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Epimeria liui sp. nov., a new calcified amphipod (Amphipoda, Amphilochidea, Epimeriidae) from a seamount of the Caroline Plate, NW Pacific

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Abstract

A calcified individual of *Epimeria* Costa, 1851 collected from an unnamed seamount of the Caroline Plate, NW Pacific, is recognized as new to science herein. This increases the number of known *Epimeria* species of the North Pacific to nine. *Epimeria liui* **sp. nov.** differs from its similar congeners by having a rostrum hardly reaching to the end margin of first peduncular article of antenna 1, the presence of large pyriform eyes, the size-increasing mid-dorsal teeth starting from pereonite 6 to pleonite 2, the projection on coxa 5 not extending to epimeral plate 1, and by having a nearly quadrate telson notched medially. To facilitate identification the new species is included in a key to Pacific species of *Epimeria*.

Keywords

Amphipoda, Caroline Plate, deep sea, *Epimeria*, new species, seamount, systematics

Introduction

The genus *Epimeria* Costa in Hope, 1851 currently contains nine subgenera and 85 described species (WoRMS 2019). This almost cosmopolitan genus is particularly diverse in the Southern Ocean (59 species), and has been recorded from the intertidal down to 5695 m depth (Stephensen 1947; Shimomura and Tomikawa 2016; d'Udekem d'Acoz and Verheye 2017). When the Chinese research vessel KEXUE surveyed the biodiversity of seamounts on the Caroline Plate, NW Pacific during 2019, one individual referable to *Epimeria* was collected. The specimen exhibits some distinctive characters differentiating it from other described *Epimeria* species, so it is identified as new to science herein. This new species is described, and morphologically compared to other very similar species are presented, and a key to all Pacific *Epimeria* species is also provided.

Material and methods

The present material was collected by ROV FAXIAN, during expeditions to seamounts on the Caroline Plate by the Institute of Oceanology, Chinese Academy of Sciences (IOCAS) during June to July 2019. The specimen is deposited in the Marine Biological Museum, Chinese Academy of Sciences, Qingdao, China. The individual was examined and dissected with a dissecting microscope (ZEISS Discovery V20). Line drawings were completed using the software Adobe Photoshop CS6 with a graphics tablet. Length measurement was made along the outline of the animal, beginning from the rostrum to the posterior margin of telson.

Systematics

Order Amphipoda Latreille, 1816
Suborder Amphilochidea Boeck, 1871
Superfamily Iphimedioidea Boeck, 1871
Family Epimeriidae Boeck, 1871

Genus *Epimeria* Costa in Hope, 1851

Diagnosis (from d'Udekem d'Acoz and Verheye 2017). Body smooth or covered with teeth or processes, but not sword-like or forming large longitudinal carinae. Head with developed ventral lobe; rostrum usually well developed; eyes usually present, bulging. Antenna 1 peduncular articles short, with accessory flagellum. Upper lip entire or symmetrically notched. Mandible with incisor and molar present; lacinia mobilis present on both mandibles. Lower lip without inner lobes. Maxilla 1 with 2-articulate palp.

Coxae 1–4 progressively longer, coxae 1–3 narrow, coxa 4 five-sided; coxae 5–6 with or without tooth or process projecting laterally. Gnathopods weak; gnathopod 2 longer than gnathopod 1. Pereiopod 6 > pereiopod 5 > pereiopod 7; basis of that with longitudinal carina on both sides. Coxal gill from gnathopod 2 to pereiopod 7. Oostegite large, from gnathopod 2 to pereiopod 6. Uropods well developed. Urosomite 1 always with a rounded or tooth-like process. Telson incised or cleft, rarely emarginate or entire.

***Epimeria liui* sp. nov.**

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Figs 1–4

Material examined. Holotype. Ovigerous ♀ (17.8 mm) (MBM 286613), dissected, unnamed seamount on Caroline Plate, NW Pacific, M6089, St. FX-Dive 218, 10°07'N, 140°14'E, depth 813–1242 m, 6 June 2019, collected by team of ROV FAXIAN.

Diagnosis. Rostrum hardly reaching to distal margin of first peduncular article of antenna 1; eyes present, pigmented, pyriform. Maxilliped palp article 4 with more than two teeth in internal margin. Coxa 5 with posterodistal corner produced. Pereonites 6, 7 and pleonites 1, 2 with size-increasing mid-dorsal teeth, the one on pereonite 6 blunt and small.

Description. Body calcified. ***Head.*** Rostrum nearly as long as head, not reaching to distal margin of first peduncular article of antenna 1; anterior cephalic margin with a small lobe medially, lateral cephalic slightly produced; eyes bulging on head, pigmented, pyriform. Antenna 1 with peduncular article 1 about twice as long as article 2, 3 times as long as article 3, without distal tooth; accessory flagellum scale-like, hardly reaching to half-length of first flagellar article; primary flagellum with 26 articles, sparsely setose. Antenna 2 nearly as long as antenna 1, peduncular article 4 slightly longer than article 5; flagellum with 29 articles.

Mouthparts. Mandible with incisor and lacinia mobilis strongly dentate; molar triturative; palp article 3 densely setose medially, with two long setae distally. Maxilla 1 with inner plate subtriangular, obliquely convex inner margin with 10 stout plumose setae; outer plate distal margin oblique, with 11 lobate robust setae; palp exceeding outer plate; palp 2-articulate, article 2 with 3 robust setae and 5 long setae distally, inner margin bearing row of dense setae. Maxilla 2 with long, slender setae distally on lateral and medial plates. Maxilliped with outer plate broadly rounded distally, bearing short setae, hardly reaching to distal margin of palp article 3; inner plate with row of short setae medially and anteriorly; palp medial margin strongly setose, article 3 with groups of long setae reaching distal end of dactylus, dactylus with serrate medial margin.

Pereonites. Pereonites 1–7 lacking lateral projection; pereonite 1 subequal in length to head (excluding rostrum), pereonite 2 shorter than pereonite 1; pereonites 1–5 lacking mid-dorsal tooth; pereonite 6 with slight blunt mid-dorsal protrusion; pereonite 7 with acute triangular mid-dorsal tooth.

Pleosome. Pleonites 1 and 2 with size-increasing, acute triangular mid-dorsal tooth, and inconspicuous posterolateral protrusions; dorsal margin of pleonite 3 sinuous. Epimeral plates 1–3 with posteroventral angle produced into small subacute tooth.

Urosome. Urosomite 1 with blunt triangular mid-dorsal tooth; urosomite 2 shortest; urosomite 3 dorsal margin slightly sinuous.

Pereopods. Gnathopod 1 coxa long and slender, posterior margin bearing row of small robust setae; basis linear, both margins with numerous slender setae; merus nearly as long as ischium, anterior margin very short, distal margin oblique, posterodistal angle acute, setose; carpus linear, longer than propodus, posterior margin strong setose, anterior margin bearing group of setae distally; propodus slightly expanded distally, posterior margin and palm with robust setae, faces bearing groups of robust setae; dactylus slender, slightly curved, posterior margin minutely serrated. Gnathopod 2 coxa wider and longer than coxa 1, posterior margin bearing row of small robust setae; basis linear, ischium and merus similar to that of gnathopod 1; carpus linear, posterior margin setose; propodus and dactylus of similar appearance to gnathopod 1. Pereopod 3 coxa wider and longer than coxa 2, posterior margin bearing small robust setae and blunt protrusion on proximal half; basis linear, both margins setose; merus longer than carpus, margins bearing small setae; carpus shorter than propodus, margins setose; propodus with posterior margin bearing robust setae; dactylus stout, curved, without setae. Pereopod 4 coxa longer than coxa 3, anterior margin nearly straight, ventral tooth slightly curved, apically subacute and oriented backwards, lateral carina without tooth, not projecting laterally, carina very distant from margin of coxa at its deepest point; basis to dactylus as for pereopod 3. Pereopod 5 coxa subrectangular, posterodistal corner produced, drawn out to pointed wing in dorsal view; basis wider than that of pereopod 4, posterodistal corner rounded, setose; ischium bearing posterodistal lobe; merus nearly as long as carpus, posterior margin produced, anterior margin bearing small setae; carpus shorter than propodus, with anterior margin bearing robust setae; propodus with anterior margin setose; dactylus stout, curved. Pereopod 6 coxa bearing carinate, lateral tooth forming a small triangular wing in dorsal view; basis wider in pereopod 5, bearing carina, setose; ischium to dactylus as for pereopod 5. Pereopod 7 coxa subrectangular; basis larger than that of pereopod 6, expanded mid-posteriorly; ischium to dactylus similar to that of pereopods 5 and 6.

Uropods and telson. Uropod 1 peduncle subequal in length to rami, outer margin setose; rami subequal in length, margins bearing small robust setae. Uropod 2 peduncle subequal to outer ramus, outer margin setose; outer ramus shorter than inner ramus, both rami outer and inner margins setose. Uropod 3 peduncle much shorter than rami, inner margin with robust setae; rami subequal in length, inner and outer margins of both rami bearing short robust setae. Telson nearly as long as wide, posterior margin notched medially.

Coloration. Freshly captured specimen of *Epimeria liui* sp. nov. show distinct orange eyes and rose- to ivory-colored body.

Etymology. The species is named in honor of the late Prof. Dr. Ruiyu Liu (J.Y. Liu), the Institute of Oceanology, Chinese Academy of Sciences, for his great contribution to the carcinology of China.

Figure 1. *Epimeria liui* sp. nov., female holotype (17.8 mm) (MBM 286613), photographed immediately after capture by Shao-qing Wang.

Distribution. NW Pacific, unnamed seamount on Caroline Plate at a depth of 813–1242 m.

Remarks. Eight *Epimeria* species have been reported from the northern Pacific, including *E. abyssalis* Shimomura & Tomikawa, 2016, *E. cora* J.L. Barnard, 1971, *E. morronei* Winfield et al., 2012, *E. ortizi* Varela & García-Gómez, 2015, *E. pacifica* Gurjanova, 1955, *E. pelagica* Birstein & Vinogradov, 1958, *E. subcarinata* Nagata, 1963 and *E. yaquinae* McCain, 1971. *Epimeria liui* sp. nov. can be distinguished from above species by the following characters: rostrum hardly reaching to the distal margin of first peduncular article of antenna 1; the presence of pyriform pigmented eyes; the projection of coxa 5 not reaching to epimeral plate 1. Actually, *E. liui* sp. nov. more closely resembles *E. bruuni* Barnard, 1961 and *E. horsti* Lörz, 2008, which occur in the southern Pacific, by the produced mid-dorsal carinae starting from pereonite 5 or 6 and having the process on coxa 5 not extending to pleonite 1. The new species differs from *E. bruuni* by the mid-dorsal teeth starting on pereonite 6 and the pleonite 3 not having a large acute mid-dorsal tooth. *Epimeria liui* sp. nov. is especially similar to *E. horsti* for the coloration of the animal body. But it morphologically differs from *E. horsti* by the rostrum not extending to the distal margin of first peduncular article of antenna 1, the anterior cephalic margin having a semicircular lobe, the coxa 5 having a ridge whereas this part in *E. horsti* appears to be smooth (Lörz 2008, figs 1, 5), the mid-dorsal blunt tooth of pereonite 6 not forming a triangular acute tooth as in *E. horsti*

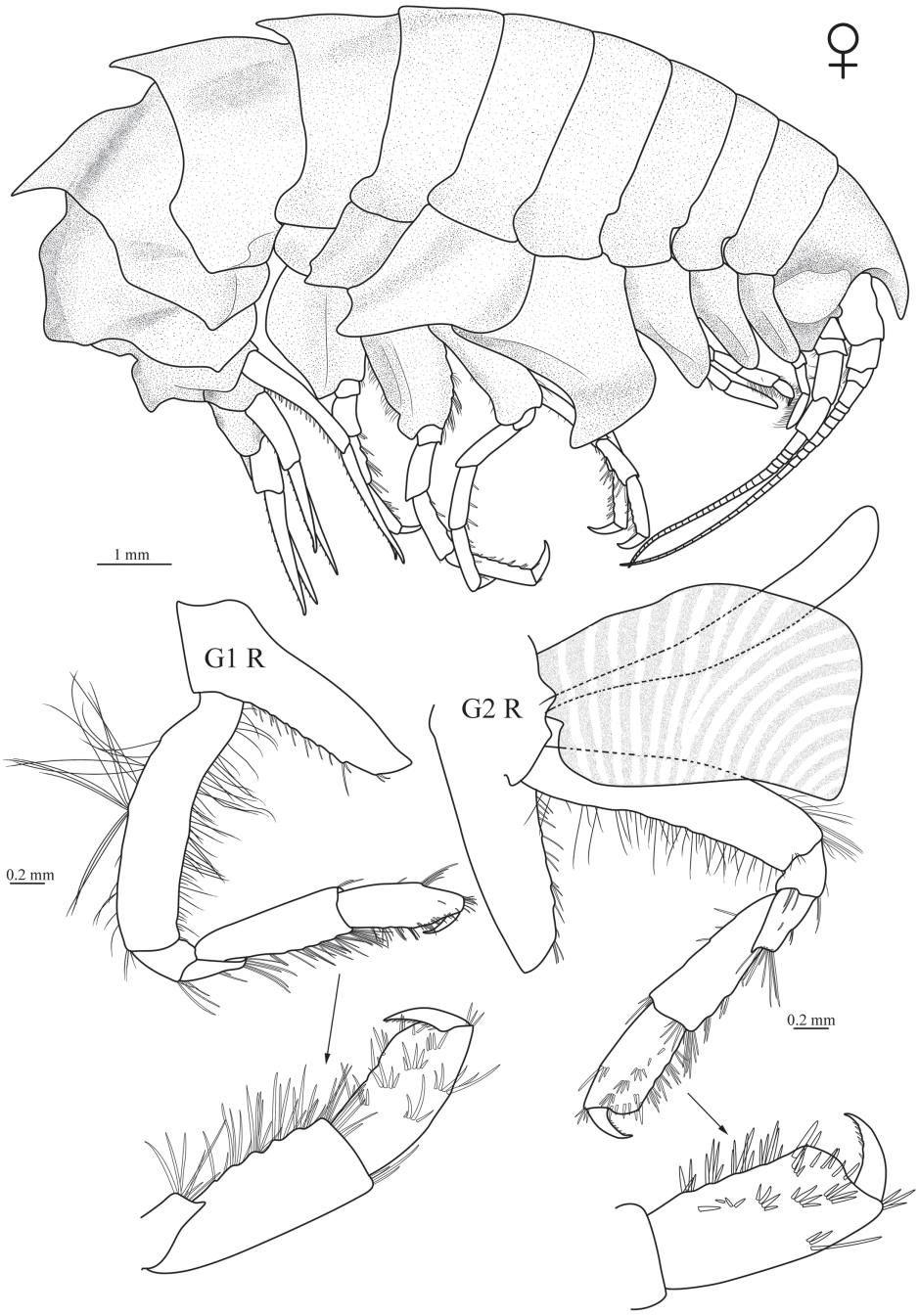

Figure 2. *Epimeria liui* sp. nov., female holotype (17.8 mm) (MBM 286613), G1 R, right gnathopod 1; G2 R, right gnathopod 2.

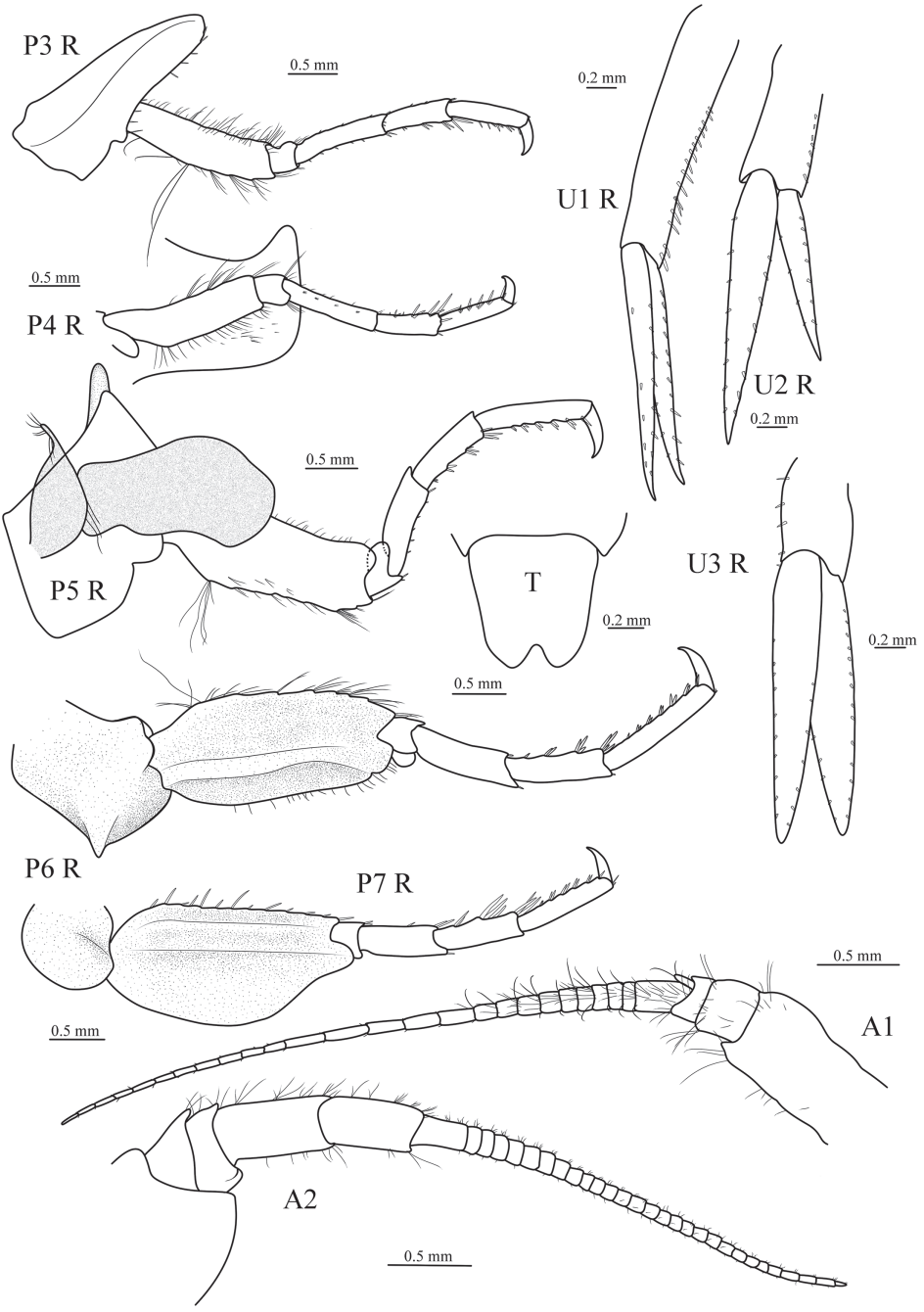

Figure 3. *Epimeria liui* sp. nov., female holotype (17.8 mm) (MBM 286613), P3 R, right pereopod 3; P4 R, right pereopod 4; P5 R, right pereopod 5; P6 R, right pereopod 6; P7 R, right pereopod 7; A1, antenna 1; A2, antenna 2; U1 R, right uropod 1; U2 R, right uropod 2; U3 R, right uropod 3; T, telson.

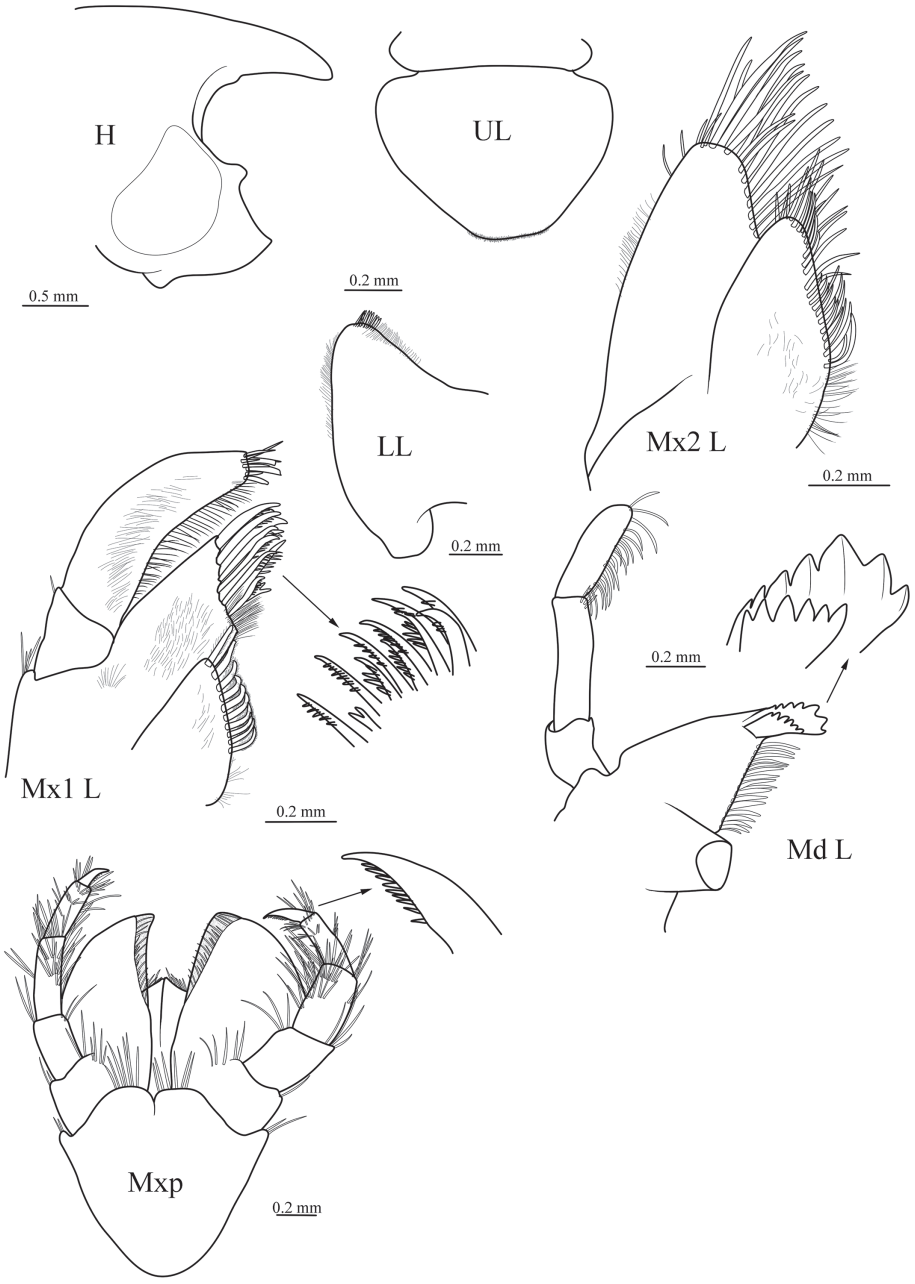

Figure 4. *Epimeria liui* sp. nov., female holotype (17.8 mm) (MBM 286613), H, head; UL, upper lip; LL, lower lip; Md L, left mandible; Mx1 L, left maxilla 1; Mx2 L, left maxilla 2; Mxp, maxilliped.

(Lörz 2008, fig. 1), the pleonite 3 not having a mid-dorsal tooth, the posteroventral angle of the epimeron 3 not being produced, and by the telson being notched medially. The key to the species of *Epimeria* based on Lörz and Coleman (2014) and Shimomura and Tomikawa (2016) is presented below.

Key to the Pacific species of *Epimeria*

1 Pereon segments lacking dorsal carinae....**2**
– Pereon segments bearing dorsal carinae....**11**
2 Eyes present....**3**
– Eyes absent....**8**
3 Urosomite 1 bearing dorsally pointed tooth; rostrum extending beyond first peduncle article of antenna 1....**4**
– Urosomite 1 lacking dorsally pointed tooth; rostrum not extending beyond first peduncle article of antenna 1....**6**
4 Coxa 5 projection not reaching to epimeral plate 1 ....***E. cora* J.L. Barnard, 1971**
– Coxa 5 projection reaching to epimeral plate 1....**5**
5 Head ventral lobe not produced....***E. ortizi* Varela & García-Gómez, 2015**
– Head ventral lobe produced....***E. pacifica* Gurjanova, 1955**
6 Coxa 5 with protrusion reaching posterior margin of epimeral plate 2; telson not cleft....***E. norfanzi* Lörz, 2011**
– Coxa 5 not produced; telson cleft....7
7 Telson with deep and broad V-shaped excavation....
....***E. pelagica* Birstein & M. Vinogradov, 1958**
– Telson with deep and narrow Y-shaped excavation....
....***E. abyssalis* Shimomura & Tomikawa, 2016**
8 Coxa 5 produced....**9**
– Coxa 5 not produced....***E. yaquinae* McCain, 1971**
9 Pleonites 1–3 with dorsal carinae; pleonite 3 not dorsally produced; coxae 1–3 ventrally rounded....**10**
– Pleonites 1–2 smooth; pleonite 3 dorsally produced; coxae 1–3 ventrally pointed....***E. subcarinata* Nagata, 1963**
10 Rostrum not extending beyond first peduncle article of antenna 1....
....***E. glaucosa* J.L. Barnard, 1961**
– Rostrum extending beyond second peduncle article of antenna 1....
....***E. morronei* Winfield, Ortiz & Hendrickx, 2012**
11 Coxa 5 produced....**12**
– Coxa 5 not produced....**15**
12 Dorsal carinae starting on pereon 4; epimeral plates bearing produced postero-lateral corners and at least two produced lateral teeth each....***E. victoria* Hurley, 1957**
– Dorsal carinae starting on pereon 6; posterolateral corners of epimeral plates 1 and 2 rounded or weakly produced....**13**
13 Pereonites 6 and 7 laterally smooth; coxa 1 ventrally rounded....**14**
– Pereonites 6 and 7 laterally bearing projections; coxa 1 ventrally subquadrate....
....***E. emma* Lörz & Coleman, 2014**
14 Rostrum not extending to distal margin of first peduncular article of antenna 1 .
....***E. liui* sp. nov.**
– Rostrum beyond distal margin of first peduncular article of antenna 1....
....***E. horsti* Lörz & Coleman, 2014**

15 Double dorsal carinae present on pleonites 1–3.....**16**
– Single dorsal carinae present on pleonites 1–3.....***E. bruuni* J.L. Barnard, 1961**
16 Pleonites laterally smooth.....***E. sophie* Lörz & Coleman, 2014**
– Pleonites laterally bearing several projections.....
..... ***E.* (*Metepimeria*) *ashleyi* (Lörz, 2012)**

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New morphological and molecular data on the little-known pontellid *Calanopia media* Gurney, 1927 (Crustacea, Copepoda, Calanoida) from the Red Sea, with notes on its diel vertical distribution

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Abstract

As a part of the routine neritic zooplankton collection program in Obhur Creek (central Red Sea, Saudi Arabia), specimens of a pontellid calanoid copepod, *Calanopia media* Gurney, 1927, were observed and studied. Since the original description was rather brief and drawings limited, especially of mouthparts and legs, which were not illustrated and described, the species is here fully redescribed. Red Sea specimens showed considerable variation in the female genital compound somite, the right caudal ramus and leg 5, as well as in the presence of a medial knob ventrally on the male right prosomal corner. DNA sequences of mtCOI of different specimens did not show any significant differences and supported their identity as one species. *Calanopia media* exhibited clear diel vertical migration, with high densities of 106 and 150 ind. m^{-3} during sunset (6:00 pm; UTC+3) and midnight (12:00 am; UTC+3) collections, respectively. However, this species was not observed in other zooplankton collections from the surface to 20 m depth, at 6:00 am and 12:00 pm (UTC+3).

Keywords

Calanopia media, copepods, pontellid, redescription, Red Sea

Introduction

The pontellid (Calanoida) fauna of the Red Sea contains a surprisingly low proportion of the Indo-Pacific fauna, from which it is apparently derived (El-Sherbiny and Ueda 2008; El-Sherbiny 2009). Five genera and 17 pontellid species have been recorded from the Red Sea (Al-Aidaroos et al. 2019; El-Sherbiny and Al-Aidaroos 2017; Razouls et al. 2019), whereas 77 pontellid species are present in the greater Indian Ocean (Razouls et al. 2019). Among the Red Sea pontellids, there are six species of *Calanopia* (Al-Aidaroos et al. 2016; El-Sherbiny and Al-Aidaroos 2017), namely: *C. elliptica* Dana, 1849, *C. minor* A. Scott, 1902, *C. media* Gurney, 1927, *C. kideysi* Ünal & Shmeleva, 2002, *C. thompsoni* A. Scott, 1909 and *C. tulina* El-Sherbiny & Al-Aidaroos, 2017. The original description of *C. media* is rather brief, does not include the cephalic and thoracic limbs, and illustrations are confined to habitus drawings of the female and male in dorsal view, the female urosome, the male right antennule ancestral segments 19 and 20 and the male and female leg 5.

During the examination of plankton, samples collected from the Saudi Arabian waters of the central Red Sea, in Obhur Creek, Jeddah, specimens of what we provisionally called *C. media* were observed. These specimens differ in some respects from Gurney's (1927) original description. Here, we provide a full description of the species and an account of variability among the Obhur Creek specimens. Comparison with the type specimens held in the Natural History Museum, London (BMNH 1926.2.16.69-88) was carried out, and information on the vertical migration in the water column was provided. In addition, the mitochondrial COI gene of some species from the Red Sea was sequenced and compared with the sequences available in GenBank (NCBI) to determine their affinity.

Material and methods

Zooplankton samples were collected from Obhur Creek (21°42'32.23"N, 39°5'41.56"E) using a 50 cm diameter plankton net of 150 μm mesh size, towed near the surface for 10 minutes at a speed of about 1–1.5 knots and vertically from 20m depth to the surface on 21 January 2016 at 7:00am, 12:00pm, 6:00pm and 12:00am (UTC+3) local time (sunrise at 7:04am and sunset at 6:05pm; UTC+3). A flowmeter (Hydrobios) was attached to the net mouth for estimating the volume of water filtered. Samples were fixed immediately in 95% alcohol. Subsequently, *Calanopia media* specimens were picked from zooplankton samples collected at midnight. For microscopic examination, specimens were dissected in lactic acid and were observed using bright-field and differential interference microscopy (Nikon DM 6000). Drawings and measurements were made with a camera lucida attached to the microscope and an ocular micrometer. Morphological terminology follows Huys and Boxshall (1991), except for maxillary and maxillipedal appendages, which follow Ferrari and Ivanenko (2008). For scanning electron microscopy, *Calanopia* specimens were washed three times in filtered seawater and clean distilled water, then dehydrated through a 30–100% ethanol series

and dried with hexamethyldisilazane. The specimens were mounted on a stub, coated with gold palladium, and observed with a SEM FEI-QUANTA 250.

For genetic analysis, four intact female specimens of *C. media*, three of *C. minor*, one of *C. elliptica* and two of *C. thompsoni* (after accurate morphological identification) were sorted out and the genomic DNA was extracted from individual specimens. A portion of the mitochondrial gene cytochrome oxidase subunit I (mtCOI) was amplified using the universal primers of Folmer et al. (1994). Individual copepods were digested in 400 µl ATL buffer (Qiagen) and 20 µl Proteinase K overnight, in a capped 0.2ml microcentrifuge tube. After digestion, 400 µl of AL buffer was added and DNA extraction continued using Qiagen's Blood and Tissue kit as per the manufacturer's instructions. DNA was precipitated in 30 µl AE buffer and mtCOI amplicons were amplified using the PCR primers LCO1490 and HCO2198 (Folmer et al. 1994). The reaction conditions were initial denaturation for 5 min at 95 °C followed by 40 cycles of 94 °C (1 min); 47 °C (2 min); 72 °C (3 min). A final extension at 72 °C for 10 min was undertaken. PCR products were purified using ExoStar (Illustra) and sequencing was carried out in an ABI 3730×l Capillary Sequencer. The machine-read sequences were compiled using Sequencing Analysis (Ver. 3.3, ABI prism) and manually checked for accuracy. Available sequences of *C. thompsoni* were obtained from the NCBI database for comparison. Pairwise distance measures and phylogenetic analyses were conducted using the MEGA X software (Kumar et al. 2018). Ambiguous sites were eliminated from the dataset.

Results

Systematics
Subclass Copepoda Milne-Edwards, 1840
Order Calanoida Sars, 1903
Family Pontellidae Dana, 1852
Genus *Calanopia* Dana, 1852

***Calanopia media* Gurney, 1927**
Figs 1–6

Material examined. 36 females (body length: 1.17–1.32 mm, mean ± SD: 1.25±0.051 mm) and 25 males (body length: 1.10–1.26 mm, mean ± SD: 1.14±0.048 mm); whole specimens in 70% ethanol were deposited in the Natural History Museum, London [Registration number: NHMUK 2018. 1538–1547]. All specimens were collected at Obhur Creek, central Red Sea (21°42'32.23"N, 39°5'41.56"E) on 21 January 2016 by M.M. El-Sherbiny.

DNA-barcode. The mitochondrial gene cytochrome oxidase subunit (mtCOI) sequences were submitted to GenBank (GenBank Accession numbers for *C. elliptica*: MN796254; *C. media*: MN445608–MN445611; *C. minor*: MN796251–MN796253; *C. thompsoni*: MN796255–MN796256).

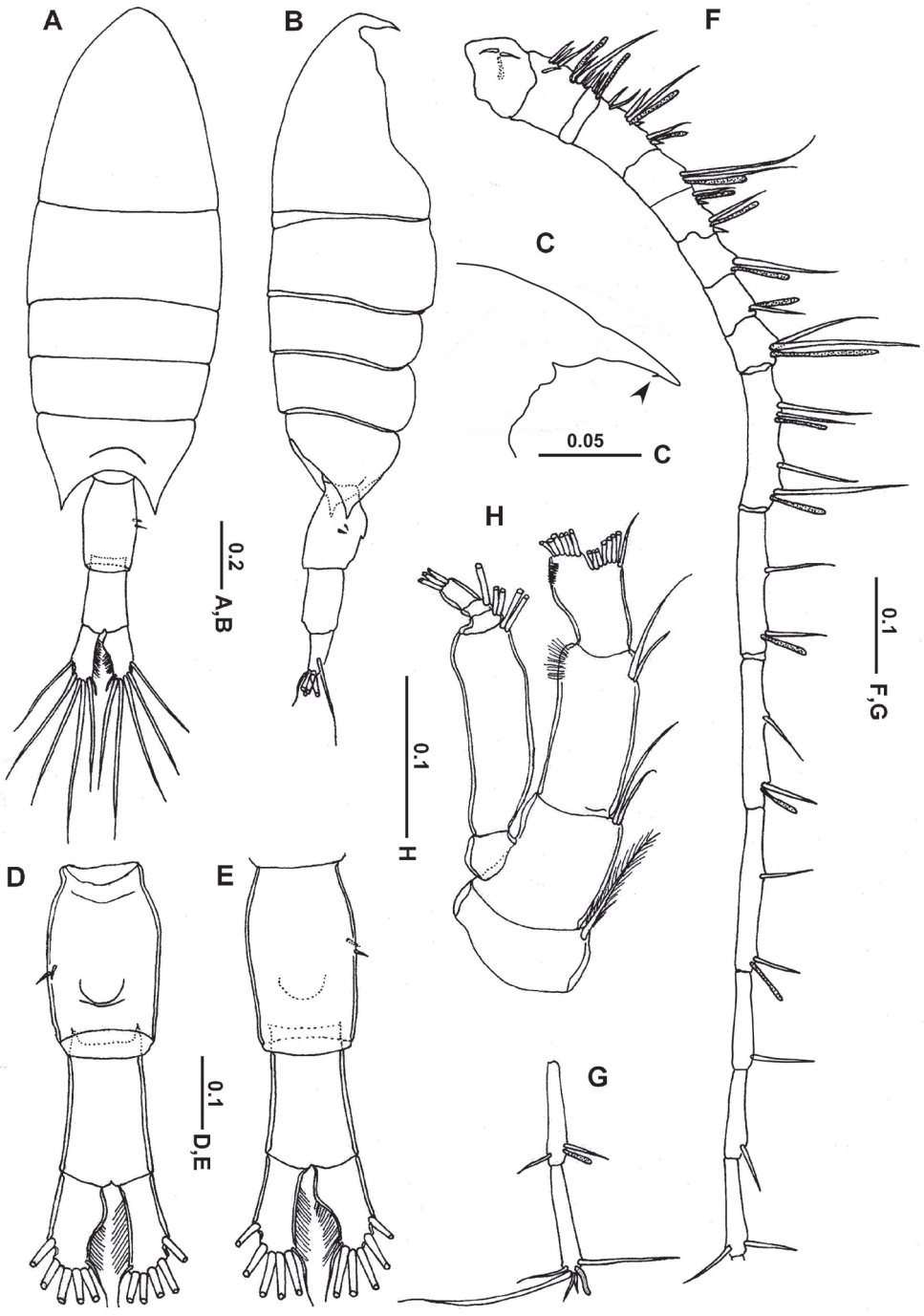

Figure 1. *Calanopia media* female from the Red Sea **A** habitus, dorsal view **B** habitus, lateral view **C** rostrum, lateral view (rudimentary rostral notch indicated by arrow) **D** abdomen, ventral view **E** abdomen, dorsal view **F–G** antennule **H** antenna. Scale bars in mm.

Description. Female. ***Prosome*** (Fig. 1A, B) elliptical, without lateral hooks; cephalosome and first pedigerous somite completely separated; fourth and fifth pedigerous somites completely fused, with dorsal suture visible; posterior corners of prosome symmetrical, sharply pointed, extending nearly one-third of way along genital compound somite. Rostrum with broad base and pair of rounded lobes, each terminating in a tapering point (Figs 1C, 2A). Urosome (Figs 1D, E, 2B, C) with 2 free somites: genital compound somite symmetrical in dorsal view, with 2 unequal ventral spinules on right side, ventral surface with smooth, evenly rounded operculum located posterior to mid-length (Figs 1E, 2C); second urosomite symmetrical and slightly shorter than genital compound somite; caudal rami asymmetrical; right ramus broader and expanded anteromedially, slightly shorter than left ramus, each ramus carrying 5 plumose setae (II–VI) along distal margin and a reduced seta (seta VII) located on dorsal surface near medial distal angle.

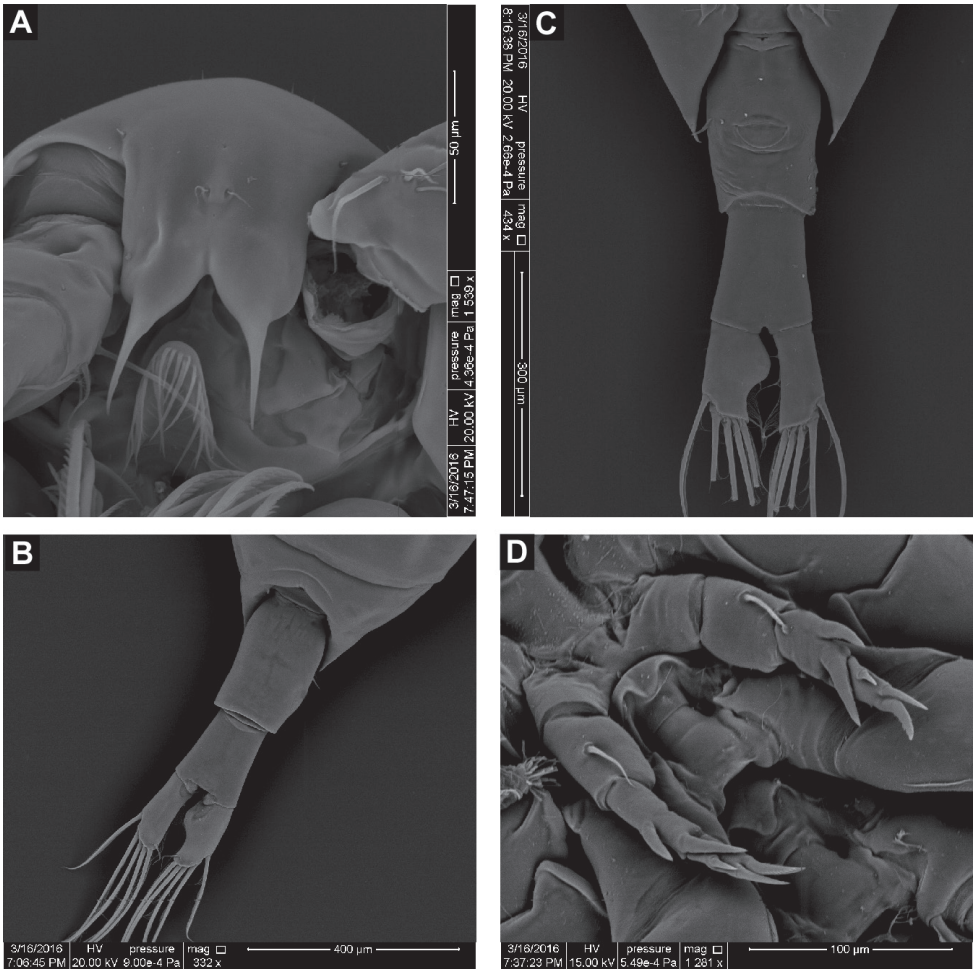

Figure 2. SEM micrographs of *Calanopia media* female from the Red Sea **A** rostrum, ventral view **B** abdomen, dorsal view **C** abdomen, ventral view **D** leg 5, posterior view.

Antennules (Fig. 1F, G) 18-segmented, slightly exceeding end of genital compound urosomite. Fusion pattern and armature elements as follows: ancestral segment I (segment 1) = 2 setae + aesthetasc (ae), II–VI (2) = 8 + ae, VII (3) = 2 + ae, VIII–X (4) = 7 (2 spiniform) + 2ae, XI (5) = 2 + ae, XII–XIII (6) = 4 (2 spiniform) + 2ae, XIV (7) = 1 +ae, XV (8) = 1 + ae, XVI (9) = 2 + ae, XVII–XVIII (10) = 4 + 2ae, XIX (11) = 2 + ae, XX (12) = 2 + ae, XXI (13) = 2 + ae, XXII (14) = 1, XXIII (15) = 1, XXIV (16) = 1 + 1, XXV (17) = 1 + ae+ 1, XXVI–XXVIII (18) = 5 + ae.

Antenna (Fig. 1H) biramous; coxa with plumose seta distomedially; basis carrying 2 subequal plumose setae at distomedial angle; exopod 5-segmented, second segment longest with setal formula of 0, 2, 2, 1, 3. Endopod 2-segmented, first endopodal segment with 2 subequal lateral setae distally and furnished with fine setules distolaterally; second endopodal segment armed with 8 and 6 setae on proximal and distal lobes, respectively, laterodistal border with row of posterior spinules.

Mandible (Fig. 3A). Gnathobase with eight teeth on cutting edge, third and fourth ventralmost teeth bicuspidate; patches of dagger-like spinules arranged at base of third to sixth ventralmost teeth; mandibular palp basis with 4 setae; endopod 2-segmented, first and second segments carrying 3 and 6 setae, respectively; exopod 5-segmented, first to fourth segments each with one seta and fifth segment with 3 setae.

Maxillule (Mx1) (Fig. 3B). Praecoxal endite well developed and extended distally with 9 marginal and 4 posterior setae; coxal exite bearing 9 setae along distal margin; coxal endite with 3 setae; basal exite with long seta, proximal and distal endites with 3 and 2 setae, respectively. Exopod 1-segmented, with a total of 9 terminal setae. Endopod fused to basis, bearing 4 medial and 5 terminal setae.

Maxilla (Mx2) (Fig. 3C). Praecoxal endite of syncoxa with 4 setae; proximal and distal coxal endites bearing 3 setae each; proximal and distal basal endites with 3 and 3 setae, respectively; endopod 3-segmented, with setal formula of 1, 1, 4.

Maxilliped (Mxp) (Fig. 3D). Praecoxa and coxa completely fused, syncoxa with three endites carrying 2, 3, 2 setae on proximal, middle and distal endites, respectively; basal endite with 2 distal setae; endopod 4-segmented, first endopodal segment long, with 2 setae distally; other three endopodal segments shorter, bearing 1, 1 and 3 setae, respectively.

Legs 1–4 as in other members of the genus, with 3-segmented exopods and 2-segmented endopods as well as lateral spines with serrated hyaline margins (Fig. 4A–D): coxa of legs 1 to 3 bearing one medial seta and a patch of fine setules; coxa of leg 4 without medial seta. Seta and spine formula as follows (spines, Roman numerals; setae, Arabic numerals):

	Coxa	Basis	Exopod			Endopod	
			1	2	3	1	2
Leg 1	0–1	0–0	I–1	I–1	II, I, 4	0–3	1, 2, 3
Leg 2	0–1	0–0	I–1	I–1	III, I, 5	0–3	2, 2, 4
Leg 3	0–1	0–0	I–1	I–1	III, I, 5	0–3	2, 2, 4
Leg 4	0–0	0–0	I–1	I–1	III, I, 5	0–3	2, 2, 3

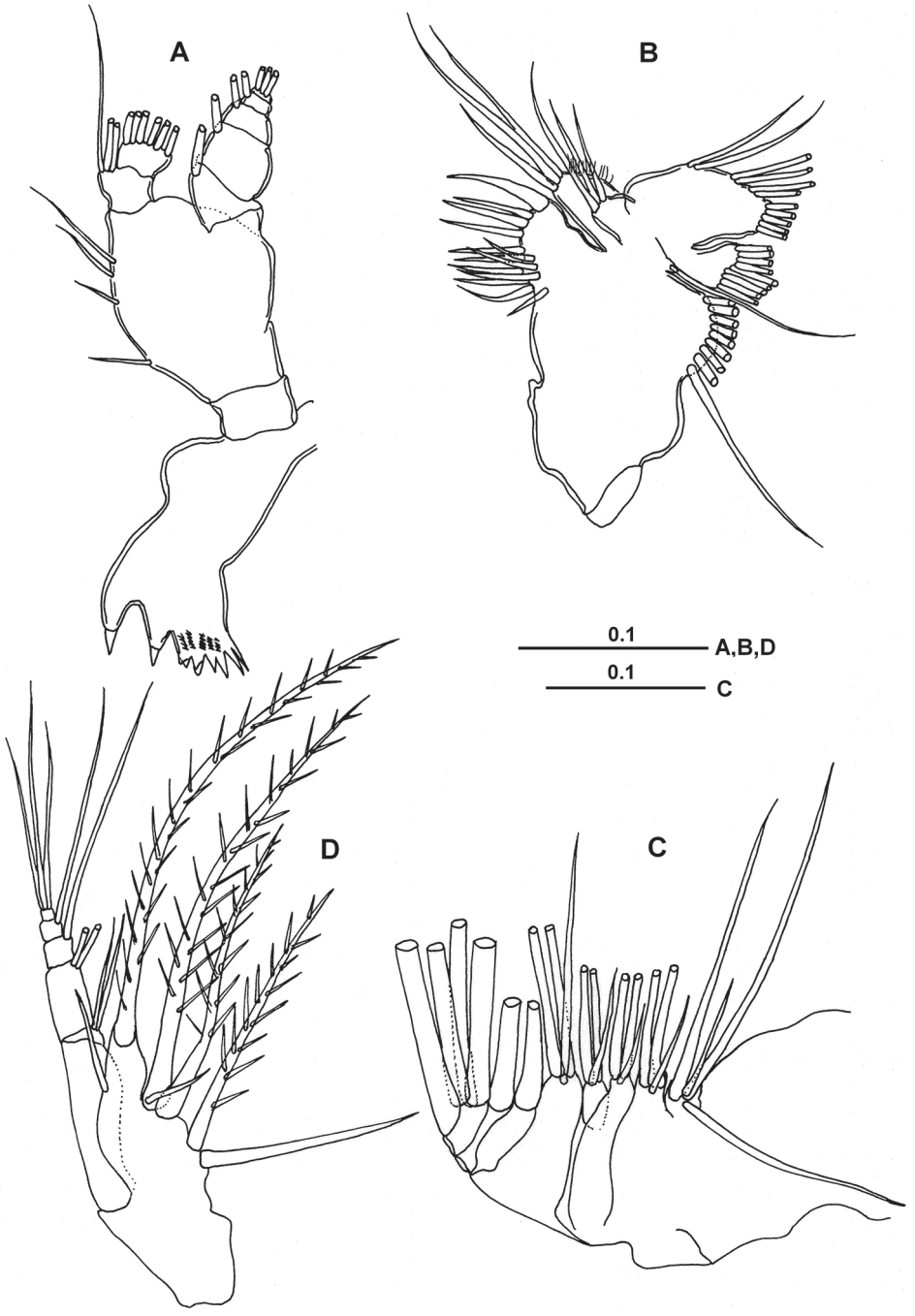

Figure 3. *Calanopia media* female from the Red Sea **A** mandible **B** maxillule **C** maxilla **D** maxilliped. Scale bars in mm.

