records posted on iNaturalist. Base map © OpenStreetMap.

Systematics. Of the seven species that have been described in this group, both genders are known for only one. For four species, only the female is known, and for one of these (*Ligodus chelififer*) this female was immature. For two species, only the male is known. It appears that there could be three useful genera here, but the current arrangement of species in these genera might also need to be revised. These would be: *Copocrossa*, in which the males have much shorter pedipalps, *Ligodus*, in which the males have much longer pedipalps, and *Mantisatta*, in which the males have longer and unusual pedipalps that look like prognathous chelicerae, and very long tails. Fortunately we now have records of the male *M. trucidans*, and we can confirm that this is closely related to *M. longicauda*. Previously we had a similar problem with *Ligodus*, but if we follow the recent description of the male *L. garvale* (Caleb et al. 2024), we can address the identity of *L. chelififer*. *Copocrossa* has been easier to identify, particularly since Davies & Žabka (1989) redescribed the type, *C. tenulineata*. However we consider many of the spiders that have been recently associated with *Copocrossa* in the field to be better placed in *Ligodus*. Here we provide a working list of species that have been placed in the Copocrosseae:

Order Araneae: Family Salticidae: Subfamily Salticinae: Salticoida: Afresia: Marpissoida: Tribe Ballini

Copocrosseae Simon 1901a (clade)

Copocrossa Simon 1900, type species *C. tenuineata*

1. *Copocrossa politiventris* (♂) Simon 1901
Copocrossa politiventris (♂) Simon 1901a
Copocrossa politiventris (♂) Simon 1901b
Copocrossa harpina (♀) Simon 1903, **new synonym**
2. *Copocrossa tenuineata* (immature ♂) (Simon 1900)
Stenodina tenuineata (immature ♂) Simon 1900
Copocrossa tenuineata (immature ♂) Simon 1901a
Copocrossa tenuineata (♀) Davies & Žabka 1989

Ligdus Thorell 1895, type species *L. chelifer*

3. *Ligdus chelifer* (immature ♀) Thorell 1895
Ligdus chelifer (immature ♀) Thorell 1895
Ligdus chelifer (immature ♀) Prószyński 1984
4. *Ligdus garvale* (♂) Caleb
Ligdus garvale (♂) Caleb et al. 2024

Mantisatta Warburton 1900, type species *M. trucidans*

5. *Mantisatta longicauda* (♂♀) Cutler & Wanless 1973
Mantisatta longicauda (♂♀) Cutler & Wanless 1973
Mantisatta longicauda (♂♀) Prószyński 1976
Mantisatta longicauda (♀) Barrion & Litsinger 1995
6. *Mantisatta trucidans* (♀) Warburton 1900
Mantisatta trucidans (♀) Simon 1901a
Mantisatta trucidans (♀) Cutler & Wanless 1973

All of the Copocrosseae are unusual spiders, with elongated or narrow, flattened bodies, a very narrow carapace that barely accommodates the pair of AME in front, unusually small lateral eyes, and long, almost ungainly legs I with swollen tibia. These legs look raptorial and appear to play a role in either prey capture or probing, but are scarcely functional with respect to walking. Here we will look at what is known of each species in more detail, and in particular will look at the remarkable nests produced by females. At the same time it is safe to say that we really know little about the "functional" aspect of the unusual morphology of these spiders. Given what we now know about the important role of the lateral or secondary eyes of salticids (Hill 2022), for example, we simply do not understand why these eyes are so reduced in this particular group. If these spiders are mimics, we do not know what they are mimicking. The size of copocrossean species varies considerably, as shown in Table 2.

Table 2. Body length of copocrossean jumping spiders (based on only a few specimens, including immatures).

| species | gender | body length | reference |
|--|----------------|--------------------------|-----------------------|
| <i>Copocrossa politiventris</i> | ♂ | 4 mm | Simon 1901b |
| <i>Copocrossa harpina</i> (= <i>C. politiventris</i>) | ♀ | 3 mm | Simon 1903 |
| <i>Copocrossa tenuineata</i> | ♂, ♀ | 3 mm, 3 mm | Whyte & Anderson 2017 |
| <i>Ligdus chelifer</i> | immature (?) ♀ | 4.5 mm | Thorell 1895 |
| <i>Ligdus garvale</i> | ♂ | 4.65 mm | Caleb et al. 2024 |
| <i>Mantisatta longicauda</i> | ♂, ♀ | 9.4 mm (+ tail), 7.48 mm | Cutler & Wanless 1973 |
| <i>Mantisatta trucidans</i> | ♀ | 3.88 mm | Cutler & Wanless 1973 |

1. *Copocrossa politiventris* Simon 1901

Simon's first account of this species came with his description of the Copocrosseae (Simon 1901a; original and translation as given previously). This included his only drawing of the species (fig. 550G), a simple (and inadequate, for purposes of identification) sketch of the right pedipalp of his male. His more formal description came later (Simon 1901b), presented here with an English translation:

95. COPOCROSSA [*Copocrossa* = *Stenodina* E. Simon (olim), nomen praeoccupatum.] POLITIVENTRIS, sp. nov. ♂. Long. 4 mm.—Cephalothorax humilis et longus, leviter ovatus atro-purpureus, prope oculos niger, supra planus et glaber, in medio crebre, antice posticeque parcius impresso-punctatus, utrinque in declivitate parum dense albo-pilosus. Oculi antici inter se validissime inaequales et contigui, medii maximi, altitudinem faciei totam occupantes. Clypeus nullus. Chelae brevissimae, nigrae, reclinatae et antice planae. Abdomen angustum et longum, teretiusculum, supra nigro-nitidum, micanti-tinctum, glabrum, sed in lateribus zonis obliquis abbreviatis albo-pilosis ornatum, subtus atrum. Sternum et partes oris nigro-nitida, luminiae extus ad apicem prominulae et divaricatae sed obtusae. Pedes 1ⁱ paris longissimi, nigro-nitidi, coxa in lateribus et subtus, metatarso (basi excepta) tarsoque pallide luteis, femore compresso longo, patella sat parva, tibia longissime ovata, subtus, in dimidio apicali, aculeis brevibus sed robustis et singulariter elevatis 3-3, armata, metatarso gracili sat longo, praesertim ad basin curvato, subtus aculeis minutissimis et erectis 2-2 munito. Reliqui pedes pallide lutei, omnino mutici. Pedes-maxillares parvi fusci, apice tarso bulboque luteis; tibia tereti, patella paulo brevior, extus ad apicem apophysii parva acuta et leviter curvata armata; tarso tibia multo longiore sed vix latiore; bulbo ad basin valde convexo et subgloboso, ad apicem stylo valido nigro, circulum magnum formante, munito. Perak : Gunong Inas.

95. COPOCROSSA [*Copocrossa* = *Stenodina* E. Simon (formerly), name preoccupied.] POLITIVENTRIS, sp. nov. ♂. Length 4 mm.—Cephalothorax low and long, slightly ovate, dark purple, black near the eyes, flat and smooth above, densely impressed-punctate in the middle, more sparsely so at the front and back, on each side of the slope somewhat densely covered with white hairs. Anterior eyes very strongly unequal among themselves and contiguous, the middle ones very large, occupying the whole height of the face. Clypeus absent. Chelicerae very short, black, reclined and flat in front. Abdomen narrow and long, somewhat cylindrical, above shiny black, with a glittering tinge, smooth, but on the sides adorned with short oblique white-haired bands, beneath jet-black. Sternum and mouthparts shiny black, palpal bulbs outwardly slightly prominent and diverging at the tip, but blunt. First pair of legs very long, shiny black, coxa on the sides and below, metatarsus (except at the base) and tarsus pale yellow; femur compressed and long, patella rather small, tibia very long and ovate, beneath, in the apical half, armed with short but stout and singularly raised spines 3-3; metatarsus slender and fairly long, curved especially at the base, beneath armed with very small erect spines 2-2. Remaining legs pale yellow, entirely unarmed. Pedipalps small, brown, with the apex of the tarsus and bulb yellow; tibia cylindrical, patella slightly shorter, outwardly at the tip armed with a small, sharp, and slightly curved apophysis; tarsus much longer than the tibia but scarcely wider; bulb at base strongly convex and somewhat globose, at the tip armed with a strong black stylus forming a large circle. Perak: Gunung Inas.

Apart from Simon's brief description, we have no other records of this species. No one has seen this species, or a type specimen that might be associated with it, in more than 120 years. Allowing for the fact that Simon was examining a specimen in alcohol, we recognize the general agreement of his description with a *Copocrossa* ♂ recently documented in Singapore, and several neighboring areas, in *iNaturalist* (Figures 2.1-2.4). In fact, with 10 separate records, this is the only copocrossean spider that has been found in Singapore. This assignment of the species name also agrees with our view that, based on the better-known Australian *C. tenuilineata* (see below), *Copocrossa* males have relatively short pedipalps.

Fortunately we have recent *iNaturalist* records for both male and female spiders living in the same localities, and the females have the two thin bands (5 and 6) across the opisthosoma as described by Simon (1903) in his later description of the ♀ *C. harpina* (Figures 2.5-2.6, 3). As with *C. politiventris*, *C. harpina* has not been seen and recognized for more than 120 years. As noted previously we consider Simon's *C. harpina* to be a junior synonym representing the female of *C. politiventris*.



Figure 2. *Copocrossa politiventris* in Singapore. 1-4, ♂. 5-6, ♀. Photo credits: 1-4, iNat. obs. 245003336, © Melvyn Yeo, CC BY-NC 4.0; 5-6, iNat. obs. 296705147, © Ong Ei Leen, CC BY-NC 4.0.



Figure 3. *Copocrossa politiventris* ♀ in Singapore. Although these images have lower resolution, they provide a good view of the thin bands (bands 5-6) at the rear of the opisthosoma (3, arrows), described by Simon (1903, description of ♀ *C. harpina*). Simon also noted the presence of a dark line on the side of the eye quadrangle, visible here but probably more prominent in his preserved specimen. Photo credits: 1-6, iNat. obs. 144479143, © klearad, CC BY-NC 4.0.

Simon's brief (1903) description of *C. harpina* is given in its entirety here, followed by an English translation:

10. *Copocrossa harpina*, sp. nov. — ♀ Long. 3 mill. — Cephalothorax humilis, longe ovatus, superne deplanatus, fulvo-lividus, parce albo-pilosus, vitta marginali lata dilutiore et densius albo-pilosa utrinque notatus, parte cephalica utrinque, prope oculos, nigra et lineolis binis abbreviatis fuscis notata. Pili oculorum et clypei albi. Oculi anteriori inter se contigui et valde inaequales. Abdomen longum et angustum, parallelum, antice truncatum, postice obtusam vix prominulum, fulvum, supra albo-pubescent et vittis fulvis transversis sex notatum, vittis 1^a et 2^a sat angustis, 3^a et 4^a latis, ultimis binis tenuibus, subtus parcius albo-pubescent. Chelae brevissimae et partes oris fusco-olivaceae. Sternum pedesque pallide lutea subpellucentia, tibia 1ⁱ paris longe ovata, subtus, in dimidio apicali, aculeis validis fuscis 3-3, metatarso longo et curvato, aculeis sat brevibus sed validis, erectis et reclinatis 2-2 subtus armato. Mamillae testaceae. Plage genitalis parva, fusco-rufula. Forêt du Nirou.

10. *Copocrossa harpina*, sp. nov. — ♀ Length 3 mm. — Cephalothorax low, long-ovate, flattened above, tawny-livid, sparsely white-haired, marked on each side with a broad, paler marginal stripe more densely covered with white hairs; the cephalic region on each side near the eyes black, marked with two short brownish streaks. Hairs on the eyes and clypeus white. Anterior eyes contiguous and very unequal among themselves. Abdomen long and narrow, parallel-sided, truncated in front, posteriorly obtuse and scarcely projecting, tawny, above white-pubescent and marked with six transverse tawny stripes, the 1st and 2nd stripes fairly narrow, the 3rd and 4th broad, the last two thin; underside partly white-pubescent. Chelicerae very short and mouthparts olive-brown. Sternum and legs pale yellowish, somewhat translucent; tibia of the 1st pair long-ovate, beneath in the apical half armed with strong dark spines 3-3; metatarsus long and curved, beneath armed with fairly short but strong spines, both erect and reclining, 2-2. Spinnerets brick-colored. Genital area small, reddish-brown. Nirou Forest, Sumatra.

