Bonn zoological Bulletin 63 (2): 123–147

December 2014

Morimotodes, a new genus for two minute wingless litter species from southwest China and Taiwan with an illustrated overview of Molytina and Plinthina genera (Coleoptera: Curculionidae: Molytini)

Vasily V. Grebennikov
Canadian Food Inspection Agency, K.W. Neatby Bldg., 960 Carling Ave., Ottawa, ON K1A 0Y9, Canada;
E-mail: vasily.grebennikov@inspection.gc.ca

Abstract. The new weevil genus *Morimotodes* g. n. is described for two new species: *M. ismene* sp. n. (Yunnan and Sichuan) and *M. polynices* sp. n. (Taiwan). *Morimotodes ismene* sp. n. is designated as the type species of *Morimotodes* g. n. Species are small (1.6–2.1 mm), wingless inhabitants of leaf litter in montane deciduous forests with characteristically globular body and obliterate elytral striae and dorsal sculpture. Analysis of DNA barcodes and external similarity suggest that *Morimotodes* g. n. is a sister to the West Palaearctic genus *Leiosoma* Stephens, 1829 with 32 similarly small-bodied and litter-inhabiting species. Dated intraspecific phylogeographic analysis utilizing DNA barcodes of *M. ismene* sp. n. reveals seven strongly supported geographical clades, four of which are allopatric and three others are parapatric on Mt. Emei in Sichuan. Potentially allied genera belonging to two of the three Molytinini subtribes, Molytina and Plinthina, are illustrated and briefly discussed. Type specimens of five exceptionally poorly known genera (*Carbonomassula* Heller, 1908, *Clarkanthus* Alonso-Zarazaga & Lyal, 1999, *Gonotrachelus* Champion, 1914, *Vouauxia* Hustache, 1920, *Pterotomus* Quedenfeldt, 1888) are re-examined and the original labels illustrated.

Key words: Yunnan, Sichuan, Taiwan, CO1, DNA barcoding, phylogeography

INTRODUCTION

In 2008, a first long series of conspicuous but unknown beetles was discovered by sifting forest leaf litter on the eastern slope of the Cang Shan Mountain Range in Yunnan (China). The peculiarly small, lustrous and rounded body in combination with the rounded elytral shoulders strongly resembled other litter-inhabiting wingless Palaearctic Molytinae, i.e. *Otibazo* Morimoto, 1961 or *Leiosoma* Stephens (Fig. 7). The subsequent four years of intensive sampling in the same and nearby forests of Southwest China revealed additional similarly shaped specimens. A long series of another seemingly congeneric species was detected among unidentified specimens collected two decades earlier in Taiwan by Aleš Smetana (Fig. 6). The generic identity of these beetles, however, remained elusive.

Since the original discovery in 2008, these beetles were repeatedly compared to many others, mainly belonging to the wingless members of Molytinae. Eventually it became evident that these finds represented a previously undetected clade presumably deserving a formal status of a new genus. This thought intensified the search for its possible relatives. That pursuit was long inconclusive, since numerous unrelated wingless Molytinae were infamous for their convergent similarity linked to the loss of hind wings (Lyal 2014). DNA-based search for relatives of the new genus was similarly inconclusive, since the dataset did not contain many critical and important taxa. Moreover, due limitations in funding, the DNA work was done with the single marker of the DNA barcode (part of cytochrome oxidase I, Hebert et al. 2003), which had significant limitations in its applicability for detecting relatively old evolutionary events (Grebennikov & Heiss 2014). Eventually, however, a representative of the genus *Leiosoma* became available for DNA analysis and consistently clustered with a clade representing the new genus. At that point the project's results were judged mature enough to be formally presented, even though some shortcomings linked to a shortage of the material and data remained (see Discussion).

Another coincidental event further triggering the completion of this project was the recent publication of the long-awaited "Phytophaga" volume of the Handbook of Zoology series, most specifically the chapter on the weevil subfamily Molytinae (Lyal 2014). This subfamily has long been and still is a phylogenetic challenge. In the aforementioned chapter the tribes of Molytinae were significantly reorganized, as compared to the earlier standard works of reference (Alonso-Zarazaga & Lyal 1999; Bouchard et al. 2011; Alonso-Zarazaga 2013). The most noticeable novelty, however, was the incorporation of the entire former "subfamily Cryptorhynchinae" into Molytinae, the latter presently containing 37 tribes plus ca. 28

Received: 07.08.2014
Accepted: 12.11.2014

Corresponding editor: D. Ahrens

incertae sedis genera (Lyal 2014: 530, 531). This decision is in line with the pivotal work of Kuschel (1987) amalgamating a multitude of former "subfamilies" into a broadly defined Molytinae (then excluding "Cryptorhynchinae"). Both steps are seen as a much needed attempt to make the formal classification more in line with the current phylogenetic hypothesis (for example, see the remarkable mosaic of both former "subfamilies" in McKenna et al. 2009). Given an acute lack of the phylogenetic framework for the subfamily and for the great majority of its tribes, numerous further changes in Molytinae classifications will undoubtedly follow. To move forward, a practical approach was outlined (Lyal 2014: 549) as to "… propose initial hypotheses for monophyletic groups within the Molytinae and then analyze them with both molecular and morphological characters…" This paper presents an attempt to answer this call for actions on Molytinae subgroups and to shed light on a small subsection of this grand, if indeed monophyletic, radiation.

This work has three main goals. First, to name formally the newly discovered genus and its two species. Second, to utilize available mtDNA sequences to test the monophyly of the genus and to search for the possible sister group. Third, to discuss and delimit species boundaries and to undertake a dated phylogeographical analysis. Forth, to advance understanding of Molytinae genera currently attributed to the subtribes Molytina and Plinthina by providing an annotated list of taxa, illustrating a representative species for all but three genera and clarifying the identity of five obscure genera by re-examination of the type specimens of their type species. Overall, this paper continues the recently initiated efforts to assess phylogeographical patterns detected from the low-dispersing flightless weevils in southwestern China and adjacent lands and to clarify the taxonomy and diversity of wingless Old World Molytinae (Grebennikov 2014).

MATERIAL AND METHODS

Museum abbreviations, followed by the name of the curator:

BMNH	Natural History Museum, London, UK (M. Barclay);
CMN	Canadian Museum of Nature, Ottawa, Canada (R. Anderson, F. Genier);
CNC	Canadian National Collection of Insects, Arachnids and Nematodes, Ottawa, Canada (P. Bouchard);
IZCAS	Institute of Zoology, Chinese Academy of Science, Beijing, P.R. China (R. Zhang);
MNHN	Muséum national d'Histoire naturelle, Paris, France (H. Perrin);
MRAC	Musée Royal de l'Afrique Centrale, Tervuren, Belgium (M. De Meyer);
MTD	Senckenberg Naturhistorische Sammlungen, Dresden, Germany (K.-D. Klass, O. Jäger);
NHMB	Naturhistorisches Museum, Basel, Switzerland (E. Sprecher);
NMW	Naturhistorisches Museum, Wien, Austria (H. Schillhammer);
ZIN	Zoological Institute, Russian Academy of Sciences, St. Petersburg, Russia (B.A. Korotyaev).

This study is based on examination of a total of 97 dry-mounted adult specimens of the new genus. Concepts of the Curculionoidea family-group names and assignment of weevil genera to tribes follow Bouchard et al. (2011) and Alonso-Zarazaga & Lyal (1999), respectively, with subsequent significant modifications by Lyal (2014). The chronostratigraphic timing is that of Cohen et al. (2013) with the Pliocene-Pleistocene boundary set at 2.588 MY. Nomenclature of male genitalia follows that of Wanat (2007). The length of the body was measured in dorsal aspect from the elytral apex to the front of the pronotum. Geographical labels of the newly described species are cited verbatim in quotation marks. The hypothetical most recent common ancestor of a monophyletic group referred to in the discussion is abbreviated as MRCA. The distribution map was generated using the online SimpleMappr tool (Shorthouse 2010). Species identification of the two sequenced specimens of *Leiosoma reitteri* (Bedel) was done based on the assumption that this is the only species of the genus known from Georgia (Alonso-Zarazaga 2013). The type species are cited using their presently valid names, which are not necesserely the same when the type species were designated; the latter can be found in Alonso-Zarazaga & Lyal (1999).

DNA dataset. All specimens submitted to DNA barcoding have a unique identifier label with the code CNC-COLVG0000XXXX; this format is shortened to #XXXX when specimens are cited in the text. All details regarding sequencing, primers, PCR protocols as well as the list of specimen information including provenience and voucher number can be seen by accessing the online dataset at: dx.doi.org/10.5883/DS-MORIMO90. In a few cases a specimen failed to amplify DNA from the first attempt and was later resubmitted; in such cases a digit "1" after a dot follows the original four digit number (like #0251.1 on Fig. 7). The dataset used for the first DNA analysis contained 90 sequences and 658 aligned positions. The ingroup was formed by 46 newly generated sequences, each representing a specimen of the continental new species of the new genus (GenBank accessions: HM417727–32, HQ986799, HQ986876–8, HQ987105,

HQ987134–5, HQ987159, HQ987179–81, KJ871620–32, KJ871634–5, KJ871637–40, KJ871642–51). All but one specimen representing another new species collected in Taiwan in 1992–1998 were submitted to DNA barcoding but failed to amplify, likely because of either their age, collecting methods or storage degraded DNA. No fresh specimens of the target genus were recovered in Taiwan during a month-long fieldwork in 2013. The majority of the ingroup sequences were 658 basepairs (bp) long and no one shorter than 407 bp. The outgroup consisted of 44 sequences and represented all Molytinae genera with available DNA barcode data (Fig. 7), while three sequences of *Graptus circassicus* Solari, 1945 (Entiminae) were used to root the topology in the first analysis (see below). All outgroup sequences were of the full DNA barcode length (658 bp). Three of the outgroup sequences representing the genus *Plinthus* Germar, 1817 (KJ871633, KJ871636, KJ871641) were newly generated. The remaining 41 outgroup sequences were taken from previous works (HM386450, HM417677–9, HQ986888–9, HQ987002–3, KJ427730–2, KJ427736–9, KJ427744, KJ427746, KJ427748, KJ445683–4, J445687, KJ445690–1, KJ445693–4, KJ445698–6, KJ445708–9, KJ445712–3, KJ445715 in Grebennikov 2014; KJ841729, KJ841731 in Grebennikov & Pham 2014). Specimen images (when present), geographical data, primers, original chromatograms and other relevant data for all 90 sequenced specimens can be found online in the publicly accessible dataset “*Morimotodes*” on the Barcode of Life Database portal (doi: dx.doi.org/10.5883/DS-MORIMO90).

DNA-based phylogenetic analyses. Two separate tree search analyses were run. The first analysis aimed at testing monophyly of the new genus represented by the type species, search for its sister-group and to examine its internal relationships. The original DNA dataset containing 90 sequences was analysed using the Maximum Likelihood (ML) approach with statistical branch support tested by 1000 replications of bootstrapping in MEGA 5 (Tamura et al. 2013). The search for the optimal substitution model for both analyses was done in MEGA 5 and resulted in the same model (GTR+G+I). The second tree search analysis was performed to date the branching events in the continental species of the new genus and to re-test the interrelationships hypothesis, as already suggested in the first analysis. The original matrix of 90 sequences was reduced to 33 to include only the full-length DNA barcodes (658 nt) of 31 ingroup specimens and two specimens of the sister group (the genus *Leiosoma*, as suggested in the first analysis). The second analysis was performed in BEAST v1.8.0 (Drummond et al. 2012) utilizing the Bayesian inference (BI) approach with no *a priori* internal grouping, all default priors and options, GRT+G+I nucleotide substitution model, strict linear molecular clock and nucleotide substitution rate of 0.018 (Papadopoulou et al. 2010). The “burn in” option was implemented eliminating the first 2500 of the 10000 obtained trees. Two resulting topologies, each representing either ML or BEAST analysis, were visualized in FigTree v1.4 (Rambaut 2013) and presented by Figs 7 and 8, respectively.

Use of morphological data. A formal morphology-based phylogentic analysis of Molytinae genera to search for the sister group of the new genus was beyond the scope of the present paper. Even restricted to 81 genera of the tribe of Molytini (80 mentioned in Lyal 2014, and the new one), the task was judged as too daunting. An attempt was made to illustrate a representative of all genera currently assigned to Molytina and Plinthina (13 and 17, respectively; see Lyal 2014: 530, 531; images of three genera were not obtainable). Five particularly poorly known genera were elucidated in more details, with their type specimens and original labels imaged. The third remaining Molytini subtribe, Hylobiina, historically considered as a tribe of its own and incorporating 51 winged genera (Lyal 2014) was not included in this treatment. This decision is partly due to the large size of this tribe. The second reason for exclusion is that until very recently, Hylobiina were formally in a separate tribe and, therefore, not specifically targeted since 2008, when this project was in preparation.

Morimotodes g. n.

Type-species: *Morimotodes ismene* sp. n., by original designation.

