Fragmenta entomologica, 52 (2): 197–211 (2020)

eISSN: 2284-4880 (online version)
pISSN: 0429-288X (print version)

Research article
Submitted: September 11th, 2020 - *Accepted*: October 18th, 2020 - *Published*: November 15th, 2020

A new weevil genus from the highlands of China casts doubts on monophyly of Cotasteromimina (Coleoptera: Curculionidae, Molytinae)

Christoph GERMANN [1], Vasily V. GREBENNIKOV [2,*]

[1] *Naturhistorisches Museum Basel - Augustinergasse 2, 4051 Basel, Switzerland* - christoph.germann@bs.ch
[2] *Canadian Food Inspection Agency, Ottawa Plant Laboratory - 960 Carling Ave., Ottawa, ON, K1A 0C6, Canada*
vasily.grebennikov@canada.ca
* Corresponding author

Abstract
We describe *Zembrus perseus* gen. et sp. nov., a new weevil from Yunnan, China. A single flightless male was sifted from under *Rhododendron* bush in the alpine zone of the Cangshan Mountain Range. The specimen's appearance suggests affinities to the molytine subtribe Cotasteromimina, which currently comprises six named species in four genera distributed between Japan, the Andaman Islands, Borneo and the Philippines. To test the species' phylogenetic affinities, we analysed 73 morphological characters of adult specimens of 23 molytine and one rooting species. Besides *Z. perseus*, the ingroup includes four named species, each representing a named genus of Cotasteromimina, and two other, likely closely related unnamed species. Phylogenetic analysis using the parsimony criterion and four character-weighting and/or ordering strategies consistently failed to detect a clade of Cotasteromimina, either with or without *Z. perseus*. The most parsimonious trees are inconsistent, the bootstrap consensus trees are almost entirely unresolved, and previously published DNA data are phylogenetically indecisive. We conclude that either adult morphological characters constitute an inadequate data source to test monophyly of Cotasteromimina or that the subtribe is not monophyletic or both. We illustrate the relevant adult structures of *Z. perseus* and most of the in- and out-group taxa used in the analysis.

Key words: *Zembrus perseus*, Cotasteromimina, Molytinae, Curculionidae, Yunnan, phylogeny.

urn:lsid:zoobank.org:pub:946CB4CF-E59B-44B2-9909-E3B3C68381D4

Introduction

This contribution was triggered by a discovery made on 17 May 2010 in Yunnan, China. A single specimen of an unusual-looking weevil (Figs 1A-O) was sifted from under a *Rhododendron* bush (Fig. 2A) in the alpine zone of the Cang Shan mountain range (Fig. 2B). Remarkably, no other similar weevils were detected in 145 sifting samples taken in Shaanxi, Sichuan, Taiwan, Yunnan and Vietnam (Table S1 in Grebennikov 2018a). The specimen was given the number 861, photographed, three DNA fragments were sequenced from it, and the specimen was placed among other mysterious weevils from Southeast China, some of which were later described as new genera (Grebennikov 2014, 2018b, c). The specimen was included in two DNA-based analyses of Molytinae (a non-monophyletic subfamily, see Shin et al. 2017) without providing any clue about its sister-group (Grebennikov 2018b, c).

Habitus photographs of this specimen 861 were distributed among colleagues to solicit their opinions about its possible relationships. A hint was obtained from Miguel A. Alonso-Zarazaga, who suggested that the weevil might have affinities with the subtribe Cotasteromimina, currently classified in the tribe Pissodini. The Cotasteromimina is an obscure taxon of six nominal species classified in four genera and known from southern Japan, South Korea, Taiwan, the Andaman Islands, the Philippines and peninsular Malaysia but not from the Chinese mainland (Fig. 2B). The Yunnan weevil shares all three original diagnostic characters of Cotasteromimini (Morimoto 1962b), namely: (1.) abdominal process between hind coxae much broader than coxal width; (2.) rostrum robust, relatively short, <1.1 times longer than pronotum and (3.) eyes in lateral view closely approximated to anterior edge of pronotum, so that width of exposed temples less than eye diameter. The question, therefore, arose whether the Yunnan specimen is indeed a member of Cotasteromimina.

An assignment to Cotasteromimina was, however, precarious as monophyly and sister-group of this subtribe are uncertain. These weevils, moreover, are rarely sampled and thus poorly known. Except for one widely distributed species (see below), all Cotasteromimina are known only from the type series (Fig. 2A). The first species, *Cotasteromimus morimotoi*, was described by Chujô & Voss

(1960) from the vicinity of Fukuoka, Kyushu, Japan. Morimoto (1962a) described the second species and the second genus, *Pseudohylobius setosus*, also from the vicinity of Fukuoka. The illustration of the latter, the first ever published for Cotasteromimina, depicts a notably parallel-sided weevil with rectangular shoulders, robust rostrum, deeply retracted head, seven-segmented funicle (the second segment retracted into the first) and an externally concealed scutellum. Morimoto (1962b) subsequently grouped the monotypic genera *Cotasteromimus* and *Pseudohylobius* into a new tribe Cotasteromimini and placed this in the subfamily Pissodinae (together with the tribe Pissodini represented in Japan only by *Pissodes* Germar, 1817). Morimoto & Miyakawa (1985) later described a second species of the type genus, *Cotasteromimus squamiger*, from a large series collected on the northern Pacific islands between (and including) Kyushu and Taiwan. Downgrading Pissodinae to a tribe of Molytinae, Alonso-Zarazaga & Lyal (1999) treated Cotasteromimina as a subtribe of Pissodini, along with the subtribes Orthorhinina and Pissodina. Hong et al. (2000) reported and illustrated *C. squamiger* from South Korea (Jeju island), and Kojima & Kaga (2011) reported the same species from Tokunoshima Island. Kojima & Idris (2005) described and illustrated a new monotypic genus, *Cotasteromorphus*, for *C. chujoi*, a new species from the Cameroon Highlands in Malaysia, and noted its effaced elytral shoulders, lack of hind wings, spinose femora, indistinct premucrones and simple third tarsomeres. Germann (2013) described the fourth genus and fifth species of Cotasteromimina, *Seticotasteromimus jarawa*, based on a single female from the Andaman Islands characterised by elongate and erect bristles. Kojima & Morimoto (2014) displayed online photographs of Japanese Cotasteromimina, including *C. morimotoi* from Shikoku and Honshu, *C. squamiger* from Honshu and Kyushu and *P. setosus* from Honshu. In an overview of the subfamily Molytinae, Lyal (2014) hesitantly retained Cotasteromimina in Pissodini, but elevating the subtribe Orthorhinina to tribal level and transferred into it a few genera formerly placed in Pissodina (see Anderson et al. 2018 on 13 phylogenetically unresolved Orthorhinini genera distributed in the western parts of the Pacific Ocean between Tasmania and the Philippines). Sprick & Floren (2018: 15, Fig. 10C, D) illustrated an unnamed putative member of Cotasteromimina collected using insecticidal knock-down (fogging) from humid rainforest canopy in Borneo. Legalov (2018), in a key to the tribes of Molytinae elevated Cotasteromimina to a tribal rank and subsequently described *Cotasteromimus philippinensis* from the Philippines (Legalov 2020). Summing up, judging from limited information available at the onset of this project, the mysterious high-altitude Yunnan weevil number 861 was likely a member of the perhaps even more mysterious subtribe Cotasteromimina.

The main goal of our present study is to use predominantly morphological data for testing in the sense proposed by Popper (1959) the following verifiable predictions:

1. the subtribe Cotasteromimina (excluding the Yunnan specimen 861) is a clade;
2. the Yunnan specimen 861 is a member of a monophyletic Cotasteromimina;
3. the tribe Pissodini (including one or more representatives of Cotasteromimina) is a clade.

Material and Methods

Museum abbreviations (name of a contact person is in brackets):

CGC	C. Germann collection, Rubigen, Switzerland
IZCAS	Institute of Zoology, Chinese Academy of Science, Beijing, P.R. China (Kuiyan Zhang)
KUZC	Kyushu University Museum, Fukuoka, Japan (Munetoshi Maruyama)
NHMB	Naturhistorisches Museum Basel, Switzerland (Christoph Germann)
NHMUK	The Natural History Museum, London, UK (Max Barclay)

Specimen sampling and morphological terms

The Yunnan weevil 861 was collected by sifting leaf and twig litter from under a *Rhododendron* bush (Fig. 2A) through a hand-held sifter, followed by subsequent extraction in suspended Winkler funnels (Grebennikov 2018a: Fig. 1). Morphological terms follow Lyal (2020).

Analysis design

Specimens were obtained from various sources (Appendix 1). Lacking DNA-grade or larval specimens of nominal Cotasteromimina, we restricted the phylogenetic analysis implemented herein to morphological characters (Appendix 2) assessable from dead adults. Besides the Yunnan specimen 861, the ingroup (abbreviated InG before terminal name) included four (of a total of six) named Cotasteromimina species, each of them being the type species of all four genera ever included in the subtribe. The ingroup also included two unnamed and morphologically similar species. One was reported by Sprick & Floren (2018) and is herein considered as congeneric with *S. jarawa*, while another is similar to *Pseudohylobius setosus* and herein referred as "*near Pseudohylobius*" (its formal description will be provided elsewhere). The close outgroup (abbreviated cOtG before terminal name) included two genera of the taxonomically nearest subtribe Pissodina and four genera of the tribe Orthorhinini, which had been treated as a subtribe of Pissodini until Lyal (2014) and Pullen et al. (2014). The distant outgroup (abbreviated dOtG before terminal name) contained ten terminals representing ten genera of seven other Molytinae tribes.

