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DNA barcoding and regional diversity of understudied Micropeplinae (Coleoptera: Staphylinidae) in Southwest China: phylogenetic implications and a new *Micropeplus* from Mount Emei

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Abstract

Extensive litter sampling at eight forested localities in Yunnan and Sichuan detected 381 specimens of Micropeplinae rove beetles. DNA barcoding data from 85 representative specimens were analysed to delimit species and infer their relationships. Statistical methods were implemented to assess regional species diversity of understudied Micropeplinae. The total number of sampled Micropeplinae species varied between 14 and 17, depending on a splitting versus lumping approach for allopatric populations. A single Micropeplinae species was sampled in six of eight studied localities, three species were found on Mount Gongga, while ten species were discovered on hyperdiverse Mount Emei in Sichuan. All Micropeplinae specimens from our samples belong either to the genus *Cerapeplus*, or to three other inclusive groups temporarily retained inside *Micropeplus sensu lato*. Each of the three groups potentially represents a separate genus: *tesserula* group, *sculptus* group and *Micropeplus sensu stricto*. A new species *Micropeplus jason* **sp. n.** from Mount Emei in Sichuan is described. Numerous illustrations introduce regional fauna and clarify the discussed morphological characters.

Key words: *Cerapeplus*, Yunnan, Sichuan, phylogeny, classification

Introduction

The mountains of Southwest China are noted for their exceptionally rich biota (Tang *et al*. 2006). This phenomenon is likely linked to the habitat diversification and fragmentation as a result of the accelerated orogeny caused by the collision of the Indian plate with Asia some 40–55 MY ago with the mountains reaching their approximate present day height by 5–15 MY (Favre *et al*. 2015). Additionally, regional species composition was extensively and repeatedly modified by the climate-induced fluctuations, including those which happened during the Pleistocene climatic cycles, fostering repeated colonisation events and promoting vicariant speciation. The resulting diverse and complex mosaic of life forms in mountains of Southwest China offers an intellectually stimulating phylogeographic sampling ground, particularly informative when one targets such stenotopic organisms as litter-inhabiting beetles (Grebennikov 2014a,b).

Here we attempt to shed light on the diversity and evolutionary history of Micropeplinae beetles richly represented in our forest leaf litter samples taken in two Southwest China provinces: Sichuan and Yunnan (Fig. 1). The Micropeplinae form an undoubtedly monophyletic group (Newton & Thayer 1995) of small and aberrant rove beetles with at least 82 species worldwide (Herman 2001). These species prefer relatively wet conditions and seem to be much restricted to such habitats. At least some species are wingless (personal observation) and seemingly narrowly distributed, suggesting accelerated vicariant speciation (Ikeda *et al*. 2011). Such characteristics would make wingless Micropeplinae a model group for unfolding the evolutionary past in the complex mountainous landscape of Southwest China, but for two significant limitations.

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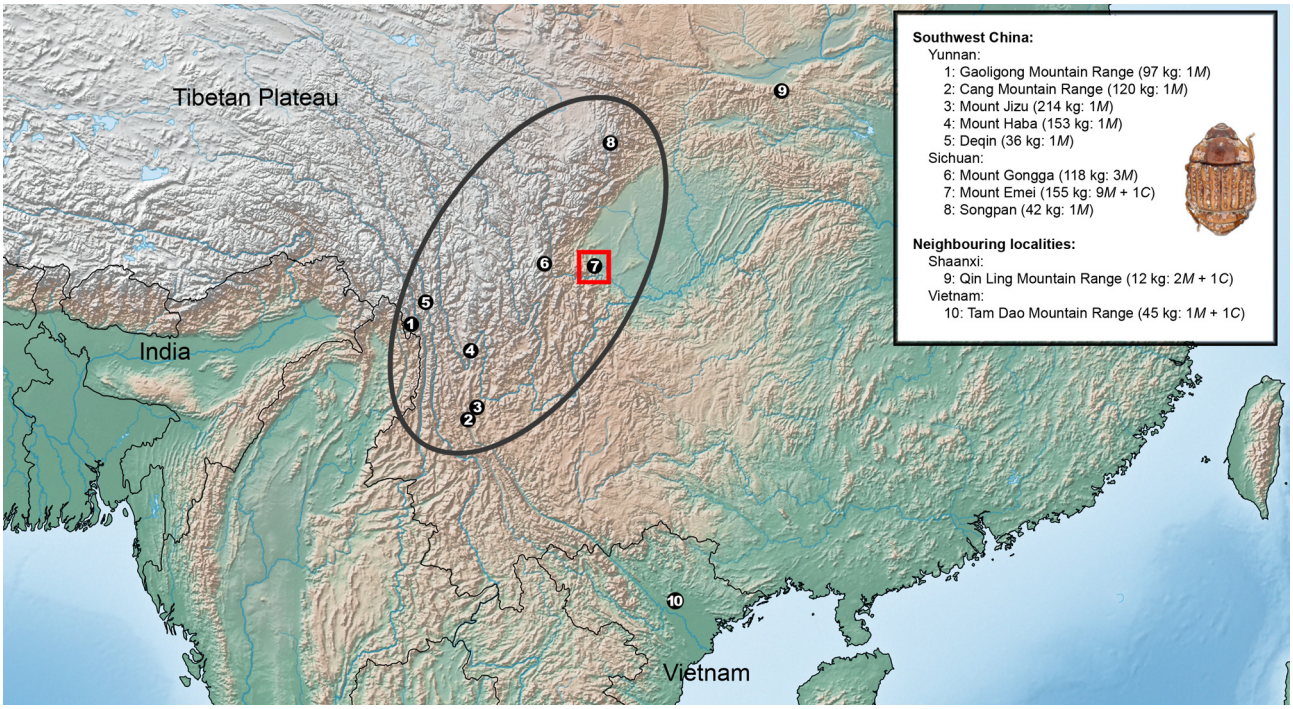

FIGURE 1. Geographical origin of the ingroup Micropeplinae specimens. Eight sampled localities in Southwest China are in the oval. The red frame denotes hyperdiverse mount Emei with at least ten species of Micropeplinae, including *Micropeplus jason* **sp. n.** The number in brackets after the regional names indicates the amount of sifted litter in kilograms, followed by Micropeplinae species diversity of *Micropeplus* (M) and *Cerapeplus* (C). We failed to amplify DNA of the single *Micropeplus* specimen #0882 detected from the Cang Mountain Range and, therefore, the entire locality is not included in the DNA analysis.

The first limitation is the lack of a robust phylogenetic hypothesis within Micropeplinae. Interrelationships inside this clade have never been addressed and, therefore, significant uncertainties exist concerning the phylogenetic validity of all six recognized genera of Micropeplinae, two of which are monobasic (Herman 2001). Most specifically, the implied monophyly of *Micropeplus* Latreille, the type genus with at least 63 species (Herman 2001) is uncertain, since this vaguely and phenetically defined genus likely serves as a dumping ground for the "typical" species lacking distinctive characters defining the other five genera.

The second limitation is the discrepancy between the likely highly diverse Micropeplinae fauna of the region and the inadequate state of their species-level taxonomy. Until 1995 no Micropeplinae species had been recorded from Southwest China (the area restricted in the present work to Yunnan and Sichuan). The most recent reports by Zheng *et al*. (2013, 2014) on *Micropeplus* list six named species for the entire region: two from Yunnan (*M. rougemonti* Watanabe, 1995, Ruili; *M. yunnanus* Watanabe & Xiao, 1996, Mount Jizu) and four from Sichuan (*M. nomurai* Watanabe, 2000, Jiuding Shan; *M. uenoi* Watanabe, 2000, Erlang Shan; *M. xiaoae* Zheng, Yan et Li, 2013, Yele Nature Reserve; *M. songi* Zheng, Li et Yan, 2014, Mount Wahui). It seems safe to assume that the real diversity of Micropeplinae in Southwest China might be at times greater. Using the six now available names is no less daunting, as they were described using the morphological differences of isolated allopatric series, without the benefit of DNA data or comparative material from nearby localities. As a result, assessment of intra- and interspecific variation for the valid six named species in a phylogenetic framework remains to be done before these names can be confidently used for identification of non-topotypical populations, including those in our samples.