Diagnosis. Adult specimens of *Morimotodes* g. n. can be immediately recognized from other Curculionoidea known both from the Eastern Palaearctic and the Oriental Region by their habitus. They are small (about 2 mm) brown or reddish beetles with lustrous dorsum, rounded body and nearly obliterated elytral shoulders and striae. In the area of their known distribution, namely in Yunnan, Sichuan and Taiwan, as well as in the adjacent regions, adults of *Morimotodes* externally resemble those of *Otibazo* Morimoto. The latter, however, has not yet been discovered in China (although its presence is possible, since the first continental species has been recently detected in northern Vietnam, see Grebennikov & Pham, 2014). Adults of *Otibazo* are immediately distinguishable from nearly all weevils by their unique fields of short dense pubescence forming characteristic whitish tufts on flagella, femora and tibiae (Fig. 7), not found in *Morimotodes*. Field recognition of *Morimotodes* can be facilitated by stressing their biological preferences. All known specimens have been found in wet leaf litter of primary deciduous forests in the altitudinal range of 1947–4072 m in southwestern China and 1110–2550 m in Taiwan. From the most closely re-

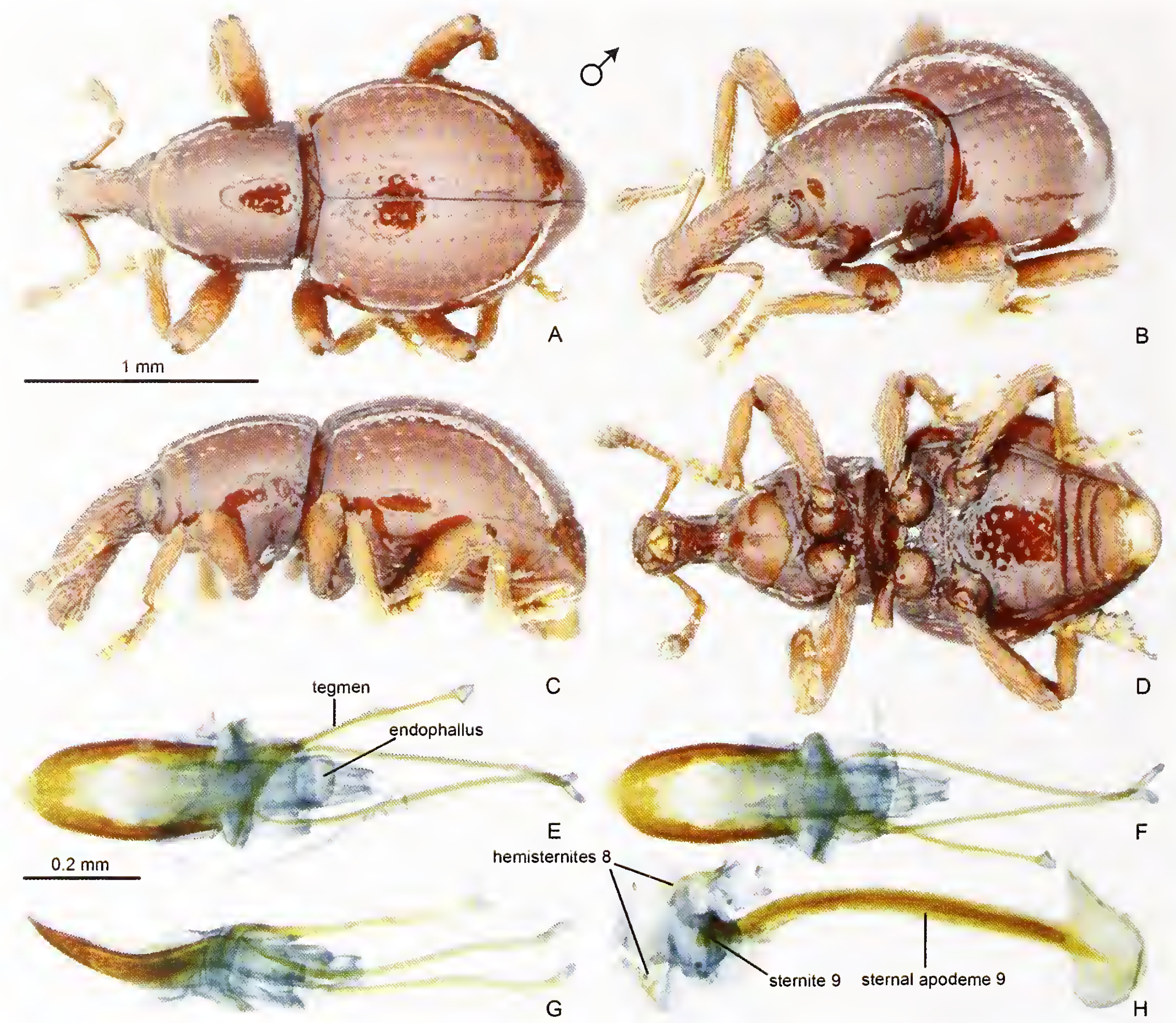

Fig. 1. *Morimotodes ismene* g. & sp. n., holotype, male, #0928 from Gaoligong Mt. Range, Yunnan. A–D: habitus; E–G: aedeagus and tegment, dorsal (E), ventral (F), lateral; (G); H: sternites 8 and 9.

lated genus *Leiosoma*, adults of *Morimotodes* g. n. can be easily distinguished by their brown or reddish colour (*Leiosoma* adults are black) and, additionally, by a wide gap in distribution (*Leiosoma* is restricted to the West Palaearctic and, therefore, is widely allopatric with *Morimotodes* g. n.).

Description. Small (1.6–2.1 mm) and uniformly brown or dark reddish, lustrous, wingless weevils. Dorsal surface of pronotum and elytra without longitudinal ridges, carinae or irregular sculpture; elytral striae weakly indicated by individual rows of fine setiferous punctures surrounded by clearly restricted zone of darker pigmentation (Figs 1A–C, 6A–C); setiferous punctures on pronotum shallower, not arranged in longitudinal rows and lacking pigmented surroundings (Figs 1A–C, 6A–C). Length of dorsal setae variable, from almost indistinguishable under 50x magnification (Figs 6A–C, “polished” specimens) to relatively long and exceeding in length longitudinal distance between setiferous punctures (Figs 4B, 5B, “hairy” specimens). Integument clean, not covered by incrustation or wax secretion. Elytra with shoulders entirely levelled, in dorsal view strongly and evenly rounded, 1.5–1.8x as wide as maximal prothoracic width. Body dorsal outline in lateral view evenly and relatively strongly curved (Fig. 5); elytra neither flattened dorsally, nor declivate apically. Head capsule moderately visible from above (Fig. 4). Eyes laterally, not reduced in size. Antennal attachments in apical third of rostrum; funicle with seven antennomeres; compact club consisting of three antennomeres. Pronotum not constricted laterally in anterior quarter; widest at middle or at base; prosternum without rostral canal or ocular

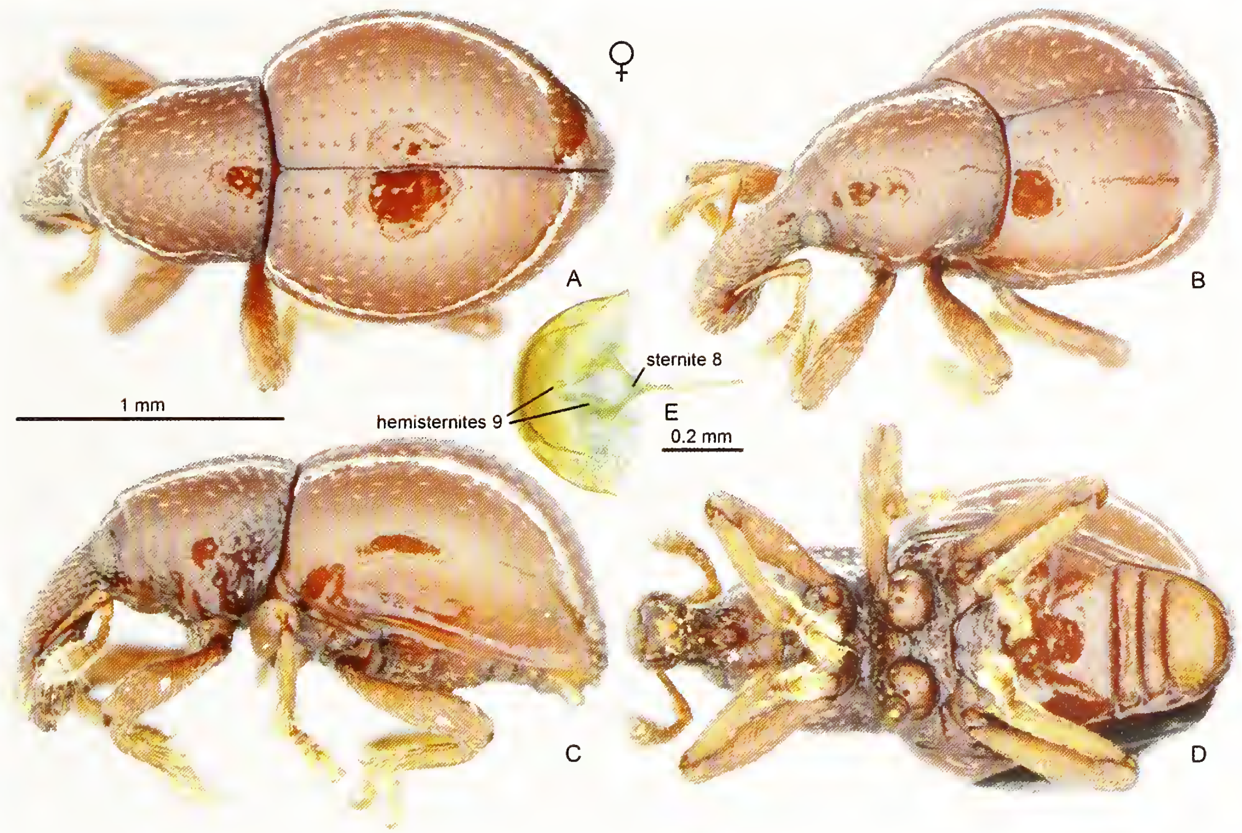

Fig. 2. *Morimotodes ismene* g. & sp. n., paratype, female, #1020 from Gaoligong Mt. Range, Yunnan. A–D: habitus, E: genital sternites 8 & 9, ventral view.

lobes; procoxae contiguous. All femora without tooth. Hind wings absent. Sclerolepidia absent (Fig. 3E). Aedeagus weakly sclerotized, dorsally and ventrally membranous and translucent; endophallus without slerotization (Figs 1E, F, 6E, F). Female hemisternites 9 each with separate and clearly distinguishable basal and apical pieces (Fig. 2E; "coxite" and "stylus", respectively).

Species composition and distribution. As currently known, the genus *Morimotodes* g. n. comprises two species, each relatively widely distributed in Southwest China (Yunnan and Sichuan) or in Taiwan, respectively.

Biology. All specimens of *Morimotodes* were collected by sifting deciduous leaf litter in montane primary forests with subsequent specimen extraction using Winkler funnels. These collecting circumstances were further corroborated by the loss of hind wings, which strongly suggest that *Morimotodes* species are habitat-dependant low-dispersing forest litter inhabitants critically dependant on this habitat. Immature stages, host plants or any specific biological preferences remain unknown.

Etymology. *Morimotodes*, patronymic, derived by adding the Latin suffix -*odes* to the family name of Katsura Morimoto (retired, formerly professor at Kyushu University, Fukuoka, Japan), in recognition of his outstanding contribution to the knowledge of weevils from the Asia-Pacific Region. Gender masculine.

Morimotodes ismene sp. n.

Figs 1–5.

Diagnostic description. Holotype, male (Fig. 1). GenBank accession: HQ987135. Length: 1.85 mm. Dorsal outline of pronotum in lateral view evenly rounded; pronotum and elytra dorsally with fine punctures and white pilosity visible at magnification below 30x; each elytron with single longitudinal groove adjacent and parallel to edge. Aedeagus parallel-sided; sternite 9 not subdivided and not wider than 1.5x width of apodeme; sternal apodeme 9 with large paddle-shaped extension anteriorly. **Intraspecific variation.** Length: 1.60–2.0 mm. Body outline in dorsal and lateral views variable (Figs 4, 5), pronotum in basal half either parallel-sided (Fig. 4D) or

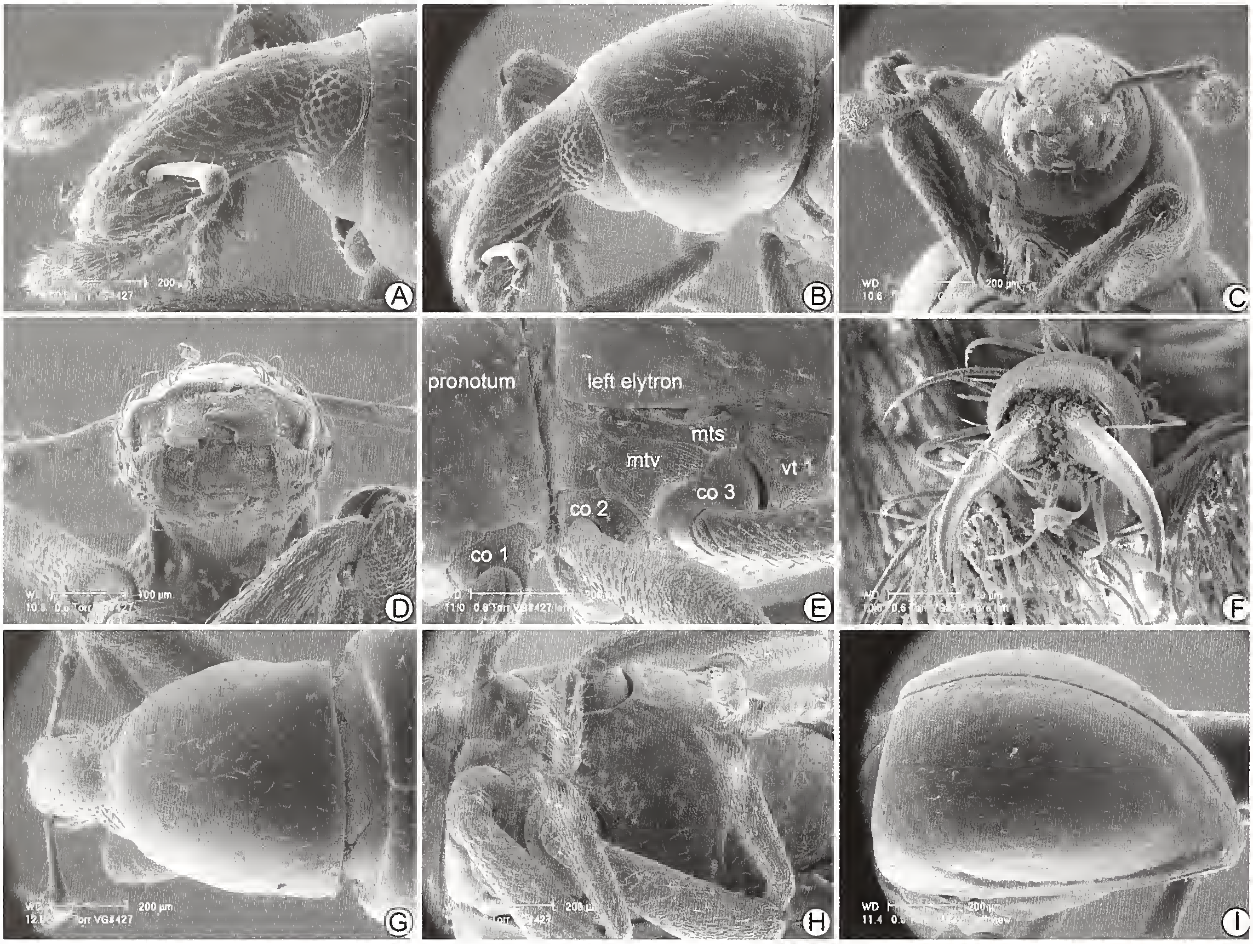

Fig. 3. *Morimotodes ismene* g. & sp. n., unsexed, #0427 from Cang Shan Mt. Range, Yunnan. SEM images. A: head, left lateral; B: head and pronotum, left lateral; C: head, frontal; D: rostrum, frontal; E: meso- and metathorax, left lateral; F: claws, lateral; G: pronotum and head, dorsal; H: meso- and metathorax, right ventro-lateral; I: elytra, left lateral. Mst: metepisternum, mtv: metaventrite, co1–co3: pro-, meso- and metaxocae, respectively, vt1: ventrite 1 (=abdominal segment 3). Note absence of sclerolepidia on metepisternal suture separating metepisternum and metaventrite; the presence of this suture in apterous weevils is unusual.

weakly broadened posterad (Fig. 4E); dorsal outline of rostrum-to-head junction even (Fig. 5B), evenly and weakly depressed (Figs 1A, 5A) or marked more abruptly (Fig. 5D). Dorsal body puncture and pilosity variable, from mostly faint (Fig. 5D) to markedly developed (Fig. 5B).