The choice of an optimal terminal to root the tree was not obvious, because the subfamily Molytinae, the next

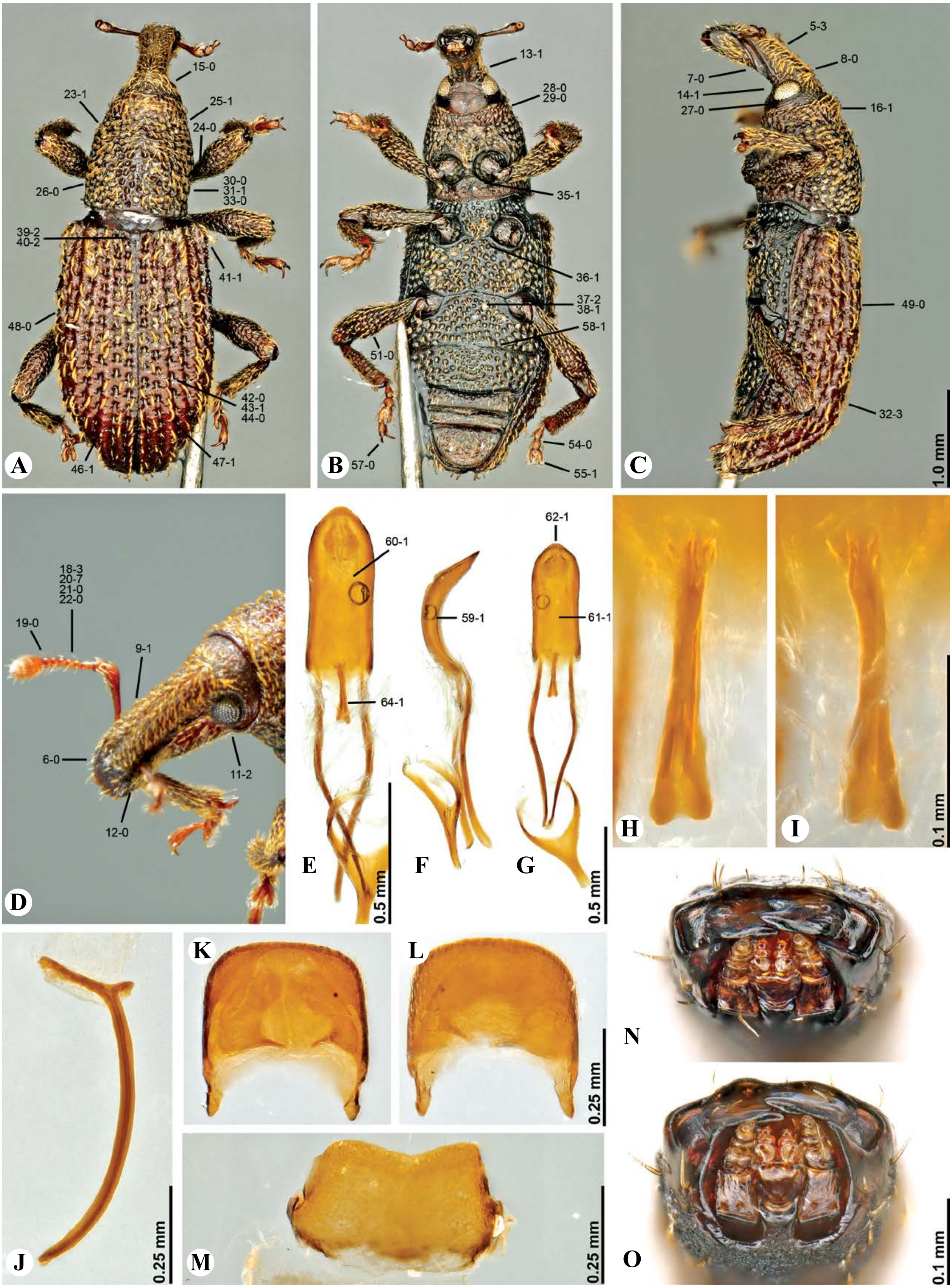

Fig. 1 – *Zembrus perseus* gen. & sp. nov., male, holotype. **A–C**, dorsal, ventral and lateral habitus; **D**, head, dorso-lateral; **E–G**, penis, dorsal, lateral and ventral view; **H–I**, copulatory sclerite, ventral and dorsal view; **J**, sternite IX; **K–L**, tergite VIII ventral (with two hemisternites VIII) and dorsal view; **M**, tergite VII, dorsal view; **N–O**, mouthparts, frontal and ventral view.

more inclusive taxon to accommodate Pissodini and Cotasteromimina, is non-monophyletic. As presently thought (Shin et al. 2017), the nearest well-supported most inclusive clade to accommodate all Molytinae genera is that consisting of Conoderinae, Cossoninae, Curculioninae, broadly defined Molytinae (e.g. including former Cryptorhynchinae) and Scolytinae (CCCMS clade). The latter is the sister group of the CEGH clade (Cyclominae, Entiminae, Gonipterini and Hyperinae; Gunter et al. 2016; Shin et al. 2017). In another broad analysis of weevil relationships (McKenna et al. 2009), non-monophyletic Molytinae were placed inside a more inclusive and well-supported clade (together with representatives of similarly non-monophyletic Curculioninae, Cossoninae and Baridinae); this well-supported clade being sister to Scolytinae. Scolytinae are not an optimal root choice for free-living Cotasteromimina weevils, because they have strongly modified and largely functionally selected wood-boring structures. We therefore chose a representative of *Gymnetron* Schoenherr, 1825 for rooting purpose, because McKenna et al. (2009) placed *Gymnetron* and *Haplonyx* Schoenherr, 1836 as sister-group to the rest of the CCCMS clade.

Whenever possible, we attempted to represent each analysed terminal by a male and a female of the type species of the genus. Dry specimens were first photographed to illustrate their habitus (Figs. 3, 4) and external morphological characters. Specimens were then softened in warm water and disarticulated to study and photograph the male and female genitalia (Figs 5, 6). Three terminals representing the genera *Devernodes* Grebennikov, 2018, *Sclerocardius* Schoenherr, 1847 and *Titilayo* Cristóvão & Lyal, 2018 were scored from publications (Grebennikov 2018c; Lyal 2018; Cristóvão & Lyal 2018, respectively). Character scoring was done in several steps following the methodological recommendations of Franz (2014). Firstly, we extracted from the literature all characters reported as diagnostic for the members of the ingroup (and those of the closer outgroup). This was followed by addition of newly recognised characters and repeated re-wording of nearly all characters and their states so as to make them logically independent from each other, and as discrete and unambiguous as possible. In order to document the characters and their states, we attempted to illustrate as many of them as possible (Figs S1–S22 in Supplementary Data), with numbered arrows pointing at relevant structures (Figs 1, 5, 6).

The matrix (Table 1) was compiled in Winclada (Nixon 2002) and consisted of 24 terminals and 73 characters (Appendix 2). Characters 4 and 34 were considered as insufficiently understood and, therefore, deactivated prior to the analysis (together with the three parsimoniously uninformative characters 52, 56, 63). Phylogenetic analysis was performed by spawning the matrix from Winclada to Hennig86 (Farris 1988). Preliminary analyses resulted in poorly resolved trees, suggesting that the phylogenetic signal of the matrix is weak. As an attempt to amplify this signal, four different analyses were implemented:

1. The first and most conservative analysis (A1) treated all characters as equally weighted and all multistate characters as non-additive (=unordered); it was implemented by using two Hennig86 commands: mh* and bb*.
2. The second analysis (A2) treated all characters as equally weighted (as in A1), but 23 multistate characters were treated as additive (see Table 1); the same two Hennig86 commands were used.
3. The third analysis (A3) treated the same 23 multistate characters as non-additive (similarly to A1), but reweighted all characters using successive approxima-

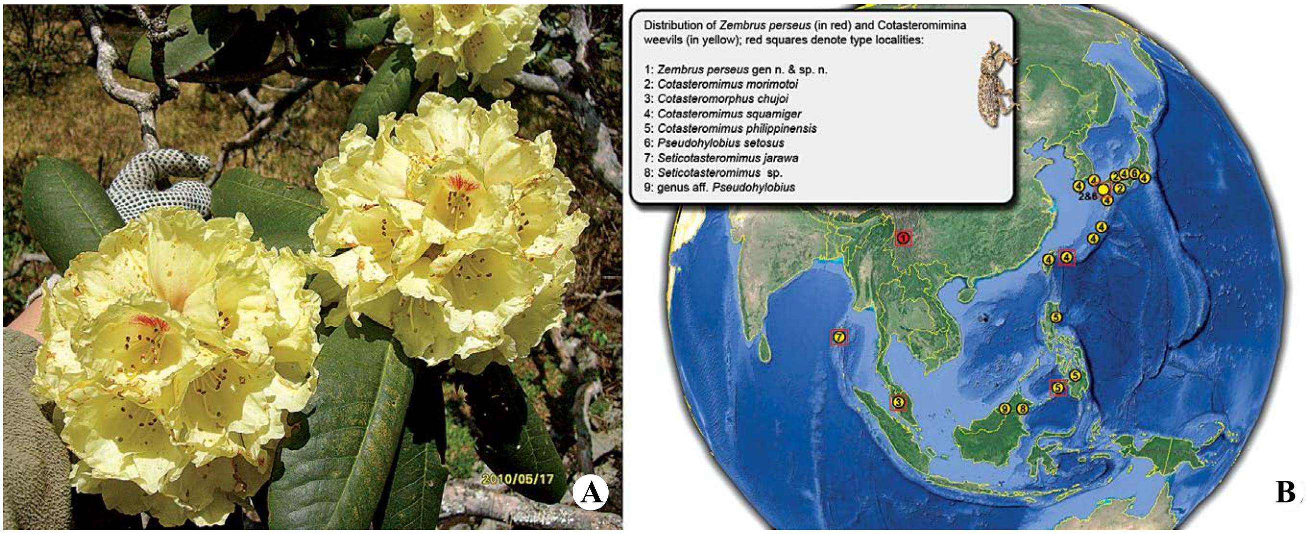

Fig. 2 – **A**, Habitat of *Zembrus perseus* gen. & sp. nov. in Yunnan, China, sampled at 3806 m from under *Rhododendron* bush; **B**, global distribution of weevils forming the ingroup of the phylogenetic analysis implemented herein (*Zembrus* gen. nov. and the subtribe Cotasteromimina).

