

On some Cuban species of the genus *Longior* Travassos & Kloss, 1958 (Oxyurida, Hystrignathidae), with description of a new species

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Abstract

Longior zayasi Coy, García & Alvarez, 1993 is established as *incertae sedis* because the males (declared as the holotype) are inconsistent with the generic diagnosis, particularly in relation to the morphology of the head and tail. Thus, the females of *L. zayasi* species (which agree with the generic diagnosis) are renamed and re-described as *L. longior* Morffe & García **sp. n.** We also described males found in the sample and considered as conspecific with the new species. A comparative table with the measurements of the most of the records of *L. longior* is given. The male of *L. similis* Morffe, García & Ventosa, 2009 is described from the type locality of the species and compared with the known males of the genus. A key to the females of the Cuban *Longior* is given.

Keywords

Nematoda, Oxyurida, Hystrignathidae, Passalidae, *Longior*, *Passalus*, Cuba, new species

Introduction

The genus *Longior* Travassos & Kloss, 1958, includes six nominal species of monoxenous parasites from passalid beetles. All of these species have been described from the Neotropical region: Brazil and the West Indies (Saint Lucia and Cuba). The genus

is distinguished by having females with the unarmed cervical cuticle, sub-cylindrical procorpus, a monodelphic-prodelphic genital tract and longitudinally ridged eggs (Adamson and Van Waerebeke 1992).

At present, the male is known only in two species: *L. longicollis* Travassos & Kloss, 1958 (Brazil) and *L. zayasi* Coy, García & Alvarez, 1993 (Cuba) (Travassos and Kloss 1958, Coy et al. 1993). However, the latter shows marked differences in the morphology of the cephalic and tail ends with regard to *L. longicollis*, to which the first male described in the genus belongs. These differences make necessary the analysis and discussion of the taxonomical status of *L. zayasi*. Several authors (Van Waerebeke 1973; Hunt 1981) have referred to the problems involved in assigning a male to its correct species in cases of multiple co-infection with multiple species of parasites. They claimed as their main reasons the lack of knowledge about the generic features of the males in most genera within the family (the male is known only in a few genera) and their morphological homogeneity. For these reasons misidentifications can be made in some cases.

In this work, we discuss the taxonomical status of *L. zayasi*, describe a new species of the genus and describe the male of *L. similis* Morffe, García & Ventosa, 2009.

Material and methods

All the passalids for this study were collected by hand from rotting logs in Cuba. Two specimens of *P. pertyi* were caught from La Jaula, La Habana Province and eight specimens of *P. interstitialis* from Escaleras de Jaruco, La Habana Province. Beetles were kept alive in plastic jars with wood chips as food. They were killed with ethyl ether and processed following Morffe et al. (2009). Intestines were dissected in normal saline and nematodes were removed from host guts and killed with hot water (60–80°C). They were fixed in 70% ethanol and clear-mounted in glycerine. The edges of the coverslips were sealed with nail polish.

Two additional specimens of *P. pertyi* from La Melba, Holguín Province, Cuba were included in the present study in order to obtain males of *L. longior* sp. n. Hosts were killed and conserved in 70% ethanol. Dissection of the beetles and processing of the parasites were made as described above, but using water instead of normal saline.

Measurements of the nematodes were made with a calibrated eyepiece micrometer and are given in millimeters. De Man's ratios a, b, c and V% were calculated. Micrographs were taken with an AxioCam digital camera attached to a Carl Zeiss AxioScop 2 Plus compound microscope. Line drawings were made on the basis of micrographs using the softwares CorelDRAW X3 and Adobe Photoshop CS2. Scale bars of all Figures are given in millimeters.

The material examined is deposited in the Colección Helmintológica de las Colecciones Zoológicas (CZACC), Instituto de Ecología y Sistemática, Havana, Cuba.

Systematics

Genus *Longior* Travassos & Kloss, 1958

Figure 1 A–D

Longior zayasi Coy, García & Alvarez, 1993 *incertae sedis*

General. Coy et al. (1993) described *L. zayasi*, from El Salón, Sierra del Rosario, eastern Pinar del Río Province, Cuba. Although the females morphology is consistent with the generic definition, examination of the male specimens showed features that disagree with the diagnosis of the male of *L. longicollis*, the type species of the genus. These features are:

First cephalic annule notably long, surpassing the stoma length, inflated, forming a truncated cone-like structure. According with Travassos and Kloss (1958), *L. longicollis* has a cephalic dilatation hardly conspicuous.

Posterior end finished in a sharply pointed tail, instead of the ventral expansion of the tail cuticle in *L. longicollis* that forms a bursa-like structure, referred by the authors as a “ventral valve”.

These discrepancies support the possibility that the males attributed to *L. zayasi* are misplaced in this genus. So far, we can not assign these males to a genus, although is possible that they belong to some species of *Artigasia* Christie, 1934 or *Hystrignathus* Leidy, 1850 where the females show a long and dilated first cephalic annule. New collections from the locality are needed to clarify the status of *L. zayasi* by comparing males with the females in the same host. Meanwhile we consider this species as an *incertae sedis*.

Coy et al. (1993) established a male specimen as holotype of *L. zayasi*. According to the Article 73.1 of the International Code of Zoological Nomenclature “A holotype is the single specimen upon which a new nominal species-group taxon is based in the original publication...”. As a new name becomes necessary for the females described as conspecific with *L. zayasi*, below we re-describe and rename such females, including the description of sympatric males that present the diagnostic features of *Longior* and we consider as conspecific with those females.

Longior longior sp. n.

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Figure 2 A–G; Figure 3 A–D; Figure 5 A–F

Type material. ♀ holotype; Cuba, La Habana Province, San José de Las Lajas, La Jaula; in *Passalus pertyi*; 15.III.2008; E. Fonseca, J. Morffe, F. Alvarez coll.; CZACC 11.4487. ♂ allotype, same data as holotype, CZACC 11.4620. 11 adult ♀♀ paratypes, same data as holotype, CZACC 11.4488–11.4498. 5 immature ♀♀ paratypes,

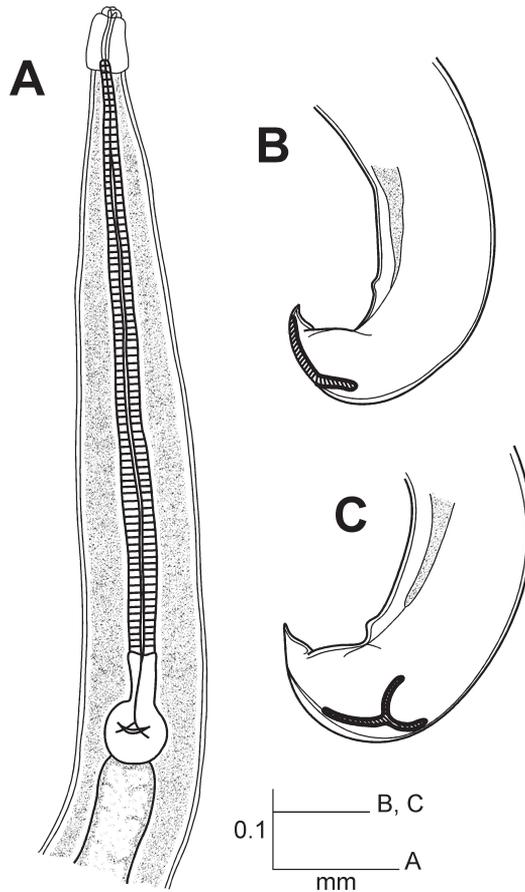


Figure 1. *Longior zayasi* Coy, García & Alvarez, 1993; *incertae sedis* (male). Drawing modified from Coy et al. (1993). **A** Esophageal region **B** Tail, lateral view **C** Tail, dorso-lateral view.

CZACC 11.4499–11.4503, same data as holotype. 5 ♂♂ paratypes, same data as holotype, CZACC 11.4621–11.4625.

Other materials examined. 4 ♂♂ vouchers; Cuba, Holguín Province, Nipe-Sagua-Baracoa, La Melba; in *Passalus pertyi*; V.2007; R. Barba, D. Ortiz coll.; CZACC 11.4626–11.4629.

3 ♀♀ paratypes of *L. zayasi*; Cuba, Pinar del Río Province, Sierra del Rosario, El Salón; in *Passalus interstitialis*; 1989; A. Coy, M. Alvarez coll.; CZACC 11.4178–11.4180.

Measurements. Holotype (female) a = 23.78, b = 4.63, c = 7.04, V% = 51.70, total length = 3.520, maximum body width = 0.148, first cephalic annule (length×width) = 0.028×0.035, stoma length = 0.078, procorpus length = 0.640, isthmus length = 0.045, diameter of basal bulb = 0.070, total length of oesophagus = 0.760, nerve ring to anterior end = 0.233, excretory pore to anterior end = 0.980, vulva to posterior end = 1.700, anus to posterior end = 0.500, eggs = 0.123–0.128×0.045–0.053 (0.125 ± 0.003×0.049 ± 0.004 n = 3).

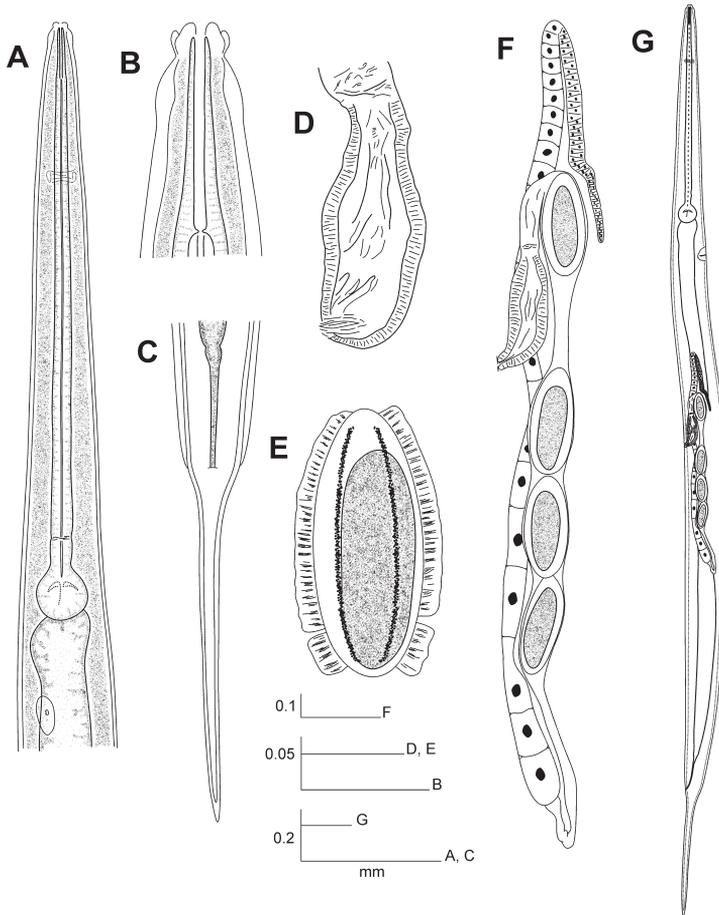


Figure 2. *Longior longior* Morffe & García sp. n. (female). **A** Esophageal region **B** Cephalic end **C** Tail, ventral view **D** Vulva **E** Egg **F** Genital tract **G** Entire nematode, lateral view.

Female adult paratypes (n = 11) a = 23.61–28.28 (25.00 ± 1.57 n = 11), b = 4.49–5.45 (4.81 ± 0.29 n = 10), c = 6.24–8.54 (7.37 ± 0.66 n = 11), V% = 49.73–58.01 (52.98 ± 2.34 n = 11), total length = 3.500–4.525 (3.863 ± 0.277 n = 11), maximum body width = 0.138–0.173 (0.155 ± 0.010 n = 11), first cephalic annule (length×width) = 0.023–0.028×0.035–0.038 ($0.024 \pm 0.002 \times 0.036 \pm 0.001$ n = 9), stoma length = 0.073–0.085 (0.079 ± 0.005 n = 11), procarpus length = 0.630–0.720 (0.678 ± 0.027 n = 10), isthmus length = 0.040–0.058 (0.053 ± 0.005 n = 10), diameter of basal bulb = 0.065–0.078 (0.071 ± 0.004 n = 10), total length of oesophagus = 0.760–0.860 (0.806 ± 0.030 n = 10), nerve ring to anterior end = 0.230–0.250 (0.242 ± 0.007 n = 9), excretory pore to anterior end = 0.970–1.125 (1.050 ± 0.047 n = 10), vulva to posterior end = 1.600–1.925 (1.813 ± 0.097 n = 11), anus to posterior end = 0.470–0.590 (0.526 ± 0.038 n = 11), eggs = 0.110–0.143×0.050–0.060 ($0.133 \pm 0.006 \times 0.053 \pm 0.003$ n = 28).

Female immature paratypes (n = 5) a = 24.31–27.02 (24.96 ± 1.16 n = 5), b = 4.13–4.42 (4.28 ± 0.12 n = 5), c = 7.07–8.86 (7.74 ± 0.68 n = 5), V% = 53.54–56.56

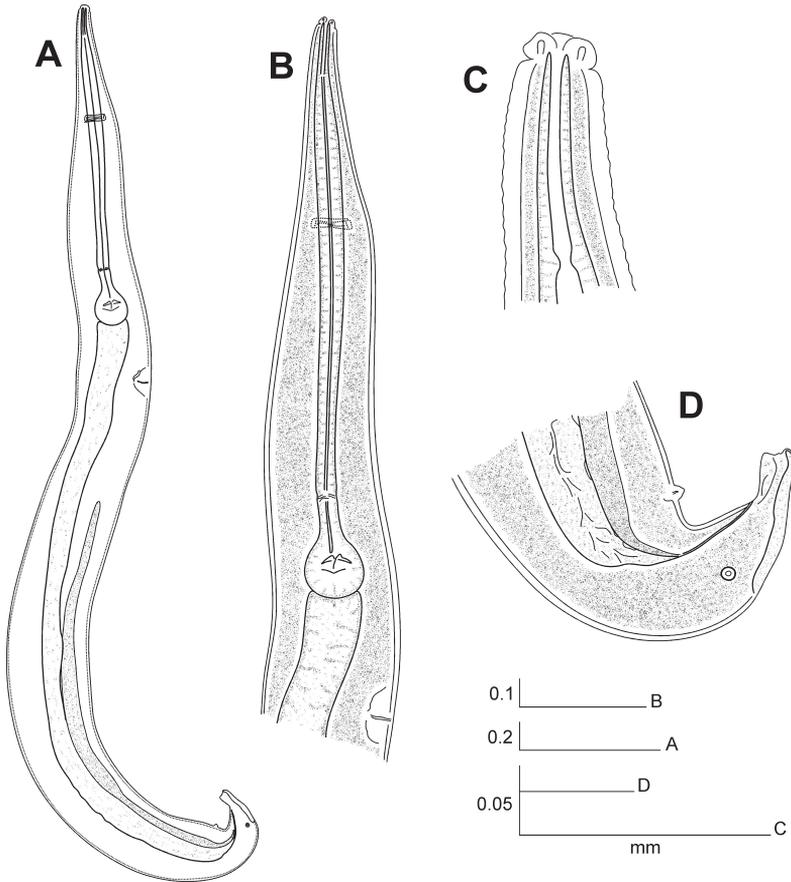


Figure 3. *Longior longior* Morffe & García sp. n. (male). **A** Entire nematode, lateral view **B** Esophageal region, lateral view **C** Cephalic end **D** Tail, lateral view.

(54.99 ± 1.07 $n = 5$), total length = 3.050–3.325 (3.165 ± 0.104 $n = 5$), maximum body width = 0.118–0.135 (0.127 ± 0.006 $n = 5$), first cephalic annule (length \times width) = 0.023–0.025 \times 0.035 ($0.024 \pm 0.001 \times 0.035 \pm 0.000$ $n = 5$), stoma length = 0.070–0.073 (0.072 ± 0.001 $n = 5$), procorpus length = 0.610–0.680 (0.638 ± 0.028 $n = 5$), isthmus length = 0.055–0.058 (0.056 ± 0.001 $n = 5$), diameter of basal bulb = 0.063–0.068 (0.065 ± 0.002 $n = 5$), total length of oesophagus = 0.690–0.760 (0.740 ± 0.029 $n = 5$), nerve ring to anterior end = 0.223–0.233 (0.227 ± 0.004 $n = 5$), excretory pore to anterior end = 0.910–0.980 (0.942 ± 0.031 $n = 5$), vulva to posterior end = 1.325–1.500 (1.425 ± 0.068 $n = 5$), anus to posterior end = 0.350–0.470 (0.412 ± 0.045 $n = 5$).

Allotype (male) $a = 15.68$, $b = 3.63$, $c = 49.67$, total length = 1.490, maximum body width = 0.095, stoma length = 0.038, procorpus length = 0.330, isthmus length = 0.033, diameter of basal bulb = 0.045, total length of oesophagus = 0.410, nerve ring to anterior end = 0.160, excretory pore to anterior end = 0.560, cloaca to posterior end = 0.030, distance from the mammiform papillae to the posterior end = 0.130, distance from the dorso-lateral papillae to the posterior end = 0.065.

Male paratypes (n = 5) a = 11.56–14.10 (12.40 ± 1.04 n = 5), b = 3.13–3.60 (3.38 ± 0.17 n = 5), c = 43.33–51.27 (47.13 ± 3.54 n = 5), total length = 1.220–1.510 (1.366 ± 0.111 n = 5), maximum body width = 0.100–0.120 (0.111 ± 0.010 n = 5), stoma length = 0.040–0.048 (0.043 ± 0.003 n = 5), procorpus length = 0.300–0.340 (0.322 ± 0.018 n = 5), isthmus length = 0.030–0.033 (0.031 ± 0.001 n = 5), diameter of basal bulb = 0.045–0.048 (0.047 ± 0.001 n = 5), total length of oesophagus = 0.390–0.420 (0.404 ± 0.015 n = 5), nerve ring to anterior end = 0.150–0.168 (0.159 ± 0.007 n = 5), excretory pore to anterior end = 0.480–0.550 (0.512 ± 0.028 n = 5), cloaca to posterior end = 0.028–0.030 (0.029 ± 0.001 n = 5), distance from the mammiform papillae to the posterior end = 0.128–0.148 (0.137 ± 0.010 n = 3), distance from the dorso-lateral papillae to the posterior end = 0.058–0.065 (0.062 ± 0.003 n = 5).

Population from La Melba, Nipe-Sagua-Baracoa, Holguín Province. Males (n = 4) a = 11.55–14.00 (13.00 ± 1.12 n = 4), b = 3.10–4.20 (3.50 ± 0.48 n = 4), c = 33.87–61.09 (44.96 ± 11.49 n = 4), total length = 1.170–1.680 (1.348 ± 0.227 n = 4), maximum body width = 0.085–0.120 (0.104 ± 0.015 n = 4), stoma length = 0.038–0.040 (0.039 ± 0.001 n = 4), procorpus length = 0.283–0.320 (0.303 ± 0.016 n = 4), isthmus length = 0.028–0.038 (0.032 ± 0.004 n = 4), diameter of basal bulb = 0.050–0.063 (0.054 ± 0.006 n = 4), total length of oesophagus = 0.378–0.400 (0.384 ± 0.010 n = 4), nerve ring to anterior end = 0.133–0.158 (0.145 ± 0.013 n = 3), excretory pore to anterior end = 0.430–0.490 (0.463 ± 0.025 n = 4), cloaca to posterior end = 0.028–0.038 (0.031 ± 0.005 n = 4), distance from the mammiform papillae to the posterior end = 0.115–0.133 (0.125 ± 0.009 n = 3), distance from the dorso-lateral papillae to the posterior end = 0.055–0.070 (0.063 ± 0.006 n = 4).

