

RESEARCH PAPER

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. taianus* 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). New records of *Eumetopus* species are provided (*E. acutimontis* Ji & Jäch, 1998 from Vietnam, *E. bullatus* (Sharp, 1875) from India: Maharashtra, *E. flavidulus* (Sharp, 1890) from India: Maharashtra and Andhra Pradesh, *E. maindroni* (Régimbart, 1903) from India: Maharashtra and Gujarat, and *E. weigeli* Skale & Jäch, 2003 from India: Uttarakhand). The habitus of all species is illustrated. An updated checklist of the *Epimetopus* species is provided, and records



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

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Introduction

The beetle superfamily Hydrophiloidea (*sensu stricto*, i.e. without histeroid families; HANSEN 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 (HANSEN 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 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 hydrophiloid 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 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 & JÄCH 1998, PERKINS 2012). Although there are studies focusing on smaller regions (e.g., SATÔ 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 outgroups. 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; HANSEN 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 ROTHMEIER & JÄCH (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

species in detail. Coincidentally, the DNA-grade specimens were also collected in Asia, where epimetopids 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* (FIKÁČEK 2019a–d). Epimetopidae 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);
HNHM	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);
NHMW	Naturhistorisches Museum Wien, Austria (M. A. Jäch);
NMPC	National Museum, Praha, Czech Republic (J. Hájek, M. Fikáček, L. Sekerka);
MRAC	Musée Royal de l’Afrique Centrale, Tervuren, Belgium (S. Hanot);
SLC	Stanislav Litovkin collection, Samara, Russia.

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 epimetopid 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 Eurapal resin after a short bath in 95% ethyl alcohol and concentrated isopropanol. Other 3-dimensional parts (pterothorax, abdomen) were kept in separate vials with glycerine. Wings were mounted as dry permanent slides. Data on outgroup taxa are largely based on similarly prepared specimens from the study of FIKÁČEK et al. (2012). All dissected specimens are deposited in the NMPC. Habitus photographs were taken using a Canon EOS 550D digital camera with attached Canon MP-E65 mm f/2.8 1–5× macro lens, followed by stacking combination in Helicon Focus software. SEM micrographs of uncoated specimens were taken using a Hitachi S-3700N environmental electron microscope at the Department of Paleontology, National Museum (Praha, Czech Republic). Photographs of slide-mounted body parts of the adults were taken using a Canon D1100 digital camera attached to an Olympus BX41 compound microscope.

For taxonomic studies of African species, we dissected male genitalia of a part of water-relaxed specimens.

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 FIKÁČEK et al. (2012). The characters were selected primarily to reconstruct the relationships among epimetopid genera and are not conclusive for the reconstruction of the relationships among families. Fourteen taxa were included: five species of Epimetopidae, two species of Hydrophilidae, and one species of Hydrochidae, Helophoridae, Georissidae and Spercheidae. *Epimetopus* seems morphologically much more diverse than other genera (see e.g. FIKÁČEK et al. 2011, PERKINS 2012), hence we included at least two representatives in which we expected different morphology (*E. mendeli* Fikáček, 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 *Syntelia* Westwood, 1864 (Synteliidae), and the tree was rooted by a representative of Agyrtidae (*Necrophilus subterraneus* 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. Anterior portion of clypeus along anterior margin: (0) on the same plane as remaining parts of clypeus; (1) more inclined, delimited from remaining parts by an edge (Figs 4A–C).
5. Eyes: (0) distinctly protruding laterad; (1) not protruding laterad from the outline of the head.
6. Eyes: (0) not or very weakly emarginate anteriorly; (1) deeply emarginate anteriorly (Fig. 4A).
7. Narrow postocular bridge: (0) present (Fig. 4E); (1) absent.
8. Labrum: (0) gradually narrowing towards base (Figs 2A, R, Z); (1) abruptly constricted basally (Fig. 2J).
9. Distal setae of lacinia: (0) trichoid and/or sickle-shaped; (1) peg-like.
10. Maxillary palpomere 4: (0) asymmetrical (Figs 2E, M, T, Z); (1) symmetrical.
11. Basal portion of maxillary palpomere 4: (0) without digitiform sensilla; (1) with digitiform sensilla (Fig. 2U).
12. Mandibular apex: (0) bidentate (Figs 2M–L); (1) tridentate (Figs 2D, e); (2) unidentate.
13. Proportions of mentum (width : length): (0) 1.3 or less (Figs 2F–G, V, b, j–l); (1) 1.31 or more (Figs 2N, O).
14. Anterior margin of mentum: (0) without long setae; (1) with a transverse row of long setae (Figs 2N, O, 4D).
15. Number of antennomeres: (0) seven; (1) eight; (2) nine (Figs 2H–I, P–Q, W, c); (3) eleven.
16. Antennal pedicel: (0) conical, narrower distally than basally; (1) bulbous (spherical to shortly conical; Figs 2H–I, P–Q, W, c, 4H–I); (2) club-like, narrower basally than distally.
17. Gular sutures: (0) widely separated; (1) conjoined or nearly so (Fig. 4E).
18. Anterior projection of pronotum concealing head: (0) absent; (1) present.

Table 1. Morphological dataset used for maximum parsimony analysis and character mapping.

	11111111112222222222333333333333444444444455555555556
	123456789012345678901234567890123456789012345678901234567890
<i>Eumetopus schuelkei</i>	011101011010112111011110100111110101211012020102002100011111
<i>Eupotemus smithi</i>	011101001011002111110100110100010101200112000011002100000000
<i>Eupotemus carinaticollis</i>	011101001011002111110100110100010101200112000011002100000000
<i>Epimetopus mendeli</i>	0100010010110021110101101111000100-1210012110001002101100000
<i>Epimetopus costaricensis</i>	01100100111100211101110111100010101210012010010012101100010
<i>Necrophilus subterraneus</i>	00100010010210310010-000000010000110200102--0000000012230010
<i>Syntelia davidis</i>	001010--010210321010-00001111000011021000202000000001222001-
<i>Sphaerites glabratus</i>	00100010110210310010-000100110000111210002020000000012220010
<i>Helophorus aquaticus</i>	110000000002102010110111000110101101010000121000100012020010
<i>Hydrobius fuscipes</i>	101010-1100010200010-0001000101010-0110100011000200012020010
<i>Georissus crenulatus</i>	010010-001101021111111212-021001-111210002000000002012100010
<i>Spercheus emarginatus</i>	1010000000010010010-020100001010-001000110000101112020010
<i>Hydrochus elongatus</i>	100000100000102010112010011000011110010100021000200012120010
<i>Berosus signaticollis</i>	10100010000110000010-000100010101100010100111000200012000010

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) with ridges only 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. Precoxal 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 the 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 stria 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 epipleura: (0) absent; (1) present.
34. Mesanepisterna: (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 pubescence of mesothorax: (0) well developed; (1) present only medially, absent on lateral portions; (2) totally absent.
38. Metaventricle 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 metaventricle: (0) absent (Figs 3J–K); (1) present (Fig. 3L).
40. Metakatepisternal suture: (0) present (Fig. 5B); (1) absent or indistinct (Fig. 5A).
41. Metanepisternum posteriorly: (0) straight; (1) bent inwards (Figs 5A–B).
42. Dense ventral pubescence on metaventricle: (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 ventrite 1: (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 ventrite 1: (0) not separated medially (Fig. 5I); (1) divided by median carina (Figs 5J–K); (2) divided by median projection of the ventrite.
55. Wing folding asperites on abdominal tergites: (0) IV–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. Sperm 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 acutimontis* 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 Hydrophiloidea 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

Table 2. GenBank accession numbers of Epimetopidae sequences newly generated for this study (in bold) and those used for the Bayesian phylogenetic analysis (*cox1*, 16S, 18S and 28S). Voucher numbers are only indicated for Epimetopidae specimens.

Species	Voucher	<i>Cox1</i>	16S	18S	28S	Wingless	Topo I	H3
<i>Sphaerites glabratus</i>	–	DQ222001	DQ202586	KP419293	KP419645	–	–	–
<i>Helophorus aquaticus</i>	–	AM287078	AM287056	AJ810714	AJ810749	–	–	–
<i>Georissus crenulatus</i>	–	DQ221983	DQ202580	AY745584	AJ810751	–	–	–
<i>Hydrochus crenatus</i>	–	AM287084	AM287062	AM287124	AM287132	–	–	–
<i>Spercheus emarginatus</i>	–	AM287085	KC992709	AJ810718	AJ810753	–	–	–
<i>Hydrobius fuscipes</i>	–	AM287092	AM287070	AJ810720	AJ810755	–	–	–
<i>Berosus luridus</i>	–	AM287087	AM287065	AJ810721	AJ810756	–	–	–
<i>Epimetopus</i> sp.	AK-2004	AM287082	AM287060	AJ810724	AJ810759	–	–	–
<i>Epimetopus</i> cf. <i>thermarum</i>	SLE0069	KC935264	KC992673	KC935040	KC992568	–	–	–
<i>Eumetopus acutimontis</i>	MF2362	MW446170	–	MW430661	MW430659	MW436481	MW436480	MW436479
<i>Eupotemus taianus</i>	MF2248	MW446169	MW430654	MW430660	MW430658	MW436478	–	–
<i>Eupotemus smithi</i>	MF2207.W	MW446168	–	–	–	–	–	–

fragments only: *cox1*, 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: *cox1* (404 bp), 16S (477 bp), 18S (1661 bp), 28S (1121 bp) and 28S (796 bp). The dataset was divided into partitions by genes, *cox1* sequences were subdivided by codon positions. The phylogenetic reconstruction was conducted using Mr-Bayes 3.2.6 (RONQUIST et al. 2012), using four chains of 25 million generations and sampling every 1000th generation. The convergence of both runs was checked in Tracer 1.7 (RAMBAUT 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

Epimetopidae Zaitzev, 1908

Epimetopina Zaitzev, 1908: 353.

Epimetopinae: ORCHYMONT (1916), KNISCH (1924), BLACKWELDER (1944), BALFOUR-BROWNE (1949), CROWSON (1967), DELÈVE (1967), PERKINS (1979), LAWRENCE & NEWTON (1982, 1995), VAN TASSEL (2000), ARCHANGELSKY et al. (2005), BOUCHARD et al. (2011), LAWRENCE & SLIPIŃSKI (2013).

Epimetopidae: HANSEN (1991), JI & JÄCH (1998a,b), HANSEN (1999), JÄCH & BALKE (2003, 2008), HEBAUER (2006a), FIKÁČEK & RYNDEVICH (2015), ARCHANGELSKY et al. (2016), SHORT (2018).

