The family Epimetopidae (Coleoptera: Hydrophiloidea): review of current knowledge, genus-level phylogeny, and taxonomic revision of Eupotemus

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Abstract. Epimetopidae are a small beetle family of the superfamily Hydrophiloidea, comprising 72 described species in three genera: the American Epimetopus Lacordaire, 1854 (56 species), Asian Eumetopus Balfour-Browne, 1949 (eight species) and African Eupotemus Ji & Jäch, 1998 (eight species, of which six are described as new here). In this study we illustrate and compare the adult morphology of all three genera and generate the first DNA sequences for Eumetopus and Eupotemus. The morphological data and sequences of four genes (cox1, 16S, 18S and 28S) are used to reconstruct phylogenetic relationships among genera. Both strongly support the monophyly of Epimetopidae, reveal Eumetopus as the earliest diverging taxon and Epimetopus + Eupotemus as a strongly supported clade with numerous synapomorphies. The reciprocal monophyly of Epimetopus and Eupotemus is strongly supported by DNA data but not in the morphological analysis which reveals Epimetopus paraphyletic. Eumetopus, despite being the earliest branching clade, is characterized by many unique derived structures, e.g. by the presence of the sperm pump in males (unique in Hydrophiloidea). The available data on the biology of Epimetopidae indicate that most species inhabit sandy to muddy margins of streams or rivers. Females of all three genera carry egg cases; Epimetopidae hence are one of three independent lineages of Hydrophiloidea in which this behavior evolved. Larvae are only known for Epimetopus and are characterized by morphological adaptations for feeding by piercing and sucking, a closed tracheal system and abdominal gills; larvae of Eumetopus and Eupotemus remain unknown and further research is needed to confirm whether they show the same adaptations as Epimetopus. The taxonomy of the African genus Eupotemus is revised, with six species described as new: E. bilobatus sp. nov. (Nigeria), E. cameroonensis sp. nov. (Cameroon), E. ophioglossus sp. nov. (Gabon, Togo), E. smithi sp. nov. (Côte d’Ivoire), E. taiamus sp. nov. (Côte d’Ivoire) and E. uluguru sp. nov. (Tanzania). Eupotemus limicola Delève, 1967 is fixed as the type species of the genus according to ICZN (1999: Art. 70.3).

Accepted: 10th January 2021
Published online: 3rd February 2021
of two specimens of the *E. costatus* group from Zambia and Saudi Arabia are considered to result from either accidental introductions or mislabelling.

**Key words.** Coleoptera, Hydrophiloidea, Epimetopidae, Georissidae, biology, DNA, morphology, new records, new species, phylogeny, revision, systematics, type species, Africa, Asia

**Introduction**

The beetle superfamily Hydrophiloidea (*sensu stricto*, i.e. without histeroid families; *Hansén* 1991, 1999) consists of six families. One of them, the Hydrophilidae, contains the largest part of the diversity in terms of number of species, morphology and lifestyles. It contains nearly 3000 described species (*Short & Fikáček* 2011, *Short* 2018) with body size ranging from less than 1 mm to nearly 50 mm (*Hansén* 1987, *Fikáček* 2019a), which can be found in a diverse array of habitats, such as running and standing waters, seepages, moist shore habitats, forest leaf litter, animal faeces, ant and termite nests or even flowers (*e.g.*, *Bloom* et al. 2014, *Minoshima* et al. 2018). Compared to the diversity of Hydrophilidae, the remaining five families (Helophoridae, Epimetopidae, Georissidae, Hydrochidae and Spercheidae) may appear less attractive for evolutionary study. They contain far fewer species: ca. 200 in Helophoridae and Hydrochidae, but as few as 18 in Spercheidae (*e.g.*, *Short* 2018, *Nasserzadeh* et al. 2019, *Perkins* 2020). Each family is rather uniform in external morphology, giving the feeling that ‘if you have seen one species, you have seen them all’. Their lifestyle is also rather uniform – representatives of all these smaller families are aquatic or riparian, mostly inhabiting standing waters or marginal habitats of streams and rivers, even though rare exceptions are known (*e.g.*, terrestrial species of Helophoridae and Georissidae; *Angus* 1973, *Fikáček* 2012). Yet, the studies of these small families are crucial. They represent ancient lineages of Hydrophiloidea which have evolved independently from other lineages for about 2000 in Helophoridae and Hydrochidae, but as few as 18 in Spercheidae (*e.g.*, *Short* 2018, *Nasserzadeh* et al. 2019, *Perkins* 2020). Each family is rather uniform in external morphology, giving the feeling that ‘if you have seen one species, you have seen them all’. Their lifestyle is also rather uniform – representatives of all these smaller families are aquatic or riparian, mostly inhabiting standing waters or marginal habitats of streams and rivers, even though rare exceptions are known (*e.g.*, terrestrial species of Helophoridae and Georissidae; *Angus* 1973, *Fikáček* 2012). Yet, the studies of these small families are crucial. They represent ancient lineages of Hydrophiloidea which have evolved independently from other lineages for about the same time as *e.g.* egg-laying and placental mammals (*McKenna* et al. 2019, *Upham* et al. 2019). Understanding the modern diversity, biology and systematics of these small hydropholid families can help us to understand the early evolution of the Hydrophiloidea. Each family also represents a lineage with a unique evolutionary history; their comparison may hence help us to understand why one of the hydrophiloid lineages, the Hydrophilidae, became dominant in terms of species diversity as well as in range of occupied habitats (*Bloom* et al. 2014).

Our knowledge of these small families is unfortunately very limited. The taxonomy was studied in much more detail only for the Helophoridae (*e.g.*, *Smetana* 1985; *Angus* 1999, 2017, 2019; *Angus* et al. 2005, 2014, 2016, 2017, 2019) and Epimetopidae (*e.g.*, *Ji & Jách* 1998, *Perkins* 2012). Although there are studies focusing on smaller regions (*e.g.*, *Satō* 1972, *Angus* 1977, *Watts* 1999, *Worthington* et al. 2016), a comprehensive, worldwide treatment is missing. We also lack studies addressing the internal phylogeny of these families. Molecular data in general remain very limited for all these families, with sequences of few species repeatedly used in larger analyses (*e.g.*, *Short* & *Fikáček* 2013; *McKenna* et al. 2015, 2019), usually only as out-groups. There are only two phylogenetic studies published so far: the morphology-based phylogeny of Helophoridae (*Fikáček* et al. 2012) and the DNA-based phylogeny of the western Palearctic Hydrochidae (*Hidalgo-Galiana & Ribera* 2011). *Fikáček* et al. (2012) revealed that our knowledge is very limited even for usual morphology of Helophoridae, and that the real morphological diversity is actually much higher than expected; the situation in other small families seems similar (*M. Fikáček*, unpubl. data). Similarly, our knowledge on the lifestyles and immature stages is mostly very limited. A notable exception is the family Helophoridae, in which all aspects of biology, larval morphology and lifestyles were studied in much detail (*Angus* 1973, 1999; *Angus* et al. 2016; *Watanabe* et al. 2000; *Minoshima* & *Watanabe* 2020). Larvae are known for few species of the other smaller families only, with detailed descriptions available for part of them (*Archangelsky* 1997, 2001; *Hansén* 2000; *Fikáček* et al. 2011). The biology of these small families remains largely unstudied, and available data are difficult to interpret, since they always refer to a single species. For example, we know that Spercheidae are the only extant filter-feeding beetles both as adults and larvae (*Fikáček* 2019b, *Yee & Kaufmann* 2019), yet the only available analysis of their filter-feeding remains the conference abstract by Rothmeyer & Jách (1986). Similarly, adult *Georissus crenulatus* (Rossi, 1794) were reported to actively camouflage using soil particles (*Bameul* 1989), but it remains unclear whether this behavior is widespread in the family or restricted to few small lineages only (*Fikáček & Falamarzi* 2010, *Litovkin* 2018, *Fikáček* 2019c). More effort is clearly needed in studies of these small and often neglected families as they have potential to discover novel data crucial for understanding the evolution of the hydrophiloid beetles.

This paper is a step forward to a better knowledge on these small families, focusing on the least known of them, the Epimetopidae. It was originally inspired by specimens collected during recent expeditions of the Natural History Museum in London, UK, in western Africa. This material not only yielded additional specimens from Africa, extremely rare in museum collections, but also specimens in DNA-grade quality, and a series of specimens which made it possible to study the morphology of the African

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**Zoobank:** http://zoobank.org/urn:lsid:zoobank.org:pub:9CB2C16A-E2B7-4C17-A310-D538AA061911

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species in detail. Coincidentally, the DNA-grade specimens were also collected in Asia, where epimetooids are also very rare, moreover with good data on biology and even a video of living beetles (see Supplementary File S1). We decided to combine all these new discoveries and include them into a study which presents not only new data, but also summarizes the previous knowledge. We decided to structure the review part of this study in a similar way as the hydrophiloid families chapters in the recently published *Australian Beetles* (Fíkáček 2019a–d). Epimetooidae are absent from Australia and hence from the book, but the similar structure allows for their easier comparison with other hydrophiloid families treated there.

**Material and methods**

*Examined specimens.* Examined specimens are deposited in the following collections:

- BMNH Natural History Museum, London, United Kingdom (M. Barclay, M. Geiser, K. Matsumoto);
- HNMU Hungarian Museum of Natural History, Budapest, Hungary (Gy. Makranczy);
- IBIW Papanin Institute for Biology of Inland Waters, Borok, Russia (A. Prokin, A. Sazhnev);
- IRSNB Institute Royal des Sciences Naturelles de Belgique, Bruxelles, Belgium (P. Limbourg);
- NMPC National Museum, Praha, Czech Republic (J. Hájek, M. Fíkáček, L. Sekerka);
- NHMW Naturhistorisches Museum Wien, Austria (M. A. Jách);
- NMNH Natural History Museum, London, United Kingdom (M. A. Jäch);
- SMF Staatliches Museum für Naturkunde Stuttgart, Germany.

Label data for type specimens are cited verbatim between quotation marks (‘…’); a single slash (/) separates lines within labels; a double slash (//) separates the data of different labels. Label data of non-type specimens are listed in a standardized form. Our comments are added in square brackets [] where necessary.

* Morphological studies.* For studies of general morphology, one or two specimens of selected epimetooid species were cleaned of soft tissues using 10% KOH, bleached in 15% hydrogen peroxide, largely disarticulated. Most body parts were mounted in permanent slides with Euparal resin on a small slide attached below the specimen. Dissected genitalia were first studied and photographed in temporary slides with glycerine or glycerine jelly, and at the end transferred via 95% alcohol to a drop of alcohol-soluble Euparal resin on a small slide attached below the respective specimen. No genitalia were treated with KOH. Photographs were taken in the same way as for morphological studies, i.e. using a Canon macro-lens for habitus photos, and a compound microscope with attached camera for genitalia photos.