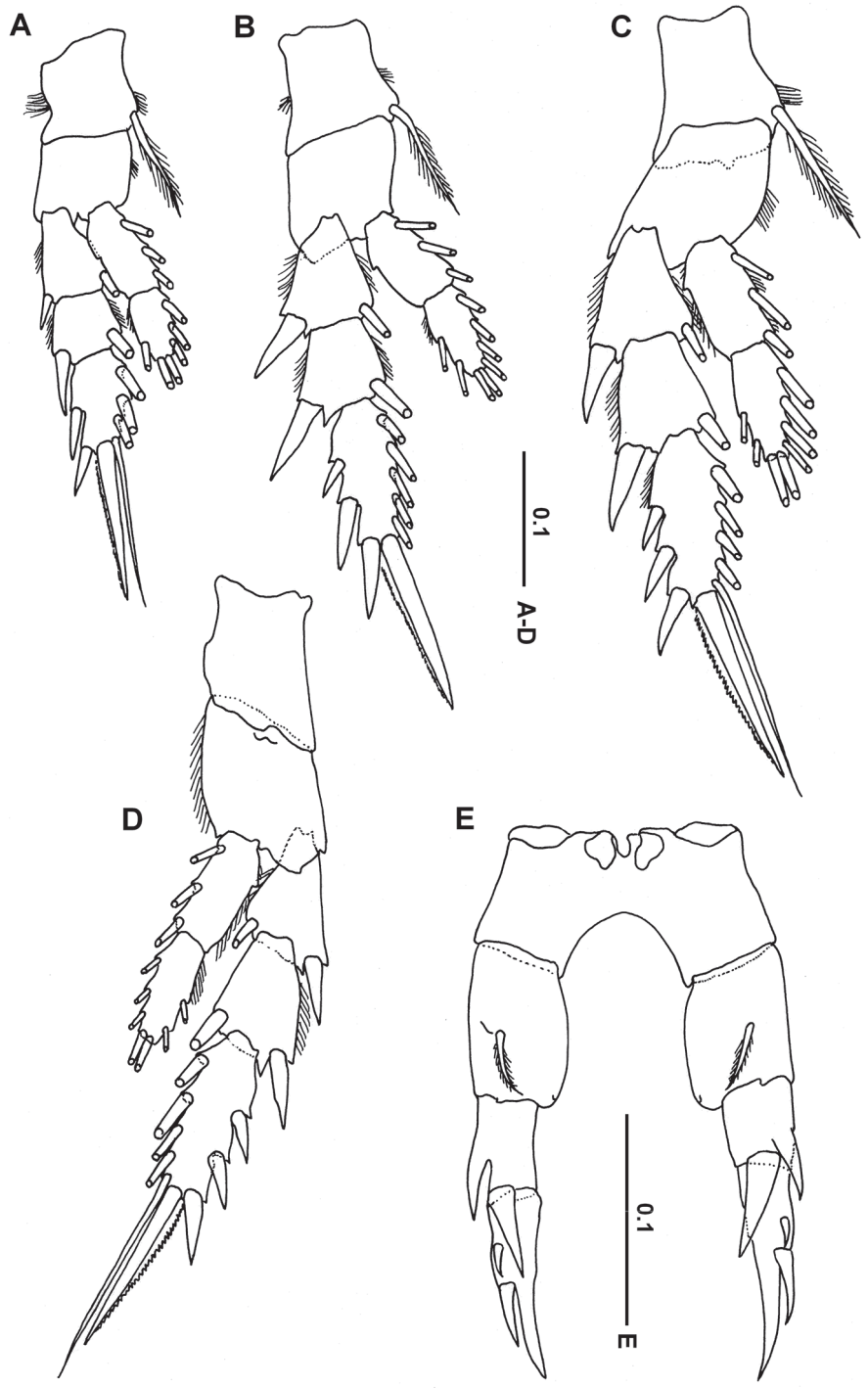

Figure 4. *Calanopia media* female from the Red Sea **A** leg 1, anterior view **B** leg 2, anterior view **C** leg 3, anterior view **D** leg 4, posterior view **E** leg 5, posterior view. Scale bars in mm.

Leg 5 (Fig. 4E) asymmetrical but with same number of spines and processes; coxa and intercoxal sclerite completely fused; right basis broader and slightly shorter than left basis, each with one posterior plumose seta; exopod 2-segmented; first exopodal segment of right leg shorter than that of left leg; with 1 lateral fused process and 1 strong spine distally; second exopodal segment of right leg slightly longer than that of left leg, extending into tapering process fused to its segment, with 2 lateral articulated spines (proximal one smaller).

Male. ***Prosome*** (Fig. 5A) 2.1 times as long as urosome; cephalosome and first pedigerous somite completely separated; fourth and fifth pedigerous somites completely fused (Figs 5A, 6B); rostrum as in female (Fig.5 B, C); posterior corners of prosome slightly asymmetrical (right one slightly longer than left), with a sharp triangular process directed posteriorly and with a distinct ventral knob or process on its right medial margin, which cannot be seen in dorsal view (Figs 5D, 6B). Urosome composed of 5 free somites, genital somite with genital aperture located ventrolaterally on posterior left side margin; second urosomite longer than other somites; anal somite shorter than preceding somite; caudal rami symmetrical, 2.2 times longer than wide, each ramus with 6 setae (II–VI) and seta VII small, inserted in ventrodistal medial margin.

Antennule (Figs 5E, F, 6C) geniculate on right side, left one similar to that of female (except for second segment, which carries longer posterior setae): right one indistinctly 17–segmented, segments 3–4 incompletely fused ventrally, segments 5–6 and 7–8 completely fused dorsally, segment 13 with long denticles on proximal 1/4 and short denticles that extend to distal fourth part, segment 14 tooth ridge possessing triangle denticles proximally, which extend back to distally-directed spure-like process, armature as follows: ancestral segment I (segment 1) = 2 setae + aesthetasc (ae), II–V (2) = 8 + 2ae, VI (3) = 2 + ae VII (4) = 2 + ae, VIII–IX (5) = 4 (2 spiniform) + 2ae, X–XI (6) = 4 (1 spiniform) + ae, XII (7) = 1 + ae, XIII (8) = 1 + ae, XIV (9) = 2+ ae, XV (10) = naked, XVI–XVII (11) = 3 + 2 ae, XVIII–XIX (12) = 1+ process] + ae, XX (13) = 1+ ae, XXI–XXIII (14) = 2 + process +ae, XXIV (15) = 1 + 1, XXV (16) = 1+ ae + 1, XXVI–XXVIII (17) = 5 + ae.

Antenna, mouthparts and legs 1–4 as in female. Leg 5 (Figs 5G, 6D) uniramous, asymmetrical; coxae and intercoxal sclerite completely fused. Left leg basis carrying 1 plumose seta posteriorly near two-thirds of its length; exopod 2-segmented, first segment shorter than basis (0.46 times) with small laterodistal spine; second segment nearly 1.35 times as long as first one, bearing 3 articulated spines (2 stout apically and one small laterally), medial hirsute margin with one distal fused spine. Right leg 5 (Figs 5G, 6D), longer than left; basis slightly longer than coxa, carrying one posterior plumose seta; right exopod 2-segmented, first segment with small thumb-like process located at approximately one-third of segment length, with small seta near base of thumb, lateral margin concave with bilobed flap-like process; second exopodal segment approximately 0.7 as long as first exopod segment, curved at about mid-length and bluntly rounded distally, bearing 2 setae in depression (one proximal and one central) and 2 unequal outer setae at mid-length (proximal one longer than distal).

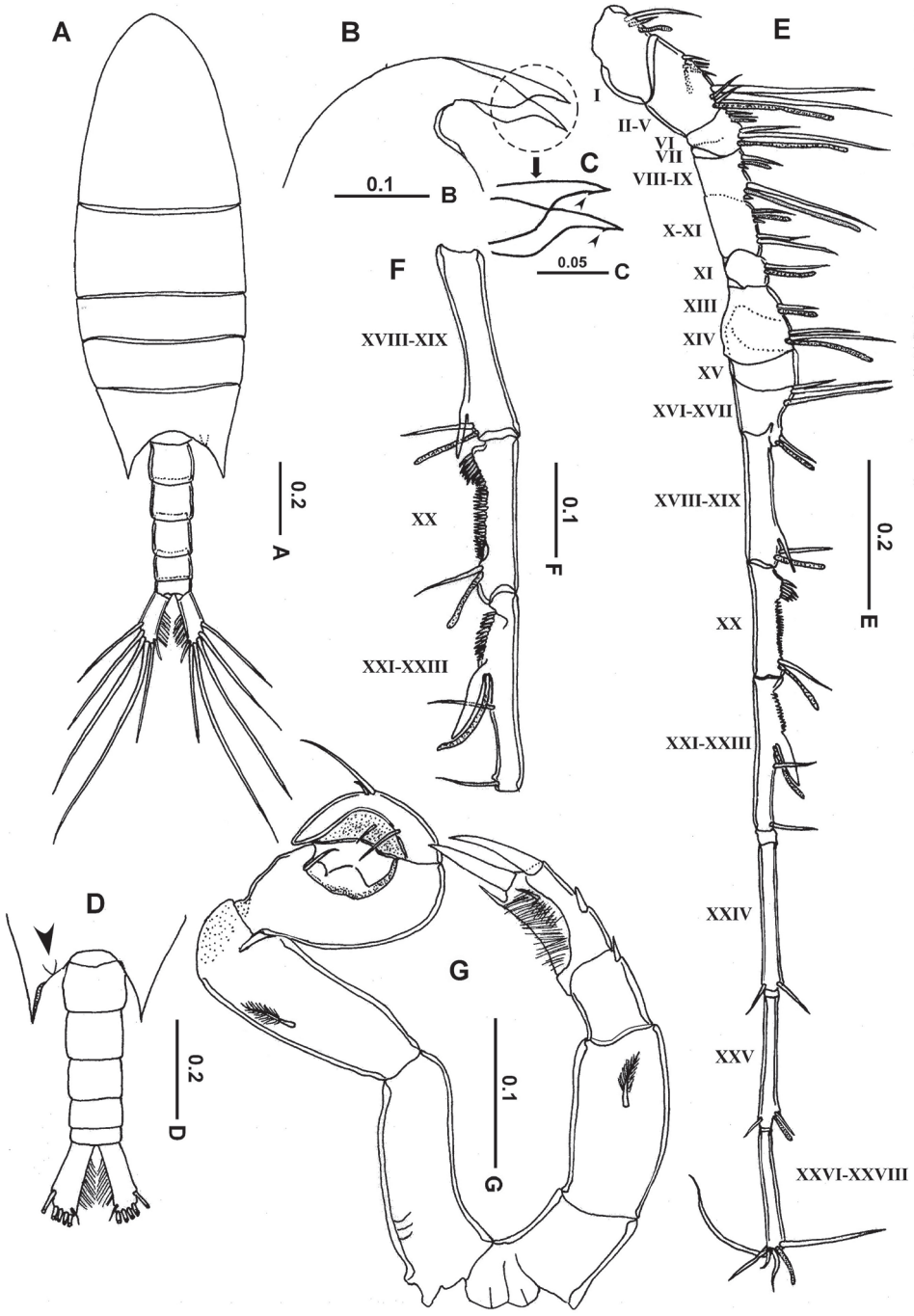

Figure 5. *Calanopia media* male from the Red Sea **A** habitus, dorsal view **B** rostrum, lateral view **C** enlarged rostral filaments (rudimentary rostral notch indicated by arrow) **D** abdomen, ventral view (knob indicated by arrow) **E** right antennule **F** enlarged segments XVIII–XXIII **G** leg 5, posterior view. Scale bars in mm.

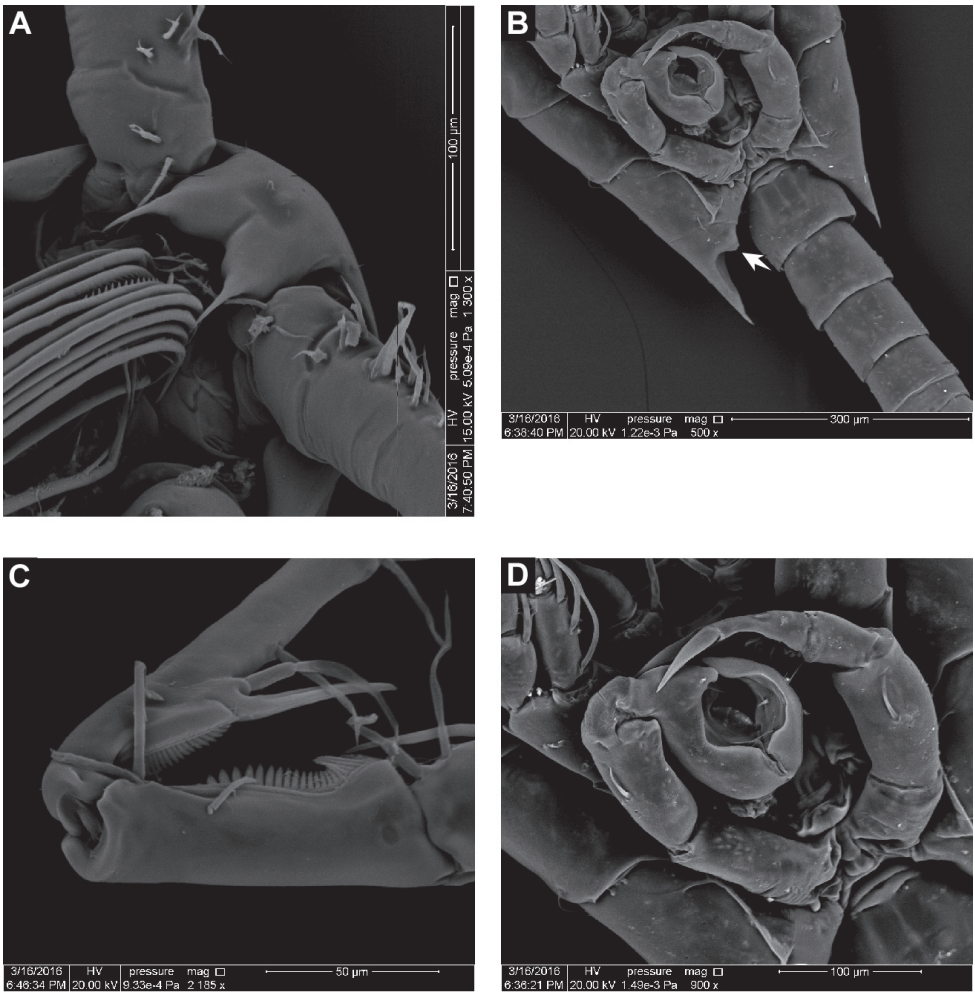

Figure 6. SEM micrograph of *Calanopia media* male from the Red Sea **A** rostrum, ventral view **B** prosomal end with abdomen, ventral view (medial notch indicated by arrow) **C** enlarged segments XX–XXIII **D** male leg 5, posterior view.

Variations. On the ventral surface of the female genital compound somite of some specimens, a small fold in the cuticle may be found on the right or left side. Also, the degree of anteromedial expansion of the female right caudal ramus varies among specimens. The anteromedial expansion of the female right caudal ramus was present in most of the specimens collected from the study area (about 90% of the population), and sometimes the degree of this expansion varied greatly among specimens. In some specimens, the right caudal ramus had a concave or straight medial margin. Moreover, the ventral knob on the right side of the male prosome posterior corners varies in size.

Table 1. Pairwise distances for mtCOI sequences between *Calanopia elliptica*, *C. media*, *C. minor* and *C. thompsoni* from the Red Sea (indicated by *). *Calanopia thompsoni* sequences from GenBank (indicated by +) were used for comparative analysis.

No.	Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
1	*C. media* (MN445608)*																				
2	*C. media* (MN445609)*	0.016																			
3	*C. media* (MN445610)*	0.013	0.016																		
4	*C. media* (MN445611)*	0.013	0.013	0.013																	
5	*C. minor* (MN796251)*	0.289	0.279	0.291	0.282																
6	*C. minor* (MN796252)*	0.288	0.279	0.290	0.282	0.000															
7	*C. minor* (MN796253)*	0.288	0.279	0.290	0.282	0.000	0.000														
8	*C. elliptica* (MN796254)*	0.263	0.278	0.260	0.263	0.294	0.293	0.293													
9	*C. thompsoni* (MN796255)*	0.227	0.238	0.238	0.233	0.270	0.269	0.269	0.232												
10	*C. thompsoni* (MN796256)*	0.231	0.242	0.241	0.236	0.267	0.267	0.267	0.235	0.002											
11	*C. thompsoni* (KP068656)+	0.213	0.225	0.223	0.218	0.276	0.275	0.275	0.235	0.034	0.036										
12	*C. thompsoni* (KP068657)+	0.211	0.223	0.220	0.216	0.273	0.272	0.272	0.232	0.032	0.034	0.002									
13	*C. thompsoni* (KP068658)+	0.211	0.223	0.220	0.216	0.275	0.275	0.275	0.235	0.030	0.033	0.003	0.002								
14	*C. thompsoni* (KP068659)+	0.223	0.235	0.233	0.228	0.290	0.290	0.290	0.248	0.040	0.042	0.008	0.010	0.008							
15	*C. thompsoni* (KF977243)+	0.221	0.224	0.226	0.215	0.253	0.252	0.252	0.225	0.195	0.193	0.229	0.227	0.226	0.238						
16	*C. thompsoni* (KF977244)+	0.240	0.242	0.244	0.233	0.255	0.255	0.255	0.244	0.208	0.206	0.241	0.239	0.239	0.251	0.022					
17	*C. thompsoni* (KF977245)+	0.235	0.238	0.240	0.228	0.258	0.258	0.258	0.244	0.198	0.196	0.234	0.232	0.231	0.244	0.026	0.009				
18	*C. thompsoni* (KF977246)+	0.231	0.233	0.235	0.224	0.264	0.263	0.263	0.239	0.200	0.198	0.224	0.222	0.222	0.234	0.022	0.021	0.018			
19	*C. thompsoni* (KF977247)+	0.242	0.245	0.247	0.235	0.252	0.252	0.252	0.239	0.211	0.208	0.239	0.236	0.236	0.248	0.022	0.006	0.009	0.021		
20	*C. thompsoni* (KF977248)+	0.233	0.235	0.237	0.226	0.255	0.255	0.255	0.244	0.203	0.201	0.243	0.240	0.240	0.252	0.021	0.004	0.010	0.019	0.007	
21	*C. thompsoni* (AY145429)+	0.231	0.233	0.235	0.224	0.267	0.266	0.266	0.233	0.205	0.203	0.221	0.219	0.219	0.231	0.026	0.018	0.018	0.011	0.018	0.020

Remarks. We compared our specimens with the paratypes deposited at the Natural History Museum, London (BMNH 1926.2.16.69-88), and concluded that our specimens are *C. media*. Both our specimens and the paratypes shared most of the diagnostic features of the species, such as: the shape of the fifth pediger, the presence of 2 ventral spinules on the right side of the female genital compound somite, and the structure of both female and male leg 5. However, the asymmetry of female leg 5 (right leg basis broader and slightly shorter than left, first exopodal segment of right leg shorter than that of left leg and second exopodal segment of right leg slightly longer than on left leg) and the presence of a ventral knob on the right side of the prosome were probably overlooked in the original description by Gurney (1927). Nevertheless, our specimens differ in the asymmetry of the caudal rami, of which the right ramus is broader and expanded anteromedially, and slightly shorter than the left one.

Distribution. *Calanopia media* was originally described from the Suez Gulf and the southern part of the Suez Canal (Gurney 1927) during the CAMBRIDGE Expedition. Subsequently, Pesta (1941) collected this species during the POLA Expedition in the southern Red Sea (15°26'12"N, 40°05'24"E). In 1956, Rose recorded this species from the Vietnamese waters. Later, it was recorded from the Levantine Basin by Berdugo (1968) and Lakkis (1984) and considered to be a Lessepsian migrant species. In the present study, *C. media* was found in considerable abundance (106 ind. m^{-3}) in samples collected at sunset (6:00 pm; UTC+3), with the highest densities at midnight (150 ind. m^{-3}). Copepodid stages were relatively low, constituting 9 and 5% of the population at sunset and midnight, respectively. It was completely absent from near the surface in morning and midday samples. The sex ratio (males/females) of *C. media* varied between 0.46 and 0.54 at 6:00 pm and 12:00 am (UTC+3), respectively.

Molecular diversity. A 624-bp region of the mtCOI was obtained for four female individuals of *C. media*, which varied in the degree of anteromedial expansion of the female right caudal ramus in specimens collected from Obhur Creek, central Red Sea. Results showed that the four analyzed specimens have nearly identical mtCOI sequences, with a distance ranging between 0.013 and 0.016 based on the pairwise distance method and Kimura 2 parameter model. The intraspecific variation in the mtCOI sequences of the other Red Sea species, *C. minor* and *C. thompsoni*, were 0.000 and 0.002, respectively.

Moreover, in the current analysis, sequences were obtained for three other *Calanopia* species collected from the study area (*C. elliptica*, *C. minor* and *C. thompsoni*) and sequences of one species (*C. thompsoni*) were obtained from NCBI. The mtCOI sequences of *Calanopia* species (i.e., *C. elliptica*, *C. media*, *C. minor* and *C. thompsoni*) from the Red Sea differ between 21.3% and 29.4% (Table 1 and Fig. 7). A Neighbor Joining phylogenetic analysis using the Kimura 2 parameter model showed that *C. media* was clearly distinct from its congeneric species (Fig. 7). Concerning *C. thompsoni*, the only sequenced mtCOI in NCBI, it is clear that the average distance between Red Sea specimens and Indian Ocean specimens (KP068656–KP068659) was 0.035 (0.030–0.042), whereas for the China seas' specimens it was 0.201 (0.193–0.211).

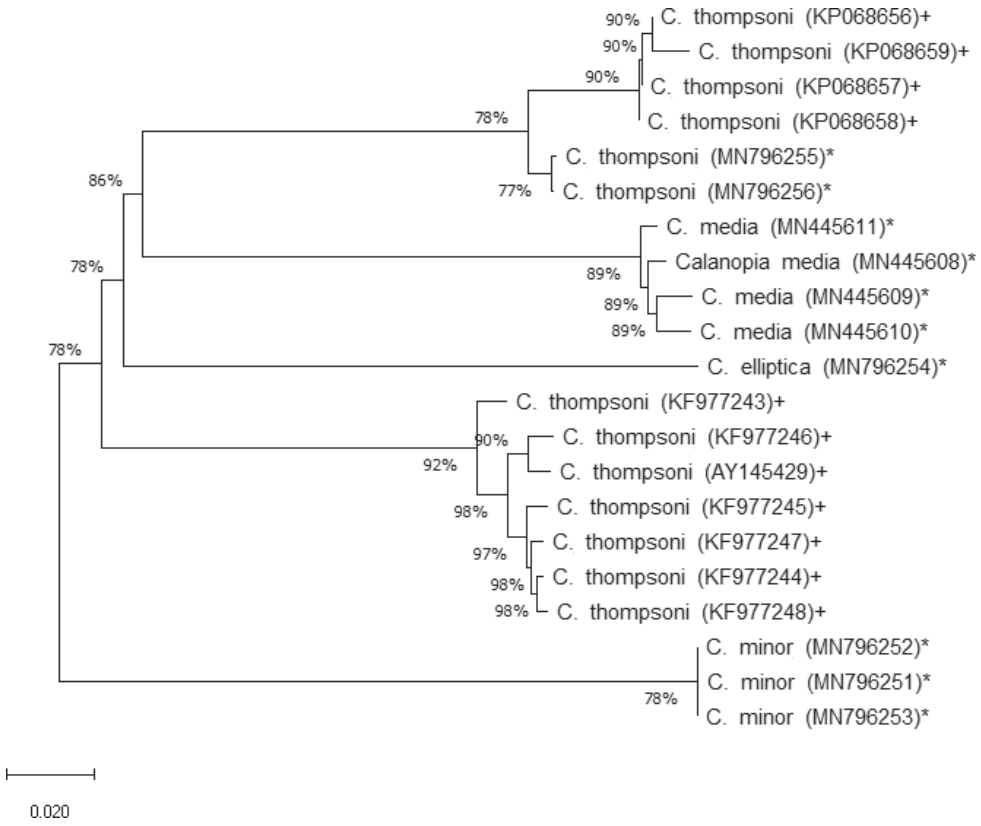

Figure 7. Neighbor Joining phylogenetic tree based on the mtCOI genes of *Calanopia elliptica*, *C. media*, *C. minor* and *C. thompsoni* from the Red Sea (indicated by *). *Calanopia thompsoni* sequences (indicated by +) from GenBank were used for comparative analysis.

Discussion

In his original description of *C. media*, Gurney (1927) provided drawings only for the whole body and leg 5 of both sexes, as well as of the female urosome and the geniculate part of the male right antennule (segments XX and XXI), and compared it with *C. elliptica*. His description was brief and focused mainly on the female genital compound somite and female leg 5. For the male, he only mentioned that the major differences between *C. media* and *C. elliptica* lay in a lack of serrations on the second exopodal segment of right leg 5. In his words, "Fifth legs closely resembling those of *C. elliptica*, but without the scalloped edge to the broad subterminal joint of the right leg". Re-examination of *C. media* from the study area allowed us to more accurately describe this species. The original characters reported by Gurney (1927) are given in brackets: 1) the female genital compound carries one or two spinules on the right side (2 spinules); 2) the female caudal rami are asymmetrical, the right one is expanding anteromedially (symmetrical); 3) the female leg 5 is slightly asymmetrical, with

the left leg slightly shorter than the right due to shortness of both the basis and first exopodal segment (mentioned as symmetrical by Gurney, but from his drawings the first exopodal segment is longer on the right side and also the right second exopod segment is longer than the left one); 4) the male prosomal corners project posterolaterally into asymmetrical pointed processes, the right one of which is slightly longer than the left, with a distinct ventral knob on its medial margin, invisible in dorsal view (symmetrical); and 5) the second exopod segment of the male right leg 5 carries one seta medially, which is lacking in Gurney's description. Moreover, Pesta (1941), in his description from the southern Red Sea, mentioned the lack of spinules on the genital compound somite, while the female leg 5 exopod proportions differed slightly from Gurney's description (in Pesta's description, the second exopod segment is 1.1 times as long as the first exopod segment) and the second distal spine on the second exopod segment is shorter than in Gurney's description.

In addition to the variability noted in the caudal rami of *C. media*, variation has been reported in *C. sewelli* Jones & Park, 1967, collected from Marquesas, central Pacific, in which the right ramus was sometimes longer and with a concave medial margin. Moreover, asymmetry of the female caudal rami has been noted in *C. asymmetrica* Mulyadi & Ueda, 1996 collected from Indonesian waters, where the right ramus was much longer than the left one and expanded posteriorly. This asymmetry was found also in *C. australica* Bayly & Greenwood, 1966 collected from Moreton Bay, Australia, in which the left ramus was longer than the right. Asymmetry of the male prosomal points in *C. media* is similar to that in *C. sarsi* C.B. Wilson, 1950 collected from Fiji waters and *C. tulina* (El-Sherbiny and Al-Aidaroos 2017) described from the Red Sea.

Calanopia media is closely related to *C. tulina* from the central Red Sea, but they can be distinguished from each other by the characters listed in Table 2. The most distinctive characters of *C. media* are: 1) the presence of 2 ventral spinules on the right side of the female genital compound somite, 2) the extreme asymmetry of the caudal rami of the female, 3) the presence of 2 long articulated and 1 short fused terminal spines on the second exopodal segment of the male left leg 5, 4) the first exopodal segment of male right leg 5 with a small thumb located approximately at one-third of the segment length and with the semicircular processes on a flap on its lateral part, and 5) the second exopodal segment of the male right leg 5 shorter than the first exopodal segment, which is curved at mid-length with a blunt apex and 2 medial setae within a shallow medial depression.

In our study, *C. media* exhibited a clear diel vertical migration (DVM). Sunset ascend and sunrise descent were performed at very low light intensities. This pattern is known as the nocturnal or normal DVM (Forward 1988). Similar observations were made in previous studies in the southern part of the Suez Canal and the southern Red Sea by Gurney (1927) and Pesta (1941), respectively, who reported that *C. media* was found in high abundance in the coastal waters mainly in the night samples. This pattern was recorded also for *C. americana* F. Dahl, 1894 in the eastern Gulf of Mexico (Turner et al. 1979) and in the Brazilian waters (Pessoa et al. 2014). This DVM may

Table 2. Comparative list of characters of *Calanopia media* and *C. tulina*. The characters of *C. tulina* are taken from the original description by El-Sherbiny and Al-Aidaroos (2017).

	Calanopia media	*Calanopia tulina*
Female		
Rostral points	With rudimentary subterminal notch	With small subterminal notch
Genital compound somite	With two spinules on right side	Without any spinules
Caudal rami	Asymmetrical, right one slightly shorter than left and expanded antero-medially (varies between individuals)	Asymmetrical, right one slightly shorter than left
Leg 5	Asymmetrical; right basis boarder and shorter than right; right first and second exopodal segments shorter than on left	Asymmetrical; left leg slightly shorter than right; left basis, first and second exopodal segment shorter than on right
Male		
Rostral points	With rudimentary subterminal notch	With small subterminal notch
Posterior prosome	Asymmetrical, right point slightly longer, with small ventral knob on medial margin	Asymmetrical, right point wider and slightly longer, with distinct knob on medial margin
Second exopodal segment of left leg 5	With 3 articulated spines (2 stout and terminal, and one small and lateral)	With 2 relatively long curved, terminal medially-serrated articulated spines and 1 lateral spine directed medially
First exopodal segment of right leg 5	With small thumb-like process located at one-third of segment length, with bilobed flap-like process	With very small rounded-tip thumb-like process located nearly mid-length, central medial part smooth, not bilobed
Second exopodal segment of right leg 5	Curved at mid-length with 2 setae on concave surface, and with 2 unequal setae at mid-length on convex surface	Curved at two-thirds length, with 2 setae on concave surface, and 2 unequal setae at mid-length on convex surface.

be performed to avoid UV radiation, light and predators, as well as for availability of food and favorable temperature (Bollens and Frost 1989; Lampert 1989; Andersen and Nival 1991; Pearre 2003; Cohen and Forward 2005). Generally, the light intensity in Obhur Creek drops steeply below 5 m depth, and very little light penetrates into waters below 15 m (Al-Aidaroos et al., unpublished data). Following the same trend, UVB radiation decreased by 74.15% at 5 m depth, while only 2% reached 15 m depth (Duarte et al., unpublished data). This suggests that *C. media* is avoiding high temperature, high light intensity and/or visual predation during the day and coming up to the surface layers for feeding during night-time. This species was observed to be abundant in night collections by light trap from a shallow coral reef in the central Red Sea (unpublished data). This might be attributed to its benthopelagic behavior, which is clearly visible in terms of the stout, large outer spines on its legs (1–4), as reported in the benthopelagic copepod genus *Platycopia* (Ohtsuka et al. 1998).

Morphology can be considered as a fundamental method for copepod species identification. However, some pontellid species display considerable intraspecific morphological variations in the female genital compound somite, caudal rami and fifth leg (Jeong et al. 2014). Such differences might be sufficient to prove the presence of a new species, as it is the case for some centropagoid species (e.g. Sakaguchi and Ueda 2010; Soh et al. 2012). The mtCOI gene was proposed as a unique tool for copepod identification with 'barcoding' (Bradford et al. 2010; Blanco-Bercial et al. 2014), which can verify the species identity within morphologically varying pontellid specimens. Within Crustacea, the level of genetic variation between congeneric species is 17.16%, while the level of intraspecific variability is 0.46% (Costa et al. 2007). Moreover, variation between calanoid copepod species varied between 13–22%, 17.6–26.7% and 21–23% in previous studies by Bucklin et al. (1999), Eyun et al. (2007) and Soh et al. (2013), respectively. In this

study, the intraspecific variation in the COI sequences from the Red Sea specimens of *C. media*, *C. minor* and *C. thompsoni* would confirm the hypothesis of Costa et al. (2007). The *Calanopia* species nucleotide sequences collected from GenBank indicate no genetic differentiation between the specimens of *C. thompsoni* from the Red Sea and the Indian Ocean. In contrast, the nucleotide data of *C. thompsoni* from the Red Sea revealed considerable variations with specimens collected from the China seas, indicating that the two populations are genetically different. This high level of deviation between both populations can by supported by the allopatric speciation hypothesis of Carpenter and Springer (2005), which states that in the Pleistocene the migration of marine organisms from the West Pacific Ocean to the Indian Ocean seems to be blocked by an ecological vicariant. Moreover, sequences included herein from the Red Sea are the first barcodes for these species, and it will be useful in future pontellid barcode studies.

During the last two decades, six species of pontellids have been originally described as new species or were first recorded from the Red Sea: *Calanopia kideysi* by Ünal and Shmeleva (2002), *Labidocera boxshalli* El-Sherbiny & Ueda, 2010 by El-Sherbiny and Ueda (2010), *Calanopia tulina* by El-Sherbiny and Al-Aidaroos (2017), *Pontella princeps* Dana, 1849 by El-Sherbiny (2009), *Labidocera karachiensis* Fazal-Ur-Rehman, 1973 by El-Sherbiny and Ueda (2008), and *Calanopia thompsoni* by Al-Aidaroos et al. (2016). However, the diversity of this family in the Red Sea is rather low (17 species) compared with that of the Indian Ocean (77 species as reported by Razouls et al. 2019), from which the Red Sea fauna has originated (Al-Aidaroos et al. 2019). This low number can be attributed to the characteristic euneustonic or facultative neustonic nature of this group (Mauchline 1998). Thus, inappropriate sampling methods and sampling time and/or limited sampling effort might have resulted in an underestimation of the fauna of Pontellidae. Therefore, this study emphasizes the necessity of understanding the diversity and distribution of pontellid copepods in the Red Sea and their mode of life.

Key to species of *Calanopia* recorded in the Red Sea

Females

1 Leg 5 exopod one-segmented **2**
– Leg 5 exopod two-segmented **3**
2 Genital compound somite shorter than second urosomite; exopodal segment of leg 5 with two small lateral spines and one long medial spine (longer than the segment itself) ..... ***C. minor***
– Genital compound somite nearly equal to second urosomite; exopodal segment of leg 5 with two small lateral spines and one medial spine (shorter than the segment itself) ..... ***C. kideysi***
3 Cephalic lateral hooks absent **4**
– Cephalic lateral hooks present ..... ***C. thompsoni***

4 Genital compound somite naked, without lateral spinules **5**
– Genital compound somite with two lateral spinules on the right side.... ***C. media***
5 Leg 5 asymmetrical; left leg distinctly longer than right one..... ***C. elliptica***
– Left leg 5 slightly asymmetrical; right leg slightly shorter than left one.... ***C. tulina***

Males (*C. kideysi* not included since the adult male is unknown)

1 Cephalic lateral hooks absent **2**
– Cephalic lateral hooks present..... ***C. thompsoni***
2 Left leg 5 shorter than right one; basis of left leg 5 not swollen proximally..... **3**
– Left leg 5 longer than right one; basis of left leg 5 swollen proximally and produced into a small curved tooth ..... ***C. minor***
3 Second urosomite with one acuminate-tip spinose process postero-laterally on right side; first exopodal segment of right leg 5 with three strong blunt teeth and second exopodal segment claw-like with three small pointed teeth.... ***C. elliptica***
– Second urosomite naked; first and second exopodal segments of right leg 5 without any teeth..... **4**
4 Second exopodal segment of left leg 5 with three articulated spines (two stout terminally, one small laterally); second exopodal segment of right leg 5 curved at mid-length with a relatively short spine laterally..... ***C. media***
– Second exopodal segment of left leg 5 with two relatively long curved, terminal, medially-serrated spines and one lateral spine directed medially; second exopodal segment of right leg 5 curved at two-thirds of length, with relatively long spine laterally ..... ***C. tulina***

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RESEARCH ARTICLE

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Rustitermes boteroi, a new genus and species of soldierless termites (Blattodea, Isoptera, Apicotermitinae) from South America

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Abstract

We present the description of a new genus and species of soldierless termites from South America. *Rustitermes boteroi* Constantini, Castro & Scheffrahn, **gen. et sp. nov.** can be identified by the morphology of the enteric valve, with six slightly asymmetric cushions, each one forming a central pouch made of scales smaller than those between the cushions. The new genus features two characteristic rows of thick bristles on the interior margin of the fore tibia, and is supported by COI molecular sequence data. This species is distributed from Tobago to northern Argentina.

Keywords

Neotropics, enteric valve, soil-feeder, barcode sequence

Introduction

Soil-feeding termites represent a large part of the termite fauna in Neotropical ecosystems (Ackerman et al. 2009; Bourguignon et al. 2011; Palin et al. 2011; Cancello et al. 2014). Species in the subfamily Apicotermitinae are almost exclusively soil feeders (Bourguignon et al. 2016a), and preferential consumption of different soil components has been suggested as a driver of great diversity in these termites (Bourguignon et al. 2009).

The Apicotermitinae subfamily was first proposed by Grassé and Noirot (1954) and defined by Sands (1972) in the most extensive taxonomic work on this group of termites carried out in Africa. Both morphological and molecular data corroborate the monophyly of Apicotermitinae (Inward et al. 2007; Bourguignon et al. 2017).

The taxonomic work of Sands (1972) described 51 new species, redescribed 9 species, and established 16 new genera. Sands (1972) considered the genus *Anoplotermes* Müller to be exclusively Neotropical. At the time, this was the sole apicotermitine genus of the region.

Taxonomic study of the worker caste has been underwhelming in the Neotropical Region (Rocha et al. 2019), and because all New World Apicotermitinae are soldierless, this subfamily has been historically understudied. Before 2009, only five genera had been described (Fontes 1992; Bourguignon et al. 2010). In recent years however, the development of Apicotermitinae taxonomy in the Neotropical Region has been increased by the description of ten new genera, with enteric valve morphology being of essential diagnostic character for the establishment of new taxa (Scheffrahn 2013; Bourguignon et al. 2016b; Scheffrahn et al. 2017; Castro et al. 2018), although other characters may also be very useful, especially in taxa with less robust enteric valve armature (Acioli and Constantino 2015; Constantini et al. 2018). The diversity of soldierless termites can be high, reaching up to 31 morphospecies for a single primary tropical rainforest (Bourguignon et al. 2013).

Herein we describe *Rustitermes boteroi* gen. nov. et sp. nov. based on the morphology of the imago, worker caste and molecular COI data.

Material and methods

The material examined in this study is deposited at Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil (**MZUSP**); Colección de artrópodos terrestres de la Amazonía Colombiana of the SINCHI Institute in Leticia, Amazonas, Colombia (**CATAC**); and at the University of Florida Termite Collection at Fort Lauderdale Research and Education Center, Davie, Florida, United States (**UF**). All the specimens are preserved in 80–85% ethanol; colonies marked with (*) in the material examined contain alates.

Some type material of old species was consulted for comparisons and remarks with *R. boteroi* sp. nov., to avoid generating new synonyms for described species. The

abbreviations of the cited institutions are: **AMNH** – American Museum of Natural History, New York, USA; **USNM** – Smithsonian National Museum of Natural History, Washington, D.C., USA; **CMNH** – Chicago Museum of Natural History, Chicago, USA. The species reviewed were: *Anoplotermes bolivianus* Snyder (alate, USNM), *Anoplotermes brucei* Snyder (alate and worker, AMNH), *Anoplotermes distans* Snyder (worker, AMNH), *Anoplotermes gracilis* Snyder (alate, AMNH), *Anoplotermes hondurensis* Snyder (alate, AMNH), *Anoplotermes meridianus* Emerson (worker, AMNH), *Anoplotermes punctatus* Snyder (worker, AMNH), *Anoplotermes pyriformis* Snyder (alate, AMNH), *Anoplotermes rotundus* Snyder (alate and worker, AMNH and USNM), *Anoplotermes subterraneus* Emerson (alates and workers, AMNH and USNM), *Anoplotermes tenebrosus* (Hagen) (alate, AMNH), *Aparatermes abbreviatus* (Silvestri) (alate and worker, AMNH), *Aparatermes cingulatus* (Burmeister), and *Aparatermes silvestrii* (Emerson) (workers, CMNH).

The terminology used to describe worker mandibles follows Sands (1972) and Deligne (1999), with some modification, while worker digestive tube descriptions follow Noirot (2001).

In Sands (1972, fig. 2), a variation of the tooth that he calls the "marginal subsidiary" is represented, which may or may not be hidden by the molar prominence (depending on the position it occupies), and suggests that the development of this tooth is a useful generic characteristic. The same tooth is called *premolar* by Deligne (1999) and *molar* by Krishna (1968). Traditionally, the term "subsidiary" is used to designate the structure present at the base of the apical tooth in the left or right mandible in some non-Termitidae families, which could generate some misunderstanding in the literature. In addition, a process not reported in the literature, closer to M3, was observed in the left mandible of some Apicotermitinae alates (Sands 1972). Therefore, we propose to call this a "pre-molar process" for the structure closest to M3 and a "molar process" for the structure closest to the molar prominence, stressing that both processes are part of the molar region (see Fig. 2C, MP).

The mandibles were examined on a microscope slide in PVA medium, after adding a cover glass and pressing them gently into position, as shown in Figure 2C, D. Nevertheless, we examined the mandibles in every possible position before separating them from the head, in order to undertake a careful examination of the "pre-molar process" and "molar process".

The terms used for pilosity are comparative: bristles are stiff hairs with well-marked bases; spine-like bristles are shorter and thicker than bristles; hairs are shorter and thinner than bristles and without conspicuous bases.

Workers and imagos were examined in a petri dish filled with 80% ethanol, whereas the dissection of the enteric valve (EV) was done with two no. 20 minuten pins (BioQuip, Rancho Dominguez, CA).

The EV was detached from the paunch (P3) and all the food particles were removed by gentle manipulation. The extracted EV was inserted in a drop of PVA mounting medium (BioQuip, Rancho Dominguez, Cat. #6371A) and then gently massaged with the side of a minuten pin for a few minutes until the EV became detached from the

muscles. Afterwards, the EV was transferred on to a microscope slide where, after adding another drop of the same mounting medium, the fully cleaned tubular EV was splayed open before final mounting.

The following morphometric characters were measured as defined by Roonwal (1970) and indicated in parentheses: *for alates*–maximum diameter of compound eyes (48); inter-eye distance (52); maximum diameter of ocellus (55); minimum diameter of ocellus (56); eye-ocellus distance (57); length of pronotum (65); width of pronotum (68); minimum length of forewing without scale (75); maximum length of forewing scale (76); *for alates and workers*–length of head to lateral base of mandibles (5); width of head (17); lengths of pro- and metatibia (85); width of protibia (86); protibia index (53, p.61).

Microphotographs were taken as multi-layer montages using a Leica M205C stereomicroscope for the worker head, fore tibia and mandibles; for the worker EV a Leica CTR 5500 compound microscope was used, controlled by the Leica Application Suite version 3 software.

The distribution map was created using ArcGIS desktop ver. 10.4.1 (ESRI, Redlands, CA). The list of examined material is sorted by country (uppercase), state or province, and locality. Collection data are organized as follows: latitude, longitude, collection date, altitude, collector name, collection, and collection number.

The COI barcoding region (Cytochrome c Oxidase subunit 1) was sequenced for four colonies of *R. boteroi* sp. nov. from Peru, Ecuador, French Guiana and Paraguay. DNA extraction and PCR were performed by the Canadian Centre for DNA Barcoding (BOLD systems), following standard high-throughput protocols (deWaard et al. 2008). The PCR employed the primers LepF1 and LepR1 (Hebert et al. 2003), which generated 622 to 652bp. To infer the relationship of *Rustitermes* gen. nov. with the other Neotropical Apicotermitinae, a Bayesian phylogeny was performed with the COI region. In addition to the four sequences of *Rustitermes boteroi* sp. nov. from colonies, UF.FG411 (BOLD:AAW5963), UF.PA534 (BOLD:ACB7291), UF.EC400 (BOLD:ABA4343) and UF.PU602 (BOLD:ACO6749), 49 GenBank and BOLD sequences were used in the analysis: 35 sequences of Neotropical Apicotermitinae (22 species, 14 genera); eight non-Neotropical Apicotermitinae genera, five non-Apicotermitinae Termitidae, and one Rhinotermitidae [*Heterotermes crinitus* (Emerson)] as outgroup. The tree was constructed under the same parameters as other recently published papers on Neotropical Apicotermitinae (Carrijo et al. 2015; Castro et al. 2018). Sequence alignment was performed under the MUSCLE algorithm; the substitution model used was the GTR+I+G, selected under the Akaike Information Criterion (AIC) by jModelTest2 (Darriba et al. 2012); the phylogeny was reconstructed with BEAST 1.8.0 (Drummond et al. 2012) under a Yule speciation process. Four 20,000,000 generations Markov chain Monte Carlo (MCMC) searches were conducted independently and combined. Sampling was conducted every 2000 generations. Convergence and stationarity were assessed with Tracer 1.5 (Rambaut et al. 2014) and the first 1000 trees of each run were discarded as burn-in.