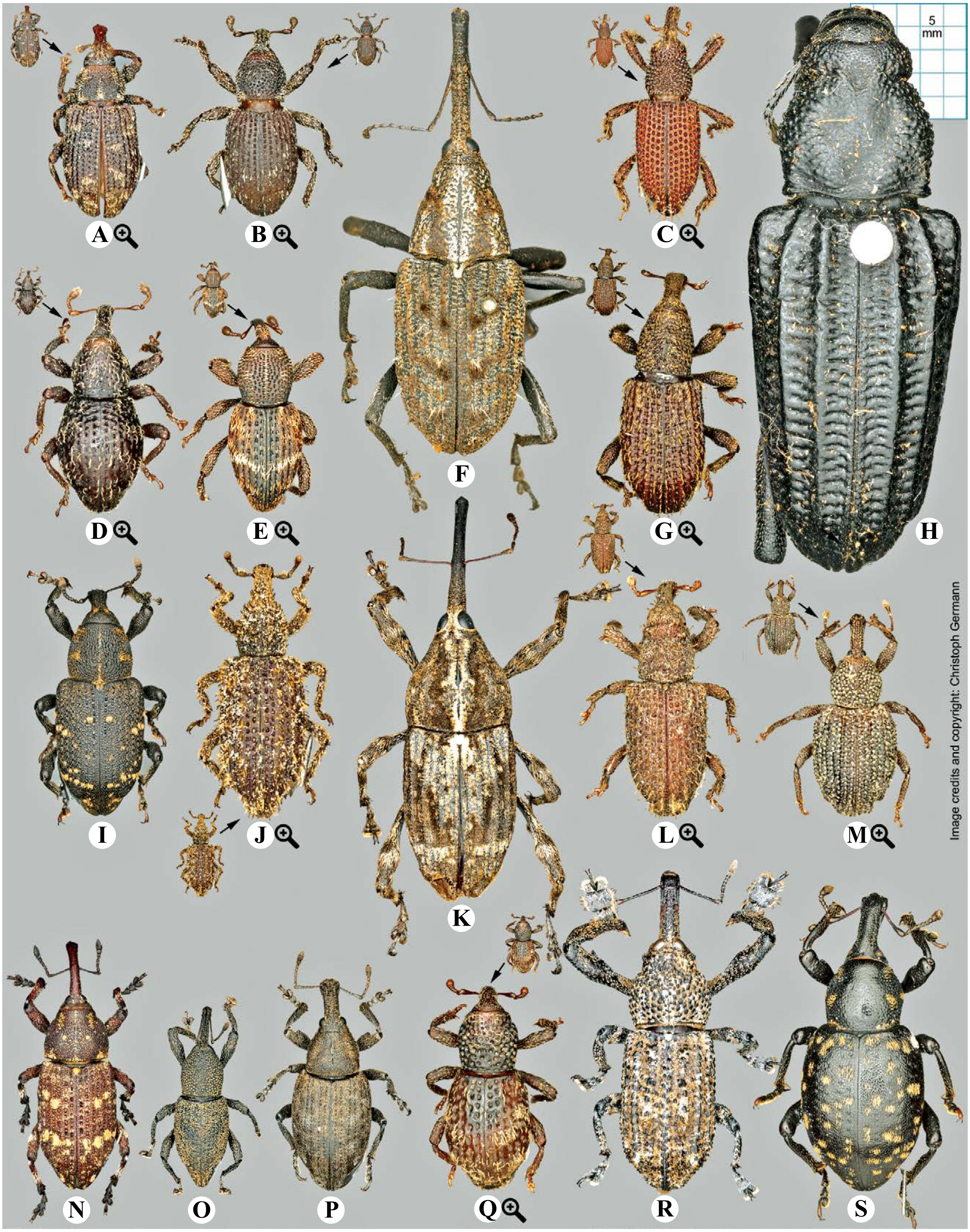

Image credits and copyright: Christoph Germann

Fig. 3 – Habitus of analysed Molytinae weevils, dorsal view. **A**, *Dorytomorpha tonsa*, **B**, *Cotasteromimus morimotoi*, **C**, *Seticotasteromimus* sp., **D**, *Cotasteromorphus chujoi*, **E**, *Himalanchonus* sp., **F**, *Eurhamphus fasciculatus*, **G**, *Zembrus perseus* gen. & sp. nov., **H**, *Vanapa oberthuri*, **I**, *Hylobius abietis*, **J**, *Pseudohylobius setosus*, **K**, *Ilacuris laticollis*, **L**, near *Pseudohylobius*, **M**, *Aparopion chevrolati*, **N**, *Pissodes pini*, **O**, *Pinacopus intermedius*, **P**, *Lepyrus capucinus*, **Q**, *Seleuca* sp., **R**, *Orthorhinus* sp., **S**, *Liparus germanus*. Magnification sign indicates enlarged images; in such cases specimen real size is indicated by a smaller image nearby. © Christoph Germann.

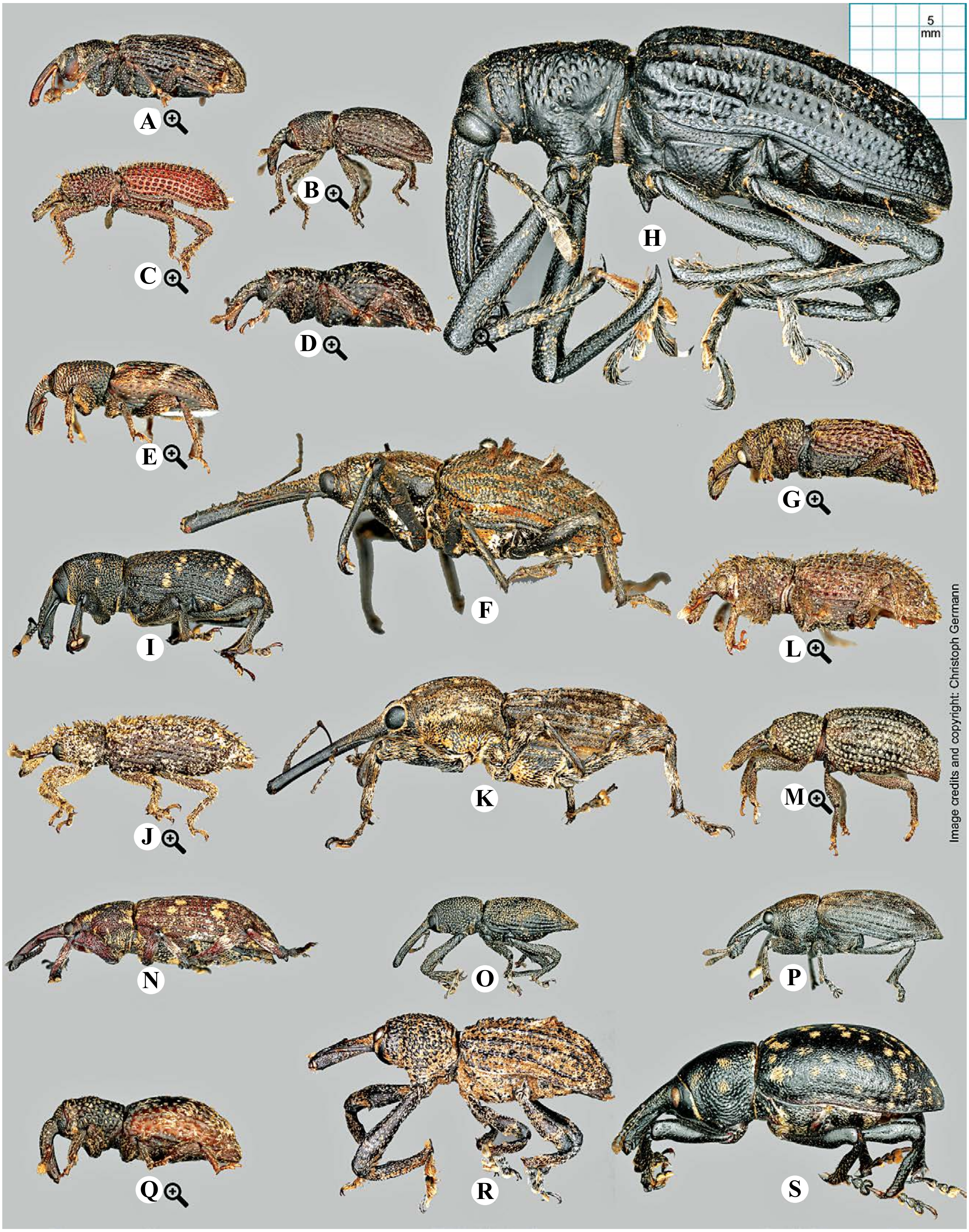

Image credits and copyright: Christoph Germann

Fig. 4 – Habitus of analysed Molytinae weevils, lateral view. **A**, *Dorytomorpha tonsa*, **B**, *Cotasteromimus morimotoi*, **C**, *Seticotasteromimus* sp., **D**, *Cotasteromorphus chujoi*, **E**, *Himalanchonus* sp., **F**, *Eurhamphus fasciculatus*, **G**, *Zembrus perseus* gen. & sp. nov., **H**, *Vanapa oberthuri*, **I**, *Hylobius abietis*, **J**, *Pseudohylobius setosus*, **K**, *Ilacuris laticollis*, **L**, near *Pseudohylobius*, **M**, *Aparopion chevrolati*, **N**, *Pissodes pini*, **O**, *Pinacopus intermedius*, **P**, *Lepyrus capucinus*, **Q**, *Seleuca* sp., **R**, *Orthorhinus* sp., **S**, *Liparus germanus*. Magnification sign indicates enlarged images; for their real size see plate with dorsal habitus. © Christoph Germann.

tion algorithm; it was implemented by cyclical use of three Hennig86 commands mh*, bb* and xs w until the tree statistics stabilized.

4. The fourth analysis (A4), the most liberal one, treated the same 23 multistate characters as additive (similarly to A2) and re-weighted all characters using the successive approximation algorithm; it was implemented by the cyclical use of three Hennig86 commands mh*, bb* and xs w until the tree statistics stabilized.

Examination of the obtained trees was done in Winclada. Bootstrap analyses (Felsenstein 1985) with 1000 replications were performed in Nona (Goloboff 1999).

Results

Phylogenetic analyses

Results of four phylogenetic analyses are summarized in Table 2 and partly illustrated in Fig. 7. The shortest topologies were most inconsistent not only among those obtained in different analyses, but also within analyses A1 and A2, when more than one most parsimonious tree has been detected. Bootstrapping four different datasets resulted in almost completely unresolved topologies having the total of either one (A1, A3, both unordered analyses) or three (A2, A4, both ordered analyses) clades, of them only one (two species of *Seticotasteromimus*) strongly supported (Table 2). Optimization of evolutionary events on branches results in preponderance of non-unique evolutionary events (either parallelisms, or reversals, Fig. 7).