Sixty characters were coded for the morphology-based phylogenetic analysis, some of which were adopted from Fíkáček et al. (2012). The characters were selected primarily to reconstruct the relationships among epimetooid genera and are not conclusive for the reconstruction of the relationships among families. Fourteen taxa were included: five species of Epimetooidae, two species of Hydrophilidae, and one species of Hydrochidae, Helphorididae, Georissidae and Spercheidae. *Eper metamopus* seems morphologically much more diverse than other genera (see e.g. Fíkáček et al. 2011, Perkins 2012), hence we included at least two representatives in which we expected different morphology (*E. mendeli* Fíkáček, Barclay & Perkins, 2011 representing the large-sized *E. mendeli* group, and *E. costaricensis* Perkins, 1972 representing the *E. costatus* group characterized by species of minute body size). As outgroup taxa, we used the histeroid genera *Sphaerites* Duftschmid, 1805 (*Sphaeritidae*) and *Sytelia* Westwood, 1864 (*Sytelidae*), and the tree was rooted by a representative of Agyrtidae (*Necrophilus subturrellus* Dahl, 1807). The final dataset is available in Table 1. The following characters were coded:

1. Systematic punctures on dorsal surface: (0) absent; (1) present.
2. Setiferous granules on head: (0) absent; (1) present.
3. Median portion of frontoclypeal suture: (0) grooved; (1) not grooved.
4. Eyes: (0) distinctly protruding laterad; (1) not protruding laterad from the outline of the head.
5. Eyes: (0) without or very weakly emarginate anteriorly; (1) deeply emarginate anteriorly.
6. Narrow postocular bridge: (0) present (Fig. 4E); (1) absent.
7. Distal setae of lacinia: (0) trichoid and/or sickle-shaped; (1) peg-like.
8. Basal portion of maxillary palpomere 4: (0) without digitiform sensilla; (1) with digitiform sensilla.
9. Proportions of mentum (width : length): (0) 1.3 or less; (1) 1.31 or more (Figs 2H–I, P–Q, W, c).
10. Anterior margin of mentum: (0) without long setae; (1) with a transverse row of long setae (Figs 2N, O).
11. Mandibular apex: (0) bidentate (Figs 2M–L); (1) tridentate (Figs 2D, e).
12. Anterior projection of pronotum concealing head: (0) absent; (1) present.
13. Anterior margin of mentum: (0) without long setae; (1) with a transverse row of long setae (Figs 2N, O).
14. Number of antennomeres: (0) seven; (1) eight; (2) nine (Figs 2H–I, Z).
15. Basal portion of maxillary palpomere 4: (0) without digitiform sensilla; (1) with digitiform sensilla (Fig. 2U).
16. Proventriculomeatal orifice: (0) conical, narrower distally than basally; (1) bulbose (spherical to shortly conical; Figs 2H–I, P–Q, W, c, 4H–I).
17. Anterior projection of pronotum concealing head: (0) absent; (1) present.
Table 1. Morphological dataset used for maximum parsimony analysis and character mapping.

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</table>
| FIKÁČEK et al.: Review of the family Epimetopidae (Coleoptera: Hydrophiloidea)  | 19. Ventral surface of pronotum: (0) with set of parallel ridges (Figs 3D, F, H); (1) without set of parallel ridges (Fig. 3B). 20. Surface of pronotum: (0) evenly convex; (1) with depressions, furrows etc. 21. Pronotum dorsally: (0) with two pairs of complete longitudinal ridges; (1) without present anteriorly; (2) with pit-like impressions. 22. Setiferous granules on pronotum: (0) absent; (1) present. 23. Lateral margin of pronotum: (0) smooth; (1) slightly to moderately crenulate; (2) strongly and sharply denticulate. 24. Antennal grooves on anterolateral portion of hypomeron: (0) absent; (1) developed. 25. Proximal portion of prosternum: (0) long, well-developed (longer than half of procoxal cavity); (1) short (at most as long as half of procoxal cavity); (2) extremely reduced. 26. Prosternal process: (0) not widened (Fig. 3C); (1) widened posteriorly between procoxae (Figs 3A, E, G, I). 27. Procoxal cavities: (0) open (Figs 3A, C); (1) closed (Figs 3E, G, I). 28. Scutellar shield: (0) triangular, with acute angle posteriorly; (1) semicircular, rounded posteriorly; (2) in shape of an elongate elevation. 29. Alternate elytral intervals: (0) elevated; (1) not elevated. 30. Elongate tubercles on alternate intervals: (0) absent; (1) present (Fig. 15). 31. Scutellary struts on elytron: (0) absent; (1) present (Fig. 15). 32. High sublateral ridge on ventral surface of elytra: (0) absent; (1) present (Figs 3M–N). 33. Inner pubescent portion of pleurite: (0) absent; (1) present. 34. Mesepsipeterna: (0) abutting mesally (Fig. 5B); (1) not abutting mesally (Figs 3J–K, 5A). 35. Anterior margin of mesoventrite: (0) narrow (Figs 3J–K, 5A); (1) wide. 36. Transverse ridge on mesoventrite: (0) absent; (1) present. 37. Ventral pubescent portion of mesothorax: (0) well developed; (1) present only medially, absent on lateral portions; (2) totally absent. 38. Metaventrite between meso- and metacoxae: (0) shorter than length of mesocoxa (Figs 3J, 5A); (1) at least as long as length of mesocoxa (Figs 3K–L, 5B). 39. Smooth areas and transverse stripes on metaventrite: (0) absent (Figs 3J–K); (1) present (Fig. 3L). 40. Metakatepisternal suture: (0) absent (Fig. 5B); (1) absent or indistinct (Fig. 5A). 41. Metakatepisternum posteriorly: (0) straight; (1) bent inwards (Figs 5A–B). 42. Dense ventral pubescence on metaventrite: (0) present on the whole surface; (1) present only laterally; (2) absent. 43. Wedge cell of hind wing: (0) absent (Figs 5C–D, F); (1) present (Fig. 5E). 44. Anal lobe of hind wing: (0) absent (Fig. 5D); (1) present, small (Figs 5E–F); (2) present, large (Fig. 5C). 45. Dense ventral pubescence on abdomen: (0) absent; (1) present. 46. Middle and hind legs: (0) without scale-like setae; (1) with scale-like setae (Figs 3O, 4P). 47. Trochanter: (0) globular; (1) plate-like. 48. Meso- and metafemora: (0) simple; (1) constricted subapically; (2) with a tooth at midlength (Fig. 4M). 49. Pubescence on basal portions of mesofemora: (0) absent; (1) present only on anterior face of the very base; (2) present on whole base. 50. Tarsal formula: (0) 5–5–5; (1) 4–4–4 (Figs 4N, O). 51. Setation of empodium: (0) bisetose; (1) multisetose; (2) with leaf-like setae (Figs 3P–Q). 52. Egg case: (0) laid in the environment; (1) carried by female (Fig. 5P). 53. Abdominal ventricle I: (0) very short, basically only containing coxal grooves (Figs 5I–K); (1) long, only its short basal part with coxal grooves. 54. Coxal grooves of abdominal ventricle I: (0) not separated medially (Fig. 5I); (1) divided by median carina (Figs 5J–K); (2) divided by median projection of the ventricle. 55. Wing folding asperites on abdominal tergites: (0) IV–V–VII; (1) on all tergites; (2) absent. 56. Sternite IX in male: (0) V- or U-shaped (Figs 6C, K); (1) circular (Fig. 6U); (2) with tongue-like median projection; (3) without median portion (only lateral struts). 57. Sperrm pump: (0) absent; (1) present (Fig. 6Y). 58. Phallobase: (0) short, compressed (Figs D–H, L–R); (1) long, cylindrical (Figs 6V–W). 59. Median lobe: (0) with simple or bifid projection ventrally (Figs 6G–H, P–R); (1) without projection (Figs L–O, X). 60. Parameres: (0) simple; (1) subdivided into two lobes (Fig. 6Z). Molecular data and phylogenetics. Some of the Eupotemus specimens examined were collected recently in 70% ethyl alcohol. The material was not collected or stored for DNA work, but we were allowed to work with the specimens before they were card-mounted and tried to get DNA data from them. At the same time, two of us (AP and AS) collected specimens of Eumetopus acutimomites Ji & Jäch, 1998 in 95% alcohol; we used these specimens for DNA work as well. We used Blood and Tissue Kit (Qiagen, Hilden, Germany) to extract DNA from the sample following the manufacturer’s instructions, except for the incubation time with proteinase K which was 4–5 hours. We tried to amplify seven fragments (mitochondrial: cox1, cox2, 16S; nuclear: 18S rRNA, 28S rRNA, histone 3, topoisomerase I) using the standard primers and PCR programs used in Hydrophilidae studies (see e.g., Fikáček et al. 2020). The success rate was low especially for the Eupotemus specimens likely due to their preservation (collected and stored in low percentage alcohol at room temperature for more than a year). The final dataset hence consists of four
fragments only: coxl, 16S, 18S and 28S. Sanger sequencing was performed by Macrogen Europe (Amsterdam, the Netherlands).

Newly obtained sequences were edited in Geneious (Kearse et al. 2012) and combined and aligned with previously published data as summarized in Table 2. For Epimetopus, we did not have any DNA-grade material at hand and hence used the previously published sequences by Bernhard et al. (2006) (voucher AK-2004) and Short & Fikáček (2013) (voucher SLE0069) for which no species identification was provided; the latter likely belongs to E. thermarum Schwarz & Barber, 1917 (A. Short, pers. comm.). The total length of the concatenated alignment is 2799 bp, consisting of the following gene fragments: coxl (404 bp), 16S (477 bp), 18S (1661 bp), 28S (1121 bp) and 28S (796 bp). The dataset was divided into partitions by genes, coxl sequences were subdivided by codon positions. The phylogenetic reconstruction was conducted using MrBayes 3.2.6 (Ronquist et al. 2012), using four chains of 25 million generations and sampling every 1000th generation. The phylogeny was edited in FigTree 1.4.3 (Ronoquist et al. 2018). The default burn-in setting (25%) was used for constructing the Bayesian maximum credibility tree. The resulting tree was edited in FigTree 1.4.3 (https://github.com/rambaut/figtree/).

Systematics of African species. Eupotemus species are very rare in collections, and although we did our best to study all known specimens, the examined material is very limited. Series of more than three specimens are only known for three species, and no species is known from more than two localities, in some cases moreover very close ones. This made it very difficult to evaluate which differences represent diagnostic characters and which are to be regarded as intraspecific variability. Examination of species available in multiple specimens from the same locality revealed that the dorsal sculpture varies a lot in the shape of the lateral pronotal lobes as well as in the form of elytral ridges (which may be lower or higher and complete or more or less interrupted into a series of elongate tubercles) in conspecific specimens from the same locality. We hence decided not to base species diagnoses on external morphology and focus on male genitalia only. These differ largely between both species groups but are rather uniform within each group. The situation was especially unclear in the case of E. limicola, E. ophioglossus and E. smithi which differ in the shape of the ventral fork of the median lobe. We originally considered this as an intraspecific variability possibly connected to geography, but we changed our opinion after the discovery of the same shape in specimens described below as E. ophioglossus from two localities more than 1000 km apart, one in Togo and the other in Gabon. In addition, one of the species diagnosed by the shape of the aedeagus fork, E. smithi, differs from all other species of the E. limicola group in the form of the elytral ridges (and is the only species which can be diagnosed by a non-genital character). We hence consider the shape of the ventral fork of the median lobe as species-specific and based the species limits on this character. The resulting taxonomic strategy is hence a splitting one in both species groups, considering any clear difference of the aedeagus morphology as species-specific. Additional material, ideally combined with species- and population-level DNA data, is needed to test our approach.