Taxonomy

***Rustitermes* Constantini, Castro & Scheffrahn, gen. nov.**
http://zoobank.org/A6BB62D4-9A1E-4FAD-A0B3-B16B56D4CB87

Type species. *Rustitermes boteroi* sp. nov.

Diagnosis. Enteric valve with six slightly asymmetrical cushions. Each cushion forming a central pouch made of scales smaller than those between the cushions. Each cushion composed of about 60–80 scales, wider at the base and narrower at the apex. Posterior portion of pads truncated, with 35 to 50 rectangular scales arranged from the middle to the apex of the cushion and increasing in density in this same direction.

Imago **(**Fig. 1; Table 1). Fontanelle inconspicuous in both sexes, the region of the fontanelle depressed; medium spot slightly conspicuous. Left mandible with apical tooth a little bit larger than M1 + 2; M3 triangular with lateral margins forming an obtuse angle; non-conspicuous premolar process; molar process not hidden by molar prominence (Fig. 2C).

Head capsule with short, sparse bristles; coloration of head capsule dark brown; frontal marks slightly lighter than rest of head capsule, with poorly defined margins. Pronotum subhexagonal, with anterior margin straight, without central incision; lateral margins very straight and well-marked; pronotum with few sparse bristles and short hairs. Tergites and sternites with short hairs covering the plates. Fore coxa with a set of 4–5 prominent long bristles; inner face of fore tibia with two rows of 6–7 thick bristles.

Worker (Figs 2–4). Monomorphic. Small and rounded fontanelle; postclypeus rather slightly inflated; head capsule covered with medium and long bristles. Left mandible with prominent apical tooth compared to M1 + 2, triangular M3 with lateral margins forming a right/acute angle, molar process not concealed by molar prominence. Pronotum with long bristles, concentrated along margin of anterior and posterior lobes. Tergites and sternites with dense cover of long bristles, facing the posterior region or upwards. Fore coxa with a set of 4–5 thick bristles; inner face of fore femur with long bristles. Fore tibia moderately inflated, inner face of fore tibia with two rows of 6–7 thick bristles.

Mixed segment (MS) separated from ileum (P1) by a simple transverse junction; P1 of uniform width along entire length, forming an inverted C in ventral view. Enteric valve without armature, with six pyriform cushions of slightly different dimensions, the two largest and two smallest cushions adjacent to each other. The center of each cushion is formed into a lumen-facing pouch consisting of about 60 fringed scales. The remainder of the cushions consists of 50–75 (depending on size of cushion) larger fringed polygons. The cuticle between the cushions is composed of even larger fringed cuboidal scales. All cushions are wider at base (near P1) and narrower at apex (near P3). Tubular and short EV seating. Worker measurements highly variable among and within different colonies (Table 2).

Comparison and remarks. The digestive tube coiling of the new genus is similar to *Hydrecotermes*, but *R. boteroi* sp. nov. can be differentiated by the worker, which

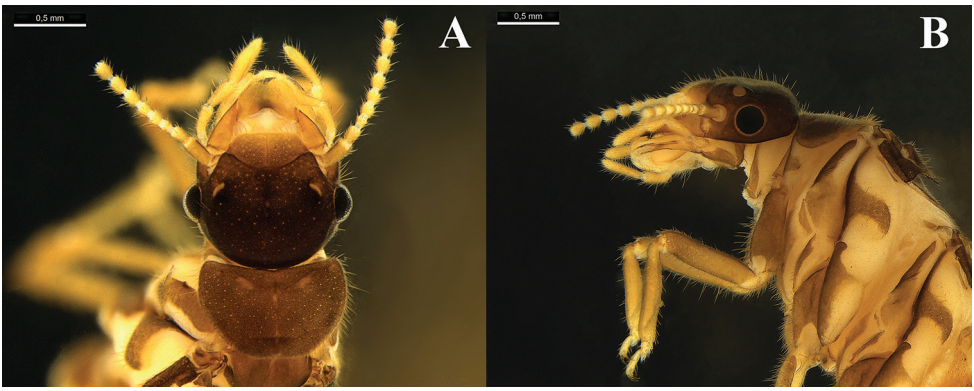

Figure 1. Female imago head capsule, pronotum and fore leg of *Rustitermes boteroi* sp. nov. **A** dorsal view **B** lateral view. Specimen from lot MZUSP 26677. Scale bars: 0.5 mm.

Table 1. Measurements (mm) of imagos of *Rustitermes boteroi* sp. nov. from colony MZUSP 26677**.**

	Female (n = 4)		Male (n = 5)	
	Range	**Mean**	**Range**	**Mean**
Length of head	0.78–0.92	0.83	0.65–0.78	0.75
Width of head with eyes	1.13–1.20	1.18	1.12–1.15	1.12
Maximum diameter of compound eye	0.27	0.27	0.27–0-28	0.27
Inter-eye distance	0.87–0.95	0.93	0.87–0.88	0.87
Maximum diameter of ocellus	0.12	0.12	0.11–0.12	0.11
Minimum diameter of ocellus	0.08–0.09	0.09	0.08–0.09	0.09
Eye-ocellus distance	0.08–0.11	0.1	0.08–0.1	0.09
Length of pronotum	0.57–0.63	0.6	0.55–0.58	0.56
Width of pronotum	1.00–1.08	1.04	0.97–0.98	0.97
Length of forewing with scale	11.60–12.13	11.82	10.40–10.53	10.47
Width of fore tibia	0.13	0.13	0.13	0.13
Length of fore tibia	0.88–0.95	0.93	0.83–0.88	0.86

has thick bristles along the inner margin of the fore tibia, absent in *Hydrecotermes*. In the workers, the enteric valve and the digestive tube may be similar to *Aparatermes*, but the cuticle between the cushions in *Aparatermes* does not have cuboidal scales. In *Aparatermes* the insertion of P1 in P3 occurs in dorsal view with a trilobate EV setting, in *Rustitermes* the enteric valve seating (EVS) is not trilobate. Also, the enteric valve of *Aparatermes* has small spines or pointy scales, which are absent in *R. boteroi* sp. nov.; in addition, the EV in *Aparatermes* has the posterior portion of the pads without scales. The imago presents a visible molar process and fore tibia with two rows of thick bristles.

Molecular analysis. The Bayesian phylogeny using the COI marker clearly separates *Rustitermes* gen. nov. from the other soldierless termites (Figure 5). The new genus was recovered as sister group of *Patawatermes*, but without high posterior probability support.

Etymology. Named in honor of Michael K. Rust, retired professor of urban entomology at the University of California, Riverside (UCR), and mentor of RHS. Mike encouraged RHS to publish his first taxonomic paper (Scheffrahn and Rust 1983).

***Rustitermes boteroi* Constantini, Castro & Scheffrahn, sp. nov.**
http://zoobank.org/95C95B44-17A3-464D-AC58-ADE9F3BC168D

Material examined. *Holotype*. Worker from colony labeled as UF no. PU602; the holotype is kept in a separate small vial in the same vial as the paratypes.

Type locality. PERU. *Ucayali*, Nueva Requena, -8.37007, -74.84366.

Type repository. University of Florida, Fort Lauderdale Research and Education Center, Termite Collection in Davie, Florida.

Paratypes. ARGENTINA. *Corrientes*, Santo Tome, (-28.57900, -56.0840), 1.JUL.1998, 93 m, J. Křeček coll. (UF no. AG360). BOLIVIA. *Cochabamba*, Chapare, Villa Tunari, (-18.15343, -60.03293), 26.MAY.2013, 408 m, Chase, Křeček, Mullins, Nishimura, Mangold, and Scheffrahn coll. (UF no. BO85). *Beni*, San Javier, (-14.70207, -64.89097), 29.MAY.2013, 152m, Chase, Křeček, Mullins, Nishimura, Mangold, and Scheffrahn coll. (UF no. BO375); (-14.54909, -64.88964), 29.MAY.2013, Chase, Křeček, Mullins, Nishimura, Mangold, and Scheffrahn coll. (UF no. BO431, BO437). *Santa Cruz*, Roboré, (-18.15343, -60.03293), 31.MAY.2013, 408 m, Chase, Křeček, Mullins, Nishimura, Mangold, and Scheffrahn coll. (UF no. BO738). BRASIL. *Alagoas*, Quebrangulo, (-9.2288, -36.4259), 19.JUN.2000, 780 m, MP Silva coll. (MZUSP 13712). *Bahia*, Conde, (-11.7718, -37.7301), 15.JUN.2016, 78 m, JP Constantini coll. (MZUSP 26648). *Espírito Santo*, Pedro Canário, (-18.3557, -39.8445), 20.JUN.2016, 43 m, JP Constantini coll. (MZUSP 26652); 21.JUN.2016, (MZUSP 26676(a), 26677*). *Paraíba*, João Pessoa, (-7.1480, -34.8614), 01-20.JUN.2000, 66 m, A Vasconcellos coll. (MZUSP 13710, 13711). *Pernambuco*, Recife, Horto Dois Irmãos, (-7.9999, -34.9473), s/d, 88m, A Vasconcellos coll. (MZUSP 13702). COLOMBIA. *Amazonas*, La Chorrera, Lago grande (-2.07066, -72.170611), 28.JUN.2016, 133 m, D. Castro coll. (CATAC-1712); Leticia, (-4.046666, -70.00566), 13.JUL.2018, 126 m, D. Castro coll. (CATAC-3137). *Caquetá*, Belén de los Andaquíes, (+1.3515, -75.81178), 23.APR.2018, 280 m, H Artunduaga coll. (CATAC-3688); (+1.26663, -75.78983), 24.FEB.2016, 252 m, Y. Virguez coll. (CATAC-1793); (+1.63063, -75.90591), 28.JAN.2017, 758 m, D. Castro coll. (CATAC-0954); Florencia, (+1.716694, -75.61369), 29.MAR.2016, 527 m, Y. Virguez coll. (CATAC-1781); San Vicente del Caguan, (+2.03560, -74.91294), 14.APR.2018, 339 m, CP Peña coll. (CATAC-1797). ECUADOR. *Orellana*, Tuptini, (-0.67177, -76.39793), 28.APR.2011, 223 m, Scheffrahn, Chase, Mangold, Křeček, Myles, Nishimura and Setter coll. (UF no. EC400). FRENCH GUIANA. *Cayenne*, Sinnamary, (+5.06314, -52.98479), 13.FEB.2008, 102 m, J. Křeček coll. (UF no. FG411). PARAGUAY. *Central*, Ypacaraí, (-25.38044, -57.20014), 27MAY2012, 248 m, Scheffrahn, Chase, Mangold, Křeček and Myles coll. (UF no. PA8). PERU. *Ucayali*, Nueva Requena, (-8.37007, -74.84366), 29.APR.2014, 185 m, Carrijo, Chase, Constantino, Mangold, Mullins, Křeček, Kuswanto, Nishimura, and Scheffrahn coll. (UF no. PU602, PU613). TRINIDAD AND TOBAGO. *Anse Fourmi*, Manson Hall, (+11.28467, -60.60133), 31.MAY.1996, 472 m, Chase, Mangold, Křeček, and Scheffrahn coll. (UF no. TT619). *Guayaguayare*, Río Claro-Mayaro (+10.23516, – 61,13266), 20.MAY.2003, 41 m, Chase, Mangold, Křeček, and Scheffrahn coll. (UF no. TT1614). VENEZUELA. *Bolívar*, Cantarrana, (+4.46750, -61.59694), 29.APR.2004, 874 m, J. Perozo coll. (UF no. VZ1443.1).

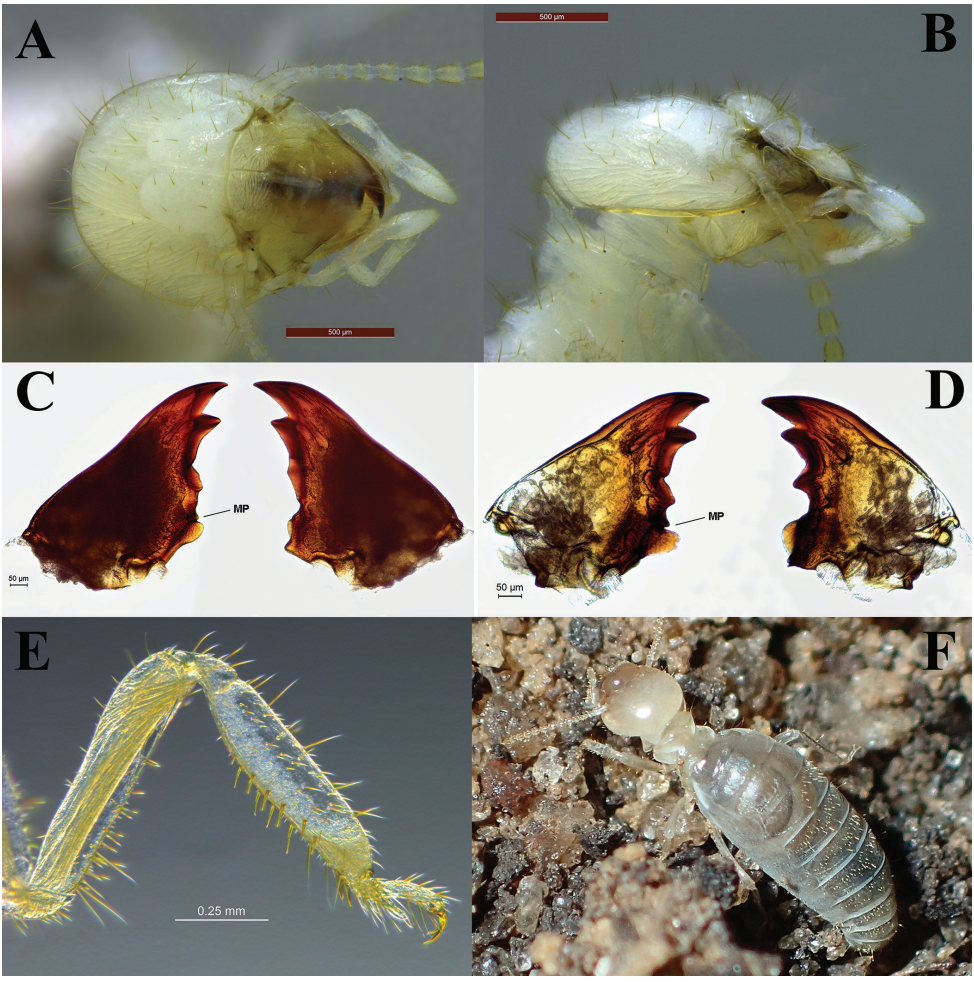

Figure 2. *Rustitermes boteroi* sp. nov. **A, B** worker head capsule in dorsal and lateral view **C** imago mandibles **D** worker mandibles **E** worker right fore tibia **F** live habitus of worker. MP = molar process. Specimens from lot CATAC 1797 (**A, B**), MZUSP 26677 (**C, D**), BO437 (**E**).

Diagnosis. Unarmed enteric valve with six slightly asymmetrical cushions, each one forms a central pouch made of about sixty scales, smaller than those between the cushions.

***Imago*.** As described for the genus.

Worker (Figs 2–4; Table 2). Monomorphic, head capsule with long and short bristles, with more abundance of long bristles. Head capsule color varying between whitish and yellowish. Antennae with 14 articles densely covered with short hairs and some long bristles. Pronotum with long bristles, concentrated along the margins of the anterior and posterior lobes, with some sparse short bristles in the center of the pronotum. Inner face of fore tibia with two rows of 6–7 thick bristles. Inner face of fore femur with thick bristles. Mesotibia and metatibia with 25–35 long, thick bristles.

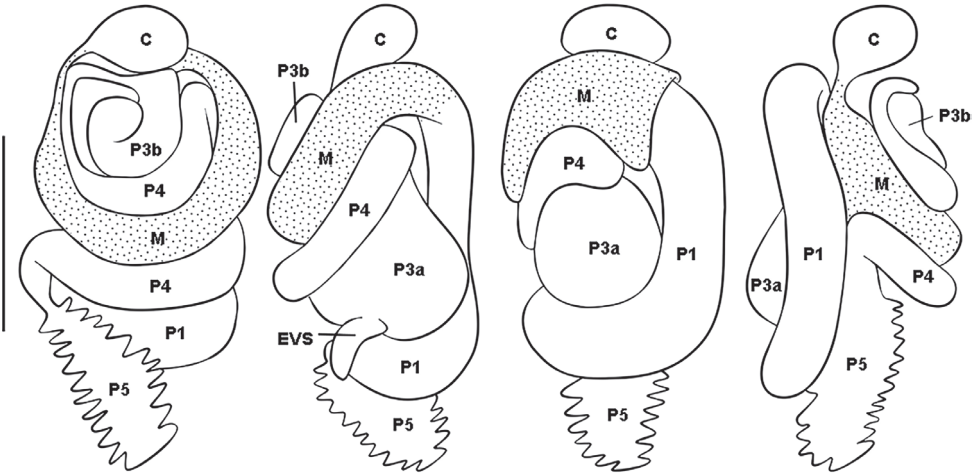

Figure 3. Digestive tube from left to right: dorsal, right, ventral and left views (gut regions indicated: *C* = crop, *M* = mesenteron, *P1* = ileum, *P3a* and *b* = paunch, *P4* = colon, *P5* = rectum, *EVS* = enteric valve seating). Scale bar: 0.5 mm.

Table 2. Measurements (mm) of 9 colonies (n = 10) of *Rustitermes boteroi* sp. nov. L = length, W = width.

	Length of head with postclypeus	Max. width of head	Hind tibia L	Fore tibia W	Fore tibia L	Ratio fore tibia W/L
Holotype	0.95	0.95	0.88	0.18	0.58	0.30
PU602	0.79–0.89 (0.86)	0.96–1.00 (0.99)	0.95–1.04 (0.99)	0.14–0.16 (0.15)	0.74–0.79 (0.78)	0.18–0.21 (0.20)
AG360	0.8–1.05 (0.86)	0.85–1.18 (0.92)	0.53–0.75 (0.63)	0.10–0.15 (0.13)	0.43–0.53 (0.46)	0.24–0.29 (0.28)
BO431	0.82–0.96 (0.90)	1.02–1.09 (1.04)	0.89–0.98 (0.95)	0.14–0.18 (0.16)	0.72–0.77 (0.75)	0.18–0.23 (0.21)
EC400	0.92–0.95 (0.89)	1.0–1.04 (1.01)	0.98–1.04 (1.01)	0.16–0.19 (0.18)	0.77–0.82 (0.80)	0.20–0.24 (0.23)
MZUSP 13712	0.80–0.84 (0.83)	0.98–1.12 (1.04)	0.77–0.88 (0.84)	0.13–0.18 (0.15)	0.63–0.72 (0.67)	0.19–0.26 (0.22)
FG411	0.80–0.85 (0.82)	0.87–0.93 (0.89)	0.68–0.80 (0.74)	0.17–0.20 (0.18)	0.55–0.58 (0.57)	0.33–0,35 (0.33)
PA8	0.82–0.89 (0.85)	0.88–0.95 (0.91)	0.88–0.96 (0.91)	0.16–0.19 (0.18)	0.68–0.75 (0.73)	0.21–0.27 (0.24)
TT1614	0.77–0.88 (0.82)	0.86–0.91 (0.89)	0.88–0.96 (0.90)	0.14–0.18 (0.16)	0.70–0.74 (0.72)	0.19–0.24 (0.22)
CATAC-0954	0.85–1.01 (0.91)	0.93–1.02 (0.99)	0.77–0.85 (0.82)	0.16–0.20 (0.18)	0.65–0.71 (0.69)	0.20–0.24 (0.22)

Enteric valve without armature, with six pyriform cushions of slightly different dimensions, each cushion consisting of 50–75 (depending on size of cushion) larger fringed polygons. The cuticle between the cushions is composed of even larger fringed cuboidal scales assembled close to P3.

Remarks. See remarks for genus.

Ecology and distribution. This species was collected mainly in soil, although it can also be found at the base of trees or occasionally under pieces of wood or fallen tree limbs above ground. Very common in pastures and open areas; found in young rubber crops in great abundance, less abundant in natural forests. Range: from Trinidad and Tobago to northern Argentina and the Atlantic Forest in Brazil (see discussion below); no known records for Chile and Uruguay (Figure 6).

Etymology. Named in honor of the great Colombian artist Fernando Botero.

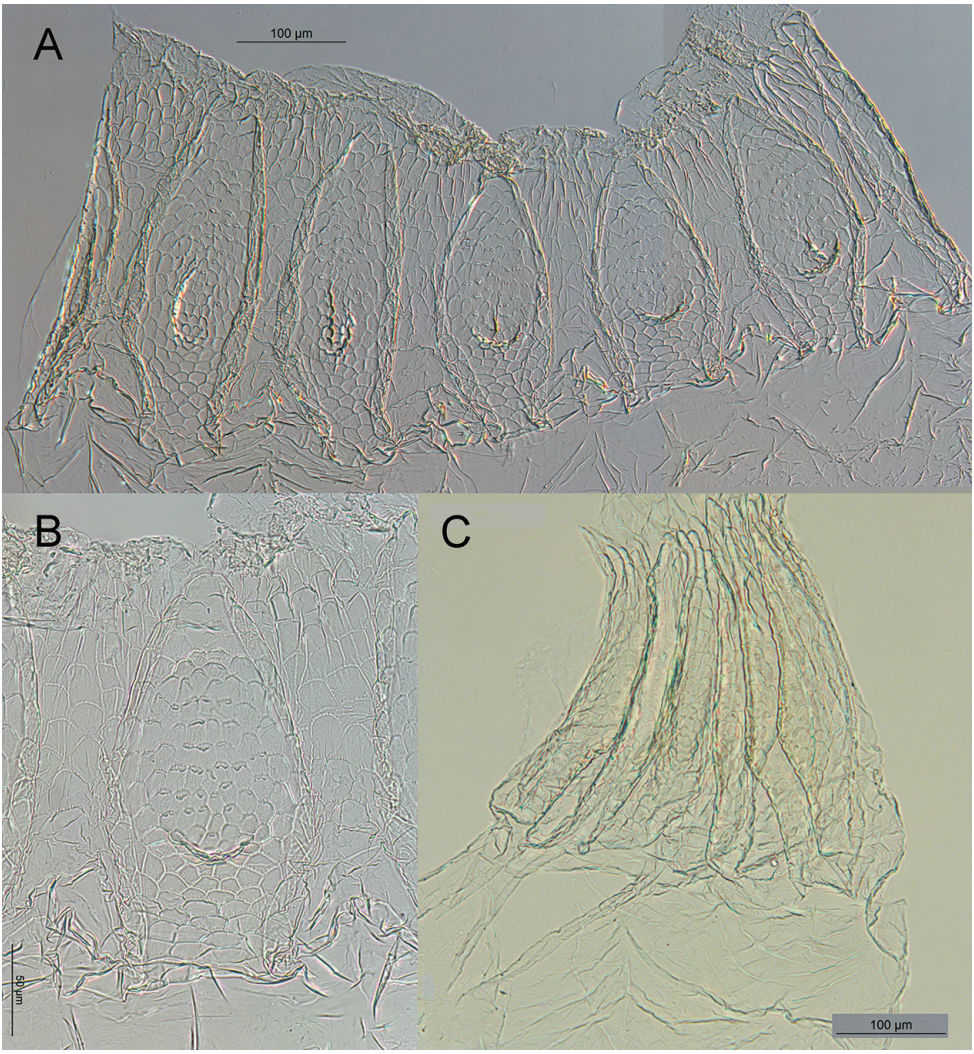

Figure 4. Worker enteric valve of *Rustitermes boteroi* sp. nov. **A** EV fully stretched laterally, showing the six cushions (end cushion bisected) **B** EV detail of smallest cushion in A **C** whole mount EV lateral profile of cushions. Food flow in each image from bottom to top.

Discussion

Despite its wide distribution and abundance in disturbed sites and open areas *R. boteroi* sp. nov. had not been previously described, indicating the lack of taxonomic work on soldierless termites. Currently, the use of the worker caste for the taxonomic identification of termites has been shown to be increasingly necessary, regardless of the presence of imago or soldier castes (Rocha et al. 2019).

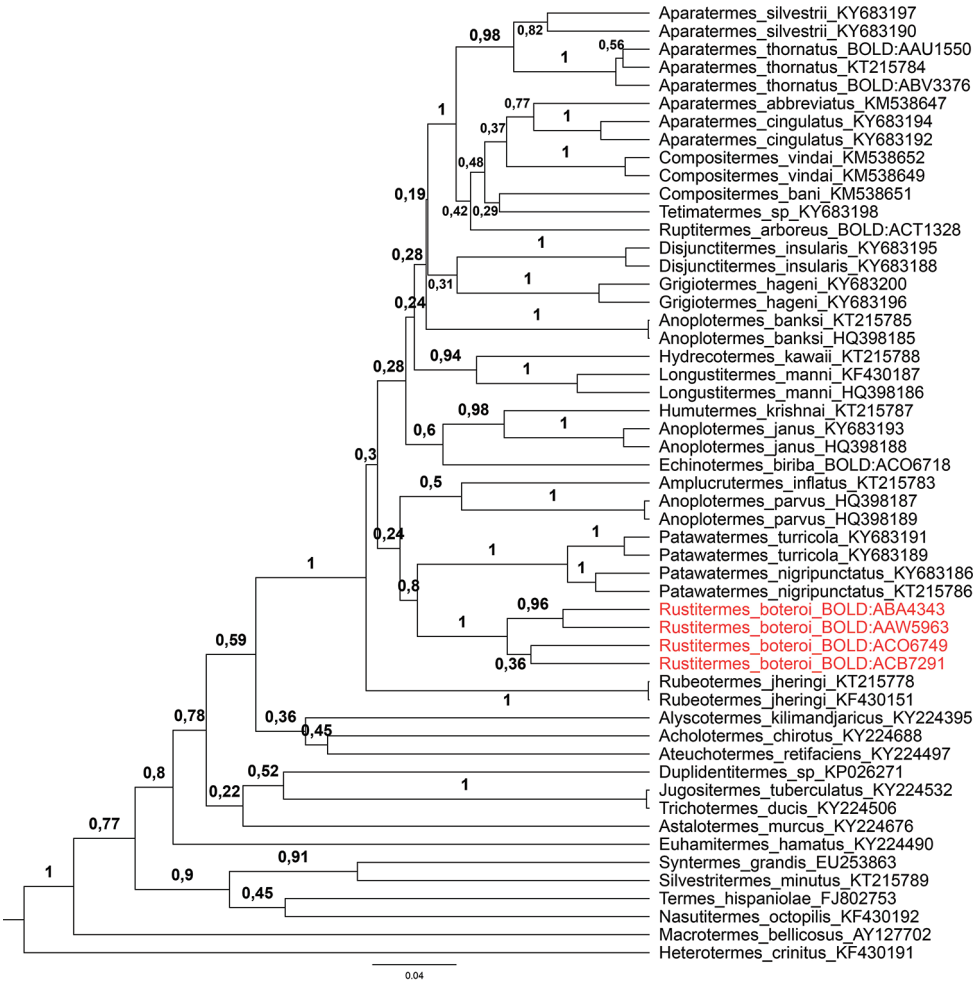

Figure 5. Bayesian phylogenetic tree of the Apicotermitinae subfamily using the COI region. In red, *Rustitermes boteroi* gen. et sp. nov. Branch support is posterior probability.

Many other Apicotermitinae species present wide distributions in South America, such as *Compositermes vindai* Scheffrahn, which has been reported from Panama to Paraguay (Scheffrahn 2013), *Aparatermes silvestrii* (Emerson), reported from Trinidad and Tobago to Paraguay (Pinzón et al. 2019), *Longustitermes manni* (Snyder), reported from Honduras to Brazil (Bourguignon et al. 2010), *Tonsuritermes tucki* Constantini and Cancello, reported from Colombia and French Guiana to southern Brazil and Paraguay (Constantini et al. 2018); and, with older records, species such as *Anoplotermes meridianus* Emerson, 1925 and *Anoplotermes parvus* Snyder, 1923, recorded from Central America to Argentina (Bourguignon et al. 2010; Krishna et al. 2013; Constantino 2019). Possibly, many others common species are not yet described, and many others,

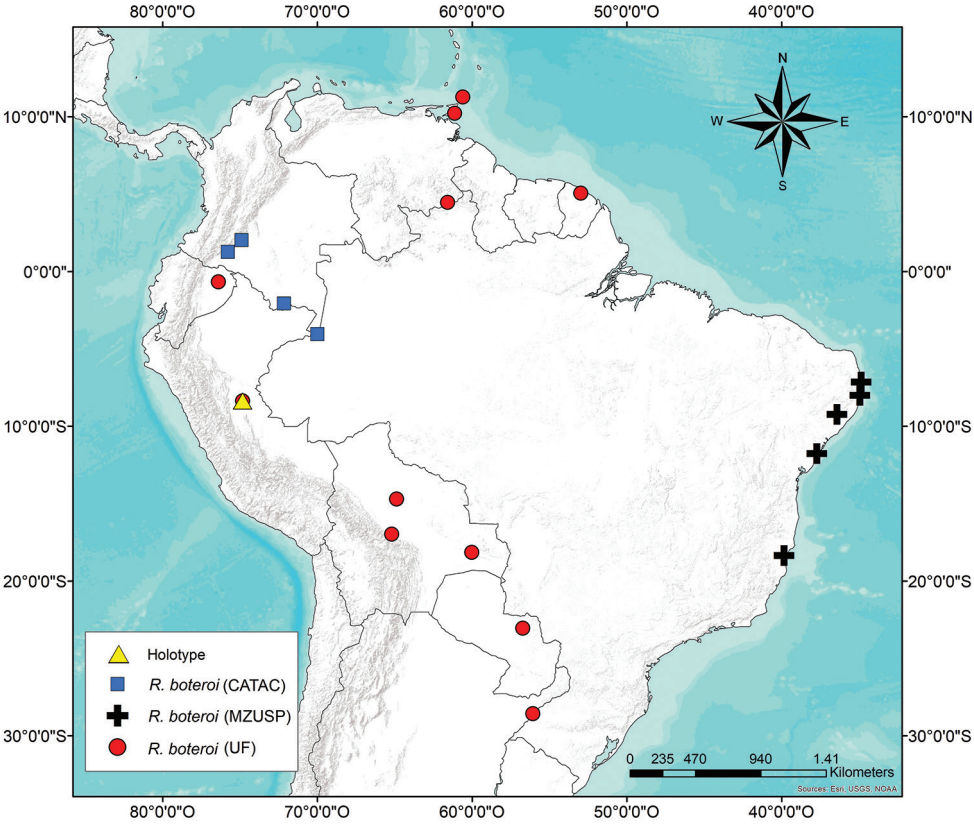

Figure 6. Distribution map of *Rustitermes boteroi* sp. nov. Collection data from the following collections: CATAC (SINCHI Institute), MZUSP (Museu de Zoologia da Universidade de São Paulo) and UF (University of Florida).

already described, have unknown ranges. Species with disjunct distributions based on few records probably have much larger distributions, as is the case with *Disjunctitermes* species (Scheffrahn et al. 2017). The New World Apicotermitinae are a typical example of both Linnean and Wallacean shortfalls (Bini et al. 2006).

According to the data presented, *R. boteroi* sp. nov. is widely distributed in the Guiana shield, the Amazon and the Atlantic forest. An effort is needed to identify Cerrado, Caatinga and Amazonian samples (there is abundant material deposited in MZUSP) to determine if this species is present in these areas.

Molecular phylogeny using the COI marker was useful to complement evidence of the separation of *R. boteroi* sp. nov. from the other Apicotermitinae genera. However, this marker alone is not enough to provide a resolved phylogeny allowing to understand the evolution of this group. The new world Apicotermitinae were determined to be monophyletic, but the relationship between most genera had very low branch support, making it impossible to provide deeper discussions.

Acknowledgments

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New record of *Didymocorypha* Wood-Mason (Mantodea, Eremiaphilidae) from China, with description of a new high-altitude wingless mantis species in Asia

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Abstract

The genus *Didymocorypha* Wood-Mason, 1877 (Eremiaphilidae, Iridinae) has only been recorded in South Asia, including a sole species *D. lanceolata* (Fabricius). Here, we firstly extend its distribution to China, with description of one new species *D. libaii* **sp. nov.** *Didymocorypha libaii* **sp. nov.** lives in an area about 3000 meters above sea level on the southern slope of the Himalayas (Tibet in China), one of the highest-altitude inhabited areas of mantis in the Northern Hemisphere. It is also the first recorded Oriental mantis species in which both sexes are wingless. Life history of the new species, necessary illustrations and ecological images are provided. The distribution of the new *Didymocorypha* species is discussed and mapped.

Keywords

apterous mantis species, life history, new species, Oriental Region, taxonomy

Introduction

The genus *Didymocorypha* was erected for a sole species *D. ensifera* Wood-Mason, 1877 from Sri Lanka with which *Pyrgocotis gracilipes* Stål, 1877 was synonymized (Wood-Mason 1882). Subsequently, *Mantis lanceolata* Fabricius, 1798, which was recorded from Eastern India, was transferred into the genus *Didymocorypha* by Bolivar (1897).

Afterwards, *D. ensifera* was considered as a synonym of *D. lanceolata* (Kirby 1904). At the time of Ehrmann's catalogue (Ehrmann 2002) the genus *Didymocorypha* only possessed one species, *D. lanceolata*, which is widely distributed in South Asia (e.g., Sri Lanka, Nepal and India). In Schwarz and Roy's (2019) new taxonomic system, the genus *Didymocorypha* belongs to subfamily Iridinae (Eremiaphilidae). This subfamily includes eight genera, among which seven range from Africa to South Asia and one genus *Iris* Saussure ranges from Africa and Europe to northwestern China (Wang 1993). Until now, no other genera of the subfamily Iridinae or the family Eremiaphilidae have been recorded from China.

Within the order Mantodea, brachypterous females are common. Apterous females are a rarity except in some families, for example Thespidae and Haaniidae. It is also rare that both sexes of a certain species are wingless. As far as we know, both sexes are apterous in three Old World mantis genera, *Apteromantis* Werner, 1931 (Amelidae), *Geomantis* Pantel, 1896 (Rivetinidae), *Holaptilon* Beier, 1964 (Gonypetidae), one African genus *Apterocorypha* Roy, 1966 (Hoplocoryphidae) and one North American genus *Yersiniops* Hebard, 1931 (Amelidae) (Ehrmann 2002; Battiston et al. 2010). Most of these apterous mantis species are small-sized, and live in grassland or shrubland in temperate regions. No mantis species with apterous males and females has been recorded within the family Eremiaphilidae or in the Oriental Realm.

When investigating fauna on the southern slope of the Himalayas in Tibet, China, we collected apterous adult specimens of *Didymocorypha* from Gyirong County at an altitude of 3000 meters in 2017. After dissecting the male specimens and comparing them with Indian samples of *D. lanceolata*, we thought that those wingless specimens should belong to a unique new species of *Didymocorypha*. The new species is the first recorded species of *Didymocorypha* from China, and the first recorded Oriental mantis species with wingless male and female adults. *Didymocorypha* is the second recorded genus of the family Eremiaphilidae from China. Here, we review the genus *Didymocorypha*, provide a redescription of the known species, and thoroughly describe the new species and its life history.

Material and methods

Classification system follows Schwarz and Roy (2019). Descriptive terminology of adult morphology and the male genitalia follows Brannoch et al. (2017) and Schwarz and Roy (2019). All specimens of the new species were collected during daytime through careful observation. Genitalia were dissected in 10% KOH solution, cleared with pure water, and finally stored in 70% ethanol in Eppendorf tubes for further research. Pictures were taken with a Nikon digital camera.

The specimens were deposited in the following institutions or private collections.

IZCAS Institute of Zoology, Chinese Academy of Sciences, Beijing, China
CJZ Collection of Jia-Zhi Zhang, Shanghai, China
CWC Collection of Chao Wu, Beijing, China

Taxonomic treatment

Didymocorypha Wood-Mason, 1877

Figs 1–7

Schizocephalus (*Didymocorypha*): Wood-Mason, 1877: 221.
Pyrgocotis: Stål, 1877: 14; Westwood 1889: 3; Brunner de Wattenwyl 1893: 59; Kirby 1904: 218 (syn.); Giglio-Tos 1921: 31 (syn.).
Didymocorypha: Wood-Mason, 1882: 24; Westwood 1889: 3; Brunner de Wattenwyl 1893: 59; Bolivar 1897: 303; Kirby 1904: 218; Giglio-Tos 1919: 57; Giglio-Tos 1921: 31; Giglio-Tos 1927: 116; Beier 1935: 5; Beier 1964: 942; Beier 1968: 8; Ehrmann 2002: 122; Otte and Spearman 2005: 328; Ehrmann and Borer 2015: 231; Schwarz and Roy 2019: 115, 143.

Type species. *Schizocephalus* (*Didymocorypha*) *ensifera* Wood-Mason, 1877 by original monotypy =*Mantis lanceolata* Fabricius, 1798.

Diagnosis. Small-sized, slender (Figs 1–3). Head elongate (Fig. 4), with lateral lobes of vertex prolonged into triangular processes, running alongside each other but not fused. Compound eyes large, oblong. Lower frons approximately trapezoid. Pronotum slender, with nearly parallel lateral margins. Fore legs weak. Fore femur (Fig. 5A, B) with 4 ventro-posterior and 4 discoidal spines; claw groove in the middle; fore tarsus much longer than tibia, and basal tarsomere longer than total length of remaining segments. Middle and hind legs slim without expansions but with genicular spines. Hind legs longer and stronger than mesolegs, similar to jumping legs of locusts. Male winged (Fig. 1A) or wingless (Figs 1C, 3A); if winged, fore wings hyaline, a little shorter than body. Female wingless (Figs 1B, 2, 3C).

Abdomen long, narrow. Cerci well-developed, with each segment wide, flat, lanceolate (Fig. 5C–E).

Distribution (Fig. 7). India, Nepal, Sri Lanka, China (new record).

Didymocorypha lanceolata (Fabricius, 1798)

Figs 1A, 4A, 5C, 6A, 7

Mantis lanceolata: Fabricius, 1798: 191.
Schizocephalus (*Didymocorypha*) *ensifera* Wood-Mason, 1877: 221–222.
Pyrgocotis gracilipes: Stål, 1877: 17; Westwood 1889: 3 (syn.); Kirby 1904: 218 (syn.); Giglio-Tos 1927: 116.
Didymocorypha ensifera: Wood-Mason, 1882: 24; Wood-Mason 1889: 34; Kirby 1904: 218 (syn.); Giglio-Tos 1927: 116.
Pyrgomantis lanceolata: Westwood 1889: 3.
Didymocorypha lanceolata: Bolivar 1897: 303; Kirby 1904: 218; Giglio-Tos 1921: 32; Giglio-Tos 1927: 116; Henry 1932: 9; Werner 1933: 898; Ehrmann 2002:123;

Otte and Spearman 2005: 328; Ehrmann and Borer 2015:231, 244, 249; Schwarz et al. 2018: 206–207, 227.

Type locality. 'India orientali' (Fabricius 1798).

Material examined. India • 5 ♂; Andhra Pradesh, Nellore District; 15.769N, 79.693E; 150 m; 10~25-IX-2012; IZCAS.

Description. Male. Slim and slender, withered-grass-like (Fig. 1A). Three ocelli large and hump (Fig. 4A). Fore femur approximately as long as fore coxa, with 4 posteroventral, 4 discoidal, 17 anteroventral spines; claw groove lying basally than middle of fore femur. Fore tibia about half as long as femur, with 5 posteroventral, 10 anteroventral spines and 1 strong tibial spur. Wings hyaline and iridescent, a little shorter than body; fore wings long and narrow, hind wings broad. Cerci flat, wide, lanceolate, with distal joints gradually becoming longer distad (Fig. 5C).

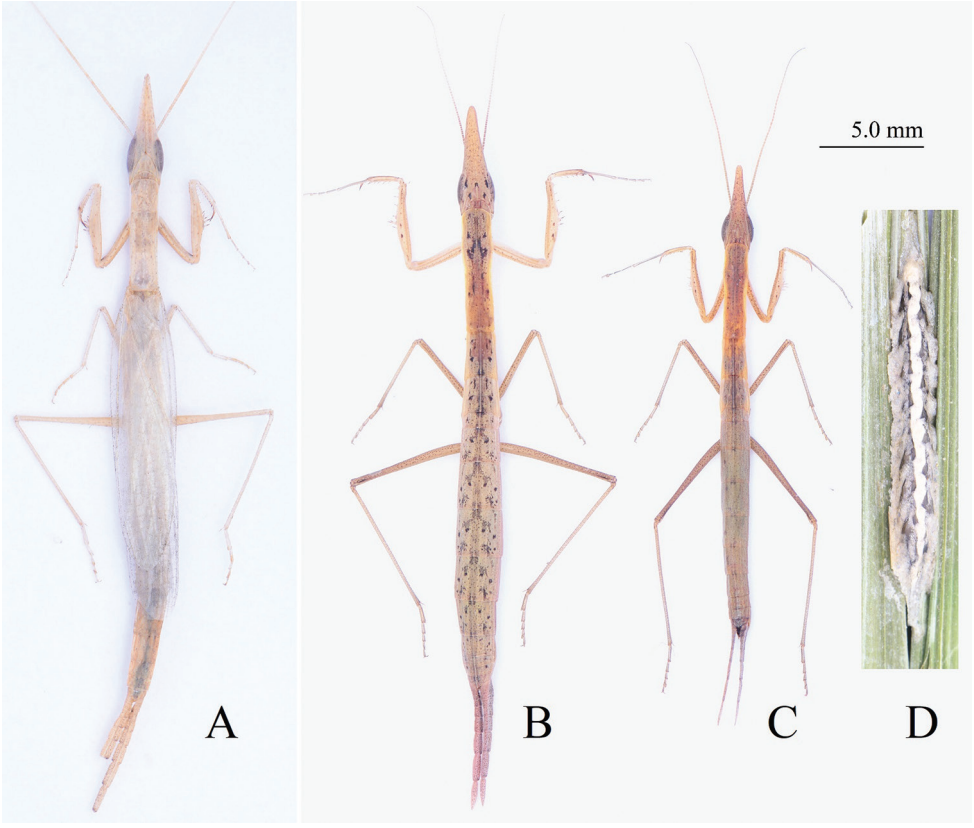

Figure 1. *Didymocorypha* spp. body in dorsal view and ootheca. **A, C** Male **B** female **D** oothecae. **A** *D. lanceolata* (Fabricius) **B–D** *D. libaii* sp. nov. (holotype and paratype).

Figure 2. *Didymocorypha libaii* sp. nov. adult female in its natural habitat.

Figure 3. Adult and nymph of *Didymocorypha libaii* sp. nov. in natural habitat. **A** Adult male **B** nymphs **C** feeding adult female **D** copulating adults **E** ecological habitat.

External genitalia (Fig. 6A) small; left phallomere narrow, long, with finger-like process paa and about 12 thick bristles on the afa; ventral phallomere with a robust short sharp spd.

Female similar as male, but larger, stronger, and wingless.

Male measurements (Length in mm). Body: 34.60–35.05; head: 7.10–7.14; pronotum: 5.90–5.95; fore coxae: 2.90–2.95; fore femora: 3.18–3.22; fore tibiae: 2.39–2.41; middle femora: 3.57–3.60; hind femora: 6.65–6.70; forewing: 14.05–14.10; hind wing: 15.33–15.38; cercus: 8.70–8.75.

Distribution (Fig. 7). India, Nepal, Sri Lanka (Ehrmann 2002), Thailand (Unnahachote et al. 2019).

Didymocorypha libaii **Wu & Liu, sp. nov.**
http://zoobank.org/B5D329E2-4E92-4853-911E-C6753EE240F3
Figs 1B–D, 2, 3–D, 4B, C, 5A, B, 5D, E, 6B, C, 7

Material examined. ***Holotype.*** China • ♂; Tibet, Gyirong County; 28.404N, 85.332E; 3300 m; 20-VII-2017; Chao Wu leg.; IZCAS. ***Paratypes.*** China • 4 ♂ 6 ♀; Tibet, Gyirong County; 28.397N, 85.351E; 2800~3300 m; 18~21-VII-2017; Chao Wu leg.; IZCAS • 3 ♂ 3 ♀; ditto; CWC • 1♀; ditto; CJZ • 1 ♀; Tibet, Gyirong County; 28.363N, 85.339E; 2672 m; 1-VIII-2018; Jin-Cheng Liu leg.; CWC.

Description. Holotype. **Male.** Slim (Figs 1B, C, 2, 3A, 3C).

Head: lanceolate. Paired juxtaocular bulges united into a conical extension with a complete median dorsal suture and a deep vertical ventral groove (Fig. 4B). Compound eyes long, oval, not bulging. Three ocelli, small, not obvious (Fig. 4B). Lower frons approximately trapezoidal, approximately as wide as high.

Thorax: pronotum longer than head, slender, about 3 times as long as wide. Prozona almost as wide as metazona. Mesothorax similar to metathorax, simple, nearly trapezoidal. Thorax with distinct medial keel. Wingless.

Prothoracic legs: fore coxa smooth, unarmed, shorter than metazona; fore femur as long as coxa, with a strongly-developed genicular spur (Fig. 5B), 4 posteroventral, 4 discoidal, 15–16 anteroventral spines, and without dilation on dorsal surface (Fig. 5A,B); claw groove lying basally to middle of fore femur; fore tibia about half as long as femur, with 5–6 posteroventral, 10 anteroventral tibial spines and 1 strong tibial spur; fore tarsus longer than tibia; basal tarsomere (= basitarsus) longer than total length of remaining segments.

Meso- and metathoracic legs: slim without expansions and with one small femoral genicular spur and one obvious tibial spur. Tarsus much shorter than tibia; basal tarsomere short, less than total length of remaining segments. Metathoracic legs longer and stronger than mesolegs.

