ARTHROPOD SYSTEMATICS & PHYLOGENY

78 (3): 427–444
2020

SENCKENBERG

Kruia rediscovered: phylogenetic implications, larval morphology, and biology of an enigmatic hydrophilid beetle from western Africa (Coleoptera: Hydrophilidae)

Martin Fikáček[1,2], Qing-Hao Zhao*[,3], Ishmeal N. Kobe[4] & Vasily Grebennikov[5]

[1] Department of Entomology, National Museum, Cirkusová 1740, CZ-19100 Praha 9, Czech Republic — [2] Department of Zoology, Faculty of Science, Charles University, Viničná 7, CZ-12844, Praha 2, Czech Republic; Martin Fikáček [mfikacek@gmail.com] — [3] Laboratory of Systematic Entomology, College of Life Sciences, Shanghai Normal University, 100 Guilin Road, Shanghai, 200234, China; Qing-Hao Zhao * [qinghaozhao1997@gmail.com] — [4] Department of Ecology, Faculty of Science, Charles University, Viničná 7, CZ-12844, Praha 2, Czech Republic; Ishmeal N. Kobe [kobe.ishmeal@gmail.com] — [5] Canadian Food Inspection Agency, 960 Carling Ave., Ottawa, ON, K1A 0Y9, Canada; Vasily Grebennikov [vasily.grebennikov@canada.ca] — * Corresponding author

Accepted on October 28, 2020.
Published online at www.senckenberg.de/arthropod-systematics on December 4, 2020.

Editors in charge: Sergio Perez Gonzales & Marianna Simões

Abstract. The enigmatic terrestrial water scavenger beetle (Hydrophilidae: Sphaeridiinae: Coelostomatini) of the genus *Kruia* Spangler & Perkins, 1981 was known by a single specimen from Liberia. We rediscovered it at two forested localities in Cameroon (Mt. Cameroon and Mt. Kupe, both of volcanic origin). Adults and larvae of a new species were collected by sifting forest leaf litter. To reveal the phylogenetic position of *Kruia*, we analyzed a dataset comprising 32 species (incl. 29 of the Coelostomatini) and seven DNA fragments. We recovered three strongly supported monophyla (*Dactylosternum*, *Coelostoma* and the Neotropical clade of Coelostomatini genera), with *Kruia* nested within *Dactylosternum* Wollaston, 1854, as sister of *D. abdominale* (Fabricius 1792). Despite of striking differences, *Kruia* adults share a unique reduction in the number of antennomeres from nine to eight with some species of the *D. abdominale* group. We, therefore, consider the genus-group name *Kruia* a junior synonym of *Dactylosternum*. We describe the Cameroonian species as *Dactylosternum riberai* sp. nov. and compare it with its sister *Dactylosternum chrysopelma* (Spangler & Perkins 1981), comb. nov. Mature larvae of the new species identified using DNA sequences are described and compared to other *Dactylosternum* larvae.

Key words. Biology, Cameroon, Coelostomatini, larval morphology, Liberia, molecular systematics, new species.

1. Introduction

Bizarre animals known only from very short type series found among unidentified museum specimens decades after being collected are known in every sizable animal clade. David Attenborough's echidna (*Zaglossus attenboroughi*) described by Flannery & Groves (1998) from a single specimen collected in 1961 in New Guinea and subsequently found in the Leiden museum, the Netherlands, or New Zealand giant gecko *Hoplodactylus delcourti* described by Bauer & Russel (1986) from a single specimen found accidentally in the Marseille museum, France, are among the best-known examples. Many of these species inhabit remote and difficult to access areas. They become subjects of research and conservation initiatives that try to rediscover them in nature and collect basic data about their distribution and lifestyle. Most species known from very short type series are, however, invertebrates, mainly insects. Such organisms attract less attention, despite being equally interesting by their isolated phylogenetic position (e.g., Erwin 2007) or the danger of extinction (e.g., Jensen et al. 2020).

Water scavenger beetles (Hydrophilidae) is a clade of ca. 3000 predominantly aquatic species (Bloom et al. 2014). Their subclade of ca. 1000 species (subfamilies Cyclominae and Sphaeridiinae) is, however, secondarily terrestrial. Terrestrial Hydrophilidae are found in tropical forest leaf litter, mammal excrements, or even flow-

ers (Arriaga-Varela et al. 2018; Minoshima et al. 2018; Fikáček 2019a). Both aquatic and terrestrial groups include genera known by singletons. Of the aquatic ones, the New Zealand *Horelophus*, Neotropical *Protistolophus*, Tasmanian *Phelea* or Mozambican *Acidocerus* were described based on one or a few historical museum specimens (Klug 1855; Orchymont 1913; Hansen 1999a; Short 2010); only the former two were subsequently rediscovered (Fikáček et al. 2012; Short et al. 2020). Terrestrial Hydrophilidae have at least 20 genera known only from a single or a few type specimens, without any biological or other information (Hansen 1999b). Recent studies of some of them revealed that their apparent rarity is often caused by an unusual lifestyle or undersampled habitat. For example, the genus *Cycreon* Orchymont, 1919 known from two historical specimens (Orchymont 1919; Shatrovskiy 2017) was recently discovered to inhabit inflorescences of various Araceae in the Malay Peninsula and Borneo (Arriaga-Varela et al. 2018), i.e. the habitat rarely inspected by hydrophilid students. Similarly, the extremely rare New Zealand *Saphydrus* eluded detection by occurring in winter or at high altitudes only (Seidel et al. 2020). On the other hand, some species likely genuinely exist in a limited number of small populations and may be critically endangered by habitat degradation. This seems to be the case of the recently described New Zealand *Enigmahydrus* known from a single population (Seidel et al. 2020) or the South African *Relictorygmus* known, despite the recent collecting effort (Seidel et al. 2018), from only three localities in Western Cape.

The genus *Kruia* Spangler & Perkins, 1981 was established for a single male collected by the 1940 Smithsonian-Firestone Expedition to Liberia (Loveridge 1941; Spangler & Perkins 1981). The peculiarity of the specimen was recognized decades later, when all information on the collecting circumstances have already been lost. The beetle clearly belonged to the terrestrial group of the Hydrophilidae but differed from all known genera by highly sculptured dorsal surface, an unusual shape of the head, mesoventrite and metaventrite and the presence of tufts of hairs on the legs. These characters urged Spangler & Perkins (1981) to establish a new genus *Kruia* based on that single specimen. Hansen (1991) assigned *Kruia* to the tribe Coelostomatini, i.e. a clade of ca. 250 described species classified in 20 genera, majority of which are terrestrial and inhabit various kinds of decaying organic matter (Fikáček 2019a). When studying *Kruia*, Hansen (1991) discovered few additional unusual characters (e.g. antennae with 8 antennomeres). No additional specimens of *Kruia* have been known.

In this study we report our rediscovery of *Kruia* during recent fieldwork in two forested Cameroonian localities. The availability of freshly collected specimens necessitated description of a new species and allowed us to analyze phylogenetic position of the genus using a newly assembled multi-gene dataset. DNA data also allowed for the association of the field-collected larvae with adults, and for obtaining basic biology data.

2. Material and Methods

2.1. Specimen sampling and DNA sequencing

Forest litter was sifted through a hand-held sifter and live specimens were subsequently extracted by suspending the fine litter fraction in Winkler funnels. Specimens were killed in 96% alcohol and stored at –20°C. 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. Seven fragments were amplified using PCR: two mitochondrial genes (3'-end of cytochrome oxidase I, cytochrome oxidase II), and five nuclear genes (18S rRNA, 28S rRNA, histone 3, topoisomerase I and wingless). For detailed amplification programs and primers, see Electronic Supplement S1. Sanger sequencing was performed by Macrogen Europe (Amsterdam, the Netherlands).

2.2. Phylogenetic analysis

Sequences were edited and aligned in Geneious (ver. 9.1.3; Kearse et al. 2012). The final alignment is 5417 bp long, consisting of the following gene fragments: *cox1* (714 bp), *cox2* (675 bp), 18S (1661 bp), 28S (1022 bp), H3 (303 bp), topoisomerase I (628 bp) and wingless (414 bp). The dataset was divided into partitions by genes, sequences of protein-coding genes (*cox1*, *cox2*, H3, topoisomerase I and wingless) were additionally divided into partitions by codon positions. DNA substitution models were tested in PartitionFinder2 (Lanfear et al. 2017; see http://www.robertlanfear.com/partitionfinder) on the Cyberinfrastructure for Phylogenetic Research (CIPRES) Science Gateway (Miller et al. 2010). The phylogenetic reconstruction was conducted using MrBayes (version 3.2.6, see https://nbisweden.github.io/MrBayes/index.html; Ronquist et al. 2012) and IQ-Tree (version 1.6.10, see www.iqtree.org; Nguyen et al. 2015) on the CIPRES Science Gateway. The MrBayes and IQ-Tree blocks with the best-fitting models for each partition are listed in Electronic Supplement S2. The Bayesian analysis was performed with four chains of 25 million generations and sampling every 1000 generation. The convergence of both runs was checked in Tracer (ver. 1.7, see https://github.com/beast-dev/tracer/ releases/tag/v1.7.1; Rambaut et al. 2018). The default burin setting (25%) was used for constructing the Bayesian consensus tree. The maximum likelihood (ML) analysis was run under default settings with 1000 ultra-fast bootstrap replicates. Resulting trees were edited in FigTree (version 1.4.3, see https://github.com/rambaut/figtree).

Table 1. List of DNA sequences used for the phylogenetic analyses, plus two additional 16S sequences available for Kruia specimens.

Taxon name	Voucher ID	cox1	cox2	18S	28S	histone 3	Topoisom I	Wingless	16S
Coelostoma austrine	MF1945	MW064266	–	–	–	–	–	–	–
Coelostoma austrine	MF2342	–	–	–	MW114813	MW052421	MW052445	MW052464	–
Coelostoma fabricii	COL481	MW064267	–	MW114821	MW114814	MW052419	–	MW052462	–
Coelostoma hispanicum	MF119	MW064268	–	–	MW114815	MW052420	MW052444	MW052463	–
Coelostoma lemuriense	MF158	MW064269	MW052395	MW114822	MW114816	MW052418	MW052443	MW052461	–
Coelostoma orbiculare	–	AM287094.1	AM287116.1	EF213785.1	KC992549.1	–	–	–	–
Coelostoma phallicum	MF326	KC935244.1	KC992398.1	KC935021.1	KC992550.1	–	–	–	–
Cyclotypus	MF842	MG208557.1	MG208585.1	MG208646.1	MG208605.1	MW052401	MW052426	MW052448	–
Cylomissus glabratus	SLE0098	KC935251.1	KC992490.1	KC935028.1	KC992556.1	–	–	–	–
Dactylosternum abdominale	MF530	MW064270	MW052396	MW114823	MW114817	MW052415	MW052440	MW052458	–
Dactylosternum auripes	MF63	KC935253.1	KC992404.1	KC935030.1	KC992558.1	–	–	–	–
Dactylosternum dytiscoides	MF811	MW064271	MW052397	MW114824	MW114818	MW052414	MW052439	–	–
Dactylosternum marginale	COL992	KF802003.1	–	MW114825	KF802166.1	MW052413	MW052438	MW052457	–
Dactylosternum striatopunctatum	MF24	MW064272	–	MW114826	MW114819	MW052406	MW052431	MW052450	–
Kruia Mt. Cameroon	MF2110	MW064273	–	MW114827	MW114820	MW052416	MW052441	MW052459	MW114810
Kruia Mt. Cameroon LARVA	MF2110L	MW064274	–	–	–	–	–	–	–
Kruia Mt. Kupe	MF2102	–	–	–	–	MW052422	–	–	MW114811
Lachnodacnum luederwaldti	MF772	MG208554.1	–	MG208643.1	MG208602.1	MW052398	MW052423	MW052446	–
Phaenonotum borinquenum	MF1729	MG208574.1	–	MG208664.1	MG208622.1	–	–	MW052453	–
Phaenonotum caribense	MF36	KC935315.1	KC992399.1	KC935090.1	KC992623.1	MW052417	MW052442	MW052460	–
Phaenonotum delgadoi	MF455	MG208552.1	MG208583.1	MG208641.1	MG208600.1	–	MW052432	–	–
Phaenonotum Ecuador	MF38	MG208551.1	MG208582.1	MG208640.1	MG208599.1	MW052400	MW052425	MW052447	–
Phaenonotum Guyana	MF1061	MG208567.1	MG208592.1	MG208656.1	MG208615.1	MW052407	MW052433	MW052451	–
Phaenonotum laevicole	MF1115	MG208572.1	MG208597.1	MG208662.1	MG208620.1	MW052408	MW052434	MW052452	–
Phaenonotum laterale	MF1013	MG208566.1	MG208591.1	MG208655.1	MG208614.1	MW052412	–	MW052456	–
Phaenonotum ondreji	MF980	MG208565.1	MG208590.1	MG208654.1	MG208613.1	MW052411	MW052437	MW052455	–
Phaenonotum Peru	MF845	MG208559.1	MG208586.1	MG208648.1	MG208607.1	MW052403	MW052428	MW052449	–
Phaenonotum Peru	MF846	MG208560.1	MG208587.1	MG208649.1	MG208608.1	MW052399	MW052424	–	–
Phaenonotum Peru	MF861	MG208563.1	MG208589.1	MG208652.1	MG208611.1	MW052405	MW052430	–	–
Phaenonotum Puerto Rico	MF654	MG208553.1	MG208584.1	MG208642.1	MG208601.1	MW052409	MW052435	–	–
Phaenonotum Suriname	MF1062	MG208568.1	MG208593.1	MG208657.1	MG208616.1	MW052410	MW052436	MW052454	–
Phaenostoma kontax	MF855	MG208561.1	–	MG208650.1	MG208609.1	MW052404	MW052429	–	–
Phaenostoma posticatum	MF1066	MG208571.1	MG208596.1	MG208661.1	MG208619.1	MW052402	MW052427	–	–
Protosternum hainanense	SLE0297	–	KC992403.1	KC935091.1	KC992624.1	–	–	–	–
Sphaeridium bipustulatum	SLE0298	KC935323.1	KC992458.1	KC935099.1	–	–	–	–	–

2.3. Morphological studies

For larval morphology, we largely followed the methods used by Minoshima & Hayashi (2011). Both available larvae were cleared by dissolving their internal tissues using the proteinase K treatment; the dissolved extract of one specimen was used for DNA extraction (see above). Cleared larvae were examined in glycerol temporary slides. Adults were dissected, with male genitalia embedded in a drop of alcohol-soluble Euparal resin on a small slide pinned below the respective specimen and photographed. One specimen was cleaned of soft tissues using 10% KOH, partly bleached in 15% hydrogen peroxide, completely disarticulated and used for the study of adult morphology. 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 adults were taken using a Hitachi S-3700N environmental electron microscope at the Department of Paleontology, National Museum (Prague, Czech Republic). Photographs of slide-mounted body parts of the adult were taken using a Canon D1100 digital camera attached to an Olympus BX41 compound microscope.

