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RESEARCH PAPER

Diversity and morphology of Eocene and Oligocene Mordellidae (Coleoptera)

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Abstract. Characteristics of the locomotor apparatus (excluding wings) and other diagnostic features of Mordellidae preserved in Eocene Baltic and Rovno amber are investigated. Main features of Eocene Mordellidae are compared with those of their extant relatives using mainly light microscopy and micro-CT scans. The entire record of Eocene and Oligocene fossils of this family is reviewed, revealing a great number of discrepancies in diagnoses of species of Eocene and Oligocene Mordellidae at the generic level, which makes a reliable discussion of their biogeography and relationship with extant species impossible. To overcome this situation, four new collective group names (i.e., without a type species designation) are established: *Baltimorda* nov., *Baltistena* nov., *Rovnostena* nov., and *Petrimordella* nov. Seven new species of Mordellistenini from Baltic amber are described, diagnosed and illustrated: *Baltistena ultima* sp. nov., *B. aurata* sp. nov., *B. longistrigata* sp. nov., *B. hoffeinsorum* sp. nov., *B. concava* sp. nov., *B. brevispina* sp. nov., and *B. atronigra* sp. nov. The number of Mordellistenini recorded from Baltic amber is doubled from seven to fourteen. The subgenus *Palaeostena* Kubisz, 2003, with the type species *Falsomordellistena eocenica* Kubisz, 2003, is elevated to a genus.

Key words. Coleoptera, Tenebrionoidea, Mordellidae, tumbling flower beetles, new collective groups, new species, tertiary, Baltic amber, Rovno amber

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Introduction

With some 2,400 species in nearly 120 genera, Mordellidae is the fourth most species rich family of Tenebrionoidea (after Tenebrionidae, Meloidae and Anthicidae). This implies that this family is taxonomically very challenging, and the situation is even more difficult when fossils are involved because usually only a very limited number of important characters are preserved or visible (e.g., natural colour is always absent and mouthparts and genitalia are usually completely hidden). In Eocene and Oligocene Mordellidae, which should be, as it is currently assumed, with one or two exceptions congeneric with extant species, any comparative studies must be even more comprehensive. Without doubt, the taxonomy of Eocene and Oligocene Mordellidae is complex and demanding in terms of specialist knowledge and technologies used.

A review of studies on Eocene and Oligocene Mordellidae, however, revealed a very different picture. The majority of descriptions are by authors who had not previously published anything on the taxonomy of extant members of the family or even related lineages (Germar 1813; Wickham 1909, 1912, 1914a,b; Cockerell 1924; Statz 1952; Nel 1985; Hong 2002; Bao et al. 2018). Karl Ermisch (*1898–†1970), a famous German specialist on this family, published his two studies on Baltic Mordellidae at the beginning of his career (Ermisch 1941a, 1943, contributions No. 9 and 13) and subsequently accumulated considerable knowledge of the systematics of this family and published nearly 60 taxonomical papers, but never returned to studying fossils. Until his two palaeoentomological contributions (Kubisz 2001, 2003), Daniel Kubisz was the author of faunistic studies related only to the fauna of Poland and did not publish anything on the taxonomy of extant mordellids. Some other eminent students of this family, such as Mario Franciscolo, Jan Horák, Emil Liljeblad, Takehiko Nakane, Sizumu Nomura, Eugene Ray and Shigehiko Shiyake, did

not publish anything on fossil Mordellidae. None of the types of Eocene and Oligocene mordellids species has ever been revisited.

Not surprisingly, this picture of publications on post-Cretaceous fossil mordellids correlates with the generally low quality of published contributions. The aim of this study is to clarify the taxonomic status of all the described Eocene and Oligocene species of this family. Available fossil record and types of previously described species were reviewed and revisited where necessary and possible. Systematic placement and taxonomical status of each genus and species of Eocene and Oligocene Mordellidae described so far are commented on and corrected. Four new generic names are established as collective group names according to ICZN (1999: Articles 10.3, 13.3.2, 23.7, 42.2.1, 42.3.1, 56.1, 66, 67.14) and seven new species of Mordellistenini from Baltic amber are described. Besides the set of specific characters usually used by students of extant Mordellidae, e.g., mouthparts, antennae and locomotive microstructures mainly on the hind legs, the present study also focused on sclerites on the pterothorax, which proved very useful for delimiting species. The aim of this publication is to provide a new base for future studies on members of this interesting family from Eocene amber deposits using modern terminology and methods of observation.

Material and methods

Labels. The data on the labels of the type material described by Karl Ermisch are cited as follows: different lines are indicated by a single slash (/), separate labels are indicated by a double slash (//). Comments are in square brackets: [p] = printed, [hw] = handwritten.

New species. Holotypes of the newly described species are deposited in the collection of Charles University, Faculty of Science, Department of Zoology, Prague (under prefix PřFUK + serial number; curator J. Prokop).

Species names. Name of each new species in the collective group *Baltimorda* nov., *Baltistena* nov. and *Rovnostena* nov. is unique for the respective tribe. In the future, this approach will enable the inclusion of new data, obtained by more advanced methods of visualization, and to determine phylogeny within extant genera without undesirable homonymy between species.

Keys. Keys to Baltic Mordellini and Mordellistenini are provided. Both keys can be used to identify species but do not reflect their possible natural relationships as is the practice for extant Mordellidae (vide, e.g., Horák 1996, Horák & Farkač 2017). This constraint on the keys to fossil Mordellidae is due to a lack of some characters necessary for delimiting species and to the uncertainty of their generic identity.

Loans. Baltic Mordellidae described by Karl Ermisch and stored in the collections of the Geologisch-Paläontologisches Institut und Museum, Hamburg, Germany (GPIH) and Senckenberg Deutsches Entomologisches Institut, Müncheberg, Germany (SDEI) were provided by the respective curators directly to DESY (Hamburg) for microtomography and subsequently borrowed for closer examination in Prague.

Main characters evaluated. Franciscolo (1957a) summarized the most important diagnostic characters of extant species of Mordellidae, but their applicability to fossil specimens preserved in amber is limited and especially so in case of compression fossils, where most of these characters are either not observable (genitalia) or too fine to be preserved or discerned on rough matrices (interfacetal setae, shape of tarsomeres, tibial spurs). In all descriptions we follow the list given by Franciscolo (1957a), which he adopted with some corrections from his predecessor Karl Ermisch. In cases where the structure is not preserved, observable, measurable or discernible this is explicitly mentioned.

The list of characters is as follows (modified from Franciscolo (1957a) in rearranged order, excluding genitalia):

Non-locomotive structures and elytra

1) form of antennae;
2) structure of maxillary palpi, notably the ultimate palpomere;
3) size of eye facets;
4) presence or absence of interfacetal setae;
5) form of scutellum;
6) form of basal margin of pronotum;
7) shape and length of elytra.

Structures of the locomotor apparatus (*excluding those used for flight*)

8) form of protarsi, particularly tarsomeres I and IV;
9) structure of protibia;
10) form of mesotarsomere IV;
11) length ratio of mesotibia and respective tarsus;
12) type of comb(s) (and dorso-lateral ridge, if present) on metatibia;
13) presence or absence of outer tibial spurs on metatibia;
14) type of comb(s) (and dorso-lateral ridge(s), if present) on metatarsus;
15) form of pygidium and its ratio to hypopygium;
16) shape of metanepisternum;
17) absence or presence and shape of metakatepisternum (newly added);
18) form of pretarsal claws (newly added);
19) setae on apex of pygidium (newly added).

Terminology. Several terms specific or important in the context of the morphology of Mordellidae are highlighted in a comment or explanation:

comb (= 'Kerbe', 'ridge') – in German and English studies, terms 'Kerbe' and 'ridge', respectively, are nearly always used for the peculiar transverse structures on the hind legs. While German 'Kerbe' means 'surface interrupted by cutting', English 'ridge' means 'elevated surface'. Both terms are misleading, however, because these structures are in fact rows of regularly arranged *scale-like setae*. The term *comb* is correctly used, for example, by Blair (1922), Nomura (1966) and Tsuru (2011) and followed here.

comb formula – e.g., 4//2/1/1/0, means four *combs* of *scale-like setae* on metatibia, two *combs* on tarsomere I, one *comb* on each tarsomere II and III and absence of *combs* on tarsomere IV. Additional incomplete patches of *scale-like setae* are commented on separately.

facets – term traditionally used in Mordellidae and kept here, meaning *cornea lenses* of ommatidia.

onychium – term inconsistently used in Mordellidae. Franciscolo (1957b: Figs 7C–E) associated this term with seta between pretarsal claws including hind legs (it is likely that he referred to the *empodium* with associated seta between the claws, as nothing else is depicted in these figures), while Horák (1994) used this term to describe the presence of a membranous area of cuticle below the lobes of the pro- and mesotarsomere IV. Dual usage of this term both for tarsal and pretarsal structures inevitably resulted in misunderstandings among students of Mordellidae. For example, according to Franciscolo (1961) the *dorsal ridge*, a structure present only in some Mordellini, should occur in *Phungia scraptiiformis* (Franciscolo, 1961) at least on metatarsomeres I–V: 'Dorsal ridge on hind tibiae runs entire length of segment, from knee to apical row of aculei and is somewhat elevated and carinate in relation to the tibial surface; same occurs also **on hind tarsal segments, except onychium** [i.e., except pretarsus sensu Franciscolo (1957b)]'. But Horák (1999) misinterpreted the original description of Franciscolo and stated that '… *P. scraptiiformis* has dorsal ridge developed **only on the first metatarsomere** …' without further explanation. The term *onychium* is considered to be confusing, outdated and too often misused (Dashman 1953), and is therefore not used in this contribution.

scale-like setae – thick flattened setae with more or less rounded tips, usually darker than other setae, regularly spaced or forming clusters (on *the tip of pygidium*) or *combs* (on hind legs).

spiniform setae – irregularly spaced setae on ventral side of hind legs, usually stronger than other setae, with acute tips.

metakatepisternal suture (sensu Lawrence et al. 2010, 2011: 34, C187) – 'transverse suture on the metasternal plate' (i.e. metaventrite) sensu Franciscolo (1962a, 1990) in extant *Glipodes* Leconte, 1862 (Mordellidae: Conaliini). This structure is not mentioned in the majority of studies on Mordellidae.

metanepisternum – in older contributions referred to as metepisternon (e.g., Franciscolo 1957a) or metepisternum (e.g., Franciscolo 2000, Odnosum & Perkovsky 2016).

row of spiniform setae – a series of equally short, regularly spaced spiniform setae along the entire ventral edge of particular metatarsomeres, different from those irregularly scattered. The term is newly introduced here, because this structure is traditionally not included in descriptions of Mordellidae.

tip of pygidium – in some species a ring of several *scale-like setae* is present on tip of tergite VII.