The goal of this paper is to report all the information we generated from Micropeplinae specimens, systematically removed from the sifted litter samples, gathered in Southwest China and nearby regions (Fig. 1) in 2009–2012. Our interest in the group was triggered in 2009 by detection of the first specimens of the new *Micropeplus* species, formally named below, which we originally thought might represent a new radiation worthy of a generic taxonomic rank. This led us to sort out all Micropeplinae from the samples in an attempt to first assess species diversity and then perhaps find the closest relatives of this new remarkable species. The availability of relatively large amounts of material and the intense application of the DNA barcoding method (Hebert *et al*. 2003) further tempted us to answer a similarly elementary question of how many Micropeplinae species are in our

samples and, moreover, how many of them can be found sympatrically. To do so, we developed the publicly available DNA barcode library to serve as a nucleus for further barcode-based research on these organisms, particularly from Southwest China. We were markedly constrained by two disadvantages of Micropeplinae as a model group elaborated above, particularly by the lack of well-understood species names coupled with faunal richness and, therefore, the necessity to deal with numerous new species. An attempt to resolve this limitation by providing a full-sized taxonomic revision would require the type specimen study accompanied, most likely, by sampling DNA-suitable specimens in the type localities for adequate DNA-based comparison with our specimens. The project was gradually growing in size and eventually we decided to limit our scope and to report the results as they are, even if some shortcuts have to be made. Most notably, we found it impossible to use Linnaean names for most of the Micropeplinae species analyzed herein, but provided an alternative interim taxonomic nomenclature. Only one new and easily recognizable species from Mount Emei is formally named. Besides determining the number of Micropeplinae species in our samples, we use this opportunity to shed light on the phylogenetic relationships within the subfamily, even though the project was not originally designed to do so. Most specifically, we discuss whether the genus *Micropeplus sensu lato* (Herman 2001) represents a clade and if not, what might be the most logical way of splitting it into smaller monophyletic units. Overall, this work serves as an introduction to Micropeplinae diversity and evolution in Southwest China aimed to catalyse and facilitate further and more detailed studies, including those on species taxonomy.

Material and methods

Museum abbreviations, followed by the name of the curator:

CNC Canadian National Collection of Insects, Arachnids and Nematodes, Ottawa, Canada (P. Bouchard);
ZCAS Institute of Zoology, Chinese Academy of Science, Beijing, P.R. China.

Specimen sampling, handling and gathering DNA data. The term "Southwest China" is delimited to two provinces, Yunnan and Sichuan, from where 381 Micropeplinae adult specimens were sampled by the first author in 2009–2012. The beetles were collected in the following eight localities (Fig. 1; in brackets are the total number of specimens, a slash, followed by the number of individuals successfully sequenced for DNA barcode of 575 nt and longer): the Gaoligong Mountain Range (8/3), the Cang Mountain Range (1/0), Mount Jizu (15/3,) Mount Haba (26/4), Deqin (7/5), Mount Gongga (204/24), Mount Emei (110/22) and Songpan (10/6). Additionally, 184 Micropeplinae specimens from two neighbouring localities were also added (Fig. 1): the Qin Ling Mountain Range in Shaanxi (181/17) and the Tam Dao Mountain Range in northern Vietnam (3/2). All these specimens were all sampled by sifting forest leaf litter with a sifter, followed by a passive extraction in Winkler funnels. The sample size was measured as the mass of litter sifted through a 7 mm square mesh. Approximately 805 kg of samples were thus obtained and processed, of which 748 kg was from Southwest China. The exact sample size for each of 10 ingroup localities is given in Fig. 1. The Micropeplinae specimens were sorted from the mixed Winkler alcohol samples in the laboratory to select specimens representing the greatest regional variety for DNA barcoding. The selection targeted the most morphologically distinct specimens, as judged by their external appearance, and without any attempt to delimit morphospecies. All Micropeplinae specimens from localities in Fig. 1 submitted for DNA barcoding have at least one unique identifier label pinned underneath with the code CNCCOLVG0000XXXX; this format is shortened to the last four informative digits when a specimen is referred to in the text (Figs. 2, 5). Specimen images, geographical data, primers, original electropherograms and other relevant data for all 92 successfully sequenced specimens from Southwest China can be seen online in the publicly accessible dataset "Micropeplinae 92 [DS-MICROP]" on the Barcode of Life Database portal (doi: dx.doi.org/10.5883/DS-MICROP). Only one Micropeplinae specimen (#0882) was sampled from the Cang Shan Mountain Range (Fig. 1) and we failed to amplify the sequence; therefore, the entire locality is not represented in the DNA analysis (Fig. 2). We failed twice to amplify DNA from the single specimen of the genus *Cerapeplus* Löbl et Burckhardt from Mount Emei (Fig. 5J); each attempt indicated by specimen labels #2852 and #4756, respectively. As judged from their external appearance and geographic data, both these specimens likely belong to two species not otherwise represented in our samples. Additionally, we failed to amplify DNA from 24 other *Micropeplus*

specimens from various localities, while one (#2890 from Mount Gongga) provided an unsatisfactory short sequence of 198 nt. These 27 specimens are not included in the online public dataset (see above).

DNA analyses and matrix construction. Three separate DNA analyses were designed. The **Neighbour Joining** (NJ) phenetic analysis was implemented solely to generate Barcode Index Numbers (BINs, see below) for the sequence clusters. The NJ matrix consisted of all 92 Micropeplinae DNA barcodes longer than 200 nt: 70 sequences represented specimens from Southwest China and 22 from the adjacent regions (the Qin Ling Mountain range and the Tam Dao Mountain range; see above and Fig. 1). The tree was not rooted and no outgroup was involved. The GenBank accessions for these 92 sequences are: HQ987112–HQ987125, KF407992–KF407996, KF407998–KF4080016, KF408018–KF408071; all of them new. The NJ analysis was performed using the online BOLD topology-building tool using uncorrected p-distances. The **Maximum Likelihood** (ML) and the **Maximum Parsimony** (MP) analyses attempted to place the diversity of Micropeplinae from Southwest China into a geographical and phylogenetic perspective. For this purpose a matrix of 658 aligned positions was constructed to include 85 barcodes from those used in the NJ analysis, none shorter than 575 nt (GenBank accessions as above for the NJ analysis, except for the following seven excluded sequences shorter than 575 nt: KF407993, KF408000, KF408006, KF408010, KF408023, KF408065, KF408067). These 85 sequences formed ingroups for both ML and MP analyses. The choice of the outgroup taxa was restricted to those relatively few with DNA barcodes freely available from public sources. In total 22 outgroup sequences were added, including six sequences representing three identified *Micropeplus* species and one sequence was that of *Kalissus nitidus* LeConte. The remaining 15 sequences were those of Pselaphinae (13), Dasycerinae (1) and Omaliinae (1); the last was used to root both ML and MP topologies. The 22 outgroup sequences were assembled using public Barcode of Life Database (BOLD) sequences. Their "specimen ID" codes and GenBank accessions followed by localities are given either in Fig. 2 or, for 13 Pselaphinae sequences, are as follows: *Bibloplectus ambiguus* ZMUO.007840 KJ966486 Finland, *Brachygluta fossulata* ZMUO.001627 KJ966445 Finland, *Bryaxis puncticollis* ZMUO.007827 KJ964069 Sweden, *Fagniezia impressa* ZMUO.001232 KJ963009 Finland, *Lucifotychus cognatus* UAM:Ento:121987 Alaska, *Ogmocerus* sp. CNCCOLVG00004001 Tanzania, *Plagiophorus* sp. CNCCOLVG00004002 Tanzania, *Pselaphus heisei* ZMUO.000572 KJ961733 Finland, *Rybaxis laminata* ZMUO.001215 KJ965473 Finland, *Rybaxis longicornis* ZMUO.000383 KJ967441 Finland, *Sonoma margemina* UAM:Ento:130493 Alaska, *Trimium brevicorne* ZMUO.007806 KJ962546 Finland, *Tyrus mucronatus* ZMUO.006223 KJ967356 Finland. Four *Micropeplus* sequences and four Pselaphinae sequences do not have GanBank accessions; they can, however, be fully accessed by using provided BOLD "specimen ID". The search for the optimal substitution model for the ML analysis resulted in choosing the GTR+G+I model as the one having the best log likelihood. Branch statistical support for both ML and MP analyses was estimated by 1000 repetitions of bootstrapping. The ML and MP analyses were performed with MEGA 5 (Tamura *et al*. 2011). Both resulting topologies were visualized in FigTree v1.4 (Rambaut 2013).

Interim taxonomic nomenclature. The unavailability of the Linnaean names for the ingroup specimens forced us to adopt an interim taxonomic nomenclature and provide its criteria. This surrogate nomenclature is to serve a temporary purpose before the proper species names become adequately introduced and fully operational for Micropeplinae from Southwest China. Three alternative approaches were used, each offering a distinct and objectivized strategy to determine an evolutionary unique lineage to be considered as presumptive (=candidate) species.

The first implemented approach was that of Ratnasingham & Hebert (2013), who introduced **Barcode Index Numbers** (BINs) for biodiversity studies hampered by inadequate taxonomy. In this phenetic method the initial sequence clusters are formed using a 2.2% uncorrected p-distance threshold, and then recalculated following a more elaborate algorithm. The end products are unique BINs formed by a combination of three capital letters and four digits (for example ABW5232, Fig. 2) assigned for each cluster of sequences, or to a single sequence, meeting the BIN quality criteria. This method is based entirely on sequence information and does not employ geographical or tree topological data, although each BIN forms a single cluster on the resulting NJ topology.