Zembrus **gen. nov.**

Type species: *Zembrus perseus* sp. nov., designated here.

Diagnosis. Considering the complete lack of phylogenetic knowledge on this weevil (see Discussion), it is necessary to provide diagnostic characters sufficient to distinguish the new taxon from all of Curculionidae. The new genus displays all three characters originally indicated by Morimoto (1961b: 62) as diagnostic for Cotasteromimina (see Introduction). In this tribe, the new genus can be distinguished:

- from *Cotasteromimus* by the robust rostrum widened apicad, by the parallel-sided elongate elytra and by the flat elytral disc;
- from *Cotasteromorphus* by the same characters as distinguish *Cotasteromimus* and by the absence of femoral spines (commonly termed “femoral tooth”);
- from *Pseudohylobius* by curved and adjacent yellowish bristles on body (hence by absence of any erect bristles or scales) and by the second segment of funicles not retracted into the first one;
- from *Seticotasteromimus* by the horizontal frons, by the robust rostrum, by the absence of erect bristles or scales on body and by the narrowly separated procoxae.

Description. Body dark auburn, surface glabrous. Rostrum robust, weakly curved in lateral view, evenly widened anteriad in dorsal view, in cross-section quadrate. Scrobes oblique. Funicles 7-segmented; club 3-segmented, oval, well-defined. Head with eyes located laterally. Pronotum with almost parallel sides, shape weakly conical, constricted before anterior margin. Dorsally and laterally surface coarsely punctate. Prothorax ventrally without rostral channel. Postocular lobes absent. Scutellum pentagonal. Mesoventrite with limited, margined depression with dense cover of punctures and setae. Procoxae separated by 1/3 of their diameter, mesocoxae separated by their diameter, metacoxae separated by twice coxal diameter. Metaventrite as long as mesoventrite, metacoxal cavities not directly reaching margins of elytra. Ventrites 1 and 2 fused, with suture between them fully visible; ventrites 3, 4 and 5 free. Elytra with prominent shoulders, with 10 deeply and regularly punctate striae, interstriae vaulted. Inner side of apical part of elytra with flattened microsclupture and without stridulation ridges. Hind wings absent. Legs strong, femora unarmed, tibiae uncinate, at inner edges with premucro. Tarsi with third tarsomere bilobed, fifth tarsomere large, claws free and simple. Body and legs covered with conspicuous strong, curved, yellowish bristles of different sizes, pointed at tip. Penis oval in cross-section, ostium present, penis body well sclerotized, copulatory sclerite visible, tegmen ring-shaped with apodeme and without parameroid lobes.

Derivation of name. The generic name is a meaningless combination of letters; its gender is masculine.

Zembrus perseus **sp. nov.** (Figs 1A-O; S1-S4)

Type material. Holotype: male, **P. R. China**: Yunnan, E slope Cangshan at Dali, N25°40’24.1” E100°05’57.6”, 17.v.2010, 3806m, sifting 15, V. Grebennikov // CNC-COLVG 00000861 // HOLOTYPE *Zembrus perseus* sp. nov. Germann & Grebennikov, 2020 [printed label on red paper] (currently in NHMB, will be deposited in IZCAS).

Description. Body length 4.2 mm (rostrum excluded). Head globose, densely punctate. Eyes oval; their lower margin lower in lateral view than ventral surface of rostrum. Contour of head and rostrum not interrupted in dorsal or lateral views. Rostrum 3.5 times longer than its width at middle. Antennae inserted in apical rostral third; insertion grooves lateral and not visible from above, in line with scrobes. Rostrum strongly punctured and striate dorsally; almost entirely covered with strong yellowish curved bristles, only absent around apex (there with several straight raised setae) and along scrobes. Scapes half as long as length of rostrum, clubbed; funicles with first segment thickest and longest, second segment shorter and narrower, following five segments globular; clubs twice as wide as apical funicular segment, oval, densely clothed

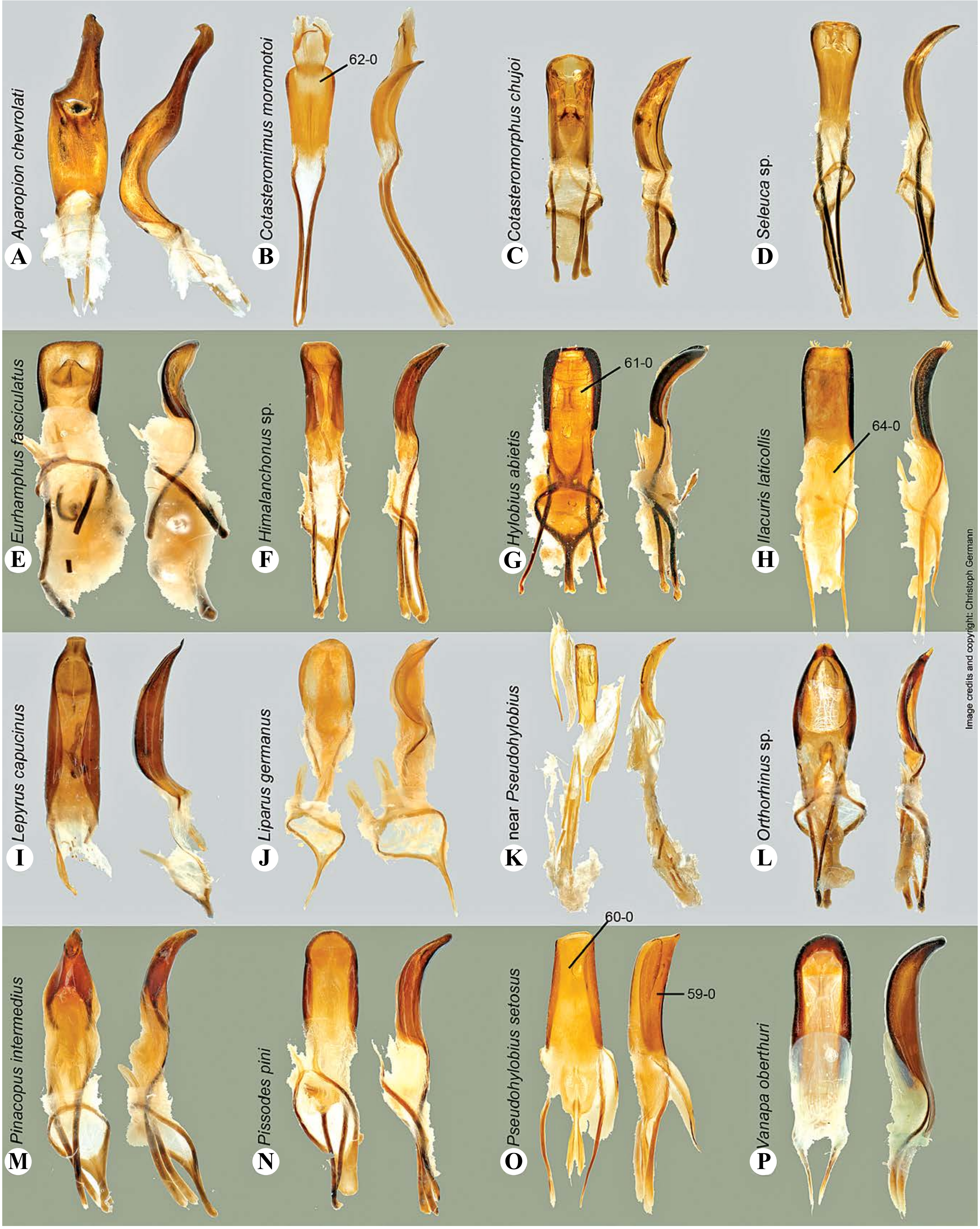

Fig. 5 – Male genitalia of analysed Molytinae weevils, not to scale. © Christoph Germann.

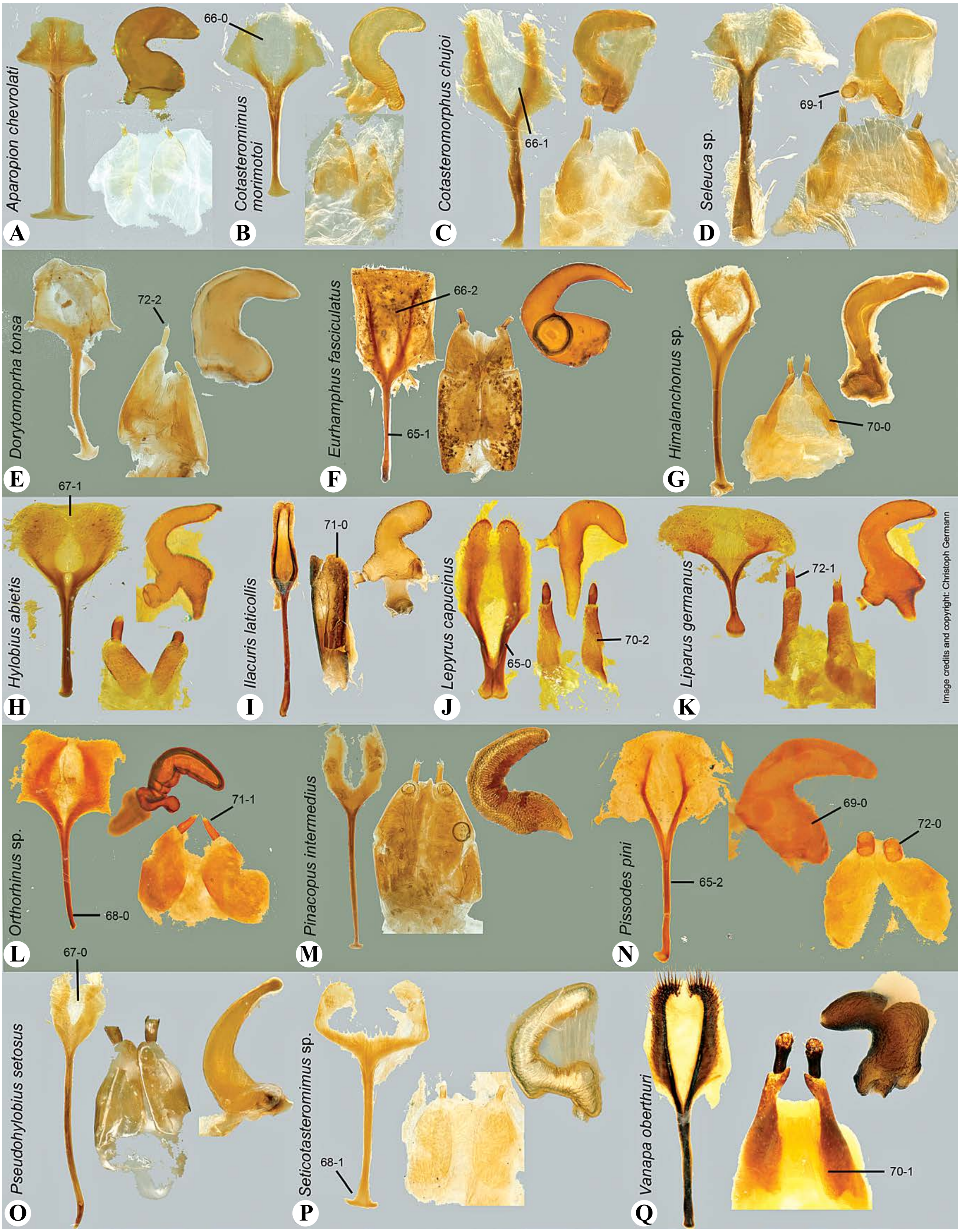

Fig. 6 – Female genitalia of analysed Molytinae weevils, not to scale. © Christoph Germann.