Systematic part

Order Coleoptera Linnaeus, 1758

Superfamily Tenebrionoidea Latreille, 1802

Family Mordellidae Latreille, 1802

Part I. Specimens preserved as inclusions in Eocene amber

Mordellidae incertae sedis

Mordellina Germar, 1813

Mordellina inclusa Germar, 1813

Mordellina inclusa Germar, 1813: 14. Syntypes: 2 specimens, Baltic amber.

Comments on identification. Germar (1813) established both the genus and species based on two specimens of unknown sex. He explicitly noted on page 12 'Daß wir die Gattungsnamen durch Anhängung der Endigung *ina*, *ites* oder *lithus* abänderten, bedarf hoffentlich keiner Rechtfertigung, die Gründe dafür auseinander zu setzen, wäre hier zu weitläufig.' Article 20 of ICZN (1999) does not include the suffix *–ina* for the purpose of describing a fossil genus: 'A name formed by adding the suffix *-ites*, *-ytes* or *-ithes* to the whole or the stem of an available name of a genus-group taxon, and applied to fossils to distinguish them from extant members of that taxon, without clear evidence of intent to establish a new genus-group taxon, is available only for the purposes of the Principle of Homonymy. Such a name cannot be used as the valid name of a taxon [Art. 23.1] or as the basis of a family-group name [Art. 11.7.1.4]' (ICZN 1999). This implies that *Mordellina* Germar, 1813 is an available name with *M. inclusa* as a type species and has priority over *Mordellina* Schilsky, 1908, a speciose genus of Mordellistenini from the Afrotropical and Oriental Region. The problem of homonymy is put aside for consideration by future students of the taxonomy of Mordellidae as its solution is beyond the scope of the present study.

The description provided by Germar (1813) does not provide any clue to where his *Mordellina inclusa* should belong according to the modern classification of this family. The species is referred to as *Mordella inclusa* (Germar, 1813) by H. Burmeister in 1832 (fide Ermisch 1941a), but the description does not contain the characters necessary for this generic placement. Therefore, eventual generic synonymy of *Mordellina* Germar with *Mordella* Linnaeus, 1758 and its tribal placement cannot be established, because until the genera *Tomoxia* A. Costa, 1854 and *Mordellistena* A. Costa, 1854 were described, the genus *Mordella* was the only available extant genus in this family. Moreover, the revision of Baltic Mordellini cited below did not reveal any direct evidence for the presence of *Mordella* in Baltic amber. Both syntypes of the species (if conspecific) were never revised and therefore the identity of *Mordellina inclusa* and validity of all subsequently described Eocene species are open to question.

Mordellinae Latreille, 1802

Mordellini Latreille, 1802

Succimorda Kubisz, 2001

Succimorda rubromaculata Kubisz, 2001

Succimorda rubromaculata Kubisz, 2001: 274. Holotype: ♀, Baltic amber.

Comments on identification. Kubisz (2001: 273) established *Succimorda* as a new monotypic genus to accommodate the newly described *S. rubromaculata*. The genus, however, is insufficiently and incorrectly diagnosed and of doubtful validity. According to the author, it 'seems closely related to *Mordella* … from which it differs markedly by naked [= glabrous] eyes and antennae being not serrate'. *Mordella* is a rather speciose genus with more than 400 species worldwide. For example, according to Liljeblad (1945), there are ten *Mordella* species in North America with glabrous eyes and all are still considered members of this genus (Hallan, unpublished catalogue). The shape of antennal segments in the different species vary, so their shape in *S. rubromaculata*, which is not very different from some extant species in having less serrate distal antennomeres, cannot justify the establishment of a new genus. There are some other discrepancies in the differential diagnosis, for example, in the statement '*Tomoxia* Costa and related genera with naked eyes …'. *Tomoxia* belongs to an informal group of three genera together with *Paratomoxioda* Ermisch, 1954 and *Tomoxioda* Ermisch, 1950, and in both *Tomoxia* and *Paratomoxioda* the eyes have interfacetal setae and are not glabrous according to Horák (2007).

Because there are no other extant species associated with this genus, we retain *Succimorda* as a purely extinct monotypic genus until a revision of the genus *Mordella* and the informal *Mordella*-group of genera sensu Franciscolo (1989).

'*Mordella* sp.'

(Fig. 1A)

Mordella sp.: Ermisch (1941a): 179, single indet. specimen, Baltic amber.

Material examined (SDEI). 'Mordella [p] /sp. [hw] / det. Ermisch 194 [p] i [hw, sic; glued on a bigger white label] // SDEI Müncheberg / SDEI-Amb-000644 [p; yellowish label]'.

Comments on identification. The micro-CT scan revealed at least five short transverse combs including the preapical one on metatibia and five similar combs on metatarsomere I. This beetle therefore belongs to Mordellistenini, not Mordellini.

It is unlikely that Ermisch made such a grave mistake. More likely the specimen was mismatched during subsequent manipulation with one of the syntypes SDEI--Amb-000635 of *Mordellistena korschefskyi* Ermisch, 1941, in which only a preapical comb on the metatibia typical for Mordellini is present (see Mordellistenini below).

The penultimate mesotarsomere of this specimen is deeply dilated so it cannot be attributed to *Mordellistena*, a genus used exclusively, but incorrectly, for Baltic Mordellistenini by Ermisch (1941a).

Baltimorda new collective group

Diagnosis. A collective group name (ICZN 1999) established to accommodate species of the family Mordellidae, tribe Mordellini, described from Eocene Baltic amber. No type species is designated in accordance with the article 13.3.2 of ICZN (1999).

Etymology. The name is composed of the words Baltic and suffix *-morda* (a form often used in nomenclature of the family). Feminine gender.

Baltimorda scheelei (Ermisch, 1941) comb. nov.

(Fig. 1B)

Mordella Scheelei Ermisch, 1941a: 178. Holotype: ♂, Baltic amber.

Type material examined. Holotype (GPIH), '37 [p; white label] // D 52 [hw] 37 [hw] / Mordellinae [hw] / Mordella scheelei [hw] / Determinator: [p] Ermisch [hw] 19 [p] 4i [hw, sic] / coll. A. SCHEELE, Berlin-Lichterfelde [p; white lable with black frame and lines, red dot] // Mordella [p] / scheelei [hw] / det. Ermisch 194 [p] i [hw, sic; white label] // Mordella scheelei Ermisch 1941 / Baltischer Bernstein / Holotypus, Typ.Kat. Nr.4297 Scheele Nr. 37 [p; red label] // Mordella scheelei / ERMISCH 1941 / Baltischer Bernstein / GPIH- Scheele -0037 / Holotyp TK-Nr.: 4297 / Familie: Mordellidae / Gattung: Mordella / Syninkl.: - [p; white label]'.

Comments on identification. Seriously damaged piece of amber (broken into 5 small pieces), one of which contains the posterior half of the body of the holotype. A dark and thin dorso-lateral ridge is clearly visible on the left metatibia along its entire length, which is identical to that in *Baltimorda* ?undescribed species A. Metatarsal segments are not visible and likely absent. Because of the presence of the dorso-lateral ridge, this species cannot be attributed to *Mordella* and is transferred here to *Baltimorda* new collective group.

Baltimorda friedrichi (Perkovsky & Odnosum, 2013) comb. nov.

Mordellaria friedrichi Perkovsky & Odnosum. 2013: 177. Holotype: Baltic amber.

Comments on identification. A casual examination of pictures of the habitus of *Mordellaria friedrichi* indicates marked differences from those of the West Palaearctic *M. aurofasciata* Comolli, 1837. The explanation for this is an incorrect generic diagnosis of *Mordellaria* provided by Perkovsky & Odnosum (2013) in which they state that: '*Mordellaria* is distinguished from the other tumbling flower beetles by the presence of fine and straight dorsal striae on metatibia that stretch from its base to its apical margin. Metatarsomeres 1 and 2 also bear fine and straight dorsal striae.' The authors also compared their species with *M. aurofasciata* in which only a dorsolateral ridge is present on the metatibia and metatarsomere I. Although it looks like a simple mistake, it had a serious effect on the taxonomic conclusions of the authors. In addition, the situation is even more complex. In the generic assignment of his *Mordellaria africana* Franciscolo, 1956, Franciscolo (1956) points out that the delimitation of this genus was incomplete at that time. Ermisch (1950a) established the genus *Mordellaria* based on *Mordella scripta* Fairmaire & Germain, 1863 from Chile, but as Franciscolo (1956)

correctly states 'Ermisch indicated that the hind tibiae bear a very distinct dorsal ridge, but does not specify whether this type of ridge is present also on the first and second hind tarsal segments, as it is the case of *Pseudomordellaria bifasciata* Erm. from Brazil.' As a consequence, Franciscolo (1956) attributed his *africana* to *Mordellaria*, providing that in the type species of the genus '(a) the middle tibiae are exactly as long as the middle tarsi (shorter in *M. scripta* Fairm. & Germ.); and (b) the first tarsal segment of the hind legs bears a distinct dorso-lateral ridge.' But in the description, he added 'the second [metatarsomere] bears a rudimentary dorso-lateral ridge (see Franciscolo 1956: fig. L-4)'. This uncertainty about the key characters attributed to putative *Mordellaria* species distributed in South American, Euro-Asian and African landmasses raises doubts about their congeneric relationship. Examination of the type of *Mordellaria scripta* stored in The Natural History Museum, London has revealed that the dorsolateral ridge is present on the metatibia and metatarsomere I only, and that the differential diagnosis provided by Perkovsky & Odnosum (2013) is incorrect also with respect to the type species of the genus.

Because characters of *M. friedrichi* do not correspond with the generic characteristic of *Mordellaria* the species is transferred here into *Baltimorda* new collective group.

Baltimorda succinea (Bao, Walczyńska, Bojarski, Jarzembowski, Wang & Rust, 2018) comb. nov.

Tomoxia succinea Bao, Walczyńska, Bojarski, Jarzembowski, Wang & Rust, 2018: 32. Holotype and paratype: Baltic amber.