Population from El Salón, Sierra del Rosario, Pinar del Río Province. Females (n = 3) a = 17.20–23.94 (21.67 ± 3.87), b = 4.79–4.86 (4.83 ± 0.05), c = 6.68–7.63 (7.25 ± 0.51), V% = 45.99–52.19 (50.04 ± 3.51), total length = 3.580–3.890 (3.737 ± 0.155), maximum body width = 0.150–0.218 (0.177 ± 0.036), first cephalic annule = 0.018–0.025×0.035–0.038 ($0.021 \pm 0.005 \times 0.036 \pm 0.002$), stoma length = 0.060–0.075 (0.066 ± 0.008), procorpus length = 0.650–0.660 (0.655 ± 0.007), isthmus length = 0.050–0.058 (0.053 ± 0.004), diameter of basal bulb = 0.070–0.073 (0.071 ± 0.002), total length of oesophagus = 0.780–0.800 (0.790 ± 0.014), nerve ring to anterior end = 0.225–0.235 (0.230 ± 0.005), excretory pore to anterior end = 0.990–1.05 (1.020 ± 0.042), vulva to posterior end = 1.720–2.020 (1.867 ± 0.150), anus to posterior end = 0.480–0.560 (0.517 ± 0.040), eggs = 0.128–0.140×0.045–0.060 ($0.133 \pm 0.005 \times 0.053 \pm 0.006$ n = 5).

Description. Female. Body long and relatively slender. Cervical cuticle without spines. Subcuticular longitudinal striae present. Lateral alae well developed, arising from about two body widths posterior to the basal bulb up to the level of the anus. Head rounded, set-off from body by a single, deep groove, bearing eight prominent, paired papillae. First cephalic annule slightly inflated, about 2 to 2.5 head-lengths long. Stoma long, slender, about 3.5 first cephalic annule lengths long, surrounded by an esophageal collar. Oesophagus consisting of a very elongated, subcylindrical, muscular procorpus less set-off from the isthmus. Basal bulb sub-spherical, valve plate well developed. Intestine simple, sub-rectilinear, its fore region slightly inflated. Rec-

tum short, anus not prominent. Nerve ring encircling procorpus at about 20% of its length. Excretory pore located at about a body width posterior to basal bulb. Vulva a median transverse slit, near midbody, lips not prominent. Vagina muscular, strongly developed, forwardly directed. Genital tract monodelphic-prodelphic. Ovary reflected at about two body widths posterior to bulb, distal flexure about two body widths long. Eggs ovoid, with eight, rough, very prominent, longitudinal ridges not reaching the poles. Oocytes in a single row. Tail conical, subulate, ending in a fine tip.

Male. Body comparatively stout, shorter than female. Posterior region of body ventrally curved. Cervical cuticle unarmed, visibly annulated up to a little distance before the nerve ring. Sub-cuticular longitudinal striae present. Head set off from body by a single groove and bearing eight small, paired papillae. First cephalic annule not conspicuous. Stoma long, surrounded by an esophageal collar. Oesophagus slightly sub-fusiform, diminishing its diameter toward its second half until equaling the diameter of the isthmus. Basal bulb rounded, valve plate developed. Nerve ring encircling procorpus at about 35% of its length. Excretory pore situated at little more than a body-width posterior to basal bulb. Testis single, full of spermatids, commencing at about 1.5 body-widths posterior to bulb. Spicule absent. A large, median, mammiform preloacal papillae situated at a little less than a body width before the posterior end. A pair of dorso-lateral preloacal papillae located at about 0.5 body-widths before the tail tip. Dorsal cuticle of posterior end thickened from level of the latter pair of papillae to the tail tip. There is a cuticular bursa-like structure in the tail end, almost reaching the level of the tail tip.

Differential diagnosis. *L. longior* sp. n. differs from *L. longicollis*, from Brazil, by having females with the body larger (3.500–4.525 vs. 2.98–3.64) and the tail comparatively longer ($c = 6.72\text{--}8.54$ vs. $9.03\text{--}9.33$). The vulva is slightly displaced forward in the present species ($V\% = 50.00\text{--}58.01$ vs. $57.72\text{--}61.81$). The tail of the male of *L. longior* sp. n. is comparatively shorter ($c = 43.33\text{--}51.27$: $30.66\text{--}32.83$), and has the tip unreflexed. In *L. longior* the nerve ring is displaced to the first half of the procorpus in both sexes, instead of *L. longicollis* sp. n. where this structure is situated in the midpoint of the procorpus.

L. longior sp. n. differs from *L. similis* by lacking wide and marked annule in the cervical cuticle of females. Its body is longer (total length = 3.500–4.525 vs. 2.675–3.075) and the first cephalic annule is more inflated. The ovary is reflexed at about two body widths beyond the excretory pore, more posterior than *L. similis* where it is reflexed at little less than a body width beyond the excretory pore. Males of the new species differ from *L. similis* by having the cervical cuticle markedly annulated instead of *L. similis* that presents the cervical cuticle smooth.

L. longior sp. n. is distinguished from *L. alius* García & Coy, 1994 (from Cuba) by having the isthmus shorter and not bent, instead of the isthmus very long and bent of the latter species. From *L. semialata* Hunt, 1981, from Saint Lucia, West Indies, differs by the lateral alae that commence before the level of the vulva, the body longer (total length = 3.500–4.525 vs. 2.26–2.63) and the oesophagus comparatively shorter ($b = 4.49\text{--}5.45$ vs. $3.30\text{--}3.70$). The lateral alae of *L. semialata* start at about the middle of the distance between the vulva and the anus.

L. longior sp. n. can be differentiated from *L. elieri* García, Ventosa & Morffe, 2009 (from Cuba) by having an inflated first cephalic annule and by lacking of wide annule in the cervical region. *L. elieri* has a not inflated first cephalic annule and the first third of the cervical cuticle widely annulated.

Etymology. Named after the Latin *longior*: the largest, being this species the largest in the genus.

Type host. *Passalus pertyi* (Coleoptera, Passalidae)

Other host. *P. interstitialis* Escholtz, 1829 (Coleoptera, Passalidae)

Site. Gut caeca

Type locality. La Jaula, San José de Las Lajas, La Habana Province, Cuba.

Other records (formerly referred as *L. zayasi*). El Salón, Sierra del Rosario, Pinar del Río Province, Cuba (Coy et al. 1993); El Mulo, Sierra del Rosario, Pinar del Río Province, Cuba (García et al. 2009a); La Melba, Nipe-Sagua-Baracoa, Holguín Province, Cuba (García et al. 2009b); La Platica, Sierra Maestra, Granma Province, Cuba (Morffe et al. 2009).

Remarks. All the records of females of *L. longior* sp. n. were formerly referred as *L. zayasi* and measures of most of them have been published. In order to compare the meristic features between localities a chart with such variables is offered (Table 1).

***Longior similis* Morffe, García & Ventosa, 2009**

Figure 4 A–D; Figure 5 G–H

Material examined. ♂ voucher; Cuba, La Habana Province, Jaruco, Escaleras de Jaruco; in *Passalus interstitialis*; 16.III.2008; E. Fonseca, J. Morffe, F. Alvarez coll.; CZACC 11.4630.

Measurements. Male (n = 1) a = 15.66, b = 4.15, c = 54.80, total length = 1.370, maximum body width = 0.088, stoma length = 0.045, procorpus length = 0.260, isthmus length = 0.028, diameter of basal bulb = 0.040, total length of oesophagus = 0.330, nerve ring to anterior end = 0.145, excretory pore to anterior end = 0.500, cloaca to posterior end = 0.025, distance from the mammiform papillae to the posterior end = 0.153, distance from the dorso-lateral papillae to the posterior end = 0.068.

Description. Male body comparatively slender, shorter than female. Cuticle thin, finely annulated. Sub-cuticular longitudinal striae present. Head short, rounded, set-off from body by a single groove, papillae not observed. First cephalic annule not differentiated. Stoma as in the female. Oesophagus with its second half slender than first, hardly set-off from the isthmus. Basal bulb rounded, valve plate developed. Intestine simple, slender, its fore region dilated. Anus inconspicuous. Nerve ring encircling procorpus at about 40% of its length. Excretory pore located at about 1.5 body widths posterior to basal bulb. Testis single, full of spermatids, commencing just behind excretory pore, its second third slightly inflated. Spicule absent. A large, mid-ventral, precloacal, mammiform papilla situated at about 1.5 body widths before the tail tip. A pair of dorso-lateral, precloacal papillae at little less than a body width before the tail tip. Dorsal cuticle of the posterior end thickened from the level of the pair of papillae

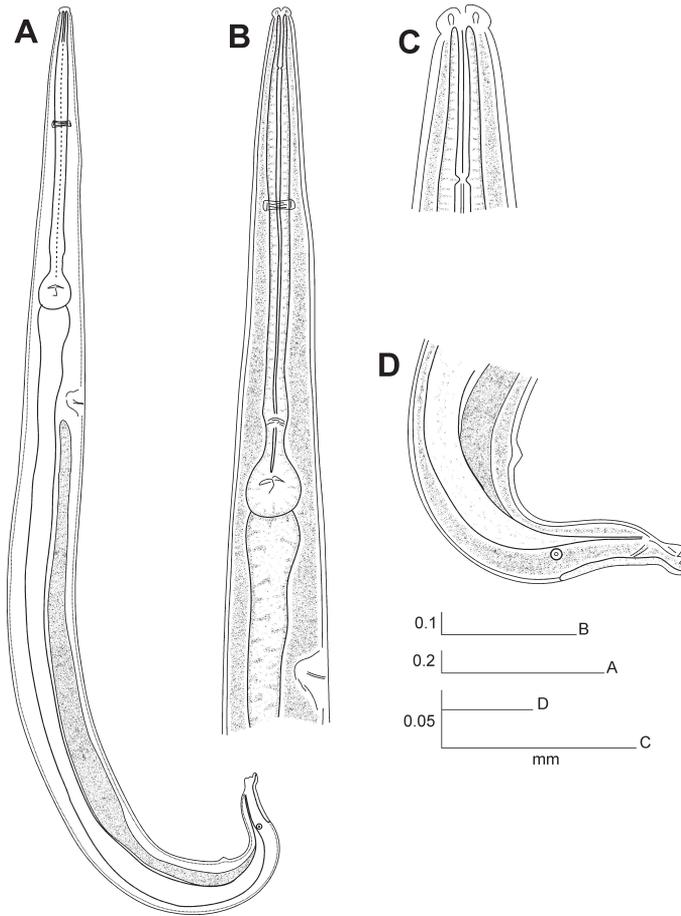


Figure 4. *Longior similis* Morffe, García & Ventosa, 2009 (male). **A** Entire nematode, lateral view **B** Esophageal region, lateral view **C** Cephalic end **D** Tail, lateral view.

to almost the tail tip. Ventral cuticle expanded, forming a bursa-like structure with the distal end terminating before the tail tip. Tail short, conical, ending in a rounded tip. Posterior end slightly reflexed toward dorsal region.

Differential diagnosis (only based on males). The male of *L. similis* resembles *L. longicollis* mainly by the form of the tail end but differs by having the nerve ring displaced to the first half of the procorpus, at about the 40% of its length (in *L. longicollis* the nerve ring is at the middle of procorpus). The procorpus of *L. longicollis* is cylindrical in all its extension, while in *L. similis* it is slightly wider in its first half. The tail is also comparatively shorter in the Cuban species ($c = 54.8: 30.66\text{--}32.83$).

From *L. longior* sp. n., the other species where the male is known differs by having the cervical cuticle without visible annule and the tail tip reflexed toward the back. *L. longior* sp. n. has the cervical cuticle annulated up to about the first third of the procorpus and the tail tip unreflexed. Also, *L. similis* has a comparatively shorter oesophagus ($b = 4.15$ vs. $3.13\text{--}3.63$).

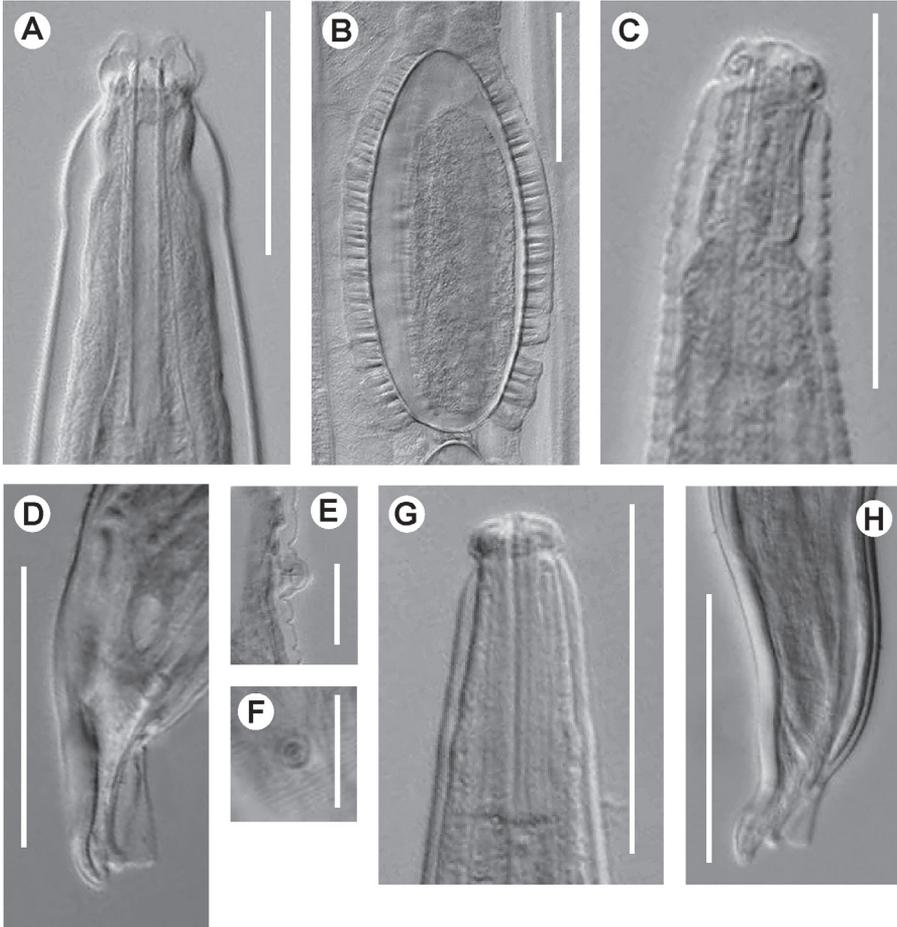


Figure 5. *Longior longior* Morffe & García sp. n. (female). **A** Cephalic end **B** Egg. *Longior longior* Morffe & García sp. n. (male) **C** Cephalic end **D** Tail, lateral view **E** Pre-cloacal median mammiform papilla, lateral view **F** Post-cloacal dorso-lateral papilla. *Longior similis* Morffe, García & Ventosa, 2009 (male) **G** Cephalic end **H** Tail, lateral view. Scale bars: A, B, C, D, G, H. 0.05 mm. E, F. 0.020 mm.

Host. *Passalus interstitialis* Escholtz, 1829 (Coleoptera, Passalidae).

Site. Gut caeca.

Locality. Escaleras de Jaruco, Jaruco, La Habana Province, Cuba.

Key to the species of *Longior* from Cuba

Note: males are described only in two of the five Cuban *Longior* species. Due to this, the present key was made only on the basis of females.

- 1 Isthmus long and bent *L. alius* Coy & García, 1994
- Isthmus short and not bent 2

Table 1. Comparative measurements of the females and males of *Longior longior* Morffe & García sp. n. from its type locality La Jaula, San José de las Lajas, La Habana Province, Cuba and the records from El Salón, Sierra del Rosario, Pinar del Río Province, Cuba; La Melba, Nipe-Sagua-Baracoa, Holguín Province, Cuba and La Platica, Sierra Maestra, Granma Province, Cuba. Measurements are given in millimetres.

Host	<i>Pussalus pertyi</i>	<i>P. interstitialis</i>	<i>P. pertyi</i>	<i>P. pertyi</i>
Locality	La Jaula, La Habana Province (type locality) (n = 12)	El Salón, Pinar del Río Province (n = 3)	La Melba, Holguín Province (n = 6)	La Platica, Granma Province (n = 6)
Female measurements				
Total length	3.500–4.525	3.580–3.890	3.390–4.090	3.620–4.150
Body width	0.138–0.173	0.150–0.218	0.150–0.170	0.100–0.140
Stoma length	0.073–0.085	0.060–0.075	0.055–0.060	0.058–0.070
Procorpus length	0.630–0.720	0.650–0.660	0.640–0.740	0.600–0.690
Isthmus length	0.040–0.058	0.050–0.058	0.050–0.063	0.048–0.060
Diameter basal bulb	0.065–0.078	0.070–0.073	0.073–0.080	0.060–0.073
Esophagus length	0.760–0.860	0.780–0.800	0.770–0.950	0.730–0.820
Nerve ring-head end	0.230–0.250	0.225–0.235	0.225–0.250	0.235–0.250
Excretory pore-head end	0.970–1.125	0.990–1.05	0.950–1.040	-
Vulva-tail end	1.600–1.925	1.720–2.020	1.720–2.040	2,000
Anus-tail end	0.470–0.590	0.480–0.560	0.480–0.610	0.600–0.640
Eggs	0.110–0.143×0.050–0.060	0.128–0.140×0.045–0.060	0.135–0.153×0.050–0.070	0.125–0.140×0.050–0.058
a	23.61–28.28	17.20–23.94	21.19–27.27	29.36–36.20
b	4.49–5.45	4.79–4.86	4.27–5.13	4.83–5.41
c	6.24–8.54	6.68–7.63	6.70–7.90	6.03–6.92
V%	49.73–58.01	45.99–52.19	45.65–55.67	49,24
Male measurements				
Total length	1.220–1.510	-	1.170–1.680	-
Body width	0.095–0.120	-	0.085–0.120	-
Stoma length	0.038–0.048	-	0.038–0.040	-
Procorpus length	0.300–0.340	-	0.283–0.320	-

Host	<i>Pussalus pertyi</i>	<i>P. interstitialis</i>	<i>P. pertyi</i>	<i>P. pertyi</i>
Locality	La Jaula, La Habana Province (type locality) (n = 12)	El Salón, Pinar del Río Province (n = 3)	La Melba, Holguín Province (n = 6)	La Platíca, Granma Province (n = 6)
Isthmus length	0.030–0.033	-	0.028–0.038	-
Diameter basal bulb	0.045–0.048	-	0.050–0.063	-
Esophagus length	0.390–0.420	-	0.378–0.400	-
Nerve ring-head end	0.150–0.168	-	0.133–0.158	-
Excretory pore-head end	0.480–0.560	-	0.430–0.490	-
Cloaca-tail end	0.028–0.030	-	0.028–0.038	-
Median papilla-tail end	0.115–0.133	-	0.128–0.148	-
Dorso-lateral papilla-tail end	0.055–0.070	-	0.058–0.065	-
a	11.56–15.68	-	11.55–14.00	-
b	3.13–3.63	-	3.10–4.20	-
c	43.33–51.27	-	33.87–61.09	-

- 2 First cephalic annule not inflated.....***L. elieri* García, Ventosa & Morffe, 2009**
 – First cephalic annule more or less inflated**3**
 3 Cervical cuticle without wide annule, ovary reflected at about two body widths beyond the excretory pore..... ***L. longior* sp. n. Morffe & García**
 – Cervical cuticle with wide annule, ovary reflected at little less than a body width beyond the excretory pore.....***L. similis* Morffe, García & Ventosa, 2009**

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On the identity of the fossil aquatic beetles from the Tertiary localities in the southern part of the Upper Rhine Graben (Coleoptera, Hydrophilidae, Dytiscidae)

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Abstract

This study focuses on the fossil beetles assigned previously to the family Hydrophilidae described from the localities in the southern part of the Upper Rhine Graben: Brunstatt (France, Alsace) and Kleinkems (Germany, Baden-Württemberg) (both dated ca. to Eocene-Oligocene boundary, 34 Ma). The identity of *Escheria convexa* Förster, 1891 is fixed by the designation of its neotype, the species is redescribed, illustrated, transferred from the hydrophilid genus *Hydrobius* Leach, 1815 to the genus *Copelatus* Erichson, 1832 (Coleoptera: Adepaga: Dytiscidae) and compared with other fossil representatives of *Copelatus*. The identity of the remaining three species, *Hydrobius crassipunctatus* (Förster, 1891), *H. dimidiatus* (Förster, 1891) and *H. punctulatus* (Förster, 1891), is briefly evaluated on the basis of the original descriptions and illustrations only, because their types were lost or destroyed during World War II; all three species are removed from the fossil record of the Hydrophiloidea and placed into Polyphaga *incertae sedis*. The geology and stratigraphy of Brunstatt and Kleinkems are discussed briefly.