2. *Copocrossa tenulineata* (Simon 1900)

Simon described this type species for his genus *Copocrossa* in 1900, from an immature specimen collected in Queensland. Fortunately Davies & Žabka, much later (1989), described a small female from the same area that matched Simon's description. Whyte & Anderson more recently (2017) published definitive photographs of the adult male and female. As a result, although we know very little about this species, it has been, nonetheless, one of the easiest of the Copocrosseae to identify (Figure 4-5).

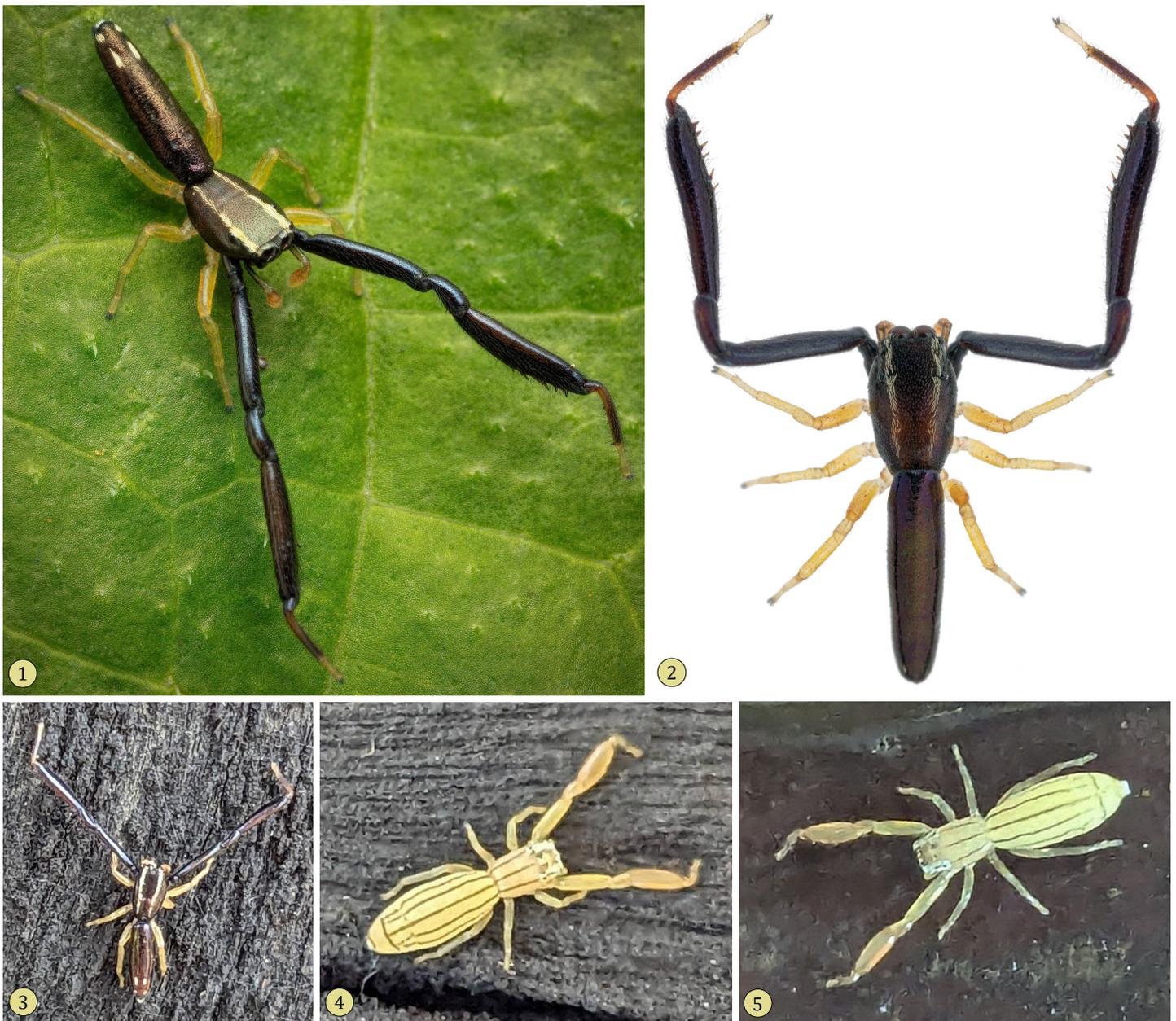


Figure 4. *Copocrossa tenulineata* in Australia. 1, ♂, Queensland. 2, ♂, Berry Springs, Northern Territory. 3, ♂, Queensland, exploring on the bark of a tree with the flexed metatarsi of extended legs I. 4-5, Two ♀, Queensland. Photo credits: 1, iNat. obs. 235630485, © Alan Henderson, CC BY-NC 4.0; 2, ♂, iNat. obs. 194240860, © Nick Volpe, CC BY-NC 4.0; 3-5, iNat. obs. 136992696 [3], 136992695 [4], 246884434 [5], © RattyExplores, CC BY-NC 4.0.

We have no records of nesting or brooding behavior for either of the two *Copocrossa* species, but given their similar appearance, this behavior may compare to that of the better-known *Ligdus*.

Here we present Simon's original (1900) description of an immature male (as *Stenodina*; changed to *Copocrossa* by Simon 1901a as noted above), with an English translation, for reference:

Stenodina nov. gen. A *Mantisatta* Warburton, praesertim differt abdomine postice leviter prominulo sed obtusissimo.—Typus *S. tenuilineata* E. S. **Stenodina tenuilineata** sp. nov. ♂ (pullus). Long. 4 mill. Cephalothorax pallide luteus, linea marginali exillima nigra lineisque dorsalibus trinis exilibus, media antice abbreviata, supra notatus, parce albido-pilosus, parte cephalica antice et utrinque crebrius luteo-pubescenti. Pili oculorum supra lutei, subtus albidi. Abdomen pallide luteum, lineis exillimis fuscis quatuor supra ornatum. Chelae, sternum pedesque pallide lutea, tibia antica insigniter longa, longe ovata, subtus, in parte apicali, aculeis robustis et brevibus 3-3 armata, metatarso brevi, subtus aculeis parvis 2-2 munito.—Australia: Cook-Town.

Stenodina, new genus. It differs from *Mantisatta* Warburton especially by having a slightly protruding but very blunt posterior part of the abdomen.—Type species: *Stenodina tenuilineata* E. S. **Stenodina tenuilineata**, new species, ♂ (juvenile). Length: 4 mm. Cephalothorax pale yellow, with a very fine black marginal line and three slender dorsal lines (the middle one shortened at the front); marked above, sparsely covered with whitish hairs; the front and sides of the head region more densely covered with yellowish down. Eye hairs yellow above, whitish below. Abdomen pale yellow, decorated above with four very fine dark brown lines. Chelicerae, sternum, and legs pale yellow. The front tibia is notably long, long-oval in shape, and armed underneath at the tip with three short, strong spines on each side (3–3). The metatarsus is short, with two small spines underneath on each side (2–2). Location: Australia — Cooktown.

3. *Ligdus chelifera* Simon 1900

Thorell (1895) described what he thought could be an immature female that, for 130 years, has remained the only known specimen representing this species. This is unfortunate, as *Ligdus* is the oldest named genus in the Copocrosseae, and *L. chelifera* is the type species for that genus. Prószyński (1984) published several drawings of what appears to be Thorell's type (Figure 5), but they are of little use for identification.

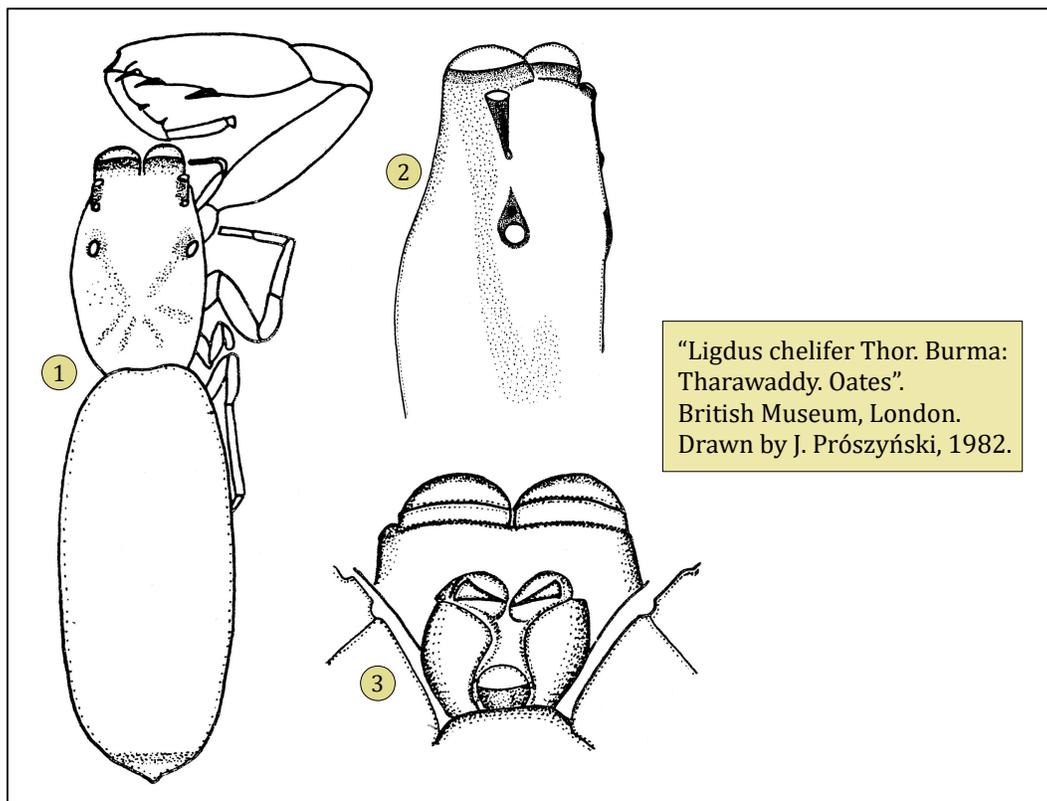


Figure 5. Prószyński's (1984) drawings of the immature ♀ type specimen for *Ligdus chelifera*.

For reference we present Thorell's original Latin description here, with an English translation:

LIGDUS [Nom. propr. pers.], gen. n. Corpus valde depressum; cephalothorax humilis, planus, multo longior quam latior, clypeo satis alto. Oculi medii antichi magni, paene totam frontis latitudinem occupantes, lateralibus anticis, qui pone eos, paullo magis extra, locati sunt, multis partibus majores. Quadrangulus oculorum plus $\frac{2}{5}$ sed non dimidium longitudinis cephalothoracis occupat; paene quadratus est, parum latior quam longior, et non parum angustior postice quam cephalothorax eodem loco. Oculi seriei 2^{ae} minutissimi longius ab oculis posticis quam a lateralibus anticis distant; series, quam formant oculi tres utriusque lateris, levissime foras curvata est. Sternum subellipticum, fere dimidio longius quam latius, coxis etiam anticis multo latius, antice truncatum, apice postico inter coxas 4ⁱ paris spatio sat parvo separatas pertinens; spatium inter coxas 1ⁱ paris maxillarum et labii latitudinem (conjunctim) paene aequat. Mandibulae breves, parallelae. Maxillae porrectae, parallelae, subovatae, basi angustae, apice rotundatae, labio plus triplo longiores; labium minutum, paullo transversum, apice rotundatum. Pedes ita: I, IV, II, III (III, II?) longitudine se excipiunt pedes 1ⁱ paris, qui in piano librato extensi et articulati sunt, depressi, sat longi et robusti, reliquis brevissimis et gracilibus multo longiores et latiores, subter (intus) in tibiis et metatarsis aculeis brevibus armati. Tibia cum patella 4ⁱ paris longior est quam tibia cum patella 3ⁱⁱ paris. Abdomen humile, paene planum, longum sed non multo angustum. Typus: *L. chelififer*, sp. n. Aranea parva valde depressa, ad quam recipiendam hoc genus creavi, fugaci oculo adspecta *Chelonetho* quodam sat similis est, pedibus 1ⁱ paris in piano librato incurvis palpos Chelonethorum repraesentantibus; positione oculorum lateralium anticorum magis pone anticos medios locatis, sterno lato et forma partium oris transitum ad *Lyssomaninas* format, praeterea, ut videtur, magis cum *Holoplatye*, Sim., conveniens.