Larval morphological terminology follows Archangelsky (1997) and Minoshima & Hayashi (2011). Although we only examined third instar larvae, we attempted the homologization of at least some sensilla with the primary chaetotaxy of the larval head (Fikáček et al. 2008; Bytteebier & Torres 2009). **Abbreviations. AN** – antenna; **FR** – frontale; **gAN** – group of antennal sensilla; **gAPP** – group of sensilla on inner appendage of maxilla; **gFR** – group of sensilla on frontale; **gLA** – group of sensilla on labium; **gMX** – group of sensilla on maxilla; **LA** – labium; **MN** – mandible; **MX** – maxilla; **PA** – parietale; **SE** – sensorium. Adult morphological terminology follows Lawrence & Slipiński (2013) and Fikáček (2019a). Classification follows Short & Fikáček (2013) and Seidel et al. (2016).

2.4. Depository of complete digital data

Original unedited photos and SEM micrographs, including those only used for comparative purposes and not included into this paper, are publicly available from Zenodo archive following this link: http://doi.org/10.5281/zenodo.4039839. Newly generated sequences were submitted to GenBank (see Table 1).

2.5. Depository Abbreviations

BMNH – the Natural History Museum, London, United Kingdom (M. Barclay); **CNC** – Canadian National Collection of Insects, Arachnids and Nematodes, Ottawa, Canada (A. Brunke, P. Bouchard); **NMPC** – National Museum, Prague, Czech Republic (J. Hájek, L. Sekerka); **USNM** – Smithsonian Institution, National Museum of Natural History, Washington D.C., USA (C. Michelli).

3. Results

3.1. Results of molecular analyses

Bayesian and maximum likelihood analyses resulted in identical topology (Fig. 1). They revealed a strongly supported monophyly of Coelostomatini (posterior probability PP/bootstrap BS = 1.0/97) comprising three strongly supported clades: *Dactylosternum* including *Kruia* (PP/BS = 0.95/75), *Coelostoma* (PP/BS = 1.0/100) and the Neotropical clade of *Phaenonotum*, *Phaenostoma* and *Lachnodacnum* (PP/BS = 1.0/100). *Cyclotypus* is revealed as sister to *Coelostoma*, but without support (PP/ BS = 0.53/44). *Dactylosternum* (including *Kruia*) is sister to the rest of analyzed Coelostomatini, and *Coelostoma* + *Cyclotypus* sister to the Neotropical clade, without support (PP/BS = 0.79/57). *Kruia* is revealed as nested in *Dactylosternum*, with *D. abdominale* as the sister species (PP/BS = 1.0/100). The *cox1* sequences of the adult and the co-occurring coelostomatine larva from Mt. Cameroon are nearly identical (uncorrected genetic distance = 0.04%), suggesting conspecificity. We did not obtain *cox1* sequence for the Mt. Kupe adult, but the histone 3 and 16S sequences of both specimens are identical which may give additional support to the morphological information about the identification.

3.2. Systematics and morphology

3.2.1. *Dactylosternum* Wollaston, 1854

Dactylosternum Wollaston, 1854: 99. Type species: *Dactylosternum roussetii* Wollaston, 1854.

= *Kruia* Spangler & Perkins, 1981: 220, **new synonym**. Type species: *Kruia chrysopelma* Spangler & Perkins, 1981 (by monotypy).

Comments on the synonymy. The phylogenetic analysis revealed *Kruia* nested within the genus *Dactylosternum* (Fig. 1), sister to the African *D. abdominale* species group, where the type species of *Dactylosternum* belongs to. Morphologically, *Kruia* is unique in Coelostomatini in some striking characters (e.g. sculptured dorsal surface, sexual dimorphism) but otherwise resembles members of the *D. abdominale* species group (see the redescription below and the detailed comparison in the Discussion). We treat, therefore, *Kruia* as a morphologically unusual member of *Dactylosternum* and synonymize it with *Dactylosternum*, the latter being the oldest name having priority. Both species treated below are undoubtedly closely related, forming a monophyletic group which we call '*Dactylosternum chrysopelma* species group' hereafter.

Adult description of *D. chrysopelma* species group. ***Body*** (Fig. 2): Moderately long (3.9–4.8 mm), widely oval, dorsally moderately convex in lateral view. Sides of pronotum and elytra widely explanate. Pronotum more convex than elytra, not forming continuous curve with elytra in lateral view. Dorsal coloration dark brown to black, explanate parts of elytra paler; ventral side dark brown; legs and appendages brown. ***Head***: Clypeus explanate anteriorly, widest in front of eyes (Figs 2F, I, K–L); eyes relatively small, deeply excised by an anterior canthus. Dorsal surface of head with dense and coarse punctation with intermixed short setae. Labrum moderately sclerotized (Fig. 3B), completely concealed under clypeus (Figs 2F, I). Mandibles with large slightly asymmetrical molar part and short and wide, thin apical portion with a single thin apical tooth (Fig. 3C). Maxilla with long projecting lacinia bearing organized series of fine setae (Fig. 3D). Mentum ca. twice as wide as long, ventral surface covered by dense pubescence (Figs 3E, 4B). Antenna with 8 antennomeres, geniculate, antennomeres 6–8 forming a pubescent rather loosely articulated club (Fig. 3A). Gular sutures contiguous. ***Prothorax*:** Pronotum transverse, explanate anterolaterally, humpy in appearance, with median longitudinal impression (Figs. 2A–B, F–I); surface with coarse punctures with intermixed short setae. Ventral surface with very wide lateral glabrous portion (Fig. 3F). Prosternum ca. as long as procoxal cavity, weakly carinate medially (Figs. 3F, 4A). Procoxal cavity closed internally, open posteriorly externally; prosternal process narrowly projecting between procoxae (Figs. 3F, 4A). ***Pterothorax*:** Mesoventrite fused with anespisternal, anapleural sutures obsolete (Figs 3G); mesoventrite with deep anterior pit and a large subhexagonal median elevation (Figs. 3G, 4C, E). Metaventrite with a glabrous median area projecting anteriorly into rather long and moderately wide metaventral process widely contacting and slightly overlapping posterior margin of mesoventral plate; median glabrous area with tufts of setae posterolaterally (Figs. 4C–E). Lateral portions of metaventrite setose, with large sparse pits. Metanepisternum wide, with large posterolateral projection. Scutellar shield large, equilateral

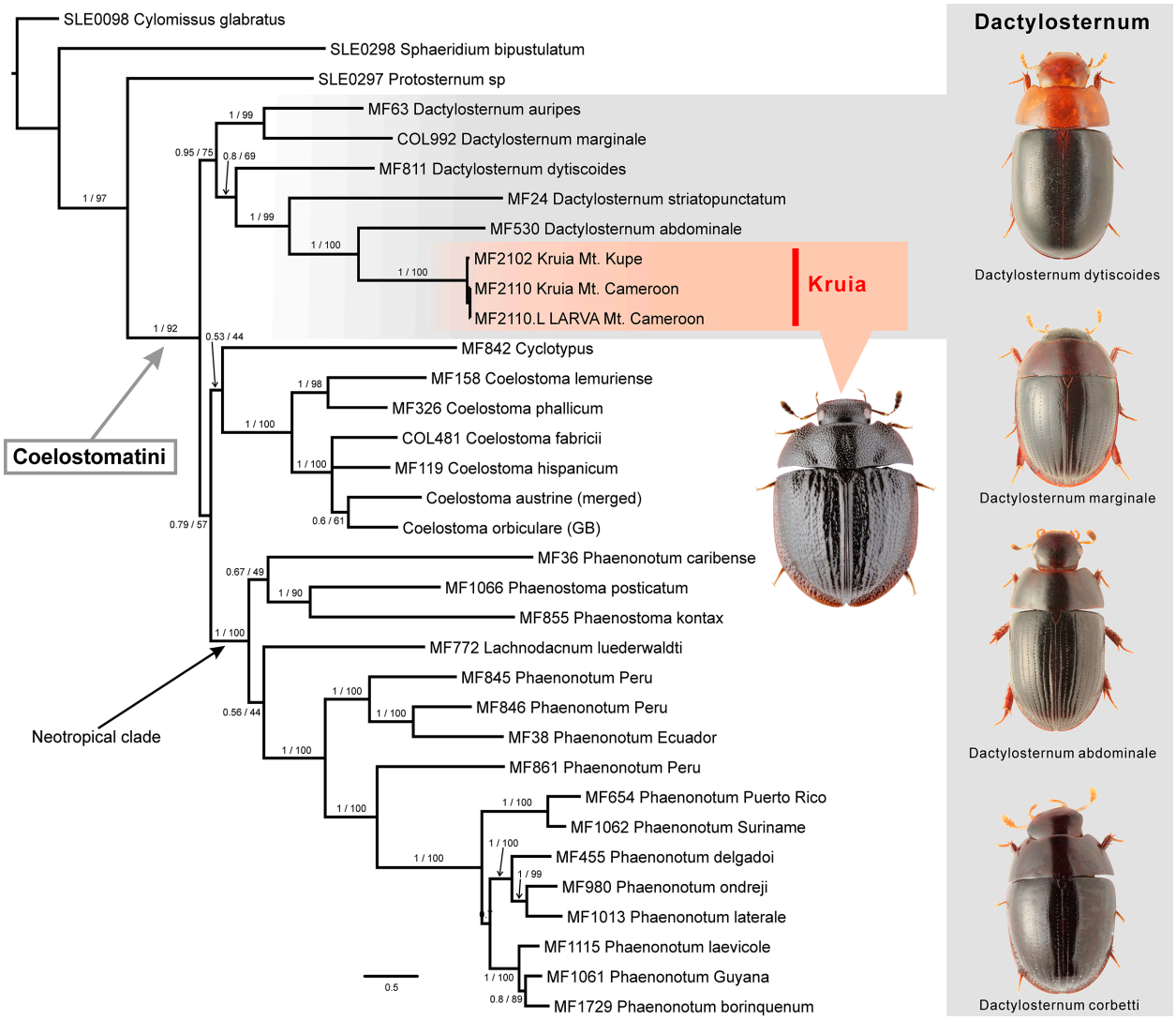

Fig. 1. Phylogenetic position of *Kruia*. Majority rule phylogram from Bayesian inference based on concatenated sequences of COI, COII, 18S, 28S, H3, topoisomerase I and wingless of Coelostomatini post-burnin (25%). Support values = Bayesian posterior probability / ML boostrap in IQ-Tree analysis.

triangle (Figs. 2A,G). Elytra slightly bumpy, coarsely punctate dorsally, with 9 regular and 2 lateral irregularly arranged series of punctures; sides of elytra widely explanate; epipleura very wide, with wide outer glabrous and gradually narrowing inner pubescent portion (Fig. 4E). Hind wings well developed, with large anal lobe and a complete set of cubital and anal veins (Fig. 3J). ***Legs*:** Femora slender, their ventral surface with very sparse setae; tips of femora not reaching body outline. Meso- and metatibia arcuate, widening distally; mesotibia with irregular series of fine setae ventrally. Tibial spur very short. Tarsi with 5 tarsomeres, with dense and long ventral pubescence; basal metatasomere robust, ca. as long as tarsomeres 2–3 combined; tarsal claws simple, arcuate (Fig. 3M). ***Abdomen*** (Fig. 3H): with 5 ventrites; ventrite 1 with median carina; apex of ventrite 5 simple, without stout setae. Female external genitalia as in Fig. 3I. Male sternite 9 wide, with median projection which widens posteriorly (Fig. 3N). Aedeagus with wide and rather long phallobase, median lobe subtriangular, parameres truncate apically (Figs. 3O–P). ***Sexual dimorphism*:** Males with a pair of small tubercles with tufts of hairs on postero-median part of metaventrite (Figs 4C, D), female with indistinct tubercles lacking hairs. Males with mesotibia more widened than females, mesally with a brush of long yellowish setae on mesal face of tibial apex (Fig. 3K); females with narrower tibiae without such hairs (Fig. 3L).