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

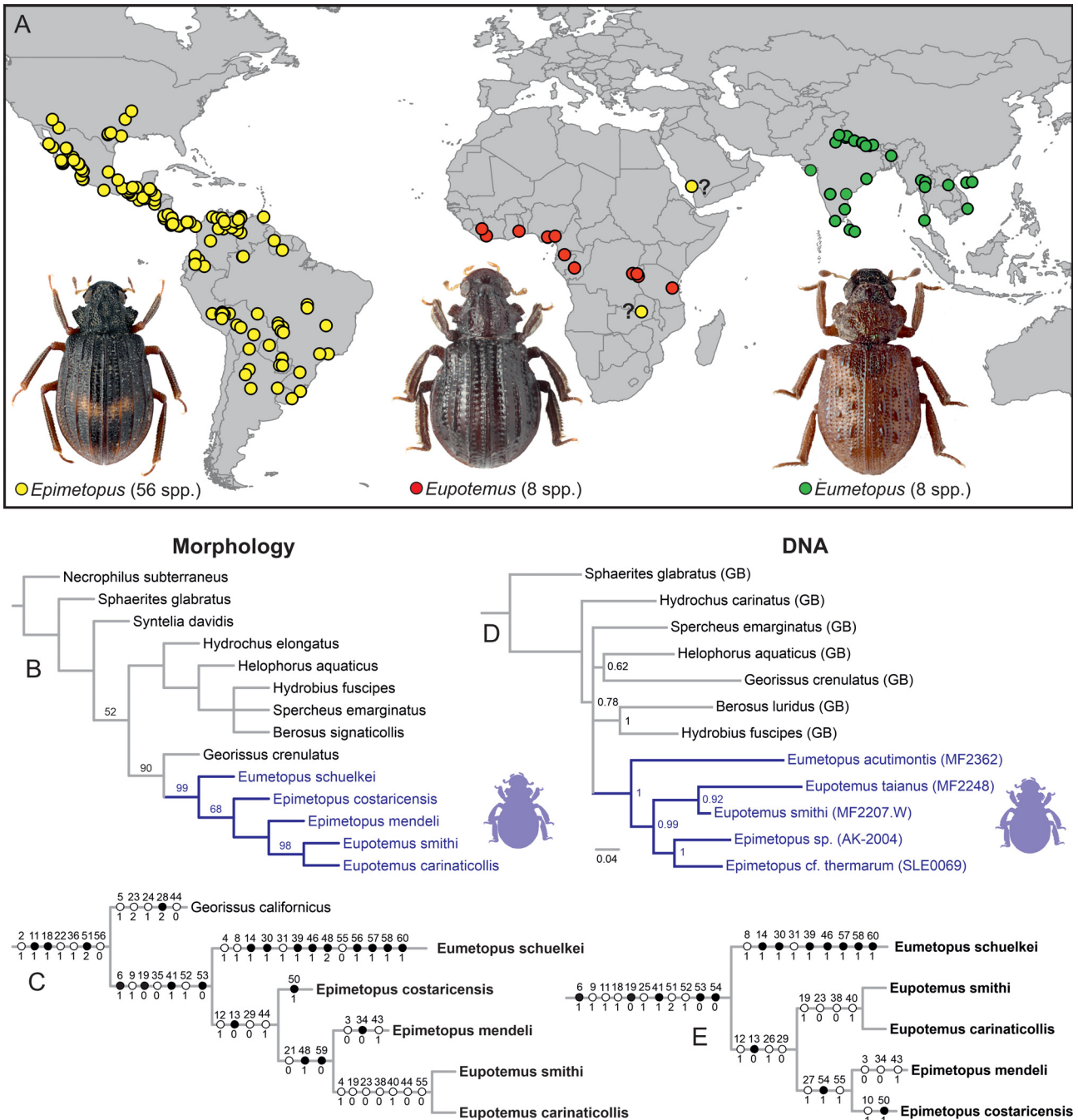


Fig. 1. Distribution and phylogenetic relationships of Epimetopidae genera. A – summary of all known records of Epimetopidae, mapped by genera. Records for American *Epimetopus* adopted from PERKINS (2012). B–E – phylogenetic relationship among genera based on morphological characters (B–C) and DNA data (D–E): B–C – strict consensus tree of the morphology-based maximum parsimony analysis (B – complete tree with bootstrap supports; C – Georissidae + Epimetopidae subtree with characters mapped). D – Bayesian maximum credibility tree based on *cox1*, 16S, 18S and 28S sequences, with posterior probability of particular clades. E – morphological characters mapped on the molecular topology of Epimetopidae constrained as sister to all other hydrophilid families following the topology by LÜ et al. (2020).

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 (*Epimetopus 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

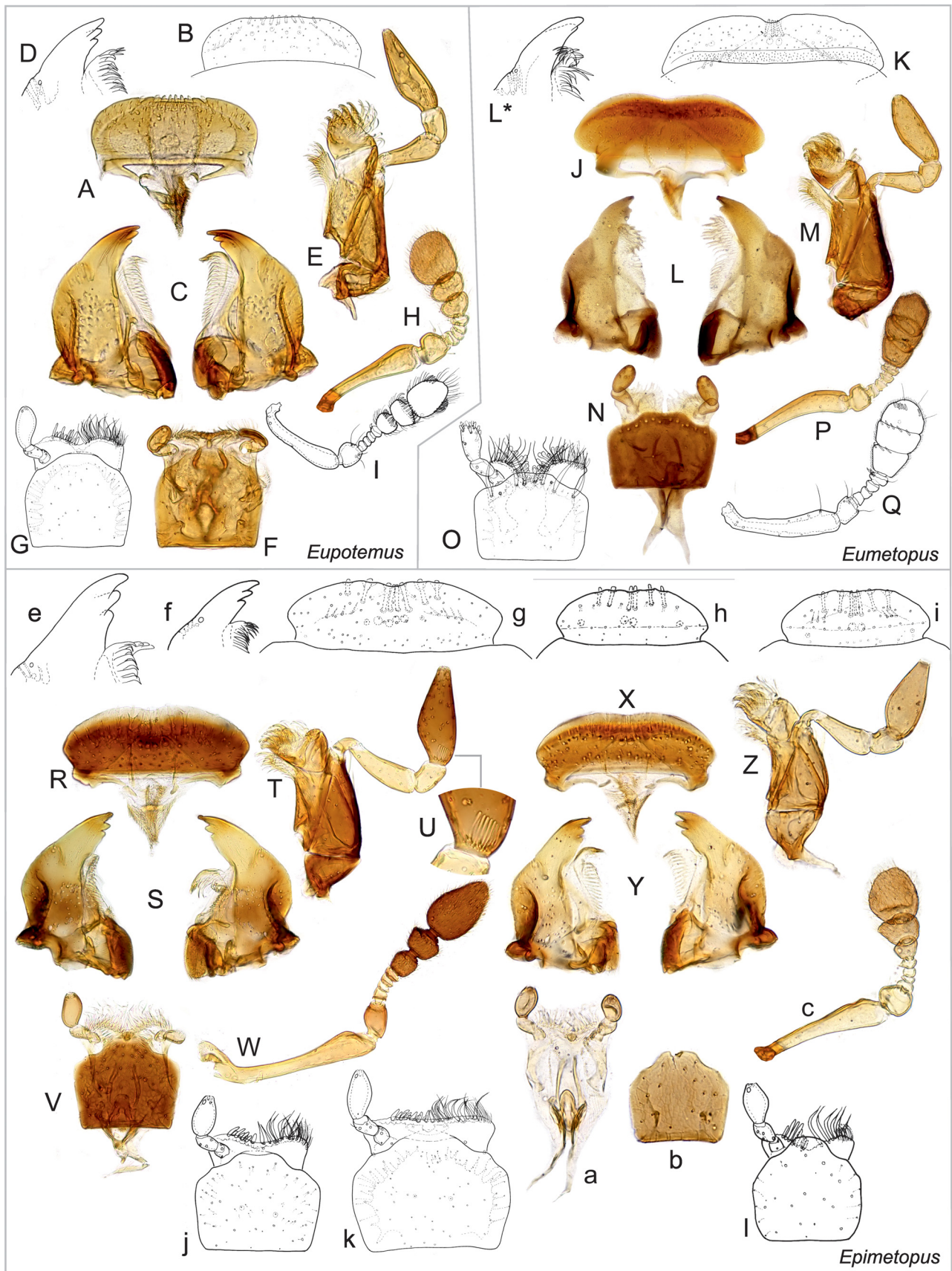


Fig. 2. Morphology of mouthparts and head appendages of the genera of Epimetopidae. A–I – *Eupotemus* Ji & Jäch, 1998: A, C, E, F, H – *E. smithi* sp. nov., B, D, G – *E. limicola* (Delève, 1967), I – *E. cameroonensis* sp. nov. J–Q – *Eumetopus* Balfour-Browne, 1949: J, L, M, N, P – *E. schuelkei* Jäch, 2002, Q – *E. bullatus* (Sharp, 1875), K, L*, O – *E.* sp. from Sri Lanka. R–Z, a–l – *Epimetopus* Lacordaire, 1854: R–W – *E. mendeli* Fikáček et al., 2011, X–Z, a–c – *E. costaricensis* Perkins, 1979, g, j – *E. thermanum* Schwarz & Barber, 1917, e, k – *E. trogoides* (Sharp, 1874), h – *E. costatus* group, f, i, l – *E. punctipennis* Perkins, 1979. Body parts: A–B, J–K, R, X, g–i – labrum; C, L, S, Y – mandibles; D, L*, e–f – mandibular apex; E, M, T, Z – maxilla; U – detail of basal part of ultimate palpomere; F–G, N–O, V, a–b, j–l – mentum and prementum; H–I, P–Q, W, c – antenna. Not to scale.

(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, bulbous; 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*, *Eupotemus*); 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 subpentagonal (Figs 2F–G, N, O, W, j–l); ligula bilobed; labial palpus with three palpomeres, apical palpomere expanded, 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*, *Eupotemus*) 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 (*Eupotemus*; Fig. 3B). Dorsal surface with setiferous tubercles, and with two pairs of longitudinal elevated costae which are complete or nearly so (*Eupotemus*, 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 ventrally; 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*, *Eupotemus*) or with (*Eumetopus*) very weakly developed median carina, anterior margin straight. Prosternal process present, widened posteriorly, largely concealed by procoxae (*Eupotemus*, *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 (*Eupotemus*, *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*) scutellary 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*, *Epimetopus*; 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 mesanepisterna, anterior portion of mesoventrite on different plane than metaventrite; without defined procoxal rests; posteromesal portion with elevated transverse or arcuately transverse ridge; mesoventral cavity absent; discrimen absent. Mesanepisterna narrowly separated from each other anteriorly (most species; Figs 3J–K) or contiguous (some *Epimetopus*; Fig. 5B). Mesocoxal 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 dorsolaterally. Metaventrite distinctly transverse, flat to slightly convex, uniformly tuberculate (*Epimetopus*; Fig. 3K), with posteromedian transverse ridge (*Eupotemus*; Fig. 3J) or with basal ridges and central elevation (*Eumetopus*; Fig. 3L); anteromesally with long projection separating mesocoxae; discrimen reduced, transverse (metakatepisternal) suture well developed (*Epimetopus*; Fig. 5B), weakly developed (*Eumetopus*) or obsolete (*Eupotemus*; Fig. 5A); metanepisternum exposed ventrally, wide throughout, arcuate in shape (Figs 5A–B). Metacoxae massive, transverse, widely separated by narrowly bifurcate posterior process of metaventrite, laterally meeting metanepisternum, not reaching elytra (Figs 5A–B). Metendosternite 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

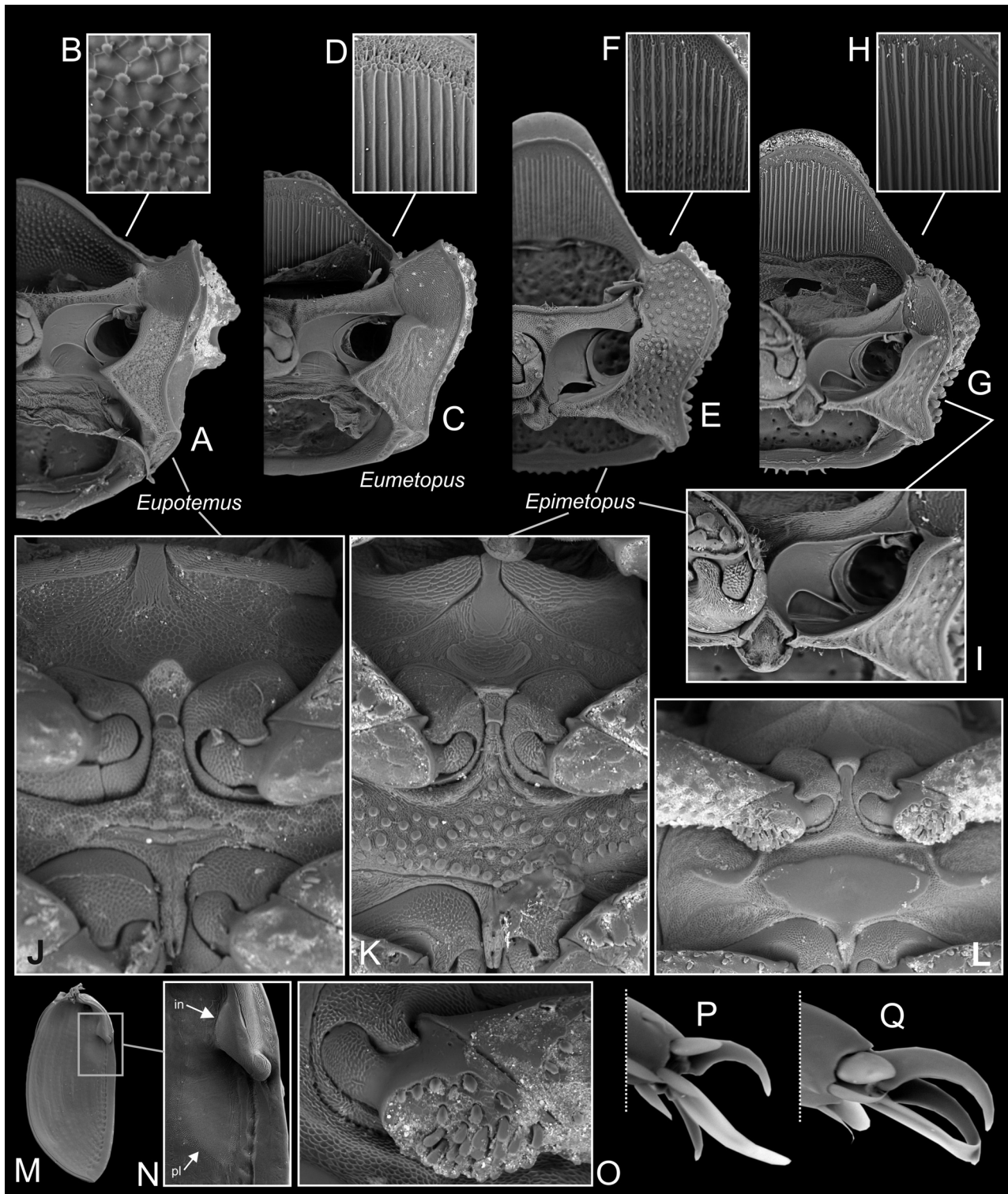


Fig. 3. Thoracic morphology of the genera of Epimetopidae. A–B, J, Q – *Eupotemus smithi* sp. nov.; C–D, L–O – *Eumetopus schuelkei* Jäch, 2002; E–F – *Epimetopus mendeli* Fikáček, Barclay & Perkins, 2012; G–I, P – *Epimetopus costaricensis* Perkins, 1979. A–I – prothorax in ventral view (B, D, E, F, H – detail of ventral sculpture of the pronotal hood; I – detail of closed procoxal cavity. J–L – meso- and metathorax in ventral view. M–N – elytron in ventral view (M – general view; N – detail of the ventral ridge, notice the spiny surface on inner face of the ridge (in) and on the elytral plectrum posteriorly of it (pl)). O – mesotrochanter. P–Q – details of pretarsus with the leaf-like empodial seta. Not to scale.