Review of the family Epimetopidae


Adult morphology. Length 1.2–4.3 mm. Body about 1.7–2.3 times as long as wide, sides not evenly rounded (lateral margin of pronotum and elytra does not form a continuous line), body well sclerotized, moderately convex; color yellowish brown to pitchy black, sometimes (some Epimetopus) with paler spots on elytra (e.g. Fig. 1A), sometimes (some Eumetopus) with weak dorsal metallic sheen (Figs 14–15); dorsal surface at least partly tuberculate (with all or some of the granules bearing a very

Table 2. GenBank accession numbers of Epimetopidae sequences newly generated for this study (in bold) and those used for the Bayesian phylogenetic analysis (coxl, 16S, 18S and 28S). Voucher numbers are only indicated for Epimetopidae specimens.

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short apical sensillum) and often costate; ventral surface without hydrofuge pubescence.

Head moderately to strongly declined, largely covered by anterior lobe of pronotum in dorsal view. Eyes well developed, slightly protuberant, subdivided into dorsal and ventral part anteriorly by a clypeal projection (*Eumetopus*, *Eupotemus*, most *Epimetopus*; Fig. 4A) or completely divided into dorsal and ventral portion by clypeal projection meeting projection of vertex (*Eumetopus trogoides* group); eyes coarsely faceted, without interfacetal setae. Antennal insertions not exposed from above, covered by lateral portions of clypeus; subantennal groove absent. Frontoclypeal and mid-cranial sutures impressed (*Epimetopus* and *Eupotemus*) or indistinct (*Eumetopus*); clypeus large, rounded to subangular anteriorly, with an additional ridge delimiting a narrow anterior semivertical portion in *Eupotemus* and *Eumetopus* (Figs 4B–C). Labrum transverse, well sclerotized, exposed in dorsal view.
(Figs 4B–C), arcuate or bisinuate on anterior margin (Figs 2A–B, J–K, R, g–i). Antennae (Figs 2H, P, W, c, 4H–I) moderately long, weakly geniculate, 9-segmented, with antennomeres 1–6 glabrous and with 3-segmented pubescent club; scapus very long (longer than antennomeres 2–9 combined), pedicel short, bulbose; antennomere preceding antennal club cup-like. Mandibles (Figs 2C, L, S, Y) large and partly concealed beneath clypeus and labrum; apex bidentate (Eumetopus) or tridentate (Epimetopus, Eumetopus); mola well-developed and asymmetrical; prostheca well-developed, membranous, pubescent and not articulated. Maxilla (Figs 2E, M, T, Z) with narrowly projecting, partly sclerotized lacinia apically bearing stout spines; galea short and wide, sclerotized basally, apically membranous with series of long curved setae; maxillary palps slender, relatively short, ca. as long as antennal scapus, consisting of four palpomeres. Palpomere 1 minute, palpomeres 2 and 4 subequal in length, palpomere 3 ca. third to half the length of palpomere 4; palpomere 4 fusiform, weakly to strongly asymmetrical, basally with a series of digitiform sensilla (Fig. 2U). Mentum subpenisiform, weakly to strongly asymmetrical, basally with 3 ca. third to half the length of palpomere 4; palpomere 4 nute, palpomeres 2 and 4 subequal in length, palpomere 4 elongate, without spines (Fig. 4J). Gular sutures confluent except at posterior end (Fig. 4E), posterior tentorial pits confluent. Cervical sclerites present. Pronotum about 0.9–1.0 times as long as wide, widest in anterior third to half; base of pronotum narrower than combined elytral bases; sides with two projections at each side, anterior one larger, subquadrate to multilobate in shape, posterior one smaller, tuberculate to spiniform or completely absent; anterior third (Eumetopus, Epimetopus) to half (Epimetopus) represented by a ‘hood’ largely covering the head, ventral surface of the hood with a set of longitudinal ridges (Eumetopus, Epimetopus; Figs 3D, F, H) or with mesh-like tuberculate sculpture (Eumetopus; Fig. 3B). Dorsal surface with setiferous tubercles, and with two pairs of longitudinal elevated costae which are complete or nearly so (Eumetopus, most Epimetopus; Figs 9, 10, 12, 16A) or partly (some Epimetopus; Figs 16D–F) or largely reduced (Eumetopus, only very anterior part of mesal pair present, lateral ones totally absent; Fig. 14). Lateral pronotal carinae complete and simple, situated venrally; anterior angles absent; posterior angles rounded, not embracing elytral bases; posterior edge arcuate, without ventral ridge interlocking with elytra and scutellar shield. Prosternum (Figs 3A, C, E, G) well-developed, exposed, shorter than shortest diameter of procoxal cavity, without (Epimetopus, Eumetopus) or with (Eumetopus) very weakly developed median carina, anterior margin straight. Prosternal process present, widened posteriorly, largely concealed by procoxae (Eumetopus, Eumetopus) or enlarged and exposed behind procoxae (Epimetopus). Notosternal sutures present, straight. Hypomeron not divided into shiny lateral and pubescent mesal portions; without anterior groove for reception of antennal club. Procoxal cavities transverse, contiguous, partly open internally, externally open (Eumetopus, Eumetopus; Figs 3A, C) or closed by an extension of hypomeron (Epimetopus; Figs 3E, G, I), without (most species) or with (some Epimetopus) narrow anterolateral extension. Scutellar shield minute, subtriangular, as wide as long, or longer than wide (Fig. 5H). Elytra about 1.1–1.4 times as long as combined width and 1.4–2.4 times as long as pronotum; sides moderately curved, apices conjointly rounded; humeri well-developed; disc with ten puncture rows, with (Eumetopus) or without (Eupotemus, Epimetopus) scutellar stria, alternate elytral intervals (1, 3, 5, and 7) with rows of elongate tubercles which are always separate (Eumetopus; Fig. 15) or partly to completely fused in elevated ridges (Eupotemus, Eumetopus; Figs 9, 10, 12, 16); side margin of elytron denticulate; epipleura present, relatively wide throughout including apex (Figs 5A–B); ventral face with elevated bar anterolaterally (Figs 3M–N). Mesoventrite (Figs 3J–L) separated by complete sutures from mesonepisterna, anterior portion of mesoventrite on different plane than metaventrite; without defined prococoxal rests; posteroventral portion with elevated transverse or arcuately transverse ridge; mesoventral cavity absent; discriment absent. Mesaneopisterna narrowly separated from each other anteriorly (most species; Figs 3J–K) or contiguous (some Epimetopus; Fig. 5B). Mesocoacal cavities subcircular, narrowly separated, closed laterally by mesepimeron (Figs 5A–B). Mesofurca well developed, its arms widely separated basally, slightly widened apically, without narrow extension projecting dorsilaterally. Metaventrite distinctly transverse, flat to slightly convex, uniformly tuberculate (Epimetopus; Fig. 3K), with posteroventral transverse ridge (Eupotemus; Fig. 3J) or with basal ridges and central elevation (Eupotemus; Fig. 3L); anteromesally with long projection separating mesocoxae; discriment reduced, transverse (metakatepisternal) suture well developed (Epimetopus; Fig. 5B), weakly developed (Eumetopus) or obsolete (Eumetopus; Fig. 5A); metaneopisternum exposed ventrally, wide throughout, arcuate in shape (Figs 5A–B). Metacoxae massive, transverse, widely separated by narrowly bifurcate posterior process of metaventrite, laterally meeting metaneopisternum, not reaching elytra (Figs 5A–B). Metendonsterne with short wide stalk, long lateral arms and short but distinct anterior tendons. Hind wing well-developed (Figs 5C–F), or in some species/populations reduced in size (brachypterous); when fully developed, wing narrowly elongate with apical field forming apical half of wing area; ScA and RA reaching nearly wing base, radial cell weakly unpigmented, RP not developed basally, proximally joint with MP and forming the R-M loop, veins posterior of R-M loop weakly sclerotized: basal cell present; wedge cell absent (Eumetopus, Eupotemus, some Epimetopus) or present (some Epimetopus); anal lobe absent (Eupotemus) or present, minute (Epimetopus) or long and narrow (Eumetopus); wing margin with long, sparsely arranged setae. Legs. Protrochantins concealed. Procoxae large, conical; meso- and metacoxae transverse. Trochanters well-developed, sometimes plate-like (some Epimetopus). Femora subcylindrical, strongly widened at mid-length, meso- and metafemora sometimes with posterior spine (Eumetopus; Fig. 4M); femoral base oblique, anteromesal portion of femur
contacting trochanter. Trochanters and femora bare (Epimetopus, Eupotemus) or with scale-like sensilla (Eumetopus; Fig. 3O). Tibiae (Figs 4P–R) cylindrical, with longitudinal rows of strong spines or plate-like setae, laterally strongly denticulate in some species, without swimming hairs, tibial apex obliquely cut off, tarsus attached mesally; tibial spurs short, indistinct. Tarsal formula 5-5-5 in most species (Eumetopus, Eupotemus, most Epimetopus; Fig. 4L) or 4-4-4 (Epimetopus costatus group; Figs 4N–O); tarsomeres simple, tarsomere 1 small or absent, tarsomeres 2–4 subequal in length; pretarsal claws simple, arcuate; empodium small, with a single wide and long leaf-like seta (Figs 3P–Q).
metopus mendeli* Fikáček, Barclay & Perkins, 2011; N–O – *Epinotopus costaricensis* Perkins, 1979. A – head in dorsolateral view (can – clypeal canthus causing the eye emargination); B–C – head in dorsal view (arrow – the ridge dividing anterior declined part of clypeus); D – mentum and maxilla; E – head in ventral view; F–G – occipital part of the head with median raised tubercle, dorsolateral view (arrows: parallel impressions corresponding to ventral ridges of pronotal hood); H–I – antenna, scapus largely omitted; J – labial palp; K – apical tibial armature, ventral view, mesothoracic leg; L – apical tibial armature and tarsus, ventral view, metathoracic leg; M – mesotibia; N–O – tarsus (N – posterior; O – anterior); P–R – metatibia, dorsal view. Not to scale.
Abdomen with five free ventrites (Figs 5I–K); ventrite 1 very short, completely or nearly completely occupied by metacoxal grooves divided medially (Epimetopus, Eupotemus) or not (Eumetopus), free portion without median carina; intercoxal process absent; ventrites 2–5 subequal in length, bare or with fine microsculpture (some Epimetopus), lacking hydrophuge pubescence; posterior margin of ventrite 5 simple, without emargination or stout setae. The shape and surface sculpture of ventrites II–III are sexually dimorphic in some Epimetopus, with slightly elevated median ridge and/or mesally reduced microsculpture in females (PERKINS 2012). Functional spiracles on abdominal segments I–VI; abdominal tergites relatively lightly sclerotised, each (Epimetopus) or only IV–VII (Eumetopus, Eupotemus) with patches of wing-folding asperities. Anterior edge of male sternite VIII without median strut (Figs 6A, I, S). Segment IX in male U-shaped asperites. Anterior edge of male sternite VIII without mesally in males in some groups; PKİlış et al. 2012). Functional spiracles on abdominal segments I–VI; abdominal tergites relatively lightly sclerotised, each (Epimetopus) or only IV–VII (Eumetopus, Eupotemus) with patches of wing-folding asperities. Anterior edge of male sternite VIII without median strut (Figs 6A, I, S). Segment IX in male U-shaped asperites. Anterior edge of male sternite VIII without mesally in males in some groups; PKİlış et al. 2012).