Comments on identification. The examination of figures and description of *Tomoxia succinea* provided by Bao et al. (2018) indicates that this species is not associated with the genus *Tomoxia*, because this placement is based on erroneous arguments and poor knowledge of the generic delimitations within the Mordellini. The diagnosis they provide is as follows: 'Diagnosis (emended). The diagnostic characters for the genus *Tomoxia* when compared to the other members of the tribe Mordellini are: (1) eyes finely granulated; (2) scutellum quadrilateral or irregular shaped; (3) hind tibia with a fine dorsal ridge and a lateral ridge; basal tarsomere of hindleg also with a fine dorsal ridge (Smith 1882, Liljeblad 1945, Franciscolo 1965, Jackman & Lu 2001).' While points (1) and (2) do not provide any information relevant to the definition of the genus (e.g., eyes with small facets are present in all three genera included in the informal *Tomoxia* complex (Horák 2007) and in many other Mordellini), point (3) is incorrect *per se* because in *Tomoxia*, a dorsolateral ridge (dorsal ridge sensu Bao et al. 2018) is present on the metatibia, but absent on the first metatarsomere. According to the generic key to the *Tomoxia* complex provided by Horák (2007), the genus *Tomoxia* is defined as follows: 'Hind tibiae besides preapical ridge with fine dorsolateral ridge. First tarsomere of posterior tarsus **without dorsolateral ridge**. Eyes very finely facetted, with interfacetal setae.' In the description of eyes of *Tomoxia succinea* the authors stated those are 'large, ellipsoidal, finely faceted and granulated, apparently not reaching occiput, hairy.' This term likely indicates the presence of interfacetal setae, which are present in *Tomoxia* and *Tomoxioda*, but absent in *Paratomoxioda*. The combination of eyes with small facets covered with setae and presence of dorsolateral ridges on hind tibia and first metatarsomere conforms with the diagnosis of the genus *Klapperichimorda* Ermisch, 1968, which contains four Oriental species (Ermisch 1968; Horák 1996, 2020).

Because of the uncertain generic identity of the holotype and paratype of *Tomoxia succinea*, this species is transferred here into *Baltimorda* new collective group.

Baltimorda ?undescribed species A

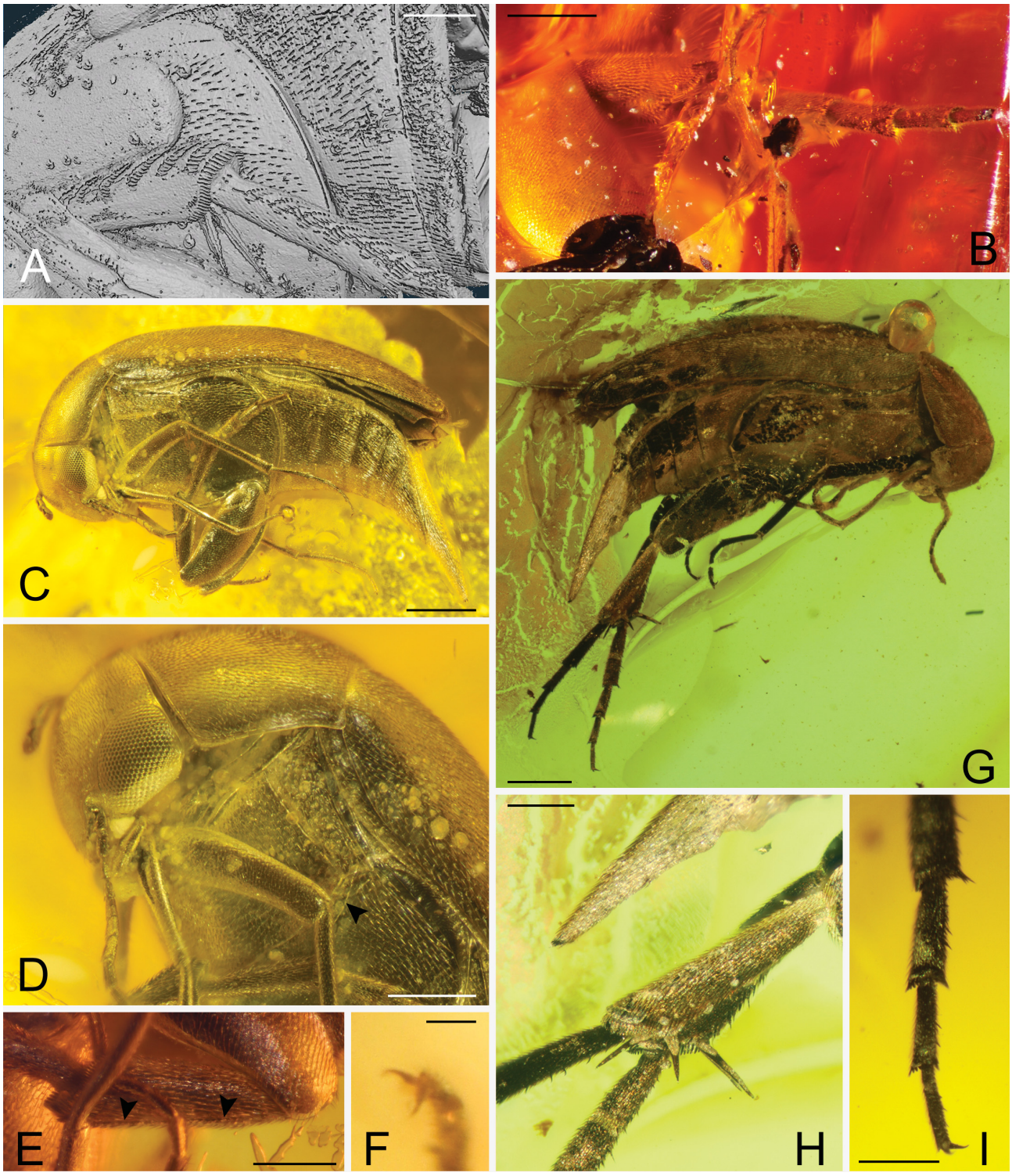
(Figs 1C–F, 10A)

Material examined. One specimen, PřfUK71, obtained from Jonas Damzen (original number JDC9160): Baltic amber.

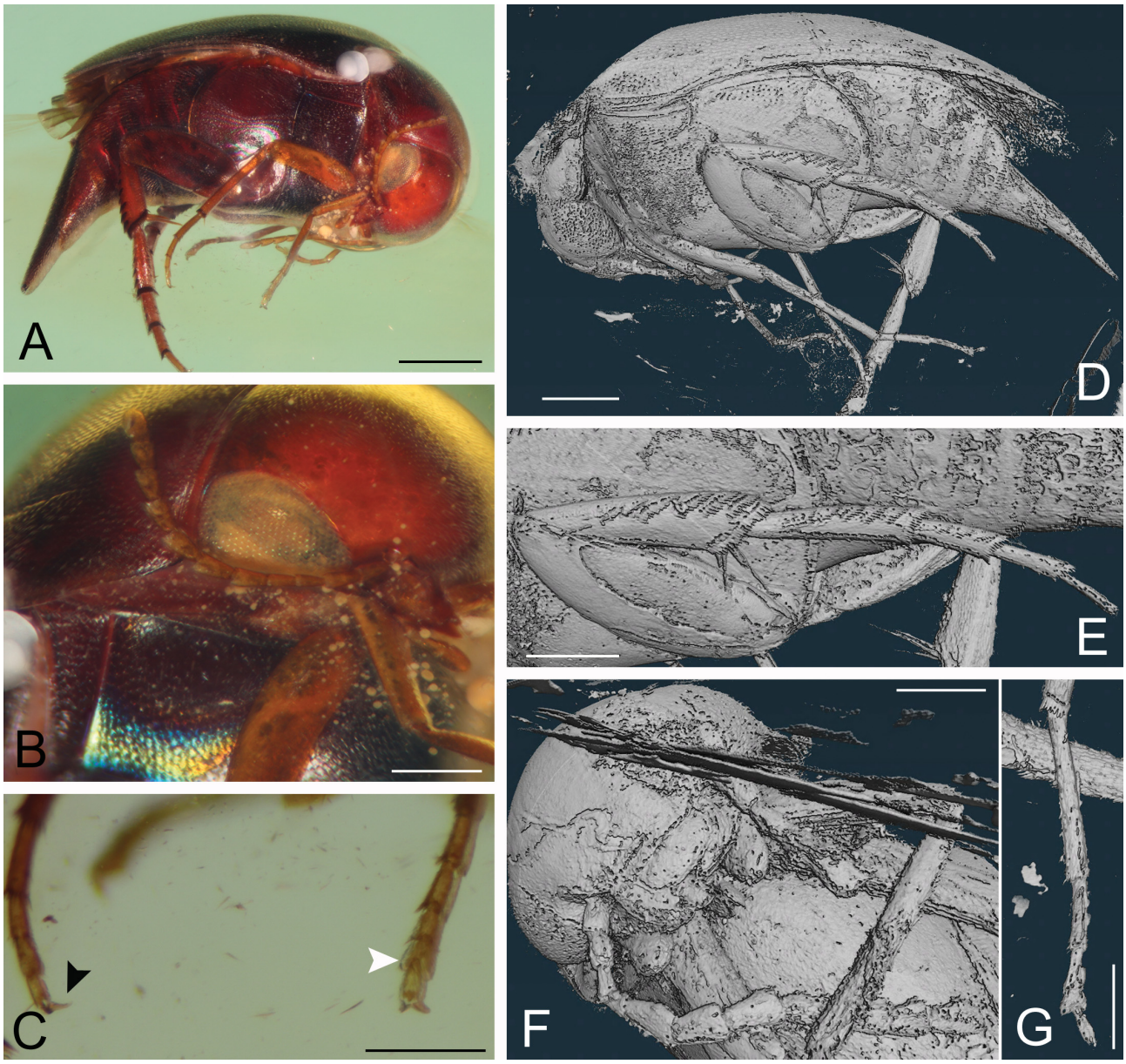
Description. Body of *Mordella*-type, cuticle shiny, head subglobular, frons continuously convex, posterior edge of eye near posterior margin of head, elytra convex, metacoxa broad, pygidium long. Main characters: All eleven antennomeres almost equal in length, antennomeres I and II robust, shiny, cylindrical, antennomere III narrow, cylindrical, antennomeres IV–VIII subserrate, slightly flattened, antennomeres IX–XI subcylindrical. Two maxillary palpomeres visible, shape indiscernible. Eyes elliptical, with about 18 facets across their widest part. Eyes glabrous, interfacetal setae absent. Form of scutellum indiscernible. Postero-lateral edges of pronotal disc at right angle. Elytra 3.2× as long as pronotal disc. All protarsomeres slender and cylindrical. Protibia narrow, about 1.5× as long as protarsus. Mesotarsomere IV cylindrical, slightly wider apically, 0.6× as long as tarsomeres III and V. Mesotibia 1.1× as long as respective tarsus. Metatibia with preapical comb parallel with apical setae and with fine dorsolateral ridge along whole length of tibia. Outer tibial spur on metatibia as long as half of metatarsomere I. Metatarsus without combs or ridges. Pygidium 2.6× as long as hypopygium. Anterior edge of metanepisternum 2× as long as its posterior edge, ventral edge 4× as long as posterior edge. Metakatepisternum present, but only dorsal part visible. Pretarsal claws simple, without visible teeth. Tip of pygidium with few dark acute setae.

Lengths (in mm): pronotal disc = 0.75, elytra = 2.56, mesotibia = 0.7, metatarsomere I = 0.5, pygidium = 1.1.