Material examined. Holotype male (IZCAS): #0928, “P.R. CHINA, Yunnan, E slope N Gaoligongshan, N27°47’22.1 E098°32’17.7, 24.v.2010, 3027m, sifting20, V.Grebennikov”. **Paratypes** (CNC, IZCAS, MTD), 19 in total: 4 exx, #0114–6, #0503: “P.R. CHINA, Yunnan, E slope N Gaoligongshan, N27°46.212’ E098°36.221’, 12.vi.2009, 2312m, sifting02, V.Grebennikov”; 5 exx, #0144 and 4 not numbered: “P.R. CHINA, Yunnan, E slope N Gaoligongshan, N27°46.782’ E098°33.087’, 14.vi.2009, 2956m, sifting04, V.Grebennikov”; 2 exx, not numbered: “P.R. CHINA, Yunnan, E slope N Gaoligongshan, N27°46.665’ E098°33.321’, 15.vi.2009, 2982m, sifting05, V.Grebennikov”; 1 ex, not numbered: “P.R. CHINA, Yunnan, E slope N Gaoligongshan, N27°46.635’ E098°33.381’, 16.vi.2009, 2946m, sifting07, V.Grebennikov”; 2 exx, #0927 and 1 not numbered: same data as holotype; 1 ex, #0977: 2010/21 “P.R. CHINA, Yunnan, E slope N Gaoligongshan, N27°47’22.1 E098°32’17.7, 24.v.2010, 3027m, sifting21, V.Grebennikov”; 4 exx, #1017–20: “P.R. CHINA, Yunnan, E slope N Gaoligongshan, N27°59’01.0 E098°32’56.9, 27.v.2010, 3018m, sifting22, V.Grebennikov”.

Additional non-type specimens: Cang Shan Mt. Range (15 in total, CNC): 14 exx, #0300–1, #0427, #0499–502, 7 not numbered: “P.R.CHINA, Yunnan, Cangshan, N25°40.381’ E100°08.016’, 30.v.2008, 2600m, sifting, V.Grebennikov”; 1 ex, #0867: “P.R. CHINA, Yunnan, E

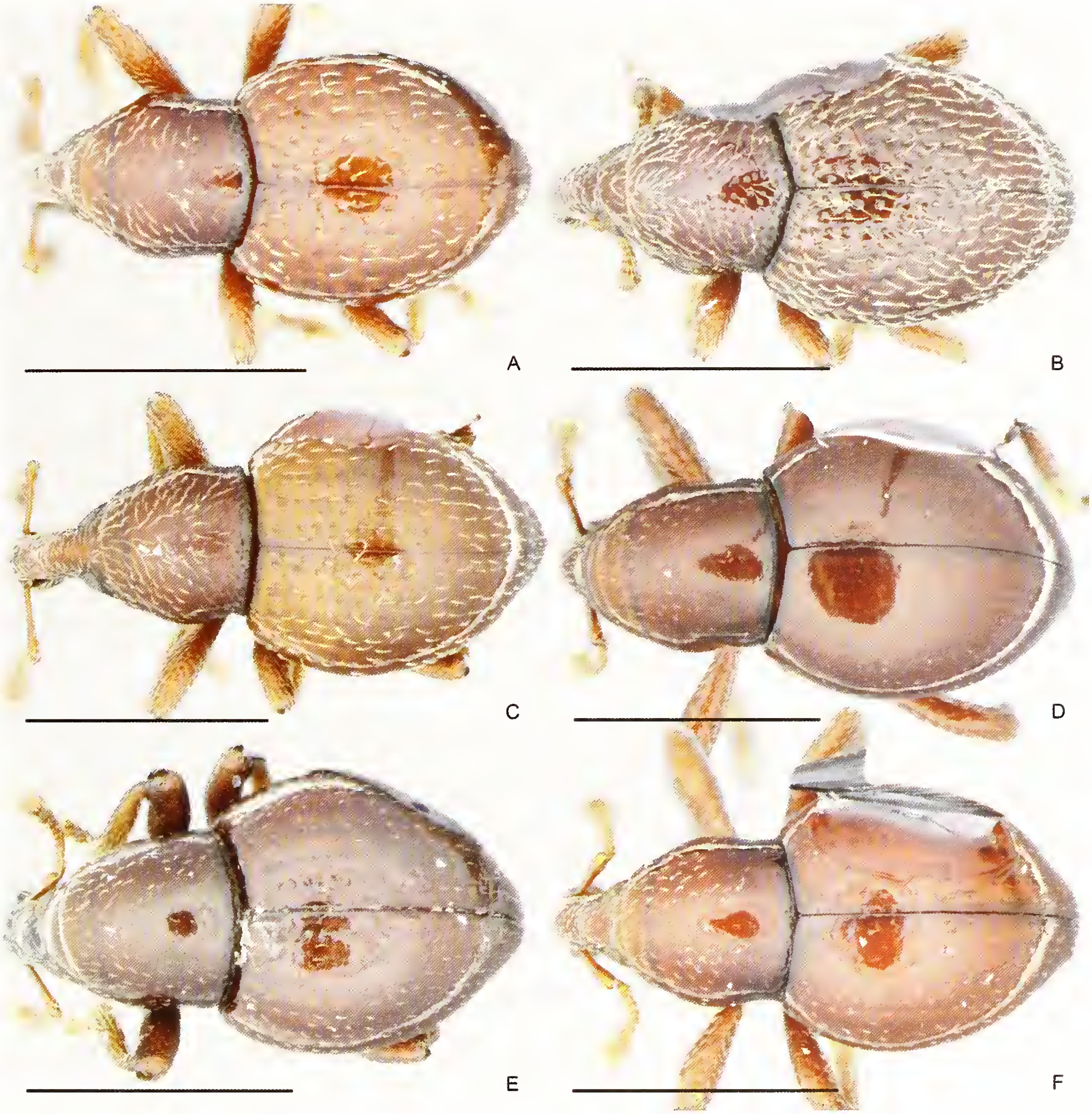

Fig. 4. *Morimotodes ismene* g. & sp. n., unsexed, dorsal view. A: #2409 from Mount Gongga, Sichuan; B: #4483 from Mount Haba, Yunnan; C: #6185 from Mount Emei, Sichuan; D: #1105 from Mount Emei, Sichuan; E: #0867 from Cang Shan Mt. Range, Yunnan; F: #0251 from Mount Emei, Sichuan. Scale: 1 mm.

slope Cangshan at Dali, N25°40’15.5 E100°07’45.4, 18.v.2010, 2657m, sifting17, V.Grebennikov”. Mount Haba (6 in total, CNC): 4 exx, #4481–4: “CHINA, Yunnan, Haba Shan, N27°21’01“ E100°05’44”, 21.vi.2012, 4072m, sift26, V. Grebennikov”; 2 exx, #4536–7: “CHINA, Yunnan, Haba Shan, N27°21’01“ E100°05’44”, 28.vi.2012, 4072m, sift35, V. Grebennikov”. Mount Gongga (9 in total, CNC): 1 ex, #2409: “P.R. CHINA, Sichuan, NE slope Gongga Shan, N29°48’15” E102°03’44”, 06.vi.2011, 2765m, sift11, V.Grebennikov; 1 ex, #2456: “P.R. CHINA, Sichuan, NE slope Gongga Shan, N29°50’50” E102°02’28”, 09.vi.2011, 3170m, sift14, V.Grebennikov”; 3 exx, #2471–3: “P.R. CHINA, Sichuan, NE slope Gongga Shan, N29°50’05” E102°02’53”, 11.vi.2011, 3019m, sift15, V.Grebennikov”; 2 exx, #2559–60: “P.R. CHINA, Sichuan, NE slope Gongga Shan, N29°49’33” E102°03’06”, 21.vi.2011, 2977m, sift24, V.Grebennikov”; 3 exx, #2562–3: “P.R. CHINA,

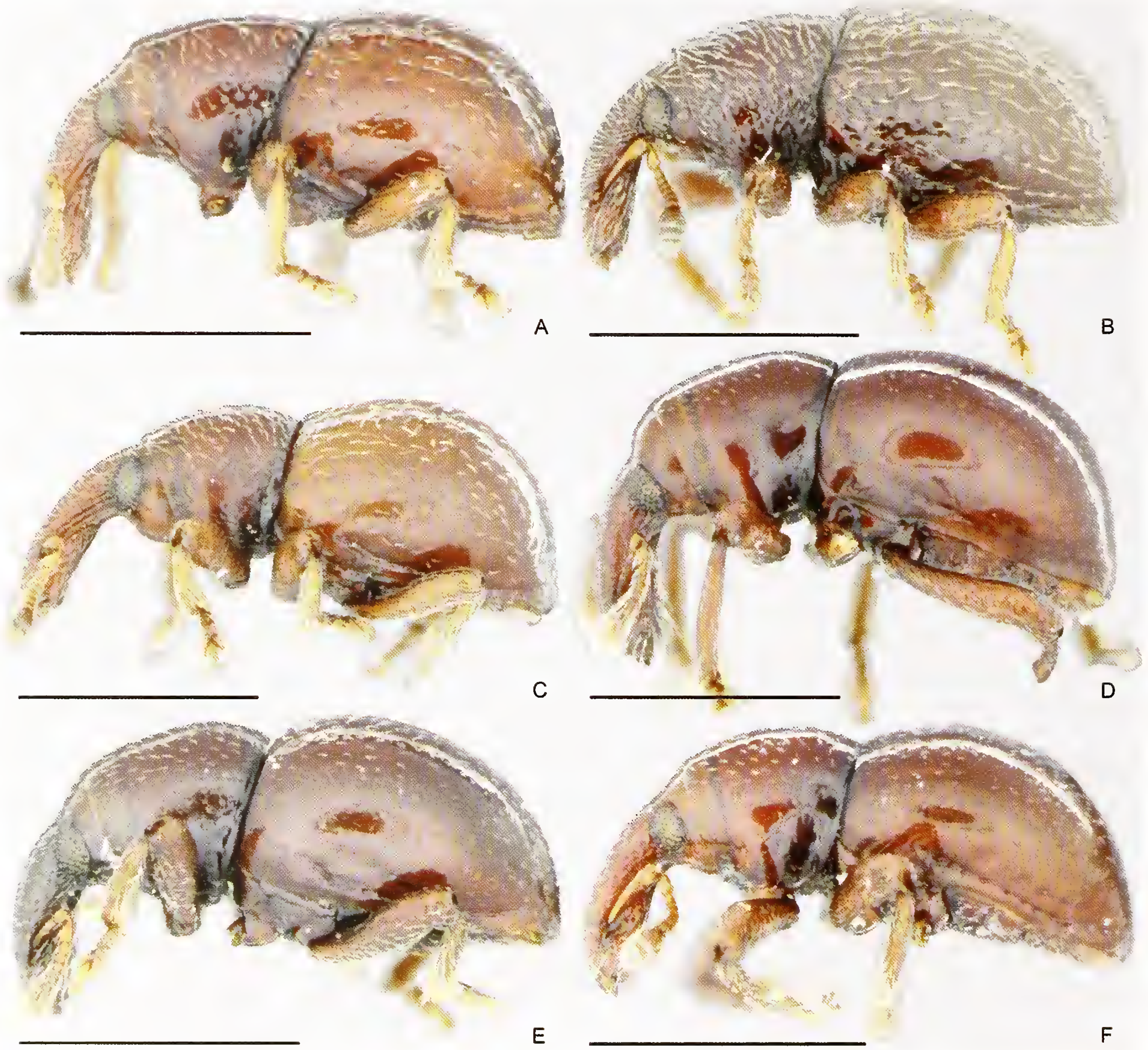

Fig. 5. *Morimotodes ismene* g. & sp. n., unsexed, left lateral view. A: #2409 from Mount Gongga, Sichuan; B: #4483 from Mount Haba, Yunnan; C: #6185 from Mount Emei, Sichuan; D: #1105 from Mount Emei, Sichuan; E: #0867 from Cang Shan Mt. Range, Yunnan; F: #0251 from Mount Emei, Sichuan. Scale: 1 mm.

Sichuan, NE slope Gongga Shan, N29°49’29” E102°03’24”, 21.vi.2011, 2986m, sift25, V.Grebennikov”. Mount Emei, clade EM-A (10 in total, CNC): 10 exx, #1216–9: #6184–9: “P.R. CHINA, Sichuan, EmeiShan, N29°32’37.3 E103°19’57.5, 18.vi.2010, 2440m, sifting37, V.Grebennikov”; clade EM-B (6 in total, CNC): 4 exx, #0251–3, #0504: “P.R. CHINA, Sichuan, Emei Shan, N29°32.932’ E103°20.466’, 01.vii.2009, 2310m, sifting14, V.Grebennikov”; 1 ex, #0505: “P.R. CHINA, Sichuan, Emei Shan, N29°32.806’ E103°20.106’, 03.vii.2009, 2342m, sifting15, V.Grebennikov”; 1 ex, #1172 and #4186 (two numbers on the same specimen): “P.R. CHINA, Sichuan, EmeiShan, N29°32’37.3 E103°19’57.5, 18.vi.2010, 2440m, sifting37, V.Grebennikov”; clade EM-C (1 in total, CNC): 1 ex, #1105: “P.R. CHINA, Sichuan, EmeiShan, N29°33’36.3 E103°20’38.0, 15.vi.2010, 1947m, sifting33, V.Grebennikov”.

Distribution. The species is known from five isolated high altitude forest regions in Yunnan and Sichuan provinces (Fig. 9).

Etymology. The species epithet is the Latinized Greek mythical name of Ismene, a daughter and half-sister of Oedipus, daughter and granddaughter of Jocasta, and sister of Polynices; noun in apposition.