270. **Ligdus chelififer, sp. n. Pallide flavens totus, modo maculis ocularibus ordinariis binis utrinque in parte cephalica aculeisque pedum 1ⁱ paris nigris; et abdomine supra plus minus evidentem pallide luteo-maculato vel variato.—♀ jun. (pulla?). Long. saltem 4½ millim. *Femina jun.*—Ad notas, quas generis *Ligdi* supra dedi, modo paucas hic addere possum, quum singulum quod vidi exemplum valde immaturum videatur.—*Cephalothorax* duplo longior est quam latior, lateribus leviter rotundatis anteriora et posteriora versus aequaliter paullo angustatus, antice truncatus (non rotundatus), postice quoque truncatus et paene aequae latus atque antice. Humillimus et supra planus est, a latere visus in dorso ante declivitatem posticam brevem et satis praeruptam libratus et rectus, impressionibus cephalicis et sulco centrali carens. Clypeus valde reclinatus, dimidiam oculi maximi diametrum altitudine superans. *Oculi* medii antichi maximi et inter se contingentes, lateralibus anticis parvis circiter sextuplo majores et ab iis spatiis parvis sed distinctis separati; linea oculos seriei 1^{ae} supra tangens recta est, si plane a fronte inspicitur facies. *Oculi* seriei 2^{ae} minuti saltem dimidio longius ubi oculis posticis quam a lateralibus anticis distant. *Oculi* postici laterales anticos magnitudine saltem aequant. Quadrangulus oculorum paullulo latior est postice quam antice, saltem aequae latus antice ac longus, et postice tripla-quadrupla diametro oculi postici (paene dupla hac diametro *utrinque*) angustior quam cephalothorax eodem loco. *Mandibulae* minutae, paene directae, parum longiores quam latiores. *Palpi* mediocres. Pedes 1ⁱ paris reliquis pedibus circa duplo longiores et (desuper visi) triplo-quadruplo latiores: coxa eorum paullo longior est quam latior, trochanter ea multo brevior et paullo angustior, transversus; femur ipsa basi (postice sive) extra cito paullo convexo-dilatatum et praeterea extra leviter convexum est, intus rectum, apicem versus sensim paullulo angustatum, saltem 4plo longius quam latius; patella femore et tibia circa triplo brevior et, etiam apice, non parum angustior, paullo longior quam latior; tibia femore paullulo longior et non parum latior, circa triplo longior quam latior in medio, cylindrato-ovata, extra modo leviter, intus paullo fortius convexo-arcuata, 3 paribus aculeorum brevium sed sat fortium intus armata. Metatarsus hujus paris subcylindratus et paullo incurvus est, tibia duplo brevior et circa triplo angustior, aculeis minutis brevissimis 2.2. intus (subter) munitus; tarsus metatarso paene duplo brevior. Reliqui pedes brevissimi et graciles sunt, longitudine non multo inter se discrepantes, aculeis carentes. *Abdomen* depressum, circa triplo longius quam latius, antice truncatum et cephalothoraci arete applicatum (quo fit, ut corpus, desuper visum, inter cephalothoracem et abdomen modo leviter constrictum videatur), postice rotundatum, lateribus parallelis antice et postice rotundatis, praeterea paene rectis. *Color.*—*Cephalothorax* pallide flavens est, maculis duabus parvis nigris utrinque in parte cephalica notatus, altera oblonga et angusta, oculum lateralem anticum cum oculo seriei 2^{ae} conjungente, altera paullo majore et rotundata, oculum seriei 3^{ae} cingente; pube tenui densa alba in lateribus (et supra?) vestitus est cephalothorax. *Sternum, partes oris, palpi et pedes* pallide flaventia, aculeis tibiis et metatarsorum 1ⁱ paris nigris. *Abdomen* pallide cinereo-flavens: secundum medium dorsum ejus inaequaliter pallide luteum vel luteo-maculatum est, et latera saltem posterius maculis pallide luteis sunt notata, hac pictura tamen valde obsoleta; vestigia pubescentiae tenuis albae hic illic vidisse videor. Venter cum *mamillis* pallide flavens. Lg. corp. 4½; lg. cephaloth. 1½, lat. ej. saltem $\frac{3}{4}$; lg. abd. paene 3, lat. ej. paene 1 millim. Ped. I circa 4½, II et III circa 2¼, IV circa 2⅝; pat. + tib. IV et metat. + tars. IV circa $\frac{7}{8}$ millim. Singulum exemplum femineum immaturum, ex Tharrawaddy.

Ligdus [proper personal name], new genus. The body is strongly flattened; the cephalothorax is low, flat, much longer than wide, with a fairly high clypeus. The anterior medial eyes are large, occupying almost the entire width of the front of the head, and are many times larger than the anterior lateral eyes, which are positioned somewhat further out behind them. The eye quadrangle occupies more than $\frac{2}{5}$ but not half the length of the cephalothorax; it is almost square, slightly wider than long, and notably narrower at the rear than the cephalothorax at the same point. The second row of eyes is extremely small, and they are farther from the posterior eyes than from the anterior lateral ones; the row formed by the three eyes on each side is very slightly curved outward. The sternum is subelliptical, nearly half again as long as wide, much wider even than the anterior coxae, truncated at the front, and reaching at the posterior tip into the small space between the coxae of the fourth pair; the space between the coxae of the first pair nearly equals the combined width of the maxillae and labium. The mandibles (chelicerae) are short and parallel. The maxillae are extended forward, parallel, somewhat egg-shaped, narrow at the base, rounded at the tip, more than three times longer than the labium; the labium is minute, slightly transverse, and rounded at the apex. The leg formula is: I, IV, II, III (or possibly III, II?); the legs of the first pair, which are extended and articulated on a level plane, are flattened, fairly long and robust, and much longer and broader than the other legs, which are very short and slender. The tibiae and metatarsi of the first pair are armed underneath (on the inner side) with short spines. The tibia plus patella of the fourth pair is longer than the tibia plus patella of the third pair. The abdomen is low, nearly flat, long but not very narrow. Type species: *Ligdus chelififer*, new species. A very small, strongly flattened spider, for the reception of which this genus was created. Seen fleetingly, it resembles in appearance a certain *Chelonethus* (a pseudoscorpion genus), with the first pair of legs curved on a flat plane, representing the palps of *Chelonethus*. By the position of the anterior lateral eyes, which are placed farther behind the anterior median eyes, the broad sternum, and the shape of the mouthparts, it shows a transition to the *Lyssomaninae*. Moreover, it appears to be more in agreement with *Holoplatys*, described by Simon).

270. **Ligdus chelififer**, new species. Entirely pale yellowish, with only the usual paired eye spots on each side of the cephalic region and the spines of the first pair of legs being black; and the dorsum of the abdomen more or less distinctly pale yellow-spotted or variegated.— Immature ♀ (young?). Total length: at least 4.5 mm. *Juvenile female*: To the characters I have already given above for the genus *Ligdus*, I can now add only a few more, since the single specimen I have seen appears to be very immature. *Cephalothorax*: twice as long as it is wide, with slightly rounded sides, narrowing equally slightly toward the front and back, truncated in front (not rounded), also truncated behind and almost as wide posteriorly as anteriorly. It is very low and flat above; seen from the side, the dorsal surface is level and straight before a short and rather steep posterior slope. It lacks cephalic indentations and a central groove. The clypeus is very steeply inclined, exceeding half the diameter of the largest eye in height. The anterior medial eyes are the largest and are touching each other; they are about six times larger than the small anterior lateral eyes and are separated from them by small but distinct spaces. A straight line drawn above the eyes of the first row appears straight when the face is viewed head-on. The eyes of the second row are minute and are at least twice as far from the posterior eyes as from the anterior lateral eyes. The posterior lateral eyes are at least equal in size to the anterior lateral eyes. The eye quadrangle is slightly wider at the back than at the front, at least as wide in front as it is long, and at the back it is three to four times as wide as the diameter of the posterior eye (almost twice this diameter on each side) narrower than the cephalothorax at the same point. The *chelicerae* are small, almost straight, slightly longer than wide. The palps are of medium size. *Legs*: The first pair of legs is about twice as long as the remaining legs and (seen from above) three to four times wider: coxa is slightly longer than wide, trochanter is much shorter and slightly narrower, transverse. Femur is slightly convex-dilated at the base (behind or externally), and otherwise slightly convex externally, straight on the inner side, and gradually narrowing toward the tip. It is at least four times longer than wide. Patella is about one-third the length of the femur and tibia combined [should be patella about one-third the length of either the femur or tibia, based on Prószyński's (1984) drawing of this specimen, shown in Figure 5], even at the tip noticeably narrower, slightly longer than wide. Tibia is a little longer and noticeably wider than the femur, about three times longer than wide at midsection, cylindrical-ovate in shape, slightly convex on the outer side and more strongly arched on the inner side, armed inside with three pairs of short but fairly strong spines. Metatarsus of this pair is subcylindrical and slightly curved, half the length and about a third the width of the tibia, armed on the inner side (underneath) with very short, minute spines in a 2.2 arrangement. Tarsus is almost half as long as the metatarsus. The remaining legs are very short and slender, not differing much from each other in length, and lack spines. *Abdomen* flattened, about three times as long as wide, truncated in front and closely applied to the cephalothorax (making the body appear only slightly constricted between the cephalothorax and abdomen when viewed from above), rounded at the rear, with sides parallel anteriorly and posteriorly rounded, otherwise almost straight. *Coloration*: The *cephalothorax* is pale yellowish, marked with two small black spots on each side of the cephalic region. One spot is oblong and narrow, connecting the anterior lateral eye with the eye of the second row. The other is slightly larger and round, encircling the eye of the third row. The cephalothorax is clothed on the sides

(and possibly above) with a thin, dense white pubescence. The *sternum*, *mouthparts*, *palps*, and *legs* are pale yellowish; the spines of the tibiae and metatarsi of the first pair are black. The *abdomen* is pale grayish-yellow; along its mid-dorsal line it is irregularly pale yellow or yellow-spotted, and at least the rear sides are marked with pale yellow spots—this pattern, however, is quite faded. I seemed to see traces of thin white pubescence here and there. The venter and spinnerets are pale yellow. Measurements (in millimeters): Body length: 4.5. Cephalothorax length: 1.5, width at least 0.75. Abdomen length: almost 3, width: almost 1. Legs: I, ~4.5. II & III, ~2.25. IV: ~2.625. Patella + tibia IV and metatarsus + tarsus IV: ~0.875. Specimen: a single immature female, from Tharrawaddy.

Since this immature was probably quite translucent, we assume that the dark areas between the lateral eyes described by Thorell represent pigments of respective eye capsules, visible through the integument of a preserved specimen. As long a Thorell's description was, it is also quite generic and might apply to a number of different species. Here, based largely on the subsequent placement of *Ligodus garvale* in this *resurrected* genus by Caleb et al. (2024), we use this name (*L. chelififer*) for a *Ligodus* that is well-known and often observed in Hong Kong (Figures 6-9). This can be justified by the general location at which the immature type for *L. chelififer* was collected ("Burma"), the agreement of the Hong Kong species with the published description of *L. chelififer*, and similarities between the Hong Kong species and *L. garvale*. Males of both species have long pedipalps, much longer than those of *Copocrossa* species. In addition females of both species construct elaborate nests on the underside of leaves with a similar structure, to include both a structural outer layer, an inner layer or sac of dense silk, and two regular entrances.

