

# First *Alaocybites* weevil (Insecta: Coleoptera: Curculionoidea) from the Eastern Palaearctic: a new microphthalmic species and generic relationships

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## > Abstract

The genus *Alaocybites* (Coleoptera: Curculionoidea), previously consisting of two eyeless Californian species, is for the first time reported from the East Palaearctic Region. A new microphthalmic species, *A. egorovi* sp.n., is described from Primorsky Krai, the Far East of Russia. An early Late Pliocene Alaskan weevil fossil previously attributed to the molytine genus *Otibazo* is assigned to *Alaocybites* and found almost undistinguishable from *A. egorovi* sp.n. Results of preliminary phylogenetic analyses aimed to clarify phylogenetic affinities of *Alaocybites* are found controversial and inconclusive. The uncertainties of the contemporary classification of orthocerous weevils are briefly discussed. *Alaocybites* is provisionally retained in Raymondionymidae, with the absence of tarsomere IV on each leg being the family's most plausible apomorphy. Monophyly, geographical distribution and internal relationships of Raymondionymidae are briefly discussed and compared with other predominantly Mediterranean groups of eyeless beetles. External and genital morphological characters of edaphic weevils with reduced eyes habitually resembling, or thought to be related to, *Alaocybites* are extensively illustrated.

## > Key words

Weevils, Curculionidae, Raymondionymidae, *Alaocybites*, microphthalmic, leaf litter.

## 1. Introduction

While entomological net or beating sheet collecting methods have long been considered an indispensable tool for productive insect sampling, both the sifter and the Winkler/Berlese eectors came into use much later. This is indeed noteworthy since gathering and processing sifted leaf litter through eector normally generates a high number of cryptic, minute and otherwise difficult-to-obtain inhabitants of the forest floor litter, flood debris, or the upper soil layer. The delay in spreading this type of sifting technique throughout the entomological community has resulted in large geographical regions to have remained not, or inadequately, sampled with respect to their litter-associated, often wingless and microphthalmic insect inhabitants. This, in turn, suggests that unexpected and intellectually stimulating zoological discoveries are still to be

made with a sifter and an eector (SMETANA 1986; STÜBEN & ASTRIN 2009; ANDERSON 2010; BRANCUCCI & HENDRICH 2010; RIEDEL et al. 2010). One such discovery within the weevil realm is reported in the present paper.

When sorting my 2007 sifting samples obtained in the forests of the Russian Far East, I noticed two conspecific specimens of what looked like a small blind and noticeably unpigmented soil-inhabiting weevil (Figs. 1, 2). The initial discovery was remarkable since not a single anophthalmic weevil species had been previously recorded from the vast territory that includes Asian Russia, Mongolia, Korea and the whole of the P.R. China. The nearest known localities of truly anophthalmic weevils are northern Vietnam (monotypic *Anonyxmolytes* Meregalli & Osella, 2007,

Molytinae: Anchonini, but see Material and Methods for discussion on the tribal affinities), Nepal (*Cotasteroloebelis* Osella, 1983, Cossoninae: Dryotribini, with three species in Nepal and northern India), Kazakhstan (monotypic *Iliolus* Bajtenov, 1968, Cossoninae: Dryotribini) and USA: California (monotypic *Schizomicrus* Casey, 1905 and *Alaocybites* Gilbert, 1955 with two species; both genera currently assigned to Raymondionymidae). The most peculiar, however, was the fact that the Russian Far East specimens had a relatively long rostrum and at the same time lacked an uncus on the tibial apices (see discussion in THOMPSON 1992 on the ‘uncus’ versus ‘mucro’ dilemma), whereby it superficially resembled members of the consistently anophthalmic weevil family Raymondionymidae and, to a lesser degree, a handful of anophthalmic Erihinae. This was unexpected, as most Raymondionymidae inhabit the Mediterranean region and closely adjacent lands of the southeastern Palaearctic (Fig. 3); only three species in two genera (*Gilbertiella* Osella, 1982 and *Schizomicrus* Casey, 1905) are known from the western Nearctic. Five additional small genera of anophthalmic weevils are questionably assigned to Raymondionymidae: *Alaocybites*, see above; *Homosomus* Richard, 1956 with three species in Madagascar; *Bordoniella* Osella, 1987 with two species in Venezuela; monotypic *Neoubychia* Gilbert & Howden, 1987 from Mexico; and monotypic *Myrtonymus* Kuschel, 1990 from New Zealand. The second best guess was that the new beetles might belong to the Erihinae, which is known to include two anophthalmic genera in the Mediterranean Region (monotypic *Absoloniella* Formánek, 1913 from Bosnia-Herzegovina known by the type series and *Ruffodytes* Osella, 1873 with five species in Italy and Greece) and one monotypic microphthalmic genus described from the Russian Far East (*Himasthlophallus* Egorov & Zherikhin, 1991; Figs. 11, 12). Raymondionymidae and Erihinae, if they are indeed monophyletic, might be closely related to each other, and the former is sometimes included within the latter (MORRONE et al. 2001) and believed to be “hypogean derivatives” of Erihinae (KUSCHEL 1995: 23). OBERPRIELER et al. (2007) demoted both groups to tribe level and grouped them, together with Ocladiini and Cryptolaryngini, into Curculionidae: Brachycerinae *sensu lato* (not followed here; see section 2.1. on the classification consistently used in this paper).

The newly discovered beetles were found to have a compound eye consisting of a single ommatidium. Among some 62,000 weevils species (OBERPRIELER et al. 2007) very few are known to have a single ommatidium, such as some of the high altitude South American genus *Andesianellus* Anderson & Morrone, 1996 (Cyclominae: Rhythirini), or some of the speciose genus *Otiorynchus* Germar, 1822, e.g. *O. (Troglo-*

*rynchus) anophthalmoides* (Reitter, 1914) (Entiminae: Otiorynchini, P. Hlaváč pers. comm.). This feature suggested the two specimens from the Russian Far East not to belong to Raymondionymidae, since the total lack of eyes was one among the few potential synapomorphies unifying the latter family (THOMPSON 1992). The comparison of the specimens with some Erihinae, particularly with the sympatrically distributed *Himasthlophallus flagellifer* Egorov & Zherikhin, 1991, revealed their gross dissimilarity, which normally suggests a rather distant relationship. The issue of the generic affinities of the two 2007 specimens thus remained puzzling.

The collecting in 2008 of a few additional specimens from the same locality (Anisimovka village) and a much larger series from a locality some 130 km distant (‘Verkhnechuguevskiy Statsionar’ field station in the ‘Chuguevskiy Rayon’ administrative district of Primorsky Krai), allowed for intensive dissection and study of internal morphology, particularly the male and female genitalia. One of the most noticeable features discovered was the truly four-tarsomeric tarsi with tarsomere IV being completely absent (Fig. 1G). This character was suggested by THOMPSON (1992: 884) as an almost certain synapomorphy for Raymondionymidae. The shape of the tarsi also suggested that the new species could be attributed to this family, although no eyed Raymondionymidae species have ever been known (but see below on *Neoubychia*; Fig. 8I). On the other hand, the aedeagus of the new species (Fig. 1H) was most dissimilar to that of Raymondionymidae, which is believed to be the ‘primitive’ pedotectal type (Figs. 7D,E, i.e. aedeagus with “...well preserved and plate-like, sclerotized tectum, separated from the pedon by lateral membranes along its whole length...”; WANAT 2007: 155). In addition, the male sternite VIII of the Far East specimens (Fig. 1I) consisted of two hemisternites and was lacking an apodeme (Fig. 1I; “spiculum relictum” of THOMPSON 1992: 842), which differs from the condition in Raymondionymidae (Fig. 7B).

At this stage it became obvious that a significant effort is required to assess the affinities of this new bizarre-looking one-faceted Far Eastern weevil species. With loans of various museum specimens of similar and, therefore, potentially related weevils (see Material and Methods below) little progress had been achieved until I saw specimens of the Californian *Alaocybites californicus* Gilbert, 1956 (Figs. 4, 5). This is the type species of the genus, which had been described as the sister taxon to all the remaining Raymondionymidae (GILBERT 1956), then was explicitly transferred to Curculionidae: Molytinae: Lymanini (OSELLA 1977: 147; “...il suo posto più naturale accanto al genere *Typhloglymma*...”, *Typhloglymma* Dury, 1901 = *Lymanites* Schoenherr, 1838) to be par-

ticularly linked with the Venezuelan genus *Bordoniola* Osella, 1987 (see OSELLA 1987), and then was explicitly returned to Raymondionymidae (THOMPSON 1992: 884), where both *Alaocybites* and *Bordoniola* currently remain (ALONZO-ZARAZAGA & LYAL 1999). True to the original description, specimens of *A. californicus* had no ommatidia (Fig. 4D), although in any other ways they markedly resembled the Far Eastern species. A study of *A. californicus* male genitalia (Fig. 4B–E; previously not depicted) revealed a remarkable similarity with the Far Eastern species and somewhat disagreed with THOMPSON'S (1992: 884) observation that this genus "...has similar genitalia and sternite 8..." to the rest of Raymondionymidae. It became, therefore, obvious that the Far Eastern species is closely related to *A. californicus* from North America.

Finding out at this stage that *Alaocybites* is morphologically noticeably dissimilar to the majority of Raymondionymidae, including the shape of male genitalia, led me to doubt the monophyly of Raymondionymidae. Having male genitalia of pedal type (i.e. without distinctly separated dorsal tectum and ventral pedon; previously commonly referred to as 'orthocerous'; see below for terminology) was a uniquely optimised morphological synapomorphy uniting the entire Curculionidae (*sensu* THOMPSON 1992; or, alternatively, its most speciose clade in the more inclusive definition of this family, KUSCHEL 1995; MARVALDI et al. 2002; OBERPRIELER et al. 2007). Monophyly of this clade was further strengthened by the characters of the male sternite 8, which is almost always divided into a pair of hemisternites in true Curculionidae (*sensu* THOMPSON 1992), versus being predominantly undivided and having an apodeme in the remaining weevils. *Alaocybites californicus* turned out to have a pedal-type aedeagus (Fig. 1H) and a sternite VIII subdivided into two hemisternites (Fig. 1I); in addition an apodeme on sternite VIII was lacking – all features as in the new Far Eastern species.

Having associated the Far Eastern species with *Alaocybites*, I was left with a gross uncertainty about the phylogenetic affinities of this genus. Two previous hypotheses suggested that it was either a member of Curculionidae: Molytinae: Lymantini (OSELLA 1977: 147; 1979) or of Raymondionymidae (THOMPSON 1992). Whereas based on current views on Curculionoidea phylogeny these hypotheses are grossly incompatible, GILBERT (1956), when describing *Alaocybites*, stated that the group presently called Raymondionymidae might be most closely related to the Molytinae tribe Lymantini ("Anchonini" in GILBERT 1956). To add to this confusion, neither Raymondionymidae nor Lymantini (or even Molytinae) have ever been demonstrated to be monophyletic in a formal cladistic analysis. Recent attempts to utilize DNA se-

quence data for phylogenetic purposes in weevils are highly promising (MCKENNA et al. 2009 and references therein), although the sampling done so far was not extensive enough to include any of the taxa here concerned (*Alaocybites*, any Raymondionymidae, any Erihrinidae with reduced eyes, any Lymantini). To make things worse, a significant number of 'higher' weevil taxa analysed using DNA sequence data (i.e. HUNSDOERFER et al. 2009; MCKENNA et al. 2009) have not been shown as monophyletic or having a clearly delimited sister-group. The *Alaocybites* phylogenetic affinities, therefore, were most unsatisfactorily understood.

This paper has several goals, all related to, or triggered by, the unexpected discovery of the soil-dwelling *Alaocybites* in the Asia Pacific Region and subsequent difficulties experienced when trying to assign the genus into the weevil taxonomic framework. The first goal is to illustrate and describe the new species and to amend the generic diagnosis in order to incorporate this microphthalmic species in the genus previously known to be comprised exclusively of eyeless species. The second goal is to compare *Alaocybites* with some other and, in part, potentially related micro- and anophthalmic soil-dwelling weevils and thus document many morphological characters for these mostly poorly studied taxa. The third goal is to attempt, through cladistic analysis, to place *Alaocybites* into the weevil system. Overall this paper illustrates the highly insufficient state of present-day weevil higher taxonomy when family/subfamily limits remain poorly defined and the same genus may become assigned to various higher categories. This means that at least some (if not the majority) of the 'higher' orthocerous weevil families and subfamilies are potentially either non-monophyletic, or lack a clearly identified sister-group. The work here reported furthermore is an exemplary case of far-reaching consequences triggered by sifting forest leaf litter in a remote and under-sampled corner of the Asia Pacific.

## 2. Material and methods

### 2.1. Terminology and taxonomic conventions

The terminology for male genitalia follows WANAT (2007), while the terms 'pedal' and 'pedotectal' follow ALONZO-ZARAZAGA (2007) to substitute the somewhat misleading terms 'orthocerous' and 'gonatocerous' in application to aedeagal structures. The

terminology for female genitalia mainly follows HOWDEN (1995).

Assignment of weevils to higher taxonomic units conventionally follows ALONSO-ZARAZAGA & LYAL (1999), i.e. with orthocerous weevils like Raymondionymidae, Eriirhinidae and some other groups with predominantly pedotectal male genitalia treated as families outside of Curculionidae *sensu stricto*, them having predominantly pedal male genitalia. This classification differs from the one adopted by MARVALDI et al. (2002) and OBERPRIELER et al. (2007), in which the family Curculionidae is delimited *sensu lato* to include all orthocerous weevils (except Nanophyinae), regardless of the genitalia type, and to form a well-defined sister-group to Brentidae *sensu lato*. The genus *Sosgenes* Broun, 1893 has been recently transferred from Cyclominae to Molytinae (OBERPRIELER 2010). The genera *Anonyxmolytes* and *Otibazo* were recently thought not to belong to Anchonini and were vaguely attributed to Molytini (MEREGALLI & OSELLA 2007); both tribal affiliations were made without providing supporting evidence and in the present paper both genera are conventionally kept in Anchonini.

## 2.2. Sources, label data and handling of specimens

All specimens studied for this project are stored in the Canadian National Collection of Insects, Arachnids and Nematodes, Ottawa, Canada (CNC, curator Patrice Bouchard), unless otherwise stated. The collection abbreviations used in the text are: CMN (Canadian Museum of Nature, Ottawa, Canada, curator Robert Anderson) and SBMNH (Santa Barbara Museum of Natural History, Santa Barbara, USA, curator Michael S. Caterino).

Label data and depository information (CNC, except as noted) for weevils examined and illustrated: **Brentidae**: *Arrhenodes minutus* (Drury, 1770), Canada, Ontario, Pinery Provincial Park, 26.viii.2008, V. Grebennikov. **Raymondionymidae**: *Alaocybites californicus* Gilbert, 1956, USA, California, Mendocino Co., 10 mi SW Legget, 20.i.1989, S. O'Keffe (CMN), Figs. 4, 5; *Raymondionymus orientalis* Hervé, 1949, Italy, Colle Melosa, Liguria Region, vii.1975 [no collector], Fig. 7; *Gilbertiolla helferi* (Gilbert, 1956), USA, California, Del Norte Co., 18 km N Crescent City, 31.v.2003, S. Peck (CMN), Fig. 8; *Neobychia mexicana* Gilbert & Howden, 1987, Mexico, Hidalgo, 55 km NE Jacala, 4.vi.1987, R. Anderson (CMN), Fig. 9; *Schizomicrus caecus* (Casey, 1892), USA, California, Sonoma Co., Hwy 116 near Duncan Mills

19.i.2007, M. Caterino & S. Chatzimanolis (CNC & SBMNH), Fig. 10; *Myrtonymus zelandicus* Kuschel, 1990, New Zealand, Auckland, Lynfield, 6.v.1980, G. Kuschel, Fig. 11. **Eriirhinidae**: *Himasthlophallus flagellifer* Egorov & Zherikhin, 1991, Russia, Primorsky Krai, Benevskoe vil., 4–7.vii.2008, V. Grebennikov, Figs. 12, 13. **Cossoninae**: *Barretonus minor* Folwaczny, 1972, Spain, Madeira, 2.5 km N Vila Baleira, 28.iii.2008, P. Stüben & J. Astrin, Fig. 14. **Cryptorhynchinae**: *Torneuma deplanatum* (Hampe, 1864), Italy, Sicilia, 6 km SW Carini, 9.x.2006, P. Stüben, Fig. 15. **Molytinae**: *Otibazo* sp., Japan, Nara, 27–31.vii.1980, Cl. Besuchet, Fig. 16; *Caecossonus dentipes* Gilbert, 1955, USA, Florida, Monroe Co., No Name Key, 5.viii.1971, S. Peck, Fig. 17; *Lymantes scrobicollis* Gyllenhal, 1838, USA, Arkansas, Pulaski Co., Pinnacle Mt., 26.xi.1987, C. Carlton (CMN), Fig. 18; *Reyesiella caecus* Broun, 1893, New Zealand, Far North District, Waipoua Forest, 20.iii.1978, 370 m, S. & J. Peck (CMN), Fig. 19; *Sosgenes carinatus* Broun, 1893, New Zealand, Far North District, Omaha State Forest, 18.iii.1978, 300 m, S. & J. Peck (CMN), Fig. 20.

For the study of the internal structures beetle specimens were kept overnight in warm proteinase K-Buffer ATL solution, as described in 'DNeasy Blood & Tissue Handbook', which served as a more gentle equivalent to the widely used beetle treatment of a 5–10% KOH water solution (A. Riedel, pers. comm.). Disarticulated specimens were either mounted on microscope slides in Euparal, or stored in glycerol in small vials pinned on entomological pins. Some specimens were disarticulated, macerated in warm 5–10% KOH water solution, rinsed with isopropanol, mounted in drops of Canada balsam on plastic rectangulars and then pinned on entomological pin. For electron microscopy, beetles were glued by the dorsal side to the point of an entomological pin, which was then inserted into a horizontally-oriented holder allowing some tilting (up to 25 degrees) and 360 degree rotation when taking images.

## 2.3. Illustrations

Morphological illustrations were organized on plates using three different image sources: (1) coloured images obtained with a Nikon DXM1200F digital camera attached to a Nikon SMZ1500 stereo dissecting microscope; (2) greyscale Philips XL30 environment electron scanning microscope (ESEM) micrographs; (3) line drawings of dissected beetle genitalia prepared with a compound microscope and a camera lucida. Colour habitus images were captured at different

focal depths and then were automatically combined into a single all-sharp image using CombineZ5 software (HADLEY 2006). Some illustrated specimens were designated with unique labels of the following format: “CNCCOLVG000xxxxx”; the last “xxxxx” corresponding to the same five digits in brackets used in the figure captions linking an illustration to a particular specimen.

#### 2.4. Phylogenetic analyses: rationale, methodology, terminals' choice and data matrices

Eight individual phylogenetic analyses were carried out using two different datasets.

