

Cirolana songkhla, a new species of brackish-water cirolanid isopod (Crustacea, Isopoda, Cirolanidae) from the lower Gulf of Thailand

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Abstract

Cirolana songkhla sp. n. was collected from brackish-water habitats including lagoons and estuaries in the coastal zone of the lower Gulf of Thailand. *C. songkhla* sp. n. is described and fully illustrated; *C. songkhla* sp. n. can be recognized by the presence of abundant chromatophores dorsally, lack of ornamentation on the posterior pereonites, pleonites and pleotelson, the number of robust setae on the uropodal and pleotelson margins (uropod exopod lateral margin with 12–14 RS, mesial margin with 5–8 RS; endopod lateral margin with 8–10 RS, mesial margin with 11–13 RS; pleotelson with 12–15 RS) and lack of setae on the endopods of pleopods 3–5. A dichotomous key of brackish *Cirolana* species in Thailand is given.

Keywords

Isopoda, Cirolanidae, *Cirolana*, new species, brackish water, Thailand

Introduction

The family Cirolanidae has received little attention in Thailand and South-East Asia in general, with only 13 species in eight genera known from Thailand. The genus *Cirolana* Leach, 1818, the largest genus in the family with 129 species (Bruce and Schotte 2013) is equally poorly known in the region. Suvatti (1967) listed the known species from Thailand, while Kensley (2001) listed the species known to date from the Indian Ocean, including the western coasts of Thailand. Recently, Bruce and Olesen (2002) have reported four marine cirolanid species from Andaman Sea including two new species of *Cirolana*. All the brackish species of *Cirolana* have been recorded only from the Gulf of Thailand: *C. willeyi* Stebbing, 1904 from the Mae Klong River, Samut Songkhram province (Upper Gulf of Thailand) (Suvatti 1967); and *C. pleonastica* Stebbing, 1900 and *C. parva* Hansen, 1890 from Songkhla Lake (Lower Gulf of Thailand) (Chilton 1924, 1926). Chilton's (1924, 1926) records are both now regarded as misidentification as Barnard (1935) suggested that the record of *C. pleonastica* was in fact *C. fluviatilis* Stebbing, 1902 and Bruce and Bowman (1982) showed that *C. parva* is restricted to the Caribbean and Central American coasts. Although there had been numerous relatively recent advances in the taxonomy of the Cirolanidae (e.g. see Bruce 1986, Brusca et al. 1995, Keable 2006, Moore and Brusca 2003, Riseman and Brusca 2002), knowledge on Thailand's fauna remains minimal.

This present report corrects Chilton's record of *C. parva*, describes *C. songkhla* sp. n., and presents a key of the brackish-water species of *Cirolana* that occur in Thailand.

Materials and Methods

Specimens were collected by using baited traps from brackish-water habitats including the lagoon and estuary in the lower Gulf of Thailand (Figure 1). Appendages were dissected and drawn under stereo and compound microscopes with a camera lucida. Morphological characters for the description (based on Bruce 2004) were prepared by using DELTA (Descriptive Language for Taxonomy: Dallwitz et al. 1997). The type material of the new species is deposited at Prince of Songkla University Zoological Collection (PSUZC) and Museum of Tropical Queensland (MTQ).

Abbreviations: PMS, plumose marginal setae; RS, robust seta/setae; CPS, circumplumose setae.

Taxonomy

Genus *Cirolana* Leach, 1818

<http://species-id.net/wiki/Cirolana>

Restricted synonymy. Bruce 1986: 139, Kensley and Schotte 1989: 132, Brusca et al. 1995: 17.

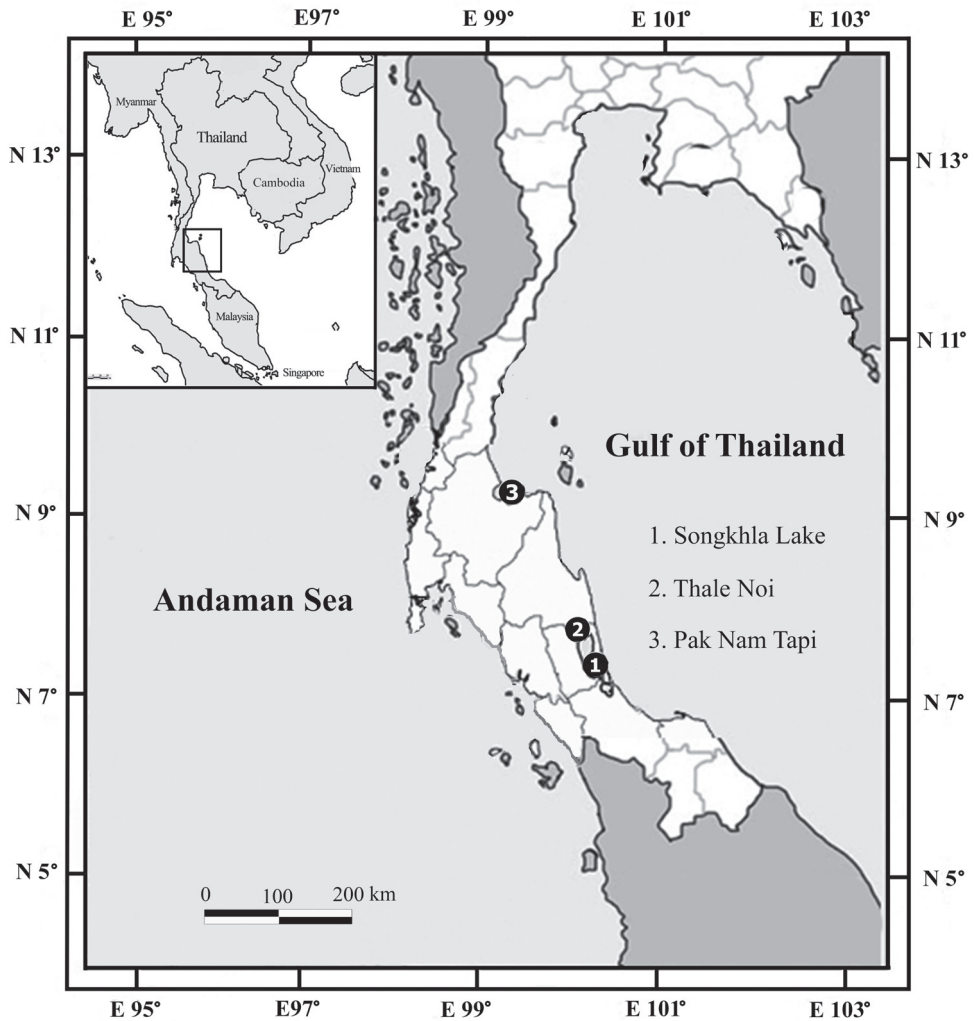


Figure 1. Map of sampling sites.

Remarks. *Cirolana* is the largest genus of the Cirolanidae (Bruce 1981, 1986, Brusca et al. 1995, Keable 2006) with 129 named species (Bruce and Schotte 2013) and many more not yet described. *Cirolana* occurs from cool-temperate to tropical regions, primarily in marine environments, but also occasionally found in low-salinity habitats, such as mangroves, estuarine reaches of rivers and creeks (Bruce 1986), and also rarely found in freshwater and cave and ground waters (Kensley and Schotte 1989, Botosaneanu and Iliffe 2000). Most low salinity and freshwater species of *Cirolana* lack setae on the endopods of pleopods 3 and 4, and were formerly placed in the genus *Anopsilana* Paulian & Delamare-Deboutville, 1956 (e.g. Bruce 1986; Bruce and Iliffe

1993), but following Botosaneanu and Iliffe (1997) the genus is now accepted as a junior synonym of *Cirolana*.

Diagnoses to the genus have been given by Bruce (1986), Brusca et al. (1995) and Kensley and Schotte (1989).

***Cirolana songkhla* sp. n.**

<http://zoobank.org/40967001-288A-433E-8B14-A411034CE8A7>

http://species-id.net/wiki/Cirolana_songkhla

Figs 2–6

?*Cirolana parva*: Chilton 1924: 883, 1926: 180 (misidentification as *Cirolana parva* Hansen, 1890 in part of freshwater records only; same species as *Cirolana songkhla* sp. n.).

Material examined. Holotype, ♂ (13.7 mm), middle part of Songkhla Lake, Phattalung province, 07°29.09'N, 100°20.11'E, 23 October 2011, gravel bottom and associated with water plants, salinity 4 ppt, coll. E. Rodcharoen (PSUZY-CR0281-01).

Paratypes, 10 ♂ (13.8, 11.2, 12.4, 10.2, 10.3, 10.0, 13.8, 11.8, 11.4, 10.6 mm [dissected]), 1 ♀ (ovig. 8.7 mm [dissected]), further specimens unmeasured, same data as holotype (PSUZY-CR0281-02; MTQ W34265). 8 ♂ (11.1, 12.8, 12.2, 13.9, 13.2, 12.4, 12.2, 9.8 mm [dissected]), 4 ♀ (ovig. 8.6, 8.7 [dissected], 8.8, 9.0 mm), further specimens unmeasured, Klong Ban Klang, Thale Noi, Phattalung province, 07°46.44'N, 100°09.27'E, 27 May 2013 clay bottom, salinity 0.6 ppt, coll. E. Rodcharoen (PSUZY-CR0281-03; MTQ W34266).

Additional material. 12 ♂ (unmeasured), same data as holotype (PSUZY-CR0281-04), 38 ♂ and 3 ♀ (unmeasured), same data as paratype PSUZY-CR0281-03; MTQ W34266 (PSUZY-CR0281-05; MTQ W34267), 1 adult ♂ and 3 juvenile (unmeasured), Pak Nam Tapi (estuary), Surat Thani province, 09°10.31'N, 99°21.36'E, 30 October 2012 coll. E. Rodcharoen (PSUZY-CR0281-06).

Description of male. *Body* 3.2 times as long as greatest width, dorsal surfaces smooth, widest at pereonite 5 and pereonite 6, lateral margins subparallel (Figure 2A). *Rostral point* (Figure 2C) present, folded ventrally and posteriorly, in contact with frontal lamina (Figure 2D, E). *Eye* colour dark brown; eyes separated by about 81% width of head (Figure 2C). *Pereonite 1 and coxae* 2–3 each with posteroventral angle rounded; coxae 5–7 with entire oblique carina; posterior margins of pereonites 5–7 smooth (Figure 2B). *Pleon* (Figure 2F) with pleonite 1 largely concealed by pereonite 7; pleonites 3–5 posterior margins smooth; posterolateral angles of pleonite 2 forming acute point, extending posteriorly to anterior of pleonite 4; pleonite 3 with posterolateral margins extending clearly beyond posterior margins of pleonites 4 and 5, narrowly rounded; posterolateral margin of pleonite 4 rounded, clearly extending beyond posterior margin of pleonite 5. *Pleotelson* (Figure 6E) 1.0 times as long as anterior width, dorsal surface without longitudinal carina; lateral margins convex; margins weakly serrate, posterior margin converging to small distinct caudomedial point, with 12 RS (Figure 6E, F).

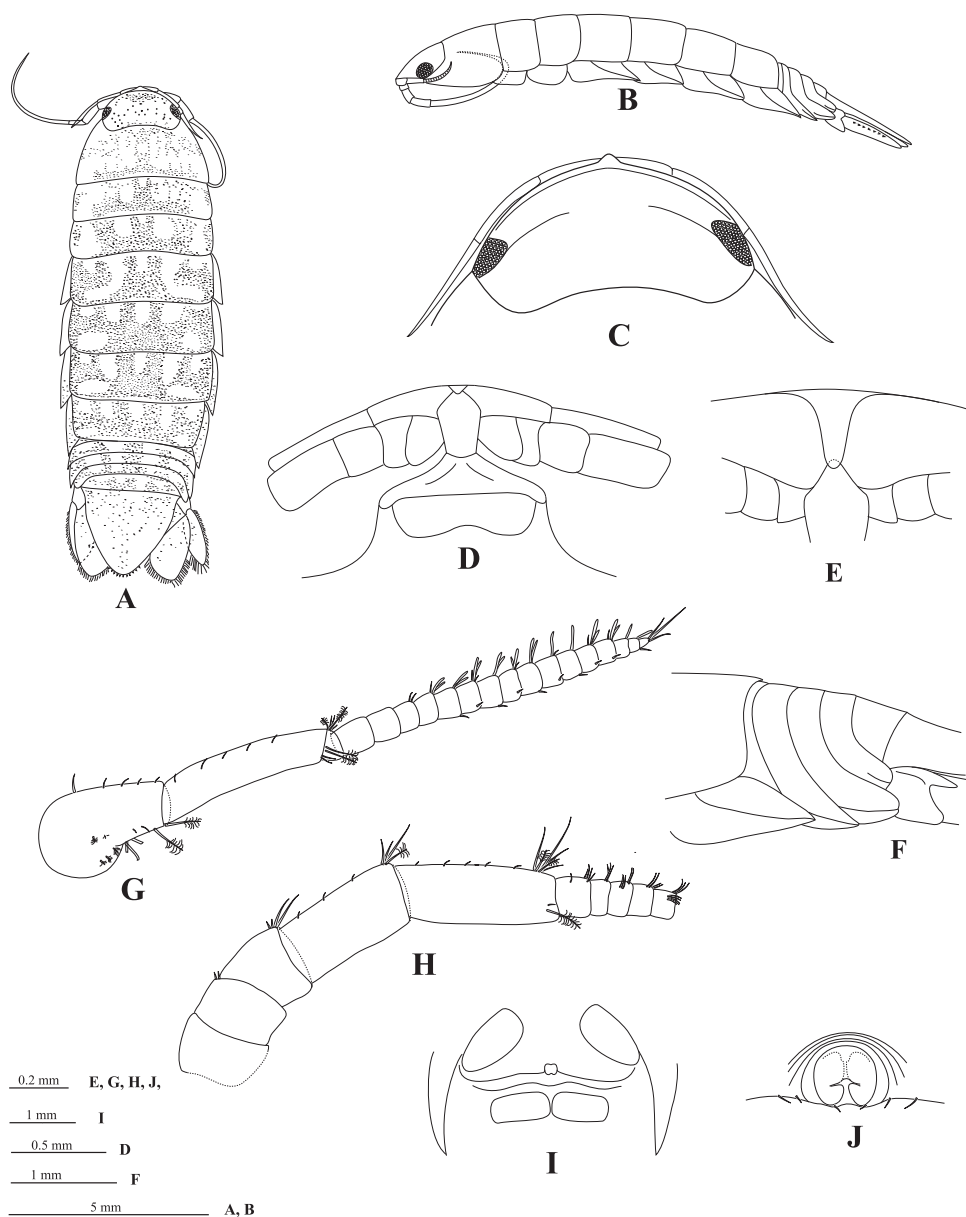


Figure 2. *Cirolana songkhla* sp. n., male holotype (PSUZC-CR0281-01) (13.7 mm) (**A–F**), male paratype (PSUZC-CR0281-2) (11.2 mm) (**G–H**), male paratype (PSUZC-CR0281-2) (13.8 mm) (**I–J**). **A** dorsal view **B** lateral view **C** head, dorsal view **D** frons **E** detail of frontal lamina **F** pleon **G** antennule **H** antennal peduncle **I** antero-ventral view of penial opening **J** ventral view of penial opening.

Antennule (Figure 2G) peduncle articles 1 and 2 entirely fused; articles 3 and 4 1.3 times as long as combined lengths of articles 1 and 2, article 3 5.0 times as long as wide; flagellum with 16 articles, extending to middle of pereonite 1. *Antenna*

(Figure 2H) peduncle article 4 1.8 times as long as wide, 2.2 times as long as article 3, anterodistal angle with 3 short simple setae and 1 plumose seta; article 5 1.2 times as long as article 4, 2.4 times as long as wide, anterodistal angle with cluster of 4 short simple setae and 2 plumose setae; flagellum with 34 articles, extending to posterior of pereonite 4.

Frontal lamina (Figure 2D, E) pentagonal, 2.2 times as long as posterior width; 1.6 times as long as greatest width, lateral margins straight, diverging slightly towards anterior, anterior margin acute, with small median point.

Mandible molar process (Figure 3A) anterior margin with 19 flat teeth; with proximal cluster of long simple setae; right mandible spine row composed of 13 spines; palp article 2 with 21 distolateral setae, palp article 3 with 22 biserrate RS (Fig 3B). *Maxillule* (Figure 3C) mesial lobe with 3 large circumplumose RS; lateral lobe with 13 RS (weakly serrated). *Maxilla* (Figure 3D) lateral lobe with 4 long setae; middle lobe with 12 long setae; mesial lobe with 4 distal plumose setae and 14 proximal plumose setae. *Maxilliped palp* (Figure 3E) article 1 mesial margin with 1 slender seta; article 2 mesial margin with 6 slender setae, lateral margin distally with 2 slender setae; article 3 mesial margin with 15 slender setae, lateral margin with 13 slender setae; article 4 mesial margin with 17 slender setae, lateral margin with 9 slender setae; article 5 distal margin with 18 setae, lateral margin with 6 setae; endite (Figure 3F) with 6 long CPS, and 2 coupling setae.

Pereopod 1 (Figure 4A, C) *basis* 2.3 times as long as greatest width, inferior distal angle with cluster of 2 acute setae; *ischium* 0.5 times as long as basis, inferior margin with 1 acute seta, inferior distolateral margin with 2 setae (1 molariform RS and 1 acute seta), median distolateral margin with 2 acute setae, superior distal margin with 3 RS; *merus* inferior margin with 6 molariform RS, (set in rows of 4 and 2), superior distal angle with 3 setae (slender); *carpus* inferior distal margin with 2 setae (1 RS and 1 acute seta); *propodus* 2.0 times as long as wide, inferior margin with 2 RS; *dactylus* (Figure 4B) 0.5 times as long as propodus. *Pereopod 2* (Figure 4D) *ischium* inferior margin with 2 stout, bluntly rounded RS, superior distal margin with 3 RS; *merus* inferior margin with 10 stout RS, set in one row, superior distal margin with 6 acute RS; *carpus* inferodistal angle with 3 RS (plus 1 slender seta); *propodus* 3.5 times as long as wide; *dactylus* 0.7 times as long as propodus. *Pereopod 3* similar to pereopod 2. *Pereopod 4* (Figure 4E) intermediate in form between pereopod 3 and pereopod 5. *Pereopod 6* (Figure 4F) similar to pereopod 7. *Pereopod 7* (Figure 4G) *basis* 3.0 times as long as greatest width, superior margin weakly convex, inferior margin with 3 palmate setae; *ischium* 0.8 times as long as basis, inferior margin with 8 RS (set in groups of 3, 3, 1 and 1), superior distal angle with 6 RS (5 simple, 1 biserrate), inferior distal angle with 2 RS; *merus* 0.5 times as long as ischium, 2.0 times as long as wide, inferior margin with 3 RS, superior distal angle with 6 RS (3 simple, 3 biserrate), inferior distal angle with 7 RS; *carpus* 0.7 times as long as ischium, 2.4 times as long as wide, inferior margin with 6 RS (set in groups of 2 and 4), superior distal angle with 11 RS (4 simple, 7 biserrate), inferior distal angle with 9 RS (6 simple, 3 biserrate); *propodus* 0.8 times as long as ischium, 5.4 times

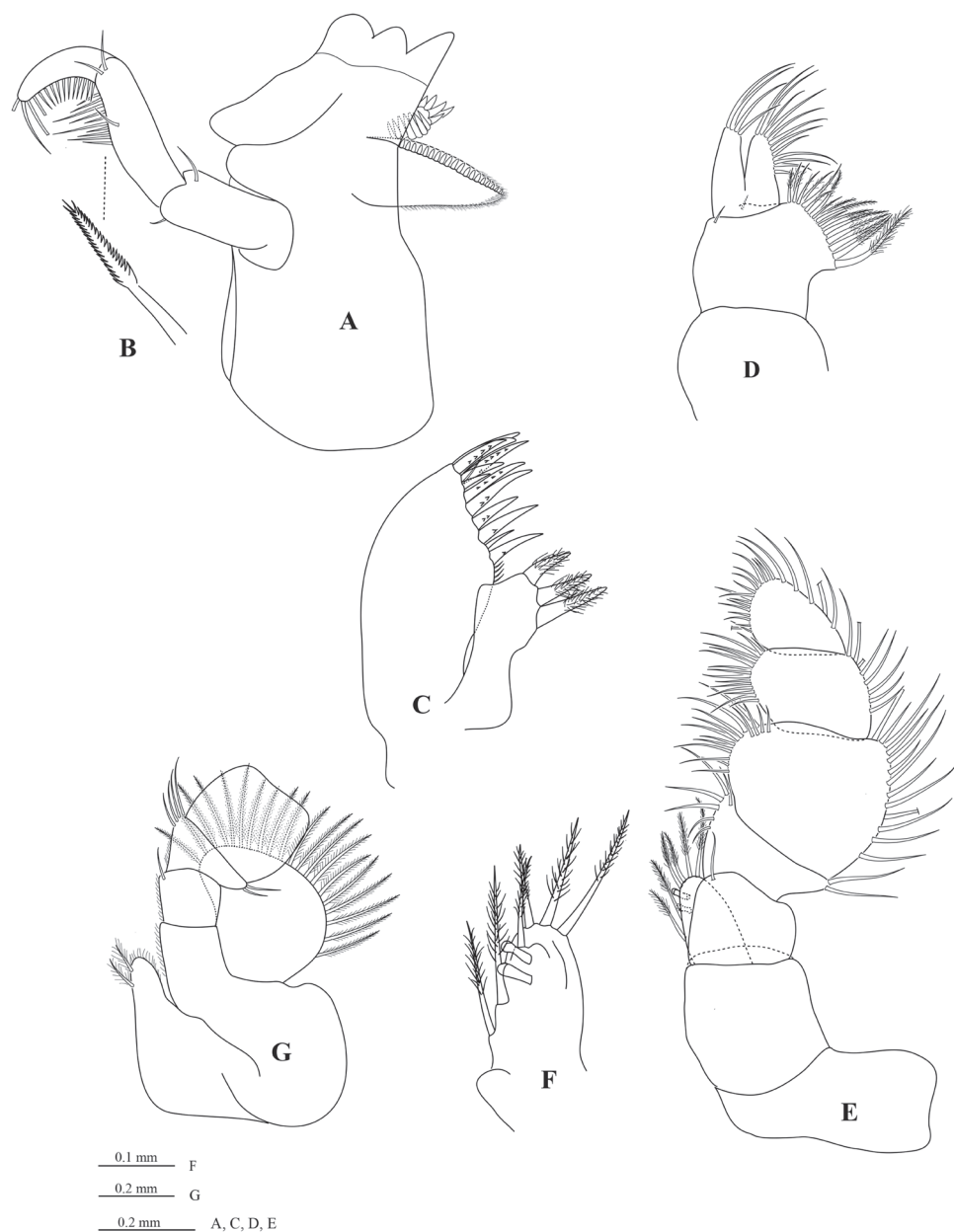


Figure 3. *Cirolana songkhla* sp. n., male paratype (PSUZC-CR0281-2) (11.2 mm) (**A–F**), ovigerous female paratype (PSUZC-CR0281-2) (8.7 mm) (**G**). **A** right mandible **B** robust setae **C** right maxillule **D** right maxilla **E** right maxilliped **F** maxilliped endite **G** left maxilliped, basal articles.

as long as wide, inferior margin with 7 RS (set in groups of 1, 2, 2 and 2), superior distal angle with 3 slender setae and 1 palm seta, inferior distal angle with 2 RS; *dactylus* 0.3 times as long as propodus.

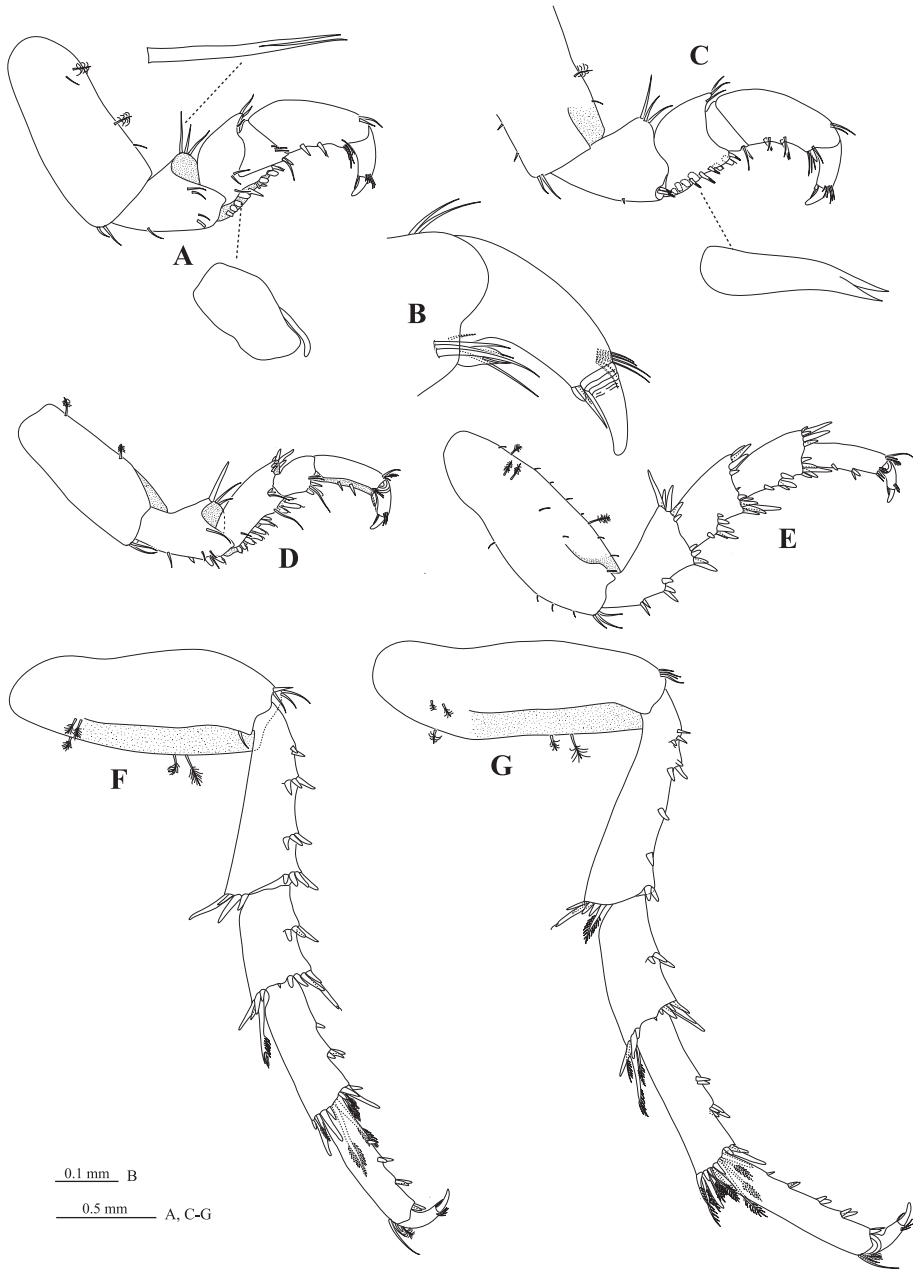


Figure 4. *Cirolana songkhla* sp. n., male paratype (PSUZC-CR0281-2) (11.2 mm). **A** pereopod 1 **B** dactylus of pereopod 1 **C** mesial view, pereopod 1 **D** pereopod 2 **E** pereopod 4 **F** pereopod 6 **G** pereopod 7.

Penes (Figure 2I, J) medially united low papillae.

Pleopod 1 (Figure 5A) exopod 1.3 times as long as wide, lateral margin weakly convex, distally broadly rounded, mesial margin weakly convex, with ~35 PMS from

distal one-third; endopod 2.1 times as long as wide, distally broadly rounded, lateral margin sinuate, with ~16 PMS on distal margin only; peduncle 1.9 times as wide as long, mesial margin with 4 coupling hooks. *Pleopod 2* (Figure 5B) exopod with ~52 PMS, endopod with ~24 PMS; *appendix masculina* with parallel margins, 1.0 times as long as endopod, distally notch. *Pleopod 3* (Figure 5C) endopod without PMS, exopod with ~60 PMS. *Pleopod 4* (Figure 5D) endopod without PMS, exopod with ~60 PMS. *Pleopod 5* (Figure 5E) endopod without PSM, exopod with ~54 PMS. Pleopods 2–5 peduncle distolateral margin with prominent acute RS, 3–5 endopods with distomesial serrate scales.

Uropod (Figure 6A) peduncle ventrolateral margin (Figure 6D) with 2 RS, lateral margin with 1 mesial short acute RS, posterior lobe about one-half as long as endopod; rami extending beyond pleotelson, marginal setae in single tiers, apices acute. *Endopod* (Figure 6A) apically sub-bifid, medial process prominent (Figure 6C); lateral margin weakly convex, with 8 RS, mesial margin strongly convex, with 12 RS. *Exopod* (Figure 6A) not extending to end of endopod, 3.3 times as long as greatest width, apically sub-bifid, medial process prominent (Figure 6B); lateral margin weakly convex, with 13 RS; mesial margin weakly convex, with 6 RS.

Female. Similar to male but on average smaller. Antennal flagellum slightly longer, extending to anterior of pereonite 5; maxilliped with lamina vibrans (Figure 3G); brood pouch composed of 5 pairs of oostegites (Figure 6G) arising on sternites 1–5 (as recorded for some other *Cirolana* species, such as *Cirolana (Anopsilana) barnardi* (Bruce, 1992) and *Cirolana kokoru* Bruce, 2004), lateral margin of oostegite 4 with ~23 slender setae.

Variation. Pleotelson (n=23 [18♂ and 5♀]) with 12–15 RS, with 14 RS (7+7) most frequent (74%), 12 (4%) and 15 (4%) occurring only once. Uropod endopod mesial margin with 11–13 RS, with 12 (52%) and 11(39%) most frequent, lateral margin with 8–10 RS, with 8 (52%) and 9 (39%) most frequent; exopod mesial margin with 5–8 RS, with 7 (39%) and 6 (35%) most frequent, lateral margin with 12–14, with 13 (74%) most frequent.

Size. Adult males (n=19) 9.8–13.9 mm (mean 11.9 mm); ovigerous females (n=5) 8.6–9.0 mm (mean 8.8 mm).

Remarks. The presence of abundant chromatophores and lack of ornamentation on the posterior pereonites, pleonites and pleotelson excludes *C. songkhla* sp. n. from the *Cirolana* ‘tuberculate-group’ (see Bruce 1986). Although *C. songkhla* sp. n., with smooth dorsal surface, seems to belong to the *Cirolana* ‘parva-group’ of Bruce (2004), there are several characters that differ to that group. The body size of *C. songkhla* sp. n. is significantly larger than most tropical ‘parva-group’ species, most which do not exceed 7 mm. Moreover, the uropods and pleotelson margins are far more heavily armed with robust setae than the ‘parva-group’; and the coxae of *C. songkhla* sp. n. are more visible in dorsal view than usually for the ‘parva-group’.

C. songkhla sp. n. is characterized by lacking plumose setae on endopods of pleopods 3–5. This character is particularly associated with brackish and freshwater cirolanid species, formerly placed in the genus and then subgenus *Anopsilana* (Bruce

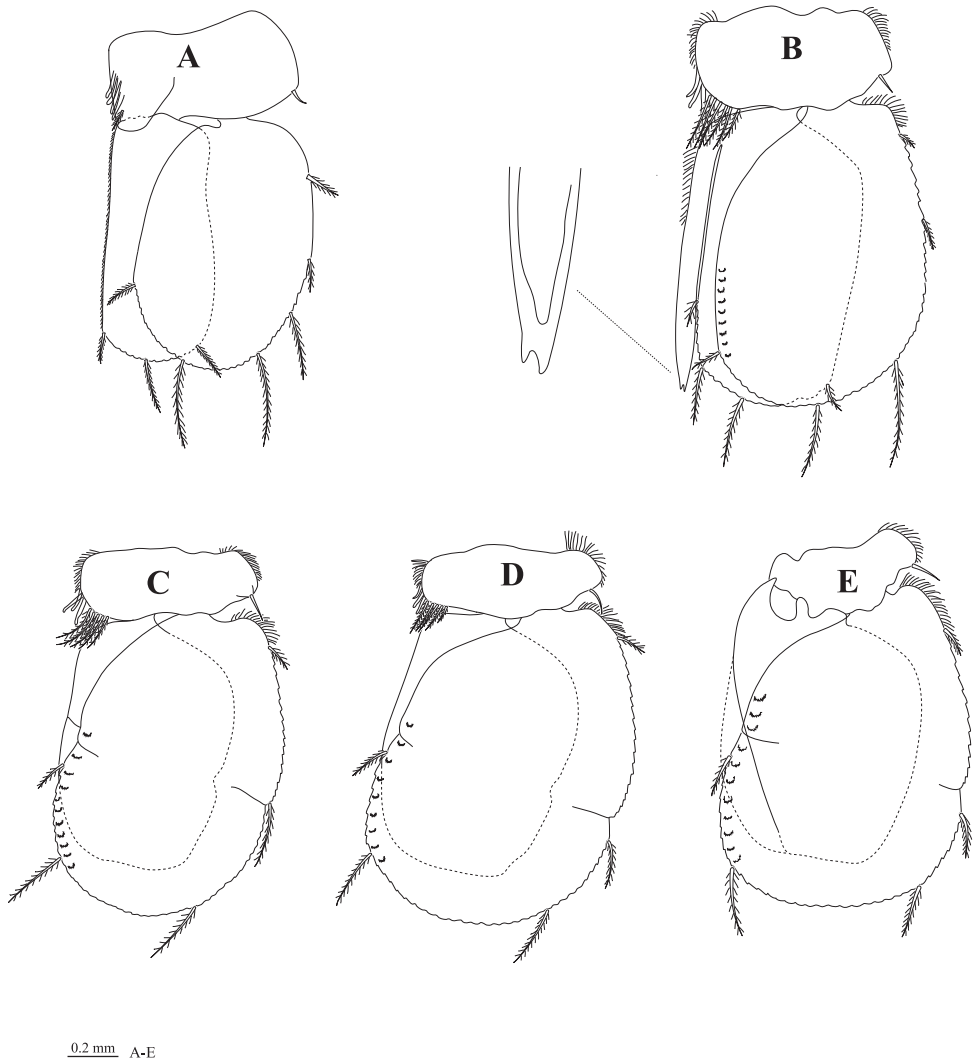


Figure 5. *Cirolana songkhla* sp. n., male paratype (PSUZC-CR0281-2) (11.2 mm) **A–E** pleopods 1–5 respectively.

1981, Botosaneanu and Iliffe 1997). However, *C. songkhla* sp. n. can be distinguished from the other species of *Cirolana* (*Anopsilana*) by having well-developed eyes (absent in freshwater cave species) and smooth dorsal surfaces [nodular and tubercular in species, such as *C. fluviatilis* Stebbing, 1902 and *C. willeyi* Stebbing, 1904].