Keywords

Dytiscidae, Hydrophilidae, *Copelatus*, *Hydrobius*, fossils, Eocene-Oligocene boundary, Brunstatt, Kleinkems, neotype designation

Introduction

In his study of the insects from the Tertiary outcrop of Brunstatt (Alsace, France), Förster (1891) described four species of the family Hydrophilidae, assigning all of them to the fossil genus *Escheria* Heer, 1847. Later, Théobald (1937) recorded two of these species from the locality of Kleinkems (spelled incorrectly as ‘Kleinkembs’ by the latter author), which is situated 16 km from Brunstatt and is believed to be of the same age and origin (see below for details). Based on the preserved characters, Théobald (1937) transferred all four of Förster’s (1891) species to the recent hydrophilid genus *Hydrobius* Leach, 1815. After 1937, the specimens were never re-examined and their identity remained unclear. Unfortunately, the Förster collection was either lost or destroyed during World War II (see Material and methods for details), which further complicates research.

For this study, we have re-examined the specimens from the locality of Kleinkems studied previously by Théobald (1937). In order to resolve the complicated situation concerning the four hydrophilid taxa, a neotype is designated for *Escheria convexa* Förster, 1891 and its taxonomic position is thus illuminated. The remaining fossils are excluded from the Hydrophiloidea due to the absence of any hydrophiloid apomorphy. Hence, our study supports the opinion by Fikáček et al. (2010) that various middle-sized Tertiary beetles were assigned into the hydrophilid genus *Hydrobius* irrespectively to their real taxonomic position.

Geology and stratigraphy of the fossil sites

The Tertiary outcrops of Brunstatt and Kleinkems were located in the south-west of central Europe and no longer exist today. Brunstatt was situated south of the city of Mulhouse in France (47°41'N 7°31'E); Kleinkems was situated in Germany (47°43'N 7°19'E) northwest of the city of Basel (Switzerland), about 16 km from Brunstatt. Several hundred fossils in total were collected at these localities (Wappler et al. 2005).

According to the reconstruction of the sedimentation history, the limnic sediments of Brunstatt and Kleinkems were deposited on the shore of a very large shallow saline lake (with an area of several hundred square kilometres) with episodic intrusion of fresh water (Lutz 1997). The landscape in this area originated during the formation of the Upper Rhine Graben (URG) which forms the central part of the Cenozoic Central European Rift System. Increased rifting during the late Middle Eocene to Early Oligocene led to the formation of the Mulhouse Potash Salt Basin (also called Potash Basin or Potassic Basin) which is located in the narrowest part of the graben and flanked by the highest of the Vosges Mountains and Black Forest Mountains (Hinsken et al.

2007). A detailed overview of the development of the URG and the Potash Basin is provided by Berger et al. (2005 a, b) and Hinsken et al. (2007).

Lutz (1997) and Mai (1995) assign the age of Brunstatt and Kleinkems to the Lower Oligocene, but Mai (1995) also allocated Brunstatt to the Mammal Reference Level MP20 which corresponds to the Priabonian (37.2–33.9 Ma) in the latest part of the Eocene. Thus, the stratigraphical position of Brunstatt and Kleinkems seems to be close to the Eocene-Oligocene boundary, as is the case of the similar fossil site of Altkirch in France (Wappler et al. 2005). According to Mai (1995) [based on Lakowitz (1895)], the palaeoclimate of Brunstatt was characterised by an average annual temperature of 18°C and abundant rainfall.

It seems very likely that the sediments of Brunstatt and nearby Kleinkems are nearly identical in age and genesis. Lutz (1995) even combined both localities in his study reconstructing their paleoenvironment, and according to Mai (1995), plant fossils from Brunstatt and Kleinkems are both deposited in the same layers of laminated clay ('plattiger Steinmergel').

Material and methods

Only the fossils from the locality of Kleinkems mentioned by Théobald (1937) deposited currently in the Naturhistorisches Museum in Basel, Switzerland (NHMB) were studied for this paper. The material originally examined by Förster (1891) was deposited at the 'Service de la Carte Géologique de Strasbourg' (Théobald 1937) and is considered to have been lost or destroyed during World War II on the basis of information we received from Jean Claude Horrenberger (École et Observatoire de la Terre, Strasbourg, France) as well as two letters sent to Volker Püthz, a specialist on Staphylinidae, by Marguerite Wolf (Université Louis Pasteur, Institut de Géologie, Strasbourg, France) in July 1967 and September 1971 (Püthz, pers. comm. 2010). The identity of species missing from the Kleinkems material is only discussed briefly on the basis of the original drawings by Förster (1891).

Fossils were examined using the Olympus SZ61 binocular microscope. Photographs were taken using the Canon MP-E 65 mm macro lens attached to the Canon EOS 550D camera. Drawings were traced from photographs. Abbreviations used in descriptions are: **EL** – length of the elytron; **TL** – total length, a single measurement of length from front of head to apex of elytra; **TL-h** – total length minus head length, length of body from anterior margin of pronotum to apex of elytra; **TW** – maximum width of body measured at right angles to TL.

Fossils whose family placement and hence also generic placement remains unclear are cited using the original combination of the name, placing the respective genus name in quotation marks.

Taxonomy

Coleoptera: Adephaga

Family Dytiscidae

Copelatus convexus (Förster, 1891) comb. n.

Figs 1–4

Escheria convexa Förster 1891: 359, plate XI, Figs 9a,b (original description from Brunstatt); Handlirsch 1908: 767 (catalogue).

Hydrobius convexus: Théobald 1937: 168, plate XII, Fig. 29 (transferred to *Hydrobius*, recorded from Kleinkems); Hansen (1999: 319, catalogue).

WWW site on Wikispecies. http://species.wikimedia.org/wiki/Copelatus_convexus

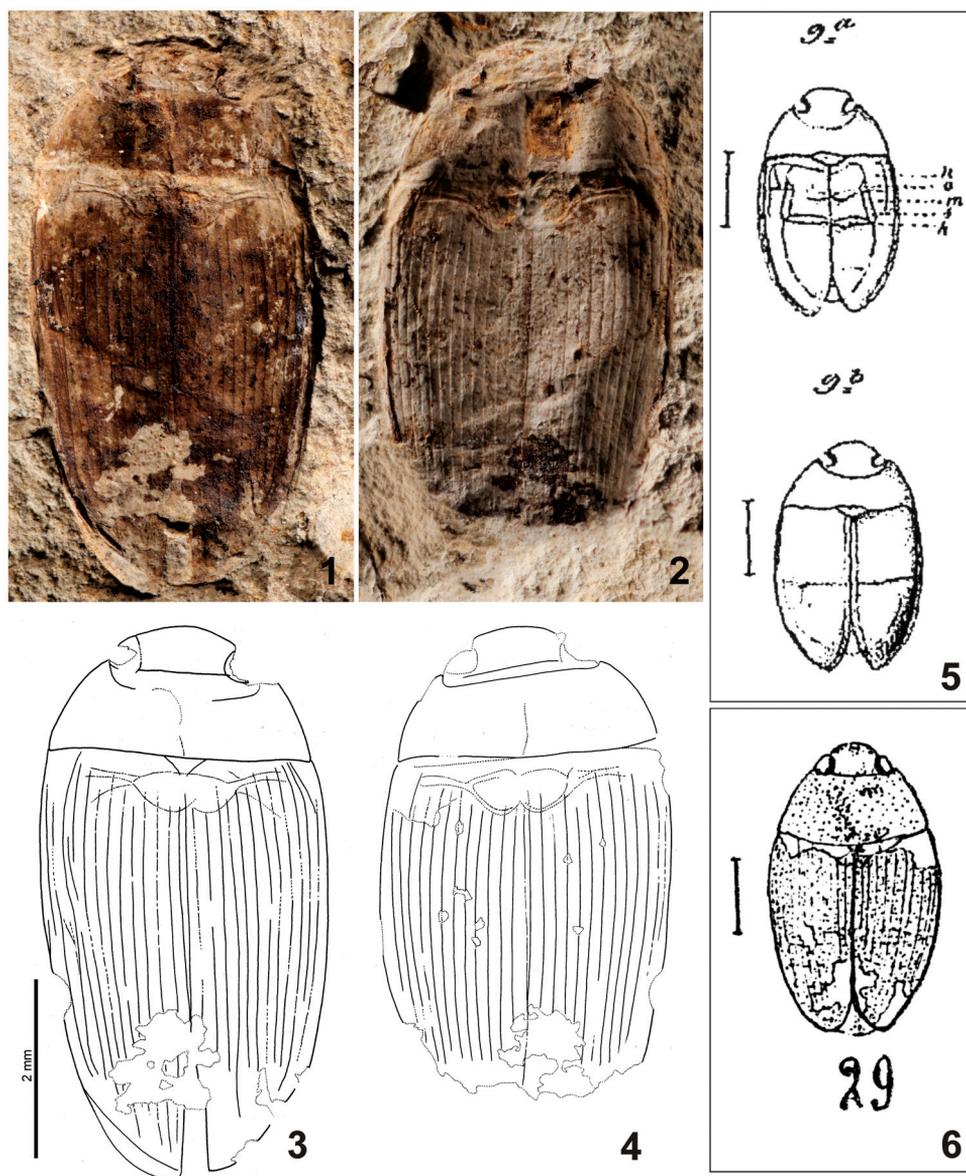
Material examined. Neotype, by present designation (NHMB): R91 (imprint) + R74 (counter-imprint) from the locality of Kleinkems (SW Germany, ca. Eocene-Oligocene boundary): fossil of the whole beetle in dorsal view, head, pronotum and elytra almost completely preserved; appendages missing.

Redescription. Body oblong-oval, broadest in basal third of elytra. Head relatively broad; compound eyes large, not exceeding body outline; clypeus rounded. Pronotum broadest between posterior angles, lateral margins regularly, moderately curved. Mesoscutellar shield well preserved, broadly triangular. Base of elytra as broad as pronotal base; lateral margins of elytra moderately curved. Only mesocoxae, part of metathoracic anepisternum, and probably part of apical abdominal ventrite perceptible from ventral part of body (Figs 1–4).

Surface sculpture. Pronotum with distinct longitudinal median impression, and poorly perceptible short longitudinal striolae on disc. Elytra with 12 moderately impressed longitudinal striae.

Measurements. TL: 6.3 mm, TL-h: 5.6 mm, TW: 3.2 mm. EL: 5.2 mm.

Notes on the type material. The neotype corresponds well with the original description and drawings by Förster (1891) in the following characters: (i) general body shape; (ii) shape of the pronotum with projecting anterior angles; (iii) elytra with large number of longitudinal striae [preserved only in posterior portion of elytra in the holotype and their number is therefore estimated by Förster (1891) to be at least 10; 12 striae are present in the specimen from Kleinkems]; (iv) shape and proportion of the scutellar shield [much wider than long]; (v) body size [TL = 6.5 mm, EL = 4.3 mm, TW = 3.8 mm for the specimen from Brunstatt according to Förster (1891)]. The body proportions differ slightly between both specimens (the specimen from Brunstatt is relatively wider), but this may easily have been caused by deformation during the fossilization process or by the inaccuracy of the drawings by Förster (1891) which is quite usual for historic authors (e.g., compare the drawings by Théobald (1937) in Figs 6 and 12 with the actual appearance of the respective



Figures 1–6. *Copelatus convexus* (Förster, 1891). **1–4** neotype (**1, 3** NHMB R91; **2, 4** NHMB R74) **5** original illustrations of the holotype by Förster (1891) **6** drawing of the specimen NHMB R91 by Théobald (1937).

fossils). Moreover, Förster (1891) mentioned that his fossil resembles the dytiscid genus *Agabus* in most characters and did not assign it to the Dytiscidae merely because of its ventral morphology which was reconstructed by him as resembling that of *Polyphaga* (Fig. 5). It seems that Théobald (1937) examined Förster's types as he mentioned certain details which are absent in Förster's (1891) original publication,

and his opinion about the conspecificity therefore also has to be considered as a strong argument.

The reasons provided above together with the same age, geological origin and geographical proximity of both outcrops (Brunnstatt and Kleinkems) provide strong support for the conspecificity of both specimens mentioned by Théobald (1937). As the specimen from Brunstatt (i.e., the holotype) is lost, we consider it adequate to designate the specimen from Kleinkems as the neotype.

Generic attribution. The preserved characters of the ventral morphology, i.e. the narrow metathoracic anepisternum arising from the median coxal cavity and the anepisterno-metaventral suture directed lateroposteriad correspond closely with the ventral morphology of the Dytiscidae (see, e.g., Fig. 7.6.1 in Balke (2005)). The hydrodynamic body shape, large eyes, broad mesoscutellar shield, medium body size and distinct elytral striae enable us to classify the specimen without any doubt as belonging to the genus *Copelatus* Erichson, 1832 of the family Dytiscidae.

Copelatus is currently pantropical in its distribution and contains more than 400 described species (Nilsson 2001). Most species of *Copelatus* are characterised by longitudinal elytral striae whose number has been used to group the species into species groups (Sharp 1882); only a few species have smooth elytra (e.g., Hájek et al. 2010). Although the presence and number of elytral striae provides only limited evidence of phylogeny (Balke et al. 2004), the species groups delimited by number and position of elytral striae are frequently used as a tool for better orientation within the genus (e.g., Guignot 1961; Guéorguiev 1968; Nilsson et al. 1997). The European species previously classified in *Copelatus* have elytra without striae and have been transferred to the genus *Liopterus* Dejean, 1833 by Balke et al. (2004); they are not closely related to the fossil dealt with in this study.

Comparison with other *Copelatus* species. Altogether five species of fossil *Copelatus* species are known: *C. aphroditae* Balke, 2003 from Baltic amber (Eocene), *C. predaveterus* Miller, 2003 from Dominican amber (Miocene) (Miller and Balke 2003), and *C. fossilis* Říha, 1974, *C. ponomarenkoi* Říha, 1974 and *C. stavropolitanus* Říha, 1974 from the Miocene deposit of Stavropol (Říha 1974). The differences between all known species are summarized in Table 1.

Copelatus convexus differs from all known fossil and extant species of the genus in the presence of 12 longitudinal striae on each elytron. Sharp (1882) erected a group characterized by 12 discal striae (group 7) for a single species *Copelatus interruptus* Sharp, 1882 which is, however, currently classified in the genus *Exocelina* Broun, 1886 (Nilsson 2007). In contrast to the fossil *C. convexus*, this recent species has elytra with numerous short striolae rather than 'true' striae, see, e.g. Wewalka et al. (2010). Therefore, *C. convexus* might be provisionally classified in a separate *C. convexus*-group. However, it is necessary to point out that the counting of the precise number of lateral elytral striae is problematic in compressed fossils as the imprint of the submarginal stria may coincide with the lateral margin of the body or with the epipleuron. Therefore, we cannot rule out that a short submarginal stria was present in *C. convexus* although it is not perceptible in the fossil. In this case, *C. convexus* would belong to the *C. simoni*-group sensu Nilsson (2001).

Table 1. List of fossil species of the genus *Copelatus*, their basic morphological characteristics and their age. Body measurements in italics are estimated from usual TL/EL ratio in *Copelatus*.

Species	Period	Body length	Number of elytral striae	Species group (Nilsson 2001; Miller and Balke 2003)
<i>C. aphroditae</i>	Eocene	5.0 mm	19 discal	<i>C. aphroditae</i> -group
<i>C. convexus</i>	Eocene-Oligocene boundary	6.3–6.5 mm	12 discal	<i>C. convexus</i> -group
<i>C. fossilis</i>	Miocene	<i>6.1–6.5 mm</i>	10 discal + 1 submarginal	<i>C. erichsoni</i> -group
<i>C. ponomarenkoi</i>	Miocene	5.5–5.6 mm	6 discal + 1 submarginal	<i>C. irinus</i> -group
<i>C. predaveterus</i>	Miocene	3.8–4.4 mm	11 discal + 1 submarginal	<i>C. trilobatus</i> -group
<i>C. stavropolitanus</i>	Miocene	5.1 mm	11 discal	<i>C. nigrolineatus</i> -group

Coleoptera: Polyphaga

Family *incertae sedis*

'*Escheria*' *crassipunctata* Förster, 1891

Fig. 7

Escheria crassipunctata Förster 1891: 364, plate XI, Fig. 11 (original description from Brunstatt); Handlirsch 1908: 767 (catalogue).

Hydrobius crassipunctatus: Théobald 1937: 169, plate II, Fig. 28 (transferred to *Hydrobius*, referred from Kleinkems); Hansen 1999: 319 (catalogue).

Taxonomic notes. As in the case of *Copelatus convexus*, Théobald (1937) transferred *Escheria crassipunctata* to the hydrophilid genus *Hydrobius* and assigned fossil specimen no. R 707 from the locality of Kleinkems (deposited in NHMB) to this species. We have examined the specimen from Kleinkems for this study (Figs 10–11) but we cannot confirm that it is conspecific with *Escheria crassipunctata* for the following reasons: (i) the elytra are slightly constricted sub-basally in the specimen from Kleinkems, but evenly rounded laterally in *E. crassipunctata*; (ii) the body outline is distinctly interrupted between the pronotum and the elytra, but it is uninterrupted in *E. crassipunctata*, (iii) eyes are large and globular in the specimen from Kleinkems, but relatively small in *E. crassipunctata*. A more detailed comparison is impossible as the holotype of *E. crassipunctata* is lost and was moreover preserved in dorsal view based on the drawing by Förster (1891), whereas the specimen from Kleinkems is preserved in ventral view.