**Analyses 1–4** (Tab. 2) were based on a matrix consisting of 16 taxa and 23 characters (of which two were deactivated, leaving only 21 parsimony informative characters, see Tab. 1) evaluated with four alternative combinations of character treatments: successively weighted (FARRIS 1969) versus equally weighted and some multistate characters ordered versus unordered. This data matrix included two named *Alaocybites* species and has been specifically designed to test (A) the monophyly of the genus and (B) two previously proposed hypotheses suggesting that *Alaocybites* is closely related to either Raymondionymidae or Curculionidae: Molytinae: Lymanitini (see Introduction). Since monophyly of both groups has never been previously tested, they were represented by their type genera (*Raymondionymus* Wollaston, 1873 and *Lymanites* Schoenherr, 1838, respectively), and supplemented further by taxa normally considered phylogenetically close to them. Raymondionymidae was additionally represented by the genera *Neoubychia* Gilbert & Howden, 1987, *Gilbertiola* Osella, 1982, *Schizomicrus* Casey, 1905 and *Myrtonymus* Kuschel, 1990; Lymanitini was supplemented by members of the more inclusive Molytinae + Cryptorhynchinae + Cossoninae clade (KUSCHEL 1987): *Barrettonus* Roudier, 1958 (Cossoninae), *Torneuma* Wollaston, 1860 (Cryptorhynchinae), *Otibazo* Morimoto, 1961 and *Caecossonus* Gilbert, 1955 (both Molytinae). The Erirhinidae genus *Himasthlophallus* Egorov & Zherikhin, 1991 from the Far East of Russia, previously known from the type series only, has been recently re-discovered and added in the analyses. *Reyesiella* Alonso-Zarazaga & Lyal, 1999 (= *Idus* Broun, 1893; Molytinae: Phrynixini) and *Sosgenes* Broun, 1893 (Molytinae incertae sedis), both endemic to New Zealand, have adults with a single ommatidium noticeably resembling those of *Alaocybites* and

were also added to the analysis. The obtained trees were rooted on *Arrhenodes minutus* (Drury, 1770) (Brentidae). Since *Alaocybites* is a markedly modified soil dweller with a number of reductions, the first four analyses included only wingless and predominantly ano- or microphthalmic leaf litter and soil dwellers (except for Brentidae, where no microphthalmic species are known). Male genitalia characters of *Myrtonymus zelandicus* Kuschel, 1990, the smallest known weevil with a body length of about 0.7–0.8 mm, were not studied but scored from its original description. The main limitation of this analysis is that it has been relatively narrowly aimed and included just a handful of taxa and characters.

**Analyses 5–8** (Tab. 2) were designed to test the fit of *Alaocybites* into a wider weevil framework by re-using MARVALDI et al.'s (2002) matrix, which contains 103 terminal taxa and 115 larval and adult morphological characters. To this the following string of *Alaocybites* adult character scores was added (character numbers in brackets and in bold): “-” for the first 37 characters (all larval characters), then **(38–40)**: 1?1; **(41–50)**: 01111?2?0?; **(51–60)**: 113010000?; **(61–70)**: 000?111??0; **(71–80)**: ----11000; **(81–90)**: 1001?0101?; **(91–100)**: 0010110020; **(101–110)**: 210?11102?; **(111–115)**: ----. The description of character #105 in MARVALDI et al. (2002) erroneously referred to females, while it concerns males (and was correctly scored for males in the 2002 matrix) and should read: “#105. Spiculum relictum or apodeme of male sternite 8: (0) present; (1) vestigial or absent (THOMPSON 1992: 842).” (A. Marvaldi pers. comm.). A number of the newly scored *Alaocybites* character states are illustrated on Figs. 1 and 2 with the respective structure indicated by an arrow accompanied by “M” (= MARVALDI et al. 2002) and then the character number followed, after a slash, by the character state. Analyses 5 and 6 used all 115 characters; analyses 7 and 8 used only adult characters 38–115. Characters were equally weighted in analyses 5 and 7 but successively weighted in analyses 6 and 8 (see Tab. 2). The trees obtained were rooted using *Dendrobium* sp. (Cerambycidae). The main limitation of these four analyses was that neither Raymondionymidae nor Lymanitini, previously regarded as being related to *Alaocybites*, were represented in the matrix. Another limitation was that the majority of the included taxa were not soil-dwellers and, therefore, this matrix was not accommodating for the possible bias caused by the morphological adaptations of *Alaocybites* to life in the soil.

Three software packages were employed to perform phylogenetic analyses. Hennig86 (FARRIS 1988) was used to search for the shortest (= most parsimonious) trees (single heuristic search; commands “mh\*” and “bb\*”) and then to perform successive approxi-

mations (FARRIS 1969; executed by a string of commands “xs w”, “mh\*” and “bb\*” repeated in cycles until the tree statistics stabilises). Branch support was assessed using Nona 2.0 (GOLOBOFF 1999) through bootstrapping 1000 randomly generated trees. Winclada (NIXON 2002) was used as a shell program to construct the matrix and to communicate with both Hennig86 and Nona.

## 2.5. Problems and limitations to phylogenetic work

Before proceeding further some additional, general problems and limitations of the phylogenetic efforts undertaken herein should be highlighted.

First, Curculionidae (either *sensu stricto* or *sensu lato*) is an enormously diversified family of the Animal Kingdom, second only to the rove beetles (Staphylinidae) (GREBENNIKOV & NEWTON 2009). Unlike Staphylinidae, however, weevil higher classification became a subject of focused studies based on the cladistic methodology only relatively recently. As a consequence the monophyly and interrelationships of many weevil family-group taxa are far from being adequately tested (see Introduction). This unavoidably and negatively affects any discussion pertaining to weevil phylogeny, and introduces much uncertainty in the choice of taxa to be included in analyses (FRANZ & ENGEL 2010).

The second significant limitation was the relatively small body size combined with a low number of specimens available. This prevented me from scoring some minute structures requiring dissection, such as ventral mouthparts or female genitalia.

A third difficulty was that the majority of weevils studied, dissected and illustrated for this project had significant morphological modifications as a result of inhabiting leaf litter and/or soil. This reduced the number of available informative morphological characters, such as eye and wing venational characters, and the results of the analyses might be affected by the high likelihood of convergence due to the edaphic way of life.

The fourth significant shortcoming of all analyses performed below is the limitation of available data. Larvae of *Alaocybites* and Lymantini are completely unknown, while only one Raymondionymidae species has its larva described (RÉMILLET 1968). No DNA sequencing, to the best of my knowledge, has ever been done to any of the ingroup taxa of the analyses 1–4 (Tab. 1). The analyses performed herein are, therefore, necessarily limited to the adult morphological characters.

The fifth shortcoming was that specimens of some eyeless weevils externally resembling *Alaocybites* were mostly known from the type series only and, therefore, could not be feasibly obtained to be incorporated in the analysis. Such are the members of the following edaphic genera: *Absoloniella* Formánek, 1913 with two species from Bosnia-Herzegovina (Eirrhinidae); *Bordoniola* Osella, 1987 with two species in Venezuela (Raymondionymidae); *Homosomus* Richard, 1956 with three species endemic to Madagascar (Raymondionymidae); *Ruffodytes* Osella, 1973 with five species in Italy and Greece (Eirrhinidae). The unavailability of *Bordoniola* is particularly regrettable, as this genus has been mentioned as a potential sister-group of *Alaocybites* (see OSELLA 1987).

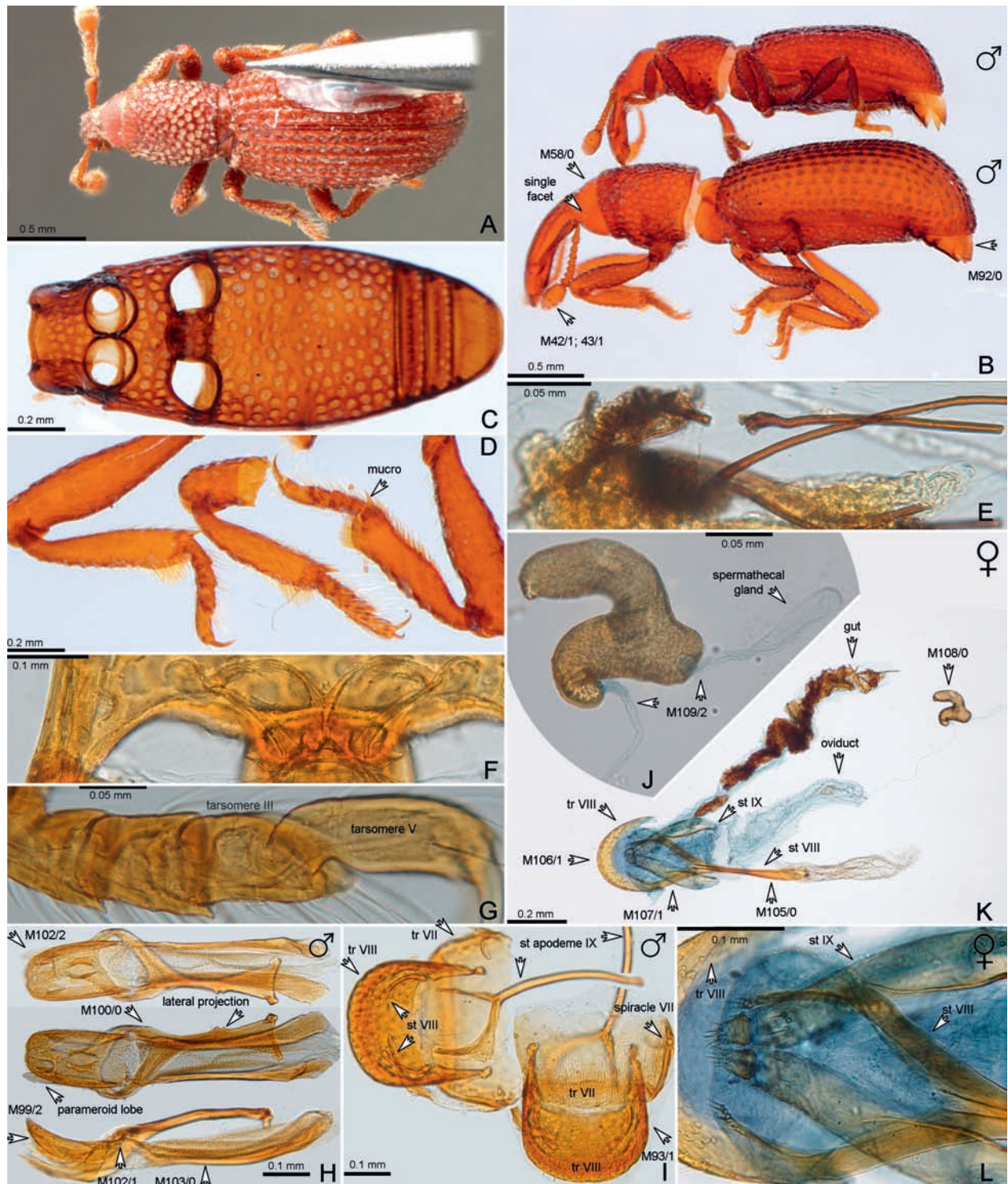
Summing up, the topology-building exercises reported in this paper should be mainly seen as an attempt to introduce, document and illustrate morphological characters of some poorly-known and rarely collected micro- and anophthalmic weevils. This should serve as a step towards a proper future analysis, rather than to be taken as the most plausible phylogenetic conclusion. By stating this I hope to avoid being criticized for performing an analysis with so many shortcomings, as those described above (see, for example, FRANZ & ENGEL 2010). I trust, however, that executing and reporting a clearly documented and fully transparent topology-building attempt is still more beneficial than not doing so.

## 3. Taxonomy

### 3.1. *Alaocybites* Gilbert, 1956

Figs. 1, 2, 4, 5

**Description.** GILBERT's (1956) generic description of the external morphological characters is adequate. Only a single amendment is needed in view of the findings here reported: the eyes in *Alaocybites* are either completely absent, as in the two previously known Californian species, or represented by a single ommatidium, as in the newly described East Palaearctic species (and also in the Alaskan *Alaocybites* fossil, see below). GILBERT (1956) also did not mention that the tarsi are truly tetramerous with tarsomere IV completely absent (Figs. 1G, 4N), and that the maxillary palp consists of, apparently, three palpomeres (Fig. 4J). He also did not mention the proventriculus, which is well-sclerotized and clearly distinguishable. Moreover, *Alaocybites* male and female genitalia have nev-



**Fig. 1.** *Alaoxybites egorovi* sp.n. (Raymondionymidae); unsexed specimens (A,C–G), male (B,H–I), female (J–L); light microscopy. Numbered arrows point to characters of MARVALDI et al.'s (2002) data matrix (= M; numbers = character / state) as scored for analyses 5–8 herein. Abbreviations: tr = tergite, st = sternite. **A:** habitus, dorsal; **B:** habitus, lateral; **C:** meso- and metaventrum and abdominal ventrites, legs and internal structures removed, ventral; **D:** disarticulated left fore (right), middle (center) and hind (left) leg; **E:** gut content; **F:** metendosternite, internal dorsal; **G:** tarsus, **H:** aedeagus and tegmen, dorsal (above), ventral (middle) and lateral (below); **I:** tergites VII and VIII and sternites VIII and IX, ventral (left & above) and dorsal (right & below); **J:** spermatheca; **K:** female genital chamber, ventral; **L:** apical part of female genital chamber, ventral.

er been adequately described; the description below is based on the type species *A. californicus* and the newly described East Palaearctic species; no specimens of the Californian *A. rothi* Gilbert, 1956 have been seen.

**Male genitalia** (Figs. 1H,I, 4B–E) with sternite VIII consisting of two hemisternites, sternal apodeme VIII absent. Sternite IX V- or U-shaped with sternal apodeme IX about twice as long as sternite itself. Tergites

VII and VIII complete, tergite IX absent. Aedeagus of pedal type with aedeagal tectum not distinguishable; dorsal part of aedeagus membranous with aedeagal pedon forming a spoon-like structure containing 2 longitudinally oriented internal sclerites. Aedeagal apodemes about twice as long as aedeagus, gradually widening distad. Tegmen narrowly encircling aedeagus, fully closed dorsally, with 2 asetose and weakly sclerotized parameroid lobes; tegminal apodeme extending some 3/4 of aedeagal apodemes, noticeably widening distad; with small asymmetrical lateral projection at middle of its left side. **Female genitalia** (Figs. 1K,L, 4F–H) with sternite VIII V-shaped, sternal apodeme about sub-equal in length to sternite VIII. Sternite IX consisting of two hemisternites, each formed by a sub-quadrate smaller setose apical part ('stylus') and a much larger basal part ('coxite'). Tergite VII complete, tergite IX absent. Spermatheca with attachments of spermathecal duct and spermathecal gland distantly separated.

**Differential Diagnosis.** Specimens of the three known extant *Alaocybites* species can be easily distinguished from the vast majority of weevils by the remarkable eye reduction leaving either one (the newly described East Palearctic species) or no externally visible eye facets (both Californian species). From similarly shaped micro- or anophthalmic weevils of the Cossoninae-Molytinae radiation (OBERPRIELER et al. 2007; = Cossoninae-Molytinae-Cryptorhynchinae radiation of HOWDEN 1992), *Alaocybites* differs by having the legs armed only with a short 'mucro'-type projection originating from the inner tibial edges and without a large 'uncus'-type projection normally originating from the outer tibial edge. From similarly shaped micro- or anophthalmic Entiminae, *Alaocybites* differs by having a relatively longer rostrum, by the antennal attachment not completely visible and open when viewed from above, and by the lack of the mandibular scar indicating presence of the deciduous process. From similarly shaped micro- (*Neoubychia* Gilbert & Howden, 1987) and anophthalmic (all other) Raymondionymidae, *Alaocybites* can be distinguished by a 7-segmented antennal flagellum in combination with the presence of a short 'mucro'-type projection upon the inner tibial edge. The monotypic genus *Schizomicrus* (Raymondionymidae) is sympatric with both Californian *Alaocybites* species and is similar to *Alaocybites* in both aforementioned characters; adults of *Schizomicrus* can be immediately distinguished from those of *Alaocybites* by having a distinct prosternal depression (Fig. 10D,M). Among similarly shaped anophthalmic (*Absoloniella* Formáněk, 1913 and *Ruffodytes* Osella, 1973) and microphthalmic (*Himasthlophallus* Egorov & Zherikhin, 1991) Eriirhinidae, *Alaocybites* can be distinguished by hav-

ing male genitalia of pedal type and male sternite VIII consisting of two hemisternites and lacking an apodeme (Fig. 1I versus Fig. 13C).

**Recent distribution and fossil record.** Recent species of *Alaocybites* are known from two widely separated regions: California and the southern part of the Sikhote-Alin Mountains in Primorsky Krai, Russia (Fig. 3). A Pliocene (3 ma B.P.) *Alaocybites* fossil has been reported from the Alaskan Lost Chicken gold mine (MATTHEWS & TELKA 1997: 942, fig. 3g) under the name "*Otibazo* sp.". The true genus *Otibazo* Morimoto, 1961 (Fig. 16) currently comprises two described and a number of undescribed narrowly localized wingless species, all endemic to Japan (MORIMOTO 1982 and pers. comm.). Based on its incorrect identification as "*Otibazo*", this fossil *Alaocybites* was given as an example of the puzzling generic distribution of poorly dispersing wingless weevils (PORCH & ELIAS 2000; MATTHEWS et al. 2003; MEREGALLI & OSELLA 2007; ELIAS 2009). The original report of this fossil depicts its head laterally (without antennae) with all accessible morphological characters nearly identical to the new *Alaocybites* species described below.

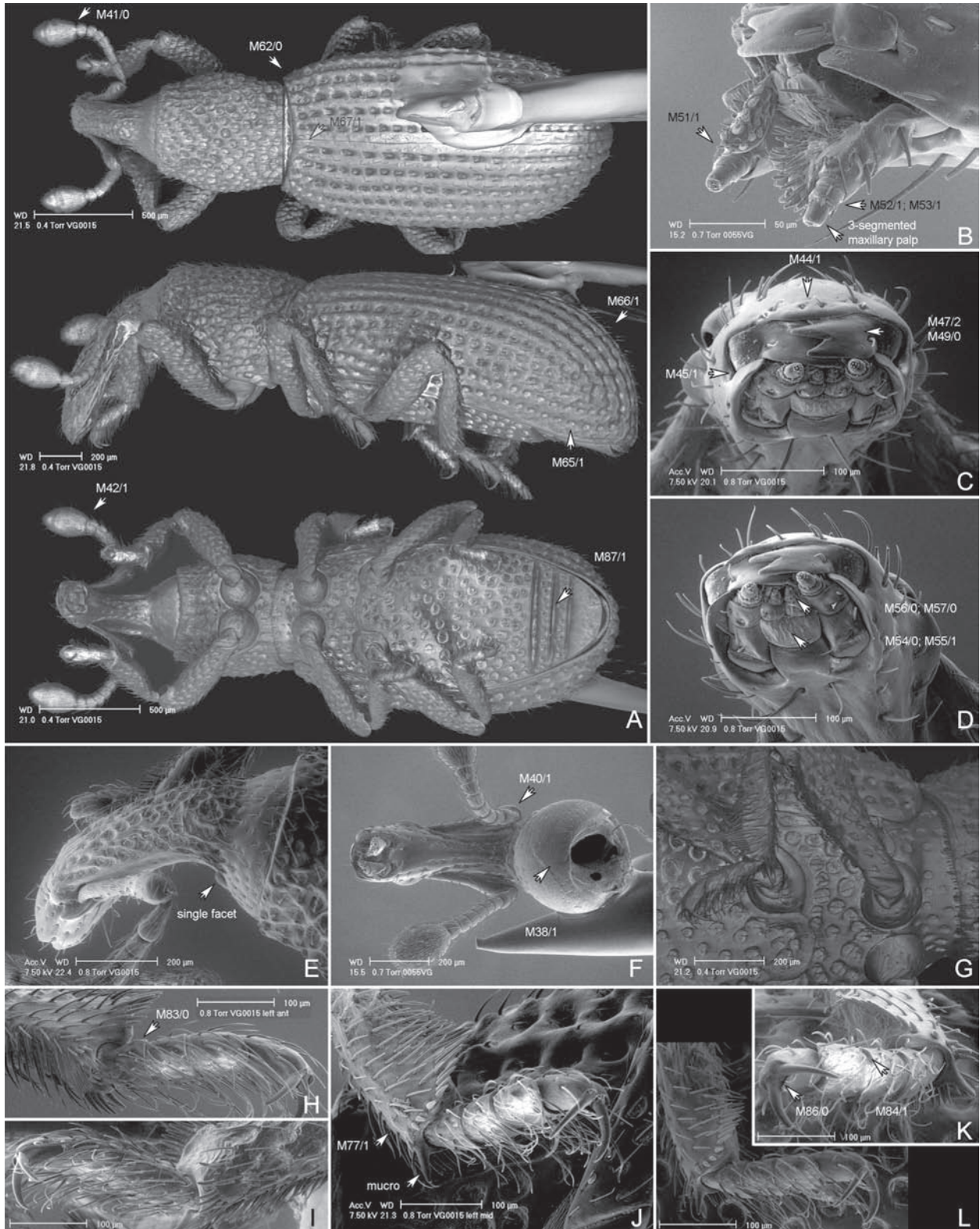
### 3.2. *Alaocybites egorovi* sp.n.