Abdomen: almost as wide as pronotum. Each abdominal segment similar, nearly square; tergite 10 (Supra-anal plate) broad, widely trianglar. Cerci possessing 15 joints, with distal joints gradually becoming longer distad. Each of last 3 joints longer than

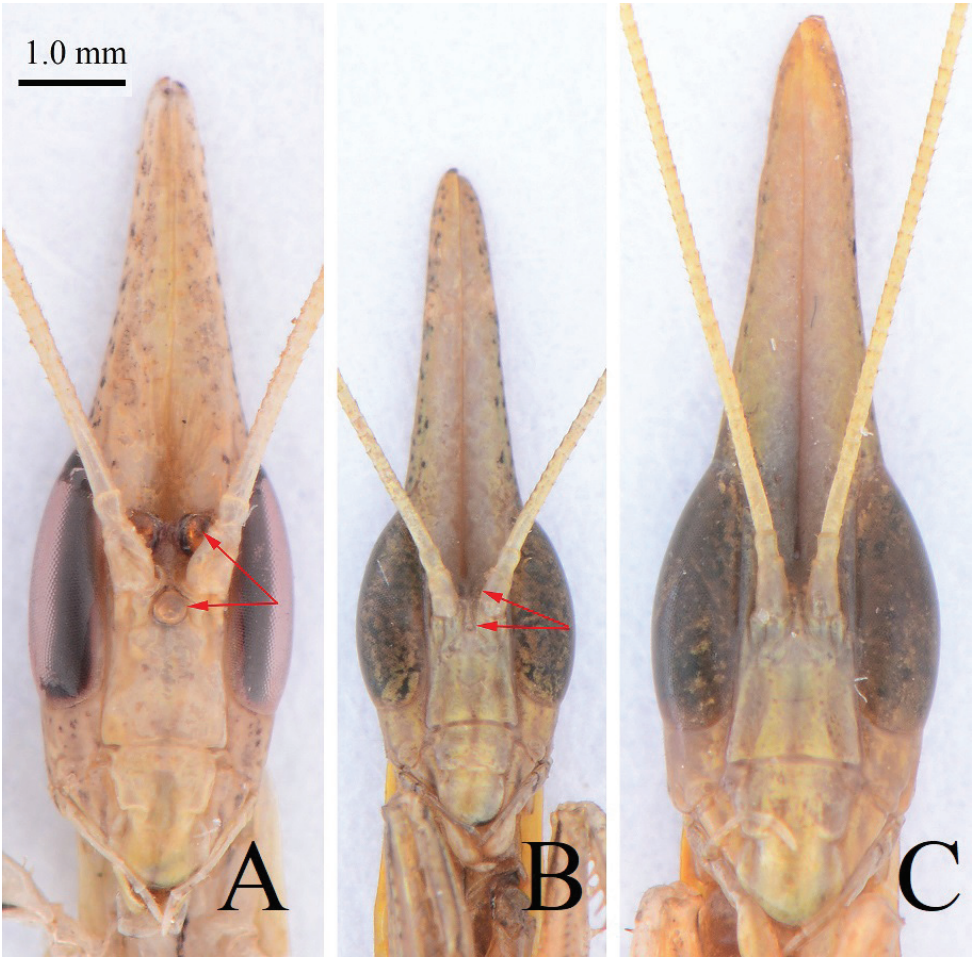

Figure 4. Head of *Didymocorypha* spp., anterior view. **A** Male, *D. lanceolata* (Fabricius) **B** male, *D. libaii* sp. nov. (holotype) **C** female, *D. libaii* sp. nov. (paratype). Red arrows point to ocelli.

wide (Fig. 5E). Coxosternite 9 (subgenital plate) nearly triangular, slightly asymmetrical, with a pair of styli.

External genitalia (Fig. 6B, C): relatively large-sized. Left phallomere narrow and long, posterior process of ventral phallomere (spd) indistinct; phalloid apophysis (afa) short, wide and strongly sclerotized, with a spine-like projection; posterior process of left phallomere (paa) with a finger-like extension, with a small obtuse tubercle in middle, and with a brush-like cluster of hairs on base.

Female. Similar to male, but distinctly larger and stronger (Figs 1B, 5C).

Measurements (Length in mm, Holotype in parentheses). Body: male 28.30–28.75 (28.45), female 32.50–35.15; head: male 5.85–5.95 (5.94), female 7.45–7.55; prono-

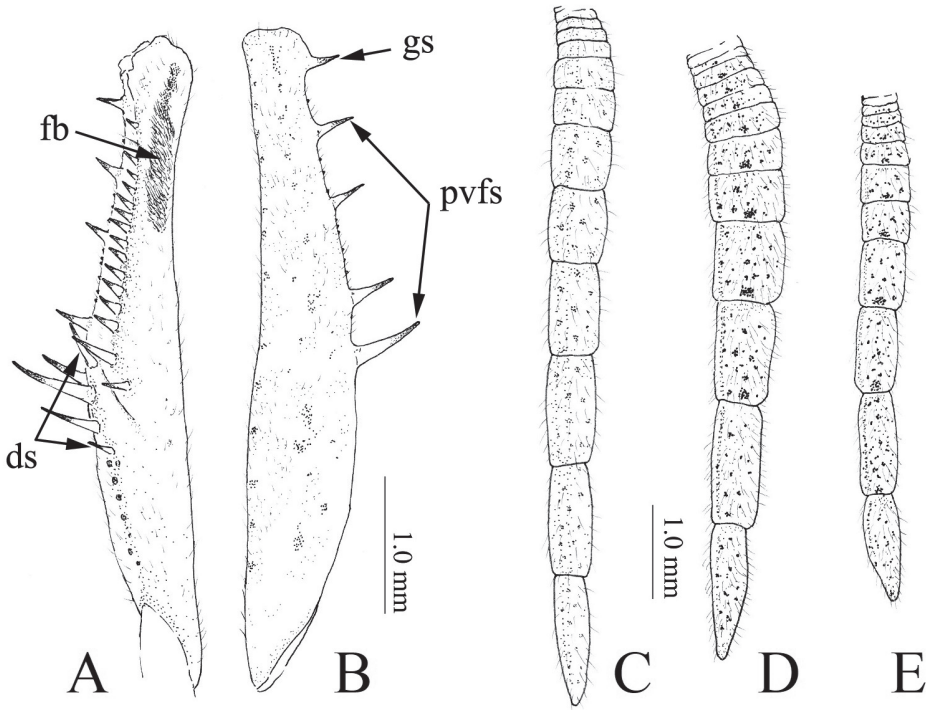

Figure 5. Fore femur (**A, B**) and cerci (**C–E**) of *Didymocorypha* spp. **A, B, D, E** *D. libaii* sp. nov. **C** *D. lanceolata* (Fabricius). **A** Ventral view **B** dorsal view **A, B, C, E** male **D** female. Abbreviations: **fb** = femoral brush; **ds** = discoidal spines; **gs** = genicular spur; **pvfs** = posteroventral femoral spines.

tum: male 5.35–5.39 (5.39), female 6.95–7.10; fore coxae: male 3.13–3.18 (3.15), female 4.11–4.20; fore femora: male 4.10–4.13 (4.11), female 4.62–4.80; fore tibiae: male 2.25–2.30 (2.27), female 2.85–3.02; middle femora: male 4.42–4.51 (4.45), female 5.70–5.79; hind femora: male 6.20–6.27 (6.25), female 7.43–7.52; cercus: male 5.45–5.50 (5.47), female 7.30–7.35.

Diagnosis. The new species is distinguished from *D. lanceolata* by small body size, small and indistinct male ocelli, wingless male adults, comparatively large-sized genitalia, ventral phallomere without secondary distal process (sdp), additional obtuse tubercle on paa and different structure of afa (Fig. 6).

Coloration (Figs 2, 3). Monotonous, tawny, dry-grass-like, densely covered with little black spots. Some specimens possessing irregular black patches. Spines of fore legs brown.

Life history. The new species often lives at the bottom of bushes in a variety of angiosperms (Figs 2, 3A–D) in high-altitude coniferous forest. Nymphs were found to be clustering (Fig. 3B), without cannibalism. This peaceful situation is an exception for mantis. The mating (Fig. 3D) is also peaceful, and needs up to 4–8

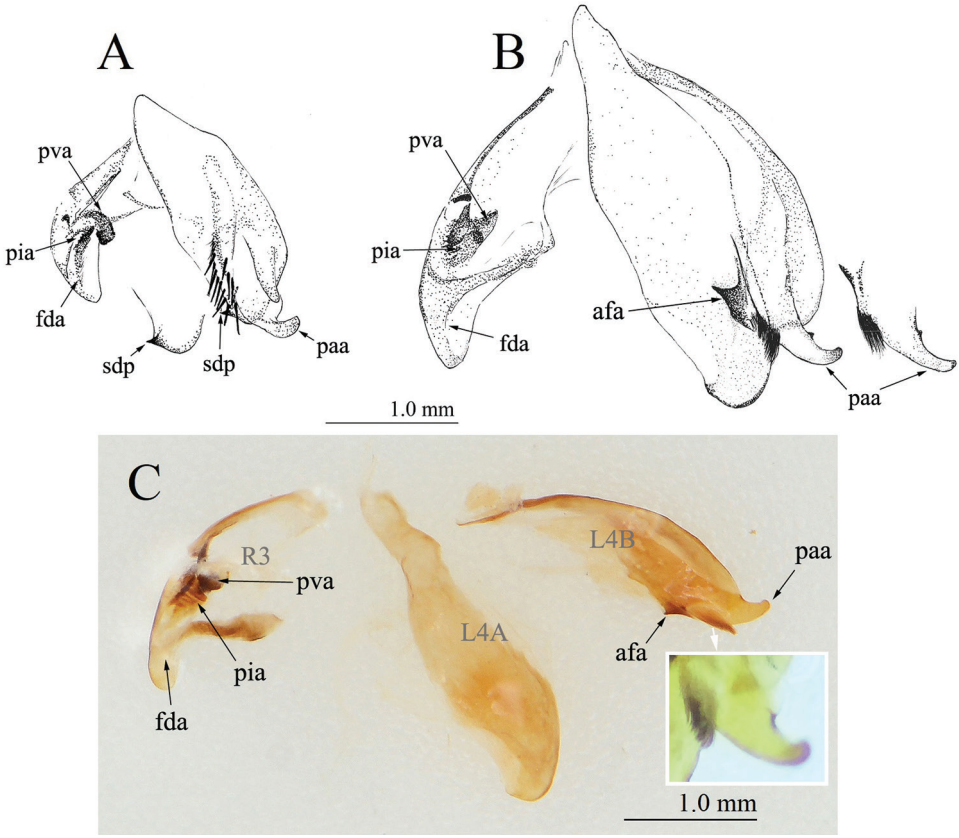

Figure 6. Male genitalia of *Didymocorypha* spp., Disarticulated genital complex, ventral view. **A** *D. lanceolata* (Fabricius) **B, C** *D. libaii* sp. nov. Abbreviations: **L4A** = sclerite extending over the ventral wall of left phallomere; **L4B** = sclerite extending over the dorsal wall of left phallomere; **R3** = anteriorly extending sclerite of right phallomere; **afa** = phalloid apophysis; **fda** = main posterior lobe of right phallomere; **pia** = process posterolateral to pva of right phallomere; **pva** = process anteromesal to pia of right phallomere; **paa** = posterior process of left phallomere; **sdp** = secondary distal process.

hours. Female lays their oothecae on the fifth day after mating. Oothecae are fusiform, withered-leaf-like. Each ootheca contains 4–10 eggs (Fig. 1D). Color of ootheca varies from light to very dark brown. External wall of cotheca is thin, sparse. Oothecae did not hatch successfully in the laboratory probably due to significant elevation differences from the mantis's natural habitat. In field, the mantis species prey on small-sized insects (e.g., Diptera, Hemiptera and Collembola) (Fig. 3C), based on our observations.

Distribution. China (Tibet: Gyirong County).

Etymology. The new species was named after Bai Li, who is a poet in the Tang dynasty of China and one of the most famous poets in Chinese history.

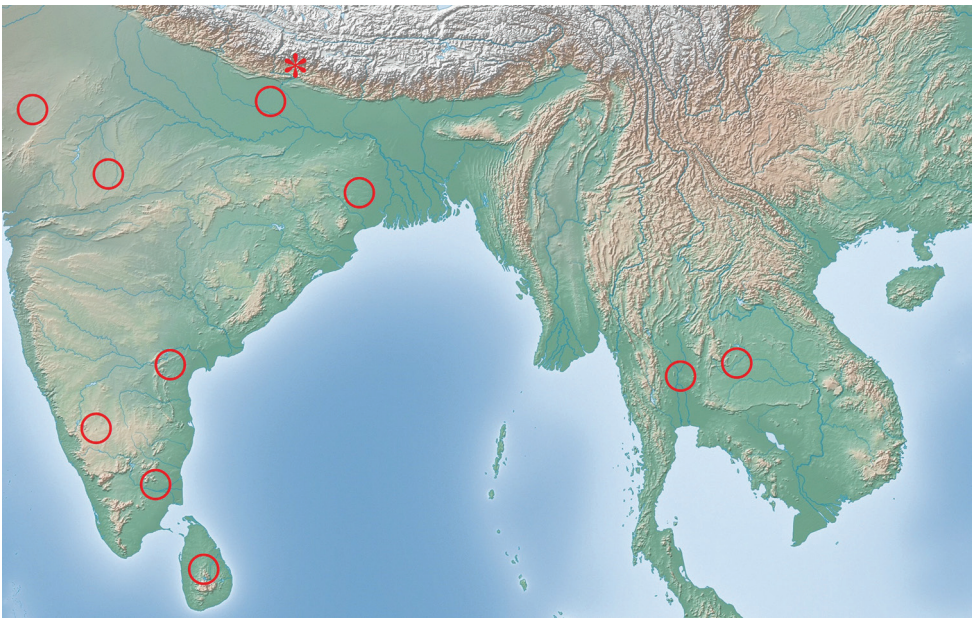

Figure 7. Distribution map of the distribution *Didymocorypha* spp. in South Asia and East Asia (Himalaya).○: *D. lanceolata* (Fabricius) ; * *D. libaii* sp. nov.

Discussion

Didymocorypha libaii sp. nov., is the first mantis species recorded at altitudes of more than 3000 meters (Fig. 3E) in China. At the type locality of *D. libaii* sp. nov., blankets of snow persist during the long winter, and the growing period is very short. In fact, it was difficult to distinguish the adults and nymphs of this new species from each other in general appearance. Initially, we judged them to be adults because they were mating when breeding indoors. Retention of nymph characteristics in the adults is called neoteny. We assume in the harsh environment of type locality of *D. libaii* sp. nov., that neotenic development could help to shorten the life cycle of the mantis, simultaneously, the large-sized male genitalia of the species can improve the success rate of copulation. In summary, the wingless adults and the large-sized male genitalia enable the species to adapt to the harsh environment.

We suppose that the new species was isolated by the uplifted Himalayas and diverged from its congener. Its ancestral population adapted to the environment at high altitudes, and was restricted to a very narrow range. In addition, a few mantis species (of genera *Arria* Stål, 1877, *Odontomantis* Saussure, 1871 and *Phyllothelys* Wood-Mason, 1877) are also found at an altitude of about 2500 m in China (including high-altitude areas of the Himalayas) based on our collections, which we will report in other papers. There are a range of suitable environments on the southern slopes of the Himalayas in China and more discoveries will possibly be made in the future.

The other recorded mantis species at high altitude include *Pseudopogonogaster hebardi* (Terra, 1982) from Ecuador at elevations 3500 m and *Armene breviptera* Lindt, 1963 from Badakhshan (West Pamir Mountains) at elevations 2300–2700 m. One ootheca of *A. breviptera* was even found at 3700 m (Lindt 1963). *Armene breviptera* was the only species of Mantodea that was previously found in the harsh environment. The dominant ecosystem there is dry mountain grassland with short and sparse vegetation cover, without trees or bushes and with very low biodiversity comparing to the lower elevations in the same region. The snow cover during winter is intermittent and often does not provide sufficient thermal protection during the cold months (Khakimov et al. 2007). *Armene breviptera* is the only micropterous species in the genus, also suggesting a connection between harsh external conditions and wing adaptation in Mantodea. By comparison, *Didymocorypha libaii* sp. nov. lives in a significantly milder environment with abundant vegetation, including trees, in spite of long winters. The conditions of *D. libaii* are also atypical for Mantodea also suggesting possible adaptations of the species to the short growth period.

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Additions and corrections to "Family-group names in Coleoptera (Insecta)"

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Abstract

Changes to the treatment of Coleoptera family-group names published by Bouchard et al. (2011) are given. These include necessary additions and corrections based on much-appreciated suggestions from our colleagues, as well as our own research. Our ultimate goal is to assemble a complete list of available Coleoptera family-group names published up to the end of 2010 (including information about their spelling, author, year of publication, and type genus).

The following 59 available Coleoptera family-group names are based on type genera not included in Bouchard et al. (2011): Prothydrinae Guignot, 1954, Aulonogyrini Ochs, 1953 (Gyrinidae); Pogonostomini Mandl 1954, Merismoderini Wasmann, 1929, †Escheriidae Kolbe, 1880 (Carabidae); Timarchopsinae Wang, Ponomarenko & Zhang, 2010 (Coptoclavidae); Stictocraniini Jakobson, 1914 (Staphylinidae); Cylindrocaulini Zang, 1905, Kaupiolinae Zang, 1905 (Passalidae); Phaeochroinae Kolbe, 1912 (Hybosoridae); Anthypnidae Chalande, 1884 (Glaphyridae); Comophorini Britton, 1957, Comophini Britton, 1978, Chasmidae Streubel, 1846, Mimelidae Theobald, 1882, Rhepsimidae Streubel, 1846, Ometidae Streubel, 1846, Jumnidae Burmeister, 1842, Evambateidae Gistel, 1856 (Scarabaeidae); Protelmidae Jeannel, 1950 (Byrrhoidea); Pseudeucinetini Csiki, 1924 (Limnichidae); Xylotrogidae Schönfeldt, 1887 (Bostrichidae); †Mesernobiinae Engel, 2010, Fabrasiinae Lawrence & Reichardt, 1966 (Ptinidae); Arhinopini Kirejtshuk & Bouchard, 2018 (Nitidulidae); Hypodacninae Dajoz, 1976, Ceuthocera Mannerheim, 1852 (Cerylonidae); Symbiotinae Joy, 1932 (Endomychidae); Cheilomenini Schilder & Schilder, 1928, Veraniini Schilder & Schilder, 1928 (Coccinellidae); Ennearthroninae Chûjô, 1939 (Ciidae); Curtimordini Odnosum, 2010, Mordellochroini Odnosum, 2010 (Mordellidae); Chanopterinae Borchmann, 1915 (Promecheilidae); Heptaphyllini Prudhomme de Borre, 1886, Olocratarii Baudi di Selve, 1875, Opatrinaires

Mulsant & Rey, 1853, Telacianae Poey, 1854, Ancylopominae Pascoe, 1871 (Tenebrionidae); Oxycopiini Arnett, 1984 (Oedemeridae); Eutrypteidae Gistel, 1856 (Mycteridae); Pogonocerinae Iablokoff-Khnzorian, 1985 (Pyrochroidae); Amblyderini Desbrochers des Loges, 1899 (Anthicidae); Trotommideini Pic, 1903 (Scraptiidae); Acmaeopsini Della Beffa, 1915, Trigonarthrini Villiers, 1984, Eunidiini Téocchi, Sudre & Jiroux, 2010 (Cerambycidae); Macropleini Lopatin, 1977, Stenopodiides Horn, 1883, Microrhopalides Horn, 1883, Colaphidae Siegel, 1866, Lexiphanini Wilcox, 1954 (Chrysomelidae); †Medmetrioxenoidesini Legalov, 2010, †Megametrioxenoidesini Legalov, 2010 (Nemonychidae); Myrmecinae Tanner, 1966, Tapinotinae Joy, 1932, Acallinae Joy, 1932, Cycloderini Hoffmann, 1950, Sthereini Hatch, 1971 (Curculionidae).

The following 21 family-group names, listed as unavailable in Bouchard et al. (2011), are determined to be available: Eohomopterinae Wasmann, 1929 (Carabidae); Prosopocoilini Benesh, 1960, Pseudodorcini Benesh, 1960, Rhyssonotini Benesh, 1960 (Lucanidae); Galbini Beaulieu, 1919 (Eucnemidae); Troglopates Mulsant & Rey, 1867 (Melyridae); Hippodamiini Weise, 1885 (Coccinellidae); Micrositates Mulsant & Rey, 1854, Héliopathaires Mulsant & Rey, 1854 (Tenebrionidae); Hypasclerini Arnett, 1984; Oxaciini Arnett, 1984 (Oedemeridae); Stilpnonotinae Borchmann, 1936 (Mycteridae); Trogocryptinae Lawrence, 1991 (Salpingidae); Grammopterini Della Beffa, 1915, Aedilinae Perrier, 1893, Anaesthetinae Perrier, 1893 (Cerambycidae); Physonotitae Spaeth, 1942, Octotomides Horn, 1883 (Chrysomelidae); Sympiezopinorum Faust, 1886, Sueinae Murayama, 1959, Eccoptopterini Kalshoven, 1959 (Curculionidae).

The following names were proposed as new without reference to family-group names based on the same type genus which had been made available at an earlier date: Dineutini Ochs, 1926 (Gyrinidae); Odonteini Shokhin, 2007 (Geotrupidae); Fornaxini Cobos, 1965 (Eucnemidae); Auletobiina Legalov, 2001 (Attelabidae).

The priority of several family-group names, listed as valid in Bouchard et al. (2011), is affected by recent bibliographic discoveries or new nomenclatural interpretations. †Necronectinae Ponomarenko, 1977 is treated as permanently invalid and replaced with †Timarchopsinae Wang, Ponomarenko & Zhang, 2010 (Coptoclavidae); Agathidiini Westwood, 1838 is replaced by the older name Anisotomini Horaninow, 1834 (Staphylinidae); Cyrtoscydmini Schaufuss, 1889 is replaced by the older name Stenichnini Fauvel, 1885 (Staphylinidae); Eremazinae Iablokoff-Khnzorian, 1977 is treated as unavailable and replaced with Eremazinae Stebnicka, 1977 (Scarabaeidae); Coryphocerina Burmeister, 1842 is replaced by the older name Rhomborhinina Westwood, 1842 (Scarabaeidae); Eudysantina Bouchard, Lawrence, Davies & Newton, 2005 is replaced by the older name Dysantina Gebien, 1922 which is not permanently invalid (Tenebrionidae). The names Macraulacinae/-ini Fleutiaux, 1923 (Eucnemidae), Anamorphinae Strohecker, 1953 (Endomychidae), Pachycnemina Laporte, 1840 (Scarabaeidae), Thaumastodinae Champion, 1924 (Limnichidae), Eudicronychinae Girard, 1971 (Elateridae), Trogoxylini Lesne, 1921 (Bostrichidae), Laemophloeidae Ganglbauer, 1899 (Laemophloeidae); Ancitini Aurivillius, 1917 (Cerambycidae) and Tropiphorini Marseul, 1863 (Curculionidae) are threatened by the discovery of older names; Reversal of Precedence (ICZN 1999: Art. 23.9) or an application to the International Commission on Zoological Nomenclature will be necessary to retain usage of the younger synonyms. Reversal of Precedence is used herein to qualify the following family-group names as *nomina protecta*: Murmidiinae Jacquelin du Val, 1858 (Cerylonidae) and Chalepini Weise, 1910 (Chrysomelidae).

The following 17 Coleoptera family-group names (some of which are used as valid) are homonyms of other family-group names in zoology, these cases must be referred to the Commission for a ruling to remove the homonymy: Catiniidae Ponomarenko, 1968 (Catiniidae); Homopterinae Wasmann, 1920, Glyptini Horn, 1881 (Carabidae); Tychini Raffray, 1904, Ocypodina Hatch, 1957 (Staphylinidae); Gonatinae Kuwert, 1891 (Passalidae); Aplonychidae Burmeister, 1855 (Scarabaeidae); Mi-

crochaetini Paulus, 1973 (Byrrhidae); Epiphanini Muona, 1993 (Eucnemidae); Limoniina Jakobson, 1913 (Elateridae); Ichthyurini Champion, 1915 (Cantharidae); Decamerinae Crowson, 1964 (Trogossitidae); Trichodidae Streubel, 1839 (Cleridae); Monocorynini Miyatake, 1988 (Coccinellidae); Gastrophysina Kippenberg, 2010, Chorinini Weise, 1923 (Chrysomelidae); Meconemini Pierce, 1930 (Anthribidae).

The following new substitute names are proposed: *Phoroschizus* (to replace *Schizophorus* Ponomarenko, 1968) and Phoroschizidae (to replace Schizophoridae Ponomarenko, 1968); *Mesostyloides* (to replace *Mesostylus* Faust, 1894) and Mesostyloidini (to replace Mesostylini Reitter, 1913).

The following new genus-group name synonyms are proposed [valid names in square brackets]: *Plocastes* Gistel, 1856 [*Aesalus* Fabricius, 1801] (Lucanidae); *Evambates* Gistel, 1856 [*Trichius* Fabricius, 1775] (Scarabaeidae); *Homoeoplastus* Gistel, 1856 [*Byturus* Latreille, 1797] (Byturidae). Two type genera previously treated as preoccupied and invalid, *Heteroscelis* Latreille, 1828 and *Dysantes* Pascoe, 1869 (Tenebrionidae), are determined to be senior homonyms based on bibliographical research. While *Dysantes* is treated as valid here, Reversal of Precedence (ICZN 1999: Art. 23.9) is used to conserve usage of *Anomalipus* Guérin-Méneville, 1831 over *Heteroscelis*.

Keywords
Beetles, family-group name, nomenclature, stem, type genus

Introduction

Nine years have passed since the publication of the catalogue of "Family-group names in Coleoptera" (Bouchard et al. 2011). During this period, we have become aware of a number of available family-group names that were unfortunately omitted at the time. Furthermore, bibliographic and other errors associated with family-group names and their type genera were discovered. The additions and corrections herein focus on available family-group names proposed up to the end of 2010 with the exception of replacement names for names proposed before 2011. Several changes to the classification of Coleoptera have been published in the years since the publication of Bouchard et al. (2011), generally based on new molecular phylogenetic analyses. A thorough summary of these changes is outside of the scope of this article and therefore the classification scheme used in Bouchard et al. (2011) is followed here to maximize uniformity of contents for users. Further action is required to resolve remaining nomenclatural issues involving the Principle of Priority and the Principle of Homonymy (summarized in Appendices 2, 3). These cases are left unresolved so that specialists on the relevant groups can review them and decide on the best course of action. A dagger symbol "†" precedes fossil taxa.

We use the same methods as in Bouchard et al. (2011) although further comments are necessary regarding the treatment of the substantial number of family-group names proposed after 1999 based on the incorrectly formed stem of their type genus. Article 29.4 states that "If after 1999 a new family-group name is based on a generic name which is or ends in a Greek or Latin word or ends in a Greek or Latin suffix, but its derivation does not follow the grammatical procedures of Articles 29.3.1 or 29.3.2, its original spelling must be maintained as the correct original spelling, provided 29.4.1. it

has a correctly formed suffix [Art. 29.2], and 29.4.2. its stem is formed from the name of the type genus as though it were an arbitrary combination of letters [Art. 29.3.3]." Following the suggestion of Newton (2017: 4), we have accepted that the best way to promote stability in the long term (especially as several more family-group names proposed since 2011 are based on the incorrectly formed stem of their type genus) is to maintain the spellings as originally proposed when conditions laid out in Art. 29.3.3 are met. In this work we have accordingly reverted back to original spellings for family-group names proposed after 1999 that fall into this category. It may be argued that the spelling of some of these family-group names, as used in our initial work (Bouchard et al. 2011), is in prevailing usage and so is to be maintained (Art. 29.5). However, in all the cases the family-group names as corrected in our initial work have been used by very few authors (as far as we known in two works or fewer) and therefore we do not believe that Article 29.5 should apply here.

Additions and corrections

Bibliographic notes

Throughout the text replace "Acloque, 1896" with "Acloque, 1895". Acloque's *Faune de France* was issued in December 1895 (Bousquet 2016: 40), not in 1896 as listed on the title page.

Throughout the text replace "Branden, 1885" with "Branden, 1884". The separate of Branden's paper in Volume 29 of the *Annales de la Société Entomologique de Belgique* was issued in 1884, prior to the publication in the journal (Bousquet 2016: 543). The paginations in the separate and the journal article are identical.

Throughout the text replace "Desmarest, 1857" with "Desmarest, 1852". We follow Bousquet (2016: 142–143) who recommended using "1852" as the correct date of publication for the second part of this work.

Throughout the text replace "Germar, 1824" with "Germar, 1823" (but see exception for the genus *Otiorhynchus* below). Germar's *Coleopterorum species novae aut minus cognitae*" was issued in 1823, not in 1824 as indicated on the title page (Bousquet 2016: 211; Prena 2018: 327, 342).

Throughout the text replace "Laporte, 1836" with "Laporte, 1838". Although 1836 is the year given on the title page of volume 4 of the *Revue Entomologique*, this volume was only published in early 1838 (Hayek 1983: 207–208).

Throughout the text replace "Lacordaire, 1856" with "Lacordaire, 1855". Lacordaire's third volume of his *Histoire naturelle des insectes* was issued in October 1855, not in 1856 as listed on the title page (Bousquet 2016: 314).

Throughout the text replace "W. S. MacLeay, 1827" with "W. S. MacLeay, 1826". MacLeay's *Annulosa. Catalogue of insects*, *collected by Captain King*, *R.N.* was first published in two volumes in 1826 (Bousquet 2016: 353–354).

Throughout the text replace "Pic, 1912" with Pic, 1912a." The family-group names attributed to "Pic, 1912" in Bouchard et al. (2011) were published in *Coleopterorum Catalogus* (18 October 1912) while Ernobiinae (Pic 1912b: 55), which appeared in Volume 28 of *L'Échange*, was issued earlier in the same year (July 1912).

Throughout the text replace "Reitter, 1909" with "Reitter, 1909a." The family-group names attributed to "Reitter, 1909" in Bouchard et al. (2011) appeared in the second Theil of Reitter's "Fauna Germanica", which should be treated as having been published on December 31, 1909 for nomenclatural purposes (recorded in *Naturae Novitates* in January 1910). The new entry for Tanygnathini Reitter, 1909b (see below) was first proposed in the Coleoptera section (i.e., part 3–4) of "Die Süsswasserfauna Deutschlands: eine Exkursionsfauna" (recorded in *Naturae Novitates* in August 1909).

Table 1

Page 8. In Table 1, replace the generic ending from "*-celis*" to "*-scelis*" and the meaning from "spot (Greek)" to "leg (Greek)".

Page 8. In Table 1, replace the meaning of "*-onyx*" with "claw (Greek)" and that of "*-teles*" with "end, tail (Greek)".

Catalogue of Coleoptera family-group names

Suborder ARCHOSTEMATA

Page 95. Below "**Suborder ARCHOSTEMATA**" add:

"**Superfamily Cupedoidea Laporte, 1838**

Cupesidae Laporte, 1838: 56 [stem: *Cuped-*]. Type genus: *Cupes* Fabricius, 1801." Note. This superfamily is proposed to include the families Crowsoniellidae, Cupedidae, Micromalthidae, Ommatidae, Jurodidae, †Triadocupedidae, †Magnocoleidae, and †Obrieniidae. The suborder ARCHOSTEMATA includes the superfamilies Cupedoidea, †Asiocoleoidea, †Rhombocoleoidea, and †Schizocoleoidea.

Page 97. Replace the valid name "**†Tribe Kenderlykaini Legalov, 2009**" with "**†Tribe Kenderlykanini Legalov, 2009**".

Page 97. In the entry "Kenderlykanini Legalov, 2009c: 285..." replace the stem with "*Kenderlykan-*" and replace the "Comment" section with "Comment: incorrect original stem formation maintained under Art. 29.4 (should be *Kenderlyka-*)."

Page 97. Move the entries "**†Superfamily Asiocoleoidea Rohdendorf, 1961**", "**†Superfamily Rhombocoleoidea Rohdendorf, 1961**" and "**†Superfamily Schizophoroidea Ponomarenko, 1968**" and their associated data to below the entry "Obrieniidae Zherikhin and Gratshev, 1994: 51..." Note. The suborder MYXOPHAGA includes only the superfamilies Lepiceroidea Hinton, 1936 (1882) and Sphaeriusoidea Erichson, 1845.

Page 97. Replace the valid name "**†Superfamily Schizophoroidea Ponomarenko, 1968**" with "**†Superfamily Schizocoleoidea Rohdendorf, 1961**".

Page 97. Replace the entry "Schizophoridae Ponomarenko, 1968: 130…" below the valid name "**†Superfamily Schizocoleoidea Rohdendorf, 1961**" with:

"Schizocoleidae Rohdendorf, 1961: 438 [stem: *Schizocole*-]. Type genus: *Schizocoleus* Rohdendorf, 1961."

Page 97. Replace the valid name "**†Family Schizophoridae Ponomarenko, 1968**" with "**†Family Phoroschizidae Bouchard and Bousquet, *nomen novum***".

Page 97. Replace the entry "Schizophoridae Ponomarenko, 1968: 130…" below the valid name "**†Family Schizophoridae Ponomarenko, 1968**" with:

"Schizophoridae Ponomarenko, 1968: 130 [stem: *Schizophor*-]. Type genus: *Schizophorus* Ponomarenko, 1968 [preoccupied genus name, not *Schizophorus* Balashova, 1953 [Trilobita]; syn. of *Phoroschizus* Bouchard and Bousquet, ***nomen novum***. Comment: permanently invalid (Art. 39): based on preoccupied type genus."

Page 97. Below the entry "Schizophoridae Ponomarenko, 1968: 130…" add:

"Phoroschizidae Bouchard and Bousquet, ***nomen novum*** for Schizophoridae Ponomarenko, 1968 [stem: *Phoroschiz*-]. Type genus: *Phoroschizus* Bouchard and Bousquet, ***nomen novum*** for *Schizophorus* Ponomarenko, 1968."

Page 97. At the end of the entry "Catiniidae Ponomarenko, 1968: 137…" add "Comment: the family-group name Catiniidae Bocquet and Stock, 1957 (type genus *Catinia* Bocquet and Stock, 1957) is available in Crustacea; this case is to be referred to the Commission to remove the homonymy (Art. 55.3.1); the unnecessary replacement name Coleocatiniidae Ponomarenko and Prokin (2015) is unavailable (Art. 11.7.1.1) since it was not based on an available genus name at the time."

Suborder ADEPHAGA

Family Tritarsusidae Hong, 2002

Page 99. Replace the valid name "**†Family Tritarsidae Hong, 2002**" with "**†Family Tritarsusidae Hong, 2002**".

Page 99. In the entry "Tritarsusidae Hong, 2002: 102..." replace the stem with "*Tritarsus*-" and replace the "Comment" section with "Comment: incorrect original stem formation maintained under Art. 29.4 (should be *Tritars*-)."

Family Gyrinidae Latreille, 1810

Page 100. Replace the valid name "**Tribe Enhydrini Régimbart, 1882**" with "**Tribe Enhydrusini Branden, 1882**".

Page 100. Replace the entry "Enhydrini Régimbart, 1882: 392…" under the valid name "**Tribe Enhydrusini Branden, 1882**" with:

"Enhydrini Branden, 1882: 48 [stem: *Enhydrus*-]. Type genus: *Enhydrus* Laporte, 1834 [placed on the Official List of Generic Names in Zoology (ICZN 1964, 2012a)]. Comment: usage of this name conserved over Dineutini Desmarest, 1851 (Art. 35.5), though considered a junior synonym of Dineutini Desmarest, 1851 by

Gustafson and Miller (2013: 81, 95–96); name placed on the Official List of Family-Group Names in Zoology (ICZN 2012a, as "Enhydrusini Régimbart, 1882")."

Page 100. In the entry "Dineutides Desmarest, 1851: 223…" replace "Type genus: *Dineutes* W. S. MacLeay, 1825." with "Type genus: *Dineutus* W. S. MacLeay, 1825."

Page 100. Below the entry "Dineutides Desmarest, 1851: 223…" add:

"Dineutini Ochs, 1926: 63 [stem: *Dineut*-]. Type genus: *Dineutus* W. S. MacLeay, 1825. Comment: family-group name proposed as new without reference to Dineutides Desmarest, 1851 (see Gustafson and Miller 2013)."

Page 100. Replace the valid name "**Subtribe Enhydrina Régimbart, 1882**" with "**Subtribe Enhydrusina Branden, 1882**".

Page 100. Replace the entry "Enhydrini Régimbart, 1882: 392…" under the valid name "**Subtribe Enhydrusina Branden, 1882**" with:

"Enhydrini Branden, 1882: 48 [stem: *Enhydrus*-]. Type genus: *Enhydrus* Laporte, 1834 [placed on the Official List of Generic Names in Zoology (ICZN 1964, 2012a)]. Comment: correct stem ruled to be *Enhydrus*- to remove homonymy with Enhydrini Gray, 1825 (type genus *Enhydra* Fleming, 1822) in Mammalia and "Enhydrusini Régimbart, 1882" placed on the Official List of Family-Group Names in Zoology (ICZN 2012a); "Enhydrini Régimbart, 1882" deemed to be an incorrect original spelling and placed on the Official Index of Rejected and Invalid Family-Group Names in Zoology (ICZN 2012a); regarding the authorship of this name, Régimbart's paper was issued by December 1882 while Branden's was published earlier, before 25 April 1882."

Page 100. Below the entry "Enhydrini Branden, 1882: 48…" under the valid name "**Subtribe Enhydrusina Branden, 1882**" add:

"Prothydrinae Guignot, 1954: 45 [stem: *Prothydr*-]. Type genus: *Prothydrus* Guignot, 1954."

Page 100. Below the entry "Gyrinites Latreille, 1810: 141…" under the valid name "**Subtribe Gyrinina Latreille, 1810**" add:

"Aulonogyrini Ochs, 1953: 8 [stem: *Aulonogyr*-]. Type genus: *Aulonogyrus* Motschulsky, 1853."

Page 100. Replace the valid name "**Tribe Orectochilini Régimbart, 1882**" with "**Tribe Orectochilini Kolbe, 1880**".

Page 100. Replace "Orectochilini Régimbart, 1882: 391" with "Orectochilini Kolbe, 1880: 264".

Family Carabidae Latreille, 1802

Page 104. Move the entry "Euryodini W. Horn, 1899: 37…" from "**Subtribe Dromicina Thomson, 1859**" to "**Subtribe Cicindelina Latreille, 1802**" below the entry "Cicindeletae Latreille, 1802: 77…" and replace "Type genus: *Euryoda* Lacordaire, 1842 [syn. of *Prothyma* Hope, 1838]" with "Type genus: *Euryoda* Lacordaire, 1842 [syn. of *Heptodonta* Hope, 1838]" Note. As discussed by Bousquet (2002: 22) *Euryoda* Lacordaire, 1842 is an unnecessary replacement name for *Heptodonta* Hope, 1838 and is therefore a junior objective synonym of that taxon.

Page 105. Delete the entry "*Colliurides Motschulsky, 1855: 34…" Note. The genus-group name *Colliuris* used by Latreille (1802) is an incorrect subsequent spelling of *Collyris* Fabricius, 1801, not in prevailing usage. Therefore, Colliurides used by Motschulsky is an incorrect subsequent spelling of Collyridina Brullé, 1834.

Page 105. Below the entry "Ctenostomidae Laporte, 1834b: 38…" add:

"Pogonostomini Mandl 1954: 7 [stem: *Pogonostomat-*]. Type genus: *Pogonostoma* Klug, 1835. Comment: incorrect original stem formation, not in prevailing usage."

Page 106. In the entry "*Cechenogenici Morawitz, 1889: 40…" replace "Type genus: *Cechenus* Fischer von Waldheim, 1822" with "Type genus: *Cechenus* Fischer von Waldheim, 1822 [preoccupied genus name, not *Cechenus* Illiger, 1807 [Hymenoptera: Braconidae]; syn. of *Cechenochilus* Motschulsky, 1850]."

Page 106. In the entry "Cechenogenici Csiki, 1927: 110…" replace "Type genus: *Cechenus* Fischer von Waldheim, 1822" with "Type genus: *Cechenus* Fischer von Waldheim, 1822 [preoccupied genus name, not *Cechenus* Illiger, 1807 [Hymenoptera: Braconidae]; syn. of *Cechenochilus* Motschulsky, 1850]. Comment: permanently invalid (Art. 39): based on preoccupied type genus."

Page 116. In the entry "Sinozolini Deuve, 1997…" replace "Type genus: *Sinozolus* Bedel, 1898" with "Type genus: *Sinozolus* Deuve, 1997".

Page 118. Replace the entry "Nomiidae Gozis, 1875: 3…" with:

"Nomiidae Gozis, 1875: 3 [stem: *Nomius-*]. Type genus: *Nomius* Laporte, 1835 [placed on the Official List of Generic Names in Zoology (ICZN 2011a)]. Comment: Nomiidae Gozis, 1875 placed on the Official Index of Rejected and Invalid Family-Group Names in Zoology (ICZN 2011a), stem emended to *Nomius-* and Nomiusidae Gozis, 1875 placed on the Official List of Family-Group Names in Zoology (ICZN 2011a)."

Page 119. Below the entry "Carabidomemninae Wasmann, 1928: 271…" add:

"Eohomopterinae Wasmann, 1929: 60 [stem: *Eohomopter-*]. Type genus: *Eohomopterus* Wasmann, 1920."

Page 120. At the end of the entry "Homopterinae Wasmann, 1920: 111…" add "Comment: the family-group name Homopterinae Boisduval, 1852 (type genus *Homoptera* Boisduval, 1852) is available in Lepidoptera; this case is to be referred to the Commission to remove the homonymy (Art. 55.3.1)."

Page 120. Below the entry "Paussili Latreille, 1806: 234…" add:

"Merismoderini Wasmann, 1929: 60 [stem: *Merismoder-*]. Type genus: *Merismoderus* Westwood, 1846 [syn. of *Melanospilus* Westwood, 1846]."

Page 128. At the end of the entry "Glypti G. H. Horn, 1881: 179…" add "Comment: the family-group name Glyptini Cushman and Rohwer, 1920 (type genus *Glypta* Gravenhorst, 1829) is available and used as valid in Hymenoptera: Ichneumonidae; this case is to be referred to the Commission to remove the homonymy (Art. 55.3.1)."

Page 133. In the entry "Callidides Chaudoir, 1873b: 97…" replace "Type genus: *Calleida* Dejean, 1824" with "Type genus: *Calleida* Latreille, 1824".

Page 138. In the entry "Melanodini Alluaud, 1916: 228…" replace "syn. of *Melanchiton* Basilewsky, 1946." with "syn. of *Melanchiton* Andrewes, 1940."

Page 138. In the entry "Melanchitonitae Jeannel, 1948b: 627…" replace "Type genus: *Melanchiton* Basilewsky, 1946" with "Type genus: *Melanchiton* Andrewes, 1940."

Page 141. In the entry "Meleagrosini Morvan, 2004: 2..." replace the stem with "*Meleagros-*" and replace the "Comment" section with "Comment: incorrect original stem formation maintained under Art. 29.4 (should be *Meleagr-*)."

Page 143. Replace "Stomidae Chaudoir, 1846: 514" with "Stomides Gené, 1839: 50"

Page 145. In the entry "Agronomaeidae Gistel, 1848: [2]…" after "...*Amara* Bonelli, 1810" add "; preoccupied genus name, not *Agronoma* Hübner, 1821 [Lepidoptera]" and at the end of the "Comment" section add "; permanently invalid (Art. 39): based on preoccupied type genus."

Page 146. Above the valid name "**Family Haliplidae Aubé, 1836**" add:

"**Carabidae *incertae sedis***

†Escheriidae Kolbe, 1880: 266 [stem: *Escheri-*]. Type genus: *Escheria* Heer, 1847."

Family Coptoclavidae Ponomarenko, 1961

Page 147. Replace the valid name "**†Subfamily Necronectinae Ponomarenko, 1977**" with "**†Subfamily Timarchopsinae Wang, Ponomarenko and Zhang, 2010**".

Page 147. In the entry "Necronectinae Ponomarenko, 1977: 22…" replace "Type genus: *Necronectes* Ponomarenko, 1977 [syn. of *Timarchopsis* Brauer, Redtenbacher and Ganglbauer, 1889]" with "Type genus: *Necronectes* Ponomarenko, 1977 [preoccupied genus name, not *Necronectes* Milne-Edwards, 1881 [Crustacea]; syn. of *Timarchopsis* Brauer, Redtenbacher and Ganglbauer, 1889]" and add "Comment: permanently invalid (Art. 39): based on preoccupied type genus."

Page 147. Below the entry "Necronectinae Ponomarenko, 1977: 22…" add:

"Timarchopsinae Wang, Ponomarenko and Zhang, 2010: 681 [stem: *Timarchops-*]. Type genus: *Timarchopsis* Brauer, Redtenbacher and Ganglbauer, 1889. Comment: replacement name for Necronectinae Ponomarenko, 1977; incorrect stem formation maintained under Art. 29.4 (should be *Timarchopse-*)."

Page 147. In the entry "Hispanoclavinae Soriano et al., 2007: 527…" replace "Type genus: *Hispanoclava* Soriano, Ponomarenko and Delclos, 2007" with "Type genus: *Hispanoclavina* Soriano, Ponomarenko and Delclòs, 2007" and add "Comment: incorrect stem formation maintained under Art. 29.4 (should be *Hispanoclavin-*)."

Family Liadytidae Ponomarenko, 1977

Page 147. In the entry "Liadytidae Ponomarenko, 1977: 37…" replace "Type genus: *Liadytes* Ponomarenko, 1977" with "Type genus: *Liadytes* Ponomarenko, 1963."

Family Noteridae Thomson, 1860

Page 148. Replace the valid name "**Subfamily Notomicrinae Zimmermann, 1919**" with "**Subfamily Notomicrinae Branden, 1884**".

Page 148. Replace "Notomicrini A. Zimmermann, 1919: 110" with "Notomicrini Branden, 1884: 13".

Family Dytiscidae Leach, 1815

Page 151. In the entry "Bidessini Sharp, 1880: cxlviii…", replace "Type genus: *Bidessus* Sharp, 1882" with "Type genus: *Bidessus* Sharp, 1880 [for comments regarding problems with the type species of this genus see Bousquet and Bouchard (2018a: 32), Fery and Grygier (2019: 62)]."

Page 152. Replace "Hydrocoptini Branden, 1885: 13" with "Hydrocoptini Kolbe, 1883b: 386."

Page 152. Replace "Pachydrini Biström et al., 1997: 66" with "Pachydrini Young, 1980: 306." Note. We do not consider the statement "should probably be placed in a new tribe" used by Young (1980: 306) as evidence of a conditional proposal (Art. 15.1).

Suborder POLYPHAGA

Family Hydrophilidae Latreille, 1802

Page 157. In the entry "Cyllomina Zaitzev, 1908: 400…" replace "[stem: *Cylomat-*]" to "[stem: *Cylom-*]" and delete the "Comment" section. Note. See comment by Seidel et al. (2016: 161) regarding the stem of the genus *Cyloma* Sharp, 1872.