We refer to these studies for illustrations and character discussion. Larvae of Epimetopus form two groups: ‘short-headed’ with one pair of abdominal gills, and ‘long-headed’ with two pairs of abdominal gills. The abdominal gills were confused with urogomphi and considered segmented by some authors, as discussed in detail by FİKAlexander et al. (2011). Here, we provide a morphological diagnosis of Epimetopus larvae in the format compatible to that used in the hydrophiloid chapters of Australian Beetles to facilitate the comparison with other hydrophiloid families.

Epimetopus larvae: Body elongate, nearly parallel-sided; head and protergum well sclerotized, meso- and metathorax (or mesothorax only) with a pair of triangular sclerites; abdomen weakly sclerotized, without tergites; lateral projections absent on thorax, present on abdomen. Head hyperprognathous, slightly longer than wide in some species (ARCHANGELSKY 1997, FİKAlexander et al. 2011), transverse and much wider than long in others (ROCHA 1967, 1969, COSTA et al. 1988), with parallel sides; epicranial stem absent; frontal arms U-shaped with bases reaching posterior margin of head; median endocarina absent. Each side of head with one ocular spot formed by fused stemmata. Frontoclypeal suture absent; labrum fused to head capsule and forming clypeolabrum; clypeolabrum with median narrow projection subquadrate apically (nasale) and with large symmetrical paired adnasalia (= epistomal lobes); adnasalia with denticulate inner margin and with membranous ciliate lateral portions, on inner face bearing few wide flat setae with ciliate inner margin (these are possibly absent in the larvae with short head: ROCHA 1967, 1969). Antennae well developed, 3-segmented; antennomere 2 longest, with laterally placed single sensornum. Mandibles symmetrical, moderately broad at base, with narrow, strongly curved and undentate apex, each with two highly modified retinacular teeth and a groove dorsally between them, going towards mandibular base; basal tooth anvil-shaped, with numerous projections directed mesad (? prostheca); basal penicillus present. Ventral mouthparts protraced, maxillary articulating area present, membranous, with two small sclerites; maxilla hexamorous, with segment-like palpifer (= palpomere 1 sensu ARCHANGELSKY 1997); cardines distinct, large; stipes long. Massive cylindrical palpifer (= palpomere 1 sensu ARCHANGELSKY 1997) long and cylindrical; galea (= inner appendage) membranous, slightly projecting; lacinia absent; palps 3-segmented (4-segmented if palpifer is considered as part of palpus, see ARCHANGELSKY 1997). Labium consisting of prementum and postmentum; palps 2-segmented; ligula absent. Ventral tentorial pits separated, situated anteriorly, gular sutures absent. Thoracic segments subequal in length; prothorax with single tergal plate divided by median ec dysial line; meso- and metatergum with a pair of separated sclerites (may be absent on metaventrite). Prothoracic venter with two pairs of sclerites submesally, not sclerotized mesally (FİKAlexander et al. 2011). Legs 5-segmented, with a distinct and long claw-like pretarsus; procoxae nearly contiguous, meso- and metacoxae separated (FİKAlexander et al. 2011). Abdominal segments I–IX lightly sclerotised, without distinct sclerites; segments VIII–IX, or only segment IX, with...
long unsegmented lateral projections (gills); abdominal sternum without prolegs, with transverse rows of asperities on segments II–VII. Abdominal apex without spiracular atrium, segment VIII not terminal, tergum IX completely visible with 1-segmented urogomphi, segment X terminal. Segment IX in some species with a pair of ventral papillae (Fikáček et al. 2011). Spiracles small and likely non-functional (Fikáček et al. 2011, Rodriguez et al. 2020), present on mesothorax and abdominal segments I–VIII.

**Diversity and distribution.** Epimetopidae contain 72 described species classified in three genera: the Asian *Eumetopus* Balfour-Browne, 1949 (8 species), African *Eupotemus* Ji & Jäch, 1998 (8 species) and the most diverse *Epimetopus* Lacordaire, 1854 (56 species) distributed in...
Central and South America and southwestern North America. The records of *Epimetopus* from Africa and the Arabian Peninsula (see below) are either accidental introductions or mislabelled specimens. A list of the known species and references to identification literature are given below under each genus.

**Phylogenetic position and age.** The phylogenetic position of Epimetopidae in the Hydrophiloida is not properly understood so far. Phylogenetic studies based on morphology of adults and larvae usually reveal the clade of Epimetopidae + Georissidae, which is either a part of the so-called ‘helophorid lineage’ together with Helophoridae (Archangelsky 1998, Beutel & Leschen 2005, Fikáček et al. 2012) or Helophoridae and Hydrochidae (Hansen 1991, Bernhard et al. 2009), or stands close to Hydrophilidae (Beutel 1994, 1999; Beutel & Komarek 2004; Fikáček et al. 2012). The following unique synapomorphies were revealed for...
Epimetopidae + Georissidae: bulbous antennal pedicel, pronotum projecting anteriorly to cover the head, sublateral ridge on ventral surface of the elytron, absence of ventral hydrophuge pubescence and highly reduced meso- and metafurca in adults (Beutel & Komarek 2004, Bernhard et al. 2009, Fikáček et al. 2012; the reduction of meso- and metafurca in Epimetopidae was not confirmed in this study), and membranous ciliate lateral portion of epistomal lobes and straight submental suture in larvae (Fikáček et al. 2011, 2012; Fikáček 2019c). The morphology-based analysis performed here also strongly supports the sister relationship of Epimetopidae and Georissidae and revealed two previously undetected unique synapomorphies: (1) basal part of maxillary palpmere 4 with digitiform sensilla (character 11:1, Fig. 2U), and (2) empodium with a single leaf-like seta (character 51:2; Figs 3P–Q). A few additional characters are indicated as non-unique synapomorphies, e.g. the dorsal surface with setiferous granules (also present in Helophoridae) and the V-shaped male sternite IX (also present in some Hydrophilidae, modified from plesiomorphic condition in Eumetopus, see Fig. 6).

In contrast, published molecular analyses contradict the sister relationships of Epimetopidae and Georissidae, never revealing them as sister taxa. Early molecular analyses of the Hydrophiloidea (Bernhard et al. 2006, 2009; Short & Fikáček 2013) placed Epimetopidae rather basally but did not provide any clear idea about its position in the superfAMILY. Recent studies on Coleoptera phylogeny mostly did not contain any representatives of Epimetopidae, with two exceptions. McKenna et al. (2014) reveal Epimetopidae as early branching lineage of Hydrophiloidea, but the basal topology of Hydrophiloidea is obscured by a biased position of Spercheidae as sister to all other families, a position rejected by the newest genomic data analyses (McKenna et al. 2019). Lu et al. (2020) revealed Epimetopidae as sister to all other hydrophiloid lineages, i.e. suggesting that Epimetopidae may be the most ancient lineage of the Hydrophiloidea, dating back to the middle Jurassic. The presence of members of the related families Helophoridae and Hydrophilidae in the early Jurassic (Fikáček et al. 2012a,h, 2014) indicates that the origin of the Epimetopidae may be even slightly older, and that additional studies are needed.

**Monophyly of Epimetopidae.** Our analyses are the first ones which include representatives of all three epimopetid genera. Both indicate a strongly supported monophyly of Epimetopidae. The following synapomorphies are revealed for the family: (1) eyes deeply emarginate anteriorly (also present in some Hydrophilidae: Sphaeridiinae); (2) peg-like setae on lacinia (also present in some Helophoridae and Hydrophilidae); (3) pronotal hoods with set of parallel ridges ventrally (unique for Epimetopidae but lost in Eupotemus); (4) metepimeron directed mesally in its posterior part (unique for Epimetopidae); (6) very short abdominal ventrite 1 (unique for Epimetopidae) and (7) egg cases carried by the female (also present in Spercheidae and a subclade of the hydrophilid subfamily Acidocerinae).

**Phylogenetic relationships among genera.** Morphological and molecular analyses are concordant in resolving Eumetopus as the earliest branching lineage of Epimetopidae. The Eupotemus + Eupotemus lineage is strongly supported in both analyses. Its morphological synapomorphies are: tridentate mandibular apex (Figs Figs 2D, e–i), mentum ca. as long as wide (Figs 2G, j–k), prosternal process broadened posteriorly (Figs 3A, E, G, I), elytra with elevated alternate intervals, and hind wing with reduced anallobe (Figs 5D–F). Both analyses revealed the monophyly of Eupotemus, as indicated by the loss of the stridulation file on the ventral surface of the pronotal hoods (Figs 3A–B), smooth lateral margin of pronotum (seen only ventrally, Fig. 3A), short metasternite (Figs 3J, 5A) and indistinct metakatepisternal suture of metaventrite (Fig. 5A). The morphology-based analysis does not recover the monophyly of Eupotemus, in contrast to the DNA-based analysis in which the monophyly of Eupotemus is strongly supported. Mapping of morphological characters on the molecular tree (Fig. 1E) suggest three synapomorphies for Eupotemus: closed procoxal cavities (unique within Epimetopidae, Figs 3E, G, I), abdominal ventricle 1 with medially separated coxal grooves (Fig. 5K) and all abdominal tergites with wing-folding asperites.

**Fossil record.** No fossils of Epimetopidae are known.

**Biology.** Based on the available data, most species of Epimetopidae live in similar habitats: wet sand or gravel at sides of various types of streams and rivers, occasionally also with algal mats or accumulations of plant debris (Perkins 2012; A. E. Z. Short, pers. comm.; Figs 7E–H). The observation of living specimens of Eumetopus acutimontis from Vietnam indicate that the specimens were digging and hiding in the wet sandy or gravelly substrate at the margin of a small river (Figs 7A–D). In contrast, some Eupotemus (e.g., E. venezuelensis Perkins, 2012) were collected in standing water, typically well vegetated shallow marshes (Figs 71–J; A. Short, pers. comm.). Females of all three genera carry their egg case on the ventral surface of the abdomen (Eupotemus: Rocha 1967, Costa et al. 1988, Perkins 2012; Eumetopus: J & Jäck 1998, Prokin & Sazhnev, pers. observ.; Eupotemus: Fikáček, unpubl. data, Fig. 5P). Larvae are predatory based on the morphology of their mouthparts (Fikáček et al. 2011, Rodriguez et al. 2020) and are likely living in the same habitats as the adults.

The ventral structure of the pronotal hoods in Epimetopus and Eupotemus strongly resembles the stridulation files of other insects and suggests that these two genera may possibly stridulate by moving the elevated tubercle on the dorsal surface of the occiput (Figs 4F–G) across the pronotal stridulation file by slightly rotating the head. However, Perkins (2012) found parallel grooves on the occiput of the examined specimen (Fig. 4G), corresponding to the elevated costae on the ventral part of the pronotal hood; these grooves were interpreted to be caused by abrasion by the parallel ridges of the pronotal hoods. These grooves would suggest rather a
strong pressure of the pronotal hood against the occiput when the head moves in an antero-posterior direction. The structures on the ventral side of the pronotal hood may hence serve to transfer force from the prothorax to the head during burrowing and/or to fix the position of the head during feeding in the substrate. In constrast, no transverse abrasion marks on the hood ridges were found (Perkins 2012, this study).