The second implemented approach is that of **Geographically Delimited Terminal Clades** (GDTCs). These units are formed on rooted phylogenetic trees to incorporate all specimens from a single locality forming a clade. If, however, any original GDTC renders paraphyletic to another group consisting of two or more specimens from another locality, the GDTC is further expanded to incorporate them. This method is expected to perform best with the low-dispersing species sampled from such discrete and relatively adjacent localities as islands or mountaintops

widely separated by dispersal barriers. This approach is threshold-free and instead capitalizes on the geographically discrete nature of the samples and on a hypothesis that unless explicitly rejected, allopatric speciation was the only means of lineage diversification. This implies that in an adequately representative sample no two sister species can be sympatric. This also means that all specimens from the same locality forming a clade represent the same species. The approach is not explicit in reference to the status of the sister allopatric clade, which can be either the same species, or a sister species. The choice between the two latter options has to be made on a case-by-case basis after considering all available data. The GDTCs from a single locality are numbered by using the smallest four digit number of the included specimens (see Fig. 2). In three cases, when the GDTC incorporates specimens from two localities and only one of these two geographic groups is monophyletic, both numbers are used and separated by an n-dash, and the number of the paraphyletic population italicized (for example GDCT #2854–*0883*, Fig. 2).

To avoid the conflict between the independently generated BINs and GDTCs, the third approach employing **Operational Taxonomic Units** (OTUs) was implemented. When GDTC and BIN fully matched each other, a separate and identical OTU was created and numbered by the same four digits matching the GDTC number (or the lesser one for those three GDTCs incorporating specimens from two localities, Fig. 2). Seven detected mismatches between GDTUs and BINs (shaded areas in Fig. 2) were resolved by expanding OTUs to incorporate additional sister GDTCs, or BINs, or both, into an expanded OTU. Each OUT, therefore, was kept monophyletic on the ML tree and, simultaneously, was required not to include other OTUs or their subgroups.

Results

The NJ analysis (tree not shown) grouped 92 specimens of the ingroup Micropeplinae into 22 BINs.

The ML analysis resulted in the tree (Fig. 2) with non-monophyletic Micropeplinae and the highest log likelihood of –9636.2660. Twenty GDTCs of 85 ingroup members were identified, 17 of which contained specimens from a single locality. The remaining three GDTCs contained specimens from two localities, one of them forming a clade and rendering the other paraphyletic.

The MP analysis found the single most parsimonious tree with monophyletic Micropeplinae, the tree length of 2196, the consistency index of 0.24 and the retention index of 0.77. Its topology and branch support values were highly comparable to the ML tree (Fig. 2), while all 20 GDTCs and seven more inclusive clades A-G (Fig. 2) were identical. The basal-most branching pattern of the MP tree is shown on the insert in Fig. 2.

In 12 cases the GDTCs found in the ML or MP analyses were formed by one or more specimens from a single locality and fully corresponded to a BIN found in NJ analysis (in brackets is the number of GDTC specimens): GDTC #4785 (5 exx) from Deqin: BIN ACM8890; GDTC #0886 (1 ex) from Mount Emei: BIN AAN4684; GDTC #2851 (1 ex) from Mount Emei: BIN ABW5237; GDTC #2857 (2 exx) from Mount Emei: BIN ABW5233; GDTC #2863 (1 ex) from Mount Emei: BIN ABW5238; GDTC #0904 (4 exx) from Mount Emei: BIN AAO1980; GDTC #4766 (1 ex) from Tam Dao: BIN ACA6041; GDTC #2837 (4 exx) from the Qin Ling Mountain Range: BIN ABW5252; GDTC #0902 (2 exx) from Mount Emei: BIN AAO1979; GDTC #0906 (4 exx) from Mount Emei: BIN AAO2028; GDTC #4760 (1 ex) from the Tam Dao Mountain Range: BIN ACA6358; GDTC #2875 (5 exx) from Mount Gongga: BIN ABW5234.

Eight other GDTCs did not match a single BIN, or were formed by specimens from more than one locality, or both. These discrepancies are indicated by seven shaded rectangles in Fig. 2 and are as follows: GDTC #2829 (7 exx) from the Qin Ling Mountain Range and GDTC #4790 (3 exx) from Mount Haba formed a single BIN ABW5232; GDTC #4793 (1 ex) from Mount Haba had 14 ambiguously read nucleotides and, therefore, did not meet the minimal quality criteria to form a BIN; GDTC #4767–*2883* corresponding to BIN ABW5231 was formed by specimens from two localities: Songpan (6 exx) and Mount Gongga (3 exx), with the former specimens paraphyletic with respect to the latter; GDTC #2893 (3 exx) from Mount Jizu was formed by two sister BINs: ABW5235 and ABW5239; GDTC #2854–*0883* corresponding to BINs AAN4682 and AAN4683 was formed by specimens from two localities: Mount Emei (3 exx) and the Gaoligong Mountain Range (3 exx), with the former paraphyletic with respect to the latter; GDTC #0889–*2831* corresponding to BINs ACE8713 and ACE8714 was formed by specimens from two localities: Mount Emei (4 exx) and the Qin Ling Mountain Range (5 exx), with the former specimens paraphyletic with respect to the latter; GDTC #2865 (16 exx) from Mount Gongga was split in two sister BINs: ACE8712 and ACE8714.

Resolving conflicts between BINs and GDTCs (shaded rectangles in Fig. 2) resulted in 18 OTUs, 12 of them corresponding to BINs and GDTCs, and six others more inclusive.

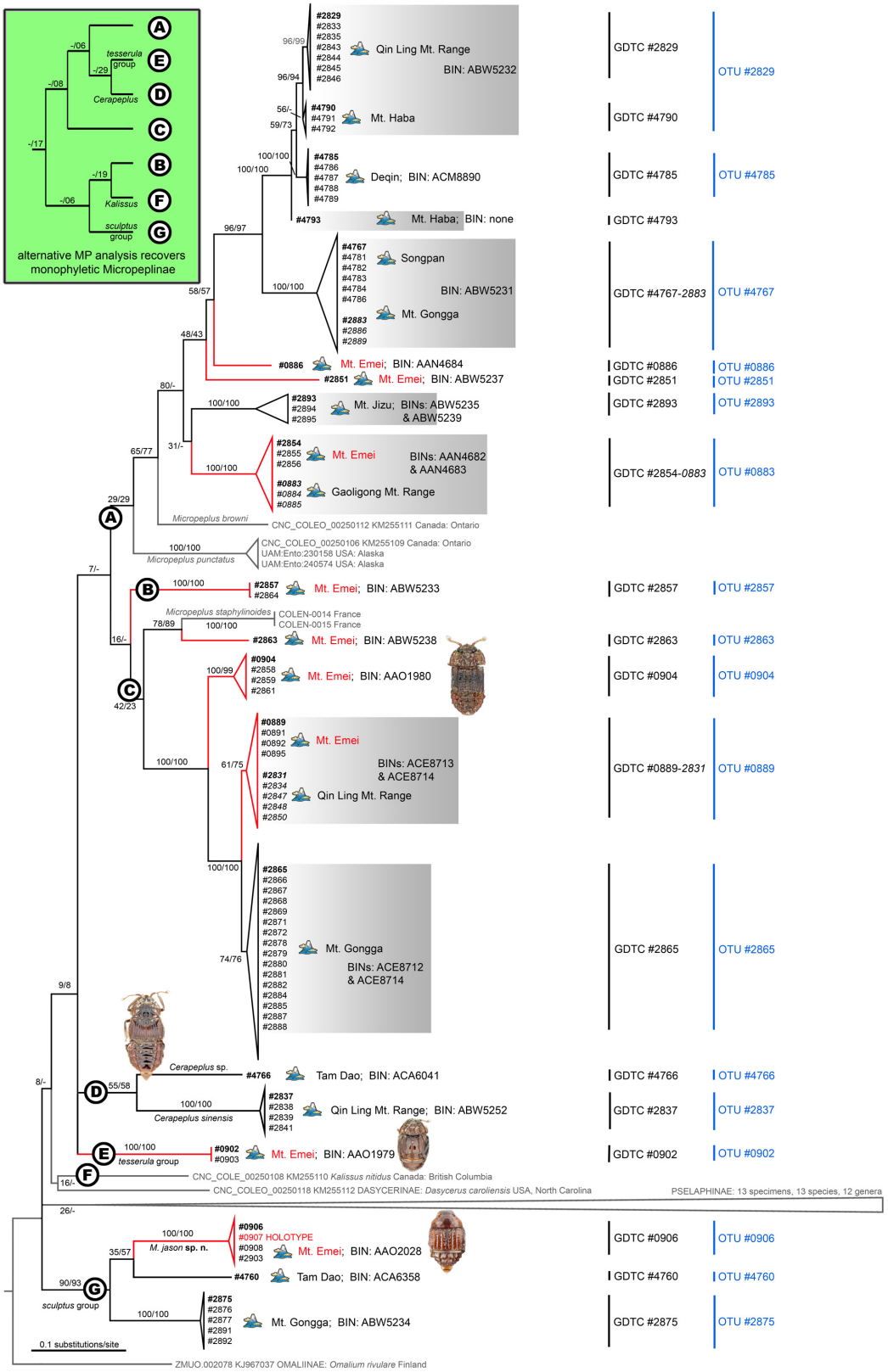

FIGURE 2. Maximum Likelihood inference phylogram of 85 Micropeplinae ingroup specimens from Southwest China and two neighbouring localities using the 658 nt of the mtDNA barcoding CO1 gene fragment. The outgroup clades and terminals are in grey. The nine red terminal clades are those from hyperdiverse Mount Emei. Clades A–G are discussed in the text. The digits at branches separated by a slash (/) are ML and MP bootstrap values, respectively; a dash (-) after a slash denotes five ML clades not recovered in MP analysis. BIN, GDTC and OUT are interim taxonomic clusters explained in Methods. Seven grey boxes indicate mismatches between GDTC and BINs. Insert in the upper left corner shows different backbone tree arrangement recovered in alternative MP analysis.

