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.

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). 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, Pseu
dohylolobius setosus, also from the vicinity of Fukuoka. The illustration of the latter, the first ever published for Cotasteromimina, depicts a notably par
tallel-sided weevil with rectangular shoulders, robust rost
trum, 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 Pseu
dohylolobius into a new tribe Cotasteromimini and placed this in the subfamily Pissodinae (together with the tribe Pissodini represented in Japan only by Pissodes German, 1817). Morimoto & Miyakawa (1985) later described a second species of the type genus, Cotasteromimus squa
miger, from a large series collected on the northern Pa
cific islands between (and including) Kyushu and Taiwan. Downgrading Pissodinae to a tribe of Molytinae, Alonso-Zarazaga & Lyal (1999) treated Cotasteromimina as a sub
tribe 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 Toku
noshima Island. Kojima & Idris (2005) later described and il
lustrated 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 pre
nemures and simple third tarsomeres. Germann (2013) described the fourth genus and fifth species of Cotasteromimina, Seti
cotasteromimus jarawa, based on a single female from the Andaman Islands characterised by elongate and erect bris
tles. Kojima & Morimoto (2014) displayed online photographs of Japanese Cotasteromimina, including C. mori
motoi from Shikoku and Honshu, C. squamiger from Hon
shu and Kyushu and P. setosus from Honshu. In an over
view of the subfamily Molytinae, Lyal (2014) hesitantly re
tained Cotasteromimina in Pissodini, but elevating the sub
tribe Orthorhinina to tribal level and transferred into it a few genera formerly placed in Pissodina (see Anderson et al. 2018 on 13 phylogenetically unresolved Cotasteromimus 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 Molyti
nae elevated Cotasteromimina to a tribal rank and subse
quently 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 predomin
antly morphological data for testing in the sense pro
posed by Popper (1959) the following verifiable predic
tions:
1. the subtribe Cotasteromimina (excluding the Yunnan specimen 861) is a clade;
2. the Yunnan specimen 861 is a member of a monophyle
letic Cotasteromimina;
3. the tribe Pissodini (including one or more representa
tives 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 twi
g litter from under a Rhododendron bush (Fig. 2A) through a hand-held sifter, followed by subsequent extrac
tion 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 (Appen
dix 2) assessable from dead adults. Besides the Yunnan specimen 861, the ingroup (abbreviated InG before termi
nal name) included four (of a total of six) named Cotas
eromimina 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 Pseudohylolobius setosus and herein referred as “near Pseudohylolobius” (its formal description will be provided elsewhere). The close outgroup (abbrevi
ated oOtG 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
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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 Cryptorrhynchinae) 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 (Fig. 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 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 re-weighted all characters using successive approxima-
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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, mesoxoae 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 microsculpture and without stridulation ridges. Hind wings absent. Legs strong, femora unarmored, tibiae uncinate, at inner edges with premicro. 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 0000861 // 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 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.
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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 apically; 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.

<table>
<thead>
<tr>
<th>Analysis</th>
<th>Weighted</th>
<th>Ordered</th>
<th>Tree length</th>
<th>CI</th>
<th>RI</th>
<th>MPT</th>
<th>S+S</th>
<th>P+(S+S)</th>
<th>E+V</th>
</tr>
</thead>
<tbody>
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<td>A1</td>
<td>no</td>
<td>no</td>
<td>345</td>
<td>28</td>
<td>44</td>
<td>1</td>
<td>99</td>
<td>50</td>
<td>no</td>
</tr>
<tr>
<td>A2</td>
<td>no</td>
<td>yes</td>
<td>372</td>
<td>27</td>
<td>46</td>
<td>9</td>
<td>99</td>
<td>59</td>
<td>55</td>
</tr>
<tr>
<td>A3</td>
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<td>350</td>
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<td>43</td>
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<td>98</td>
<td>no</td>
<td>no</td>
</tr>
<tr>
<td>A4</td>
<td>yes</td>
<td>yes</td>
<td>379</td>
<td>26</td>
<td>44</td>
<td>1 (Fig. 7)</td>
<td>99</td>
<td>60</td>
<td>59</td>
</tr>
</tbody>
</table>

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 obhurthi.
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 phylogenetic 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 2018h,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 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.

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


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 antennal = 0 (Fig. 1D); parallel-sided = 1; narrowing antennal = 2 [nonadditive].

7. Head, rostrum, 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, 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) [deactivated].

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, prepuce: 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. 5O); 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. 6G); 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.