Family Histeridae Gyllenhal, 1808

Page 160. In the entry "Scolytini Jakobson, 1911a: 652…" replace "Type genus: *Scolytus* Müller, 1764 [preoccupied genus name, not *Scolytus* Geoffroy, 1762 [Coleoptera: Curculionidae]; syn. of *Onthophilus* Leach, 1817]. Comment: permanently invalid (Art. 39): based on preoccupied type genus." with "Type genus: *Scolytus* sensu Jakobson, 1911 [not *Scolytus* Geoffroy, 1762; syn. of *Onthophilus* Leach, 1817]. Comment: based on a misidentified type genus." Note. Since stability or universality is not threatened, no application to the Commission is needed to suppress this family-group name (Art. 65.2.1).

Page 161. Replace the valid name "**Nymphistrini Tishechkin, 2007**" with "**Nymphisterini Tishechkin, 2007**".

Page 161. In the entry "Nymphisterini Tishechkin, 2007" replace the stem with "*Nymphister-*" and replace the "Comment" section with "Comment: incorrect original stem formation maintained under Art. 29.4 (should be *Nymphistr-*)." Note. See Newton (2017: 5).

Family Ptiliidae Erichson, 1845

Page 166. In the entry "*Pterycini Dybas, 1966: 16, 44…" replace the "Comment" section with "Comment: unavailable family-group name, proposed after 1930 without description or bibliographic reference to such a description (Art. 13.1); incorrect original stem formation, not in prevailing usage; the earlier usage of "pterycine group" by Dybas (1955: 562) is unavailable because it is not a noun (Art. 11.7.1.1); also this name has been used subsequently by Hall (2003: 85) but the name Pterycini has not been made available yet (see Hall 2005: 257)."

Family Leiodidae Fleming, 1821

Page 168. Replace the valid name "**Tribe Agathidiini Westwood, 1838**" with "**Tribe Anisotomini Horaninow, 1834**".

Page 168. Below the entry "*Anisotomidae Stephens, 1828: 99…" add:

"Anisotomidae Horaninow, 1834: 124 [stem: *Anisotom-*]. Type genus: *Anisotoma* Panzer, 1797. Comment: Horaninow (1834) used *Anisotoma* as valid and in the sense of Panzer (1797)."

Page 168. In the entry "Agathidiidae Westwood, 1838: 10…" replace "Type genus: *Agathidium* Illiger, 1798" with "Type genus: *Agathidium* Panzer, 1796."

Page 168. Delete the entry "Anisotomidae Reitter, 1884: 6…"

Page 169. In the entry "Anisotomidae Erichson, 1845: 41…" delete "; an application will need to be submitted to the Commission to suppress this name for the Principles of Priority and Homonymy (Art. 65.2.1) if Anisotomidae Reitter, 1884 in Leiodinae: Agathidiini is to be used as valid in the future."

Page 170. Replace the valid names "**Tribe Anemadini Hatch, 1928**" and "**Subtribe Anemadina Hatch, 1928**" with "**Tribe Anemadini Hatch, 1927**" and "**Subtribe Anemadina Hatch, 1927**" respectively.

Page 170. Replace "Anemadina Hatch, 1928: 159" with "Anemadina Hatch, 1927: 14" under the valid name "**Tribe Anemadini Hatch, 1927**" and "**Subtribe Anemadina Hatch, 1927**" respectively.

Page 170. At the end of entry "Anemadinae Jeannel, 1936: 179…" replace "Anemadina Hatch, 1928" with "Anemadina Hatch, 1927".

Page 171. In the entry "Antroherpona Jeannel, 1910: 25..." replace the stem with "*Anthroherpon-*".

Page 171. In the entry "Antroherpona Guéorguiev, 1974: 841, in key..." replace the stem with "*Anthroherpon-*" and add at the end of the "Comment" section "incorrect original stem formation, not in prevailing usage."

Family Staphylinidae Latreille, 1802

Page 175. In the entry "Omalidae W. S. MacLeay, 1825…" replace "Type genus: *Omalium* Gravenhorst, 1802" with "Type genus: *Omalium* Gravenhorst, 1802 [placed on the Official List of Generic Names in Zoology (ICZN 2015b)]."

Page 176. In the entry "Omalidae W. S. MacLeay, 1825…" replace "Type genus: *Omalium* Gravenhorst, 1802" with "Type genus: *Omalium* Gravenhorst, 1802 [placed on the Official List of Generic Names in Zoology (ICZN 2015b)]." and at the end of the "Comment" section add: "; name placed on the Official List of Family-Group Names in Zoology (ICZN 2015b; as Omaliidae MacLeay, 1825)".

Page 178. In the entry "Megarthrini Joy, 1932: 93…" replace "Type genus: *Megarthrus* Curtis, 1829" with "Type genus: *Megarthrus* Stephens, 1829".

Page 181. In the entry "Neocerini Jeannel, 1954a: 316…" add the following at the end of the "Comment" section: "; the older family-group name Neocerini Salmon, 1941 (type genus *Neocerus* Salmon, 1941, preoccupied genus name, not

Neocerus Wasmann, 1893) is available though permanently invalid (Art. 39) in Collembola."

Page 182. Replace the valid name "**Tribe Jubini Raffray, 1904**" with "**Tribe Jubini Raffray, 1898**".

Page 182. Replace "Jubini Raffray, 1904: 489, in key" with "Jubini Raffray, 1898: 199".

Page 183. Replace the valid name "**Tribe Mayetiini Winkler, 1925**" with "**Tribe Mayetiini Scheerpeltz, 1925**".

Page 183. Replace "Mayetiini Winkler, 1925: 348" with "Mayetiini Scheerpeltz, 1925: 348." Note. The section on Staphylinidae, except for the Steninae (pp. 349–357), Euaesthetinae (pp. 357–358) and the genus *Staphylinus* (pp. 381–386), was compiled ("Conscripsit") by Scheerpeltz (p. 323) and therefore he should be treated as the author of the new taxa in this section.

Page 184. Replace the valid name "**Subtribe Trimiina Bowman, 1934**" with "**Subtribe Trimiina Brendel and Wickham, 1890**".

Page 184. Replace "Trimii Bowman, 1934: 8" with "Trimiini Brendel and Wickham, 1890: 225".

Page 184. In the entry "Trimiina Jeannel, 1950a: 139…" replace "without reference to Trimii Bowman, 1934" with "without reference to Trimii Brendel and Wickham, 1890".

Page 184. Replace the valid names "**Tribe Trogastrini Jeannel, 1949**" and "**Subtribe Trogastrina Jeannel, 1949**" with "**Tribe Trogastrini Brendel and Wickham, 1890**" and "**Subtribe Trogastrina Brendel and Wickham, 1890**" respectively.

Page 184. Below the valid names "**Tribe Trogastrini Jeannel, 1949**" and "**Subtribe Trogastrina Jeannel, 1949**" replace "Trogastrini Jeannel, 1949a: 41, in key" with "Trogasterini Brendel and Wickham, 1890: 225" and add "Comment: incorrect stem formation, not in prevailing usage."

Page 186. In the entry "Bythinini Raffray, 1890: 83, in key…" under the valid names "**Tribe Bythinini Raffray, 1890**" and "**Subtribe Bythinina Raffray, 1890**" add "Comment: published March 1890; this family-group name was also proposed in the same year by Brendel and Wickham (1890 [June]: 224, as Bythinini)."

Page 188. At the end of the entry "Tychini Raffray, 1904: 490, in key…" add "Comment: junior homonym of Tychinae Dana, 1851 (type genus: *Tyche* Bell, 1835), which has been used as valid in Crustacea: Decapoda recently (e.g., Davie et al. 2015); this case is to be referred to the Commission to remove the homonymy (Art. 55.3.1)."

Page 193. In the entry "Athetae Casey, 1910: 2…" under the valid names "**Tribe Athetini Casey, 1910**" and "**Subtribe Athetina Casey, 1910**" replace the "Comment" section with "Comment: name placed on the Official List of Family-Group Names in Zoology (ICZN 2012e)." Note. The name "Athetae" used earlier by Rambousek (1907: 40) is considered a plural term for subgenera of *Atheta*, Rambousek's name is therefore unavailable as a family-group name (Art. 11.7.1.2).

Page 193. In the entry "Callicerina Jakobson, 1908: 448…" replace "Type genus: *Callicerus* Gravenhorst, 1802" with "Type genus: *Callicerus* Gravenhorst, 1802 [placed on the Official List of Generic Names in Zoology (ICZN 2012e)]." and replace the "Comment" section with "Comment: following an application by Gusarov (2011) the names Callicerini Jakobson, 1908, Callicerini Horion, 1967 and Callicerini Lohse, 1969, which are junior homonyms of Callicerini Rondani, 1856 (type genus *Callicera* Panzer, 1806) in Diptera: Syrphidae, were suppressed for the purposes of both the Principle of Priority and the Principle of Homonymy and placed on the Official Index of Rejected and Invalid Family-Group Names in Zoology (ICZN 2012e)."

Page 194. At the end of the entry "Geostibae Seevers, 1978: 126…" add "Comment: following an application by Gusarov (2011) the name Geostibina Seevers, 1978 was placed on the Official List of Family-Group Names in Zoology (ICZN 2012e)."

Page 195. In the entries "Corotocini Fenyes, 1918: 61…" replace "Type genus: *Corotoca* Schiødte, 1847" with "Type genus: *Corotoca* Schiødte, 1853".

Page 197. Replace the valid name "**Cryptonotopseini Pace, 2003**" with "**Cryptonotopsisini Pace, 2003**".

Page 197. In the entry "Cryptonotopsisini Pace, 2003: 38..." replace the stem with "*Cryptonotopsis*-" and replace the "Comment" section with "Comment: incorrect original stem formation maintained under Art. 29.4 (should be *Cryptonotopse*-)." Note. See Newton (2017: 5).

Page 203. Replace the valid names "**Tribe Mimecitini Wasmann, 1917**" and "**Subtribe Mimecitina Wasmann, 1917**" with "**Tribe Mimecitini Wasmann, 1909**" and "**Subtribe Mimecitina Wasmann, 1909**" respectively.

Page 203. Replace "Mimecitonini Wasmann, 1917: 325" with "Mimecitonini Wasmann, 1909: 55".

Page 205. Replace the valid name "**Tribe Oxypodinini Fenyes, 1921**" with "**Tribe Oxypodinini Fenyes, 1918**".

Page 210. In the entry "Prognathites Blanchard, 1845a: 290…" replace "Type genus: *Prognathus* Berthold, 1827" with "Type genus: *Prognathus* Blondel, 1827".

Page 215. In the entry "Chevrolatini Reitter, 1882c: 142…" replace "Type genus: *Chevrolatia* Jacquelin du Val, 1859" with "Type genus: *Chevrolatia* Jacquelin du Val, 1850".

Page 215. Replace the valid name "**Tribe Cyrtoscydmini Schaufuss, 1889**" with "**Tribe Stenichnini Fauvel, 1885**" and move names for the entire tribe down to just above the valid name "**Subfamily Steninae MacLeay, 1825**" to maintain alphabetical order of valid tribes. Note. The name Cyrtoscydmini Schaufuss, 1889 was replaced by Glandulariini Schaufuss, 1889 by Newton (2015) but Glandulariini needs to be replaced by Stenichnini Fauvel, 1885 based on priority.

Page 215. Replace "Stenichnini Ganglbauer, 1898: 25" with "Stenichnini Fauvel, 1885: 182" and move the entry "Stenichnini Fauvel, 1885: 182…" above to immediately under the valid name "**Tribe Stenichnini Fauvel, 1885**".

Page 216. In the entry "Austroaesthetini Cameron, 1944: 69..." replace "as *Austroaesthetus*, unjustifed emendation of genus name not in prevailing usage" with "as *Austroaesthetus*, incorrect subsequent spelling of genus name not in prevailing usage".

Page 216. Replace the valid name "**Tribe Fenderiini Scheerpeltz, 1974**" with "**Tribe Stictocraniini Jakobson, 1914**".

Page 216. Above the entry "Fenderiini Scheerpeltz, 1974: 103..." add:

"Stictocraniini Jakobson, 1914: 529 [stem: *Stictocrani-*]. Type genus: *Stictocranius* J. L. LeConte, 1866." Note. See Newton (2017: 5).

Page 223. In the entry "Philonthidae Kirby, 1837: 91…" replace "Type genus: *Philonthus* Curtis, 1829" with "Type genus: *Philonthus* Stephens, 1829".

Page 224. In the entry "Ocypina Hatch, 1957: 173, in key…" replace the "Comment" section with "Comment: incorrect original stem formation, not in prevailing usage; usage of the corrected stem *Ocypod-* proposed by Newton and Thayer (1992: 65) creates a homonymy problem with Ocypodidae Rafinesque, 1815 (type genus *Ocypode* Weber, 1795), which has been used as valid in Crustacea (e.g., Naderloo 2017), and therefore this case is to be referred to the Commission to remove the homonymy (Art. 55.3.1)."

Page 224. Replace "Tanygnathinini Reitter, 1909: 105" with "Tanygnathinini Reitter, 1909b: 164".

Series SCARABAEIFORMIA

Page 225. In the entry "Scarabaeïdes Latreille, 1802…" replace "Type genus: *Scarabaeus* Linnaeus, 1758." with "Type genus: *Scarabaeus* Linnaeus, 1758 [placed on the Official List of Generic Names in Zoology (ICZN 2014)]."

Family Geotrupidae Latreille, 1802

Page 226. Replace the valid name "**Tribe Bolbelasmini Nikolajev, 1996**" with "**Tribe Bolbelasmini Iablokoff-Khnzorian, 1977**".

Page 226. Replace "Bolbelasmini Nikolajev, 1996: 96" with "Bolbelasmini Iablokoff-Khnzorian, 1977: 165".

Page 227. Replace the valid name "**Tribe Odonteini Shokhin, 2007**" with "**Tribe Odonteini Streubel, 1846**".

Page 227. Above the entry "Odonteini Shokhin, 2007: 111…" add:

"Odontaeidae Streubel, 1846: 960 [stem: *Odonte-*]. Type genus: *Odonteus* Samouelle, 1819 [as *Odontaeus*, incorrect subsequent spelling of type genus name, not in prevailing usage; placed on the Official List of Generic Names in Zoology (ICZN 2006a)]. Comment: incorrect original stem formation, not in prevailing usage."

Page 227. In the entry "Odonteini Shokhin, 2007: 111…" replace "…*Bolboceras* Kirby, 1819 was fixed differently by the Commission (ICZN 2006a)." with "…*Bolboceras* Kirby, 1819 was fixed differently by the Commission (ICZN 2006a); family-group name proposed as new without reference to Odonteini Streubel, 1846."

Family Passalidae Leach, 1815

Page 228. In the entry "Ceracupini Boucher, 2006: 319..." replace the stem with "*Ceracup-*" and replace the "Comment" section with "Comment: incorrect original stem formation maintained under Art. 29.4 (should be *Ceracuped-*)."

Page 228. Below the entry "Ceracupedini Boucher, 1006: 319..." add:

"**Tribe Cylindrocaulini Zang, 1905**

Cylindrocaulinae Zang, 1905: 229 [stem: *Cylindrocaul-*]. Type genus: *Cylindrocaulus* Fairmaire, 1880." Note. Boucher et al. (2017) recently proposed the family-group name Ceracyclini for the genera *Cylindrocaulus* Fairmaire, 1880 and the new fossil genus *Ceracyclus*. However, Cylindrocaulini Zang, 1905 is older and should be used as valid instead of Ceracyclini.

Page 229. At the end of the entry "Gonatinae Kuwert, 1891: 169…" add "Comment: the family-group name Gonatidae Hoyle, 1886 (type genus: *Gonatus* Gray, 1849) is available in Cephalopoda; this case is to be referred to the Commission to remove the homonymy (Art. 55.3.1)."

Page 229. In the entry "Pelopinae Kuwert, 1896: 229…" replace "… [stem: *Pelopid-*]. Type genus: *Pelopides* Kuwert, 1896. Comment: incorrect original stem formation, not in prevailing usage." with "…[stem: *Pelop-*]. Type genus: *Pelops* Kaup, 1871 [preoccupied genus name, not *Pelops* Koch, 1835 [Acari: Oribatida], syn. of *Protomocoelus* Zhang, 1905]. Comment: the older genus group-name *Pelops* Gistel, 1834 [Coleoptera: Tenebrionidae] was recently treated as a *nomen oblitum* by Bousquet and Bouchard (2017: 132); permanently invalid (Art. 39), based on preoccupied type genus."

Page 229. Below the entry "Pleurariinae Kuwert, 1896: 224..." add:

"Kaupiolinae Zang, 1905: 227 [stem: *Kaupiol-*]. Type genus: *Kaupiolus* Zang, 1903 [syn. of *Labienus* Kaup, 1871]."

Page 229. Replace "Gnaphalocneminae Gravely, 1914: 194" with "Gnaphalocneminae Heller, 1900: 11".

Family Glaresidae Prudhomme de Borre, 1886

Page 231. Replace the valid name "**Family Glaresidae Kolbe, 1905**" with "**Family Glaresidae Prudhomme de Borre, 1886**".

Page 231. Replace the entry "Glaresini Kolbe, 1905: 543..." with: "Glaresini Prudhomme de Borre, 1886: 56 [stem: *Glares-*]. Type genus: *Glaresis* Erichson, 1848."

Family Lucanidae Latreille, 1804

Page 232. Below the entry "Aesalidae W. S. MacLeay, 1819: 102…" under the valid name "**Tribe Aesalini MacLeay, 1819**" add:

"Plocasteidae Gistel, 1856a: 365 [stem = *Plocast-*]. Type genus: *Plocastes* Gistel, 1856 [Gistel (1856a: 365) included one species under the generic name *Plocastes*, *scarabaoides*, which refers to *Lucanus scarabaeoides* Panzer, 1795 and this species is the type species by monotypy; **syn. nov.** of *Aesalus* Fabricius, 1801]. Comment: incorrect original stem formation, not in prevailing usage."

Page 234. Replace the entry "*Chalcodinae Didier and Séguy, 1953: 91…" with:

"Chalcodinae Didier and Séguy, 1953: 12, in key, 91 [stem: *Chalcod-*]. Type species: *Chalcodes* H. C. C. Burmeister, 1847." Note. This family-group name is available since the authors provided a description in the key.

Page 234. In the entry "*Prosopocoilini Benesh, 1960: 50..." remove the asterisk (*) and replace the "Comment" section with "Comment: name proposed after 1930 without description or bibliographic reference to such a description (Art. 13.1), however available because it was used as valid before 2000 as in Klausnitzer (1995: 10, as Prosopocoilini) and was not rejected by an author who, between 1961 and 1999, applied Article 13 of the then current edition of the Code (Art. 13.2.1)."

Page 234. In the entry "*Pseudodorcini Benesh, 1960: 97..." remove the asterisk (*) and replace the "Comment" section with "Comment: name proposed after 1930 without description or bibliographic reference to such a description (Art. 13.1), however available because it was used as valid before 2000 as in Klausnitzer (1995: 10, as Pseudodorcini) and was not rejected by an author who, between 1961 and 1999, applied Article 13 of the then current edition of the Code (Art. 13.2.1)."

Page 234. In the entry "*Rhyssonotini Benesh, 1960: 148..." remove the asterisk (*) and replace the "Comment" section with "Comment: name proposed after 1930 without description or bibliographic reference to such a description (Art. 13.1), however available because it was used as valid before 2000 as in Klausnitzer (1995: 10, as Rhyssonotini) and was not rejected by an author who, between 1961 and 1999, applied Article 13 of the then current edition of the Code (Art. 13.2.1); incorrect original stem formation, not in prevailing usage."

Page 234. Delete the entry "*Chalcodinae J. P. Lacroix, 1979: 258…"

Family Ochodaeidae Mulsant and Rey, 1871

Page 235. Replace the valid names "**Family Ochodaeidae Mulsant and Rey, 1871**", "**Subfamily Ochodaeinae Mulsant and Rey, 1871**" and "**Tribe Ochodaeini Mulsant and Rey, 1871**" with "**Family Ochodaeidae Streubel, 1846**", "**Subfamily Ochodaeinae Streubel, 1846**" and "**Tribe Ochodaeini Streubel, 1846**" respectively.

Page 235. Below the valid names "**Family Ochodaeidae Streubel, 1846**", "**Subfamily Ochodaeinae Streubel, 1846**" and "**Tribe Ochodaeini Streubel, 1846**" replace the entry "Ochodéens Mulsant and Rey, 1871b: 493…" with:

"Ochodaeidae Streubel, 1846: 960 [stem: *Ochodae*-]. Type genus: *Ochodaeus* Dejean, 1821."

Family Hybosoridae Erichson, 1847

Page 237. Replace the entry "Acanthocérides Lacordaire, 1856: 155…" with:

"Acanthoceridae Streubel, 1846: 960 [stem: *Acanthocer*-]. Type genus: *Acanthocerus* W. S. MacLeay, 1819 [preoccupied genus name, not *Acanthocerus* Palisot de Beauvois, 1818 [Hemiptera]; syn. of *Ceratocanthus* A. White, 1842]. Comment: permanently invalid (Art. 39): based on preoccupied type genus."

Page 237. In the entry "Ceratocanthini Martínez, 1968: 14…" replace "Acanthocerini Lacordaire, 1856" with "Acanthocerini Streubel, 1846".

Page 237. Below the entry "Hybosoridae Erichson, 1847a: 104..." add: "Phaeochroinen Kolbe, 1912: 153 [stem: *Phaeochro*-]. Type genus: *Phaeochrous* Laporte,

1840. Comment: name listed as "Phaeochroinae" in the Sachregister (p. v), likely written by the editor Karl Grünberg."

Family Glaphyridae MacLeay, 1819

Page 238. Below the entry "Glaphyridae W. S. MacLeay, 1819: 76…" add:

"Anthypnidae Chalande, 1884: 46, 99 [stem= *Anthypn*-]. Type genus: *Anthypna* Eschscholtz, 1818."

Family Scarabaeidae Latreille, 1802

Page 238. In the entry "Scarabaeïdes Latreille, 1802…" replace "Type genus: *Scarabaeus* Linnaeus, 1758." with "Type genus: *Scarabaeus* Linnaeus, 1758 [placed on the Official List of Generic Names in Zoology (ICZN 2014)]."

Page 239. Replace the valid name "**Subfamily Eremazinae Iablokoff-Khnzorian, 1977**" with "**Subfamily Eremazinae Stebnicka, 1977**".

Page 239. Replace the entry "Eremazini Iablokoff-Khnzorian, 1977 [3 October]: 168…" with:

"*Eremazini Iablokoff-Khnzorian, 1977 [3 October]: 168 [stem: *Eremaz*-]. Type genus: *Eremazus* Mulsant, 1851. Comment: unavailable family-group name, proposed after 1930 without description or bibliographic reference to such a description (Art. 13.1)." Note. The only descriptive terms provided for this name are "*Bei den Eremizi ist das Metendosternit wie bei den Aphodiinae gebildet, denen sie viel näher stehen als die anderen Aegialitinae, auch ihrer Gesamtbildung nach*" [In the case of the Eremizi the metendosternite is formed as in the Aphodiinae, to which they stand much closer than the other Aegialitinae, also in their general structure]. This statement does not fulfill article 13.1.1, which states "be accompanied by a description or definition that states in words characters that are purported to differentiate the taxon." Therefore this name is unavailable.

Page 239. In the entry "Eremazina Stebnicka, 1977 ["31 December"]: 412…" delete the "Comment" section.

Page 239. In the entry "Aphodida Leach, 1815: 97…" below the valid names "**Subfamily Aphodiinae Leach, 1815**", "**Tribe Aphodiini Leach, 1815**" and "**Subtribe Aphodiina Leach, 1815**" replace "Type genus: *Aphodius* Illiger, 1798" with "Type genus: *Aphodius* Hellwig, 1798." Note. See Alonso-Zarazaga and Krell (2011).

Page 242. In the entry "Scarabaeïdes Latreille, 1802…" replace "Type genus: *Scarabaeus* Linnaeus, 1758." with "Type genus: *Scarabaeus* Linnaeus, 1758 [placed on the Official List of Generic Names in Zoology (ICZN 2014)]."

Page 243. Replace the valid name "**Tribe Gymnopleurini Lacordaire, 1856**" with "**Tribe Gymnopleurini Streubel, 1846**".

Page 243. Replace the entry "Gymnopleurides Lacordaire, 1856: 72…" with:

"Gymnopleuridae Streubel, 1846: 961 [stem: *Gymnopleur*-]. Type genus: *Gymnopleurus* Illiger, 1803."

Page 244. Replace the valid name "**Tribe Onthophagini Burmeister, 1846**" with "**Tribe Onthophagini Streubel, 1846**".

Page 244. Replace the entry "Onthophagidae H. C. C. Burmeister, 1846: [1]…" with:

"Onthophagidae Streubel, 1846: 961 [stem: *Onthophag-*]. Type genus: *Onthophagus* Latreille, 1802. Comment: published by 13 August 1846; this family-group name was also used in the same year by Burmeister (1846 [by 26 November 1846]: [1], as Onthophagidae)."

Page 245. In the entry "Scarabaeïdes Latreille, 1802…" replace "Type genus: *Scarabaeus* Linnaeus, 1758." with "Type genus: *Scarabaeus* Linnaeus, 1758 [placed on the Official List of Generic Names in Zoology (ICZN 2014)]." and at the end add: "Comment: name placed on the Official List of Family-Group Names in Zoology (ICZN 2014, as Scarabaeidae Latreille, 1802)."

Page 248. Replace the valid name "**Tribe Comophorinini Britton, 1957**" with "**Tribe Comophini Britton, 1978**".

Page 248. Replace the entry "Comophorini Britton, 1957: 10…" with the following entries:

"Comophorini Britton, 1957: 10 [stem: *Comophor-*]. Type genus: *Comophorus* Blanchard, 1850 [preoccupied genus name, not *Comophorus* Agassiz, 1846 [Pisces]; syn. of *Comophorina* Strand, 1928]. Comment: permanently invalid (Art. 39): based on preoccupied type genus.

Comophini Britton, 1978: 7 [stem: *Comoph-*]. Type genus: *Comophus* Britton, 1978 [syn. of *Comophorina* Strand, 1928]. Comment: replacement name for Comophorini Britton, 1957 because of the homonymy of the type genus.

Comophorinini Britton, 1987: 761 [stem: *Comophorin-*]. Type genus: *Comophorina* Strand, 1928."

Page 249. In the entry "Hétéronycides Lacordaire, 1856: 225..." at the end of the "Comment" section add "; the family-group name Heteronychidae André, 1891 (type genus *Heteronyx* Saussure, 1887) is available in Hymenoptera though permanently invalid (based on preoccupied type genus)."

Page 250. Below the entry "Lepisiidae H. C. C. Burmeister, 1844: 166…" add:

"Chasmidae Streubel, 1846: 960 [stem: *Chasm-*]. Type genus: *Chasme* Lepeletier and Audinet-Serville, 1828."

Page 250. Replace the entry "Lepitrichiden Oken, 1843: 483…" with:

"Lepitrichina Perty, 1840: 933 [stem: *Lepitrich-*]. Type genus: *Lepitrix* Lepeletier and Audinet-Serville, 1828." Note. The family-group name Lepitrichina Perty, 1840, published by 17 November 1840 (Bousquet 2016: 413), is a senior synonym of Pachycnemina Laporte, 1840, issued by 26 December 1840 (Bousquet 2016: 321). Reversal of Precedence (ICZN 1999: Article 23.9) or an application to the Commission is necessary to conserve usage of Pachycnemina Laporte as valid.

Page 250. Replace the entry "Haplonychidae H. C. C. Burmeister, 1855: 224…" with:

"Haplonychidae H. C. C. Burmeister, 1855: 224 [stem: *Aplonych-*]. Type genus: *Aplonycha* Boisduval, 1835 [as *Haplonycha*, unjustifed emendation of type genus name by Agassiz (1846b: 29)]. Comment: the unjustified emendation *Haplonycha* Agassiz, 1846 is in prevailing usage but attributed to Dejean (1836), not to Boisduval (1835) who first made the name *Aplonycha* available and therefore,

Art. 33.2.3.1 (ICZN 1999) cannot be used to consider *Haplonycha* as a justified emendation; incorrect original stem formation, not in prevailing usage; the junior homonym Aplonychini De Stefani, 1908 (type genus *Aplonyx* De Stefani, 1908) is available in Diptera; this case is to be referred to the Commission to remove the homonymy (Art. 55.3.1)."

Page 252. In the entry "Rhizotrogidae H. C. C. Burmeister, 1855: 308…", replace "Type genus: *Rhizotrogus* Latreille, 1825" with "Type genus: *Rhizotrogus* Berthold, 1827"

Page 257. Below the entry "Phyllurgaeidae Gistel, 1848: [5]…" add:

"Mimelidae Theobald, 1882: 112 [stem = *Mimel*-]. Type genus: *Mimela* Kirby, 1823."

Page 257. Replace the valid name "**Subtribe Popilliina Ohaus, 1918**" with "**Subtribe Popilliina Ohaus, 1902**".

Page 257. Replace "Popilliina Ohaus, 1918: 133" with "Popilliidae Ohaus, 1902: 270"

Page 258. Below the entry "Anoplognathidae W. S. MacLeay, 1819: 81…" under the valid name "**Subtribe Anoplognathina MacLeay, 1819**" add:

"Rhepsimidae Streubel, 1846: 960 [stem: *Repsim*-]. Type genus: *Repsimus* W. S. MacLeay, 1819. Comment: incorrect original stem formation, not in prevailing usage."

Page 259. Replace "Macraspididae H. C. C. Burmeister, 1844: 343" with "Macraspida Perty, 1840: 933".

Page 259. Below the entry "Pelidnotidae H. C. C. Burmeister, 1844: 388…" add:

"Ometidae Streubel, 1846: 960 [stem: *Omet*-]. Type genus: *Ometis* Latreille, 1829 [syn. of *Lagochile* Hoffmannsegg, 1817]."

Page 260. In the entry "Dynastidae W. S. MacLeay, 1819…" under the valid name "**Subfamily Dynastinae MacLeay, 1819**" replace "Type genus: *Dynastes* W. S. MacLeay, 1819." with "Type genus: *Dynastes* W. S. MacLeay, 1819 [placed on the Official List of Generic Names in Zoology (ICZN 2014)]." and in the same entry under the valid name "**Tribe Dynastini MacLeay, 1819**" replace "Type genus: *Dynastes* W. S. MacLeay, 1819." with "Type genus: *Dynastes* W. S. MacLeay, 1819 [placed on the Official List of Generic Names in Zoology (ICZN 2014)]." and at the end add: "Comment: name placed on the Official List of Family-Group Names in Zoology (ICZN 2014)."

Page 260. Replace "Chalepidae H. C. C. Burmeister, 1847: 71" with "Chalepidae Streubel, 1846: 960".

Page 261. In the entry "Oryctésaires Mulsant, 1842: 372…" replace "Type genus: *Oryctes* Illiger, 1798" with "Type genus: *Oryctes* Hellwig, 1798." Note. See Alonso-Zarazaga and Krell (2011).

Page 264. In the entry "Aspilina Krikken, 1984: 25, in key…" replace "Type genus: *Aspilus* Westwood in Schaum, 1848" with "Type genus: *Aspilus* Schaum, 1848"

Page 265. In the entry "Spilophorina Krikken, 1984: 25, in key…" replace "Type genus: *Spilophorus* Westwood in Schaum, 1848" with "Type genus: *Spilophorus* Schaum, 1848".

Page 265. In the entry "Trogodina Krikken, 1984: 27, in key…" replace "Type genus: *Trogodes* Westwood, 1874" with "Type genus: *Trogodes* Boheman, 1851".

Page 266. Replace the valid name "**Subtribe Coryphocerina Burmeister, 1842**" with "**Subtribe Rhomborhinina Westwood, 1842**".

Page 266. In the entry "Coryphoceridae H. C. C. Burmeister, 1842: 215..." add "Comment: published by 8 December 1842."

Page 266. Below the entry "Coryphoceridae H. C. C. Burmeister, 1842: 215..." add:

"Jumnidae H. C. C. Burmeister, 1842: 195 [stem: *Jumn-*]. Type genus: *Jumnos* Saunders, 1839. Comment: published by 8 December 1842; we act as First Revisers (Coryphoceridae H. C. C. Burmeister, 1842 vs Jumnidae H. C. C. Burmeister, 1842) and select Coryphoceridae H. C. C. Burmeister, 1842 to have precedence.

Page 266. Replace the entry "Rhomborrhinae Shoch, 1894: 170…" with:

"Rhomborrhinae Westwood, 1842: 340 [stem: *Rhomborhin-*]. Type genus: *Rhomborhina* Hope, 1837 [as *Rhomborrhina*, incorrect subsequent spelling of the type genus, not in prevailing usage]. Comment: published on 1 January 1842; incorrect original stem formation, not in prevailing usage." and move entire entry above "Coryphoceridae H. C. C. Burmeister, 1842: 215..." to keep the chronological order. Note. We have decided to use Rhomborhinina Westwood, 1842 as valid (as determined by the Principle of Priority) based on the fact that Cetoniinae taxonomy is in flux and many changes to the classification will be necessary in the future (A. B. T. Smith, pers. comm. September 2019).

Page 271. Below the entry "Paniscidae Gistel, 1848: [5]…" add:

"Evambateidae Gistel, 1856a: 365 [stem = *Evambat-*]. Type genus: *Evambates* Gistel, 1856 [Gistel (1856a: 365) originally included *Scarabaeus fasciatus* Linnaeus, 1758 and *Trichius zonatus* Germar, 1831 in his genus *Evambates*; we hereby select *Scarabaeus fasciatus* Linnaeus, 1758 as the type species of *Evambates* Gistel, 1856; **syn. nov**. of *Trichius* Fabricius, 1775]. Comment: incorrect original stem formation, not in prevailing usage."

Page 271. In the entry "Myodermini Péringuey, 1907: 313…" replace "[stem: *Myoderm-*]. Type genus: *Myodermum* H. C. C. Burmeister and Schaum, 1840." with "[stem: *Myodermat-*]. Type genus: *Myoderma* Dejean, 1833. Comment: incorrect original stem formation, not in prevailing usage." Note. See Bousquet and Bouchard (2013: 38) for comments regarding the correct spelling and authorship of the type genus.

Family Eucinetidae Lacordaire, 1857

Page 273. In the entry "Cryptomeridae Broun, 1893: 1358…" replace "Type genus: *Cryptomera* Broun, 1893 [syn. of *Eucinetus* Germar, 1818]" with "Type genus: *Cryptomera* Broun, 1893 [preoccupied genus name, not *Cryptomera* Rafinesque, 1820 [Chilopoda]; syn. of *Eucinetus* Germar, 1818]. Comment: permanently invalid (Art. 39): based on preoccupied type genus."

Family Buprestidae Leach, 1815

Page 278. In the entry "Xenopsina Volkovitsh, 2008: 628..." replace the stem with "*Xenops-*" and replace the "Comment" section with "Comment: incorrect original stem formation maintained under Art. 29.4 (should be *Xenopse-*)."

Page 281. In the entry "Polybothrisidae Gistel, 1848…" replace "Type genus: *Polybothris* Spinola, 1837." with "Type genus: *Polybothris* Dupont, 1833 [placed on the Official List of Generic Names in Zoology (ICZN 2015a)]."

Page 281. Replace "Capnodina Jakobson, 1913: 779" with "Capnodini Csiki, 1909c: 168".

Page 285. In the entry "Melobasini Bílý, 2000: 113..." replace the stem with "*Melobas*-" and replace the "Comment" section with "Comment: incorrect original stem formation maintained under Art. 29.4 (should be *Melobase*-)."

Page 288. Under the valid name "**Subtribe Aphanisticina Jacquelin du Val, 1859**" in the entry "Aphanisticites Jacquelin du Val, 1859: 104…" replace "Type genus: *Aphanisticus* Latreille, 1829" with "Type genus: *Aphanisticus* Latreille, 1810." Note. The genus *Aphanisticus* is often credited in the literature to Latreille (1829a: 448). However, the name was first made available by Latreille (1810: 169).

Page 288. Replace the valid name "**Subtribe Amorphosomatina Majer, 2000**" with "**Subtribe Amorphosomina Majer, 2000**".

Page 288. In the entry "Amorphosomina Majer, 2000: 210..." replace the stem with "*Amorphosom*-" and replace the "Comment" section with "Comment: incorrect original stem formation maintained under Art. 29.4 (should be *Amorphosomat*-)."

Page 289. Replace the valid name "**Subtribe Clematina Majer, 2000**" with "**Subtribe Clemina Majer, 2000**".

Page 289. In the entry "Clemina Majer, 2000: 215..." replace the stem with "*Clem*-" and replace the "Comment" section with "Comment: incorrect original stem formation maintained under Art. 29.4 (should be *Clemat*-)."

Family Byrrhidae Latreille, 1804

Page 291. Replace "Lioonini Leng, 1920: 193" with "Lioonini Casey, 1912: 59".

Page 291. At the end of the entry "Microchaetini Paulus, 1973: 353, in key…" add "Comment: the senior homonym Microchaetini Beddard, 1895 (type genus *Microchaetus* Rapp, 1849) in Oligochaeta is currently used as valid (see Plisko 2013: 85); this case is to be referred to the Commission to remove the homonymy (Art. 55.3.1)."

Superfamily Byrrhoidea Latreille, 1804

Page 292. Above the valid name "**Family Elmidae Curtis, 1830**" add:

"**Family Protelmidae Jeannel, 1950**

Protelmini Jeannel, 1950: 170, in key [stem: *Protelm*-]. Type genus: *Protelmis* Grouvelle, 1911."

Family Elmidae Curtis, 1830

Page 293. Replace the entry "Limniidae Hope 1838a: 153…" with:

"Limniidae C. G. Thomson, 1859: 21 [stem: *Limni*-]. Type genus: *Limnius* Illiger, 1802." Note. Limniidae Hope, 1838a: 153 is unavailable since it was not based on a genus used as valid at the time. Hope (1838a) listed *Limnius* (as "*Limneus*") as a synonym of *Stenelmis* Dufour, 1835.

Family Limnichidae Erichson, 1846

Page 295. Above the entry "Thaumastodinae Champion, 1924: 25…" add:

"Pseudeucinetini Csiki, 1924: 14 [stem: *Pseudeucinet-*]. Type genus: *Pseudeucinetus* Heller, 1921. Comment: the names Thaumastodinae Champion and Pseudeucinetini Csiki were published in the same year, Csiki's publication was issued on 24 February 1924 (verso of title page) while that of Champion was published in the February 1924 issue of the journal *The Entomologist's Monthly Magazine*; Article 35.5 of the Code (ICZN 1999), proposed by Hernando and Ribera (2016: 32) as a reason to preserve usage of the subfamily name Thaumastodinae, cannot be used in this case, the main reason is that Thaumastodini and Pseudeucinetini are not, and cannot, be used as two separate valid tribes within the subfamily Thaumastodinae since they are based on a single taxonomic entity (i.e., the genus *Pseudeucinetus* of which *Thaumastodus* Champion, 1924 is a junior synonym); an application to the Commission is necessary to maintain usage of Thaumastodinae Champion, 1924 name as valid."

Family Eulichadidae Crowson, 1973

Page 297. Delete the entry "*Lichadiden Kolbe, 1908: 249...".

Page 298. Replace "Lichadidae Forbes, 1926: 102" with "Lichadidae Csiki, 1902: 191".

Superfamily Elateroidea Leach, 1815

Page 298. In the entry "Elaterides Leach, 1815: 85…" replace the "Comment" section with "Comment: Elateroidea Leach, 1815 given precedence for superfamily name over Cebrionoidea Latreille, 1802 (Art. 35.5; ICZN secretariat pers. comm.)." Note. See Kundrata et al. (2019: 87).

Family Brachypsectridae Horn, 1881

Page 299. Replace the valid name "**Family Brachypsectridae LeConte and Horn, 1883**" with "**Family Brachypsectridae Horn, 1881**".

Page 299. Replace "Brachypsectrini J. L. LeConte and G. H. Horn, 1883: 170" with "Brachypsectrini G. H. Horn, 1881b: 87".

Family Eucnemidae Eschscholtz, 1829

Page 301. Replace the entry "Arhipini Cobos, 1965: 396…" with:

"Arhipini Cobos, 1965: 396 [stem: *Arrhipid-*]. Type genus: *Arrhipis* Bonvouloir, 1871 [as *Arhipis*, unjustified emendation of type genus name by Fleutiaux (1921: 173), not in prevailing usage; preoccupied genus name, not *Arrhipis* Agassiz, 1846, unjustified emendation of *Arripis* Jenyns, 1840 in Pisces]. Comment: permanently invalid (Art. 39): based on preoccupied type genus; incorrect original stem formation, not in prevailing usage." Note. Since *Arrhipis* Bonvouloir, 1871 is a junior homonym, Reversal of Precedence of the generic name (ICZN 1999: Article 23.9) or an application to the Commission is necessary to conserve usage of this family-group name. Alternatively, a replacement name will be needed.

Page 302. At the end of the entry "Epiphanini Muona, 1993: 45…" add "Comment: the senior homonym Epiphanidae Harring, 1913 (type genus *Epiphanes* Ehrenberg, 1832) in Rotifera is currently used as valid (e.g., Wilts et al. 2012: 180); this case is to be referred to the Commission to remove the homonymy (Art. 55.3.1)."

Page 302. In the entry "Hylocharites Jacquelin du Val, 1859: 119..." replace in the "Comment" section "original vernacular name available (Art. 11.7.2): generally accepted as in Muona (2007: 84, as Hylocharini)" with "original vernacular name available (Art. 11.7.2): first used in latinized form and generally accepted as in Muona (1993: 43)".

Page 302. In the entries "*Neocharini Muona, 1991a: 167…" and "Neocharini Muona, 1993: 44…" replace "Type genus: *Neocharis* Sharp, 1887" with "Type genus: *Neocharis* Sharp, 1877".

Page 303. In the entry "*Galbites Blanchard, 1845b: 71…" replace "Comment: original vernacular name unavailable (Art. 11.7.2): not subsequently latinized; if found to be available in the future then permanently invalid (Art. 39): based on preoccupied type genus." with "Comment: original vernacular name unavailable (Art. 11.7.2): not subsequently latinized and attributed to Blanchard (1845)."

Page 303. Under the entry "*Galbites Blanchard, 1845b: 71…" add:

"Gabini [sic] Beaulieu, 1919: 191 [stem: *Galb-*]. Type genus: *Galba* Latreille, 1829 [preoccupied genus name, not *Galba* Schrank, 1803 [Mollusca]; syn. of *Galbites* Fleutiaux, 1918]. Comment: incorrect original stem formation; permanently invalid (Art. 39): based on preoccupied type genus."

Page 305. Above the entry "Macraulacinae Fleutiaux, 1923: 304..." under the valid name "**Tribe Macraulacini Fleutiaux, 1923**" add the following entries:

"Fornacini Beaulieu, 1919: 191 [stem: *Fornac-*]. Type genus: *Fornax* Laporte, 1835.

Dromaeolini Beaulieu, 1919: 191 [stem: *Dromaeol-*]. Type genus: *Dromaeolus* Kiesenwetter, 1858."

Page 305. At the end of the entry "Macraulacinae Fleutiaux, 1923: 304…" under the valid name "**Tribe Macraulacini Fleutiaux, 1923**" add "Comment: Fornacini Beaulieu, 1919 and Dromaeolini Beaulieu, 1919 take precedence over the valid subfamily and tribe names Macraulacinae/-ini Fleutiaux, 1923, an application to the Commission is necessary to preserve usage of Macraulacinae/-ini Fleutiaux, 1923 as valid."

Page 305. In the entry "Fornaxini Cobos, 1965: 294..." add at the end of the "Comment" section "; family-group name proposed as new without reference to Fornacini Beaulieu, 1919".

Page 305. Delete the entry "Dromaeolini Leiler, 1976: 48…"

Page 306. In the entry "Nematodini Leiler, 1976: 48…" replace "Type genus: *Nematodes* Berthold, 1827" with "Type genus: *Nematodes* Guérin-Méneville, 1827." Note. The name *Nematodes* is usually credited to Berthold (1827: 335). However, it was made available first by Guérin-Méneville in Volume 11 (p. 498) of Bory de Saint-Vincent's *Dictionnaire classique d'histoire naturelle* published on January 1827 (title page). The earliest known date of publication for Berthold's publication is 22 September 1827 (Bousquet 2016: 73).

Family Throscidae Laporte, 1840

Page 306. In the entry "Stereolia Rafinesque, 1815: 112..." replace "[unjustified emendation of *Throscus* Latreille, 1797 not in prevailing usage;" with "[unnecessary replacement name for *Throscus* Latreille, 1797;".

Family Elateridae Leach, 1815

Pages 306–307. In the entry "Elaterides Leach, 1815: 85…" replace the "Comment" section with "Comment: Elateridae Leach, 1815 given precedence for family name over Cebrionidae Latreille, 1802 (Art. 35.5; ICZN secretariat pers. comm.)." Note. See Kundrata et al. (2019: 87).

Page 309. In the entry "Oophoridae Gistel, 1848: [5]…" replace "Type genus: *Oophorus* Eschscholtz, 1833" with "Type genus: *Oophorus* Dejean, 1833."

Page 310. In the entry "Nyctophyxina C. Costa, 1975: 85…" replace "Type genus: *Nyctophysis* C. Costa, 1975" with "Type genus: *Nyctophyxis* C. Costa, 1975".

Page 312. In the entry "Campyloxeninae C. Costa, 1975: 114…" replace "Type genus: *Campyloxenus* Fairmaire, 1860" with "Type genus: *Campyloxenus* Fairmaire and Germain, 1860".

Page 313. At the end of the entry "Limoniina Jakobson, 1913: 755…" add "Comment: the senior homonym Limoniidae/-inae Speiser, 1909 (type genus *Limonia* Meigen, 1803) in Diptera is currently used as valid (e.g., Ribeiro and Amorin 2002: 1); this case is to be referred to the Commission to remove the homonymy (Art. 55.3.1)."

Page 316. Replace the valid name "**Subtribe Loebliquasimusina Schimmel and Tarnawski, 2009**" with "**Subtribe Loebliquasina Schimmel and Tarnawski, 2009**"

Page 316. In the entry "Loebliquasina Schimmel and Tarnawski, 2009: 18..." delete the "Comment" section.

Page 316. Replace the valid name "**Subtribe Striatoquasimusina Schimmel and Tarnawski, 2009**" with "**Subtribe Striatoquasimina Schimmel and Tarnawski, 2009**".