Figs. 1, 2

**Differential Diagnosis.** *Alaocybites egorovi* can be easily distinguished from both completely eyeless extant congeneric species by the presence of a single eye facet on each side of the head (Fig. 2E). No reliable morphological features are known to distinguish *A. egorovi* and the Alaskan fossil *Alaocybites* species known from a single head.

**Description.** Body length (from base of rostrum to elytral apex as seen from above): 2.32 mm (2.15–2.40 mm; n=10; holotype: 2.4 mm). **Eyes** consist of a single ommatidium on each head side. **Rostrum** widening apicad, with 6–8 semi-regular longitudinal rows of setiferous punctures forming 2–4 short keels between antennal insertions; basal part of rostrum ventrally with 2 pairs of longitudinal rows of setiferous punctures and with 2 longitudinal keels between each pair; dorsal surface of apical rostral part (frons) with 2 longitudinal rows of 3 setae inclined medially and with 5 setae at anterior edge. **Scrobe** gradually widening proximad to about twice its apical width; not extending to ventral side. **Antennae** without distinct ridges, antennomere I (scape) sub-equal in length to antennomeres II–VIII (flagellum); antennomere II

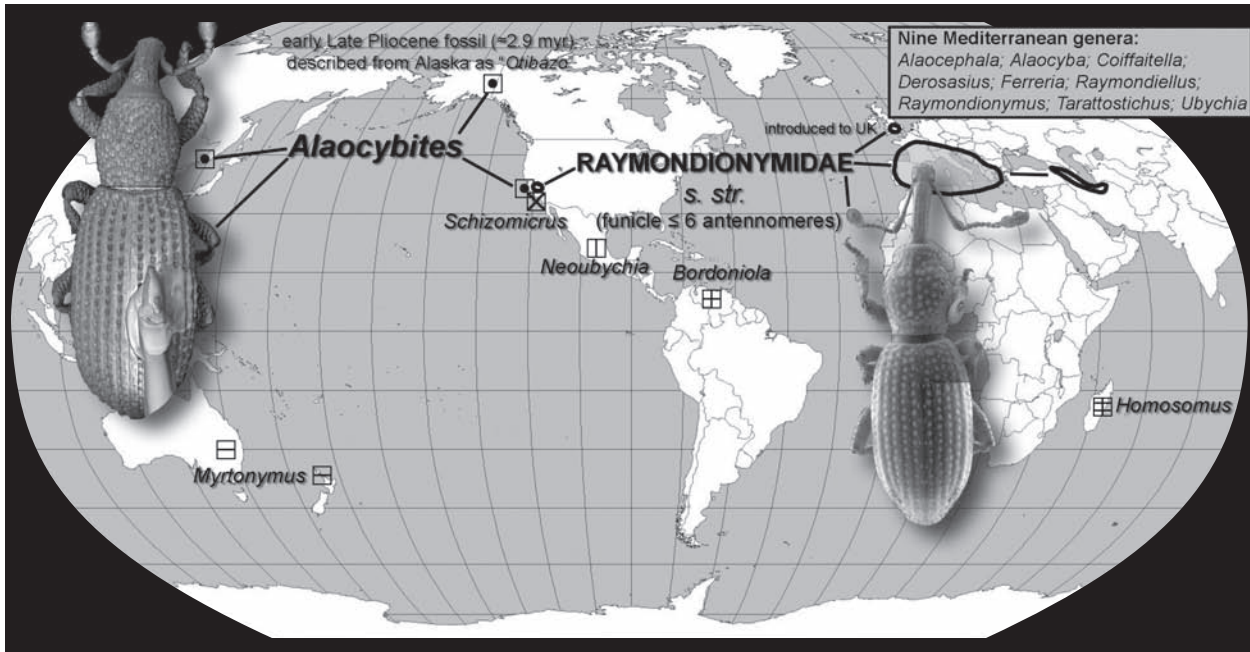




**Fig. 2.** *Alaoocybites egorovi* sp.n. (Raymondionymidae); unsexed specimens #00015 (A,C–E,G–L) and #00055 (B,F); ESEM. Numbered arrows point to characters of MARVALDI et al.’s (2002) data matrix (= M; numbers = character / state) as scored for analyses 5–8 herein. **A:** habitus, dorsal (above), lateral (middle) and ventral (below); **B–D:** mouthparts, lateral (B, ventral mouthparts forcibly opened), frontal (C) and ventro-lateral (D); **E,F:** head, dorso-lateral (E) and ventral (F); **G:** meso- and metathorax, ventro-lateral; **H,I:** fore left tarsus, anterior (H) and posterior (I); **J:** middle left tarsus, latero-posterior; **K:** hind right tarsus, postero-ventral; **L:** hind left tarsus, postero-ventral.

(first flagellar antennomere) about 1.2 × length of antennomeres II and III combined; antennomeres II–VII

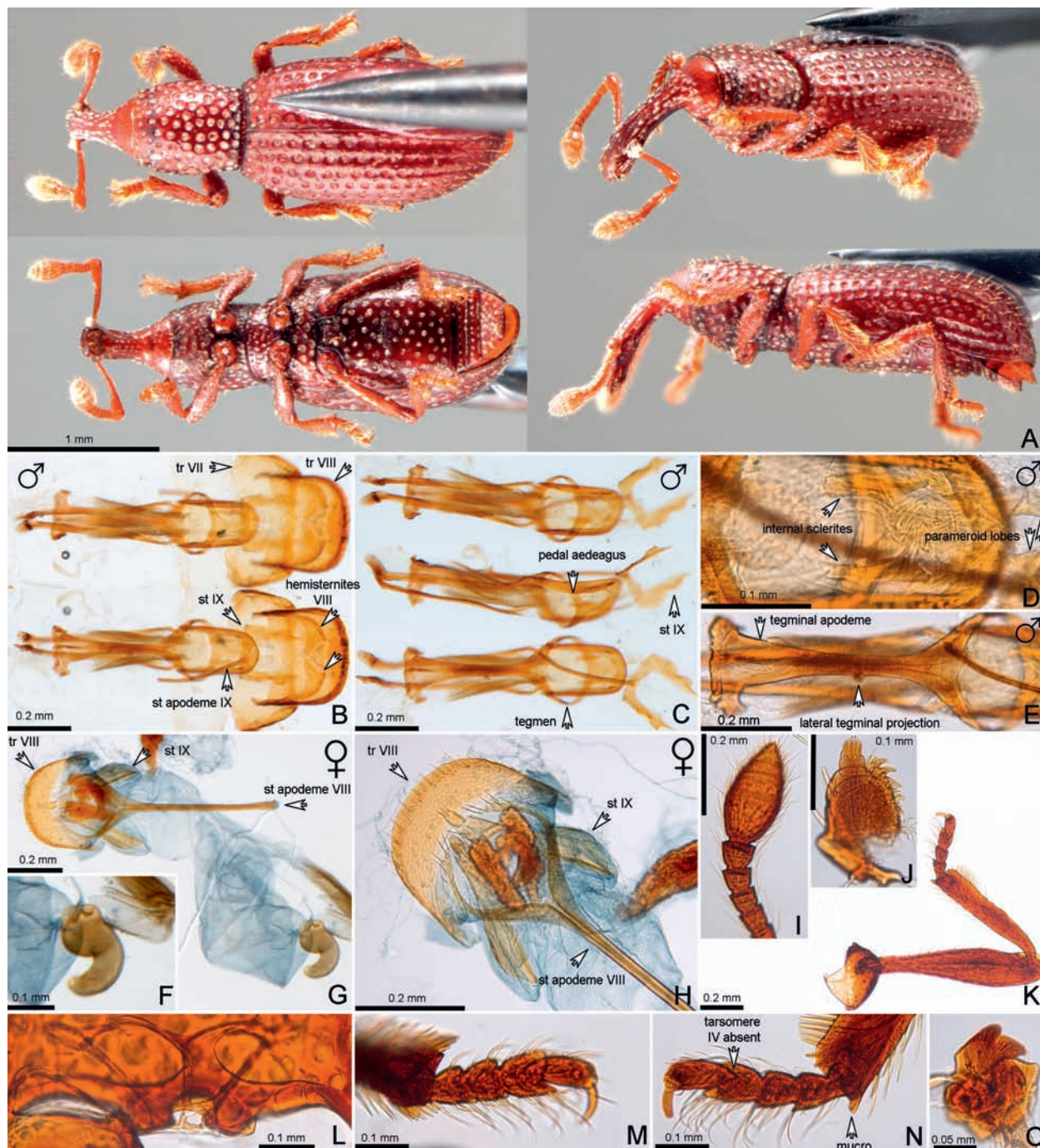
gradually increase in width and decrease in length; club distinctly transversely subdivided into four sub-



**Fig. 3.** World distribution of Raymondionymidae weevils (sensu ALONZO-ZARAZAGA & LYAL 1999). Solid line encircles distribution of Raymondionymidae s.str. (funicle consisting of six or less antennomeres). Note that all Raymondionymidae s.str. genera, except for the Californian *Gilbertiola*, are restricted to the Mediterranean Region (with a presumably human-assisted introduction to the United Kingdom: THOMPSON 1995).

parts with the proximal sub-part forming about 40% of club length. **Mandibles** with 3 sub-equal distinctly shaped apical teeth and with a seta on lateral surface. **Prothorax** nearly cylindrical in shape and almost circular in cross-section, slightly flattened dorsally; dorsal length sub-equal to dorsal maximal width (although appearing rather elongate); about 1.3 × longer dorsally than ventrally; covered with punctures, each bearing a single seta directed dorso-anteriorly and inclined at about 45°; distance between punctures sub-equal to 0.5–1 diameter of individual puncture; dorsal length of pronotum accommodates about 12 individual punctures in irregular longitudinal row, lateral length accommodates about 10 punctures; prothorax with straight anterior and posterior edges when viewed dorsally, widest at middle; ocular lobes absent. **Legs** with trochanter distally oblique, thus femur dorsally sub-contiguous to coxa; femora slightly bent outwards, not grooved to accommodate tibia in repose; punctured similar to most of body; with anterior and posterior oblique rows of about 9 fossorial contiguous setae; 3 further shorter fossorial setae located between the row and ventral projection of tibia; tarsomeres sub-cylindrical, not widened and without adhesive surfaces; 3 proximal tarsomeres with numerous setae about 2 × as long as individual tarsomere and directed parallel to claws; both proximal tarsomeres distally abruptly transverse, tarsomere III deeply notched dorsally and obliquely joined distally with distal tarsomere; claws not joined or notched at base. **Meso- and metathorax** with numerous irregu-

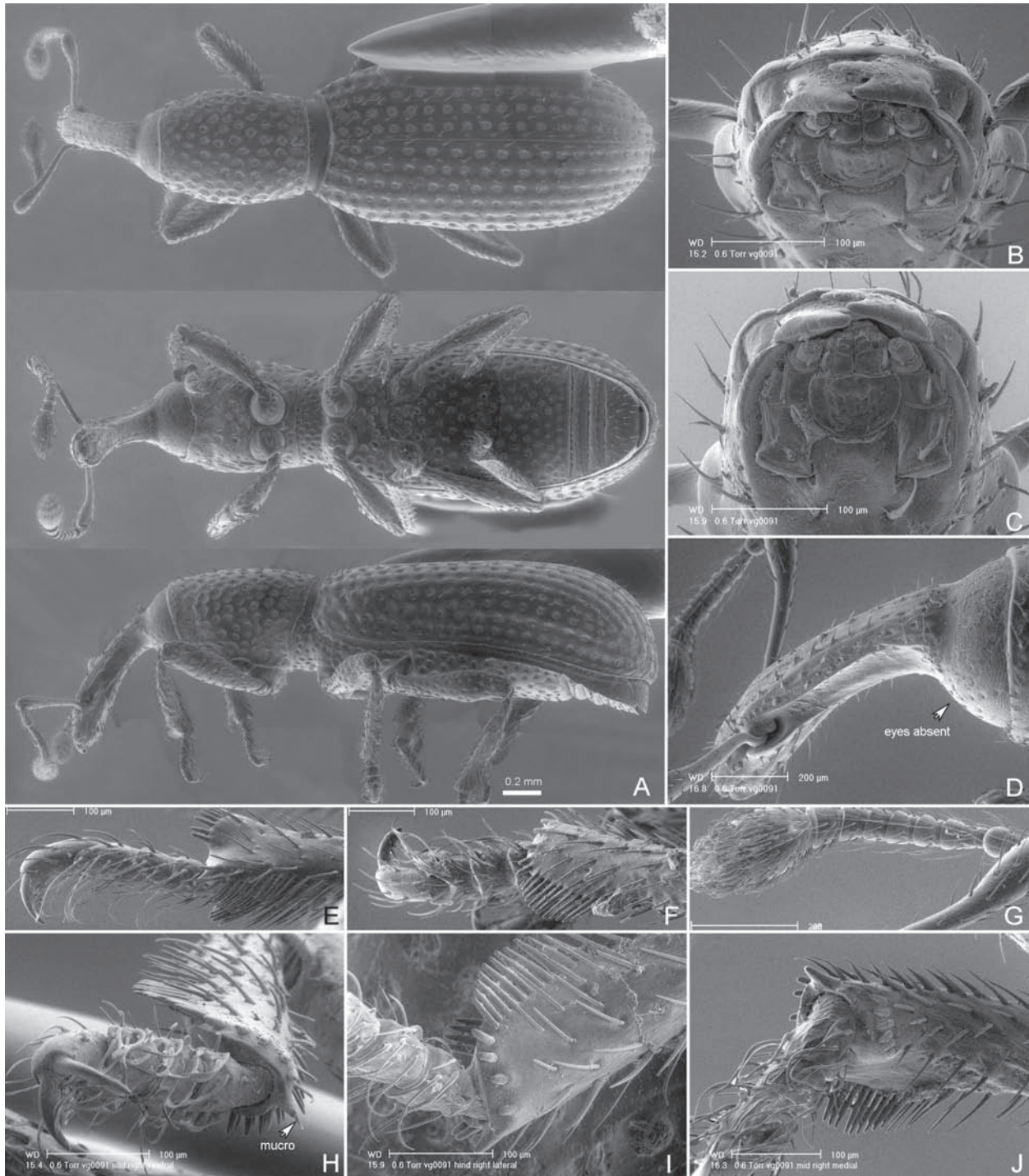
lar setiferous punctures; mesocoxae sub-contiguous and separated by about 1/10 of mesocoxal diameter, separation formed by anterior projection of metaventrum and posterior projection of mesoventrum; mesepisternite and mesepimerite not demarcated from each other; metepisternite partly covered by elytra, its exposed part parallel-sided and about 8–10 × as long as wide, metepimerite not demarcated externally. **Elytra** about 1.47 × as wide as pronotum and about 1.70 × as long as their maximum combined width (length measured from anterior transverse elytral keel); evenly widening posterad with maximal width (viewed dorsally) and height (viewed laterally) at beginning of declivity; elytral declivity evenly rounded and vertical to body axis (viewed laterally); elytra jointly rounded at apex; apparently fused together and not capable of being opened; without visible scutellum or scutellar row; epipleura absent. **Abdomen** with morphological sternites III and IV (normally referred to as the first two visible ventrites) sub-equal in length and amalgamated into single ventral abdominal plate with the trace of suture between them weakly visible only on disarticulated specimens with elytra removed under high magnification and in transparent light; ventral abdominal plate with numerous irregular setiferous punctures, with sub-quadrate, anteriorly notched anterior projection separating metacoxae on a distance sub-equal to longitudinal length for metacoxae; ventral abdominal plate (measured from posterior edge of metacoxal cavity) about 2.5 × combined length of the three remaining visible ster-



**Fig. 4.** *Alaocybites californicus* Gilbert, 1956 (Raymondionymidae); unsexed specimen (A), male #00467 (B–E), female (F–N); light microscopy. Abbreviations: tr = tergite, st = sternite. A: habitus, dorsal (left & above), ventral (left & below), fronto-lateral (right & above) and lateral (right & below); B: male genital chamber, dorsal (above) and ventral (below); C: aedeagus, tegmen and sternite IX, dorsal (above), lateral (middle) and ventral (below); D: aedeagal internal sclerotization, dorsal; E: tegmen and tegminal apodeme (with aedeagus forming background), ventral; F: spermatheca, ventral; G: female genital chamber, ventral; H: female tergite VIII, sternites VIII and IX, ventral; I: apical part of left antenna, dorsal; J: right maxilla, ventral; K: hind left leg, ventral; L: metendosternite, internal dorsal; M: middle right tarsus, ventro-lateral; N: hind left tarsus, ventral; O: right mandible, ventral.

nites (morphological sternites V–VII); sternites V and VI each with a single transverse row of 8–9 punctures; sternite VII sub-equal in length to sternites V and VI combined, without punctures; tergite VIII (pygidium) partly exposed, vertical to body axis. **Male and female genitalia** as described for the genus and illustrated for the species.