Differential diagnosis. Until there is a detailed investigation of all Baltic Mordellini based on characters other than ridges on the posterior legs, the identity of *Baltimorda* ?undescribed species A will remain uncertain. This specimen has a fine dorsolateral ridge along the whole length of the metatibia, as is the case in *Baltimorda scheelei*, *B. succinea* and *B. friedrichi*, but the presence or absence of ridges on tarsomeres cannot be verified with the material at hand. In its habitus it is more similar to *B. scheelei* than to the other two described species. The dorsolateral ridge on the metatibia and sometimes also metatarsus is present in many extant Mordellini genera (see also Differential diagnoses above) and the presence or absence of this structure is no longer sufficient for the identification and placement of Baltic Mordellini.



Figs 1. Mordellidae, Baltic amber. A – *Baltistena* sp., SDEI-Amb-000644, hind leg. B – *Baltimorda scheelei* (Ermisch, 1941), holotype, hind leg. C–F – *Baltimorda*, undescribed species A, PřfUK71: C – habitus; D – head and thorax; E – hind leg (black arrows marking fine dorsolateral ridge); F – pretarsal claws. G–I – *Baltimorda*, undescribed species B, PřfUK94: G – habitus; H – hind legs; I – metatarsus. Scale bars: A, E, H, I – 0.2 mm; B, D, – 0.3 mm; C, G – 0.5 mm; F – 0.05 mm.



Figs 2. A–G – Mordellistenini. A–C – *Palaeostena eocenica* Kubisz, 2003, PřfUK107, Rovno amber: A – habitus; B – head and antenna; C – mesotarsus with smooth pretarsal claws (black arrow) and protarsus with emarginated tarsomere IV (white arrow). D–G – *Baltistena amplicollis* (Ermisch, 1941), holotype, Baltic amber: D – habitus; E – hind leg; F – head ventrally; G – middle leg with emarginated tarsomere IV. Scale bars: A, D – 0.5 mm; B, C, G – 0.2 mm; E, F – 0.3 mm.

Baltimorda undescribed species B

(Figs 1G–I)

Material examined. One specimen, PřfUK94, obtained from Jonas Damzen (original number JDC9688): Baltic amber.

Description. Body shape similar to *Hoshihananomia* Kôno, 1935, cuticle matt, head subglobular, frons continuously convex, posterior edge of eye near posterior margin of head, elytra convex, metacoxa broad, pygidium long. Main characters: All eleven antennomeres cylindrical, antennomere XI acute at tip. Maxillary palpomeres not visible. Eyes elliptical, very finely faceted. Interfacetal setae not visible due to poor preservation. Form of scutellum indiscernible. Postero-lateral edges of pronotal disc obtuse. Elytra 3.0× as long as pronotal disc. Protarsomere I cylindrical; protarsomere IV flattened, deeply dilated. Protibia narrow, slightly curved, about 1.2× as long as protarsus. Mesotarsomere IV cylindrical, 0.75× as long as tarsomere III and V. Mesotibia 1.2× as long as respective tarsus. Metatibia only with preapical comb running parallel with row of apical setae. Outer tibial spur on metatibia as long as half of metatarsomere I; both metatibial spurs almost equal in length. Metatarsus without combs or ridges, ventral side of all metatarsomeres with spiniform setae. Pygidium 4.0× as long as hypopygium. Anterior edge of metanepisternum 2.5× as long as posterior edge, ventral edge 6.5× as long as posterior edge. Metakatepisternum not delimited. Pretarsal claws simple, without visible teeth. Tip of pygidium with few dark acute setae.

Lengths (in mm): pronotal disc = 0.86, elytra = 2.7, mesotibia = 0.7, metatarsomere I = 0.5, pygidium = 1.2.

Differential diagnosis. This specimen is the second species of Baltic Mordellini known to lack dorsolateral ridge on

the metatibia. In addition to the different habitus, there are also some evident differences in the measurements of this species B and *Succimorda rubromaculata* Kubisz, 2001 (see the Key below). The comparison with extant Mordellini has to wait until this tribe is reviewed.

A key to Mordellini from Baltic Eocene amber

Due to incomplete preservation of *Baltimorda scheelei* (Ermisch, 1941) the paragraphs 3 and 4 presented below have only tentative validity.

1 Metatibia with preapical comb running parallel with row of apical setae, but lacking dorsolateral ridge. .. 2
– Metatibia with preapical comb running parallel with row of apical setae and with fine dorsolateral ridge along whole length of tibia [a group of species including *Baltimorda scheelei*]. 3
2 Metatarsomere I 0.6× as long as metatibia. .... ***Baltimorda*** undescribed species B
– Metatarsomere I as long as metatibia. .... ***Succimorda rubromaculata*** Kubisz, 2001
3 Dorsolateral ridge on metatarsomere I absent. .... ***Baltimorda*** ?undescribed species A
– Dorsolateral ridge on metatarsomere I present. 4
4 Dorsolateral ridge on metatarsomere II absent. .... ***Baltimorda succinea*** (Bao et al., 2018)
– Dorsolateral ridge on metatarsomere II present. ..... ***Baltimorda friedrichi*** (Perkovsky & Odnosum, 2013)

Mordellistenini Ermisch, 1941

Palaeostena Kubisz, 2003 stat. nov.

Palaeostena Kubisz, 2003: 185 (as subgenus of *Falsomordellistena* Ermisch, 1941). Type species: *Falsomordellistena eocenica* Kubisz, 2003, original designation.

Palaeostena eocenica (Kubisz, 2003) comb. nov.

(Figs 2A–C, 10B)

Falsomordellistena (*Palaeostena*) *eocenica* Kubisz, 2003: 186. Holotype: ♂, Baltic amber.

Material examined. One specimen, PřfUK107, obtained from Jonas Damzen (original number JDC8742): ?Rovno amber. The specimen conforms with the description and figures of *P. eocenica* and is thus considered to be conspecific. It represents the first possible record of this species from Rovno amber.

Comments on identification. The author compared this species with extant members of *Falsomordellistena* because of the similar shape of their antennomeres. However, antennae in Mordellidae are often similar in different genera (see below for an example of a different diagnosis of *Baltistena concava* sp. nov.). In addition, in males of species of *Falsomordellistena* antennomeres V–X vary greatly in shape (from feebly serrate to filiform) and are usually 2× as long as wide or longer (e.g., Nomura 1967, 1975), while in *Palaeostena eocenica* they are only 'one half longer than wide', which must be considered a difference rather than a similarity.

Kubisz (2003) also lists several characters of *P. eocenica*, in which this species should differ from all extant *Falsomordellistena* species: eyes without interfacetal setae; peculiar shape of maxillary palpomere IV (surprisingly, its length is compared with the length of basal antennomeres, not palpomeres); asymmetry of metatibial spurs; absence of body pubescence; and body size. Only the last three of these differences are included in the diagnosis of this species, as according to the author, they delimit *P. eocenica* from all known species of *Falsomordellistena*. In summary, Kubisz (2003) states that *P. eocenica* differs from extant species of *Falsomordellistena* in at least five characters usually used for delimiting genera and therefore its inclusion into this extant genus would invalidate the generic diagnosis.

Accepting the validity of this species and the fact that its generic assignment to *Falsomordellistena* is not supported by the given diagnosis, the subgenus *Palaeostena* is here raised to generic status.

Baltistena new collective group

Diagnosis. A collective group name (ICZN 1999) established to accommodate species of the family Mordellidae, tribe Mordellistenini described from Eocene Baltic amber. No type species is designated in accordance with article 13.3.2. of ICZN (1999).

Etymology. The name is composed of the words Baltic and suffix *-stena* (a form often used in nomenclature of the family). Feminine gender.

Baltistena amplicollis (Ermisch, 1941) comb. nov.

(Figs 2D–G)

Mordellistena amplicollis Ermisch, 1941a: 182. Holotype: Baltic amber.

Type material examined. Holotype (SDEI): 'MORDELLISTENA [p] / amplicollis [hw] / det. Ermisch 194 [p] i [hw, sic; white label glued on a bigger white label] // TYPE [p; in black frame, red label glued on the bigger white label] // SDEI Müncheberg / SDEI-Amb-000640 [p; yellowish label]'.

Comments on identification. As pro- and mesotarsomere IV are distinctly broader and shallowly emarginated, this species cannot be attributed to *Mordellistena*. To distinguish it from other Eocene Mordellistenini see the Key below. Because of the uncertain generic identity of this species, it is transferred here into *Baltistena* new collective group.

Baltistena antiqua (Ermisch, 1941) comb. nov.

(Figs 3A–C)

Mordellistena antiqua Ermisch, 1941a: 181. Holotype: Baltic amber.

Type material examined. Holotype (GPIH): 'TYPE [p; in black frame, red label] // 36 [p; white label] // D 52 [hw] / Mordellinae [hw] / Mordellistena antiqua [hw] / Determinator: [p] Ermisch [hw] 19 [p] 4i [hw, sic] / coll. A. SCHEELE, Berlin-Lichterfelde [p; white label with black frame and lines, red dot] // MORDELLISTENA [p] / antiqua [hw] / det. Ermisch 194 [p] i [hw, sic; white label] // *Mordellistina* [sic] *antiqua* Ermisch 1941 / Baltischer Bernstein / Holotypus,, Typ.Kat.Nr.3890, Scheele Nr. 36 [p; red label] // Mordellistena antiqua / ERMISCH 1941 / Baltischer Bernstein / GPIH- Scheele -0036 / Holotyp TK-Nr.: 3890 A / Familie: Mordellidae / Gattung: Mordellistena / Syninkl.: Lepidoptera (Köcher) [p; white label]'.

Comments on identification. At least mesotarsomere IV is deeply dilated and bilobed so this species cannot be attributed to *Mordellistena*. To distinguish it from other Eocene Mordellistenini see the Key below.

Because of its uncertain generic identity this species is transferred here into *Baltistena* new collective group.

Baltistena goeckei (Ermisch, 1941) comb. nov.

Mordellistena goeckei Ermisch, 1941a: 179. Holotype: ♂, Baltic amber.

Comments on identification. According to the curator of the GPIH collection only an empty bag with label 'broken' was found and the type is considered lost. At the moment we cannot add any comment to this species. To distinguish this species tentatively from other Eocene Mordellistenini see the note after the key below.

Because the generic identity of this species cannot be investigated and supported, it is transferred here into *Baltistena* new collective group.

Baltistena korschefskyi (Ermisch, 1941) comb. nov.

(Figs 3D–J)

Mordellistena korschefskyi Ermisch, 1941a: 180. Syntypes: 3 specimens, Baltic amber.

Type material examined. Lectotype (here designated) (SDEI):, 'MORDELLISTENA [p] / Korschefskyi [hw] / det. Ermisch 194 [p] i [hw, sic; white label glued on bigger white label] // TYPE [p; in black frame, red label glued on the bigger white label] // SDEI Müncheberg / SDEI--Amb-000639 [p; yellowish label]'. Paralectotypes: 2 spec. (SDEI), 'MORDELLISTENA [p] / Korschefskyi [hw] / det. Ermisch 194 [p] i [hw, sic; white label glued on bigger white label] // Cotype [p; in black frame] Cotype [p; in black frame; white label glued on the bigger white label] // SDEI Müncheberg / SDEI-Amb-000635 [p; yellowish label]'.