Only *Cirolana barnardi* (Bruce, 1992) from tropical eastern Australia is similar to *C. songkhla* sp. n. having in common a smooth dorsal surface, rostral point and pentagonal frontal lamina. However, the two species can be clearly distinguished by body size of *C. songkhla* sp. n., which is larger than that of *C. barnardi* (male average at 11.9 VS 3.9 mm, ovigerous female at 8.8 VS 4.0 mm). Furthermore, *C. songkhla*

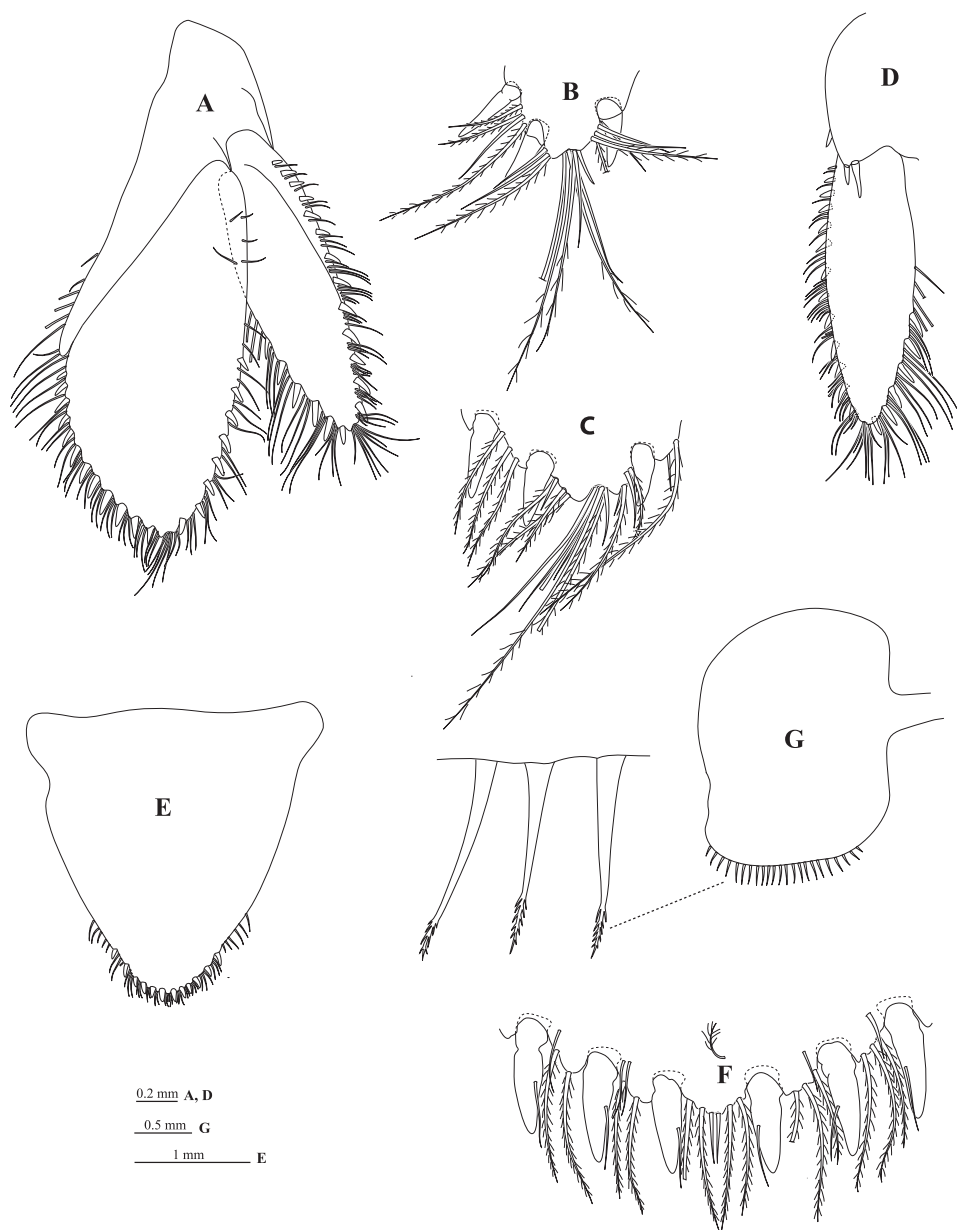


Figure 6. *Cirolana songkhla* sp. n., male paratype (PSUZC-CR0281-2) (11.2 mm) (**A–F**), ovigerous female (PSUZC-CR0281-2) (8.7 mm) (**G**). **A** uropod **B** uropod exopod apex **C** uropod endopod apex **D** uropod exopod **E** pleotelson **F** detail of pleotelson apex **G** oostegite 4.

sp. n. has more numerous robust setae on the uropodal rami and pleotelson margin than *C. barnardi*; uropod exopod lateral margin with 12–14 RS (VS 7–10), mesial margin with 5–8 RS (VS 5–6); endopod lateral margin with 8–10 RS (VS 3–4),

mesial margin with 11–13 RS (VS 5–7) and pleotelson, posterior margin converging to small distinct caudomedial point (VS posterior margin subtruncate), with 12–15 RS (VS 7–10).

Cirolana parva Hansen, 1890 has been recorded in freshwater from Thailand by Chilton (1924, 1926) from Songkhla Lake and Talé Sap. *C. parva* is, unequivocally, restricted to marine habitats in Central America and the Caribbean (Bruce and Bowman 1982), with all Indo-Pacific records being misidentifications (see also Bruce 1986, 1995, 2004; Schotte and Kensley 2005). It is probable that Chilton's specimens, misidentified as *C. parva*, are the same species as *C. songkhla* sp. n. Chilton (1924) gives a figure (figure 5, but the locality of the specimens is not stated) of the pleotelson and uropods of the Songkhla Lake species, which has a more acute pleotelson apex but is otherwise compatible with the present material and records the size of the Talé Sap specimens as 9 mm, also compatible with the present species. For those reasons, we provisionally include these records from freshwater in the synonymy for *C. songkhla* sp. n. Chilton (1924) also included several marine localities and some uncertain localities, and these other records are regarded as being of unknown identity.

Etymology. *Cirolana songkhla* sp. n. is named for the type locality.

Key to brackish species of *Cirolana* in Thailand

- 1 Anterior margin of head without rostral point; frontal lamina anterior margin rounded..... *C. fluviatilis*
- Anterior margin of head with rostral point, folded ventrally and posteriorly, in contact with frontal lamina; frontal lamina pentagonal..... **2**
- 2 Body dorsal surface without ornamentation; pleotelson lateral margins convex..... *C. songkhla* sp. n.
- Body dorsal surface with tubercles on pereonites, pleonites and pleotelson; pleotelson lateral margins concave *C. willeyi*

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Systematics of the Neotropical genus *Catharylla* Zeller (Lepidoptera, Pyralidae s. l., Crambinae)

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Abstract

The Neotropical genus *Catharylla* Zeller, 1863 (type species: *Crambus tenellus* Zeller, 1839) is redescribed. *Catharylla contiguella* Zeller, 1872, *C. interrupta* Zeller, 1866 and *Myelois sericina* Zeller, 1881, included by Munroe (1995) in *Catharylla*, are moved to *Argyria* Hübner. *Catharylla paulella* Schaus, 1922 and *C. tenellus* (Zeller, 1839) are redescribed. Six new species are described by Léger and Landry: *C. bijuga*, *C. chelicerata*, *C. coronata*, *C. gigantea*, *C. mayrabonillae* and *C. serrabonita*. The phylogenetic relationships were investigated using morphological as well as molecular data (COI, wingless, EF-1 α genes). The median and subterminal transverse lines of the forewing as well as the short anterior and posterior apophyses of the female genitalia are characteristic of the genus. The monophyly of *Catharylla* was recovered in all phylogenetic analyses of the molecular and the combined datasets, with three morphological apomorphies highlighted. Phylogenetic analyses of the morphology of the two sexes recovered three separate species groups within *Catharylla*: the *chelicerata*, the *mayrabonillae*, and the *tenellus* species groups. The possible position of *Micrelephas* Schaus, 1922 as sister to *Catharylla*, based on both morphological and molecular data, and the status of tribe Argyriini are discussed. The biogeographical data indicate that the *chelicerata* species group is restricted to the Guyanas and the Amazonian regions whereas the *tenellus* group is restricted to the Atlantic Forest in the South-Eastern part of Brazil. The

mayrabonillae group is widespread from Costa Rica to South Bolivia with an allopatric distribution of the two species. COI barcode sequences indicate relatively strong divergence within *C. bijuga*, *C. mayrabonillae*, *C. serrabonita* and *C. tenellus*.

Keywords

Argyria, Argyriini, Atlantic forest, biogeography, Crambini, *Micrelephas*, morphology, new species, phylogeny, Pyraloidea, taxonomy

Introduction

Pyraloidea is one of the largest superfamilies of the order Lepidoptera. The monophyly of the group and that of its two main lineages, the Pyraliformes and Crambiformes (or Pyralidae and Crambidae, depending on authors), are well supported by morphological characters (Börner 1925, Hasenfuß 1960, Minet 1982) and molecular investigations (Regier et al. 2009, 2012; Mutanen et al. 2010). The abdominal tympanal organs represent a distinctive autapomorphy for the superfamily (Munroe and Solis 1998). The phallus attached medially to the juxta, the crambine-type tympanal organs, as well as the presence of a hair tuft on the dorsal hindwing cubital stem support the monophyly of subfamily Crambinae (Landry 1995). This is corroborated by Regier et al. (2012) based on sequences of several genes, but only three taxa and two of them Crambini. The only available, although partial, phylogenetic analysis of the Crambinae Latreille, 1810 is that of Landry (1995), which, however, did not include *Catharylla*. The relationships of *Catharylla* with other genera of Crambinae are not known, except for the placement of the genus in the Argyriini by Munroe (1995) together with *Argyria* Hübner, 1818, *Vaxi* Bleszynski, 1962 and *Urola* Walker, 1863. This placement was based on a suggestion by Bleszynski (1962: 12) that *Catharylla* may be closely related to *Vaxi* (Munroe 1995:161). Tribe Argyriini was thought to be monophyletic on the basis of the snow white color of the wings, the broad forewings, and the short labial palpi (Landry 1995, Munroe 1995), but its phylogenetic relationships remain unresolved. Stanislas Bleszynski investigated *Catharylla*, but he never published his findings, probably due to his accidental death in 1969.

Catharylla moths are of medium size, with snow white to cream-colored wings with two ochreous to brown transverse lines on the forewings. Species of *Catharylla* occur in tropical Central and South America. Nothing is known on the immature stages and biology. The original description of Zeller (1863) gives little information and was restricted to external features. Munroe (1995) included five species in *Catharylla* (*C. contiguella*, *C. interrupta*, *C. paulella*, *C. sericina*, *C. tenellus*), but these share no evident common characteristics other than the snow white color of the wings.

In this work, *Catharylla* is revised using both morphological and molecular data. Phylogenetic relationships within *Catharylla* and with putatively related taxa as well as the distribution of each species along with biogeographical hypotheses are analysed.

Material and methods

Morphological investigations

Material

Catharylla and outgroup taxa investigated were borrowed from museums and private collectors as listed in Table 1, which also gives the acronyms used throughout the text.

Several of the MHNG specimens were kindly given to this institution by collaborators mentioned in the acknowledgments section. The specimens were usually well preserved, the color being sometimes faded. Many specimens from the BMNH were dissected by S. Bleszynski. Unfortunately, his preparations were usually poorly made and badly mounted, sometimes hampering the investigation of genitalia characters.

The dissection and slide mounting methods follow Landry (1995). Genitalia pictures were taken with a Leica MZ APO, a JVC digital camera (KY-F70B), and Auto-Montage version 4.02.0014. The adult pictures were made with a NIKON D300 and a 105mm Micro NIKON f/2.8G AF-S VR lens. The images were enhanced with Adobe Photoshop Elements.

Apart from the eight *Catharylla* species, four additional crambine species were included in the dataset for phylogenetic analyses. The material investigated to build the morphological matrix is reported below in Table 2.

Table 1. Collections from which *Catharylla* specimens were borrowed.

Acronym	Museum or Collection	Locality	Number of specimens
AMNH	American Museum of Natural History	USA, New York, New York	1
Becker Coll.	Collection of V. O. Becker	Brazil, Bahia, Camacan	57
BMNH	Natural History Museum	Great Britain, London	34
CMNH	Carnegie Museum of Natural History	USA, Pennsylvania, Pittsburgh	9
CNC	Canadian National Collection of Insects, Arachnids and Nematodes	Canada, Ontario, Ottawa	14
ISZP	Institute of Systematic Zoology	Poland, Krakow	9
INBio	Instituto Nacional de Biodiversidad	Costa Rica, Santo Domingo de Heredia	5
MHNG	Muséum d'histoire naturelle de Genève	Switzerland, Geneva	28
NMW	Naturhistorisches Museum Wien	Austria, Vienna	4
Schouten Coll.	Collection R. T. A. Schouten	Netherlands, The Hague	6
SMNS	Staatliches Museum für Naturkunde, Stuttgart	Germany, Stuttgart	1
SMTD	Staatliches Museum für Tierkunde, Dresden	Germany, Dresden	1
USNM	National Museum of Natural History	USA, D. C., Washington	33

Table 2. Material used for the morphology-based phylogenetic analysis of *Catharylla* species and related genera.

Subfamily	Genus	Species	Sex	Collecting locality	Collection	Dissection number
Crambinae	<i>Argyria</i>	<i>lacteella</i>	M	USA, Florida, Lake Placid, Archbold Biological Station	MHNG	BL 064
Crambinae	<i>Argyria</i>	<i>lacteella</i>	F	USA, Florida, Lake Placid, Archbold Biological Station	MHNG	BL 067
Crambinae	<i>Argyria</i>	<i>lacteella</i>	F	Brazil, Bahia, Camacan, Serra Bonita Reserve	MHNG	TL 15 (wing prep.)
Crambinae	<i>Catharylla</i>	<i>bijuga</i>	M	French Guiana, Saint-Jean-du-Maroni	BMNH	BL 1719
Crambinae	<i>Catharylla</i>	<i>bijuga</i>	F	Suriname, Sipaliwini District, Thibiti area, partly swampy, primary forest on hilly slopes, ca. 2km from river	Schouten Coll.	BL 1732
Crambinae	<i>Catharylla</i>	<i>chelicerata</i>	M	Brazil, Reserva Ducke, km. 26 Manaus–Itacoatiara Highway	CNC	BL 1721
Crambinae	<i>Catharylla</i>	<i>chelicerata</i>	F	Brazil, Reserva Ducke, km. 26 Manaus–Itacoatiara Highway	CNC	BL 1711
Crambinae	<i>Catharylla</i>	<i>chelicerata</i>	M	French Guiana, 36 km SE Roura (Camp Patawa)	MHNG	MHNG 6272 (wing prep.)
Crambinae	<i>Catharylla</i>	<i>coronata</i>	M	Brazil, Espírito Santo, Linhares, 40m	Becker Coll.	BL 1743
Crambinae	<i>Catharylla</i>	<i>coronata</i>	F	Brazil, Rio Negro, 900 m	ISZP	BL 1731
Crambinae	<i>Catharylla</i>	<i>gigantea</i>	M	Guyana, Potaro	BMNH	BL 1716
Crambinae	<i>Catharylla</i>	<i>gigantea</i>	F	French Guiana, Saint-Jean-du-Maroni	BMNH	Pyralidae Brit. Mus. Slide N° 11342
Crambinae	<i>Catharylla</i>	<i>mayrabonillae</i>	M	Peru, Agnaitia, Huallaga, Peru, 400m	CNC	BL 1724
Crambinae	<i>Catharylla</i>	<i>mayrabonillae</i>	F	French Guiana, Saint-Jean-du-Maroni	BMNH	BL 1720
Crambinae	<i>Catharylla</i>	<i>pauella</i>	M	Bolivia, Provincia del Sara, 450 m	BMNH	Pyralidae Brit. Mus. Slide N° 15890
Crambinae	<i>Catharylla</i>	<i>pauella</i>	F	Brazil, Mato Grosso, Urucum, 15 miles South of Columbá, 650 feet	BMNH	BL 1712
Crambinae	<i>Catharylla</i>	<i>serrabonita</i>	M	Brazil, Espírito Santo, Linhares, 40m	USNM	BL 1745
Crambinae	<i>Catharylla</i>	<i>serrabonita</i>	F	Brazil, Espírito Santo, Linhares, 40m	Becker Coll.	BL 1759
Crambinae	<i>Catharylla</i>	<i>serrabonita</i>	M	Brazil, Bahia, Camacan, Serra Bonita Reserve	MHNG	TL 8 (wing prep.)
Crambinae	<i>Catharylla</i>	<i>tenellus</i>	M	Brazil, Minas Gerais, Caraça, 1300 m	Becker Coll.	BL 1746
Crambinae	<i>Catharylla</i>	<i>tenellus</i>	F	Brazil, São Paulo, Bertioga, 5 m	Becker Coll.	BL 1742
Crambinae	<i>Crambus</i>	<i>uliginosellus</i>	M	Germany, Oberstdorf, Allgäu	SMTD	MTD prep. N°327
Crambinae	<i>Crambus</i>	<i>uliginosellus</i>	F	Switzerland, St. Gallen	SMTD	MTD prep. N°329
Crambinae	<i>Crambus</i>	<i>pascuella</i>	M	Germany, Coswig, Dresden	SMTD	MTD prep. N°325

Subfamily	Genus	Species	Sex	Collecting locality	Collection	Dissection number
Crambinae	<i>Crambus</i>	<i>pascuella</i>	F	Germany, Koetzschenbroda, Dresden	SMTD	MTD prep. N°326
Crambinae	<i>Micrelephas</i>	<i>pictellus</i>	M	Brazil, Bahia, Camacan, 400–700m	MNHG	MHNG ENTO N°2831
Crambinae	<i>Micrelephas</i>	<i>pictellus</i>	F	Panama, Barro Colorado Island	MNHG	MHNG ENTO N°2829
Crambinae	<i>Micrelephas</i>	<i>pictellus</i>	M	Brazil, Bahia, Camacan, Serra Bonita Reserve	MNHG	TL 17 (wing prep.)

Taxonomy

The types of the two species *C. contiguella* Zeller, 1872, and *C. interrupta* Zeller, 1866 could not be found. With the help of the descriptions and illustrations, they were excluded from *Catharylla* because of the forewing pattern, which is like that of *Argyria* Hübner, 1818, with only one median transverse line. For *C. sericina* Zeller, 1881, based on the description and a photograph of the type in the BMNH, the species was rejected from *Catharylla* based on the elongated forewing shape and the silvery white pattern without transverse lines. For *C. paulella* Schaus, 1922, a photograph of the habitus and the genitalia of the female type from the USNM allowed to find other specimens of the same species; the male and female were then associated based on wing pattern. For *C. tenellus* Zeller, 1839, a photograph of the habitus and the genitalia of the female type were available and the male of the species was associated based on wing pattern. For the descriptions, we followed the nomenclature and terminology used by Landry (1995), except for the use of the term phallus (see Kristensen 2003). New species were recognized based on major differences in male and female genitalia.

The following measurements were made with the use of an ocular micrometer: length of labial palpus (base of segment I to apex of segment III), diameter of eye (greatest vertical width), length of forewing (from base to apex), length of uncus (from tegumen-uncus junction to apex of uncus), length of tegumen connection (from tegumen arms connection medially to tegumen-uncus junction), length of papillae anales (dorso-ventral length), lengths of anterior and posterior apophyses (from base to apex).

Regarding the holotype data, the information was copied exactly as found on the labels with vertical slashes to express changes of lines. Abbreviations are spelled out in square brackets. We assume that the labels are rectangular and white, and that the text is in black ink, otherwise differences are indicated in brackets. Paratype data are reported by country in alphabetical order and the information is recorded without indication of line change. Collecting localities are reported as written on labels, with a question-mark when the locality could not be recovered. Dates and collectors' information were standardized and the latter placed in parentheses. The specimen depositories are reported with the use of the corresponding acronyms.

Biogeographical investigations

The coordinates of the localities were found using Google Earth (2011). The localities that were not registered in Google Earth were localized more or less precisely with the help of internet search engines or with gazeeters from the GEOnet Names Server (GNS) of the National Geospatial Intelligence Agency (<http://earth-info.nga.mil/gns/html/>). The localities were reported on a text file (*.txt) and loaded on a map using DIVA-GIS 7.4.0.1 (Hijmans et al. 2011). Distances between localities were calculated with Google Earth. The localities and their coordinates are reported in Appendix I - Table 1. We refer to the provinces of Morrone (2006) in the biogeography section.

Molecular investigations

Material

The genes investigated are the mitochondrial COI gene (1474 bp) and the two nuclear genes wingless (353 bp) and EF-1 α (679 bp). These genes show different rates of substitution through time, with COI >> wingless > EF-1 α (Wahlberg and Wheat 2008). COI performs well at the species level and the two nuclear genes recover accurate phylogenies in deeper nodes of Lepidoptera (Wahlberg and Wheat 2008).

Specimens used for molecular investigations are listed in Table 3, with the sequencing success for the different investigated genes. Specimens were preserved in 95% ethanol under cool conditions until molecular investigations, or were pinned and dried. Sequences for the additional species were obtained from GenBank (see Table 3).

For *Catharylla* specimens collected no more than twenty years ago, a leg was sent to the Canadian Centre for DNA Barcoding (CCDB) at the Biodiversity Institute of Ontario (BIO) in Guelph. The barcode sequences of *Catharylla* are reported in each species description. The protocol for DNA extraction is found in the supplementary material of Ivanova et al. (2006). The primers LepF1, LepR1 (Hebert et al. 2004) and MLepF1, MLepR1 (Hajibabaei et al. 2006) were used by the CCDB. The protocol for COI amplification is found at http://dev.ccdb.ca/docs/CCDB_Amplification.pdf

DNA sequencing

DNA extractions were performed following the method of Knölke et al. (2005) and with the NucleoSpin Tissue kit by Magerey-Nagel according to the manufacturer's protocol. For alcohol preserved specimens, only tissue from the thorax was used for DNA extraction. For dried specimens, DNA was extracted from the abdomen or a leg, when the abdomen was missing.

The primers used are recorded in Table 4.

Table 3. List of the material used in the molecular work with voucher numbers, database of origin, collecting depository, and sequencing results for each gene. LEP references refer to the Lepidoptera DNA database of M. Nuss at the SMTD. BC MTD references refer to the barcode sequence voucher of the Barcoding Of Life Database (BOLD). HG references refer to the European Nucleotide Archive. Amplicon length (in basepairs) is given in brackets. The sequences with an asterisk were those used to build the datasets used in the phylogenetic analyses.

species	Voucher number	Collecting locality and specimen depository	sequencing results			
			COI		wingless	EF-1 α
			1st part	2nd part		
		<i>Catharylla</i>				
<i>bijuga</i>	-	French Guiana, Roura, road to Crique Gabrielle, 3.6 km East Roura (AMNH)	BC MTD 01839 (1–654)			
<i>bijuga</i>	-	Brazil, Amazonas, Parque nacional do Jaú, 1°57'S, 61°49'W (USNM)	BC MTD 01840 (1–654)*			
<i>chelicerrata</i>	LEP 963	French Guiana, 36 km SE Roura (Camp Patawa) (MHNG)	BC MTD 01703 (1–654)			
<i>chelicerrata</i>	-	French Guiana, 36 km SE Roura (Camp Patawa) (MHNG)	BC MTD 01704 (1–654)			
<i>chelicerrata</i>	LEP 1290	French Guiana, 600, Parcelles CIRAD de Combi, plantations expérimentales, pk 1.8 5°18'N, 52°55'30"W (MHNG)	HG793015 (1–1474)*		HG793008 (46–353)*	HG793003 (1–452)*
<i>coronata</i>	-	Brazil, Espiritu Santo, Linhares, 40m (USNM)	BC MTD 01890 (1–654)*			
<i>mayrabonillae</i>	LEP 1126	Peru, Huánuco, Río Lullapichis, Panguana, 74,945°W / 9,614°S (SMTD)	HG793014 (6–1474)*		HG793009 (1–353)*	HG793004 (1–199)*
<i>mayrabonillae</i>	-	Costa Rica, Alajuela, Area de Conservacion Guanacaste, Estacion Caribe (INBio)	07-SRNP-113921 (1–654)			
<i>pauella</i>	LEP 965	Brazil, Sao Paulo, Sao Luiz do Paraitinga, 900 m, 23°20'S-45°06'W(V. O. Becker n°132357) (Becker Coll.)	HG793016 (1–978)*			
<i>serrabonita</i>	LEP 970	Brazil, Bahia, Porto Seguro, A. d'Ajuda, 16°27'S, 39°03'W, 20m (V. O. Becker n°144140) (Becker Coll.)	BC MTD 01887 (1–654)			
<i>serrabonita</i>	LEP 979	Brazil, Bahia, Camacan, Reserva Serra Bonita, 800m (MHNG)	HG793017 (35–556)*	HG793018 (751–1333)*	HG793010 (734–1474)*	HG793005 (106–679)*

species	Voucher number	Collecting locality and specimen depository	sequencing results			
			COI		wingless	EF-1 α
			1st part	2nd part		
<i>sermabonita</i>	-	Brazil, Espírito Santo, Linhares, 40m (USNM)	BC MTD 01843 (1–654)			
<i>tenellus</i>	-	Brazil, Bahia, Porto Seguro, A. d'Ajuda, 16°27'S, 39°03'W, 20m (V. O. Becker n°142784) (Becker Coll.)	BC MTD 01708 (15–654)			
<i>tenellus</i>	LEP 973	Brazil, Bahia, Porto Seguro, A. d'Ajuda, 16°27'S, 39°03'W, 20m (V. O. Becker n°144140) (Becker Coll.)	BC MTD 01709 (1–654)		HG793011 (23–353)*	
<i>tenellus</i>	-	Brazil, Bahia, Porto Seguro, A. d'Ajuda, 16°27'S, 39°03'W, 20m (V. O. Becker n°140808) (Becker Coll.)	BC MTD 01710 (1–654)			
<i>tenellus</i>	-	Brazil, São Paulo, Ubatuba, Picinguaba, 23°22'S, 44°50'W (Becker Coll.)	BC MTD 01842 (1–654)			
<i>tenellus</i>	LEP 972	Brazil, Bahia, Porto Seguro, A. d'Ajuda, 16°27'S, 39°03'W, 20m (V. O. Becker n°140808) (Becker Coll.)	BC MTD 01888 (1–654)*	HG793020 (792–1473)*		
Other Crambinae						
<i>Argyria lacteella</i>	LEP 976	Brazil, Bahia, Camacan, Reserva Serra Bonita, 800m (MHNG)	HG793013 (6–689; 709–1474)*		HG793006 (57–355)*	HG793001 (1–654)*
<i>Crambus pascuella</i>	-	USA: North Carolina, Swain County, 1720m, 35°35'45"N, 83°27'42"W	GU089400 (1–657)*			
<i>Crambus uliginosellus</i>	-	unknown	GU828691 (1–668)*	GU828487 (716–1474)*	GU829571 (1–353)*	GU829302 (269–679)*
<i>Microlephas pictellus</i>	LEP 977	Brazil, Bahia, Camacan, Reserva Serra Bonita, 800m (MHNG)	HG793012 (26–1474)*		HG793007 (1–353)*	HG793002 (1–626)*

Table 4. Primers used for DNA sequencing. (F) stands for Forward primers, (R) for Reverse primers. The primers of the Nymphalidae Systematics Group can be found at <http://nymphalidae.utu.fi/Nymphalidae/Molecular.htm>

Origine	gene	Primers	References
mitochondrial	COI	HybLCO (F)	Wahlberg and Wheat 2008
		Nancy (R)	Wahlberg and Wheat 2008
		HybJerry (F)	Wahlberg and Wheat 2008
		HybPat (R)	Wahlberg and Wheat 2008
		K699 (R)	The Nymphalidae Systematics Group
		Ron (F)	The Nymphalidae Systematics Group
		Mila (R)	The Nymphalidae Systematics Group
		Brian (F)	The Nymphalidae Systematics Group
nuclear	wingless	HybLepWG1 (F)	Wahlberg and Wheat 2008
		HybLepWG2 (R)	Wahlberg and Wheat 2008
	EF-1 α	Oscar-6143 (F)	Hundsörfer et al. 2009
		Bosie-6144 (R)	Hundsörfer et al. 2009

PCRs were performed using *peqGOLD* Taq DNA polymerase (PeqLab). In cases of weak or absent PCR result, a re-examination PCR was done using *BIO-X-ACT* Short Taq polymerase (Bioline). PCR protocols are given in Appendix II - Tables 1 and 2. Potential contamination was tested along with PCRs by control sample without DNA.

Success of gene amplification was evaluated by an electrophoresis with 1% agarose gel, subsequent gel dying with GelRed and analysis under ultraviolet light. PCR products were purified using *ExoSAP-IT* (USB Corporation).

Sequence PCR was done with the *BigDye Terminator-Kit* of Applied Biosystems. The amount of each product is reported in Appendix II - Table 3. The PCR programme is reported in the *BigDye Terminator Sequencing Kit* protocol. The sequences were obtained from the sample analysis on a 3130 Genetic Analyzer (Applied Biosystems).

Sequence analyses

Sequence alignment was done with *BIOEDIT* 7.1.3 (Hall 1999) and *PhyDE* (Phylogenetic Data Editor) 0.9971 (Müller et al. 2011). Nucleotide positions that proved ambiguous in the pherogram were coded according to the IUPAC nucleotide ambiguity code. Depending on the quality of the sequences, the 5' and 3' ends of the sequences were deleted in cases of high error rates for the nucleotide assignment from the pherogram. We used the programme *DAMBE* (Xia and Xie 2001) to generate the molecular data with third codon position deleted. The alignment was exported as fasta, nexus and phylip files. Sequences were deposited on European Nucleotide Archive, and can be accessed via the following links (for the COI and the nuclear sequences respectively):

<http://www.ebi.ac.uk/ena/data/view/HG793012-HG793020>; <http://www.ebi.ac.uk/ena/data/view/HG793012-HG793020>

Genetic distances

Genetic distances between barcoding sequences of COI are given in Table 5. Distances were calculated using DAMBE. The GTR model was used as the substitution model.

Phylogenetic analyses

Morphology-based analysis

The 21 characters are listed in Table 6. Characters 12, 16 and 17 were polarized into two sets of continuous values of ratios, with the limit selected subjectively where the gap between two groups of values appeared to be the largest. Phylogenetic analyses were run under PAUP 4.0b10 (Swofford 2002). A 12-taxa dataset was analysed, with *Crambus pascuella* and *Crambus uliginosellus* set as outgroups. Maximum parsimony analyses were performed using the Branch-and-bound method as searching algorithm with parameters left unchanged. The bootstrap resampling method with 1000 replicates was used. The resulting tree was a 50% majority-rule consensus tree with bootstrap (BS) values assigned to each node. BS supports are reported on the tree of Figure 42.

Molecular-based analysis

Because of the age of some of the material used, only the COI barcode sequences were available for *C. bijuga* and *C. coronata*, and the whole COI gene for *C. paulella*. For *C. bijuga*, we used the sequence BC MTD 1840 to build the datasets as this sequence performed better than BC MTD 1839 in phylogenetic analyses. The COI sequence of LEP 972 was combined with that of wingless for LEP 973 given that the two samples come from the same population and are genetically very similar as attest the barcode sequences. We generated four different datasets from the sequence data: a complete dataset with all three genes sequences available for the 12 taxa (mol_1), a 12-taxa dataset with the 3rd codon position of COI deleted (mol_2), a dataset restricted to the 7 taxa for which the sequence of the COI gene and at least of one nuclear gene were available (nucl_1), and the same data as nucl_1 but with the 3rd codon position of the COI deleted (nucl_2). We used the programme RAxML (Stamatakis 2006) to perform phylogenetic analyses of these four datasets under the Maximum Likelihood algorithm. The analyses were run on the online platform CIPRES (Miller et al. 2010) with the web-server adapted interface of RAxML (Stamatakis et al. 2008). The version 7.2.8 of RAxML with the Black Box were used. As in the morphology-based analysis, *Crambus pascuella* and *Crambus uliginosellus* were set as outgroups in the analyses of mol_1 and mol_2, and *Crambus uliginosellus* was set as outgroup in the analyses of nucl_1 and nucl_2. For each dataset, three analyses were performed: one without partition, one with the data partitioned into the three genes, and one with the data partitioned into

the three genes and the three codon positions in each gene. According to Mr-AIC (Nylander 2004), the model which best fits our data is GTR+I+G, hence this model was used as evolution model, with parameters estimated for each partition, and the proportion of invariable sites estimated. Bootstrapping was automatically halted by RAxML when a sufficient number of bootstrap replicates was reached. The number of bootstrap replicates is indicated for each analysis. The resulting trees were 50% majority-rule consensus trees with bootstrap values assigned to each node. BS supports of each analysis are reported on the tree (Fig. 42).

Combined bayesian analysis

A nexus file was created for the 12 taxa investigated, with the four following partitions: (1) the morpho-matrix (Table 6), (2) COI, (3) wingless, (4) EF-1 α , and was analysed using Mr-Bayes 3.2.1 (Huelsenbeck and Ronquist 2001). The settings were set as follows to fit to the GTR+I+G model: number of states ("nst") = 6, rate variation among sites ("rates") = gamma-shaped rate variation with a proportion of invariable sites ("invgamma"). The relative rates of substitution ("revmat"), the transition/transversion rate ratio ("tratio"), the stationary nucleotide frequencies ("statefreq"), and the alpha shape parameter of the gamma distribution ("shape") were unlinked in order to allow them to vary among partitions. The number of generations was set to 3,000,000. *Crambus uliginosellus* was chosen as outgroup. The results were considered good when the standard deviation of split frequencies between the two independent runs was below 0.01. Nodes with a posterior probability (PP) over 0.95 are considered well supported. PP values are reported on the tree (Fig. 42).

Results

Catharylla Zeller, 1863

<http://species-id.net/wiki/Catharylla>

Catharylla Zeller 1863: 50, Bleszynski and Collins 1962: 226, Landry 1993: 1088, Munroe 1995: 35, Nuss et al. 2013.

Type species. *Crambus tenellus* Zeller, 1839, by subsequent designation by Schaus 1922: 131.

Diagnosis. *Catharylla* species have snow white to creamy white wings and short labial palpi. They can be separated from other Argyriini by the presence on the forewing of median and subterminal thin transverse lines, slightly curved, convex on costal 1/3. The labial palpi are also shorter in comparison to those of *Vaxi*. The highly variable male genitalia do not show any synapomorphy or generic diagnostic character. In females, a possible synapomorphy is the strongly reduced anterior and posterior

apophyses of abdominal segments VIII and IX, but this is shared with some Crambini and a few other Crambinae (see Landry 1995).

Redescription. Head white, chaetosemata present. Antenna brown, covered with light ochreous to brown scales. Maxillary palpus light ochreous to brown, white tipped. Labial palpus 1.0–1.95 × width of head, curved upward; white basally, light ochreous to ochreous, white tipped, with some brown or dark brown. Thorax white, with ochreous to brown scales at collar. Foreleg coxa white to whitish brown, femur dorsally brown to dark brown, tibia and tarsomeres distally ringed with dark brown. Midleg white to light ochreous with tibia-femur joint ashen brown, with pair of spurs at apex of tibia, tarsomeres II–V dorsally brown to dark brown, with white tips. Hindleg white, with 2 pairs of spurs on tibia, tarsomeres as on midleg. Male frenulum simple, frenulum hook present; female frenulum with 3 or 4 acanthae. Forewing length: 7.5–15 mm in males; 9.5–22 mm in females. Wing venation (of *C. chelicerata*) (Fig. 9): R1 present and free, not connected to Sc; R2 free; R3 connected with R4 at 3/4; R5 stalked with R3+R4 at 1/4; M1 from upper corner of cell; cell opened between M1 and M2; M2 and M3 not stalked; CuA1 from lower corner of cell; CuA2 at distal 1/3 of cell; 1A+2A strong. Hindwing Sc+R1 connected to Rs at distal 1/3; M1 connected to Sc+R1 by short narrow vein; M3 connecting to M2 at distal 1/3, CuA1 connecting to M2 at half of length and CuA2 connecting at basal 2/5; 1A unforked; 2A unforked, strong; 3A present, unforked. Forewing (Figs 1–8) background snow white; pattern with costal margin ochreous to brown, sometimes faded; median and subterminal transverse lines thin, ochreous to brown, convex toward costa; outer margin ochreous, sometimes with dark brown spots between veins, or spots forming a continuous line; fringes white; verso light ochreous to ochreous; with marginal spots pronounced. Hindwing snow white to cream-colored; with hairs along 2A and root of M2; with small dark brown spots on outer margin, sometimes in continuous line; sometimes with postmedian transverse line; verso white with marginal spots pronounced.

Tympanal organs (Fig. 10): Transverse ridge regularly rounded. Tympanal pockets more or less extending beyond transverse ridge. Tympanal bridge present, straight, lightly sclerotized. Tympanal drum more or less ovoid.

Male genitalia (Figs 11–33): Uncus long, basally wide, straight or downcurved, bare or setose. Gnathos arms connecting at 1/4 to 1/2 from base, thin, slightly curved to hook shaped, with apex pointing upward. Tegumen arms enlarging toward uncus, connecting dorsally. Valva with cucullus long, densely setose on inner side, apically more or less rounded, slightly curved upward; costal arm present, variable in shape. Transtilla present only in *C. tenellus* group, strongly developed. Juxta medially curved downward, narrowing toward rounded apex, slightly directed downward apically, basally triangular, sometimes with additional lobes at base or ventro-lateral projections. Vinculum of medium width; saccus short, rounded, directed anterad and slightly upward. Phallus straight or curved, usually more strongly sclerotized at apex; vesica without cornuti, with one cornutus, or with crest of cornuti.

Female genitalia (Figs 34–41): Papillae anales strongly setose, connecting dorsally and ventrally, usually slightly produced dorsally, with basal band of sclerotization. Poste-

rior apophyses $0.25\text{--}0.45 \times$ length of papillae anales, straight, regularly thin. Tergite VIII narrow, with postero-dorsal line of setae. Anterior apophyses reduced, $0.01\text{--}0.1 \times$ length of papillae anales. Sternite VIII about twice length of tergite, not connecting ventrally in *tenellus* species group. Sterigma present, strongly sclerotized except in *tenellus* species group, usually forming pockets of variable shape; reduced to sclerotized lamella antevaginalis in *C. bijuga*. Ductus seminalis connecting posteriorly at base of ductus bursae. Ductus bursae long, at least $2 \times$ length of corpus, wide, basally curved. Corpus bursae usually rounded, egg-shaped, often enlarging progressively from ductus bursae, usually with one signum, sometimes without; corpus and ductus bursae covered with minute spicules.