Based on the original drawing by Förster (1891), *Escheria crassipunctata* does not bear any synapomorphy of the Hydrophiloidea. For this reason, the species is removed from the fossil record of the Hydrophiloidea and is placed in Polyphaga *incertae sedis*.

Specimen no. R707 from Kleinkems does not bear any synapomorphy of the Hydrophiloidea, and moreover bears a combination of characters which excludes its assignment to the Hydrophiloidea: (i) prosternal process wide, (ii) mesocoxal cavities rather wide apart, and (iii) eyes large and globular. The preserved characters of this specimen do not allow an unambiguous family assignment (see Lawrence et al. 1999).

'*Escheria*' *dimidiata* Förster, 1891

Fig. 8

Escheria dimidiata Förster 1891: 363, plate XI, Figs 10a,b (original description from Brunstatt); Handlirsch 1908: 767 (catalogue)

Hydrobius dimidiatus: Théobald 1937: 169 (transferred to *Hydrobius*); Hansen 1999: 319 (catalogue).

Taxonomic note. Based on the original drawing by Förster (1891), the morphology of *Escheria dimidiata* agrees with that of Hydrophilidae: Hydrophilinae in many aspects: (i) mesocoxal cavities transverse, narrowly isolated from each other, (ii) metanepisternum rather narrow, (iii) epipleuron narrow but reaching elytral apex, and (iv) elytron with 10 longitudinal punctural series. None of these characters or their combination is, however, unique for the Hydrophiloidea and may be found in other beetle families as well (see e.g. Lawrence et al. 1999). Moreover, the medium body size (EL: 9 mm according to Förster (1891)) would indicate that the fossil should belong to the subtribes Hydrobiusina or Hydrophilina, whose representatives are characterized by a relatively large and well developed triangular mesoscutellar shield; in contrast, the scutellar shield is very small or reduced in *Escheria dimidiata*. Moreover, the re-examination of the fossil is impossible as the holotype was lost or destroyed. For all these reasons, *Escheria dimidiata* is removed from the fossil record of the Hydrophiloidea and is placed in *Polyphaga incertae sedis*.

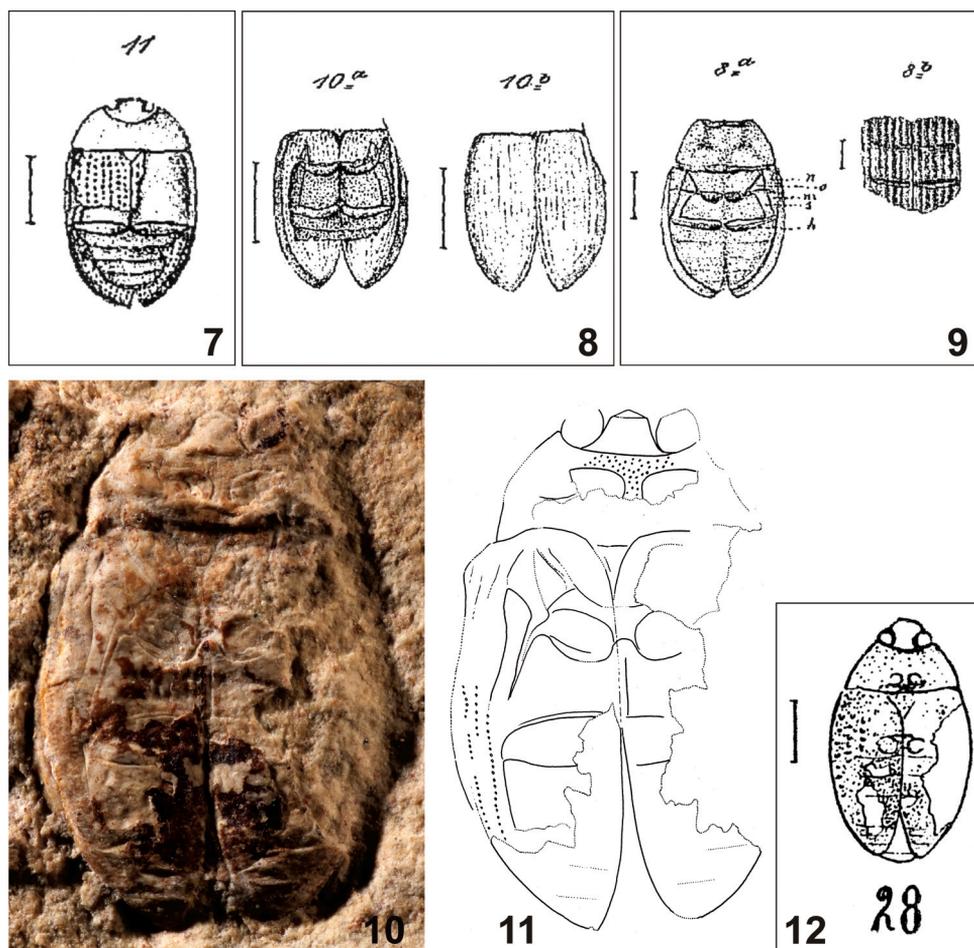
'*Escheria*' *punctulata* Förster, 1891

Fig. 9

Escheria punctulata Förster 1891: 361; plate XI, Figs 8a,b (original description from Brunstatt); Handlirsch 1908: 767 (catalogue).

Hydrobius punctulatus: Théobald 1937: 169 (transferred to *Hydrobius*); Hansen 1999: 319 (catalogue).

Taxonomic note. Based on the drawing by Förster (1891), the ventral morphology of this species agrees with that of Hydrophilidae: Hydrophilinae in many characters: (i) mesocoxae transverse and very narrowly separated, (ii) mesepimeron well separated, triangular, (iii) metanepisternum rather narrow; (iv) abdomen with five ventrites.



Figures 7–12. 7 '*Escheria*' *crassipunctata* Förster, 1891, original illustration of the holotype 8 '*Escheria*' *dimidiata* Förster, 1891, original illustration of the holotype 9 '*Escheria*' *punctulata* Förster, 1891, original illustration of the holotype 10–12 specimen NHMB R707 (10 photograph 11 drawing 12 original drawing by Théobald (1937)).

However, none of these characters or their combination is unique for the Hydrophiloidea and may be found in other beetle families as well (see Lawrence et al. 1999). Moreover, two characters illustrated on the drawing and/or mentioned in the original description exclude the placement of *E. punctulata* in the Hydrophiloidea: (i) elytra bear only 6 deeply impressed striae [9–11 striae are present in all Hydrophiloidea with striate elytra, only rarely is the number of series higher but in such cases they are never impressed to striae]; (ii) mesoventrite fused with mesepisternal (i.e. not separated from them by sutures) [in Hydrophiloidea, the mesoventrite is fused to mesepisterna only in derived groups of the Sphaeridiinae which are characterized by a highly elevated median portion of the mesoventrite; the elevated median elevation is missing from the fossil]. For these reasons, *Escheria punctulata* is removed from the fossil record of

the Hydrophiloidea and is placed into Polyphaga *incertae sedis*; its family placement remains unclear.

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Redefinition of the genus *Allonychiurus* Yoshii, 1995 (Collembola, Onychiuridae) with description of a new species from China

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Abstract

In this paper, we describe a new species of the genus *Allonychiurus* Yoshii, 1995, characterized by the presence of an apical swelling on the fourth antennal segment as well as a combination of chaetotaxic and pseudocellar characters. The genus *Allonychiurus* is redefined. Four of its species are considered as *incertae sedis*: *A. michelbacheri* (Bagnall, 1948), *A. spinosus* (Bagnall, 1949), *A. caprariae* (Dallai, 1969) and *A. sensitivus* (Handschin, 1928). The three species *A. borensis* (Beruete, Arbea & Jordana, 1994), *A. sensilatus* (Thibaud & Massoud, 1979) and *A. vandeli* (Cassagnau, 1960) are removed from *Allonychiurus* and placed in *Micronychiurus* Bagnall, 1949, *Thalassaphorura* Bagnall, 1949 and *Spinonychiurus* Weiner, 1996 respectively. The synonymy of *Thibaudichiurus* Weiner, 1996 with *Allonychiurus* is rejected and *A. foliatus* (Rusek, 1967) and *A. mariangeae* (Thibaud & Lee, 1994) are re-allocated to *Thibaudichiurus*. List and identification key to the world species of the genus are given.

Keywords

Collembola, *Allonychiurus*, *Micronychiurus*, *Spinonychiurus*, *Thalassaphorura*, *Thibaudichiurus*, chaetotaxy, taxonomy, China

Introduction

The genus *Allonychiurus* Yoshii, 1995 includes 23 species according to Bellinger et al. (2010). They are distributed in Asia, Europe and America. However, as stressed by Sun et al. (2009), generic assignment of most of these species is disputable. To improve this confusing situation, we re-examined all available taxonomic descriptions and type specimens of several species. We redefined the genus accordingly. As a result, five species are translocated to other genera and four are considered as *incertae sedis*. A new species discovered in China, *Allonychiurus antennalis* sp. n., is described.

Redefinition of *Allonychiurus* Yoshii, 1995

Type-species: *Onychiurus flavescens* Kinoshita, 1916: p. 458

Diagnosis

Onychiurinae Thalassaphorurini. Postantennal organ oval, with numerous compound vesicles perpendicular to the long axis; antennal basis rather well delimited. Clubs of antenna III organ smooth or granulated. No invaginated apical bulb on Ant. IV. Labral chaetae formula 4/3,4,2; labium of AC type (*sensu* Fjellberg 1999); chaeta d_0 present on head. No multiplication of dorsal pseudocelli; 3 (rarely 2) anterior pseudocelli on head, located inside the area antennalis; Th. I tergite usually with 1 or 2 pseudocelli per half-tergite (rarely absent). Abd. III sternite not subdivided into two subsegments; 4 (rarely 2, 3 or 5) pseudocelli per half-tergite on Abd. IV; 3 (rarely 2 or 4) pseudocelli per half-tergite on Abd. V (2–3 postero-internal and 0–1 postero-lateral). Abd. VI with 1 or 2 uneven axial chaetae (a_0 or p_0 , or both); anal spines present. Tibiotarsus with 9 or 11 chaetae in the distal whorl, clavate tenent hairs absent. Furcal rudiment as finely granulated area with 4 posterior minute dental chaetae regularly arranged in 2 rows. Two or three rows of manubrial chaetae posteriorly to the 4 dental chaetae.

Discussion

The genus *Allonychiurus* is very similar to *Onychiurus* Gervais, 1841 differing from it by a furcal area with 4 small posterior chaetae arranged in two rows versus arranged in one row. It is also the only difference between Thalassaphorurini and Onychiurini. The attempt to restrict the genus *Allonychiurus* to species with 11 distal chaetae on tibiotarsus (Sun et al. 2009) versus 9 in *Onychiurus* cannot be retained on current available evidence, as discussed below.

The problem of species assigned to *Allonychiurus*

The genus *Allonychiurus* was described by Yoshii (1995) as a subgenus of *Onychiurus* Gervais, 1841, to include species of the *flavescens*-group of *Paronychiurus* previously recognized by Weiner (1989). This last author upgraded it to genus level in 1996, characterizing it mostly on the basis of its furcal area similar to that of *Thalassaphorura* Bagnall, 1949, and its post-antennal organ with several compound vesicles. Recently, Sun et al. (2009) restricted the definition of *Allonychiurus* to species with 11 chaetae in the distal whorl of tibiotarsus (a character erroneously stated as being drawn from the Weiner 1996 diagnosis); according to this conception, only four species (out of the 24 species listed at this time on the Janssens and Christiansen website at <http://www.collembola.org>) could be confirmed as *Allonychiurus* (*flavescens*, *jongaksanensis*, *shanghaiensis* and *shinbugensis*), in addition to *A. megasomus* that Sun et al. (2009) described in their paper. The authors also reallocated tentatively two species, *A. edinensis* (Bagnall, 1935) and *A. subedinensis* (Arbea & Jordana, 1985) to the genus *Spinonychiurus* Weiner, 1996, a move formally confirmed by Kaprus' and Tsalan (2009); they stressed that 12 species did not match the genus as they defined it, nine because they had fewer than 11 chaetae in the distal whorl of tibiotarsus, two because they had smooth clubs in antenna III organ, and one because it had simple PAO vesicles. The remaining 6 species were not documented for distal tibiotarsal chaetae, and their status was considered as doubtful. In short, 80% of species assigned to *Allonychiurus* did not match the Sun et al. (2009) definition of the genus before our study.

Thalassaphorurini versus Onychiurini

A further concern is that furcal area chaetotaxy, i.e. the diagnostic character that Pomorski (1998) proposed to distinguish the tribes Thalassaphorurini, where *Allonychiurus* is placed, and Onychiurini, is not documented in most of the 23 species assigned to *Allonychiurus* by Bellinger et al. in 2010. These species could belong as well to a genus of Onychiurini, like *Onychiurus*. In this respect, a few *Onychiurus* species described in the recent paper of Pomorski, Furgoł and Christiansen (2009) have a furcal area similar to that of *Allonychiurus*, but the authors do not formally discuss the important taxonomic implications of this finding. They nevertheless recognize that «Many of the features he (Pomorski) used to redefine the genus (*Onychiurus*) are not given in many descriptions». A large number of species assigned to *Allonychiurus* and *Onychiurus* in Bellinger et al. (2010) need therefore to be re-examined in detail, as it is not known if they match the modern diagnoses of these genera. In parallel, differences between both genera as well as between Onychiurini and Thalassaphorurini have to be re-assessed.

The chaetotaxy of tibiotarsus

The use of the number of chaetae in the distal whorl of tibiotarsus as a diagnostic character to define *Allonychiurus* deserves further comments. This character is not mentioned in the published descriptions of *Allonychiurus* by Yoshii (1995) and Weiner (1996). Bellinger et al. (2010) key out the genus as having “more than 7” chaetae in this whorl. Sun et al. (2009) characterize *Allonychiurus* as having 11 chaetae in the distal whorl of tibiotarsus. Actually, only six species have these 11 chaetae including the type species of the genus, *A. flavescens* (though it needs to be confirmed on type locality specimens) and the new species *A. antennalis* described here. Among the species listed as *Allonychiurus* in the web site of Janssens and Christiansen at this time, Sun et al. (2009) recognized 9 species with less than 11 distal tibiotarsal chaetae (easily seen on original drawings of *A. mediasetus* (Lee, 1974), and *A. pseudocellitriadis* (Lee, 1974), less obvious for other species). Other morphological characters are very similar between 9- and 11-chaetae species. In order to avoid the splitting of *Allonychiurus* in weakly defined entities, and given our poor knowledge of other diagnostic characters (furcal area and antenna III organ) in several species, we define *Allonychiurus* as having 9 or 11 chaetae in the distal whorl of tibiotarsus. This is in line with the other large genus of Thalassaphorurini, i.e. *Thalassaphorura*, where distal tibiotarsal chaetae are 7 or 9 (Sun et al. 2010), suggesting that this character may have lower taxonomical value in some genera than recently thought.

Taxonomical approach

In this contribution and as a first step, we address the taxonomic problems raised above in three ways. First, in order to accommodate several species that would otherwise necessitate the creation of new poorly defined genera, we extended the diagnosis of *Allonychiurus* of Sun et al. (2009) to include species with sensory clubs of antenna III organ smooth or granulated (*versus* only granulated), and species with 9 or 11 distal chaetae on tibiotarsus (*versus* only 11). This new definition is compatible with the characters of *Allonychiurus* extracted from the key of Bellinger et al. (2010). Second, we remove from the *Allonychiurus* list of Bellinger et al. (2010) nine species that do not match diagnostic characters of *Allonychiurus*: four are considered *incertae sedis*, and five are reallocated to other genera. Third, we provisionally keep in *Allonychiurus* several insufficiently described species listed by Bellinger et al. (2010) that do not conflict with the definition of the genus, but could belong as well to other genera like *Onychiurus* or *Thibaudichiurus* Weiner, 1996; their generic assignment will have to be checked from fresh material.

Critical checklist of the world species of *Allonychiurus* Yoshii, 1995

In the checklist given below, an asterisk (*) indicates that species assignment requires confirmation.

Allonychiurus flavescens (Kinoshita, 1916) (type species of the genus *Allonychiurus* by original designation). Originally described in the genus *Onychiurus* from Japan, later found in Korean caves (Yosii and Lee 1963, Yosii 1966, Weiner 1989) and largely distributed across USA (Muzzio 1984, Christiansen and Bellinger 1998). The different populations of Eastern Asia might however represent closely related geographic species (Weiner 1989, Yoshii 1995). Those of USA exhibit geographical variability according to Christiansen and Bellinger (1998), at a level unusual in other Thalassaphorurini species, and would deserve closer examination.

Allonychiurus donjiensis (Lee & Kim, 1994)*. Described in the genus *Onychiurus* from South Korea, later placed in *Allonychiurus* by Babenko (2007, following the tentative key of Onychiurinae on www.collembola.org). Morphological similarity with *Thibaudichiurus mariangeae* (Thibaud & Lee, 1994) was stressed in the original description. Smooth sensory clubs of third antennal segment and four protecting papillae in the sense organ of third antennal segment are shared by the two species. Ecology (coastal habitats) and distribution are also similar. A redescription of the species would probably result in its reallocation to *Thibaudichiurus*.

Allonychiurus hangchowensis (Stach, 1964). Described in the genus *Onychiurus* from China (Zhejiang: Hangzhou), later placed in *Allonychiurus* by Bellinger et al. (2010).

Allonychiurus indicus (Choudhuri & Roy, 1965)*. Described in the genus *Onychiurus* from India (West Bengale), later placed in *Allonychiurus* by Bellinger et al. (2010).

Allonychiurus jindoensis (Lee & Kim, 1994)*. Described in the genus *Onychiurus* from South Korea, later placed in *Allonychiurus* by Babenko (2007, following the tentative key of Onychiurinae on www.collembola.org). Remarks regarding the species affinities of *A. donjiensis* with *Thibaudichiurus mariangeae* apply here.

Allonychiurus jongaksanensis (Weiner, 1989). Described in the genus *Paronychiurus* from North Korea, later placed in *Allonychiurus* by Weiner (1996).

Allonychiurus kimi (Lee, 1973). Described in the genus *Onychiurus* from South Korea, reported from North Korea by Weiner (1989), later placed in *Allonychiurus* by Yoshii (1995).

Allonychiurus mediasetus (Lee, 1974). Described as *Onychiurus mediaseta* from South Korea, reported from North Korea by Weiner (1989), later placed in *Allonychiurus* as *Allonychiurus mediaseta* by Weiner (1996).

Allonychiurus megasomus Sun, Yan & Chen, 2009. Described from China (Nanjing).

Allonychiurus pamirensis (Martynova, 1975)*. Described in the genus *Onychiurus* from Tajikistan at high altitude (East Pamir), later placed in *Allonychiurus* by Bellinger et al. (2010).

Allonychiurus pseudocellitriadis (Lee, 1974). Described in the genus *Onychiurus* from South Korea, later placed in *Allonychiurus* by Weiner (1996).