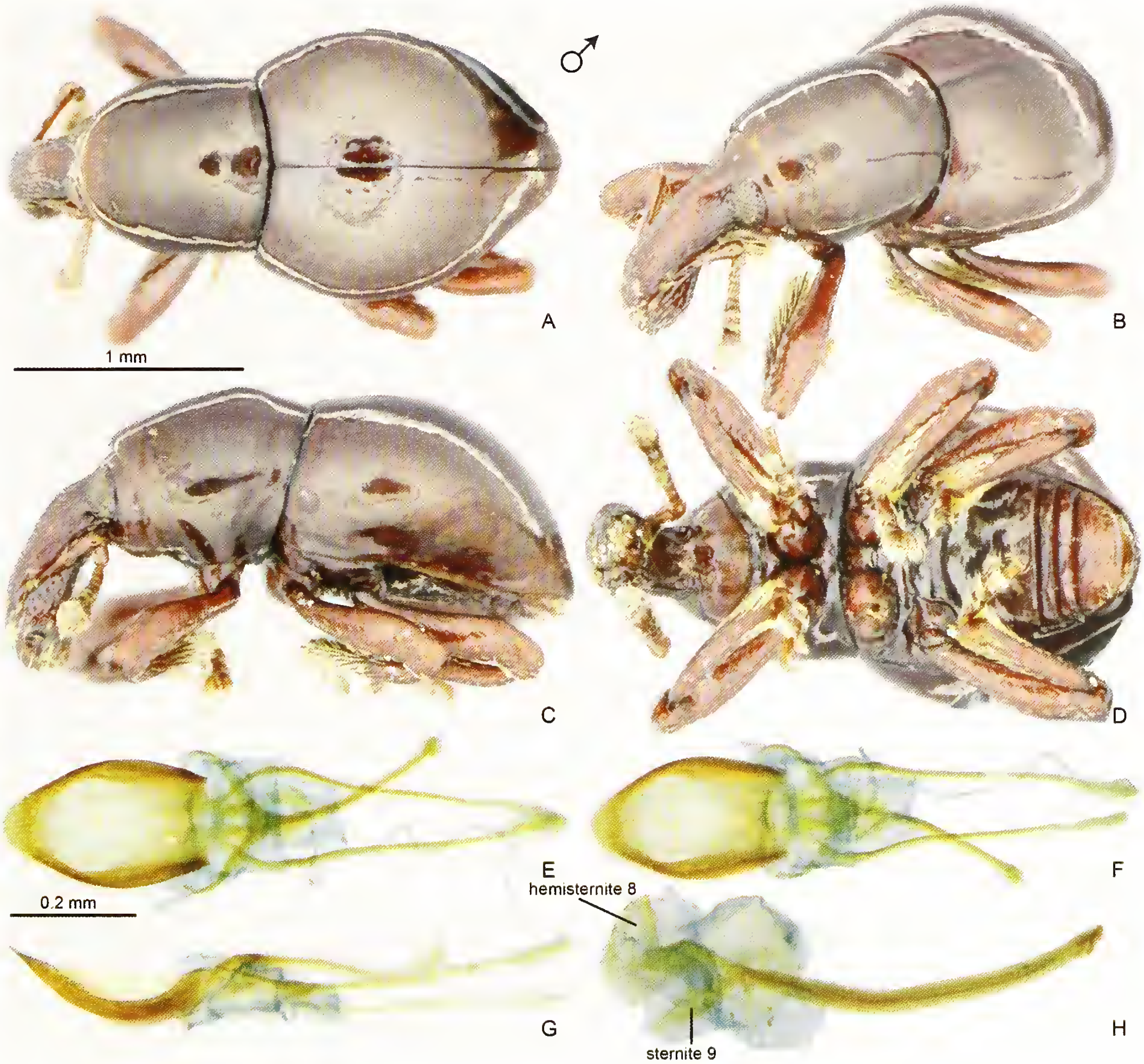

Fig. 6. *Morimotodes polynices* g. & sp. n., holotype, male, #5949 from Taiwan. A–D: habitus; E–G: aedeagus and tegment, dorsal (E), ventral (F), lateral; (G); H: sternites 8 and 9.

Morimotodes polynices sp. n.

Fig. 4.

Diagnostic description. Holotype, male (Fig. 6). DNA not sequenced. Length: 2.00 mm. Dorsal outline of pronotum in lateral view with hump in basal third; pronotum and elytra dorsally with fine punctures and pilosity not visible at magnification below 30x; each elytron without longitudinal groove parallel to edge. Aedeagus rounded laterally, sternite 9 Y-shaped and about 3–5x wider than apodeme; sternal apodeme 9 without extention anteriorly. **Intraspecific variation.** Length: 1.98–2.12 mm.

Material examined. Holotype male (CMN): #5949 "TAIWAN, Kaohsiung Hs. Rd. Abv. Tona For. Sta. Km16–17, 1700–1800m 28.V.1998, A.Smetana (T190)". **Paratypes** (CNC, CMN), 26 in total: 2 exx, #5925–6: "TAIWAN, Kaohsiung Hsien, Kuanshan trail at Kaunshanchi Riv. 2400 m 24.VI.1992 A. Smetana (T94)"; 9 exx, #5927–35: "TAIWAN, Kaohsiung Hsien, Peinantashan trail, 2000m 7.VII.93 A. Smetana (T144)"; 1 ex, #0587: "TAIWAN, Kaohsiung Hsien, Kuanshan trail above Kaunshanchi Riv., 2550m, 22.VII.93 A. Smetana (T160)"; 1 ex, #5936: "TAIWAN, Kaohsiung Hsien, Peinantashan trail 2450m, 2.V.1995 A. Smetana (T170)"; 13 exx, #5940–8, #5950–3:

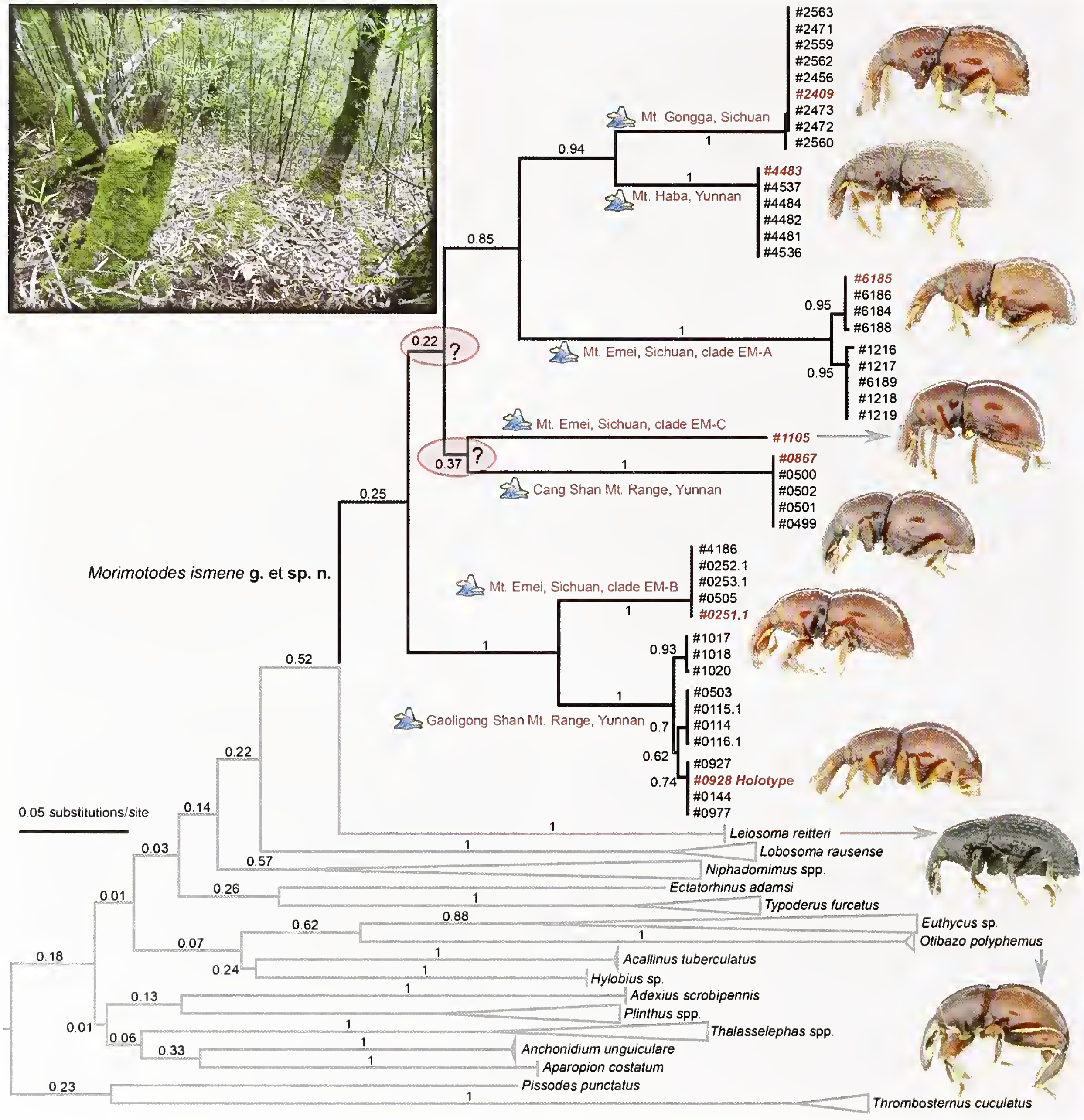

Fig. 7. Maximum Likelihood inference phylogram positioning monophyletic *Morimotodes ismene* g. & sp. n. (in black) as a sister to *Leiosoma reitteri* among other analysed Molytinae genera (in grey) using the 658 nt of the mtDNA barcoding CO1 gene fragment. Digits at internodes are bootstrap values. The tree is rooted on *Graptus circassicus* (Entiminae; not shown). Seven geographically linked lineages of *M. ismene* g. & sp. n. are marked in red; note that Mount Emei uniquely harbours three unrelated lineages. Red and italicized numbers are those of imaged specimens (Figs 1, 4, 5) illustrating respective clades. Two pink ovals with question marks denote two nodes not recovered in the alternative BI analysis (Fig. 8). Inserted image of the forest illustrates exact spot where the type specimen #0928 was found.

same data as holotype. **Additional non-type specimens:** 3 exx, (CMN), #5937–9: "TAIWAN, Ilan Hsien Shen-Mi Lake 24°22'43"N 121°44'12"E, 1110m 10.V.1995 A. Smetana (T177)".

Distribution. The species is known from two widely separated regions in southern and northern Taiwan, respectively (Fig. 9).

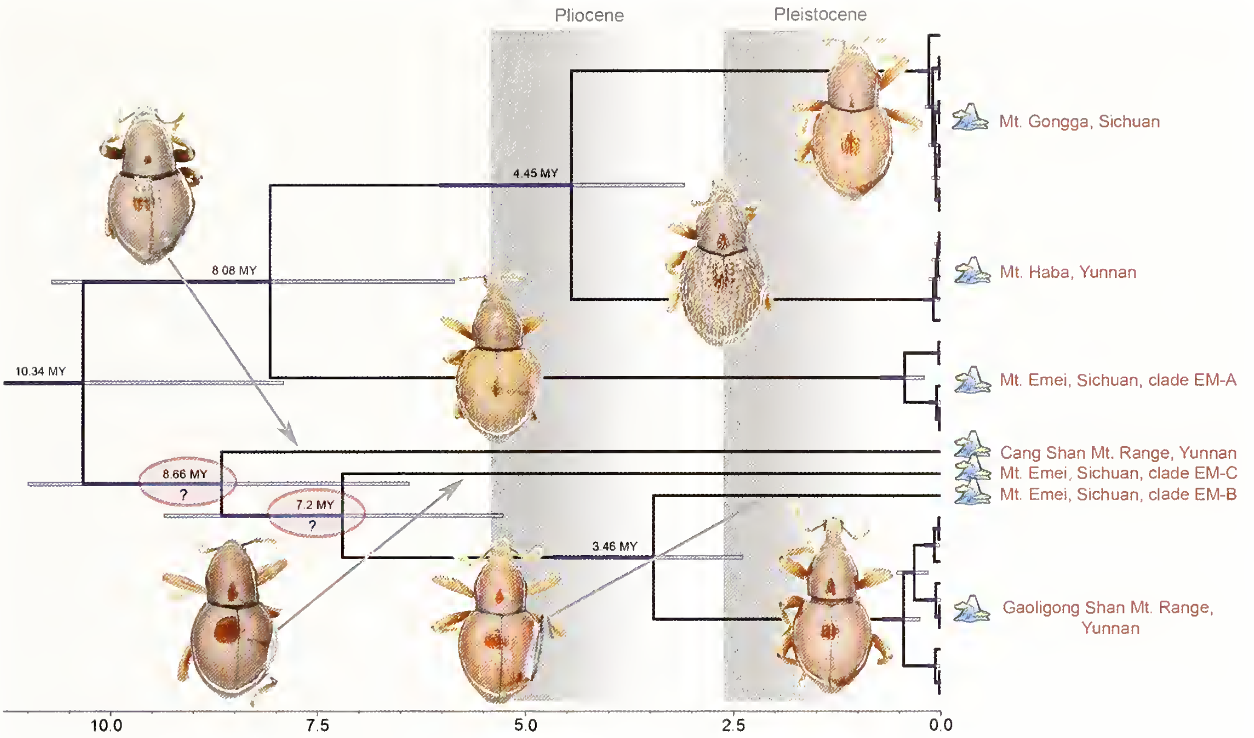

Fig. 8. Ultrametic tree of *Morimotodes ismene* g. & sp. n. reconstructed using Baeysian inference method strict linear molecular clock approach to analyse 658 nt of the mtDNA barcoding CO1 gene fragment and calibrated at a rate of 0.018 substitutions/site/MY. Numbers at nodes and on the scale below are million years before present. Node bars represent 95% confidence intervals of the age estimate. Two pink ovals with question marks denote two nodes not recovered in the alternative ML analysis (Fig. 7).

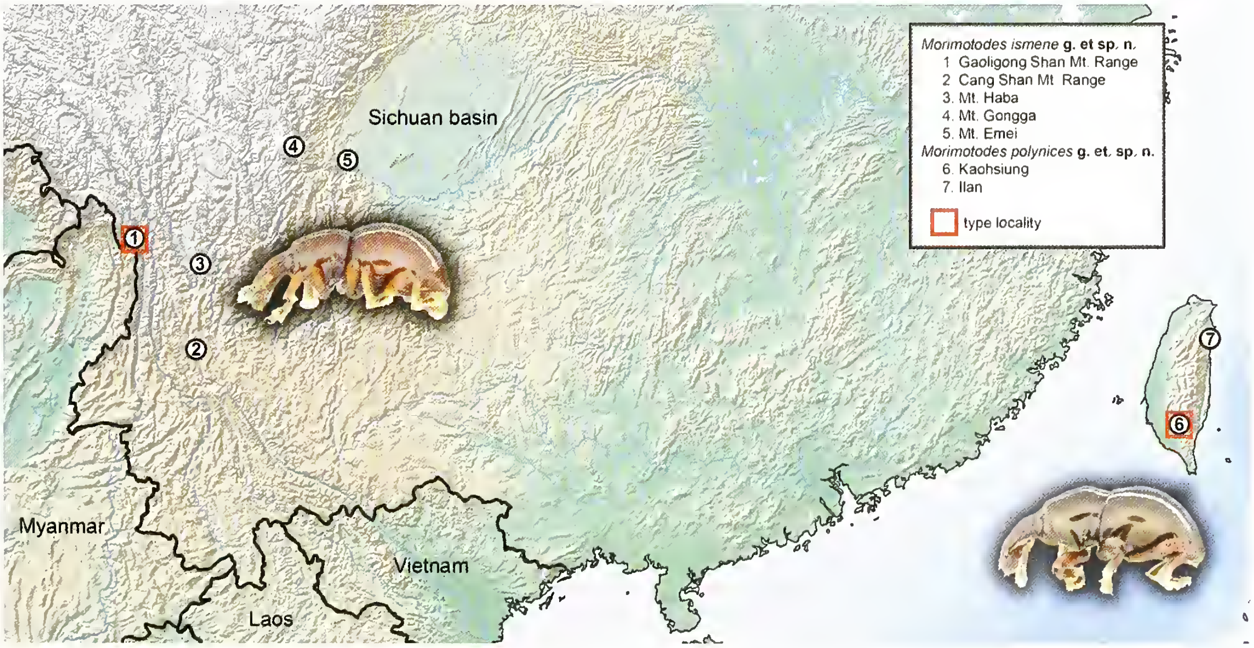

Fig. 9. Known distribution of *Morimotodes* g. n.

Etymology. The species epithet is the Latinized Greek mythical name of Polynices, the son of Oedipus and Jocasta, as well as a grandson of Jocasta; noun in apposition.