Distribution. The genus is restricted to the Neotropical Region, from Costa Rica to Santa Catarina, Brazil, from sea level to 1300 m (Figs 43–46).

Biology. The biology of the species remains unknown. In the Serra Bonita Reserve in march 2011, we observed *C. serrabonita* in its environment, i.e. forested hills up to about 950 m in elevation, surrounded by cacao or coffee plantations in the lowlands. The moths were coming to light, usually very late (after 23:00).

Phylogenetic relationships and monophyly. Presumably, given the reduced labial palpi and the forewing color and pattern, *Catharylla* has been placed in the Argyriini (Munroe 1995). But our phylogenetic analyses do not support tribe Argyriini with *Catharylla* included, and the genus seems to be most closely related to *Micrelephas*.

***Catharylla bijuga* T. Léger & B. Landry, sp. n.**

<http://zoobank.org/9FC3D8A6-A172-443C-A52A-BE510976DD0A>

http://species-id.net/wiki/Catharylla_bijuga

Figs 1, 11, 12, 34, 45

Type material. Holotype. ♂, with labels as follows: “Pied Saut, | Oyapok [sic] River, | French Guiana, | S. M. Klages | C. M. Acc. 6111.”; “Dec[ember]. | 1917”; “HOLOTYPE | *Catharylla bijuga* | T. Léger & B. Landry” [red label]; “*Catharylla* | *ramona* sp. n. | det. Bleszynski, 1969”; “MANUSCRIPT | NAME” [white card with red lettering and thin red rectangle submarginally]; “BL 1744 ♂”. Deposited in CMNH.

Paratypes. 16 ♂, 9 ♀. BRAZIL: 1 ♂ (genitalia on slide BL 1748, used for DNA Barcoding BC MTD 01840), Amazonas, P[ar]q[ue] Nac[ional] do Jaú, Rio Jaú, bg. Miratucú, $1^{\circ}57'S$, $61^{\circ}49'W$, 26–27.vii.1995, U[ltra] V[iolet] light sheet (R. W. Hutchings) (USNM). FRENCH GUIANA: 2 ♂ (1 with genitalia on slide Pyralidae Brit. Mus. slide N°15893) with same data as holotype (BMNH); 5 ♂, 1 ♀ (2 ♂ with genitalia on slides Pyralidae Brit. Mus. Slide N°15891, N°15892, ♀ with genitalia on slide BL 1735) with same locality as holotype except i.1918 (1 ♂), ii.1918 (4 ♂, 1 ♀) (S. M. Klages) (BMNH, CMNH); 1 ♂, 2 ♀, Parcelles CIRAD de Combi, plantations expérimentales pk 1.5, $5^{\circ}18'N$, $52^{\circ}55'30'W$, 4.iii.2011, piège lumineux [light trap] (B. Hermier) (♂ with Hermier n° 24340, 2 ♀ with labels Hermier n° 24341 & 24345) (MHNG); 3 ♂, 2 ♀ (2 ♂ with genitalia on slides BL 1719 and Pyralidae Brit. Mus. Slide N° 7815, 2 ♀ with genitalia on slides BL 1739 and BL 1740), Saint-Jean-du-Maroni (Le Moulst)

(BMNH); 1 ♂, Saint-Laurent-du-Maroni (USNM); 1 ♂ (genitalia on slide BL 1694, (used for DNA barcoding BC MTD 01839) Roura, 3.6km E[ast] Roura at r[oa]d to Crique Gabrielle, 50m, 20.iv.1994, at light (J. S. Miller & C. Snyder) (AMNH); 1 ♀ (genitalia on slide BL 1734), Cayenne, iii.1917 (CMNH). GUYANA: 1 ♂, New River 1938 (C.A. Hudson) (BMNH); 1 ♂, Mallali [sic] (USNM). SURINAME: 1 ♀ (genitalia on slide USNM 52888), Geldersland, Surinam River (USNM); 1 ♀ (genitalia on slide BL 1732), Sipaliwini Distr[ict], Thibiti area, Kabo Creek, partly swampy, primary forest on hilly slopes, ca. 2km from river, 29.v.1989 (J. Beerlink) (Schouten Coll.).

COI barcode sequence of paratype BC MTD 01839 (654 bp): ACATTA-TATTTTATCTTCGGAATTTGAGCAGGAATAGTTGGAACATCCCTAA-GACTTTTAATTTCGAGCAGAATTAGGTAATCCAGGTTCTCTTATTG-GTGACGACCAAATTTATAATACTATTGTTACTGCTCATGCATTTATTA-TAATTTTTTTTATAGTTATGCCAATTATAATTGGAGGATTCGGTAATT-GATTAGTTCCATTAATATTGGGAGCACCAGATATAGCATTCCCAC-GAATAAATAATATAAGATTTTGATTACTCCCCCCTCTTTAATCCTAT-TAATTTCTAGAAGAGTTGTAGAAAATGGAGCTGGAACAGGATGAACA-GTTTACCCCCCACTTTCATCAAATATTGCTCATAGTGGTAGATCTG-TAGATTTAGCAATTTTTCTCTACACTTAGCAGGAATTTTCATCAATCT-TAGGAGCTATTAATTTTATTACAACAATTCTTAATATACGAATTAATG-GTTTATCTTTCGATCAAATACCTTTATTTGTTTGATCTGTAGGAAT-TACAGCTTTACTTCTTCTTATCCTTACCCGTATTAGCTGGTGCTAT-TACTATACTTTTAACTGATCGAAATTTAAATACATCTTTTTTTTGATCCT-GCTGGAGGAGGAGATCCTATCCTTTACCAACACTTA

Diagnosis. On the forewing (Fig. 1), the seven, thin, marginal dark brown dashes with the most tornal two shaped like spots will separate this species from the others. In male genitalia (Fig. 11), the strongly sclerotized double costal arm of the valva with the ventral arm tubular is a distinctive character. In female genitalia, the best diagnostic character is the sclerotized projection latero-ventrally on sternite VIII (Fig. 34).

Description. Male (n=17) (Fig. 1): Antenna brown with light ochreous scales; with patch of dark brown scales at base. Maxillary palpus ringed with brown at base and half of length, white tipped. Labial palpus: 1.4–1.6 mm long; ochreous, slightly lighter basally, ringed with dark brown at 2/3, white tipped. Thorax slightly ochreous at collar. Foreleg coxa white; femur ochreous, dark brown dorsally; tibia and tarsomeres ochreous, distally ringed with brown. Midleg and hindleg light ochreous; tibia-femur joint brown on midleg; tarsomeres II–V brown to dark brown on upperside, with white ringed tips. Abdomen dull white to greyish brown. Forewing length: 9.0–10.5 mm; snow white, with yellow ochreous to brown costal margin, partially disrupted when meeting transverse lines; median line yellow ochreous; subterminal line yellow ochreous to brown, forming small triangular spot on costal margin; subapical triangle on costal margin ochreous; outer margin slightly ochreous with five dark brown dashes regularly spaced or sometimes forming faintly continuous line, and one cubital and one anal spots, with cubital spot slightly displaced toward base; fringes brass colored; underside dull white to light ochreous along costal margin, with marginal dashes pro-



Figures 1–8. Habitus of *Catharylla* species: **1** *C. bijuga* sp. n., holotype, French Guiana, Pied Saut, Oyapock River (CMNH) **2** *C. chelicerata* sp. n., Parcelles CIRAD de Combi, plantations expérimentales pk 1.8, 5°18'N, 52°55'30"W (MHNG) **3** *C. gigantea* sp. n., holotype, Brazil, Amazonas, Manaus, Reserva Ducke, AM-010, km 26, 2°55'S, 59°59'W **4** *C. tenellus* Zeller, Brazil, São Paulo, Bertioga (Becker Coll.) **5** *C. coronata* sp. n., holotype, Brazil, Espírito Santo, Linhares (USNM) **6** *C. serrabonita* sp. n., holotype, Brazil, Bahia, Camacan, Reserva Serra Bonita, 15°23'S, 39°33'W, 800m (Becker Coll.) **7** *C. mayrabonillae* sp. n., holotype, Ecuador, Napo, Misahualli (Becker Coll.) **8** *C. paulella* Schaus, holotype, Brazil, São Paulo state, São Paulo (USNM).

nounced. Hindwing snow white, veins slightly ochreous, with shiny aspect; marginal line thin, brown, pronounced up to CuA1, then shiny white; fringes white; underside white, with same margin as on recto.

Tympanal organs (n=8): Tympanic pockets extending slightly beyond transverse ridge, rounded. Tympanic drum elongate, more or less oval, postero-laterally extended beyond transverse ridge.

Male genitalia (n=8) (Figs 11, 12): Uncus slightly down-curved, about $3/5$ length of tegumen arms, with few setae laterally; tip pointed; uncus arms not separated at base, forming low bump medio-ventrally. Gnathos arms joining at half their length; distal half with short, rounded, dorsal projection at base; directed upward subapically at about 50° angle; slightly shorter than uncus and thinner. Tegumen pedunculi progressively widening toward uncus; dorsal connection of tegumen about $1/3$ length of pedunculi; ventral margin straight; dorsal margin slightly convex, bare. Cucculus moderately wide, narrowing in distal $1/4$; costal arm of valva double, bare, about as long as cucculus, joined to cucculus until $3/5$ of its length; ventral arm thin, tubular, strongly sclerotized, slightly curved inward, apex directed upward, narrowed, pointed; dorsal arm broader, slightly shorter than ventral arm, straight, apically rounded, less thickly sclerotized than ventral arm. Vinculum enlarging latero-dorsally, ventrally narrow; saccus short, rounded. Juxta triangular, apically broadly rounded, slightly curved downward, basally projected into two large lateral lobes. Phallus almost straight, with slightly upturned sclerotized apex; vesica covered with microspicules barely visible, with one large, curved, pointed cornutus.

Female (n=10): Labial palpi: 1.1–1.4 mm long. Forewing length: 11–15 mm; frenulum triple.

Female genitalia (n=6) (Fig. 34): Papillae anales slightly projected ventrally and dorsally, dorsally forming prominent sclerotized rounded bulge. Posterior apophyses widened basally, $0.35\text{--}0.5 \times$ length of papillae anales. Segment VIII circular in cross section, enlarging progressively toward papillae. Tergite VIII narrow, about $2/5$ length of sternite VIII, with short setae along posterior edge. Anterior apophyses wide at base, about $0.1 \times$ length of papillae. Sterigma with thin slightly sclerotized membrane covered with minute spicules dorsad of ostium bursae, with posterior margin slightly indented; with sclerotized projection laterad from sternite VIII antero-ventrally, with tip bifid, longer part directed downward, shorter part lateral, curved posterad. Basal part of ductus bursae ventrally sclerotized, looping and narrow, progressively widening toward corpus bursae. Corpus bursae poorly differentiated from ductus, twice as long as wide, without signum.

Distribution. The species occurs in lowlands in the three Guianas and Brazil (Fig. 45).

Etymology. *Bijuga* comes from the Latin *bijugus*, *a*, *um* which means “yoked together, double”, in reference to the bifid costal arm of the male genitalia.

Notes. In some paratypes from French Guiana the collecting data mention a “pk” (=“point kilométrique”). This kilometeric marker refers to the distance of the collecting spot on the forest road to the nearest main road. CIRAD (Centre de coopération internationale en recherche agronomique pour le développement) refers to the name of the research institution leading agronomical research on the Combi site. the Combi site. When S. Bleszynski looked into *Catharylla*, he gave the manuscript name *Catharylla ramona* to this species, but never published it. The comparison of the tip of the tubular costal arm of the male genitalia and the female lateral projections of sternite VIII shows

rather nicely that the male hooks the female genitalia during the mating process. The specimen collected in Parque Nacional do Jaú, Brazil, shows a divergence in COI barcode sequence of 5.05% with that of Roura, French Guiana. In morphology we find no significant difference corroborating this divergence. The relationships of this species to the others remain uncertain in our phylogenetic analyses.

***Chelicerata* species group**

Diagnosis. The synapomorphies of the group are the quadrangular valva with a truncated apex and the hook-shaped gnathos in the male genitalia. The *chelicerata* species group can be separated from the other *Catharylla* species based on additional diagnostic characters. Externally, the forewing has a clear, dark brown costal band, and its length is usually over 14 mm. In male genitalia, the apex of the uncus is regularly rounded with a short, narrow projection medially and the vesica shows one large, curved, pointed cornutus, preceded by a string of 13–14 smaller cornuti increasing in size toward apex. In female genitalia, the ductus bursae shows a pronounced, tongue-shaped projection postero-ventrally.

Notes. This group includes two species. The phylogenetic analyses restricted to the nuclear genes and the combined Bayesian analysis place the group as sister-group of the *mayrabonillae* species group (Fig. 42).

***Catharylla chelicerata* T. Léger & B. Landry, sp. n.**

<http://zoobank.org/10B2350D-F0E5-4E09-BDE8-CE7D3F58A33F>

http://species-id.net/wiki/Catharylla_chelicerata

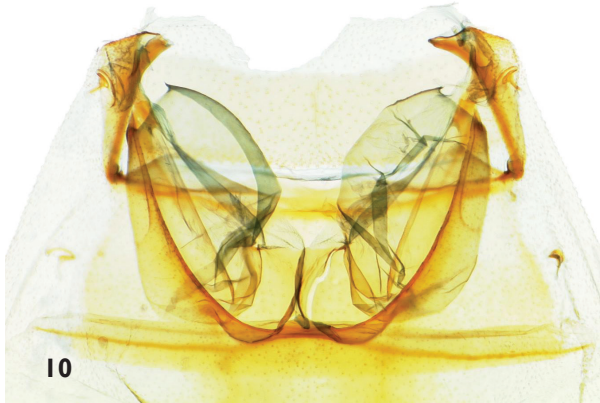
Figs 2, 9, 13, 14, 35, 43

Type material. Holotype. ♂, with labels as follows: “/600/ Parcelles CIRAD de Combi, | plantations expérimentales pk 1,8 | 5°18'N, 52°55'30"W | 3.XII.2010 | B[ernard]. Hermier | [piège lumineux]”; 1 ♂, “Hermier | n° 23939”; “MHNG | ENTO ♂ | 00007213”; “Don de Bernard | Hermier | MHNG 2013”; “HOLOTYPE | *Catharylla* | *chelicerata* | T. Léger & B. Landry” [red label]. Deposited in MHNG.

Paratypes. 20 ♂, 4 ♀. BRAZIL: 1 ♂ (genitalia on slide BL 1714), Amazonas, Rio Negro, Mirapinima, 8.iv.1972 (E. G., I. & E. A. Munroe) (CNC); 9 ♂, 1 ♀, Reserva Ducke, km 26 Manaus–Itacoatiara Highway, 15.iv.1972 (1 ♂), 18.iv.1972 (1 ♂, with genitalia on slide BL 1721), 21.iv.1972 (2 ♂, one with genitalia on slide BL 1709), 16.v.1972 (2 ♂), 17.v.1972 (2 ♂, one with genitalia on slide BL 1738), 18.v.1972 (1 ♂, 1 ♀ with genitalia on slide BL 1711) (E.G., I. and E.A. Munroe) (CNC). FRENCH GUIANA: 5 ♂, 1 ♀, 36km SE, Roura (Camp Patawa), 21.xi.2007 (1 ♂, genitalia on slide MHNG ENTO 6239), 29–30.xi.2007 (3 ♂, 1 ♀, one ♂ with wings on slide MHNG ENTO 6272, 2 ♂ used for DNA sequencing and barcoding, one with labels LEP 963, BC MTD 01703, genitalia on slide TL 1, one with labels



Figure 9. Male wing venation of *Catharylla* species: *C. chelicerata* sp. n., paratype ♂, French Guiana, Roura, Camp Patawa; slide MHNG 6272 (MHNG).



Figures 10. Tympanal organs of *Catharylla* species: *C. paulella* Schaus, ♀, Brazil, Distrito Federal, Planaltina, slide BL 1751 (Becker Coll.).

LEP 964, BC MTD 01704, genitalia on slide TL 2, ♀ with genitalia on slide MHNG ENTO 6240), 30.xi.2007 (1 ♂) (MHNG); 1 ♀ (abdomen used for DNA sequencing LEP 1290, genitalia on slide BL 1750) with same data as holotype; 1 ♂, same data as holotype except 2.ix.2011 (Hermier n° 24755); 1 ♀, same data as holotype except /604/ and 4.iii.2011 (Hermier n° 24344); 2 ♂, Beauséjour, N[ationale] 1 pk 28.5, 4°42'30"N 52°23'30"W, 3.vi.2011, piège lumineux (Hermier n° 24545 & 24546) (B. Hermier) (MHNG); 1 ♂, Route d'Apatou pk 25.5 spk 2+4.4, 1.x.2011, piège lumineux (B. Hermier) (Hermier n° 24956) (MHNG); 1 ♂ (genitalia on slide BL 1749), R[ou]te forestière de Saut Léodate pk 4.5, 4°55'N, 52°33'W, 31.x.1995 piège lumineux (B. Hermier) (Hermier n° 8457) (MHNG).

Other specimens. 1 ♀ (genitalia on slide GS-5949-SB), Nova Olinda, Rio Purus, v.1922 (S. M. Klages) (CMNH); 1 ♀ (genitalia on slide Pyralidae Brit. Mus. Slide N° 17693), Teffé [sic], vi.1906 (W. Hoffmanns) (BMNH).

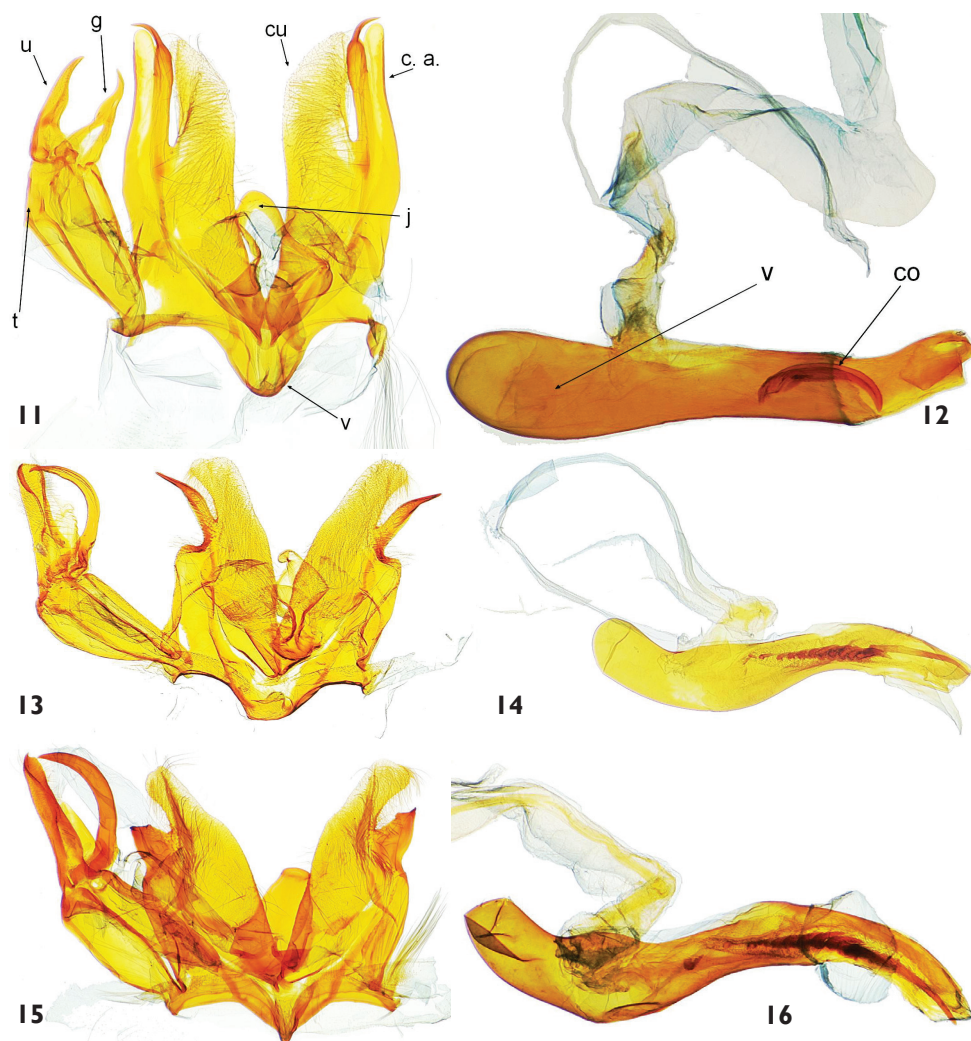
COI barcode sequence of paratype BC MTD 01703 (654 bp): ACTTTA-TATTTTATCTTTGGAATTTGAGCAGGAATAATTGGAACATCCTTAA-GACTACTAATTCGAGCAGAATTAGGTAATCCTGGATCTCTTATCGGG-GATGACCAAATTTATAACACTATTGTTACTGCTCATGCATTTG-TAATAATCTTTTTTATAGTTATACCAATTATAATTGGTGGATTTG-GAACTGATTAGTACCTTTAATGCTAGGGGCACCAGATATAGCATTC-CCTCGTATAAATAATATAAGATTTTGACTTCTTCCCCCTCTTTAAC-CCTATTAATTTCAAGTAGAATTGTAGAAAATGGGGCAGGAACAGGAT-GAACCGTTTATCCACCTTTATCATCTAATATTGCCCATGGAGGCA-GATCAGTAGATCTGGCAATTTTTTCACTACATTTAGCTGGAATTTTCAT-CAATTTTAGGGGCAATTAATTTTATTACAACAATTATTAATATACGAAT-TAATAATCTTTCATTTGATCAAATACCCCTATTTGTTTGATCAGTAGGT-ATTACAGCATTACTATTACTTCTATCTTTACCAGTATTGGCGGGAGCT-ATTACCATACTTCTAACTGACCGAAATCTCAATACTTCCTTTTTTGATC-CAGCAGGGGGGGGAGACCCTATTTTATATCAACACCTA

Diagnosis. From *C. gigantea*, *C. chelicerata* differs in having the male costal arm hook shaped, longer, and thinner than in *C. gigantea*, and the juxta is strongly down-curved, apically conical whereas it is long, almost straight, without apical conical projection downward in *C. gigantea*. In female genitalia the sterigma forms a strongly sclerotized symmetrical structure made of two asymmetrical bell-shaped cavities, opened anterad in *C. chelicerata* whereas it forms a pair of shallow pockets opened posterad in *C. gigantea*.

Description. Male (n=21) (Figs 2, 9): Head with ochreous to brown chaetosemata. Antenna greyish brown with light brown scales, with patch of brown scales at base. Maxillary palpus ochreous to dark brown, lightly ringed with dark brown at 2/3, white tipped. Labial palpus: 1.3–2.0 mm long; ochreous, basally white, tip of segment II light greyish-brown; white tipped. Thorax with dark brown patch at collar. Foreleg coxa white; femur white, ashen brown dorsally, tibia and tarsomeres ochreous, distally ringed with dark brown. Midleg femur white, tibia ashen brown basally, tarsomeres ochreous, brown to ashen brown on upperside, with white ringed tips. Hindleg white, tarsomere I ochreous; II–V brown on upperside, with white ringed tips. Abdomen dull white to light ochreous. Forewing length: 10.5–15.0 mm; costal band wide, brown from base to apex; median and subterminal transverse lines faded brown, sometimes completely faded; dark brown spots on apical margin forming more or less continuous line; fringes brass colored; underside white with costal margin brown; outer margin with somewhat triangular spots. Hindwing snow white, with marginal spots between veins; fringes white; underside silvery white with marginal spots pronounced.

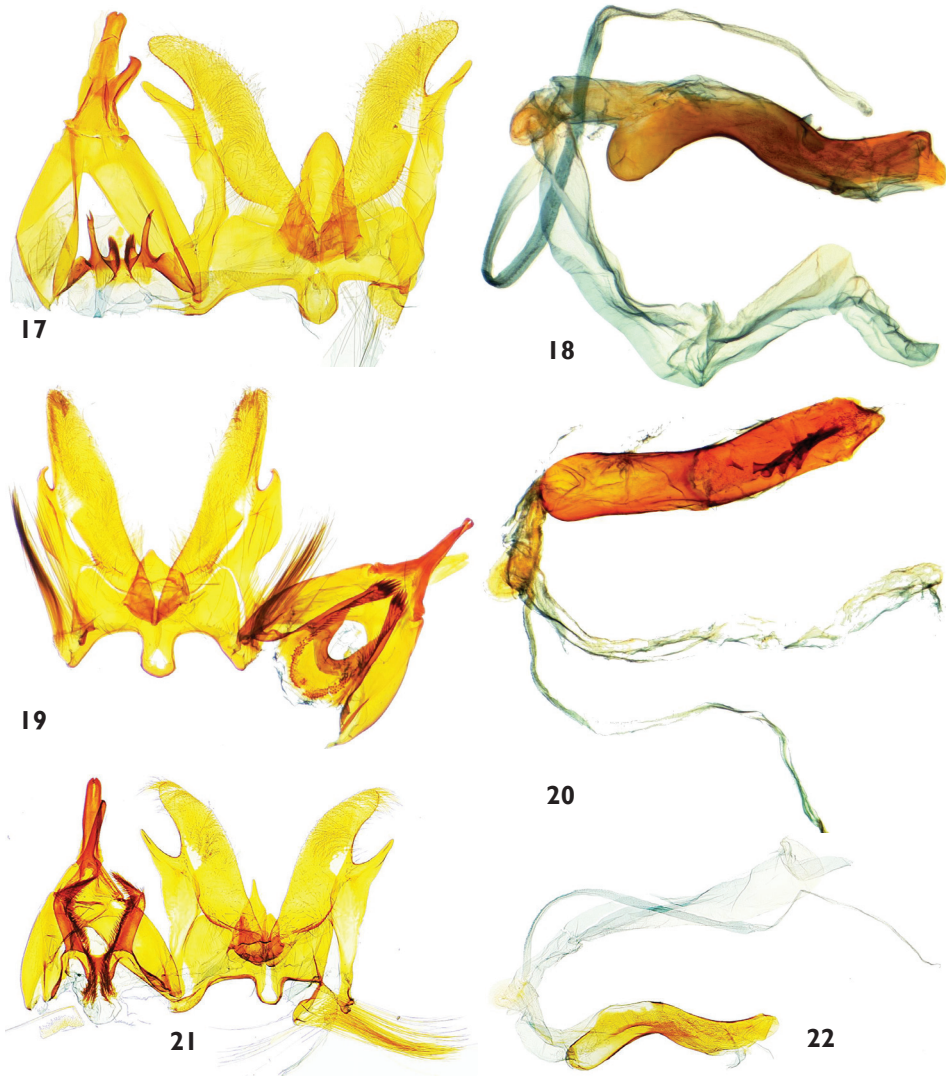
Tympanal organs (n=9): Transverse ridge almost straight medially. Tympanic pockets conical, extending slightly beyond transverse ridge. Tympanic bridge lightly sclerotized, dorsal base of praecinctorium sclerotized. Tympanic drums elongate, bean shaped, posteriorly reaching transverse ridge or slightly beyond.

Male genitalia (n=9) (Figs 13, 14): Uncus straight, of about 4/5 length of tegumen arms, dorso-ventrally compressed, with setae dorsally and laterally; apex truncated, slightly rounded, tip with short projection pointing posterad, ventrally convex,



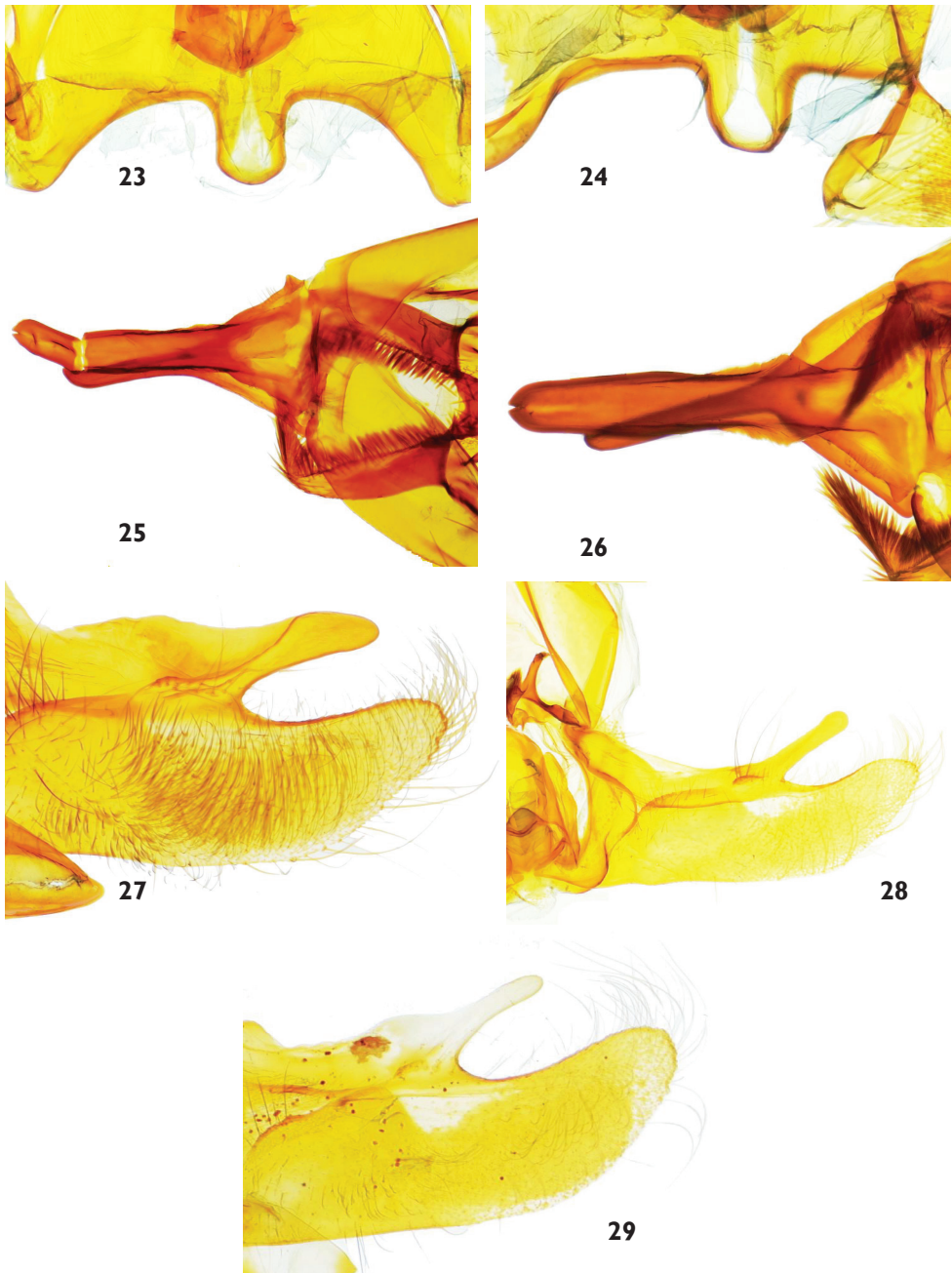
Figures 11–16. Male genitalia features of *Catharylla* species: **11–12** *C. bijuga* sp. n., paratype, French Guyana, St-Jean-de-Maroni, slide BL 1719♂ (BMNH) **11** Genitalia without phallus. cu: cucullus; c. a.: costal arm; g: gnathos; j: juxta; t: tegumen; u: uncus; v: vinculum **12** Phallus in lateral view. v: vesica; c: cornutus **13–14** *C. chelicerata* sp. n., paratype, Brazil, Amazonas, Rio Negro, Mirapinima, slide BL 1714 ♂ (MHNG) **13** Genitalia without phallus **14** Phallus in lateral view **15–16** *C. gigantea* sp. n., holotype, Brazil, Amazonas, Reserva Ducke, slide BL 1747 ♂ (BMNH) **15** Genitalia without phallus. **16** Phallus in lateral view.

sometimes with median bump. Gnathos arms joining at 1/5 of length, regularly hook shaped, forming angle of about 100° with axis of basal arms, about 1/4 longer than uncus. Tegumen arms narrow at base, enlarging progressively toward dorsum to 2 × basal width, projected dorsally with bump at connection, connecting at distal 1/6. Cucculus densely setose, slightly directed upward on distal 1/3, apically truncated; basal 2/3 of costa of valva dorso-ventrally and laterally widened; costal arm hook-shaped,



Figures 17–22. Male genitalia features of *Catharylla* species: **17–18** *C. tenellus* Zeller **17** Genitalia without phallus, Brazil, Minas Gerais, Caraça, slide BL 1755 ♂ (Becker Coll.) **18** Phallus in lateral view, Brazil, São Paulo, Bertioga, slide BL 1746 ♂ (USNM) **19–20** *C. coronata* sp. n. paratype, Brazil, Paraná, Rio Negro, slide BL 1730 ♂ (ISZP) **19** Genitalia without phallus **20** Phallus in ventral view **21–22** *C. serrabonita* sp. n. paratype, Brazil, Bahia, Camacan, Serra Bonita Reserve, slide BL 1776 ♂ (MHNG) **21** Genitalia without phallus **22** Phallus in lateral view.

strongly sclerotized, directed upward at about 45° from costal arm base. Juxta triangular, curved downward, tip rounded and sac-like, basal lateral lobes curved ventrally. Saccus short, curved upward medially. Phallus narrow, S-shaped; vesica covered with tiny spicules, with one large, curved, pointed cornutus apically, preceded by string of 13–14 smaller cornuti increasing in size toward apex.



Figures 23–29. Male genitalia features of *Catharylla* species: **23–24** Vinculum of *C. serrabonita* sp. n. **23** Brazil, Espírito Santo, Linhares, slide BL 1745 ♂ (USNM) **24** Brazil, Bahia, Camacan, Serra Bonita Reserve, slide BL 1776 ♂ (MHNG) **25–26** Uncus of *C. serrabonita* sp. n. **25** Brazil, Espírito Santo, Linhares, slide BL 1745 ♂ (USNM) **26** Brazil, Bahia, Camacan, Serra Bonita Reserve, slide BL 1776 ♂ (MHNG) **27–29** Costal arm of *C. tenellus* **27** São Paulo, Ubatuba, Picinguaba, slide BL 1757 ♂ **28** Minas Gerais, Caraça, slide BL 1746 ♂ **29** Brazil, Bahia, Porto Seguro, A. d'Ajuda, slide TL 9 ♂.