Page 316. In the entry "Striatoquasina Schimmel and Tarnawski, 2009: 20..." replace the stem with "*Striatoquasim-*"

Page 316. Replace the valid name "**Subtribe Wittmeroquasimusina Schimmel and Tarnawski, 2009**" with "**Subtribe Wittmeroquasimina Schimmel and Tarnawski, 2009**".

Page 316. In the entry "Wittmeroquasina Schimmel and Tarnawski, 2009: 20..." replace the stem with "*Wittmeroquasim-*" and the type-genus with "*Wittmeroquasimus* Dolin, 1993".

Page 319. Replace the entry "Dicronychidae Schwarz, 1897: 11…" with:

"Dicronychidae Schwarz, 1897: 11 [stem: *Dicronych-*]. Type genus: *Dicronychus* sensu Laporte, 1840 [not *Dicronychus* Brullé, 1832; syn. of *Eudicronychus* Méquignon, 1931]. Comment: based on a misidentified type genus, name treated here as invalid until an application is submitted to the Commission to suppress it for the Principle of Priority (Art. 65.2.1)."

Page 319. Replace the valid name "**Subfamily Morostomatinae Dolin, 2000**" with "**Subfamily Morostominae Dolin, 2000**".

Page 319. In the entry "Morostominae Dolin, 2000: 18..." replace the stem with "*Morostom-*" and replace the "Comment" section with "Comment: incorrect original stem formation maintained under Art. 29.4 (should be *Morostomat-*)."

Family Lycidae Laporte, 1836

Page 321. In the entry "Libnetinina Bocák and Bocáková, 1990: 652…" replace "Type genus: *Libnetis* C. O. Waterhouse, 1878." with "Type genus: *Libnetis* C. O. Waterhouse, 1878 [incorrect subsequent spelling of *Libnetus* by C. O. Waterhouse (1879: 77), incorrect subsequent spelling in prevailing usage, treated as correct original spelling (Art. 33.3.1)]."

Page 321 Replace the entry "Lycoprogenthini Bocák and Bocáková, 2008: 709…" with:"Lycoprogenthini Bocák and Bocáková, 2008: 709 [stem: *Lycoprogenth-*]. Type genus: *Lycoprogenthes* Pic, 1915 [incorrect subsequent spelling of *Lycoprogentes* Pic (1915b: 6), incorrect subsequent spelling in prevailing usage, treated as correct original spelling (Art. 33.3.1)]."

Page 322. In the entry "Paralycinae L. N. Medvedev and Kazantsev, 1992: 59…" replace "Type genus: *Paralycus* L. N. Medvedev and Kazantsev, 1992 [syn. of *Lyropaeus* C. O. Waterhouse, 1878]." with "Type genus: *Paralycus* L. N. Medvedev and Kazantsev, 1992 [preoccupied genus name, not *Paralycus* Womersley, 1944 [Acarina]; syn. of *Lyropaeus* C. O. Waterhouse, 1878]. Comment: permanently invalid (Art. 39): based on preoccupied type genus." Note. The name *Paralycus* Womersley, 1944 is not listed in Neave's *Nomenclator Zoologicus*. It was made available in Transactions of the Royal Society of South Australia 68: 135.

Family Lampyridae Rafinesque, 1815

Page 327. Replace the valid name "**Tribe Cratomorphini Greene, 1948**" with "**Tribe Cratomorphini Olivier, 1911**".

Page 327. Replace "Cratomorphi Green, 1948: 68, in key" with "Cratomorphinae Olivier, 1911: 75".

Page 327. In the entry "Dadophorini E. Olivier, 1907: 26…" replace "Type genus: *Dadophora* E. Olivier, 1907" with "Type genus: *Dadophora* Duponchel, 1844." Note. The genus *Dadophora* is credited to Olivier (1907: 27) in the literature but the generic name was first made available by Duponchel (1844: 574) when he described the species *Dadophora hyalina*.

Page 328. Replace the entry "Photini J. L. LeConte, 1881: 30…" with:"Photini J. L. LeConte, 1881: 30 [stem: *Photin-*]. Type genus: *Photinus* Laporte, 1833 [placed on the Official List of Generic Names in Zoology (ICZN 2018)]. Comment: placed on the Official List of Family-Group Names in Zoology (as Photinini LeConte, 1881) and correct stem of senior homonym (based on the type genus *Photina* Burmeister, 1838) in Mantodea determined to be *Photina-* to remove the homonymy (ICZN 2018)."

Page 329. In the entry "Photurides Lacordaire, 1857: 338…" replace "Type genus: *Photuris* J. L. LeConte, 1851" with "Type genus: *Photuris* Dejean 1833".

Family Cantharidae Imhoff, 1856 (1815)

Page 331. At the end of the entry "Ichthyurini Champion, 1915: 128…" add the following: "Comment: the senior homonym Ichthyurinae Packard, 1895 (type genus *Ichthyura* Hübner, 1819) in Lepidoptera is currently a junior synonym of

Pygaerinae Duponchel, 1845 (see Schintlmeister 2013: 17); this case is to be referred to the Commission to remove the homonymy (Art. 55.3.1)."

Series ELATERIFORMIA

Page 331. Above the valid name "**Subfamily Cydistinae Paulus, 1972**" add the following: "**Elateriformia *incertae sedis***". Note. The unassigned family-group taxa Cydistinae Paulus, 1972, Pterotinae LeConte, 1861, Ototretinae McDermott, 1964, Ototretadrilinae Crowson, 1972, and †Lasiosynidae Kirejtshuk, Chang, Ren and Kun, 2010 belong to Elateriformia *incertae sedis* (Lawrence et al. 2010a) and are not actually considered subfamilies of Cantharidae.

Family Jacobsoniidae Heller, 1926

Page 333. In the entry "Derolathriinae Sen Gupta, 1979: 692…" replace "Type genus: *Derolathrus* Sharp, 1900" with "Type genus: *Derolathrus* Sharp, 1908".

Family Bostrichidae Latreille, 1802

Page 335. Replace the valid name "**Subfamily Dysidinae Lesne, 1921**" with "**Subfamily Dysidinae Lesne, 1894**"

Page 335. Replace "Dysididae Lesne, 1921b: 286" with "Dysidini Lesne, 1894: 20"

Page 337. Under the entry "Lyctides Billberg, 1820a: 48…" add:

"Xylotrogidae Schönfeldt, 1887: 128 [stem: *Xylotrog-*]. Type genus: *Xylotrogus* Stephens, 1830."

Page 337. Move the entry "Tristariini Lesne, 1921b: 287…" above the entry "Trogoxylini Lesne, 1921a: 231…" and, at the end of the entry "Tristariini Lesne, 1921b: 287…", add "Comment: Tristariini was proposed before Trogoxylini since Lesne (1921a: 231) included the proper citation and page of Tristariini; in fact, Lesne unnecessarily changed his name Tristariini to Trogoxylini simply because *Trogoxylon* LeConte, 1862 was older than *Tristaria* Reitter, 1878; however, we recommend that an application be submitted to the Commission to conserve usage of the well-established name Trogoxylini Lesne, 1921."

Family Ptinidae Latreille, 1802

Page 338. Above the valid name "**Subfamily Ptininae Latreille, 1802**" add:

"**†Subfamily Mesernobiinae Engel, 2010**

Mesernobiinae Engel, 2010: 32 [stem: *Mesernobi-*]. Type genus: *Mesernobius* Engel, 2010."

Page 338. In the entry "Meziini Bellés, 1985: 37, in key…" replace "Type genus: *Mezium* Curtis, 1828" with "Type genus: *Mezium* Samouelle, 1819." Note. The generic name *Mezium* is credited to Curtis in 1828 in the literature but the name was first made available by Samouelle in 1819 (p. 180) with *Ptinus sulcatus* Fabricius, 1781 as type species by original designation.

Page 338. Replace "Gnostidae Gemminger and Harold, 1868: 700" with "Gnostidae King, 1866: 317".

Page 339. Replace the entry "Cosmoceroideos Solier, 1849: 476..." with:

"*Cosmoceroideos Solier, 1849: 476 [stem: *Cosmocer-*]. Type genus: *Cosmocerus* Solier, 1849 [preoccupied genus name, not *Cosmocerus* Guérin-Méneville, 1844 [Coleoptera: Cerambycidae]; syn. of *Cerocosmus* Gemminger, 1873]. Comment: original vernacular name unavailable (Art. 11.7.2): subsequently latinized and attributed to Solier (e.g., Lawrence and Newton (1995: 864), as Cosmocerinae) but not generally accepted as valid; if found to be available, permanently invalid (Art. 39): based on preoccupied type genus."

Page 339. Replace "Ernobiinae Pic, 1912: 12" with "Ernobiinae Pic, 1912b: 55."

Page 342. In the entry "Fabiinae Martínez and Viana, 1964: 7…" replace "Type genus: *Fabia* Martínez and Viana, 1964" with "Type genus: *Fabia* Martínez and Viana, 1964 [preoccupied genus name, not *Fabia* Dana, 1851 [Crustacea]; syn. of *Fabrasia* Martínez and Viana, 1965]" and add "Comment: permanently invalid (Art. 39): based on preoccupied type genus."

Page 342. Below the entry "Fabiinae Martínez and Viana, 1964: 7…" add:

"Fabrasiinae Lawrence and Reichardt, 1966: 32 [stem: *Fabrasi-*]. Type genus: *Fabrasia* Martínez and Viana, 1965. Comment: replacement name for Fabiinae Martínez and Viana, 1964 because of the homonymy of the type genus."

Family Lymexylidae Fleming, 1821

Page 342. In the entry "Hylecoeti Germar, 1818: 344…" replace "Type genus: *Hylecoetus* Latreille, 1806" with "Type genus: *Hylecoetus* Latreille, 1806 [syn. of *Elateroides* Schaeffer, 1777]."

Family Trogossitidae Latreille, 1802

Page 343. Replace the valid names "**Subfamily Peltinae Latreille, 1806**" and "**Tribe Peltini Latreille, 1806**" with "**Subfamily Peltinae Kirby, 1837**" and "**Tribe Peltini Kirby, 1837**" respectively.

Page 343. Below the valid name "**Subfamily Peltinae Kirby, 1837**" replace the entry "Peltides Latreille, 1806: 8…" with:

"Peltidae Kirby, 1837: 104 [stem: *Pelt-*]. Type genus: *Peltis* Kugelann, 1792 [placed on the Official List of Generic Names in Zoology (ICZN 1994a)]."

Page 343. At the end of the entry "Decamerinae Crowson, 1964: 287…" add "Comment: the junior homonym Decameridae Rasmussen, 1978 (type genus *Decameros* d'Orbigny, 1850) is available in Echinodermata; this case is to be referred to the Commission to remove the homonymy (Art. 55.3.1)."

Page 343. In the entry for "Peltides Latreille, 1806: 8…" under the valid name "**Tribe Peltini Kirby, 1837**" add an asterisk (*) in front of the name and replace the comment with the following: "Comment: family-group name unavailable (Art. 11.7.1.1): not based on a genus used as valid at the time (see Lawrence and Newton 1995: 868)."

Page 343. Below the entry "*Peltides Latreille, 1806: 8…" add:

"Peltidae Kirby, 1837: 104 [stem: *Pelt-*]. Type genus: *Peltis* Kugelann, 1792 [placed on the Official List of Generic Names in Zoology (ICZN 1994a)]."

Page 344. Replace the valid name "**Tribe Calityini Reitter, 1922**" with "**Tribe Calityini Houlbert, 1922**".

Page 344. Replace "Calityni Reitter, 1922a: 66" with "Calityni Houlbert, 1922a: 103" and add at the beginning of the "Comment" section "issued by 15 July 1922; this family-group name was also used the same year by Reitter (1922a ["31 December 1922"] 66, as Calityni;".

Page 344. In the entry "Gymnochilides Lacordaire, 1854b: 344…" replace "Type genus: *Gymnochila* Klug, 1844" with "Type genus: *Gymnochila* Erichson, 1844 [syn. of *Gymnocheilis* Dejean, 1835]."

Page 345. Replace the valid name "**†Tribe Lithostomatini Kolibáč and Huang, 2008**" with "**†Tribe Lithostomini Kolibáč and Huang, 2008**".

Page 345. In the entry "Lithostomini Kolibáč and Huang, 2008: 142..." replace the stem with "*Lithostom-*" and replace the "Comment" section with "Comment: incorrect original stem formation maintained under Art. 29.4 (should be *Lithostomat-*)."

Family Chaetosomatidae Crowson, 1952

Page 345. Replace the entry "Chaetosomatidae Crowson, 1952: 66…" with:

"Chaetosomatidae Crowson, 1952: 66 [stem: *Chaetosomat-*]. Type genus: *Chaetosoma* Westwood, 1851 [the senior homonym *Chaetosoma* Chevrolat, 1843 in Cerambycidae was recently suppressed for both the Principle of Priority and the Principle of Homonymy, placed on the Official Index of Rejected and Invalid Generic Names in Zoology, and *Chaetosoma* Westwood, 1851 placed on the Official List of Generic Names in Zoology (ICZN 2011b)]. Comment: the senior homonym Chaetosomatidae Claus, 1872 (type genus *Chaetosoma* Claparède, 1863) in Nematoda was recently suppressed for both the Principle of Priority and the Principle of Homonymy, placed on the Official Index of Rejected and Invalid Family-Group Names in Zoology and Chaetosomatidae Crowson, 1952 placed on the Official List of Family-Group Names in Zoology (ICZN 2011b)."

Family Cleridae Latreille, 1802

Page 346. In the entry "Cylidrina Reitter, 1894: 38…" replace "Type genus: *Cylidrus* Latreille, 1829" with "Type genus: *Cylidrus* Latreille, 1817." Note. The genus-group name *Cylidrus* was first made available by Latreille (1817: 43).

Page 347. Replace the entry "*Trichodites Blanchard, 1845b: 84…" with:

"Trichodidae Streubel, 1839: 136 [stem: *Trichod-*]. Type genus: *Trichodes* Herbst, 1792 [placed on the Official List of Generic Names in Zoology (ICZN 1984a)]. Comment: the younger name originally proposed as Trichodina van der Hoeven, 1849 (type genus *Trichoda* Müller, 1773) is available in Protozoa: Ciliophora; this case is to be referred to the Commission to remove the homonymy (Art. 55.3.1)."

Page 347. Delete the entry "Trichodini Portevin, 1931: 457, in key…"

Page 348. In the entry "Necrobiaeidae Gistel, 1848: [6]..." replace "Type genus: *Necrobia* A. G. Olivier, 1795 [placed on the Official List of Generic Names in

Zoology (ICZN 1961c)]" with "Type genus: *Necrobia* Latreille, 1797 [placed on the Official List of Generic Names in Zoology (ICZN 1961c) as "*Necrobia* A. G. Olivier, 1795"]." Note. The genus-group name *Necrobia* was first made available by Latreille (1797: 35), not by Olivier since Olivier's section Nécrobie [No 76bis] in the fourth volume of his *Entomologie, ou histoire naturelle des insectes* was issued in 1800, not in 1795 (Bousquet 2018: 140).

Page 348. In the entry "Dermestoidini Jakobson, 1911a: 719…" replace "Type genus: *Dermestoides* Schaeffer, 1771" with "Type genus: *Dermestoides* Schaeffer, 1777".

Family Melyridae Leach, 1815

Page 350. In the entry "Pelecophorini Majer, 1987: 797, in key…" replace "Type genus: *Pelecophora* Lepeletier and Audinet-Serville, 1825" with "Type genus: *Pelecophora* Dejean, 1821."

Page 352. Replace the entry "*Troglopates Mulsant and Rey, 1867b: 281…" with:

"Troglopates Mulsant and Rey, 1867b: 281 [stem: *Troglop-*]. Type genus: *Troglops* Erichson, 1840. Comment: original vernacular name available (Art. 11.7.2): first used in latinized form by Porta (1929: 84) and generally accepted as in Mayor (2007: 451, as Troglopini)."

Page 353. In the entry "Laiina Jakobson, 1911a: 688…" replace "Type genus: *Laius* Guérin-Méneville, 1838" with "Type genus: *Laius* Guérin-Méneville, 1830." Note. The generic name *Laius* Guérin-Méneville was made available through an illustration (pl. 2, fig. 10) of *Laius cyaneus* issued in November 1830.

Family Byturidae Gistel, 1848

Page 354. Below the entry "Byturidae Gistel, 1848: [3]..." under the valid name "**Byturinae Gistel, 1848**" add:

"Homoeoplastidae Gistel, 1856a: 360 [stem = *Homoeoplast-*]. Type genus: *Homoeoplastus* Gistel, 1856 [Gistel (1856a: 360) included two available species under the generic name *Homoeoplastus*, *tomentosus*, which refers to *Dermestes tomentosus* DeGeer, 1774, and *fumatus*, which refers to *Dermestes fumatus* Linnaeus, 1767; we here select *Dermestes tomentosus* DeGeer, 1774 as type species; **syn. nov.** of *Byturus* Latreille, 1797]."

Family Sphindidae Jacquelin du Val, 1860

Page 355. In the entry "Odontosphindini Sen Gupta and Crowson, 1979: 180, in key…" replace "Type genus: *Odontosphindus* Sen Gupta and Crowson, 1979" with "Type genus: *Odontosphindus* J. L. LeConte, 1878."

Family Erotylidae Latreille, 1802

Page 358. In the entry "Encaustini Crotch, 1876: 476..." replace in the "Comment" section "published after February 1876" with "published in February 1876"

Page 358. Replace the entry "Triplacinae Erichson, 1847a: 179…" with:

"Triplacina Streubel, 1839: 135 [stem: *Triplac-*]. Type genus: *Triplax* Herbst, 1793."

Family Cryptophagidae Kirby, 1826

Page 360. Replace "Paramecosomina Reitter, 1875: 4" with "Paramecosomini Reitter, 1874: 381".

Page 360. Replace the valid name "**Tribe Picrotini Crowson, 1980**" with "**Tribe Picrotini Sen Gupta and Crowson, 1971**".

Page 360. Replace "Picrotini Crowson, 1980: 283" with "Picrotinae Sen Gupta and Crowson, 1971: 30".

Family Phalacridae Leach, 1815

Page 364. In the entry "Eustilbini Guillebeau, 1892: 149…" replace "Type genus: *Eustilbus* Sharp, 1888" with "Type genus: *Eustilbus* Sharp, 1888 [syn. of *Stilbus* Seidlitz, 1872]."

Family Laemophloeidae Ganglbauer, 1899

Page 364. Move the entry "Nartheciinae Grouvelle, 1908: 453…" above the entry "Laemophloeini Ganglbauer, 1899: 606…" and replace it with:

"Narthecini Casey, 1890: 497 [stem: *Nartheci*-]. Type genus: *Narthecius* J. L. LeConte, 1861. Comment: this name is older than the well-established family name Laemophloeidae Ganglbauer, 1899; an application to the Commission is necessary to preserve usage of Laemophloeidae Ganglbauer, 1899 over Narthecidae Casey, 1890."

Family Nitidulidae Latreille, 1802

Page 367. Replace the valid name "**Arhinini Kirejtshuk, 1987**" with "**Arhinopini Kirejtshuk and Bouchard, 2018**".

Page 367. In the entry "Arhinini Kirejtshuk, 1987: 63…" replace "Type genus: *Arhina* Murray, 1876" with "Type genus: *Arhina* Murray, 1867 [preoccupied genus name, not *Arhina* Agassiz, 1846 (an unjustified emendation for *Arina* Robineau-Desvoidy, 1830) [Diptera]; syn. of *Arhinops* Kirejtshuk and Bouchard, 2018]. Comment: permanently invalid (Art. 39): based on preoccupied type genus."

Page 367. Below the entry "Arhinini Kirejtshuk, 1987: 63…" add:

"Arhinopini Kirejtshuk and Bouchard, 2018: 157 [stem: *Arhinop*-]. Type genus: *Arhinops* Kirejtshuk and Bouchard, 2018."

Page 367. Replace "Pityophagini Reitter, 1891: 163" with "Pityophagini Schilsky, 1888: 60".

Page 368. Replace "Glischrochilini Iablokoff -Khnzorian, 1966: 314" with "Glischrochilini Chagnon, 1934: 309, in key".

Family Cerylonidae Billberg, 1820

Page 369. Below the entry "Tachyoryctidiini Jeannel and Paulian, 1945…" add:

"Hypodacninae Dajoz, 1976: 184, in key [stem: *Hypodacn*-]. Type genus: *Hypodacne* J. L. LeConte, 1875."

Page 370. Above the entry "Murmidiides Jacquelin du Val, 1858: 227…" add:

"Ceuthocera Mannerheim, 1852: 383 [stem: *Ceutocer*-]. Type genus: *Ceutocerus* Germar, 1823 [as *Ceuthocerus*, incorrect subsequent spelling of type genus name, not in prevailing usage; syn. of *Murmidius* Leach, 1822]. Comment: incorrect original stem formation, not in prevailing usage; the discovery of this family-group name threatens the well-established name Murmidiinae Jacquelin du Val, 1858; as far as we know, a family-group name based on *Ceutocerus* has not been used as valid after 1899 and we found 25 references, published by at least 10 authors in the immediately preceding 50 years and encompassing a span of not less than 10 years, using the family-group name based on *Murmidius* as valid; therefore Reversal of Precedence (Art. 23.9) is used (see Appendix 1 for supporting references) to qualify Murmidiinae as *nomen protectum* and Ceutocerinae as *nomen oblitum*.

Family Endomychidae Leach, 1815

Page 372. Below the valid name "**Subfamily Anamorphinae Strohecker, 1953**" add:

"Symbiotinae Joy, 1932: 558, in key [stem: *Symbiot*-]. Type genus: *Symbiotes* Redtenbacher, 1849."

Page 372. At the end of the entry "Anamorphini Strohecker, 1953: 15, in key…" add "Comment: the genus *Symbiotes* Redtenbacher, 1849 is currently placed in the subfamily Anamorphinae Strohecker, 1953 (e.g., Tomaszewska 2007: 559), therefore the older name Symbiotinae Joy, 1932 takes precedence over Anamorphinae based on the Principle of Priority; an application to the Commission is necessary to preserve usage of Anamorphinae Strohecker, 1953 as valid."

Page 373. In the entry "Epipocidae Gorham, 1873: 20…" replace "Type genus: *Epipocus* Germar, 1843" with "Type genus: *Epipocus* Chevrolat, 1836".

Page 373. In the entry "Corynomalidae Gorham, 1873: 14…" replace "Type genus: *Corynomalus* Gerstaecker, 1857" with "Type genus: *Corynomalus* Chevrolat, 1836".

Family Coccinellidae Latreille, 1807

Page 374. Replace the valid name "**Tribe Serangiini Pope, 1962**" with "**Tribe Serangiini Blackwelder, 1845**".

Page 374. In the entry "*Serangiini Blackwelder, 1945: 450…" remove the asterisk (*) and replace the "Comment" section with "Comment: name proposed after 1930 without description or bibliographic reference to such a description (Art. 13.1), however available because it was used as valid before 2000 as in Pope (1962: 627, as Serangiini) and was not rejected by an author who, between 1961 and 1999, applied Article 13 of the then current edition of the Code (Art. 13.2.1)."

Page 374. Delete the entry "Serangiini Pope, 1962: 627…"

Page 376. In the entry "*Mysiates Mulsant, 1846: 125…" replace "[stem: *Myzi*-]. Type genus: *Myzia* Mulsant, 1846 [as *Mysia*, alternative original spelling of type genus name; we follow Kovář (2007: 620) in using *Myzia* as the correct spelling for this genus]. Comment: original vernacular name unavailable (Art. 11.7.2): not subsequently latinized; incorrect original stem formation, not in prevailing usage."

with "[stem: *Mysi*-]. Type genus: *Mysia* Mulsant, 1846. Comment: original vernacular name unavailable (Art. 11.7.2): not subsequently latinized." Note. Mulsant (1846) used two original spellings, *Myzia* and *Mysia*. Subsequently Mulsant (1850: 137) used the spelling *Mysia* and so acted as First Reviser (Art. 24.2.4); *Mysia* is therefore considered the correct original spelling.

Page 377. Below the entry "Synonychini Weise, 1885: 7…" add:

"Hippodamiini Weise, 1885: 11 [stem: *Hippodami*-]. Type genus: *Hippodamia* Chevrolat, 1836."

Page 377. Above the entry "Anisolemniina Mader, 1954: 93, in key…" add:

"Cheilomenini F. A. Schilder and M. Schilder, 1928: 218 [stem: *Cheilomen*-]. Type genus: *Cheilomenes* Chevrolat, 1836.

Veraniini F. A. Schilder and M. Schilder, 1928: 218 [stem: *Verani*-]. Type genus: *Verania* Mulsant, 1850 [preoccupied genus name, not *Verania* Krohn, 1846 [Mollusca]; syn. of *Micraspis* Chevrolat, 1836]. Comment: permanently invalid (Art. 39): based on preoccupied type genus."

Page 378. In the entry "Subcoccinellini Jakobson, 1915: 968…" replace "Type genus: *Subcoccinella* Huber, 1841" with "Type genus: *Subcoccinella* Agassiz, 1846." Note. Huber (1841) proposed the new genus-group name in a vernacular form only (i.e., Subcoccinelle) and therefore the name is unavailable. Agassiz (1846a: 156) is the first who used the name as valid, latinized it, and provided a reference to a previously published description.

Page 379. At the end of the entry "Monocorynini Miyatake, 1988: 28…" add: "Comment: the family group name Monocoryninae Rees, 1956 (type genus *Monocoryne* Broch, 1910) is available in Cnidaria; this case is to be referred to the Commission to remove the homonymy (Art. 55.3.1)."

Family Corylophidae LeConte, 1852

Page 382. In the entry "Periptyctinae Ślipiński *et al.*, 2001: 312…" replace "Type genus: *Periptyctus* Blackburn, 1825" with "Type genus: *Periptyctus* Blackburn, 1895."

Page 382. Replace "Clypeastres L. Redtenbacher, 1845: 122" with "Clypeastrina Perty, 1840: 928".

Page 383. Replace the valid name "**Tribe Sericoderini Matthews, 1888**" with "**Tribe Sericoderini Matthews, 1886**".

Page 383. Replace "Sericoderina A. Matthews, 1888: 103" with "Sericoderina A. Matthews, 1886: 224".

Family Akalyptoischiidae Lord, Hartley, Lawrence, McHugh, Whiting and Miller, 2010

Page 383. Replace the valid name "**Family Akalyptoischiidae Lord, Hartley, Lawrence, McHugh and Miller, 2010**" with "**Family Akalyptoischiidae Lord, Hartley, Lawrence, McHugh, Whiting and Miller, 2010**".

Family Latridiidae Erichson, 1842

Page 384. Under the valid name "**Family Latridiidae Erichson, 1842**" replace the entry "Lathridien Erichson, 1842: 122…" with:

"Lathridien Erichson, 1842: 122 [stem: *Latridi-*]. Type genus: *Latridius* Herbst, 1793 [placed on the Official List of Generic Names in Zoology (ICZN 2011c)]. Comment: family name Latridiidae given precedence over Corticariidae Curtis, 1829 and other family-group names based on *Corticaria* Marsham, 1802 whenever their type genera are placed in the same family-group taxon, and placed on the Official List of Family-Group Names in Zoology (ICZN 2011c)."

Page 384. Under the valid name "**Subfamily Latridiinae Erichson, 1842**" replace the entry "Lathridien Erichson, 1842: 122…" with:

"Lathridien Erichson, 1842: 122 [stem: *Latridi-*]. Type genus: *Latridius* Herbst, 1793 [placed on the Official List of Generic Names in Zoology (ICZN 2011c)]. Comment: original vernacular name available (Art. 11.7.2): first used in latinized form by L. Redtenbacher (1845: 123, as Lathridii), generally accepted as in Lawrence and Newton (1995: 886, as Latridiidae); incorrect original stem formation, not in prevailing usage." Note. The name "Latridii" used earlier by Westerhauser (1832: 151) is considered a plural term for the members of the genus *Latridius*, Westerhauser's name is therefore unavailable as a family-group name (Art. 11.7.1.2).

Page 384. Replace the entry "Corticaridae Curtis, 1829: pl. 283…" with:

"Corticaridae Curtis, 1829: pl. 283 [stem: *Corticari-*]. Type genus: *Corticaria* Marsham, 1802 [placed on the Official List of Generic Names in Zoology (ICZN 2011c)]. Comment: incorrect original stem formation, not in prevailing usage; Corticaridae Curtis, 1829 placed on the Official List of Family-Group Names in Zoology, with the endorsement that it and other family-group names based on *Corticaria* are not to be given priority over Latridiidae Erichson, 1842 and other family-group names based on *Latridius* Herbst, 1793 whenever their type genera are placed in the same family-group taxon (ICZN 2011c)."

Page 384. Replace the entry "*Melanophthalmidae Arnett, 1962b: 835…" with:

"Melanophthalmidae Stickney, 1923: 45 [stem: *Melanophthalm-*]. Type genus: *Melanophthalma* Motschulsky, 1866."

Page 384. Replace the valid name "**†Subfamily Tetrameropseinae Kirejtshuk and Azar, 2008**" with "**†Subfamily Tetrameropsinae Kirejtshuk and Azar, 2008**"

Page 384. In the entry "Tetrameropsinae Kirejtshuk and Azar, 2008: 36..." replace the stem with "*Tetramerops-*" and replace the "Comment" section with "Comment: incorrect original stem formation maintained under Art. 29.4 (should be *Tetrameropse-*)."

Family Mycetophagidae Leach, 1815

Page 385. Replace "Triphyllini Harold, 1880: 757" with "Triphyllidae Crotch, 1873a: 82".

Family Ciidae Leach, 1819

Page 386. Below the entry "Cisidae Leach, 1819: 206…" under the valid name "**Tribe Ciini Leach, 1819**" add:

"Ennearthroninae Chûjô, 1939a: 9 [stem: *Ennearthr-*]. Type genus: *Ennearthron* Mellié, 1847. Comment: Ennearthroninae was also used later in the same year by Chûjô (1939b: 24, in key); incorrect original stem formation, not in prevailing usage."

Family Mordellidae Latreille, 1802

Page 390. Above the valid name "**Tribe Mordellini Latreille, 1802**" add:

"**Tribe Curtimordini Odnosum, 2010**

Curtimordini Odnosum, 2010: 69, 119 [stem: *Curtimord*-]. Type genus: *Curtimorda* Méquignon, 1946."

Page 390. Above the valid name "**Tribe Reynoldsiellini Franciscolo, 1957**" add:

"**Tribe Mordellochroini Odnosum, 2010**

Mordellochroini Odnosum, 2010: 71, 125 [stem: *Mordellochro*-]. Type genus: *Mordellochroa* Emery, 1876."

Family Ripiphoridae Laporte, 1840

Page 390. Replace the valid name "**Family Ripiphoridae Gemminger, 1870 (1855)**" with "**Family Ripiphoridae Laporte, 1840**".

Page 390. Replace the entry "Rhipiphoridae Gemminger, 1870: 2117…" with:

"Rhipiphorites Laporte, 1840: 261 [stem: *Ripiphor*-]. Type genus: *Ripiphorus* Bosc, 1791 [as *Rhipiphorus*, unjustified emendation of type genus name by Duméril (1827: 374), not in prevailing usage]."

Page 391. Replace the valid name "**Subfamily Pelecotominae Seidlitz, 1875**" with "**Subfamily Pelecotominae Guérin-Méneville, 1857**".

Page 391. Replace "Pelecotomini Seidlitz, 1875 [Gatt.]: 104" with "Pelecotomini Guérin-Méneville, 1857: 91".

Page 391. Replace the valid name "**Subfamily Ripiphorinae Gemminger, 1870 (1855)**" with "**Subfamily Ripiphorinae Laporte, 1840**".

Page 391. Replace the entry "Rhipiphoridae Gemminger, 1870: 2117…" with:

"Rhipiphorites Laporte, 1840: 261 [stem: *Ripiphor*-]. Type genus: *Ripiphorus* Bosc, 1791 [as *Rhipiphorus*, unjustified emendation of type genus name by Duméril (1827: 374), not in prevailing usage]."

Page 391. Below the valid name "**Tribe Macrosiagonini Heyden, 1908**" delete the entry "Rhipiphorites Laporte, 1840b: 261…"

Page 392. In the entry "Macrosiagonini L. Heyden, 1908: 45…" delete the "Comment" section.

Page 392. Replace the valid name "**Tribe Ripiphorini Gemminger, 1870 (1855)**" with "**Tribe Ripiphorini Laporte, 1840**".

Page 392. In the entries "*Mioditini A. Costa, 1853: 2…" and "Myoditini Gerstaecker, 1855: 15…" replace "Type genus: *Myodites* Latreille, 1829" with "Type genus: *Myodites* Latreille, 1819".

Page 392. In the entry "Myoditini Gerstaecker, 1855: 15…" delete the "Comment" section.

Page 392. Replace the entry "Rhipidophoridae Gemminger, 1870: 2117…" with:

"Rhipiphorites Laporte, 1840: 261 [stem: *Ripiphor*-]. Type genus: *Ripiphorus* Bosc, 1791 [as *Rhipiphorus*, unjustified emendation of type genus name by Duméril (1827: 374), not in prevailing usage]. Comment: original vernacular name available (Art. 11.7.2): first used in latinized form by Gerstaecker (1855: 5, as Rhipiphori-

DUM [incorrect stem formation]), generally accepted as in Telnov (2004: 78, as RHIPIPHORIDAE [incorrect stem formation]; an application to the Commission was published recently (Bousquet and Bouchard 2018b) requesting the Commission to rule that Laporte (1840: 261), when proposing the new name RHIPIPHORITES, used the genus *Ripiphorus* in the currently-accepted sense." and move entire entry above "*MIODITINI A. Costa, 1853: 2..." to keep the chronological order.

Family ZOPHERIDAE Solier, 1834

Page 394. Replace the valid name "**Tribe SYNCHITINI Erichson, 1845**" with "**Tribe SYNCHITINI L. Redtenbacher, 1845**".

Page 394. Replace the entry "SYNCHITINI Erichson, 1845: 254…" with:

"SYNCHITAE L. Redtenbacher, 1845: 123 [stem: *Synchit*-]. Type genus: *Synchita* Hellwig, 1792. Comment: published by September 1845; this family-group name was also used in the same year by Erichson (1845 [by 15 October]: 254, as SYNCHITINI)."

Page 394. Replace the entry "CORTICINI Ganglbauer, 1899: 870…" with:

"CORTICIDES Reitter, 1882a: 116 [stem: *Cortic*-]. Type genus: *Corticus* Germar, 1823."

Page 395. Replace the entry "ENDOPHLOEINI Reitter, 1922a: 17..." with:

"ENDOPHLOEIDAE Wollaston, 1868: 264 [stem: *Endophloe*-]. Type genus: *Endophloeus* Dejean, 1834" and move the entry above "COXELINI Seidlitz, 1872 [Gatt.]: 38..." on the previous page.

Family PROMECHEILIDAE Lacordaire, 1859

Page 396. Below the entry "PROMÉCHILIDES Lacordaire, 1859: 698..." add:

"CHANOPTERINAE Borchmann, 1915: 47, in key [stem: *Chanopter*-]. Type genus: *Chanopterus* Boheman, 1858." Note. The genus *Chanopterus* is currently placed in the family PROMECHEILIDAE (Lawrence *et al*. 2010b: 563).

Family TENEBRIONIDAE Latreille, 1802

Page 398. In the entry "*PHOBÉLIIDES Lacordaire, 1859: 393…" replace "Type genus: *Phobelius* Blanchard, 1845" with "Type genus: *Phobelius* Blanchard, 1842" Note. The generic name *Phobelius* is credited to Blanchard (1845b: 39) in the literature but it was made available first by Blanchard (1842: pl. 14, fig. 9) when he illustrated the species *Phobelius crenatus*.

Page 398. Below the entry "*PHOBÉLIIDES Lacordaire, 1859: 393…" add:

"PHOBELIIDES F. Bates, 1890: 76 [stem: *Phobeli*-]. Type genus: *Phobelius* Blanchard, 1842."

Page 398. Delete the entry "PHOBELIINA Ardoin, 1961: 33..."

Page 399. Replace the valid name "**Tribe LUPROPINI Ardoin, 1958**" with "**Tribe LUPROPINI Lesne, 1926**".

Page 399. Replace the entry "LUPROPSINI Ardoin, 1958: 59…" with:

"LYPROPINI Lesne, 1926: 68 [stem: *Luprop*-]. Type genus: *Luprops* Hope, 1833 [as *Lyprops*, incorrect subsequent spelling not in prevailing usage]. Comment: incorrect original stem formation, not in prevailing usage."

Page 404. Replace "Eusatti Doyen, 1984: 11" with "Eusatti Casey, 1908: 55".

Page 408. In the entry "Nyctélites Solier, 1834…" replace "Type genus: *Nyctelia* Latreille, 1825" with "Type genus: *Nyctelia* Berthold, 1827".

Page 409. In the entry "Leucolaephusini Pierre, 1961: 558…" replace "Type genus: *Leucolaephus* Lucas, 1859. Comment: incorrect original stem formation, not in prevailing usage." with "Type genus: *Leucolaephus* Lucas, 1859 [*Leucolaephus* is an incorrect subsequent spelling of the original spelling *Leucoloephus*, in prevailing usage and so deemed to be the correct original spelling (Art. 33.3.1)]. Comment: incorrect original stem formation, not in prevailing usage."

Page 415. Below the entry "Eutomides Lacordaire, 1865: 369..." add:

"Heptaphyllini Prudhomme de Borre, 1886: 56 [stem: *Heptaphyll-*]. Type genus: *Heptaphylla* Friedenreich, 1883 [syn. of *Rhipidandrus* J. L. LeConte, 1862]."

Page 416. In the entry "Heleadae Fleming, 1821: 51" replace "Type genus: *Helea* Latreille, 1816" with "Type genus: *Helea* Latreille, 1804".

Page 417. In the entry "Hypulia Rafinesque, 1815…" replace "[syn. of *Helops* Fabricius, 1775]." with "[preoccupied genus name, not *Hypulus* Paykull, 1798 [Coleoptera: Melandryidae]; syn. of *Helops* Fabricius, 1775]. Comment: permanently invalid (Art. 39): based on preoccupied type genus."

Page 421. In the entry "*Omocratates Mulsant and Rey, 1854: 266, in key…" replace "syn. of *Phylan* Dejean, 1821" with "syn. of *Phylan* Sturm, 1826".

Page 421. In the entry "Pandarites Mulsant & Rey, 1854: 153…" replace "[stem: *Pandar-*]" with "[stem: *Dendar-*]".

Page 421. Replace the entry "*Micrositates Mulsant and Rey, 1854: 274…" with:

"Micrositates Mulsant and Rey, 1854: 274 [stem: *Microsit-*]. Type genus: *Micrositus* Mulsant and Rey, 1854. Comment: original vernacular name available (Art. 11.7.2): first used in latinized form and generally accepted as in Baudi di Selve (1875: 158, as Micrositarii)."

Page 422. Replace the entry "*Héliopathaires Mulsant and Rey, 1854: 265…" with:

"Héliopathaires Mulsant and Rey, 1854: 265 [stem: *Heliopat-*]. Type genus: *Heliopates* Dejean, 1834 [as *Heliopathes*, incorrect subsequent spelling of type genus name, not in prevailing usage]. Comment: original vernacular name available (Art. 11.7.2): first used in latinized form and generally accepted as in Baudi di Selve (1875: 159, as Heliopatharii)."

Page 422. Above the entry "Bioplanina A. N. Reichardt, 1936: 24…" add:

"Olocratarii Baudi di Selve, 1875: 158 [stem = *Olocrat-*]. Type genus: *Olocrates* Mulsant, 1854 [syn. of *Phylan* Sturm, 1826]." Note. *Olocrates* Mulsant, 1854 (p. 383) was proposed in the *Errata and addenda* of Mulsant's work as a replacement name for *Omocrates* Mulsant, 1854 (p. 150) a junior homonym of *Omocrates* H. C. C. Burmeister, 1844 [Coleoptera: Scarabaeidae].

Page 422. In the entry "Phylacides Lacordaire, 1859: 270…" replace "Type genus: *Phylax* Brullé, 1832 [syn. of *Dendarus* Dejean, 1821]." with "Type genus: *Phylax* Brullé, 1832 [unnecessary replacement name for *Phylan* Sturm, 1826; syn. of *Phylan* Sturm, 1826]." Note. It is evident, particularly from the footnote attached to

the generic name, that *Phylax* Brullé, 1832 is an unnecessary replacement name for *Phylan* Sturm, 1826. This means that *Phylax* Brullé is not a junior synonym of *Dendarus* Dejean, 1821 but a junior synonym of *Phylan* Sturm, 1826.

Page 422. Replace "Psectropini Kaszab, 1941: 33" with "Psectropini Kaszab, 1940: 141".

Page 422. In the entry "Leichenaires Mulsant, 1854: 179…" replace "Type genus: *Leichenum* Blanchard, 1845" with "Type genus: *Leichenum* Dejean, 1834".

Page 423. Replace the entry "*Hétéroscélites Solier, 1836: 502…" with:

"*Hétéroscélites Solier, 1836: 502 [stem: *Heteroscelid-*]. Type genus: *Heteroscelis* Latreille, 1828 [*nomen oblitum*; this genus name is a senior subjective synonym of *Anomalipus* Guérin-Méneville, 1831 *nomen protectum*; we provide references to support the conservation of *Anomalipus* Guérin-Méneville, 1831 as the valid name for this genus (Art. 23.9.1) (see Appendix 1)]. Comment: original vernacular name unavailable (Art. 11.7.2): not subsequently latinized; incorrect original stem formation, not in prevailing usage." Note. The Coleoptera genus-group name *Heteroscelis* Latreille (1828: 574), previously credited to Latreille (1829b: 18), is the senior homonym of the name *Heteroscelis* Latreille (1829b: 194) in Hemiptera, and not the reverse as has been accepted in the literature.

Page 423. Below the entry "Trigonopaires Mulsant and Rey, 1853: 104…" add:

"Opatrinaires Mulsant and Rey, 1853: 294 [stem = *Opatrin-*]. Type genus: *Opatrinus* Dejean, 1821. Comment: original vernacular name available (Art. 11.7.2): first used in latinized form and generally accepted as in Giebel (1855: 90, as Opatrinini)."

Page 425. Replace the valid name "**Subtribe Eudysantina Bouchard, Lawrence, Davies and Newton, 2005**" with "**Subtribe Dysantina Gebien, 1922**".

Page 425. Replace the entry "Dysantinae Gebien, 1922: 289…" with:

"Dysantinae Gebien, 1922: 289 [stem: *Dysant-*]. Type genus: *Dysantes* Pascoe, 1869." Note. The genus *Dysantes* Pascoe (1869a: 31) was first made available in 1869 [on 1 January], not in 1871 as previously noted. The name is a senior homonym of the Hymenoptera name *Dysantes* Förster, 1869 [May] which has been incorrectly dated 1868 in some works.

Page 425. In the entry "Eudysantina Bouchard et al., 2005: 508…" replace the "Comment" section with "Comment: unnecessary replacement name for Dysantina Gebien, 1922".

Page 427. In the entry "Mycetocharisidae Gistel, 1848: [10]…" replace "Type genus: *Mycetochara* Berthold, 1827" with "Type genus: *Mycetochara* Guérin-Méneville, 1827". Note. The name *Mycetochara* is usually credited to Berthold (1827: 371). However the name was made available first by Guérin-Méneville in Volume 11 (p. 346) of Bory de Saint-Vincent's *Dictionnaire classique d'histoire naturelle* published on January 1827 (see Bousquet and Bouchard 2016: 138).

Page 428. Above the entry "Omophliens Mulsant, 1856a: 65…" add:

"Telacianae Poey, 1854: 322 [stem: *Telac-*]. Type genus: *Telacis* Poey, 1854 [syn. of *Cteniopus* Solier, 1835]. Comment: incorrect original stem formation, not in prevailing usage."

Page 428. Replace "Petriidae Semenov, 1893b: 359" with "Petriidae Semenov, 1894a: 359"

Page 433. In the entry "Stenochiadae Kirby, 1837: 238…" replace "Type genus: *Stenochia* Kirby, 1819." with "Type genus: *Stenochia* Kirby, 1819 [syn. of *Strongylium* Kirby, 1819]."

Page 433. Below the heading "Tenebrionidae *incertae sedis*" add:

"Ancylopominae Pascoe, 1871: 354 [stem: *Ancylopomat-*]. Type genus: *Ancylopoma* Pascoe, 1871. Comment: incorrect original stem formation, not in prevailing usage." Note. The systematic position of the genus *Ancylopoma* has not been studied after its description except for comments by Bates (1872: 97) who mentioned that "it should be placed after *Anaedus*, Blanch." It was included in Heterotarsinae by Gebien (1911: 472) and Blackwelder (1945: 537) along with *Anaedus*. Recently, the genus *Anaedus* has been included in the tribe Goniaderini Lacordaire, 1859 (e.g., Doyen and Tschinkel 1982: 182, Bousquet et al. 2018: 29) or Lupropini Ardoin, 1958 (e.g., Schawaller 2011: 271).

Family Oedemeridae Latreille, 1810

Page 435. In the entry "Ascleraeidae Gistel, 1848: [11]…" replace "Type genus: *Asclera* Stephens, 1839" with "Type genus: *Asclera* Dejean, 1834 [syn. of *Ischnomera* Stephens, 1832]".

Page 435. In the entry "Ganglbaueriidae Semenov, 1894: 450…" replace "[stem: *Ganglebaueri-*]" with "[stem: *Ganglbaueri-*]."

Page 435. Below the entry "*Hypasclerini Macnamara, 1971: 164, in key…" add:

"Oxaciini Arnett, 1984: 4, in key [stem: *Oxacid-*]. Type genus: *Oxacis* J. L. LeConte, 1866. Comment: incorrect original stem formation, not in prevailing usage." Note. The genus *Oxacis* is currently placed in the tribe Asclerini Gistel, 1848 (e.g., Kriska 2002: 518).

Oxycopiini Arnett, 1984: 4, in key [stem: *Oxycopid-*]. Type genus: *Oxycopis* Arnett, 1951. Comment: incorrect original stem formation, not in prevailing usage." Note. The genus *Oxycopis* is currently placed in the tribe Asclerini Gistel, 1848 (e.g., Kriska 2002: 518)."

Page 435. Replace the entry "*Hypasclerini Švihla, 1986: 161…" with:

"Hypasclerini Arnett, 1984: 4, in key [stem: *Hypascler-*]. Type genus: *Hypasclera* Kirsch, 1866."