**Collecting.** Most specimens in the collections were found at light, or less frequently with flight intercept traps; in Costa Rica, some specimens were collected by using a car net at dusk (M. Schülke, pers. comm.). In the original habitats, specimens can be either searched for directly, which can be however difficult and very time consuming. The beetles float at the water surface when the microhabitat is flooded (A. Prokin, unpubl. data; A. E. Z. Short, pers. comm.), and may be hence most effectively collected by washing the stream or river banks, digging water-filled pits along the margin in which the sand or gravel is washed, or by washing the sandy sediments in a pale-colored tray (Fig. 7F). The tray is filled with water and an adequate amount of the upper layer of the wet sand or gravel from near the water edge (including plant debris) and the content of the tray is stirred, roots of riparian plants may be washed out in the tray as well. Epimetopid beetles appear floating at the water surface, along with representatives of other riparian beetles (Sphaeriusidae, Limnichidae, Georissidae, some Hydrophilidae: Agraphydrus Régimbart, 1903, Laccobius Ericsson, 1837, Chaetarthria Stephens, 1835, Thysanarthria Orchymont, 1926; M. Fikáček, A. Prokin, pers. observ.).

**Key to genera of Epimetopidae**

1. Elytra with scutellary stria, odd intervals with series of elevated tubercles, never with keels (Fig. 15). Pronotum without longitudinal keels (Fig. 14). Aedeagus with very long rounded conical phallobase and complex multilobate parameres (Figs 6V–Z). Male sternite IX O-shaped (Fig. 6U). Asia. .................................

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**Eumetopus** Balfour-Browne, 1949

- Elytra without scutellary stria, odd intervals with longitudinal keels which may be interrupted here and there (Figs 9, 10, 12, 16). Pronotum with longitudinal keels (Figs 9, 10, 12, 16). Aedeagus with simple flat open phallobase and simple parameres (Figs 6D–H, L–R). Male sternite IX U- or V-shaped (Figs 6C, K). Africa and America. ................................. 2

2. Procoxal cavities open posteriorly (Fig. 3A). Male sternite IX V-shaped (Fig. 6C). Median lobe with a single ventral projection which is simple or bifid at apex (Figs 6G–H). Africa. ................................. 2

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**Eupotemus** Ji & Jách, 1998

- Procoxal cavities closed posteriorly (Figs 3G, I). Male sternite IX U-shaped (Fig. 6K). Median lobe either without any projections, or with a pair of projections (Figs 6L–R). America. ................................. **Epimetopus** Lacordaire, 1854

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**Genera and species**

**Eupotemus** Ji & Jách, 1998

(Figs 2A–I; 3A–B, J, Q; 4C, K–L; 5D, J, M; 6A–H; 8–13)


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**Fixation of type species according to ICZN (1999: Art. 70.3).** Ji & Jách (1998a) designated **Eumetopus limicola** as type species of their newly erected genus *Eupotemus*. Their generic description was based on the examination of one male from Gabon, identified as *E. limicola*, and a bibliographic reference (Delève 1967: Figs 2, 7, 8) to the aedeagi of both species of the new genus known at that time (*E. limicola* and *E. carinaticollis*). However, it has now turned out, that *E. limicola* sensu Delève (1967) and Ji & Jách (1998a) represents a complex of sibling species (*E. limicola* group), and the specimen examined by Ji & Jách (1998a) is described below as a new species (*E. ophioglossus*). Therefore, the species designated as the type species, *E. limicola*, was strictly speaking, at least in part, misidentified by Ji & Jách (1998a). In order to avoid further nomenclatural uncertainties, we herewith fix *E. limicola* Delève, 1967 as type species of *Eupotemus* according to Article 70.3.1 (ICZN 1999).

**Diagnosis.** Moderately large species (body length 2.6–3.4 mm); body brown to black, without metallic sheen (Figs 9–10, 12); eyes not divided completely into dorsal and ventral portion; anterior oblique portion of clypeus divided from posterior parts by a ridge (Fig. 4C); labrum not narrowed posteriorly (Fig. 2A); mandibular apex tridentate (Figs C–D); apical maxillary palpomere long, strongly asymmetrical (Fig. 2E); mentum ca. as long as wide, without anterior series of setae (Figs 2F–G); pronotum 0.9× as long as wide; ventral surface of the hood without set of parallel ridges, with tuberculate mesh-like microsculpture (Figs 3A–B); prosternum without median carina, ca. 0.25× as long as procoxal cavity (Fig. 3A); procoxal cavity open posteriorly (Figs 3A–B); elytron without scutellary stria; alternate elytral intervals with elevated ridges (Figs 9–10, 12); mesanepisterna narrowly separated by anterior portion of mesoventrite (Figs 3J, 5A); mesoventrite postero mesomesoventrite with high projection (Fig. 3J); metaventrite between meso- and metacoxae very short (Figs 3J, 5A); postero mesoventrite with a low transverse ridge (Fig. 3J); middle and hind femora without posterior spine; phallobase short and wide (Figs 6D–H); parameres simple; median lobe flat (*E. carinaticollis* group; Fig. 11) or strongly 3D (*E. limicola* group; Fig. 8), with a single ventral projection which is simple or bifid, sperm pump absent; male sternite IX V-shaped (Fig. 6C).

**List of species** (8 described species)

**Eupotemus carinaticollis** species group

- **E. carinaticollis** (Basilewsky, 1956) Burundi, DR Congo (Basilewsky 1956, this paper)
- **E. taianus** sp. nov. Côte d’Ivoire (this paper)
- **E. uluguru** sp. nov. Tanzania (this paper)
Eupotemus limicola species group

E. bilobatus sp. nov.
E. cameroonensis sp. nov.
E. limicola (Delève, 1967)
E. ophioglossus sp. nov.
E. smithi sp. nov.

Nigeria (this paper)
Cameroon (this paper)
DR Congo (Delève 1967)
Gabon, Togo (this paper)
Côte d’Ivoire (this paper)

Key to species groups of Eupotemus

1. Lateral ridge of the pronotum not interrupted (Fig. 10H). Median lobe in lateral view resembling a bottle opener (Figs 8B, E, H, K, N); ventral projection of median lobe bifid (Figs 8P–R, T, V, X).

............................................................................................................. E. limicola group

- Lateral ridge of the pronotum interrupted in the middle (Fig. 10G). Median lobe in lateral view compressed dorsoventrally (Figs 11B, E, H); ventral projection of median lobe bar-like (Fig. 6H).

............................................................................................................. E. carinatricollis group

Eupotemus limicola group

Eupotemus bilobatus sp. nov.

(Figs 8A–C, 9A–C)

Material examined. HOLOTYPE: BMNH: ’Umudike / J. L. Gregory / 10-13.iv.1960 // Para-

Differential diagnosis. Very similar to the other species of the E. limicola species group from which it can be reliably distinguished by male genitalia only. The aedeagus is unique in the following characters: deeply bilobate apex of the median lobe (Figs 8A, C; not bilobate in all other species), apices of parameres not widened in lateral view (Figs 8B, S; more or less widened in all other species) and ventral fork rather narrow and shallowly excised (Fig. 8R; in contrast to E. cameroonensis, E. limicola and E. ophioglossus).Externally, it can be only distinguished from E. smithi by the complete ridge on elytral interval 3 (interrupted posteriorly in E. smithi). The coloration of all examined specimens is paler (brown to dark brown Figs 9A–C) than in all other species examined.

Description. Body 2.8–3.3 mm long (holotype 2.9 mm) and 1.5–1.8 mm wide (holotype 1.6 mm). Dorsal coloration brown to dark brown. Habitus and sculpture as in Figs 9A–C; ridge on elytral interval 3 not interrupted throughout; ridge on interval 5 interrupted anteriorly and

Table 3. Differences of the aedeagi of the species of the Eupotemus limicola group.

<table>
<thead>
<tr>
<th>E. bilobatus sp. nov.</th>
<th>E. cameroonensis sp. nov.</th>
<th>E. limicola (Delève, 1967)</th>
<th>E. ophioglossus sp. nov.</th>
<th>E. smithi sp. nov.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Apical disc of median lobe (length to width)</td>
<td>Bilobed apically, very slightly longer than wide.</td>
<td>Unlobed apically, &gt;2× longer than wide.</td>
<td>Bilobed apically, ca. 1.5× longer than wide.</td>
<td>Unlobed apically, 1.5–2.0× longer than wide.</td>
</tr>
</tbody>
</table>

in some specimens posteriorly; ridge on interval 7 complete until posterior third of elytral length. Elytral punctures of each row connected by low elevated line. Aedeagus (Figs 8A–C, R–S): 0.90–0.95 mm long. Parameres ca. 3× longer than phallobase, weakly bisinuate on outer face, not widened apically in lateral view. Median lobe with ventral impression wide in lateral view; apical disc ca. 1.3× longer than wide, concave in lateral view, its apex deeply bisinuate. Phallobase basally with narrow, slightly asymmetrical manubrium.

Etymology. The species name refers to the bilobate apex of the median lobe which is a unique character of this species. Adjective.

Biology. No data available.

Distribution. Only known from two close localities in southern Nigeria (Fig. 13A).

Eupotemus cameroonensis sp. nov.

(Figs 8D–F, 9D–F)

Material examined. HOLOTYPE: BMNH: ’Holotype / type / BRITISH CAMEROON / Manfe, 7-11.i.1949 / B. Malkin coll. // Rain forest; clear / stream: Gravel and / sand. / Metepitopus / occidentalis Type! / JK. Balfour-Browne det. // HOLOTYPE / Afrometopus / cameroonensis / P. D. Perkins // New species to / coll. + n.g. was a / specimen in D.2.2.1 / see its pinlabels’.

Differential diagnosis. Very similar to the other species of the E. limicola species group from which it can be reliably distinguished by male genitalia only. The aedeagus (Figs 8D–F) differs from other species except E. ophioglossus in the moderately widened apex of the paramere in lateral view (Figs 8E, U) and the very elongate and distally rounded (not bilobate) apical disc of the median lobe. In all these aspects it resembles E. ophioglossus from which it only differs in the shape of the ventral fork (Fig. 8T) which is only shallowly emarginate. Externally, it can be only distinguished from E. smithi by the complete ridge on elytral interval 3 (see under E. smithi for details).

Description. Body 2.65 mm long and 1.60 mm wide. Dorsal surface black. Habitus and sculpture as in Figs 9D–F; ridge on elytral interval 3 not interrupted; ridge on interval 5 interrupted anteriorly and just before its posterior end; ridge on interval 7 complete until posterior 0.1 of elytral length. Elytral punctures connected by low elevated line. Aedeagus (Figs 8D–E, T–U): 0.80 mm long. Parameres ca. 1.5× longer than phallobase, moderately bisinuate on outer face, moderately widened apically in lateral view. Median lobe with ventral impression rounded in lateral view; apical


disc ca. twice as long as wide, concave in lateral view, its apex rounded. Phallobase basally with narrow, slightly asymmetrical manubrium.

**Etymology.** The species name refers to Cameroon where the only known specimen was collected. Adjective.

**Biology.** No data available.

**Distribution.** Only known from the type locality (Fig. 13A).

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**Eupotemus limicola** (Delèye, 1967)

(Figs 8M–Q, 9G–I)


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Fig. 9. Habitus photographs of the species of the *Eupotemus limicola* species group, holotypes: A–C – *E. bilobatus* sp. nov.; D–F – *E. cameroonensis* sp. nov.; G–I – *E. limicola* (Delève, 1967).
Fig. 10. Habitus photographs of the species of the *Eupotemus limicola* species group, holotypes (A–F) and differences between species groups in pronotal morphology (G–H). A–C – *E. smithi* sp. nov.; D–F – *E. ophioglossus* sp. nov.; G–I – pronotal sculpture: G – *E. carinaticollis* species group; H – *E. limicola* species group.