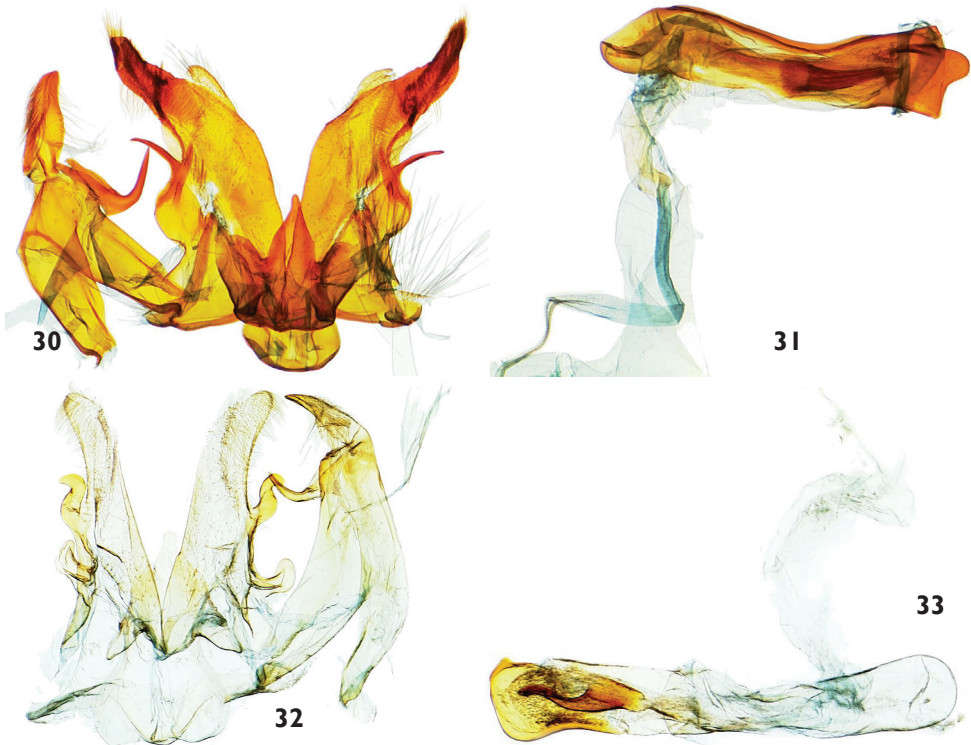
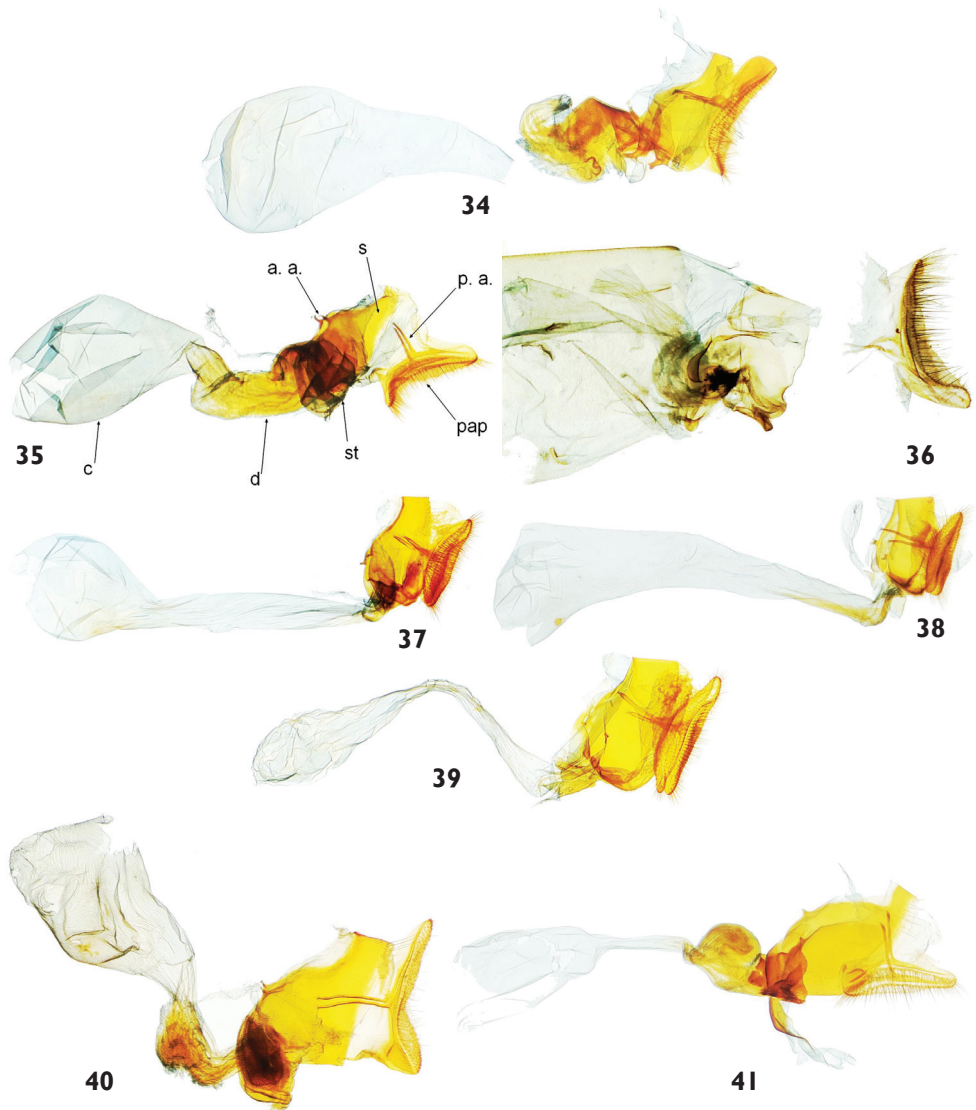


Figure 30–33. Male genitalia features of *Catharylla* species. **30–31** *C. mayrabonillae* sp. n., paratype, Peru, Agnaytia, Huallaga, 400 m, slide BL 1724 ♂ (CNC) **30** Genitalia without phallus **31** Phallus in lateral view **32–33** *C. paulella* Schaus, Bolivia, provincia del Sara, slide GS-6682-SB (BMNH) **32** Genitalia without phallus **33** Phallus in lateral view.

Female (n=4): Labial palpi: 1.8–2.2 mm long. Forewing: 15–19.5 mm. Frenulum quadruple.

Female genitalia (n=3) (Fig. 35): Papillae anales dorsally strongly produced posterad, with rounded bulge dorso-apically; ventrally slightly produced. Posterior apophyses $0.3\text{--}0.45 \times$ length of papillae. Tergite VIII about half of length of sternite VIII. Anterior apophyses about $0.1 \times$ length of papillae anales, slightly wider and rounded apically. Sternite VIII narrowing ventrally, densely covered with spinules, slightly connected medially at lamella antevaginalis; lamella antevaginalis slightly projected downward. Sterigma forming strongly sclerotized ventro-laterally symmetrical structure made of two asymmetrical bell-shaped cavities in ventral view, opened anterad, with dorsal lobe longer, expanding upward, slightly indented along latero-anterior margin; covered with minute punctuation. Ventro-basal section of ductus bursae tongue shaped, strongly sclerotized; ductus bursae long, ventrally sclerotized, widened and looped in basal half; enlarging progressively into corpus bursae. Corpus bursae egg-shaped with one signum.

Distribution. The species was found in French Guiana and Brazil (Amazonas) (Fig. 43).



Figures 34–41. Female genitalia of *Catharylla* species. **34** *C. bijuga* sp. n. in lateral view, paratype, Suriname, Sipaliwini District, Thibiti area, Kabo-Creek, slide BL 1732 ♀ (Schouten Coll.) **35** *C. chelicerata* sp. n., paratype, Brazil, Reserva Ducke, slide BL 1711 ♀ (CNC); pap: papillae anales; p. a.: posterior apophyses; s: segment VIII; a. a.: anterior apophyses; st: sterigma; d: ductus bursae; c: corpus bursae **36** *C. gigantea* sp. n. paratype, French Guyana, Saint-Jean-du-Maroni, slide n°6679SB (BMNH) **37** *C. tenellus* Zeller, Brazil, Rio de Janeiro, slide BL 1733 ♀ (CMNH) **38** *C. coronata* sp. n. paratype, Brazil, Paraná, Curitiba, slide BL 1753 ♀ (Becker Coll.) **39** *C. serrabonita* sp. n. paratype, Brazil, Espírito Santo, Linhares, slide BL 1759 ♀ (Becker Coll.) **40** *C. mayrabonillae* sp. n. paratype, French Guyana, Saint-Jean-du-Maroni, slide BL 1720 ♀ (BMNH) **41** *C. paulella* Schaus, Brazil, Distrito Federal, Planaltina, slide BL 1751 ♀ (Becker Coll.).

Etymology. “*Chelicerata*” refers to the shape of the costal arms of the male valva, which look like mygalomorph chelicerae.

Notes. Two females included here have been named *Catharylla robustella* (genitalia on slide GS-5949-SB, CMNH) and *Catharylla tenellina* (genitalia on slide Pyralidae Brit. Mus. Slide N°17693, BMNH) by S. Bleszynski, as indicated on labels, but these names were never published. These two specimens are probably *C. chelicerata*, but the bad genitalia preparations do not allow to see details, and therefore they are not included as paratypes.

***Catharylla gigantea* T. Léger & B. Landry, sp. n.**

<http://zoobank.org/06B7837B-A5DE-4347-824E-B74127F028E2>

http://species-id.net/wiki/Catharylla_gigantea

Figs 3, 15, 16, 36, 43

Type material. Holotype. ♂, with labels as follows: “Brazil: Amazonas, Manaus, | Reserva Ducke, AM-010, k[ilo]m[eter]. 26 | 2°55'S, 59°59'W, Dec[ember].13, 1993 | J. Bolling Sullivan & | Roger W. Hutchings | U[ltra]V[iolet] Light (Plateau Hut)”; “HOLOTYPE | *Catharylla gigantea* | T. Léger & B. Landry” [red label]; “BL 1747 ♂” [light green label]. Deposited in USNM.

Paratypes. 5♂, 2♀. BRAZIL: 1♂, Amazonas, Reserva Ducke, km. 26, Manaus–Itacoatiara Highway, 15.v.1972 (E. G., I. and E. A. Munroe) (CNC). FRENCH GUIANA: 1♂, 1♀ (genitalia respectively on Pyralidae Brit. Mus. slides N° 11224 and 11342), Saint-Jean-du-Maroni (E. Le Mout) (BMNH); 1♂ (genitalia on slide GS-6694-SB), Oyapok [sic] River, Pied Saut, iii.1918 (S. M. Klages) (CMNH). GUYANA: 2♂, 1♀ (1♂ with genitalia on slide BL 1716, ♀ with genitalia on Pyralidae Brit. Mus. Slide N° 19017), Potaro, ii.1908 (2♂), v.1908 (1♀) (S. M. Klages) (BMNH).

Diagnosis. From *C. chelicerata*, *C. gigantea* differs in having the male costal arm shorter, basally wide and tooth shaped while it is long, narrow throughout and hook shaped in *C. chelicerata*. The juxta is long, tongue shaped, almost straight, and apically rounded, whereas it is downcurved and apically conical in *C. chelicerata*. In female genitalia, the sterigma forms a pair of shallow pockets opened posterad whereas in *C. chelicerata* the sterigma forms a strongly sclerotized symmetrical structure made of two asymmetrical bell-shaped cavities opened anterad.

Description. Male (n=6) (Fig. 3): Head with ochreous chaetosemata. Antenna brown with light brown scales, with patch of dark brown scales at base. Maxillary palpus brown with dark brown spot at half of length, white tipped. Labial palpus: 1.6–2.4 mm long; ochreous to brown ochreous, basally white, with patch of dark brown scales at half of length, white tipped. Thorax with some brown at collar. Foreleg coxa white, femur white, ashen brown dorsally; tibia and tarsomeres brown-ochreous, distally ringed with dark brown. Midleg white with tibia-femur joint and base of tibia ashen; tarsomeres ochreous to brown ochreous with upperside brown to dark brown, white tipped. Hindleg white with tarsomeres II–V ochreous to brown ochreous, up-

perside brown, with white tips. Forewing length: 13.5–14.5 mm; snow white with wide brown to dark brown costal line from base to apex; median and subterminal transverse lines faded brown; dark brown spots on termen forming more or less continuous line; fringes brass colored; underside white, with costal margin brown ochreous, outer margin with subtriangular spots. Hindwing snow white; marginal spots dark brown between R5, M1, M2, M3, and CuA1; fringe white; underside snow white, with same spots as on upperside.

Tympanal organs (n=5): Transverse ridge medially convex. Tympanal pockets extending slightly beyond transverse ridge, rounded. Tympanal bridge lightly sclerotized, dorsal base of praecinctorium sclerotized. Tympanal drums elongate, bean shaped.

Male genitalia (n=5) (Figs 15, 16): Uncus straight, about $3/4$ length of tegumen arms, dorso-ventrally flattened, dorsally convex, ventral margin convex in basal half, concave in distal half; basally and laterally setose; apex slightly rounded, medially with short projection pointing postero-ventrally. Gnathos arms joining at $1/5$, about $1/4$ longer than uncus, regularly curved. Tegumen arms narrow at base, widening regularly to reach $1.5 \times$ basal width dorsally, with connection at distal $1/6$. Cucullus densely setose, broad at base, slightly widening and truncate at apex; costal arm of valva basally wide, short, tooth shaped, slightly curved inward. Juxta long, tongue shaped, almost straight, apically rounded, with basal lateral lobes curved ventrally. Saccus short, curved upward. Phallus narrow, S-shaped; vesica covered with tiny spicules, with string of 14 small cornuti increasing in size toward apex, with apical cornutus up to $5 \times$ length of previous one.

Female (n=2): Labial palpi: 2.5–3.1 mm long. Forewing length: 17.5–22 mm; frenulum triple.

Female genitalia (n=2) (Fig. 36): Papillae anales ventrally projected. Posterior apophyses about $0.35 \times$ length of papillae anales, narrow. Segment VIII narrowing ventrally, densely covered with spinules; narrow connection at lamella antevaginalis; lamella antevaginalis slightly projected downward. Sterigma forming pair of shallow pockets opened posterad at base of segment VIII. Anterior apophyses about $0.08 \times$ length of papillae anales, of medium width, basally wide. Ductus bursae wide, as long as twice segment VIII, regularly enlarging into corpus bursae. Corpus bursae with one rounded signum.

Distribution. *Catharylla gigantea* has been found in French Guiana, Guyana, and Brazil (Amazonas) (Fig. 43).

Etymology. The name comes from the Latin *giganteus*, *a*, *um* meaning very large.

Notes. The name was given to the species on manuscript labels by S. Blezynski, probably in reference to the large size of the female.

Tenellus species group

Diagnosis. The synapomorphies of the group are the dorsal furrow on the uncus, the uncus apex slightly bifid, the presence of a transtilla in male genitalia, and the absence of a ventral connection of sternite VIII in female genitalia. The *tenellus* species group

can also be separated from the other *Catharylla* species based on the following additional diagnostic characters: the hindwings are creamy-white, and in female genitalia, the papillae anales are not produced.

Notes. This group includes three species, including two new ones. *Catharylla ser-rabonita* and *C. tenellus* form a monophyletic group within the *tenellus* species group (Fig. 42). Relationships to other species groups are unknown.

***Catharylla tenellus* (Zeller, 1839)**

http://species-id.net/wiki/Catharylla_tenellus

Figs 4, 17, 18, 27–29, 37, 45

Crambus tenellus Zeller, 1839: 174–175

Catharylla tenella: Zeller 1863: 50; Bleszynski and Collins 1962: 226; Landry 1993: 1088; Munroe 1995: 35; Nuss et al. 2013

Argyria tenella: Zeller 1877: 58; Dyar 1914: 317

Platytes tenella: Hampson 1896: 944

Type material. Holotype. ♀, “Type” [red ringed]; “*Catharylla* | *tenella* Z[eller]. | Mon[ograph]. p[age]. 50 Am. anfr.” [not clearly readable]; “Zell[er]. Coll[ection]. | 1884”; “♀ | Pyralidae | Brit[ish]. Mus[eum]. | Slide N° | 1094”. Deposited in BMNH.

Other specimens examined. 20 ♂, 7 ♀. BRAZIL: 3 ♂ (1 ♂ with leg used for DNA barcoding BC MTD 01842, 1 ♂ with genitalia on slide BL 1757), São Paulo, Ubatuba, Picinguaba, 23°22'S, 44°50'W, 2–20m, 22–24.ix.2001 (V. O. Becker n°132820) (Becker Coll.); 2 ♂ with same data except 10–12.xi.2001 (V. O. Becker n°133712) (Becker Coll.); 2 ♂, 1 ♀ (1 ♂ with genitalia on slide BL 1741, ♀ genitalia on slide BL 1742), São Paulo, Bertioiga, 5 m, 5.xi.1995 (V. O. Becker n°99090) (USNM); 1 ♂ (genitalia on slide BL 1778) with same data (Becker Coll.); 1 ♂ (genitalia on slide BL 1775) with same data except 15–17.v.1996 (V. O. Becker n° 99386) (Becker Coll.); 1 ♂ with same data except 7–9.x.1996 (V. O. Becker Coll. n°99757) (Becker Coll.); 1 ♂ (used for DNA sequencing and barcoding LEP 975, BC MTD 01711, genitalia on slide TL 13), São Paulo, São Luiz do Paraitinga, 23°20'S, 45°06'W, 900 m, 13–20.iii.2001 (V. O. Becker n°132356) (Becker Coll.); 1 ♂ (genitalia on slide Pyralidae Brit. Mus. Slide N° 19065), São Paulo, 700 m (E. D. Jones) (BMNH); 1 ♂ (genitalia on slide BL 1746), Minas Gerais, Caraça, 1300 m, 1–2.iv.1992 (V. O. Becker n°85081) (USNM); 1 ♀ (genitalia on slide BL 1754) with same data (Becker Coll.); 1 ♂ (genitalia on slide BL 1755) with same data except 25.x.1994 (V. O. Becker & K. S. Sattler, n°93291) (Becker Coll.); 1 ♂, 1 ♀ (♂ used for DNA sequencing and barcoding LEP 973, BC MTD 01709, genitalia on slide TL 11, ♀ genitalia on slide BL 1758), Bahia, Porto Seguro, A. d'Ajuda, 16°27'S, 39° 03'W, 20 m, 12.vii.2009 (V. O. Becker n°144140) (Becker Coll.); 2 ♂ (used for DNA sequencing and barcoding, one with labels LEP 972, BC MTD 01888, genitalia on slide TL 10, other with labels LEP 974, BC MTD 01710, genitalia on slide TL 12) with same data except 15.viii.2008 (V. O.

Becker n°140808) (Becker Coll.); 1 ♂ (used for DNA sequencing and barcoding LEP 971, BC MTD 01708, genitalia on slide TL 9) with same data except 1–3.v.2009 (V. O. Becker n°142784) (Becker Coll.); 1 ♂, Paranà, Castro (USNM); 1 ♀ (genitalia on slide BL 1733), Rio de Janeiro, xi[day and year data missing] (H. H. Smith) (CMNH); 1 ♀ (genitalia on Pyralidae Brit. Mus. Slide N°19069), Rio de Janeiro, Corcovado, 457 m, 26.xii.1958 (E. P. Wiltshire) (BMNH). No locality data: 1 ♂, 1 ♀ (♂ genitalia on slide Nat[ur]. hist[orisches]. Mus[eum]. Wien Gen[italia]. Praep[aration]. MV 9022a, ♀ genitalia on slide Nat. hist. Mus. Wien Gen. Praep. MV 9022b); 1 ♀ (genitalia on slide Nat. hist. Mus. Wien Gen. Praep. MV 9022c), 1869 (NMW).

COI barcode sequence of specimen BC MTD 1710 (654 bp): ACTCTA-TATTTTATCTTTGGAATTTGATCAGGAATAATTGGAACATCTTTAA-GATTATTAATTCGAGCAGAATTAGGGAATCCTGGATCTCTAATTG-GAGATGATCAAATTTATAACACTATTGTAACAGCCCATGCATTTATTA-TAATTTTTTTTATGGTTATACCAATTATAATTGGTGGATTTGGAAATT-GATTGGTTCCATTAATATTAGGAGCCCCAGATATAGCTTTCCCC-CGAATAAATAACATAAGATTTTGGTTATTACCCCTTCCTTAACTCTTT-TAATTTCTAGAAGAATTGTAGAAAATGGAGCTGGAACAGGATGAACG-GTCTACCCCCCTTTCATCTAATATTGCCCATAGTGGAAGATCTG-TAGATTTAGCAATCTTTTCTCTTCATTTAGCTGGAATTTTCATCAATTT-TAGGAGCTATTAATTTTATTACAACAATTATTAATATACGAATTAG-TAATTTATCTTTTGATCAAATACCTTTATTTGTTTGATCAGTCGGTAT-TACAGCTTTACTTCTTCTTCTATCTTTACCTGTATTAGCAGGAGCTAT-TACTATACTTTTAACTGATCGAAATTAAATACATCTTTTTTTTGATCCT-GCAGGAGGAGGAGATCCTATCTTATATCAACATTTA

Diagnosis. From *C. serrabonita* and *C. coronata*, *C. tenellus* can be separated by the median transverse line, which is faintly convex towards costa, whereas it is more strongly convex in *C. coronata* and *C. serrabonita*. The male genitalia provide the best diagnostic characters. The most obvious refers to the transtilla, which forms a pair of short, narrow sclerotized arms with pointed tips, projecting posterad, with, in between, a pair of brushes directed medio-ventrally, whereas it forms a pair of arms pointing posterad with a string of spines ventrally in *C. serrabonita* and *C. coronata*. In female genitalia, the anterior angle of sternite VIII is directed downward into a more or less rounded projection covered with short spinules of same length, whereas it is projected anterior in *C. serrabonita*, and it is not projected in *C. coronata*.

Redescription. Male (n=20) (Fig. 4): Head white with ochreous chaetosemata. Antenna brown with ochreous scales. Maxillary palpi ochreous to brown, white tipped. Labial palpi: 1.1–1.4 mm long; basally white, medially brown ochreous with white tips. Thorax slightly ochreous at collar. Foreleg coxa white; femur ochreous, dorsally dark brown; tibia and tarsomeres ochreous, distally ringed with dark brown. Midleg light ochreous with tibia-femur joint brown; tarsomeres II–V dark brown on upper-side, with white ringed tips. Hindleg white; tarsomeres as midleg. Forewing length: 10.5–12 mm; snow white; costal line ochreous, lightly pronounced from base to apex; median and subterminal transverse lines ochreous, median transverse line faintly con-

vex towards costa; outer margin ochreous with 7 dark brown spots often triangular, strongly pronounced; fringes brass colored; underside ochreous with costal margin pronounced in basal half and marginal spots pronounced. Hindwing cream-coloured; outer margin with small ochreous brown spots forming more or less continuous line between Sc+R1, Rs, M1, M2, M3, CuA1 and CuA2; underside light ochreous, with marginal spots pronounced; fringes white.

Tympanal organs (n=13): Transverse ridge more or less regularly rounded, medially more straight. Tympanic pocket extending slightly beyond transverse ridge. Tympanic drum ovoid, posteriorly not extended beyond transverse ridge. Tympanic bridge faintly sclerotized.

Male genitalia (n=13) (Figs 17, 18, 27–29): Uncus about half of length of tegumen arms, broadly downcurved; uncus arms connecting at base, with ventro-lateral tuft of setae; dorsal furrow with few short setae on each side, tip rounded, slightly indented medially, slightly convex in apical 1/3. Gnathos short and thick, arms joining at half of length, laterally compressed toward apex, almost straight, slightly downcurved, with apex pointing upward. Tegumen arms slightly enlarging toward apex; connecting at 3/4, slightly projected dorsally at connection. Costa of valva at 2/3 with arm directed postero-dorsally with rounded tip, without basal projection on dorsal edge or narrow with low basal projection, or wide with basal projection; cucullus upcurved in apical 1/4. Juxta ogival, posteriorly directed downward, with pair of thumb-like lobes ventrally reaching about 2/3 of length. Transtilla strongly sclerotized, with pair of narrow arms on each side of middle, pointing posterad, with 3 spines apically, also with pair of shorter brushes of tightly set spines medio-ventrally; in some specimens triangular median projection dorsally with few tiny setae. Phallus S-shaped, subapically with dorsal bump, apically lightly sclerotized, truncated, covered with microspicules barely visible; vesica without cornuti.

Female (n=7): Labial palpi: 1.6–2 mm; forewing length 12–16 mm; frenulum triple.

Female genitalia (n=7) (Fig. 37): Papillae anales straight, thick. Posterior apophyses narrow $0.3\text{--}0.45 \times$ length of papillae anales, slightly wider basally. Intersegmental membrane between segments VIII and IX covered with microspines. Tergite VIII laterally about 2X longer than dorsally; sternite VIII formed by 2 lobes regularly narrowing downward in more or less triangular shape, not connected ventrally, densely covered with short spinules of same length; ventro-anterior angle of sternite VIII slightly projected downward, rounded, covered with short spinules; anterior margin of segment VIII latero-dorsally strongly sclerotized, thicker; posterior margin with dorsal line of setae. Anterior apophyses $0.02\text{--}0.05 \times$ length of papillae anales. Sterigma membranous, covered with spinules. Ductus bursae about $3 \times$ length of corpus bursae, narrow. Corpus bursae elongate, sometimes with one signum.

Distribution. The species is known from Brazil in the Atlantic Forest (Bahia, Minas Gerais, Paraná, Rio de Janeiro, São Paulo) (Fig. 45).

Notes. The species was described from “one female collected in Brazil, near Rio de Janeiro”. Hence, the lectotype designated by a label by S. Bleszynski is not warranted. This designation is presumably based on the fact that Zeller (1863:50) mentions a pair deposited in the Vienna Museum. The association of sexes in this species is not 100% certain.

Specimens from Porto Seguro, Brazil show a divergence of 3.34% in COI barcode sequences with the specimen from Ubatuba, Brazil. In morphology, differences in male genitalia are also observed: in the specimens from Bertioga, Caraça, São Paulo and Ubatuba the costal arm of the valva is wide and 1/3 of the length of the cucullus, almost reaching its tip, and the dorsal edge at base is slightly produced (Fig. 27). In the specimens from Porto Seguro, the costal arm is about 1/5 the length of the cucullus, relatively narrow, and the dorsal edge is slightly produced at base (Fig. 29). Another form, from Caraça, Minas Gerais (Fig. 28) was also found. No differences were found in the female genitalia. We feel that specimens and data are currently lacking to conclude that possibly more than one taxon should be recognized under *C. tenellus*, or that there is indeed a deep divergence in the COI barcode between populations of this species.

***Catharylla coronata* T. Léger & B. Landry, sp. n.**

<http://zoobank.org/7E0EB0BE-44C4-42EC-9F4D-2C923E9299E6>

http://species-id.net/wiki/Catharylla_coronata

Figs 5, 19, 20, 38, 45

Type material. Holotype. ♂, with labels as follows: “Col. BECKER | 81552”; “BRASIL:ES | Linhares, 40m | 20-29.ii.1992 | V.O.Becker Col”; “HOLOTYPE | Catharylla | coronata | Léger & Landry” [red label]. Deposited in Becker Collection.

Paratypes. 21 ♂, 4 ♀. BRAZIL: 5 ♂ with same data as holotype (1 used for DNA barcoding BC MTD 01890, 1 with genitalia on slide BL 1743); 2 ♂ with same data as holotype (1 used for DNA barcoding BC MTD 01891) except 05–09.iv.1992 (V. O. Becker n°82486); 6 ♂, 1 ♀ (1 ♂ with genitalia on slide BL 1730, ♀ with genitalia on slide BL 1731), Paranà, Rio Negro, 900 m, 8.ii.1973 (2 ♂), 10.ii.1973 (1 ♂), 11.ii.1973 (3 ♂), 13.ii.1973 (1 ♀) (A. & J. Razowski) (ISZP); 2 ♂, 2 ♀, Paranà, Curitiba, 920 m, 17.ii.1975 (1 ♂) (V. O. Becker n°10167), 20.ii.1975 (1 ♀, genitalia on slide BL 1756) (V. O. Becker n°10168), 12.iii.1975 (1 ♀, genitalia on slide BL 1753) (V. O. Becker n°10166), 10.x.1975 (1 ♂) (V. O. Becker n°4010) (Becker Coll.); 1 ♂ (genitalia on Pyralidae Brit. Mus. Slide No. 11357), Paranà, Castro, 950 m (E. D. Jones) (BMNH); 1 ♂, Paranà, Quatro Barras, 850 m, 27.ii.1970 (Laroca & Becker) (V. O. Becker n°15442) (Becker Coll.); 1 ♂ (genitalia on Pyralidae Brit. Mus. Slide No. 11337) Rio de Janeiro, Novo Friburgo (BMNH); 1 ♂ (genitalia on Pyralidae Brit. Mus. Slide No. 19019) Sao Paulo, 700 m (E. D. Jones) (BMNH); 1 ♂, 1 ♀ (♂ with genitalia on slide BL 1774, ♀ with genitalia on slide BL 1736), Santa Catarina, Rio Vermelho, 968 m, 18.ii.1973 (♂), 28. ii. 1973 (♀) (A. & J. Razowski) (ISZP); 1 ♂, no locality data (V. O. Becker) (Becker Coll.).

COI barcode sequence of paratype BC MTD 01890 (654 bp): ACTTTA-TATTTTATTTTGGGAATTTGAGCAGGAATAGTAGGAACATCATTAAGATTATTAATTCGAGCTGAATTAGGTAATCCTGGATCTCTTATTGGAGATGATCAAATCTATAATACTATTGTAACCGCTCATGCATTATTATAATTTTTTTTATAGTTATACCAATTATAATTGGTGGATTGGAAATT-

GATTAGTTCCCTTAATATTAGGAGCACCAGATATAGCTTTTCCTC-
 GAATAAATAACATAAGATTTTGATTATTACCCCCCTCTTTAACTCTTT-
 TAATTTCAAGAAGAATTGTAGAAAATGGAGCTGGAACAGGATGAACA-
 GTTTACCCCCCACTTTCATCTAATATTGCCCATAGTGGAAGATCCG-
 TAGATTTAGCAATCTTTTCCCTTCATTTAGCTGGAATTTCTTCAATTT-
 TAGGAGCAATTAATTTTATTACAACAATTATTAATATACGAAT-
 CAATAATCTTTCATTTGATCAAATACCTCTTTTTTGTTTGATCAG-
 TAGGAATTACAGCTTTACTTCTTCTTTTATCATTACCAGTATT-
 AGCTGGAGCTATTACTATACTTTTAACTGATCGAAATTTAAATA-
 CATCTTTTTTTTGATCCCGCAGGAGGAGGAGATCCTATTTTATAT-
 CAACATTTA

Diagnosis. From *C. serrabonita* and *C. tenellus*, *Catharylla coronata* can be separated with characters of the male genitalia: the uncus is apically bifid and grooved on distal 1/5 in *C. coronata* whereas it is only indented medially at apex in *C. serrabonita* and *C. tenellus*; the costal arm of the valva is short and the apex is curved inward in *C. coronata* whereas the costal arm is longer and points postero-dorsally in the other two species; the transtilla forms a pair of sclerotized arms slightly bent inward distally, ventrally with a row of short spines increasing in size from base to apex whereas it forms a pair of short, narrow sclerotized arms with pointed tips, projecting posterad, and with a pair of brushes directed medio-ventrally in *C. tenellus* and a pair of sclerotized arms strongly bent inward on distal 1/4 and with a string of long spines of same length medially along it in *C. serrabonita*; the juxta is shorter than in *C. tenellus*, and regularly narrowing toward apex whereas it is strongly narrowing on distal 1/4 in *C. serrabonita*; the ventral projections of the juxta form a pair of shallow pockets whereas they are bell-shaped in *C. serrabonita* and thumb-like in *C. tenellus*; the vesica has a row of 6–7 cornuti in *C. coronata* whereas it does not show any cornuti in *C. serrabonita* and *C. tenellus*. In the female genitalia of *C. coronata*, the anterior angle of sternite VIII is not projected whereas it is rounded, projected anterad and covered with short spinules in *C. serrabonita*, and projected downward in *C. tenellus*. The anterior apophyses are quadrangular, anvil shaped whereas they are spine like in the other two species.

Description. Male (n=21) (Fig. 5): Head white with ochreous chaetosemata. Antenna brown, with whitish ochreous scales and patch of brown scales at base. Maxillary palpi light ochreous to ochreous, white tipped. Labial palpi: 1.6–1.85 mm long; light ochreous, white tipped. Thorax white, with ochreous patch at collar. Foreleg coxa white; femur white, dorsally dark brown; tibia and tarsomeres ochreous, distally ringed with brown; midleg and hindleg white to light ochreous, tarsomeres II–V ochreous, upperside brown, with white ringed tips. Forewing length: 10–13 mm; costal margin line thin, light ochreous, apically faded; median transverse line light ochreous, concave on costal half, more or less disrupted; subterminal transverse line ochreous, curving toward base on costal half; R5 vein faintly marked apically with ochreous; outer margin ochreous with 7 pronounced dark brown spots more or less triangular between veins, sometimes connecting; fringes brass colored; underside white ochreous to ochreous,

costal margin basally brown; outer margin with pronounced spots. Hindwing white to creamy white, usually with marginal brown spots between Sc+R1, Rs, M1, M2, M3, CuA1 and CuA2, forming more or less continuous line; fringes white; underside light ochreous, with dark brown marginal spots pronounced.

Tympanal organs (n=7): Transverse ridge more or less regularly rounded. Tympanic pocket extending faintly beyond transverse ridge, rounded. Tympanic drum glomerular, not reaching transverse ridge.

Male genitalia (n=7) (Figs 19, 20): Uncus about 3/4 length of tegumen arms, downcurved; uncus arms basally with ventro-lateral tuft of setae; dorsal furrow pronounced medially with row of few setae on each side; thin, bifid on distal 1/5, slightly grooved, with apex slightly pointed; with shallow cavity ventro-apically. Gnathos arms connecting at 1/3 of length; shaft slightly downcurved, with apex pointing upward. Tegumen arms enlarging progressively toward uncus; tegumen connection about 1/3 arms length. Costa of valva basally narrow, with quadrangular projection, apically narrowing into arm pointing posterad with short tip curved inward; cucullus curved upward in distal 1/3, with apex rounded. Juxta triangular, regularly narrowing toward apex with shallow pockets projected ventro-laterally; with baso-lateral angles curved upward. Transtilla modified into two arms projecting posterad, slightly curved inward in distal 1/4, with longitudinal string of short spines ventrally at base, medially along arms, and at apex, increasing in size from base to apex in factor of about 1 to 4–5. Phallus almost straight, apex dorsally triangular; vesica basally covered with tiny spicules, microspicules barely visible all along vesica, also with row of 5–6 straight, short spine-like cornuti wider at their base.

Female (n=4): Labial palpi: 1.6–2.2 mm long. Forewing length 14–16 mm. Frenulum triple.

Female genitalia (n=4) (Fig. 38): Papillae anales straight, thick. Posterior apophyses 0.3–0.5 × length of papillae anales, wide at base, about half of length of papillae. Intersegmental membrane between segment VIII and IX covered with microspines. Sternite VIII laterally about 1/3 longer than tergite VIII. Sternite VIII formed by 2 lobes regularly narrowing downward into triangle, not connected ventrally, densely covered with spinules, with spinules longer ventrally. Anterior apophyses about 0.05 × length of papillae anales, quadrangular, anvil shaped. Anterior margin of sternite VIII latero-dorsally strongly sclerotized, thicker; posterior margin with dorsal line of setae. Sterigma membranous, covered with spinules. Ductus bursae regularly enlarging into corpus bursae, basally directed downward. Corpus bursae more or less rounded, faintly delimited from ductus bursae, with one oval signum.

Distribution. The species occurs in Brazil in the following states: Bahia, Espírito Santo, Paraná, Rio de Janeiro, Santa Catarina, São Paulo (Fig. 45).

Etymology. The name comes from the latin *coronatus*, *a*, *um*: crowned, referring to the longitudinal string of short spines of the transtilla in the male genitalia.

Notes. Based on our combined phylogenetic analysis, *C. coronata* is the sister species of the *C. tenellus* + *C. serrabonita* pair (Fig. 42).

***Catharylla serrabonita* T. Léger & B. Landry, sp. n.**

<http://zoobank.org/8B0F3E46-1CA6-47C3-A5AC-D9A9A01AAA29>

http://species-id.net/wiki/Catharylla_serrabonita

Figs 6, 21–26, 39, 45, 46

Type material. Holotype. ♂, with labels as follows: “BRASIL :BA, Camacan | Res[erva]. Serra Bonita | 15°23'S, - 39°33'W, | 800m, 06.iv.2011 | B. Landry, V. Becker”; “HOLOTYPE | *Catharylla serrabonita* | T. Léger & B. Landry” [red label]. Deposited in Becker Collection.

Paratypes. 21 ♂, 1 ♀. BRAZIL: 5 ♂ (1 used for DNA barcoding BC MTD 01843, 1 with genitalia on slide BL 1745), Espírito Santo, Linhares, 40m, 25–30.i.1998 (V. O. Becker n°113929) (Becker Coll., USNM); 2 ♂, 1 ♀ (♀ with genitalia on slide BL 1759) with same except 20–29.ii.1992 (V. O. Becker n°81552) (Becker Coll., USNM); 2 ♂ with same data as holotype except 05–09.iv.1992 (V. O. Becker n°82486) (USNM); 10 ♂ (1 in alcohol, thorax used for DNA sequencing LEP 979, genitalia on slide TL 7, wing on slide TL 8) Bahia, Camacan, Serra Bonita Reserve, 15°23'S, 39°33'W, 800 m, B. Landry, V. O. Becker, 1.iv.2011 (1 ♂), 2.iv.2011 (2 ♂), 3.iv.2011 (1 ♂, genitalia on slide BL 1776), 5.iv.2011 (3 ♂), 6.iv.2011 (1 ♂), 7.iv.2011 (1 ♂) (MHNG); 1 ♂ with same data except vii.2010 (V. O. Becker) (Becker Coll.); 1 ♂ (used for DNA sequencing and barcoding LEP 970, BC MTD 01887, genitalia on slide TL 6) Bahia, Porto Seguro, A. d'Ajuda, 16°27'S, 39°03'W, 20 m, 12.vii.2009 (V. O. Becker n°144140) (Becker Coll.).