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).

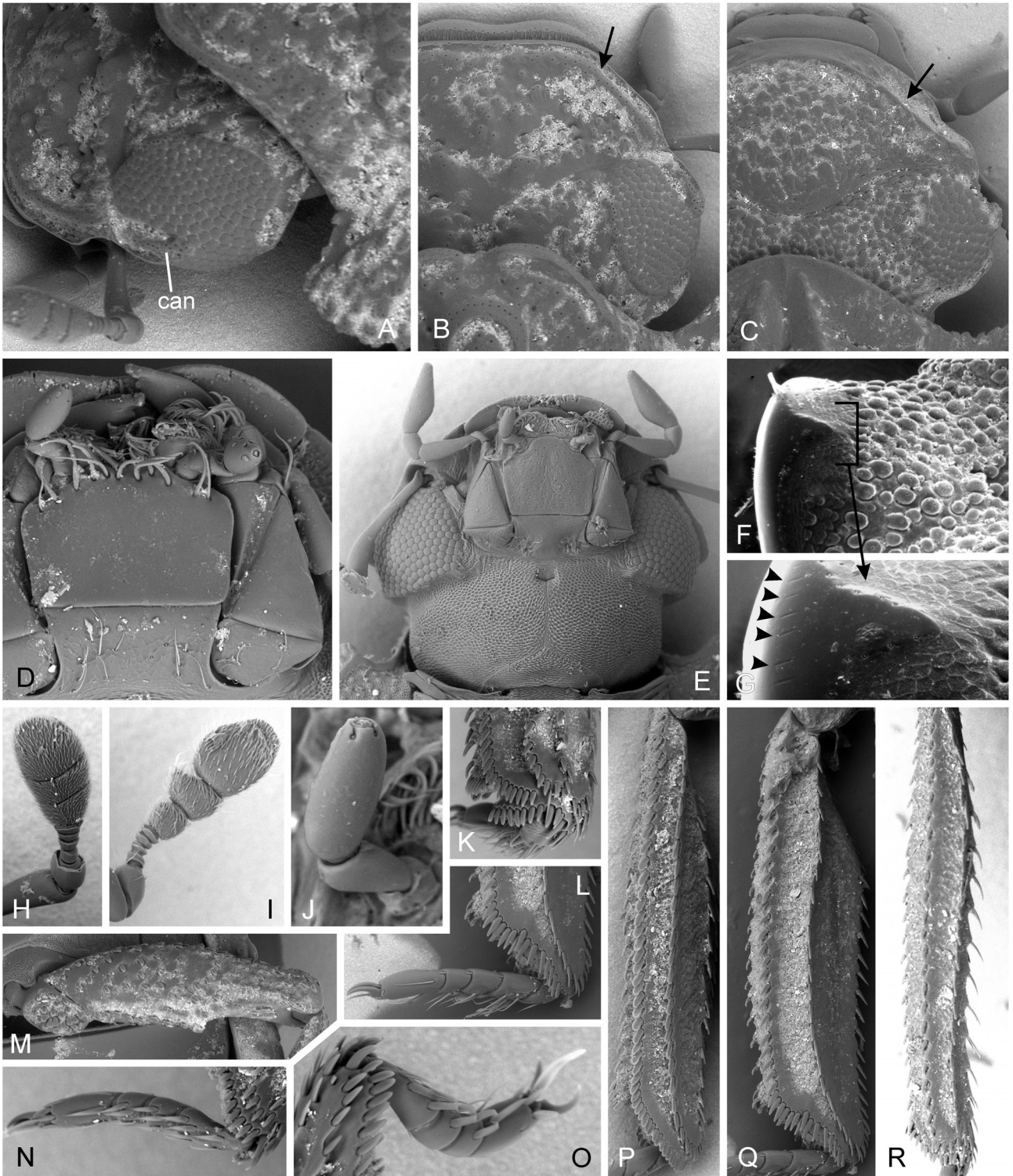


Fig. 4. Head and leg morphology of the genera of Epimetopidae. A–B, H, L – *Eumetopus acutimontis* Ji & Jäch, 1998; D, M – *Eumetopus schuelkei* Jäch, 2002; C, K–L, Q – *Eupotemus smithi* sp. nov.; F–G – *Epimetopus punctipennis* Perkins, 1979 (adopted from PERKINS 2012); E, I–J, R – *Epimetopus mendeli* Fikáček, Barclay & Perkins, 2011; N–O – *Epimetopus 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 hydrofuge 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 asperites. Anterior edge of male sternite VIII without median strut (Figs 6A, I, S). Segment IX in male U-shaped (*Epimetopus*; Fig. 6K), V-shaped (*Eupotemus*; Fig. 6C) or O-shaped (*Eumetopus*; Fig. 6U), with weakly delimited long lateral struts. Aedeagus of trilobate type, symmetrical, with short open phallobase and simple parameres (*Eupotemus*, *Epimetopus*; Figs 6D–F, L–N) or with long conical phallobase and complicated multilobate parameres (*Eumetopus*; Figs 6V–X, Z); penis with short basal struts. Male gonoduct with large and strongly sclerotized sperm pump (*Eumetopus*; Fig. 6Y) or without it (*Eupotemus*, *Epimetopus*). Ovipositor (Figs 5L–M) moderately elongate, lightly sclerotized; paraprocts much shorter than coxites, which are subdivided into a long basal lobe (gonocoxite), and a short (*Eupotemus*) or rather long (*Eumetopus*) distal lobe (gonostylus).

A slight sexual dimorphism is present in some species of *Eumetopus* (elytra apically with more elevated tubercles or ridges or elytral apices acuminate in females; hind tibia more strongly compressed in females; tarsi wider and more densely setose and claws larger in males; Ji & JÄCH 1998a) and in some *Epimetopus* (females with abdominal ventrite slightly concave and in some species with slightly elevated median portion; abdominal ventrites microreticulate throughout in males but with microsculpture reduced mesally in males in some groups; PERKINS 2012).

Larval morphology. Larvae are known for few species of *Epimetopus*, but they are unknown for *Eumetopus* and *Eupotemus*. All descriptions of *Epimetopus* larvae are based on first instar larvae which were found inside of egg-cases carried by females or were reared from them. *Epimetopus* larvae bear characters shared with Helophoridae and Georissidae (general morphology of nasale and epistomal lobes, long maxillary palpomere 1, head chaetotaxy) or Georissidae only (form and setation of epistomal lobes, submentum divided from head capsule by a straight line). The morphology of the mandibles is, however, highly derived, adapted to underwater processing of food by piercing and sucking. The reduction of abdominal spiracles and the presence of abdominal gills is likely also related to the underwater lifestyle (RODRIGUEZ et al. 2020).

Larvae of *Epimetopus* were described and illustrated by ROCHA (1967, 1969), COSTA et al. (1988), ARCHANGELSKY (1997), FIKÁČEK et al. (2011) and RODRIGUEZ et al. (2020).

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 FIKÁČEK 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, FIKÁČEK 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 sensorium. Mandibles symmetrical, moderately broad at base, with narrow, strongly curved and unidentate 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 protracted, maxillary articulating area present, membranous, with two small sclerites; maxilla hexamerous, 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; palp 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 ecdysial 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 (FIKÁČEK et al. 2011). Legs 5-segmented, with a distinct and long claw-like pretarsus; procoxae nearly contiguous, meso- and metacoxae separated (FIKÁČEK et al. 2011). Abdominal segments I–IX lightly sclerotised, without distinct sclerites; segments VIII–IX, or only segment IX, with

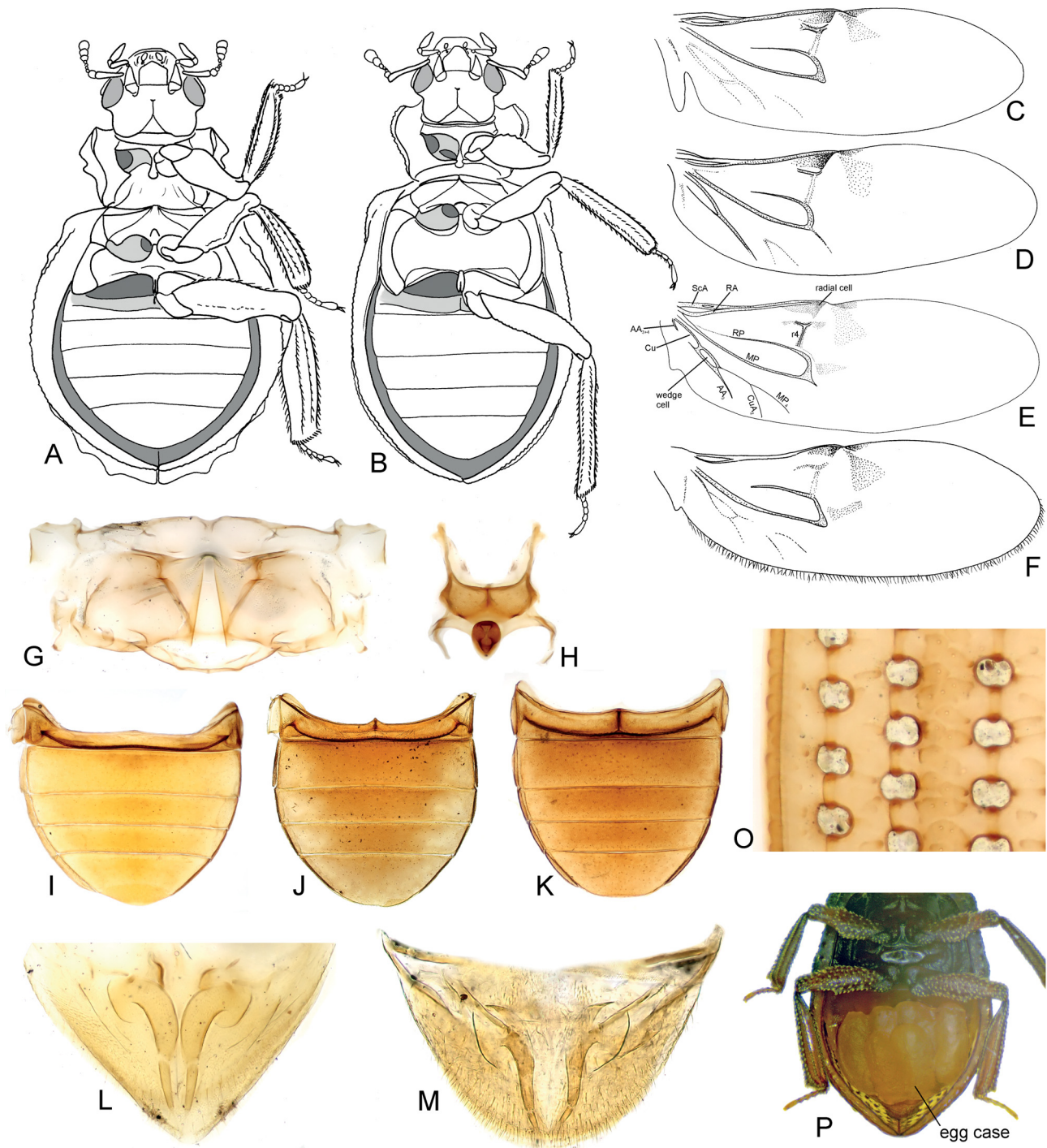


Fig. 5. Morphology of Epimetopidae. A–B – ventral morphology: A – *Eupotemus smithi* sp. nov.; B – *Epimetopus mendeli* Fikáček, Perkins & Barclay, 2011. C–F – hind wings: C – *Eumetopus schuelkei* Jäch, 2002; D – *Eupotemus smithi* sp. nov.; E – *Epimetopus mendeli*, adopted from FIKÁČEK et al. (2011); F – *Epimetopus costaricensis* Perkins, 1979. G – dorsal part of the metathorax. H – scutellum. I–K – abdominal ventrites (I – *Eumetopus schuelkei*; J – *Eupotemus smithi* sp. nov.; K – *Epimetopus mendeli*). L–M – ovipositor (L – *Eumetopus schuelkei*; M – *Eupotemus smithi*). O – elytral punctation, slide-mounted elytra of *Epimetopus costaricensis*. P – female of *Eumetopus acutimontis* in ventral view, with the egg cases carried under the abdomen. Not to scale.