Comments on identification. According to Ermisch (1941a), all three type specimens must be considered syntypes because he explicitly noted 'Es sind drei Exemplare vorhanden (Sammlung D.E.I.) zwei davon stark getrübt.' The terms 'type' and 'cotype' have been used only at the labels of respective specimens. Due to the uncertain conspecificity of the three syntypes (see below), the lectotype is designated to preserve stability of the nomenclature of this species, according to the Article 74.7.3 of the Zoological Code (ICZN 1999).

The specimen SDEI-Amb-000639 is designated here as the lectotype because 1) it is complete and very well preserved, 2) Ermisch labelled this specimen as a 'type' and both specimens of 635 as 'cotype' and 3) Ermisch chose this specimen for his plate VII (fig. 6) as the only representative of this species.

Both pro- and mesotarsomere IV of the lectotype are distinctly broader and shallowly emarginated so it cannot be attributed to *Mordellistena*. To distinguish this species from other Eocene Mordellistenini see the key below. Because of the uncertain generic identity of this species, it is transferred here into *Baltistena* new collective group.

The micro-CT scan revealed that one of the paralectotypes SDEI-Amb-000635 (Figs 4A,B) has a preapical comb only on the metatibia. The specimen is therefore a member of Mordellini, not Mordellistenini. Subsequent mismatch with Ermisch's '*Mordella* sp.' is expected (see above). Malleiform maxillary palpomere IV differs from triangular palpomere IV of *Mordella* spp.

It is likely that the second specimen SDEI-Amb-000635 (Figs 4C–G) is not conspecific with the lectotype because in the lectotype the metatarsomere I is about 0.8× as long as metatibia, whereas in the cotype 635 it is only 0.6× as long as the metatibia. In both specimens, the angles of the combs differ. At least protarsomere IV of the Mordellistenini specimen SDEI-Amb-000635 is deeply dilated so it cannot be attributed to *Mordellistena*.

Baltistena soror (Ermisch, 1941) comb. nov.

(Figs 5A–E)

Mordellistena soror Ermisch, 1941a: 180. Syntype (number of specimens not mentioned): Baltic amber.

Type material examined. Syntype: (SDEI): 'MORDELLISTENA [p] / soror [hw] / det. Ermisch 194[p] i [hw, sic; white label glued on a bigger white label] // TYPE [p; in black frame, red label glued on a bigger white label] // SDEI Müncheberg / SDEI-AMB-000638 [p; yellowish label]'.

Comments on identification. At least mesotarsomere IV is very dilated so this species cannot be assigned to *Mordellistena*. To distinguish it from other Eocene Mordellistenini see the key below.

Because of the uncertain generic identity of this species, it is transferred here into *Baltistena* new collective group.

Baltistena sergeli (Ermisch, 1943) comb. nov.

(Figs 5F–J)

Glipostena sergeli Ermisch, 1943: 65. Holotype: ♂, Baltic amber.

Type material examined. Holotype: (SDEI):, [two white labels with double black frames glued on left and right side of microscope slide, the other labels glued on top of them] 'Glipostena [hw] / Sergeli sp. n. [hw] / det. Ermisch 1942 [p; white label] // Ermisch (Type) [hw; double framed white label on the left side of microscope slide] // TYPE [p; in black frame, red label] // SDEI Müncheberg / SDEI-Amb-000647 [p; yellowish label] / coll.Dr.Sergel / ded.Novemb.1942 [hw; double framed, white label on the right side of the microscope slide]'.

Comments on identification. Terminal palomere of maxillary palpus is malleiform (bean-like in shape), i.e., of type C sensu Franciscolo (1957a), versus equilateral triangular in extant species of *Glipostena* Ermisch, 1941, i.e., of type B (Franciscolo (1957a). Comb formula 7//5/3/2/0 and length and orientation of all combs are very different from those in extant species: combs of *G. sergeli* are too short, more transverse and more abundant on metatibia and the first three metatarsomeres (for details see under *Rovnostena ponomarenkoi* (Odnosum & Perkovsky, 2009)). To distinguish it from other Eocene Mordellistenini see the key below.

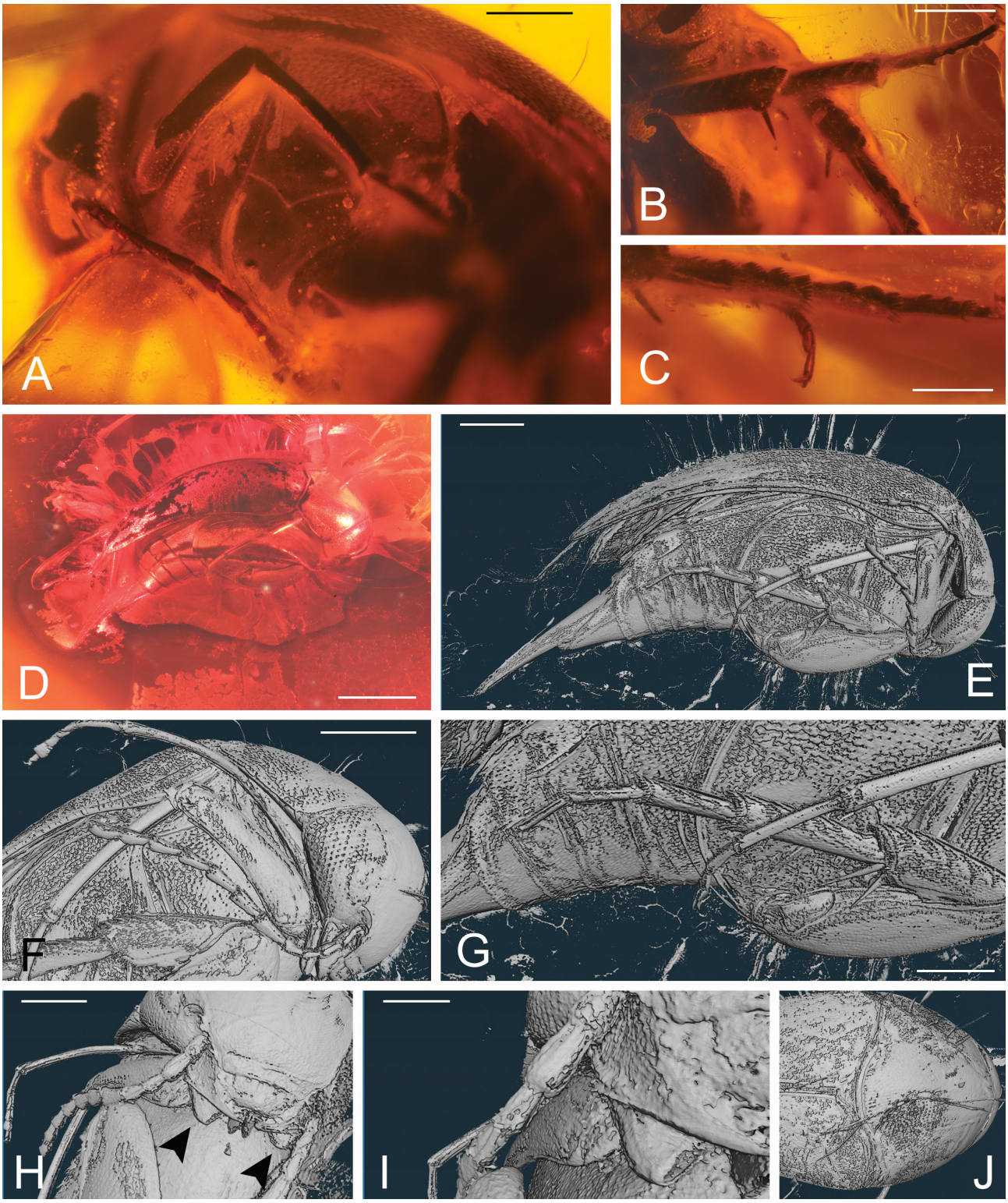
Because of the uncertain generic identity of this species, it is transferred here into *Baltistena* new collective group.

Baltistena ultima sp. nov.

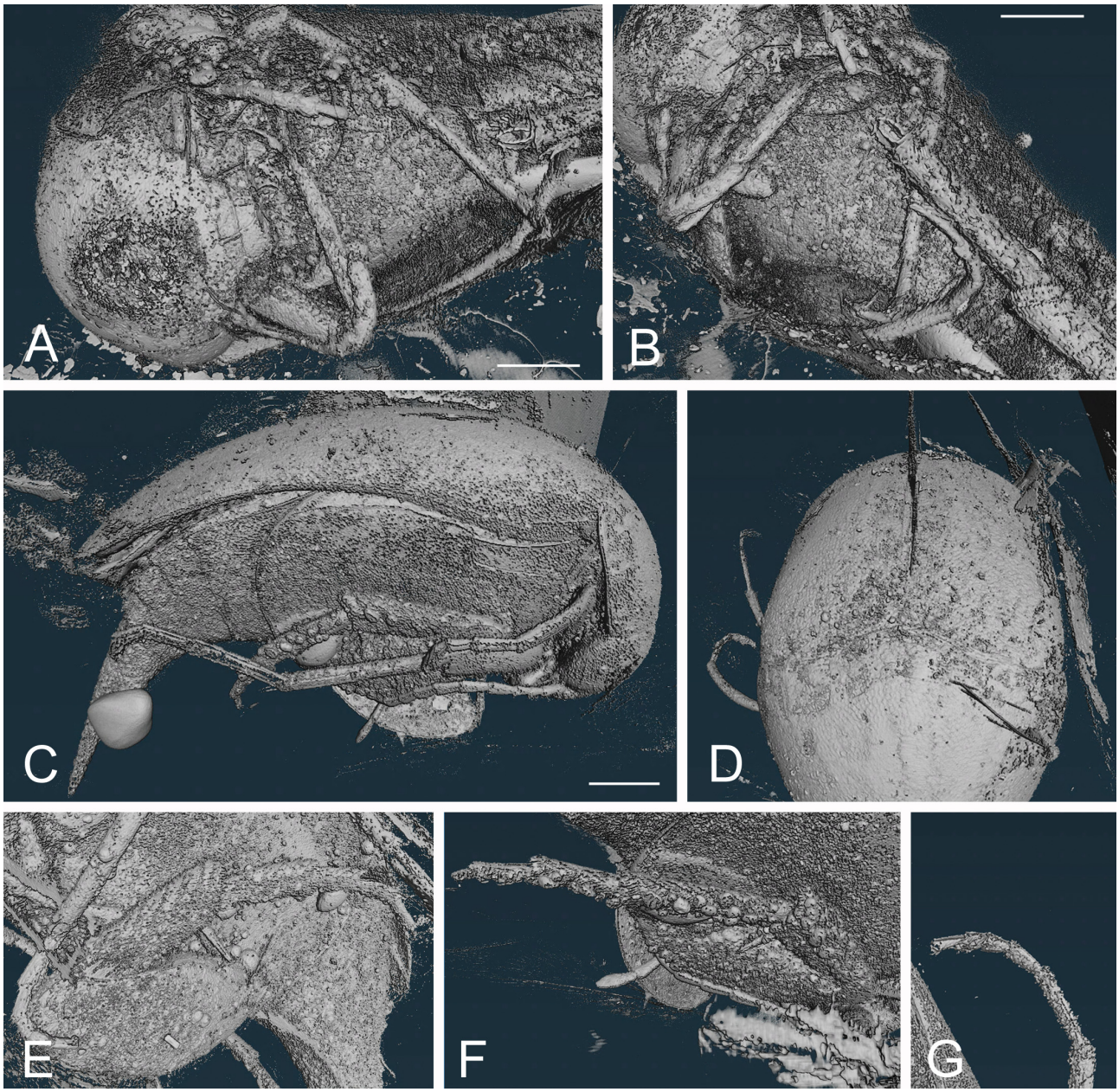
(Figs 6A–C)

Type material. Holotype: PřfUK65, obtained from rmvveta (www.ambertreasure4u.com) (original number 274532540629): Baltic amber.