Page 435. Delete the entry "*Oxacini Švihla, 1986: 161…"

Family Meloidae Gyllenhal, 1810

Page 437. In the entry "Spasticina Kaszab, 1959: 72…" replace "Type genus: *Spastica* Lacordaire, 1859" with "Type genus: *Spastica* Lucas, 1859." Note. The genus *Spastica* is currently credited to Lacordaire (1859 [issued by 27 June]: 679). However, the name was first treated as a junior synonym of *Gnathium* Kirby, 1819 by Lucas (1859 [issued by 7 March 1859]: 147). Since the name has been treated as an available name by Lacordaire (1859: 679), it is made available but dates from its publication as a synonym (Art. 11.6.1).

Page 439. Replace the valid name "**Tribe Lyttini Solier, 1851**" with "**Tribe Lyttini Streubel, 1846**".

Page 439. Delete the entry "*Lyttes Motschulsky, 1849: 59…"

Page 439. Replace the entry "Lyttoides Solier, 1851: 278…" with:

"Lyttidae Streubel, 1846: 961 [stem: *Lytt-*]. Type genus: *Lytta* Fabricius, 1775. Comment: although this is not the oldest name for the tribe, we recommend that an application be submitted to the Commission to suppress Cantharini Latreille, 1802 because it is based on a misidentifed type genus (Art. 65.2.1)."

Family Mycteridae Perty, 1840

Page 443. Replace the valid names "**Family Mycteridae Oken, 1843**" and "**Subfamily Mycterinae Oken, 1843**" with "**Family Mycteridae Perty, 1840**" and "**Subfamily Mycterinae Perty, 1840**" respectively.

Page 443. Below the valid names "**Family Mycteridae Perty, 1840**" and "**Subfamily Mycterinae Perty, 1840**" replace "Mycteriden Oken, 1843: 484" with "Mycterina Perty, 1840: 919" and delete the "Comment" section.

Page 443. Below the entry "Artaxidae Gistel, 1848: [8]…" add:

"Eutrypteidae Gistel, 1856a: 375 [stem = *Eutrypt-*]. Type genus: *Eutryptes* Gistel, 1856 [subgenus of *Mycterus* Clairville, 1798]. Comment: incorrect original stem formation, not in prevailing usage."

Page 443. Replace the entry "*Stilpnonotinae Blackwelder, 1945: 503…" with:

"Stilpnonotinae Borchmann, 1936: 13, in key [stem: *Stilpnonot-*]. Type genus: *Stilpnonotus* Gray, 1832."

Family Pythidae Solier, 1834

Page 444. Replace "Osphyoplesiini Reitter, 1917: 59, in key" with "Osphyoplesiini A. Winkler, 1915: 333".

Family Pyrochroidae Latreille, 1806

Page 445. Above the valid name "**Subfamily Agnathinae Lacordaire, 1859**" add:

"**Subfamily Pogonocerinae Iablokoff-Khnzorian, 1985.**

Pogonocerinae Iablokoff-Khnzorian, 1985: 197 [stem: *Pogonocer-*]. Type genus: *Pogonocerus* Fischer von Waldheim, 1812."

Page 445. Replace "Elacatidae Cockerell, 1906: 242" with "Elacatidae Reitter, 1879: 212".

Family Salpingidae Leach, 1815

Page 446. In the entry "*Trogocryptinae Crowson, 1953: 51…" delete "; this name has been used subsequently, e.g., Lawrence (1977: 43, 1980: 307), Lawrence and Newton (1995: 900), but it has not been made available".

Page 446. Below the entry "*Trogocryptinae Crowson, 1953: 51…" add:

"Trogocryptinae Lawrence, 1991: 260, 294, in key [stem: *Trogocrypt-*]. Type genus: *Trogocryptus* Sharp, 1900."

Page 446. In the entries "*Rhinosimites Solier, 1834: 496…" and "Rhinosimidae Hope, 1840a: 134…" replace "Type genus: *Rhinosimus* Latreille, 1802" with "Type genus: *Rhinosimus* Latreille, 1802 [syn. of *Salpingus* Illiger, 1802]."

Page 446. Replace "Lissodemina Seidlitz, 1917b: 422" with "Lissodemina Seidlitz, 1916b: 337".

Family Anthicidae Latreille, 1819

Pages 446 and 448 (twice). Replace "Anthicites Latreille, 1819: 363" with "Anthicites Latreille, 1819: 437" and replace "Type genus: *Anthicus* Paykull, 1798." with "Type genus: *Anthicus* Paykull, 1798 [placed on the Official List of Generic Names in Zoology (ICZN 2017)]."

Page 447. Replace the valid name "**Tribe Mitraelabrini Abdullah, 1969**" with "**Tribe Mitraelabrini Abdullah and Abdullah, 1968**".

Page 447. Replace "Mitraelabrini M. Abdullah, 1969a: 350" with "Mitraelabrini M. Abdullah and A. Abdullah, 1968: 73, in key".

Page 447. Replace the valid name "**†Tribe Camelomorphini Kirejtshuk and Azar, 2008**" with "**†Tribe Camelomorphini Kirejtshuk, Azar and Telnov, 2008**"

Page 447. Replace "Camelomorphini Kirejtshuk and Azar, 2008: 40" with "Camelomorphini Kirejtshuk, Azar and Telnov, 2008: 40" and "Type genus: *Camelomorpha* Kirejtshuk and Azar, 2008" with "Type genus: *Camelomorpha* Kirejtshuk, Azar and Telnov, 2008"

Page 447. Replace the valid name "**Subfamily Lemodinae Lawrence and Britton, 1991**" with "**Subfamily Lemodinae Matthews, 1987**"

Page 447. Replace "Lemodinae Lawrence and Britton, 1991: 603, in key" with "Lemodinae Matthews, 1987: 40"

Page 448. Below the entry "Anthicini Latreille, 1819: 363..." under the valid name "**Tribe Anthicini Latreille, 1819**" add:

"Amblyderini Desbrochers des Loges, 1899: 28 [stem: *Amblyder-*]. Type genus: *Amblyderus* LaFerté-Sénectère, 1847."

Page 448. In the entry "Microhorini Bonadona, 1974: 110, in key…" replace "Type genus: *Microhoria* Chevrolat, 1877" with "Type genus: *Microhoria* Chevrolat, 1877 [placed on the Official List of Generic Names in Zoology (ICZN 2017)]."

Family Aderidae Csiki, 1909

Page 449. In the entry "Xylophilidae Shuckard, 1839b: 47…" replace "Type genus: *Xylophilus* Latreille, 1825" with "Type genus: *Xylophilus* Latreille, 1829".

Page 449. Replace "Hylophilidae Pic, 1900: 754" with "Hylophilidae Streubel, 1846: 961".

Family Scraptiidae Gistel, 1848

Page 450. Below the entry "Scraptiaeidae Gistel, 1848: [11]…" under the valid name "**Tribe Scraptiini Gistel, 1848**" add:

"Trotommideini Pic, 1903: 76 [stem: *Trotommide-*]. Type genus: *Trotommidea* Reitter, 1883."

Superfamily Tenebrionoidea Latreille, 1802

Page 451. Insert "**Tenebrionoidea *incertae sedis***" above the valid name "**Subfamily Lagrioidinae Abdullah and Abdullah, 1968**". Note. The unassigned family-group taxa Lagrioidinae Abdullah and Abdullah, 1968, Afreminae Levey, 1985, and Ischaliinae Blair, 1920 belong to Tenebrionoidea *incertae sedis* (Lawrence et al. 2010c).

Family Cerambycidae Latreille, 1802

Page 457. Replace the entry "*Ancistrotides Lacordaire, 1868: 81…" with:

"Ancistrotides Lacordaire, 1868: 81 [stem: *Ancistrot-*]. Type genus: *Ancistrotus* Audinet-Serville, 1832. Comment: original vernacular name available (Art. 11.7.2): first used in latinized form by Lameere (1919: 90, as Ancistrotini), generally accepted as in Cerda (1986: 30, as Ancistrotini)."

Page 457. Delete the entry "Ancistrotini Lameere, 1919: 90…"

Page 460. In the entries "*Cyrtognathites Blanchard, 1845b: 138..." and "Cyrthognathitae J. Thomson, 1861: 328…" replace "*Cyrtognathus* Faldermann, 1835" with "*Cyrtognathus* Dejean, 1835." Note. For priority of author's name, see Bousquet and Bouchard (2013: 79–80).

Page 462. Below the entry "*Grammoptérates Mulsant, 1863b: 569..." add:

"Grammopterini Della Beffa, 1915: 42 [stem: *Grammopter-*]. Type genus: *Grammopterus* Audinet-Serville, 1835."

Page 463. Below the entry "Toxoti J. L. LeConte and Horn, 1883: 313..." add:

"Acmaeopsini Della Beffa, 1915: 42 [stem: *Acmaeop-*]. Type genus: *Acmaeops* J. L. LeConte, 1850. Comment: incorrect original stem formation, not in prevailing usage."

Page 464. In the entry "*Criocéphalites Fairmaire, 1864: 125…" replace "Type genus: *Criocephalus* Mulsant, 1839" with "Type genus: *Criocephalum* Dejean, 1835".

Page 464. Replace the entry "Criocephalinae Sharp, 1905: 147…" with:

"Criocephalinae Perrier, 1893: 1262 [stem: *Criocephal-*]. Type genus: *Criocephalum* Dejean, 1835 [syn. of *Arhopalus* Audinet-Serville, 1834]."

Page 467. Replace the valid name "**Tribe Auxesini Lepesme and Breuning, 1952**" with "**Tribe Auxesini Lacordaire, 1872**".

Page 467. Replace the entry "*Auxésides Lacordaire, 1872: 463…" with:

"Auxésides Lacordaire, 1872: 463 [stem: *Auxes-*]. Type genus: *Auxesis* J. Tomson, 1858. Comment: original vernacular name available (Art. 11.7.2): first used in latinized form and generally accepted as in Gahan (1902: 278, as Auxesinae); current spelling maintained (Art. 29.5): incorrect original stem formation in prevailing usage (should be *Auxese-*)."

Page 467. Delete the entry "Auxesina Lepesme and Breuning, 1952: 140…"

Page 467. Replace the valid name "**Tribe Brachypteromatini Sama, 2008**" with "**Tribe Brachypteromini Sama, 2008**".

Page 467. In the entry "Brachypteromini Sama, 2008: 229..." replace the stem with "*Brachypterom-*" and replace the "Comment" section with "Comment: incorrect original stem formation maintained under Art. 29.4 (should be *Brachypteromat-*)."

Page 473. Replace the valid name "**Tribe Hexoplini Martins, 2006**" with "**Tribe Hexoplonini Martins, 2006**".

Page 473. In the entry "Hexoplonini Martins, 2006: 22..." replace the stem with "*Hexoplon*-" and replace the "Comment" section with "Comment: incorrect original stem formation maintained under Art. 29.4 (should be *Hexopl*-)."

Page 474. Replace the valid name "**Tribe Hylotrupini Zagajkevich, 1991**" with "**Tribe Hylotrupini Rose, 1983**".

Page 474. Replace "Hylotrupini Zagajkevich, 1991: 67" with "Hylotrupini Rose, 1983: 48".

Page 474. Replace the valid name "**Tribe Ibidionini Thomson, 1861**" with "**Tribe Tropidini Martins and Galileo, 2007**" and move all associated records above "**Tribe Tropocalymmatini Lacordaire, 1868**" on page 485 in order to maintain the alphabetical order of valid tribes.

Page 474. Replace "Ibidionitae J. Thomson, 1861: 199..." under the valid name "**Tribe Tropidini Martins and Galileo, 2007**" with:

"Tropidina Martins and Galileo, 2007: 7 [stem: *Tropid*-]. Type genus: *Tropidion* J. Thomson, 1867."

Page 474. Replace the valid name "**Subtribe Ibidionina Thomson, 1861**" with "**Subtribe Neoibidionina Monné, 2012**".

Page 474. Replace the entry "Ibidionitae J. Thomson, 1861: 199..." under the valid name "**Subtribe Neoibidionina Monné, 2012**" with:

"Ibidionitae J. Thomson, 1861: 199 [stem: *Ibidion*-]. Type genus: *Ibidion* Audinet-Serville, 1834 [preoccupied genus name, not *Ibidion* Gory, 1833; syn. of *Neoibidion* Monné, 2012]. Comment: incorrect stem formation (should be *Ibidi*-); permanently invalid (Art. 39): based on preoccupied type genus."

Page 474. Below the entry "*Sydacini Martins, 2003a: 204..." add:

"Neoibidionini Monné, 2012: 35 [stem: *Neoibidion*-]. Type genus: *Neoibidion* Monné, 2012. Comment: incorrect original stem formation maintained under Art. 29.4 (should be *Neoibidi*-)." Note. Monné (2012) proposed the replacement name Neoibidionini for the tribe Ibidionini J. Thomson because of the homonymy of the type genus *Ibidion* Audinet-Serville. However, the replacement name could apply only to the rank of subtribe since there are two older available names which could be used as valid for the tribe, Compsina Martins and Galileo, 2007 and Tropidina Martins and Galileo, 2007. We here select Tropidini Martins and Galileo, 2007 as the valid name for the tribe.

Page 479. Replace "Leptideina Reitter, 1913a: 24" with "Leptideinae Perrier, 1893: 1262".

Page 482. In the entry "*Ptérosténides Lacordaire, 1868: 410…" replace "Type genus: *Pterostenus* Laporte, 1840" with "Type genus: *Pterostenus* Dejean, 1835" Note. See Bousquet and Bouchard (2013: 91).

Page 485. Above the valid name "**Tribe Tropocalymmatini Lacordaire, 1868**" add:

"**Tribe Trigonarthrini Villiers, 1984.**

Trigonarthrini Villiers, 1984: 1 [stem: *Trigonarthr*-]. Type genus: *Trigonarthron* Boppe, 1912."

Page 486. In the entry "Trypanidiitae J. Thomson, 1860a: 7" replace "Type genus: *Trypanidius* Blanchard, 1846" with "Type genus: *Trypanidius* Blanchard, 1842" Note. The generic name *Trypanidius* is usually attributed to Blanchard (1846 [should be 1847]: 209) in the literature but it was made available first by Blanchard (1842: pl. 22, fig. 6) when he illustrated the species *Trypanidius andicola*.

Page 486. In the entry "Liopi J. L. LeConte, 1873: 338…" add at the end of the "Comment" section "; the family-group name Leiopidae [should be Leiopodidae] Lang, 1970 (type genus *Leiopus* Beddard, 1886) is available in Crustacea though permanently invalid (based on preoccupied type genus)."

Page 486. Below the entry "Liopi J. L. LeConte, 1873: 338…" add:

"Aedilinae Perrier, 1893: 1263 [stem: *Aedil-*]. Type genus: *Aedilis* Audinet-Serville, 1835."

Page 488. In the entry "Ancitini Aurivillius, 1917: 28…" replace "Type genus: *Ancita* J. Thomson, 1864" with "Type genus: *Ancita* J. Thomson, 1864 [syn. of *Hebecerus* Dejean, 1835]." See additional notes for name Hebesecinae Pascoe, 1871 below.

Page 491. Move the entry "Hebesecinae Pascoe, 1871: 277…" to page 488 above the entry "Ancitini Aurivillius, 1917: 28…" Note. The type genus *Hebesecis* Pascoe, 1865 is a replacement name for *Hebecerus* Dejean, 1835, which used to be attributed to "Thomson, 1864" and treated as a junior homonym of *Hebecerus* Kolenati, 1845 [Hemiptera] until recently (see Bousquet and Bouchard 2013: 83). *Hebecerus* Dejean, 1835 is a senior synonym of *Ancita* Thomson, 1864 and Hebesecini Pascoe, 1871 is a senior synonym of Ancitini Aurivillius, 1917. An application to the Commission is necessary to conserve usage of *Ancita* Thomson, 1864 and Ancitini Aurivillius, 1917, which have been treated as valid in recent literature (e.g., Ślipiński and Escalona 2013: 93).

Page 492. In the entry "Crinotarsides Lacordaire, 1872: 475…" replace "Type genus: *Crinotarsus* Blanchard, 1853" with "Type genus: *Crinotarsus* Blanchard, 1846" Note. The generic name *Crinotarsus* is usually attributed to Blanchard (1853: 275) in the literature but it was made available first by Blanchard (1846: pl. 16, fig. 10) when he illustrated the species *Crinotarsus plagiatus*.

Page 492. Replace the entry "Apodasyides Lacordaire, 1872: 623 …" with:

"Apodasyides Lacordaire, 1872: 623 [stem: *Apodasy-*]. Type genus: *Apodasya* Pascoe, 1863 [the senior objective synonym *Chaetosoma* Chevrolat, 1843 was recently suppressed for both the Principle of Priority and the Principle of Homonymy, placed on the Official Index of Rejected and Invalid Generic Names in Zoology and *Apodasya* Pascoe, 1863 placed on the Official List of Generic Names in Zoology (ICZN 2011b)]. Comment: original vernacular name available (Art. 11.7.2): first used in latinized form by Kolbe (1897: 321, as Apodasinae [incorrect stem formation]), generally accepted as in Aurivillius (1922a: 305, as Apodasyini)."

Page 492. Below the entry "Eupogonii J. L. LeConte, 1873: 342…" add:

"Anaesthetinae Perrier, 1893: 1263 [stem: *Anaesthet-*]. Type genus: *Anaesthetis* Dejean, 1835."

Page 494. Above the valid name "**Eupromerini Galileo and Martins, 1995**" add:

"**Tribe Eunidiini Téocchi, Sudre and Jiroux, 2010.**

Eunidiini Téocchi, Sudre and Jiroux, 2010: 13 [stem: *Eunidi-*]. Type genus: *Eunidia* Erichson, 1843."

Page 500. At the end of the entry "Niphoninae Pascoe, 1864: 56…" add "Comment: the family-group name Niphonidae Jordan, 1923 (type genus *Niphon* Cuvier et Valenciennes, 1828) is available in Pisces but has been incorrectly formed in the literature, the correct stem based on *Niphon* is *Niphont-* (Alonso-Zarazaga pers. comm. December 2019)."

Page 503. In the entry "Ichthyosomitae J. Thomson, 1864: 33…" replace "[stem: *Ichthyosom-*]. Type genus: *Ichthyosomus* Boisduval, 1835" with "[stem: *Ichthyosomat-*]. Type genus: *Ichthyosoma* Boisduval, 1835. Comment: incorrect original stem formation, not in prevailing usage."

Family Chrysomelidae Latreille, 1802

Page 506. In the entry "Amblycerinae Bridwell, 1932: 103, in key…" under the valid name "**Subtribe Amblycerina Bridwell, 1932**" replace "although this is the oldest name for the tribe" in the "Comment" section with "although this is not the oldest name for the tribe".

Page 509. Below the entry "Haemoniini Chen, 1941: 8…" add:

"Macropleini Lopatin, 1977: 53 [stem: *Macrople-*]. Type genus: *Macroplea* Samouelle, 1819".

Page 510. Replace "Aprioidini Weise, 1911: 41" with "Aproidini Weise, 1911: 41".

Page 513. Replace the valid name "**Tribe Chalepini Weise, 1910**" with "**Tribe Chalepini Weise, 1910 *nomen protectum***".

Page 513. Above the entry "Chalepini Weise, 1910: 69…" add the entries:

"Stenopodiides Horn, 1883: 290 [stem: *Stenopodi-*]. Type genus: *Stenopodius* Horn, 1883. Comment: this and the following family-group name have precedence over Chalepini Weise, 1910; as far as we know family-group names based on *Stenopodius* Horn and *Microrhopala* Chevrolat have not been used as valid after 1899 and we found 25 references (Appendix 1), using Chalepini as valid, in the preceding 50 years published by at least 10 authors and encompassing a span of not less than 10 years; therefore Stenopodiides Horn, 1883 and Microrhopalides Horn, 1883 are *nomina oblita* and Chalepini Weise, 1910 a *nomen protectum* following Art. 23.9.2 (ICZN 1999)."

"Microrhopalides Horn, 1883: 290 [stem: *Microrhopal-*]. Type genus: *Microrhopala* Chevrolat, 1836."

Page 513. In the entry "Chalepini Weise, 1910: 69…" replace "Comment: Chalepini Weise, 1910 is a junior homonym of Chalepidae H. C. C. Burmeister, 1847…" with "Comment: *nomen protectum* (see Appendix 1); Chalepini Weise, 1910 is a junior homonym of Chalepidae Streubel, 1846…"

Page 515. In the entry "Hispoleptites Chapuis, 1875: 283…" replace "Type genus: *Hispopleptis* Baly, 1864" with "Type genus: *Hispoleptis* Baly, 1864".

Page 516. Replace the entry "*Physonotitae Spaeth, 1942: 32…" with:

"Physonotitae Spaeth, 1942: 32 [stem: *Physonot-*]. Type genus: *Physonota* Boheman, 1854. Comment: name proposed after 1930 without description or bibliographic reference to such a description (Art. 13.1), however available because it was used as valid before 2000 as in Balsbaugh and Hays (1972: 191) and was not rejected by an author who, between 1961 and 1999, applied Article 13 of the then current edition of the Code (see Art. 13.2.1)."

Page 516. Replace the valid name "**Tribe Nothosacanthini Gressitt, 1952 (1929)**" with "**Tribe Notosacanthini Gressitt, 1952 (1929)**"

Page 517. Replace the entry "Oncocéphalites Chapuis, 1875: 308…" with:

"Oncocéphalites Chapuis, 1875: 308 [stem: *Oncocephal-*]. Type genus: *Oncocephala* Agassiz, 1846. Comment: original vernacular name available (Art. 11.7.2): first used in latinized form by Weise (1911: 50, as Oncocephalini), generally accepted as in Świętojańska et al. (2006: 49, as Oncocephalini)." Note. *Oncocephala* Agassiz, 1846 is an unjustified emendation of *Onchocephala* Guérin-Méneville, 1844, which is a junior homonym of *Onchocephala* de Blainville, 1828 (Annelides).

Page 518. In the entry "Promecothécites Chapuis, 1875: 300…" replace "Type genus: *Promecotheca* Chevrolat, 1847" with "Type genus: *Promecotheca* Guérin-Méneville, 1840" Note. This genus name is credited by most authors to Blanchard (1853: 312) or Chevrolat (1847b: 482); however, it was first made available by Guérin-Méneville (1840: 334).

Page 518. In the entry "Prosopodontini Weise, 1910: 69…" replace "Type genus: *Prosopodonta* Baly, 1885" with "Type genus: *Prosopodonta* Baly, 1858".

Page 519. Below the entry "*Octotomites Chapuis, 1875: 310…" add:

"Octotomides Horn, 1883: 290 [stem: *Octotom-*]. Type genus: *Octotoma* Dejean, 1836. Comment: this family-group name has precedence over Uroplatini Weise, 1910; Octotomidae was used as valid after 1899 (e.g., Ienistea 1986: 31) and therefore Octotomini Horn, 1883 cannot be treated as a *nomen oblitum* (Art. 23.9.1.1); an application to the Commission is necessary to conserve usage of the well-established name Uroplatini Weise, 1910."

Page 520. Above the entry "*Australicites Chapuis, 1874: 428…" add:

"Colaphidae Siegel, 1866: 102 [stem: *Colaph-*]. Type genus: *Colaphus* L. Redtenbacher, 1845 [preoccupied genus name, not *Colaphus* Dejean, 1836 [Coleoptera: Chrysomelidae]; syn. of *Colaphellus* Weise, 1916]. Comment: permanently invalid (Art. 39): based on preoccupied type genus."

Page 522. At the end of the entry "Gastrophysina Kippenberg, 2010a: 68…" add: "Comment: the senior homonym Gastrophysini Harting, 1864 (type genus *Gastrophysus* Müller, 1843) is available in Pisces; this case is to be referred to the Commission to remove the homonymy (Art. 55.3.1)."

Page 522. Delete the entry "Hesperidae Swainson, 1840: 310…"

Page 524. In the entry "Oxygonites Chapuis, 1875: 43…" at the end of the comment for the type genus replace "…Chevrolat (1847: 368)]." with "…Chevrolat (1847: 368); syn. of *Platiprosopus* Chevrolat, 1834]."

Page 527. In the entry "Chorini Weise, 1923: 124…" add at the end of the "Comment" section "; the family group name Chorininae Dana, 1851 (type genus *Chorinus* Latreille, 1825) is available in Crustacea but currently considered a synonym of Pisinae Dana, 1851; this case is to be referred to the Commission to remove the homonymy (Art. 55.3.1)."

Page 530. Replace "Androlyperini Leng, 1920: 298" with "Androlyperites G. H. Horn, 1893: 59" and move the entry above "Phyllecthrites G. H. Horn, 1893: 60, in key…"

Page 533. At the end of the entry "Monachites Chapuis, 1874: 172…" replace "Monachinae Trouessart, 1897 (type genus *Monachus* Fleming, 1822) is available in Mammalia." with "Monachinae Trouessart, 1897 (type genus *Monachus* Fleming, 1822) is available in Mammalia but a junior homonym of the Coleoptera family-group name based on *Monachus* Chevrolat, 1836; an application to the Commission is needed to conserve usage of the well established name in Mammalia."

Page 533. Below the entry "Monachulini Leng, 1920: 290…" add:

"Lexiphanini Wilcox, 1954: 379, in key [stem: *Lexiphan*-]. Type genus: *Lexiphanes* Gistel, 1848."

Page 534. In the entry "Eumolpidae Hope, 1840a: 162…" replace "Type genus: *Eumolpus* Kugelann, 1798 [an application to suppress *Eumolpus* Kugelann, 1798 and conserve *Eumolpus* Weber, 1801 was recently submitted to the Commission by Moseyko et al. (2010)]." with "Type genus: *Eumolpus* Weber, 1801 [placed on the Official List of Generic Names in Zoology (ICZN 2012b)]. Comment: it appears that Hope (1840) intended to create the family-group name Eumolpidae based on *Eumolpus* Weber, 1801, not *Eumolpus* Kugelann, 1798 (M. Alonso-Zarazaga, pers. comm. 2016); since *Eumolpus* Kugelann, 1798 (as "*Eumolpus* Illiger, 1798") has been suppressed for the purposes of both the Principle of Priority and the Principle of Homonymy and placed on the Official Index of Rejected and Invalid Generic Names in Zoology in Opinion 2298 (ICZN 2012b), *Eumolpus* Weber, 1801 is not a junior homonym and the name Eumolpidae Hope, 1840 can be retained as valid."

Page 534. In the entry "Bromiinae Baly, 1865: 438…" replace "Type genus: *Bromius* Chevrolat, 1836 [an application to conserve *Bromius* Chevrolat, 1836, threatened by the older name *Eumolpus* Kugelann, 1798, was recently submitted to the Commission by Moseyko et al. (2010)]." with "Type genus: *Bromius* Chevrolat, 1836 [placed on the Official List of Generic Names in Zoology (ICZN 2012b)]".

Page 536. Replace the entry "Eumolpidae Hope, 1840a: 162…" with:

"Eumolpidae Hope, 1840a: 162 [stem: *Eumolp*-]. Type genus: *Eumolpus* Weber, 1801 [placed on the Official List of Generic Names in Zoology (ICZN 2012b)]. Comment: First Reviser (Eumolpini Hope, 1840 vs Colaspidini Hope, 1840) not determined, current usage maintained." Note. See additional comments in suggested correction for the entry "Eumolpidae Hope, 1840a: 162..." on page 534 above.

Page 536. Replace the entry "Edusites Chapuis, 1874: 306…" with:

"Edusites Chapuis, 1874: 306 [stem: *Edus*-]. Type genus: *Edusa* Chevrolat, 1836. Comment: original vernacular name available (Art. 11.7.2): first used in latinized

form and generally accepted as in Lefèvre (1885: 111, as Edusitae)." Note. As mentioned by Bousquet and Bouchard (2013: 111) the type genus *Edusa* was first made available in Coleoptera by Chevrolat (1836), as opposed to Chapuis (1874) as previously understood. This removes the homonymy problem with other genera named *Edusa* after 1836 and therefore the family-group name based on *Edusa* Chevrolat, 1836 can be used as valid in the future.

Family Nemonychidae Bedel, 1882

Page 541. Replace the valid name "**†Tribe Kuschelomacrini Riedel, 2010**" with "**†Tribe Kuschelomacerini Riedel, 2010**".

Page 541. In the entry "Kuschelomacerini Riedel, 2010: 31..." replace the stem with "*Kuschelomacer-*" and replace the "Comment" section with "Comment: incorrect original stem formation maintained under Art. 29.4 (should be "*Kuschelomacr-*")."

Page 544. Above the valid name "**†Subfamily Cretonemonychinae Gratshev and Legalov, 2009**" add the following entries:

"**†Tribe Metrioxenoidini Legalov, 2009**

Metrioxenoidinae Legalov, 2009c: 288 [stem: *Metrioxenoid-*]. Type genus: *Metrioxenoides* Gratshev et al., 1998."

"**†Tribe Medmetrioxenoidesini Legalov, 2010**

Medmetrioxenoidesini Legalov, 2010: 471 [stem: *Medmetrioxenoides-*]. Type genus: *Medmetrioxenoides* Gratshev and Legalov, 2009. Comment: incorrect original stem formation maintained under Art. 29.4 (should be "*Medmetrioxenoid-*")."

†Tribe Megametrioxenoidesini Legalov, 2010

Megametrioxenoidesini Legalov, 2010: 471 [stem: *Megametrioxenoides-*]. Type genus: *Megametrioxenoides* Gratshev and Legalov, 2009. Comment: incorrect original stem formation maintained under Art. 29.4 (should be "*Megametrioxenoid-*")."

Family Anthribidae Billberg, 1820

Page 546. At the end of the entry "Meconemini Pierce, 1930: 4, in key…" add: "Comment: the junior homonym Meconemini Burmeister, 1838 (type genus *Meconema* Audinet-Serville, 1831) is available in Orthoptera; this case is to be referred to the Commission to remove the homonymy (Art. 55.3.1)."

Family Caridae Thompson, 1992

Page 553. Replace the valid name "**Tribe Carodini Legalov, 2009**" with "**Tribe Carodesini Legalov, 2009**".

Page 553. In the entry "Carodesina Legalov, 2009: 126..." replace the stem with "*Carodes-*" and replace the "Comment" section with "Comment: incorrect original stem formation maintained under Art. 29.4 (should be *Carod-*)."

Family Attelabidae Billberg, 1820

Page 555. In the entry "Archeuopsina Legalov, 2003: 359..." replace the stem with "*Archeuops-*" and replace the "Comment" section with "Comment: proposed as a

subtribe of Euopini; incorrect original stem formation maintained under Art. 29.4 (should be *Archeuop-*)."

Page 556. In the entry "Suniopsina Legalov, 2003: 364..." replace the stem with "*Suniops-*" and replace the "Comment" section with "Comment: proposed as a subtribe of Euopini; incorrect original stem formation maintained under Art. 29.4 (should be *Suniop-*)."

Page 556. In the entry "Synaptopsina Legalov, 2003: 368..." replace the stem with "*Synaptops-*" and replace the "Comment" section with "Comment: proposed as a subtribe of Euopini; incorrect original stem formation maintained under Art. 29.4 (should be *Synaptop-*)."

Page 556. In the entry "Ljudmilinina Legalov, 2007: 219..." replace the stem with "*Ljudmilin-*" and replace the "Comment" section with "proposed as a subtribe of Euopini; incorrect stem formation maintained under Art. 29.4 (should be *Ljudmilini-*)."

Page 556. In the entry "Parasynaptopsisina Legalov, 2007: 227..." replace the stem with "*Parasynaptopsis-*" and replace the "Comment" section with "proposed as a subtribe of Euopini; incorrect stem formation maintained under Art. 29.4 (should be *Parasynaptopse-*)."

Page 556. In the entry "Riedelinina Legalov, 2007: 218..." replace the stem with "*Riedelin-*" and replace the "Comment" section with "proposed as a subtribe of Euopini; incorrect stem formation maintained under Art. 29.4 (should be *Riedelini-*)."

Page 556. In the entry "Sawadaeuopsina Legalov, 2007: 241..." replace the stem with "*Sawadaeuops-*" and replace the "Comment" section with "Comment: proposed as a subtribe of Euopini; incorrect original stem formation maintained under Art. 29.4 (should be *Sawadaeuop-*)."

Page 558. Replace the valid name "**Subtribe Auletobiina Legalov, 2001**" with "**Subtribe Auletobiina Voss, 1930**".

Page 558. Above the entry "Auletobiina Legalov, 2001: 37…" add:

"Auletobini Voss, 1930: 60 [stem: *Auletobi-*]. Type genus: *Auletobius* Desbrochers des Loges, 1869. Comment: incorrect original stem formation, not in prevailing usage."

Page 558. At the end of the entry "Auletobiina Legalov, 2001: 37…" add "Comment: family-group name proposed as new without reference to Auletobiina Voss, 1930."

Page 559. Move the entry "*Rhynchitallini Voss, 1960: 415..." to before the entry "Rhynchitallina Legalov, 2003: 226..." on page 560.

Page 559. Delete the entry "Proteugnamptini Legalov, 2003: 80..."

Page 560. In the entry "†Sanyrevilleina Legalov, 2003: 85…" replace "[stem: *Sanyreville-*]. Type genus: *Sanyrevilleus* Gratshev and Zherikhin, 2000. Comment: proposed as a subtribe of Auletanini; raised to tribal level by Legalov (2007)." with "[stem: *Sayreville-*]. Type genus: *Sayrevilleus* Gratshev and Zherikhin, 2000. Comment: proposed as a subtribe of Auletanini; raised to tribal level by Legalov (2007); incorrect original stem formation, not in prevailing usage."

Family Brentidae Billberg, 1820

Page 569. Replace the valid name "**Tribe Noterapiini Kissinger, 2004**" with "**Tribe Noterapionini Kissinger, 2004**".

Page 569. In the entry "Noterapionini Kissinger, 2004: 243..." replace the stem with "*Noterapion-*" and replace the "Comment" section with "Comment: incorrect original stem formation maintained under Art. 29.4 (should be *Noterapi-*)."

Family Curculionidae Latreille, 1802

Page 579. Replace "Brachonychina Voss, 1944: 38" with "Brachonychinae Joy, 1932: 159, in key".

Page 579. In the entry "Camarotides Schönherr, 1833: 4…" replace "Type genus: *Camarotus* Germar, 1817" with "Type genus: *Camarotus* Germar, 1833"

Page 582. Below the entry "Otidocéphalides Lacordaire, 1863: 568…" add:

"Myrmecinae Tanner, 1966: 6, in key [stem: *Myrmec-*]. Type genus: *Myrmex* Sturm, 1826."

Page 585. Replace "Orthocaetina Morimoto, 1962a: 56, in key" with "Orthochaetinae Joy, 1932: 159 (in key), 208" and remove the "Comment" section.

Page 591. Below the entry "Poophagidae Schultze, 1902: 226…" add:

"Tapinotinae Joy, 1932: 160, in key [stem: *Tapinot-*]. Type genus: *Tapinotus* Schönherr, 1826." Note. See Colonnelli (2013: 58) for a discussion regarding the correct spelling of the type genus name.

Page 594. Below the entry "*Sympiézopides Lacordaire, 1865: 166…" add:

"Sympiezopinorum Faust, 1886b: 367. [stem: *Sympiezopod-*]. Type genus: *Sympiezopus* Schönherr, 1837. Comment: Sympiezopinorum is the genitive of Sympiezopini (Alonso-Zarazaga pers. comm. December 2019); incorrect original stem formation, not in prevailing usage."

Pages 599–600. Below the entry for "Tylodides Lacordaire, 1865: 90" add:

"Acallinae Joy, 1932: 160, in key [stem: *Acall-*]. Type genus: *Acalles* Schönherr, 1825."

Page 600. In the entry "Psépholacides Lacordaire, 1865: 72…" replace "Type genus: *Psepholax* Lacordaire, 1865" with "Type genus: *Psepholax* White, 1843".

Page 602. In the entry "Hipporhinides Lacordaire, 1863: 323…" replace "Type genus: *Hipporhinus* Schönherr, 1823" with "Type genus: *Hipporhis* Billberg, 1820 [as *Hipporhinus*, unjustified emendation of the type genus by Schönherr, 1823, not in prevailing usage; syn. of *Bronchus* Germar, 1817]".

Page 604. In the entry "Strophosomidae Gistel, 1848: [8]…" replace "Type genus: *Strophosomum* Gistel, 1856 [syn. of *Strophosoma* Billberg, 1820]" with "Type genus: *Strophosoma* Billberg, 1820."

Page 610. Replace the valid name "**Tribe Mesostylini Reitter, 1913**" with "**Tribe Mesostyloidini Bouchard & Bousquet, *nomen novum*"**

Page 610. Replace the entry "Mesostylini Reitter, 1913b: 8..." with:

"Mesostylini Reitter, 1913b: 8 [stem: *Mesostyl-*]. Type genus: *Mesostylus* Faust, 1894 [preoccupied genus name, not *Mesostylus* Bronn and Roemer, 1852 [Crustacea]; syn. of *Mesostyloides* Bouchard and Bousquet, ***nomen*** [***novum***]. Comment: per-

manently invalid (Art. 39); based on preoccupied type genus." Note. Although the crustacean name *Mesostylus* Bronn and Roemer, 1852 was treated as a nomen oblitum by Karasawa (2003: 181), this genus was used as valid more recently by Schweitzer and Feldmann (2012: 17).

Page 610. Below the entry "Mesostylini Reitter, 1913b: 8..." add:

"Mesostyloidini Bouchard and Bousquet, ***nomen novum*** for Mesostylini Reitter, 1913 [stem: *Mesostyloid-*]. Type genus: *Mesostyloides* Bouchard and Bousquet, ***nomen novum*** for *Mesostylus* Faust, 1894."

Page 612. Replace the entry "Loborhynchides Schönherr, 1823: column 1144…" with:

"Loborhynchides Schönherr, 1823: column 1144 [stem: *Loborhynch-*]. Type genus: *Loborhynchus* Dejean, 1821 [placed on the Official Index of Rejected and Invalid Generic Names in Zoology (ICZN 1972, ICZN 2012c)]. Comment: Loborhynchinae Schönherr, 1823 placed on the Official Index of Rejected and Invalid Family-Group Names in Zoology (ICZN 1972)."

Page 613. Replace the entry "Otiorhynchides Schönherr, 1826: 203…" with:

"Otiorhynchides Schönherr, 1826: 203 [stem: *Otiorhynch-*]. Type genus: *Otiorhynchus* Germar, 1822 [placed on the Official List of Generic Names in Zoology (ICZN 1972, ICZN 2012c)]. Comment: name placed on the Official List of Family-Group Names in Zoology (ICZN 1972, as Otiorhynchinae Schönherr, 1826)." Note. The entry on the Official List of Generic Names in Zoology for the genus *Otiorhynchus* was emended from "*Otiorhynchus* Germar, 1824, *Insectorum species novae aut minus cognitae, descriptionibus illustratae*, vol. 1." to "*Otiorhynchus* Germar, 1822, *Fauna Insectorum Europae*, 7: no. 12" (ICZN 2012c).

Page 615. In the entry "Sitonisidae Gistel, 1848: [8]…" replace "Type genus: *Sitones* Schönherr, 1840 [syn. of *Sitona* Germar, 1817]" with "Type species: *Sitona* Germar, 1817 [as *Sitones*, unjustified emendation of the type genus by Schönherr (1840b: 253), not in prevailing usage]".

Page 616. Below the entry for "Pandeleteini Pierce, 1913: 399…" add:

"Cycloderini Hoffmann, 1950: 417 [stem: *Cycloder-*]. Type genus: *Cycloderes* C. R. Sahlberg, 1823."

Pages 617. In the entry "Tropiphoridae Marseul, 1863: 220…" delete the "Comment" section. Note. The date of 15 June 1863 on the first page of Marseul's *Catalogue* does not pertain to the date of publication but to the date of the preliminaries. The work was published in November 1863 (Marseul 1864: xxv, as "Nov. 1843" [sic]). The new date of publication found means that the family-group names Strangaliodini Lacordaire, 1863, Byrsopagini Lacordaire, 1863, Pantopoeini Lacordaire, 1863 and Synaptonychini Lacordaire, 1863 have precedence over Marseul's Tropiphorini since Lacordaire's book was issued by 1 August 1863 (Bousquet 2016: 314). An application to the Commission is necessary to preserve usage of Tropiphorini Marseul, 1863 in Curculionidae: Entiminae, or alternatively, one or more of the available family-group names

proposed by Lacordaire (1863) could be used as valid (e.g., Alonso-Zarazaga et al. 2017: 543).

Page 618. In the entry "Stenocorynini McKeown, 1939: 408…" replace "Type genus: *Stenocorynus* Schönherr, 1842" with "Type genus: *Stenocorynus* Schönherr, 1823"

Page 619. Replace the valid name "**Tribe Hyperini Marseul, 1863 (1848)**" with "**Tribe Hyperini Lacordaire, 1863 (1848)**".

Page 619. Replace the entry "Hyperidae Marseul, 1863: 224…" with:

"Hypérides Lacordaire, 1863: 395 [stem: *Hyper-*]. Type genus *Hypera* Germar, 1817. Comment: original vernacular name available (Art. 11.7.2): first used in latinized form by Marseul (1863: 224, as Hyperidae), generally accepted as in Morrone and Roig Juñent (1995: 12, as Hyperinae)." Note. As mentioned above the date of 15 June 1863 on the first page of Marseul's *Catalogue* does not pertain to the date of publication but to the date of the preliminaries. The work was published in November 1863 and so Lacordaire's name was proposed earlier [by 10 August 1863] and takes priority.

Page 619. In the entry "Macrotarrhusina Legalov, 2007: 401..." replace the stem with "*Macrotarrhus-*" and replace the "Comment" section with "Comment: incorrect original stem formation maintained under Art. 29.4 (should be *Macrotarrh-*)."

Page 623. In the entry "Brachyceropseinae Aurivillius, 1926b: 2…" replace "Type genus: *Brachyceropsis* Aurivillius, 1926" with "Type genus: *Brachyceropsis* Aurivillius, 1886".

Page 628. Replace the entry "Plinthides Lacordaire, 1863: 359…" with:

"Plinthides Lacordaire, 1863: 359 [stem: *Plinth-*]. Type genus: *Plinthus* Germar, 1817 [placed on the Official List of Generic Names in Zoology (ICZN 2012d)]. Comment: name placed on the Official List of Family-Group Names in Zoology (ICZN 2012d, as Plinthini Lacordaire, 1863)."

Page 628. Below the entry "Minyopidae Marseul, 1863: 221…" add:

"**Subtribe Sthereina Hatch, 1971**

Sthereini Hatch, 1971: 309 [stem: *Sthere-*]. Type genus: *Sthereus* Motschulsky, 1845."

Page 635. In the entry "*Sueinae Murayama, 1959: 26..." remove the asterisk (*) and replace the "Comment" section with "Comment: name proposed after 1930 without description or bibliographic reference to such a description (Art. 13.1), however available because it was used as valid before 2000 as in Murayama (1963: 4, as Sueinae) and was not rejected by an author who, between 1961 and 1999, applied Article 13 of the then current edition of the Code (Art. 13.2.1)."

Page 635. Delete the entry "Sueinae Murayama, 1963: 4…"

Page 637. Replace the entry "*Eccoptopterina Browne, 1961: 49…" with:

"Eccoptopterini Kalshoven, 1959: 166 [stem: *Eccoptopter-*]. Type genus: *Eccoptopterus* Motschulsky, 1863. Comment: name proposed after 1930 without description or bibliographic reference to such a description (Art. 13.1), however available because it was used as valid before 2000 as in Browne (1961: 49, as Eccoptopterina) and was not rejected by an author who, between 1961 and 1999, applied Article 13 of the then current edition of the Code (Art. 13.2.1)."

Coleoptera *incertae sedis*

Page 639. Insert an asterisk (*) in front of "Serratopalpidae Gistel, 1856a: 384" since the family-group name is not available.

Page 639. Delete the entry "Homoeoplastidae Gistel, 1856a: 360…" since this family-group name is available (see above, under p. 354).

Page 639. Delete the entry "Plocasteidae Gistel, 1856a: 365…" since this family-group name is available (see above, under p. 232).

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Delete the following references:

Biström O, Nilsson AN, Wewalka G (1997)…
Hatch MH (1928)…
Latreille PA (1819)…
Régimbart M (1882)…
Winkler A (1925)…
Zimmermann A (1919)…

Add the following references:

Alonso-Zarazaga MA, Barrios H, Borovec R, Bouchard P, Caldara R, Colonnelli E, Gültekin L, Hlaváč P, Korotyaev B, Lyal CHC, Machado A, Meregalli M, Pierotti H, Ren L, Sánchez-Ruiz M, Sforzi A, Silfverberg H, Skuhrovec J, Trýzna M, Velázquez de Castro AJ, Yunakov

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Additions and corrections to appendices in Bouchard et al. (2011)

Appendix 1

Conservation of younger names using Reversal of Precedence (Art. 23.9). Cases listed in alphabetical order by family with their supporting references.

Cerylonidae

Supporting references for the conservation of Murmidiinae Jacquelin du Val, 1858 over Ceutocerinae Mannerheim, 1852 (Art. 23.9.2). The taxon name Ceutocerinae Mannerheim, 1852 has not been used as valid after 1899 to our knowledge.

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Chrysomelidae

Supporting references for the conservation of Chalepini Weise, 1910 over Stenopodiini Horn, 1883: 290 and Microrhopalini Horn, 1883. The taxon names Stenopodiini Horn, 1883: 290 and Microrhopalini Horn, 1883 have not been used as valid after 1899 to our knowledge.

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Appendix 2

Coleoptera family-group name changes required based on the Principle of Priority. The action that has been taken to fix the problem, or recommendation for future work, is mentioned for each case. Cases listed in alphabetical order by family.