Allonychiurus shanghaiensis (Rusek, 1971)*. Described in the genus *Onychiurus* from China (Shanghai), later placed in the genus *Allonychiurus* by Sun et al. (2009).

Allonychiurus shinbugensis (Lee, 1974). Described in the genus *Onychiurus* from South Korea, reported from North Korea by Weiner (1989), later placed in the genus *Allonychiurus* by Weiner (1996).

Allonychiurus tianshanicus (Martynova, 1971)*. Described in the genus *Onychiurus* from Kyrgyzstan at high altitude, later placed in the genus *Allonychiurus* by Bellinger et al. (2010).

Incertae sedis

Four of the species currently placed in the genus *Allonychiurus* by Bellinger et al. (2010) are very insufficiently described or exhibit characters that are not those of the genus. They are considered here as *Thalassaphorurini incertae sedis*.

Allonychiurus caprariae (Dallai, 1969). Described in the genus *Onychiurus*, later placed in *Allonychiurus* by Bellinger et al. (2010). Only known from the type locality (Capraia Island in Italy). For its antennal basis not differentiated and the presence of 4+4 anterior pseudocelli on head, this species departs from *Allonychiurus*.

Allonychiurus michelbacheri (Bagnall, 1948). Described in the genus *Onychiuroides* Bagnall, 1948 from the USA, later placed in the genus *Allonychiurus* by Bellinger et al. (2010). In the original description, considered to be closely related to *Onychiurus edinensis* Bagnall, 1935 (type of the genus *Spinonychiurus* Weiner, 1996).

Allonychiurus sensitivus (Handschin, 1928). Described in the genus *Onychiurus* from Bulgaria, later placed in *Allonychiurus* by Bellinger et al. (2010).

Allonychiurus spinosus (Bagnall, 1949). Described in the genus *Onychiuroides* from Ireland, later placed in *Allonychiurus* by Bellinger et al. (2010). The ‘dorsal spines’ of the abdomen mentioned in the original description are likely to be thickened S-chaetae. The “exceptionally long” lateral chaetae on head and body remind a first instar chaetotaxy.

Species removed from *Allonychiurus*

Thalassaphorura sensilata (Thibaud & Massoud, 1979), comb. n.

This species was originally described from Lesser Antilles (Central America) in the genus *Protaphorura* and later transferred to *Allonychiurus* by Bellinger et al. (2010). PAO with simple vesicles undoubtedly places this species in *Thalassaphorura* Bagnall, 1949 according to original description, to observation of Sun et al. (2009) and to re-examination of type specimens.

Micronychiurus borensis (Beruete, Arbea & Jordana, 1994), comb. n.

Described in the genus *Onychiurus* from Spanish Pyrenees, later placed in *Allonychiurus* by Bellinger et al. (2010). It rather belongs to *Micronychiurus* Bagnall, 1949 *sensu* Weiner (1996), as indicated by the number of pso on Abd. IV and V (5–7 and 5–6 respectively in *Micronychiurus* versus a lower number in *Allonychiurus*). It was correctly placed in the “*Onychiurus*” *minutus* species-group (equivalent to *Micronychiurus*) in the original description.

Spinonychiurus vandeli (Cassagnau, 1960), comb. n.

Described in the genus *Onychiurus* from the French Pyrenees at high altitude, later placed in *Allonychiurus* by Bellinger et al. (2010). We have checked Cassagnau’s type specimens in the Muséum national d’Histoire naturelle of Paris. Because of the absence of d_0 on head and the subdivision of Abd. III sternite into two subsegments, the species should be assigned to *Spinonychiurus* as redefined by Kaprus’ and Tsalan (2009).

Thibaudichiurus foliatus (Rusek, 1967). Described in the genus *Onychiurus* from China (Shanghai), reallocated to *Thibaudichiurus* by Weiner (1996), later placed in *Allonychiurus* by Bellinger et al. (2010). See discussion about the validity of *Thibaudichiurus* at *T. mariangeae*.

Thibaudichiurus mariangeae (Thibaud & Lee, 1994). Described in the genus *Onychiurus* from South Korea, given as type species of the genus *Thibaudichiurus* Weiner, 1996, later placed in *Allonychiurus* by Babenko (2007, following the tentative key of Onychiurinae on www.collembola.org), cited again as *Thibaudichiurus* from Santo island (Vanuatu) by Thibaud (2009). The proposed synonymy of *Thibaudichiurus* and *Allonychiurus* has never been documented in the literature, and is not accepted here, after re-examination of the type specimens from the Muséum national d’Histoire naturelle of Paris. The key difference between *Thibaudichiurus* and *Allonychiurus* according to Weiner (1996) is the presence of 2+2 *versus* 1+1 pseudocelli on first thoracic tergite. The same character is supposed to separate two other genera of Thalassaphorurini (*Jailolaphorura* Yosii & Suhardjono, 1992 and *Thalassaphorura* Bagnall, 1949), but was not considered of generic value by Sun Xin et al. (2010), as typical and closely related species of *Thalassaphorura* may have either 1+1 or 2+2 on this tergite. In the same way, we did not retained this character as discriminant for *Thibaudichiurus*. However, *Thibaudichiurus* is maintained here on the basis of its single row of manubrial chaetae posterior to dental chaetae (several in *Allonychiurus*) (Weiner 1996 and comm. pers.), and the presence of characteristic, thickened chaetae on the male genital plate that are not recorded in *Allonychiurus* species. According to Pomorski (1998) *Thibaudichiurus* is also closely related to *Tantulonychiurus* Pomorski, 1996 from which it differs by modified chaetae of male restricted to the genital plate and position of dorso-median pseudoscelli on abdomen IV and V tergites; we confirm also the difference suspected by Pomorski in number of distal chaetae of tibiotarsi (11 in *Thibaudichiurus*, 7 in *Tantulonychiurus*). Arrangement of chaetae on and around furcal area (but not their morphology) is identical between the two genera.

Note on species ecology and distribution

Allonychiurus occurs in a wide range of habitats. Most described species live in soil and litter of lowland areas (Weiner 1989). The type species of the genus (*A. flavescens*) has been found in caves in Korea, but is described from soil in Japan. The identity of the Korean specimens and the original specimens from Japan may be questioned given the diversity of the genus (Yoshii 1995). No other location in cave habitats is mentioned in the literature for *Allonychiurus*, in contrast to *Onychiurus* which is highly diversified in caves. Two species (*A. pamirensis* and *A. tianshanicus*) live at high altitude in central Asia. Two others (*A. donjiensis* and *A. jindoensis* from Korea) are coastal halophilous species (Lee and Kim 1994); their generic assignation needs however confirmation, as this ecology and several morphological characters rather points to *Thibaudichiurus* from the same habitat and same region.

Abbreviations and vocabulary used

Material. The codes between brackets are field codes of the samples which contained the specimens, for instance (C9581).

Material deposit. Nanjing University (China)—NJU, Museum national d’Histoire naturelle de Paris (France)—MNHN.

Morphology. Labial papillae types are named after Fjellberg (1999). Labium areas and chaetal nomenclature follow Massoud (1967) and D’Haese (2003). Chaetae on anal valves are named after Yoshii (1996).

Ant antennal segments, **AllIO** Sensory organ of third antennal segment, **PAO** postantennal organ, **Th** thoracic segments, **Abd** abdominal segments, **p-chaeta** chaeta of row p on head, **Sp** posterior S-chaeta (on Abd. V or on head), **ms** S-microchaeta (microsensillum auct.), **psO** pseudocelli, **a-psO** postero-internal psO on head, **psp** pseudopore, **AS** anal spines, **x** axial psp of Abd. IV.

The uneven axial chaeta m_0 (Sun et al. 2010) of Abd. VI tergite is named here p_0 in agreement with the literature.

Labral chaetae formula is the number of chaetae from prelabrals to distal row of labrum; for instance: 4/342.

Pseudocellar and pseudopore formulae are the number of pseudocelli and pseudopores by half-tergite (dorsally) or half-sternite (ventrally) as follows: head anterior, head posterior/Th. I, Th. II, Th. III/Abd. I, Abd. II, Abd. III, Abd. IV, Abd. V (for instance: 32/022/33343).

S-chaetae formula is the number of S-chaetae by half-tergite from head to Abd. VI (for instance: 11/012/222120).

Formula of tibiotarsal chaetotaxy: total number of chaetae (number of chaetae in the distal whorl (A+T), number of chaetae in the proximal whorl B, number of basal chaetae); for instance: 21 (11, 8, 2).

Systematics

Onychiuridae Börner, 1913

Allonychiurus Yoshii, 1995

Allonychiurus antennalis sp. n.

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Figs 1–2. Table 1.

Type material: Holotype female, 3 female paratypes. China: Jiangsu Province: Nanjing: Zijinshan: 10.iv.2009, litter, Berlese extraction, Zhang Feng et al. leg. (C9581). – ibid: Nanjing: Baima Park: 14 paratypes (2 males, 3 females and 9 juveniles) on slides, 13.v. 2007, litter, Berlese extraction, Chen Jian-xiu et al. leg. (C9544).

Holotype and 13 paratypes on slides are deposited in the Department of Biological Science and Technology of NJU, 4 paratypes on slides in MNHN.

Diagnosis: pso formula as 32/133/33343 dorsally, 11/000/01000 ventrally; subcoxa 1 of legs I, II and III with 1, 1 and 1 pso respectively; parapseudocelli (psx) absent; presence of small, finely granulated, apical swelling at the apex of Ant. IV; Th. II and III each with 3 dorsal chaetae on both side of axial line; tibiotarsus with 11 chaetae in the distal whorl, no clavate tenent hair; ventral tube with 6+6 distal chaetae, without anterior or basal chaetae.

Description: Body length: 1.3–1.7 mm (females), 1.0 mm (males). Body shape cylindrical, Abd. III–IV more or less broadened. Body colour white in alcohol.

Pseudocellar formulae as 32/133/33343 dorsally, 11/000/01000 ventrally (Figs 1A, B), subcoxa 1 of legs I, II and III with 1, 1 and 1 pso respectively. Parapseudocelli absent. Pseudopore formulae as 00/011/11110 dorsally, 00/111/000x0 ventrally (Figs 1A, B).

S-chaetae formula as 11/012/222120 dorsally. Sp present on head. S-microchaetae tiny and blunt, present on Th. II and III dorsally (Fig. 1A).

Head. Antennae short and distinctly segmented, as long as head (Fig. 1A). Length ratio of antennal segments I: II: III: IV = 1: 1.8–2: 1.8–2: 3.8–4.0. Ant. I with 9–10 chaetae. Ant. II with 14–15 chaetae. Ant. III sensory organ composed of 5 papillae, 5 guard chaetae, 2 small rods and 2 weakly granulated sensory clubs, both morel-like; lateral ms just posterior to sensory organ (Fig. 1C). Ant. IV subapical organite rod-like; basolateral ms at about 2/5 length from base; presence of a small, finely granulated (probably only primary granulation), flat apical swelling at the apex of antenna (possibly remnant of apical bulb fused to the apex) (Fig. 1D); invaginated apical bulb absent. Antennal base with distinct granulation. PAO composed of 18–22 compound vesicles arranged in 2 rows along axis of organ (Fig. 1A). Dorsal cephalic chaeta d_0 present. 4+4 p-chaetae between posterior a-pso on head (Fig. 1A). Mandible with strong molar plate and 4 apical teeth. Maxilla bearing 3 teeth and 6 lamellae. Maxillary palp simple with 1 basal chaeta and 2 sublobal hairs. Labral chaetae formula 4/342. Labium with 6 proximal, 4 basomedian (E, F, G, and f) and 6 basolateral (a, b, c, d, e, e') chaetae;

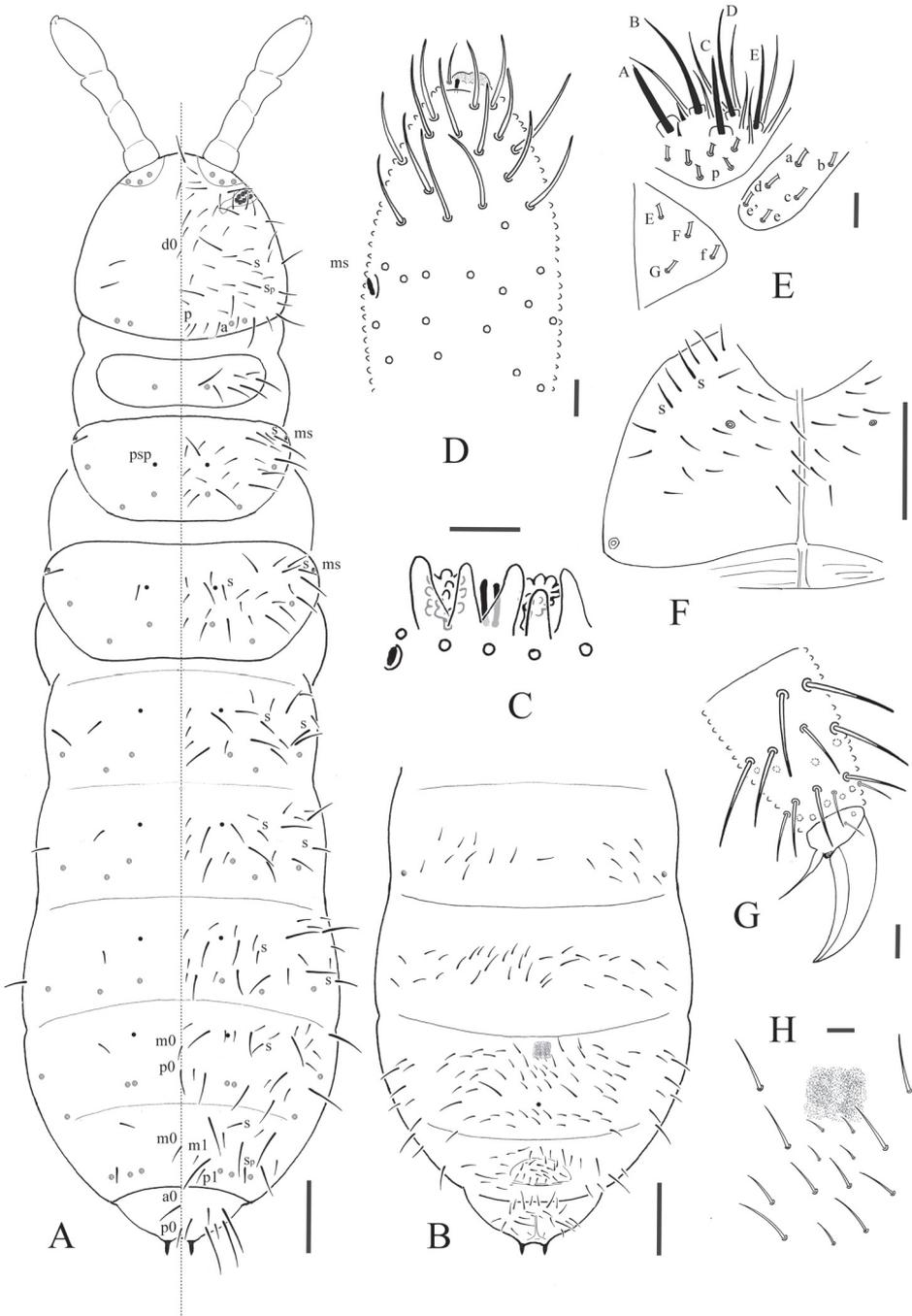


Figure 1. *Allonychiurus antennalis* sp. n. **A** dorsal side of body with chaetotaxy, S-chaetae, pso and psp **B** ventral side of Abd. II–VI **C** organ of Ant. III **D** dorsal side of left Ant. III **E** labium (p, proximal group of chaetae of labial palp) **F** ventral side of head **G** distal part of leg III **H** furcal area. Scales: 0.1 mm (A, B & F), 0.01 mm (C–E & G–H).

labial papillae of AC type, papillae A–E respectively with 1, 3, 0, 3 and 3 guard chaetae (Fig. 1E). Postlabial chaetae 4+4 along ventral groove (Fig. 1F).

Body chaetotaxy. Ordinary chaetae differentiated in meso- and macro-chaetae, ratio Sp: m1: p1 on Abd. V = 1: 0.6: 1.1 (Fig. 1A). Th. I with 7+7 chaetae dorsally. Three chaetae on both side of axial line and no uneven axial chaetae from Th. II to Abd. III tergites. Abd. IV tergite with two uneven axial chaetae (m_0 and p_0), Abd. V tergite with one uneven axial chaeta (m_0), Abd. VI with two uneven axial chaetae (a_0 and p_0) (Fig. 1A). Th. I, II and III sternites with 0+0, 1+1 and 1+1 chaetae respectively.

Appendages. Subcoxa 1 of legs I, II and III with 4, 4 and 4 chaetae, subcoxa 2 with 1, 4 and 4 chaetae, respectively. Tibiotarsi of legs I, II and III with 22 (11, 8, 3), 21 (11, 8, 2) and 21 (11, 8, 2) chaetae. Unguis without tooth. Unguiculus slender and pointed, 0.6 times as long as inner edge of unguis, with narrow inner basal lamella (Fig. 1G). Ventral tube with 6+6 distal chaetae, anterior and basal chaetae absent (Fig. 2A). Furca reduced to a finely granulated area, with 4 short chaetae in two rows posterior to furcal rudiment (Fig. 1H).

Male genital plate with 30 circumgenital and 8 genital chaetae (Fig. 2B); female genital plate with 16–18 anterior and 2 genital chaetae (Fig. 2C). No modified chaetae ventrally in males. Anal valves with numerous acuminate chaetae; each lateral valve with chaetae a_0 and 2 a_1 ; upper (posterior) valve with chaetae a_0 , 2 b_1 , 2 b_2 , c_0 , 2 c_1 , 2 c_2 (Fig. 2D). Anal spines set on distinct papillae, 0.6 times as long as inner edge of leg III unguis (Fig. 2E).

Derivatio nominis. Named for its peculiar antennal morphology.

Ecology. In broadleaved litter, in a recreational park in town, and at the forested foot of a hill close to the town, altitude 10 to 50 m a.s.l.

Remarks. Bisexual species. *Allonychiurus antennalis* sp. n. can be easily recognized by the presence of its apical swelling on Ant. IV, not reported in other species of the genus. It has the same dorsal pseudocellar formula (32/133/33343) as *A. shinbugensis*, *A. megasomus* and *A. mediasetus*. Diagnostic characters are summarized in Table 1.

Table 1. Comparison of the four species of *Allonychiurus* with a dorsal pseudocellar formula of 32/133/33343.