Description. Head subglobular, frons continuously convex, posterior edge of eye near posterior margin of head, elytra convex, metacoxa expanded, comb formula 4//3/3/0/0, pygidium long. Main characters: Form of antennae: only 10 distal antennomeres visible, length ratios as follows: ?-1.6-1-1.2-1.6-1.2-1.4-1.4-1.4-1.4-2.2 (i.e., antennomere III probably shortest), antennomere XI longest, notched (emarginated) laterally at apex, thus distal half of antennomere half as wide as basal half. Structure of



Figs 3. A–J – Mordellistenini, Baltic amber. A–C – *Baltistena antiqua* (Ermisch, 1941), holotype: A – thorax ventrally. B, C – hind legs. D–J – *Baltistena korschefskyi* (Ermisch, 1941), SDEI-Amb-000639, lectotype: D, E – habitus; F – head and thorax anteroventrally; G – hind legs; H – maxillary palpomeres IV (black arrows); I – maxillary palpomere IV and antennomeres I–IV; J – pronotal disc dorsally. Scale bars: A, B, G – 0.3 mm; C, H – 0.2 mm; D – 1 mm; E, F – 0.5 mm; I – 0.1 mm.



Figs 4. A, B – Mordellini, *Baltimorda* sp., SDEI-Amb-000635, head and thorax ventrally including legs. C–G – Mordellistenini, *Baltistena* sp., SDEI-Amb-000635: C – habitus. D – hind margin of pronotal disc and elytra. E, F – hind legs. G – fore leg. Scale bars: A – 0.4 mm; B – 0.3 mm; C – 0.5 mm.

maxillary palpi indiscernible. Size of eye facets indiscernible. Presence or absence of interfacetal setae uncertain. Form of scutellum indiscernible. Basal side of pronotum indiscernible. Elytra 3.1× as long as pronotal disc. Form of protarsi: protarsomere I cylindrical, 7× as long as wide; protarsomere II cylindrical, 4× as long as wide; protarsomere III subcylindrical, 2× as long as wide at apex; protarsomere IV as long as wide, dilated at apex; protarsomere V elliptical, about as long as protarsomere III. Protibia very narrow, slightly curved, distinctly longer than protarsus. Form of mesotarsomere IV indiscernible. Mesotibia 1.1× as long as respective tarsus. Metatibia with at least four dorso-lateral combs of scale-like setae including preapical one. Metatibia with two long, very thin and sharply pointed spurs. Metatarsomere I with row of spiniform setae consisting of ca 15 short strong setae ventrally and with five combs of lateral scale-like setae, the first three of them with only a few setae; metatarsomere II with row of spiniform setae consisting of ca. 15 short strong setae ventrally, and with two short lateral combs of scale-like setae; metatarsomeres III and IV with row of spiniform setae consisting of ca. 15 short strong setae ventrally, lateral combs of scale-like setae absent. Pygidium 2.3× as long as hypopygium, distinctly bowed ventrally. Shape of metanepisternum indiscernible. Absence or presence and shape of metakatepisternum (newly added). Pretarsal claws long and straight, bidentate at apex. Tip of pygidium with distinct cluster of black scale-like setae.

Lengths (in mm): pronotal disc = 0.5, elytra = 1.8, metatarsomere I = 0.4, pygidium = 0.9.

Etymology. The species name refers to the specific modification of antennomere XI; adjective.

Differential diagnosis. *Baltistena ultima* sp. nov. can be readily separated from other members of the family by the presence of dorso-lateral combs of scale-like setae (= 'ridges') including a preapical one on the metatibia and metatarsomeres (character of Mordellistenini), antennomere XI laterally notched at apex, and protarsomere IV emarginated at apex. Apically notched antennomere XI occur only in a few taxa of Mordellidae. In Mordellistenini this character is present only in *Mordellistena* (*Mordellokoiles*) *grandii* Franciscolo, 1942 – a monotypic subgenus from southern Italy (Franciscolo 1942), and in Mordellini only in the species of *Tomoxia* (e.g., Liljeblad 1945: Plate III, fig. 16a; Franciscolo 1957a: Fig. 5.5). The genus *Mordellistena* differs from *Baltistena ultima* sp. nov. in having cylindrical protarsomeres with a truncate (= straight cut) apex. The above-mentioned species are unlikely to be related as this peculiar modification of antennomere XI apparently appeared in both tribes independently. The function is unknown.

Baltistena aurata sp. nov.

(Figs 6D–G)

Type material. Holotype: PřfUK66, obtained from rmvveta (www.ambertreasure4u.com) (original number 224239532480): Baltic amber.

Description. Head subglobular, frons continuously convex, posterior edge of eye near posterior margin of head, elytra convex, metacoxae broad, comb formula 3//3/1/0/0, pygidium long. Main characters: Right antenna clearly visible, length ratios of antennomeres as follows: 1.25-1.4-1->1->1-1.4-1.25-1.4-1.4-1.25-<2 (antennomeres IV and V only slightly longer than antennomere III), antennomeres I–X cylindrical, antennomere XI malleiform, widest in middle, all antennomeres distinctly longer than wide with ratio: 1.75-2-1.5-1.45-1.5-2-2.3-2.6-2.6-1.9-3.9. Maxillary palpomere II robust, almost as long as wide, palpomere III short, triangular, palpomere IV malleiform of *Mordellochroa*-type (Franciscolo 1957a: 216). Eyes roughly faceted. Eyes glabrous. Form of scutellum indiscernible. Form of basal side of pronotum indiscernible. Elytra 3.1× as long as pronotal disc. Form of protarsi: protarsomeres cylindrical, tarsomere I 6.25× as long as wide; tarsomere II 4× as long as wide; tarsomere III 3× as long as wide; tarsomere IV oblique at apex but without visible emargination; tarsomere V about 3× as long as wide. Structure of protibia indiscernible. Form of mesotarsomere IV: mesotarsomeres cylindrical, tarsomere I 5.6× as long as wide; tarsomere II 3.6× as long as wide; tarsomere III 3.5× as long as wide; tarsomere IV 2× as long as wide excised almost down to middle of its length; tarsomere V about 2.5× as long as wide. Mesotibia 1.5× as long as mesotarsal segments combined. Type of comb on metatibia: three distinct lateral combs of scale-like setae including preapical comb, combs do not reach middle of metatibia; preapical comb runs parallel with apical fringe of setae, remaining two combs oriented at different angles; few isolated patches of scale-like setae present behind proximal dorso-lateral comb. Metatibia with two spurs, outer spur shorter and sharply pointed. Metatarsomere I with row of spiniform setae consisting of about 20 short strong setae ventrally, metatarsomeres II–IV with row of spiniform setae consisting ventrally of about 17 short strong setae; metatarsomere I with three short lateral combs of scale-like setae; metatarsomere II with one short lateral comb of scale-like setae, metatarsomeres III–IV without combs; length ratio of metatarsal segments 1.75-1-1-1. Pygidium long and straight, 3.1× as long as hypopygium. Shape of metanepisternum: long and narrow, lower corner of posterior edge rounded, anterior edge 3× as long as posterior edge, ventral edge 5.5× as long as posterior edge. Metakatepisternum not discernible. Pretarsal claws long and straight, with 2–3 indistinct teeth on ventral edge. Tip of pygidium with distinct cluster of black scale-like setae.

Lengths (in mm): pronotal disc = 0.54, elytra = 2.16, mesotibia = 0.8, metatarsomere I = 0.34, pygidium = 0.9.

Etymology. The species name refers to the golden appearance of the body; adjective.

Differential diagnosis. Although the structure of mouthparts, shape of antennae, legs and pronotal disc, and overall habitus of *Baltistena aurata* sp. nov. appear familiar, this species cannot be placed in any extant genus of Mordellistenini because of the following characters: length over 4 mm; eyes glabrous; frons convex; terminal maxillary palpomere malleiform; antenna filiform, antennomeres cylindrical; antennomeres V–X 1.5–2.6× as long as wide; antennomere XI 1.6× as long as preceding one; anterior edge of pronotal disc rounded; pro- and mesotarsomere IV emarginated, shallowly bilobed; metatibial combs short; both metatibial spurs long, only slightly dissimilar. For its comparison with 37 extant genera and subgenera having pro- and mesotarsomere IV emarginated see Table 1.

Baltistena longistrigata sp. nov.