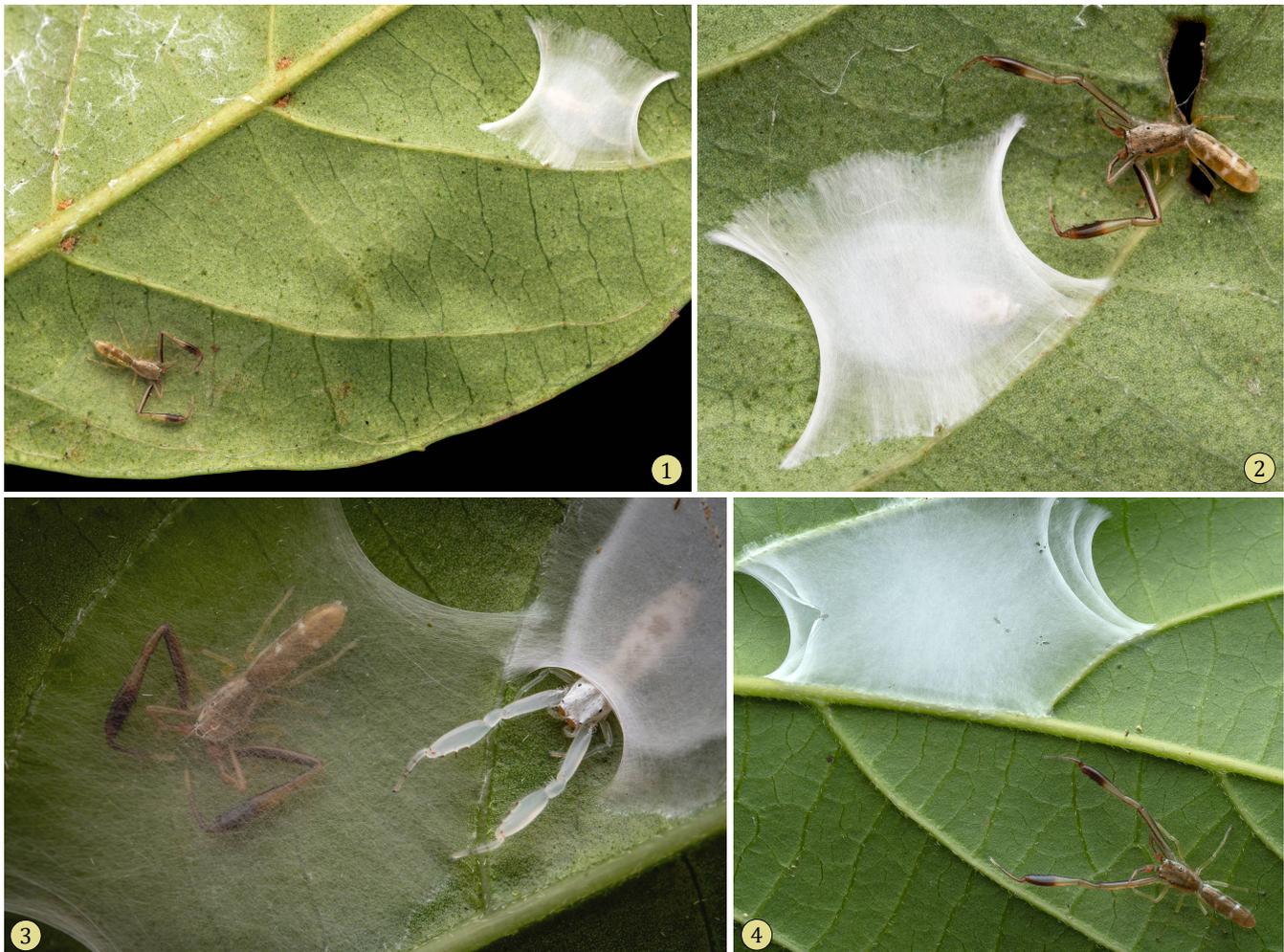


Figure 6. Four different ♂ *Ligodus chelififer* near ♀ nests, Hong Kong. Two ♂ (2, 4) have constructed their own simple shelters nearby. Photo credits: 1-3, iNat. obs. 181510560 [1], 142058849 [2-3], © Lawrence Hylton, CC BY 4.0; 4, iNat. obs. 250577250, © Artur Tomaszek, used with permission; 5, iNat. obs. 250577249, © hei_wildlife, CC BY-NC 4.0.

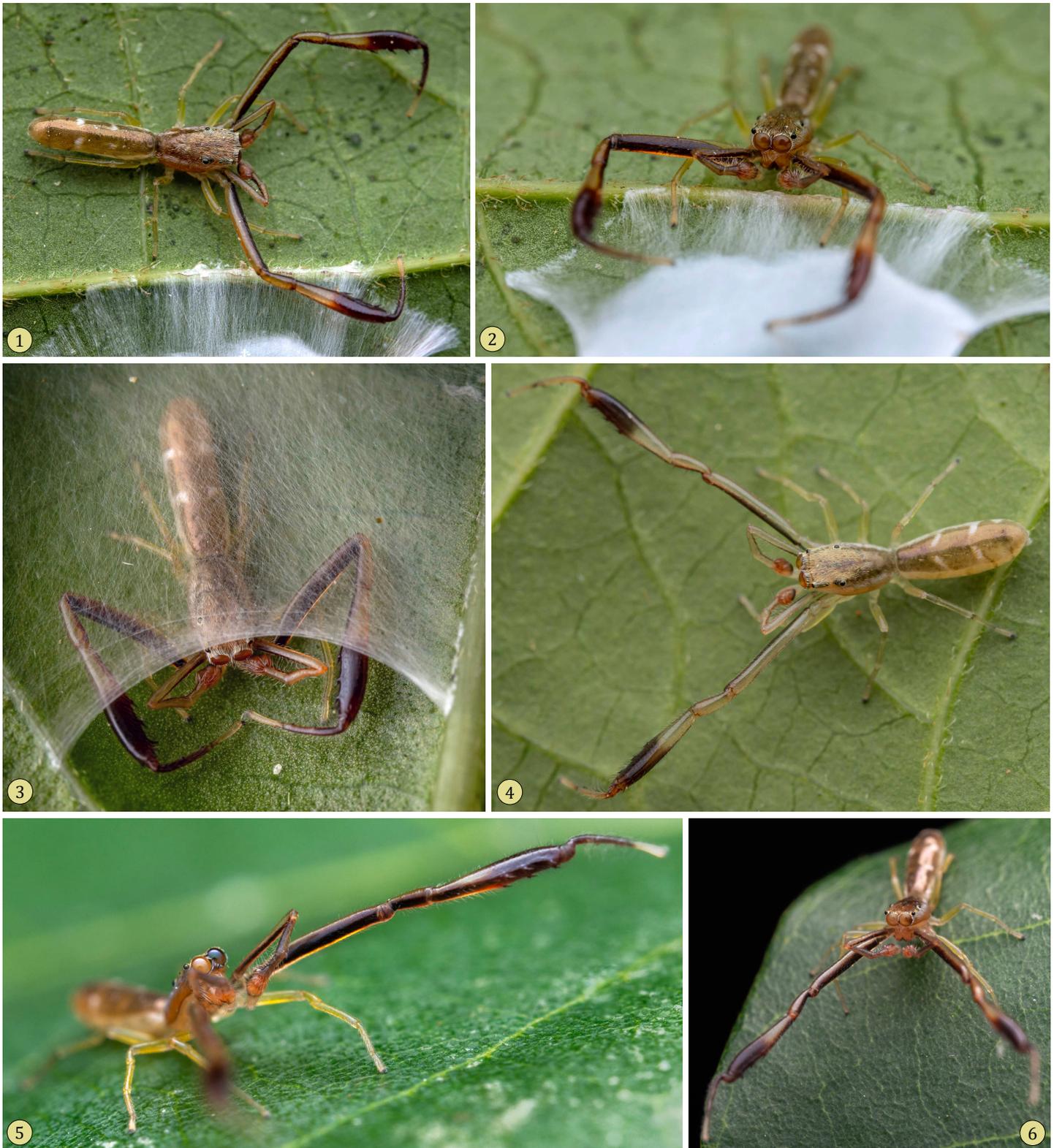


Figure 7. ♂ *Ligdus chelifera* in Hong Kong. **1-2**, ♂ near ♀ nest. **3**, ♂ at the entrance of his shelter. Photo credits: 1-4, iNat. obs. 102476754 [1-2], 250577249 [3], 139690174 [4], © Artur Tomaszek, used with permission; 5-6, iNat. obs. 99312782, © Lawrence Hylton, CC BY 4.0.

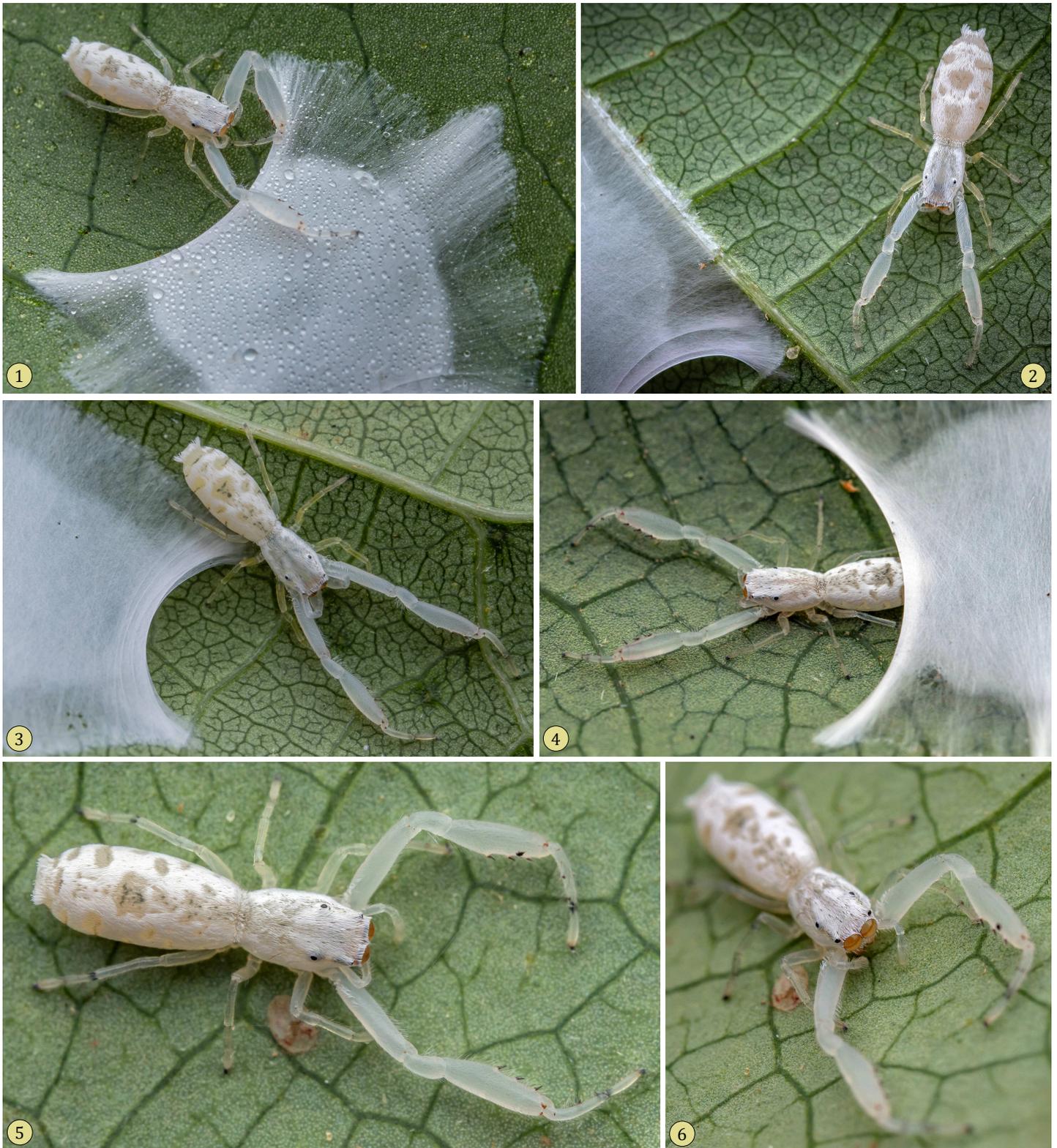


Figure 8. ♀ *Ligdus chelifer* in Hong Kong. **1-4**, ♀ near nest or nest entrance. Photo credits: 1-6, iNat. obs. 198099537 [1], 248223830 [2], 93594351 [3], 192644943 [4], 200778402 [5-6], © Artur Tomaszek, used with permission



Figure 9. ♀ *Ligdus chelifer* in Hong Kong. **1**, ♀ at the entrance of a shelter on the underside of a leaf. **6-7**, Two ♀ in nests on the underside of a leaf. Both nests have two entrances and both inner and outer layers of silk, but both the outer structure and the inner chamber of (7) have been heavily reinforced, suggesting that the ♀ is either ready to brood, or is brooding. Photo credits: 1-2, iNat. obs. 250577227 [1], 139690175 [2], © Artur Tomaszek, used with permission; 3, iNat. obs. 84866597, © blackdogto, CC BY-NC 4.0; 4-6, iNat. obs. 101998394 [4], 181510573 [5], 143922156 [6], © Lawrence Hylton, CC BY 4.0.