	<i>antennalis</i> sp. n.	<i>mediasetus</i> (Lee, 1974)	<i>megasomus</i> Sun et al., 2009	<i>shinbugensis</i> (Lee, 1974)
Ant. IV apical swelling	present	not mentioned	absent	not mentioned
Ventral pso formula	11/000/01000	11/000/01110	11/000/01110	10/000/01010
Inner basal lamella of unguiculus	present	present	absent	present
Number of chaetae on ventral tube	6+6	8+8	8+8	8+8
Number of chaetae on Th. I tergite	7+7	9+9	7-8+7-8	7+7
Number of p-chaetae between posterior a-pso on head	4+4	4+4	4+4	3+3
Number of axial chaetae on Th. II and III tergites	3+3	4+4	4+4	4+4
Uneven axial chaetae on Abd. IV	m_0 and p_0	p_0	m_0 and p_0	m_0 and p_0
Maximum length (mm)	1.7	1.6	2.1	1.5

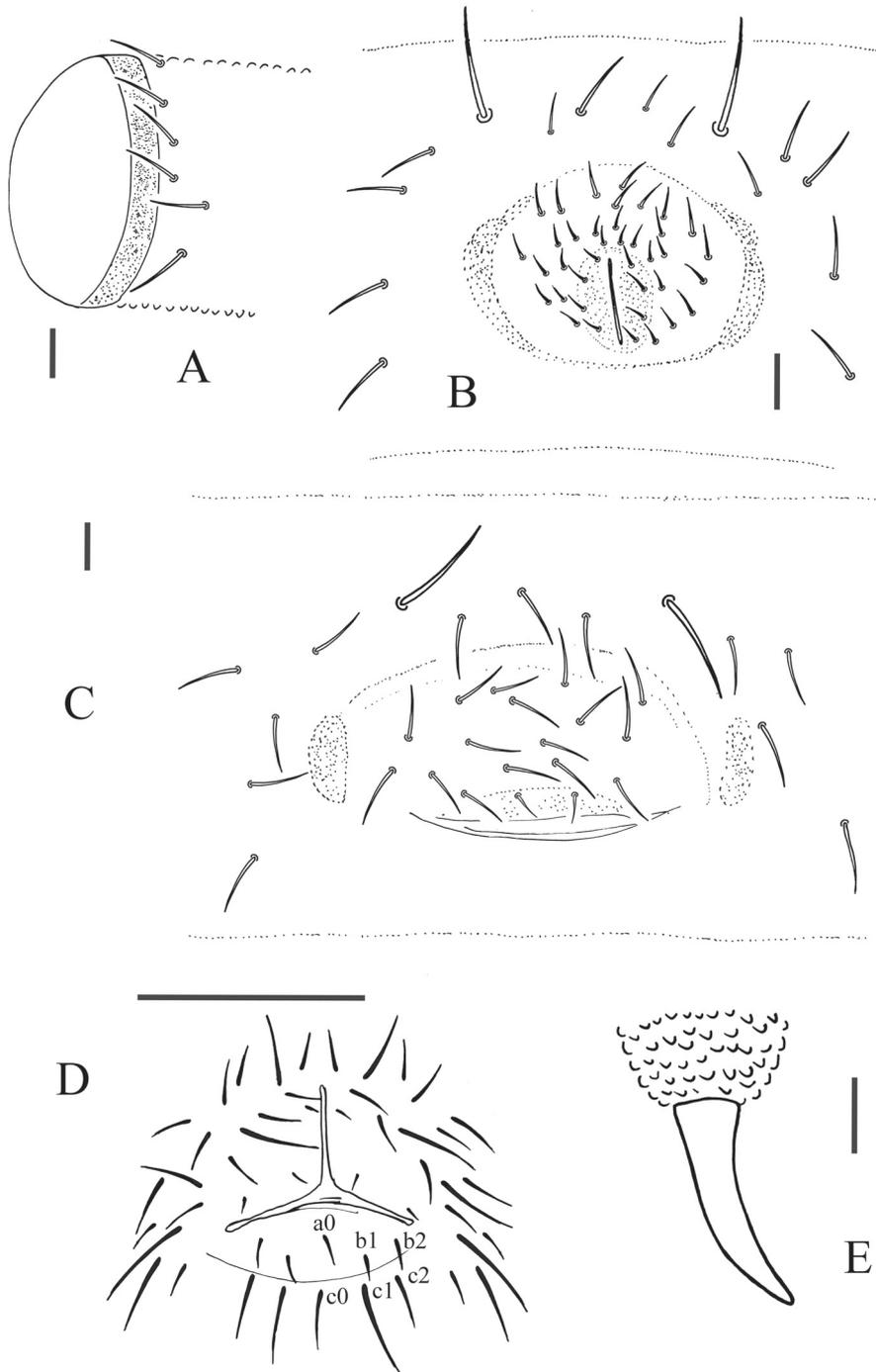


Figure 2. *Allonychiurus antennalis* sp. n. **A** ventral tube, lateral side **B** male genital plate **C** female genital plate **D** anal valves **E** anal spine. Scales: 0.1 mm (D), 0.01 mm (A–C & E).

Key to world species of *Allonychiurus* Yoshii, 1995

Note. Some forms of *Allonychiurus flavescens* from USA may lack pso on Th. I or are polymorphic (Christiansen and Bellinger, 1998). In the absence of more detailed information regarding other characters, they are not included in this key.

- 1 AIII O with 4 papillae, 2+2 or 3+3 pso on Abd IV 2
 – AIII O with 5 papillae, more than 3+3 pso on Abd IV 3
 2(1) Dorsal pso formula 22/222/22222 after original description
 *A. donjiensis* (Lee & Kim) (South Korea)
 – Dorsal pso formula 32/233/33333
 *A. jindoensis* (Lee & Kim) (South Korea)
 3(1) Th. I tergite with 2+2 pso 4
 – Th. I tergite with 1+1 pso or without pso 5
 4(3) Th. I tergite with 12+12 chaetae, Abd. I tergite with 4+4 pso, dorsal pso formula 33/233/4444-54 *A. pamirensis* (Martynova) (Russia)
 – Th. I tergite with 8+8 chaetae, Abd. I tergite with 3+3 pso, dorsal pso formula 32/233/34445 after original figure (given as 32/233/34445 in original description), ventral pso formula 1/000/00010, ventral tube with 8+8 distal chaetae *A. tianshanicus* (Martynova) (Russia)
 5(3) Th. I tergite without pso, dorsal pso formula 32/022/33343, ventral pso formula 11/000/00000, 4+4 p-chaetae between posterior a-pso on head, Th. I tergite with 8+8 chaetae, subcoxa 1 of legs I, II and III with 2, 2 and 2 pso respectively, ventral tube with 8+8 distal chaetae
 *A. pseudocellitriadis* (Lee) (South Korea)
 – Th. I tergite with 1+1 pso 6
 6(5) Th. II and III each with 3+3 pso dorsally; dorsal pso formula 32/133/33343...7
 – Number of pso on Th. II and III not as above 10
 7(6) Ventral pso formula 11/000/01110, 4+4 p-chaetae between posterior a-pso on head 8
 – Ventral pso formula not as above 9
 8(7) Distal whorl of tibiotarsi with 9 chaetae (interpretation of original drawing), Th. I tergite with 9+9 chaetae, unguiculus with basal lamella, Abd. IV tergite with one uneven axial chaeta (p0) dorsally
 *A. mediasetus* (Lee) (South and North Korea)
 – Distal whorl of tibiotarsi with 11 chaetae, Th. I tergite with 7-8+7-8 chaetae, unguiculus without basal lamella, Abd. IV tergite with two uneven axial chaetae (m0 and p0) dorsally *A. megasomus* Sun, Yan & Chen (China)
 9(7) Ventral pso formula 10/000/01010, Ant. IV without apical swelling, 3+3 p-chaetae between posterior a-pso on head, 4+4 axial chaetae on Th. II and Th. III tergites, ventral tube with 8+8 distal chaetae
 *A. shinbugensis* (Lee) (South and North Korea)

- Ventral pso formula 11/000/01000, Ant. IV with a flat apical swelling, 4+4 p-chaetae between posterior a-pso on head, 3+3 axial chaetae on Th. II and Th. III tergites, ventral tube with 6+6 distal chaetae.....
.....*A. antennalis* sp. n. (China)
- 10(6) Th. II and III with 2+2 and 2+2 pso dorsally; dorsal pso formula 32/122/33343 **11**
- Number of pso on Th. II and III not as above..... **13**
- 11(10) Unguiculus with basal lamella, Th. I tergite with 9+9 chaetae, Abd. V tergite without uneven axial chaeta dorsally after original drawing.....
.....*A. shanghaiensis* (Rusek) (China)
- Unguiculus without basal lamella, Th. I tergite with 8+8 chaetae, Abd. V tergite with one uneven axial chaeta (m0) dorsally **12**
- 12(11) Ventral pso formula 10/000/01000, Abd. IV tergite with two axial chaetae (m0 and p0) dorsally..... *A. kimi* (Lee) (South and North Korea)
- Ventral pso formula 10/000/01110, Abd. IV tergite with one axial chaeta (p0) dorsally *A. flavescens* (Kinoshita) (Japan, South Korea, USA)
- 13(10) Dorsal pso formula 32/123/33343, distal whorl of tibiotarsi with less than 11 chaetae (interpretation of original figure) *A. hangchowensis* (Stach) (China)
- Dorsal pso formula 32/132/33343, distal whorl of tibiotarsi with 11 chaetae, 4+4 p-chaetae between posterior a-pso on head, 3+3 axial chaetae on Th. II and Th. III tergites.....*A. jongaksanensis* (Weiner) (North Korea)

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Cachiporrini, a remarkable new tribe of Lamprosomatinae (Coleoptera, Chrysomelidae) from South America

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“The best collecting is in museums”, Charles O’Brien (paraphrased)

Abstract

A new genus and species of Lamprosomatinae, *Cachiporra extremaglobosa* Chamorro & Konstantinov, is described from Brazil. A new tribe, Cachiporrini, is proposed. The first phylogenetic analysis of Lamprosomatinae based on adult morphological characters is conducted. Comparisons are made among lamprosomatine tribes and genera. A key to tribes is provided.

Keywords

New tribe, new genus, new species, antennal clubs, capitulum, leaf beetles, Brazil, phylogeny

Introduction

As taxonomists we can only hope to make the kind of discoveries that prompt suspended awe and prolonged excitement. Such was our reaction when we stumbled upon this new lamprosomatine genus buried within the Cryptocephalinae addenda drawers

of the Coleoptera collection at the National Museum of Natural History (NMNH), Smithsonian Institution. Confirmation of this taxon as new was facilitated by the comprehensive chrysomelid collection at NMNH, by the relatively small number of higher-level taxa in Lamprosomatinae, and by the comprehensive studies by Monrós (1956, 1958) on the group.

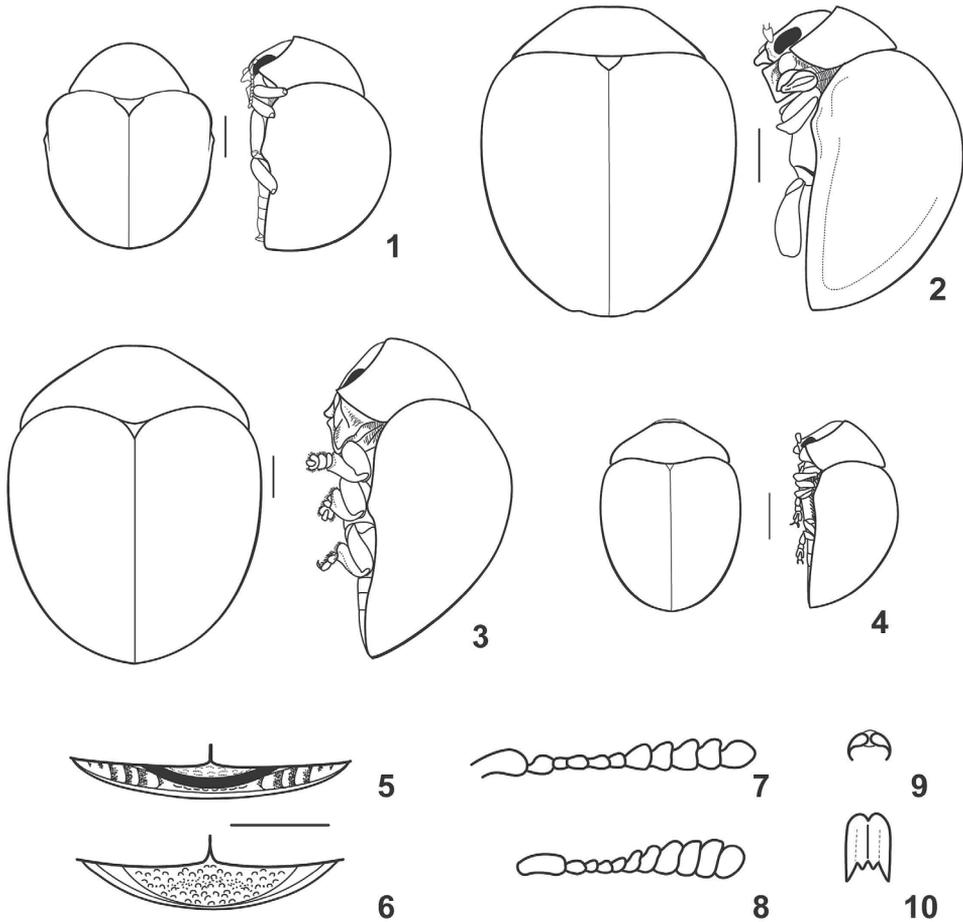
Monrós devoted much of his short life and taxonomic expertise to the study of this group of small, round, and shiny beetles. Therefore, it was surprising and somewhat ironic that these specimens are from the Monrós collection acquired by the NMNH in 1959. It is fair to state however, that the Monrós collection is extensive and would require many consecutive lifetimes to study it all.

Lamprosomatinae consists of four tribes and 14 genera (Table 1): Cachiporrini Chamorro & Konstantinov, 2011 (1 genus); Neochlamysini Monrós, 1958 (2 genera); Sphaerocharini Clavareau, 1913 (1 genus); and Lamprosomatini Lacordaire, 1848 (10 genera) (Seeno and Wilcox 1982). Sphaerocharini has been treated as an independent subfamily (Chapuis 1874; Kasap and Crowson 1976), as a tribe of Lamprosomatinae (Lacordaire 1848; Clavareau 1913; Monrós 1956) or as a tribe of the former subfamily Chlamisinae (now a tribe in Cryptocephalinae) (Chen 1940). Monrós (1956) correctly argued for: 1) accepting Sphaerocharini as a tribe of Lamprosomatinae and rejecting the notion that *Sphaerocharis* represents a transitional group between chlamisines and lamprosomatines and 2) not placing it in its own subfamily. Including Sphaerocharini in Lamprosomatinae is now the prevailing classification (Seeno and Wilcox 1982; Lawrence and Newton 1995). Monrós (1958) later transferred *Pseudolychnophaes* and *Neochlamys* from Sphaerocharini to a new tribe, Neochlamysini.

All lamprosomatines are highly convex and ventrally flattened [species of Cryptocephalinae, including Chlamisini, sister taxon to lamprosomatines (Farell 1998), are cylindrical and not ventrally flattened], they are shiny and usually iridescent (cryp-

Table 1. Summary of classification and distribution of Lamprosomatinae. **NA** Nearctic **NT** Neotropical **AT** Afrotropical **PA** Palearctic **OR** Oriental **AU** Australasian.

Tribe	Genus	Author	Year	NA	NT	AT	PA	OR	AU
Cachiporrini	<i>Cachiporra</i>	Chamorro & Konstantinov	2011		×				
Neochlamysini	<i>Pseudolychnophaes</i>	Achard	1914			×			
	<i>Neochlamys</i>	Jacoby	1882			×			
Sphaerocharini	<i>Sphaerocharis</i>	Lacordaire	1848		×				
	<i>Xenoomorphus</i>	Monrós	1956			×			
	<i>Oyarzuna</i>	Bechyné	1950		×				
	<i>Oomorphus</i>	Curtis	1831	×	×	×	×	×	×
	<i>Asisia</i>	Bezdek, Löbl, Konstantinov	2010					×	
Lamprosomatini	<i>Oomorphoides</i>	Monrós	1956					×	×
	<i>Lychnophaes</i>	Lacordaire	1848		×				
	<i>Dorisina</i>	Monrós	1956		×				
	<i>Lamprosoma</i>	Kirby	1818	×	×				
	<i>Scrophoomorphus</i>	L. Medvedev	1968					×	



Figures 1–10. 1–4 Lamprosomatinae habiti, dorsal (left) and lateral (right) views, drawn after Monrós, 1956: 1 *Sphaerocharis marginicollis* (Sphaerocharini) 2 *Neochlamys strigicollis* (Neochlamysini) 3 *Lycnophaes globulosus* (Lamprosomatini) 4 *Pseudolychnophaes africanus* (Neochlamysini); 5–6 Apical margin of ventrite V, drawn after Monrós, 1956: 5 with stridulatory device, *Lamprosoma nicaraguensis* (Lamprosomatini) 6 without stridulatory device, *Sphaerocharis marginicollis* (Sphaerocharini); 7–8 Antennae, drawn after Monrós, 1956: 7 *Lycnophaes purpureus* (Lamprosomatini) 8 *Sphaerocharis marginicollis* (Sphaerocharini); 9–10 Claws, drawn after Monrós, 1956: 9 *Oomorpha floridanus* (Lamprosomatini) 10 *Sphaerocharis marginicollis* (Sphaerocharini).

tocephalines are rarely iridescent), their abdominal ventrites are all the same width medially with sternal longitudinal muscles within ventrite 4 [constricted ventrite 4 appearing hidden between ventrites 3 and 5 and sternal longitudinal muscles lacking in cryptocephalines (Kasap and Crowson 1976)]; females lack a fovea or egg-depression on ventrite 5 (present in cryptocephalines); and antennal grooves are present on the prosternum (feature also present in Chlamisini and Ischiopachina of Clytrini).

Upon discovery, *Cachiporra* could not be placed into any previously recognized lamprosomatine tribe. Clavate antennae are common in many camptosomata (e.g. Chlamisini, Clytrini, Lamprosomatini, but not in Cryptocephalini) (Figs 7, 8), however, *Cachiporra* is the first known camptosomata with capitate antennae represented by completely fused antennomeres forming an abrupt terminal bulb (capitulum), which is much wider than preceding antennomeres (Figs 16, 18; autapomorphy of Cachiporini, character 2 state 0). This kind of club is very uncommon in Chrysomelidae; it is known in only a few flea beetle (Alticini) genera commonly living in relatively dense substrate, such as leaf litter or moss cushions (e.g., *Clavicornaltica* Scherer, *Kiskeya* Konstantinov and Chamorro-Lacayo) (Konstantinov and Chamorro-Lacayo 2006) and a few Hispini.

A phylogenetic analysis of Lamprosomatinae was undertaken to find taxonomic position for *Chachiporra* within the subfamily. Designation of a new tribe was considered appropriate and justified to accommodate this new genus from Brazil. Current higher-level classification is based on Monrós's (1956, 1958) interpretation of relationships. The first evolutionary relationship among Lamprosomatinae is here inferred based on cladistic principles.

Material and Methods

Taxon sampling and outgroup

This study includes 12 of 14 lamprosomatine genera in 4 tribes (Tables 1 and 3). *Exema* Lacordaire and *Melittochlamys* Monrós (Chlamisini) were selected as outgroup to determine character polarity. All examined material is from the National Museum of Natural History (NMNH), Smithsonian Institution, Washington, DC.