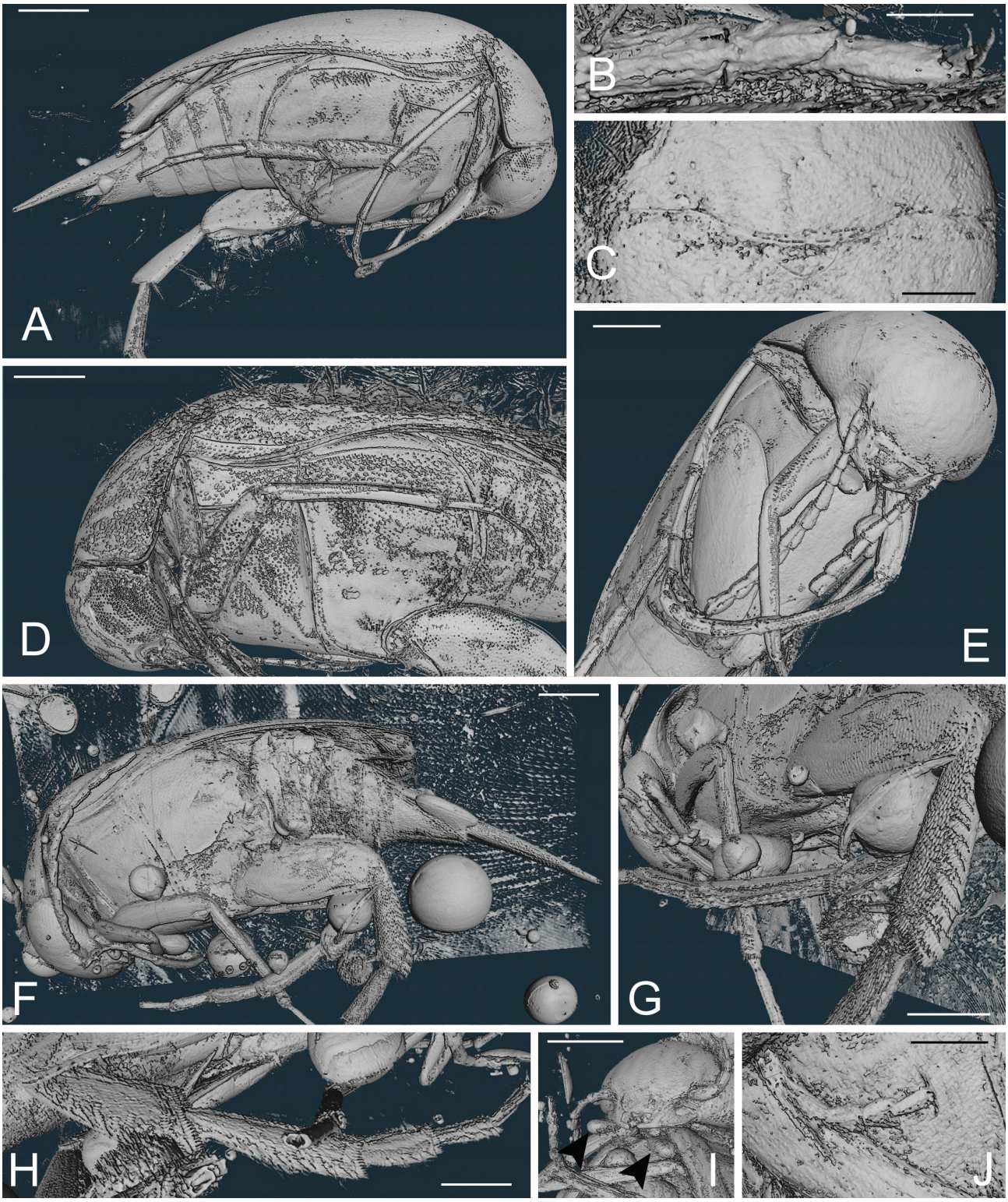
(Figs 7A–D)

Type material. Holotype: PřfUK69, obtained from rmvveta (www.ambertreasure4u.com) (original number 293822360959): Baltic amber.

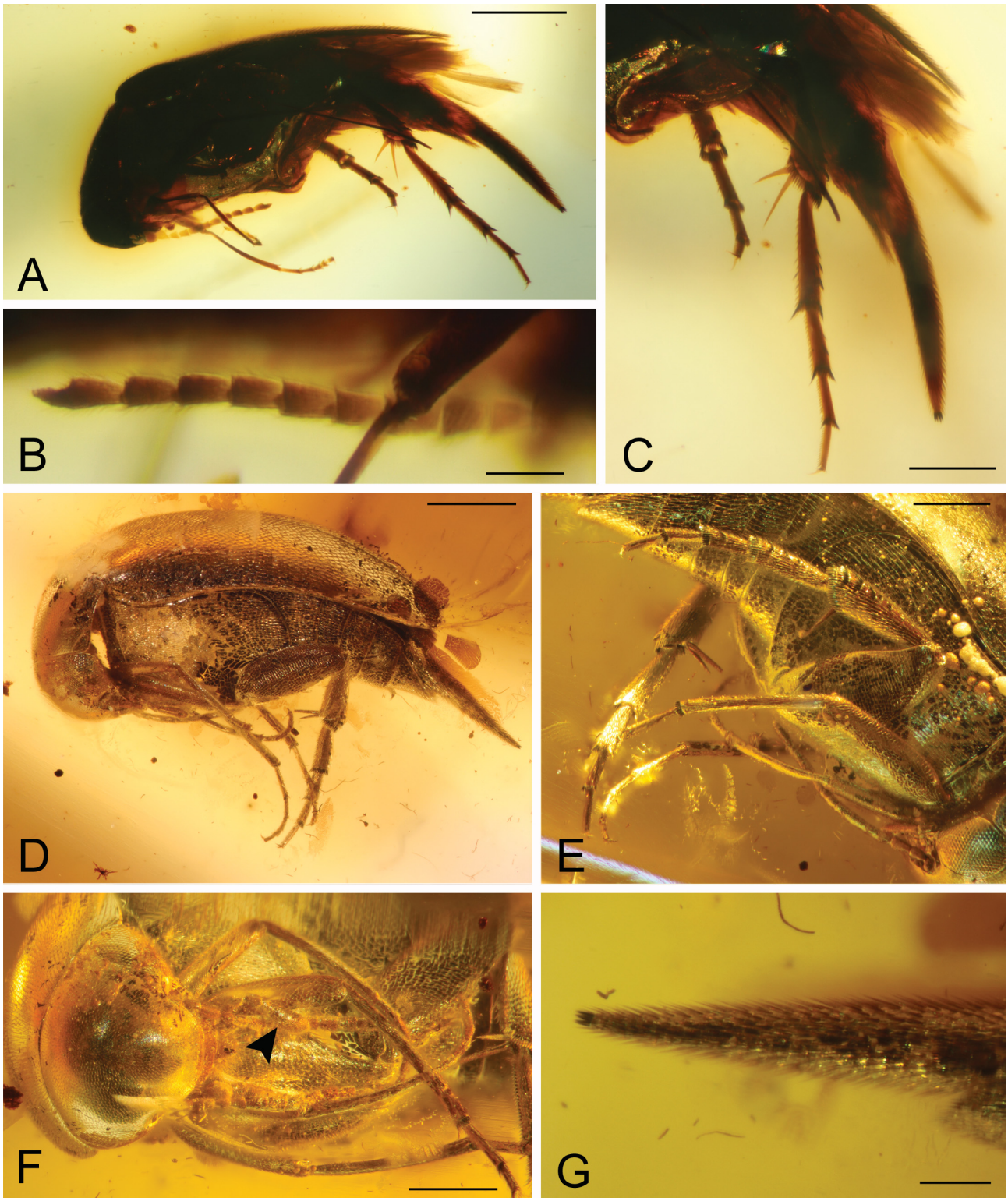
Description. Head subglobular, frons continuously convex, posterior edge of eye near posterior margin of head, elytra convex, metacoxae expanded, comb formula 1+2//3/1/0/0, pygidium long. Male genitalia partly extruded. Main characters: Form of antennae: five or six basal antennomeres visible, cylindrical, about 2× as long as wide. Structure of maxillary palpi indiscernible. Eyes rounded, with about 20 facets across middle of eye. Interfacetal setae absent. Form of scutellum indiscernible. Form of basal side of pronotum indiscernible. Elytra 4× as long as pronotal disc. Form of protarsomeres indiscernible. Protibia straight and robust. Mesotarsomere IV shortest, oblique at apex, deeply dilated. Length ratio of mesotibia and respective tarsus unknown. Type of combs on metatibia: preapical comb shortest, two subsequent combs about 2× as long as preapical one, straight, formed by shorter and finer setae. Presence or absence of outer tibial spurs on metatibia indiscernible. Type of combs on metatarsus: metatarsomere I with three short transverse combs, metatarsomere II with one short comb formed by four scale-like setae situated close to posterior edge of tarsomere. Pygidium 3.3× as long as hypopygium. Anterior edge of metanepisternum 1.7× as long as its posterior edge, ventral edge 4.5× as long as its

Table 1. Comparison of *Baltistena aurata* sp. nov. with extant genera of Mordellistenini.