long unsegmented lateral projections (gills); abdominal sterna 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

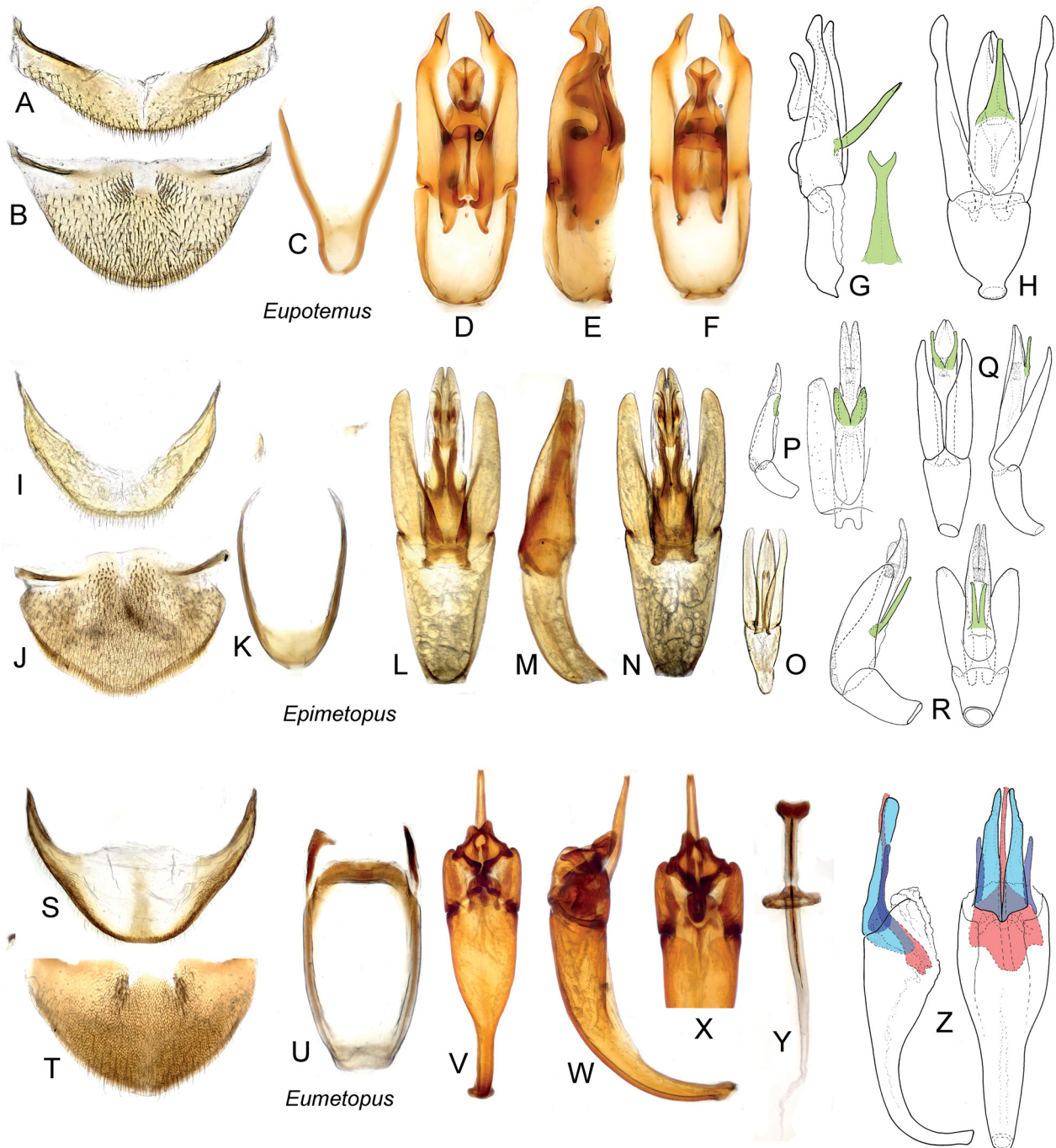


Fig. 6. Male genitalia and associated structures of Epimetopidae. A–H – *Eupotemus* Ji & Jäch, 1998 (A–F – *E. smithi* sp. nov.; G – *E. cameroonensis* sp. nov.; H – *E. carinaticollis* (Basilewsky, 1956)). I–R – *Epimetopus* Lacordaire, 1854 (I–N – *E. mendeli* Fikáček et al., 2011; O – *E. cf. burruyacu* Oliva, 1986; P – *E. multiporus* Perkins, 2012; Q – *E. clandestinus* Perkins, 2012; R – *E. thermarum* Schwarz & Barber, 1917). S–Z – *Eumetopus* Bal-four-Browne, 1949 (S–Y – *E. acutimontis* Ji & Jäch, 1998; Z – *E. bullatus* (Sharp, 1875)). A, I, S – sternite VIII; B, J, T – tergite VIII; C, K, U – sternite IX; D, L, V – aedeagus dorsally; E, M, W – aedeagus laterally; F, N, X – aedeagus ventrally (basal part omitted in X); Y – sperm pump. Color coding: green – ventral projections of the median lobe; red – median lobe; blue – paramere (pale blue – dorsal lobe; dark blue – ventral lobe). Not to scale.

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 Hydrophiloidea 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 hydrofuge 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 by 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 palpomere 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). LÜ 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,b, 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 epimetopid 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 hood with set of parallel ridges ventrally (unique for Epimetopidae but lost in *Eupotemus*); (4) mesoventrite narrow anteriorly (also present in some Helophoridae and Hydrophilidae); (5) metanepisternum 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 *Epimetopus* + *Eupotemus* lineage is strongly supported in both analyses. Its morphological synapomorphies are: tridentate mandibular apex (Figs 2D, e–f), 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 anal lobe (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 hood (Figs 3A–B), smooth lateral margin of pronotum (seen only ventrally, Fig. 3A), short meta-ventrite (Figs 3J, 5A) and indistinct metakatepisternal suture of meta-ventrite (Fig. 5A). The morphology-based analysis does not recover the monophyly of *Epimetopus*, in contrast to the DNA-based analysis in which the monophyly of *Epimetopus* is strongly supported. Mapping of morphological characters on the molecular tree (Fig. 1E) suggest three synapomorphies for *Epimetopus*: closed procoxal cavities (unique within Epimetopidae, Figs 3E, G, I), abdominal ventrite 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 *Epimetopus* (e.g., *E. venezuelensis* Perkins, 2012) were collected in standing water, typically well vegetated shallow marshes (Figs 7I–J; A. Short, pers. comm.). Females of all three genera carry their egg case on the ventral surface of the abdomen (*Epimetopus*: ROCHA 1967, COSTA et al. 1988, PERKINS 2012; *Eumetopus*: JI & JÄCH 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 hood 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 hood. These grooves would suggest rather a



Fig. 7. Biology of Epimetopidae. A–D – *Eumetopus acutimontis* Ji & Jäch, 1998 in Vietnam, Khánh Hòa Prov., Ba Ho Waterfalls National Park, 12°23.131'N 109°08.052'E: A–B – alive specimens on wet sandy shores; C – specimen buried in wet sand; D – general view of the locality. E–F – locality of *Epimetopus surinamensis* Perkins, 2012 in Suriname: Sipaliwini, Wehepai, 2°21.776'N 56°41.861'W (SR10-0904-01A) (E – general view; F – detail of sandy banks from which specimens were collected). G–H – locality of *Epimetopus simplex* Perkins, 1979 in Venezuela, Guarico, Rio San Antonio, 9°46.32'N 67°21.177'W (VZ09-0108-02A) (G – detail of gravelly shore show which specimens were collected; H – general view). I–J – marshy roadside ditch with *Epimetopus venezuelensis* Perkins, 2012 in Venezuela, Apure, ca. 1 km N Rio Claro, 7°10.162'N 67°38.69'W (AS-06-009). (I – general view; J – detail of the microhabitat). Photos by A. Sazhnev (A–C), A. Prokin (D), A. Short (E–J).

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 contrast, 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 (Sphaeriidae, Limnichidae, Georissidae, some Hydraenidae and Hydrophilidae: *Agraphydrus* Régimbart, 1903, *Laccobius* Erichson, 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 curved conical phallobase and complex multilobate parameres (Figs 6V–Z). Male sternite IX O-shaped (Fig. 6U). Asia.
..... *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.
..... *Eupotemus* Ji & Jäch, 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

Genera and species

Eupotemus Ji & Jäch, 1998

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

Eupotemus Ji & Jäch, 1998a: 95. Type species: *Eumetopus limicola* Delève, 1967 (here confirmed).

Eupotemus: Ji & Jäch (1998b); HANSEN (1999), HEBAUER (2006a), FIKÁČEK et al. (2011).

Fixation of type species according to ICZN (1999: Art. 70.3). Ji & Jäch (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 & Jäch (1998a) represents in fact a complex of sibling species (*E. limicola* group), and the specimen examined by Ji & Jäch (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 & Jäch (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 posteromesally with high projection (Fig. 3J); metaventrite between meso- and metacoxae very short (Figs 3J, 5A), posteromesally 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

- | | |
|---|---|
| <i>E. carinaticollis</i> (Basilewsky, 1956) | Burundi, DR Congo (BASILEWSKY 1956, this paper) |
| <i>E. taianus</i> sp. nov. | Côte d'Ivoire (this paper) |
| <i>E. uluguru</i> sp. nov. | Tanzania (this paper) |

***Eupotemus limicola* species group**

<i>E. bilobatus</i> sp. nov.	Nigeria (this paper)
<i>E. cameroonensis</i> sp. nov.	Cameroon (this paper)
<i>E. limicola</i> (Delève, 1967)	DR Congo (DELÈVE 1967)
<i>E. ophioglossus</i> sp. nov.	Gabon, Togo (this paper)
<i>E. smithi</i> sp. nov.	Côte d'Ivoire (this paper)

Key to species groups of *Eupotemus*

- 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. carinaticollis* group**

Eupotemus limicola* group**Eupotemus bilobatus* sp. nov.**

(Figs 8A–C, 9A–C)

Material examined. HOLOTYPE: ♂ (BMNH): 'Umuahia / J L.G / 3.ix.–4.x.1960 // C. E. Tottenham / collection / B. M. 1974-587.' PARATYPES: NIGERIA: ABIA: 1 ♂ 1 ♀ 4 spec. (BMNH, NMPC): 'Umuahia / 3.ix.–4.x.1960 // J.L. Gregory // C. E. Tottenham / collection / B. M. 1974-587'; 3 ♀♀ (BMNH): 'Umudike / J. L. Gregory / 10-13.iv.1960 // C. E. Tottenham / collection / B. M. 1974-587'.

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 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

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): 'Holo- / 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

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

	<i>E. bilobatus</i> sp. nov.	<i>E. cameroonensis</i> sp. nov.	<i>E. limicola</i> (Delève, 1967)	<i>E. ophioglossus</i> sp. nov.	<i>E. smithi</i> sp. nov.
Fork of ventral process	Shallowly bifurcate, branches short and wide.	Shallowly bifurcate, branches short and wide.	Moderately bifurcate, branches moderately long, narrow.	Deeply bifurcate, branches long and narrow.	Deeply bifurcate, branches long and narrow.
Apical disc of median lobe (length to width)	Bilobed apically, very slightly longer than wide.	Unilobed apically, >2× longer than wide.	Bilobed apically, ca. 1.5× longer than wide.	Unilobed apically, ca. 2× longer than wide.	Unilobed apically, 1.5–2.0× longer than wide.
Apex of parameres in lateral view	Simple.	Slightly widened apically.	Very broad apically.	Slightly widened apically.	Very broad apically.

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).

***Eupotemus limicola* (Delève, 1967)**

(Figs 8M–Q, 9G–I)

Material examined. HOLOTYPE: ♂ (MRAC): 'HOLOTYPE // Biot. No 14 / banks de / vase // I. R. S. A. C. – MUS. CONGO / Kivu: Kitutu, terr. Mwenga / riv. Lubushwa 650 m / B. 14 N. Leleup 12-IV-58 // TYPE // J. Delève det. 1966 / Eumetopus / limicola n. sp. // Aedeagus / drawn by / P. D. Perkins'. PARATYPES: 9 ♀♀ (MRAC), 1 ♂ 1 ♀ (IRSNB): same locality data as the holotype.