4. *Ligdus garvale* Caleb 2024

A single ♂ *Ligdus garvale* (Figure 10) was recently described in detail from one locality in Karnataka (Caleb et al 2024). This male was seen resting in a retreat or shelter on the underside of a leaf of the introduced torch ginger plant (*Etilingera elatior*). Returning to that location, the junior authors have now been able to document the appearance of the ♀ *L. garvale* for the first time (Figure 11), as well as several aspects of the brooding behavior of this species, which appears to be much like that of the related *L. chelififer*. The banded appearance of both the ♂ and ♀ is distinctive, making this species easy to identify.

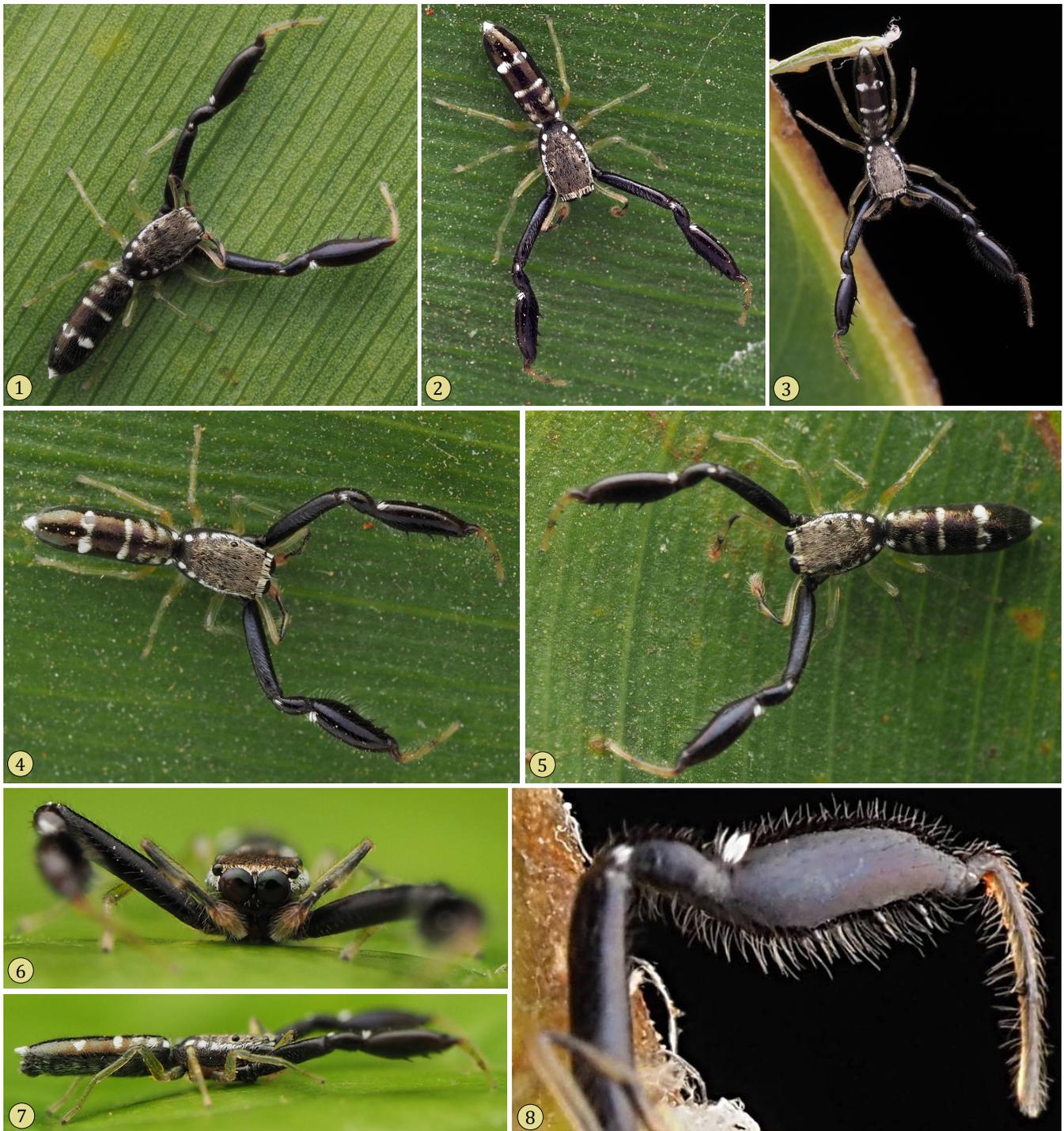


Figure 10. Holotype ♂ *Ligdus garvale*, Kodagu, Karnataka. **8**, Prolateral side of leg L1, showing the inflated tibia.



Figure 11 (continued on next page). ♀ *Ligus garvale* in Kodagu, Karnataka. Like the males of this species, females are distinctly banded, on both the sides of the carapace and the opisthosoma. Both males and females also have a short tufted tail. 7, Note the presence of three pairs of black spines on the underside of each inflated tibia I.

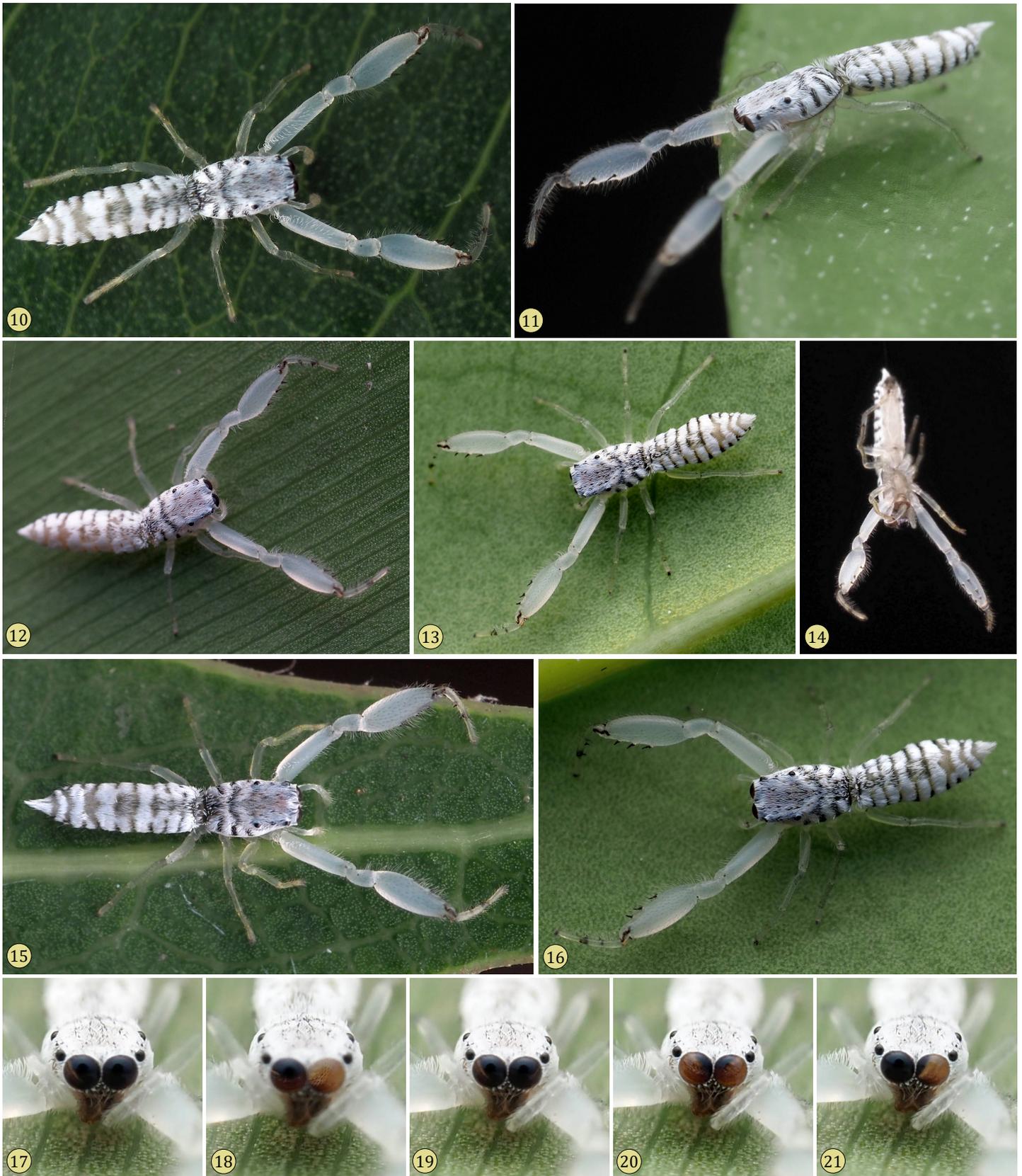


Figure 11 (continued from previous page). ♀ *Ligidus garvale* in Kodagu, Karnataka. 17-21, Sequence showing changing appearance of the AME as this female scanned the photographer.

The nests of female *Ligidus garvale* are similar to those of *L. chelifer* (Figures 6-9). The photos of *L. garvale* shelters and nests shown here (Figures 12-13) were taken recently in Kodagu (mostly 2-3 March, 2025).

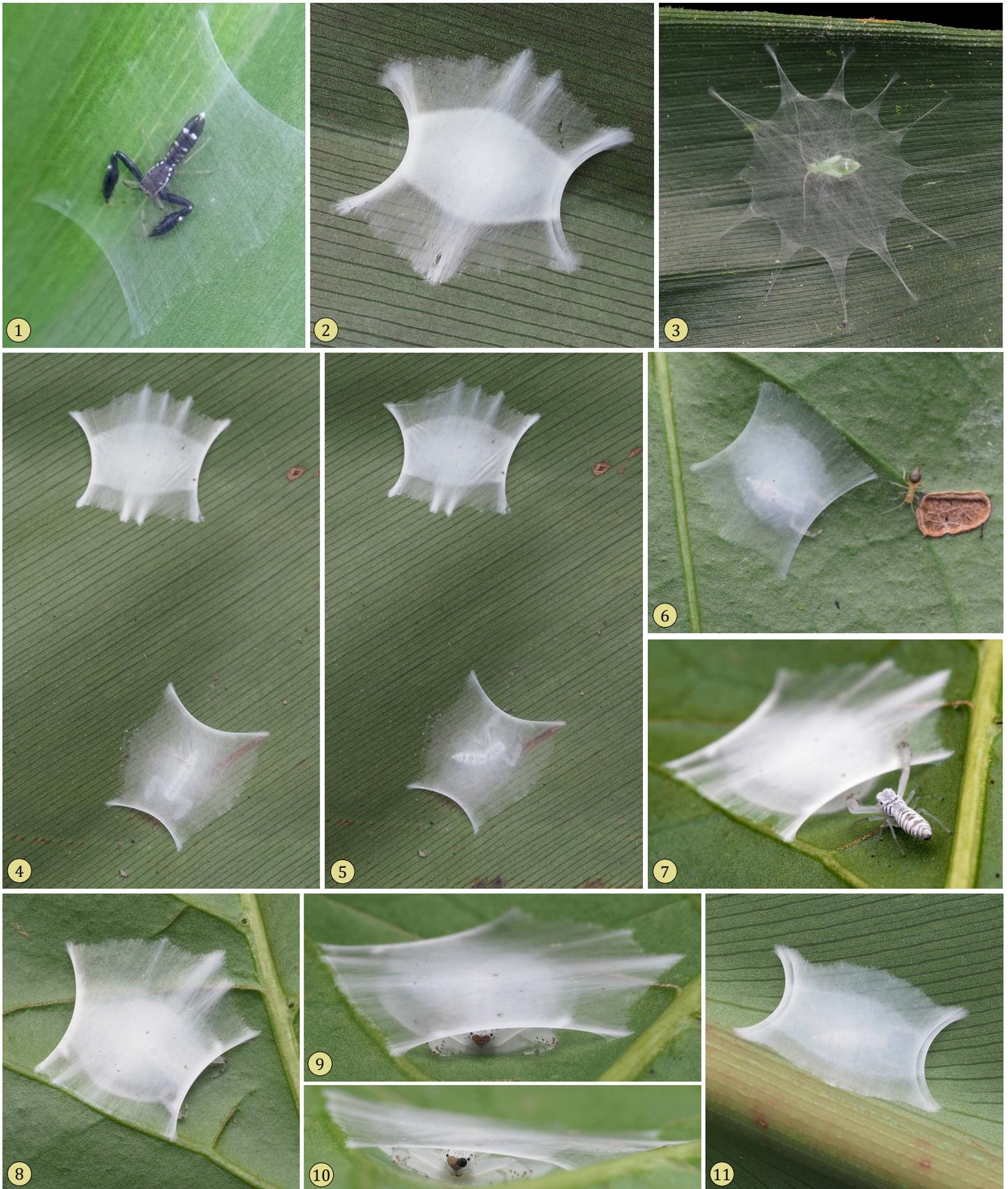


Figure 12. Flat shelters and nests on the underside of leaves, Kodagu, Karnataka. **1**, ♂ *Ligidus garvale* in shelter. **2**, *L. garvale* nest. **3**, Barklouse (Psocodea: Psocidae) in its elaborate silk shelter. Psocids produce silk from glands in their mouths. **4-5**, Two views of a ♀ *L. garvale* in a less formed nest, near a completed nest. Females may move from one nest to another. **6-11** (7-10 show one nest), ♀ *L. garvale* with nest.