Characters

General morphological terminology follows Konstantinov (1998). Terminology for female genitalia combines Moseyko (2008) and Chamorro-Lacayo et al. (2006), for kotopresse we follow Schöller (2008), and for thorax Chamorro-Lacayo and Konstantinov (2004). Hind wing nomenclature follows Kukalová-Peck and Lawrence (1993). A number of characters used in this analysis have traditionally been used to distinguish among genera and tribes (characters 1, 7, 8, 10, 16, 21 and 22), particularly by Monrós (1956, 1958). However, the majority of the 26 characters and 70 states are new. All characters have equal weights (Wilkinson 1992) and are unordered (Fitch 1971). Characters were coded based on variations in external morphology among the taxa. Approaches to coding and treatment of characters and missing data is outlined in Chamorro and Holzenthal (2010).

Table 2. Characters and states used in the cladistic analysis

1	Canthus of eye: 0, acute; 1, absent (Fig. 17); 2, wide and short; 3, wide and long, longer than half of transverse diameter of eye.
2	Antennomeres 7 to 11 (Figs 7, 8, 16): 0, fused into tight capitulum; 1, free.
3	Antennomeres 6 to 8 (Figs 7, 8, 16): 0, strongly transverse, more than twice as wide as long; 1, about as long as wide; 2, weakly transverse.
4	Base of pronotum in dorsal view: 0, entire; 1, extending posteriorly beyond base of elytra (Fig. 15); 2, extending posteriorly, but not beyond base of elytra.
5	Explanation of lateral margin of pronotum: 0, situated laterally (as in vast majority of Lamprosomatinae and other leaf beetles); 1, situated ventrally, essentially covered from above by expansion of upper side of pronotum laterally (Figs 15, 16).
6	Posterolateral corner of pronotum: 0, extending posterad beyond elytral base; 1, not extending posterad beyond elytral base.
7	Posterior margin of last abdominal ventrite: 0, concave; 1, more or less straight; 2, convex; 3, sinusoidal.
8	Shape of scutellum: 0, acutely triangular; 1, triangular (equilateral); 2, rectangular.
9	Size of scutellum: 0, minute; 1, small; 2, large.
10	Elytral punctation: 0, arranged in regular rows or with tendency to form such rows; 1, completely confused.
11	Sides of elytra: 0, extended into wide long lobe concealing most of middle to posterior part of metepisternite (Fig. 11); 1, extended into wide relatively short lobe not concealing much of metepisternite (Fig. 12); 2, extended into narrow long lobe concealing nearly all posterior part of metepisternite (Fig. 13); 3, extended into wide long lobe not concealing entire metepisternite (Fig. 14).
12	Elytra: 0, covered with bumps; 1, smooth (Fig. 15).
13	Elytral suture: 0, smooth (Fig. 15); 1, dentate.
14	Upper side of beetle body with metallic luster: 0, present; 1, absent.
15	Pronotal and elytral puncture setae: 0, present (Fig. 15); 1, absent.
16	Tarsal claws: 0, bifid and fused (Fig. 10); 1, simple and free (Fig. 9); 2, appendiculate, free, narrowly separated; 3, appendiculate, widely separated.
17	Wing (Fig. 19), number of cells between Cu and A: 0, one; 1, two.
18	Wing, RA 3+4: 0, present; 1, absent.
19	Wing, CuA 3+4 and spur of RP: 0, situated close to each other; 1, placed far away from each other.
20	Epipleura (Figs 11–14) directed: 0, vertically, forming nearly straight line with side of elytron, visible from outside; 1, horizontally, forming nearly straight angle with side of elytron, not visible from outside; 2, vertically, folded behind lateral side of elytron, not visible from outside.
21	Stridulatory file on distal border of last abdominal ventrite: 0, present (Fig. 5); 1, absent (Fig. 6).
22	Pygidium: 0, completely covered by elytra; 1, partly covered by elytra; 2, completely exposed.
23	Sclerotized thin rim of kotpresse: 0, present; 1, absent (Fig. 22).
24	Sclerotized part of spermathecal duct: 0, long, straight, about as wide, but longer than duct of gland (Fig. 20); 1, short, about as long as duct of gland; 2, very long, forming coils, longer than duct of gland; 3, long, consists of narrow and wider parts attached under angle to each other; 4, long, straight, much narrower and longer than duct of gland.
25	Stylus: 0, wider or nearly as wide as long; 1, longer than wide (Fig. 21); 2, absent.
26	Membranous window on apex of coxite (base of stylus): 0, present; 1, absent.

Table 3. Matrix of 26 characters for 11 taxa of the Lamprosomatinae and two outgroup taxa

Species name	Character states		
	0000000001	1111111112	222222
	1234567890	1234567890	123456
<i>Cachiporra extremaglobosa</i> sp. n.	1001101111	0101010110	121011
<i>Pseudolychnophaes africanus</i> Jacoby	11?0010121	110111??11	12????
<i>Neochlamys strigicollis</i> Jacoby	11?0010121	1101111011	120100
<i>Sphaerocharis marginicollis</i> (Guerin-Meneville)	0100010121	2100101011	11????
<i>Xenoomorphus gingindhlovanus</i> Monrós	2110011000	2100111011	000120
<i>Oomorphus concolor</i> (Sturm)	2110011000	210111??11	000201
<i>Asisia vietnamica</i> (Medvedev)	2110011010	2101111011	00????
<i>Oomorphoides yoasanicum</i> (Chen)	2110001010	2101121011	000200
<i>Lychnophaes globosus</i> (Olivier)	2110002010	2100111011	000200
<i>Dorisina pusilla</i> (Jacoby)	2111002000	2100111011	000300
<i>Lamprosoma chorisiae</i> Monrós	2111002010	2100121011	000100
<i>Melittochlamys semen</i> (Lacordaire)	3121013221	3001130002	120420
<i>Exema conspersa</i> (Mannerheim)	3122010221	3011130002	120420

Phylogenetic analysis

The data matrix was created using MacClade 4.08 (Maddison and Maddison 2000) and analyzed using PAUP* (beta test version) (Swofford 2003). Heuristic search was implemented using stepwise addition and 1000 random addition sequence replicates, 5 trees held at each step and Tree-Bisection-Reconnection (TBR) branch swapping algorithm. Nodal support for the preferred topology based on the given dataset was determined by bootstrapping (Felsenstein 1985) and Bremer support indices (Bremer 1988, 1994). Bootstrapping was carried out with 500 replicates and random-taxon addition. Decay or Bremer support indices were calculated by executing in PAUP* a MacClade generated batch file of 20 replicate heuristic searches and random-taxon addition for each constraint tree.

Results

Five equally parsimonious trees resulted from this analysis (Figs 23–27) of length 55 (CI: 0.80; RI: 0.82; RC: 0.65). A strict consensus tree is shown on Fig. 28. All topological results support the designation of a new tribe, Cachiporrini. Both Bremer and bootstrap values (respectively, separated by comma) strongly support the monophyly of Lamprosomatinae and Lamprosomatini. The placement of *Sphaerocharis* and the monophyly of Neochlamysini remains uncorroborated in the strict consensus. Majority-rule consensus tree retains a monophyletic Neochlamysini with *Sphaerocharini* as the sister taxon to Lamprosomatini (Figs 29–31). A majority-rule consensus cladogram is shown with distribution of unambiguous characters in Fig. 29 and ambiguous characters under slow (Fig. 30) and fast (Fig. 31) optimization.

Key to Tribes of Lamprosomatinae

- 1 With stridulatory file (device) on distal border of last ventrite (Fig. 5); last ventrite not excised in shape of arc. Pygidium completely covered by elytra. Scutellum acutely triangular, small to very small (Fig. 3). Elytral punctation arranged in regular rows or with a tendency to form such rows
..... **Lamprosomatini** (Worldwide)
- Without stridulatory file (device) on distal border of last ventrite (Fig. 6); last ventrite varies in shape. Pygidium not completely covered by elytra. Scutellum triangular, equilateral (Figs 1, 2, 4); size either very small or relatively large. Elytral punctation confused (or with a weak tendency to form rows) **2**
- 2(1) Eyes with deep canthus. Tarsal claws bifid and fused (Fig. 10). Metallic in color, shiny. Pygidium partly exposed, partly covered by elytra
..... **Sphaerocharini** Neotropical (South America)
- Eyes entire, without deep canthus. Tarsal claws simple and free (Fig. 9). Black, moderately shiny or not shiny. Pygidium completely exposed **3**
- 3(2) Antennae capitate with last 3 or 4 antennomeres tightly fused to form a sphere (Figs 16, 18). Scutellum small. Pronotum basally sinuate, medially extending posterad beyond elytral base. Pygidium exposed. Each puncture of pronotum and elytra with seta **Cachiporrini** Neotropical (South America)
- Antennae not capitate and last 4 antennomeres not fused to form a sphere, instead dentate (Figs 7, 8). Scutellum relatively large. Pronotum not basally sinuate, medially not extending posterad beyond elytral base. Punctures of pronotum and elytra without setae **Neochlamysini** Afrotropical

Cachiporrini Chamorro & Konstantinov, trib. n.

urn:lsid:zoobank.org:act:74B93547-7A5F-430D-9980-46831A35F370

Type genus. *Cachiporra* Chamorro & Konstantinov

Diagnosis. Body small, about 1.8 mm in length, moderately shiny, black. Head without midcranial and frontal sutures. Frontoclypeus swollen, notched in middle. Eye entire, not notched. Antenna capitate with last 4 antennomeres tightly fused to form sphere (Figs 16, 18).

Pronotum basally sinuate (Fig. 15), medially extending posterad beyond elytral base. Side swollen and bent ventrally so that lateral border not visible from above (Figs 17, 18). Lateral border of pronotum situated close to posterior margin of prosternum leaving hypomera extremely thin and limiting prosternum to small triangle.

Scutellum triangular, equilateral, small (Fig. 15). Side of elytron with long lobe directed ventrally covering significant part of metepisternite. Epipleura vertical, evenly narrow throughout (Fig. 11). Elytral punctation confused with weak tendency to form rows (Fig. 15). Each puncture of pronotum and elytra with light-colored seta. Tibial apices without long setae and without excavation. Tarsal claws simple

and free. Last abdominal ventrite without stridulatory file on distal border. Pygidium exposed (Fig. 18).

***Cachiporra* Chamorro & Konstantinov, gen. n.**

urn:lsid:zoobank.org:act:FE5E7031-33C2-4340-B822-D6705222A699

Figs 11, 15–22

Type species. *Cachiporra extremaglobosa* Chamorro & Konstantinov

Description. Body small, 1.81–1.85 mm long, 1.43–1.47 mm wide, and 1.01–1.04 mm thick, broadly oval.

Color. Body entirely black with bluish or bronzish tint, antennal capitulum and mouth parts deep reddish brown.

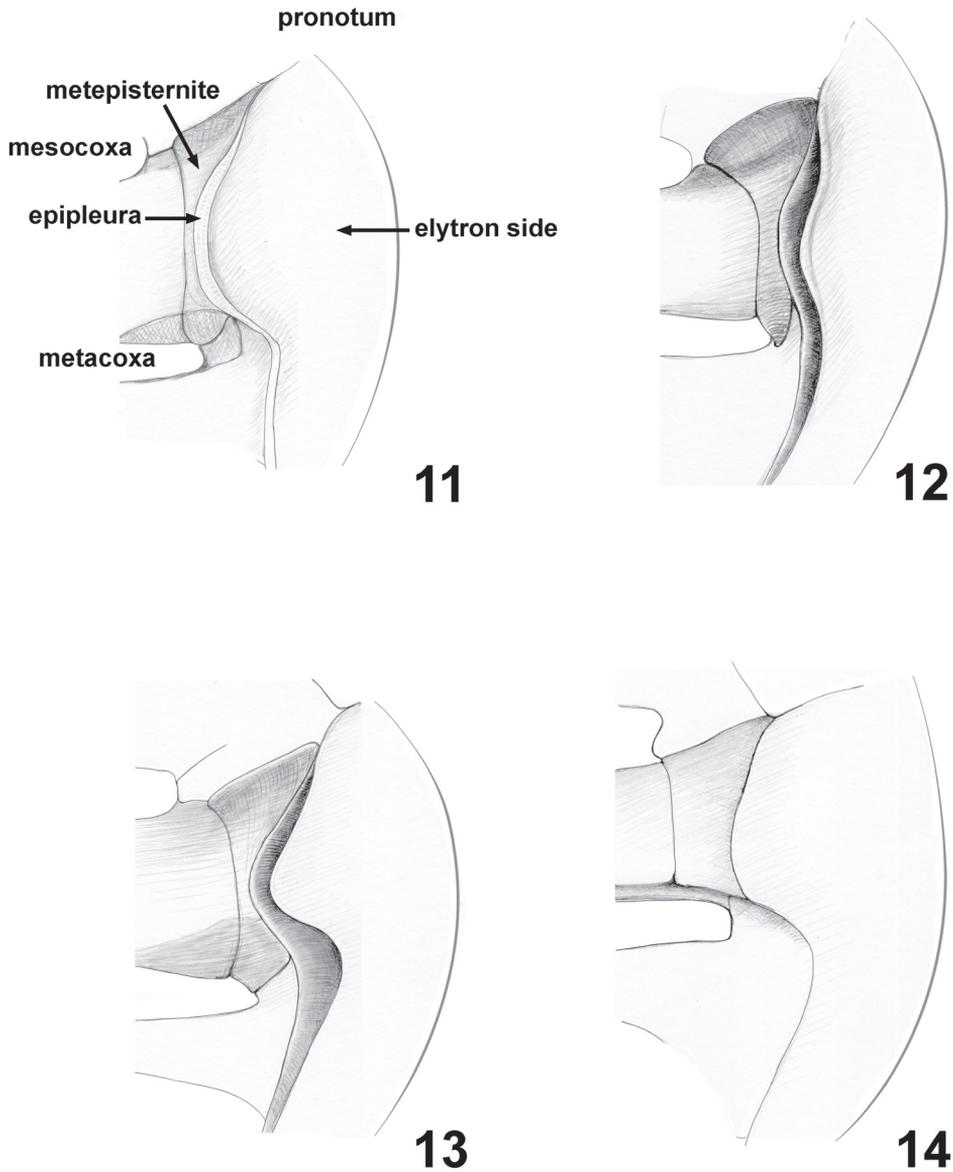
Head flat in lateral view, 1.42 times wider than long in frontal view, completely lacking hairs (except on labrum). Midcranial and frontal sutures absent. Top of frons and bottom of vertex with oval impression. Orbital area swollen and situated above eye level. Internal margin of eye entire, not notched. Distance between eyes 2.64 times as large as transverse diameter of eye. Labrum with three setae on each side placed symmetrically on anterior margin. Antennae extremely capitate with last 4 antennomeres tightly fused to form sphere (Figs 16, 18), inserted slightly above lower eye level with side of antennal socket adjacent to eye margin. Antennomere 1 wide with triangular lobe directed dorsolaterally. Antennomere 2 cylindrical, shorter than wide. Antennomeres 3 to 7 dorsoventrally flat, about as long as antennomere 2, but narrower.

Prothorax. Pronotum apically shallowly sinusoidal, basally sinuate, medially extending posterad beyond elytral base. Each pronotal puncture with short seta. Sides swollen and bent ventrally so that lateral border not visible from above. Lateral border situated close to posterior margin of prosternum leaving hypomera extremely thin and limiting prosternum to small triangle. Intercostal prosternal process in ventral view slightly longer than wide (length to width ratio 1.26), sides constricted above middle, anterior margin evenly concave with obtuse denticle in middle, posterior margin straight. Intercostal prosternal process in lateral view nearly straight in middle, abruptly bending posterodorsally. Procoxal cavity open posteriorly.

Mesothorax. Scutellum triangular, equilateral, small (Fig. 15). Elytra with well developed humeral calli. Side of elytron with long lobe directed ventrally covering significant part of metepisternite (Fig. 11). Elytral punctation confused, with a tendency to form longitudinal rows. Each elytral puncture bearing short seta. Epipleura narrow. Mesosternum vertical, nearly completely covered with intercoxal prosternal process and anterior process of metasternum separating mesocoxae.

Metathorax. Anterior process of metasternum rectangular with straight anterior margin (Fig. 16). Posterior margin curved. Surface shallowly shagreened with relatively large punctures placed more densely anteriorly.

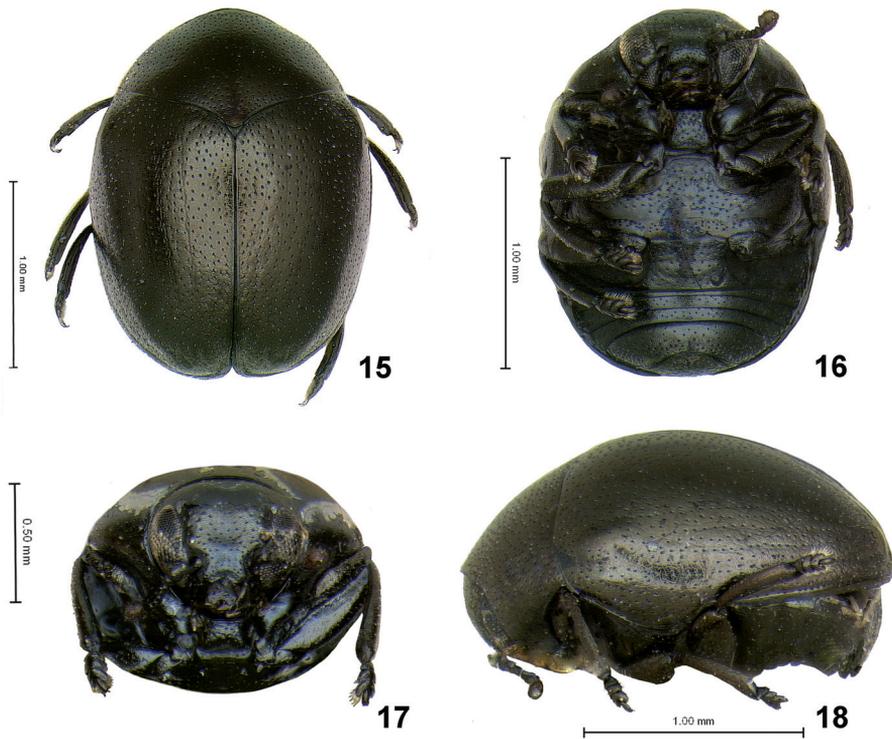
Wing fully developed (Fig. 19). Radial (RA) sinusoidal, wide, and strongly sclerotized laterally, bending posteriorly. RP connected to posterior arm of radial cell,



Figures 11–14. Thoracic characters of Lamprosomatinae and Chlamisini: **11** *Cachiporra extremaglobosa* **12** *Neochlamys strigicollis* **13** *Sphaerocharis marginicollis* **14** *Melittochlamys semen*

divided into two parts: poorly sclerotized median and strongly sclerotized lateral. AA better developed than CuA. RA 3+4 absent. Cu and A form only one complete cell.

Abdomen. First visible abdominal ventrite as long (medially) as rest of abdomen. Second visible ventrite narrowest, half as narrow medially as either third and fourth. Third and fourth of equal length (Fig. 12). Last abdominal ventrite three



Figures 15–18. *Cachiporra extremaglobosa*: 15 dorsal 16 ventral 17 frontal 18 lateral views.

times longer than preceding, without stridularoty file (device) on distal border. Pygidium exposed.