Differential diagnosis of *D. chrysopelma* species group. Members of this group are easily recognized as a member of the Coelostomatini based on the long metatarsomere 1 (diagnostic for Sphaeridiinae; Fig. 3M), head not excised in front of eyes (in contrast to Megasternini and Omicrini; Figs. 2F, I), mesoventrite with high wide elevating broadly contacting metaventral projection (present in multiple clades of the Sphaeridiinae including all Coelostomatini; Figs. 4C, E) and a deep pit in front of this elevation (unique for Coelostomatini within Sphaeridiinae; Figs 4C, E).

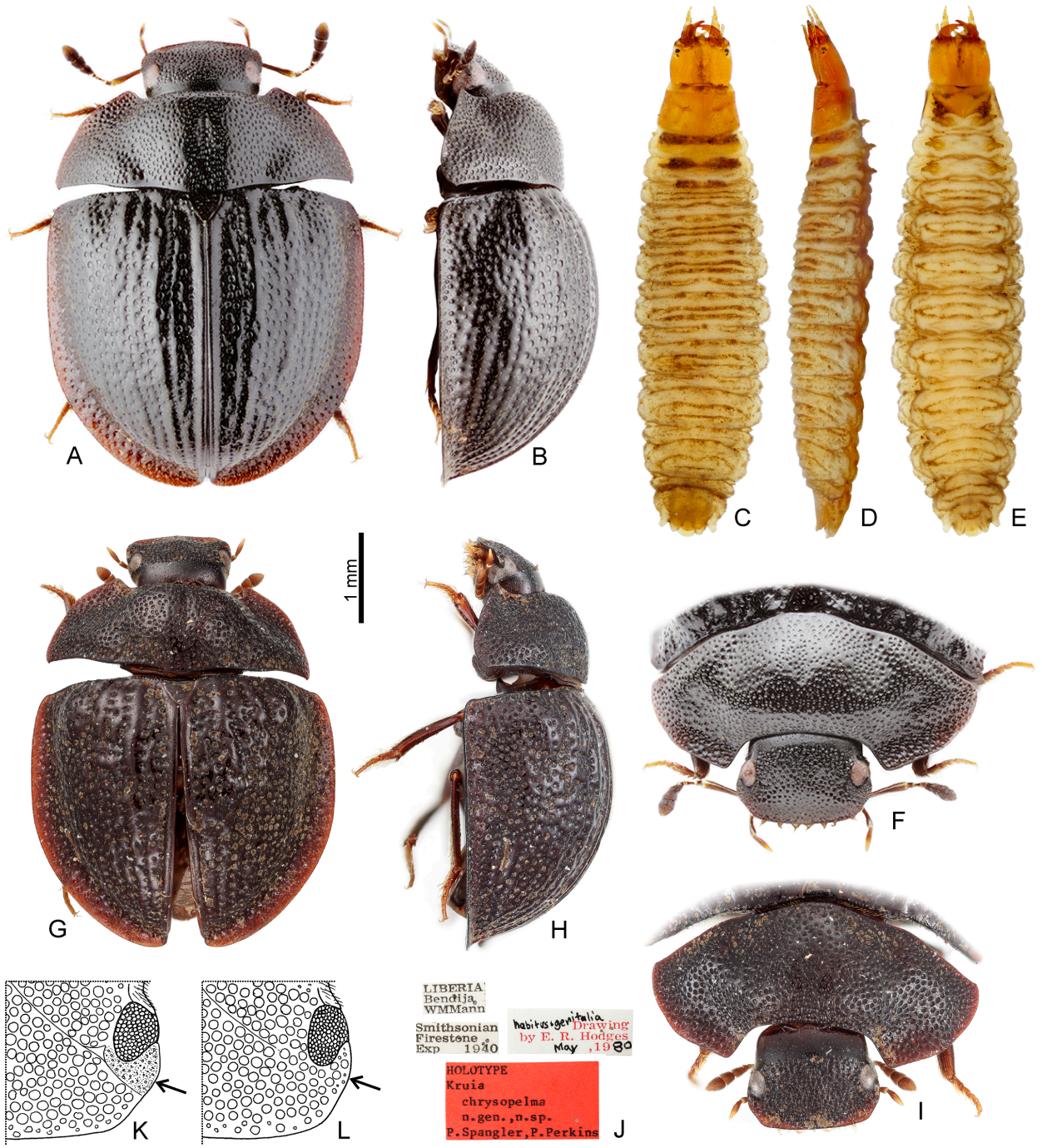

Fig. 2. Habitus and diagnostic characters of *Kruia* species. A–F, K: *Dactylosternum riberai* sp. nov. from Cameroon. G–J, L: *Dactylosternum chrysopelma* Spangler & Perkins, 1981, holotype. A, G: habitus, dorsal view; B, H: habitus, lateral view; C–E: third instar larva (dorsal, lateral and ventral view); F, I: dorsofrontal view; K–L: detail of lateral portion of the head; J: labels of the holotype.

Members of the *D. chrysopelma* species group are easy-to-distinguish from other Coelostomatini including other *Dactylosternum* species by the anteriorly widening clypeus; pronotum more convex than elytra and with median longitudinal impression (Figs. 2A–B, G–H); elytra weakly costate to bumpy on the surface, widely explanate laterally (Figs. 2A–B, G–H); rather loosely articulated antennal club (Figs. 2, 3A) and carinate abdominal ventrite 1 (Fig. 3H). *Dactylosternum chrysopelma* species group is also unique in having 8 antennomeres only (Fig. 3A), which it only shares with two species of *D. abdominale* species group (*D. antennale* Orchymont, 1924 and *D. scutellare* Régimbart, 1907).

3.2.2. Key to species of the *D. chrysopelma* group

1 Elytral keels interrupted, giving the elytra bumpy appearance anteromesally (Fig. 2G). Lateral portion of frons in front of eyes with large punctures similar to those on mesal surface (Fig. 2L). Liberia. .... ***Dactylosternum chrysopelma*** (Spangler & Perkins 1981), **comb. nov.**

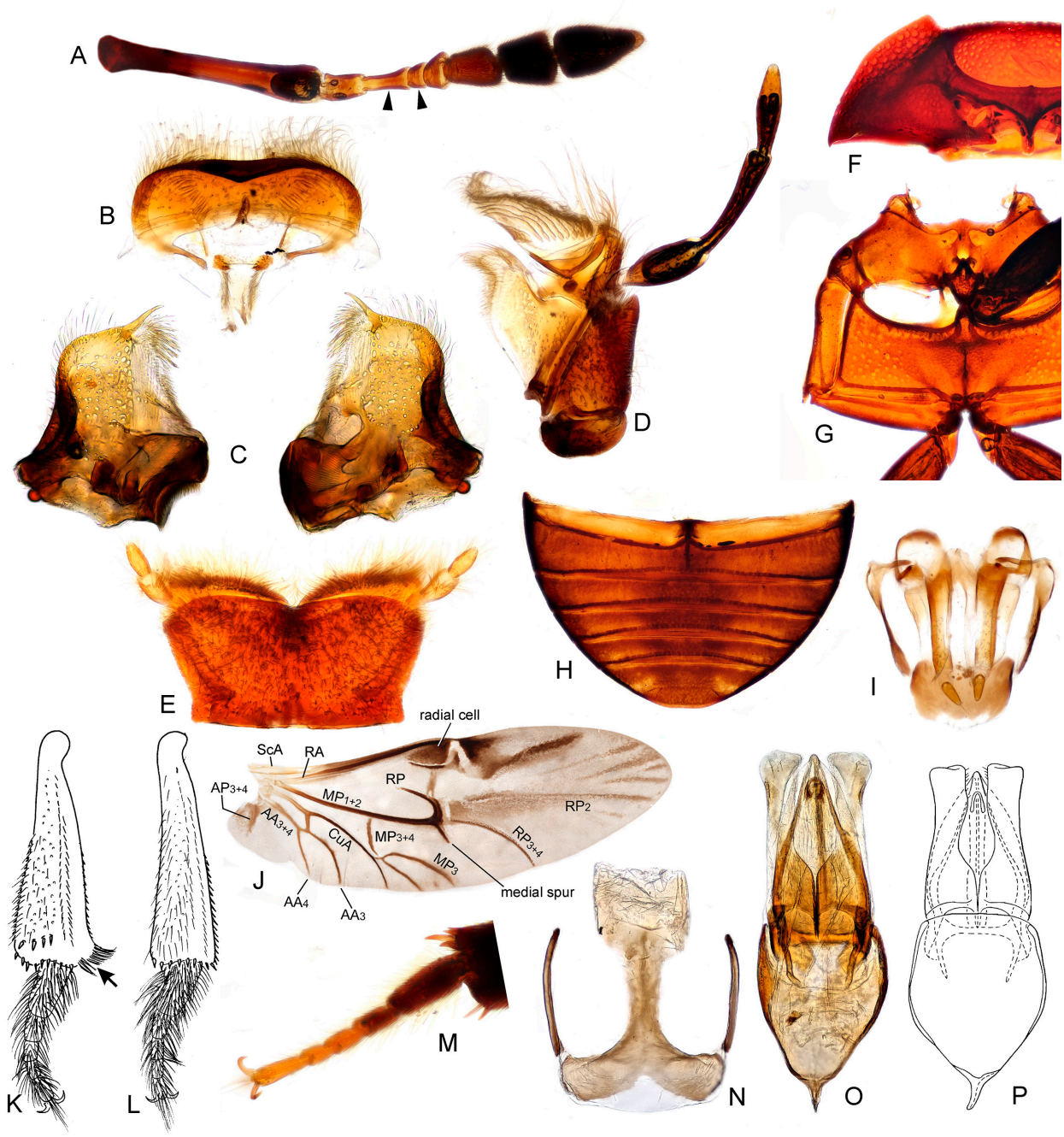

Fig. 3. Details of adult morphology of *Dactylosternum riberai* sp. nov. (A–O) and *Dactylosternum chrysopelma* (Spangler & Perkins, 1981) (P). A: antenna; B: labrum; C: mandibles; D: maxilla; E: mentum and prementum; F: prothorax in ventral view; G: meso- and metathotax in ventral view; H: abdominal ventrites; I: ovipositor; J: metathoracic wing; K–L: mesoibia (K: male, L: female); M: metatatarsus; N: male sternite 9; O–P: aedeagus (P adopted from Spangler & Perkins 1981).

1' Elytral keels developed as longitudinal slightly convex stripes (Fig. 2A). Lateral portion of frons in front of eyes with tiny punctures and interstices bearing fine microsculpture (Fig. 2K). Cameroon. .... ***Dactylosternum riberai* sp. nov.**

3.2.3. Dactylosternum chrysopelma (Spangler & Perkins, 1981), comb. nov.

(Figs. 2G–J, L, 3P)

Kruia chrysopelma Spangler & Perkins, 1981: 223.

Type locality. Liberia, Bendija [= Liberia: Grand Cape Mount county: Bendaja/Bendaje, GPS ca. 7.168635°N, 11.246249°E; see Loveridge 1941].

Material examined. ***Type material***: Holotype ♂ (USNM), 'LIBERIA, Bendija, WMMann | Smithsonian Firestone Exp 1940 | HOLOTYPE | Kruia chrysopelma n. gen., n. sp. | P. Spangler, P. Perkins | habitus + genitalia Drawing by E. R. Hodges May 1980'. We did not examine the specimen physically but were provided with high quality photographs of all needed views done by the USNM staff. All these photographs are available at http://doi.org/10.5281/zenodo.4039839.