COI barcode sequence of holotype LEP 979 (516 bp): TAGTTGGAACAT-CATTAAGACTATTAATTCGAGSAGAGTTAGGGAATCCTGGATCTCT-TATTGGAGATGATCAAATTTATAATACTATTGKAACAGCTCATGSATT-TATTATAATTTTTTTTATAGTTATACCAATTATAATTGGTGGATTTG-GAACTGACTAGTTCCATTAATATTAGGAGCCCCAGACATAGCTTTC-CCCCGAATAAATAATATAAGATTTTGATTACTCCCCCCTCTTTAAC-CCTTTTAATTTCCAGAAGAATTGTAGAGAATGGAGCTGGAACAG-GATGAACGGTTTACCCCCCCTTTTCATCTAATATTGCTCATAGKGGAA-GATCTGTAGATTTAGCAATTTTTTCTCTTCATTTAGSAGGAATTTTCAT-CAATTTTAGGAGCAATTAATTTTATTACAACAATTATTAATATACGAAT-TAATAATTTATCTTTTGATCAAATACCGTTATTTGTCTGATCAGTTGG-TATTACAGCTTTACTCCTTCTTTTATCTTTAC

Diagnosis. From *Catharylla coronata* and *C. tenellus*, *C. serrabonita* can be separated by the zigzagging median transverse line with the short triangular dent at CuA2 and the pronounced creamy color of the hindwing. The male genitalia provide the best discriminant characters: in *C. serrabonita*, the transtilla forms a pair of sclerotized arms bent inward in distal 1/4 and with a string of long spines of same length medially along it, whereas it forms a pair of short, narrow sclerotized arms with pointed tips projecting posterad, and with a pair of brushes directed medio-ventrally in *C. tenellus*, and two sclerotized arms slightly bent inward distally, with a row of short spines increasing in size from base to apex in *C. coronata*, and the juxta is apically narrow and pointed

whereas it is triangular and regularly narrowed in *C. coronata* and *C. tenellus*. In female genitalia, the anterior angle of sternite VIII is projected anterad into a rounded protrusion covered with short spinules in *C. serrabonita*, whereas it is projected downward in *C. tenellus* and it is not projected in *C. coronata*.

Description. Male (n=21) (Fig. 6): Head white with ochreous chaetosemata. Antenna brown with whitish-ochreous scales and patch of brown scales at base. Maxillary palpus light ochreous, with patches of dark brown scales at 1/3 and 2/3, white tipped. Labial palpus: 1.7–2.5 mm long; light ochreous, white tipped. Thorax white, with ochreous patch at collar. Foreleg coxa white; femur white, dorsally dark brown; tibia and tarsomeres ochreous, distally ringed with brown. Midleg and hindleg white to light ochreous; tarsomeres II–V ochreous, brown on upperside, with white ringed tips. Forewing length: 10–14 mm; costal line ochreous; median transverse line ochreous to brown, zigzagging with short brown pronounced spot at M1 and short triangular dent at CuA2; subterminal transverse line ochreous to brown, regularly curved up to CuA2, then curved again; R5 faintly marked apically with ochreous; outer margin ochreous with 7 more or less triangular and connected dark brown spots between veins; fringes brass colored; underside ochreous, outer margin with pronounced spots. Hindwing cream-coloured, usually with more or less connected marginal brown spots between Sc+R1, Rs, M1, M2, M3, CuA1 and CuA2; fringes white; underside light ochreous, with marginal spots pronounced.

Tympanal organs (n=4): Transverse ridge more or less rounded, medially slightly flattened. Tympanic pocket extending faintly beyond transverse ridge, rounded. Tympanic drum glomerular, not reaching transverse ridge.

Male genitalia (n=4) (Figs 21–26): Uncus about as long as tegumen arms, downcurved; uncus arms connecting basally, with ventro-lateral tuft of setae at base; dorsal furrow pronounced medially with row of few hairs on each side; apex rounded, slightly indented medially, slightly convex ventro-apically. Gnathos arms connecting at 1/3; main shaft slightly downcurved with apex pointing upward. Tegumen arms regularly enlarging toward apex, connection at about 4/5 length of arms. Costa with apically rounded arm pointing postero-dorsally; cucullus curved upward in distal 1/3, with apex rounded. Juxta triangular, narrowing in distal 1/4 with bell-shaped ventro-lateral projections, regularly curved with apex horizontally straightened; baso-lateral angles curved upward. Transtilla with two very large sclerotized arms projecting posterad, bent inward in apical 1/4, with longitudinal string of long spines medially. Phallus slightly S-shaped, with apex dorsally sclerotized; vesica covered with microspicules, without cornuti.

Female (n=1): Labial palpi: 1.9 mm long. Forewing length: 14 mm. Frenulum triple.

Female genitalia (n=1) (Fig. 39): Papillae anales straight, thick. Posterior apophyses $0.4 \times$ length of papillae anales, narrow, wider at base. Intersegmental membrane between segment VIII and IX covered with microspines. Sternite VIII laterally about $5/3$ length of tergite VIII; posterior margin of tergite VIII with line of setae; sternite VIII forming 2 triangular lobes regularly narrowing downward, not connected, densely covered with short spinules of same length; anterior angle of sternite VIII slightly projected anterad, rounded, covered with short spinules of same length. Anterior apophyses $0.03 \times$ length of papillae anales. Sterigma membranous, covered with spinules.

Ductus bursae about $3 \times$ length of corpus bursae, narrow, basally directed downward and then bent upward. Corpus bursae elongate, ovoid, with one tiny signum.

Distribution. The species occurs in Brazil (Bahia, Espírito Santo) (Figs 45 & 46).

Etymology. The name comes from that of the Serra Bonita Reserve founded by Vitor O. Becker and Clemira de Souza. It is managed by Instituto Uiraçu in the State of Bahia, Brazil.

Notes. Serra Bonita Reserve is located in the Atlantic Forest, in a hilly region of cacao plantations and scattered forest. Adults came late to light, usually after 23:00. Our molecular analysis of the COI barcode sequences highlighted that specimens from Serra Bonita respectively show 3.24 and 2.21 % base differences with those of Porto Seguro and Linhares. This divergence is possibly associated with slight morphological differences in male genitalia as shown in Figs 23–26. No females were found at Serra Bonita.

Mayrabonillae species group

Diagnosis. We have not recovered any obvious synapomorphy for this group. It can be separated from the other *Catharylla* species based on the shorter forewing length, usually between 7.5 and 9.0 mm (maximum 10.5 mm). In male genitalia, the tegumen connection is more than two times longer than the uncus, the uncus is beak-shaped, with the apex narrowing to a point, the gnathos is bent at an angle of about 90° . In female genitalia, the basal line along the anal papillae is ventrally expanded onto a triangle, and the sterigma forms a pair of sclerotized pockets on each side of the middle, covered with short spines or spicules. The sterigma does not bear tiny setae on the ventral membrane of segment VIII.

Notes. This group includes two species. The phylogenetic analyses restricted to the nuclear genes and the combined Bayesian analysis place the *mayrabonillae* group as sister to the *chelicera* group (Fig. 42).

Catharylla mayrabonillae T. Léger & B. Landry, sp. n.

<http://zoobank.org/5078E6D0-DDA4-4B9F-8089-F7FFECC725C6>

http://species-id.net/wiki/Catharylla_mayrabonillae

Figs 7, 30, 31, 40, 44

Type material. Holotype. ♂, with labels as follows: “Col. BECKER | 101668”; “ECUADOR: NAPO | Misahualli | 450m xii.1992 | V.O.Becker Col”; “HOLOTYPE | *Catharylla* | *mayrabonillae* | Léger & Landry” [red label]. Deposited in Becker Collection.

Paratypes. 16 ♂, 37 ♀. BRAZIL: 1 ♀ (genitalia on slide BL 1729), [Acre] Rio Branco, 1924 (Dengler) (SMNS); 2 ♀, Amazonas, Manaus, Reserva Ducke, AM-010, km 26, $2^\circ 55'S$, $59^\circ 59'W$, 15.xii.1993, U[ltra]V[iolet] Light (J. B. Sullivan & R. W. Hutchings) (USNM); 1 ♂ (genitalia on Pyralidae Brit. Mus. Slide No. 11341), Amazonas, Fonte Boa, ix.1906 (S. M. Klages) (BMNH); 1 ♀ (genitalia on slide BL 1713), Federal

District, Estação Florestal, Cabeça do Vedaio, 1100m, 18.x.1971 (E.G., I. & E.A. Munroe) (CNC); 2 ♂, Maranhão, Feira Nova, Faz[enda]. Retiro, 480m, 07°00'S, 46°26'W, 1–3.xii.2011 (V. O. Becker n°148263) (Becker Coll.); 2 ♀, Pará, Belém, 20m, i.1984 (V. O. Becker n°46981) (Becker Coll.); 1 ♀, Pará, Capitao Poco, 25–31.i.1984 (V. O. Becker n°97880) (Becker Coll.); 1 ♂, Rondonia, Cacauplândia, 140m, xi.1991 (V. O. Becker n°79592) (Becker Coll.); 1 ♀, Rondonia, 62km S[outh] Ariquemes, Fazenda Rancho Grande, 165m, 10°32'S, 62°48'W, 18–26.iv.1991 (R. Leuschner) (USNM). COLOMBIA: 1 ♂, Valle, J[un]ct[ion]. Old B'[uena]v[en]tura R[oa]d. and Rio Dagua, 50m, 8.ii.1989 (J. B. Sullivan) (USNM). COSTA RICA: 1 ♀ (used for DNA Barcoding by Janzen, 07-SRNP-113921), Alajuela, Area de Conservacion Guanacaste, Estacion Caribe, 12.xi.2007 (S. Rios & H. Cambronero) (INBio); 1 ♀, Alajuela, Area de Conservacion Guanacaste, Rio Negro, 25.i.2009 (H. Cambronero & F. Quesada) (INBio); 2 ♂ (one used for DNA sequencing LEP 966, with genitalia on slide TL 3, other used for DNA sequencing LEP 967, with genitalia on slide TL 4), Alajuela, San Carlos, Arenal National Park, Send[ero] Pilón, Rio Celeste, 700m, light trap, 17–19.x.2001 (G. Rodriguez) (INBio); 1 ♂, Prov[incia] Guanacaste, F[in]ca Pasmompa, Est[acion] Pitilla, 5km SO S[an]ta Cecilia, 400m, xii.1990 (P. Rios & C. Moraga) (INBio). EC-UADOR: 4 ♀ with same data and deposition as holotype; 4 ♂, 8 ♀ (1 ♂ used for DNA barcoding BC MTD 01844) with same data (USNM); 1 ♀ (genitalia on slide BL 1726, used for DNA sequencing and barcoding LEP 969, BC MTD 1707), Napo, 6km NW Tena, Lumu Caspi, 0°54'37"S, 77°49'32"W, 590m, 29.ix.2002 (Schouten Coll.); 1 ♀ (genitalia on slide BL 1715, used for DNA sequencing and barcoding LEP 968, BC MTD 1706), Pastaza, 1km N Santa Clara, 1°16'02"S, 77°52'57"W, 630m, 28.ix.2002 (Schouten Coll.). FRENCH GUIANA: 1 ♂, 4 ♀ (♂ genitalia on Pyralidae Brit. Mus. Slide No 7816, ♀ genitalia on slides BL 1720, BL 1725, and Pyralidae Brit. Mus. Slides No. 5953 and 19020), Saint Jean de Maroni (E. Le Moulton) (BMNH); 2 ♀, Piste Nancibo, km 6, 4°41'N, 52°25'W, in logged rain forest, at 125W[atts] mer[cury]-vapor light and 15W[atts] U[ltra]V[iolet], 11.i.1985 (J.[-]F. Landry) (USNM); 1 ♂, Roura, Montagne des Chevaux, xii.2008 (S. Delmas) (MHNG); 1 ♂ (genitalia on slide Pyralidae Brit. Mus. Slide No 7792), Cayen[ne] (BMNH). GUYANA: 1 ♀ (genitalia on slide BL 1723), Omai, vi.1908 (S. M. Klages) (BMNH); 1 ♀ (genitalia on slide BL 1722), Potaro i.1908 (S. M. Klages) (BMNH). PANAMA: 1 ♀, Rio Trinidad, 12.iii [no year data] (A. Busck) (USNM). PERU: 1 ♂ (genitalia on slide BL 1724), Agnaitia, Huallaga, 400m, ix.1961 (F. H. Walz) (CNC); 1 ♀ (genitalia on slide GS-6908-SB), Yurimaguas, Huallaga 14.iv.[19]20 (CMNH). SURINAME: 2 ♀ (genitalia on slides BL 1727 and BL 1728), Kabo, 5°16'N, 55°44'W, Saramaca, black light, respectively 15–16.iii.1983 and 13–14.i.1983 (K.E.Neerling) (Schouten Coll.); 1 ♀ (genitalia on slide BL 1710), Sipaliwini Distr[ict], Tibiti area, Kabo Creek, partly swampy primary forest on hilly slopes, ca 2km from river, vi.1989 (J. Beerlink) (Schouten Coll.).

Other specimen examined. 1 ♀ (used for DNA sequencing Lep 1126), Peru, Huánuco, Rio Lullapichis, Panguana, 74,945°W / 9,614°S, 23.9.–10.10.2011 (SMTD).

COI barcode sequence of paratype 07-SRNP-113921 (654 bp): ACATTA-TATTTTATTTTCGGGATTTGAGCAGGTATAGTAGGAACCTTCACTTA-

GATTATTAATTCGTGCTGAATTAGGTAACCCTGGCTCTCTTATTGGA-
 GATGATCAAATTTATAATACTATTGTAACAGCCCATGCATTTATTA-
 TAATTTTTTTTATAGTTATACCTATTATAATCGGTGGATTGGAATT-
 GATTAGTTCCTTTAATATTAGGGGCACCAGATATAGCTTCCCTC-
 GAATAAATAACATAAGATTTTGATTATTACCACCATCATTAACCTCTT-
 TAATTTCTAGAAGAATTGTAGAAAATGGAGCTGGAACAGGATGAACA-
 GTTTATCCACCTTTATCATCTAATATTGCCCATGGGGGTAGATCTGTA-
 GATTTAACAATTTTTTCATTACATTTAGCTGGAATTTTCATCAATTTTAG-
 GAGCTATTAATTTTATTACAACAATTATTAATATACGAATTAATAATT-
 TATCATTTGATCAATTATCATTATTTATTTGATCAGTAGGAATTACT-
 GCTTTACTTTTATTATTATCATTACCAGTTTTAGCTGGGGCTAT-
 TACTATACTTTTAACTGATCGAAATCTTAATACATCATTTTTTGATC-
 CAGCAGGAGGAGGAGATCCAATTTTATATCAACATTTA

Diagnosis. The best discriminant characters externally between the two species of the *mayrabonillae* group are the shape of the forewing outer margin, which is slightly produced apically in *C. mayrabonillae* and not produced in *C. paulella*, and the forewing median transverse line with two strongly pronounced spots at 1/3 and 2/3 in *C. paulella*, whereas these spots are lacking in *C. mayrabonillae*. The hindwing of *C. mayrabonillae* has a faded subterminal transverse line on costal half whereas the hindwing of *C. paulella* lacks this marking. In male genitalia, the heavily sclerotized sacculus bears a dorso-lateral sclerotized string of short spines on distal 1/4 whereas the two processes of the costa are S-shaped in *C. paulella*, and the apex of the phallus is trifid, rounded medially, shortly triangular laterally, whereas it is simply rounded in *C. paulella*. In female genitalia, the sterigma forms double rounded cavities with a mustachio-shape arrangement of short spines in ventral view, and the ductus bursae is wide, progressively widening toward corpus in *C. mayrabonillae*, whereas the sterigma forms a pair of shallow rounded pockets on each side of middle and the ductus bursae is narrow, with the rounded corpus bursae clearly differentiated from it in *C. paulella*.

Description. Male (n=17) (Fig. 7): Head with light ochreous chaetosemata. Antenna brown, with white scales dorsally and patch of dark brown scales at base. Maxillary palpus light ochreous, ringed with dark brown at 2/3; white tipped. Labial palpus: 1–1.4 mm; white, with patch of dark brown scales at 1/3 and 2/3 laterally. Thorax with patch of light ochreous scales at collar. Foreleg coxa whitish brown, femur white, dorsally ashen brown, tibia and tarsomeres ochreous, distally ringed with dark brown. Midleg femur white, tibia light ochreous, basally brown, tarsomeres II–V ochreous with tips ringed white. Hindleg white, except tarsomeres, as in midleg. Abdomen dull white. Forewing length: 7.5–8.5 mm; with apex slightly produced; costal line thin, ochreous or white in basal half, white in apical half; median transverse line ochreous, slightly undulated; subterminal transverse line ochreous; transverse lines enlarging into brown spot on costal margin with ochreous bar on costa following subterminal transverse line; terminal sector with light ochreous between veins, margin with thin, dark brown line from apex to CuA1, with two dark brown spots in cubital sector, with spot between CuA1 and CuA2 slightly displaced toward base; fringes brass colored; under-

side light ochreous with some brownish scales, with thin brown margin. Hindwing white with thin transverse subterminal line faded ochreous, in continuity with forewing median transverse line; outer margin line pronounced, dark brown; underside dull white with thin faded brown margin; fringes white.

Tympanal organs ($n=7$): Transverse ridge regularly rounded, medially slightly flattened. Tympanic pockets broadly rounded, extended widely beyond transverse ridge, connected medially at base of praecinctorium. Tympanic drum bean-shaped, elongated, extended beyond tympanic pockets.

Male genitalia ($n=7$) (Figs 30, 31): Uncus thick and wide, about $2/5$ length of tegumen arms, densely setose, with shortly projecting apex dorsally rounded. Gnathos reaching about $1/4$ longer than uncus; arms wide, joining at $2/5$ of length; distal $2/5$ at angle of about 85° . Tegumen almost regularly narrow, joined in last $1/4$. Cucculus narrow, shorter than sacculus, apically rounded; sacculus greatly enlarged, thickly sclerotized, directed upward, then apically straight, slightly narrowing toward apex, laterally with string of short spines and 2–3 longer basal spines pointing downward; costal arm of valva directed upward, located at about $1/3$ of costal margin, thin, strongly sclerotized, slightly curved. Vinculum arms narrow; saccus short and wide, tongue shaped, projecting posterad apically. Juxta elongate, distal $1/4$ narrowed with rounded tip; wide base with ear-like lobes laterally and baso-lateral angle projected anterad. Phallus slightly bent sideways in distal $1/4$, with trifid sclerotized apex rounded medially and shortly triangular laterally; vesica basally covered with tiny spicules, microspicules barely visible all along, with long spine-like, down-curved cornutus of about $2/5$ length of phallus.

Female ($n=37$): Labial palpi length: 1.1–1.3 mm. Forewing length: 9.5–10.5 mm; frenulum triple.

Female genitalia ($n=16$) (Fig. 40): Papillae anales strongly curved in lateral view; sclerotized line along papillae expanding ventrally into triangle. Posterior apophyses $0.35\text{--}0.45 \times$ length of papillae anales. Tergite VIII about $1/3$ length of sternite VIII; postero-dorsal margin with few setae of moderate length; anterior apophyses $0.03\text{--}0.1 \times$ papillae anales; sternite VIII with patches of minute setae antero-ventrally on each side of bare median band. Sterigma forming double rounded cavities with mustachio-shaped arrangement of short spines (in ventral view); remaining cavity wall with tiny spines. Ductus bursae short and wide, enlarged near middle; partly sclerotized on right side of enlargement and posterior section. Corpus bursae circular to elongate, about as long as tergite VII; single signum faintly pronounced.

Distribution. The species has been found so far in Panama, Costa Rica, Colombia, Venezuela, Guyana, Suriname, French Guiana, Ecuador, Peru and Brazil (Acre, Amazonas, Distrito Federal, Pará, Rondônia) (Fig. 44). It is the most widespread species of *Catharylla* and the only one so far found in Central America and in Venezuela, Columbia, Ecuador and Peru.

Etymology. *Catharylla mayrabonillae* is named in honor of Ms. Mayra Bonilla of San Jose, Costa Rica, in recognition of her artistic portrayal of the biodiversity and ecosystems of Costa Rica and her many years of support for the existence of the rain forest in Area de Conservacion Guanacaste.

Notes. The relatively strong COI barcode divergence of 4.34% between samples LEP 1126 from Peru and 07-SRNP-113921 from Costa Rica (Table 5) is notable but it is not associated with morphological variation.

***Catharylla paulella* Schaus, 1922**

http://species-id.net/wiki/Catharylla_paulella

Figs 8, 10, 32, 33, 41, 44

Catharylla paulella Schaus, 1922: 131; Bleszynski and Collins 1962: 226; Bleszynski 1967: 97; Munroe 1995: 35; Nuss et al. 2013.

Type material. Holotype. ♀, with labels as follows: “Sao Paulo | S.E. Brazil.”; “Collection | W[illia]mSchaus”; “Type No. | 25533 | U.S.N.M.” [orange label]; “SLIDE | SB ♀ | No.4641” [light blue label]; “Catharylla | paulella | type Sch[au]s” [hand written]; “Genitalia Slide | By SB | USNM 111,535” [green rectangular label with thin black line submarginally]. Deposited in USNM.

Other specimens examined. 2 ♂, 7 ♀. BOLIVIA: 2 ♂ (genitalia on slides GS-6652-SB and Pyralidae Brit. Mus. Slide No. 15890), Prov.[incia] del Sara, 450 m, iv.1910 (J. Steinbach) (CMNH, BMNH). BRAZIL: 1 ♀ (genitalia on slide BL 1752), Federal District, Planaltina, 15°35'S, 47°42'W, 1000 m, 3.xi.1977 (V. O. Becker n°22055) (Becker Coll.), 1 ♀ (genitalia on slide BL 1751) with same locality, 16.x.1990 (V. O. Becker n°96854) (Becker Coll.); 1 ♀, Maranhão, Feira Nova, Faz[enda]. Retiro, 480m, 07°00'S, 46°26'W, 1–3.xii.2011 (V. O. Becker n°148263) (Becker Coll.); 1 ♀ (genitalia on slide BL 1712), Mato Grosso, Urucum, 15 miles S[outh]. of Columbá, 650 f[ee]t, 19. iv. [19]27, at light (C. L. Collenette) (BMNH); 1 ♀, Pará, Belém, 20m, i.1984 (V. O. Becker n°46993) (Becker Coll.); 1 ♀ (genitalia on Pyralidae Brit. Mus. Slide N° 17692), São Paulo (BMNH); 1 ♀ (used for DNA sequencing and barcoding LEP 965, BC MTD 1705, genitalia on slide TL 5), São Paulo, São Luiz do Paraitinga, 23°20'S, 45°06'W, 900 m, 13–20.iii.2001 (V. O. Becker n°132357) (Becker Coll.).

COI barcode sequence of specimen LEP 965 (654 bp): ACATTATATTT-TATTTTTTGGAAATTTGAGCAGGTATACTAGGAACCTTCACTTAGAT-TATTAATTCGTGCTGAATTAGGTAATCCTGGATCTCTTATTGGT-GATGATCAAATTTATAATACTATTGTAACAGCTCATGCATTTAT-TATAATTTTTTTTATAGTTATACCTATTATAATTGGTGGATTTG-GAAATTGATTAGTTCCTTTAATATTAGGTGCACCAGATATAGCTTTC-CCTCGAATAAATAATATGAGATTTTGATTATTACCCCATCATTAAC-TCTTTTATTTT?TAGAAGAATTGTGCGAAAATGGAACAGGAT-GAACAGTTTACCCACCCTTATCATCCAATATTGCTCATAGAGGTA-GATCAGTAGATCTAGCAATTTTTTCTTTACATTTGGCTGGAATTTTCAT-CAATCTTAGGAGCTATTAATTTTATTACAACAATTATCAATATACGAAT-TAATAATTTATCTTTTGATCAATTATCATTATTTATTTGATCTGTAGGT-ATTACAGCTTTACTTTTATTATTATCATTACCAGTTCTAGCTGGAGCT-

ATTACTATACTTTTAACTGATCGAAATCTTAATACATCATTTTTTTGATC-
CTGCAGGAGGAGGTGATCCTATCTTGTATCAACATTTA

Diagnosis. This species can be easily separated from the other *Catharylla* species by the forewing median transverse line with two strongly pronounced spots at 1/3 and 2/3. The forewing is also sparkled with dark brown scales, which is unique in the genus. In male genitalia, the two S-like projections of the costal arm of the valva discriminate this species from the other species of *Catharylla*. In female genitalia, the sterigma forms a pair of shallow rounded pockets on each side of middle, and the ductus bursae is narrow, with the rounded corpus bursae clearly differentiated from it in *C. paulella*, whereas it forms double rounded cavities with a mustachio-shape arrangement of short spines in ventral view, and the ductus bursae is wide, progressively widening toward corpus in *C. mayrabonillae*.

Redescription. Male (n=2): Head with ochreous chaetosemata. Antenna ochreous with white scales, with patch of dark brown scales at base. Maxillary palpus light ochreous, white tipped. Labial palpus: 1.4–1.7 mm long, light ochreous, white tipped. Thorax light ochreous at collar. Foreleg coxa whitish ochreous, femur light ochreous, dorsally ochreous; tibia and tarsomeres greyish brown, distally ringed with dark brown. Midleg and hindleg whitish ochreous; midleg tibia basally brown, hindleg tibia white; midleg and hindleg tarsomeres with white tips. Forewing length: 7–8 mm; costal line thin, brown or dirty white; median transverse line ochreous, with two dark brown strongly pronounced spots at 1/3 and 2/3; subterminal transverse line thin, ochreous, with small triangular spot on costal margin; with ochreous bar on costal margin following subterminal transverse line; outer margin ochreous with short dark brown lunules or dashes; fringes brass colored; underside light ochreous with brownish suffusion; with pronounced marginal spots. Hindwing white; outer margin with thin ochreous line in apical half; fringes white; underside dull white with dark brown marginal spots more or less connected on apical half.

Male genitalia (n=2) (Figs 32, 33): Uncus almost straight, densely setose, about 1/4 length of tegumen arms. Gnathos with arms joining at 3/5, then directed upward at slightly less than 90° angle; apically narrowly rounded. Tegumen arms regularly widening toward uncus, connecting at about half their length. Cucculus of medium width, slightly curved upward in distal 1/4; costal arm of valva divided with short spatula at base and S-shaped projection with rounded apex apically. Juxta triangular with distal third narrower, apically rounded, with baso-lateral narrow, triangular projections pointing anterad. Phallus with apex more thickly sclerotized, with blunt apical margin, with short triangular ventral projection; vesica covered on basal 1/4 with tiny spicules, with barely visible microspicules all along, with one wide and curved cornutus at about 1/4 length of phallus.

Female (n=7) (Figs 8, 10): Labial palpi: 1.4–1.7 mm long; forewing length: 9–9.5 mm; frenulum triple.

Tympanal organs (n=5) (Fig. 10): Transverse ridge medially straight. Tympanic pockets not reaching beyond transverse ridge, rounded. Tympanic drum bean shaped, somewhat oval, just reaching transverse ridge.

Female genitalia (n=5) (Fig. 41): Papillae anales ventrally slightly projected; sclerotized line at base enlarging medially to triangular shape covered by minute punctuation. Posterior apophyses 0.4–0.5 × length of papillae anales, narrow, tubular, with

rounded tips. Tergite VIII short, about half of length of greatly enlarged sternite VIII. Anterior apophyses $0.05\text{--}0.1 \times$ length of papillae anales. Lamella antevaginalis of sterigma dorsally covered with minute spicules; pair of shallow rounded pockets on each side of middle opened posterad. Base of ductus bursae sclerotized, forming circular membranous and narrow pocket. Corpus bursae regularly rounded, without signum.

Distribution. The species has been found in Brazil (Federal District, Maranhão, Mato Grosso, Pará, São Paulo) and in Bolivia (Fig. 44).

Notes. The original description doesn't mention the original number or sex of the specimens but it is assumed that there was only one. S. Bleszynski gave the new name of *Catharylla hibisca* to specimens that appear to be *C. paulella*. The BMNH São Paulo specimen is associated with slide n° 17692, but the genitalia on this slide seem to be wrongly associated, given the inscription "wrong abdomen?" on the label, as well as the size of the abdomen, which is much bigger than those of *C. paulella*. Therefore, this specimen cannot be identified with certainty. An error is possible in the association of the sexes of this species as there are no series of both sexes from the same locality or other means of associating them with 100% confidence.

Key to the species of *Catharylla*

- 1 Forewing costa with thick, brown to greyish brown stripe (Figs 2, 3); forewing length usually > 14 mm. Hindwing white. In male genitalia, gnathos regularly curved, juxta without latero-ventral projections (Figs 13, 15) **2**
- Forewing costa with thin, ochreous stripe or none (Figs 1, 4–8); forewing length 7–14 mm. Hindwing white, cream-coloured, or yellowish. In male genitalia, gnathos more or less straight, or bent at about 90° angle; juxta with latero-ventral projections (Figs 11, 17, 19, 21, 30, 32) **3**
- 2 Male genitalia with costal arm long, narrow throughout, hook shaped, slightly curved, posteriorly reaching beyond cucullus (Fig. 13). In female genitalia, sterigma forming strongly sclerotized ventro-laterally symmetrical structure made of two asymmetrical bell-shaped cavities (Fig. 35) ***C. chelicerata***
- Male genitalia with costal arm short, basally wide, tooth shaped, not reaching cucullus tip (Fig. 15). In female genitalia, sterigma forming a pair of shallow pockets opened posterad, antero-ventrad of segment VIII (Fig. 36) ... ***C. gigantea***
- 3 Forewing length 7–10 mm, forewing costa slightly ochreous or white on basal $1/2$, white on distal $1/2$ (Figs 7, 8). In male genitalia, gnathos bent at about 90° angle; uncus less than twice length of tegumen connection, beak shaped (Figs 30, 32) **4**
- Forewing length 10–16 mm, forewing costa with thin ochreous to brown stripe (Figs 1, 4–6). In male genitalia, gnathos more or less straight; uncus more than twice length of tegumen connection (Figs 11, 17, 19, 21) **5**
- 4 Forewing outer margin slightly produced at apex, median transverse line without spots at $1/3$ and $2/3$ (Fig. 7). In male genitalia, costal arm of valva

- simple, narrow; sacculus heavily sclerotized, large, laterally with string of sclerotized spines with 2–3 longer basal spines pointing downward (Fig. 30). In female genitalia, sterigma forming mustachio-shaped double rounded cavities set with short spines (Fig. 40) ***C. mayrabonillae***
- Forewing outer margin not produced at apex, median transverse line with two clearly pronounced spots at 1/3 and 2/3 (Fig. 8). In male genitalia, costal arm of valva with two well-separated projections; sacculus not strongly sclerotized, densely setose, apically rounded (Fig. 32). In female genitalia, sterigma forming double rounded pockets opened posterad (Fig. 41) ***C. paullella***
- 5 Hindwing white (Fig. 1). In male genitalia, costal arm of valva double, with ventral arm tubular, apically pointing upward, and dorsal arm slightly shorter, flattened, apically rounded; transtilla absent; vesica with one cornutus (Fig. 11). In female genitalia, sternite VIII ventrally connecting, with latero-ventral projections (Fig. 34) ***C. bijuga***
- Hindwing cream colored or yellowish (Figs 4–6). In male genitalia, costal arm of valva simple; transtilla present; vesica without cornutus, or with crest of cornuti (Figs 17–22). In female genitalia, sternite VIII narrowing ventrally, ventrally not connected, without latero-ventral projection (Figs 37–39) **6**
- 6 Forewing median transverse line more or less straight, shortly curved inward in costal 1/3 (Fig. 4). In male genitalia, transtilla laterally with short, narrow sclerotized arms with pointed tips, projecting posterad, and medially with pair of brushes directed medio-ventrally (Fig. 17). In female genitalia, anterior angle of sternite VIII projected downward into more or less rounded projection covered with short spinules of same length (Fig. 37) ... ***C. tenellus***
- Forewing median transverse line not regular, slightly curved outward at M1 and CuA2, curved inward in costal 1/3 (Figs 5–6). In male genitalia, transtilla forming pair of sclerotized arms slightly bent inward with longitudinal row of spines ventrally or medially (Figs 19, 21). In female genitalia, anterior angle of sternite VIII not projected or projected anterad (Figs 38, 39) **7**
- 7 Forewing median transverse line without short marked triangular dent at CuA2 (Fig. 5). In male genitalia, uncus bifid and grooved in distal 1/5; transtilla forming pair of sclerotized arms slightly bent inward distally, ventrally with row of short spines increasing in size from base to apex; juxta regularly narrowing toward apex; vesica with row of 6–7 cornuti (Figs 19, 20). In female genitalia, anterior angle of sternite VIII not projected; anterior apophyses quadrangular, anvil shaped (Fig. 38) ***C. coronata***
- Forewing median transverse line with short triangular dent at CuA2 (Fig. 6). In male genitalia, uncus apically indented medially; transtilla forming pair of sclerotized arms strongly bent inward in distal 1/4 and with string of long spines of same length medially along it; juxta strongly narrowing in distal 1/4; vesica without cornuti (Figs 21, 22). In female genitalia, anterior angle of sternite VIII projected anterad into rounded projection covered with short spinules; anterior apophyses spine-like (Fig. 39) ***C. serrabonita***

COI barcode sequences and genetic distances within *Catharylla*

The number of bases obtained for each barcode sequence is given in Table 3 and the genetic distances between specimens in Table 5.

As most of the data were restricted to few sequence samples per species, and some of the sequences came from the same populations, we don't have the definitive picture of the intraspecific variation in the COI barcode sequences of *Catharylla* species. We observe a relatively high divergence between different barcode haplotypes in *C. bijuga* (5.05%), *C. mayrabonillae* (4.34%), *C. serrabonita* (3.24%) and *C. tenellus* (3.34%), sometimes possibly associated with differences in morphological characters (see Notes of the descriptions of *C. bijuga*, *C. tenellus*) and with geographical distances. The divergence between *C. chelicerata* samples LEP 1703 and LEP 1704 is of 0.15% (1 base) because they are issued from the same population. Sample LEP 1290 differs from sam-

Table 5. Distance matrix between *Catharylla* species calculated with GTR correction. Values are given in %.

	<i>C. bijuga</i> BC MTD 1839	<i>C. bijuga</i> BC MTD 1840	<i>C. chelicerata</i> LEP 1290	<i>C. chelicerata</i> BC MTD 1703	<i>C. chelicerata</i> BC MTD 1704	<i>C. coronata</i> BC MTD 1890	<i>C. mayrabonillae</i> LEP 1126	<i>C. mayrabonillae</i> 07-SRNP-113921	<i>C. paulella</i> LEP 965	<i>C. serrabonita</i> LEP 979	<i>C. serrabonita</i> BC MTD 1887	<i>C. serrabonita</i> BC MTD 1843	<i>C. tenellus</i> BC MTD 1842
<i>C. bijuga</i> BC MTD 1840	5.05												
<i>C. chelicerata</i> LEP 1290	16.61	14.63											
<i>C. chelicerata</i> BC MTD 1703	16.84	14.83	0.62										
<i>C. chelicerata</i> BC MTD 1704	16.63	14.63	0.46	0.15									
<i>C. coronata</i> BC MTD 1890	11.55	10.61	13.34	13.35	13.14								
<i>C. mayrabonillae</i> LEP 1126	15.55	15.8	16.6	16.83	16.61	11.22							
<i>C. mayrabonillae</i> 07-SRNP-113921	14.82	15.07	15.63	15.63	15.42	9.79	4.34						
<i>C. paulella</i> LEP 965	13.66	13.32	16.41	16.63	16.42	11.13	7.57	6.29					
<i>C. serrabonita</i> LEP 979	10.16	9.75	13.46	13.46	13.46	8.48	14.58	13.11	12.59				
<i>C. serrabonita</i> BC MTD 1887	11.1	10.41	15.06	14.65	14.86	7.74	14.64	13.68	13.57	3.24			
<i>C. serrabonita</i> BC MTD 1843	10.37	9.7	14.48	14.07	14.28	7.59	14.49	13.11	13.01	2.21	0.77		
<i>C. tenellus</i> BC MTD 1842	12.29	9.87	14.72	14.95	14.73	7.3	13.42	13.06	12.93	7.45	6.44	6.47	
<i>C. tenellus</i> BC MTD 1709 1710 1888	11.8	10.52	15.01	15.24	15.03	7.31	13.15	12.08	12.14	6.72	7.17	6.49	3.34

ples LEP 1703 and LEP 1704 respectively by 0.62 and 0.46%. We observe no variation between samples LEP 1708, LEP 1709, LEP 1710 and LEP 1888 because they are all issued from the same population. The inter-specific variation in COI barcode sequences (6.29–16.84%) is always higher than the intraspecific variation (0.15–5.05%).