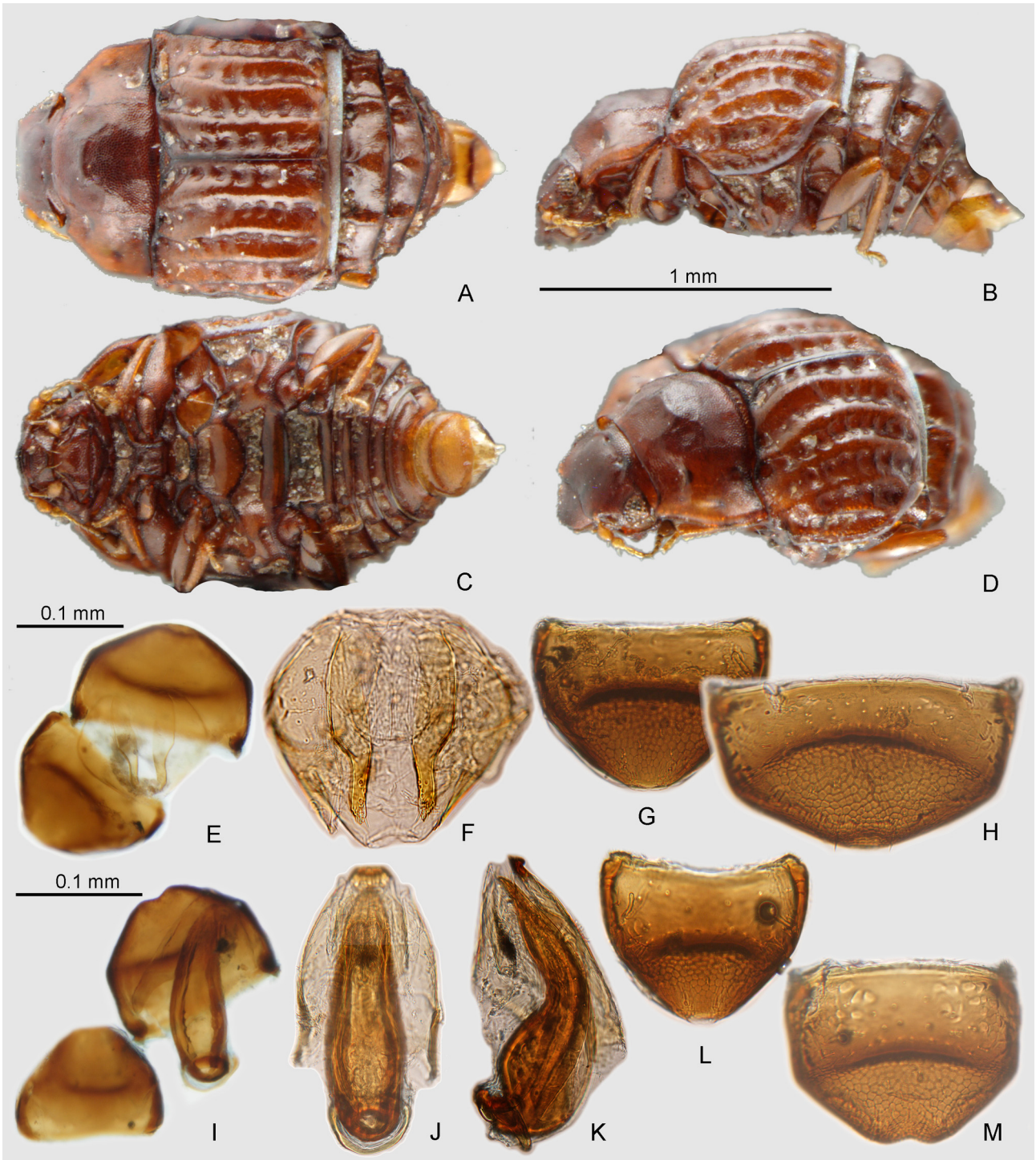

FIGURE 3. *Micropeplus jason* **sp. n.** from Mount Emei, Sichuan. A–D: holotype, female, #0907, habitus; E–H: paratype, female, #0906, tergite and sternite 8 with enclosed hemisternites (E), hemisternites (F), tergite (G) and ventrite (H) 8; I–M: paratype, male, #0911, tergite and sternite 8 with enclosed aedeagus (I), aedeagus (J, K), tergite (L) and sternite (M) 8.

Regional fauna of the ingroup Micropeplinae is summarized in Fig. 1. Five of eight sampled regions in Southwest China harbour a single species of *Micropeplus*. Mount Jizu has two *Micropeplus* species: *M. yunnanus* with impunctate elytral intercostae (species absent in our samples) as well as another species with punctate intercostae represented by OTU #2893. The two remaining regions have richer fauna: Mount Gongga has three *Micropeplus* species, while Mount Emei has nine *Micropeplus* species and one species of *Cerapeplus*. Two nearby regions, the Qin Ling Mountain Range and the Tam Dao Mountain Range, each have one species of *Cerapeplus* and either two or one species of *Micropeplus*, respectively.

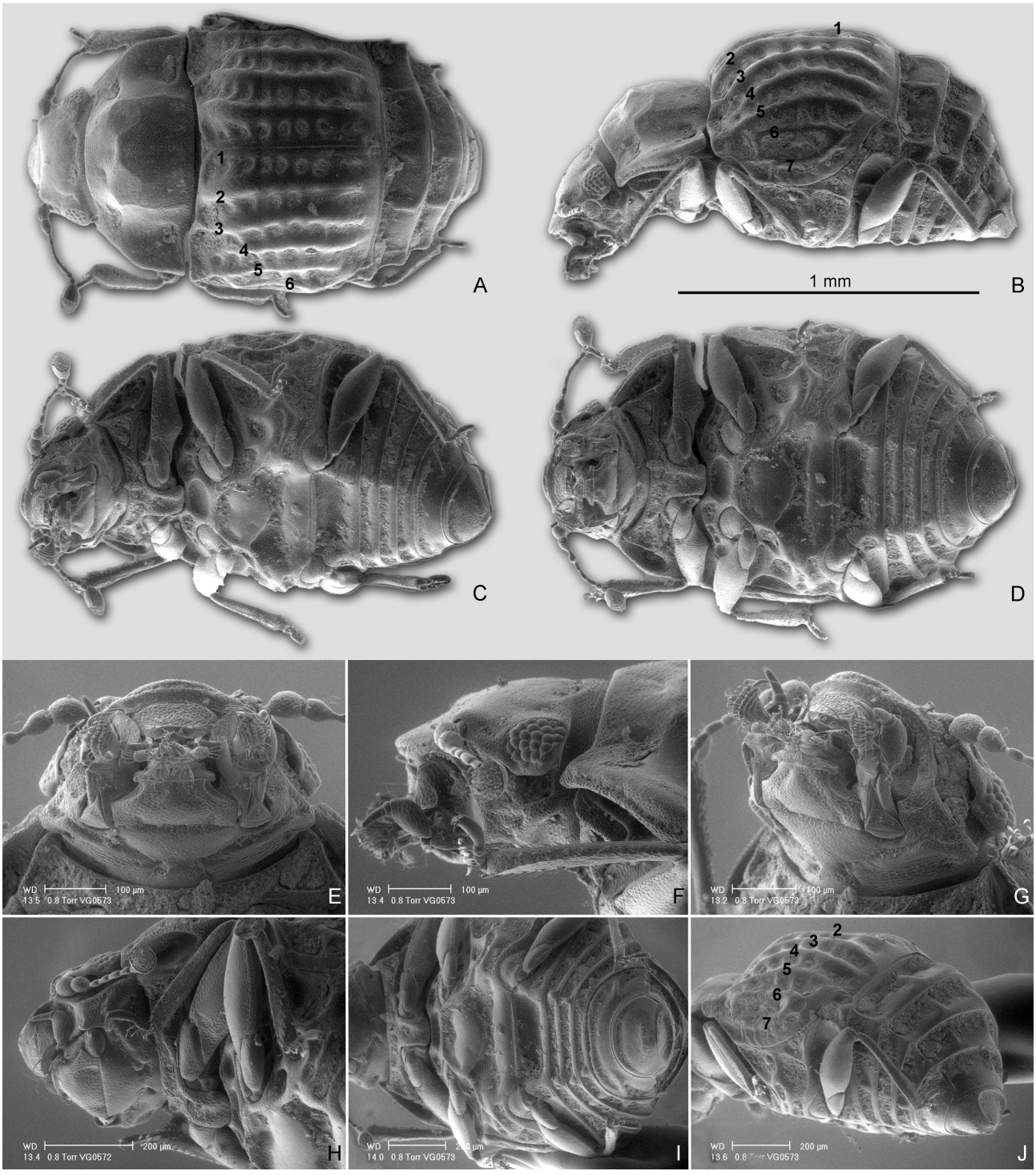

FIGURE 4. *Micropeplus jason* **sp. n.** from Mount Emei, Sichuan. Unsexed paratypes #0572 (H) and #0573 (A–G, I–J). Habitus (A-D), head fronto-ventral (E), lateral (F) and ventro-lateral (G), anterior body latero-ventral (H), posterior body ventro-terminal (I) and latero-terminal (J). Numbers on elytra indicate elytral costae starting with the weakly developed median (=sutural or adsutural) costa.