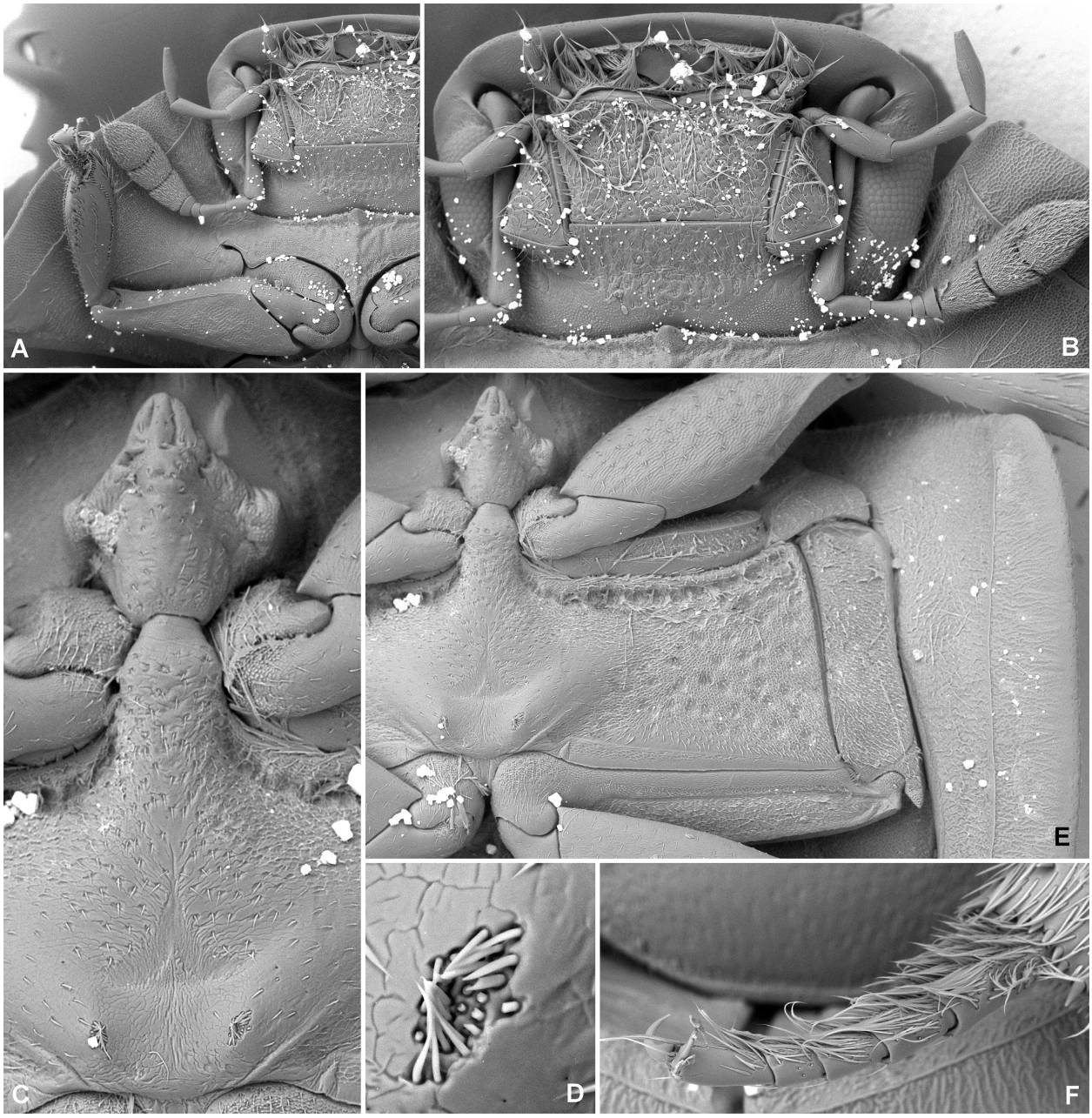

Fig. 4. Adult morphology of male *Dactylosternum riberai* sp. nov., SEM micrographs. A: head and prothorax, ventral view; B: head in ventral view, detail; C: meso-metaventral elevation; D: detail of tufts of setae of metaventrite; E: meso- and metathorax in ventral view; F: metatarsus.

Differential diagnosis. Body length 4.6 mm; maximum body width 3.4 mm. The species is very similar to *D. riberai* sp. nov. and can be distinguished from it based on the following characters (only the easy-to-use ones are mentioned in the key above): Head with frontoclypeal suture obsolete laterally; frons in front of eyes with large punctures similar to those on mesal surface (Fig. 2L). Pronotum moderately convex, not bulging anteriorly in lateral view (Fig. 2H). Elytra widest at midlength; surface of elytra with low longitudinal keels which are partly interrupted, giving elytra bumpy appearance (Figs. 2G–H). Aedeagus with lateral face of parameres indistinctly concave; apex of parameres abruptly truncated; median lobe relatively shorter and wider (Fig. 3P).

Distribution. *Dactylosternum chrysopelma* **comb. nov.** is known only from the type locality at the Liberia – Sierra Leone borders.

Biology. Unknown.

3.2.4. *Dactylosternum riberai* sp. nov.

(Figs. 2A–F, K; 3A–O; 4–7)

Type locality. Cameroon, Mt. Cameroon, 4.0935°N 9.0573°E, 524 m a.s.l.

Material examined. ***Type material***: Holotype: ♂ (NMPC), 'CAMEROON | Mt. Cameroon, | sifting, | 524 m | 28.xii.2015, | 4.0935 9.0573 | Grebennikov (CM05)'. Paratypes: 14 spec.

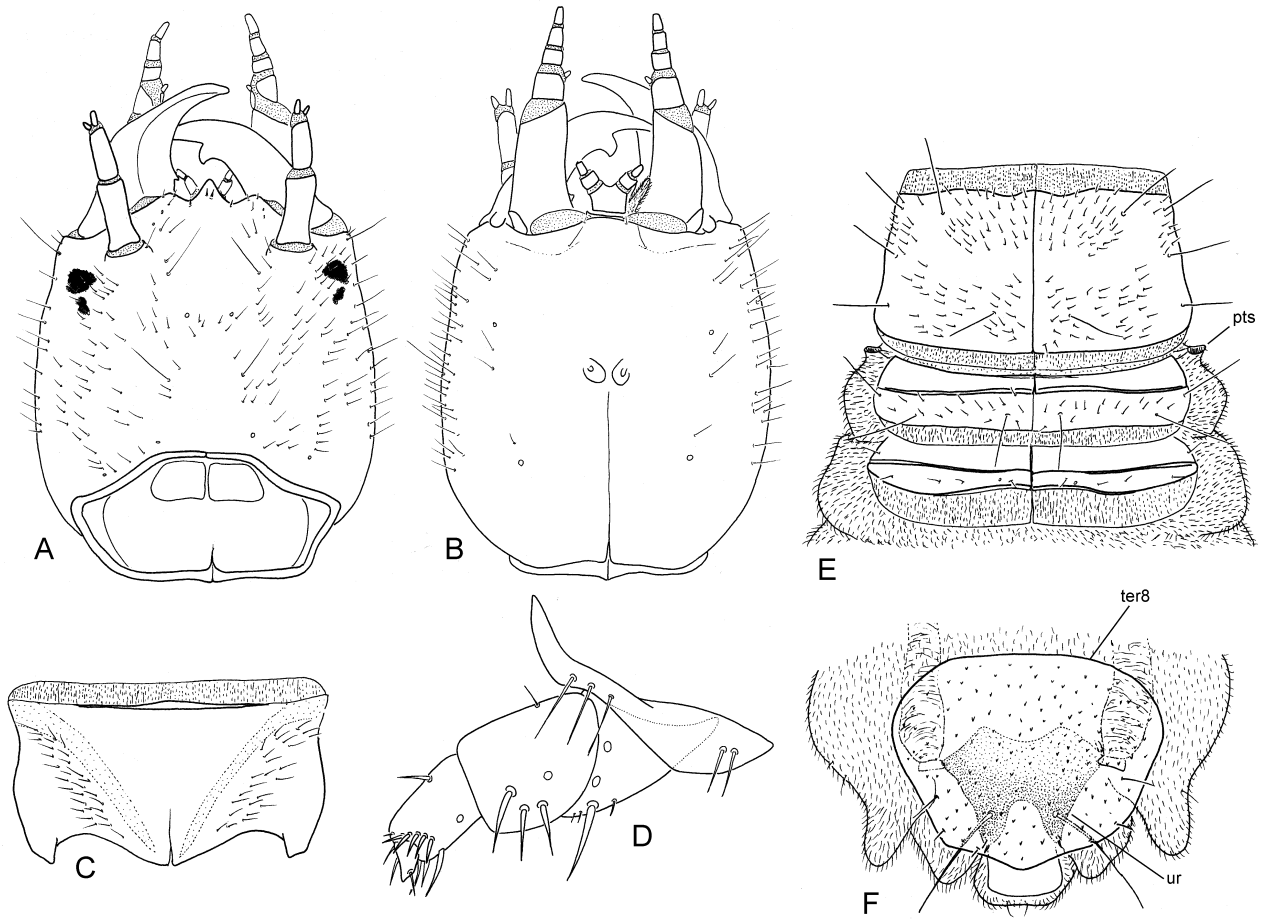

Fig. 5. Third instar larva of *Dactylosternum riberai* sp. nov. A: head in dorsal view; B: head in ventral view; C: proscutum; D: mesothoracic leg; E: thorax in dorsal view; F: abdominal apex in dorsal view. Abbreviations: ter8: dorsal sclerite on abdominal segment VIII; ur: urogomphus.

(NMPC, CNC, BMNH, USNM): same data as the holotype [incl. 1 spec. sequenced: MF2110.1, 1 spec. dissected and slide-mounted, 1 spec. in DNA tissue collection, all in NMPC]. 6 spec. (NMPC): Cameroon, Mt. Kupe, sifting, 1423m, 29.xii.2015, GPS: 4.8223, 9.7047, V. Grebennikov lgt. (CM11) [incl. one spec. sequenced: MF2102 (DNA extract labelled as NZ641) and 2 spec. in DNA tissue collection].

Larval material examined. 2 third instar larvae (NMPC): same data as the holotype [one larva was sequenced: MF2110.L].

Adult differential diagnosis. Body length 3.9–4.8 mm (holotype: 4.2 mm), maximum body width 2.9–3.5 mm (holotype: 3.0 mm). The species is very similar to *D. chrysopelma* and can be distinguished from it based on the following characters (only the easy-to-use ones are mentioned in the key above): Head with frontoclypeal suture complete, reaching lateral margin of head; frons in front of eyes with tiny punctures and interstices bearing fine microsculpture (Fig. 2K). Pronotum highly convex, bulging slightly anteriorly in lateral view (Fig. 2B). Elytra widest in anterior half; surface of elytra with keels developed as complete, non-interrupted slightly convex stripes (Figs. 2A–B). Aedeagus with lateral face of parameres distinctly concave, apex of parameres truncated but slightly convex; median lobe relatively longer and narrower (Fig. 3O).

Third instar larva. ***Body*****:** elongate cylindrical, pale yellowish, sclerotized parts reddish brown (Figs. 2C–E). Body length 7.3 mm, width of head capsule 0.75 mm. ***Head*****:** Head capsule ca. as long as wide (Figs. 5A–B); occipital foramen large; cervical sclerites present, large and subrectancular (Figs. 5A, 6C). Head capsule smooth, only with weak mesh-like structure at sides of frons, on posterolateral face of parietale, laterally of gular sulcus and anteriorly of posterior tentorial pits. Frontal lines absent. Ventral surface with gular sulcus reaching posterior tentorial pits only; posterior tentorial pits large, situated ca. at midlength of head capsule, very narrowly separated from each other. Stemmata on each side aggregated in two groups, larger anterior one and smaller posterior one (Fig. 5A), without any associated cuticular structures. *Frontoclypeus* (Fig. 6A) symmetrical; nasale in form of a simple widely triangular projection; epistomal lobes lower than nasale, their lateral portions membranous. *Antenna* (Fig. 7A) with antennomere 1 as long as antennomeres 2, antennomere 3 the shortest, sensorium slender, as long as antennomere 3. *Mandibles* (Fig. 7C) asymmetrical; right one with single large retinacular tooth bent backwards, sharply angulate subbasally on inner face; left one only with a very small tooth situated in basal third, inner face anteriorly of this tooth densely pubescent (Fig. 7C).

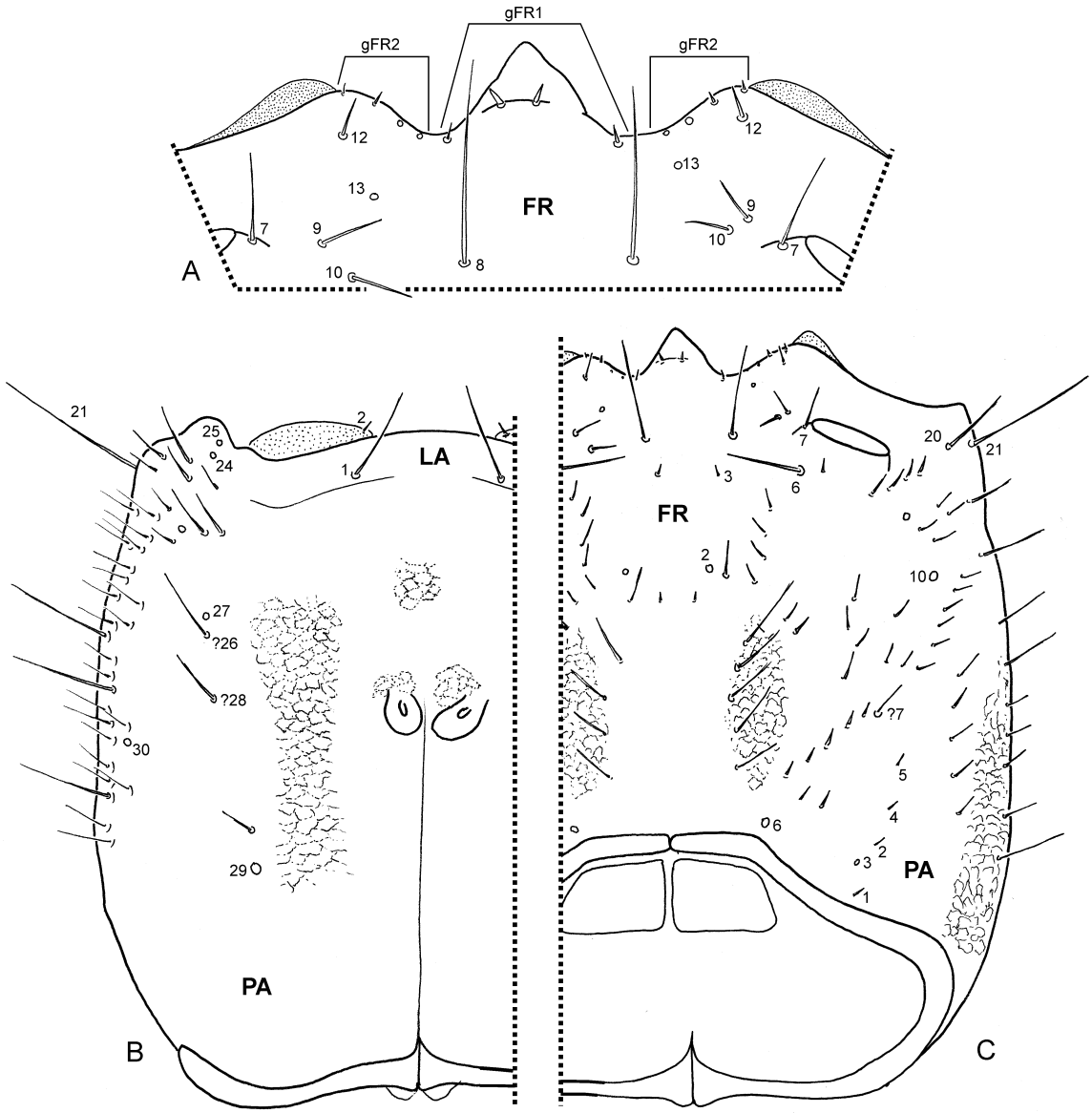

Fig. 6. Third instar larva of *Dactylosternum riberai* sp. nov. and its chaetotaxy A: clypeolabrum, dorsal view; B: head capsule, ventral view; C: head capsule, dorsal view. Only sensilla which homology with primary one can be estimated are numbered.