Morphological results

The 21 analysed characters are listed in Table 6.

Phylogenetic results

Phylogenetic analysis of *Catharylla* and related genera based on molecular data

The monophyly of *Catharylla* is supported by the analysis of mol_1 and the combined Bayesian analysis (BS support = 90, PP = 0.95) and by the analyses of nucl_1 and nucl_2 (*C. chelicerata*, *C. mayrabonillae*, *C. serrabonita* and *C. tenellus* represented). Three synapomorphies (11: 1, 17: 1, 19: 1, with one reversal to the ancestral state in the *chelicerata* group for character 11) and one non-unique apomorphy (16: 1, apomorphy observed in the two outgroups as well) support the group. The *mayrabonillae* group is well supported in all analyses (BS supports = 100 in mol_1 and mol_2 analyses, PP = 1.00 in the combined Bayesian analysis) except in the morphology-based analysis (BS support = 60), because no clear synapomorphy was found for the group. However, two non-unique synapomorphies and one reversal (observed only once in *Catharylla*) are observed (9: 1, 12: 1, 19: 0). The *tenellus* group is well supported by the morphology-based analysis (BS support = 97) with four clear synapomorphies (5: 1, 7: 3, 10: 1, 20: 1) and two reversals (3: 0, 15: 0), but show no support in other analyses, probably because only the barcode sequence was available for *C. coronata*. The closer relationship between *C. serrabonita* and *C. tenellus* within the *tenellus* group is supported by the combined Bayesian analysis and by one non-unique apomorphy (but unique in *Catharylla*). The *tenellus* group as represented in the analyses of nucl_1 and nucl_2 (*C. serrabonita* + *C. tenellus*) is well supported (BS supports of 99 and 93, respectively). The *chelicerata* group is well supported by the morphology-based analysis (BS support = 96) and the combined Bayesian analysis (PP = 1.00). The group shows two synapomorphies (8: 1, 9: 2), one non-unique apomorphy (7: 1) and one reversal (11: 0). Unfortunately, no sequence was available for *C. gigantea*, thus we cannot compare the morphology with the molecular-based analyses. The closer relationships between the *chelicerata* and the *mayrabonillae* groups is strongly supported by the nucl_1 analysis (BS support = 100) and the combined Bayesian analysis (PP = 1.00). Two reversals (4: 0, 6: 0) support the group. The position of *C. bijuga* as sister group of the other *Catharylla* species is weakly supported by the combined Bayesian analysis (PP = 0.90), and show no support in other analyses. The position of *Micrelephas pictellus* as sister

Table 6. Character matrix of *Catharylla* and related taxa. A question mark refers to an unknown state for character 21, or an uncoded state (*Crambus pascuella*, character 7).

characters \ taxa	<i>C. biyuga</i>	<i>C. chelicerata</i>	<i>C. coronata</i>	<i>C. gigantea</i>	<i>C. maynabonillae</i>	<i>C. paulilla</i>	<i>C. serrabonita</i>	<i>C. tenellus</i>	<i>Argyria lactella</i>	<i>Micrelephas pictellus</i>	<i>Crambus pascuella</i>	<i>Crambus uliginosellus</i>
1. Labial palpi ringed with brown at 1/3 and 2/3; absent (0); present (1)	1	0	0	0	1	0	0	0	0	0	0	0
2. Length of labial palpi/eye diameter: >2/1 (0) ; < 2/1 (1)	1	1	1	1	1	1	1	1	1	1	0	0
3. Hindwing color: yellowish / creamy white (0); white (1)	1	1	0	1	1	1	0	0	1	0	0	0
4. Uncus in lateral view: horizontally straight (0); downcurved (1)	1	0	1	0	0	0	1	1	1	0	0	0
5. Dorsal furrow on uncus: absent (0); present (1)	0	0	1	0	0	0	1	1	0	0	0	0
6. Uncus dorsally setose (0); bare, or with few setae (1)	1	0	1	0	0	0	1	1	0	1	0	0
7. Uncus apex: unilobed, regularly rounded (0); regularly rounded with narrow tip (1); narrowing to a point (2); apically slightly bifid (3)	2	1	3	1	2	2	3	3	2	0	?	1
8. Apex of valva: narrowed or rounded (0); quadrangular, truncated (1)	0	1	0	1	0	0	0	0	0	0	0	0
9. Gnathos: almost straight with apex pointing upward (0); bent of about 90° angle (1); regularly curved (2)	0	2	0	2	1	1	0	0	1	0	0	0
10. Transtilla: absent (0); present (1)	0	0	1	0	0	0	1	1	0	0	0	0
11. Lateroventral projections on juxta: absent (0); present (1)	1	0	1	0	1	1	1	1	0	0	0	0
12. Ratio of dorsal roof of tegumen on uncus length: < 1/2 (0); > 1/2 (1)	0	0	0	0	1	1	0	0	0	0	1	1
13. Latero-basal tuft of hairs on uncus: absent (0); present (1)	0	1	1	1	0	0	1	1	1	1	0	0
14. Vesica: with one cornutus (0); with crest of cornuti (1); without cornuti (2)	0	1	1	1	0	0	2	2	1	2	2	0
15. Ventral shape of papillae anales in lateral view: not produced (0); slightly produced (1)	1	1	0	1	1	1	0	0	1	0	0	0
16. Ratio of anterior apophyses/papillae anales: > 0.1 (0); < 0.1 (1)	1	1	1	1	1	1	1	1	0	0	1	1
17. Ratio of posterior apophyses/papillae anales: > 0.5 (0); < 0.5 (1)	1	1	1	1	1	1	1	1	0	0	0	0
18. Ventral tongue shaped pronounced sclerotization postero-ventrally on ductus bursae: absent (0); present (1)	1	1	0	1	0	1	0	0	0	0	0	0
19. Ventral membrane of segment VIII: without tiny setae (0); with tiny setae (1)	1	1	1	1	0	0	1	1	0	0	0	0
20. Postvaginal sterigma: present (0); absent (1)	0	0	1	0	0	0	1	1	0	0	0	0
21. Forewing R4: free (0); stalked with R2+3 (1)	?	1	?	?	1	?	1	?	0	0	?	?

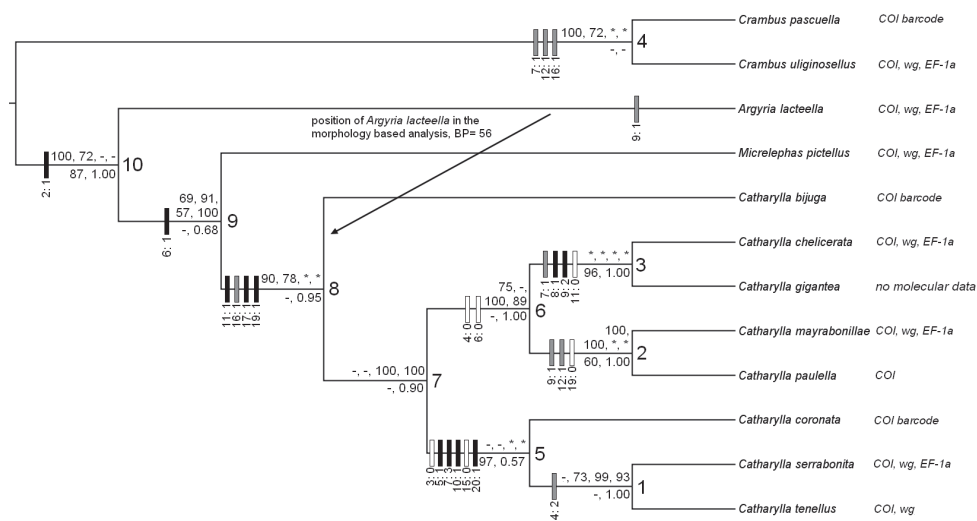


Figure 42. 50% majority-rule consensus tree of the combined Bayesian analysis of the morphological and molecular datasets combined with 3'000'000 generations. Values above branches are the respective BS supports of the phylogenetic analyses with Maximum Likelihood algorithm of mol_1 (gene + codon partition, 800 BS replicates), mol_2 (gene partition, 450 BS replicates), nucl_1 (gene partition, 150 BS replicates), and nucl_2 (gene partition, 150 BS replicates). Values below branches are the BS supports of the phylogenetic analysis of the morphological data and the PP of the combined Bayesian analysis. “-” represent values under the majority rule; “*” represent the absence of value because of the absence of one or several taxa in the considered analysis. Boxes upon branches represent character changes: black boxes represent unique transformations to the apomorphic state; grey boxes represent multiple transformations to the apomorphic state; white boxes represent reversals to the plesiomorphic state.

group of *Catharylla* is supported by the analysis of mol_2 and nucl_2 (respective BS supports of 91 and 100). This node is supported by one synapomorphy (6: 1, with one reversal in the *chelicerata* + *mayrabonillae* clade). Node 10 (*Argyria lacteella* + *Micrelephas pictellus* + *Catharylla*) is supported by the analysis of mol_1 (BS support = 100) and the combined Bayesian analysis (PP = 1.00). One synapomorphy (2: 1) supports the group. The monophyly of the two *Crambus* species chosen as outgroups is well supported in the mol_1 analysis (BS support of 100). The settings of MrBayes do not allow to choose two outgroups, therefore the monophyly of the two *Crambus* species is not supported by the combined Bayesian analysis. Three non-unique synapomorphies support the genus based on these two species (7: 1, 12: 1, 16: 1). The synapomorphies of the different groups highlighted by the phylogeny are reported here below:

Chelicerata group (node 3)

8: 1. Apex of valva quadriangular, truncated

9: 2. Gnathos regularly curved

Tenellus group (node 5)

5: 1. Presence of a dorsal furrow on the uncus

7: 3. Apex of uncus slightly bifid

10: 1. Transtilla present

20: 1. Postvaginal sterigma absent

Catharylla (node 8)

11: 1. Lateroventral projections on juxta

17: 1. Posterior apophyses/papillae anales < 0.5

19: 1. Ventral membrane of segment VIII with tiny setae

Catharylla + *Micrelephas* (node 9)

6: 1. Uncus dorsally bare, or with few setae

Catharylla + *Micrelephas* + *Argyria* (node 10)

2: 1. Length of labial palpi/eye diameter < 2/1

Geographical distribution and biogeography

Catharylla occurs northward from Middle America with locality records in Costa Rica (Area de Conservacion Guanacaste) at a latitude of 10°54' N, southward to Rio Vermelho (Brazil, Santa Catarina) at a latitude of 27°30' S, from sea level up to 1300 m (Brazil, Minas Gerais, Serra do Caraça). Within *Catharylla*, species and species groups show distinct distribution patterns. The *chelicercata* group is widespread in the Northern Amazonian rainforest of Brazil, and in the three Guyanas (Fig. 43). The *tenellus* group is restricted to the south-eastern Atlantic coast of Brazil in the Atlantic Forest, which is formed by tropical moist forests (Thomas and Britton 2008) (Fig. 45). These two groups seem to be restricted to moist forest habitats. The sister species *C. mayrabonillae* and *C. paulella* show an allopatric distribution: *C. mayrabonillae* is widespread northwards up to Costa Rica and southwards down to Brasília (15°47' S), whereas *C. paulella* is widespread from Feira Nova (07°00' S) down to São Paulo (23°35' S) (Fig. 44). They are both recorded from the Federal District, and from Maranhão (Feira Nova). Both species show wide geographical distribution covering a large range of ecosystems: *C. mayrabonillae* occurs in the tropical moist forests of the Caribbean, the Northwestern South American and the Amazonian subregions, as well as in the Cerrado province of Central Brazil (records from Brasília, Distrito Federal) (Figs 43, 44), where savannahs predominate with a semi-humid tropical climate and a pronounced dry period during winter (april–september) (Ratter et al. 1997). *Catharylla paulella* occurs in the Cerrado (Planaltina, Distrito Federal), in the Chaco formation (Urucum, Matto Grosso, Brazil and Provincia del Sara, Bolivia) (Figs 43, 44), which is a hot and dry area with xerothermic deciduous forests (Candolle 1993). *Catharylla bijuga* is restricted to the Guyana province. The distribution areas of the *chelicercata* group and that of *C. bijuga* are allopatric with respect to that of the *tenellus* group. The dry diagonal (Prado and Gibbs 1993) formed by the Caatinga, the Cerrado and the Gran Chaco, highlighted by the low rainfall rates (represented in yellow, orange and brown on Fig. 43), constitutes the climatic barrier between the Atlantic and the Amazonian Forests. Both barcode haplotypes of *C. bijuga* are from the Amazonian Forest, but they are distant from each other by about 1290 km

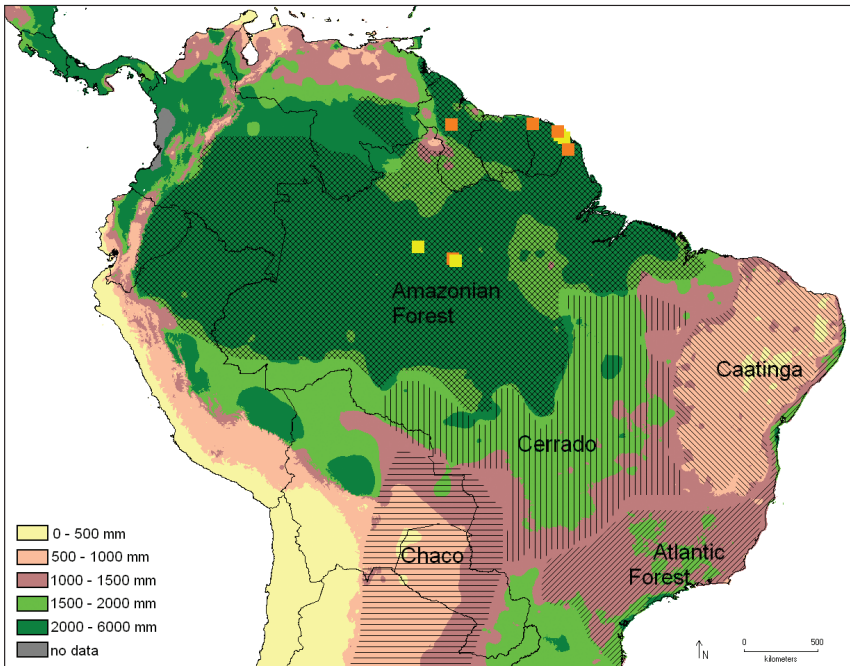


Figure 43. Distribution of *C. chelicerata* (yellow) and *C. gigantea* (orange) with the pluviometry and the biomes reported. Distribution of the biomes taken from Vanzolini and Heyer (1987: map n°3).

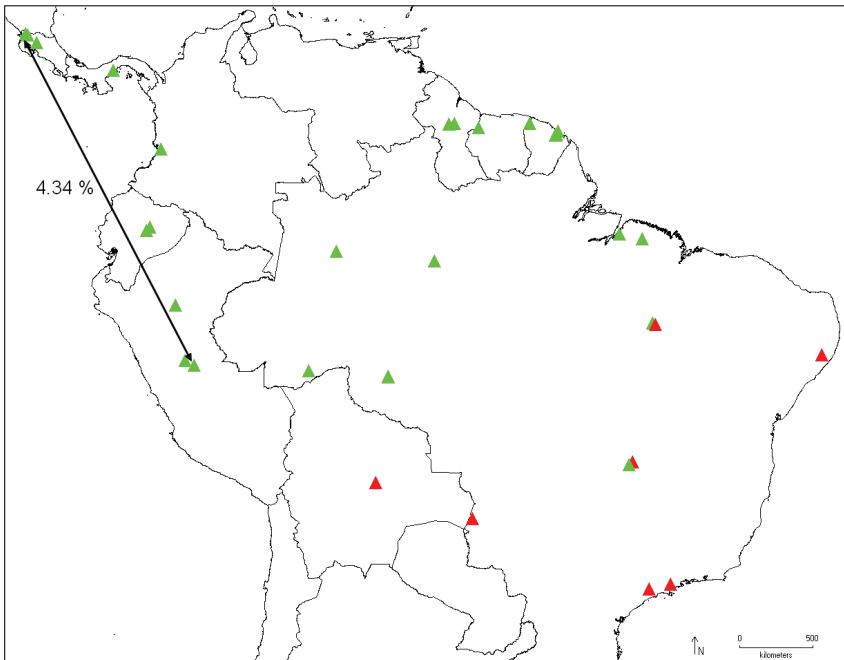


Figure 44. Distribution of *C. mayrabonillae* (green) and *C. paulella* (red), and distance between barcode haplotypes 07-SRNP-113921 and LEP 1226 (*C. mayrabonillae*).

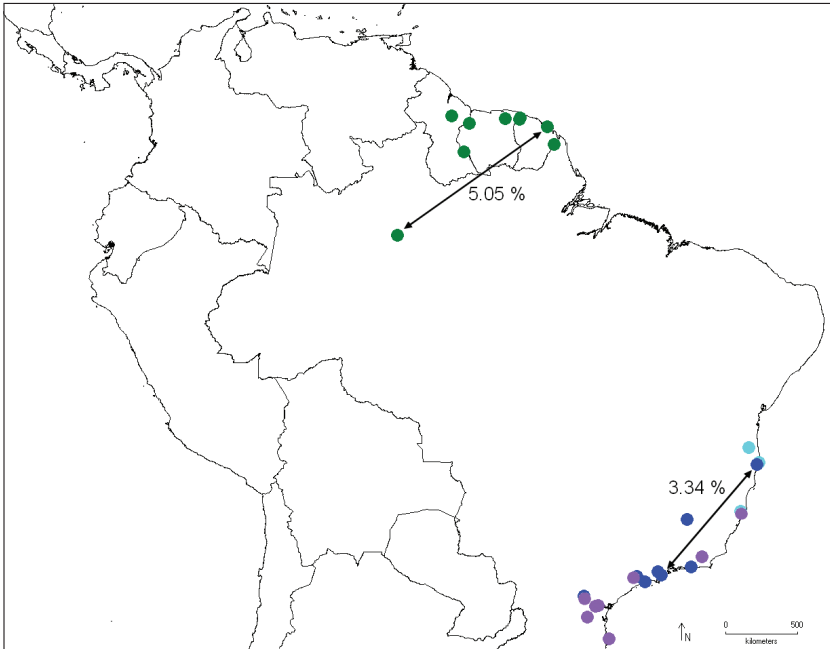


Figure 45. Distribution of *C. bijuga* (green), *C. coronata* (light purple), *C. serrabonita* (sky blue) and *C. tenellus* (blue), and distances between barcode haplotypes BC MTD 01839 and BC MTD 1840 (*C. bijuga*), and BC MTD 1709 and BC MTD 1842 (*C. tenellus*).

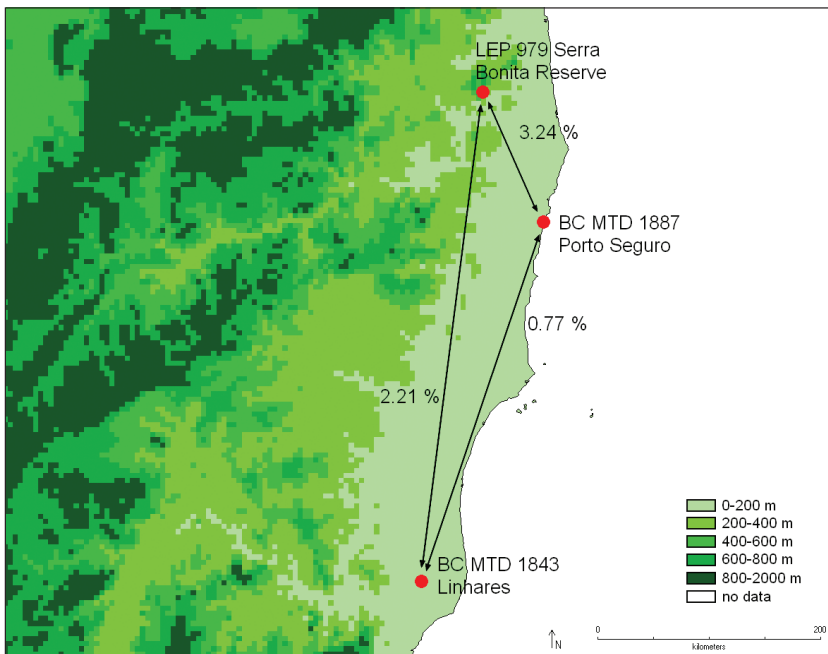


Figure 46. Distribution of *Catharylla serrabonita* and percentage of nucleotide differences in barcode sequences between different samples.

and from different provinces: haplotype BC MTD 1839 is from the Varzea province, near the Rio Negro (Brazil, Parque nacional do Jaú) while haplotype BC MTD 1840 is from the Humid Guyana province (French Guyana, Roura). *Catharylla mayrabonillae* barcode haplotype 07-SRNP-113921 is found in the Caribbean subregion, whereas haplotype LEP 1126 is found in the Amazonian subregion. The barcode haplotypes of the *Catharylla serrabonita* populations from the two coastal localities of Linhares and Porto Seguro are more closely related, whereas the haplotype from the population of the forested hills of the Serra Bonita Reserve clearly diverges from the other two (Fig. 46).

Discussion

Reliability of phylogenetic analyses

The analyses of nucl_1 and nucl_2 datasets brought better BS supports than the analyses of mol_1 and mol_2 on nodes 1, 6, 9, and for the monophyly of *Catharylla* (nodes 7 & 8). The reduced number of taxa (7 taxa in nucl datasets vs 11 in mol datasets, with 4 *Catharylla* species in nucl_1 and nucl_2 vs 7 in mol_1 and mol_2), as well as the quality of the datasets (complete sets of genes for nucl_1 and nucl_2 vs partly complete sets of genes in mol_1 and mol_2) explain the better results obtained in nucl_1 and nucl_2, because taxa with incomplete data tend to lower the resolution and the bootstrap supports of the tree (Regier et al. 2009). The barcode sequence evolves rapidly and therefore fails to accurately reconstruct phylogenetic relationships. The analysis of a higher number of genes would increase the support values (Wahlberg and Wheat 2008). The morphology-based analysis yielded good support for two species groups within *Catharylla*, but failed to reconstruct the phylogenetic relationships between different *Catharylla* species groups and between *Catharylla* and other genera. The weak number of characters of the matrix used (21, reported in Table 6) compared to the number of taxa, as well as the homoplastic characters explain the lack of bootstrap-supported groups (Bremer et al. 1999). The combined Bayesian analysis yielded good supports within *Catharylla* and between *Catharylla* and other genera.

Taxa positions on the phylogenetic tree

Our molecular-based analyses failed to place with certainty two of the four taxa lacking nuclear sequences (*C. bijuga* and *C. coronata*) because of the great divergence of these sequences from those of other *Catharylla* species. However, the clear support brought by the morphological analysis places *C. coronata* together with *C. serrabonita* and *C. tenellus*. The neighbor-joining (NJ) analysis of barcode sequences of *Catharylla* species (not represented here) places *C. coronata* together with *C. serrabonita* (divergence of 7.59% with the sequence BC MTD 1843) and *C. tenellus* (divergence of 7.3% with the sequence BC MTD 1842), and thus corroborates the findings of the morphology-

based analysis. Moreover, the species is morphologically very similar to *C. serrabonita* especially regarding the transtilla in the male genitalia. The basal position of *C. bijuga* in *Catharylla*, as sister taxon of other *Catharylla* species, is doubtful (PP = 0.90) and may be an artefact due to the great divergence of the barcode sequence (the lowest divergence with other *Catharylla* species is of 9.7% with sample BC MTD 1843 of *C. serrabonita*). The supports brought by the combined Bayesian analysis have to be carefully considered since the results are sensitive to small variations of the taxon and character sampling, and the posterior probabilities tend to overestimate the strongness of the nodes (Buckley et al. 2002, Whittingham et al. 2002). For *C. bijuga* and *C. coronata*, a complete gene dataset would be needed because the barcode sequence alone is not sufficient to undoubtedly assess their position within *Catharylla*. The closer relationships of the *chelicera* and the *mayrabonillae* groups (Fig. 42, node 6) is well supported by the analysis of nucl_1 and by the combined Bayesian analysis (BS support = 100, PP = 1.00), but a decrease of the BS support is observed when comparing mol_1 to mol_2, and nucl_1 to nucl_2, showing that the third codon position of the COI gene supports this node. This suggests a rapid evolution of this group where mutations accumulated only at the less constrained third codon position, or this could result from convergent substitutions in each lineage. *Micrelephas pictellus* is here placed as sister group of *Catharylla*, an unexpected topology, given that *Catharylla* has been placed in the Argyriini (type genus: *Argyria*) along with *Argyria*, *Urola* and *Vaxi*, and *Micrelephas* in Crambini (Landry 2003). The Argyriini as defined here are not monophyletic and would need to be redescribed, whether to include *Micrelephas*, or to exclude *Catharylla*. A more extensive analysis of the tribe with *Urola*, *Vaxi* and more genera of Crambini would be desirable to assess the validity and the composition of the Argyriini. The position of *Micrelephas* as sister group of *Catharylla* is subject to caution as only three Crambinae genera of the 179 currently recognized (Nuss et al. 2013) are represented in the analyses. The short labial palpi (i. e. the length of labial palpi/eye diameter < 2/1), which constitutes a synapomorphy for node 10 is observed in few other genera of Crambinae (*Euchromius*, *Myelobia* and *Urola*, see Landry 1995), for which long, porrect palpi are the norm.

Species delimitation and possible cryptic species in *Catharylla*

The intra-specific divergence in barcode sequences within *Catharylla* (Table 5; distances mapped on Figs 44, 45 and 46) is higher than the threshold of 2–3% predicted to delimit the species level in Lepidoptera according to Hebert et al. (2003), with intraspecific divergence often representing overlooked species (Hebert et al. 2003, Mutanen et al. 2012). The maximum intraspecific COI barcode divergences observed in *C. bijuga* (5.05%), *C. mayrabonillae* (4.34%), *C. serrabonita* (3.24%) and *C. tenellus* (3.34%) could therefore suggest that these different barcode haplotypes represent different species. Some morphological variation in male genitalia was found in *C. serrabonita* and *C. tenellus* (Figs 23–29) haplotypes, but none in *C. bijuga* and *C. mayrabonillae*, which is counter-intuitive given that the latter two species have more divergence than the other

two. Moreover, none of the intraspecific divergence observed in *Catharylla* is higher than the interspecific divergence. A greater number of specimens would be required to properly investigate the COI and nuclear gene variation along with morphological and ecological variations to judge if these COI barcode haplotypes and morphological variations represent meaningful differences linked with speciation or incipient speciation or if these species are really older than average. For now, given the available data, we are confident in our decision to recognize the eight species treated here in genus *Catharylla*.

Biogeography

The different species groups of *Catharylla* highlighted by the phylogenetic analyses show distinct distribution patterns, with species widely spread, such as *C. mayrabonillae* and *C. paulella* (Fig. 44) and other species confined to smaller areas, such as *C. bijugata* (Fig. 45), and the *chelicera* and *tenellus* species groups (Figs 43 & 45). The humid formations of the Amazonian and Atlantic Forests constituted two different refuges separated by the Caatinga and the Cerrado xerothermic formations, and vicariant evolutionary processes in plants (Rizzini 1997; Perret et al. 2012) and in birds (Eberhard and Bermingham 2005) have been documented. The distribution of *C. mayrabonillae* and *C. paulella* (Fig. 44), respectively northwards and southwards of the dry diagonal could also result from the split of a former population between the Amazon and the Atlantic Forests where speciation events occurred during dry spells, with expansion of the species afterwards. The patterns of distribution of the *chelicera* group (Fig. 43) suggest that its diversification might have occurred in the Amazonian Forest. The two species are sympatric as they are both recorded from Reserva Ducke. Similarly, *C. coronata* and *C. tenellus* are sympatric (both collected in Rio de Janeiro and São Paulo), as well as *C. serrabonita* and *C. tenellus* (both collected in Porto Seguro), while *C. coronata* and *C. serrabonita* are vicariant, *C. serrabonita* being distributed north of Linhares, whereas *C. coronata* is found south of this locality. The patterns of distribution suggest that the diversification of the *tenellus* group might have occurred in the Atlantic Forest, or have occurred in a wider area that reduced afterwards. In *C. tenellus*, two forms of male valva linked to different COI barcode sequences seem to be geographically separated, with the form from Ubatuba (associated to barcode sequence BC MTD 1842), Bertioga, São Paulo (São Paulo State), and Caraça (Minas Gerais) occurring more to the south than the form from Porto Seguro (associated with barcode sequences BC MTD 1709, 1710, 1711, 1888). The third form, observed in Caraça (Minas Gerais) suggests that this locality could represent a point of contact between the two other forms. Regarding *C. serrabonita*, the locality of Serra Bonita is a moist forest of middle elevation (800 m) (Fig. 46), while the localities of Porto Seguro and Linhares are part of a drier biome along the Atlantic Coast (V. O. Becker, pers. comm.). Therefore, the genetic distance found between these populations of this species could barely be explained by the distance between the two localities (130 km between Serra Bonita and Porto Seguro), but could be related to different ecological conditions.

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Appendix I

Table I. Coordinates of the localities pertaining to the *Catharylla* specimens studied.

Country	Locality	Province / State / Subdivision	latitude	longitude
Bolivia	?	Sara	-16°55', -63°37'	
Brazil	Belem	Pará	-1°27', -48°30'	
	Bertioga	São Paulo	-23°51', -46°8'	
	Cacaulândia	Rondônia	-10°20', -62°53'	
	Capitão Poço	Pará	-1°44', -47°3'	
	Caraça	Minas Gerais	-20°07', -43°28'	
	Castro	Paraná	-24°47', -50°0'	
	Corcovado	Rio de Janeiro	-22°57', -43°13'	
	Curitiba	Paraná	-25°25', -49°16'	
	Fazenda Rancho Grande	Rondônia	-10°18', -62°52'	
	Feira Nova	Maranhão	-07°00', -46°26'	
	Fonte Boa	Amazonas	-2°31', -66°05'	
	Ibateguara	Alagoas	-8°58', -35°55'	
	Lago Teffé	Amazonas	-3°27', -64°53'	
	Linhares	Espírito Santo	-19°23', -40°3'	
	Manaus	Amazonas	-3°7', -60°0'	
	Mirapinima	Amazonas	-2°10', -61°9'	
	Nova Friburgo	Rio de Janeiro	-22°17', -42°32'	
	Nova Olinda do Norte	Amazonas	-3°54', -59°05'	
	Parque Nacional de Jaú	Amazonas	-1°57', -61°49'	
	Planaltina	Federal District	-15°36', -47°40'	
	Porto Seguro	Bahia	-16°27', -39°3'	
	Quatro Barras	Paraná	-25°22', -49°4'	
	Reserva Ducke	Amazonas	-2°55', -59°58'	
	Rio Branco	Acre	-9°58', -67°48'	
	Rio Negro	Paraná	-26°6', -49°48'	
	Rio Vermelho	Santa Catarina	-27°29', -48°24'	
	Sao Luiz do Paraitinga	São Paulo	-23°13', -45°18'	
	São Paulo	São Paulo	-23°32', -46°38'	
	Serra Bonita	Bahia	-15°23', -39°33'	
	Ubatuba	São Paulo	-23°26', -45°5'	
	Urucum	Mato Grosso do Sul	-19°8', -57°38'	

Country	Locality	Province / State / Subdivision	latitude	longitude
Colombia	Buenaventura	Valle del Cauca	3°49, -77°00	
	Estacion Caribe	Alajuela	10°54'06, -85°16'30	
Costa Rica	Pitilla	Guanacaste	10°59'21, -85°25'32	
	Parque Nacional Arenal	Alajuela	10°26, -84°44	
Ecuador	Misahualli	Napo	-1°1, -77°40	
	Santa Clara	Pastaza	-1°15, -77°53	
French Guiana	Beauséjour		4°42, -52°23	
	Cayenne		4°55, -52°19	
	Montagne des Chevaux		4°43, -52°25	
	Nancibo		4°40, -52°28	
	Oyapock, Pied Saut		3°48, -51°53	
	Parcelles CIRAD de Combi		5°18, -52°55	
	Roura, road to Crique Gabrielle		4°44, -52°19	
	Roura, Camp Patawa		4°33, -52°9	
	Route d'Apatou pk 25.5		5°15, -54°13	
	Route de Saut Léodate		4°55, -52°33	
	Saint-Jean-du-Maroni		5°24, -54°4	
	Saint-Laurent-du-Maroni		5°30, -54°01	
Guyana	Malali	Upper Demerara–Berbice	5°37, -58°21	
	New River	East Berbice–Corentyne	3°21, -57°35	
	Omai	Cuyuni–Mazaruni	5°25, -58°45	
	Potaro	Potaro–Siparuni	5°22, -59°7	
Panama	Rio Trinidad	Nuevo Emperador	8°43, -79°58	
Peru	Aguaytía	Ucayali	-9°20, -75°30	
	Panguana	Huánuco	-9°36, -74°56	
	Yurimaguas	Loreto	-5°54, -76°7	
Suriname	Gelderland	Para	5°27, -54°59	
	Kabo	Sipaliwini	5°16, -55°44	
	Kabo Kreek	Sipaliwini	5°8, -57°16	

Appendix II

Molecular material and techniques.

Table 1. PCR mix for respective genes and primer pairs.

Product	LCO/Pat, LCO/ Nancy, Jerry/ Pat (COI) HybLepWg1 / HybLepWg2 (wingless)	LCO/K699, Ron/Nancy, Jerry/Mila, Brian/Pat (COI), HybLepWg1/ HybLepWg2 (wingless), Oscar-6143 / Bosie-6144 (EF-1 α)	HybLepWg1/ HybLepWg2 (wingless), Oscar-6143/ Bosie-6144 (EF-1 α)
H2O (ultraclean)	15.9 μ l	12.55 μ l	11.95 μ l
10X Taq buffer (15 mM MgCl ₂)	2.5 μ l	2.5 μ l	2.5 μ l (10X OptiBuffer)
MgCl ₂ (25 mM)	1 μ l	0.75 μ l	0.75 μ l (50 mM)
Forward primer (10 pmol/ μ l)	0.5 μ l	1.2 μ l	1.5 μ l

Product	LCO/Pat, LCO/ Nancy, Jerry/ Pat (COI) HybLepWg1 / HybLepWg2 (wingless)	LCO/K699, Ron/Nancy, Jerry/Mila, Brian/Pat (COI), HybLepWg1/ HybLepWg2 (wingless), Oscar-6143 / Bosie-6144 (EF-1 α)	HybLepWg1/ HybLepWg2 (wingless), Oscar-6143/ Bosie-6144 (EF-1 α)
Reverse primer (10 pmol/ μ l)	0.5 μ l	1.2 μ l	1.5 μ l
dNTP (each 10 mM)	0.5 μ l	2.5 μ l	2.5 μ l
Taq DNA polymerase (5 units/ μ l)	0.1 μ l	0.3 μ l	0.3 μ l (BIO-X-ACT Short TaqDNA polymerase; 4 units/ μ l)
DNA	4 μ l	4 μ l	4 μ l

Table 2. PCR programmes for COI, wingless and EF-1 α .

Gene		COI, wingless	wingless	EF-1 α
Polymerase		Taq polymerase	BIO-X-ACT Short Taq	Taq polymerase
programme	initial:	95 °C (5 min)	95 °C (5 min), 48 °C (1 min)	95 °C (5 min)
	40 cycles:	94 °C (30 sec)	95 °C (30 sec)	94 °C (30 sec)
		48 °C (30 sec)	51 °C (30 sec)	51 °C (30 sec)
		72 °C (1 min 30)	70 °C (1 min)	72 °C (1 min 30)
	final:	72 °C (10 min)	70 °C (10 min)	72 °C (10 min)
	cooling:	8 °C (∞)	8 °C (∞)	8 °C (∞)

Table 3. PCR-mix for sequencing reaction.

Product	low DNA concentration	high DNA concentration
cleaned PCR-product	4 μ l	1 μ l
H ₂ O (ultraclean)	2 μ l	5 μ l
Forward primer (10 pmol/ μ l)	1 μ l	1 μ l
T-mix (2.5X)	1 μ l	1 μ l
Buffer (5X)	2 μ l	2 μ l

***Acanoides* gen. n., a new spider genus from China with a note on the taxonomic status of *Acanthoneta* Eskov & Marusik, 1992 (Araneae, Linyphiidae, Micronetinae)**

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Abstract

A new “micronetine” genus *Acanoides* **gen. n.** is erected to accommodate two species from China: *Acanoides beijingensis* **sp. n.** as the type species and *Acanoides hengshanensis* (Chen & Yin, 2000), **comb. n.**, with the females described for the first time. The genitalic characters and somatic features of the new genus were studied by means of light microscopy and scanning electron microscopy (SEM). The monophyly of the new genus was tested by a phylogenetic analysis based on molecular data. Descriptions of the new genus, the new species and the new combination are presented; SEM images and microscopy pictures of somatic and genitalic characters are provided in detail. To distinguish from other genera with similar genitalic characters, we compare the new genus with the species of *Acanthoneta* Eskov & Marusik, 1992, *Epibellowia* Tanasevitch, 1996 and *Wubanoidea* Eskov, 1986. Four putative synapomorphies for *Acanoides* **gen. n.** are suggested to support its monophyly that could be tested in the future. Furthermore, redescrptions of the epigynal morphology of *Acanthoneta aggrassa* Chamberlin & Ivie, 1943 (Nearctic) and on the male of *A. dokutchaei* Eskov & Marusik, 1993 (Far East Asia, firstly recorded from China) are provided. Based on comparison with *Poecilonetia*, from which *Acanthoneta* **stat. n.** was separated by Saaristo and Tanasevitch (1996), a revised diagnosis is proposed to support the generic status.