with whitish scales. Funicles with long straight setae on each segment. Pronotum 1.1 times longer than wide, parallel-sided in basal half, evenly and weakly narrowed apicad; dorsal and lateral surface roughly and densely punctate; punctures of polygonal shape, separated by narrow ridges; indistinct middle pronotal line without punctures. Elytra at base jointly broader than pronotum; anterior margin weakly emarginate; humeral calli pronounced; parallel-sided on basal two thirds; in lateral view flattened on disc and fused along suture. Elytral striae consisting of regular oblong to rectangular punctures, interstriae broader than striae, vaulted and with irregular sharp tubercles; with smaller, bright yellowish curved bristles originating at front margin of punctures. Elytral interstriae with broader and longer yellowish curved bristles originating from hind margin of tubercles. Mesoventrite, metaventrite, epipleura and abdominal ventrites dark brown, deeply and coarsely punctate, covered with narrow, pointed bristles directed posteriad; fifth (last) ventrite broadly rounded. Legs robust, surface coarsely punctate with curved nar-

Table 1 – Data matrix of adult morphological characters used in four phylogenetic analyses (A1-A4) to determine affinities of *Zembrus perseus* gen. et sp. nov. Abbreviations before taxa include InG: Ingroup; cOtG: close outgroup, dOtG: distant outgroup. The first two lines read vertically provide the character number. The bottom line three lines indicate additive, deactivated and uninformative characters, respectively.

```
                                       0000000001 1111111112 2222222223 3333333334 4444444445 5555555556 6666666667 777
                                       1234567890 1234567890 1234567890 1234567890 1234567890 1234567890 1234567890 123
ROOT Gymnetron veronicae               0000020011 2110010305 0001100001 1301011021 1000-10013 0100110110 1100020011 110
InG1 Zembrus perseus                   0120300111 2011010307 0010100000 1301112122 1010-11000 0110100111 1101?????? ???
InG2 Cotasteromimus morimotoi          0120211121 2010020007 1011110101 120101200- 0000-20110 0100100111 1000201110 110
InG3 Cotasteromorphus chujoi           0000301011 2010011107 1011111100 120101210- 0201010110 1101000111 1101211110 120
InG4 Pseudohylobius setosus            0110300111 2010020107 1110000001 1322012122 1111101003 1110000000 1001220110 110
InG5 near Pseudohylobius               0113000110 2010011306 0110100110 1322111022 1101000013 1111100111 1000?????? ???
InG6 Seticotasteromimus jarawa         0231000110 2110020107 1021100001 1320122122 1201001003 0100100?? ????211100 110
InG7 Seticotasteromimus sp             0221000110 2110020107 1011100001 1320122122 1201011003 0100100?? ????201111 120

cOtG1 Pissodini Dorytomorpha tonsa     0110200021 2001010107 1001100111 1301112121 1210-10003 1111010?? ????210100 120
cOtG2 Pissodini Pissodes pini          1110200021 2111000207 0001100101 1100012021 1100-11003 0111100111 0001210100 100
cOtG3 Orthorhinini Eurhamphus fasciculatus 4210000032 0102100207 0011100101 1301012121 1011111113 0112100110 1001120000 110
cOtG4 Orthorhinini Ilacuris laticollis 3102000032 2101010107 0001100001 0-02012121 1010--1013 1112100110 1000221112 0-0
cOtG5 Orthorhinini Orthorhinus sp      2210310011 1111021107 0001101101 0-01022021 1010--1013 1112100110 1101110010 120
cOtG6 Orthorhinini Vanapa oberthuri    4230000032 1001101117 0021101001 1202011022 1010-11013 1112100110 1100120001 120

dOtG1 Anchonini Himalanchonus sp       0120201121 2011020206 0011001111 0-0101200- 0100--0100 0110101010 1001120110 110
dOtG2 Anchonini Titilayo garnerae      0102311131 2011010207 0001100001 101101200- 0011101110 0101100101 1100220000 111
dOtG3 Hylobiini Hylobius abietis       3100300011 2011000217 0001101101 1300001020 1000--0003 1101000110 0001101111 120
dOtG4 Ithyporini Sclerocardius bohemani 2000210130 2110010307 0001001111 1110011020 1001010113 1111100101 1001020100 110
dOtG5 Lepyrini Lepyrus capucinus       2013300001 2001110317 0000100000 1301011020 0000-10110 0101100110 1101021112 110
dOtG6 Lithinini Seleuca sp             01133-1121 2010020207 0011101100 1201011020 0001110110 1100000011 1000201111 110
dOtG7 Lymantini Devernodes chthonia    0213011122 21-1110206 0011100000 110101210- 0200-10110 0110000110 0000220002 0-0
dOtG8 Molytini Liparus germanus        3000000011 2011000217 0001100001 0-00002120 0000--0110 1111100110 1100121111 110
dOtG9 Molytini Pinacopus intermedius   1110010131 2011012307 0011001101 110111210- 0001010110 1111000010 1100221100 110
dOtG10 Typodeini Aparopion chevrolati  0103300121 2001100307 0001100000 120101210- 0110-11110 0101100011 1111200101 111

23 additive characters: A              AAA-----AA AA-A-AAAAA –A-------- ----AAA--- -A-------A ---------- ----AA---A –A-
2 deactivated characters: D            ---D------ ---------- –--------- ---D------ ---------- ---------- ---------- ---
3 uninformative characters: U          ---------- ---------- –--------- ---------- ---------- -U---U---- --U------- ---
```

Table 2 – Parameters, statistics and results of four phylogenetic analyses to determine affinities of Zembrus perseus gen. et sp. nov. "Weighted" indicates whether characters were successively re-weighted; "ordered" indicated whether 23 additive characters were ordered. CI: Consistency Index; RI: retention Index; MPT: number of the most parsimonious (=shortest) shortest trees. Last three columns indicate bootstrap support >50% for all three clades recovered in otherwise unresolved bootstrap analyses: S+S: InG6 *Seticotasteromimus jarawa* + InG7 *Seticotasteromimus* sp.; P+(S+S): InG4 *Pseudohylobius setosus* + (InG6 *Seticotasteromimus jarawa* + InG7 *Seticotasteromimus* sp.); E+V: cOtG3 *Eurhamphus fasciculatus* + cOtG6 *Vanapa oberthuri*.

Analysis	Weighted	Ordered	Tree lenght	CI	RI	MPT	S+S	P+(S+S)	E+V
A1	no	no	345	28	44	1	99	50	no
A2	no	yes	372	27	46	9	99	59	55
A3	yes	no	350	28	43	1	98	no	no
A4	yes	yes	379	26	44	1 (Fig. 7)	99	60	59