Maxillae (Figs. 7D–G) with asymmetrical stipites: left stipes shorter and wider, densely pubescent on distal half of inner face; right stipes longer and narrower, sparsely pubescent along inner face; maxillary palpus with four palpomeres, all subequal in length; inner appendage short, sclerotized. *Labium* (Figs. 5B, 6B, 7B). Submentum completely fused to head capsule, submental suture absent; mentum very short, present as a narrow cuticular rim only; prementum well developed and strongly sclerotized, ligula absent; hypopharyngeal lobe present, narrowly projecting towards the inner face of left mandible; labial palps widely separated, each with two palpomeres. ***Thorax*:** slightly wider than head capsule (Fig. 2C). Prothorax with large proscutum subdivided by sagittal line, with membranous portion along anterior and posterior margins; prosternum in form of a large sclerite with a fine sagittal suture present only posteriorly, with a pair of weakly sclerotized stripes reaching from anterolateral corners to posteromedian margin. Meso- and metathorax each with a narrow pair of sclerites dorsally, subdivided by transverse ridges into three parts, anterior sclerotized and bare, intermediate sclerotized and pubescent, and posterior membranous (Fig. 5E). Mesothoracic spiracles open, situated on small tubercles (Fig. 5E, pts). *Legs* (Fig. 5D) with 5 segments (coxa, trochanter, femur, tibiotarsus and tarsal claw), but extremely shortened, situated on ventrolateral part of each segment and hence widely separated from each other; femur robust, tibiotarsus narrower and shorter, claw extremely shortened; all setae very stout. ***Abdomen*:** ten-segmented; segments I–VII subequal in size and shape, without distinct sclerites, each segment subdivided in two main transverse folds, posterior lobe further subdivided into three lobes; segments I–VI ventrally with two transverse stripes consisting of weakly sclerotized spines; segments I–VII with spiracles opening on small lateral tubercles. Segment VIII form-

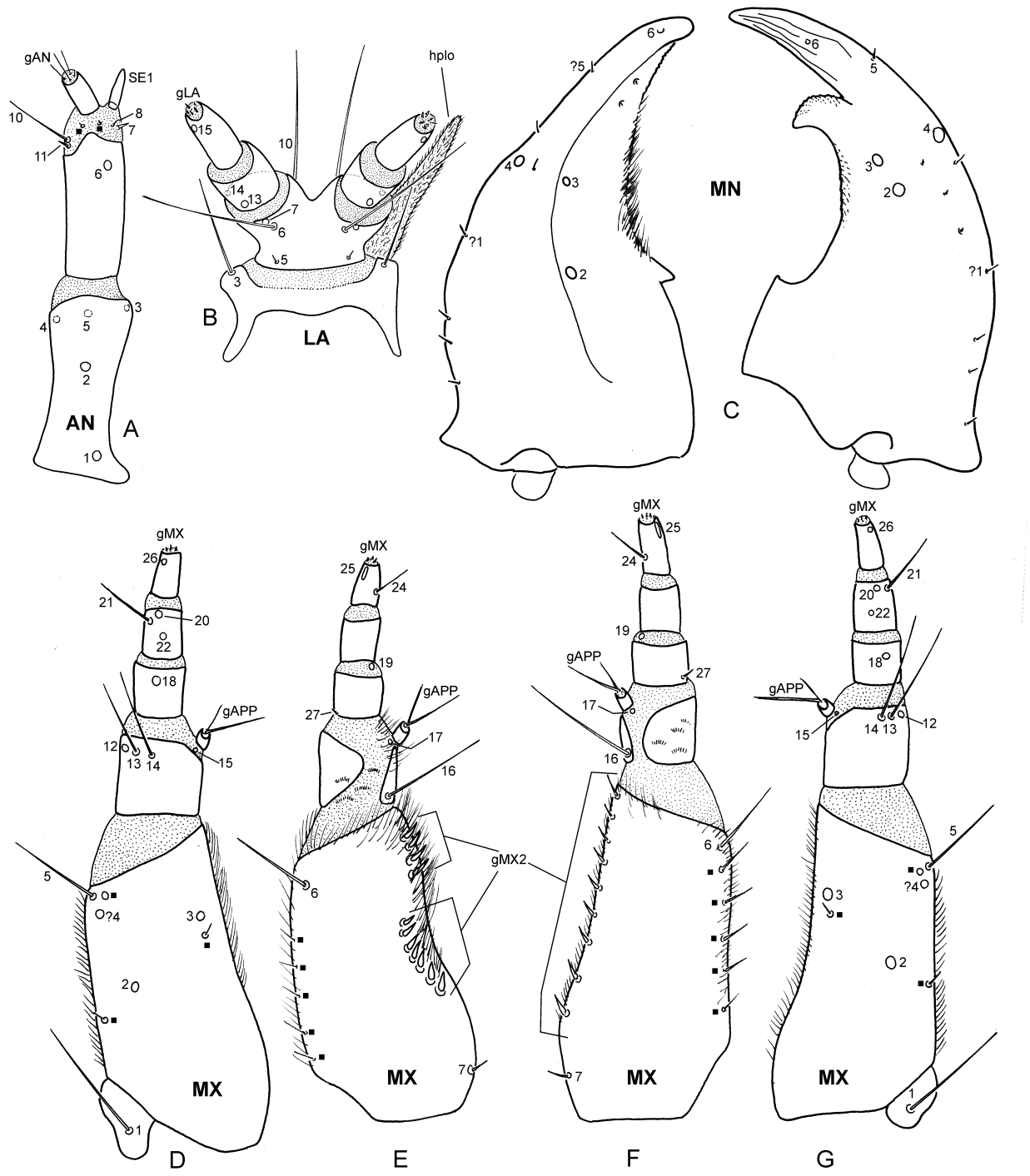

Fig. 7. Head appendages of the third instar larva of *Dactylosternum riberai* sp. nov. and their chaetotaxy A: antenna, dorsal view; B: mentum and prementum, ventral view; C: mandibles, ventral view; D–E: left maxilla (D: ventral, E. dorsal view); F–G: right maxilla (F: dorsal; G: ventral view). Black square marks additional sensilla not homologous to primary ones.

ing the anterior part of spiracular atrium into which the 8th pair spiracles open (those are large and annular); its dorsal surface with large plate ca. 1.2 × wider than long, posterior margin weakly projecting medially (Fig. 5F). Urogomphi large, strongly sclerotized and fused basally.

Head chaetotaxy of third instar larva. ***Frontale*****:** Nasale (Fig. 6A) with 2 pairs of setae in gFR1, lateral pair fine and short, in emargination between nasale and epistomal lobes, mesal pair short and stout, on dorsal face of the triangular nasal projection. Epistomal lobes each with 4 sensilla (gFR2) along anterior margin, mesal two pore-like, lateral two short setae; surface of epistomal lobe with one short stout seta (FR12) and one pore posteromesally of it (FR13), two moderately long setae (FR9–10) more posteriorly near antennal socket; a pair of long and widely separated setae (FR8) between antennal sockets. Remaining sensilla of the anterior part of the frontale not observed. Inner margin of antennal socket with moderately long seta (FR7) and a long setae posteriorly of it (FR6); FR3 minute seta slightly posterior of FR8, FR2

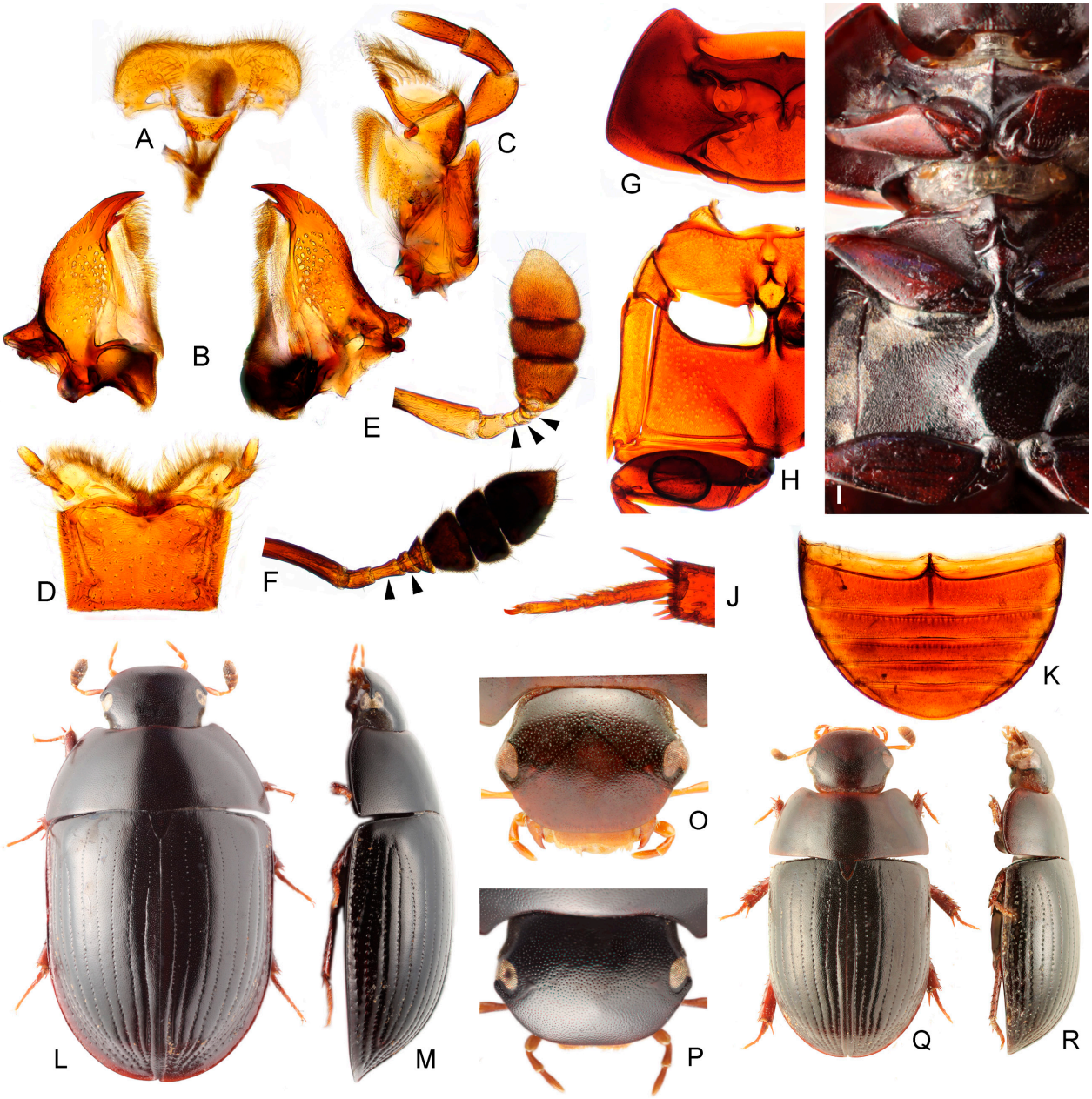

Fig. 8. Morphology of members of the *Dactylosternum abdominale* species group, *D. abdominale* (A–E, G–H, J–K, O, Q–R) and *D. antennale* (F, I, L–M, P). A: labrum; B: mandibles; C: maxilla; D, mentum; E–F: antenna; G: prothorax in ventral view; H: meso- and metathorax in ventral view; I: thorax in ventral view; J: metatarsus, K: abdominal ventrites; L–M, Q–R: habitus (dorsal and lateral); O–P: head in dorsal view.