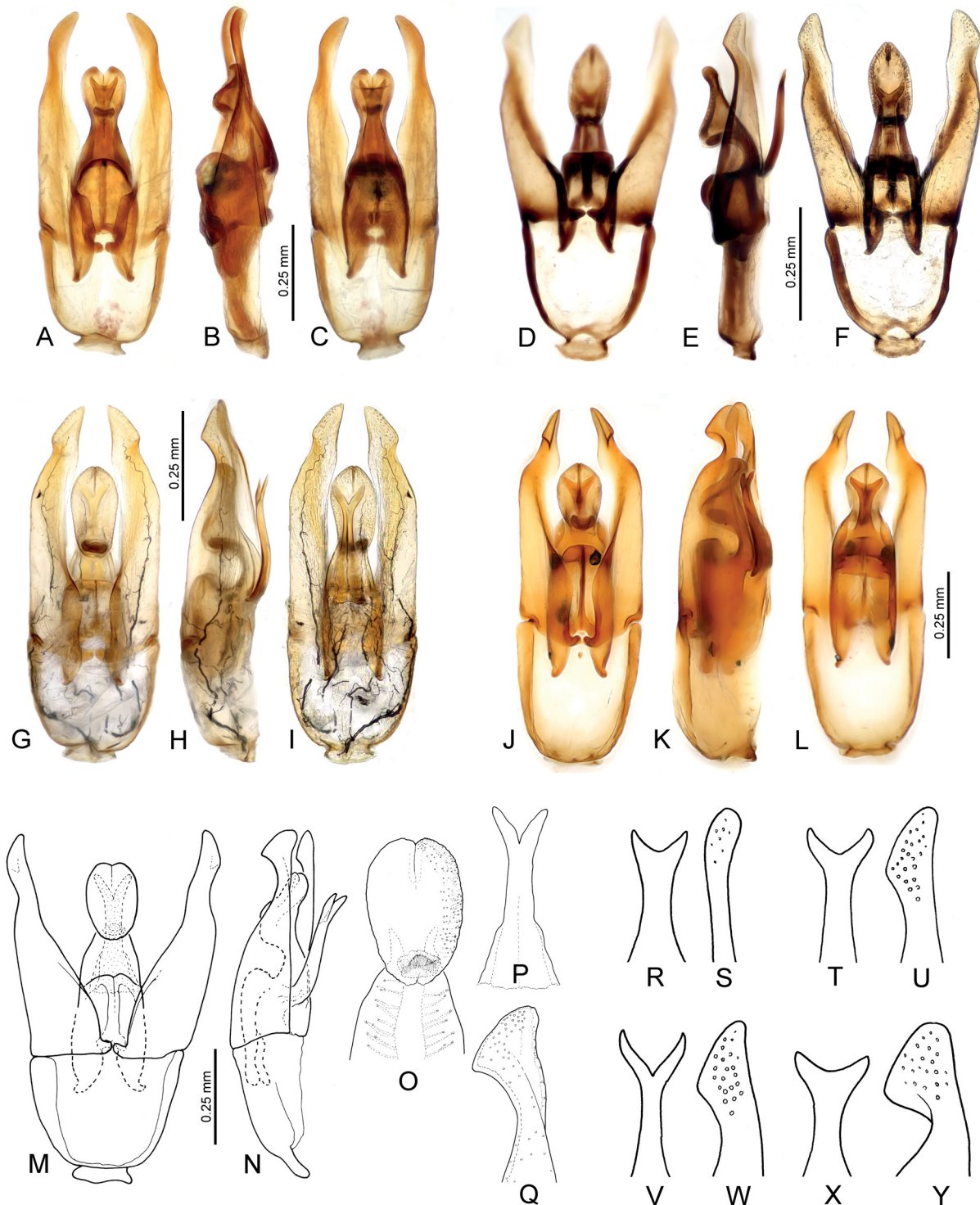


Fig. 8. Male genitalia of the species of the *Eupotemus limicola* species group, holotypes. A–C, R–S – *E. bilobatus* sp. nov.; D–F, T–U – *E. cameroonensis* sp. nov.; G–I, V–W – *E. ophioglossus* sp. nov.; J–L, X–Y – *E. smithi* sp. nov.; M–Q – *E. limicola* (Delève, 1967). A, D, G, J, M – dorsal view; B, E, H, K, N – lateral view; C, F, I, L – ventral view; O – apex of the median lobe, dorsal view; P, R, T, V, X – fork of the median lobe; Q, S, U, W, Y – apex of parameres in lateral view.

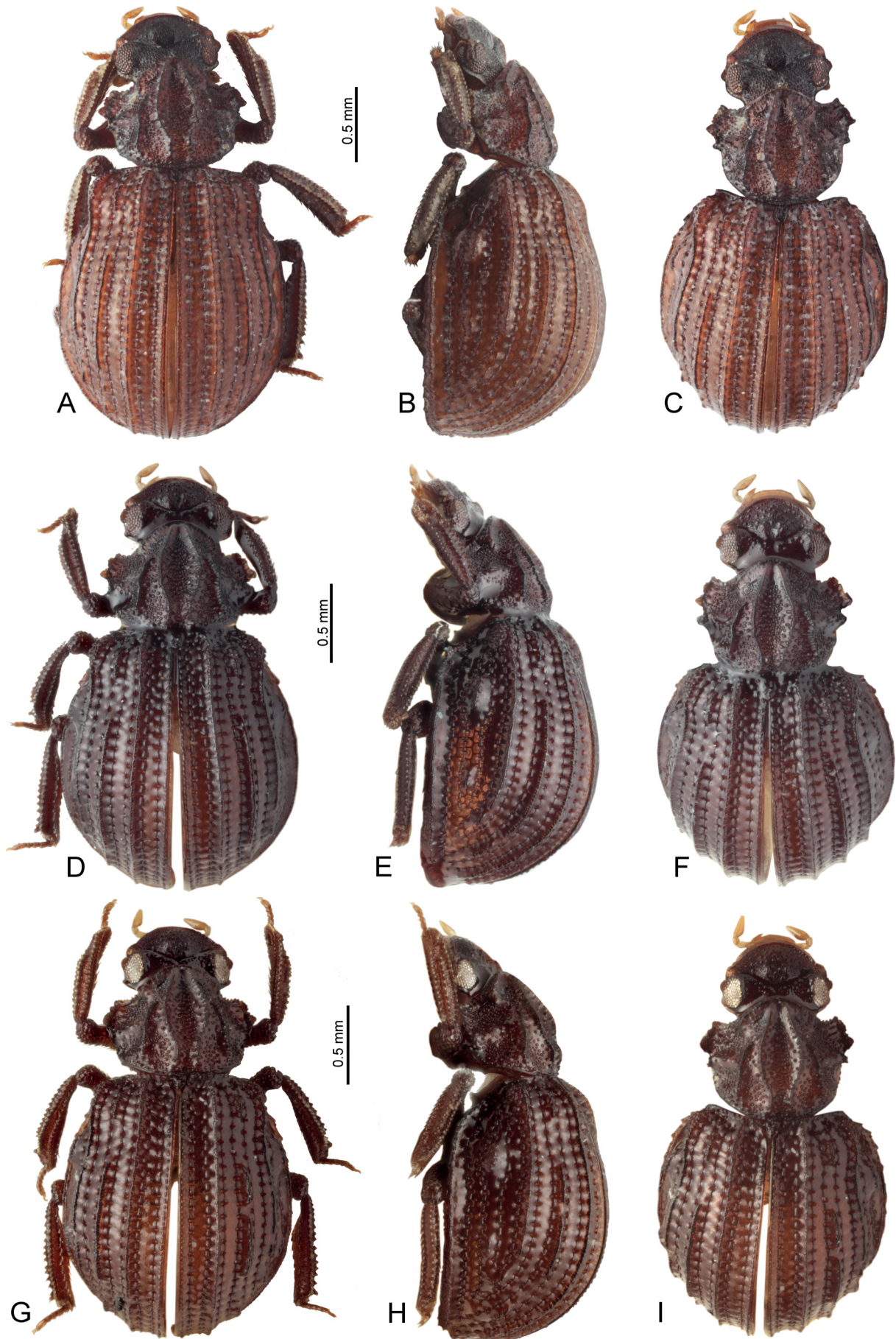


Fig. 9. Habitus photographs of the species of the *Eupotemus limicola* species group, holotypes: A–C – *E. bilobatus* sp. nov.; D–F – *E. cameroonensis* sp. nov.; G–I – *E. limicola* (Delève, 1967).

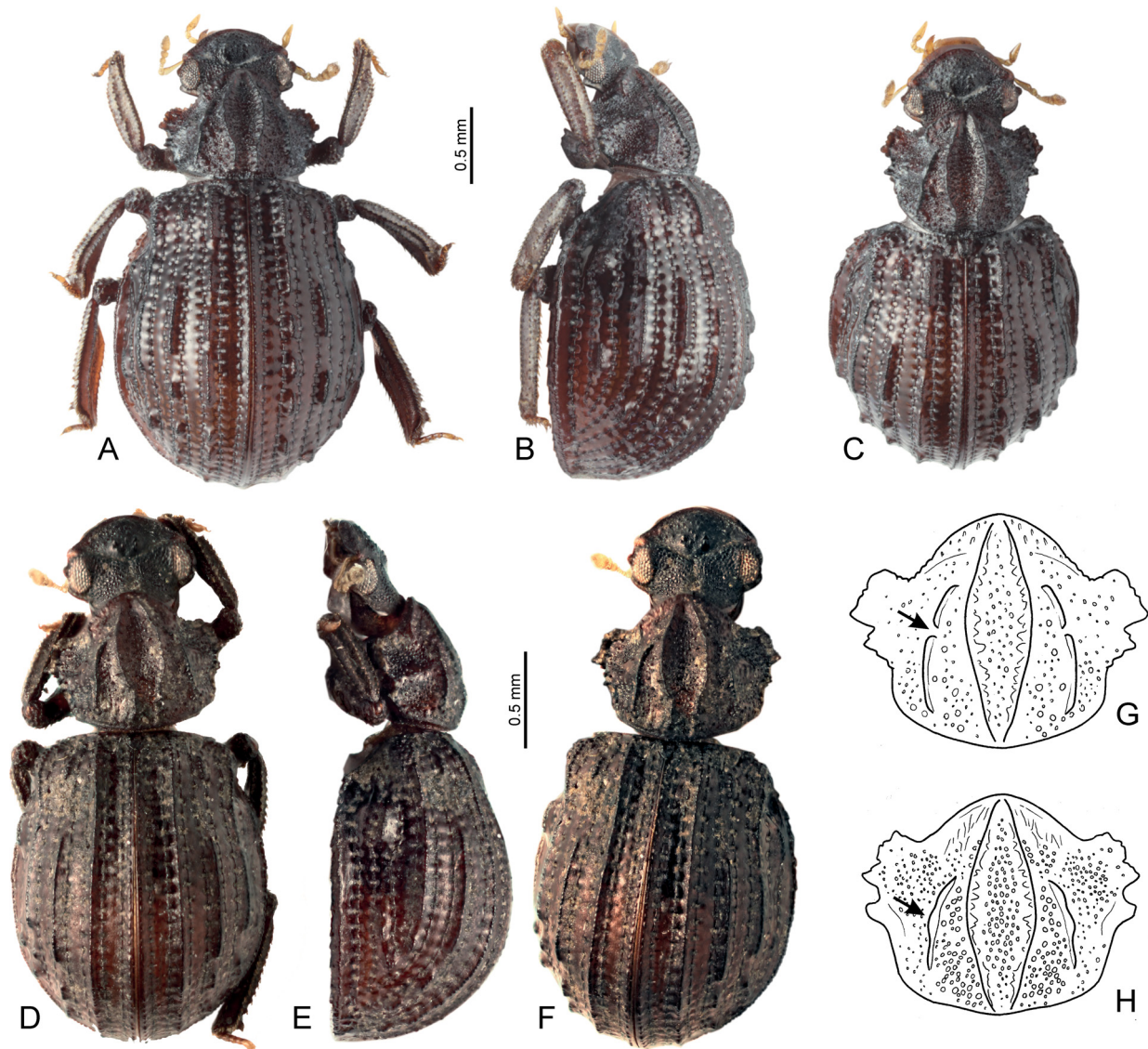


Fig. 10. Habitus photographs of the species of the *Eupotemus limicola* species group, holotypes (A–F) and differences between species groups in pronotal morphology (G–H). A–C – *E. smithi* sp. nov.; D–F – *E. ophioglossus* sp. nov.; G–I – pronotal sculpture: G – *E. carinaticollis* species group; H – *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 DELÈVE (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 / Konda (village), 9.II.2006 / leg. Komarek & Hougue (28) // 06°58'05.3"N 00°34'18.2"E, ca. 510 m a.s.l. / small stream in prim. forest'.