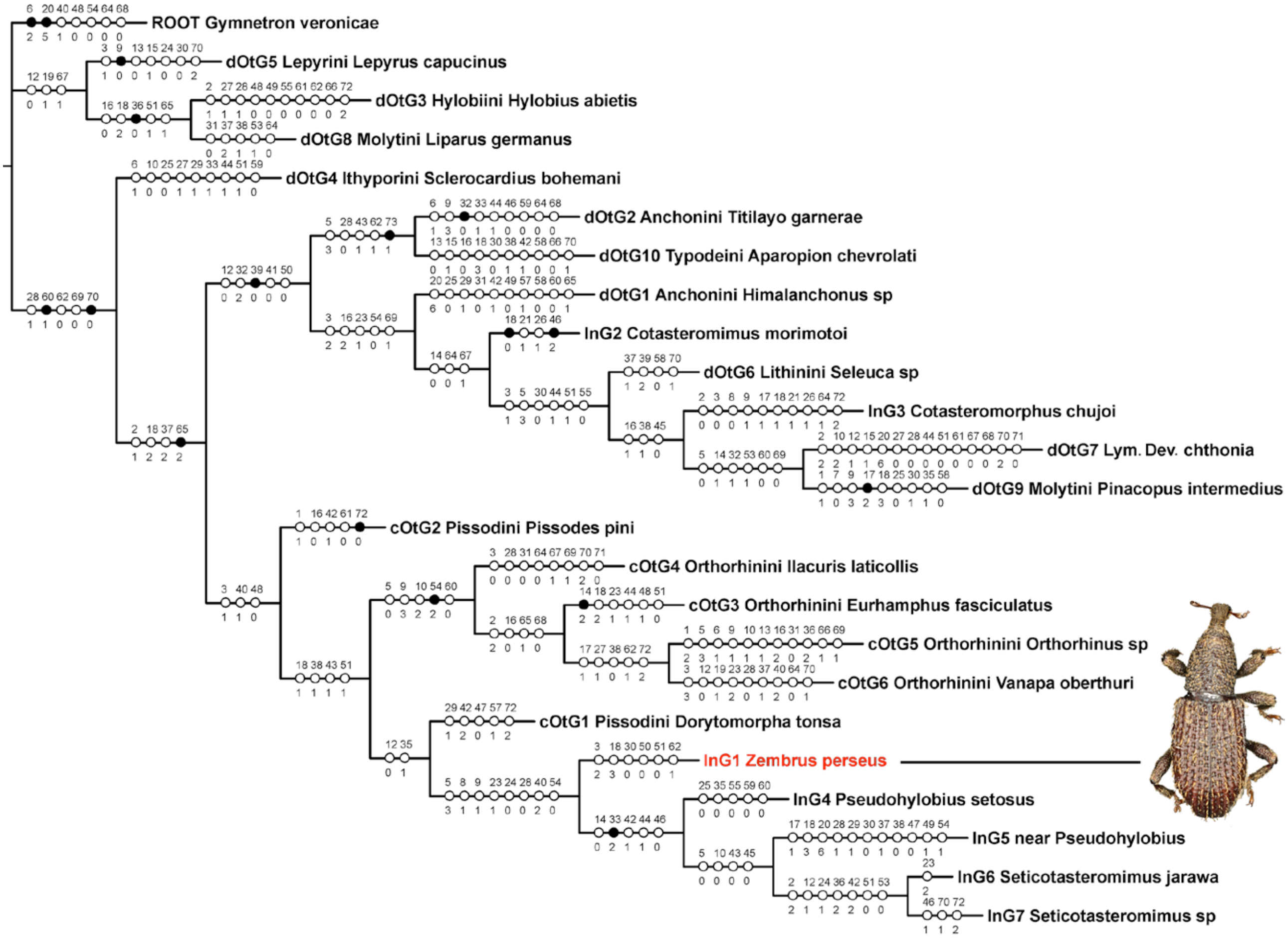

Fig. 7 – Single most parsimonious tree resulting from analysis A4. Unambiguously optimized evolutionary events plotted along internodes. Character numbers are above circles, newly acquired character states are below circles. Black circles indicate unique evolutionary events; white circles indicate parallelisms or reversals.

row yellowish bristles; femora clubbed in middle; tibiae with straight hairs along inner edge; apex on inner and outer edge with short fringe of orange stiff spines; tarsomere 5 longer than 2/3 of combined length of remaining tarsomeres. Male genitalia: penis with dorsal and ventral sides evenly sclerotized; apodemes (temones) longer than penis body; penis evenly bent in vertical dimension; apex of penis regularly and broadly pointed; tegmen ring with short apodeme (Figs 1E-G); single copulatory sclerite thickened at base, its apex with three separate tips (Figs 1H-I); sternite IX with long curved apodeme and two basal arms (Fig. 1J). DNA sequences: COI: HQ987100, ITS2: MG648823, 28S: MG648736.

Derivation of name: The species name is that of Perseus, son of Zeus and Danae, one of the greatest Greek mythological heroes; it is a noun in apposition.

Remark: Due to damage suffered during posting, the antennae of the holotype are lost, but they were documented (Fig. 1D, Figs S1–S4 in the Supplementary Data).

Discussion

The interpretation of our results presented herein leads to the following conclusions: Predictions 1, 2 and 3 (monophyly of Cotasteromimina and Pissodini, with or without *Z. perseus*) cannot be adequately tested, because the branching of the resulting trees of four bootstrap analyses are almost entirely unresolved (Table 2).

Considering the sizable analytical effort undertaken and its notably inconclusive results, our main overall conclusion is that Cotasteromimina are either:

- rampantly non-monophyletic;
- or our dataset restricted to adult morphological characters is acutely inadequate for the purpose;
- or both of the above.

When starting this project, we did not expect to obtain taxonomically congruent and well supported phylogeny estimates. If Cotasteromimina could not be consistently recovered as a clade, at least we expected to resolve some stable clades formed by its non-congeneric members. We also thought it likely that *Z. perseus* might consistently cluster with at least one genus of Cotasteromimina. Recovering the grossly incompatible shortest trees among (and even in, Table 2) the four analyses implemented was sobering and unexpected. Perhaps even more sobering was to see the nearly completely unresolved bootstrap branchings (Table 2). It appears that we grossly overestimated our capacity to extract even vestiges of phylogenetically relevant information from these beetles, despite trying all we could. Rarely are so inconclusive phylogenetic results published, this scarcity likely due to authors being reluctant to admit what they consider an analytical impotence. Equally inconclusive were earlier attempts to the find sister group of *Z. perseus* using one (Grebennikov 2014) or three DNA fragments (Grebennikov 2018b,c), both mitochondrial and nuclear. All in all, the phylogenetic position of our Yunnan specimen 861 remains as mysterious as it was at the onset of this study. However, with the description and thorough illustration *Zembrus perseus* has finally reached the level of alphataxonomical recognition.

Facing the practical necessity to allocate our new genus to the next more inclusive taxon, we herein arbitrarily assign it to the subtribe Cotasteromimina. This decision, even if not supported by the analyses, is partly based on the utilitarian preference of maintaining the existing classification. An alternative taxonomic assignment is that of yet another genus of Molytinae *incertae sedis* (Grebennikov 2018c, 2020), which seems less practical. Our taxonomic decision is also motivated by a possibility that Cotasteromimina might be a clade after all. Their monophyly is suggested by the species' external similarity (small parallel-sized weevils sharing at least three diagnostic characters, see introduction) and by their geographically coherent distribution in South-East Asia (Fig. 2B). Time is expected to test this assumption.

Acknowledgements – Miguel A. Alonso-Zarazaga (Madrid, Spain) shared his opinion on possible affinities of the new species. Munetoshi Maruyama and Naomichi Tsuji (both Fukuoka, Japan) loaned the Japanese Cotasteromimina specimens. Andreas Floren (Würzburg, Germany) and Peter Sprick (Hannover, Germany) provided Cotasteromimina specimens obtained through their canopy fogging project on Borneo. Michael Geiser and Max Barclay (both London, UK) loaned specimens from The Natural History Museum, London. Christopher H. C. Lyal (London, UK) critically read an earlier draft of the manuscript prior to its submission. The referees are cordially acknowledged for their criticism.

References

Alonso-Zarazaga M.A., Lyal C.H.C. 1999. A world catalogue of families and genera of Curculionoidea (Insecta: Coleoptera) (excepting Scolytidae and Platypodidae). Entomopraxis, Barcelona, 315 pp.

Anderson R.S., Oberprieler R.G., Setliff G.P. 2018. A review of the *Araucaria*-associated weevils of the tribe Orthorhinini (Coleoptera: Curculionidae: Molytinae), with description of new species of *Ilacuris* Pascoe, 1865 and *Notopissodes* Zimmerman & Oberprieler, 2014 and a new genus, *Kuschelorhinus* Anderson & Setliff. Diversity, 10, 5, 25 pp. Doi: https://doi.org/10.3390/d10030054

Chujô M., Voss E. 1960. Neue Curculioniden-Subfamilie, -Gattungen und -Arten von Japan (Coleoptera, Curculionidae). Memoirs of the Faculty of Liberal Arts and Education, Kogawa University (part II), 94: 1–17.

Cristóvão J.P., Lyal C.H.C. 2018. Anchonini in Africa: new species and genus confirming a transatlantic distribution (Coleoptera: Curculionidae: Molytinae). Diversity, 10, 82, 34 pp. Doi: https://doi.org/10.3390/d10030082

Farris J.S. 1988. Hennig86. Documentation for Version 1.5. Published by the author, Port Jefferson Station, New York.

Felsenstein J. 1985. Confidence limits on phylogenies: an approach using the bootstrap. Evolution, 39: 783–791. Doi: http://dx.doi.org/10.2307/2408678

Franz N.M. 2014. Anatomy of a cladistic analysis. Cladistics, 30: 294–321. Doi: https://doi.org/10.1111/cla.12042

Germann C. 2013. *Seticotasteromimus* gen. n. *jarawa* sp. nov. from the Andaman Islands (Coleoptera, Curculionidae). Revue Suisse de Zoologie, 120: 125–129.

Goloboff P.A. 1999. 'Nona. Version 2.0.' (Published by the author: Instituto Miguel Lillo, Tucumán, Argentina.)

Grebennikov V.V. 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). Bonn Zoological Bulletin, 63: 123–147.

Grebennikov V.V. 2018a. Dryophthorinae weevils (Coleoptera: Curculionidae) of the forest floor in Southeast Asia: Three-marker analysis reveals monophyly of Asian Stromboscerini and new identity of rediscovered *Tasactes*. European Journal of Entomology, 115: 437–444. Doi: http://doi.org/10.14411/eje.2018.044

Grebennikov V.V. 2018b. Discovery of Lymantini weevils (Coleoptera: Curculionidae: Molytinae) outside the Americas: *Devernodes*, a new genus for five new species from Southeast Asia. Zootaxa, 4500: 363–380. Doi: https://doi.org/10.11646/zootaxa.4500.3.4

Grebennikov V.V. 2018c. Phylogenetically problematic *Aater cangshanensis* gen. et sp. nov. from Southwest China suggests multiple origins of prosternal canal in Molytinae weevils (Coleoptera: Curculionidae). Fragmenta entomologica, 50: 103–110.

Grebennikov V.V. 2020. *Tazarcus*, a new phylogenetically unplaced genus of two flightless weevils with metapleural ridge from the Eastern Arc Mountains, Tanzania (Coleoptera: Curculionidae: Molytinae). Zootaxa, 4766 (3): 421–434. Doi: https://doi.org/10.11646/zootaxa.4766.3.2

Hong K.-J., Egorov A.B., Korotyaev B.A. 2000. Illustrated Catalogue of Curculionidae in Korea (Coleoptera). Insects of Korea, Series 5, pp. 340.

Kojima H., Idris A.G. 2005. *Cotasteromorphus*, a new Cotasteromimina (Coleoptera, Curculionidae, Molytinae, Pissodini) from the Malaysian moss forests. Elytra, 33: 133–141.

Kojima H., Kaga Y. 2011. Record of some weevils new to the fauna of Tokunoshima Island, Southwest Japan. Elytra (N.S.), 1: 159–161.

Kojima H., Morimoto K. 2014. An online checklist and database of the Japanese weevils (Insecta: Coleoptera: Curculionoidea) (excepting Scolytidae and Platypodidae). Bulletin of the Kyushu University Museum, 2: 33–147 [in Japanese]. Database available from: http://de05.digitalasia.chubu.ac.jp/index.html (accessed 20 March 2019).