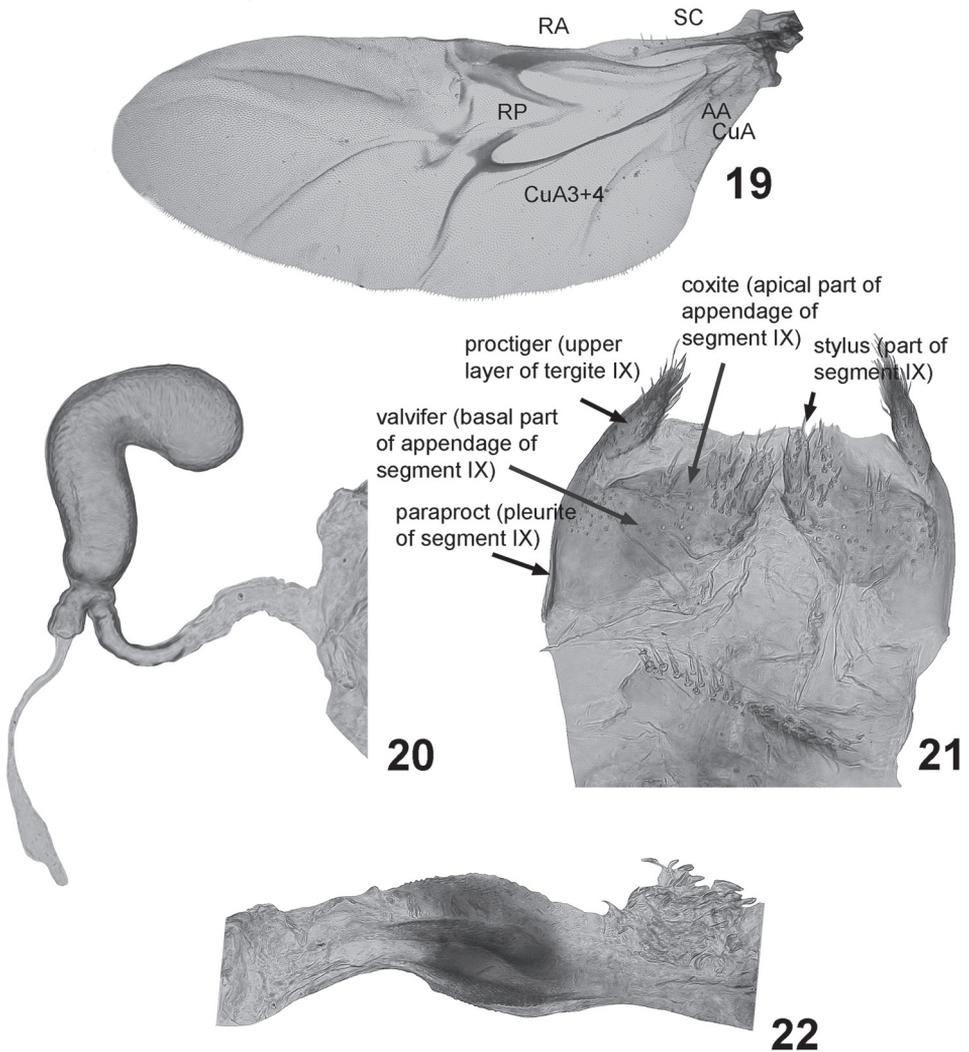
Kotpresse without dorsal or ventral sclerites with chitinpolster dorsally and ventrally; long lateral fold sclerotized and bent upward and with small denticles (Fig. 22).

Legs. Femora dorsoventrally flat with anterior and posterior sides nearly parallel to each other. Tibiae slightly curved in ventral view gradually widening apically. All tibial apices with small spur, but without long setae and excavation. Tarsal claws relatively small, simple, and free.

Female genitalia (Figs 20, 21). Paraproct (pleurite of segment IX) narrow. Proctiger (upper layer of tergite IX) widely triangular, with setae on their apical margins, moderately sclerotized and narrow membranous stripe between them. Stylus parallel-sided, at base much narrower than long, separated by distinct border from coxite (apical part of appendage of segment IX). Spermatheca without border between pump and receptacle. Base of spermatheca constricted forming short canal branching into gland and duct. Gland and duct relatively short making no loops. Tignum absent.

Etymology. “Cachiporra” is the Spanish word for “billy” club (capitulum). “Cachiporra” alludes to the club-shaped antenna of this lamprosomatine. Feminine.

Distribution. Brazil, Rio Grande do Norte, Natal.



Figures 19–22. *Cachiporra extremaglobosa*: **19** wing **20** spermatheca **21** sclerites of female genitalia **22** kotpresse.

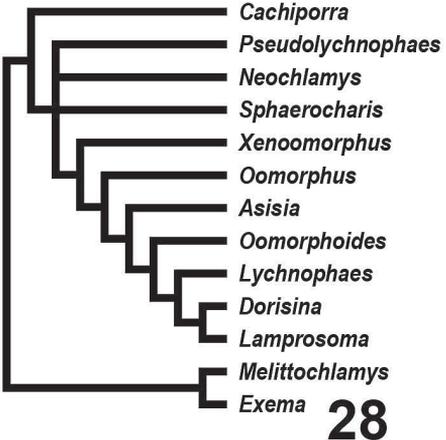
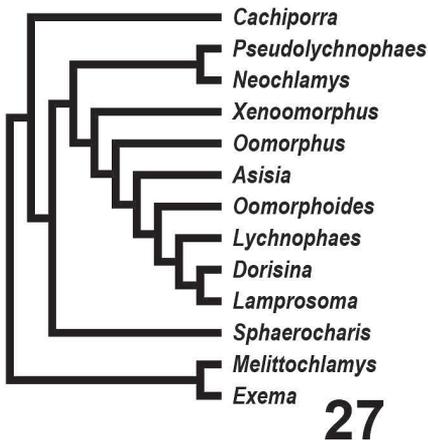
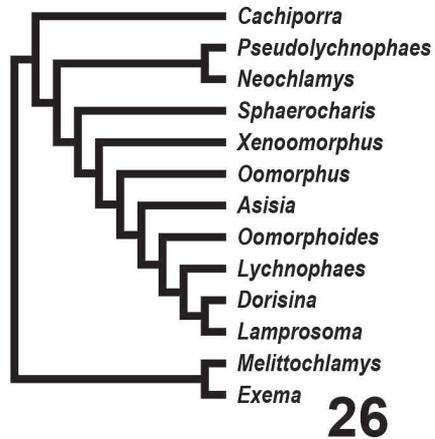
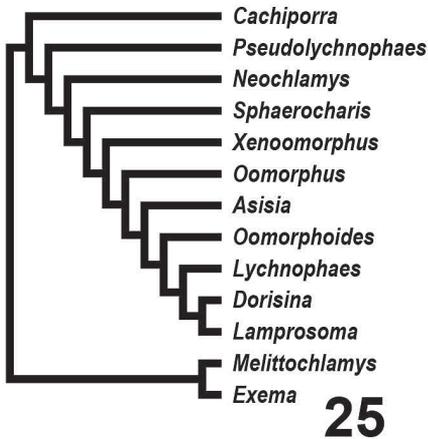
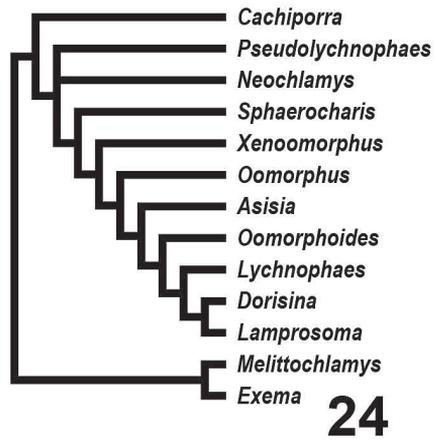
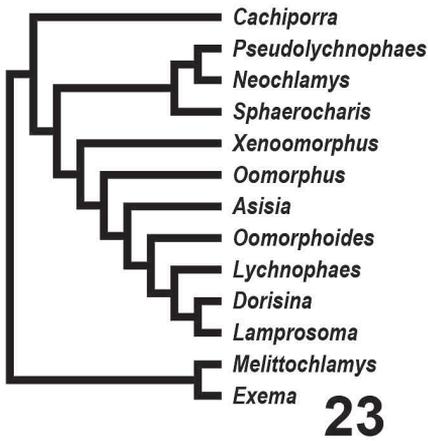
***Cachiporra extremaglobosa* Chamorro & Konstantinov, sp. n.**

urn:lsid:zoobank.org:act:464C4E20-8CAB-40C4-A072-27D057015464

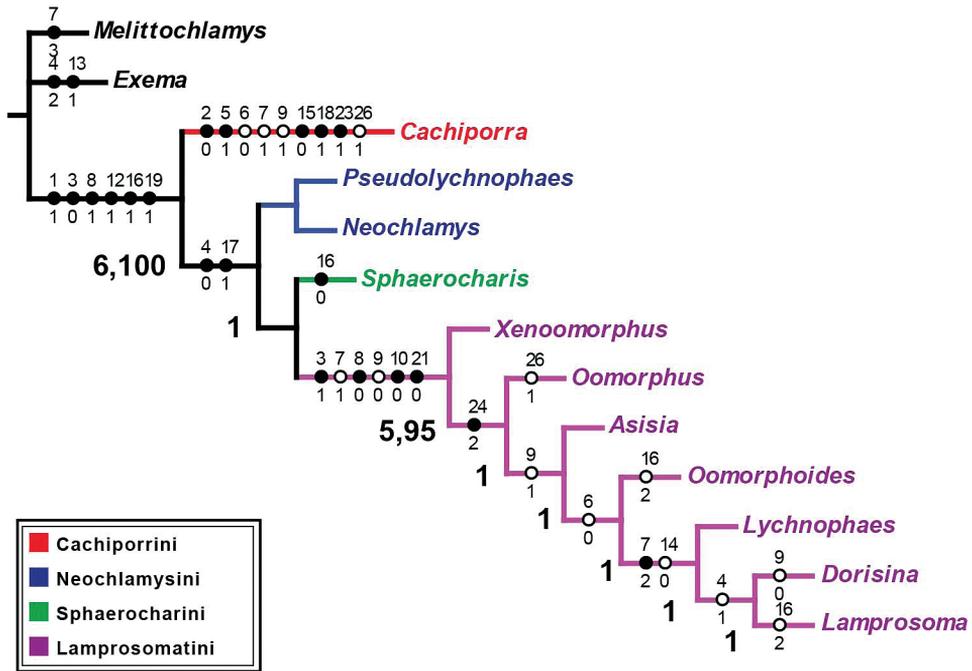
Figs 11, 15–22

Type locality. Brazil, Rio Grande do Norte, Natal.

Description. Length 1.81-1.85 mm. Color black, with bluish and bronzish tint. Head with frons and vertex shagreened, covered by sparse, sharply defined punctures.



Figures 23–28. Cladograms of Lamprosomatinae relationships. Outgroup *Exema* and *Melittochlamys* (Chlamisini) **23–27** Five equally parsimonious trees **28** Strict consensus of 5 equally parsimonious trees.



29

Figure 29. Majority (50%) rule consensus tree with unambiguous character state optimizations. Black circles represent synapomorphies; open circles indicate homoplasious character state transformations. Numbers above correspond to list of characters on table 2; numbers below indicate the state for character indicated above. Bremer support values are indicated by the first numbers on some nodes. Second numbers (only for two clades) separated by a comma indicate bootstrap values (showing only those >5%).

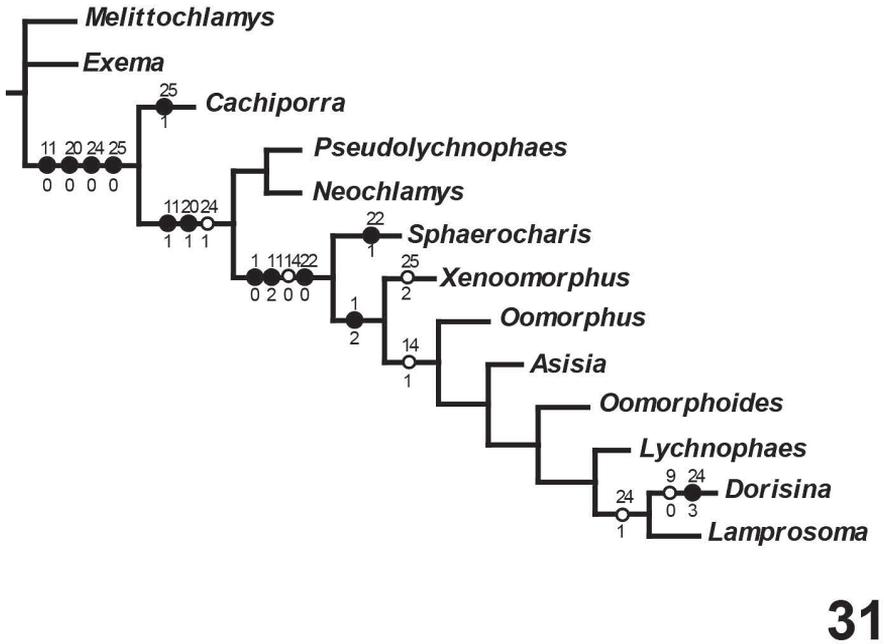
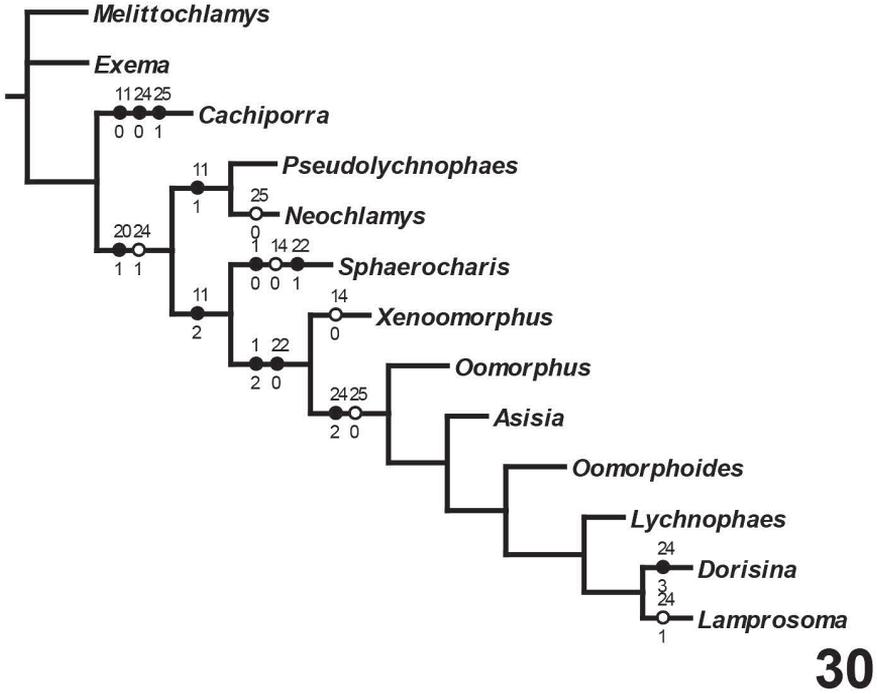
Pronotum strongly shagreened, evenly covered with sharply impressed small punctures, each bearing a single, small seta. Diameter of punctures four to ten times smaller than distance between them.

Elytral surface strongly shagreened, with numerous wrinkles, some of which short and placed diagonally, some exceptionally long and stretched from base of elytron to and beyond middle. Punctures with tendency to form rows.

Female genitalia. Median side of the lateral sclerotization of tergite IX strongly oblique. Stylus attached slightly anteriorly from apex. Receptacle of spermatheca slightly longer than pump, slightly S-shaped with small bump near base and apically. Apex of spermathecal pump bulbous, wider than receptacle and base of pump.

Material examined. Holotype, female: 1) Brazil RG Norte, Papari: III. 1952. M. Alvarengo; 2) F. Monrós Collection, 1959; 3) Holotype *Cachiporra extremaglobosa* Chamorro & Konstantinov, des. 2010 (NMNH).

Paratype, female: 1) Brazil Natal, R.G. Norte, 24.IX. 1951. M. Alvarengo; 2) F. Monrós Collection, 1959; 3) Paratype *Cachiporra extremaglobosa* Chamorro & Konstantinov, des. 2010 (NMNH).



Figures 30–31. Majority (50%) rule consensus tree. Black circles represent synapomorphies; open circles indicate homoplasious character state transformations. Unambiguous characters deleted **30** Character states under slow (DELTRAN) optimization **31** Character states under fast (ACCTRAN) optimization.

Etymology. Named for the extremely globular antennal club (capitulum). The epithet is treated as a noun in apposition.

Discussion. Unique features of Cachiporrini include the following: antennomeres 7–11 fused into a tight capitulum (2:0); explanation of lateral margin of pronotum situated ventrally essentially covered from above by expansion of upper side of pronotum laterally (5:1); pronotal and elytral punctures with setae (15:0); wings with RA 3+4 absent (18:1); absence of sclerotized rim of kotpresse (23:1); and stylus of female genitalia longer than wide.

Among various lamprosomatine genera, *Cachiporra* is superficially most similar in color, size, wing venation, and overall body shape to *Oomorplus*. The pronotum of *Cachiporra* is considerably different from that of *Oomorplus* and all other lamprosomatines in having the sides swollen and bent ventrally so that the lateral border is not visible from above. The lateral border is therefore located very close to the posterior margin of the prosternum, leaving hypomera extremely thin and limiting the intercoxal prosternal process to the shape of a small triangle. In *Oomorplus* the sides of the pronotum are not bent ventrally and the hypomera and the prosternum itself occupy most of the ventral side of the lateral part of prothorax. Furthermore, dorsally the pronotum in *Cachiporra* is basally sinuate and medially extending posterad beyond elytral base (Fig. 15) and side of elytron have an extended lobe directed ventrad nearly concealing all of metepisternite (Fig. 11).

Cachiporra has a number of pleisiomorphies also present in African Neochlamysini. These are absence of a stridulatory device (also absent in Sphaerocharini), entire eyes, completely exposed pygidium, and free and simple claws.

Synapomorphies of Lamprosomatinae (Fig. 29) include the loss of canthus of the eye, character 1 state 1 (1:1); antennomeres 6–8 strongly transverse, more than twice as wide as long, 3:0; triangular scutellum, 8:1; smooth elytra, 12:1; tarsal claws simple and free, 16:1; and have CuA 3+4 and spurt RP distant from each other, 19:1. Of the four tribes, Lamprosomatini has the greatest support with at least four synapomorphies and a number of homoplasious character states (Figs 29–31). Sides of elytra extended in wide relatively short lobe, not concealing much of metepisternite (character 11:1) (Fig. 12) supports the monophyly of Neochlamysini under slow optimization (Fig. 30). The transformation of the sides of elytra into a narrow lobe concealing nearly all posterior part of metepisternite (character 11:2) (Fig. 13) is a shared derived feature of Sphaerocharini + Lamprosomatini (Fig. 30) under slow optimization. In Cachiporrini this lobe is wide and long concealing most of middle to posterior part of metepisternite (character 11:0) (Fig. 11); a unique feature of this tribe.

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Agricultural University, Kerala, India) for reviewing earlier versions of this manuscript and providing valuable suggestions. We thank Dr. X. Mengual for his generosity and help with software. MLC thanks T. Erwin and the Encyclopedia of Life, Rubenstein fellowship program (National Museum of Natural History, Smithsonian Institution, Washington DC) for funding and support.

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