**Material.** Holotype, unsexed specimen: “RUSSIA, Primorsky Krai, Chuguevskiy r-n, N44°02.118' E134°12.166', 21–25.v. 2008, 650 m, sifting, V. Grebennikov” / “HOLOTYPE *Alaocybites egorovi* sp.n. Grebennikov det.”; currently in CNC, will be eventually deposited, together with some paratypes, in the collection of the Laboratory of Entomology, Institute of Biology and Soil Science, Vladivostok, Russia. – Paratypes (60 specimens in total, males and females, but mainly un-



**Fig. 5.** *Alaocybites californicus* Gilbert, 1956 (Raymondionymidae); female #00091; ESEM. **A:** habitus, dorsal (above), ventral (middle) and lateral (below); **B,C:** mouthparts, frontal (B) and ventral (C); **D:** head, latero-dorsal; **E:** fore right tarsus, medial; **F:** middle left tarsus, dorsal; **G:** right antenna, dorsal; **H:** middle right tarsus and tibia, ventral; **I:** hind right tarsus and tibia, lateral; **J:** middle right tibia, medial.

sexed): 49 specimens: same locality data as the holotype (five unsexed specimens deposited in each of the following: CMN, the Natural History Museum in London, Zoological Institute in St. Petersburg, Senckenberg Natural History Collections Dresden; two further specimens each in Massimo Meregalli's private collection in Torino and in SBMNH); 2 ♂♂: "RUSSIA, Primorsky Krai, 5 km S of Anisimovka vil., N43°07' E132°48', 21–30.vi.2007, 500–1000 m, V. Grebennikov" / "Sifting and berlesing forest leaf litter"; 5 specimens: "RUSSIA, Primorsky Krai, Anisimovka vil., N43°07.490' E132°

47.637', 09–11.vii. 2008, 500 m, sifting, V. Grebennikov"; 4 specimens: "RUSSIA, Primorsky Krai, Anisimovka, N43°07.490' E132°47.687', 2008–2009 soil trap, 500 m, V. Grebennikov".

**Geographical distribution.** *Alaocybites egorovi* is presently known from two localities some 130 km apart in the southern part of the Sikhote-Alin Mountain Range, Primorsky Krai, Russia (Fig. 3).

**Bionomics.** Specimens were collected by sifting leaf litter in the mixed (Anisimovka) and predominantly oak (Chuguevsky Rayon) forests together with other leaf-litter inhabiting weevils such as *Lobosoma rauseense* (Nakane, 1963; Molytinae: Plinthini: Plinthina), *Acallinus tuberculatus* Morimoto, 1962 (Molytinae: Ithyporini: Colobodina) and *Asphalmus* sp. (Entiminae). No larvae or noticeably teneral adult specimens were recorded. Unidentifiable gut content is depicted on Fig. 1E. Host plant and immature stages are unknown. *Alaocybites* specimens were relatively rarely seen in Anisimovka vil. (about one specimen per 20 kg of sifted leaf litter), while they were about five times more frequently encountered in Chuguevsky Rayon.

**Etymology.** The species name is a patronym derived from the family name of Andrey Borisovich Egorov, a Soviet/Russian weevil specialist who worked extensively on weevils of the Russian Far East and the neighbouring lands (Korea: HONG et al. 2000). Egorov authored a number of pioneering discoveries and influential general treatments (ZHERIKHIN & EGOROV 1990; EGOROV et al. 1996) pertaining to the Asia Pacific weevils. For a long period, Egorov was aware of this species existing in the fauna of the Russian Far East, although the scarcity of material prevented its earlier description.

#### 4. List of morphological characters for phylogenetic analysis

The scoring of the characters across the included taxa (matrix) is presented in Tab. 1. The word “additive” in square brackets at the end of a character indicates that it is treated as ordered in analyses 2 and 4 (see Tab. 1).

1. Rostrum, shape and orientation in relation to head, lateral view (THOMPSON 1992): relatively straight, directed more anterad (Figs. 7A, 10H, 16A) = 0; bent and directed ventrad (Figs. 1A, 2A, 8A) = 1.
2. Rostrum, its length relative to dorsal pronotal length, lateral view: shorter than pronotum (max. 90%; Figs. 8A, 14A, 17A) = 0; sub-equal (90–120%) in length to pronotum (Figs. 1B, 2A, 4A, 5A, 7A, 8A, 9A, 10H, 11A, 13A, 14A, 18A, 19A, 20A) = 1.
3. Antennal attachment and rostral scrobes, dorso-frontal view (GILBERT & HOWDEN 1987): both not visible (Fig. 7L) = 0; antennal attachment partly visible, scrobes not visible (Fig. 2A) = 1.
4. Eyes, composition: eyes fully absent (Fig. 5D) = 0; eyes present, each consisting of a single ommatidium (Figs. 1B, 2D, 9I, 19G, 20G) = 1; eyes present, each consisting of two to ten ommatidia (Fig. 16G) = 2; eyes present, each consisting of eleven and more ommatidia = 3 [additive].
5. Dorsal separation of rostrum from remaining head, lateral view (HOWDEN 1992): absent (Fig. 11I) = 0; present, indicated by a fine notch or depression of dorsal outline (Fig. 9A) = 1; present, deep and sulcate (Figs. 17J, 18A) = 2 [additive].
6. Cephalic capsule, whether retracted in prothorax, dorsal view (OSELLA 1977; HOWDEN 1992): not or weakly retracted, at least anterior 30% of head visible (Fig. 14A) = 0; moderately retracted, at least anterior 20% of head visible (Fig. 1B) = 1; markedly retracted, only rostrum visible (Figs. 7L, 10K) = 2 [additive].
7. Antennal funicle, number of antennomeres (GILBERT 1956; THOMPSON 1992): five (Figs. 8M, 19G) = 5; six (Figs. 7N, 18A) = 6; seven (Figs. 2F, 11I) = 7; eight (Figs. 17K,N) = 8 [additive].
8. Maxillary palp (THOMPSON 1992): two-segmented = 2; three-segmented = 3 [deactivated]. While the maxillary palp is normally three-segmented in weevils, a two-segmented palp is believed to be characteristic to the majority of Raymondionymidae (THOMPSON 1992); this is a potential synapomorphy for Raymondionymidae. I was not able to study this extremely minute and difficult-to-dissect structure in all taxa included in the analyses 1–4, although the palp appears as three-segmented in both *Alaocybites* species (Figs. 2B, 4J), as well as in *Neoubychia*, *Schizomicrus* (Fig. 10H) and *Barretonus*, while it indeed appears two-segmented in *Raymondionymus* (Fig. 7J).
9. Galea (THOMPSON 1992): absent = 0; present = 1 [deactivated]. In the majority of Raymondionymidae, the galea is believed to be absent (THOMPSON 1992), while it is normally present in other weevils; its lack is thus a potential synapomorphy for Raymondionymidae (THOMPSON 1992). A separate galea appears to be absent in *Alaocybites* (Fig. 4K), while no attempt has been made to trace this character throughout all included taxa. It should be noted that in many weevils the galea fuses with the lacinia and palpifer forming a compound structure (THOMPSON 1992) termed “mala” (MORIMOTO 1962) or “galeo-lacinal complex” (FRANZ 2006).
10. Prosternum, wide notch or laterally sulcate channel, ventral view: absent (Figs. 2A, 7L) = 0; present (Figs. 8H, 9H, 10D, 12A, 15A, 19F, 20G) = 1.
11. Procoxae, whether connate, ventral view (OSELLA 1977): connate (Fig. 2A) = 0; not connate, narrowly separated by about 0.5 coxal diameter (Fig.

| Character number:                       | 000000001                | 111111112  | 222    |
|---|--------------------------|------------|--------|
|   | 1234567890               | 1234567890 | 123    |
| BRE <i>Arrhenodes minutus</i>           | 00-300-??0               | 1210000011 | 010    |
| RAY <i>Alaocybites egorovi</i>          | 1111117300               | 0110011000 | 101    |
| RAY <i>Alaocybites californicus</i>     | 1110117300               | 0110011000 | 101    |
| RAY <i>Raymondionymus orientalis</i>    | 01000262?0               | 0111110001 | 010    |
| RAY <i>Gilbertiella helferi</i>         | 1000115??1               | 1112220001 | 010    |
| RAY <i>Neoubychia mexicana</i>          | 11011173?1               | 1202221000 | 110    |
| RAY <i>Schizomicrus caecus</i>          | 01000273?1               | 0112221001 | 000    |
| RAY <i>Myrtonymus zelandicus</i>        | 1100007??0               | 0000000001 | 010    |
| ERI <i>Himasthlophallus flagellifer</i> | 1102017??1               | 0110001011 | 010    |
| COS <i>Barretonus minor</i>             | 1000007??0               | 1110000110 | 100    |
| CRY <i>Torneuma deplanatum</i>          | 11010273?1               | 2210000110 | 100    |
| MOL <i>Otibazo</i> sp.                  | 0102117??0               | 1210020110 | 110    |
| MOL <i>Caecossonus dentipes</i>         | 1010208??0               | 1210000110 | 100    |
| MOL <i>Lymantes scrobicollis</i>        | 1110206??0               | 1110001110 | 100    |
| MOL <i>Reyesiella caecus</i>            | 11010153?1               | 0110001000 | 100    |
| MOL <i>Sosgenes carinatus</i>           | 1111017??1               | 1210001000 | 100    |
| Character                               | 0-ordered; D-deactivated | OOO ODD    | OO OOO |

**Tab. 1.** Data matrix of adult morphological characters used for phylogenetic analyses 1–4 seeking to determine phylogenetic affinities of *Alaocybites* (Curculionoidea); three-letter abbreviations before taxon name indicate BRE = Brentidae, RAY = Raymondionymidae, ERI = Eirrhinidae, MOL = Molytinae, COS = Cossoninae, CRY = Cryptorhynchinae. The first two lines read vertically provide the character number.

- 9K) = 1; not connate, widely separated by about coxal diameter (Fig. 15A) = 2 [additive].
12. Mesocoxae, whether connate, ventral view: connate (Fig. 11C) = 0; not connate, narrowly separated by less than 0.5 coxal diameter (Fig. 14A) = 1; not connate, widely separated by more than 0.5 coxal diameter (Fig. 16A) = 2 [additive].
13. Elytral striae, dorsal view: not identifiable (Figs. 9A, 11A,L) = 0; clearly identifiable (Figs. 1A, 7A, 8A, 19A, 20A) = 1.
14. Legs, ventral femoral face, whether grooved to receive tibia: not grooved (Figs. 2G, 19I, 20F) = 0; grooved in distal half (Fig. 7S) = 1; grooved through most of femoral length (Figs. 8K, 9L, 10M) = 2 [additive].
15. Legs, dorsal tibial face, whether expanded posteriorly into flat lobe: not expanded (Fig. 5) = 0; noticeably expanded in distal half into flat lobe (Figs. 7P,S) = 1; expanded along most of its length into flat lobe (Figs. 8K, 9L, 10K) = 2 [additive].
16. Legs, outer tibial face, whether with longitudinal setal fringe along posterior margin, lateral view: without setal fringe (Figs. 11N, 19I, 20H,J) = 0; with setal fringe along distal quarter (Figs. 2J, 7P) = 1; with setal fringe along distal half or more (Figs. 8K, 16L) = 2 [additive].
17. Legs, inner distal projection of tibia ('mucro') (OSSELLA 1977): absent (Figs. 7Q, 8J, 16J, 17M, O) = 0; present (Figs. 2J, 9J, 10N, 12C, 19I, 20I) = 1.
18. Legs, outer distal projection of tibia ('uncus'), lateral view (GILBERT 1956; OSSELLA 1977; HOWDEN 1992): absent (Figs. 2J, 4K, 5H, 7P, 8K, 9L,M, 10O, 11N, 12C, 19I, 20H,I) = 0; present (Figs. 14G, 15A, 16J, 17O, 18H) = 1.
19. Tarsomere IV (microscopy of a cleared slide preparation is required to confirm absence; THOMPSON 1992): absent (Figs. 1G, 4M,N, 8F,

10B, 19E, 20D) = 0; present (although small and partly or completely hidden between tarsomeres III and V) = 1.

20. Medial apodeme of male sternum VIII (dissection required; KUSCHEL 1971): absent (Figs. 1I, 4B, 9E, 14E, 15D, 16E, 17D, 18E, 19C, 20C) = 0; present (Figs. 7B, 8C, 9G, 10F, 13C) = 1.
21. Male sternum VIII (dissection required; THOMPSON 1992): entire (Figs. 7B, 8C, 10G, 13C) = 0; divided by membrane in two hemisternites (Figs. 1I, 4B, 9E, 14E, 15D, 16B, 17D, 18E, 19C, 20C) = 1.
22. Lateral membrane dividing aedeagus into dorsal (tectum) and ventral (pedon) plates (dissection required; KUSCHEL 1971): absent (genitalia of pedal type having only pedon; Figs. 1H, 4C, 10J, 14B, 15E, 17B, 18C,D 19B, 20B) = 0; present (genitalia of pedotectal type with discrete tectum clearly separated from pedon; Figs. 7D, 8B, 9B, 16D) = 1. This character was scored as 1 for *Otibazo* sp. (Fig. 16D), although judging by the aedeagal shape it seems unlikely that this condition is homologous to other pedotectal genitalia.
23. Right asymmetrical lateral projection of tegminal apodeme: absent (Figs. 7D, 8B, 9D, 10F, 13A, 14B, 15E, 16C, 17B, 18C, 19B, 20B) = 0; present (Figs. 1H, 4E) = 1.

No specific effort has been made to complete an overview of the **female genitalia** and associated structures among the taxa sampled for the analyses 1–4. This was partly due to the lack of available female specimens. Except for KUSCHEL's (1990) description of *Myrtonymus zelandicus* and GILBERT & HOWDEN's (1987) of *Neoubychia mexicana*, I am not aware of another published illustration of Raymondionymidae female genitalia. Dissection of a single *Raymondionymus orientalis* female revealed the presence of scler-

**Tab. 2.** Parameters and statistics of eight phylogenetic analyses performed to hypothesise relationships of *Alaocybites*. Analyses 1–4 used a restricted adult dataset of 16 taxa and 23 characters (two deactivated thus leaving 21 characters parsimony informative; see matrix Tab. 1). Analyses 5 and 6 used MARVALDI et al.’s (2002) matrix of larval and adult morphological characters, with the addition of *Alaocybites egorovi* sp.n. adult morphological characters (total 104 taxa and 115 characters; character #91 uninformative and deactivated); analyses 7 and 8 used only the 78 adult characters from the same matrix. Column “Additive” indicates whether the multistate characters (4–7, 11, 12, and 14–16 in analyses 1–4) were ordered or not. Column “Weighted” indicates whether successive approximation (FARRIS 1969) has been applied to calculate character weight, or not. Columns “CI” and “RI” indicate consistency and retention indices, respectively, with their values multiplied by 100. Column “MPT” indicates the number of the obtained most parsimonious trees. Column “SRA” indicates (for analyses 1–4 only) number of MPTs maintaining the “SRA clade” = *Sosgenes* + *Reyesiella* + *Alaocybites*. Columns “Raymond.” and “Lymantini” indicate (for analysis 1–4 only) number of MPTs associating the “SRA clade” with either Raymondionymidae (Fig. 6A) or Curculionidae: Molytinae: Lymantini (Fig. 6B), respectively.

| Analysis # | Additive | Weighted | Tree length | CI | RI | MPT   | SRA | Raymond. | Lymantini |
|------------|----------|----------|-------------|----|----|-------|-----|----------|-----------|
| 1          | no       | no       | 69          | 46 | 58 | 6     | 6   | 6        | 0         |
| 2          | yes      | no       | 77          | 41 | 57 | 4     | 1   | 0        | 1         |
| 3          | no       | yes      | 153         | 65 | 78 | 2     | 2   | 2        | 0         |
| 4          | yes      | yes      | 147         | 63 | 81 | 1     | 1   | 0        | 1         |
| 5          | no       | no       | 233         | 58 | 92 | > 920 | n/a | n/a      | n/a       |
| 6          | no       | yes      | 1198        | 79 | 97 | > 924 | n/a | n/a      | n/a       |
| 7          | no       | no       | 157         | 58 | 93 | > 921 | n/a | n/a      | n/a       |
| 8          | no       | yes      | 810         | 82 | 97 | > 921 | n/a | n/a      | n/a       |

ites with uncertain homology (Fig. 7G,F), including a structure potentially homologous to tergite IX, or forming a part of the invaginated anterior edge of sternite VII (often disarticulated during dissection), or being a corpus of sternite VIII (spiculum ventrale).

## 5. Results of phylogenetic analysis

Parameters, main statistics and main results of eight performed phylogenetic analyses are represented in Tab. 2, while three main topologies are shown in Fig. 6.

Analyses 1–4 were designed (A) to test monophyly of *Alaocybites* and (B) to evaluate two conflicting hypotheses suggesting the genus belonging to either Raymondionymidae or Curculionidae: Molytinae: Lymantini. The results strongly suggest that *Alaocybites* forms a clade. The group of both included *Alaocybites* species is present in the most parsimonious tree from each of the four analyses. Furthermore, this clade was strong enough to withstand variously applied bootstrapping, which almost invariably collapsed the rest of obtained topologies in a completely unresolved bush. *Alaocybites* consistently grouped together with the New Zealand genera *Reyesiella* (Molytinae: Phrynixini) and *Sosgenes* (Molytinae incertae sedis) forming the so-called ‘SRA clade’. The ‘SRA clade’ was variously associated with either Raymondionymidae (Fig. 6A) or Molytinae: Lymantini (Fig. 6B) (see also Tab. 2).

Analyses 5–8 were designed to hypothesise the placement of *Alaocybites* in a broader weevil framework based on MARVALDI et al.’s (2002) larval and adult morphological dataset. The strict consensus of MPTs places *Alaocybites* in a polytomy of some 30 Curculionidae lineages (analyses 5 and 7) or as sister to all Curculionidae (analyses 6 and 8). Bootstrapping the obtained topologies places *Alaocybites* either as sister of Cossoninae + (Platypodinae + Scolytinae) (analysis 5; 71% bootstrap support) or as sister of the remaining Curculionidae (analyses 6–8; Fig. 6C; bootstrap support for clades ‘*Alaocybites* + Curculionidae’ and ‘Curculionidae’ in analyses 6–8 is 96/92, 84/54 and 80/61, respectively).

## 6. Discussion

### 6.1. Present and past distribution of *Alaocybites*

*Alaocybites* has three extant species: *A. californicus* and *A. rothi* in California and *A. egorovi* sp.n. in the southernmost part of the Russian Far East (Fig. 3). Known localities of extant *Alaocybites* are too far south from the past Beringian land bridge to be called ‘Beringian distribution’, a pattern commonly found among beetles (ANDERSON 1997a) and weevils in particular (ANDERSON 1997b). The widely disjunctive distribution of poorly-dispersing organisms such as

*Alaocybites* can be categorised by the vague term ‘relict’, implying that in earlier times *Alaocybites* beetles were more widely distributed. This would agree with the presence of a fossil *Alaocybites* in Alaska. Alternatively, the widely disjunctive distribution of extant *Alaocybites* could be only apparent, merely reflecting a vast lack of data. The discovery of the previously unreported East Palaearctic *Alaocybites* being quite commonly collected in two localities some 130 km apart suggests that with adequate collecting techniques these weevils can be found inhabiting much wider territories. Extant populations of *Alaocybites* may be eventually discovered in parts of Beringia unglaciated during the ice ages. This hypothesis is partly based on the presence of the extant soil-dwelling Lepotyphlinae rove-beetle *Chionotyphlus alaskensis* Smetana, 1986 in the vicinity of Fairbanks (SMETANA 1986). This blind and wingless beetle is similar to *Alaocybites* in dispersal capacities, thus indicating the possibility of *Alaocybites* being able to survive repeated ice ages.