Legalov A.A. 2018. Annotated key to weevils of the world.

Part 2. Subfamily Molytinae (Coleoptera, Curculionidae). Ukrainian Journal of Ecology, 8: 340–350.

Legalov A.A. 2020. New species and new subgenus of the genus *Cotasteromimus* Chûjô et Voss, 1960 (Coleoptera: Curculionidae) from the Philippines. Far Eastern Entomologist, 405: 15–19. Doi: https://doi.org/10.25221/fee.405.3

Lyal C.H.C. 2014. 3.7.7 Molytinae Schoenherr, 1823. In: Leschen R.A.B., Beutel R.G. (Eds), Handbook of Zoology, Arthropoda: Insecta: Coleoptera. Volume 3: Morphology and Systematics (Phytophaga). Walter de Gruyter, Berlin, pp. 529–570.

Lyal C.H.C. 2018. The problematic genus *Sclerocardius* (Coleoptera: Curculionidae: Molytinae: Ithyporini). Diversity, 10: 74, 30 pp. Doi: https://doi.org/10.3390/d10030074

Lyal C.H.C. 2020. Glossary of Weevil Characters. International Weevil Community Website. http://weevil.info/glossary-weevil-characters (accessed June 24, 2020).

McKenna D.D., Sequeira A.S., Marvaldi A.E., Farell B.D. 2009. Temporal lags and overlap in the diversification of weevils and flowering plants. Proceedings of the National Academy of Sciences, 106: 7083–7088. Doi: http://dx.doi.org/10.1073/pnas.0810618106

Morimoto K. 1962a. Descriptions of a new subfamily, new genera and species of the family Curculionidae of Japan. (Comparative morphology, phylogeny and systematics of the superfamily Curculionoidea of Japan. II). Journal of the Faculty of Agriculture, Kyushu University, 11: 375–407.

Morimoto K. 1962b. Key to families, subfamilies, tribes and genera of the superfamily Curculionoidea of Japan excluding Scolytidae, Platypodidae and Cossoninae. (Comparative morphology, phylogeny and systematics of the superfamily Curculionoidea of Japan. III). Journal of the Faculty of Agriculture, Kyushu University, 12: 21–66.

Morimoto K., Miyakawa S. 1985. Weevil fauna of the Izu Islands, Japan (Coleoptera). Mushi, 50: 19–85.

Nixon K.C. 2002. Winclada, Version 1.00.08. Published by the author, Ithaca, New York.

Popper K. 1959. The logic of scientific discovery. Basic Books, New York, 484 pp.

Pullen K.R., Jennings D., Oberprieler R.G. 2014. Annotated catalogue of Australian weevils (Coleoptera: Curculionoidea). Zootaxa, 3896: 1–481. Doi: http://dx.doi.org/10.11646/zootaxa.3896.1.1

Shin S., Clarke D.J., Lemmon A.R., Lemmon E.M., Aitken A.L., Haddad S., Farrell B.D., Marvaldi A.E., Oberprieler R.G., McKenna D.D. 2017. Phylogenomic data yield new and robust insights into the phylogeny and evolution of weevils. Molecular Biology and Evolution, 35: 823–836. Doi: http://dx.doi.org/10.1093/molbev/msx324

Sprick P., Floren A. 2018. Diversity of Curculionoidea in humid rain forest canopies of Borneo: a taxonomic blank spot. *Diversity*, 10, 116, 22 pp. Doi: http://dx.doi.org/10.3390/d10040116

APPENDIX 1 – Specimen data for weevils used for photography and scoring of morphological characters. Lack of data (such as dates) indicates that these data are not provided on the specimen label.

ROOT: *Gymnetron veronicae* (Germar, 1821), ♂ & ♀: Switzerland, Bern, Heimenschwand, Wachseldornmoos, 17.v.2014, C. Germann (CGC). **Ingroup: InG1**: *Zembrus perseus* gen. et sp. nov., ♂: China, Yunnan, E slope Cangshan at Dali, 3806 m, 17.v.2010, V. Grebennikov (NHMB, later IZCAS). **InG2**: *Cotasteromimus morimotoi* Chûjô et Voss, 1960, ♂: Japan, Yamanashi, Narusawa, Fuji-rindo, 1300–1600 m, 14-16.vi.2016, N. Tsuji (CGC); ♀: Japan, Mie, Mt. Nyuudou, Suzuka, 13.ix.2009, N. Tsuji (CGC). **InG3**: *Cotasteromorphus chujoi* Kojima, 2005, ♂ & ♀ paratypes: Malaysia, Pehang, Cameron Highlands, Gunung Brinchang, 27.iii.2002, H. & M. Kojima (KUZC). **InG4**: *Pseudohylobius setosus* Morimoto, 1962, ♂ & ♀: Japan, Oita-ken, Yufu-shi, Mt. Kuro-dak, 900 m, 29.x.2016, N. Tsuji (CGC). **InG5**: near *Pseudohylobius* sp., ♂: Malaysia, Sabah, Mt. Kinabalu, A. Floren (NHMB). **InG6**: *Seticotasteromimus jarawa* Germann, 2013, ♀ holotype: India, South Andaman Island, Sippighat, 11.xii.2006 (NHMB). **InG7**: *Seticotasteromimus* sp., ♀: Malaysia, Tawau, Tawau Hills, A. Floren (NHMB). **Close outgroup: cOtG1**: *Dorytomorpha tonsa* (Chevrolat, 1880), ♀: Guadaloupe, Gourbeyre, L. Dufour & A. Hustache (NHMUK). **cOtG2**: *Pissodes pini* (Linnaeus, 1758), ♀: Switzerland, Grisons, Ftan, 4.ix.2005, C. Germann (CGC)l ♂: Greece, Xanthi, E-Livatidis, 25.v.2016, C. Germann (CGC). **cOtG3**: *Eurhamphus fasciculatus* Shuckard, 1838, ♂: Australia, Queensland, G.A.K. Marshall (NHMUK); ♀: Tasmania, D. Sharp (NHMUK). **cOtG4**: *Ilacuris laticollis* Pascoe, 1865, ♂: Australia, S. Queensland, Fletcher, i.1956, E. Sutton (NHMUK); ♀: Australia, Queensland, Townsville, D. Sharp (NHMUK). **cOtG5**: *Orthorhinus* sp., ♂ & ♀: Australia, Cairns, High Island, 25.vii.2004, D. Wegmann (CGC). **cOtG6**: *Vanapa oberthuri* Pouillaude, 1915, ♂: Papua New Guinea, Bulolo Morobe, Hoop Pine, iii.1964, K. White (NHMUK); ♀: Papua New Guinea, Bulolo N. P., ix.1979, E. Gowing Scopes (NHMUK); ♂: Papua New Guinea, Goroka East Highl. D., 10.ii.1964, I. Szent (NHMUK). **Distant outgroup: dOtG1**: *Himalanchonus* sp., ♂ & ♀: China, Yunnan, E slope Cangshan at Dali, 2728 m, 9.v.2010, V. Grebennikov (CGC). **dOtG2**: *Titilayo garnerae* (Cristóvão & Lyal, 2018), see Cristóvão & Lyal (2018). **dOtG3**: *Hylobius abietis* (Linnaeus, 1758), ♂: Italy, Calabria, Aspromonte, Montalto, 20.iii.2001, C. Germann (CGC); ♀: Switzerland, Schwyz, Vorderthal, 13.vi.2007, C. Monnerat (CGC). **dOtG4**: *Sclerocardius bohemani* Schoenherr, 1847, see Lyal (2018). **dOtG5**: *Lepyrus capucinus* (Schaller, 1783), ♂: Italy, Piemonte, Biella, Santuario di Oropa, 25.v.2010, W. Marggi (CGC); ♀: Switzerland, Ticino, Blenio, Dongio, 22.v.2010, C. Germann (CGC). **dOtG6**: *Seleuca* sp., ♂ & ♀: Taiwan, Taichung, Huisun forest, 1647 m, 3.ix.2013, V. Grebennikov (CGC). **dOtG7**: *Devernodes chthonia* Grebennikov, 2018, see Grebennikov (2018b). **dOtG8**: *Liparus germanus* (Linnaeus, 1758), ♂: Switzerland, Vaud, St. Cergue, 10.v.2002, C. Germann (CGC); ♀: Switzerland, Aargau, Würenlingen, viii.1961, G. Bächli (CGC). **dOtG9**: *Pinacopus intermedius* Kojima & Morimoto, 2002, ♂ & ♀ paratypes: Malaysia, Pahang, Gunung Jasar, 8.iv.1976, M. Hata (KUZC). **dOtG10**: *Aparopion chevrolati* (Jacquelin du Val, 1855), ♂ & ♀: Italy, Liguria, Savona, San Filippo, 29.ix.2010, C. Germann (CGC).

APPENDIX 2 – List of characters.

1. Body, length between anterior margin of pronotum and elytral apex, dorsal view: < 6 mm = 0; 6 to < 9 mm = 1; 9 to < 12 mm = 2; 12 to < 15 mm = 3; 15 mm and more = 4 [additive].
2. Body, ratio of body length to elytral width at midlength, dorsal view: < 2.0 = 0; 2.0 to < 2.5 = 1; 2.5 to < 3.0 = 2 [additive].
3. Body, ratio of body length to maximum height, lateral view: < 2.5 = 0; 2.5 to < 3.0 = 1; 3.0 to < 3.5 = 2; 3.5 and more = 3 [additive].