***Micropeplus jason* sp. n.**
Figs. 3, 4.

Diagnosis. This species is easily recognizable by its small size and the unique combination of two characters: effaced pronotal ridges and single line of large punctures on elytral intercostae.

Description. Holotype, female (Figs. 3A–D). GenBank accession: HQ987124. Length: 1.6 mm. Body not flattened, pronotal ridges effaced, each elytron with seven costae, elytral intercostae with single line of large punctures, metacoxae widely separated. **Intraspecific variation.** GenBank accessions: HQ987123, HQ987125, KF408053. Length: 1.4–1.6 mm.

Material examined. Holotype female (ZCAS): #0907, "P.R. CHINA, Sichuan, EmeiShan, N29°33'36.3 E103°20'38.0, 15.vi.2010, 1947m, sifting33, V.Grebennikov". Paratypes (CNC, ZCAS): 9 exx in total: 3 exx: #0905, 0906, #0908: same data as holotype; 2 exx: #0572, #0911: "P.R. CHINA, Sichuan, Emei Shan, N29°33.605' E103°20.633', 05.vii.2009, 1947m, sifting17, V.Grebennikov"; 2 exx: #0573, #0574: "P.R. CHINA, Sichuan, Emei Shan, N29°32.932' E103°20.466', 01.vii.2009, 2310m, sifting14, V.Grebennikov"; 2 exx: #2903, #2904: "P.R. CHINA, Sichuan, Emei Shan, N29°33'00" E103°21'38", 28.v.2011, 1639m, sift08, V.Grebennikov".

Distribution. This species is known only from Mount Emei in Sichuan, Southwest China. Elevation: 1639–1947 m.

Etymology. The species epithet is the Latinized Greek mythical name of Jason, the leader of Argonauts in their quest for the Golden Fleece; noun in apposition.

Phylogenetic position. See Discussion.

Discussion

Why only one new species is formally described? As highlighted in the introduction, the current state of Micropeplinae taxonomy pertaining to China, and particularly to the mountainous regions of both Yunnan and Sichuan, is highly inadequate. With the exception of *Cerapeplus sinensis* Löbl identified in our samples by its characteristic morphology and geographical proximity to the type locality, most, if not all, the other species are likely new to science. An attempt to perform a full-scale taxonomic revision of all our Micropeplinae specimens is now too prodigious and it was, therefore, left outside our scope. This decision is partly due to the difficulties in applying six available Micropeplinae species names known for Southwest China. Furthermore, six OTUs representing candidate species (see below) are formed by singletons. Two likely new species are each based on a unique, not amplified, specimen (#0882 and #2852) and are not represented in the DNA analysis. In only one case (for the OTU #0906 from Mount Emei, see below) we felt that introducing a new species name would be beneficial considering the present state of taxonomic knowledge.

How many Micropeplinae species are in Southwest China? Counting the number of Micropeplinae species in our samples is not a straightforward task. Part of the challenge is attributable to the inadequate regional taxonomy of the group with the total of only six species names ever recorded for the entire Southwest China. No less daunting is the necessity to define species limits by determining the status of closely related allopatric populations, which might be counted as either belonging to the same species, or to sister ones. Instead of attempting an impossible task of an objectivized species count (De Queiroz 2007), we implement an alternative approach of minimizing the conflict between three available lines of evidence. These lines are as follows (in the decreasing order of contribution): DNA sequence data; geographical distribution and morphology. The former data source is underrepresented, since no thorough effort was made to do an extensive morphological study including that of male genitalia. Biological data, occasionally of much use for species segregation, are not now informative, as all sampled ingroup specimens were indistinguishable in their biological characteristics.

We think that neither 22 BINs, nor 20 GDTCs (Fig. 2) detected for the ingroup can all be directly accepted as candidate species. It appears that both BINs and GDTCs tend to variously overestimate the number of evolutionary lineages worthy of recognition as a Linnaean species. The BINs emphasise minute differences in DNA sequence data suggesting sympatric sister species, which is contradictory to the logic of allopatric speciation (for example BINs ACE8712 & ACE8714 from Mount Gongga, Fig. 2). The GDTCs, in turn, err in recognizing every allopatric lineage as a separate species-level entity (like the most closely related GDTC #2829 from the Qin Ling Mountain Range and GDTC #4790 from Mount Haba). Seven conflicts between BINs and GDTCs (shaded areas in Fig. 2) highlight points of specific interest and attention. These conflicts were resolved in the total of 18 OTUs (Fig. 2), which might be seen as candidate species under, however, the most extreme splitting approach.

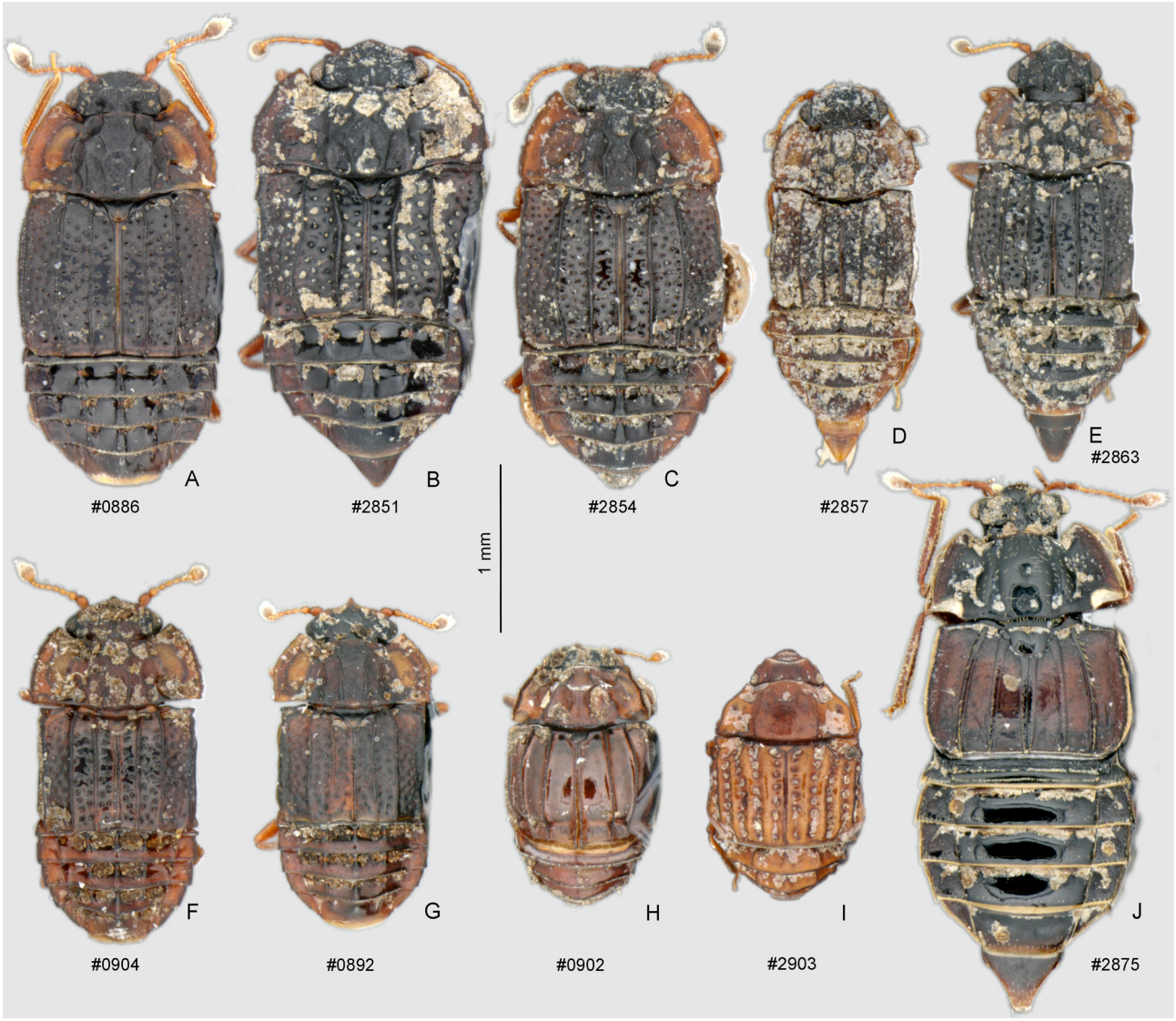

FIGURE 5. Ten species of Micropeplinae detected on Mount Emei, Sichuan. A–H: *Micropeplus* spp.; I: *Micropeplus jason* **sp. n.**, J: *Cerapeplus* sp. Phylogenetic position of respective specimens can be found by tracing unique specimen numbers in Fig. 2, except for *Cerapeplus* #2874, which did not amplify and was not represented in the DNA analysis.