Is the Pliocene Alaskan fossil *Alaocybites* known from a single head (“*Otibazo* sp.” in MATTHEWS & TELKA 1997) conspecific with *A. egorovi*? This question can hardly be answered with the small amount of fossil data currently available. The time gap of about 3 million years separating the Alaskan fossil and the extant *A. egorovi* by itself does not exclude their conspecificity. *Micropeplus dokuchaevi* Rjaburkhin, 1991, an eyed and wingless rove-beetle presently existing on the Kamchatka Peninsula, is thought to be conspecific to subfossil and fossil specimens from middle Pleistocene Britain (about 1.5 Mya) and upper Miocene Alaska (about 5.7 Mya; COOPE 1995). HÖRNSCHEMEYER et al. (2010) provided a long list of extant insect species having morphologically undistinguishable fossils of the age comparable to, or even greater than, the age of the *Alaocybites* fossil. These authors concluded that Ice Age and even older pre-Ice Age specimens might belong to extant species. It is likely, therefore, that *Alaocybites egorovi* may be found to be among these species.

PERKOVSKY et al. (2003: fig. 2) illustrated “a new genus and species of Molytinae” from Rovno amber, Ukraine, of presumed Late Eocene to Early Oligocene age. The illustration shows a beetle much resembling *Alaocybites*, although the picture is not detailed enough to see the specifics, particularly the eyes, uncus and mucro. An attempt has been made to check whether this unnamed fossil might be another *Alaocybites* and the following information has been obtained: “hook-like uncus present, about as long as quarter of tibial length, mucro (= premucro) short and tooth-like, presence of eyes could not be verified” (E. Perkovsky, pers. comm.). This information excludes *Alaocybites* as the genus to accommodate the fossil,

while its true affinities might be potentially traced within the ‘uncinate’ weevil radiation predominantly consisting of Molytinae, Cryptorhynchinae and Cossoninae (KUSCHEL 1987).

## 6.2. *Alaocybites* monophyly and internal relationships

The results of the phylogenetic analyses 1–4 (Tab. 2) strongly suggest *Alaocybites* (represented therein by *A. californicus* and *A. egorovi*) to be monophyletic. Yet, these analyses do not provide a rigorous test for *Alaocybites* monophyly due to the low number of sampled taxa.

Monophyly of *Alaocybites* is mainly suggested by the remarkable external similarity of all three extant species, further corroborated by the similarity in male and female genital structure between the type species and the newly described one (genitalia of *A. rothi* are unknown). Among the genital similarities, the presence of a small, asymmetric lateral projection at mid-length of the tegminal apodeme (Figs. 1H, 4E), which among the taxa here sampled has not been observed outside of *Alaocybites*, likely represents an autapomorphy of the genus.

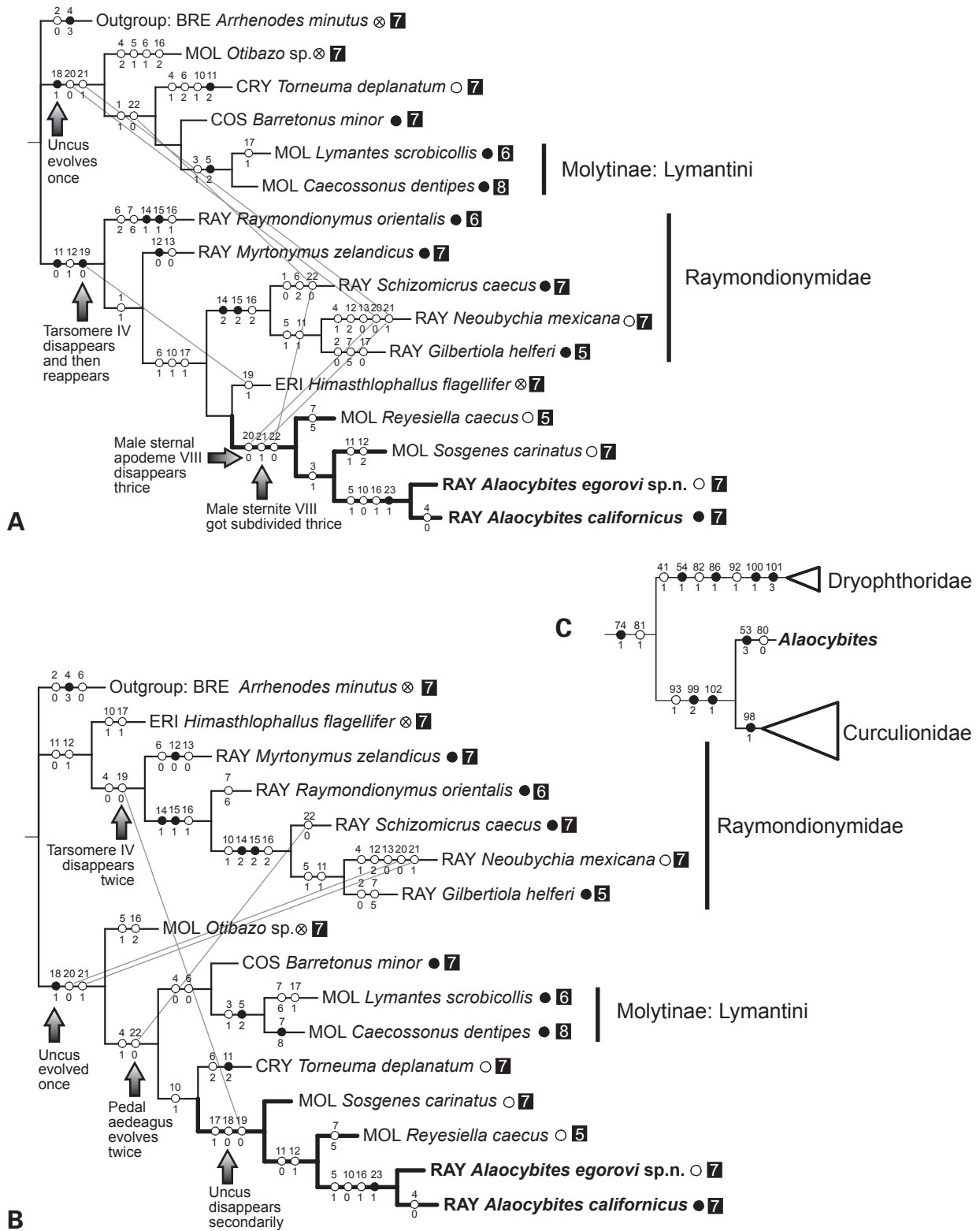
Little can be presently hypothesised on the relationships among three known extant *Alaocybites* species. Eye morphology straightforwardly suggests that the single-faceted *A. egorovi* is the sister group to a clade composed of the two completely eyeless Californian species.

## 6.3. Phylogenetic relationships and taxonomic position of *Alaocybites*

The only pre-existing hypothesis on the sister-group relationship of *Alaocybites* is that of OSELLA (1987), who proposes *Bordoniola* from Venezuela to take this position. This hypothesis could not be tested due to the unavailability of *Bordoniola* specimens.

In the absence of *Bordoniola*, analyses 1–4 consistently grouped *Alaocybites* with the endemic New Zealand soil weevil genera *Reyesiella* and *Sosgenes* (‘SRA clade’, Fig. 6A,B, Tab. 2). Like *A. egorovi*, adults of these genera have a single ommatidium per side, no uncus and no tarsomere IV and – unlike true Raymondionymidae – pedal male genitalia. Both *Sosgenes* and *Reyesiella* are arguably among the least known weevils. The genera were originally described by Capitan Thomas BROWN (1893), who later added





**Fig. 6.** Three conflicting hypotheses relating *Alaocybites* to either Raymondionymidae (A: one of six shortest trees from analysis 1) or to Curculionidae: Molytinae: Lymantini (B: single shortest tree from analysis 4) or, as sister group, to the entire Curculionidae (C: part of one of more than 924 shortest trees from analysis 8). Unambiguously optimized evolutionary events are plotted along internodes; character numbers are above circles and newly acquired character states are below circles. Character numbers for topologies A and B are those described in the present work (chapter 4); character numbers for topology C are those of MARVALDI et al. (2002). Black circles indicate unique evolutionary events; white circles indicate parallelisms or reversals. Three-letter abbreviations before taxon name indicate BRE = Brentidae, RAY = Raymondionymidae, ERI = Eriirhinidae, MOL = Molytinae, COS = Cossoninae, CRY = Cryptorhynchinae. Oblique lines connect presumably conflicting evolutionary events and are further discussed in the text. Circles at terminalia indicate number of ommatidia: none (filled circle), single one (empty circle), or ≥ two (circle including cross). Numbers 5–8 at the end of terminalia correspond to the number of funicular antennomeres. The clade *Sosgenes* + *Reyesiella* + *Alaocybites* (SRA) most commonly recovered in analyses 1–4 is traced in bold line.

three more *Sosgenes* species. Since then both genera appear nearly forgotten. Online search in *Zoological Record* revealed five titles referring to either *Sosgenes* or *Reyesiella* (= *Idus*): four original descriptions by Broun and the ALONSO-ZARAZAGA & LYAL (1999) catalogue. The genera are not mentioned in the review by OSELLA (1979), which otherwise is the most comprehensive, although slightly outdated entry point into soil weevil issues. When the present paper had been submitted, *Sosgenes* was re-studied and transferred from Cyclominae to Molytinae (OBREPRIELER 2010). The detected linkage of the two New Zealand genera with *Alaocybites* is puzzling, presently hardly explainable. Indeed, the apomorphies supporting the SRA clade vary among the analyses (compare A and B in Fig. 6), essentially depending on whether the clade is associated with Lymantini or with Raymondionymidae (see below). Moreover, none of the apomorphies is unique to the SRA clade (see Fig. 6 for strong homoplasy). Therefore this phylogenetic grouping is altogether not very convincing.

In the analyses 1–4 both previously proposed hypotheses of *Alaocybites* (as a part of the SRA clade herein) being a member of either the Raymondionymidae or the Lymantini radiation received nearly identical support (Tab. 2). Since these analyses included almost exclusively members of the two tested radiations, even a clear result would be preliminary anyway. The optimization of character changes on each of the two topologies (Figs. 6A,B) necessarily involves considerable homoplasy (either as parallelisms or reversals). Assuming that *Alaocybites* is a member of Raymondionymidae (Fig. 6A) suggests that male sternite VIII lost its apodeme three times (character 20/0); male sternite VIII became subdivided into two hemisternites three times (character 21/1); the pedal type of male genitalia has evolved three times (character 22/0); and tarsomere IV reappeared once (character 19/1). Alternatively, the hypothesis that *Alaocybites* is a member of the Lymantini radiation (Fig. 6B) suggests that a single eye facet was once regained following eyeless ancestors (character 4/1); an uncus evolves and then disappears (characters 18/1 and 18/0); tarsomere IV disappeared twice (character 19/0); male sternite VIII lost its apodeme twice (character 20/0) and became twice subdivided into two hemisternites (character 21/1); and the pedal type of male genitalia has evolved twice (character 22/0). Summing up the results of analyses 1–4, one has to accept that they were not consistent enough to test the hypotheses and are, in fact, markedly inconclusive.

Analyses 5–8 utilized a large dataset by MARVALDI et al. (2002), which does not include *Bordoniola*, *Reyesiella*, *Sosgenes*, Raymondionymidae and Lymantini (hence the most important taxa when analysing phylogenetic affinities of *Alaocybites*), and to

which data for adult *Alaocybites* were added. The weakly supported position of *Alaocybites* as sister to Cossoninae + (Platypodinae + Scolytinae) in the bootstrapped topology from analysis 5 is surprising and represents, most likely, an artefact. Bootstrapped topologies resulting from analyses 6–8 place *Alaocybites* as sister to the large Curculionidae radiation (Fig. 6C), although lack of Raymondionymidae and Lymantini representatives does not allow testing their respective placement in relation to *Alaocybites*. This position of *Alaocybites* is largely based on character 98/1 (MARVALDI et al. 2002): the male tegminal apodeme in *Alaocybites* is larger than the apodeme of sternite IX (optimized as a plesiomorphy), while the reverse is true for the rest of Curculionidae (optimized as an apomorphy for the clade). With just a single character in support and very few taxa analysed, such a hypothesis is premature, although it might suggest that *Alaocybites* represents a relatively old and species-poor lineage inadequately sampled in the present analysis.

The remarkable controversies and uncertainties obtained as a result of eight phylogenetic analyses based on two different datasets strongly suggest that the undertaken analyses, although designed to the best of the present-day knowledge and available data, were still inadequate to test existing and/or provide new hypotheses on *Alaocybites* relationships. Most of the critique put forward by FRANZ & ENGEL (2010) to some recent attempts to address weevil phylogeny might be equally well applied to the present study. I would, however, argue that even with all its shortcomings, it is still better to make an analytical effort by using as much data as presently available, even if the obtained results are expected to be far from conclusive.

In view of the gross uncertainties regarding *Alaocybites* relationships, it appears as a *status quo* solution to keep maintaining the current classification (ALONSO-ZARAZAGA & LYAL 1999) and consider the genus as a member of poorly defined Raymondionymidae, with the complete loss of tarsomere IV being the family's most remarkable potential apomorphy.

#### 6.4. On the composition and conventional limits of Raymondionymidae

With phylogenetic affinities of *Alaocybites* being so controversial and uncertain, what then are the Raymondionymidae weevils (sensu ALONSO-ZARAZAGA & LYAL 1999)? It might be a relatively ancient clade with a biogeographical history potentially similar to that of the Leptotyphlinae rove beetles (see below) and united, among other features yet to be discovered, by the lack

of tarsomere IV. Alternatively, 'Raymondionymidae' might be an artificial assemblage of unrelated unpigmented soil-inhabiting weevils lacking a tibial uncus and for these reasons tentatively assigned with the family's presumably monophyletic 'core', Raymondionymidae *s.str.*, consisting of nine exclusively Mediterranean genera (Fig. 3) with the possible addition of the North American *Gilbertiola*. This 'core' group seems to form a clade supported, along with the remarkable similarity in external and genital characters, by a potentially synapomorphic reduction of the number of funicular antennomeres from seven to six or less. Among the 'non-core' genera currently assigned to Raymondionymidae a similarly shaped antennal funicle with six antennomeres was noted only for all three *Homosomus* species from Madagascar (RICHARD 1956), which otherwise remains the least understood genus with the family, known only from type specimens and with no genital characters described. The remaining five 'non-core' Raymondionymidae genera, with seven funicular antennomeres, namely *Alaocybites*, *Bordoniola*, *Schizomicrus*, *Neoubychia* and *Myrtonymus* (Fig. 3) may well represent lineages unrelated with the Raymondionymidae *s.str.* and are about as dissimilar to them as, for example, the New Zealand Molytinae genera *Reyesiella* and *Sosgenes*. The present analysis failed to provide clear evidence for an alternative outline of Raymondionymidae, although it suggested that the existing taxonomy is hardly satisfactory and should be eventually re-assessed.

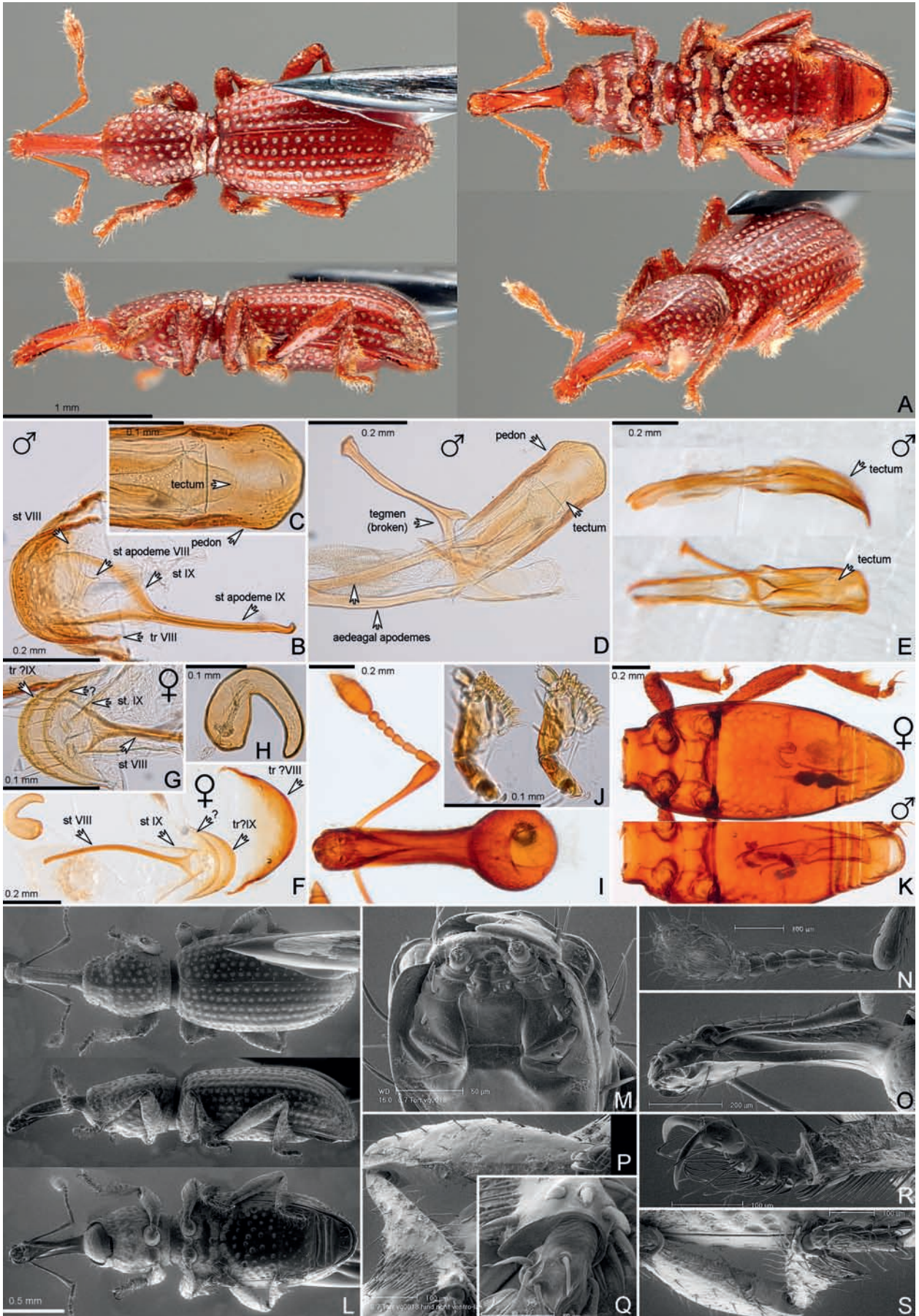
### 6.5. On other predominantly Mediterranean radiations of eyeless beetles