Add the following entries:

Family	Change from:	Change to:	Action	Reference
Bostrichidae	Trogoxylini Lesne, 1921	Tristariini Lesne, 1921	An application to the Commission is needed to conserve usage of the well-established name Trogoxylini Lesne, 1921	
Cerambycidae	Ancitini Aurivillius, 1917	Hebesecini Pascoe, 1871	An application to the Commission is needed to conserve usage of the well-established name Ancitini Aurivillius, 1917	
Chrysomelidae	Uroplatini Weise, 1910	Octotomini Horn, 1883	An application to the Commission is needed to conserve usage of the well-established name Uroplatini Weise, 1910	
Curculionidae	Tropiphorini Marseul, 1863	Leptopini Lacordaire, 1863	An application to the Commission is needed to conserve usage of the well-established name Tropiphorini Marseul, 1863	
Elateridae	Eudicronychinae Girard, 1971	Dicronychidae Schwarz, 1897	An application to the Commission is needed to suppress the older name because it is based on a misidentified type genus (Art. 65.2.1)	
Endomychidae	Anamorphinae Strohecker, 1953	Symbiotinae Joy, 1932	An application to the Commission is needed to conserve usage of the well-established name Anamorphinae Strohecker, 1953	
Eucnemidae	Macraulacinae/-ini Fleutiaux, 1923	Fornacini Beaulieu, 1919 and Dromaeolini Beaulieu, 1919	An application to the Commission is needed to conserve usage of the well-established names Macraulacinae/-ini Fleutiaux, 1923	
Laemophloeidae	Laemophloeidae Ganglbauer, 1899	Nartheciidae Casey, 1890	An application to the Commission is needed to conserve usage of the well-established name Laemophloeidae Ganglbauer, 1899	
Limnichidae	Thaumastodinae Champion, 1924	Pseudeucinetinae Csiki, 1924	An application to the Commission is needed to conserve usage of the well-established name Thaumastodinae Champion, 1924	

Family	Change from:	Change to:	Action	Reference
Meloidae	Lyttini Streubel, 1846	Cantharini Latreille, 1802	An application to the Commission is needed to suppress the older name because it is based on a misidentified type genus (Art. 65.2.1)	
Scarabaeidae	Pachycnemina Laporte, 1840	Lepitrichina Perty, 1840	Reversal of Precedence or an application to the Commission is needed to conserve usage of the well-established name Pachycnemina Laporte, 1840	

Delete the following entries:

Family	Change from:	Change to:	Action	Reference
Elateroidea/-idae	Elateroidea/-idae Leach, 1815	Cebrionoidea/-idae Latreille, 1802	An application to the Commission will be sent to conserve usage of the well-established names Elateroidea/-idae Leach, 1815	P. J. Johnson (in Lawrence and Newton 1995, pers. comm. 2009)
Latridiidae	Latridiidae Erichson, 1842	Corticariidae Curtis, 1829	An application to the Commission was submitted by Bousquet et al. (2010) to conserve usage of the well-established name Latridiidae Erichson, 1842	
Meloidae	Lyttini Solier, 1851	Cantharini Latreille, 1802	An application to the Commission is needed to suppress the older name because it is based on a misidentified type genus (Art. 65.2.1)	

Appendix 3

Coleoptera family-group name changes required based on the Principle of Homonymy. The action that has been taken to fix the problem, or recommendation for future work, is mentioned for each case. Cases listed in alphabetical order by family.

Add the following entries:

Family	Coleoptera name:	Homonym:	Type genera	Action	Reference
Anthribidae	Meconemini Pierce, 1930	Meconemini Burmeister, 1838 [Orthoptera]	different	An application to the Commission is needed to remove the homonymy (Art. 55.3.1)	
Byrrhidae	Microchaetini Paulus, 1973	Microchaetini Beddard, 1895 [Oligochaeta]	different	An application to the Commission is needed to remove the homonymy (Art. 55.3.1)	

Family	Coleoptera name:	Homonym:	Type genera	Action	Reference
Cantharidae	Ichthyurini Champion, 1915	Ichthyurinae Packard, 1895 [Lepidoptera]	different	An application to the Commission is needed to remove the homonymy (Art. 55.3.1)	
Carabidae	Homopterinae Wasmann, 1920	Homopterinae Boisduval, 1852 [Lepidoptera]	different	An application to the Commission is needed to remove the homonymy (Art. 55.3.1)	
Carabidae	Glyptini Horn, 1881	Glyptini Cushman and Rohwer, 1920 [Hymenoptera]	different	An application to the Commission is needed to remove the homonymy (Art. 55.3.1)	
Catiniidae	Catiniidae Ponomarenko, 1968	Catiniidae Bocquet and Stock, 1957 [Crustacea]	different	An application to the Commission is needed to remove the homonymy (Art. 55.3.1)	
Chrysomelidae	Chorinini Weise, 1923	Chorininae Dana, 1851 [Crustacea]	different	An application to the Commission is needed to remove the homonymy (Art. 55.3.1)	
Chrysomelidae	Gastrophysina Kippenberg, 2010	Gastrophysini Harting, 1864 [Pisces]	different	An application to the Commission is needed to remove the homonymy (Art. 55.3.1)	
Cleridae	Trichodidae Streubel, 1839	Trichodina Maitland, 1851 [Protozoa]	different	An application to the Commission is needed to remove the homonymy (Art. 55.3.1)	
Coccinellidae	Monocorynini Miyatake, 1988	Monocoryninae Rees, 1956 [Cnidaria]	different	An application to the Commission is needed to remove the homonymy (Art. 55.3.1)	
Elateridae	Limoniina Jakobson, 1913	Limoniidae Speiser, 1909 [Diptera]	different	An application to the Commission is needed to remove the homonymy (Art. 55.3.1)	
Eucnemidae	Epiphanini Muona, 1993	Epiphanidae Harring, 1913 [Rotifera]	different	An application to the Commission is needed to remove the homonymy (Art. 55.3.1)	
Passalidae	Gonatinae Kuwert, 1891	Gonatidae Hoyle, 1886 [Cephalopoda]	different	An application to the Commission is needed to remove the homonymy (Art. 55.3.1)	

Family	Coleoptera name:	Homonym:	Type genera	Action	Reference
Scarabaeidae	Aplonychidae H. C. C. Burmeister, 1855	Aplonychini De Stefani, 1908 [Diptera]	different	An application to the Commission is needed to remove the homonymy (Art. 55.3.1)	
Staphylinidae	Tychini Raffray, 1904	Tychinae Dana, 1851 [Crustacea]	different	An application to the Commission is needed to remove the homonymy (Art. 55.3.1)	
Staphylinidae	Ocypodina Hatch, 1957	Ocypodidae Rafinesque, 1815 [Crustacea]	different	An application to the Commission is needed to remove the homonymy (Art. 55.3.1)	
Trogossitidae	Decamerini Crowson, 1964	Decameridae Rasmussen, 1978 [Echinodermata]	different	An application to the Commission is needed to remove the homonymy (Art. 55.3.1)	

Delete the following entries:

Family	Coleoptera name:	Homonym:	Type genera	Action	Reference
Carabidae	Nomiini Gozis, 1875	Nomiidae Robertson, 1904 [Hymenoptera]	different	An application was submitted to the Commission to emend the stem of the beetle family-group name	Engel and Bouchard (2009)
Cleroidea	Chaetosomatidae Crowson, 1952	Chaetosomatidae Claus, 1872 [Nematoda]	same, Coleoptera genus older	An application to the Commission was submitted by YB and PB to conserve the Coleoptera name	
Gyrinidae	Enhydrini Régimbart, 1882	Enhydrini Gray, 1825	different	An application was recently submitted to the Commission by Özdikmen and Darilmaz (2010) to remove the homonymy	
Lampyridae	Photinini LeConte, 1881	Photininae Giglio-Tos, 1915 [Mantodea]	different	An application to the Commission was submitted by Svenson and Branham (2007) to remove the homonymy (Art. 55.3.1)	

Appendix 4

Coleoptera names as they appear on the Official List of Family-Group Names in Zoology. Cases listed in alphabetical order by family.

Family	Name on Official List	Opinion(s) or Direction	Reference
Carabidae	Nomiusidae Gozis, 1875	2272	ICZN 2011a
Chaetosomatidae	Chaetosomatidae Crowson, 1952	2287	ICZN 2011b
Curculionidae	Plinthini Lacordaire, 1863	2300	ICZN 2012d
Gyrinidae	Enhydrusini Régimbart, 1882	2297	ICZN 2012a
Lampyridae	Photinini LeConte, 1881	2397	ICZN 2018
Latridiidae	Corticariidae Curtis, 1829	2288	ICZN 2011c
Latridiidae	Latridiidae Erichson, 1842	2288	ICZN 2011c
Scarabaeidae	Dynastidae MacLeay, 1819	2344	ICZN 2014
Scarabaeidae	Scarabaeidae Latreille, 1802	2344	ICZN 2014
Staphylinidae	Athetini Casey, 1910	2305	ICZN 2012e
Staphylinidae	Geostibina Seevers, 1978	2305	ICZN 2012d
Staphylinidae	Omaliidae MacLeay, 1825	2370	ICZN 2015b

Appendix 5

Coleoptera type genus names as they appear on the Official List of Generic Names in Zoology. Cases listed in alphabetical order by family.

Family	Name on Official List	Opinion(s)	Reference(s)
Anthicidae	*Anthicus* Paykull, 1798	2377	ICZN 2017
Anthicidae	*Microhoria* Chevrolat, 1877	2377	ICZN 2017
Buprestidae	*Polybothris* Dupont, 1833	2366	ICZN 2015a
Carabidae	*Nomius* Laporte, 1835	2272	ICZN 2011a
Cerambycidae	*Apodasya* Pascoe, 1863	2287	ICZN 2011b
Chaetosomatidae	*Chaetosoma* Westwood, 1851	2287	ICZN 2011b
Chrysomelidae	*Bromius* Chevrolat, 1836	2298	ICZN 2012b
Chrysomelidae	*Eumolpus* Weber, 1801	2298	ICZN 2012b
Curculionidae	*Otiorhynchus* Germar, 1822 [year emended]	2299	ICZN 2012c
Curculionidae	*Plinthus* Germar, 1817	2299	ICZN 2012d
Lampyridae	*Photinus* Laporte, 1833	2397	ICZN 2018
Latridiidae	*Corticaria* Marsham, 1802	2288	ICZN 2011c
Latridiidae	*Latridius* Herbst, 1793	2288	ICZN 2011c
Scarabaeidae	*Dynastes* MacLeay, 1819	2344	ICZN 2014
Scarabaeidae	*Scarabaeus* Linnaeus, 1758	2344	ICZN 2014
Staphylinidae	*Callicerus* Gravenhorst, 1802	2305	ICZN 2012e
Staphylinidae	*Omalium* Gravenhorst, 1802	2370	ICZN 2015b

Appendix 6

Summary of cases involving Coleoptera family-group names and/or their type genera awaiting a ruling by the Commission. Cases listed in alphabetical order by family.

Replace the cases listed in Bouchard et al (2011: 894–895) with:

Chrysomelidae

An application to conserve *Eupales* Lefèvre, 1885 and Eupalini Verma et al. 2005 was submitted by Jolivet and Verma (Bulletin of Zoological Nomenclature 2009: 204; see notice of "New applications to the Commission") but this Case (number 3498) was never published (ICZN secretariat pers. comm. 2019).

Dytiscidae

An application to conserve usage of the genus *Bidessus* Sharp, 1880 was submitted by Bousquet and Bouchard (2018a). An alternative request to the Commission was subsequently published by Fery and Grygier (2019).

Eucnemidae

An application to conserve usage of Eucnemidae Eschscholtz, 1829 over Melasidae Fleming, 1821 was submitted by Muona (Bulletin of Zoological Nomenclature 1994: 185; see notice of "New applications to the Commission") but this Case (number 2938) was never published (ICZN secretariat pers. comm. 2019).

Hybosoridae

Ballerio (Bulletin of Zoological Nomenclature 2018: 3; see "Notice of New Applications to the Commission (Cases 3753–3772)") submitted an application to conserve usage of *Acanthocerus* W. S. MacLeay, 1819 (now *Ceratocanthus* A. White, 1842). This Case (number 3766) has not been published yet.

Ripiphoridae

A request was submitted to the Commission by Bousquet and Bouchard (2018b) to conserve usage of Ripiphoridae Laporte, 1840 and its type genus *Ripiphorus* Bosc, 1791.

Tenebrionidae

Bousquet and Bouchard (Bulletin of Zoological Nomenclature 2018: 206; see "Notice of New Applications to the Commission (Cases 3782–3787)") submitted an application to conserve usage of *Cnodalon* Latreille, 1797. This Case (number 3784) has not been published yet.

Curculionidae

Caldara and Alonso-Zarazaga (2018) submitted an application to the Commission to conserve usage of *Orchestes* Illiger, 1798 by giving it precedence over *Salius* Schrank, 1798.

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RESEARCH ARTICLE

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Simulium reptans (Linnaeus, 1758) and *Simulium reptantoides* Carlsson, 1962 from the Balkan Peninsula

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Abstract

Simulium reptans (Linnaeus, 1758) and *Simulium reptantoides* Carlsson, 1962 are two species of the *Simulium reptans* group whose distribution is unclear because of their confusing taxonomy and systematics. Their genetic variability is well known for populations in northern and central Europe and shows that both species have two forms; however, the genetic variability of these species in southern and eastern Europe is unknown. To identify the status of these two species in southeast Europe, mtDNA was extracted from 19 individuals from 12 localities across the Balkan Peninsula. Phylogenetic analysis confirmed the existence of two species with 7.38–7.94% divergence. Each species was comprised of two clades, with 2.31% and 1.43% interclade divergence for *S. reptans* and *S. reptantoides*, respectively. This study revealed the presence of both species across the Balkans and that *S. reptans* occurs in this area in only one form (*S. reptans* B), while *S. reptantoides* is found in two genetic forms (A and B).

Keywords

genetic variability, Simuliidae, southeast Europe

Introduction

The systematics, population genetics, distribution and evolution of black flies (Diptera: Simuliidae) represent interesting research fields for scientists worldwide (e.g., Hernández-Triana et al. 2012; Ya'cob et al. 2016; Ivković et al. 2016; Conflitti et al. 2017; Ruiz-Arrondo et al. 2018; Adler 2019). The great morphological similarity among certain species leads to frequent misidentification; nowadays, the description of new taxa is aided by cytogenetic and molecular identification methods. These methods have shown that some morphologically defined taxa consist of several sister species, which are usually reproductively isolated (Rothfels 1979; Adler et al. 2010). A similar situation occurs within the *Simulium reptans* group, which contains 16 species widely present in Europe and the Caucasus area (Adler 2019). The whole group consists of mammophilous and anthropophilous species, placing them in the focus of interest primarily because of their medical, sanitary and economic significance (Day et al. 2008; Kúdela et al. 2014).

Two species of this group, *Simulium reptans* (Linnaeus, 1758) and *Simulium reptantoides* Carlsson, 1962, have been extensively discussed in the literature. One of the problems with these species has been their frequent misidentification. Taxonomic features that distinguish them are given in only a few identification keys or scientific articles (Edwards 1920; Knoz 1965; Jedlička et al. 2004), while most of the keys did not include both species, which has led to inaccurate reports of their presence. According to Day et al. (2008), two main features could morphologically distinguish these two species: pigmentation of the cephalic apotome of larvae (Edwards 1920) and microtubercles on the thorax of pupae (Day et al. 2008). Likewise, *S. reptans* has a large and conspicuous dark spot in the middle of the cephalic apotome, while *S. reptantoides* has very little pigmentation except along the posterior margin. On the other hand, the pupae of these species can be distinguished by the average number of microtubercles on the thorax. Both species have two types of microtubercles (pointed and rounded), but their density on the thorax in *S. reptantoides* exceeds that in *S. reptans* pupae. Day et al. (2008) applied barcoding to individuals that were previously identified based on these morphological features, confirming that they could be distinguished by them.

The second problem regarding these species has been their nomenclature, which is reflected by the high number of synonyms (Adler 2019). Hence, *S. reptans* was previously described as *S. galeratum* (Edwards, 1920) (Crosskey and Howard 2004; Day et al. 2008; Bernotienė and Stunžėnas 2009), and *S. reptantoides* as *S. reptans* (Jedlička 1965; Day et al. 2008; Bernotienė and Stunžėnas 2009). The latest revision by Kúdela et al. (2014) described in detail the taxonomic and nomenclatural status of *S. reptans* and *S. reptantoides*. The recall of *S. reptantoides* from synonymy by Kúdela et al. (2014) was accepted by Adler and Crosskey (2014) in their annual inventory of world Simuliidae. In the present study we used the taxonomical approach of Kúdela et al. (2014), which was also adopted in the current inventory list (Adler 2019).

Both Day et al. (2008) and Kúdela et al. (2014) reported the existence of two different forms among *S. reptantoides*, termed A and B. The molecular diagnosis given by

Day et al. (2008) was limited to British populations. Further examination by Kúdela et al. (2014) included European mainland populations as well. According to Kúdela et al. (2014), *S. reptantoides* is not found in the Baltic area and is limited to the UK and central Europe. *Simulium reptans* has a wider distribution (Scandinavia, UK, the Baltic area and Slovakia) and can also be found in its own forms, also named A and B (Kúdela et al. 2014).

According to the last inventory list (Adler 2019), *S. reptans* has a wide distribution and is present in south and eastern Europe, including the Balkan Peninsula, while *S. reptantoides* is limited to the UK and Slovakia.

Because of the work of Day et al. (2008) and Kúdela et al. (2014), the genetic variability of *S. reptans* and *S. reptantoides* is established for northern and central European populations. However, there are no data about the genetic variability of these species in southern and eastern Europe, even though *S. reptans* was frequently found in Balkan rivers (Crosskey 1998; Jedlička and Seitz 2008; Ivković et al. 2016). To the best to our knowledge, there are only a few published findings of *S. reptantoides* from the Balkans (Jedlička and Seitz 2008; Ivković et al. 2016).

The aim of the present study was to fill in the knowledge gap in the distribution and genetic variation of these two species in southeastern Europe, i.e., to determine whether they are present in the Balkans or not and if so, in which molecular form(s).

Materials and methods

Sample collection

From 2015 to 2017, samples of larvae and pupae of *S. reptans* and *S. reptantoides* were collected at 12 localities across the Balkan Peninsula as follows: Slovenia (SVN), Croatia (CRO), Bosnia and Herzegovina (BIH), Montenegro (MNE), Serbia (SRB), North Macedonia (MKD) and Bulgaria (BGR) (Table 1 and Fig. 1). The collected material was preserved in the field in 96% ethanol. Identification was performed twice in the Institute for Biological Research "Siniša Stanković". The material was identified before the molecular analyses of the specimens using the Rivosecchi (1978) and Lechthaler and Car (2005) identification keys, and once more after the molecular analyses using the identification keys and scientific articles as guidelines of Edwards (1920), Knoz (1965) and Day et al. (2008).

Molecular procedures

DNA extractions from larvae and pupae were performed in the Institute for Biological research "Siniša Stanković". To avoid the risk of contamination by other DNA sources, the intestinal tracts of the larvae were removed. For the extractions we used the isolation kit "KAPA2G Express Extract Kit" (Kapa Biosystems, United States, Wilmington, Massachusetts). The quality of the DNA was checked by agarose gel (1%) electrophoresis.

Table 1. Data for species *S. reptans* and *S. reptantoides* collected in the period 2015–2017. Species names are given according to the results of the study.

Accession Numbers	Species	Stage	River	Location	Country Alpha-3 code	Latitude /Longitude	Collection date	Collector
MK936587	*Simulium reptans*	pupa	Sava River	near Čatež	SVN	45.884078, 15.640831	03 Sep. 2015	Paunović et al.
MK936590		pupa	Sava River	near Čatež	SVN	45.884078, 15.640831	03 Sep. 2015	Paunović et al.
MK936588		pupa	Sava River	near Zagreb	CRO	45.759639, 16.047861	04 Sep. 2015	Paunović et al.
MK936589		pupa	Humljani	Humljani	CRO	45.578080, 17.798738	25 Sep. 2016	Đuknić et al.
MK947040		pupa	Strumica River	near Vasilevo	MKD	41.497500, 22.643333	24 Jun. 2017	Đuknić et al.
MK936596	*Simulium reptantoides*	larva	Sava River	near Čatež	SVN	45.884078, 15.640831	03 Sep. 2015	Paunović et al.
MK947041		pupa	Neretva River	near Počitelj	BIH	43.149052, 17.737837	31 Jul. 2016	Đuknić et al.
MK936595		larva	Zamna River	near Negotin	SRB	44.297883, 22.354969	26 Apr. 2015	Đuknić et al.
MK947046		pupa	Urovica River	near Urovica	SRB	44.399425, 22.407786	25 Apr. 2015	Đuknić et al.
MK947048		pupa	Urovica River	near Urovica	SRB	44.399425, 22.407786	25 Apr. 2015	Đuknić et al.
MK947045		pupa	Ibar River	near Raška	SRB	43.286957, 20.618514	11 Jun. 2017	Đuknić et al.
MK947047		pupa	Ibar River	near Raška	SRB	43.286957, 20.618514	11 Jun. 2017	Đuknić et al.
MK936591		pupa	Rila River	Rila	BGR	42.131866, 23.156651	17 Sep. 2017	Đuknić et al.
MK947044		larva	Neretva River	near Počitelj	BIH	43.149052, 17.737837	31 Jul. 2016	Đuknić et al.
MK947043		pupa	Neretva River	near Počitelj	BIH	43.149052, 17.737837	31 Jul. 2016	Đuknić et al.
MK946294		pupa	Tara River	near Kolašin	MNE	42.863386, 19.527027	08 Aug. 2017	Đuknić et al.
MK947042		pupa	Cjevna River	near Podgorica	MNE	42.382999, 19.278886	25 Mar. 2017	Đuknić et al.
MK940493		pupa	Lim River	near Prepolje	SRB	43.393293, 19.642978	09 Aug. 2016	Đuknić et al.
MK937592		pupa	Rila River	Rila	BGR	42.131866, 23.156651	17 Sep. 2017	Đuknić et al.

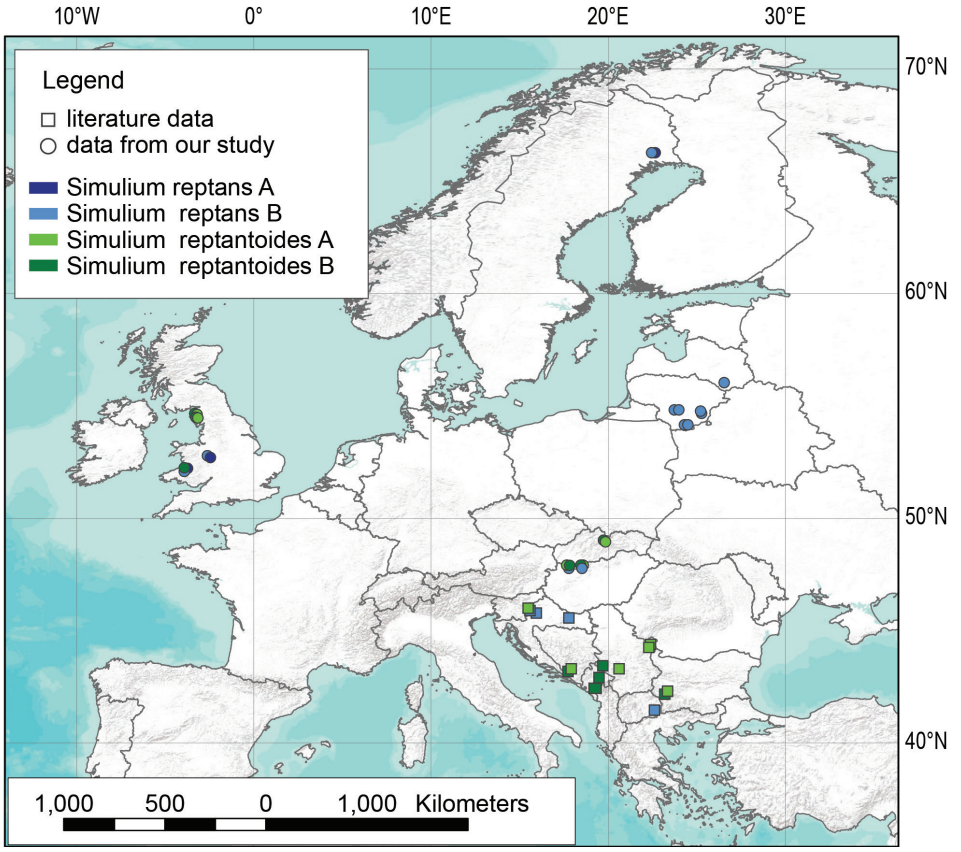

Figure 1. Map of the different localities. Localities of the collected specimen of *S. reptans* and *S. reptantoides* from the Balkan Peninsula (our study) and localities of the origin for the downloaded sequences from NCBI GenBank (literature data).

The barcoding region of the mitochondrial COI gene of two morphologically identified species, *Simulium reptans* (five individuals) and *S. reptantoides* (14 individuals), was amplified using the following primers: LCO1490 (5-GGTCAACAAATCATAAAGATATTGG-3) and HCO2198 (5-TAAACTTCAGGCTGACCAAAAAAT CA-3) (Folmer et al. 1994). The total volume of mtDNA amplification was 25 µL, which contained 1 µL of extracted DNA, 16.9 µL of dH_2O, 0.5 µL dNTPs, 0.5 µL GoTaq buffer, 0.7 µL of both primers and 0.2 µL of GoTaq polymerase. The PCR cycles were as follows: 2 min of denaturation at 95 °C, followed by 35 cycles of denaturation at 94 °C for 1 min, primer annealing at 50 °C for 1 min and extension at 72 °C for 1 min, the final extension step for 5 min at 72 °C. Ethidium bromide was used to visualise the PCR products on 1% agarose gels. DNA sequencing was performed at the Faculty of Biology, University of Belgrade (Center for Human Molecular Genetics). ABI Sequence Scanner Software v. 2.0 was used to check and arrange the sequences (Applied Biosystems). All DNA sequences were stored at GenBank; accession numbers are shown in Table 1.

Genetic and phylogenetic analyses

In total, 90 sequences were analysed: five sequences of *S. reptans* and 14 of *S. reptantoides* collected from the Balkan Peninsula, 38 sequences of *S. reptans* and 33 of *S. reptantoides* downloaded from GenBank, and six sequences from the GenBank database were used as outgroups: two *Simulium vernum* Macquart, 1826, two *Thaumalea testacea* Ruthe, 1831 and two *Culicoides brevitarsis* Kieffer. The COI gene sequences for *S. reptans* and *S. reptantoides* that were downloaded from GenBank originated from Slovakia (19 sequences), Lithuania (8), Latvia (3), Sweden (12) and the UK (29), and are listed in Suppl. material 1: Table S1. MEGA6 (Tamura et al., 2013) with the ClustalW algorithm was used to align the sequences. The best-fitting model of sequence evolution was found in MEGA6 according to the model comparison procedure by the Bayesian information criterion (BIC) and log-likelihood (lnL) and was used in subsequent analyses.

Maximum likelihood (ML) and maximum parsimony (MP) phylogenetic analyses were also carried out using MEGA6 software (Tamura et al. 2013), while Bayesian phylogenetic analyses were performed using BEAST v2.4.2 (Bouckaert et al. 2014).

To assess branch support in the resulting ML and MP trees, 1,000 bootstrap replicates were performed. To calculate average genetic distances between clades and within each clade (bootstrap method: 1,000 replicates), the best-fitting model of base substitution was applied in MEGA6.

The best-fitting site evolution model priors within BEAST were selected according to a model selection run in MEGA6. We ran preliminary tests to examine the performance of strict versus uncorrelated log-normal relaxed clock priors. These preliminary analyses consisted of two independent runs, each for 6,000,000 generations, with sampling every 1,000 generation. We examined posterior density histograms in TRACER v1.6 (Rambaut et al. 2014) and concluded that strict clock priors better suit our data, and subsequently used these clock priors to reconstruct Bayesian phylogeny.

DnaSP v6.10.01 was used (Rozas et al. 2017) for the analyses of nucleotide diversity and tests of neutrality for each clade. The following parameters were obtained: number of used sequences (n), number of haplotypes (h), number of segregating sites (S), haplotype diversity (Hd) with the standard deviation, nucleotide diversity (Pi) with the standard deviation, Tajima's D statistic (Tajima 1989), and Fu's Fs (Fu 1997). The networks of *S. reptans* and *S. reptantoides* haplotypes from DnaSP were drawn in Network v5.0.0.1. (Librado and Rozas 2009). To reduce the number of nodes in the networks, star contraction (Forster et al. 2001) of haplotypes was conducted. The median-joining algorithm (Bandelt et al. 1999) was preformed to calculate the network.

Results

Using the Lechthaler and Car (2005) identification key for morphological taxonomic identification, all sampled specimens were identified as *S. reptans*. However, barcoding of these individuals revealed that two species (*S. reptans* and *S. reptantoides*) were present among the identified material. Identification was then repeated using keys by

Table 2. Five nucleotide substitution models that best fit the input data.

Model		BIC	lnL
T92+G	Tamura 3-parameter	7364.018442	-2643.969915
T92+G+I	Tamura 3-parameter	7372.132269	-2642.563464
HKY+G	Hasegawa-Kishino-Yano	7373.999596	-2638.033763
HKY+G+I	Hasegawa-Kishino-Yano	7381.914365	-2636.527782
TN93+G	Tamura-Nei	7384.845828	-2637.993514

Edwards (1920), Knoz (1965) and Day et al. (2008). After this revision, both species were morphologically identified. In the analysed material from all 12 localities, *S. reptantoides* made up 73% of the specimens, and morphological and genetic identification coincided 100%.

All retrieved sequences had lengths ranging from 453 bp to 606 bp. The Tamura 3-parameter model with the gamma distribution of variation between the nucleotide positions (Tamura 1992) fitted our collection of samples the best, as it had the lowest BIC score (Table 2).

The topology of the phylogenetic tree for *S. reptans* and *S. reptantoides* involves seven clades (Fig. 2). The names for the clades (A and B) are given with respect to previous studies (Kúdela et al. 2014).

The Bayesian phylogenetic tree (Fig. 2) consisted of two highly supported monophyletic branches (with BI > 0.99) of *S. reptans* and *S. reptantoides*. One branch consisted of the clades *S. reptans* A and *S. reptans* B. The second branch consisted of *S. reptantoides* A and *S. reptantoides* B. Samples from the Balkan Peninsula occurred within three clades: *S. reptans* B, *S. reptantoides* A, and *S. reptantoides* B.

Nucleotide diversity within the monophyletic clades ranged from 0.50% within *S. reptantoides* B to 0.70% within *S. reptans* A (Table 3). The COI gene revealed a higher haplotype diversity (0.949) within the clade *S. reptantoides* B, while the lowest diversity (0.663) was detected within *S. reptans* B. The highest number (27) of haplotypes was also found in *S. reptantoides* B (Table 3). The negative values of Tajima's D and Fu's Fs (observed in all clades) indicate low nucleotide diversity but high haplotype diversity.

The interclade divergence for the COI sequence of *S. reptans* and *S. reptantoides* ranged from 1.43% (*S. reptantoides* A vs. *S. reptantoides* B) to 7.94% (*S. reptans* A vs. *S. reptantoides* A) (Table 4). Clades within species showed genetic distances that were 2.31% for *S. reptans* and 1.43% for *S. reptantoides* (Table 4).

A total of 18 haplotypes of *S. reptans* were recognised in DnaSP (Table 3). After applying the star contraction method, the number of haplotypes was reduced to eleven. The minimum distance between haplotypes of *S. reptans* A and *S. reptans* B was seven mutation events. The overall lowest number of mutations (only one) was recorded between two haplotypes of the *S. reptans* A clade. All sequences were grouped in one haplotype except sequence number EU025945. The highest number of mutations in *S. reptans* B clade (nine) was found between haplotype 8B and haplotypes 2B, 3B, and 4B (Fig. 3).

A total of 33 haplotypes of *S. reptantoides* was recognised in DnaSP (Table 3). After applying the star contraction method, the number of haplotypes was reduced

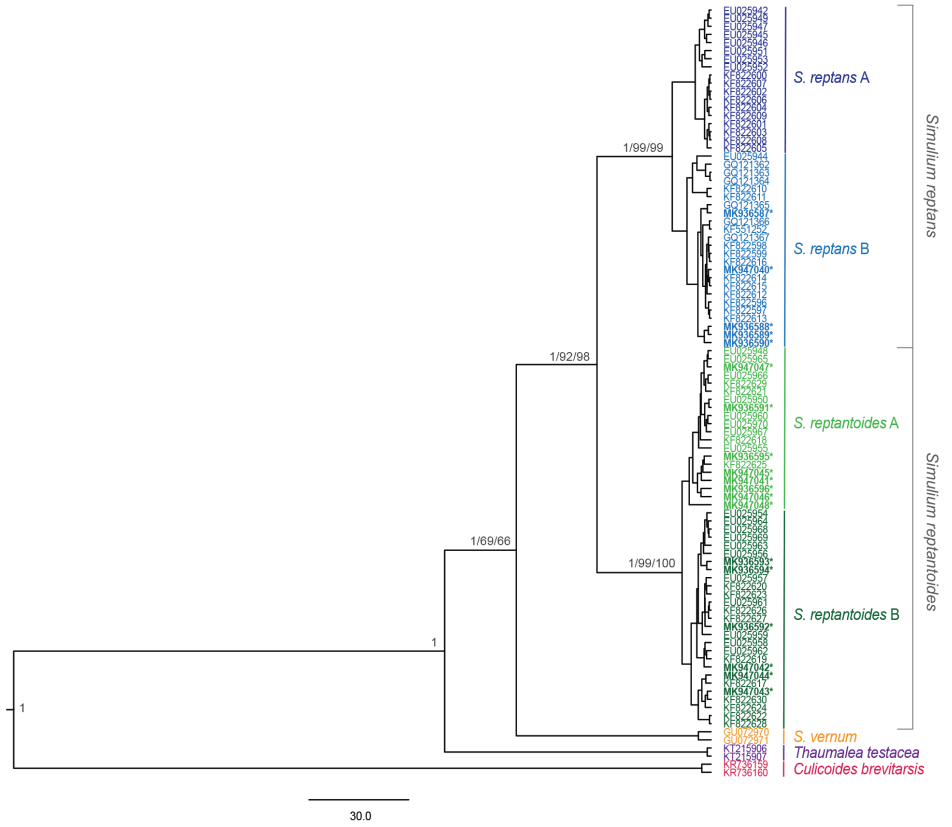

Figure 2. Bayesian phylogenetic tree based on the COI gene of two species, *S. reptans* and *S. reptantoides*. Species *S. vernum*, *Culicoides brevitarsis* and *Thaumalea testacea* were used as outgroups. Numbers above the branches represent posterior BA probabilities followed by ML and MP > 50% bootstrap support. Sequences (tree leaves) are given as GenBank accession numbers. Sequences in bold type with asterisks at the end of the accession number were obtained in this study. The colours of the clades are given according to the species and forms.

Table 3. Nucleotide diversity calculations and tests of neutrality; n – number of sequences, h – number of haplotypes, S – number of segregating sites, Hd – haplotype diversity ± standard deviation, Pi – nucleotide diversity ± standard deviation, Tajima's D test and Fu's Fs test.

Clades	n	h	S	Hd	Pi	Tajima's D	Fu's Fs
S. reptans A	18	9	20/453	0.797±0.090	0.00698±0.00252	-1.88682*	-1.912
S. reptans B	24	9	14/418	0.663±0.107	0.00667±0.00171	-1.07936	-1.485
S. reptantoides A	20	14	19/487	0.889±0.068	0.00631±0.00112	-1.72802	-8.315
S. reptantoides B	27	19	19/544	0.949±0.032	0.00500±0.00057	-1.79156	-16.054

Note: Statistical significance: *, p < 0.05

to 16 (Fig. 4). The minimum distance between haplotypes of *S. reptantoides* A and *S. reptantoides* B was three mutations. *Simulium reptantoides* A clade has five different haplotypes while the *S. reptantoides* B clade has 11.

Table 4. Evolutionary divergence between clades based on the pairwise analysis of COI sequences.

Clades	1.	2.	3.	4.
1. *Simulium reptans* A				
2. *Simulium reptans* B	0.0231			
3. *Simulium reptantoides* A	0.0794	0.0738		
4. *Simulium reptantoides* B	0.0775	0.0792	0.0143	

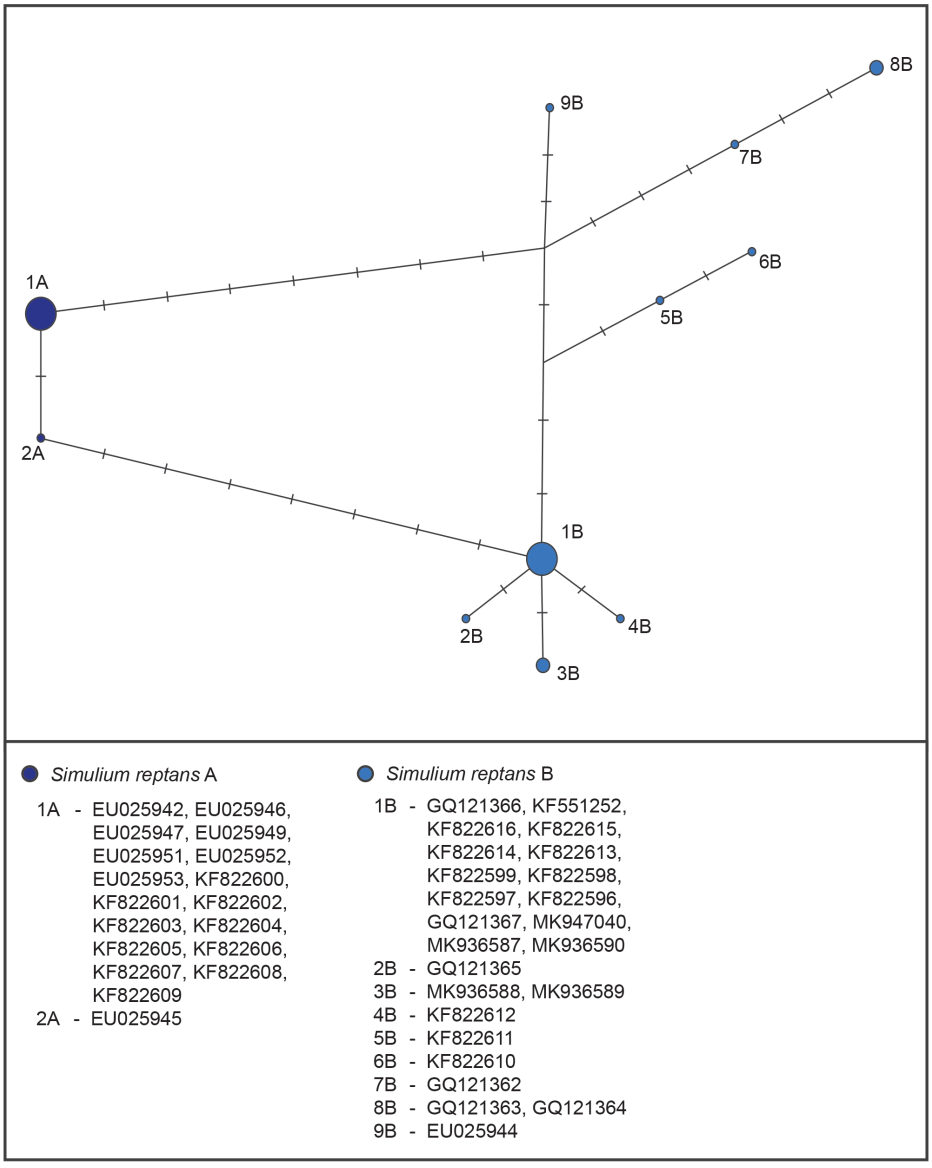

Figure 3. Haplotype network obtained from *S. reptans* mtCOI gene sequences using Network (Librado & Rozas, 2009). Circle sizes are proportional to the haplotype frequency. Colours and clade names correspond to the phylogenetic tree.

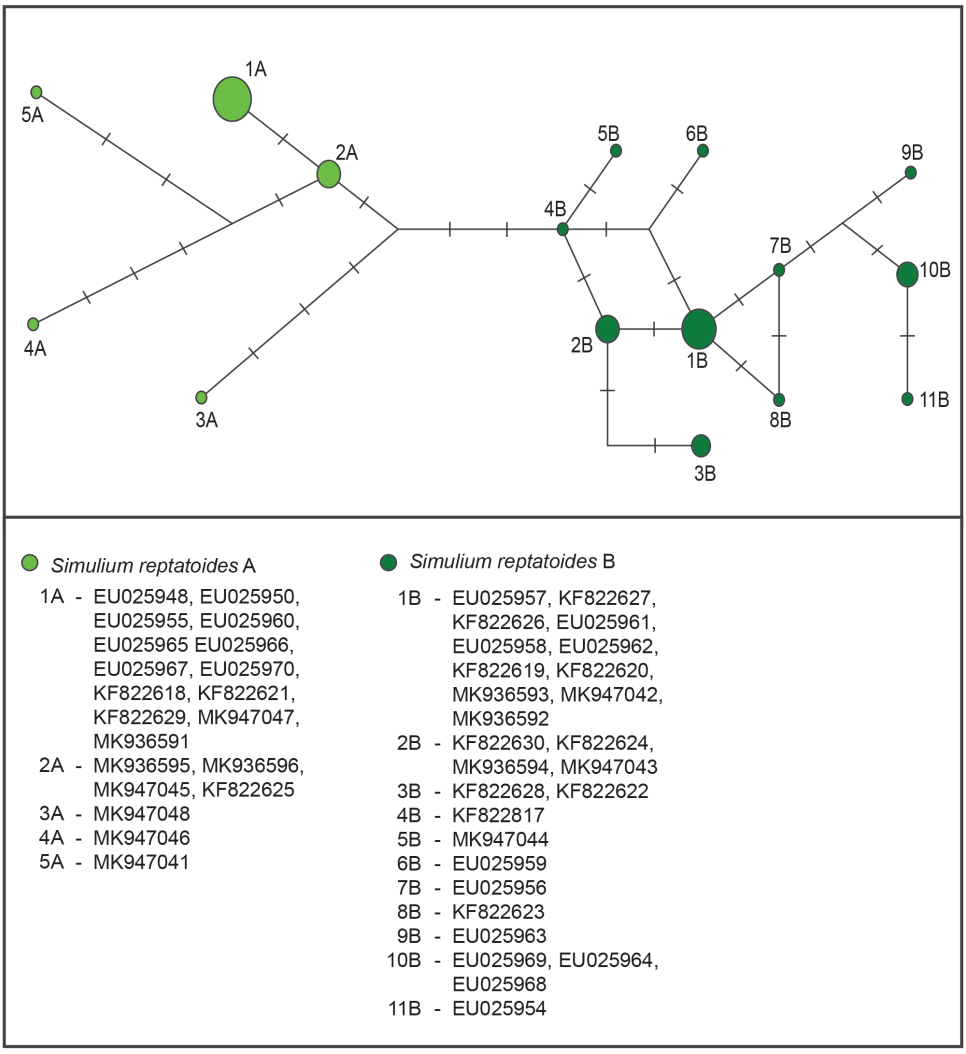

Figure 4. Haplotype network obtained from *S. reptantoides* mtCOI gene sequences using Network (Librado & Rozas, 2009). Circle sizes are proportional to haplotype frequency. Colours and clade names correspond to the phylogenetic tree.

Discussion

Phylogenetic analyses of sequences from samples of the *Simulium reptans* group revealed the presence of two major branches with four well-distinguished clades. Two branches represent previously defined species, *S. reptans* and *S. reptantoides* (Edwards 1920; Knoz 1965; Day et al. 2008). The divergence between them (7.38–7.94%) confirmed the existence of two species. According to previous studies (Rivera and Currie 2009; Hernández-Triana et al. 2012; Đuknić et al. 2019), genetic divergences in the

range of 2.83–15.33% suggest the existence of different species, while genetic divergences in the range of 0–3.84% suggest intraspecific differences.

The typology of trees using different methods (ML, MP and Bayesian) showed the same position of the main clades, with high bootstrap values. We explain above the Bayesian tree topology. The positions of some lineages within these clades differed among the ML, MP and Bayesian phylogenetic trees. However, these differences do not have high bootstrap support and need to be analysed further.

Each species consisted of two clades that represented different molecular forms, A and B. The existence of these forms was described by Day et al. (2008) and Kúdela et al. (2014), and no new forms were defined within samples from the Balkan Peninsula. The interclade divergences for the COI sequence of these two forms in *S. reptans* (2.31%) and *S. reptantoides* (1.43%) were insufficient to consider them as different species. However, these percentages suggest a high intraspecific variability in both species. The high variability could be related to wide distribution.

According to the latest inventory list, *S. reptans* is present in some Balkan countries, including Bosnia and Herzegovina, Greece, North Macedonia, Montenegro and Serbia. Kúdela et al. (2014) showed that the *S. reptans* A form occurs only in the UK and Sweden, while *S. reptans* B, although it is present in the UK and Sweden as well, albeit with infrequent findings, is mainly distributed in central Europe and the Baltic area. Our results revealed the presence of the *S. reptans* B form in the Balkans as well. One haplotype (3B) was found exclusively in Balkan samples (Croatia), while another (1B) was found in both Balkan samples (Slovenia and North Macedonia) and in Slovakia and Lithuania. We confirmed the low variability in the *S. reptans* A form (with only two haplotypes present and only one mutational step difference between them) and its restricted distribution in western and northern Europe. According to our results and with the inclusion of all the samples from the Balkan Peninsula, the *S. reptans* B form demonstrated a wider distribution than was previously known.

Simulium reptantoides was originally described by Carlsson from an unspecified European country; thus, its type locality is unknown (Adler 2019). The species was subsequently confirmed from Britain and Slovakia (Kúdela et al. 2014). Although some rare and sporadic findings of *S. reptantoides* exist, they are mostly limited to the northern Balkan area, the Danube and the Sava rivers in Croatia (Ivković et al. 2016) and the Danube drainage system (Jedlička and Seitz 2008). In the study of Kúdela et al. (2014), *S. reptantoides* was limited to the UK (predominantly the A form) and central Europe (predominantly the B form). Our research showed a uniform distribution of both forms throughout Europe, from the UK, through Slovakia, to the Balkan Peninsula (Slovenia, Serbia, Bosnia and Herzegovina, Montenegro and Bulgaria). Both forms were found at the same sampling site, overlapping at all life stages. Furthermore, haplotype diversity was higher than the one observed in *S. reptans*. The samples collected from the Balkan Peninsula appeared as the most basal within the *S. reptantoides* A form, while being interspersed within the B form clade. This points to the importance of the Balkan Peninsula as a potential place of origin for clade A, but also as a place of high simuliid genetic diversity.

Conclusions

With the use of molecular barcoding, this study confirmed the presence of *S. reptans* throughout the Balkans and revealed that *S. reptantoides* is more widely distributed and has a higher frequency of occurrence in the Balkans than *S. reptans*. Based on previous studies (Day et al. 2008; Bernotienė and Stunžėnas 2009; Kúdela et al. 2014), we established a wider distribution for both species. The genetic variation of *S. reptans* and *S. reptantoides* suggests the existence of different forms (A and B). This study showed that in the Balkans, only one form of *S. reptans* is present (form B), while *S. reptantoides* occurs in both forms (A and B).

The presence of *S. reptantoides* on the Balkan Peninsula indicates that some previous findings were misidentified or synonymised. Further analyses are needed in order to precisely delimit the distribution of this species and to explain the high intraspecific variability.

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Supplementary material 1

The COI gene sequences for *S. reptans* and *S. reptantoides* downloaded from GenBank

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Data type: table

Explanation note: Sequence downloaded from GenBank, Author of the sequence and Country where the original material was collected.

Link: https://doi.org/10.3897/zookeys.922.49306.suppl1