RESULTS

The first tree search resulted in a Maximum Likelihood tree (Fig. 7) with the highest log likelihood of – 9190.09. All analyzed specimens of *M. ismene* g. & sp. n. formed a weakly supported clade (bootstrap value 25%). The genus *Morimotodes* g. n., represented by only its type-species, formed a moderately supported (52%) clade with the genus *Leiosoma*. Forty-six analyzed specimens of *M. ismene* sp. n. from five mountain regions formed seven geographical lineages (one monotypical, six others supported with 100% bootstrap). Four of these lineages corresponded to four mountain regions (Fig. 7), while all 15 analyzed specimens from Mount Emei formed three groups not most closely related to each other. Temporal (second) analysis in BEAST (Fig. 8) recovered all *Morimotodes* specimens forming a clade with the same seven lineages as in the first analysis, although the grouping among themselves was not identical with the results of the first analysis. The inferred timing of the splits forming the seven geographically linked lineages within monophyletic *M. ismene* g. & sp. n. detected in the second analysis date between 10.34 MY to 3.46 MY (Fig. 8).

DISCUSSION

Monophyly and sister group of *Morimotodes* g. n.

As presently defined, the genus *Morimotodes* g. n. is most likely monophyletic. This assertion is not tested by the cladistic methods, and is based entirely on circumstantial evidence. None of the 29 specimens of *M. polynices* g. & sp. n. responded positively to a DNA amplification effort and, therefore, the species was not represented in the DNA analyses. Continental populations of *Morimotodes* g. n. from Yunnan and Sichuan all assigned to a broadly defined *M. ismene* g. & sp. n. were consistently recovered as a monophyletic clade in the first tree analysis (Fig. 7). The assumption of both *Morimotodes* g. n. species forming a clade is based entirely on their adult external similarities, further corroborated by the analogous collecting circumstances suggesting similar biology. The geographical gap of about 2000 km separating known distributional areas of both species is not large enough to shed significant doubts on their sister group relationships. Such are all presently available data to justify the implemented taxonomic decisions of grouping both species into a presumably monophyletic new genus.

The most surprising aspect of the first analysis is the relatively weak statistical support for *M. ismene* g. & sp. n. (25%, Fig.7), which can be at least partly attributed to the known phylogenetic limitations of CO1 (Maddison 2012), including the saturation effect.

The sister-group relationships between *Morimotodes* g. n. and the West Palaearctic *Leiosoma* is moderately supported (bootstrap 52% (Fig. 7). Close affinities of both genera have been hypothesised ever since the first representatives of *Morimotodes* g. n. came to notice in 2008, and was grounded entirely on adult morphological similarities (small weevils less than 3 mm in body length with laterally rounded and not flattened bodies and with shiny dorsum) and biological preferences (inhabitants of the deciduous leaf litter). Analogous expectations for the similarly shaped genus *Otibazo* were, however, rejected by the ML tree, the latter clustered with the genus *Euthycus* (Fig. 7). At present, it is impossible to suggest phylogenetic affinities of the clade *Morimotodes* g. n. + *Leiosoma*, since the available data are highly inadequate. Pending further investigation, the genus *Morimotodes* g. n. is placed in the same higher taxonomic group containing its sister group Molytinae: Molytini: Molytina.

If *Morimotodes* g. n. is indeed sister to *Leiosoma*, then attribution of both new species from China to the former genus could be a phylogenetically sound taxonomic alternative. It was, however, rejected because establishing a new genus better reflects the significant external dissimilarity between their members and the wide gap in their known geographical distribution.

Species delimitation of *Morimotodes* g. n.

Both species of *Morimotodes* g. n. as presently defined are much dissimilar to each other. The species from Taiwan, *M. polynices* sp. n., is known from a museum series of externally remarkably similar specimens, all but three of which were sampled from a geographically confined region (Kaohsiung, Fig. 9) not more than 50 km in its greatest detention and within the limited altitudinal range (1700–2550 m). This evidence suggests that all type specimens most likely share the MRCA. Three additional non-type specimens from north of Taiwan (Ilan, Fig. 9) are externally most similar to those from the type locality and, therefore, are thought to be conspecific, although with lesser certainty. These two hypotheses could not be tested using DNA data, since the sequences were not obtainable. Judging from the morphological and geographical data, it seems unlikely that the Taiwanese specimens of *Morimotodes* g. n. could be grouped within the clade formed by their continental counterparts. This evidence, although not tested phylogenetically, strongly suggests separate evolutionary history for the Taiwanese lineage worthy, therefore, of establishing a formal species.

Deciding what to all a species for the continental members of *Morimotodes* g. n. is ambiguous. The most inclusive and conservative approach is, therefore, employed. All specimens of *Morimotodes* g. n. from continental China are presently assigned to the broadly defined *M. ismene* sp. n. This uncertainty on species boundaries is not made any easier by the relatively large amount of available relevant data for the continental species. The implemented decision to assign all continental *Morimotodes* g. n. to a single species is a balanced temporary solution implemented to minimize the conflict among four independent lines of evidence (in the increasing order of their contribution): (1) biological characteristics, (2) morphological similarity/dissimilarity (3) geographical distribution, and (4) mtDNA sequences. The logic of their combined evaluation is described below.

The condition determining the gene flow among *Morimotodes* g. n. populations inhabiting five continental localities (the Cang Shan and the Gaoligong Mountain Ranges, as well as Mounts Haba, Gongga and Emei; Fig. 9) can be considered analogous to those acting for terrestrial organisms confined to oceanic islands. This approximation is commonly used for the low-dispersing and flightless moisture- and habitat-dependent species found in relatively wet isolated forests widely separated by seemingly unsuitable lowlands. Such estimate might perhaps be even an understatement of the dispersal difficulties for the mountain species, since the salt water barriers are occasionally crossed by seemingly most unseaworthy organisms such as chameleons possibly rafting on dislodged floating trees, or blind subterranean Arthropods perhaps surviving the passage in soil attached to their roots (Raxworthy et al. 2002 and Peck 1990, respectively). The very first task with such allopatric mountainous low-dispersing organisms as *Morimotodes* g. n. was, therefore, to assess whether the specimens from each separate locality form distinct evolutionary clusters and whether any of the localities supports more than one such cluster.

The four aforementioned lines of evidence contributed conflicting data. Biological data were the least informative, since all sampled specimens of *M. ismene* sp. n. were sifted from seemingly similar forest litter and within comparable altitude range. The only exception was shown by the Mount Haba specimens recovered from the upper forest zone at altitude notably higher than known for other continental populations. Adult external morphology was the second least informative line of evidence (see below on the use of genital characters). Although the imaged specimens representing each of seven clades were somewhat dissimilar to each other (note the hairy specimen #4484 from Mount Haba, or the large and non-hairy specimen #1105 representing the clade EM-C from Mount Emei; Figs 4, 5), it was impossible to consistently distinguish the others. The most powerful signal came from the mtDNA sequences, which grouped specimens from four localities into four strongly supported corresponding clades (Fig. 7). The exception was Mount Emei, where 14 specimens clustered in two unrelated groups (EM-A and EM-B on Fig. 7) with an additional third equally unrelated lineage (EM-C) represented by a single specimen #1105. The emerging distributional pattern indicated that each locality supports at least one lineage of *Morimotodes* g. n., while Mount Emei has at least three such lineages. The main operational problem was that the majority of the seven detected radiations could neither be uniquely characterized morphologically, nor biologically.

It should be noted that detecting seven evolutionary separate lineages of continental *Morimotodes* g. n. inhabiting five discrete mountain regions is not prohibitive in itself. There are no reasons to expect that no more than a single radiation of closely related low-dispersing organisms should exist in any suitable locality. Among all five continental localities, Mount Emei should be rightfully expected to be the most diverse in *Morimotodes* g. n., because it is overwhelmingly rich in other forms of life and by that exceeds many other comparable localities. For example, its relatively well documented flora condensed on just 154 km^2 and lacking the entire alpine zone, encompasses an astonishing 3703 species of higher plants (Wang et al. 2013). This diversity exceeds Canada (3,156; Mosquin et al. 1995) and is comparable with that of the British Isles (3842, Fitter & Peat 2014). Summing up, the phylogeographic pattern as represented on Fig. 7 did not pose significant biological inconsistencies. By far the major challenge was the necessity to implement the Linnaean taxonomy and decide on how many nominal species are there.

At this stage the purely practical limitations of available material has to be mentioned. Mostly, specimens of *Morimotodes* g. n. are relatively rarely encountered. For example, the radiation inhabiting the Cang Shan Mountain Range responded well to the original sifting in 2008, however, DNA sequencing of the 2008 specimens resulted in only short fragments of 407 bp (four specimens #0499–0502). During the subsequent two visits to Cang Shan in 2010 and 2012, a significant greater sampling effort resulted in the collection of only a single specimen (#0867), but provided a full-length DNA barcode. Mount Emei has also been visited three times with one month of intense fieldwork in total. Among the 27 sifting samples, only five contained representatives of *Morimotodes* g. n. Four focussed samples were taken in two years within 50 meters from where the unique specimen #1105 (lineage EM-C, Fig. 7) had been sifted, but I failed to discover additional specimens. The entire lineage EM-A was recovered from a single sample. Only the lineage EM-B was detected in three samples, two of them taken in exactly the same place in different years and the third one some 650 m away. Such sampling results strongly suggest that specimens of the continental *Morimotodes* g. n. are most unevenly distributed in time and across seemingly identical landscape of mountainous forest.

Species delimitation in insects often relies on the shape of male genitalia. However, due to the scarcity of *Morimotodes* g. n. specimens coupled with possible structural damages during dissection of the minute genitalia, I refrained to examine genitalia of all sequenced specimens. It was impossible to sex specimens externally and, therefore, male genitalia dissection had to be attempted with a randomly chosen specimen, some of them females. Even more problematic were the difficulties linked to the mechanical body properties of these highly compact minute beetles with globular elytra firmly fused to the hind body and forming together a most robust, inflexible and, accordingly, highly breakable capsule. After the muscle tissue was nearly completely dissolved and the remaining internal structures much loosened, the genitalia were successfully dissected for the two holotypes, only. It was, therefore, judged inadvisable to perform extensive male genitalia dissections.

The practical conclusion reached after considering all was to define preliminarily a single species for all continental representatives of *Morimotodes* g. n., even though this taxon might be later split into more separate species. The Haba Shan lineage having distinct external adult morphology further corroborated by the unique biological preferences of higher altitudes can perhaps merit its own species even at present. This action, however, will render the rest of the continental *Morimotodes* g. n. paraphyletic and, therefore, is not implemented. Considering a likelihood of further taxonomic changes in the broadly defined *M. ismene* sp. n., the type series is purposely restricted to the specimens forming a separate lineage uniquely characterised by DNA and geographical data. Specimens from the Gaoligong Mountain Range forming the extreme west of the known generic distribution (Fig. 9) were chosen for this purpose, specifically because they are numerous in the DNA analysis. Additionally, this lineage is represented by specimens recovered in at least six separate samples taken from the area measuring 25 km in its greatest dimension and, therefore, having the least chances of harbouring an undetected sympatric congeneric lineage (i.e., like Mount Emei with at least three such lineages). Consequently, all specimens of *M. ismene* sp. n. from localities other than the Gaoligong Mountain Range are not designated as paratypes.

Dated phylogeography of *Morimotodes ismene* g. & sp. n.

Little can be presently said about the temporal aspect of *Morimotodes* g. n. evolution. The single and seemingly most interesting aspect of it, namely the time of the implied separation between continental *M. ismene* sp. n. and *M. polynices* sp. n. from Taiwan cannot be addressed at present because of the lack of mtDNA data to represent the latter species. Even though all seven lineages constituting monophyletic *M. ismene* sp. n. were consistently recovered in the first (ML) and the second (BI) analyses, their grouping was consistent in only three nodes (Fig. 8): (a.) the split between lineages inhabiting Mount Haba and Mount Gongga, (b.) their MCRA separating from the lineage EM-A inhabiting Mount Emei and (c.) the split between Mount Emei clade EM-B and the lineage from the Gaoligong Mt. Range. All four consistently recovered evolutionary events (three aforementioned and the origin of the entire *M. ismene* sp. n.) date 4.45 MY, 8.08 MY, 3.46 MY and 10.34 MY, respectively. These estimations provide a very approximate time frame for the origin and diversification of the continental *Morimotodes* g. n., which is comparable to those of the sympartically distributed weevil genera *Niphadomimus* Zherikhin, 1987 (Grebennikov 2014) and *Notaris* Germar, 1817 (Grebennikov & Kolov, unpublished) likely linked to the advanced stages of the uplift of the Tibetan Plateau (Favre et al. 2014).

Illustrated overview of genera of the subtribes Molytina and Plinthina

The catalog of Alonso-Zarazaga & Lyal (1999, 2002) had all genera currently assigned to Molytina and Plinthina already listed as such (except for two proposed later) and all included in the broadly defined Molytini. Since then the following changes were proposed: (1) the monotypic *Stenanchonus* Voss, formerly of Anchonini, was synonymized with *Enthycus* Pascoe of Molytina (Meregalli 2003); (2) some species of the genus *Minyops* Schoenherr of Plinthina was assigned to the newly erected *Paraminyops* Osella & Bellò (Osella & Bellò 2010); (3) the tribe Sthereini was re-erected to incorporate nine genera, four of them formerly of Plinthina (Alonso-Zarazaga 2013; Lyal 2014); (4) the former Molytini subtribe Typoderini was elevated to tribe level; (5) the former Molytini subtribe Leiosomatina was synonymized with Molytina (Lyal 2014); (6) the former tribe Hylobiini was synonymized with Molytini by forming its third and the last subtribe (Lyal 2014); (7) one new genus, *Morimotodes* g. n., being described herein. Moreover, the Palaearctic representatives of both subtribes accounting for about 80% of their species were recently catalogued (Alonso-Zarazaga 2013).

All 30 genera presently assigned to both subtribes are listed below and 27 of them are illustrated. This summary was done with the intention to bring them to the notice of the contemporary scientific community and hopefully trigger their reinvestigation in a phylogenetic framework using modern data and analytical methods. Up to now very little of such work has been done for the entire subfamily Molytinae, including both Molytina and Plinthina. Most importantly, reciprocal monophyly of both subtribes has never been demonstrated and, therefore, their taxonomic existence as currently defined seems very precarious yet. Moreover, with the exception of Craw's (1999) detailed analysis of the New Zealand's *Hadramphus* & *Lyperobius*, none of the non-monotypical genera shown in detail below has ever been tested for its monophyly. Some phylogenetically relevant statements were, however, made: Meregalli (1985) suggested a sister-group relation between *Minyops* (then containing *Paraminyops*) and *Plinthus*. Davidian (2008) proposed that the lineage presently consisting of *Paraminyops* and *Minyops* is most closely related to a subgroup of the genus *Plinthus* (rendering the former paraphyletic) and that *Hoplopteridius* forms a clade with all of them. Osella & Bellò (2010), when separating their new genus *Paraminyops* from *Minyops*, suggested that both genera together with *Hoplopteridius* form a group ("subtribe Minyopina", a synonym of Plinthina, Bouchard et al. 2011). None of these hypotheses have been analytically tested.