pore-like, posteriorly of FR3. Lateral parts of fronts between FR6 and FR2 and posteriorly of FR2 with irregular series of secondary setae. ***Parietale*:** (Figs 6B–C). Dorsal and lateral portions with numerous secondary setae which makes the homology inference impossible for most primary sensilla, except the following: PA1–5 posteriorly at mid-width of parietale, pore PA3 more posteriorly than seta PA2; pore PA6 posteromesally; PA10 pore-like in stemmatal area; PA20–21 long setae situated laterally close to anterior margin of parietale. Ventral surface with two pores (PA24–25) close to mandibular articulation, pore PA17 slightly posteriorly of them, among numerous secondary setae. Ventral face at midwidth of parietale with a row (from the front to the back) of a pore (PA27), two moderately long setae (?PA26 and ?PA28), one secondary seta and one pore (PA29). Lateral portion at ca. mid-length with a pore PA30 situated among secondary setae. Remaining sensilla not observed or not homologized. ***Antenna*:** (Fig. 7A). Antennomere 1 with pore AN1 basally at dorsal face, pore AN2 ca. at midlength, pores AN3–5 along distal margin on lateral and dorsal face. Antennomere 2 with pore PA6 distally on dorsal surface; long seta AN10 close to short seta AN11 on inner face of intersegmental membrane, short setae AN7–8 on its outer face. Sensorium as long as antennomere 3. ***Mandibles*:** (Fig. 7C). Right mandible with

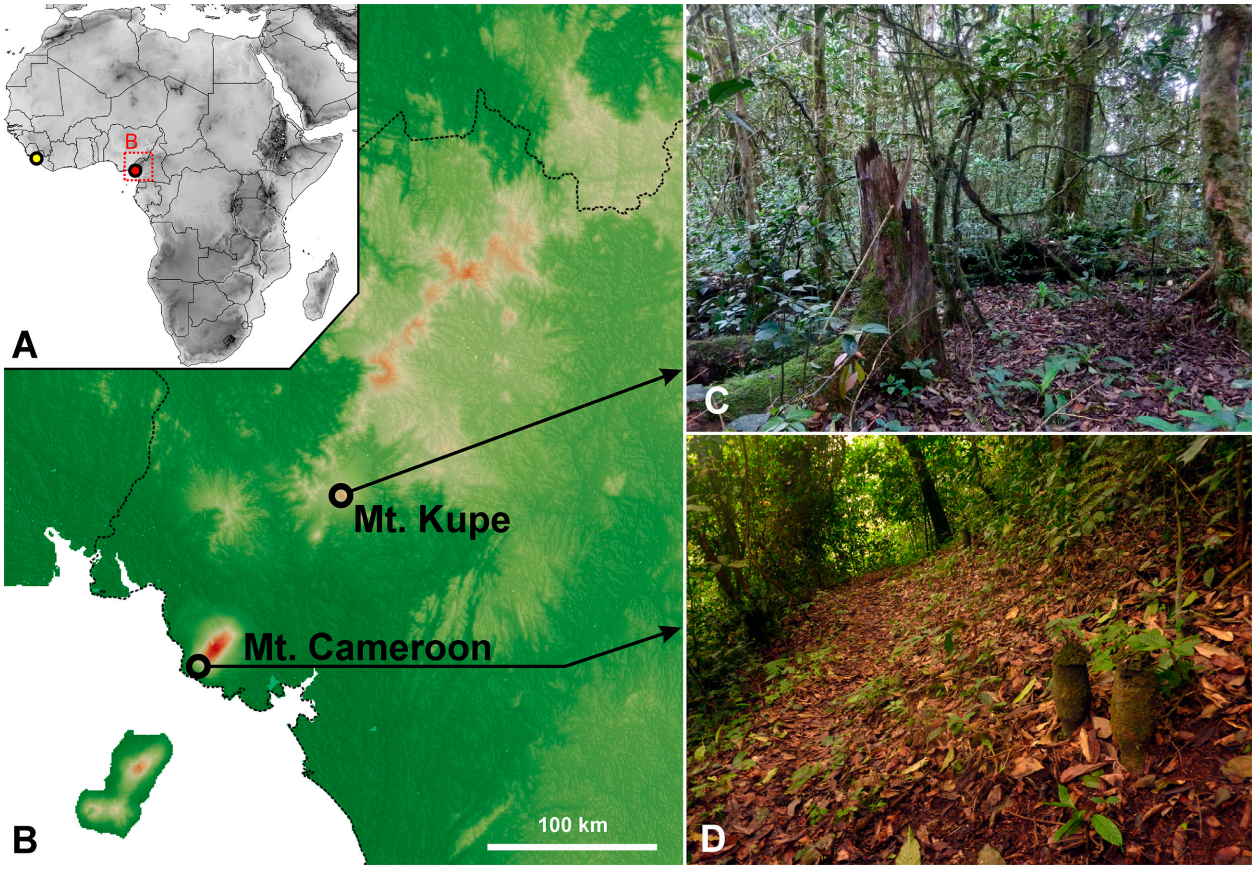

Fig. 9. Distribution and habitats of *D. chrysopelma* species group. A, general distribution in Africa (yellow = *Dactylosternum chrysopelma*, red = *D. riberai* sp. nov.). B, detail of known localities of *D. riberai* sp. nov. in the volcanic arc in Cameroon. C, submontane forest at Mt. Kupe, 1420 m. D, lowland forest at the foothills of Mt. Cameroon, 524 m.

a triangle of three pores (MN2–4) slightly basally of the retinacular tooth; ?MN1 small seta situated at mid-length between MN4 and mandibular base; ?MN5 tiny seta situated at mid-length between MN4 and mandibular apex; MN6 pore-like, subapical. Left mandible with pore MN2 shifted more basally to the level of the small retinacular tooth, otherwise the chaetotaxy corresponding to the right mandible. ***Maxilla*:** (Figs. 7D–G). Cardo with one long seta (MX1). Chaetotaxy of the inner face stipites asymmetrical: right one with a fine basal seta (MX7) and a more distal series of 9 short setae (gMX2) arranged along the whole length; left one with 12–13 short and very stout setae in gMX2, subdivided into basal row of 7 setae situated more dorsally than the distal row of 5–6 setae situated mesally; outer face of stipes with two long setae (MX5–6) and two pores (MX4 and a secondary one) distally, and a series of secondary setae more basally; ventral face with two pores (MX2–3) and two small secondary setae posterior of each of them. Palpomere 1 with one long mesal seta basally (MX16) and two long setae (MX13–14) and one pore (MX12) at distal ventral face; inner appendage with two pores basally, one ventrally and one dorsally (MX15 and MX17), its distal part with few moderately long to long setae (gAPP). Palpomere 2 ventrally with a pore (MX18), dorsally with a very short seta (MX27) basally and a pore (MX19) distally on intersegmental membrane; palpomere 3 with two pores (MX20, MX22) ventrally, and a moderately long seta on outer face (MX21), MX23 not observed; palpomere 4 with subbasal moderately long seta (MX24) and a pore (MX26) and digitiform sensillum (MX25) distally, apical membranous part with numerous short setae (gMX). ***Labium*:** (Figs. 6B, 7B). Submentum with one pair of long setae (LA1) and one pair of minute setae on membranous lobe (LA2). Mentum only with a pair of long setae (LA3) observed. Prementum ventrally with a pair of minute setae (LA5) basally, and a long seta LA6 contiguous with pore LA7 on anterior margin basally of labial palpus; dorsal surface only with very long seta LA10 observed. Labial palpomere 1 with a pore (LA13) basally, and another (LA14) on intersegmental membrane dorsally; palpomere 2 with a pore (LA15) on outer face and a group of tiny setae (gLA) apically.

Etymology. The new species is named after Ignacio Ribera, an evolutionary biologist, ecologist and a water beetle specialist who passed away during the coronavirus pandemic in 2020.

Distribution and biology. The new species is known from two localities some 100 km apart on the Cameroonian Volcanic Line in western Cameroon. Adults and larvae were sifted from the forest leaf litter in primary lowland (Mt. Cameroon) and submontane forest (Mt. Kupe).

4. Discussion

4.1. Phylogeny of Coelostomatini

The phylogeny of the tribe Coelostomatini is insufficiently known. Short & Fikáček (2013) revealed the monophyly of the tribe but included only five species representing three genera in their molecular phylogeny of the Hydrophilidae. Deler-Hernández et al. (2018) included 33 terminal taxa, but their sampling was focused on the Neotropical genera *Phaenonotum*, *Phaenostoma*, *Lachnodacnum* and *Cyclotypus* and did not include relevant sampling for remaining coelostomatine subgroups. For this study, we expanded the sampling for the genera *Dactylosternum* and *Coelostoma* and added three nuclear protein-coding genes for the species sequenced previously. Our analysis reveals three strongly supported clades: (1) genus *Dactylosternum* which is revealed monophyletic, in contrast to doubts about its monophyly discussed by Short & Fikáček (2013); (2) genus *Coelostoma* which monophyly is moreover supported by the aquatic lifestyle of all representatives; and (3) the Neotropical clade revealed as monophylum already in the study by Deler-Hernández et al. (2018). In contrast, the relationships among these groups are less robust. The genus *Cyclotypus* is herein surprisingly revealed as sister to *Coelostoma*, rather than to the Neotropical clade as suggested in the previous analysis by Deler-Hernández et al. (2018), but its position was recovered without support in both analyses. This indicates that reconstructing the backbone topology of the Coelostomatini may be challenging and will likely require a wider taxon and gene sampling. The monophyly of *Dactylosternum* revealed here is unexpected as the genus is diverse in adult and larval morphology. The five *Dactylosternum* taxa in the phylogenetic analysis include species with both larval morphotypes (see chapter 4.3. for details) and different adult morphology, yet they still represent less than 10% of the known diversity (77 species without those of *Kruia*; Short & Fikáček 2011). Better taxon sampling of *Dactylosternum* species is hence needed to test the results of the current analysis.

4.2. Phylogenetic position of *Kruia*

Our analyses reveal *Kruia* as strongly supported sister clade to *Dactylosternum abdominale*, indicating that it is a morphologically highly modified internal group of *Dactylosternum*. Its sister taxon, *Dactylosternum abdominale*, represents an African group of four very similar species (*D. abdominale, D. depressum*, *D. antennale* and *D. scutellare*; Orchymont 1924). *Dactylosternum chrysopelma* group differs from them in the head widened in front of eyes (narrowing in front of eyes in all *Dactylosternum*), concealed labrum (exposed in *D. abdominale* group; Figs. 8O–P), very coarse punctuation of the dorsal body surface (simple in all *Dactylosternum*; Figs. 1, 8L,Q), pronotum more convex than elytra and explanate laterally (as convex as elytra and not explanate in all *Dactylosternum*; Figs. 8M, R), elytra explanate laterally and with convex intervals or bumps (very narrowly explanate and with flat intervals in all *Dactylosternum*) and tarsi with dense long hair-like setae only (with series of stout setae intermixed with sparse hair-like setae in *D. abdominale* group; Fig. 8J). In addition, members of *D. chrysopelma* group differ from all other *Dactylosternum* (and all Coelostomatini) in the sexual dimorphism in the setation of the metaventrite and mesotibia (Figs. 3K–L). They also differ from *Dactylosternum abdominale* in the morphology of the mandible (robust with bifid apex in *D. abdominale,* shortened with simple slender apex in *D. chrysopelma* group; compare Figs 3C and 8B), indicating different food preferences. It is possible that either sexual selection or different biology (or combination of both) may be responsible for the highly modified morphology of *Kruia*. Interestingly, two of the aforementioned species of *D. abdominale* group (*D. antennale* and *D. scutellare*) have antennae with eight antennomeres as in *Kruia* (Fig. 8F); eight antennomeres are otherwise only present in males of *Bourdonnaisia mahensis* Scott, 1913 endemic to Seychelles (Scott 1913) in the Coelostomatini. Eight-segmented antennae in *Kruia* may be a further evidence about the close relationship of *Kruia* and members of the *Dactylosternum abdominale* species group. In other aspects, the morphology of *Kruia* corresponds to that of *D. abdominale* group (Fig. 8): prosternum is short and weakly elevate mesally, the mesoventral elevation is similar in size and shape, the morphology of mouthparts except mandibles is very similar, and all species have carinate first abdominal ventrite. All these observations are congruent with the position of *Kruia* close to the *Dactylosternum abdominale* group as indicated by the molecular analysis. They also justify the proposed synonymy of *Kruia* with *Dactylosternum.*

DNA data are not available for the type species of *Kruia*, but the high morphological similarity of that species with *Dactylosternum riberai* including the nearly identical male genitalia (Figs. 3O–P) indicate that both species form a clade, referred as *D. chrysopelma* species group hereafter.