Figure 13. Nests and broods of *Ligidus garvale* on the underside of leaves, Kodagu, Karnataka. **1-2**, Removal of the outer layer of this nest exposed a clutch of 7 eggs, beneath the parchment-like silk of the egg sac. **3-5**, By the next morning the female had returned to her nest, and replaced the outer layer above her chamber. **6-8**, Three views of a brood of eight advanced (note eye pigment) first instars, after the nest cover was pulled to one side. **9-10**, Free living early instars. **11-12**, Removal of the outer (11), then inner (12) layers of an older nest, now empty.

The nests of *Ligdus garvale* are remarkable, with one (and sometimes two, Figure 12.11) outer layers of structural and protective silk above the chamber inhabited by the female, accessible by two separate entrances. Below this the brood sac, which the female does not enter, is encapsulated with a layer of dense, parchment-like silk. As shown here (Figures 13.1-13.5), a female may return to a damaged nest and replace the chamber above the brood sac if this is damaged. First instars are gregarious, at the center of the brood sac, and it appears that it is solely by their activity that egg membrane remnants and exuviae are pushed to the sides of this sac (Figures 13.6-13.8). After instar 2 spiders (Figures 13.9-13.10) leave the nest through a break in the sac, all of their discarded egg membranes and the exuviae from their first two molts remain there (Figures 13.11-13.12).

5. *Mantisatta longicauda* Cutler & Wanless 1973

By its physical appearance alone, *Mantisatta longicauda*, endemic to the Philippines and neighboring islands, is the most remarkable member of the Copocrosseae. It is also much larger than other members of this group. Yet we know almost nothing of its life history. Cutler & Wanless (1973) described a single male specimen (the holotype) and a single female specimen that had been collected near the end of World War II (June-July of 1945) by one R. B. Burrows in Lingayen, Luzon, Philippines, and subsequently deposited in the collection of the American Museum of Natural History in New York. Just months earlier, the Japanese had occupied Luzon: the Battle of Luzon lasted from January to March of 1945.

Cutler & Wanless knew that a part of the *caudal process* (or tail) of their male was missing, and they did not know how long this was when intact. They described the unique appearance of the male, but did not produce a drawing of this. Thus, until the recent work of macrophotographers whose images are presented here (Figures 14-16), this species remained little-known. Although Cutler & Wanless suggested that *Mantisatta* species *might* be placed in the Lyssomanidae as a family separate from the Salticidae (pending further information), we now recognize this genus as a close relative of *Ligdus* and we are confident in its placement within the Copocrosseae.

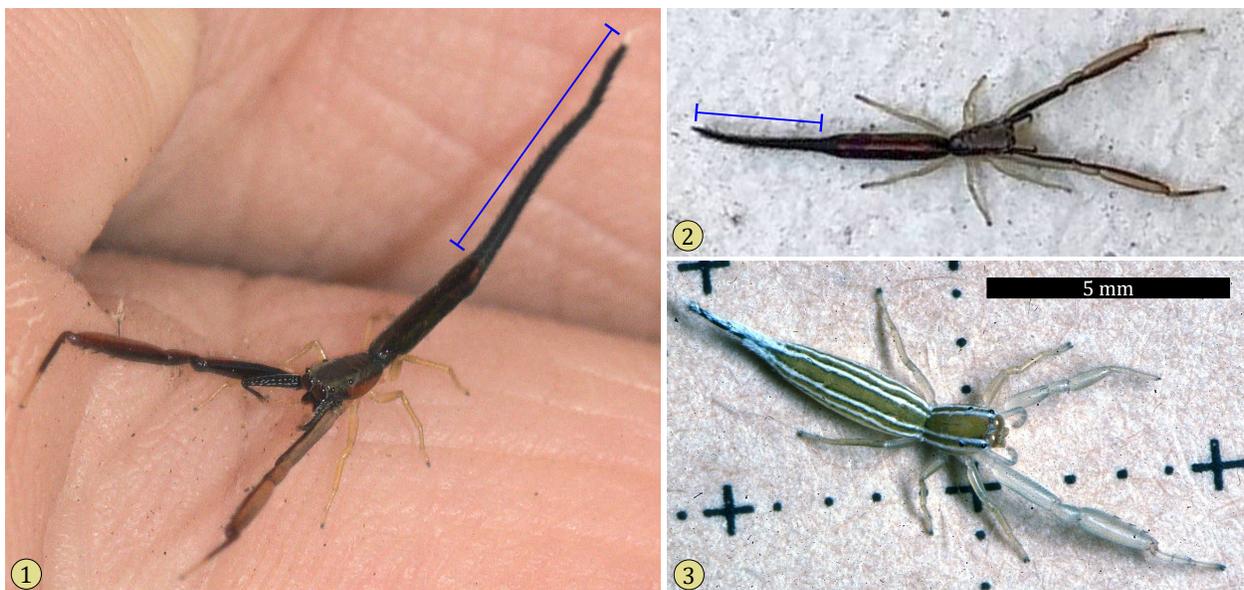


Figure 14. *Mantisatta longicauda*. **1**, ♂, Kepulauan Sangihe Talaud, Sulawesi Utara, Indonesia. **2**, ♂, Silang, Cavite, Philippines. **3**, ♀, Los Baños, Laguna Province, Luzon. We do not know how long the tail of the male (blue lines in 1 and 2) can get, if this varies by individual, or whether the tip of this tail is normally white as shown in (1). The female has a distinct dorsal pattern, and a much shorter tail. Photo credits: 1, iNat. obs. 193770942, © Isaac Krone, CC BY 4.0; 2, iNat. obs. 20344352, © lenisutcliffe, CC BY-NC 4.0; 3, WPM#93-146, © 2015 W. Maddison, CC BY 3.0.



Figure 15. ♂ *Mantisatta longicauda*, Philippines. The long caudal process or tail of this island species can be raised by the male (4), but we are unsure of its function. It may be used in courtship display, to mimic the tail of a scorpion, or for both purposes. Photo credits: 1-6, © Nicky Bay, used with permission.

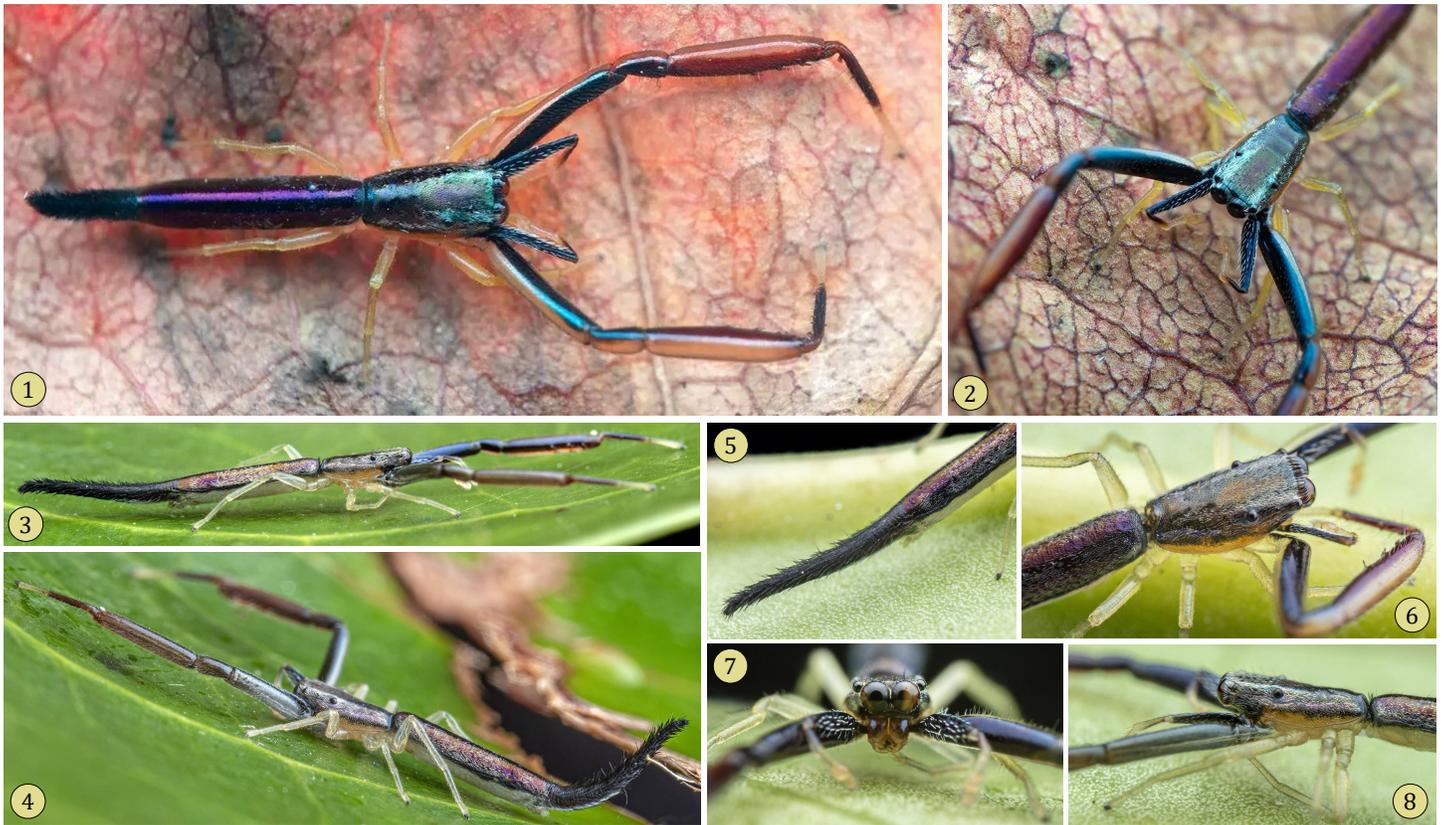


Figure 16. ♂ *Mantisatta longicauda*, Philippines. 1-2, Dorsal view of a male that may be missing most of its tail. Note the white setae on the prolateral side of each pedipalp femur (also visible in 7). The color of the femur and patella of the pedipalps makes them look like prognathous chelicerae with extended fangs. 3, Lateral view showing the dorso-ventral compression of this spider. 4, Here the tail is elevated in a manner that might mimic a small scorpion. 5, Detail of tail showing cover of black setae. Photo credits: 1-2, iNat. obs. 105310764, © Alope Sahu, CC BY-NC 4.0; 3-8, © Nicky Bay, used with permission.