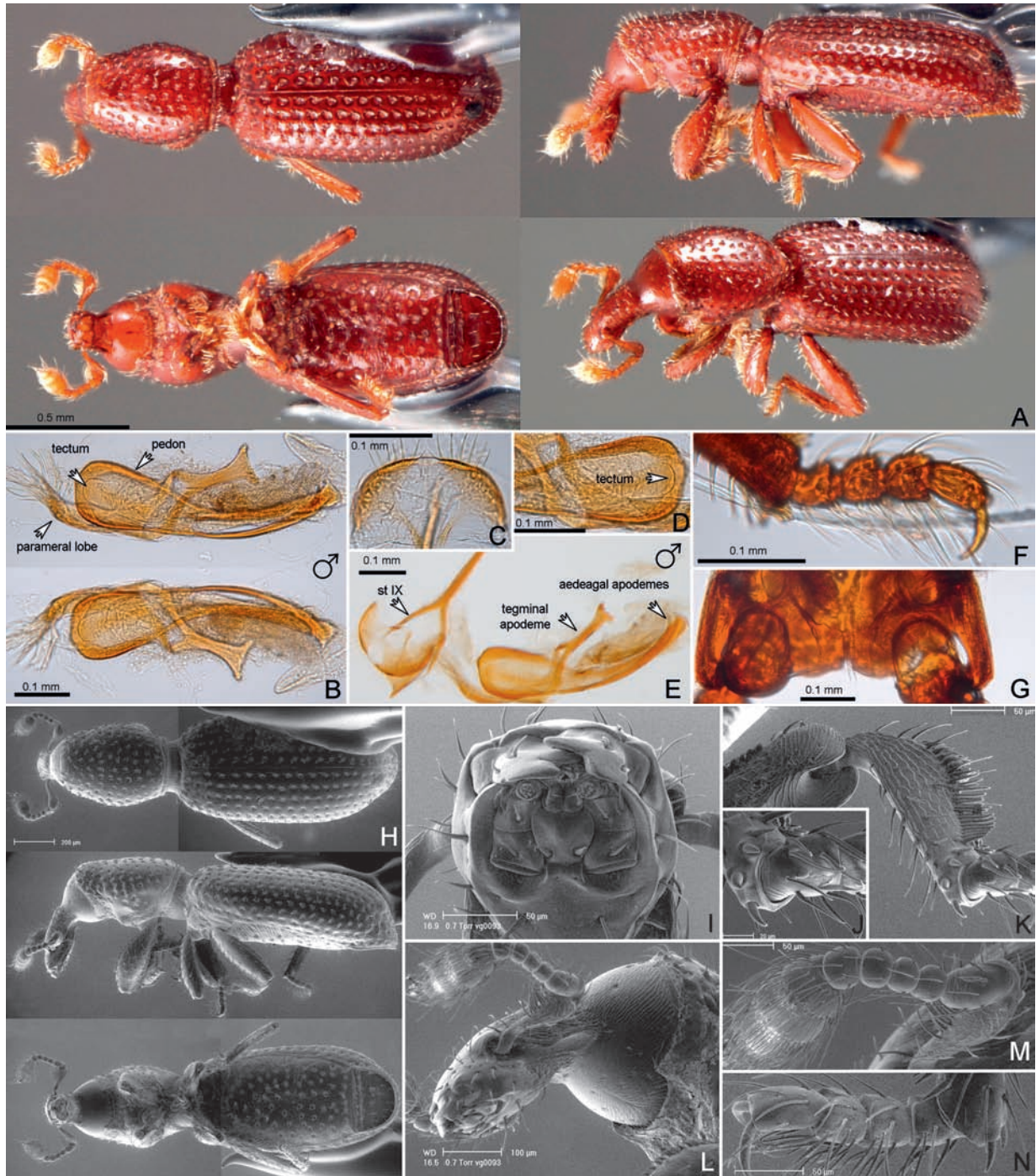
Phylogenetic and biogeographic uncertainties comparable to those surrounding a group of the predominantly eyeless weevils presently amassed under Raymondionymidae are seen among a handful of other Mediterranean-centered groups of unpigmented and chiefly subterranean beetles with reduced eyes. Most usually such groups become first recognised and defined based on their Mediterranean members, and later somewhat similarly looking, although likely unrelated taxa from well outside of the Mediterranean Region become discovered and questionably assigned to them. The lack of a well-developed phylogenetic hypothesis seems to be the most common cause for such 'extraterritorial' assignments. Within weevils this pattern can be further illustrated by the eyeless Chilean *Neotorneuma porteri* Hustache, 1939 originally described in the otherwise exclusively Mediterranean and likely monophyletic Torneumatini (Curculionidae: Cryptorhynchinae; STÜBEN 2007). In Carabidae this pattern is illustrated by

the Scaritinae subtribe Reicheiina with a few questionable members known from eastern Asia (GREBENNIKOV et al. 2009), and by the Trechitae tribe Anillini recorded from all zoogeographical regions and only questionably monophyletic (GREBENNIKOV 2002). The tribe Leptodirini (Leiodidae), one of the most intensely studied predominantly cave Mediterranean beetle radiations, has a handful of doubtful members in eastern Palearctic, western North America and, supposedly, Venezuela (NEWTON 1998). At least two among the east Palearctic 'Leptodirini' genera, namely *Sciaphyes* Jeannel, 1910 and *Fusi* Perkovsky, 1989, however, do not appear to belong to this tribe, as judged by a preliminary analysis of sequence data from a variety of gene fragments (I. Ribera & J. Fresneda pers. comm.). Among such examples the rove-beetle subfamily Leptotyphlinae is, potentially, the only group with convincing evidence of monophyly and adequately resolved sister-group affinities (GREBENNIKOV & NEWTON 2009) while in almost all other comparable cases no similarly robust phylogenetic hypothesis exists.

## 7. Concluding remarks

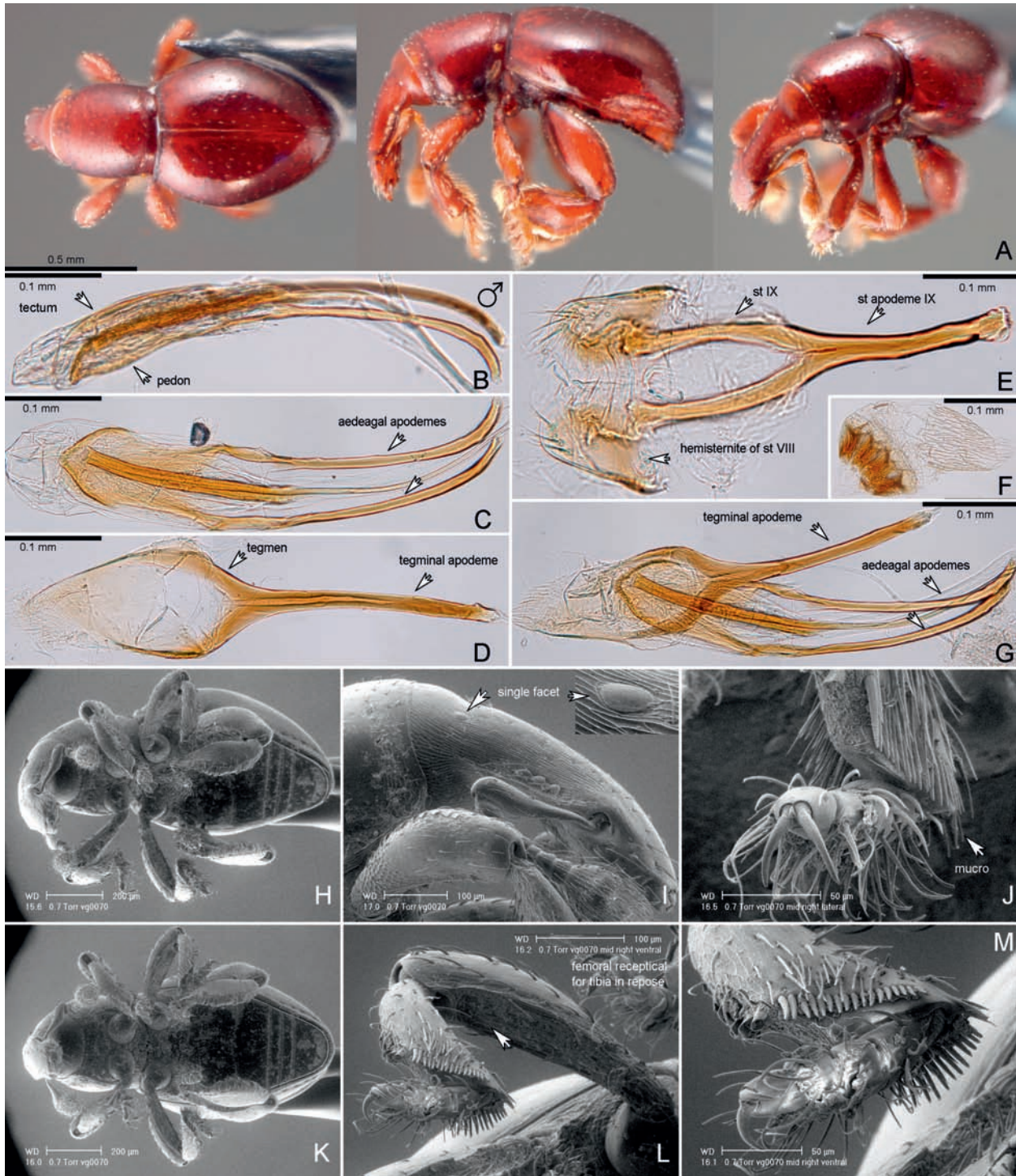
I cannot help feeling somewhat amused by the sequence of the events described in this paper. First an odd-looking and obviously new edaphic weevil has been discovered by sifting forest leaf litter in a 'remote' corner of the Eastern Palearctic. Then the species was assigned to a previously exclusively Californian genus which, as it turned out, contains a previously misidentified Alaskan fossil nearly three million years old that is practically undistinguishable from the extant species. Then it became obvious that the phylogenetic affinities of the genus are in the most unsatisfactory state of affairs and, therefore, should be clarified. Then a sizable effort was conducted to utilize all feasibly available data sources and to run a series of computations. Obtained results, however, turned out so unconvincing and vague that the whole phylogenetic attempt has to be judged as 'inconclusive' and, as a result, the existing provisional classification continued to be maintained. I still believe, however, that some progress has been gained, as at the very least this work should call attention to the fact that our present understanding of weevil phylogeny, particularly pertaining to cryptic species inhabiting 'remote' areas of the Globe, is far from being satisfactory, thus suggesting a number of stimulating phylogenetic discoveries still to lie ahead.





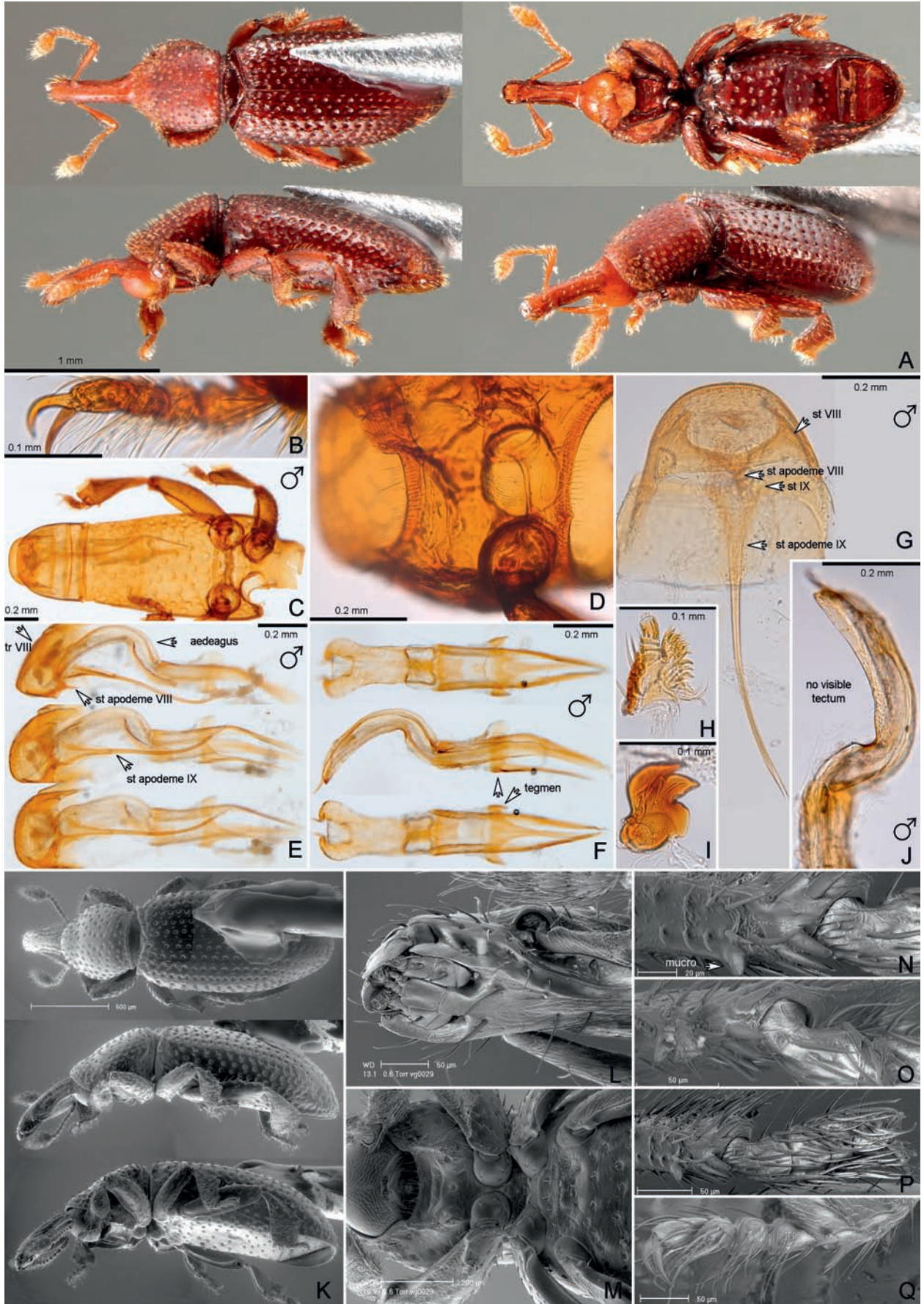
**Fig. 8.** *Gilbertiola helferi* (Gilbert, 1956) (Raymondionymidae: Raymondionyminae); unsexed specimen #00093 (A,H–N), male #00466 (B–G); light microscopy (A–G) or ESEM (H–N). Abbreviation: st = sternite. **A:** habitus, dorsal (left & above), ventral (left & below), lateral (right & above), fronto-lateral (right & below); **B:** aedeagus and tegmen, dorso-lateral (above) and ventro-lateral (below); **C:** sternite VIII, ventral; **D:** aedeagal apex, dorsal; **E:** aedeagus, tegmen, sternites VIII (with broken part of tergite VIII attached below) and IX, ventral; **F:** middle left tarsus, ventral; **G:** metendosternite, dorsal interior; **H:** habitus, dorsal (above), lateral (middle) and ventral (below); **I:** mouthparts, ventro-frontal; **J:** hind right tibio-tarsal joint, ventral; **K:** hind right leg, ventral; **L:** head, latero-ventral; **M:** left antenna, lateral; **N:** hind right tarsus, lateral.

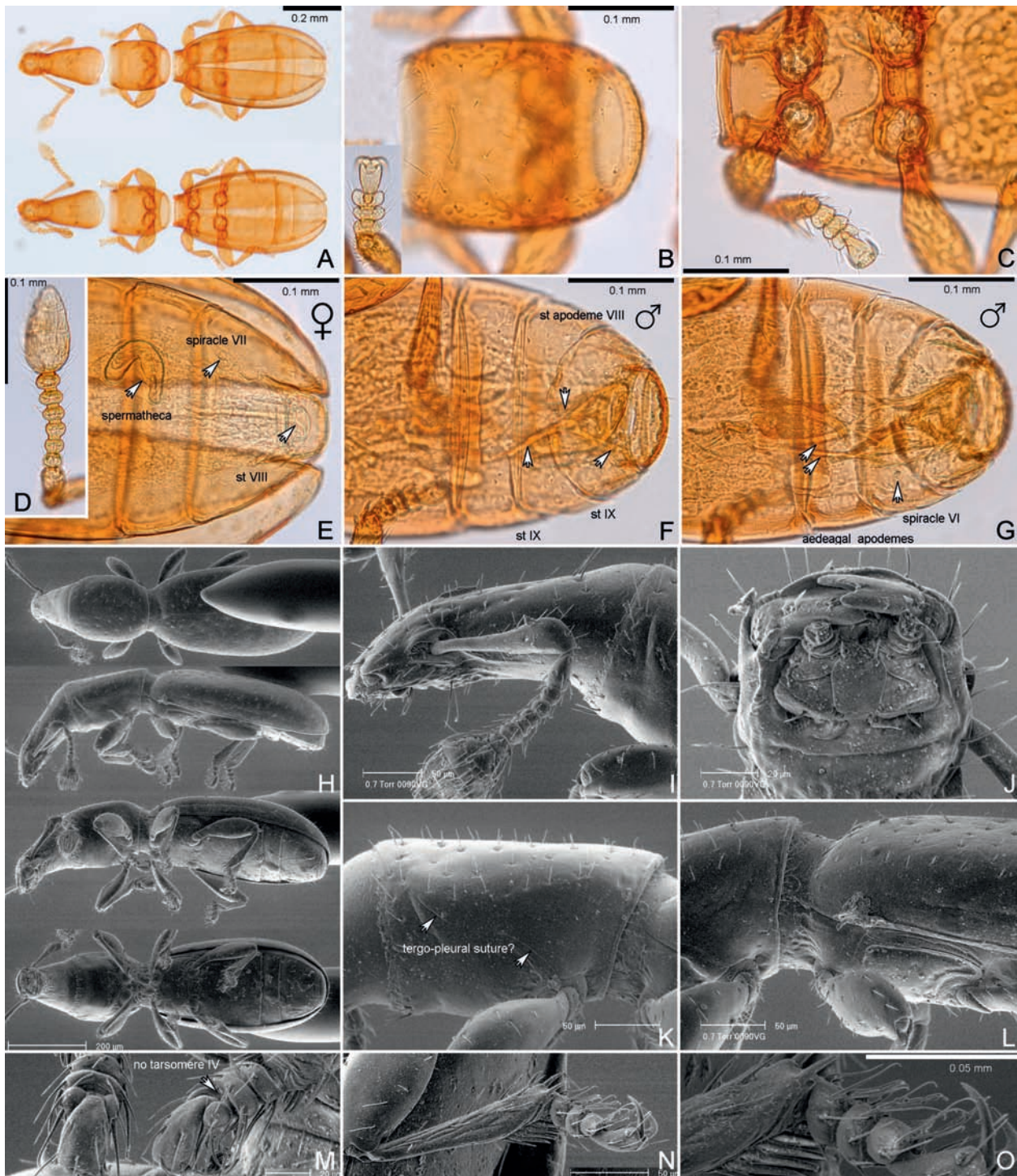
**Fig. 7.** [←] *Raymondionymus orientalis* Hervé, 1949 (Raymondionymidae: Raymondionyminae); unsexed specimen (A,I, J,L–S), male (B–E,K), female (F–H); light microscopy (A–K) or ESEM (L–S). Abbreviations: tr = tergite, st = sternite. **A:** habitus, dorsal (left & above), lateral (left & below), ventral (right & above), fronto-lateral (right & below); **B:** male genital chamber, aedeagus and tegmen removed, ventral; **C:** aedeagal apex, dorsal; **D:** aedeagus and tegmen (broken), dorsal; **E:** aedeagus, lateral (above) and dorsal (below); **F:** female genital chamber, ventral; **G:** apex of female genital chamber, ventral; **H:** spermatheca; **I:** head, ventral; **J:** left maxilla, dorsal (two images with different focal depth); **K:** pterothorax and genitalia, female (above) and male (below); **L:** habitus, dorsal (above), lateral (middle) and ventral (below); **M:** mouthparts, fronto-ventral; **N:** left antenna, dorsal; **O:** rostrum, ventro-lateral; **P:** hind right leg, latero-ventral; **Q:** hind right tibio-tarsal joint, latero-ventral; **R:** fore left tarsus, latero-dorsal; **S:** hind right leg, ventral.