Subtribe Molytina

The tribe includes 13 genera, which are numbered and listed alphabetically below. Nine of them, as noted by Lyal (2014), are widely scattered from New Zealand and Australia, through New Guinea, Borneo, Java, and Indochina, to Sri Lanka, eastern India, China and Japan. Three other genera (*Anisorhynchus*, *Leiosoma* and *Liparus*) are distributed in the Western Palaearctic, with the former also known from Central Asia (Alonso-Zarazaga & Lyal 1999). One genus known only from the holotype (*Pterotomus*) is restricted to Angola.

Anisorhynchus **Schoenherr, 1842** (Figs 10A, B). This is a genus of 13 large-bodied species and one non-nominative subspecies restricted to the West Palaearctic and distributed mainly around the Mediterranean Sea (Alonso-Zarazaga 2013).

Apterylobius **Marshall, 1942** (Figs 10C, D). Fewer than a dozen specimens of this genus are known, all exclusively from Mount Kinabalu in northern Borneo. Since its description (Marshall 1942), the genus contains two species and one non-nominative subspecies, and no newly collected specimens have been since reported.

Carbonomassula **Heller, 1908** (Figs 10E, F, 16A). Specimens of this genus, apart from their much greater size, markedly resemble those of *Morimotodes* g. n. in having similarly evenly rounded and dorsally lustrous body of reddish or brownish color (compare Figs 6A and 10E). The genus contains the single species from Papua New Guinea, *C. glaberrima* Heller, 1908. The original description was based on an unknown number of syntypes and accompanied by a high quality habitus drawing (Heller 1908). The type locality is "Nova Guinea Britannica, ad flumen Aroa". Two syntypes are in MTD, the smaller one best fitting the body length given in the original description is illustrated herein (Figs 10E, F). Both syntypes have a blue rectangular label "14523" (Fig. 16A), even though the original description mentions "14525". One additional and seemingly conspecific specimen supplied to BMNH by M.E. Bacchus in 1965 has the locality label "NEW GINEA: Morobe Dist., Herzog Mts., Vagau, C.4,000 ft. 4–7.i.1965". No other specimens of this genus have been reported (Setliff 2007).

Clarkanthus **Alonso-Zarazaga & Lyal, 1999** (Figs 10G, H, 16B). This genus consists of two poorly known species from Sri Lanka and the adjacent part of India. Its type species, *C. taprobanus* (Faust, 1895) was described from the holotype collected on "Ceylon". The genus has long been known under a preoccupied generic name *Ischnopus* Faust, year (non Amyot). Second species, *C. madrasensis* Pajni & Sood, 1982, was described from a holotype collected in the South Indian state of Tamil Nadu just across the Palk Strait from Sri Lanka. Except for the two type specimens, representatives of the genus have not been reported in the literature. Two additional historical specimens are present in MTD: one seemingly conspecific with the type species and labelled "Ceylon Plason" in Faust's handwriting, and another at least congeneric and with a printed label "India or. Madura". The locality might perhaps refer to the Madurai District in Tamil Nadu, which is the type locality of *C. madrasensis*. These four specimens are the sole representatives of this obscure genus.

Euthycus **Pascoe, 1885** (Figs 11A, B). This genus embraces 12 species distributed at the junction between the Palaearctic and Oriental Regions and recorded from Japan, southern China and Taiwan, southwards to Borneo and Java, and westwards to Assam, Sikkim and Andaman Islands of India (Meregalli 2003). Little is known of their natural history, aside from appearing to be associated with mid-altitude primary mountainous forests. Observation of two live specimens personally collected by sifting litter in Taiwan and represented in the DNA analyses revealed remarkably strong adhesive power of their tarsi. This suggests that the beetles are climbers rather than true litter inhabitants (such as *Morimotodes* g. n.), where they might be encountered only accidently.

Hadramphus **Broun, 1911** (Figs 11C, D). This genus includes four relatively large-bodied species restricted to New Zealand and some nearby islands and was revised by Craw (1999, including a summary on the immature stages and host plants). Together with *Lyperobius*, this genus can be considered as a weevil analogous to the moa or weta (i.e., flightless giant birds or crickets), that evolved

Fig. 10. Representatives of the Molytini: Molytina genera. A–B: *Anisorhynchus barbatus* (Rossi), Italy, Abruzzo, no date, no collector, type species of *Anisorhynchus*, MTD; C–D: *Apterylobius basalis* (Heller, 1922), Malaysia, Borneo, no date, no collector, ?syntype, MTD; E–F: *Carbonomassula glaberrima* Heller, Papua New Guinea, syntype, see text, type species of *Carbonomassula*, MTD; G–H: *Clarkanthus taprobanus* (Faust), Sri Lanka, holotype, see text, type species of *Clarkanthus*, MTD.

in the unique New Zealand biota mostly deprived of terrestrial mammals and, therefore, highly vulnerable to invasive predatory species. Unlike the moa with all nine species quickly driven to extinction by invasive humans, all but one (*Tymbopiptus valeas* Kuschel, 1987) known large New Zealand weevils continue to survive, despite

Fig. 11. Representatives of the Molytini: Molytina genera. A–B: *Euthycus macilentus* Pascoe, 1885, Indonesia, Java, Mt. Guntur, no date, Overbeck, type species of *Euthycus*, MTD; C–D: *Hadramphus tuberculatus* (Pascoe), New Zealand, Christchurch, 1910, no collector, BMNH, image: Vasily Grebennikov, © The Natural History Museum, London; E–F: *Leiosoma deflexum* (Panzer, 1795), Poland, Muszkowice, 6.v.1986, M.Wanat, type species of *Leiosoma*, CNC; G–H: *Liparus glabrirostris* (Küster, 1849), Poland, Sudetes, 15.vii.1975, M.Kupczyński, CNC.

loosing most of their former range (Kuschel & Worthy 1996). Recently an extant population of *H. tuberculatus* (Pascoe, 1877), a species thought to be extinct, was discovered (Fountain et al. 2013).

Kyliparus **Moromoto, 1982** (not illustrated). This genus was proposed to accommodate a single species from Japan, *K. lewisii* (Roelofs), previously attributed to *Liparus*. The original description of *Kiliparus* contains a habitus dorsal image of a single female studied by Morimoto (1982, fig. 46E).

***Leiosoma* Stephens, 1829** (Figs 11H, F). All 32 species and one non-nominative subspecies of this genus are restricted to the West Palaearctic, particularly the northern Mediterranean, with two species extended eastwards to the Caucasus (Alonso-Zarazaga 2013). Numerous species descriptions were made for localized allopatric populations and, therefore, a revision is desirable to assess their status as that of biologically valid entities.

***Liparus* Olivier, 1807** (Figs 11G, H), the type genus of the subtribe Molytina, the tribe Molytini and the subfamily Molytinae. The genus includes 17 species and two non-nominative subspecies (Alonso-Zarazaga 2014) of large-bodied weevils. The genus is most diverse in the West Palaearctic, while two species of the subgenus *Liparorhynchus* Reitter form the extreme eastward boundary of the generic distribution and are found in Central Asia (Uzbekistan, Tajikistan, Afghanistan, Iran; Bajtenov 1974; Alonso-Zarazaga 2013).

***Lyperobius* Pascoe, 1876** (Figs 12A, B). Along with *Hadramphus*, *Lyperobius* is another genus of large-bodied and flightless weevils endemic to New Zealand. The majority of its 16 species have highly restricted distributions due to human-induced habitat changes, including predation by introduced rodents (Craw 1999).

***Morimotodes* g. n.** (Figs 1–9). The genus includes two small-bodied litter species from Southwestern China and Taiwan, respectively, and is a sister to the West Palaearctic *Leiosoma*. See the taxonomic comments above.

***Pinacopus* Marshall, 1932** (Figs 12C, D). This genus has 14 named species found in Malaysia (8 spp.), Thailand (1 sp.), Laos (4 spp.) and northern India (1 sp.), with at least some specimens “collected from shrubs, which are more or less covered with lichens, by beating method” (Kojima 2010).

***Pterotomus* Quedenfeldt, 1888 (**Figs 12E, F, 16C). The genus includes a single species, *P. moebiusi* Quedenfeldt, 1888, known from the holotype collected in Angola’s province Malange and never reported since. The original description included a high quality habitus drawing (Quedenfeldt 1888).

Subtribe Plinthina

The subtribe Plinthina consists of 17 genera listed below. Eleven of them are restricted to the Mediterranean region and some, like *Minyops*, are also found in Central Europe, Ukraine, southern Russia and western Kazakhstan. Two genera, *Kurilio* and *Metahylobius*, with a total of three species are limited to the eastern Pacific (Honshu, Hokkaido and Kunashir). Four other inadequately known mono- and oligotypic genera are restricted to the Afrotropical Region, namely Seychelles (*Gonotrachelus*), East Africa (*Molytophilus* and *Pliuthinella*) and Madagascar (*Vouauxia*).

***Adexius* Schoenherr, 1834** (Figs 13A, B). This genus consists of three West Palaearctic species, two of them poorly known and narrowly distributed. The third one, *A. scrobipennis* Gyllenhal, 1834 is found in forest leaf litter in most of Central and Southern Europe between Belgium and Ukraine (Alonso-Zarazaga 2013).

***Alloplinthus* Solari, 1941** (Figs 13C, D). This genus consists of three species (originally described as *Plinthus*) from Tenerife and Gran Canaria (Alonso-Zarazaga 2013).

***Caulomorphus* Faust, 1886** (Figs 13E, F). The genus contains 11 eyeless species from Turkey, Greece, Iran and Azerbaijan (Alonso-Zarazaga 2013). Osella (1970) revised the genus taxonomically and later described three more species.

***Freyianus* Zumpt, 1932** (Figs 13G, H). This is a monobasic genus for *F. liparoides* Zumpt, 1932. It was described based on 10 syntypes (one of them adequately illustrated by a habitus photo) collected by “Kulzer” in “Ak-Schehir” (Zumpt 1932) and thought to be in Turkey (Alonso-Zarazaga & Lyal 1999). Since its description, this genus has not been reported in the original literature and its identity is inadequately known. The newly imaged specimen (Figs 13G, H), even if labelled as a “holotype”, is in fact a syntype and, together with two other syntypes, is stored in NHMB.

***Gonotrachelus* Champion, 1914** (Figs 13I, J, 16D). The genus includes a single species, *G. quinquecarinatus* Champion, 1914 described from two syntypes found on the Seychelles (Long Island, near Mahé). An additional specimen of this species was reported from Madagascar (Hustache 1925). The genus is characterized by the funicle consisting of fine antennomeres (Champion 1914, figs 11, 11b) and was originally compared with *Styphloderes* Wollaston (Typoderini). The type series (presently in BMNH) was taken from seashores and was thought to be introduced via driftwood (Champion 1914).

***Hoplopteridius* K. Daniel, 1908** (Figs 14A, B). This genus consists of five species and three non-nominative subspecies distributed in the northern and eastern Mediterranean (Alonso-Zarazaga 2013).

***Iberoplinthus* Meregalli, 1986** (Figs 14C, D). This recently erected genus (Meregalli 1986) consists of six species (Alonso-Zarazaga 2013) all found in northern Spain, while

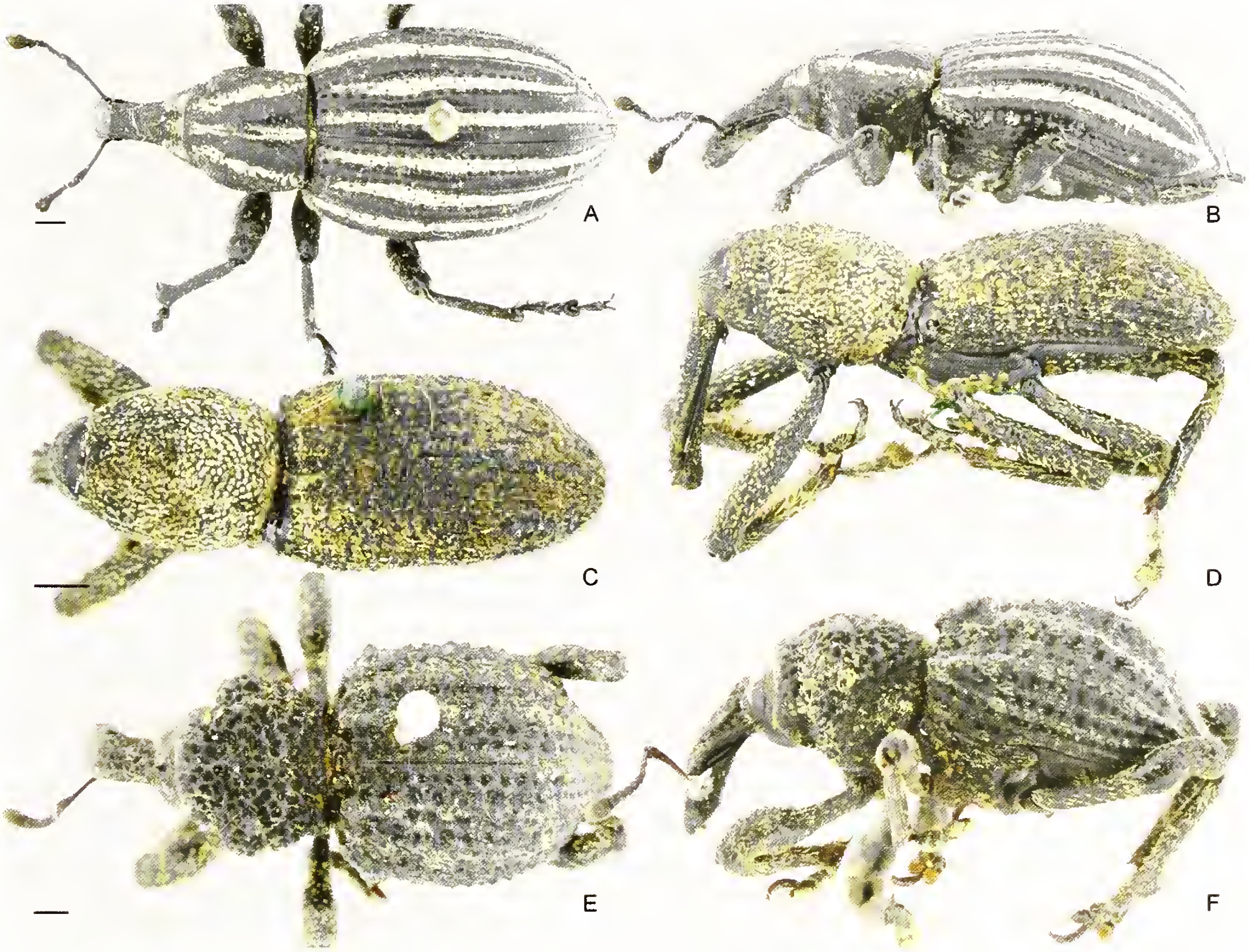

Fig. 12. Representatives of the Molytini: Molytina genera. A–B: *Lyperobius huttoni* Pascoe, 1876, New Zealand, Humboldt Mts., 30.xii.1944, C.E.Clarke, type species of *Lyperobius*, BMNH, image: Vasily Grebennikov, © The Natural History Museum, London; C–D: *Pinacopus dentirostris* Marshal, 1932, Malaysia, Perak, no date, no collector, MTD; E–F: *Pterotomus moebiusi* Quedenfeldt, Angola, holotype, see text, type species of *Pterotomus*, MNHN.

the type species, *I. imbricatus* (Dufur, 1851), and is reported also from Andorra and southern France.