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 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., / Geiser, M., Moretto, P., leg., / BMNH(E) 2016-109, / Trip Ref. CI-003 (ANHRT 17)'. PARATYPES: 14 spec. (incl. DNA voucher MF2207.W) (BMNH, NMPC): same data as the holotype.; 1 spec. (BMNH): 'CÔTE D'IVOIRE, 380m, / Yéalé Village, Mt. Nimba / 07°31'35.3"N 08°25'20.1"W, / 8.V.2016 // Aristophanous, M., / Geiser, M., Moretto, P., leg., / BMNH(E) 2016-109, Trip / Ref.:CI-003 (ANHRT 17)'; 1 ♂ (brachypterous) (BMNH): 'CÔTE 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'.

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 8J–L, X–Y) differs from all species except *E. limicola* by the largely 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 Yéalé 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 specimen 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**

Material examined. CAMEROON: 1 ♀ (NMPC): Mamengole, iv.1949, lgt. Tesárek. GABON: 1 ♀ (NHMW): Batéké Plateau National Park, camp Ntsa, 'forêt dense' [= dense forest], 8–13.ix.2008, A. Bilardo lgt.

Eupotemus carinaticollis* group**Eupotemus carinaticollis* (Basilewsky, 1956)**

(Figs 11A–C, 12A–C)

Material examined. HOLOTYPE: ♂ (MRAC): 'HOLOTYPUS // COLL. MUS. CONGO / Urundi: Rumonge 800 m / 7-III-1953 / P. Basilewsky // Georyssus / carinaticollis / n. sp. Type / P. Basilewsky det., 19 // J. Delève det. 1966 / Eumetopus / carinaticollis / Basilewsky // Aedeagus / drawn by / P. D. Perkins'.

Additional specimens examined: DEMOCRATIC REPUBLIC OF THE CONGO: 1 ♂ 1 ♀ (MRAC): Kivu: Uvira, vest. de forêt sclerophylle [= remnants of a sclerophyll forest] / I-1958 N. Leleup.

Differential diagnosis. Very similar to the other species of the *E. carinaticollis* species group from which it can

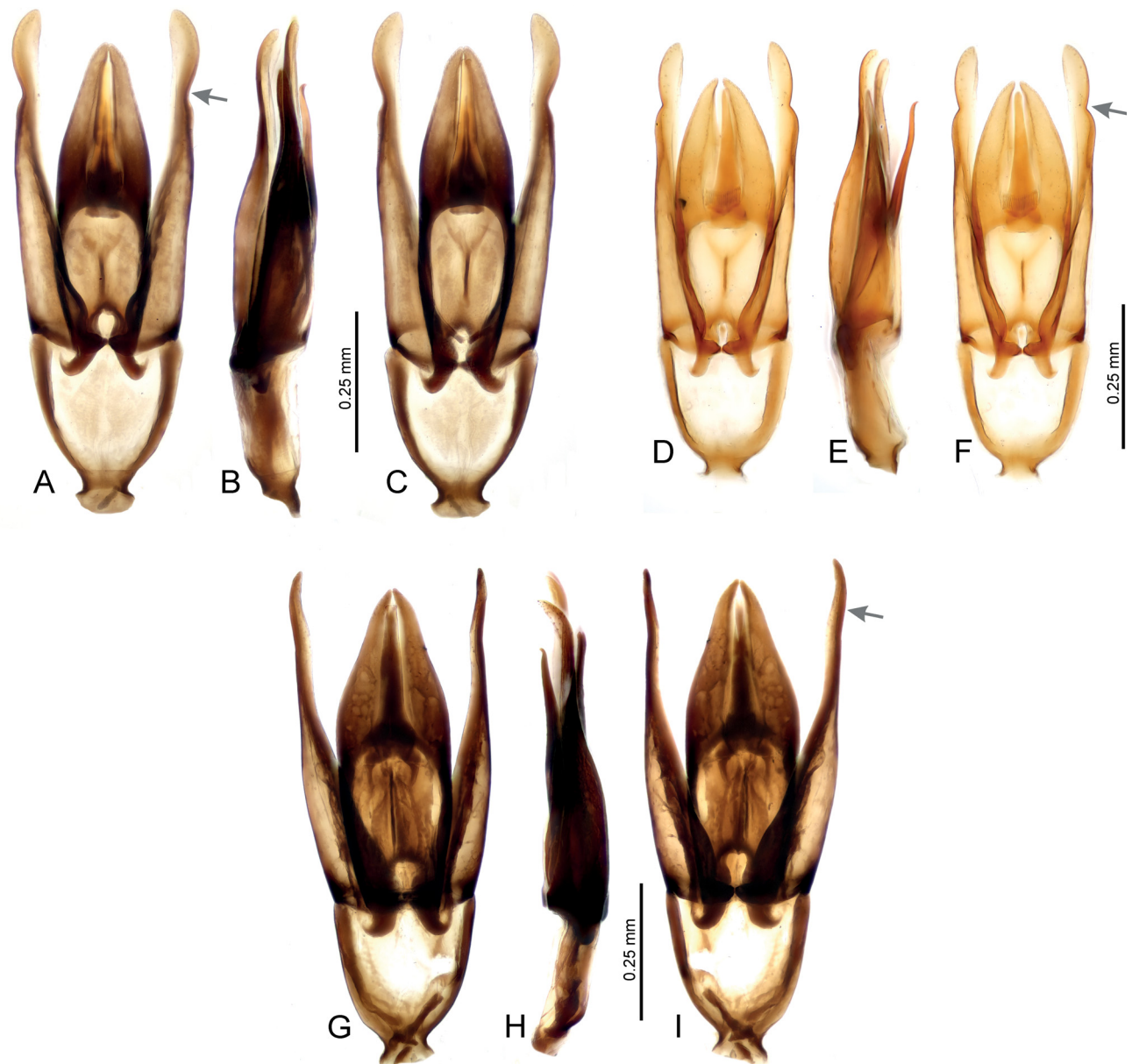


Fig. 11. Male genitalia of the *Eupotemus carinaticollis* species group, holotypes. A–C – *E. carinaticollis* (Basilevsky, 1956); D–F – *E. taianus* sp. nov.; G–I – *E. uluguru* sp. nov. A, D, G – dorsal view; B, E, H – lateral view; C, F, I – ventral view.

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, / Taï NP, Taï 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* (Basilevsky, 1956); D–F – *E. uluguru* sp. nov.; G–I – *E. taianus* sp. nov.

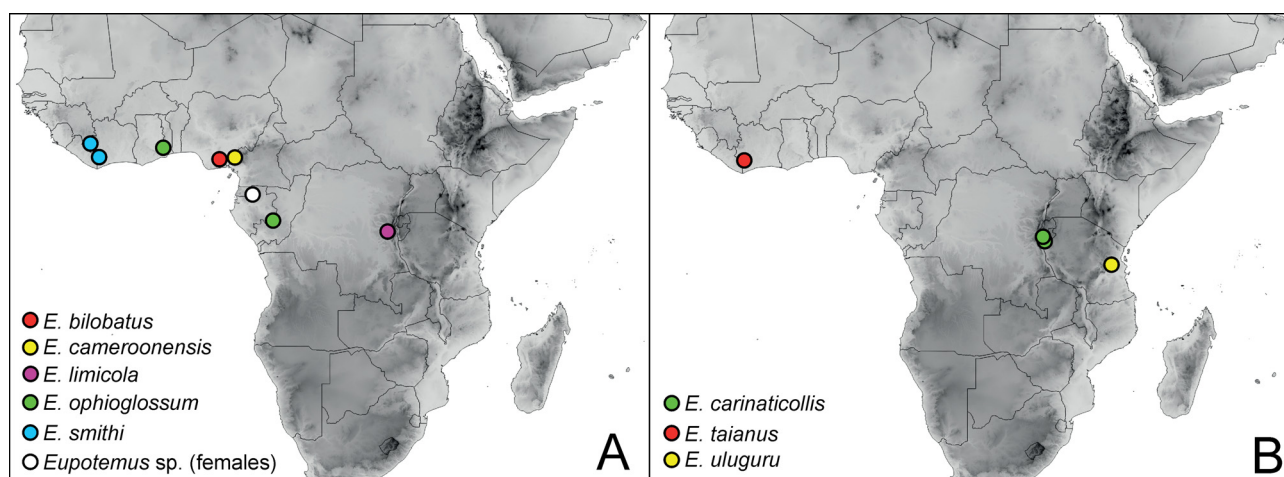


Fig. 13. Known distribution of *Eupotemus* species. A – species of *E. limicola* species group; B – species of *E. carinaticollis* species group.

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

	<i>E. carinaticollis</i>	<i>E. uluguru</i> sp. nov.	<i>E. taianus</i> sp. nov.
Median lobe proportions (length to width)	Narrow (>3× longer than wide).	Narrow (>3× longer than wide).	Wide (<3× longer than wide).
Sides of median lobe subapically	Straight to very weakly convex.	Straight to weakly concave.	Strongly convex.
Apex of parameres in dorsal view	Constricted subapically, widened at apex.	Not constricted, narrow at apex.	Constricted subapically, widened at apex.

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.

Etyymology. 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).

Eupotemus uluguru sp. nov.

(Figs 11G–I, 12D–F)

Material examined. HOLOTYPE: ♂ (MRAC): 'HOLOTYPUS // Coll. Mus. Tervuren / Mission Mts. Uluguru / L. Berger, N. Leleup / J. Debecker V / VIII/71 // Tanzanie: Mts. Uluguru / Morogoro Campus Fac. / Agric. Piège. Lum. U.V. / alt. 600 m V-VI/71 // J. Delève det. 1966 / Eumetopus / carinaticollis (Basil.) // HOLOTYPE / Afrometopus / uluguru / P. D. Perkins'. PARATYPE: 1 ♂ (NHMW): 'TANZANIA: Morogoro / 560 m a.s.l. / light

trap, III-IV.1987 / coll. Pócs & Sontera // Eupotemus / carinaticollis (Bas.) / det. M. Jäch 1999'.

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. Makranczy, 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 (Figs 11G–I): 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.

Etyymology. 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

(Figs 2M–Q; 3C–D, L–O; 4A–B, D, H, L–M; 5C, I, L; 6S–Z; 7A–C; 14–15)

Eumetopus Balfour-Browne, 1949: 13. Type species: *Sepidulum bullatum* Sharp, 1875.

Eumetopus: HANSEN (1991), Ji & JÄCH (1998a,b), HANSEN (1999), JÄCH (2002), SKALE & JÄCH (2003), HANSEN (2004), FIKÁČEK & RYNDEVICH (2015).

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 palpomere 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 wide, hood covering head forming anterior third of its length; ventral surface of the hood with set of parallel ridges (Fig. 3D); prosternum (Fig. 3C) slightly elevated medially, ca. 0.25× as long as procoxal cavity; procoxal cavity open posteriorly (Fig. 3C); elytron with scutellary stria (Fig. 15); elytra with tubercles on alternate intervals (Fig. 15); mesanepisterna narrowly separated by anterior portion of mesoventrite; mesoventrite posteromesally with high bulge (Fig. 3L); metaventrite ca. as long as mesocoxa, posteromesally with large central and a pair of lateral smooth elevated areas (Fig. 3L); middle and hind femora with posterior spine (Fig. 4M); phallobase long and conical; parameres subdivided into dorsal and ventral lobe; median lobe thin, peg-like, without projections (Figs 6V–Z); sperm pump present (Fig. 6Y); male sternite IX circular (Fig. 6U).

Identification. The genus was revised by Ji & JÄCH (1998) who also illustrated the male genitalia for all species known at that time. One additional species was described by JÄCH (2002) who provided an updated identification key. The latest recognized species was described by SKALE & JÄCH (2003) and compared to its closest relative.

List of species (8 described species)

<i>E. acutimontis</i> Ji & Jäch, 1998	China (Hainan; Ji & JÄCH 1998a), Vietnam (this paper)
<i>E. asperatus</i> (Champion, 1919)	India: Himachal Pradesh, Uttarakhand; Nepal (Ji & JÄCH 1998a, SKALE & JÄCH 2003, HEBAUER 2006b, this paper)
<i>E. bullatus</i> (Sharp, 1875)	India: Maharashtra (this paper).
<i>E. flavidulus</i> (Sharp, 1890)	India: Andhra Pradesh, Kerala, Maharashtra, Meghalaya, Odisha; Sri Lanka (Ji & JÄCH 1998a, this paper)
<i>E. maindroni</i> (Régimbart, 1903)	India: Gujarat, Maharashtra, Tamil Nadu (RÉGIMBART 1903, Ji & JÄCH 1998a, this paper)
<i>E. schuelkei</i> Jäch, 2002	Laos (JÄCH 2002)
<i>E. tibialis</i> Ji & Jäch, 1998	northern Thailand (Ji & JÄCH 1998a)
<i>E. weigeli</i> Skale & Jäch, 2003	Nepal (SKALE & JÄCH 2003), India: Uttarakhand (this paper).