The alternative lumping approach is perhaps preferable, at least at the present stage of knowledge. Its application suggests joining allopatric OTUs (Fig. 2) into monophyletic and more inclusive candidate species. Thus, OTU #2829 should be united with OTU #4785 and, perhaps, also with OTU #4767 (no OTU is assigned to GDTC #4793 from Mount Haba since its position outside the sympatric GDTC #4790 is most likely an artefact of having too many ambiguously read nucleotides). The resulting broadly defined and relatively widely distributed candidate species is monophyletic and consists of monophyletic allopatric populations. The observed paraphyly of the population from Mount Gongga (specimen #2883 and two more nearby) is likely linked to incomplete lineage sorting (Funk & Omland 2003).

Moving further down the tree (Fig. 2), the next five OTUs (#0886, #2851, #2893, #0883, #2857, #2863) do not have statistically well-supported and potentially conspecific sister OTUs and, therefore, can all be accepted as candidate species. OTU #0904 from Mount Emei, likely forming a separate species, is the strongly supported sister group of another candidate species consisting of two allopatric OTUs: #0889 and #2865. This hypothesis is further corroborated by the fact that both candidate species co-occur on Mount Emei. The remaining six OTUs at the bottom of Fig. 2 (#4766, #2837, #0902, #0906, #4760, #2875) are best considered as representing a candidate species.

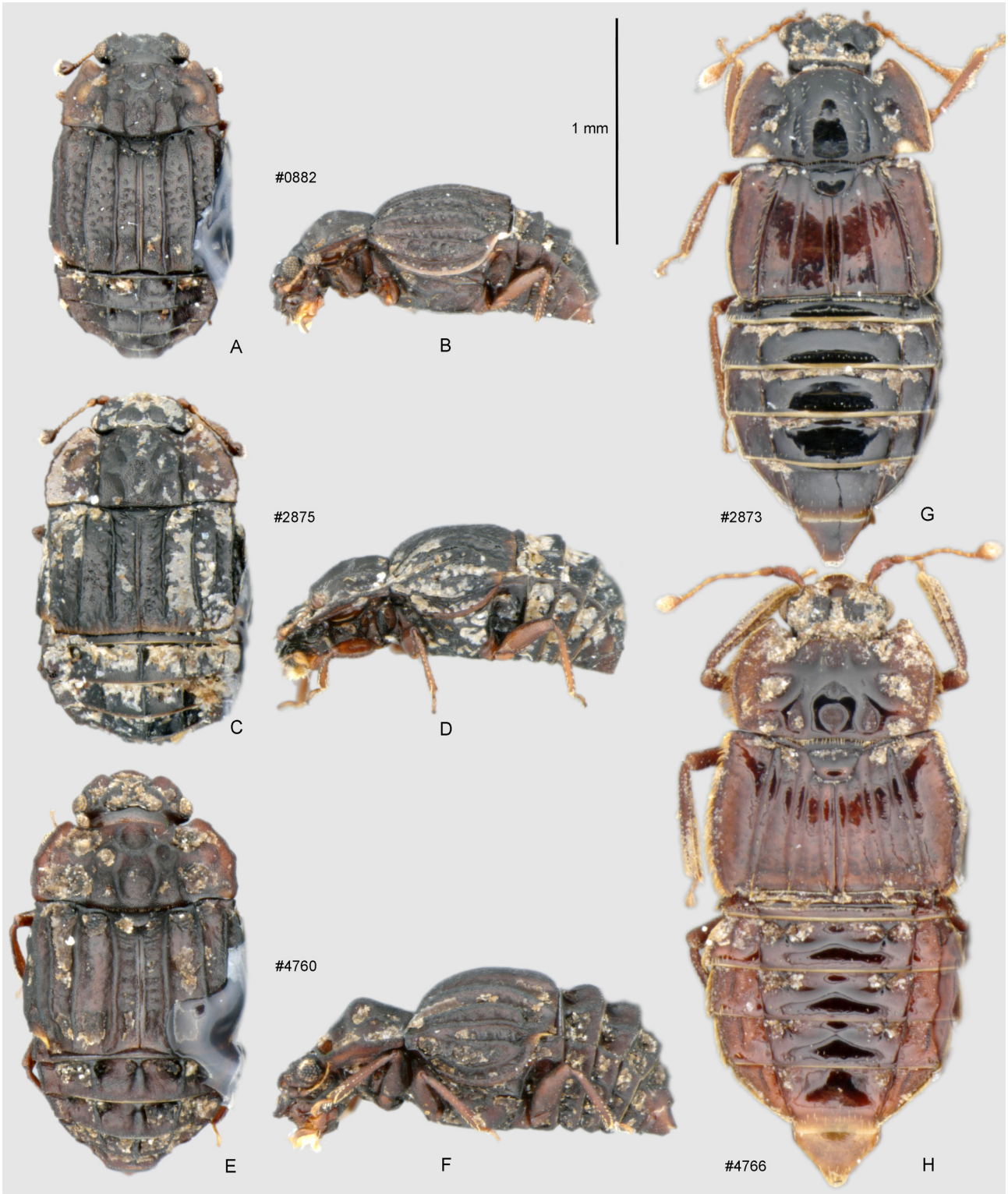

FIGURE 6. Five species of Micropeplinae from China and Vietnam. A–F: three *Micropeplus* species most closely related to *M. jason* **sp. n.**, forming the *sculptus* species-group and inhabiting the Chang Shan Mountain Range (A–B), Mount Gongga (C–D) and the Tam Dao Mountain Range (E–F); G–H: *Cerapeplus* spp., *C. sinensis* from the Qin Ling Mountain Range (G) and *Cerapeplus* sp. from the Tam Dao Mountain Range (H). Phylogenetic position of respective specimens can be found by tracing unique specimen numbers in Fig. 2, except for *Micropeplus* #0882 from the Cang Shan Mountain Range (A–B), which did not amplify and was not represented in the DNA analysis.

In summary, depending on the choice of approach (lumping versus splitting) all our sequenced ingroup Micropeplinae specimens from Southwest China and two nearby localities (Fig. 1) represent between 15–18 candidate species. Two more candidate species absent in Fig. 2 should be added (represented by the unique and not amplified specimens #0882 and #2852 from the Cang Shan Mountain Range and Mount Emei, respectively). Three species represented by OTUs #4766, #2838 and #4760 have not been yet found in Southwest China, but occur in the nearby areas (Fig. 1). The total diversity of Micropeplinae in our samples from Southwest China consists, therefore, of two species of *Cerapeplus* and between 12 and 15 species of *Micropeplus*, more than a half of them (one *Cerapeplus* and 9 *Micropeplus*, Fig. 5) found on hyperdiverse Mount Emei (see below). These numbers appear comparable, although somewhat richer, to numbers from other regions such as Poland (7 spp., Jałoszyński *et al*. 2011), Turkey (5 spp., Smetana 2004), Russian Far East (4 spp., Smetana 2004), Japan (8 spp. + 1 ssp., Smetana 2004), Taiwan (7 spp., Smetana 2004) and Canada (11 spp., Bousquet *et al.* 2013).

Although the size of our regional samples varies nearly 20 fold (Fig. 1), we directly compare the number of recovered Micropeplinae species, because the rate of increase of the species richness accumulation curve quickly slows with each additional sample (Moreno & Halfter 2000). Six of eight sampled localities in Southwest China yielded a single species, while three and ten species were discovered on Mount Gongga and Mount Emei, respectively (Fig. 1). Moreover, Mount Jizu is known to harbour an additional species, *M. sculptus* (see: Watanabe & Xiao 1996), which is absent in our samples thus highlighting the fact that at least this locality was undersampled by us. Two nearby localities in Shaanxi and Vietnam have two and three Micropeplinae species, respectively (Fig. 1). These results strongly suggest that Mount Emei (even though the most thoroughly sampled with about 155 kg of litter <7 mm) possesses by far the greatest so far Micropeplinae diversity. This statement is true not only in terms of species (10), but also with reference to the four regional Micropeplinae clades preliminary considered as candidate genera and all represented on Mount Emei (*Micropeplus sensu stricto*, Clade E, Clade G and *Cerapeplus*). The exceptionally high Micropeplinae diversity on Mount Emei is consistent with results reported for higher plants (Wang *et al* 2013) suggesting that Mount Emei possesses an exceptionally high biota densely packed into a mere 154 square kilometers (Wang *et al.* 2013).