**Fig. 9.** *Neoubychia mexicana* Gilbert & Howden, 1987 (Raymondionymidae: Raymondionyminae); male; light microscopy (A–G) or ESEM (H–M). Abbreviation: st = sternite. **A:** habitus, dorsal (left), lateral (middle) and fronto-lateral (right); **B,C:** aedeagus, lateral (B) and ventral (C); **D:** tegmen, ventral; **E:** sternites VIII and IX; **F:** proventriculus; **G:** aedeagus and tegmen, dorsal; **H,K:** habitus, latero-ventral (H) and ventral (K); **I:** head, lateral (eye represented by a single ommatidium, see enlarged insert); **J:** middle right tarsus, lateral; **L:** middle right leg, ventral; **M:** middle right tarsus, ventral.

**Fig. 10.** [→] *Schizomicrus caecus* (Casey, 1892) (Raymondionymidae: Raymondionyminae); unsexed specimens #00458 (A) and #00029 (K–Q), male (B–J); light microscopy (A–J) or ESEM (K–Q). Abbreviations: tr = tergite, st = sternite. **A:** habitus, dorsal (left & above), lateral (left & below), ventral (right & above), fronto-lateral (right & below); **B:** right fore tarsus, fronto-ventral; **C:** meso-, metathorax and abdomen, ventral; **D:** prothorax, ventro-lateral, left coxa removed; **E:** male genital chamber, lateral (above), ventro-lateral (middle), ventral (below); **F:** aedeagus and tegmen, dorsal (above), lateral (middle), ventral (below); **G:** sternites VIII and IX and tergites VII and VIII, ventral; **H:** left maxilla, dorsal; **I:** left mandible, dorsal; **J:** aedeagal apex, lateral; **K:** habitus, dorsal (above), lateral (middle), latero-ventral (below); **L:** mouthparts and antennal insertion, latero-ventral; **M:** thorax, ventral; **N:** middle left tibio-tarsal joint, ventral; **O:** hind left tibio-tarsal joint, ventral; **P:** middle left tarsus and tibial apex, ventral; **Q:** hind right tarsus, lateral.

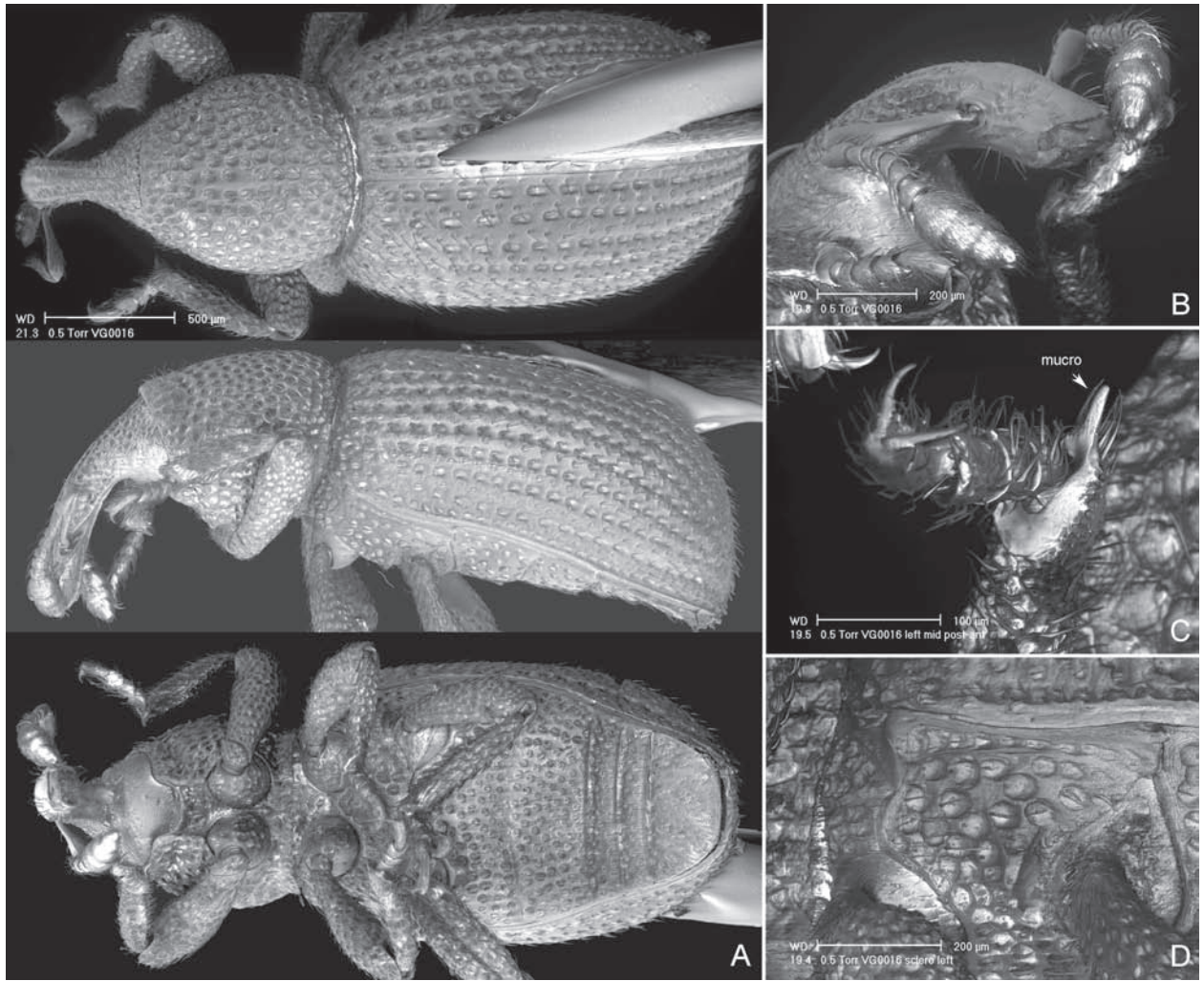




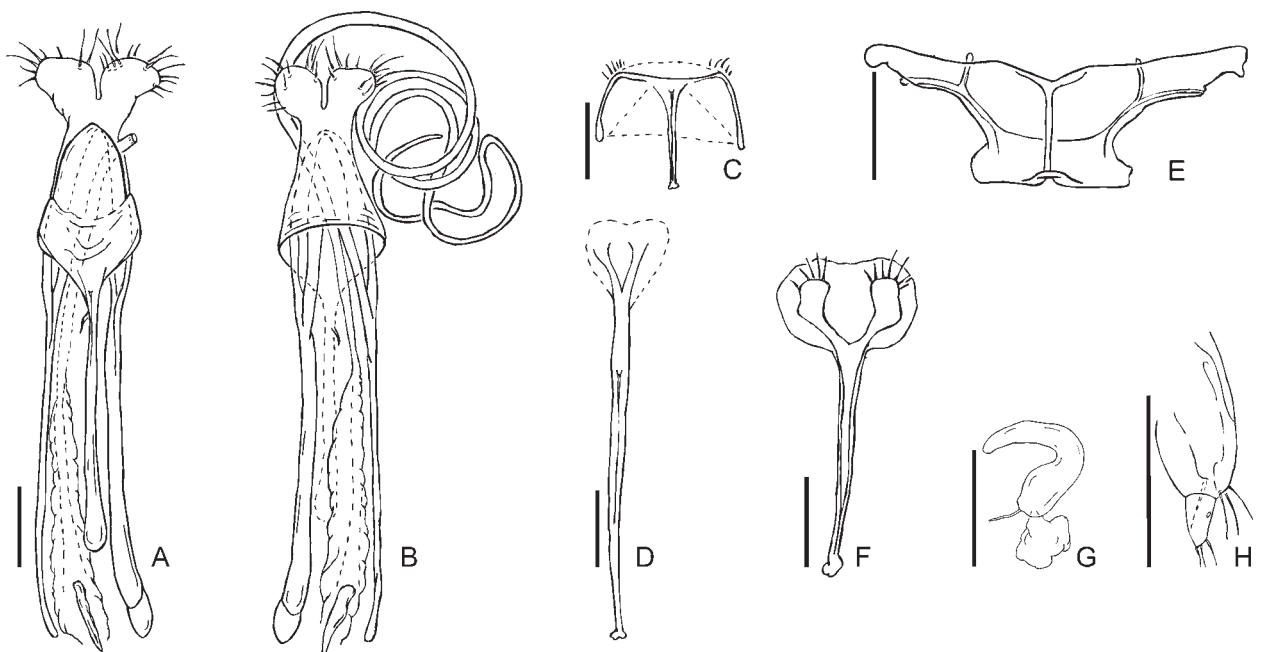
**Fig. 11.** *Myrtonymus zelandicus* Kuschel, 1990 (Raymondionymidae: Myrtonyminae); female (A–E), male (F,G), unsexed specimen (H–O); light microscopy (A–G) or ESEM (H–O). Abbreviation: st = sternite. **A:** habitus, dorsal (above) and ventral (below); **B:** prothorax, dorsal (insert: right protarsus, ventral); **C:** meso- and metathorax, ventral; **D:** left antenna, ventral; **E–G:** abdominal apex, dorsal (E) and ventral (F,G); **H:** habitus, dorsal, lateral, latero-ventral and ventral (from above); **I:** head, left-lateral; **J:** mouthparts, fronto-ventral; **K:** prothorax, left-lateral; **L:** thorax, left-lateral; **M:** protarsi, frontal; **N,O:** middle right leg, right-lateral.

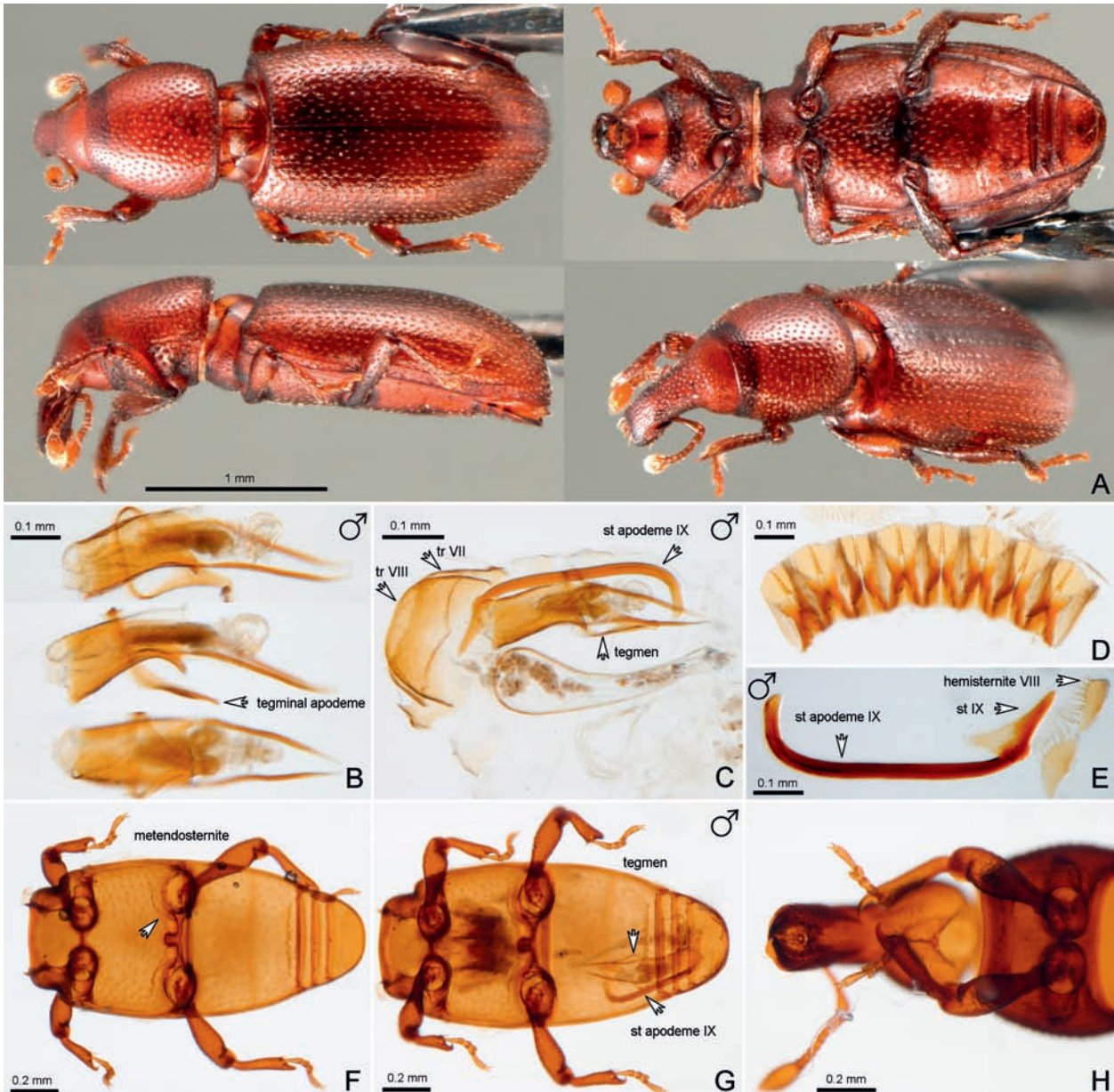
**Fig. 13.** [→] *Himasthlophallus flagellifer* Egorov & Zherikhin, 1991 (Eriirhinidae: Himasthlophallini); male #00067 (A–D), unsexed specimen (E), female #00016 (F–H); camera lucida drawings. **A,B:** aedeagus and tegmen, ventral (A, flagellum omitted) and dorsal (B); **C:** sternite VIII; **D:** sternite IX; **E:** metendosternite; **F:** sternite VIII; **G:** spermatheca; **H:** one of two hemisternites IX. Scale bars 0.2 mm.



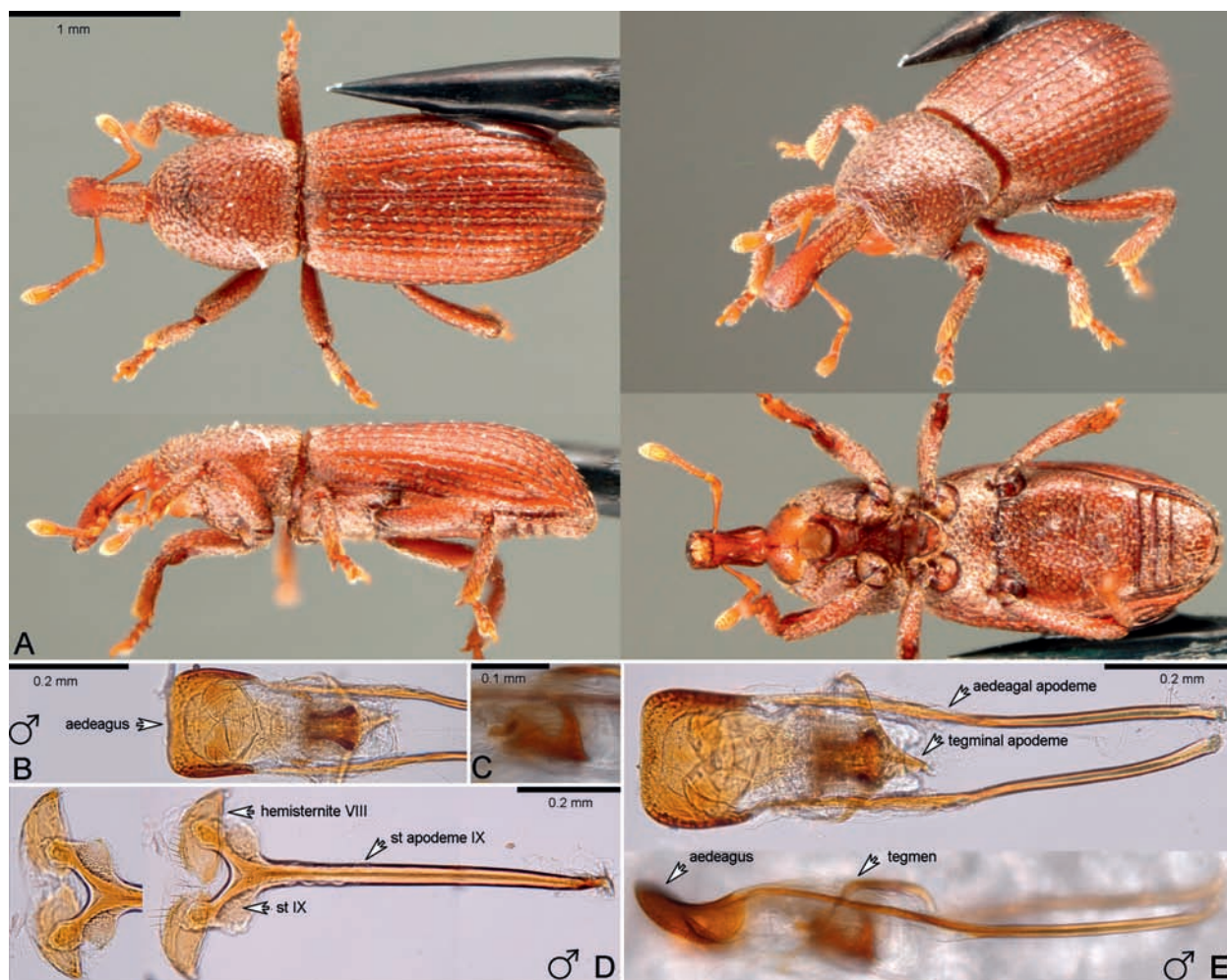


**Fig. 12.** *Himasthlophallus flagellifer* Egorov & Zherikhin, 1991 (Eirirhinidae: Himasthlophallini); unsexed specimen; ESEM. **A:** habitus, dorsal (above), lateral (middle), ventral (below); **B:** head, latero-ventral; **C:** middle left tarsus, posterior; **D:** left meso- and metathorax, lateral.