**Differential diagnosis.** Very similar to the other species of the *E. limicola* species group from which it can be reliably distinguished by the male genitalia only. The aedeagus (Figs 8M–Q) differs in rounded apex from *E. bilobatus* and in the widely expanded parameres in lateral view from all species except *E. smithi*. From *E. smithi* it may be distinguished by the much shorter phallobase, more deeply excised ventral fork of the median lobe, and the complete ridge on elytral interval 3.

**Redescription.** Body 2.5–3.1 mm long (holotype 2.7 mm) and 1.4–1.7 mm wide (holotype 1.5 mm). Dorsal surface brown to dark brown. Habitus and sculpture as in Figs 9G–I; ridge on elytral interval 3 not interrupted; ridge on interval 5 interrupted anteriorly and sometimes also throughout its length or just before its posterior end; ridge on interval 7 complete throughout or interrupted in posterior 0.2–0.3 of elytral length. Elytral punctures connected by low elevated line. Aedeagus (Figs 8M–Q): 0.90 mm long. Parameres ca. 1.8× longer than phallobase, moderately bisinuate on outer face, strongly widened apically in lateral view. Median lobe with ventral impression narrow in lateral view; apical disc ca. 1.6× longer than wide, concave in lateral view, its apex very weakly sinuate. Phallobase basally with narrow, slightly asymmetrical manubrium.

**Biology.** No data available.

**Distribution.** The species was originally described from the Democratic Republic of Congo (locality of most specimens examined) and Côte d’Ivoire (based on a single female). The female from Côte d’Ivoire was not found in the collections. However, the newly collected specimens from Côte d’Ivoire all belong to a very similar but different species (*E. smithi* sp. nov.) and we suppose the same applies for the female paratype examined by Dëleve (1967). We hence exclude Côte d’Ivoire from the distribution range of *E. limicola*. 
*Eupotemus ophioglossus* sp. nov.  
(Figs 8G–I, 10D–F)

**Material examined.** HOLOTYPE: ♂ (NHMW): 'GABON / Bissok (Oyem) / 3.-10.2.1991 / leg. Bilardo // Eupotemus limicola (Del.) / det Jäch 1998'. PARATYPE: 1 ♂ (NHMW): 'TOGO: Plateux / Pref. Kloto, ca. 5 km from / Kouda (village), 9.II.2006 / leg. Komarek & Hougne (28) // 06°58'05.3"N 00°34'18.2"E, ca. 510 m a.s.l / small stream in prim. forest'.

**Diagnosis.** Very similar to the other species of the *E. limicola* species group from which it can be reliably distinguished by the male genitalia only. The aedeagus is unique in the shape of the ventral fork of the median lobe which is very deeply excised (Fig. 8V), otherwise it resembles that of *E. cameroonensis* by the moderately widened apex of the paramere in lateral view (Figs 8H, W) and in the narrow elongate apical disc of the median lobe (Fig. 8G). Externally, it can be only distinguished from *E. smithi* in the complete ridge on elytral interval 3 (see under *E. smithi* for details).

**Description.** Body 2.6–2.7 mm long (holotype 2.6 mm) and 1.3–1.4 mm wide (holotype 1.3 mm). Dorsal surface brown to black. Habitus and sculpture as in Figs 10D–F; ridge on elytral interval 3 not interrupted; ridge on interval 5 interrupted anteriorly and posteriorly; ridge on interval 7 interrupted in posterior 0.2–0.4 of elytral length. Elytral punctures connected by low elevated line. Aedeagus (Figs 8G–I, V–W): 0.80 mm long. Parameres ca. 2.2× longer than phallobase, strongly sinuate on outer face subapically, moderately widened apically in lateral view. Median lobe with ventral impression narrowly rounded in lateral view; apical disc ca. twice as long as wide, weakly concave in lateral view, its apex rounded. Phallobase basally with narrow, slightly asymmetrical manubrium.

**Etymology.** The latinised Greek noun *ophioglossus* means 'a snake tongue', in reference to the unique shape of the ventral fork of the median lobe in this species.

**Biology.** The paratype was collected at the small stream in a primary forest.

**Distribution.** Known from two rather distant localities, one in southern Togo and one in northern Gabon (Fig. 13A).

*Eupotemus smithi* sp. nov.  
(Figs 2A, C, E–F, H; 3A–B, J; Q; 4C–K, L; Q; 5A, D, J, M; 6A–F; 8J–L, X–Y; 10A–C)

**Material examined.** HOLOTYPE: ♂ (macropterous) (BMNH): 'CÔTE D’IVOIRE, 380m, / Yeale Village, Mt. Nimba / 07°31’35.3”N 08°25’20.1”W, / 18-29. IV.2016, Light Trap, / Aristophanous, M., Moretto, P., leg., / BMNH(E) 2016-109, / Trip Ref. CI-003 (ANHRT 17)’. PARATYPES: 14 spec. (incl. DNA voucher MF2207.W) (BMNH, NHMW): ʽCÔTE D’IVOIRE, 174m, / Tai NP, Tai Research Station, / 05°49’59.8”N, 07°20’32.0”W, / 14-23.xi.2015 // Leaf litter by river bank / Aristophanous, M., / Moretto, P., Ruzzier, E. leg., / BMNH(E) 2015-177’.

**Diagnosis.** Very similar to the other species of the *E. limicola* species group from which it can be reliably distinguished by the male genitalia only. The aedeagus (Figs 8J–L, X–Y) differs from all species except *E. limicola* by the widely widened apex of the parameres in lateral view. From *E. limicola* it differs in a shallowly excised ventral fork. *Eupotemus smithi* differs from all species of the group externally in the largely interrupted keels on the elytral intervals 3, 5 and 7.

**Description.** Body 2.6–3.1 mm long (holotype 2.8 mm) and 1.4–1.7 mm wide (holotype 1.5 mm). Dorsal surface brown to black. Habitus and sculpture as in Figs 10A–C; ridge on elytral interval 3 interrupted posteriorly; ridge on interval 5 interrupted in posterior half to fourth; ridge on interval 7 interrupted in posterior half to third of elytral length. Elytral punctures connected by low elevated line. Aedeagus (Figs 8J–L, X–Y): 0.90 mm long. Parameres ca. 1.8× longer than phallobase, strongly sinuate on outer face, strongly widened apically in lateral view. Median lobe with narrow ventral impression in lateral view; apical disc ca. 1.5× longer than wide, concave in lateral view, its apex rounded. Phallobase basally with narrow, slightly asymmetrical manubrium.

**Variation.** The single male from Tai National Park is brachypterous, smaller than the remaining specimens examined (2.6 mm long), and the ridges on its elytral intervals 3, 5 and 7 are completely subdivided into a series of elongate tubercles. Yet, it corresponds with the macropterous specimens from Yéale village, with which it also agrees in all details of the aedeagus morphology. We hence consider this specimen conspecific to the holotype and hypothesize that the differences may correlate to the brachyptery.

**Etymology.** This species is named after Richard E. L. Smith, who is the founder of the African Natural History Research Trust (ANHRT).

**Biology.** Specimens from Yéale village were all collected at light in the middle of the village which is surrounded by a belt of secondary forests and plantations followed by intact forest. The brachypterous specimens in the Tai NP was collected by sifting and washing plant debris accumulated after a flood (M. Geiser & E. Ruzzier, pers. comm.).

**Distribution.** The species was collected in two lowland localities in western Côte d’Ivoire close to the border to Liberia, situated ca. 220 km apart (Fig. 13A).

Unidentified specimens of the *Eupotemus limicola* group


*Eupotemus carinaticollis* group

*Eupotemus carinaticollis* (Basilewsky, 1956)  
(Figs 11A–C, 12A–C)


**Differential diagnosis.** Very similar to the other species of the *E. carinaticollis* species group from which it can
be reliably distinguished by the male genitalia only. The aedeagus differs from *E. uluguru* sp. nov. in the apically widened and subapically constricted parameres (Fig. 11A). This character is shared with *E. taianus* sp. nov. from which *E. carinaticollis* differs in the narrower and more elongated median lobe.

**Redescription.** Body 2.9–3.4 mm long (holotype 2.9 mm) and 1.6–1.8 mm wide (holotype 1.7 mm). Dorsal surface black. Habitus and sculpture as in Figs 12A–C; ridge on elytral interval 3 and 5 complete throughout; ridge on interval 7 interrupted posteriorly. Elytral punctures connected by low elevated line. Aedeagus (Figs 11A–C): 0.85–0.90 mm long. Parameres ca. 1.8× longer than phallobase, constricted subapically, widened at apex. Median lobe 3.4× longer than wide, apical part narrowing in apical fourth, sides of median lobe narrowing to apex in a straight line. Phallobase basally with narrow symmetrical manubrium.

**Biology.** Unknown. The labels of the Burundi specimens indicate that they were collected in remnants of a sclerophyll forest (i.e. in a dry forest with hard-leaved trees).

**Distribution.** The species is known from two localities situated around the northern part of Lake Tanganyika, one in the Democratic Republic of Congo, the other in Burundi (Fig. 13B).

**Eupotemus taianus sp. nov.** (Figs 11D–F, 12G–I)

**Material examined.** Holotype: / (DNA voucher MF2248) (BMNH): 'CÔTE D’IVOIRE, 174m, / Tai NP, Tai Research Station / (SRET) / 05°50’00”N 07°20’32.0”W, / 25.III-17.IV. 2017, MV light // Aristophanous, A., / Aristophanous, M., / Geiser, M., Moretto, P., leg., / BMNH(E) 2019-93’.

**Differential diagnosis.** Very similar to the other species of the *E. carinaticollis* species group from which it can
Fig. 12. Habitus photographs of the species of the *Eupotemus carinaticollis* species group, holotypes: A–C – *E. carinaticollis* (Basilewsky, 1956); D–F – *E. uluguru* sp. nov.; G–I – *E. tuianus* sp. nov.
be reliably distinguished by the male genitalia only. The aedeagus resembles that of *E. carinaticollis* by the subapically constricted and apically widened parameres but differs in the wider median lobe with convex sides subapically. From *E. uluguru* it differs in the apically widened parameres.

**Description.** Body 2.8 mm long and 1.5 mm wide. Dorsal surface black. Habitus and sculpture as in Figs 12G–I; ridge on elytral interval 3 complete throughout; ridge on interval 5 interrupted posteriorly; ridge on interval 7 interrupted in posterior fourth. Elytral punctures connected by low elevated line. Aedeagus (11D–F): 0.90 mm long. Parameres ca. 2.0× longer than phallobase, indistinctly constricted at midlength, strongly constricted subapically, apex widened. Median lobe 2.5× longer than wide, narrowing from midlength to apex, sides convex subapically. Phallobase basally with narrow symmetrical manubrium.

**Etymology.** The species name refers to the Taï National Park in which the only known specimen of this species was collected. Adjective.