Eumetopus acutimontis Ji & Jäch, 1998

(Figs 6S–Y, 14A, 15A, I)

Material examined. VIETNAM: KHÁNH HÒA PROV.: 1 ♂ 1 ♀ 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 ♂♂ 9 ♀♀ (2 ♀♀ with egg case) (IBIW, NMPC): same locality, 2.v.2018,

A. Prokin & A. Sazhnev leg.; 4 ♂♂ 1 ♀ with egg case (IBIW): same locality, 13.iv.2019, A. Prokin lgt.

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 & JÄCH (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. (Limnichiidae) 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)

(Figs 14B, 15B)

Material examined. INDIA: UTTARAKHAND: 5 spec. (NHMW, NMPC): 30 km NNE Bageshwar, west of Loharket Village, 1800–1900 m, 24.vi.2003, Z. Kejval & M. Trýzna lgt.

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

Eumetopus bullatus (Sharp, 1875)

(Figs 6Z, 14C, 15C)

Material examined. INDIA: MAHARASHTRA: 4 ♂♂ 4 ♀♀ (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.], riverside, 40 m, 22.v.2006, Z. Kejval lgt.

Comments. The species was so far only known from the holotype with the type locality 'India' (SHARP 1875, Ji & JÄCH 1998). This is the first precise record, confirming the occurrence in India.

Eumetopus flavidulus (Sharp, 1890)

(Figs 14D, 15D, J)

Material examined. INDIA: MAHARASHTRA: 4 ♂♂ 4 ♀♀ (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.], riverside, 40 m, 22.v.2006, Z. Kejval lgt. **ANDHRA PRADESH:** 1 ♂ 1 ♀ (SLC): Vijayawada, Krishna River, 16.511°N 80.614°E, 16.ii.2014, K. Tomkovich lgt.

Comments. First record for Andhra Pradesh and Maharashtra.

Eumetopus maindroni (Régimbart, 1903)

(Figs 14E, 15E)

Material examined. INDIA: MAHARASHTRA: 3 ♂♂ 1 ♀ (NHMW): 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.], riverside, 40 m, 22.v.2006, Z. Kejval lgt. **GUJARAT:** 1 ♂ 5 ♀♀ (SLC): Junagadh, Girmar Mt., 21.526°N 70.48°E, 20–31.x.2012, at light, K. Tomkovich lgt.

Comments. The species was so far known only from the type specimens (RÉGIMBART 1903, Ji & JÄCH 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)

Material examined. THAILAND: RANONG: 1 ♀ (NMPC): Ban Na env., 9°34'N 98°42'E, K. Majer lgt.

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.

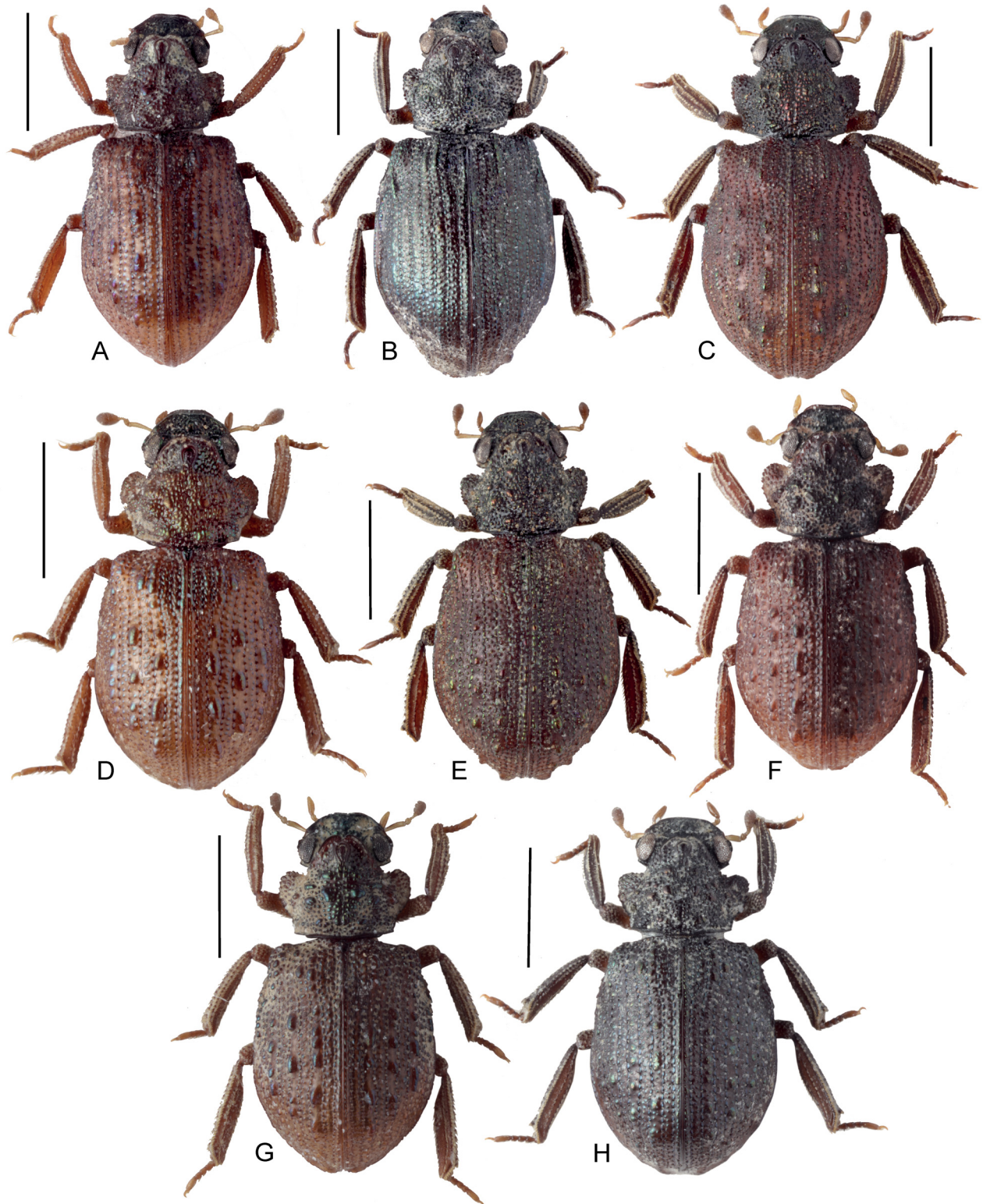


Fig. 14. Habitus photographs of the known species of *Eumetopus* Balfour-Browne, 1949. A – *E. acutimontis* Ji & Jäch, 1998, paratype from China: Hainan (NHMW); B – *E. asperatus* (Champion, 1919), specimen from Nepal: Koshi Valley (NMPC); C – *E. bullatus* (Sharp, 1875), specimen from India: Maharashtra, Sawantwadi (NMPC); D – *E. flavidulus* (Sharp, 1890), specimen from India: Meghalaya, Bagmara (NHMW); E – *E. maindroni* (Régimbart, 1903), specimen from India: Maharashtra, Sawantwadi (NHMW); F – *E. schuelkei* Jäch, 2002, paratype from central Laos; G – *E. tibialis* Ji & Jäch, 1998 from Thailand, Ban Na env. (NMPC); H – *E. weigeli* Skale & Jäch, 2003, holotype from Nepal (NHMW). Scale bars: 1 mm.

Eumetopus weigeli Skale & Jäch, 2003

(Figs 14H, 15H, L)

Material examined. INDIA: UTTARAKHAND: 5 ♂♂ 2 ♀♀ (1 ♀ with egg case), 1 spec. (BMNH): 'India: U.P., Dehra Dun, Phandowala. Suawa R. 1.iv.1928. H.G.Champion. // Brit.Mus. 1928-518'.

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.

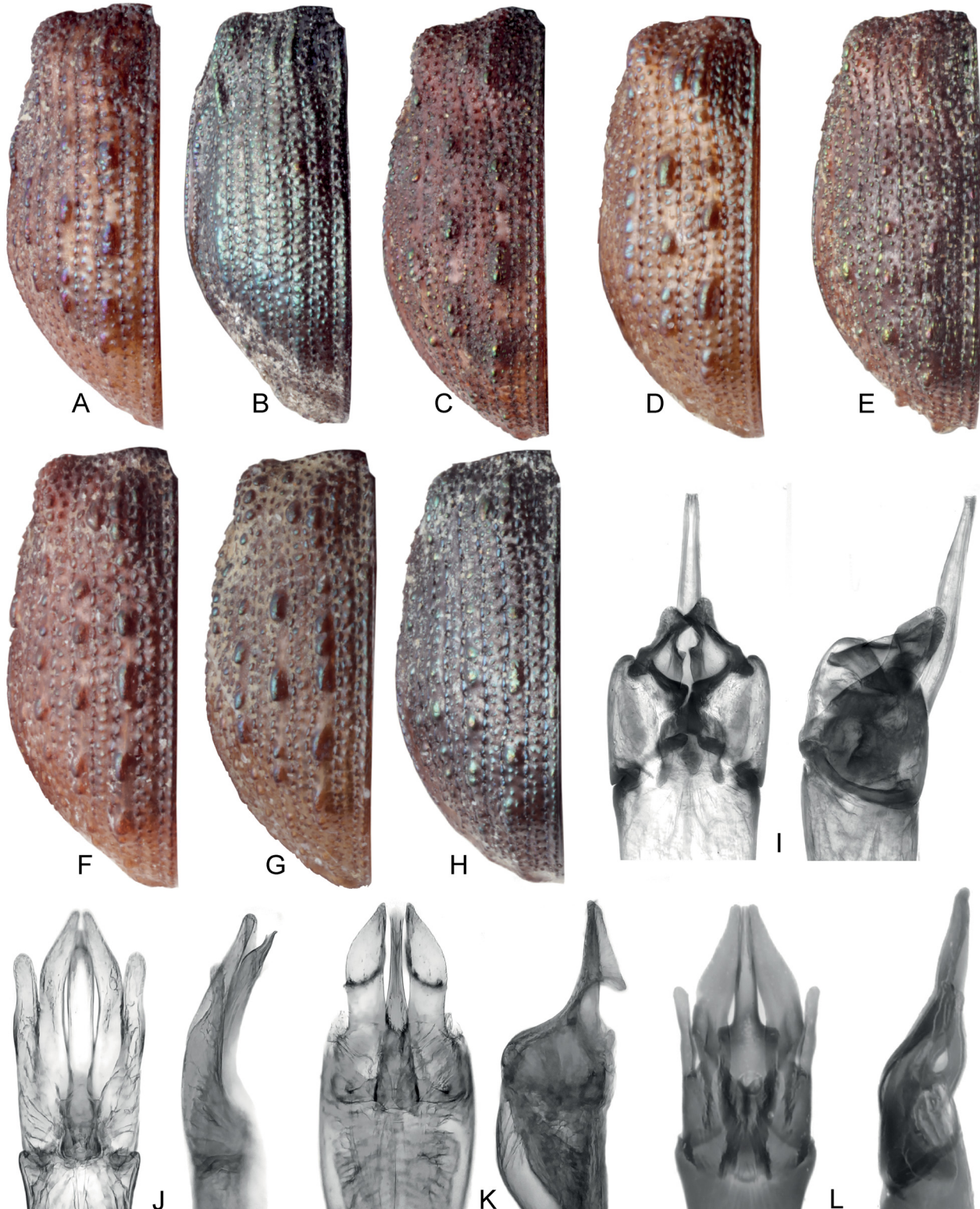


Fig. 15. Elytral sculpture and male genitalia of *Eumetopus* Balfour-Browne, 1949. A–H – elytral sculpture, same specimens as in Fig. 14: A – *E. acutimontis* Ji & Jäch, 1998; B – *E. asperatus* (Champion, 1919); C – *E. bullatus* (Sharp, 1875); D – *E. flavidulus* (Sharp, 1890); E – *E. maindroni* (Régimbart, 1903); F – *E. schuelkei* Jäch, 2002; G – *E. tibialis* Ji & Jäch, 1998; H – *E. weigeli* Skale & Jäch, 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.

***Epimetopus* Lacordaire, 1854**

(Figs 2R–Z, a–l; 3E–I, K, P; 4E–G, I–J, N–P, R; 5B, E–F, G–H, K, O–P; 6I–R; 16)

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. trogoides* 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 procoxal cavity (Figs 3E, G); procoxal cavity closed posteriorly (Figs 3E, G, I); mesanepisterna narrowly separated by anterior portion of mesoventrite (*E. costatus* group; Fig. 3K) or meeting mesally (*E. mendeli* group; Fig. 5B) (other groups not examined); mesoventrite posteromesally 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.