4.3. Larval morphology

The larva of *Dactylosternum riberai*, i.e. the member of the *D. chrysopelma* clade is very similar to the larvae of *D. cacti* (Archangelsky 1994, 1997; Archangelsky et al. 2016) and *D. abdominale* (briefly illustrated by de Marzo 2000 and Fikáček 2019a) in (1) nasale with one triangular tooth; (2) the morphology of mandibles; (3) submentum completely fused with head capsule; (4) prementum without ligula; and (5) presence of the hypopharyngeal lobe. In contrast to *D. cacti*, *D. riberai* has completely symmetrical epistomal lobes (similar to *D. abdominale*), antennal sensorium as long as antennomere 3 (shorter in *D. cacti* and *D. abdominale*, similarly

long in other *Dactylosternum* species), asymmetrical maxillary stipites as well as the arrangement of gMX2 setae, many more secondary setae on the dorsal surface of the head and shorter legs with more reduced claw (states of all latter characters are unknown for *D. abdominale* at the moment). Based on the illustrations by de Marzo (2000), it seems probable that the larva of *D. riberai* resembles that of *D. abdominale* in most characters; that would correspond to the results of our phylogenetic analysis and further corroborate *Kruia* as an internal group of *Dactylosternum*.

Two largely different larval morphotypes are known for *Dactylosternum* larvae: (1) the one represented by *D. riberai*, *D. abdominale* and *D. cacti*, and (2) the one represented by larvae of *D. subrotundum* (Costa et al. 1988), *Dactylosternum* sp. described by Archangelsky (1997) and *D. dytiscoides* (Fikáček 2019a). The first morphotype has strongly asymmetrical mandibles, the left one lacks large teeth and is pubescent, the epistomal lobes are symmetrical or nearly so, nasale is triangular, the ligula is absent and a hypopharyngeal lobe is always present. This morphotype resembles larvae of *Sphaeridium* (Archangelsky 1997) and of the tribe Megasternini (e.g., Archangelsky 1997, 2018; Fikáček 2019b) in the morphology of the head appendages, perhaps suggesting similar food preferences (i.e. eggs and larvae of Diptera or weevils: Koppenhöfer et al. 1995; Sowig et al. 1997). The second morphotype is characterized by nearly symmetrical mandibles with two retinacular teeth each, strongly asymmetrical epistomal lobes, narrowly quadrate to multidentate nasale, the presence of ligula and in two of the three species by the absence of the hypopharyngeal lobe (absent in *D. subrotundum* and *D. dytiscoides*, present in *Dactylosternum* sp. described by Archangelsky 1997).

4.4. Distribution of *D. chrysopelma* species group

Both species assigned here to the morphologically aberrant *D. chrysopelma* lineage of *Dactylosternum* inhabit moist tropical broadleaf forests in the West African Gulf of Guinea, i. e. the region considered as biodiversity hotspot (Guinean Forest of West Africa hotspot; Mittermeier et al. 2011). The newly discovered localities in Cameroon (Fig. 9) are part of the Cameroon Volcanic Line, i.e. the series of mostly dormant volcanos of Early Cretaceous origin (Tye 1984), spanning from the island of Annobón through Principe, Sao Tome and Bioko to the continent, where they include a chain of montane ranges and solitary peaks from Mt. Cameroon in the south-west (the highest mountain in West and Central Africa and the only active volcano in the region) to Mandara Mts. in the north-east (Burke 2001). Of the islands, Bioko is part of the continental shelf and was connected to the continent during the Pleistocene (Jones 1994). The known Cameroonian localities of *D. riberai* are situated in the primary lowland forest at the foothills of Mt. Cameroon (Fig. 8D; this kind of forest reaches ca. 350–1100 m a.s.l.) and submontane Afrotropical rain forest on the slopes of Mt. Kupe (Fig. 9C; it ranges from 800 m a.s.l to the submit at 2050 m a.s.l.) (Cheek et al. 2004). Both Mt. Cameroon and Mt. Kupe, as well as the whole region, are known for the high diversity and endemism in plants, amphibians, birds, primates and insects (Bergl et al. 2007; Oates 2011; Schiøtz 1999; Stattersfield et al. 1998; Onana & Cheek 2011; Cable & Cheek 1998; Ustjuzhanin et al. 2018, 2020; Safián et al. 2019), likely in consequence to the recent history of the region - the volcanoes served as rainforest refugia during the Pleistocene dry periods (Maley 1996). Lowland and highland forests have been turned into farmland and agriculture area in most areas and larger forests are nowadays mostly present on the slopes of the volcanoes of which some are protected (Mount Cameroon National Park on Mt. Cameroon, Bakossi National Park managed by the Bakossi people and monitored by WWF on western slopes of Mt. Kupe; Cronin et al. 2014). Both Pleistocene refugia and the presence of protected forests on the volcanoes may be reasons for finding *D. riberai* at foothills of Mt. Cameroon and Mt. Kupe only. Despite of our extensive recent sampling of forest litter fauna along much of the Cameroon Volcanic Line (Mt. Oku, Mt. Kupe, Mt. Cameroon in Cameroon, as well as islands of Bioko and Annobon in Equatorial Guinea), only two herein reported localities yielded *Dactylosternum riberai*, i.e. the member of the *D. chrysopelma* clade.

The only known locality of *Dactylosternum chrysopelma* is situated in the border area of Liberia and Sierra Leone where the trans-boundary Gola Forest National Park was declared in 2010–2016. It protects the largest areas of Western Guinean lowland forests also known for its high diversity and endemism (Klop et al. 2008). Similarly to the Cameroonian volcanoes, this area comprised several rainforest refugia during the Pleistocene dry events when most of the lowlands turned to dry savannah (Maley 1996). The widespread pre-Pleistocene rainforest-inhabiting ancestor which population split into widely separated refugia in Upper Guinea (Sierra Leone, Liberia, Ivory Coast), Cameroon (Cameroon Volcanic Line) and mountain areas in equatorial Africa during the Pleistocene was hypothesized for some groups of plants and vertebrates (e.g., Violaine et al. 2008; Hassanin et al. 2015; Allen et al. 2019; Piñeiro et al. 2019), although groups with similar distribution of pre-Pleistocene origin are also known (Migliore et al. 2019). We may expect a similar scenario for the species of the *Kruia* clade, although this can be studied only after obtaining the DNA-grade specimens of *D. chrysopelma* in the future.

5. Acknowledgements

We are indebted to V. Sýkora (Charles University, Prague) and M. Seidel (University of Hamburg, Germany) for providing us with few unpublished DNA sequences, and to K. Darrow (USNM) for taking the photographs of the holotype of *Kruia chrysopelma* and the permission to publish them in this study, and to R. Tropek

(Charles University, Prague) for comments on the Cameroonian localities. We are grateful to Dr. Miguel Archangelsky (Centro de Investigación Esquel de Montaña y Estepa Patagónica, Argentina) and Bruno Clarkson (Instituto Oswaldo Cruz, Rio de Janeiro, Brazil) for their comments and suggestions which helped us to improve the original manuscript. Qinghao Zhao is indebted to the Department of Zoology, Charles University, Prague for funding his stay in Prague in September 2019 during which the DNA lab work for this project was finalized. The study was partly supported by the Ministry of Culture of the Czech Republic (DKRVO 2019–2023/5.I.b, National Museum, 00023272) to M. Fikáček, National Nature Science Foundation of China (31872965) and Shanghai 'Phosphorus' Science Foundation, China (19QA1406600) to Q. Zhao, and Charles University (PRIMUS/17/SCI/8) to Ishmeal N. Kobe. Specimens were collected under the collecting permit no. 86/MINRESI/B00/C00/C10/C14 issued by the Cameroon Ministry of Scientific Research and Innovation.

6. References

Allen K.E., Walter P., Tapondjou N., Greenbaum E., Welton L.J., Bauer A.M. 2019. High levels of hidden phylogenetic structure within Central and West African *Trachylepis* skinks. – Salamandra **55**(4): 231–241.

Archangelsky M. 1994. Description of preimaginal stages of *Dactylosternum cacti* (Coleoptera, Hydrophilidae: Sphaeridiinae). – Entomologica Scandinavica **25**: 121–128.

Archangelsky M. 1997. Studies on the biology, ecology, and systematics of the immature stages of New World Hydrophiloidea (Coleoptera: Staphyliniformia). – Bulletin of the Ohio Biological Survey (New Series) **12**: 1–207.

Archangelsky M. 2018. Larval chaetotaxy and morphometry of *Oosternum costatum* (Coleoptera: Hydrophilidae) including a discussion of larval characters with phylogenetic relevance. – Acta Entomologica Musei Nationalis Pragae **58**(2): 499–511.

Archangelsky M., Rodriguez G., Torres P. L.M. 2016. Primary chaetotaxy and larval morphometry of *Phaenonotum exstriatum* and *Dactylosternum cacti* (Coleoptera: Hydrophilidae). – Acta Entomologica Musei Nationalis Pragae **56**(1): 167–193.

Arriaga-Varela E., Wong S.Y., Kirejtshuk A., Fikáček M. 2018. Review of the flower-inhabiting water scavenger beetle genus *Cycreon* (Coleoptera: Hydrophilidae), with descriptions of new species and comments on its biology. – Deutsche Entomologische Zeitschrift **65**(1): 99–115.

Bauer A.M., Russell A.P. 1986. *Hoplodactylus delcourti* n. sp. (Reptilia: Gekkonidae), the largest known gecko. – New Zealand Journal of Zoology **13**: 141–148.

Bergl R.A., Oates J.F., Fotso R., 2007. Distribution and protected area coverage of endemic taxa in West Africa's Biafran forests and highlands. – Biological Conservation **134**: 195–208.

Bloom D.D., Fikáček M., Short A.E.Z. 2014. Clade age and diversification rate variation explain disparity in species richness among water scavenger beetle (Hydrophilidae) lineages. – PLOS One **9**(6): e98430. doi:10.1371/journal.pone.0098430

Burke K. 2001. Origin of the Cameroon Line of volcano-capped swells. – Journal of Geology **109**: 349–362.

Byttebier B., Torres P.L.M. 2009. Description of the preimaginal stages of *Enochrus (Hugoscottia) variegatus* (Steinheil, 1869) and *E. (Methydrus) vulgaris* (Steinheil, 1869) (Coleoptera: Hydrophilidae), with emphasis on larval morphometry and chaetotaxy. – Zootaxa **2139**: 1–22.

Cable S., Cheek M. 1998. The Plants of Mt. Cameroon: a conservation checklist. – Royal Botanical Gardens, Kew. 277 pp.

Cheek M., Pollard B.J., Darbyshire I., Onana J.M., Wild C. 2004. The plants of Kupe, Mwanenguba and the Bakossi Mountains, Cameroon: a conservation checklist. – Kew, Royal Botanic Gardens, 508 pp.

Costa C., Vanin S.A., Cassari-Chen S.A. 1988. Larvas de Coleoptera do Brasil. – Museo di Zoologia, Universidade de Sao Paulo, Sao Paulo, 282 pp.

Cronin D.T., Moses B.L., Bergl R.A., Hearn G.W. 2014. Biodiversity and Conservation of Tropical Montane Ecosystems in the Gulf of Guinea, West Africa. – Arctic, Antarctic, and Alpine Research **46**: 891–904.

De Marzo L. 2000. Larvae di coleotteri indetriti vegetali di origine agricola: lineamenti morfologici e presenza stagionale (Polyphaga: 20 famiglie). – Entomologica, Bari **34**: 65–131.

Deler-Hernández A., Sýkora V., Seidel M., Cala-Riquelme F., Fikáček M. 2018. Multiple origins of the *Phaenonotum* beetles in the Greater Antilles (Coleoptera: Hydrophilidae): phylogeny, biogeography and systematics. – Zoological Journal of the Linnean Society **183**: 97–120.

Erwin T. 2007. Xenaroswellanini, *Xenaroswelliana deltaquadrant*, new tribe, new genus, and new species from the Cerrado of Estado de Goias, Brazil (Insecta: Coleoptera: Carabidae). – Proceedings of the California Academy of Sciences **58** (23–30): 561–568

Fikáček M. 2019a. 20. Hydrophilidae Leach, 1815. Pp. 271–337 in: Ślipiński A., Lawrence J. (eds), Australian Beetles. Volume 2. Archostemata, Myxophaga, Adephaga, Polyphaga (part). – CSIRO Publishing, Clayton, 765 pp.

Fikáček M. 2019b. Neotropical leaf litter beetle genus *Motonerus* (Coleoptera: Hydrophilidae): new species, distribution data and description of third instar larva. – Neotropical Entomology **48**(5): 788–808.

Fikáček M., Archangelsky M., Torres P.L.M. 2008. Primary chaetotaxy of the larval head capsule and head appendages of the Hydrophilidae (Coleoptera) based on larva of *Hydrobius fuscipes* (Linnaeus, 1758). – Zootaxa **1874**:16–34.

Fikáček M., Leschen R.A.B., Newton A.F., Gunter N. 2012. *Horelophus walkeri* rediscovered: adult morphology and notes on biology (Coleoptera: Hydrophilidae). – Acta Entomologica Musei Nationalis Pragae **52**: 129–146.

Flannery T.F., Groves C.P. 1998. A revision of the genus *Zaglossus* (Monotremata, Tachyglossidae), with description of new species and subspecies. – Mammalia **62**(3): 387–390.

Hansen M. 1991. The Hydrophiloid Beetles. Phylogeny, Classification and a Revision of the Genera (Coleoptera, Hydrophiloidea). – Biologiske Skrifter, Det Kongelige Danske Videnskabernes Selskab **40**: 1–368.