**Biology.** Unknown, collected at light.

**Distribution.** Known only from the type locality in southwestern Côte d’Ivoire (Fig. 13B).

### Table 4. Differences of the aedeagi of the *Eupotemus carinaticollis* group.

<table>
<thead>
<tr>
<th></th>
<th><em>E. carinaticollis</em></th>
<th><em>E. uluguru</em> sp. nov.</th>
<th><em>E. tainanus</em> sp. nov.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Median lobe proportions</td>
<td>Narrow (&lt;3× longer than wide).</td>
<td>Narrow (&lt;3× longer than wide).</td>
<td>Wide (&gt;3× longer than wide).</td>
</tr>
<tr>
<td>Sides of median lobe sub-apically</td>
<td>Straight to very weakly convex.</td>
<td>Straight to weakly concave.</td>
<td>Strongly convex.</td>
</tr>
<tr>
<td>Apex of parameres in dorsal view</td>
<td>Constricted subapically, widened at apex.</td>
<td>Not constricted, narrow at apex.</td>
<td>Constricted subapically, widened at apex.</td>
</tr>
</tbody>
</table>

**Fig. 13.** Known distribution of *Eupotemus* species. A – species of *E. limicola* species group; B – species of *E. carinaticollis* species group.

**Eupotemus uluguru sp. nov.**

(Figs 11G–I, 12D–F)


**Additional material.** Additional specimens from the same collecting event (same collectors, date and locality data) should be deposited in the HNHM but could not be located instantaneously (Gy. Makranzyc, pers. comm.).

**Differential diagnosis.** Very similar to the other species of the *E. carinaticollis* species group from which it can be reliably distinguished by the male genitalia only. The aedeagus differs from both remaining species in the continuously narrowing parameres which are not widened at apex (Figs 11G, I).

**Description.** Body 2.9 mm long (holotype 2.9 mm) and 1.6 mm wide (holotype 1.6 mm). Dorsal surface black. Habitus and sculpture as in Figs 12D–F; ridge on elytral interval 3 complete throughout; ridges on interval 5 and 7 interrupted posteriorly. Elytral punctures connected by low elevated line. Aedeagus (11G–F): 0.90 mm long. Parameres ca. 1.8× longer than phallobase, continuously narrowing towards apex, not widened apically. Median lobe 3.0× longer than wide, apical part narrowing in apical third, sides slightly concave subapically. Phallobase basally with narrow asymmetrical manubrium.

**Etymology.** The species name refers to the Uluguru Mts. where this species was collected. Noun in apposition.

**Biology.** Unknown, both specimens were collected at light.

**Distribution.** Both known specimens were collected at the same locality in eastern Tanzania (Fig. 13B).

**Eumetopus Balfour-Browne, 1949**


**Diagnosis.** Moderately large species (body length 2.6–4.3 mm); body brown to black, partly with a metallic sheen (especially on pronotum and elytral tubercles; Figs 14–15); eyes not divided completely into dorsal and ventral portion (Fig. 4A); anterior oblique portion of clypeus divided from posterior parts by a ridge (Fig. 4B); labrum strongly narrowed posteriorly (Fig. 2J); mandibular apex bidentate (Figs 2M–L); apical maxillary palpmere long, strongly asymmetrical (Fig. 2M); mentum slightly wider than long, with series of long setae along anterior margin (Figs 2N–O, 4D); pronotum 0.7–0.8× as long as mesoventrite; mesoventrite posteromesally divided from posterior parts by a ridge (Fig. 6U). with egg case (IBIW): Ba Ho Waterfalls National Park, river Shuoi-Ngang, 12°23.131′N 109°08.052′E, 18.iv.2018, A. Prokin & A. Sazhnev leg.; 12 km E Sawantwadi, 15°55′N 73°53′E [coordinates on original labels (15°55′N 75°53′E) are incorrect, Z. Kejval, pers. comm.], 40 m, 22.v.2006, Z. Kejval lgt.

**Comments.** Except for the holotype, this species has not been recorded from Uttarakhand.

**Eumetopus flavidulus** (Sharp, 1890)


**Comments.** First record for Andhra Pradesh and Maharashtra.

**Eumetopus maindroni** (Régimbart, 1903)


**Comments.** First record for Andhra Pradesh and Maharashtra.

**Eumetopus acutimontis** Ji & Jách, 1998


**Comments.** Eumetopus acutimontis was so far only known from Hainan Island, China. The specimens from Vietnam correspond well with the drawing of the male genitalia by Ji & Jách (1998a), and their external morphology agrees with the female paratype deposited in the NHMW. This is the first record of E. acutimontis from continental Asia and from Vietnam.

**Biology.** All specimens were found on the wet sandy banks of the Shuoi-Ngang river, by washing out the shore sediment (Figs A–D); the specimens were floating at the water surface when they were washed from the sandy shore. Adults of some Hydrophilidae, Byrrhinus sp. (Limnichidae) and a larva of Eulichas Jakobson, 1913 (Eulichadidae) were collected from the same microhabitat. For video of a living specimen, see Supplementary File S1.

**Eumetopus asperatus** (Champion, 1919)

Material examined. INDIA: UTTARAKHAND: 5 spec. (NHMW, NMPC): ca. 15 km E Sawantwadi, 15°55′N 73°53′E [coordinates on original labels (15°55′N 75°53′E) are incorrect, Z. Kejval, pers. comm.], 40 m, 22.v.2006, Z. Kejval lgt.

**Comments.** The species was so far only known from the type locality ‘India’ (Sharp 1875, Ji & Jách 1998). This is the first precise record, confirming the occurrence in India.

**Eumetopus vulgaris** (Champion, 1919)


**Comments.** The species was so far only known from the type specimens (Régimbart 1903, Ji & Jách 1998a) from the Indian state of Tamil Nadu. Here we report it from Gujarat and Maharashtra for the first time.
Eumetopus tibialis Ji & Jäch, 1998

(Figs 14G, 15G, K)


Comments. The species was so far only known from northern Thailand. The above specimen from southern Thailand is a female, but corresponds to the paratypes of E. tibialis in all aspects, including the body size and the dorsal sculpture of the elytron.

**Eumetopus weigeli** Skale & Jách, 2003

(Figs 14H, 15H, L)


**Comments.** These specimens agree with the holotype of *E. weigeli* examined by us in all details of external morphology and male genitalia. The species was previously known only from Nepal, we record it as new for India.

![Fig. 15. Elytral sculpture and male genitalia of *Eumetopus* Balfour-Browne, 1949. A–H – elytral sculpture, same specimens as in Fig. 14: A – *E. acutimontis* Ji & Jách, 1998; B – *E. asperatus* (Champion, 1919); C – *E. bullatus* (Sharp, 1875); D – *E. flavidulus* (Sharp, 1890); E – *E. maindroni* (Régimbart, 1903); F – *E. schuelkei* Jách, 2002; G – *E. tibialis* Ji & Jách, 1998; H – *E. weigeli* Skale & Jách, 2003. I–L – male genitalia of examined specimens, large basal portion of the phallobase omitted (dorsal and lateral view): I – *E. acutimontis* from Vietnam; J – *E. flavidulus* from India: Andhra Pradesh; K – *E. maindroni* from India: Gujarat; L – *E. weigeli* from India: Uttarakhand.](image-url)
Epimetopus Lacordaire, 1854
Ceratoderus Mulsant, 1851: 1. Type species: Ceratoderus graniger Mulsant, 1851.
Epimetopus Lacordaire, 1854: 467. New replacement name for Ceratoderus Mulsant, 1851 due to the homonymy with Ceratoderus Westwood, 1841.
Sepidulum Leconte, 1874: 47. Type species: Sepidulum costatum Leconte, 1874; synonymized by Horn (1876: 251).

Diagnosis. Small to moderately large species (body length 1.2–3.7 mm); body reddish to black, without metallic sheen (Figs 16A–F); eyes completely divided into dorsal and ventral portion (E. trogoïdes group; Fikáček et al. 2011: fig. 12) or not (remaining groups; Fikáček et al. 2011: fig. 11); anterior portion of clypeus not divided from posterior parts; labrum not strongly narrowed posteriorly (Fig. 2R, X, g–i); mandibular apex tridentate (Figs 2S, Y, e–f); apical maxillary palpomere long, strongly to weakly asymmetrical (Figs 2T, Z); mentum ca. as long as wide, without setae along anterior margin (Figs 2V, j–l); pronotum 0.7–0.8× as long as wide, hood covering head forming anterior third of its length; ventral surface of the hood with set of parallel ridges (Figs 3F, H); prosternum without median elevation, ca. 0.3× as long as procoxa cavity (Figs 3E, G); procoxa cavity closed posteriorly (Figs 3E, G, I); mesanepisternum narrowly separated by anterior portion of mesoventrite (E. costatus group; Fig. 3K) or meeting mesally (E. mendelii group; Fig. 5B) (other groups not examined); mesoventrite posteromally with high transverse ridge (Fig. 3K); metaventrite ca. as long as mesocoxa, without large smooth elevated areas (Figs 3K, 5B); middle and hind femora without posterior spine; phallobase short and wide; parameres simple; median lobe flat, with a pair of ventral projections or without any projections (Figs 6L–R); sperm pump absent; male sternite IX U-shaped (Fig. 6K).

Identification. The genus was revised by Perkins (2012) who also provided a key to the species groups and illustrated all species.

E. costatus
E. steineri
E. spatulus
E. steineri Perkins, 1979
E. rectus Perkins, 2012
E. latus Perkins, 2012
E. laticollis Perkins, 2012
E. rectus Perkins, 2012
E. laticollis Perkins, 2012
E. elongatus Balfour-Browne, 1949
E. eucaptaeus E. flaviscapus Fikáček, Barclay & Perkins, 2011
E. graniger (Mulsant, 1851)
E. mendeli Fikáček, Barclay & Perkins, 2011
E. pereuvianus Perkins, 2012
E. angustus Perkins, 2012
E. balfourbrownei Rocha, 1969
E. elongatus Balfour-Browne, 1949
E. coleaneus Perkins, 2012
E. flaviscapus Fikáček, Barclay & Perkins, 2011
E. graniger (Mulsant, 1851)
E. mendeli Fikáček, Barclay & Perkins, 2011
E. pereuvianus Perkins, 2012

**List of species (56 described species)**

**Epimetopus costatus species group**

- E. acuminatus Perkins, 2012
- E. angustus Perkins, 2012
- E. apocinus Perkins, 2012
- E. arizonicus Perkins, 2012
- E. ballatoris Perkins, 2012
- E. bifidus Perkins, 2012
- E. burruyacu Oliva, 1986
- E. costaricensis Perkins, 1979
- E. costatus (Leconte, 1874)
- E. eucaptaeus E. flaviscapus Fikáček, Barclay & Perkins, 2011
- E. graniger (Mulsant, 1851)
- E. mendeli Fikáček, Barclay & Perkins, 2011
- E. pereuvianus Perkins, 2012
- E. angustus Perkins, 2012
- E. balfourbrownei Rocha, 1969
- E. elongatus Balfour-Browne, 1949
- E. coleaneus Perkins, 2012
- E. flaviscapus Fikáček, Barclay & Perkins, 2011
- E. graniger (Mulsant, 1851)
- E. mendeli Fikáček, Barclay & Perkins, 2011
- E. pereuvianus Perkins, 2012

**Epimetopus mendeli species group**

- E. angustus Balfour-Browne, 1949
- E. eucaptaeus E. flaviscapus Fikáček, Barclay & Perkins, 2011
- E. graniger (Mulsant, 1851)
- E. mendeli Fikáček, Barclay & Perkins, 2011
- E. pereuvianus Perkins, 2012

**Epimetopus thermarum species group**

- E. arcuatus Perkins, 2012
- E. balfourbrownei Rocha, 1969
- E. chyropus Perkins, 2012
- E. surinamensis Perkins, 2012
- E. thermarum Schwarz & Barber, 1917

**Epimetopus plaumanneni species group**

- E. multiportus Perkins, 2012
- E. plaumanneni (Costa Lima, 1954)

**Epimetopus lanceolatus species group**

- E. lanceolatus Perkins, 2012

**Epimetopus trogoides species group**

- E. clandestinus Perkins, 2012
- E. deceptus Perkins, 2012
- E. fimbrirates Perkins, 2012
- E. tridens Perkins, 2012
- E. torgoides (Sharp, 1874)

**Epimetopus tuberculatus species group**

- E. tuberculatus (Costa Lima, 1954)
- E. rubidus (Sharp, 1874)
- E. rubidus (Sharp, 1874)

**Records of Epimetopus from Africa and the Arabian Peninsula**


**Discussion**

The aim of this study was to publish the newly accumulated data on the family Epimetopidae which became available due to the newly collected material. Fresh alcohol specimens enabled us to provide the first DNA sequences of Eumetopus and Euoptemus. The new material from Africa made it possible to dissect some specimens and perform morphological comparative studies based on all three genera. New records complementing the data...
on the distribution of all three genera became available. Yet, it is very clear that the knowledge about the family remains rather limited in some aspects; these are defined and discussed below.