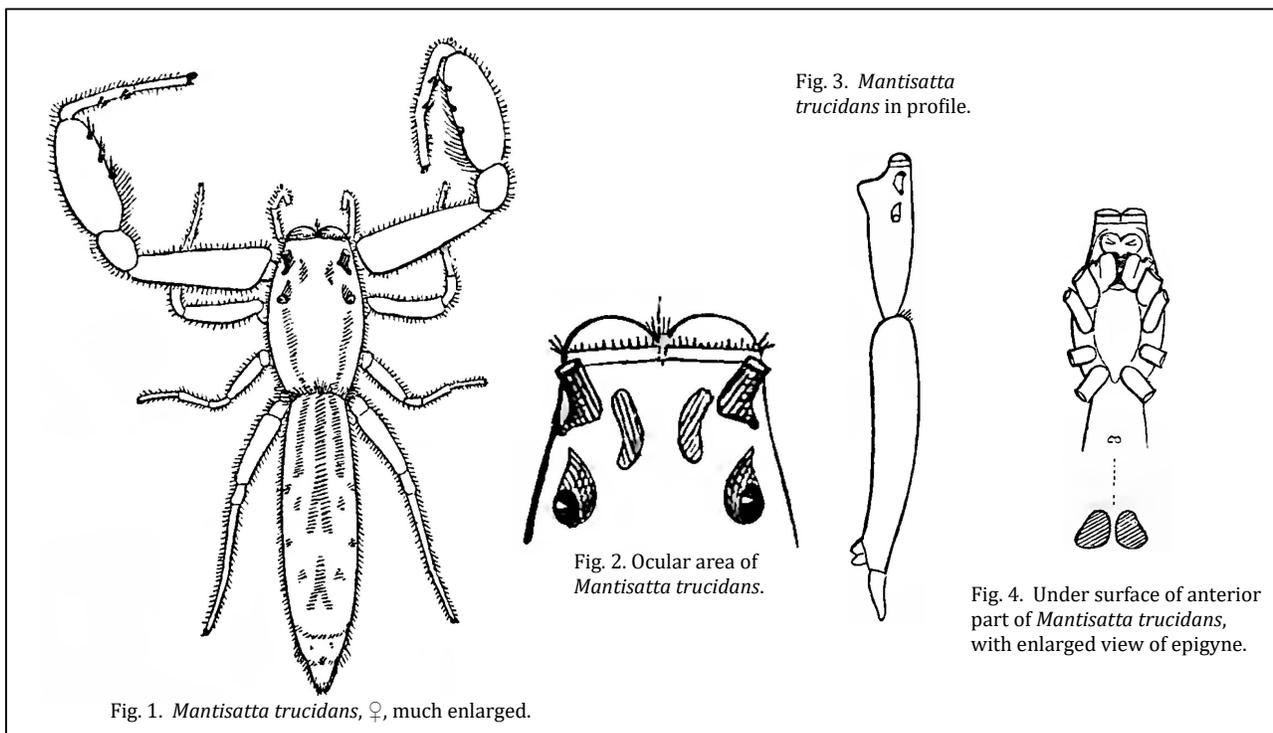
5. *Mantisatta trucidans* Warburton 1900

This species, the type for *Mantisatta*, is known from a single female specimen collected more than 125 years ago in Sarawak. Cutler & Wanless (1973) were able to obtain and redescribe the type specimen held in the University Museum of Zoology, Cambridge. Here we present Warburton's description, to include his figures, in its entirety:

Fam. Attidae — Subfam. Lyssomanae — Genus *Mantisatta*, n. gen. Body elongated and depressed. Eyes arranged as in *Lyssomanes*. Spinnerets *beneath* the posterior end of the abdomen, which is produced beyond them into a caudal process. Legs of the first pair much the most strongly developed, with strong forwardly directed spines under the tibia and *backwardly* directed spines under the metatarsus, forming a prehensile weapon when these joints are apposed.

Mantisatta trucidans, n. sp. (Fig. 1.) *Female*. Total length 4 mm.; length of thorax 1½ mm.; length of abdomen 2½ mm. Greatest breadth of thorax (about the level of the second pair of legs) about 1 mm.; of the abdomen about .75 mm. The cephalothorax is much depressed and is about half as long again as broad. The first pair of eyes are very large, occupying the whole breadth of the facies, and are mounted on short cylinders which project forward. The second and third pairs of eyes are on confluent dark-coloured eminences. The second eyes [ALE], which are pale-coloured, are about a quarter of the anterior eyes [AME] in diameter. The third eyes [PME] are very small and black. The fourth pair of eyes [PLE], somewhat farther behind the third pair than these are behind the second, are dark and moderately large, their diameter being about one third of that of the anterior eyes [AME]. The whole ocular area (fig. 2. p. 386) forms almost an exact square. The abdomen is a depressed cylinder; more than three times as long as broad. The spinnerets are not visible from above, being hidden by a caudal process (fig. 3, p. 386). The anterior legs are about as long as the whole animal, the femora, patellae, and tibiae being very strongly developed, and giving the Spider a chelifer-like appearance. Beneath each tibia,

towards its distal end, are three pairs of strong black spines, directed forward. The metatarsus, which can be closed upon the tibia, bears two pairs of shorter black spines directed backward. One pair is beneath the middle of the joint, and the other near its distal extremity. The other legs (4, 2, 3) are small and weak, and do not appear to be adapted for leaping. The whole Spider is exceedingly pale —almost white—in colour, at all events as it appears after immersion in spirit. Dorsally it is variegated by a pattern marked out in faint dusky lines and dots. On the cephalothorax there are two dark patches between the third pair of eyes, and the second, third, and fourth pairs of eyes are on black eminences. Behind the fourth pair commence two faint dusky lines, which converge slightly as they approach the abdomen, along which they are continued for nearly a third of its length. Along the first half of the abdomen there is a median line, forking posteriorly. This is succeeded by a shorter line which forks similarly, and behind this there is a transverse line. On each side of the central marking there are a series of dots, the distribution of which is shown in fig. 1. The body is thinly pubescent. The under surface of the body is whitish except the small yellow-brown epigyne (fig. 4). The legs are similar in colour, and, except for the spines on the tibiae and metatarsi of the first pair, are furnished only with a thin clothing of hairs. All exhibit black scopulae on the tarsi. Male unknown. A single adult female was found among a collection of insects made by Dr. G. D. Haviland in Sarawak. Nothing is known of its habits, but from the nature of the collection it is probable that it was found inside a termites' nest. Its structure would suggest that it does not pounce upon its prey in the usual Attid fashion, but that it remains still and seizes passing insects with its predaceous front legs.



Photographs of *Mantisatta trucidans* have been posted on *iNaturalist*, but never recognized as this species until now (Figure 17). However a single record of a male *M. trucidans*, probably from Sabah, was posted on *FLICKR* in 2014, and this includes two excellent photographs (Shim 2014). *M. trucidans* and *M. longicauda* are very closely related. Except for the much longer tails of *M. longicauda* males and females the two are very similar. The dorsal pattern of the females is, however, quite different. The extreme development of *M. longicauda*, with respect to both size ("gigantism") and the length of the tail appears to represent a case of what is known as *the island syndrome* (Novosolov et al. 2012; Baeckens & Van Damme 2020; Jezierski et al. 2023; Terborgh 2023). Although the Palawan island group is part of the Sunda Shelf, connected to mainland Asia during most of the Pleistocene, the islands where *M. longicauda* have been found have been isolated from the mainland for millions of years (Vane-Wright 1990; Hall & Morley 2004).

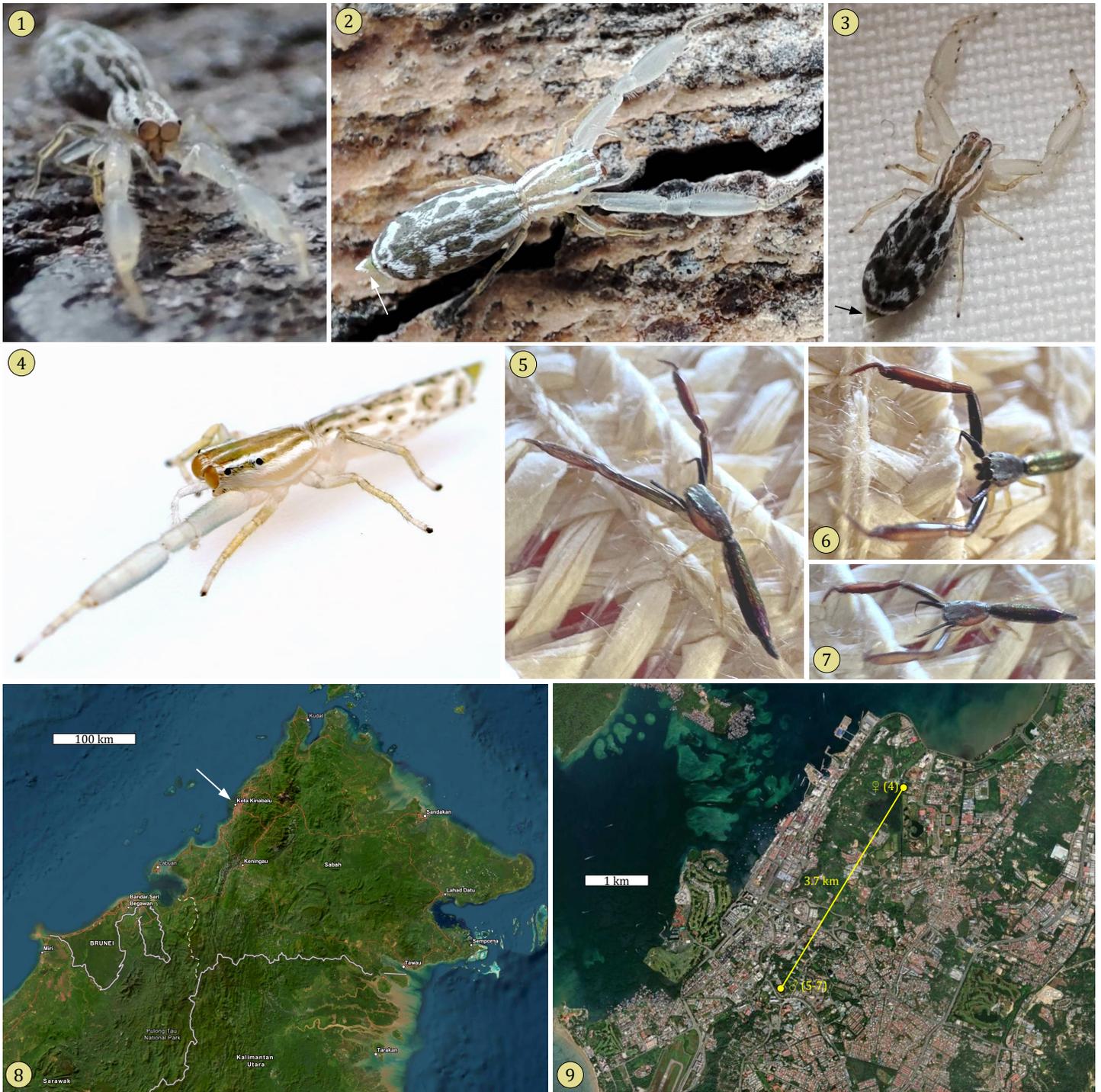


Figure 17. Recent records for *Mantisatta trucidans*. **1-3**, ♀, Dauin, Negros Oriental, Philippines. Note the presence of a short tail (arrows), and a distinctive pattern on the dorsum. As shown here, this pattern can be much darker than the drawings by either Warburton or Cutler & Wanless would suggest. **4**, ♀, Kota Kinabalu, Sabah. This female is much lighter in color than the female from the Philippines. **5-7**, ♂, Sabah. Previously not described, these look much like the ♂ *M. longicauda*, except that the tail is very short (but also black). For better pictures of the ♂, see Simon (2014). **8-9**, The female (4) and male (5-7) shown here were found at two localities in Kota Kinabalu, separated by on 3.7 km. Photo credits: 1-3, iNat. obs. 254793542, © Benoît Segerer, CC BY-NC 4.0; 4, iNat. obs. 240883347, © oly_pos, CC BY-NC 4.0; 5-7, iNat. obs. 258812622, © samding, CC BY-NC 4.0; 8-9, Base maps © OpenStreetMap.

Other Copocrosseae

Here we identify several iNaturalist records that appear to represent undescribed species in this group (Figure 18). These are posted under their respective reference numbers on the map (Figure 1).