Hansen M. 1999a. Fifteen new genera of Hydrophilidae (Coleoptera), with remarks on the generic classification of the family. – Entomologica scandinavica **30**: 121–172.

Hansen M. 1999b. World Catalogue of Insects,Vol. 2: Hydrophiloidea (Coleoptera). – Apollo Books, Stenstrup. 416 pp.

Hassanin A., Souraya K., Gembu G.C., Goodman S.M., Kadjo B., Nesi N., Pourrut X., Nakouné E., Bonillo C. 2015. The comparative phylogeography of fruit bats of the tribe Scotonycterini (Chiroptera, Pteropodidae) reveals cryptic species diversity related to African Pleistocene forest refugia. – Comptes Rendus Biologies **338**(3): 197–211.

Jensen A., Jenkins Shaw J., Żyła D., Solodovnikov A. 2020. A total-evidence approach resolves phylogenetic placement of *'Cafius' gigas*, a unique recently extinct rove beetle from Lord Howe Island. – Zoological Journal of the Linnean Society **190**(4): 1159–1174.

Jones P.J. 1994. Biodiversity in the Gulf of Guinea: an overview. – Biodiversity and Conservation **3**: 772–784.

Kearse M., Moir R., Wilson A., Stones-Havas S., Cheung M., Sturrock S., Buxton S., Cooper A., Markowitz S., Duran C., Thierer T., Ashton B., Meintjes P., Drummond A. 2012. Geneious Basics: an integrated and extendable desktop software for the organization and analysis of sequence data. – Bioinformatics **28**(12), 1647–1649. doi:10.1093/bioinformatics/bts199

Klop E., Lindsell J., Siaka A. 2008. Biodiversity of Gola Forest, Sierra Leone: A survey of Gola's mammals, birds, butterflies, dragonflies and damselflies, trees and non-woody plants, forest struc-

ture. – Royal Society for the Protection of Birds, Conservation Society of Sierra Leone, Governmentof Sierra Leone, 195 pp.

Klug J.C.F. 1855. Diagnosen neuen Coleoptera aus Mossambique. Bericht über die zur Bekanntmachung geeigneten Verhandlungen der Königl. – Preuss. Akademie der Wissenschaften zu Berlin (1855): 643–660.

Koppenhöfer A.M., Sikora R.A., Seshu Reddy K.V. 1995. Eidonomy and ekology of Dactylosternum abdominale (Coleoptera: Hydrophilidae), a predator of the Banana weevil Cosmopolites sordidus (Coleoptera: Curculionidae). – Entomologia Generalis **19**(4): 303–313.

Lanfear R., Frandsen P.B., Wright A.M., Senfeld T., Calcott B. 2017. PartitionFinder2: New methods for selecting partitioned models of evolution for molecular and morphological phylogenetic analyses. – Molecular Biology and Evolution **34**(3): 772–773. doi:10.1093/molbev/msw260

Lawrence J. F., Ślipiński A. 2013. Australian Beetles. Volume 1: Morphology, classification and keys. – CSIRO Publishing, Clayton, 520 pp.

Loveridge A. 1941. Report on the Smithsonian-Firestne expedition's collection of reptiles and amphidians from Liberia. – Proceedings of the United States National Museum **91**: 113–140.

Maley L. 1996. The African rain forest: main characteristics of changes in vegetation and climate from the Upper Cretaceous to the Quaternary. – Proceedings of the Royal Society of Edinburgh **104B**: 31–73.

Migliore J., Kaymak E., Mariac C., Couvreur T.L.P., Lissambou B., Piñeiro R., Hardy O.J. 2019. Pre–Pleistocene origin of phylogeographic breaks in African rain forest trees: New insights from *Greenwayodendron* (Annonaceae) phylogenomics. – Journal of Biogeography **46**: 213–223.

Miller M.A., Pfeiffer W., Schwartz T. 2010. Creating the CIPRES Science Gateway for inference of large phylogenetic trees. – Gateway Computing Environments Workshop', 14 November 2010, New Orleans, LA, USA. pp. 1–8. doi:10.1109/GCE.2010.5676129

Minoshima Y., Hayashi M. 2011. Larval morphology of the Japanese species of the tribes Acidocerini, Hydrobiusini and Hydrophilini (Coleoptera: Hydrophilidae). – Acta Entomologica Musei Nationalis Pragae **51**: 1–118.

Minoshima Y.N., Seidel M., Wood J.R., Leschen R.AB., Gunter M. Fikáček M. 2018. Morphology and biology of the flower-visiting water scavenger beetle genus *Rygmodus* (Coleoptera: Hydrophilidae). – Entomological Science **21**(4): 363–384.

Mittermeier R.A., Turner W.R., Larsen F.W., Brooks T.M., Gascon C. 2011. Global biodiversity conservation: the critical role of hotspots. Pp. 3–22 in: Zachos F.E., Habel J.C. (eds), Biodiversity Hotspots. – Springer Publishers, London. 546 pp.

Nguyen L.T., Schmidt H.A., von Haeseler A., Minh B.Q. 2015. IQTREE: a fast and effective stochastic algorithm for estimating maximumlikelihood phylogenies. – Molecular Biology and Evolution 32(1), 268–274. doi:10.1093/molbev/msu300

Oates J.F. 2011. Primates of West Africa: A Field Guide and Natural History. – Arlington, Virginia: Conservation International.

Onana J.M., Cheek M. 2011. Red Data Book of the Flowering Plants of Cameroon: IUCN Global Assessments. –Royal Botanic Gardens, Kew. 578 pp.

Orchymont A.d'. 1913. Un nouvel Hydrophilide de la Faune Antarctique Néozélandaise. – Annales de la Société entomologique de Belgique **57**: 94–100.

Orchymont A.d'. 1919d. Contribution a l'étude des sous-familles des Sphaeridiinae et des Hydrophilinae (Col. Hydrophilidae). – Annales de la Société entomologique de France **88**: 105–168.

Orchymont A.d'. 1924. Hydrophilidae d'Afrique orientale. – Annali del Museo civico di Storia naturale di Genova **51**(1923): 257–268.

Piñeiro R., Hardy O.J., Tovar C., Gopalakrishnan S., Vieira F.G., Gilbert M.T.P. 2019. Contrasting dates of rainforest fragmentation in Africa inferred from trees with different dispersal abilities. – bioRxiv 811463; doi: https://doi.org/10.1101/811463

Rambaut A., Drummond A.J., Xie D., Baele G., Suchard M.A. 2018. Posterior summarization in Bayesian phylogenetics using Tracer 1.7. – Systematic Biology **67**(5): 901–904. doi:10.1093/sysbio/syy032

Ronquist F., Teslenko M., van der Mark P., Ayres D.L., Darling A., Höhna S., Larget B., Liu L., Suchard M.A., Huelsenbeck J.P. 2012. MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. – Systematic Biology **61**(3): 539–542. doi:10.1093/sysbio/sys029

Sáfián Sz., Collins S.C., Belcastro C., Brattström O., Tropek R. 2019. Description of previously unknown females of three *Euriphene* Boisduval, 1847 species and the unknown male of *Bebearia inepta* Hecq, 2001 from Western Africa, with notes on their taxonomy, bionomy and distribution (Lepidoptera: Nymphalidae, Limenitidinae). – SHILAP Revista de Lepidopterología **47**: 581–591.

Scott H. 1913. The Percy Sladen Trust Expedition to the Indian Ocean in 1905, under the Leadership of Mr. J. Stanley Gardiner, M. A. Vol. 5. No. X. – Coleoptera, Hydrophilidae, Histeridae. – Transactions of the Linnean Society of London **16**(2): 193–235, pl. 14.

Seidel M., Arriaga-Varela E., Fikáček M. 2016. Establishment of Cylominae Zaitzev, 1908 as a valid name for the subfamily Rygmodinae Orchymont, 1916 with an updated list of genera (Coleoptera: Hydrophilidae). – Acta Entomologica Musei Nationalis Pragae **56**(1): 159–165.

Seidel M., Minoshima Y.N., Arriaga-Varela E., Fikáček M. 2018. Breaking a disjunct distribution: a review of the southern hemisphere genera *Cylorygmus* and *Relictorygmus* gen. nov. (Hydrophilidae: Cylominae). – Annales Zoologici **68**(2): 375–402.

Seidel M., Minoshima Y.N., Leschen R.A.B., Fikáček M. 2020. Phylogeny, systematics and rarity assessment of New Zealand endemic *Saphydrus* beetles and related enigmatic larvae (Coleoptera: Hydrophilidae: Cylominae). – Invertebrate Systematics **34**(3): 260–292.

Shatrovskiy A. 2017. A new species of *Cycreon* d'Orchymont, 1919 from Singapore (Coleoptera: Hydrophilidae: Megasternini). – Zootaxa **4217**(3): 588–592.

Schiøtz A. 1999. Treefrogs of Africa. – Chimaira, Frankfurt am Main. 350 pp.

Short A.E.Z. 2010. Phylogeny, evolution and classification of the giant water scavenger beetles (Coleoptera: Hydrophilidae: Hydrophilini: Hydrophilina). – Systematics and Biodiversity **8**(1): 17–37.

Short A.E.Z., Fikáček M. 2011. World catalogue of the Hydrophiloidea (Coleoptera): additions and corrections II (2006–2010). – Acta Entomologica Musei Nationalis Pragae **51**(1): 83–122.

Short A.E.Z., Fikáček M. 2013. Molecular phylogeny, evolution, and classification of the Hydrophilidae (Coleoptera). – Systematic Entomology **38**: 723–752.

Short A.E.Z., Santana L., Benetti C.J. Hamada N. 2020. Rediscovery of the Neotropical water scavenger beetle *Protistolophus spangleri* Short with notes on its habitat and behavior (Coleoptera: Hydrophilidae: Hydrophilinae). – Zootaxa **4759**(1): 139–142.

Sowig P., Himmelsbach R., Himmelsbach W. 1997. Predator-prey relationship between insect larvae: growth of Sphaeridium larvae (Coleoptera: Hydrophilidae) under time constraints through predation on *Musca autumnalis* maggots (Diptera: Muscidae). – Canadian Journal of Zoology **75:** 2069–2076.

Spangler P.J., Perkins P.D. 1981. A new genus and species of water scavenger beetle from Africa (Coleoptera: Hydrophilidae: Sphaeridiinae). – Pan-Pacific Entomologist **57**: 220–226

Stattersfield A.J., Crosby M.J., Long A.J., Wege D.C. 1998. Endemic Bird Areas of the World: Priorities for Biodiversity Conservation. –Birdlife International, Cambdridge. 846 pp.

Tye H. 1984. Geology and landforms in the highlands of western Cameroon. Pp. 15–17 in: Stuart S.N. (ed), Conservation of Cameroon Montane Forests. – International Council for Bird Preservation, Cambridge. 263 pp.

Ustjuzhanin P., Kovtunovich V., Sáfián S., Maicher V., Tropek R. 2018. A newly discovered biodiversity hotspot of many-plumed moths in the Mount Cameroon area: first report on species diversity, with description of nine new species (Lepidoptera, Alucitidae). – ZooKeys **777**: 119–139.

Ustjuzhanin P., Kovtunovich V., Maicher V., Sáfián S., Delabye S., Streltzov A., Tropek R. 2020. Even hotter hotspot: description of seven new species of many-plumed moths (Lepidoptera, Alucitidae) from Mount Cameroon. – ZooKeys **935**: 103–119.

Violaine N., Mboumba J.F., Verheyen E., Denys C. 2008. Phylogeographic Structure and Regional History of *Lemniscomys striatus* (Rodentia: Muridae) in Tropical Africa. – Journal of Biogeography **35**(11): 2074-2089.

Electronic Supplement File

at http://www.senckenberg.de/arthropod-systematics

ASP_78-3_Fikacek_Electronic_Supplement.zip

DOI: 10.26049/ASP78-3-2020-05/1

Supplementary file: fikacek&al-kruia-electronic-supplement.doc. — **Table S1.** Amplification programs and primers. — **Table S2.** PartionFinder2 output: IQ-Tree block and MrBayes block for dataset used. — **Fig. S1.** Maximum likelihood phylogenetic tree of the Coelostomatini. — **Fig. S2.** Bayesian analysis phylogenetic tree of the Coelostomatini.

Zoobank registrations

at http://www.zoobank.org

Present article: http://zoobank.org/urn:lsid:zoobank.org:pub:2DD49DB2-9025-47F1-9408-BB0EC717F8EC

***Dactylosternum riberai* Fikáček, Zhao, Kobe & Grebennikov, 2020:** http://zoobank.org/urn:lsid:zoobank.org:pub:2DD49DB2-9025-47F1-9408-BB0EC717F8EC

Digitally Archived Data

at Zenodo scientific archive (http://doi.org/10.5281/zenodo.4039839)

The dataset submitted to Zenodo contains (1) final DNA alignment used for this study, (2) all data included in the electronic Supplementary file above, and (3) original unedited versions of the photographs and SEM micrographs taken for this study, including those taken for comparative purposes only and not presented directly in the manuscript.

Authors' contributions

VG performed the field work. MF designed the study and prepared the systematic part, QZ generated most of the new DNA data, performed DNA analyses and drafted molecular parts of the manuscript, KI provided detailed information about the area based on his field work experience, all co-authors drafted the Discussion and commented on the text before submission.