Phylogenetic position of the family. It was mentioned above that there is an apparent and strong conflict between the position of the Epimetopidae revealed by morphological and molecular characters. Analyses based on morphology always place Epimetopidae as sister to Georissidae, irrespectively of what kind of characters are used, and whether adult or larval data are included (Hansen 1991; Beutel 1994, 1999; Archangelsky 1998; Beutel & Komarek 2004; Beutel & Leschen 2005; Bernhard et al. 2009; Fikáček et al. 2012). In contrast, molecular analyses, despite not being conclusive about the phylogenetic position of the Epimetopidae never place them close to Georissidae (Bernhard et al. 2006, 2009; Short & Fikáček 2013; McKenna et al. 2014; Lü et al. 2020). If the molecular data are correct, it would imply that the supposed synapomorphies of Epimetopidae + Georissidae evolved in both groups independently, as a result of convergent evolution. We document here that Epimetopidae inhabit moist sandy shores of streams of standing waters, i.e. the same environment as most Georissidae (Messner 1965, 1972; Fikáček & Falamarzo 2010; Litovkin & Fikáček 2011; Litovkin 2018) and some riparian groups of Hydrophilidae (e.g., Chaetarthria Stephens, 1835 and Thysanarthria Orchymont, 1926; Perkins 1976, Fikáček & Liu 2019). Chaetarthria and Thysanarthria are deeply nested clades of the Hydrophilidae (Short & Fikáček 2013) and are not closely related to Epimetopidae. Still, they bear some of the characters considered as synapomorphies of Georissidae + Epimetopidae: they have a very long antennal scape, a bulbous pedicel, strongly reduced (yet not totally absent) pubescence on the ventral body surface, reduced gula and hence fused gular sutures, and they bear numerous digitiform sensilla on the base of the maxillary palpmere IV (Fikáček & Liu 2019). Moreover, the mentum of Thysanarthria bears series of long setae along its anterior margin (Fikáček & Liu 2019: fig. 3A), strongly resembling the situation found in Eumetopus (Fig. 4D). These convergences with Hydrophilidae indicate that the convergent evolution of these characters cannot be a priori excluded for Georissidae and Epimetopidae. Additional studies on the biology and functional morphology of both latter families are needed to understand whether their biology and the morpho-functional adaptations to deal with the riparian environment are indeed identical or just analogous. For example, the pronotal hood is a unique character shared by both families. The studies of the function of the hood including the parallel ridges on its ventral side (see Biology of Epimetopidae above for current hypotheses) and a detailed comparative study of these structures between Georissidae and Epimetopidae may reveal useful information. The gas exchange is another unusual aspect which is shared by Georissidae and Epimetopidae: both clades lack the hydrofuge pubescence, which, in other Hydrophiloidea, holds the ventral air bubble (Fikáček 2019c, this paper). In Hydrophiloidea, the air bubble is usually partly formed with the help of the antenna (HRBÁČEK 1950), and the antennal modifications in Georissidae and Epimetopidae may hence correspond to the adapted way of the gas exchange not necessarily indicating a close relationship of both families.

Larvae. Larvae are so far only known for a few species of the genus Eumetopus (Rocha 1967, 1969; Costa et al. 1988; Archangelsky 1997; Fikáček et al. 2011; Rodriguez et al. 2020) but unknown for the other two genera. Epimetopus larvae are all characterized by the adaptations for the underwater processing of the prey by piercing and sucking: the adapted form of the mandibles, the enlargement of the epistomal lobes and the reduction of the labrum (Rodriguez et al. 2020). They are often associated with reductions of spiracles and the closure of the tracheal system (Rodriguez et al. 2020). Similar morphology of the head and mouthparts, associated with underwater prey processing evolved independently in Epimetopidae and in three unrelated groups of the Hydrophilidae (Fikáček et al. 2018, Rodriguez et al. 2020). Moreover, Rodriguez et al. (2020) noticed that the lineages sister to those with piercing-sucking mouthparts often have very different morphology of the head and a tracheal system well corresponding to the usual hydrophilid morphology. In addition, at least in two cases in the Hydrophilidae (Lacobini and Berosini), the lineage with piercing-sucking larval adaptations contains significantly more species than its sister clade in which larvae process the food above the water. This observation resembles the situation in the Epimetopidae. The species-rich Eumetopus with 56 species has larvae with piercing-sucking mouthparts. Its sister Eupotemus has only eight known species and the larvae are unknown. Hence, we cannot exclude that larvae of Eupotemus and Eumetopus may be not adapted for piercing-sucking food processing, and hence may look different from those of Eumetopus in head and mouthpart morphology and in the development of the larvae tracheal system. The first instar larvae of Eumetopus and Eupotemus can be obtained from the egg cases carried by the females and should be studied in detail.

Egg cases carried by females. Egg cases are carried by females of all three epimetopid genera, and hence represent a synapomorphy of Epimetopidae. Similar behavior is present in two unrelated lineages of Hydrophiloidea: the Spercheidae (Fikáček 2019d) and the Helochares group of the hydrophilid subfamily Acidocerinae (Short et al. 2021). The egg-carrying behavior is considered as derived in the Hydrophiloidea (Hansen 2000), i.e., it evolved independently in each mentioned lineage and may be adaptive. This seems to be corroborated by the slightly different way in which the egg cases are carried in each group (Hansen 2000). The purpose of this adaptation and whether similar or clade-specific evolutionary pressures led to the evolution of this behavior remains to be tested.

Monophyly and internal topology of Epimetopus. Our morphological analysis failed to reveal the monophyly of the genus Eumetopus (Figs 1B–C). In contrast, the DNA-based analysis indicated Eumetopus as monophyletic. The taxon sampling was different in both analyses. Hence,
both topologies may not be incongruent: the paraphyly of *Epimetopus* in the morphology analysis is caused by the member of the *E. costatus* group which is likely not involved in the molecular analysis. All *Epimetopus* species have posteriorly closed procoxal cavities, unlike any other epimetopids, based on which we consider the paraphyly of *Epimetopus* as unlikely. However, we cannot totally exclude it based on our data. *Epimetopus* is morphologically much more diverse than *Eumetopus* and *Eupotemus*. This is evident even from our limited taxon sampling containing two *Epimetopus* species, i.e., representatives of the *E. costatus* and *E. mendeli* groups. The comparison of these two species revealed numerous differences, e.g., in the form of the prothoracic hypomeron (compare Figs 3E and G), in the form and sculpture of the meso- and metaventrite (compare Figs 3K and 5B, for additional SEMs of *E. mendeli* see also Fikáček et al. 2011), in the form of the trochanters (with dorsal plates in *E. costatus* group, without such plates in *E. mendeli*) and in the tarsal formula (5-5-5 in *E. mendeli*, 4-4-4 in *E. costatus* group). These differences indicate that the *E. costatus* group may indeed have a rather isolated position within *Epimetopus*; that needs to be tested by analyses with a wider species sampling covering all species groups of *Epimetopus*. Some other species groups also show apparent differences, e.g., in the eye morphology (completely divided in *E. trogoides* group, partially divided in other species; compare Figs 11 and 12 in Fikáček et al. 2011) and in the morphology of the male genitalia (with ventral projections likely corresponding to those of *Eupotemus* or without such projections; Figs 6L–R and genitalia illustrations in P公社ඃං඄ඇඌ 2012). Additional studies are needed to understand the evolution of these characters within the genus and to confirm the monophyly of *Epimetopus*.

**Acknowledgements**

We are indebted to Pol Limbourg (IRSNB) and Stéphane Hanot (MRAC) for the possibility to loan and study the types of previously described *Eupotemus* species. Zbyněk Kejval (Domažlice, Czech Republic), György Makranzy (HNHM) and Michael Schülke (Berlin, Germany) provided additional information about some specimens. Andrew Short (University of Kansas, Lawrence, USA) provided the information about the biology of *Epimetopus* and the photographs of its habitats. Stanislav Litovkin is indebted to K. Tomkovich (Moscow, Russia) for donating the *Eumetopus* species used for this study. We are grateful to Robert Angus (BMNH) and Andrew Short for critical comments on the manuscript and for linguistic corrections. The work of Martin Fikáček on this study was supported by the Ministry of Culture of the Czech Republic (DKRVO 2019–2023/5.1.c, National Museum, 00023272). The field work of Alexander Prokin and Alexey Sazhnev was performed within framework of the EKOLAN-3.2 project of the Russian-Vietnam Tropical Research and Technological Center”. The work of A. Prokin was supported by the Russian Science Foundation grant (no 21-74-20108), of A. Prokin and A. Sazhnev by the Russian State assignment (no AAA–A18–118012690105–0). The sampling and study of material from Côte d’Ivoire and Zambia were made possible thanks to the support of the African Natural History Research Trust (Leominster, UK) and Richard E. L. Smith. Scientific research in Côte d’Ivoire was authorized by the Ministère de l’Enseignement Supérieur et de la Recherche Scientifique. The Office Ivorien des Parcs et Réserves (OIPR) is thanked for authorizing access and sampling of specimens in Mt. Nimba Strict Nature Reserve (Réserve Naturelle Intégrale) under permit no. 216/MINEDD/OIPR/DG, and exportation of specimens under permit no. 308/ MINEDD/OIPR/DG.

**Electronically archived data**


Link to Youtube: https://youtu.be/Ua2uxtz8Ar0

Supplementary File S2. Morphological matrix used for the phylogenetic analysis (in TNT format).

Link to the file on the journal webpage. https://www.aemnp.eu/acta-entomologica/61-1/61_1_1.html

Supplementary File S3. Complete picture documentation taken for this study, including unedited versions of all photographs and SEMs, additional photographs and SEMs used for the study but not included on the plates, original plates at high resolution and original drawings.

Link to Zenodo: http://doi.org/10.5281/zenodo.4408834

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