Keywords

Taxonomy, new species, new genus, genitalic morphology, movable epigynum

Introduction

Micronetinae Hull, 1920 is a fairly large subfamily of Linyphiidae Blackwall, 1859, including 1199 species placed in 90 genera (Tanasevitch 2014). It was redelimited by Saaristo and Tanasevitch (1996), who established eight new genera for 89 species, and raised three subgenera to generic status. Subsequently, a series of revisions were published (e.g. Saaristo and Tanasevitch 2002a, 2002b; Saaristo and Marusik 2004; Saaristo et al. 2006; Tu et al. 2006; Tu and Li 2006) that resulted in many new genera and a new subfamily Ipainae Saaristo, 2007. Results of these series of review works have not been tested in a phylogenetic context; neither Micronetinae nor Ipainae monophyly, as well as that of the genera included in the two subfamilies have been tested so far.

Poeciloneta hengshanensis (Chen & Yin, 2000) from China, originally placed in *Lepthyphantes* Menge, 1866, has its male palp very similar to that of *Poeciloneta* (*Acanthoneta*) *aggressa* (Chamberlin & Ivie, 1943). *Acanthoneta* Eskov & Marusik, 1992 is one of the three genera raised from subgeneric status by Saaristo and Tanasevitch (1996) with the type species *Acanthoneta aggressa*. Tu et al. (2006) transferred *P. hengshanensis* to *Acanthoneta* based on the similarity of the male palpal morphology. However, raising *Acanthoneta* to a generic status “was not accompanied by a diagnosis or justification”, and hence not accepted in The World Spider Catalog (Platnick 2014). All members of *Acanthoneta* are currently placed in *Poeciloneta* Kulczyński, 1894.

Females of *P. hengshanensis* (previously unknown) were found in new material from China. However, its epigynal conformation is neither congruent with that of *P. aggressa*, nor with any other species of *Poeciloneta*. Based on the presence of an extensible basal part, the movable epigynum accords with the diagnosis of the subfamily Ipainae Saaristo, 2007 (for example *Ipa* Saaristo, 2007 and *Solenysa* Simon, 1894). Additionally, we found another new species with genitalic morphology very similar to that of *P. hengshanensis*: the male palpal morphology similar to *Acanthoneta* and a movable epigynum in accordance with ipaine type.

A new genus *Acanoides* gen. n. is erected here for these two species. To test the placement of the new genus within Linyphiidae, a phylogenetic analysis based on newly sequenced molecular data of the two species and that of other linyphiids downloaded from NCBI was conducted. In the present study, the two species and the new genus are described. Characters of copulatory organs and somatic features of both species are illustrated by means of SEM and light microscopy. To distinguish the new genus from other “micronetine” genera with similar male palpal morphology and ipaine genera with a similar movable epigynum, the new genus is compared with the genera *Acanthoneta* (Micronetinae), *Wubanooides* Eskov, 1986 and *Epibellowsia* Tanasevitch, 1996 (Ipainae). Due to limited material available for examination, comparisons are largely based on descrip-

tions and illustrations provided by Tanasevitch (1996), Saaristo and Tanasevitch (2000) and Saaristo (2007); images of the epigynum of *Acanthoneta aggressa* and the male of *A. dokutchaevi* Eskov and Marusik, 1994 are presented here. Four putative synapomorphies are suggested for *Acanoides* gen. n. that could be tested in future study. In addition, diagnoses for *Acanthoneta* stat. n. are provided based on comparison with illustrations of genitalic characters provided by Saaristo and Tanasevitch (2000), to support its generic status proposed by Saaristo and Tanasevitch (1996). The composition and monophyly of both *Acanoides* gen. n. and *Acanthoneta* stat. n. could be tested in future study.

Materials and methods

Specimens were examined and measured using a Leica M205A stereomicroscope. Male palps and epigyna were examined after they were dissected from the body. Left structures (e.g. palps, legs, etc.) were depicted. Embolic divisions were excised by breaking the membranous column which connects the suprategulum and radix. Male palps and epigyna were cleared in methyl salicylate. Digital images were taken with a Leica DFC 500 camera, as composites of multiple focus images assembled using the software package LEICA APPLICATION SUITE. Scanning electron microscopy (SEM) images were taken using a S-3400N scanning electron microscope at the China Agricultural University. For SEM examination the specimens were prepared following Álvarez-Padilla and Hormiga (2008). SEM images of the embolic division taken from the right palp were mirrored to match those taken from the left palp. All measurements were taken with a micrometer and are expressed in millimeters. The leg measurements are given in the following sequence: total (femur, patella+tibia, metatarsus, tarsus). All specimens examined here are deposited in the College of Life Sciences, Capital Normal University, China (CNU) and in the College of Life Sciences, Hunan Normal University, China (HNU), except for the female material of *A. aggressa*, the epigynal pictures of which were provided by Don Buckle (Saskatoon, Canada). Distribution data for these species within China are presented at the provincial level. Terminology for the epigynal characters follows Tu and Hormiga (2010) and male palpal and somatic characters follows that of Saaristo and Tanasevitch (1996) and Hormiga (2000). Anatomical abbreviations used in the text and figures:

Somatic morphology

AER	anterior eye row
ALE	anterior lateral eye(s)
AME	anterior median eye(s)
AMEd	diameter of AME
PER	posterior eye row
PLE	posterior lateral eye(s)

Male palp

AX	apex of embolus
DM	distal membrane of terminal apophysis
DSA	distal suprategular apophysis
EM	embolic membrane
EP	embolus proper
FiG	Fickert's gland
LC	lamella characteristica
P	paracymbium
PCA	proximal cymbial apophysis
PH	pit hook
R	radix
SE	serrated area on embolus
SPT	supratégulum
TA	terminal apophysis
TH	thumb of embolus

Epigynum

CO	copulatory opening
CG	copulatory groove
DP	dorsal plate
EA	extensible area of epigynal basal part
EB	epigynal basal part
FG	fertilization groove
MP	median plate
S	spermathecae
SC	scape
ST	stretcher
VP	ventral plate

Phylogenetic analysis

Based on the dataset of Arnedo et al. (2009) which includes 34 linyphiid taxa (*Erigone dentipalpis* was not included as it has only one of the five genes available), newly sequenced data of the two *Acanoides* and data of another 65 linyphiid taxa downloaded from NCBI were added. A total of 111 taxa were sampled in our matrix, ten outgroup taxa of other araneoid families as in that of Arnedo et al. (2009) and 101 ingroup taxa, which cover the representatives of all the seven subfamilies currently proposed; one *Solenysa*, as a representative of ipaine, and *Acanthoneta* were included to test the placement of *Acanoides*.

Five genes: cytochrome c oxidase subunit I (CO1) and 16S rRNA (16S) and three nuclear genes 18S rRNA (18S), 28S rRNA (28S) and Histone H3 (H3) were sequenced for *Acanoides beijingensis* sp. n. and *A. hengshanensis*. Molecular procedures for sequencing follow that of Arnedo et al. (2009), with the same molecular markers to maximize the overlap of dataset. Taxa sampled and sequence accession numbers are presented in Appendix - Table S1. Data were automatic multiple aligned using the computer program Clustal X version 1.81 (Thompson et al. 1997). Gaps were treated as missing data. Maximum Likelihood analysis was performed using RAxML v7.2.7 as implemented on the Cipres Gateway (Miller et al. 2010). Bootstrap support analysis was performed with the commands: `raxmlHPC-HYBRID-7.3.1 -T 6 -s infile -n result -x 12345 -p 876 -f a -N 1000 -m GTRCAT -q part`.

Results

All five genes were sequenced for *Acanoides beijingensis* sp. n. and *A. hengshanensis* (Appendix - Table S1). The monophyly of Linyphiidae and its sister relationship with Pimoidae were not recovered in the result of phylogenetic analysis as two outgroup taxa: cyatholipid *Alaranea* and theridiosomatid *Theridiosoma* are embedded within Linyphiidae (Appendix - Fig. S1). Besides some weakly supported deeper branches, four robustly supported clades are recognized: *Stemonyphantes* clade (clade S), “micronetines-erigonines” clade (clade ME), “linyphiines”-1 clade (clade L1) and “linyphiines”-2 (clade L2). For the seven subfamilies currently proposed, only *Stemonyphantinae* Wunderlich, 1986 (the *Stemonyphantes* clade) and *Mynogleninae* Lehtinen, 1967 are monophyletic, while the mynoglenines clade and the *Dubiaranea* clade fall into clades L1 and L2 respectively that make Linyphiinae Blackwall, 1859 become a paraphyletic group; taxa of Micronetinae form a paraphyletic group, nested with taxa of Ipainae and Erigoninae within clade ME. The two *Acanoides* species form a robustly supported monophyly, distantly related to *Acanthoneta* and *Solenysa*.

Discussion

The result of the phylogenetic analysis based on molecular data suggests that the new species from Beijing is the sister taxon of *P. hengshanensis* which had ever been transferred to *Acanthoneta* by Tu et al. (2006). The lineage comprised by the two species is distantly related to *Acanthoneta* sp. (Appendix - Fig. S1). Accordingly, we erected here *Acanoides* gen. n. to accommodate the two species: *A. beijingensis* sp. n. and *A. hengshanensis* comb. n. The three known *Acanthoneta* species have very distinct male palpal morphology, only differ from that of the type species in small details (Eskov and Marusik 1992, 1993). Regardless the *Acanthoneta* taxon is congeneric with, or is the type species *Acanthoneta aggresus*, the new genus differs from all the three known species of *Acanthoneta* as well as all other “micronetines” in the females having a movable

epigynum (Figs 4G, 5G) and the males having a longer and sharper embolus proper (Figs 2D, 3D) which generally is pointed in “micronetines” (Fig. 6F); Fickert’s gland located in the membranous area outside the radix (Figs 2D, 3D), rather than embedded within the radix as usually the case in “micronetines” (Fig. 6G). This suggests that the two species are not congeneric with *Acanthoneta*.

Our results suggest an unknown *Lepthyphantes* species as a sister group to the *Acanoides* clade. *Lepthyphantes* Menge, 1866, which includes almost 500 species, is not a natural group (Saaristo and Tanasevitch 1996). All *Lepthyphantes* species, except five, have been transferred or are waiting to be transferred to other genera (e.g. Saaristo and Tanasevitch 1996, 2002a, b; Saaristo and Marusik 2004; Tu et al. 2006). The position of *Lepthyphantes* sp. on the tree indicates it is neither *Acanthoneta*, nor *Lepthyphantes*. Nevertheless, without morphological data, we fail to determine whether *Lepthyphantes* sp. is as a sister group of, or a number of *Acanoides* gen. n., so the close relative of *Acanoides* remains unresolved.

The genitalic characters of *Acanoides* make its subfamily placement problematic due to the epigynal character in accordance with Ipainae type, but the male palpal morphology of the “micronetine” type. Redelimitation of Mironetinae (Saaristo and Tanasevitch 1996) and the series of revisions of “micronetine” genera (e.g. Saaristo and Tanasevitch 2002a, 2002b; Saaristo and Marusik 2004; Saaristo et al. 2006; Tu et al. 2006; Tu and Li 2006) resulted in many new genera and even a new subfamily Ipainae (Saaristo 2007). However, none of them has been tested in a phylogenetic framework. Results of the first phylogenetic analysis for linyphiids based on molecular data indicate that neither Micronetinae nor Ipainae is a monophyletic group (Arnedo et al. 2009). Such a result was recovered in the present study too: “micronetine” taxa formed a paraphyletic group, and movable epigynum independently evolved in *Acanoides* and *Solenysa* (Appendix - Fig. S1). The extensible solenoid serving as a synapomorphy for *Solenysa* (Tu & Hormiga, 2011), the ventrally folded extensible epigynal basal part, together with long and sharp embolus proper, slender and unbranched lamella characteristic, and outside radix located Fickert’s gland are four putative synapomorphies for *Acanoides* gen. n.

With greatly increased ingroup sampling, the result of the present study produce a similar topology with that of Arnedo et al. (2009): four strongly supported clades S, L1, L2 and ME that correspond to the *Stemonyphantes* clade, clades C and D, and the “micronetines-erigonines” clade in the latter (Appendix - Fig. S1). Most newly added taxa fell into the clade ME that enriched the topology. However, the problems left by the previous study (Arnedo et al. 2009), such as the monophyly of Linyphiidae, placements of the weakly supported deeper branches, and taxa of different subfamilies placed together rendering most of the traditionally recognized subfamilies non monophyletic, persist. Six of the seven subfamilies currently proposed are not monophyletic groups. The higher level relationships within linyphiids reflected by phylogenetic result are still far away from the classic subfamily system (see Millidge 1984, 1993; Saaristo and Tanasevitch 1996; Saaristo 2007). Nevertheless, revising the whole higher level linyphiid systematics is beyond the scope of the present study. In the text below we keep using Micronetinae and Ipainae following the current taxonomic system.

Although with ingroup sampling about two times increased, the sampling size of the current dataset seems not to be enough to resolve the placements of *Acanoides* and *Acanthoneta*, as well as *Poeciloneta*, from which *Acanthoneta* were separated (Eskov and Marusik 1992), their close relatives, and the relationships among them. To better understand the higher level phylogenetic relationships of linyphiid spiders, more information, such as morphology and behavior, and a comprehensive sampling design are necessary. Here, we provide four putative synapomorphies for the new genus *Acanoides* that could be tested in future phylogenetic studies.

Taxonomy

Linyphiidae Blackwall, 1859

Acanoides gen. n.

<http://zoobank.org/4632240B-5228-4EB7-A1BC-CBD9176FEC2B>

<http://species-id.net/wiki/Acanoides>

Type species. *Acanoides beijingensis* sp. n.

Composition. Two species, *Acanoides beijingensis* sp. n. and *Acanoides hengshanensis* (Chen & Yin, 2000) comb. n.

Diagnosis. The males of *Acanoides* gen. n. can be distinct from *Acanthoneta* by the sharp embolus proper, the slender lamella characteristica unbranched, and by the Fickert's gland located in the membranous area outside the radix (Figs 2D, 3D). The females can be distinguished by the ventrally folded extensible epigynal basal part (Figs 2F, 3F).

Description. Male total length 2.34–2.73; female total length 2.10–2.42. Carapace yellowish-brown. Male carapace unmodified. AMEs smallest, others subequal; from the dorsal view AER recurved, PER straight, eyes separated by AMEd, ALE and PLE juxtaposed. Chelicerae medium-sized, with strong stridulatory ridges, female fang groove with three promarginal and three retromarginal teeth in *A. beijingensis* sp. n., and two promarginal and two retromarginal teeth in *A. hengshanensis*. Chaetotaxy: Ti I–IV: 2-2-2-2; Mt I–IV: 1-1-1-1; Mt I of males with two rows of ventral bristles, one prolateral, one retrolateral (Fig. 1C, 1D); Tm I about 0.25, Tm IV absent. Both species have a haplotracheate system.

Male palp (Figs 2A–E, 3A–E, 4A–B, 5A–B). Cymbium with proximal apophysis. Paracymbium medium to large-sized, with one tooth on lateral margin. Distal supratragular apophysis not modified as pit hook, or absent. Embolic division: radix long and narrow, Fickert's gland located in the membranous area connecting radix and embolus; embolus wide and strongly sclerotized with serrated area, embolus proper sharp with a thumb and an apex at each side; lamella characteristica unbranched, long and narrow with sharp sclerotized apex, almost parallel to radix; terminal apophysis with distal membrane.

Epigynum (Figs 2F–H, 3F–G, 4G–H, 5G–H). Protruding, with deeply wrinkled basal part, extensible and ventrally folded in constricted state. Epigynum well scler-

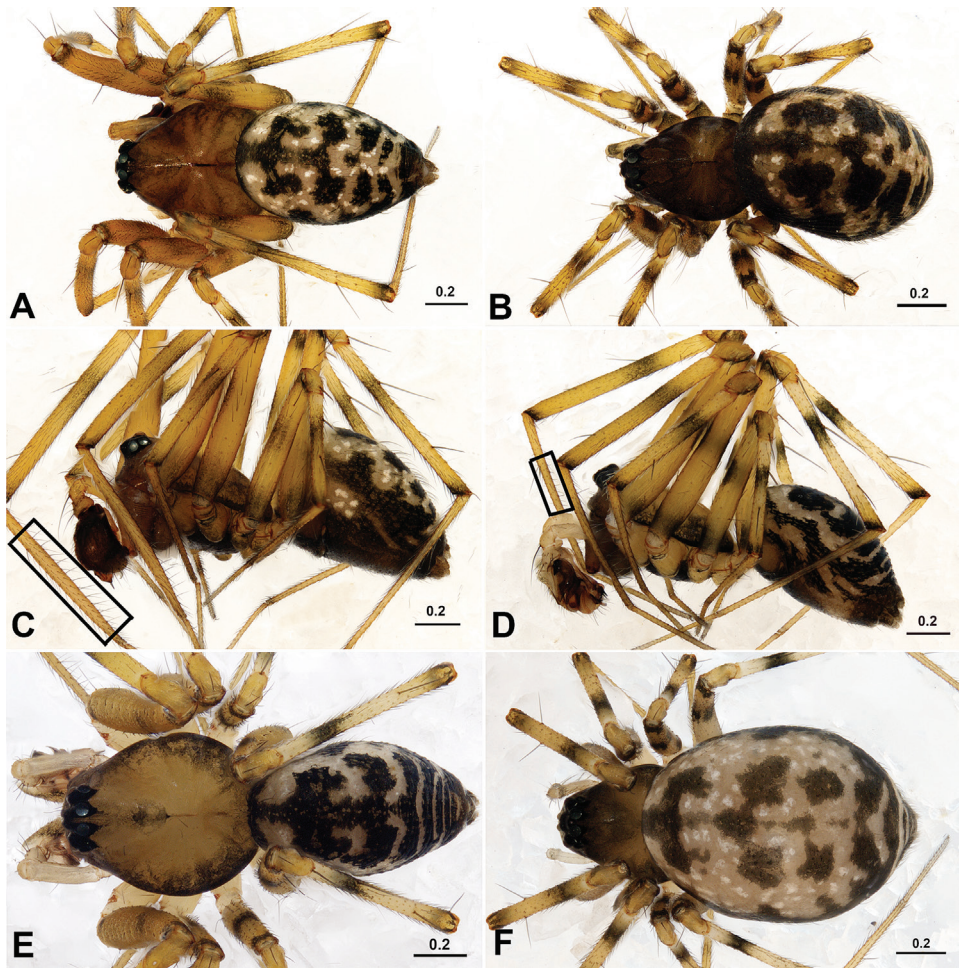


Figure 1. *Acanoides beijingensis* sp. n. (A–C) and *Acanoides hengshanensis* (D–F). **A** male, dorsal **B** female, dorsal **C** male, lateral, rectangle indicates ventrolateral rows of bristles on Mt I **D** male, lateral, rectangle indicates ventrolateral rows of bristles on Mt I **E** male, dorsal **F** female, dorsal. [Scale bars: mm].

rotized, epigynal cavity present (in *A. beijingensis* sp. n.) or absent (in *A. hengshanensis*), both scape and stretcher absent.

Etymology. The genus name, *Acanoides*, is a combination of the first four letters of “*Acanthoneta*” and the last five letters of “*Wubanoides*”. “-oides” itself in Latin means “similar to”, masculine in gender.

Phylogenetics. Due to limitations of the current dataset the monophyly of *Acanoides* could not be tested explicitly in our phylogenetic analyses, however it is supported by the following four putative synapomorphies: sharp embolus proper, slender and unbranched lamella characteristic, outside radix located Fickert’s gland and ventrally folded extensible epigynal basal part.

Distribution. China (Beijing, Hunan, Hebei) (Fig. 7).

Remarks. The males of *Acanoides* gen. n. have the palp of a “micronetine” type: presence of the Fickert’s gland, the boat-shaped radix, the trunk-like embolus with a pointed proper and a thumb, as well as the well developed terminal apophysis and lamella characteristica (Saaristo and Tanasevitch 1996). However, these sclerites in *Acanoides* (Fig. 2D) have some features different from the normal “micronetine” type (Fig. 6F, Saaristo and Tanasevitch 1996): Fickert’s gland is not embedded within the radix, but located in the membranous area connecting the radix and the embolus; and the embolus has a wide, strongly sclerotized body, with a longer and sharper embolus proper, whereas in most “micronetines” the embolus is usually trunk-like with a pointed embolus proper. The male palp of both *Acanoides* and *Acanthoneta*, have a long and slender lamella characteristica parallel to the long radix, but with an additional long and thin branch in *Acanthoneta* (Fig. 6F), unbranched in *Acanoides* (Figs 2D, 3D). The epigynum of *Acanthoneta* is in a normal “micronetine” type, with a sigmoid scape surrounded by an epigynal cavity (Fig. 6H), but with an extensible basal part in *Acanoides*.

The result of phylogenetic analysis based on molecular data indicates that Ipinae is not a monophyletic group as the movable epigynum independently evolved in *Acanoides* and *Solenysa* (Appendix - Fig. S1). This is also supported by the tracheal characters: haplotracheate type in *Acanoides*, but intermediate type in *Solenysa*, with the median pair extending into the prosoma (Tu and Hormiga 2011). We infer that the extensible basal part of the epigynum may have also evolved convergently with that in other ipaines. In *Acanoides* it differs by being ventrally folded, while it forms a solenoid in *Solenysa* (Tu & Hormiga, 2011), and folds inwards in other ipaines, e.g. *Ipa* (Saaristo 2007: fig. 29), *Wubanoides* and *Epibellowia* (Tanasevitch 1996: figs 7–9). Furthermore, the male palp of typical ipaines has filiform embolus proper (Saaristo 2007: fig. 7; Tanasevitch 1996: figs 1, 4) much longer than that of *Acanoides* (Fig. 2D).

***Acanoides beijingensis* sp. n.**

<http://zoobank.org/CE596A12-9C21-4B8F-97FC-F31CBC61CD7E>

http://species-id.net/wiki/Acanoides_beijingensis

Figs 1A–C, 2, 4

Type-locality. China, Beijing: Mt. Yangtaishan, 39°20.15'N; 115°34.52'E, alt. ca 320m, 15 Oct. 2007, L. Tu leg.

Type-specimens. Holotype, ♂ (CNU), China, Beijing, Mt. Yangtaishan, 39°20.15'N; 115°34.52'E, alt. ca 320 m, 15 Oct. 2007, L. Tu leg. Paratypes, 2 ♂♂ and 3 ♀♀ (CNU), same data as holotype.

Additional material examined. 1 ♂ and 2 ♀♀ (CNU), China, Hebei Province, Mt. Wulingshan, 40°33.61'N; 117°29.69'E, alt. ca 1100 m, 12 Aug. 2009, L. Tu leg.

Diagnosis. The male of *A. beijingensis* sp. n. can be distinguished from *A. hengshanensis* by the spine-shaped lamella characteristica (Figs 2D, 4C), ribbon-like in the latter (Figs 3D, 5C); by the hook-shaped terminal apophysis (Fig. 4C), straight in the latter (Fig. 5D); and by the presence of a distal suprategular apophysis (Fig. 4A), absent in

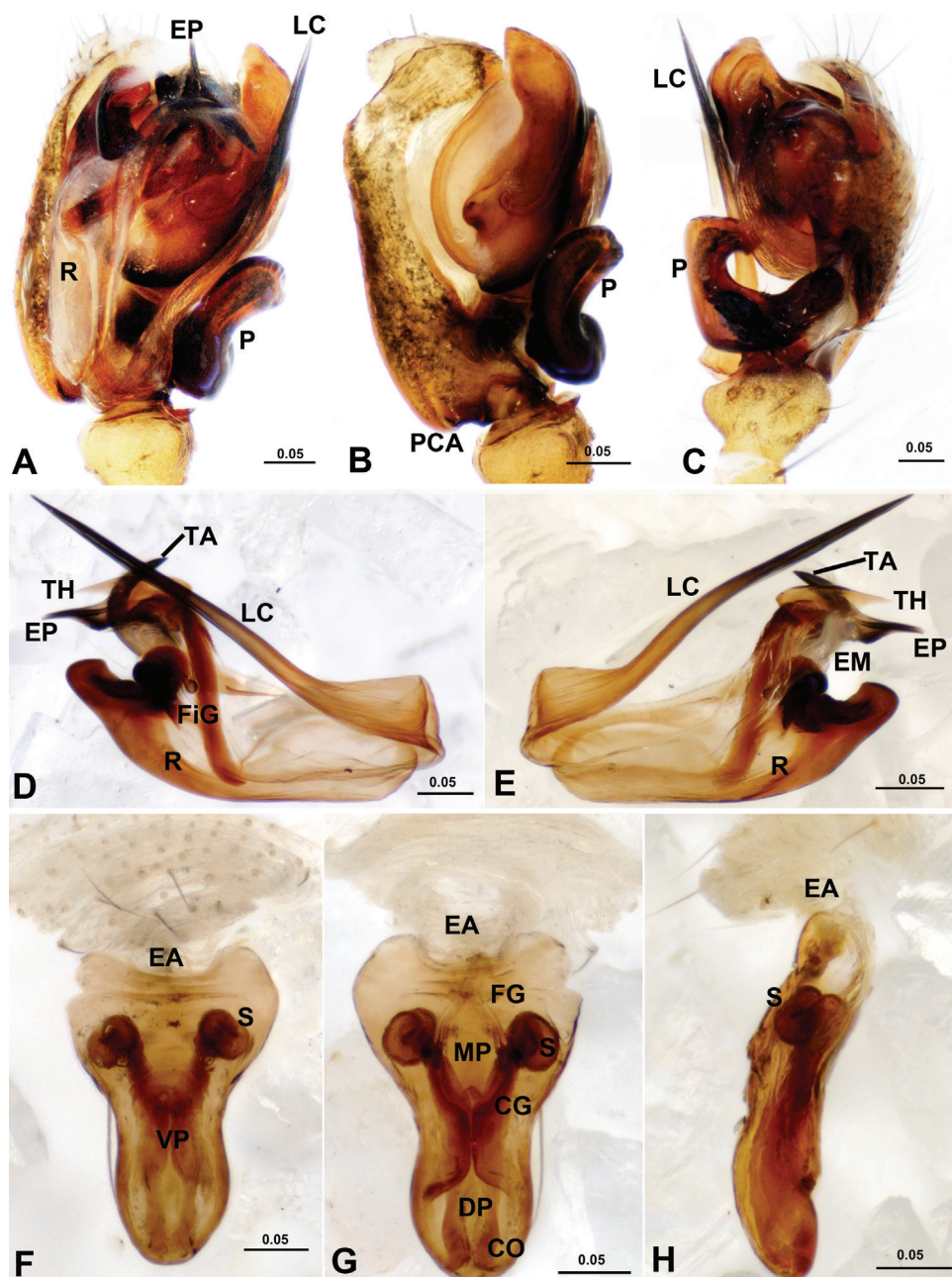


Figure 2. *Acanaoides beijingensis* sp. n. **A** male palp, prolateral **B** male palp, prolateral, with embolic division removed **C** male palp, retrolateral **D** embolic division, ventral **E** embolic division, dorsal **F** epigynum, ventral **G** epigynum, dorsal **H** epigynum, lateral. CG copulatory groove; CO copulatory opening; DP dorsal plate; EA extensible area of epigynal basal part; EM embolic membrane; EP embolus proper; FG fertilization groove; FiG Fickert's gland; LC lamella characteristica; MP median plate; P paracymbium; PCA proximal cymbial apophysis; R radix; S spermathecae; TA terminal apophysis; TH thumb of embolus; VP ventral plate. [Scale bars: mm].

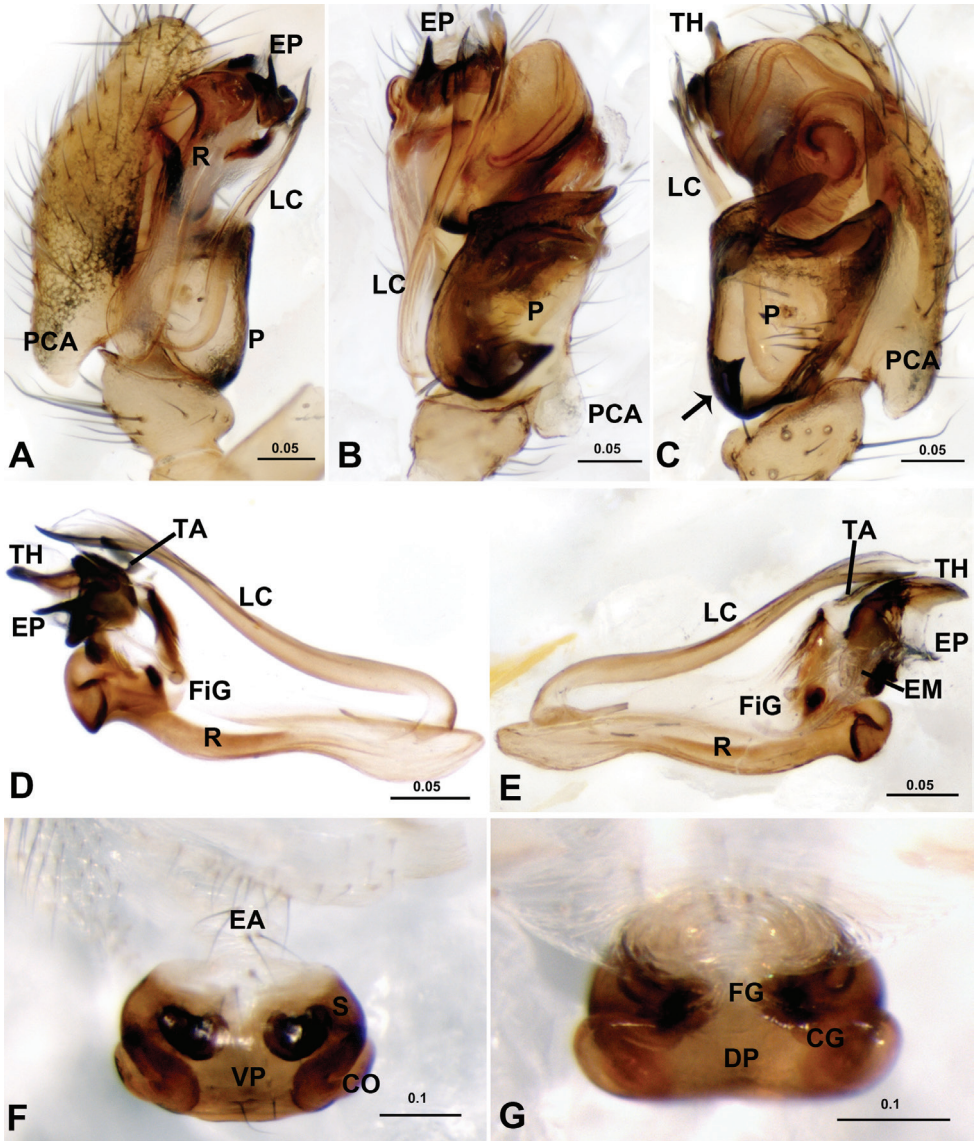


Figure 3. *Acanoides hengshanensis*. **A** male palp, prolateral **B** male palp, ventral **C** male palp, retrolateral, arrow indicates pointed tooth on posterolateral margin **D** embolic division, ventral **E** embolic division, dorsal **F** epigynum, ventral **G** epigynum, dorsal. CG copulatory groove; CO copulatory opening; DP dorsal plate; EA extensible area of epigynal basal part; EM embolic membrane; EP embolus proper; FG fertilization groove; FIG Fickert's gland; LC lamella characteristica; P paracymbium; PCA proximal cymbial apophysis; R radix; S spermatheca; TA terminal apophysis; TH thumb of embolus; VP ventral plate. [Scale bars: mm].

the latter. The female is distinct by having the epigynum two times longer than wide (Fig. 2F), shorter than wide in *A. hengshanensis* (Fig. 3F); and by the presence of a remnant epigynal cavity (Fig. 2G), totally absent in *A. hengshanensis* (Fig. 3G).

Description. Male holotype (Fig. 1A, C): Total length 2.69. Carapace 1.22 long, 1.01 wide. Abdomen 1.39 long, 0.88 wide. Lengths of legs: I 3.88 (1.05 + 1.18 + 0.99 + 0.66); II 3.02 (1.03 + 0.73 + 0.69 + 0.57); III 2.66 (0.87 + 0.88 + 0.51 + 0.40); IV 3.78 (1.12 + 1.09 + 0.93 + 0.64). Female (Fig. 1B): Total length 2.12. Carapace 0.93 long, 0.78 wide. Abdomen 1.25 long, 0.83 wide. Lengths of legs: I 6.10 (1.68 + 2.04 + 1.43 + 0.95); II 5.43 (1.56 + 1.74 + 1.24 + 0.89); III 4.39 (1.24 + 1.13 + 1.10 + 0.75); IV 5.88 (1.79 + 1.78 + 1.46 + 0.83). Tm I: 0.20. For other somatic features see description of the genus.

Male palp (Figs 2A–C, 4A–B). Cymbium with proximal apophysis. Paracymbium narrow, half rounded lateral tooth strongly sclerotized. Distal suprategular apophysis blunt, not modified as pit hook. Embolic division: radix long and narrow; Fickert's gland located in the membranous area connecting radix and embolus; embolus main body short and wide, strongly sclerotized, with serrated area on ventral surface; embolus proper sharp with pointed thumb and tail-like apex at each side; unbranched lamella characteristic long and slender, with sharp and strongly sclerotized apex; terminal apophysis hook-shaped with distal membrane.

Epigynum (Figs 2F–H, 4G–H). Two times longer than wide, wrinkled basal part extensible and ventrally folded in constricted state. Median plate and epigynal cavity present, without scape and stretcher. Copulatory openings opened dorsally.

Etymology. The species name refers to the type locality.

Variation. *Males* (n = 3). Total length 2.61–2.73. Carapace: 1.13–1.27 long, 0.95–1.05 wide. Abdomen 1.34–1.45 long, 0.71–0.99 wide.

Females (n = 3). Total length 2.10–2.23. Carapace: 0.90–0.96 long, 0.74–0.78 wide. Abdomen: 1.10–1.38 long, 0.79–0.88 wide.

Distribution. China (Beijing, Hebei) (Fig. 7).

Remarks. Although *A. beijingsensis* sp. n. looks quite different from *A. hengshanensis* in the shape of the male paracymbium and in terms of female epigynal morphology, the strongly sclerotized embolus main body and the sharp embolus proper, the location of Fickert's gland, the presence of a ventrally folded extensive area of the epigynal basal part and the absence of a scape and stretcher, shared by the two species suggest they are closely related. A close relationship between the two species is additionally supported by the phylogenetic analysis (Appendix - Fig. S1).

***Acanoides hengshanensis* (Chen & Yin, 2000), comb. n.**

http://species-id.net/wiki/Acanoides_hengshanensis

Figs 1D–F, 3, 5

Lepthyphantes hengshanensis Chen & Yin, 2000: 87, figs 12–16 (♂)

Acanthoneta hengshanensis: Tu et al. 2006: 412, figs 24–27 (♂).

Type-specimen. Holotype of *L. hengshanensis* Chen & Yin, 2000, ♂ (HNU), China, Hunan Province, Mt. Hengshan, 27°18'N; 112°42'E, 1–7 Aug. 1995, C. Yin leg. (examined).