***Kurilio* Zherikhin & Egorov, 1991** (Figs 14E, F). Its only species, *K. monachus* Zherikhin & Egorov, 1991, is restricted to Hokkaido and Kunashir Islands (Zherikhin & Egorov 1990).

***Metahylobius* Nakane, 1964** (Figs 14G, H). This genus consists of two species, both restricted to the alpine zone of Honshu: *M. jonensis* Nakane, 1964 and *M. rubiginosus* Morimoto, 1982. The adults of the former species "were captured by turning stones on the ground" (Morimoto 1982).

***Minyops* Schoenherr, 1823** (Figs 14I, J). This genus consists of 29 species and two non-nominative subspecies distributed through most of southern Europe and also Turkey (Alonso-Zarazaga 2013). The genus was recently taxonomically revised with 22 of its 31 species-group taxa described as new and eight others re-validated from synonymy (Osella & Bellò 2010).

***Mitoplinthus* Reitter, 1897** (Figs 15A, B). This genus consists of two species and one non-nominative subspecies of somewhat cylindrical medium-sized weevils distributed in southern parts of Europe between Spain and Ukraine. Meregalli (1986) provided the most recent treatment of the genus.

***Molytophilus* Hartmann, 1904** (Figs 15C, D). The genus consists of three species, the type species *Molytophilus carinatus* Hartmann, 1904, described from Tanzania, and two more from Ethiopia: *M. affinis* Hustache, 1936, and *M. puncticollis* Hustache, 1936, whose affinities with the genus have not yet been demonstrated.

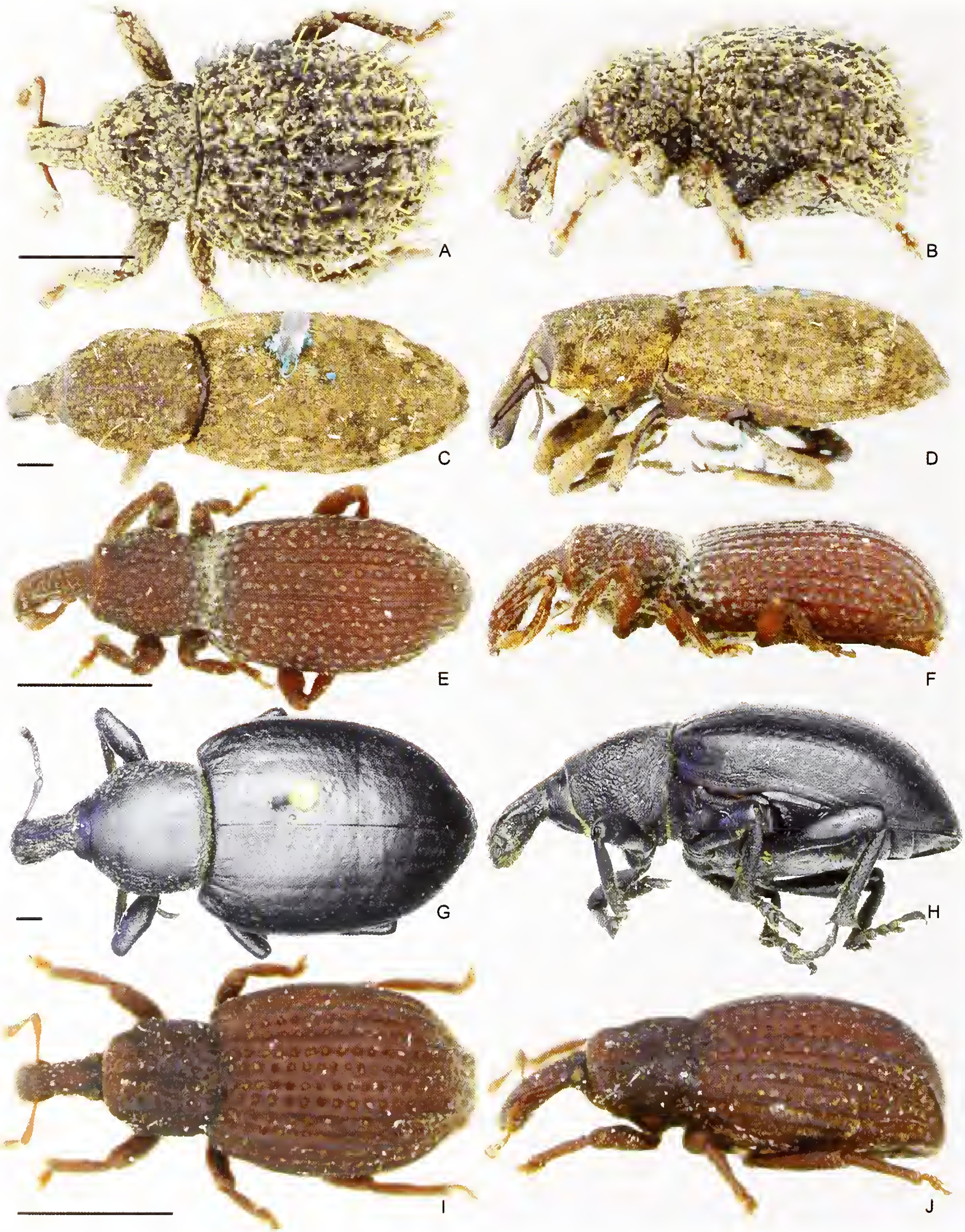

Fig. 13. Representatives of the Molytini: Plinthinae genera. A–B: *Adexius scrobipennis* Gyllenhal, Poland, Holubla ad Przemyśl, 4.vi.1997, M.Wanat, type species of *Adexius*, CNC; C–D: *Alloplinthus musicus* (Wollaston, 1860), Spain, Teneriffe, 17.v.1924, E.Appenhagen, type species of *Alloplinthus*, BMHN, image: Vasily Grebennikov, © The Natural History Museum, London; E–F: *Caulomorphus lederi* (Chevrolat, 1880), Georgia, "Meskisch. Gb.", no date, H.Leder, ?syntype, type species of *Caulomorphus*, MTD; G–H: *Freyianus liparoides* Zumpt, Turkey, "Ak-Sehehir", 22.v.1926, Kulzer, syntype, type species of *Freyianus*, NHMB; I–J: *Gonotrachelus quinquecarinatus* Champion, Seychelles, see text, syntype, type species of *Gonotrachelus*, BMNH, image: Vasily Grebennikov, © The Natural History Museum, London.

Fig. 14. Representatives of the Molytini: Plinthinae genera. A–B: *Hoplopteridius lutosus* (Frivaldszky, 1835) Italy, Rom, no date, no collector, type species of *Hoplopteridius*, MTD; C–D: *Iberoplinthus curvirostris* Meregalli, 1986 Spain, Asturias, 14.vii.1986, M.Meregalli, paratype, BMNH, image: Vasily Grebennikov, © The Natural History Museum, London; E–F: *Kurilio monachus* Zherikhin & Egorov, Russia, Kunashir Isl., 16.ix.1975, no collector, type species of *Kurilio*, CNC; G–H: *Metahylobius jonensis* Nakane, Japan, Honshu Isl., 1.vii.1986, S.J.Martin, type species of *Metahylobius*, BMNH, image: Vasily Grebennikov, © The Natural History Museum, London; I–J: *Minyops carinatus* (Linnaeus, 1767), Austria, Wien, no date, no collector, type species of *Minyops*, MTD.

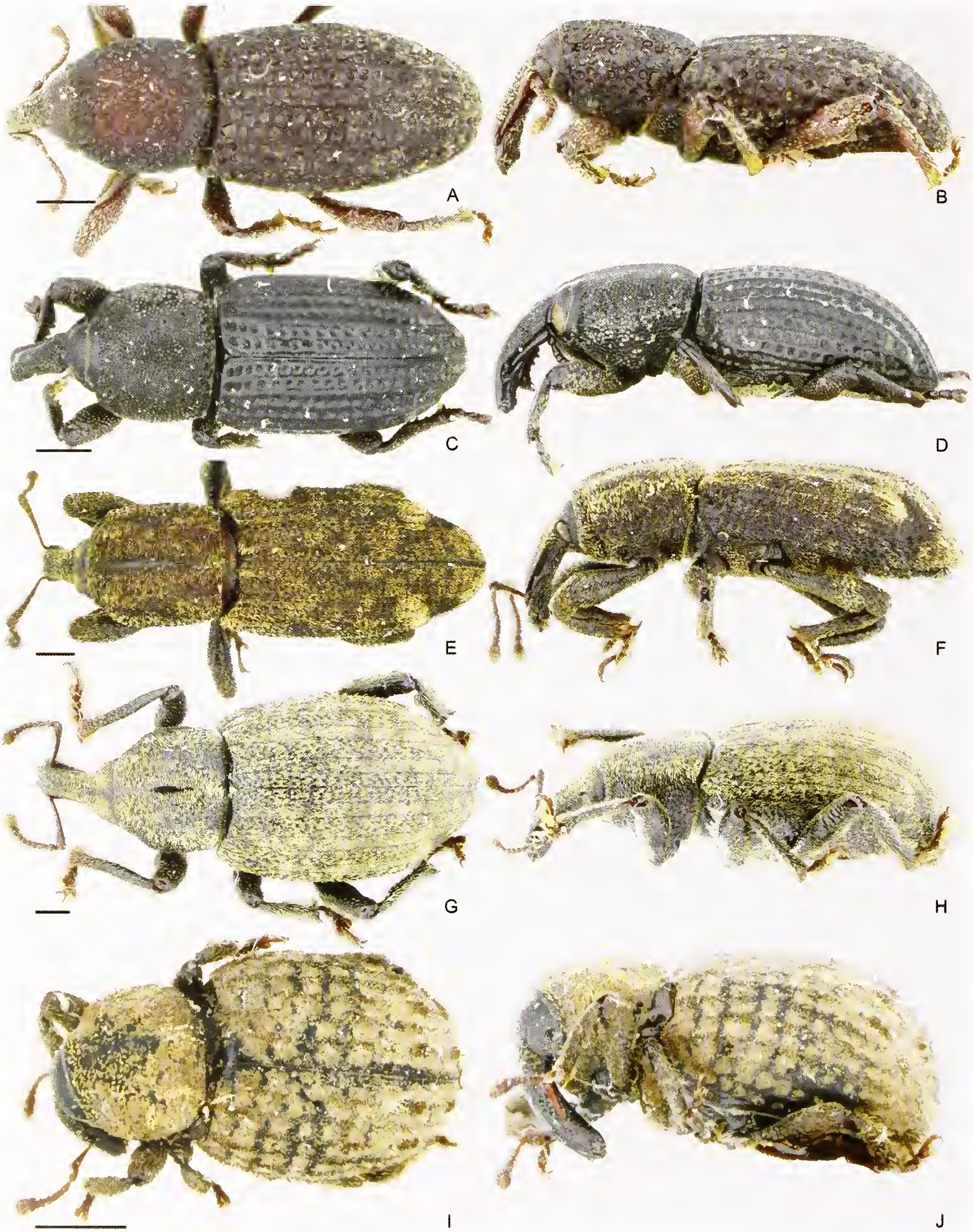

Fig. 15. Representatives of the Molytini: Plinthinae genera. A–B: *Mitoplinthus caliginosus* (Fabricius, 1775), Germany, Arnstadt, 16.x.1949, W.Liebmann, MTD; C–D: *Molytophilus carinatus* Hartmann, Tanzania, Usambara, no date, no collector, syntype, type species of *Molytophilus*, MTD; E–F: *Neoplinthus tigratus porculus* (Fabricius, 1801), Austria, Graz, no date, no collector, MTD; G–H: *Plinthus confusus* Meregalli, 1985, Russia, Caucasus, 21.vi.1974, J.Vořišek, paratype, CNC; I–J: *Vouauxia onopatroidea* Hustache, Madagascar, see text, syntype, type species of *Vouauxia*, MNHN.

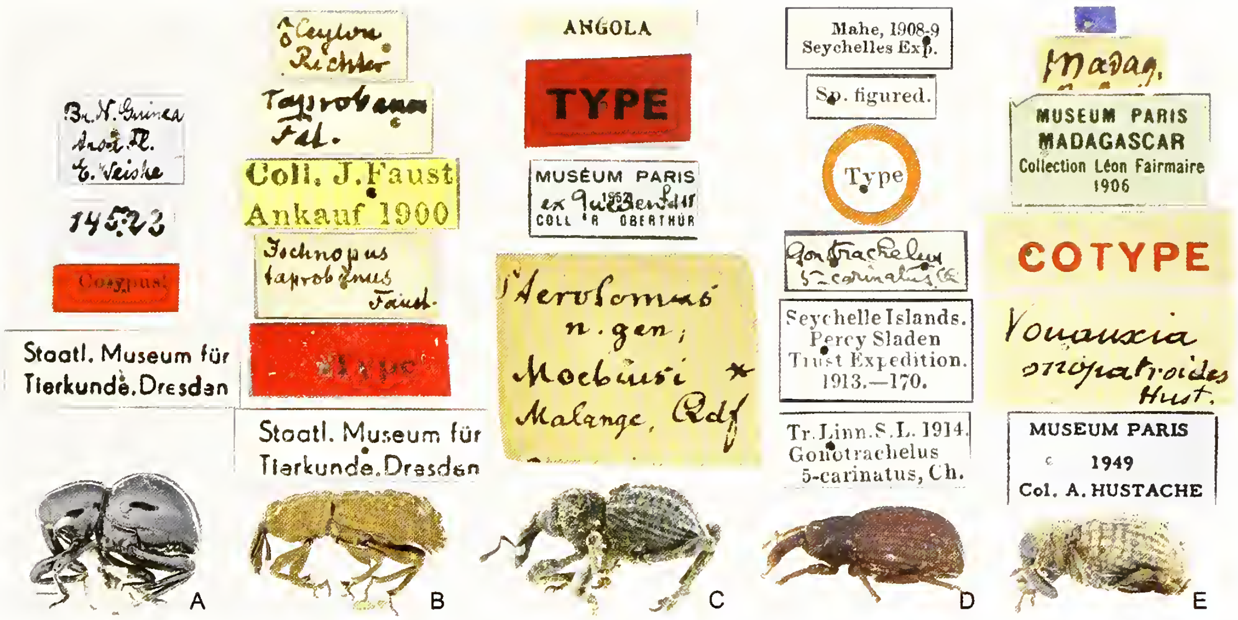

Fig. 16. Type specimen labels. A: *Carbonomassula glaberrima* Heller, ST; B: *Clarkanthus taprobanus* (Faust), holotype; C: *Pterotomus moebiusi* Quedenfeldt, holotype; D: *Gonotrachelus quinquecarinatus* Champion, syntype, image: Vasily Grebennikov, © The Natural History Museum, London; E: *Vonauxia onopatroidea* Hustache, syntype. Labels within each species are of proportional size; habitus images are not to scale.