4. Body, scales (including those on head and legs), orientation: appressed, < 45° = 0; erect, > 45° = 1; both, appressed and erect = 2; no scales = 3 [nonadditive] [deactivated].
5. Head, rostrum, shape in cross-section at midlength: circular = 0; vertical oval = 1; horizontal oval = 2; rectangular/quadrate = 3 (Fig. 1C) [nonadditive].
6. Head, rostrum, shape, fronto-dorsal view: widening anteriad = 0 (Fig. 1D); parallel-sided = 1; narrowing anteriad = 2 [nonadditive].
7. Head, rostrum, shape, lateral view: straight or weakly curved = 0 (Fig. 1C); strongly curved = 1.
8. Head, transverse dorsal depression separating rostrum and frons, lateral view: absent = 0 (Fig. 1C); present = 1.
9. Head, rostrum, length to width at middle ratio, fronto-dorsal view: < 3.0 = 0; 3.0 to < 4.0 = 1 (Fig. 1D); 4.0 to < 5.0 = 2; 5.0 and more = 3 [additive].
10. Head, rostrum, length compared to that of pronotum in dorsal view: < 0.9 = 0; 0.9 to 1.1 = 1; > 1.1 = 2 [additive].
11. Head, rostrum, position of frons relative to position of upper margin of eyes, lateral view: below = 0; at level = 1; above = 2 (Fig. 1D) [additive].
12. Head, rostrum, antennal attachment in relation to rostral length: in apical third = 0 (Fig. 1D); in median third = 1.
13. Head, rostrum, scrobes, orientation relative to rostrum, lateral view: parallel, posterior ends do not approximate each other = 0; oblique, posterior ends approximate each other = 1 (Fig. 1B).
14. Head, eyes, position in relation to imaginary posterior extension of rostrum: below = 0; at level = 1 (Fig. 1C); above = 2 [additive].
15. Head, eyes, contour in relation to that of head capsule, dorsal view: not or weakly protruding = 0 (Fig. 1A); markedly protruding = 1.
16. Head, retraction into pronotum, lateral view: not retreated, temples exposed by eye diameter or more = 0; weakly retracted, temples exposed for less than eye diameter = 1 (Fig. 1C); moderately retracted, eyes not concealed, temples fully concealed = 2 [additive].
17. Head, antenna, antennal scape, ratio of its length to that of funicle and club: < 0.9 = 0 (Fig. 1D); 0.9 to < 1.1 = 1; 1.1 to < 1.3 = 2 [additive].
18. Antenna, funicle with club, ratio of their length to that of 3 basal funicular segments: 1.0 to 1.5 = 0; 1.5 to 2.0 = 1; 2.0 to 2.5 = 2; > 2.5 = 3 (Fig. 1D) [additive].
19. Antenna, funicle, number of distal-most segments with vestiture similar to that of club: 0 = 0 (Fig. 1D); 1 = 1.
20. Head, antenna, funicle, number of segments: 5 = 5; 6 = 6; 7 = 7 (Fig. 1D) [additive].
21. Antenna, first funicular segment, ratio of its maximum width to that of second segment: < 1.7 = 0 (Fig. 1D); 1.7 and more = 1.
22. Head, antenna, funicle, ratio of second segment length to that of first, dorsal view: < 0.5 = 0 (Fig. 1D); 0.5 and more = 1.
23. Prothorax, notum, ratio of maximum length to maximum width, dorsal view: < 0.9 = 0; 0.9 to 1.1 = 1 (Fig. 1A); > 1.1 = 2 [additive].
24. Prothorax, notum, its sides, dorsal view: parallel = 0 (Fig. 1A); rounded = 1.
25. Prothorax, notum, constriction at fore margin, dorsal view: absent = 0 (Fig. 1A); present = 1.
26. Prothorax, notum, constriction at hind margin, dorsal view: absent = 0 (Fig. 1A); present = 1.
27. Prothorax, anterior edge, postocular lobes, lateral view: absent = 0 (Fig. 1C); present = 1.
28. Prothorax, anterior edge, ventral view: straight = 0 (Fig. 1B); emarginate = 1.
29. Prothorax, longitudinal channel on sternum anterior to procoxae, ventral view: absent = 0 (Fig. 1B); present = 1.
30. Prothorax, dorsal and lateral surface, scales: absent = 0 (Fig. 1A); present = 1.
31. Prothorax, dorsal and lateral surface, bristles: absent = 0; present = 1 (Fig. 1A).
32. Pronotum and elytra, shape of bristles, ratio of their length to their width in middle: < 3 = 0; 3 to < 4 = 1; 4 to < 5 = 2; 5 and more = 3 (Fig. 1C) [nonadditive].
33. Prothorax, dorsal and lateral surface, vestiture, orientation: appressed, nearly parallel to surface = 0 (Fig. 1A); semi-erect, at about 45° to surface = 1; erect, nearly 90° to surface = 2 [nonadditive].
34. Prothorax, dorsal and lateral surface, vestiture, shape: straight = 0; curved = 1; both, straight and curved = 2 [nonadditive] [deactivated].
35. Prothorax, distance between inner edges of coxae in relation to coxal diameter, ventral view: < 0.3 (subcontiguous) = 0; 0.3 to 0.9 (moderately separated) = 1 (Fig. 1B).
36. Mesothorax, distance between inner edges of coxae in relation to coxal diameter, ventral view: < 0.3 (subcontiguous) = 0; 0.3 to 0.9 (moderately separated) = 1 (Fig. 1B); > 0.9 (widely separated) = 2 [additive].
37. Metathorax, distance between inner edges of coxae in relation to coxal diameter, ventral view: 0.9 to 1.1 = 1; > 1.1 = 2 (Fig. 1B).
38. Metathorax, abdominal process between metacoxae, width relative to that of coxa: 1.5 and less = 0; > 1.5 = 1 (Fig. 1B).
39. Scutellum, if visible externally, dorsal view: not visible = 0; barely visible, shape indistinct = 1; clearly visible, shape distinct = 2 (Fig. 1A) [nonadditive].
40. Scutellum, its external part, shape, if distinct, dorsal view: triangular = 0; clearly rounded, not dot-like = 1; pentagonal = 2 (Fig. 1A) [nonadditive].
41. Elytra, shoulders, dorsal view: absent = 0; present = 1 (Fig. 1A).
42. Elytra, striae, ratio of their width to that of elytral intervals, dorsal view: < 0.9 = 0 (Fig. 1A); 0.9 to 1.1 = 1; > 1.1 = 2 [additive].
43. Elytra, elytral intervals, tubercles or bulges on at least some intervals, dorsal view (excepting elytral bulge at declivity): absent = 0; present = 1 (Fig. 1A).
44. Elytra, raised bristles, dorsal or lateral view: absent = 0 (Fig. 1A); present = 1.
45. Elytra, raised bristles, arrangement: in rows = 0; in tufts = 1 [deactivated].
46. Elytra, raised and bowed bristles, shape of tip: rounded = 0; pointed = 1; bifid = 2 (Fig. 1A) [nonadditive].
47. Elytra, elevation of odd versus even intervals, oblique dorsal view: similar = 0; odd intervals more elevated = 1 (Fig. 1A).
48. Elytra, contour at middle, dorsal view: parallel-sided = 0 (Fig. 1A); rounded = 1.
49. Elytra, dorsal contour at middle third, lateral view: straight = 0 (Fig. 1C); curved = 1.
50. Hind wings, dissection required: absent = 0; present, vestigial, about half elytral length = 1; present, short, subequal to elytral length = 2; present, long, about 2x elytral length = 3 [additive].
51. Legs, all femora, posteriorly oriented spines: absent = 0 (Fig. 1B); present = 1.
52. Legs, all tibiae, uncus: absent = 0; present = 1 [deactivated].

53. Legs, all tibiae, premucro: absent = 0; present = 1.
54. Legs, all tarsi, tarsomere 2, shape in cross-section: round = 0 (Fig. 1B); vertical oval = 1; horizontal oval = 2 [nonadditive].
55. Legs, all tarsi, tarsomere 3, shape, dorsal view: entire (not bilobed) = 0; bilobed = 1 (Fig. 1B).
56. Legs, all claws, fusion in basal third: absent (claws free) = 0; present (claws fused) = 1 [deactivated].
57. Legs, all claws, angle between them, dorsal view: < 20° = 0 (Fig. 1B); 45° and more = 1.
58. Abdomen, trace of fusion between visible ventrites 1 and 2 in its mid-third, ventral view: absent = 0; present = 1.
59. Male genitalia, penis, cross-section at middle, shape: circular = 0 (Fig. 5O); oval = 1 (Fig. 1F).
60. Male genitalia, penis, dorsal surface, sclerotization compared to that of lateral surface: weaker, surface appears membranous = 0 (Fig. 5O); similar, surface appears sclerotized = 1 (Fig. 1E).
61. Male genitalia, penis, ventral surface, sclerotization compared to that of lateral surface: weaker, surface appears membranous = 0 (Fig. 5G); similar, surface appears sclerotized = 1 (Fig. 1G).
62. Male genitalia, penis, shape of apex: rounded = 0 (Fig. 5B); pointed = 1 (Fig. 1G).
63. Male genitalia, penis, apex, dorsal or ventral view: symmetrical = 0; asymmetrical = 1 [deactivated].
64. Male genitalia, penis, one or more copulatory sclerites in endophallus: absent = 0 (Fig. 5H); present = 1 (Fig. 1E).
65. Female genitalia, sternite VIII, ratio of length of apodeme to that of plate: < 0.9 = 0 (Fig. 6J); 0.9 to 1.1 = 1 (Fig. 6F); > 1.1 = 2 (Fig. 6N) [additive].
66. Female genitalia, sternite VIII, plate, length to width ratio: < 0.9 = 0 (Fig. 6B); 0.9 to 1.1 = 1 (Fig. 6C); > 1.1 = 2 (Fig. 6F) [additive].
67. Female genitalia, sternite VIII, plate, extend of its sclerotization (but not pigmentation): small, middle not sclerotized, sternite VIII fork-like = 0 (Fig. 6O); great, middle sclerotized, sternite VIII paddle-like = 1 (Fig. 6H).
68. Female genitalia, sternite VIII, apodeme, abrupt widening in its part opposite to plate (“handle of a spade”): absent = 0 (Fig. 6L); present = 1 (Fig. 6P).
69. Female genitalia, spermatheca, nodulus and ramus: indistinct = 0 (Fig. 6N); distinct = 1 (Fig. 6D).
70. Female genitalia, each of hemisternites IX (=each gonocoxite, excluding styli), ratio of length to width: < 2.5 = 0 (Fig. 6G); 2.5 to 3.5 = 1 (Fig. 6Q); > 3.5 = 2 (Fig. 6J) [additive].
71. Female genitalia, styli: absent = 0 (Fig. 6I); present = 1 (Fig. 6L).
72. Female genitalia, styli, ratio of length to width in middle: < 1.5 = 0 (Fig. 6N); 1.5 to 2.5 = 1 (Fig. 6K); > 2.5 = 2 (Fig. 6E) [additive].
73. Female genitalia, sclerotization on bursa copulatrix: absent = 0; present = 1.