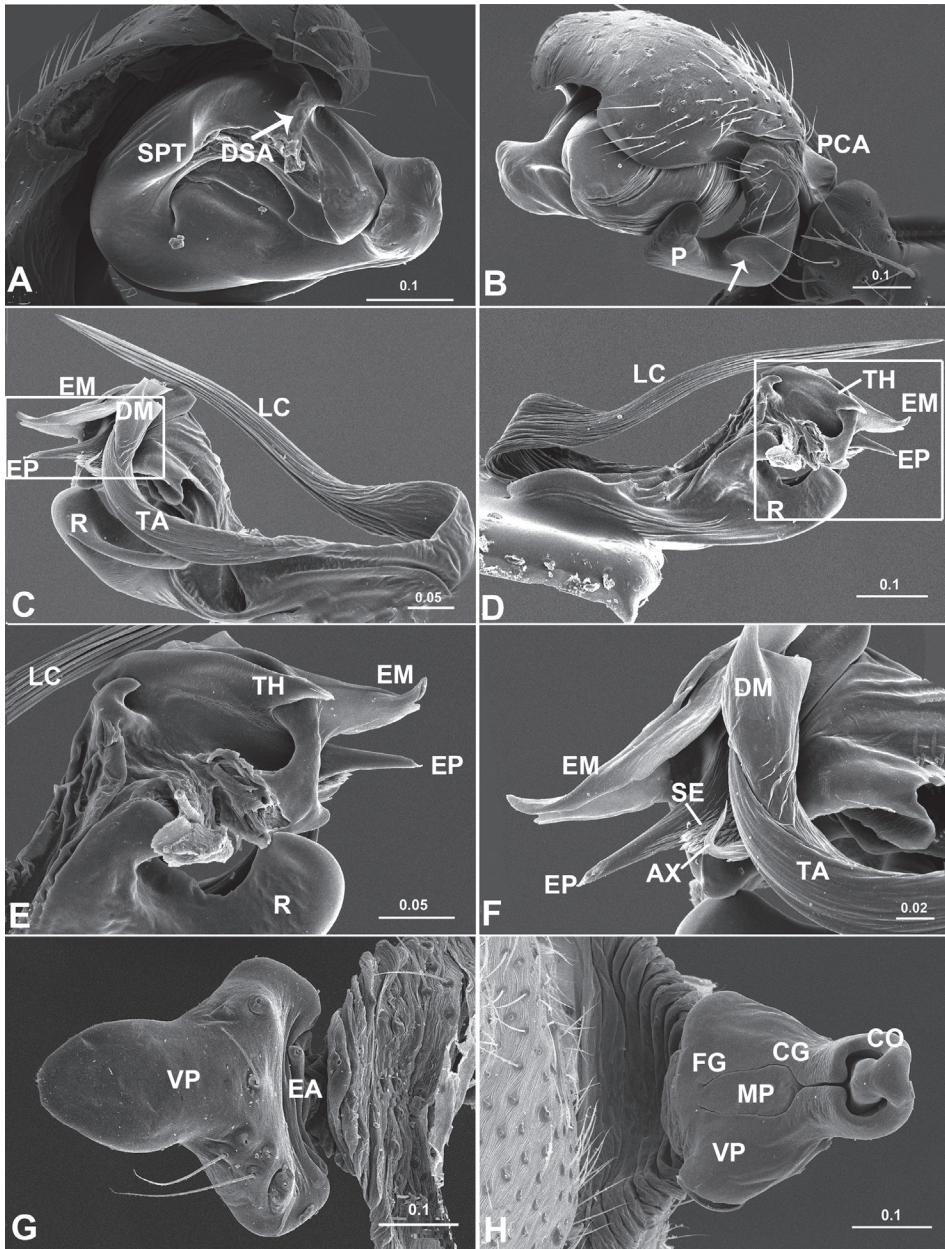


Figure 4. *Acanoides beijingsensis* sp. n. **A** palp (embolic division removed), prolateral **B** palp, retrolateral, arrow indicates half rounded lateral tooth on paracymbium **C** embolic division, ventral **D** embolic division, dorsal **E** detail of **D** **F** detail of **C** **G** epigynum, ventral **H** epigynum, dorsal. AX apex of embolus; CG copulatory groove; CO copulatory opening; DM distal membrane of terminal apophysis; DSA distal suprategular apophysis; EA extensible area of epigynal basal part; EM embolic membrane; EP embolus proper; FG fertilization groove; LC lamella characteristica; MP median plate; P paracymbium; PCA proximal cymbial apophysis; R radix; S spermatheca; SE serrated area on embolus; SPT suprategulum; TA terminal apophysis; TH thumb of embolus; VP ventral plate. [Scale bars: mm].

Additional material examined. 3 ♂♂ and 4 ♀♀, China, Beijing, Mt. Yangtaishan, Dajue Temple, 40°03.06'N; 116°05.97'E, alt. 50 m, 15 Oct. 2007, L. Tu leg.

Diagnosis. See diagnosis for *A. beijingensis* sp. n.

Description. Male (Fig. 1D–E): Total length 2.39. Carapace 1.02 long, 0.78 wide. Abdomen 1.37 long, 0.78 wide. Lengths of legs: I 5.03 (1.37 + 1.56 + 1.32 + 0.78), II 3.33 (0.98 + 0.98 + 0.83 + 0.54), III 3.47 (0.98 + 1.07 + 0.88 + 0.54), IV 4.63 (1.27 + 1.41 + 1.22 + 0.73). Tm I: 0.24. Female (Fig. 1F): Total length 2.42. Carapace 0.96 long, 0.78 wide. Abdomen 1.80 long, 1.25 wide. Lengths of legs: I 4.21 (1.18 + 1.42 + 0.96 + 0.65), II 3.19 (0.98 + 1.06 + 0.66 + 0.49), III 2.81 (0.84 + 0.85 + 0.68 + 0.44), IV 3.70 (1.08 + 1.19 + 0.89 + 0.54). Tm I: 0.23. For other somatic characters see description of the genus.

Male palp (Figs 3A–C; 5A–B). Cymbium with distinct proximal apophysis pointing backwards. Paracymbium wide and U-shaped, with triangular tooth on posterolateral margin. Distal supratregular apophysis absent. Embolic division: radix long and narrow; Fickert's gland located in the membranous area connecting radix and embolus; embolus main body large and strongly sclerotized with serrated area; embolus proper sharp with large thumb and pointed apex; lamella characteristica long and slender with bifurcated ends, one sharp and sclerotized, one membranous; terminal apophysis straight, with distal membrane.

Epigynum (Figs 3F–G, 5G–H). Short and wide, box-shaped, strongly sclerotized; wrinkled basal part extensible and ventrally folded in constricted state. Neither median plate nor epigynal cavity present. Copulatory openings located on ventral surface, slits of epigynal grooves extending laterally, passing from ventral to dorsal surface, then convergent mesally. No scape, no stretcher.

Variation. *Males* (n = 3). Total length 2.34–2.41. Carapace: 1.09–1.12 long, 0.72–0.93 wide. Abdomen 1.14–1.42 long, 0.68–0.83 wide.

Females (n = 4). Total length 2.32–2.42. Carapace: 0.87–1.01 long, 0.75–0.81 wide. Abdomen: 1.63–1.82 long, 0.76–1.22 wide.

Distribution. China (Beijing, Hunan) (Fig. 7).

Genus *Acanthoneta* Eskov & Marusik, 1992 stat. n.

Acanthoneta Eskov & Marusik, 1992: 34. Described as a subgenus of *Poecilometes*.

Acanthoneta: Saaristo and Tanasevitch 1996: 175. Raised to generic status without any comments or argumentation.

Type species. *Poecilometes aggressus* (Chamberlin & Ivie, 1943).

Composition. Three species: *A. aggressa* Chamberlin & Ivie, 1943 (Nearctic), *A. dokutchaei* Eskov & Marusik, 1993 (Far East Asia) and *A. furcata* Emerton, 1913 (Nearctic).

Comments. Originally *Acanthoneta* was described as a subgenus of *Poecilometes*, including two species: *Poecilometes* (*A.*) *aggressa* and *Poecilometes* (*A.*) *furcata*. One ad-

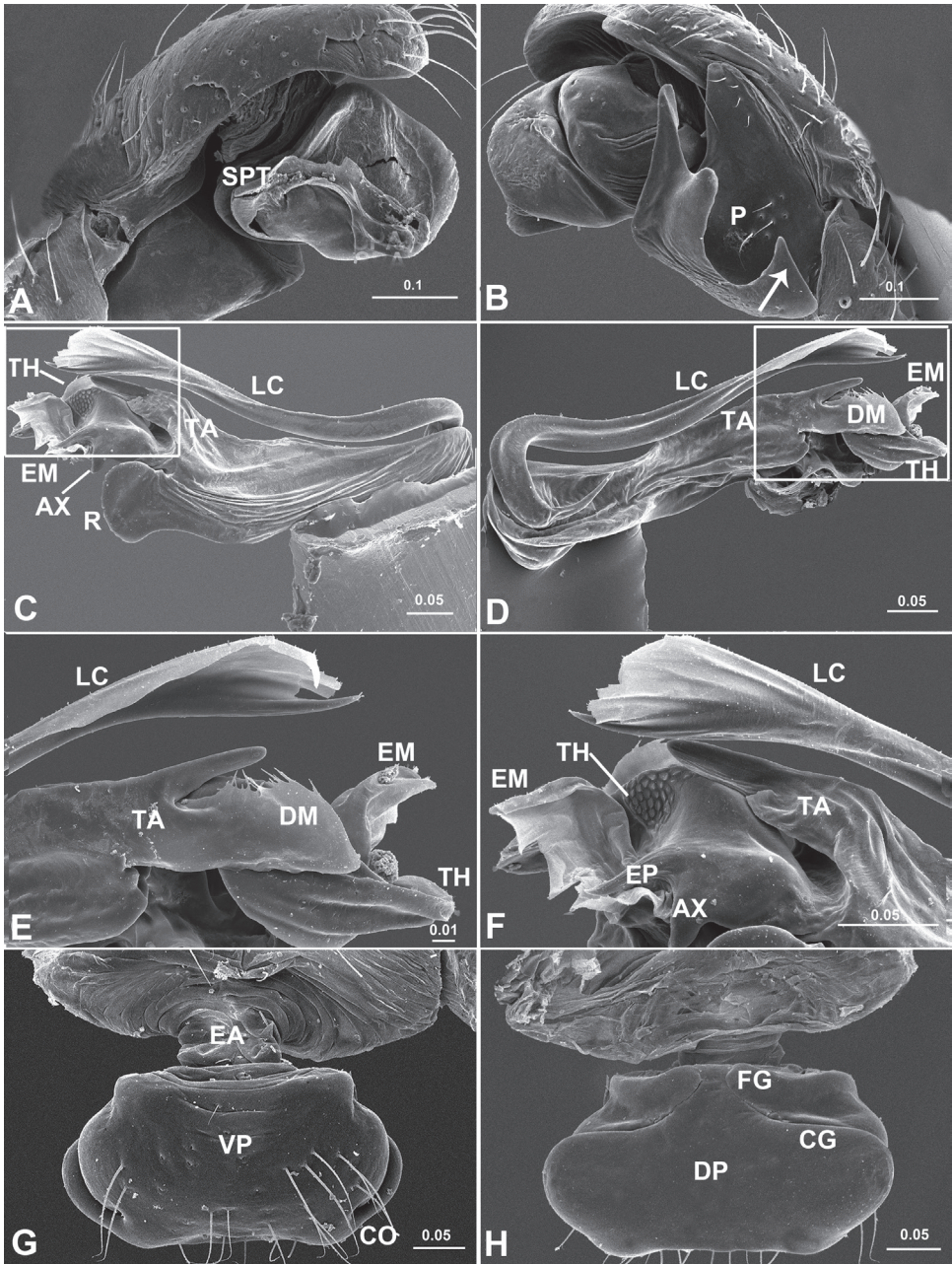


Figure 5. *Acanoides hengshanensis*. **A** palp (embolic division removed), prolateral **B** palp, retrolateral, arrow indicates pointed tooth on posterolateral margin **C** embolic division, ventral **D** embolic division, dorsal **E** detail of **D** **F** detail of **C** **G** epigynum, ventral **H** epigynum, dorsal. AX apex of embolus; CG copulatory groove; CO copulatory opening; DM distal membrane of terminal apophysis; EA extensible area of epigynal basal part; EM embolic membrane; EP embolus proper; FG fertilization groove; LC lamella characteristica; P paracymbium; PCA proximal cymbial apophysis; R radix; S spermatheca; SPT supratégulum; TA terminal apophysis; TH thumb of embolus; VP ventral plate. [Scale bars: mm].

ditional species *A. dokutchaevi* was assigned to the subgenus by Eskov and Marusik (1993). Saaristo and Tanasevitch (1996) raised *Acanthoneta* to genus status without any argumentations and hence the new status was not accepted by Platnick (2014). Here we provide a diagnosis for *Acanthoneta* and a comparison with *Poeciloneta*.

Diagnosis. Males of *Acanthoneta* differ from *Poeciloneta* by the long radix almost parallel with the long lamella characteristica (Fig. 6F), in the latter the radix is normal boat-shaped, lamella characteristica large and ribbon-like (Saaristo and Tanasevitch 2000: fig. 11). Females of the two genera differ by the epigynum in *Acanthoneta* having a sigmoid scape surrounded by an epigynal cavity, the lateral wall of which is posteriorly extended (Fig. 6H), whereas in *Poeciloneta* the scape is exposed, enlarged and strongly sclerotized (Saaristo and Tanasevitch 2000: fig. 18).

***Acanthoneta aggressa* (Chamberlin & Ivie, 1943)**

http://species-id.net/wiki/Acanthoneta_aggressa

Fig. 6H–J

Lepthyphantes aggressus Chamberlin & Ivie, 1943: 14, figs 19–20.

Poeciloneta aggressa: Crawford 1988: 19.

Acanthoneta aggressa: Saaristo and Tanasevitch 1996: 175.

Poeciloneta aggressa: Paquin and Dupérré 2003: 147, figs 1623–1625.

Material examined. No material examined, epigynum pictures were provided by Don Buckle (Saskatoon, Canada): 1 ♀, Canada, Alberta, Chinook Lake, under log in spruce or fir woods, 49°40'N; 114°30'W, 25 Jul. 1988, D. J. Buckle leg.

Description. *Epigynum* (Fig. 6H–J). Slightly protruding, without extensible area at basal part. Epigynal cavity, with posteriorly extended lateral wall, surrounding sigmoid folded scape; scape long and narrow, with well developed lateral lobes hosting copulatory openings and distal stretcher.

Distribution. Across North America from Washington State to Québec (Buckle et al. 2001; Paquin and Dupérré 2003).

***Acanthoneta dokutchaevi* Eskov & Marusik, 1993**

http://species-id.net/wiki/Acanthoneta_dokutchaevi

Fig. 6A–G

Poeciloneta (Acanthoneta) aggressa non Chamberlin & Ivie, 1943: Eskov and Marusik 1992: 34–35, figs 11–13 (♂).

Poeciloneta (Acanthoneta) dokutchaevi: Eskov and Marusik 1993: 52, figs 49–51 (♂).

Material examined. 1 ♂, China, Jilin Province, Mt. Changbaishan, Ski. 42°01.54'N; 128°04.25'E, alt. ca 1260 m, 31 July 1971.

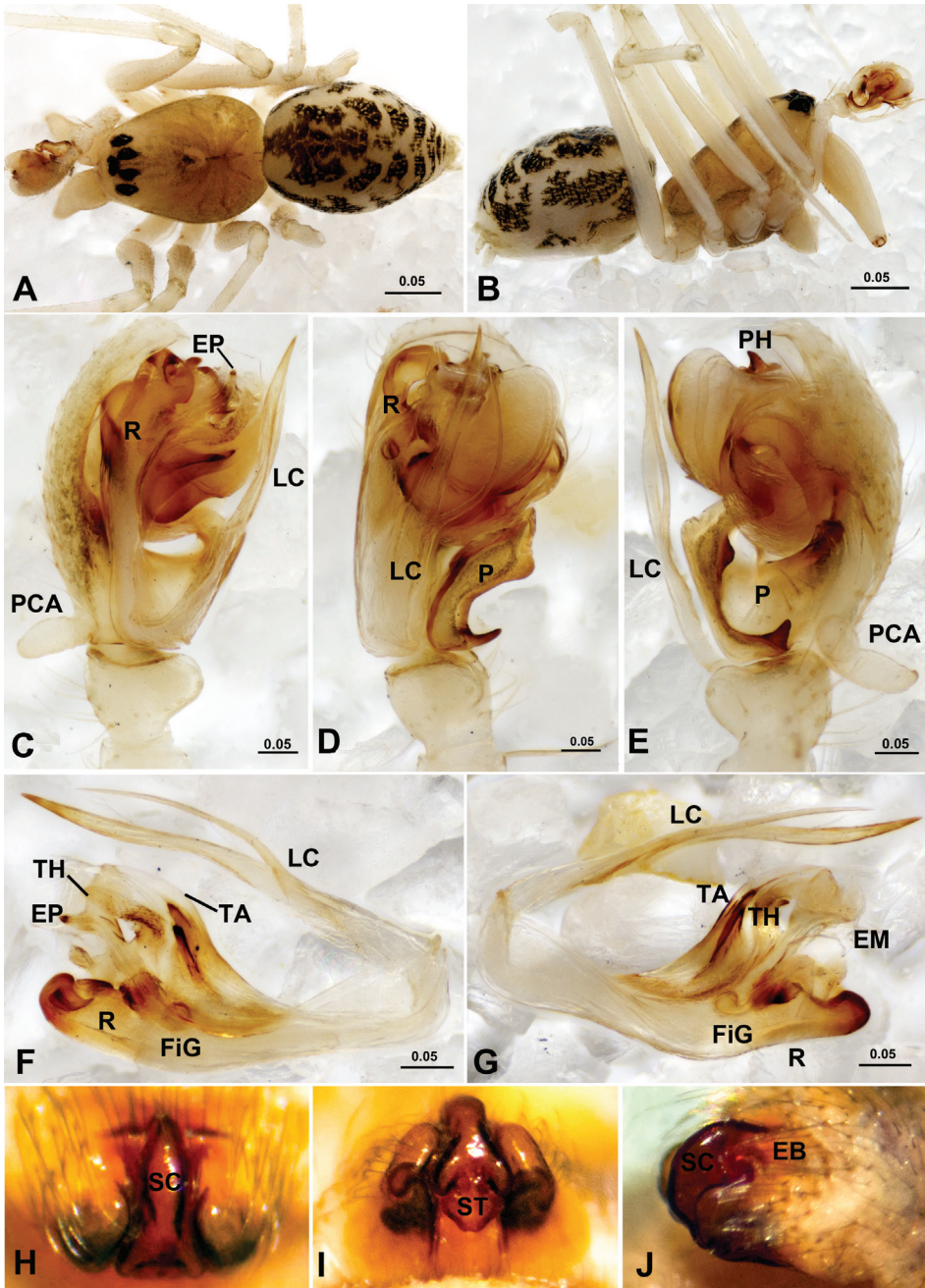


Figure 6. *Acanthoneta dokutchaei* (A–G) and *Acanthoneta aggressa* (H–J). **A** male, dorsal **B** male, lateral **C** male palp, prolateral **D** male palp, ventral **E** male palp, retrolateral **F** embolic division, ventral **G** embolic division, dorsal **H** epigynum, ventral **I** epigynum, posterior **J** epigynum, lateral (**H–J** photos provided by Don Buckle). EB epigynal basal part; EM embolic membrane; EP embolus proper; FiG Fickert's gland; LC lamella characteristica; P paracymbium; PCA proximal cymbial apophysis; PH phallosome hook; R radix; SC scape; ST stretcher; TA terminal apophysis; TH thumb of embolus. [Scale bars: mm].



Figure 7. Collecting localities of *Acanoides* species and *Acanthoneta aggrassa*, *Acanoides beijingsensis* sp. n. (Beijing, Hebei); *Acanoides hengshanensis* (Hunan, Beijing); *Acanthoneta dokutchaevi* (Jilin).

Description. Male (Fig. 6A–B). Chelicera long, with strong stridulatory ridges. Chaetotaxy: Ti I–IV: 2-2-2-2; Mt I–IV: 1-0-0-1; Tm I about 0.80, Tm IV present. For other somatic characters see description by Eskov and Marusik (1993).

Male palp (Fig. 6C–E). Cymbium with proximal apophysis erected. Paracymbium wide, with two pointed teeth on lateral margin. Distal suprategular apophysis modified as pit hook. Embolic division: radix long and narrow; Fickert's gland located within radix; embolus main body trunk-like with serrated area, pointed embolus proper and well developed thumb; lamella characteristic fork-like branched, long and slender, almost parallel to radix; terminal apophysis with distal membrane and two strongly sclerotized teeth on ventral side.

Female. Unknown.

Remarks. The male of this species is similar to the type species *A. aggrassa*. It differs only by the shape of the paracymbium. For a detailed comparison see Eskov and Marusik (1993).

Distribution. Far East Asia: Magadan Area (Eskov and Marusik 1993) and China (Fig. 7) (new record).

Acknowledgements

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Appendix

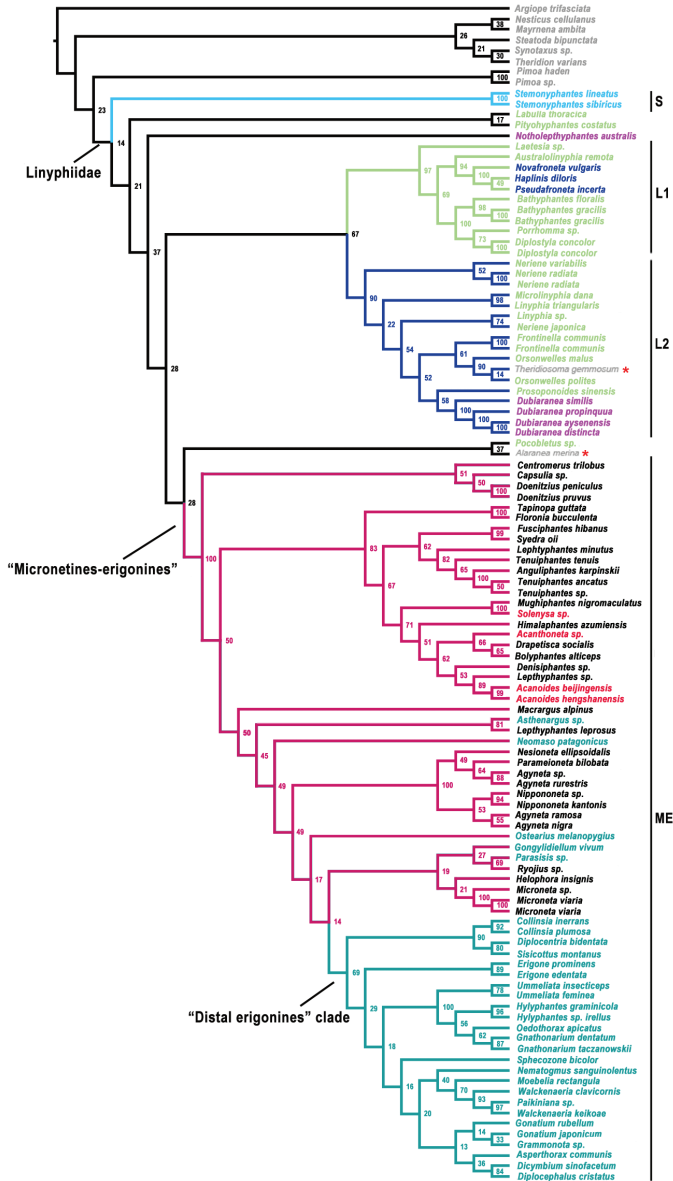


Figure S1. Linyphiid phylogeny resulting from Maximum Likelihood analysis based on molecular data. Numbers at the nodes are bootstrap value. Branches in color indicate the four robustly supported clades within linyphiids: **S** *Stemonyphantes* clade (blue) **L1** ‘linyphiines’-1 clade (pale green) **L2** ‘linyphiines’-2 clade (dark blue) **ME** ‘micronetines-erigonines’ clade (red, with ‘Distal erigonines’ clade in green). Taxa in different colors sampled from different groups: grey, outgroup; blue, Stemonyphantinae; pale green, Linyphiinae; dark blue, Mynogleninae; pink, Dubiaraneinae; black, Micronetinae; red, Ipinae, *Acanthoneta* and *Acanoides* gen. n.; green, Erigoninae. Red stars indicate the two out-group taxa: cyatholipid *Alaranea* and theridiosomatid *Theridiosoma* embedded within Linyphiidae.

Table S1. GenBank accession numbers. Data of the taxa labeled with “#” are newly sequenced; the taxa labeled with “*” come from Arnedo et al. 2009.

Family	Genus	Species	16s	18s	28s	COI	H3
Araneidae	<i>Argiope</i>	<i>trifasciata</i>		FJ525386	FJ525368	FJ525316	FJ525335
Cyatholipidae	<i>Alaranea</i>	<i>merina</i> *	AY230942	AY230890	AY231074	AY231022	AY230982
	<i>Maymena</i>	<i>ambita</i>	GU456746	GU456765	GU456824	GU456876	GU456921
Mysmenidae	<i>Nesticus</i>	<i>cellulanus</i>	EU746444	AF005447	AF124961	EU746435	
Nesticidae	<i>Pimoida</i>	<i>baden</i>	GU338640	GU338524	EF128112	EF128155	
Pimoidae		sp.*	AY230940	AY230893	AY231072	AY231025	AY230985
Synotaxidae	<i>Synotaxus</i>	sp.	AY230943	AY230894	AY231076	AY231026	AY230986
Theridiidae	<i>Steatoda</i>	<i>bipunctata</i> *	AY230951	AY230926	AY231084	AY231057	AY231014
Theridiidae	<i>Theridion</i>	<i>varians</i> *	AY230976	AY230932	AY231111	AY231063	AY231017
Theridiosomatidae	<i>Theridiosoma</i>	<i>gemmosum</i>	HM030408	HM030417	HM030428	HM030436	HM030443
Linyphiidae	<i>Acanoides</i>	<i>beijingensi</i> ‡	KJ027589	KJ027587	KJ027580	KJ027582	KJ027583
	<i>Acanoides</i>	<i>hengshanensis</i> ‡	KJ027585	KJ027588	KJ027584	KJ027586	KJ027581
	<i>Acanthoneta</i>	sp.		GU338479	GU338560	GU338678	
	<i>Agmeta</i>	sp.	GU338621		GU338529		
	<i>Agmeta</i>	<i>ramosa</i> *	FJ838670	FJ838694	FJ838717	FJ838648	FJ838740
	<i>Anguliphantes</i>	<i>karpinskii</i>		GU338516	GU338566	GU338680	
	<i>Asperthorax</i>	<i>communis</i>		GU338482	GU338545	GU338684	
	<i>Asthenargus</i>	sp.		GU338493	GU338561		
	<i>Australolinyphia</i>	<i>remota</i> *	FJ838671	FJ838695	FJ838718	FJ838649	FJ838741
	<i>Bathypantes</i>	<i>floralis</i>	GU338604	GU338465	GU338583	GU338659	
	<i>Bathypantes</i>	<i>gracilis</i> *	FJ838672	FJ838696	FJ838719	FJ838650	FJ838742
	<i>Bathypantes</i>	<i>gracilis</i>	GU338630	GU338464	GU338582	GU338689	
	<i>Bolbophantes</i>	<i>alticeps</i> *	AY078660	AY078667	AY078678	AY078691	AY078700
	<i>Capsulia</i>	sp.		GU338470	GU338586		
	<i>Centromerus</i>	<i>trilobus</i>	GU338599	GU338468	GU338571	GU338656	
	<i>Collinsia</i>	<i>inerrans</i>	GU338601	GU338518		GU338645	
	<i>Collinsia</i>	<i>plumose</i>	GU338638	GU338499	GU338543		
	<i>Denisiphantes</i>	sp.	GU338619	GU338508	GU338563	GU338669	
	<i>Dicymbium</i>	<i>sinofacetus</i>	GU338614	GU338487	EF128119	GU338665	

Family	Genus	Species	16s	18s	28s	COI	H3
	<i>Diplocentria</i>	<i>bidentata</i>	GU338629	GU338494	GU338542	GU338688	
	<i>Diplocephalus</i>	<i>cristatus</i>	GU338637	GU338490		GU338696	
	<i>Diplostyla</i>	<i>concolor</i> *	FJ838673	FJ838697	FJ838720	FJ838651	FJ838743
	<i>Diplostyla</i>	<i>concolor</i>	GU338639	GU338467	GU338585	GU338697	
	<i>Doenitzius</i>	<i>peniculus</i>	GU338631	GU338469		GU338690	
	<i>Doenitzius</i>	<i>pruvus</i>	GU338632	GU338474		GU338691	
	<i>Drapetisca</i>	<i>socialis</i> *	FJ838674	FJ838698	FJ838721	FJ838652	FJ838744
	<i>Dubiaranea</i>	<i>ayenensis</i>	FJ838675	FJ838699	FJ838722	FJ838653	FJ838745
	<i>Dubiaranea</i>	<i>distincta</i>	GU338624	GU338459	GU338579	GU338648	
	<i>Dubiaranea</i>	<i>propinqua</i>	GU338627	GU338460	GU338580	GU338675	
	<i>Dubiaranea</i>	<i>similis</i>		GU338521	GU338581	GU338681	
	<i>Erigone</i>	<i>edentate</i>		GU338486	GU338540	GU338686	
	<i>Erigone</i>	<i>prominens</i>		GU338498	GU338539	GU338679	
	<i>Floronia</i>	<i>bucculenta</i> *	FJ838676	FJ838700	FJ838723	FJ838654	FJ838746
	<i>Frontinella</i>	<i>communis</i>	GU338628	GU338517	GU338573		
	<i>Frontinella</i>	<i>communis</i> *	FJ838677	FJ838701	FJ838724	FJ838655	FJ838747
	<i>Fusciphantes</i>	<i>hibanus</i>		GU338512	GU338570	GU338683	
	<i>Gnathonarium</i>	<i>dentatum</i>	GU338593	GU338477	EF128120	GU338651	
	<i>Gnathonarium</i>	<i>taczanowskii</i>	GU338620	GU338480	GU338547	GU338670	
	<i>Gonatium</i>	<i>japonicum</i>	GU338613	GU338492			
	<i>Gonatium</i>	<i>rubellum</i> *	FJ838679	FJ838703	FJ838726	FJ838656	FJ838749
	<i>Gongylidicellum</i>	<i>vivum</i> *	FJ838678	FJ838702	FJ838725		FJ838748
	<i>Grammonota</i>	sp.		GU338491		GU338685	
	<i>Haplins</i>	<i>diloris</i> *	FJ838680	FJ838704	FJ838727	FJ838657	FJ838750
	<i>Helophora</i>	<i>insignis</i> *	FJ838681	FJ838705	FJ838728	FJ838658	FJ838751
	<i>Himalaphantes</i>	<i>azumiensis</i>		GU338522	GU338564	GU338677	
	<i>Hylyphantes</i>	<i>graminicola</i>	GU338595	GU338478	GU338550	GU338653	
	<i>Hylyphantes</i>	sp.	GU338618	GU338481	GU338549	GU338668	
	<i>Labulla</i>	<i>thoracica</i> *	AY078662	AY078674	AY078680	AY078694	AY078707
	<i>Laetesia</i>	sp.*	FJ838682	FJ838706	FJ838729	FJ838659	FJ838752
	<i>Lepthyphantes</i>	<i>minutus</i> *	AY078663	AY078673	AY078681	AY078689	AY078705

Family	Genus	Species	16s	18s	28s	COI	H3
	<i>Leptotyphantes</i>	<i>leprosus</i>		GU338488	GU338565	GU338682	
	<i>Leptotyphantes</i>	sp.	GU338610	GU338509	GU338562	GU338664	
	<i>Linyphia</i>	<i>triangularis</i> *	AY078664	AY078668	AY078682	AY078693	AY078702
	<i>Linyphia</i>	sp.	GU338597	GU338461	GU338572	GU338654	
	<i>Macrargus</i>	<i>alpinus</i>		GU338505	GU338559		
	<i>Agneta</i>	<i>nigra</i>	GU338608	GU338504	GU338577	GU338662	
	<i>Agneta</i>	<i>rurestris</i> *	FJ838683	FJ838707	FJ838730	FJ838660	FJ838753
	<i>Microliniphia</i>	<i>dana</i> *	AY078665	AY078677	AY078683	AY078690	
	<i>Microneta</i>	sp.	GU338609	GU338472	GU338538	GU338663	
	<i>Microneta</i>	<i>viaria</i> *	FJ838684	FJ838708	FJ838731	FJ838661	FJ838754
	<i>Microneta</i>	<i>viaria</i>	GU338598	GU338502	GU338537	GU338655	
	<i>Moebelia</i>	<i>rectangular</i>	GU338591	GU338485	GU338557		
	<i>Mughiphantes</i>	<i>nigromaculatus</i>	GU338600	GU338510	GU338527	GU338644	
	<i>Nematognus</i>	<i>sanguinolentus</i>	GU338635	GU338489	GU338544	GU338694	
	<i>Neomaso</i>	<i>patagonicus</i>	GU338626	GU338473	GU338578	GU338674	
	<i>Neriene</i>	<i>japonica</i>	GU338633	GU338462	GU338575	GU338692	
	<i>Neriene</i>	<i>radiata</i> *	AY078710	AY078670	AY078684	AY078696	AY078709
	<i>Neriene</i>	<i>radiate</i>	GU338623	GU338463	GU338574	GU338672	
	<i>Neriene</i>	<i>variabilis</i> *	AY078711	AY078669	AY078685	AY078699	AY078706
	<i>Nesoneta</i>	<i>ellipsoidalis</i>		GU338519	GU338532	GU338687	
	<i>Nippononeta</i>	<i>kantonis</i>	GU338634	GU338471	GU338530	GU338693	
	<i>Nippononeta</i>	sp.	GU338602	GU338520	GU338531	GU338657	
	<i>Notholeptophantes</i>	<i>australis</i> *	FJ838685	FJ838709	FJ838732	FJ838662	FJ838755
	<i>Novafoneta</i>	<i>vulgaris</i> *	FJ838686	FJ838710	FJ838733	FJ838663	FJ838756
	<i>Oedothorax</i>	<i>apicatus</i> *	FJ838687	FJ838711		FJ838664	FJ838757
	<i>Orsonvelles</i> *	<i>malus</i>	AY078737	AY078676	AY078795	AY078697	AY078708
	<i>Orsonvelles</i> *	<i>polites</i>	AY078725	AY078671	AY078786	AY078755	AY078701
	<i>Ostearius</i>	<i>melanopygius</i> *	FJ838688	FJ838712	FJ838735		FJ838758
	<i>Paikiana</i>	sp.	GU338617	GU338495	GU338555	GU338647	
	<i>Parametioneta</i>	<i>bilobata</i>	GU338605	GU338503	GU338533	GU338660	
	<i>Parasitis</i>	sp.	GU338592	GU338500	GU338534	GU338650	

Family	Genus	Species	16s	18s	28s	COI	H3
	<i>Pityophyphantes</i>	<i>costatus</i> *	AY078666	AY078675		AY078695	
	<i>Pocobletus</i>	sp.*	FJ838689	FJ838713	FJ838736	FJ838665	FJ838759
	<i>Porrhomma</i>	sp.	GU338607	GU338466	GU338584	GU338661	
	<i>Prosoptonoides</i>	<i>sinensis</i>	GU338606		GU338576	GU338649	
	<i>Pseudafroneta</i>	<i>incerta</i> *	FJ838690	FJ838714	FJ838737	FJ838666	FJ838760
	<i>Ryojius</i>	sp.	GU338611		GU338536		
	<i>Sicottus</i>	<i>montanus</i>	GU338625	GU338497	GU338541	GU338673	
	<i>Solenysa</i>	sp.	GU338616	GU338506	GU338528	GU338667	
	<i>Sphecozone</i>	<i>bicolor</i>	GU338622	GU338496	GU338553	GU338671	
	<i>Stemonyphantes</i>	<i>lineatus</i> *	FJ838691	FJ838715	FJ838738	FJ838667	FJ838761
	<i>Stemonyphantes</i>	<i>sibiricus</i> *	FJ838692			FJ838668	FJ838762
	<i>Syedra</i>	<i>oii</i>	GU338615	GU338513	GU338569	GU338666	
	<i>Tapinopa</i>	<i>guttata</i>		GU338511	GU338558	GU338676	
	<i>Tenuiphantes</i>	<i>ancatus</i>		GU338515	GU338567		
	<i>Tenuiphantes</i>	sp.	GU338612	GU338514	GU338568	GU338646	
	<i>Tenuiphantes</i>	<i>tenuis</i> *	FJ838693	FJ838716	FJ838739	FJ838669	FJ838763
	<i>Ummeliata</i>	<i>feminea</i>	GU338594	GU338475	GU338551	GU338652	
	<i>Ummeliata</i>	<i>insecticeps</i>		GU338476	GU338552		
	<i>Walckenaeria</i>	<i>clavicornis</i>	GU338596	GU338483	GU338554		
	<i>Walckenaeria</i>	<i>keikoae</i>	GU338636	GU338484	GU338556	GU338695	