Neoplinthus **Bedel, 1884** (Figs 15E, F). This genus includes five species and two non-nominative subspecies of elongated and parallel-sided weevils distributed in Central, Eastern and Southern Europe; all of them recorded from Italy (Alonso-Zarazaga 2013).

Paraminyops **Osella & Bellò, 2010** (not illustrated). This genus was recently separated from *Minyops* by Osella & Bellò (2010) to accommodate nine species and two non-nominative subspecies from northern and eastern Mediterranean.

Plinthinella **Hofmann, 1965** (not illustrated). This genus includes its sole member, the type species by original designation *P. tenella* Hoffmann, 1965. This is a small beetle of some 2.0–2.2 mm in body length and funicle with seven antennomeres described from the holotype and 12 paratypes collected in 1962 by Herbert Frantz. The type locality in "Tanganyika: Kilimandjaro" (= Mt. Kilimanjaro in Tanzania) and the altitude is unknown. When described, this taxon was compared with *Marvaldiella glacialis* (Hustache, 1929) (cited as "*Minus glacialis*") from Mount Kenya in Kenya (depicted in Hustache 1929: fig. 15). Since its description, *Plinthinella tenella* has not been reported in the original literature and its identity is inadequately known. The curatorial search to locate the type series in NMW failed, while my extensive recent sampling in the type locality did not rediscover the species. Both the generic and species names should, therefore, be considered as *nomina dubia*.

Plinthus **Germar, 1817** (Figs 15G, H). This genus includes 68 species and 17 non-nominative subspecies of medium- to large-bodied weevils widely distributed in the West Palaearctic. The majority of species are found in mountains between the Pyrenees and Alborz in northern Iran (Alonso-Zarazaga 2013). The Caucasus appears to have disproportionally large number of species normally restricted to alpine mountaintops. This is one of a few genera receiving significant attention in recent years, including detailed (although mainly unpublished) studies on internal classification, structure of male genitalia, species distribution and biology (Davidian 2008).

Vonauxia **Hustache, 1920** (Figs 15I, J, 16E). The genus includes a single species, *O. onopatroidea* Hustache, 1920, described from Madagascar from unknown number of syntypes. The original brief description (Hustache 1920) was followed by a more detailed one (Hustache 1925), both relating this taxon to *Gonotrachelus* Champion. At least three syntype are present in MNHN. No other specimens of this genus have been reported in the literature.

CONCLUDING REMARKS

This review revealed, how little is actually known about wingless Molytinae genera, especially those, which are presently assigned to the subtribes Molytina and Plinthina. The discovery of a peculiar new genus from China strongly suggests that similar findings still remain to be made, especially using specialized collecting techniques and addressing specific habitats harbouring cryptic and small-sized organisms. Equally remarkable is the acute scarcity of data on the majority of other genera herein discussed. In many cases species and even genera were mentioned only once when formally described. Many mono- and oligobasic genera such as *Apterylobius*, *Carbonomassula*, *Clarkanthus*, *Kyliparus*, *Pterotomus*, *Freyianus*, *Gonotrachelus*, *Molytophilus*, *Plinthinella* and *Vouauxia* are particularly poorly known and at least some of them appear only distantly related to the type genera of their respective subtribes. A detailed morphological and, particularly, DNA analysis of Molytinae is indeed long overdue. Much remains to be done with wingless Molytinae weevils and hopefully this paper helps to reinforce this seemingly self-evident conclusion.

Acknowledgement. Aleš Smetana collected all specimens of *Morimotodes polynices* g. & sp. n. in Taiwan. Curators of the collections mentioned above variously helped in accessing specimens under their care. Genrikh Ed. Davidian (St. Petersburg, Russia) identified the sequenced specimens of *Plinthus*. Marek Wanat (Wrocław, Poland) sent imaged specimens of *Adexius, Liparus* and *Leiosoma*. Eva Sprecher contacted on my behalf Isabelle Zürcher-Pfander (both Basel, Switzerland), who counted syntypes and took images of *Freyianus liparoides* (Figs 13G, H). Thierry Deuve (Paris, France) sent a reprint of Hustache (1920). Bradley J. Sinclair and Eduard Jendek (both Ottawa, Canada) read an early draft of this work.

REFERENCES

Alonso-Zarazaga MA (2013) Molytinae. Pp. 475–497 in: Löbl I & Smetana A (eds.) Catalogue of Palaearctic Coleoptera, Volume 8, Curculionoidea II. Brill, Leiden

Alonso-Zarazaga MA, Lyal CHC (1999) A world catalogue of families and genera of Curculionoidea (Insecta: Coleoptera) (excepting Scolytidae and Platypodidae). Entomopraxis, Barcelona

Alonso-Zarazaga MA, Lyal CHC (2002) Addenda and corrigenda to “A World Catalogue of Families and Genera of Curculionoidea (Insecta: Coleoptera)”. Zootaxa 63: 1–37

Bajtenov MS (1974) Zhuki-dolgonosiki (Coleoptera: Attelabidae, Cucrulionidae) Srednej Azii i Kazakhstana Illjustrirovannyj Opredelitel' Rodov i Katalog Vidov. Izdatel'stvo Nauka Kazakhskoy SSR, Alma-Ata

Bouchard P, Bousquet Y, Davies AE, Alonso-Zarazaga MA, Lawrence JF, Lyal CHC, Newton AF, Reid CAM, Schmitt M, Ślipiński SA, Smith ABT (2011) Family-group names in Coleoptera (Insecta). ZooKeys 88: 1–972

Champion GC (1914) Reports on the Percy Sladen Trust expedition to the Indian Ocean in 1905, under the leadership of Mr. J. Stanley Gardiner, M.A. No. XIX. Coleoptera, Curoulionidae. Transactions of the Linnean Society London 16: 393–497

Cohen KM, Finney S, Gibbard PL (2013) International Chronostratigraphic Chart, International Commission on Stratigraphy. Online at http://www.stratigraphy.org/ICSchart/ChronostratChart2013-01.pdf last accessed March 12 2014

Craw RC (1999) Molytini (Insecta: Coleoptera: Curculionidae: Molytinae). Fauna of New Zealand, 39. Manaaki Whenua Press, Lincoln

Davidian GE (2008) Weevils of the genus Plinthus Germ. (Coleoptera, Curculionidae) from the Caucasus. Autoreferat of unpublished PhD Thesis, 19 pp. [in Russian]

Drummond AJ, Suchard MA, Xie D, Rambaut A (2012) Bayesian phylogenetics with BEAUti and the BEAST 1.7. Molecular Biology and Evolution 29: 1969–1973

Faust J (1895) Rüsselkäfer der alten und neuen Welt. Stettiner Entomologische Zeitung 55: 140–160

Favre A, Päckert M, Pauls SU, Jähnig SC, Uhl D, Michalak I, Muellner-Riehl AN (2014) The role of the uplift of the Qinghai-Tibetan Plateau for the evolution of Tibetan biotas. Biological Reviews doi: 10.1111/brv.12107

Fitter AH, Peat HJ (2014) Ecological Flora of the British Isles. Online at http://www.ecoflora.co.uk last accessed 2 July 2, 2014

Fountain ED, Wiseman BH, Cruickshank RH, Paterson AM (2013) The ecology and conservation of Hadramphus tuberculatus (Pascoe 1877) (Coleoptera: Curculionidae: Molytinae). Journal of Insect Conservation 17: 737–745

Grebennikov VV (2014) DNA barcode and phylogeography of six new high altitude wingless Niphadomimus (Coleoptera: Curculionidae: Molytinae) from Southwest China. Zootaxa 3838: 151–173

Grebennikov VV, Heiss E (2014) DNA barcoding of flat bugs (Insecta: Hemiptera: Aradidae) with phylogenetic implications. Arthropod Systematics & Phylogeny 72: 213–219

Grebennikov VV, Pham H.T. (2014) First record of Otibazo (Coleoptera: Curculionidae: Molytinae) outside of Japan, with description of a new species from Vietnam. Zootaxa 3869: 597–600.

Hebert PDN, Cywinska A, Ball SL, deWaard, JR (2003) Biological identifications through DNA barcodes. Proceedings of the Royal Society B, 270: 313–321

Heller KM (1908) Viertel Beitrag zur Papuanischen Käferfauna. Abhandlungen und Berichte des Königl. Zoologischen und Anthropologisch-Etnographischen Museums zu Dresden 12: 1–33+pl

Hoffmann A (1965) Curculionides nouveaux du Tanganyika [Col.]. Annales de la Société entomologique de France, Nouvelle série 1: 393–409

Hustache A (1920) Diagnoses abrégées de Curculionides de Madagascar. L'Échange 36(398): 1–4

Hustache A (1925) Synopsis des Cuculionides de Madagascar. Bullétin de l'Académie Malagache, Nouvelle Série 7 (1924): 1–582

Hustache A (1929) Insectes Coléopteres XIX Curculionidae. Pp. 366–560, plates X, XI in: Voyage de Ch. Alluaud et R. Jeannel en Afrque Orientale (1911–1912). Résultats scientifique. Librarie P. Lechevallier, Paris

Kojima H (2010) Weevils of the genus Pinacopus (Coleoptera, Curculionidae) from Laos. Elytra 38: 151–160

Kuschel G (1987) The subfamily Molytinae (Coleoptera: Curculionidae): general notes and descriptions of new taxa from New Zealand and Chile. New Zealand Entomologist 9: 11–29

Kuschel G, Worthy TH (1996) Past distribution of large weevils (Coleoptera: Curculionidae) in the South Island, New Zealand, based on Holocene fossil remains. New Zealand Entomologist 19: 15–22

Lyal CH (2014) 3.7.7 Molytinae Schoenherr, 1823. Pp. 529–570 in: Leschen RAB & Beutel RG (eds.) Handbook of Zoology, Arthropoda: Insecta: Coleoptera. Volume 3: Morphology and Systematics (Phytophaga). Walter de Gruyter, Berlin

Maddison DR (2012) Phylogeny of Bembidion and related ground beetles (Coleoptera: Carabidae: Trechinae: Bembidiini: Bembidiina). Molecular Phylogenetics and Evolution 63: 533–576

Marshall GAK (1942). New Malaysian Hylobiinae (Col., Curcul.). Annals & Magazine of Natural History, Series 11 9: 370–390

McKenna DD, Sequeira AS, Marvaldi AE, Farrell BD (2009) Temporal lags and overlap in the diversification of weevils and flowering plants. Proceedings of the National Academy of Sciences USA 106: 7083–7088

Meregalli M (1985) Revisione del genere Plinthus Germar (Coleoptere: Curculionidae). Memorie del Museo Civico di Storia Naturale di Verona, IIA Serie, Sezione Scienze della Vita, Supplement 5, 1–133

Meregalli M (1986) Iberoplinthus, n. gen. di Plinthini e note sul genere Mitoplinthus Reitter, 1897 (Coleoptera: Curculionidae: Hylobiinae) (5 contributo alla conoscenza dei Curculionidi della Penisola Iberica). Bollettino del Museo Regionale di Scienze Naturali (Torino) 4: 489–522

Meregalli M (2003) Stenanchonus Voss 1937, a junior synonym of Euthycus Pascoe 1885 (Insecta, Coleoptera, Curculionidae, Molytinae). Senckenbergiana Biologica 82: 1–7

Morimoto K (1982). The family Curculionidae of Japan. I. Subfamily Hylobiinae. Essakia 19: 51–121

Mosquin T, Whiting PG, McAllister DE (1995) Canada's biodiversity: the variety of life, its status, economic benefits, conservation costs and unmet needs. Canadian Museum of nature, Ottawa

Osella G (1970) Revisione del genere Caulomorphus Faust e descrizione di cinque nuove specie delle regioni montuose della Turchia lungo il Mar Nero (Coleoptera, Curculionidae). Memorie del Museo Civico di Storia Naturale di Verona 17(1969): 359–395

Osella G, Bellò C (2010) Revisione di Minyops Schoenherr e Paraminyops nov. gen. (Coleoptera, Curculionidae, Molytinae). Memorie del Museo Civico di Storia Naturale di Verona, 2.serie, Sezione Scienze della Vita 19: 3–133

Pajni HR, Sood S (1982) First record of genera Niphadonyx Dalla Torre and Ischnopus Fst. and description of two new species from India (Coleoptera: Curculionidae: Hylobiinae). Journal of the Bombay Natural History Society 79: 363–369

Papadopoulou A, Anastasiou I, Vogler AP (2010) Revisiting the insect mitochondrial molecular clock: the mid-Aegean trench calibration. Molecular Biology and Evolution 27: 1659–1672

Peck SB (1990) Eyeless Arthropods of the Galapagos Island, Ecuador: composition and origin of the cryptozoic fauna of a young, tropical oceanic archipelago. Biotropica 22: 366–381

Quedenfeldt G (1888) Verzeichniss der von Herrn Major a.D. von Mechow in Angola und am Quango-Strom 1878–1881 gesammelten Curculioniden und Brenthiden. Berliner Entomologische Zeitschrift 32: 271–308+pl

Rambaut A (2013) FigTree, version 1.4. Online at http://tree.bio.ed.ac.uk/software/figtree/ last accessed March 12, 2014

Raxworthy CJ, Forstner MRJ, Nussbaum RA (2002) Chameleon radiation by oceanic dispersal. Nature 415: 784–787

Setliff, G.P. (2007) Annotated checklist of weevils from the Papuan region (Coleoptera, Curculionoidea). Zootaxa 1536: 1–296

Shorthouse DP (2010) SimpleMappr, an online tool to produce publication-quality point maps. Online at http://www.simplemappr.net last accessed May 12, 2014

Tamura K, Peterson D, Peterson N, Stecher G, Nei M, Kumar S (2011) MEGA5: molecular evolutionary genetics analysis using Maximum Likelihood, Evolutionary Distance, and Maximum Parsimony Methods. Molecular Biology and Evolution 28: 2731–2739

Wanat M (2007) Alignment and homology of male terminalia in Curculionoidea and other Coleoptera. Invertebrate Systematics 21: 147–171

Wang L, Liao W, Chen C, Fan Q (2013) The seed plant flora of the Mount Jinggangshan Region, Southeastern China. PLoS ONE 8(9): e75834

Zherikhin VV, Egorov AB (1990) Zhuki-dolgonosiki (Coleoptera, Curculionoidea) dal'nego vostoka SSSR (obzor podsemejstv s opisaniem novykh taksonov). Akademija Nauk SSSR, Dal'nevostochnoe Otdelenie, Biologo-Pochvennyj Institut, Vladivostok.

Zumpt F (1932) Curculioniden - Studien IV. (Col.) Drei neue Käferarten aus Kleinasien. Mitteilungen der Deutschen Entomologischen Gesellschaft 3: 87–94

Zeitschrift/Journal: Bonn zoological Bulletin - früher Bonner Zoologische Beiträge.

Jahr/Year: 2014

Band/Volume: 63

Autor(en)/Author(s): Grebennikov Vasily V.

Artikel/Article: Morimotodes, a new genus for two minute wingless litter species from southwest China and Taiwan with an illustrated overview of Molytina and Plinthina genera (Coleoptera: Curculionidae: Molytini) 123-147