Phylogenetic interpretation of Micropeplinae. The Micropeplinae are undoubtedly monophyletic and have a well-established position within the Omaliine Group of rove beetle subfamilies (Fig. 7, Newton & Thayer 1995, but see McKenna *et al*. 2015 for an alternative hypothesis). On the other hand, the interrelationships of their six genera (Herman 2001) are most uncertain, and even more so is their reciprocal monophyly. A dedicated phylogenetic study addressing the issue is long overdue. In its absence, we attempt to provide guarded phylogenetic interpretation of our results, even though this study was not specifically designed for the purpose.

Only the MP analysis recovered the subfamily as a clade (with low bootstrap support of 17%), while on the ML tree (Fig. 2) Micropeplinae are not monophyletic. Since the monophyly of the subfamily is a strongly supported hypothesis based on morphological characters (Newton & Thayer 1995), we attribute this discrepancy to the data and method limitations. Most likely CO1 is not an optimal single marker because its quick saturation at a rate of about 1.8% MY^{-1} (Papadopoulou *et al.* 2010) masks the relatively old evolutionary signal. We, therefore, attribute the observed differences between both ML and MP topologies, particularly the failure of ML to recover monophyletic Micropeplinae to purely stochastic causes (Lanyon 1988).

The Micropeplinae clades A–G designated in Fig. 2 and all consistently recovered in both ML and MP analyses conceivably represent seven monophyletic groups of species. Low support values of the more inclusive clades conflicting between ML and MP trees likely reflect the same source of data and method uncertainty as in the case of the subfamily monophyly, namely fast the evolution of CO1. Clades D and F correspond to the genera *Cerapeplus* and *Kalissus*, respectively, while the remaining five clades are now assigned to the broadly defined *Micropeplus sensu lato*. The latter genus is recognized following Herman's (2001) catalogue, i.e. without *Peplomicrus* Bernhauer, but including the *tesserula* species-group (Campbell 1968), which is sometimes considered a separate genus *Arrhenopeplus* Koch (Smetana 2004, Jałoszyński *et al*. 2011).

No formal morphological analysis was done and, therefore, contribution of this data source is limited to a few most easily observed characters. Their phylogenetic interpretation is markedly hampered by the hypothesis that the most recent common ancestor of Micropeplinae was a highly modified beetle, as compared to its closest relatives (Fig. 7). Some characters discretely variable within Micropeplinae, such as number of elytral costae or shape of intercostal punctures, are entirely absent in the outgroup and, therefore, cannot be easily polarized. Only contiguous metacoxae, as found in the closest relatives (Fig. 7) suggest their plesiomorphic nature in Micropeplinae.

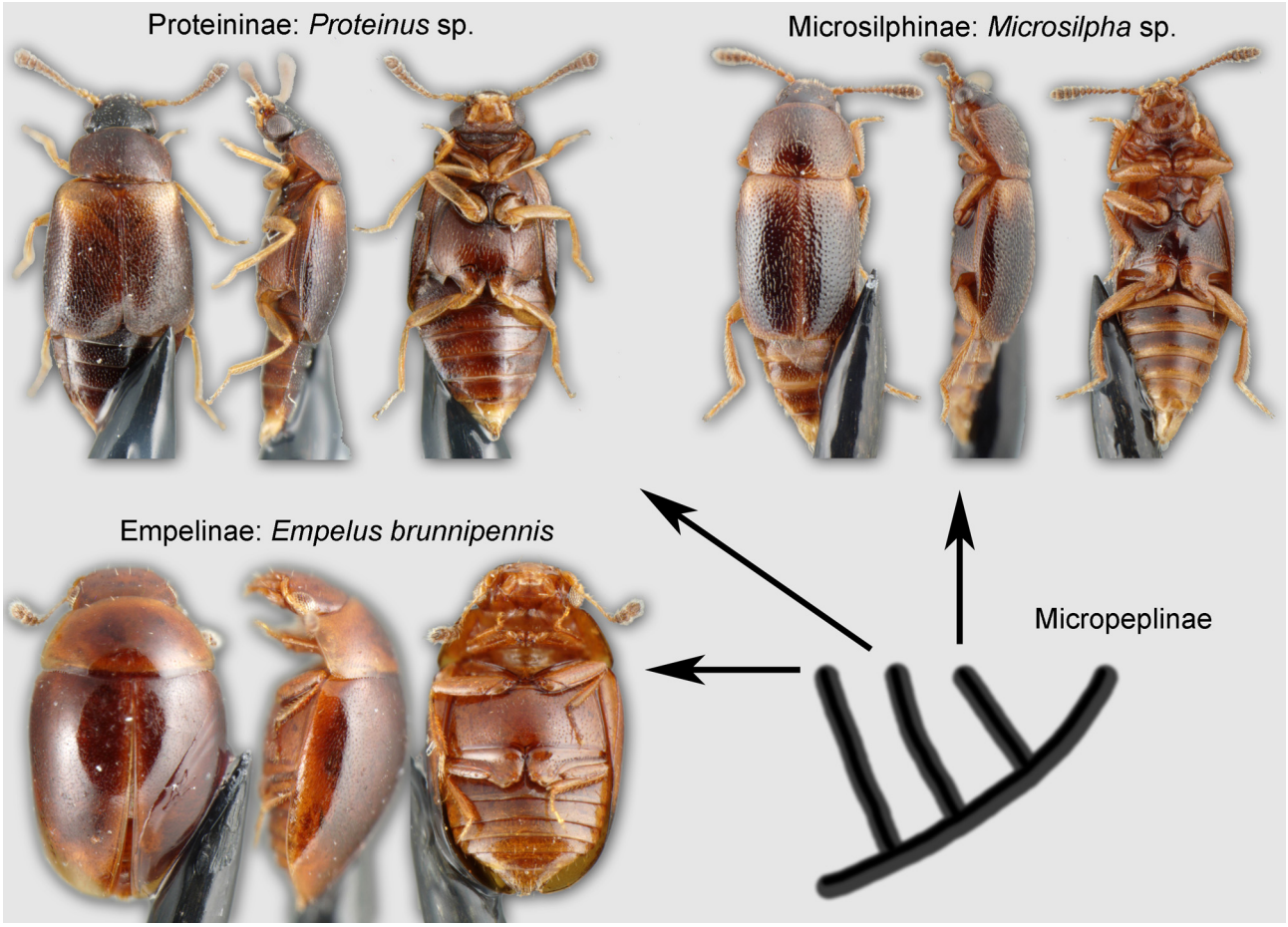

FIGURE 7. Adult habitus of representatives of three consecutive sister groups of Micropeplinae, as hypothesised by Newton & Thayer (1995). Body length of *Empelus* 2.7 mm, *Proteinus* 2.0 mm and *Microsilpha* 2.9 mm.

Below we attempt to preliminarily delimit and discuss four ingroup Micropeplinae clades recovered by the DNA analysis (Fig. 2). One of them, Clade D (Fig. 2), represents the genus *Cerapeplus*, which now appears as a phylogenetically valid genus. Two others represented by Clades G and E, respectively, might be eventually shown as two phylogenetically sound genera (see below). The remaining weakly supported clade represented in Fig. 2 by the union of individual clades A, B and C is now considered as the genus *Micropeplus sensu stricto*; it has questionable monophyly and is retained in the Discussion as a temporary matter of convenience until a thorough phylogenetic analysis elucidates its nature.

Clade G: does *Micropeplus jason* sp. n. represent an unnamed genus? When in 2009 we discovered the first specimens of *M. jason* **sp. n.**, their unusual appearance strongly suggested a new and previously unrecognized genus of Micropeplinae. The following combination of six rarely encountered characters is unique to the subfamily: body not flattened, body length less than 2 mm, effaced pronotal ridges, seven elytral costae, a single line of large punctures between costae and widely separated metacoxae. A series of analyses using DNA (Fig. 2) and morphological data (results are highly inconclusive and are not shown) failed to corroborate the new genus hypothesis. Instead, the DNA data consistently grouped *M. jason* **sp. n.** with two other possibly new species represented by OTU #4760 (Figs. 6E–F) and #2875 (Figs. 6C–D) into a strongly supported Clade G (Fig. 2). This clade likely includes the similarly shaped *M. sculptus* LeConte from Canada and the USA, *M. dokuchaevi* Ryabukhin from the Russian Far East (Figs. 8E–H) and an unnamed species from the Cang Shan Mountain Range uniquely represented by the specimen #0882 (Figs. 6A–B) DNA of which we could not amplify. All members of this clade share four among six morphological characters mentioned above: body not flattened, body length less than 2 mm, seven elytral costae and widely separated metacoxae. Two unique characters of *M. jason* **sp. n.**, namely the effaced pronotal ridges and single line of large punctures on elytral intercostae are most parsimoniously interpreted as evolutionary changes from the homologous structures found in other members of the Clade G. Thus,