Figure 18. Undescribed Copocrosseae. **1-3**, ♂ *Copocrossa* sp. A (#7), Andaman Islands. **4**, ♂ *Copocrossa* sp. B (#8), Sunshine Coast, Queensland. **5**, ♀ *Ligdus* sp. A (#9), Jamberoo, New South Wales. **6-7**, ♀ *Ligdus* sp. A (#9) with nest, Queensland. Photo credits: 1, iNat. obs. 177300629, © arnoldashu, CC BY-NC 4.0; 2, iNat. obs. 195840791, © Shelley Rutkin, CC BY-NC 4.0; 3, iNat. obs. 200611589, © Linda, CC BY-NC 4.0; 4, iNat. obs. 96556442, © donnamareetomkinson, CC BY-NC 4.0; 5, iNat. obs. 247572904, © hollythefrog, CC BY 4.0; 6-7, iNat. obs. 287468986, © Lawrence Hylton, CC BY 4.0.

Copocrossa sp. A and sp. B. have the relatively small pedipalps characteristic of males in that genus. The third species shown here (*Ligdus* sp. A) has a nest (Figures 18.6-18.7) like those constructed by females of the two known *Ligdus* species; the nests of *Copocrossa* are unknown. Female *Ligdus* sp. A have about five incomplete or indistinct bands on either side of the opisthosoma, and a distinct black stripe running along the lower prolateral surface of the femur of each first leg.

Mimicry of pseudoscorpions by copocrossean jumping spiders. When the small *Ligdus* are observed in the field, they can easily be mistaken for pseudoscorpions in their general appearance and manner of movement (Figure 19).



Figure 19. *Ligdus* and pseudoscorpions from Karnataka. 1, ♀ *Ligdus garvale*, for comparison. 2-3, Pseudoscorpions on the underside of leaves. 4, Family of pseudoscorpions in exposed nest, showing multiple generations. 5, ♀ Pseudoscorpion (*Ellingsenius*) with two nests, one opened to show the egg cluster that she is brooding. 6, ♀ Pseudoscorpion (*Ellingsenius*) with her recently hatched brood inside of an exposed nest.

Ligdus scuttle forwards and backwards on their relatively short legs II-IV and seem to avoid jumping altogether. Their small size, compressed bodies, small mouthparts, enlarged tibiae I (like the chelate terminate segments of the pseudoscorpion pedipalps), and the position in which they hold their first legs as they walk are pseudoscorpion-like. In the case of *L. garvale*, the transverse bands also resemble the segmentation of pseudoscorpions. Curiously, the flattened nests of pseudoscorpions may also look like those of *Ligdus* (Figures 19.5-19.6). Pseudoscorpions lack spinnerets, but produce their silk with cheliceral glands.

Cheliferoidea F. O. Pickard-Cambridge 1901 is a distantly related genus of North American jumping spiders that are also thought to mimic pseudoscorpions (Figure 20). These are not so distantly related, as both genera are in the clade Marpissoida. Within this clade, the copocrosseans are in the tribe Ballini, *Cheliferoidea* in the tribe Dendryphantini (see Figures 21-22). In his description of *C. segmentatus*, F. O. Pickard-Cambridge (1901) wrote that *one would expect by its general appearance that this spider mimics one of the pseudoscorpions*. Much later, Platnick (1984) wrote:

Cambridge's hypothesis has remained uninvestigated (as has the species), but it has gained recent support from the discovery of a male and juvenile specimens living together with several chernetid pseudoscorpions of similar size and appearance under the bark of mesquite in Maricopa County, Arizona. the pseudoscorpions belong to *Parachernes* (Muchmore, *in litt.*). The flatness of the spiders, the modification of the first legs into structures resembling pseudoscorpion palpal chelae, and the abdominal pigmentation, which provides a strongly segmented appearance, all contribute to the resemblance.

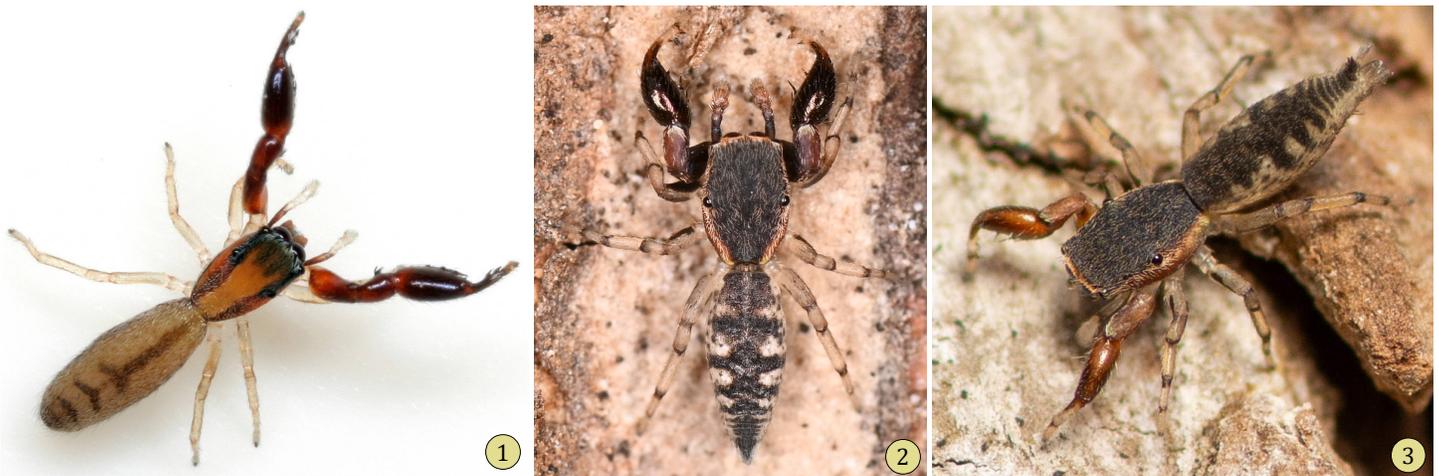


Figure 20. *Cheliferoidea* from Texas. 1, ♀ *C. longimanus*. 2, ♂ *C. segmentatus*. 3, ♀ *C. segmentatus*. Photo credits: 1, iNat. obs. 87204422, © Mike Quinn, San Marcos, CC BY-NC; 2, iNat. obs. 263550844, © yukioz, CC BY-NC 4.0; 3, iNat. obs. 199963443, © Justin Williams, CC BY 4.0.

If *Ligdus* do mimic pseudoscorpions, they may derive some benefit from the fact that pseudoscorpions discharge venom through the "fingers" of their chelate pedipalps (Krämer et al. 2021). This would represent a form of Batesian mimicry, deterring potential predators of the spider. On the other hand, similarities might also reflect evolutionary convergence to arrive at a similar morphology and lifestyle, which may include sharing of the same prey species. It is also possible that, to some extent, evolutionary convergence preceded Batesian mimicry. We have yet to learn the extent to which copocrossean salticids and pseudoscorpions share the same microhabitat, as has been reported for *Cheliferoidea*.

Phylogeny and biogeography of the Copocrosseae. Our working hypothesis, based on many sources (see Hill 2025), shows the Ballini as an Afroeurasian radiation of the Marpissoida, parallel to the American radiation of the Dendryphantini (Figure 21). Benjamin (2004) published a hypothesis of balline phylogeny based on morphology, but this was quite different from the more recent phylogeny of several genera in this group based on DNA sequencing (Bopearachchi & Benjamin 2019; Figure 22). According to one analysis (Bodner 2009, *Beast Analysis 1*), divergence or separation of Marpissoida from Mopsida (the latter including Astoida) took place ca. 34Ma, at the end of the Eocene when the *Antarctic Land Bridge* joining Australasia to the Americas was lost. According to this analysis, separation of the Ballini and the Dendryphantini took place ca. 29Ma, and *Mantisatta*, representing the Copocrosseae, diverged from most of the other Afroeurasian Ballini ca. 23Ma. It is thus likely that the presence of *Copocrossa* or *Ligdus* in Australasia is the result of more recent dispersal from tropical Asia, through Wallacea, to Australasia.

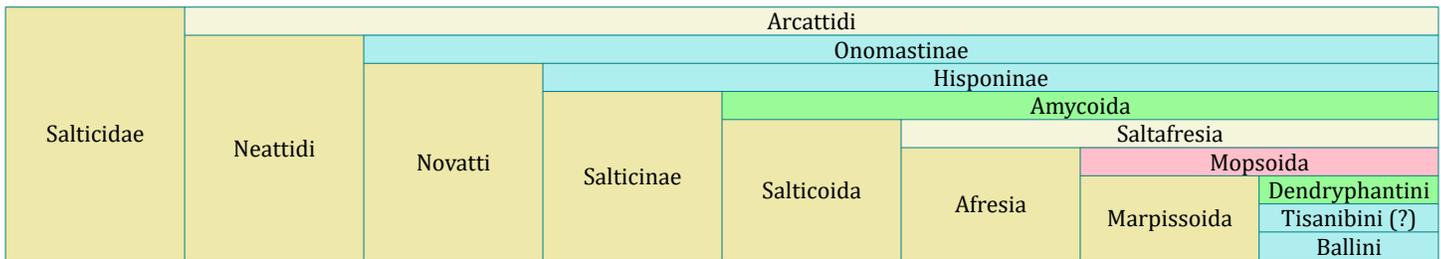


Figure 21. Working hypothesis for evolution of the Salticidae, after Hill 2025 (see references cited therein). The placement of the Tisanibini is uncertain. Primary continental distribution of clades is as follows: blue, Afroeurasia; green, Americas; pink, Australasia.

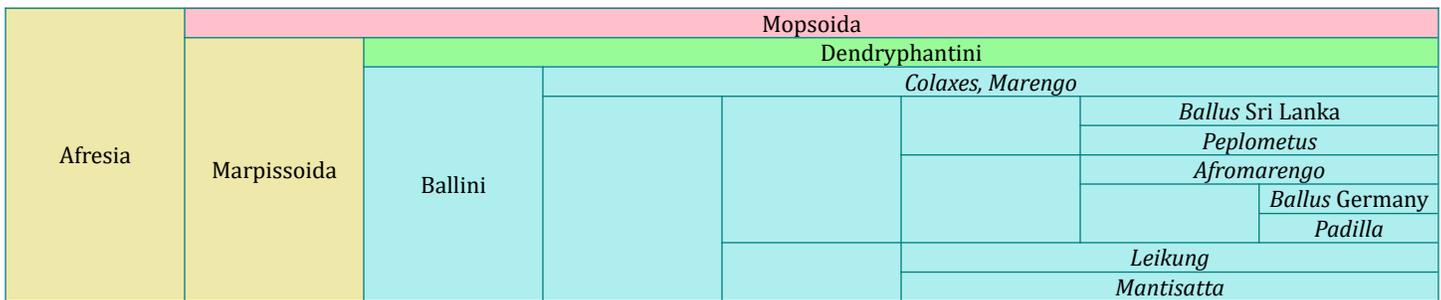


Figure 22. Phylogeny of a set of balline genera that includes the copocrossean *Mantisatta*, after Bopearachchi & Benjamin (2019).

Other ballines also have an inflated tibia I and may resemble pseudoscorpions, but these are generally ant-like and their inflated tibiae I may resemble the head of an ant or another insect when viewed from one side or the other (Figure 23).



Figure 23. Balline jumping spiders with inflated tibiae I. Unlike the Copocrosseae, the pedicel in these species is quite evident, and they appear to be ant mimics. **1**, ♀ *Philates*, Kanchanaburi, Thailand. **2-3**, ♂ *Leikung porosa*, Kinabalu Park Sabah. **4**, ♀ *Pengmarengo chelifer*, Singapore. **5**, ♂ *Pengmarengo chelifer*, Johor, Malaysia. **6-7**, ♂ *Pengmarengo chelifer*, Singapore. Photo credits: 1, iNat. obs.156396266, © watsaisaeng, CC BY-NC 4.0; 2-3, iNat. obs. 61848277, © Ben Tsai蔡維哲, CC BY-NC 4.0; 4-7, iNat. obs. 255168362 [4], 240730880 [5], 231633333 [6-7], © Melvyn Yeo, CC BY-NC 4.0.

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