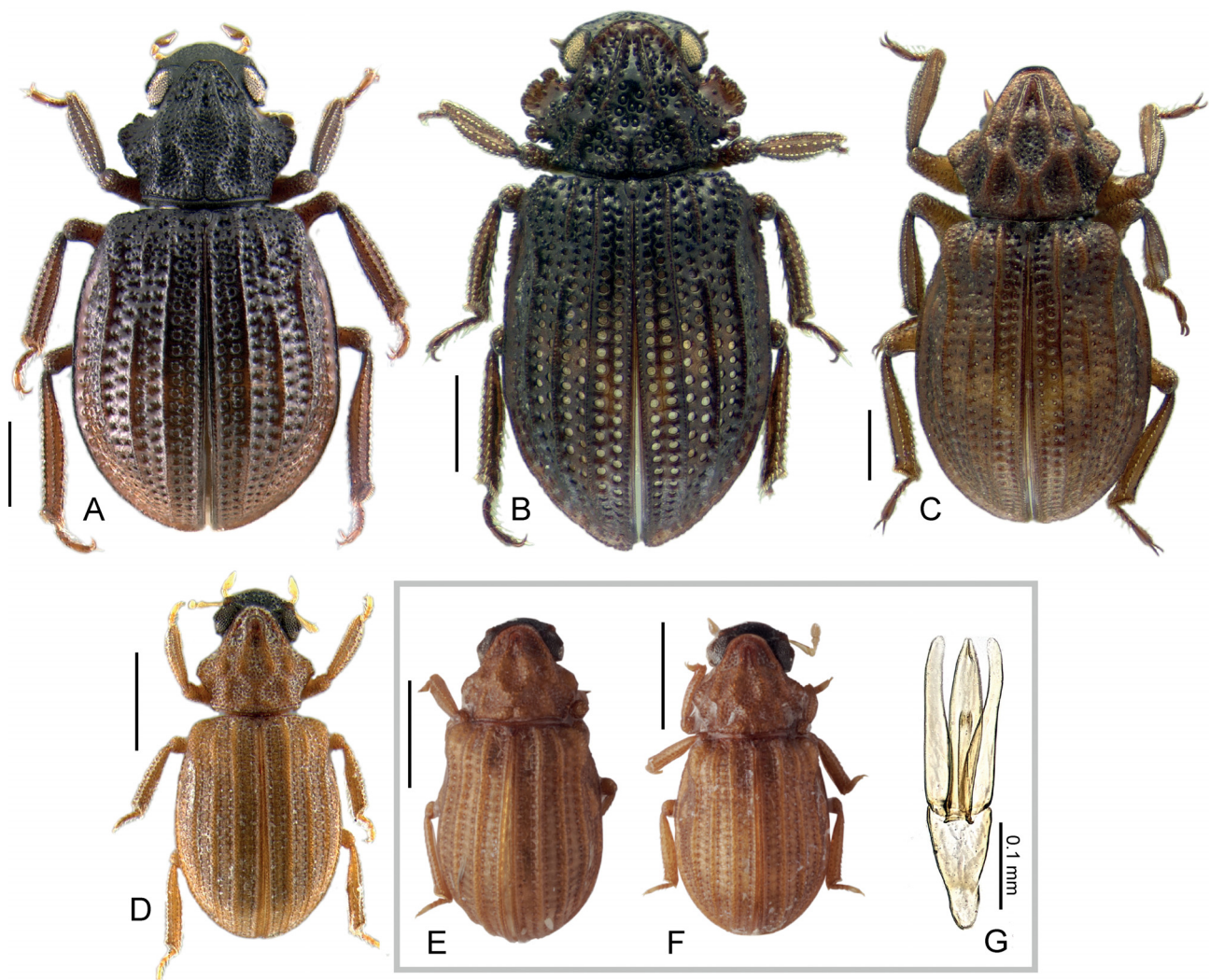


Fig. 16. Photographs of *Epimetopus* species, including two specimens of questionable provenance (E–G). A – *E. flavicaptus* Fikáček, Barclay & Perkins, 2011; B – *E. deceptus* Perkins, 2012; C – *E. tridens* Perkins, 2012; D – *E. hintoni* Balfour-Browne, 1949; E – *Epimetopus* sp. ('Zambia'); F – *E. cf. burruyacu* Oliva, 1986 ('Saudi Arabia') (F – dorsal view; G – aedeagus). Scale bars for A–F = 0.5 mm. A–D adopted from PERKINS (2012).

List of species (56 described species)

***Epimetopus costatus* species group**

- E. acuminatus* Perkins, 2012 Guatemala (PERKINS 2012)
E. angustus Perkins, 2012 Panama, Venezuela, Ecuador, Peru (PERKINS 2012)
E. apocinus Perkins, 2012 Mexico, Costa Rica (PERKINS 1979, 2012)
E. arizonicus Perkins, 2012 USA (Arizona) (PERKINS 2012)
E. ballatoris Perkins, 2012 Venezuela, Trinidad and Tobago (PERKINS 2012)
E. bifidus Perkins, 2012 Mexico (PERKINS 2012)
E. burruyacu Oliva, 1986 Argentina (Tucuman) (OLIVA 1986)
E. costaricensis Perkins, 1979 Mexico, Belize, Costa Rica, Guatemala, Honduras, Panama (PERKINS 1979, 2012)
E. costatus (Leconte, 1874) USA (Texas, Arkansas) (PERKINS 2012)
E. ecuadoriensis Perkins, 2012 Ecuador (PERKINS 2012)
E. fisheri Perkins, 1979 Mexico, Honduras (PERKINS 2012), USA (Arizona) (PERKINS 1979)
E. hintoni Balfour-Browne, 1949 Argentina (OLIVA 1986, needs confirmation), Bolivia (BALFOUR-BROWNE 1949, PERKINS 2012)
E. inaequalis Perkins, 2012 Ecuador, Peru (PERKINS 2012)
E. lacordairei Orchymont, 1933 Bolivia, Brazil (Mato Grosso), Paraguay (ORCHYMONT 1933, PERKINS 2012)
E. latilobus Perkins, 2012 Costa Rica (PERKINS 2012)
E. latisoides Perkins, 2012 Panama (PERKINS 2012)
E. latus Perkins, 2012 Colombia, Venezuela (PERKINS 2012)
E. lobilatus Perkins, 2012 Costa Rica (PERKINS 2012)
E. microporus Perkins, 2012 Honduras, Panama (PERKINS 2012)
E. mucronatus Perkins, 2012 Mexico, Honduras (PERKINS 2012)
E. oaxacus Perkins, 2012 Mexico (PERKINS 2012)
E. panamensis Perkins, 1979 Panama (PERKINS 1979, 2012)
E. plicatus Perkins, 2012 Venezuela (PERKINS 2012)
E. punctipennis Perkins, 1979 USA (Arizona, Texas, Oklahoma), northern Mexico (PERKINS 1979, 2012)
E. rectus Perkins, 2012 Costa Rica (PERKINS 2012)
E. robustus Perkins, 2012 Panama (PERKINS 2012)
E. simplex Perkins, 1979 Costa Rica, Nicaragua, Panama, Venezuela (PERKINS 1979, 2012)
E. spatulus Perkins, 2012 Peru (PERKINS 2012)
E. steineri Perkins, 2012 Ecuador (PERKINS 2012)
E. transversoides Perkins, 2012 Peru (PERKINS 2012)
E. transversus Perkins, 2012 Bolivia (PERKINS 2012)
E. trilobus Perkins, 2012 Venezuela (PERKINS 2012)

***Epimetopus mendeli* species group**

- E. angulatus* Balfour-Browne, 1949 Bolivia (BALFOUR-BROWNE 1949, PERKINS 2012)
E. coleuncus Perkins, 2012 Argentina, Bolivia (? OLIVA 1986 as *E. angulatus*, PERKINS 2012)
E. flavicaptus Fikáček, Barclay & Perkins, 2011 Ecuador (FIKÁČEK et al. 2011)
E. graniger (Mulsant, 1851) Colombia (PERKINS 2012)
E. mendeli Fikáček, Barclay & Perkins, 2011 Peru (FIKÁČEK et al. 2011, PERKINS 2012)
E. peruvianus Perkins, 2012 Peru (PERKINS 2012)

***E. thermanum* species group**

- E. arcuatus* Perkins, 2012 Paraguay (PERKINS 2012)
E. balfourbrownei Rocha, 1969 Brazil (Mato Grosso) (ROCHA 1969, PERKINS 2012)
E. clypeatus Perkins, 2012 Guyana (PERKINS 2012)
E. surinamensis Perkins, 2012 Suriname (PERKINS 2012)
E. thermanum Schwarz & Barber, 1917 USA (Arizona, Texas), Mexico, Belize, Guatemala, Costa Rica, Panama, Venezuela, (SCHWARZ & BARBER 1918, ROCHA 1969, PERKINS 2012)

***Epimetopus plaumanni* species group**

- E. multiportus* Perkins, 2012 Uruguay, Paraguay (PERKINS 2012)
E. plaumanni (Costa Lima, 1954) Brazil (Santa Catarina, Nova Teutonia) (COSTA LIMA 1954, PERKINS 2012)
E. vianai Balfour-Browne, 1949 Argentina (BALFOUR-BROWNE 1949, OLIVA 1986, PERKINS 2012)
E. vulpinus Perkins, 2012 Brazil (Rio Grande do Sul), Uruguay (PERKINS 2012)

***Epimetopus lanceolatus* species group**

- E. lanceolatus* Perkins, 2012 Brazil (Mato Grosso), Paraguay (PERKINS 2012)
E. lanceolatus Perkins, 2012 Brazil (Mato Grosso) (PERKINS 2012)

***Epimetopus trogoides* species group**

- E. clandestinus* Perkins, 2012 Brazil (Mato Grosso), Venezuela (PERKINS 2012)
E. deceptus Perkins, 2012 Brazil (Mato Grosso) (PERKINS 2012)
E. fimbriatus Perkins, 2012 Brazil (Mato Grosso) (PERKINS 2012)
E. tridens Perkins, 2012 Brazil (São Paulo) (PERKINS 2012)
E. trogoides (Sharp, 1874) Brazil (Mato Grosso, São Paulo) (PERKINS 2012); records by ROCHA (1969) from Brazil and by OLIVA (1986) from Argentina need verification
E. venezuelensis Perkins, 2012 Venezuela (PERKINS 2012)

***Epimetopus tuberculatus* species group**

- E. tuberculatus* Rocha, 1969 Brazil (Minas Gerais) (ROCHA 1969, PERKINS 2012)

Records of *Epimetopus* from Africa and the Arabian Peninsula

Specimens examined. ZAMBIA: 1 ♀ (BMNH): Kabwe, Kasanka NP, 12°32'28"S 30°12'42"E, light trap – Edwards funnel, 30.xi.–1.xii.2012, Smith & Takano lgt. **SAUDI ARABIA:** 1 ♂ (NMPC): Jizan Prov., 'Wadi Atoud', 8.ii.2016, 17°48'N 42°22'E, 245 m, J. Bezděk & D. Král lgt.

Comments. Both specimens belong to the *Epimetopus costatus* species group, i.e. the group for which the morphology of the male genitalia needs to be examined for species identification. The specimen from Zambia (Fig. 16E) is a female and hence cannot be identified. The specimen from Saudi Arabia (Figs 16F–G) seems to correspond to *E. burruyacu*, i.e. the species endemic to Argentina. Both specimens were collected at light. We contacted the collectors of both specimens who excluded the possibility of confusing or mixing the samples with those from South America. The specimen from Saudi Arabia is from the same collecting event (same collectors, date and locality data) as the four specimens of the South American (likely Argentinian) *Chaetarthria* reported by FIKÁČEK & LIU (2019: 251). Most likely, these specimens have been mislabeled.

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 *Eupotemus*. 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 & FALAMARZI 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 palpomere 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 *Epimetopus* (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 (Laccobiini 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 *Epimetopus* 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 *Epimetopus* in head and mouthpart morphology and in the development of the larval 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 *Epimetopus* (Figs 1B–C). In contrast, the DNA-based analysis indicated *Epimetopus* 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 PERKINS 2012). Additional studies are needed to understand the evolution of these characters within the genus and to confirm the monophyly of *Epimetopus*.

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Electronically archived data

- Supplementary File S1.** Video of a living specimen of *Eumetopus acutimontis* Ji & Jäch, 1998 in Vietnam, Khánh Hòa Prov., Ba Ho Waterfalls National Park, 12°23.131'N 109°08.052'E.
Link to the file on the journal webpage. https://www.aemnp.eu/acta-entomologica/61-1/61_1_1.html
Link to Youtube: <https://youtu.be/Ua2uxt8Ar0>
- 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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