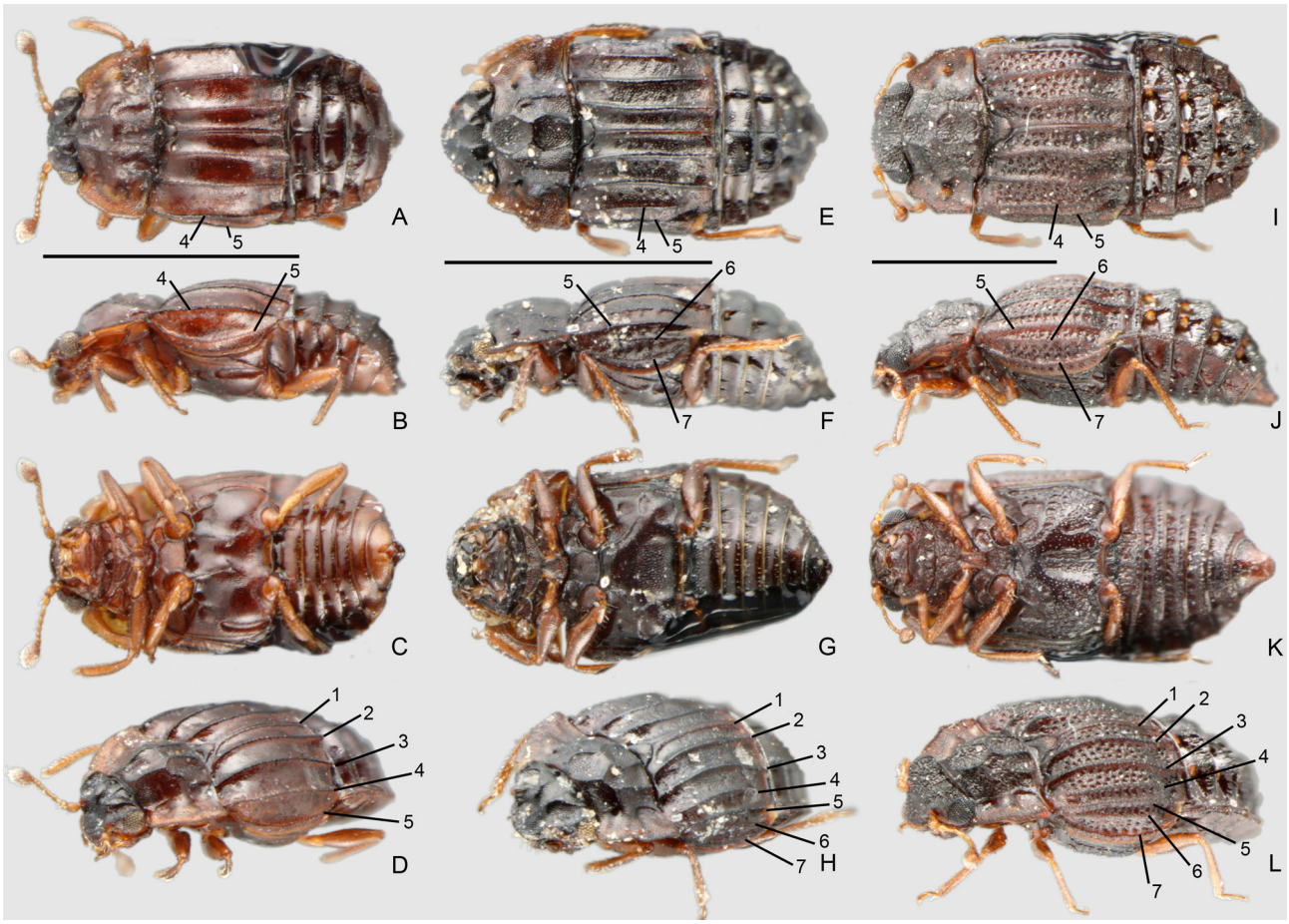

FIGURE 8. Habitus of *Micropeplus* spp. A–D: *M. tesserula* ("Ünökö, Ost-Karpat" [= Rodna mountains, Romania], collector and date unknown, CNC); E–H: *M. dokuchaevi* (#3996, Russia, Magadan region, 26.vi.1990, A.S. Rjabukhin, CNC); I–L: *M. porcatus* (#2396, "Feistr. Styr." [= unknown locality], Diener, 9.viii.1904, CNC). Numbers indicate elytral striae. Scale bars: 1 mm.

the pronotum of *M. jason* **sp. n.** retains its reticulate structure suggesting a novel reduction of the former ridges (Fig. 4A), while a single line of large although weak punctures can be distinguished on the median-most intercosta of the remaining species of the Clade G (Figs. 6A, C, E). If *M. jason* **sp. n.** is to be eventually assigned to a genus, the latter should incorporate the entire Clade G. The unique evolutionary history of this group was already noted by Campbell (1968), who established for it a distinct *sculptus* species-group. So delimited, the group is likely monophyletic and perhaps worthy of formal recognition as a genus (particularly if the *tesserula* species-group of Campbell is also removed from *Micropeplus* under the now synonymous generic name *Arrhenopeplus*; see below). Two significant uncertainties, however, preclude us from proposing this taxonomic action: (1.) the internal phylogeny of the subfamily is still inadequately known, while (2.) *M. porcatus* Paykull (Figs. 8I–L), the type species of the genus *Micropeplus*, exhibits external morphological character seemingly "intermediate" between those of the Clade G and at least some other representatives of *Micropeplus sensu stricto* (see below).

Clade E: *tesserula* species-group (=*Arrhenopeplus*). The Clade E (Fig. 2) corresponds to the *tesserula* species group of Campbell (1968; the latter species is also the type species of the genus *Arrhenopeplus* Koch recognized as valid in Smetana 2004 and Jałoszyński *et al*. 2011, but not here). This radiation is uniquely characterized by the following five adult characters (those marked with asterisk are shared with the *sculptus* species-group; see above): body not flattened*, body length not exceeding 2 mm*, elytra with five costae, impunctate elytral intercostae, widely separated metacoxae*. Smetana (2004) listed six species belonging to this radiation, all narrowly localized except for *M. tesserula* Curtis. As now known, *M. tesserula* is by far the most widely distributed species of Micropeplinae with published records from Mexico, USA, Canada (Campbell 1968), nearly all of Europe, southern Siberia, Russian Far East, as well as northern Neotropical and northern Afrotropical

regions (Smetana 2004). It might be plausible to assume that all recognized species of this group other than *M. tesserula*, like *M. dentatus* Zhao & Zhou, 2004 from Zhejiang province in China, are in fact only gradistic regional lineages rendering a more inclusive *M. tesserula* paraphyletic (Ross 2014). In other words, the entire species group might be considered as a single and extremely widely distributed species. Unlike most *Micropeplus sensu lato* in Southwest China, specimens of the *tesserula* species-group are fully winged and are likely capable of active flight, which fosters genetic exchange over large distributional area. Considering the above, the *tesserula* species-group might be further characterized by an additional character of having a highly efficient mechanism to retain an abnormally high rate of genetic exchange efficiently preventing allopatric speciation. All these pieces of evidence corroborate a hypothesis that the Clade E represents a phylogenetically valid radiation worthy of formal generic status as *Arrhenopeplus* Koch.

Clades A, B and C: the genus *Micropeplus sensu stricto.* The assemblage of clades A, B and C in Fig. 2 was weakly recovered in ML analysis and collapsed in MP analysis. The present temporary delineation of this assemblage as the narrowly defined *Micropeplus* is adopted to stress the separation of both Clades E and G, which represent unrelated radiations possibly worthy of full generic status (see above). Not only monophyly, but also the naming of *Micropeplus sensu stricto* is controversial, since *M. porcatus*, the type species of the genus, was not represented in our DNA analyses. Assessment of its external morphology was inconclusive, since the species exhibits a conflicting mix of characters linking it with either *Micropeplus sensu stricto* (numerous small punctures forming two or three longitudinal lines on elytral intercostae, Fig. 8I), or with Clade G (seven elytral costae, Fig. 8L). Some other characteristics are intermediate (body length about 2.1 mm, weakly developed pronotal ridges, moderately separated metacoxae). The type species of *Micropeplus* has, therefore, approximately equal chances of belonging to either of these two groups: *Micropeplus sensu stricto* or Clade G, which, in turn, will determine the valid generic name of the lineage.

Clade D: the genus *Cerapeplus.* The relatively recently discovered genus *Cerapeplus* consists of two named species. The type species *C. siamensis* Löbl & Burckhardt is known from 15 specimens widely distributed in Southeast Asia (Thailand, Indonesia, possibly Malaysia: Sabah). *Cerapeplus sinensis* Löbl is restricted to the Qin Ling Mountain Range in China: Shaanxi and is known from three type specimens (Löbl & Burckhardt 1988, Löbl 1997). This genus was trice recorded in our samples: a single specimen #2875 from Mount Emei (Fig. 5J); a single specimen #4766 from the Tam Dao Mountain Range in Vietnam (Fig. 6H, a new generic record for the country) and about two dozen specimens of *C. sinensis* from the Qin Ling Mountain Range (Fig. 6G). Even if the first two specimens might represent unnamed species, we postpone their taxonomic assessment until more data become available. Overall, our *Cerapeplus* samples exceed in number of specimens and species all that was previously recorded for this genus and suggest a significantly higher diversity than previously known.

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