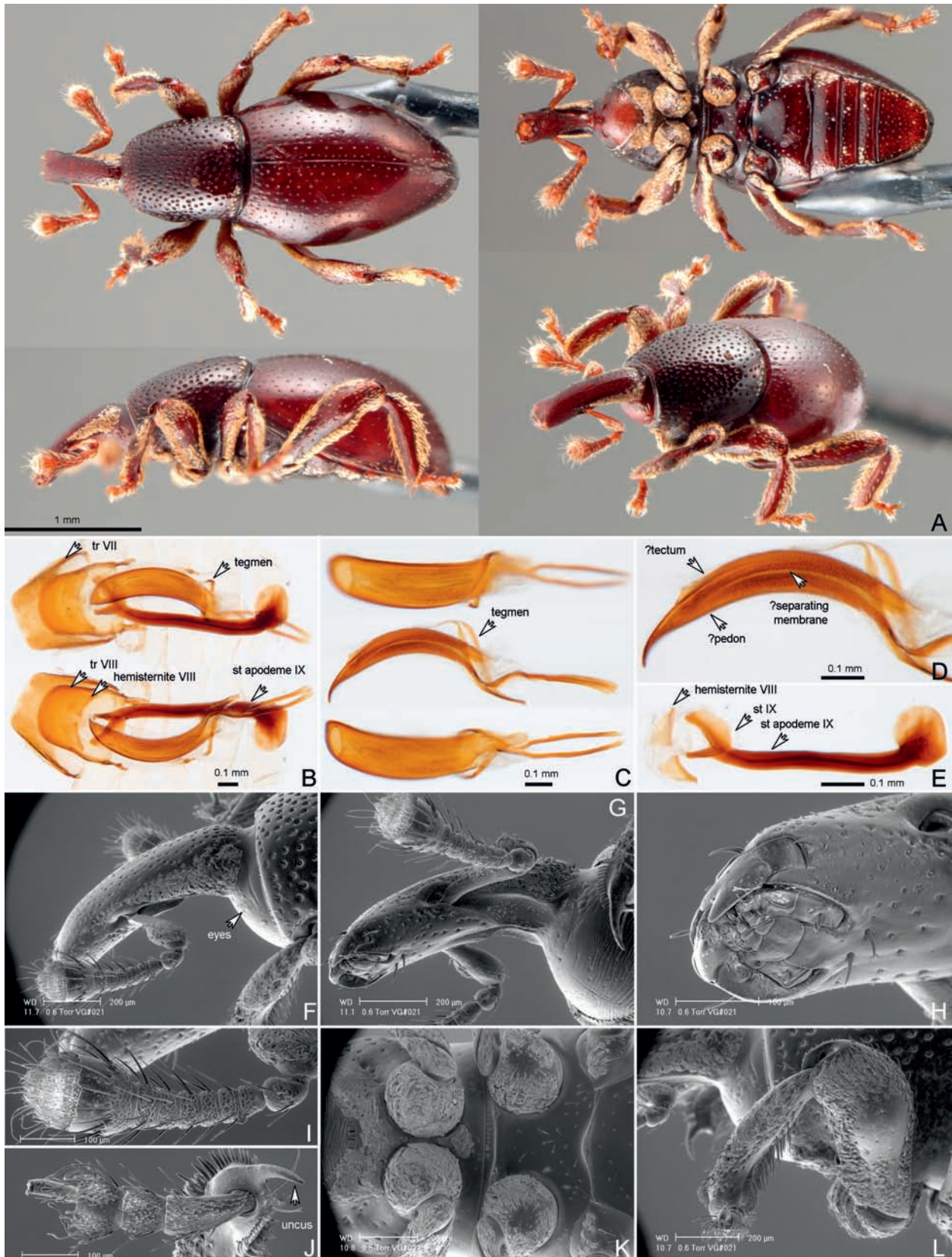




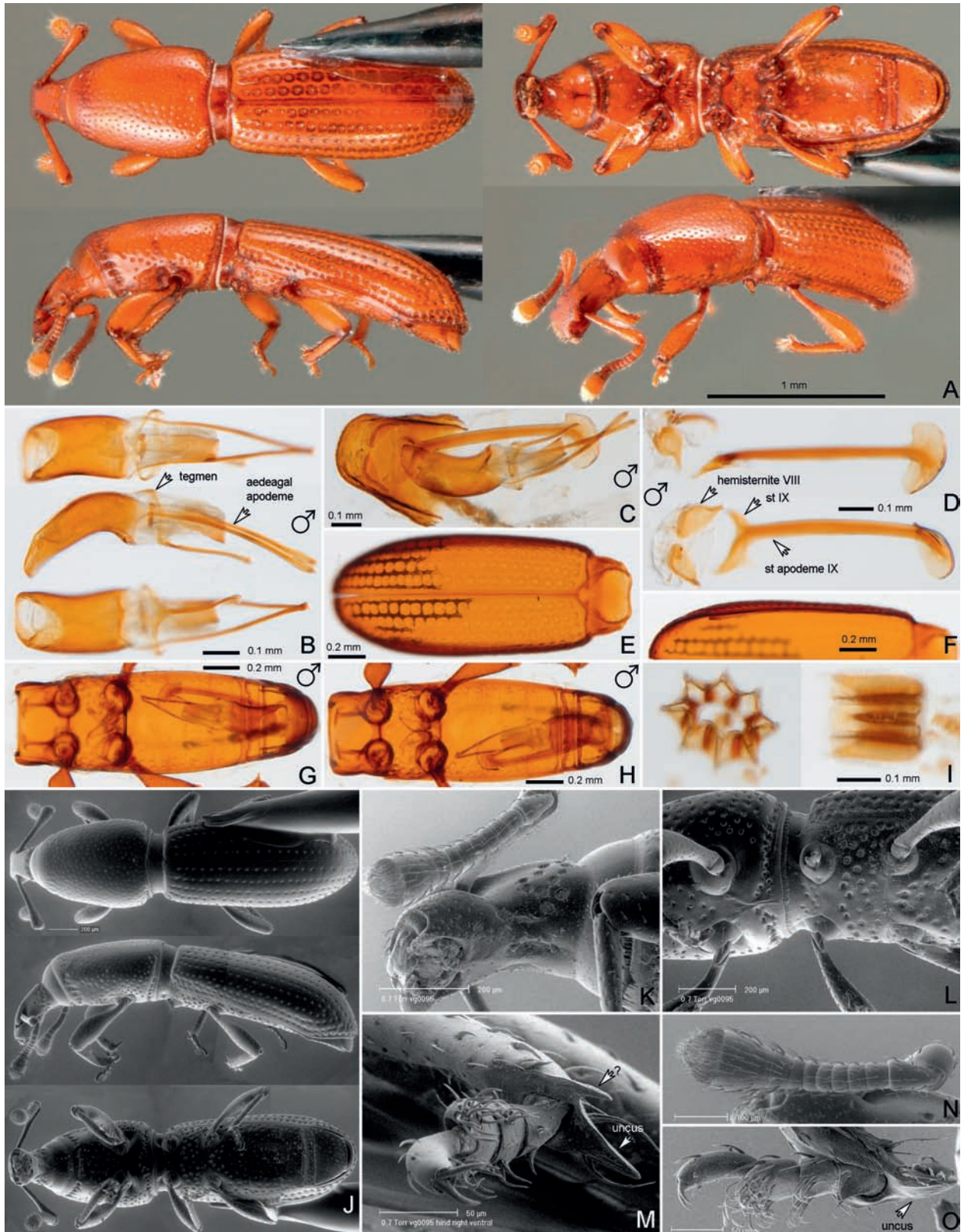
**Fig. 14.** *Barretonus minor* Folwaczny, 1972 (Curculionidae: Cossoninae: Dryotribini); unsexed specimen #00459 (A), male #00463 (B–H); light microscopy. Abbreviations: tr = tergite, st = sternite. **A:** habitus, dorsal (left & above), lateral (left & below), ventral (right & above), fronto-lateral (right & below); **B:** aedeagus, dorso-lateral (above), lateral (middle), ventral (below); **C:** male genital chamber; **D:** proventriculus; **E:** sternites VIII and IX; **F,G:** pterothorax and abdomen, ventral (F) and dorsal (G), tergites and internal soft tissue removed; **H:** head and prothorax, ventral.



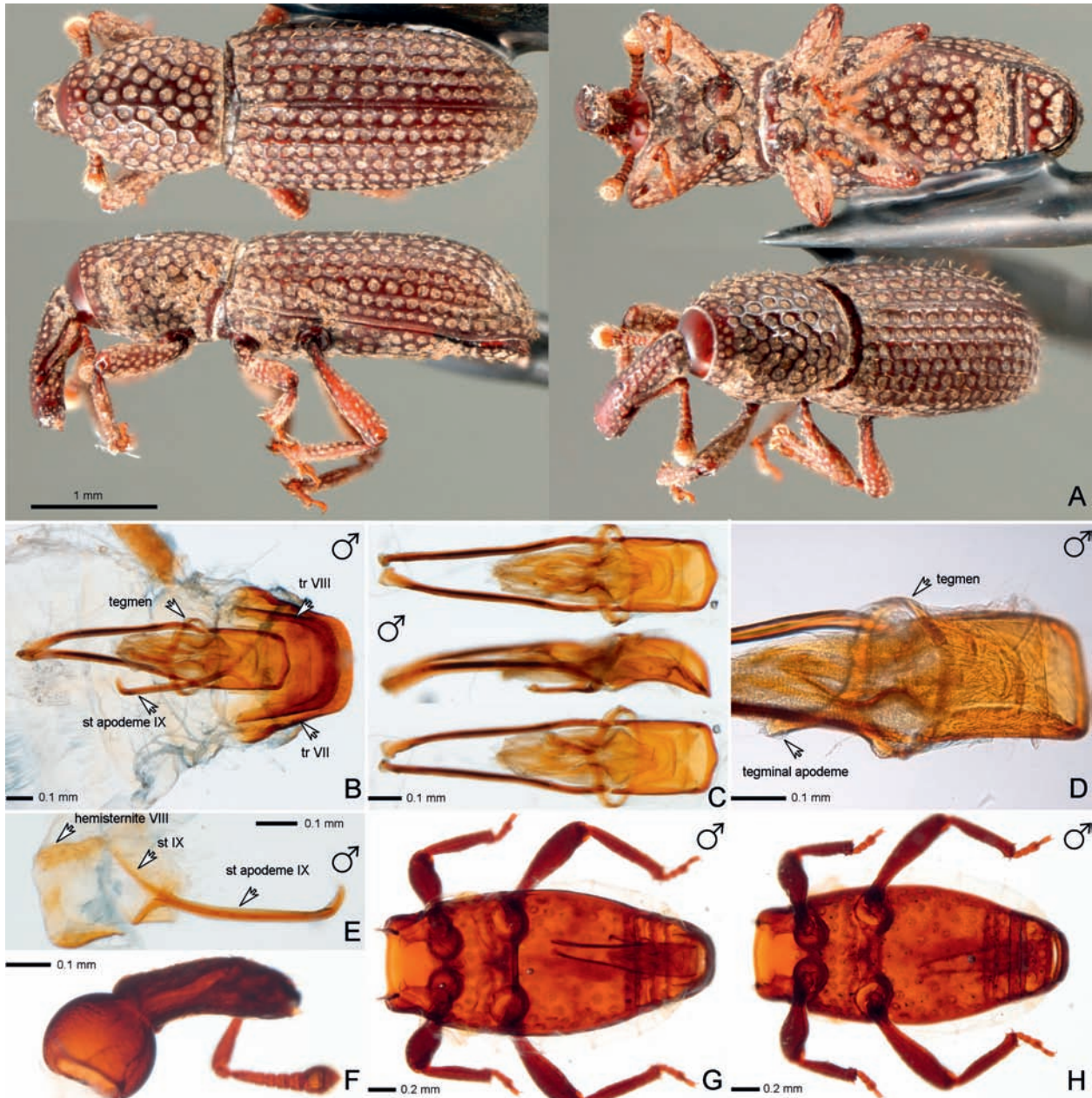
**Fig. 15.** *Torneuma deplanatum* (Hampe, 1864) (Curculionidae: Cryptorhynchinae: Torneumatini); male #00461; light microscopy. Abbreviation: st = sternite. **A:** habitus, dorsal (left & above), lateral (left & below), fronto-lateral (right & above) and ventral (right & below); **B:** aedeagus, ventral; **C:** aedeagal internal sclerotization, lateral; **D:** two hemisternites VIII and sternite IX, ventral (left) and dorsal (right); **E:** aedeagus and tegmen, dorsal (above) and lateral (below).



**Fig. 16.** *Otibazo* sp. (Curculionidae: Molytinae: Anchonini); unsexed specimen #00021 (A,F–L), male #00465 (B–E); light microscopy (A–E) or ESEM (F–H). Abbreviations: tr = tergite, st = sternite. **A:** habitus, dorsal (left & above), lateral (left & below), ventral (left & above), fronto-lateral (right & below); **B:** male genital chamber, dorsal (above), ventral (below); **C:** aedeagus and tegmen, dorsal (above), lateral (middle), ventral (below); **D:** apical part of aedeagus and tegmen, lateral; **E:** male sternites VIII and IX, dorsal; **F:** head, latero-dorsal; **G:** head, latero-ventral; **H:** mouthparts, latero-ventral; **I:** left antenna, lateral; **J:** fore right tibio-tarsal joint and tarsus, ventral; **K:** thorax, ventral; **L:** fore left leg, lateral.



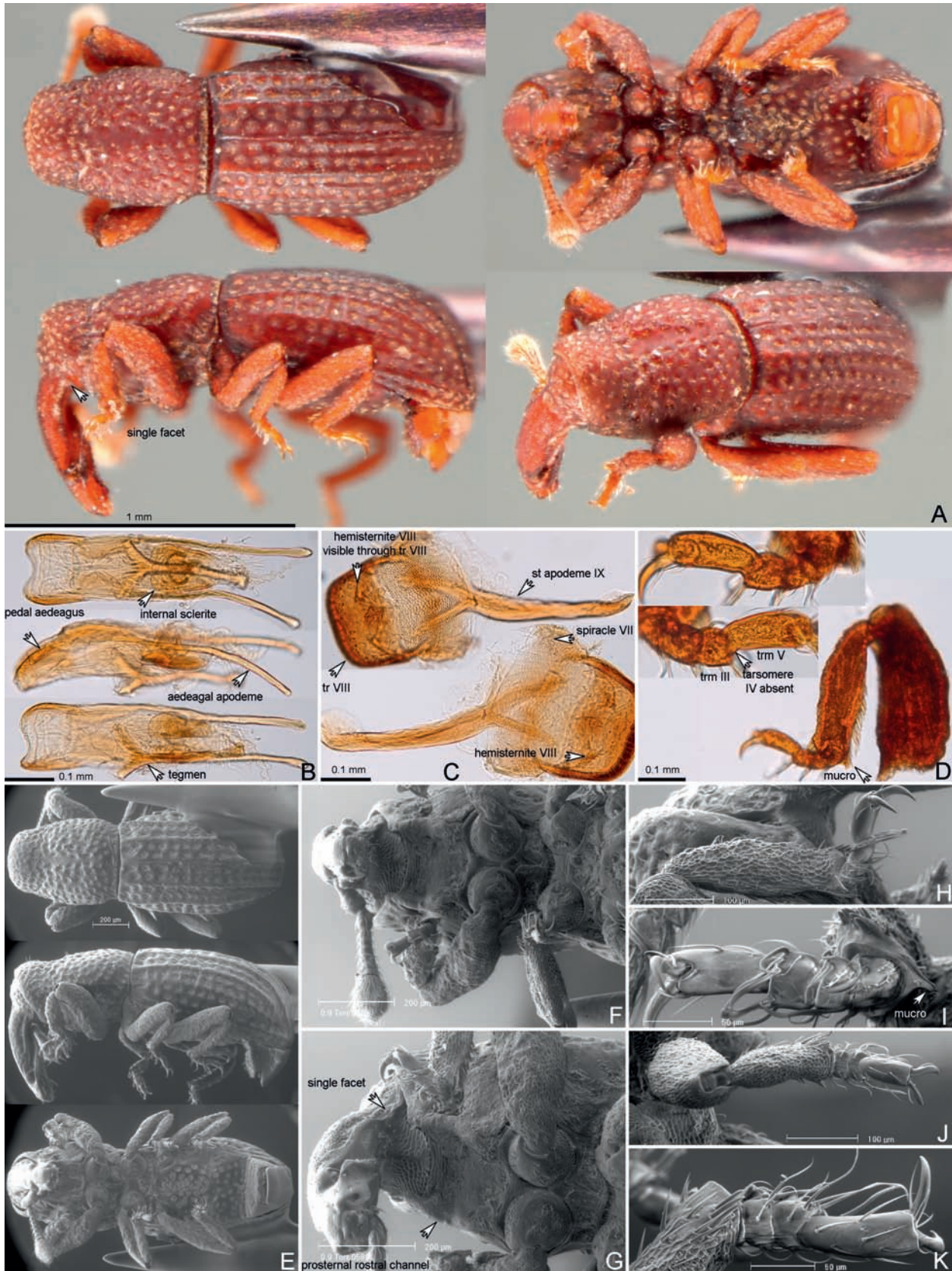
**Fig. 17.** *Caecossonus dentipes* Gilbert, 1955 (Curculionidae: Molytinae: Lymanitini); unsexed specimen #00095 (A,J–O), male #00096 (B–I); light microscopy (A–I) or ESEM (J–O). Abbreviation: st = sternite. **A:** habitus, dorsal (left & above), lateral (left & below), ventral (right & above), fronto-lateral (right below); **B:** aedeagus, dorsal (above), lateral (middle), ventral (below); **C:** male genital chamber, ventral; **D:** male sternites VIII and IX, ventro-lateral (above), ventral (below); **E:** elytra, dorsal; **F:** right elytron, ventral; **G:** pterothorax and abdomen, elytra removed, ventral; **H:** pterothorax and abdomen, elytra and soft tissue removed, dorsal; **I:** proventriculus, frontal (left), dorsal (right); **J:** habitus, dorsal (above), lateral (middle), ventral (below); **K:** head, ventro-lateral; **L:** thorax, ventro-lateral; **M:** hind right tibio-tarsal joint and tarsus, ventral; **N:** left antenna, lateral; **O:** fore left tibio-tarsal joint and tarsus, lateral.



**Fig. 18.** *Lymanthes scrobicollis* Gyllenhal, 1838 (Curculionidae: Molytinae: Lymanitini); unsexed specimen #00460 (A), male #00462 (B–H); light microscopy. Abbreviations: tr = tergite, st = sternite. **A:** habitus, dorsal (left & above), lateral (left & below), ventral (right & above), fronto-lateral (right & below); **B:** male genital chamber, dorsal; **C:** aedeagus and tegmen, dorsal (above), lateral (middle), ventral (below); **D:** tegmen and aedeagal apex, dorso-lateral; **E:** male sternites VIII and IX, ventral; **F:** head, latero-ventral; **G,H:** pterothorax and abdomen, elytra and soft tissue removed, dorsal (G) and ventral (H).



**Fig. 19.** *Reyesiella caecus* (Broun, 1893) (Molytinae: Phrynixini); males #00589 (A,F–K) and #00593 (B–E); light microscopy (A–E) or ESEM (F–K). Abbreviations: tr = tergite, st = sternite. **A:** habitus, dorsal (left & above), lateral (left & below), ventral (right & above), fronto-lateral (right & below); **B:** male genital chamber, dorsal (above), lateral (middle) and ventral (below); **C:** aedeagal apex, ventral; **D:** right antennomere, dorsal; **E:** right fore leg, medial, inserted enlarged tarsus; **F:** habitus, dorsal (above), lateral (middle) and ventral (below); **G:** head, lateral; **H:** mouthparts, latero-ventral; **I:** right fore leg, lateral; **J:** right fore tarsus, ventral; **K:** fore (above), middle (middle) and hind (below) tarsus, dorso-lateral.



**Fig. 20.** *Sosgenes carinatus* Broun, 1893 (Molytinae incertae sedis); male #00588; light microscopy (A–D) or ESEM (E–K). Abbreviations: tr = tergite, st = sternite. **A:** habitus, dorsal (left & above), lateral (left & below), ventral (right & above), fronto-lateral (right & below); **B:** aedeagus and tegmen, dorsal (above), lateral (middle) and ventral (below); **C:** tergites VIII and IX and sternites VIII and IX, dorsal (above) and ventral (below); **D:** right fore leg, medial, inserted enlarged tarsus; **E:** habitus, dorsal (above), lateral (middle) and ventral (below); **F,G:** head and prothorax, ventral (F) and ventro-lateral (G); **H:** right fore leg, lateral; **I:** right fore tarsus, ventral; **J:** right middle leg, lateral; **K:** right middle tarsus, dorsal.



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