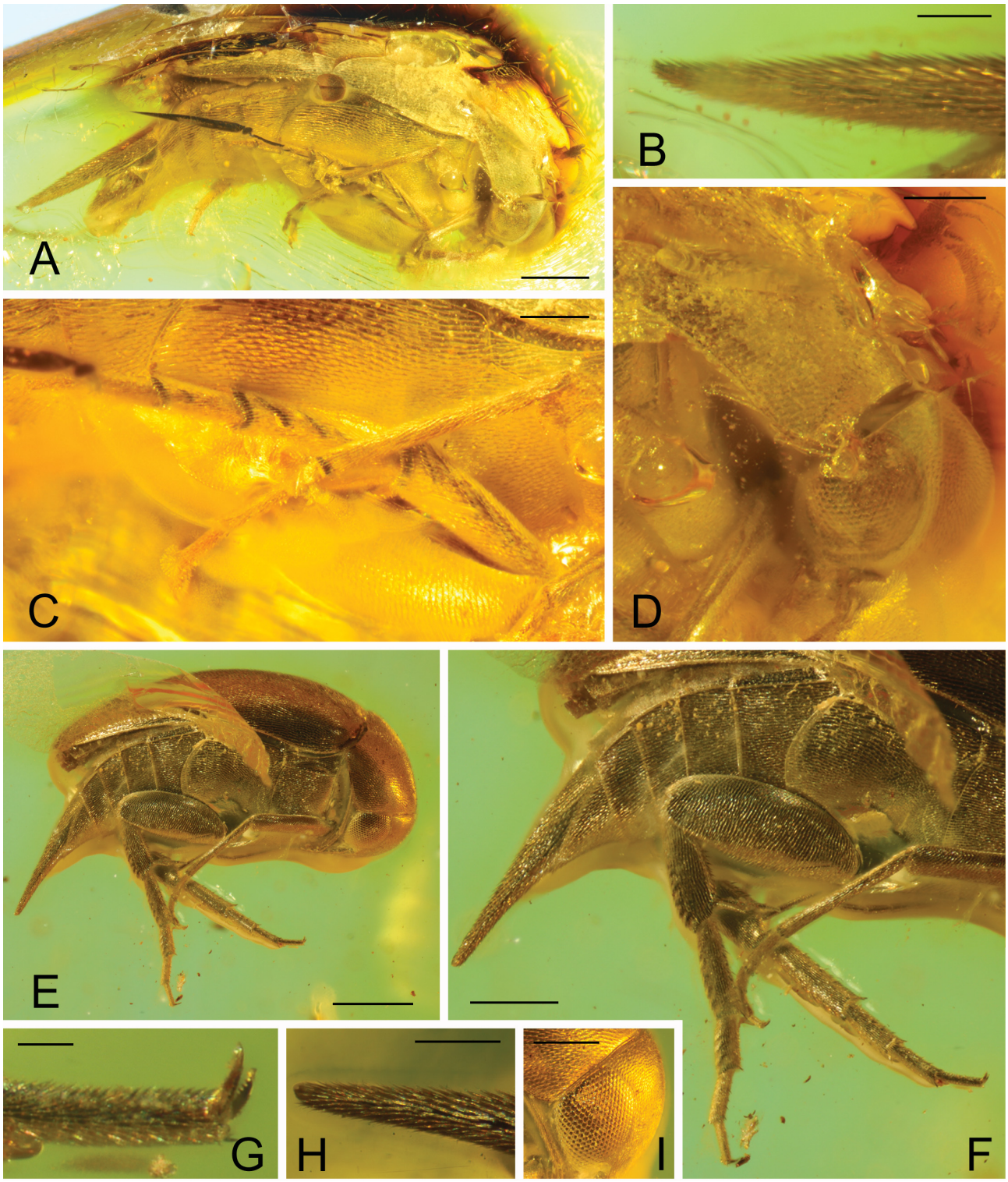
Mordellistenini with emarginated, bilobed or excavated pro- and mesotarsomere IV	**Prominent generic character(s) of respective genus/subgenus**	**Difference in *Baltistena aurata* n.sp.**
Asiatolida Shiyake, 2000	distinctly dissimilar metatibial spurs	both metatibial spurs long, only slightly dissimilar
Calyce Champion, 1891	ultimate maxillary palpomere lamellate with long processes (males) or cultriform (females)	terminal maxillary palpomere malleiform
Calycemorda Ermisch, 1969	antennae distinctly serrate from antennomere V to antennomere X	antennae filiform, antennomeres cylindrical
Calyceoidea Ermisch, 1969	antennae distinctly serrate from antennomere V to antennomere X	antennae filiform, antennomeres cylindrical
Dellamora Normand, 1916	size less than 2.5 mm	size more than 4.0 mm
Diversimorda Ermisch, 1969	anterior edge of pronotal disc prolonged (neck-like)	anterior edge of pronotal disc shalowly rounded
Ermischiella Franciscolo, 1950	terminal maxillary palpomere elongate-securiform or broadly securiform, eyes with distinct interfacetal setae	terminal maxillary palpomere malleiform, eyes glabrous
Fahraeusiella Ermisch, 1953	one metatibial spur	two metatibial spurs
Falsomordellina Nomura, 1966	eyes with interfacetal setae, metatibial combs long and oblique	eyes glabrous, metatibial combs short
Falsomordellistena (*Falsomordellistenoda* Ermisch, 1950)	terminal maxillary palpomere elongate-securiform, eyes with distinct interfacetal setae	terminal maxillary palpomere malleiform, eyes glabrous
Falsomordellistena (s.str.) Ermisch, 1941	terminal maxillary palpomere elongate-securiform, eyes with distinct interfacetal setae	terminal maxillary palpomere malleiform, eyes glabrous
Gladiostena Horák, 2007	antennomere IX in males 5–6 times, in females only 2–2.5 times as long as the preceding one	antennomere XI only 1.6 times as long as preceding one
Glipostena Ermisch, 1941	combs long reaching the midwidth of the metatibia, oblique and not parallel to its apical margin	combs short reaching not more than one third of the metatibia width and parallel to its apical margin
Glipostenoda Ermisch, 1950	terminal maxillary palpomere elongate-securiform, eyes with distinct interfacetal setae	terminal maxillary palpomere malleiform, eyes glabrous
Horionella Ermisch, 1954	frons with deep depression	frons convex
Jenisia Horák, 2008	frons with deep depression	frons convex
Lubosiella Horák, 2007	one metatibial spur	two metatibial spurs
Lycidomorda Horák, 2007	terminal maxillary palpomere elongate-securiform or broadly securiform	terminal maxillary palpomere malleiform
Mordellistenalia Ermisch, 1958	terminal palpomere elongate-securiform or broadly securiform	terminal palpomere malleiform
Mordellistenoda Ermisch, 1941	combs much prolonged and oblique along the length of metatibia	combs short, mostly parallel with apex of metatibia
Mordellochroidea Ermisch, 1969	combs much prolonged and oblique along the length of metatibia	combs short, mostly parallel with apex of metatibia
Morphomordellochroa Ermisch, 1969	combs much prolonged and oblique along the length of metatibia	combs short, mostly parallel with apex of metatibia
Neomordellistena (*Neomordellina* Franciscolo, 1967)	eyes with distinct interfacetal setae	eyes glabrous
Neomordellistena (s.str.) Ermisch, 1950	eyes with distinct interfacetal setae	eyes glabrous
Ophthalmomorda Horák & Farkač, 2017	terminal maxillary palpomere elongate-securiform or broadly securiform	terminal maxillary palpomere malleiform
Palpomorda Ermisch, 1969	eyes with interfacetal setae	eyes glabrous
Pselaphokentron Franciscolo, 1955	eyes with interfacetal setae	eyes glabrous
Pseudodellamora Ermisch, 1941	size less than 2.5 mm	size more than 4.0 mm
Pseudotolida Ermisch, 1949	combs much prolonged and oblique along the length of metatibia	combs short, mostly parallel with apex of metatibia
Pulchrimorda Ermisch, 1968	terminal maxillary palpomere elongate-securiform or broadly securiform	terminal maxillary palpomere malleiform
Rolcikomorda (*Hauckina* Horák, 2007)	antennae distinctly serrate from antennomere V to antennomere X	antennae filiform, antennomeres cylindrical
Rolcikomorda (s.str.) Horák, 2007	antennae distinctly serrate from antennomere V to antennomere X	antennae filiform, antennomeres cylindrical
Scaphiostena Horák, 1994	size less than 2.5 mm	size more than 4.0 mm
Sinopalpus Horák, 2007	one metatibial spur	two metatibial spurs
Tolida Mulsant, 1856	eyes with distinct interfacetal setae	eyes glabrous
Tolidopalpus Ermisch, 1951	antennomeres V–X as long as wide	antennomeres V–X 1.5–2.6 times as long as wide
Xanthomorda Ermisch, 1969	combs much prolonged and oblique along the length of metatibia	combs short, mostly parallel with apex of metatibia



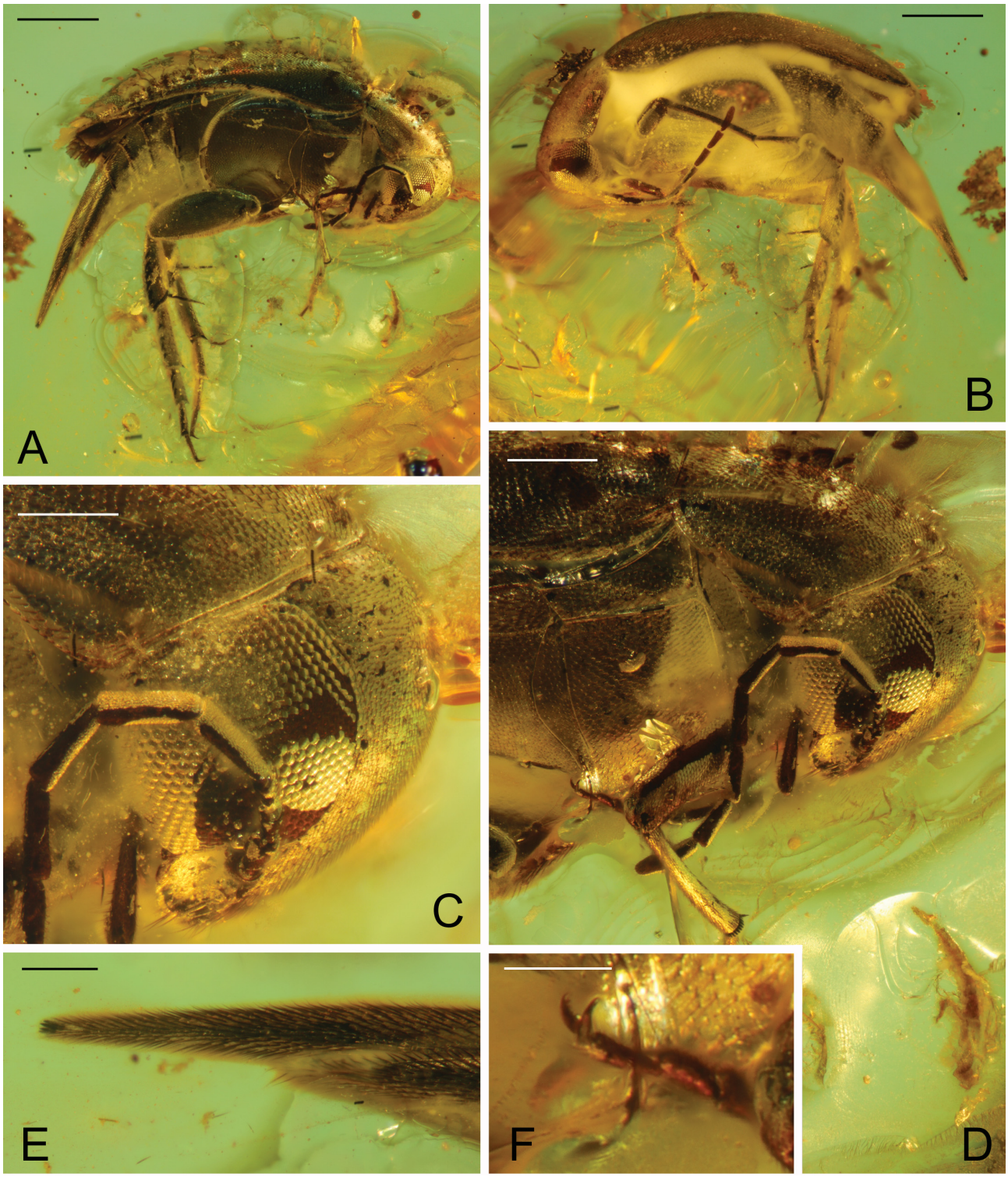
Figs 5. A–J – Mordellistenini, Baltic amber. A–E – *Baltistena soror* (Ermisch, 1941), type: A – habitus. B – middle leg. C – posterior pronotal margin. D, E – head and thorax. F–J – *Baltistena sergeli* (Ermisch, 1943), holotype: F – habitus; G, H – hind legs; I – maxillary palpomeres IV (black arrows); J – protarsus. Scale bars: A, F, I – 0.5 mm, B – 0.05 mm; C, J – 0.2 mm; D, E, G, H – 0.3 mm.



Figs 6. A–G – Mordellistenini, Baltic amber. A–C – *Baltistena ultima* sp. nov., holotype, PřFUK65: A – habitus; B – antenna; C – hind leg and hypopygium. D–G – *Baltistena aurata* sp. nov., holotype, PřFUK66: D – habitus; E – hind leg; F – head frontally (maxillary palpomere IV marked by black arrow); G – hypopygium. Scale bars: A, D – 0.5 mm; C, E, F – 0.3 mm; B, G – 0.1 mm.



Figs 7. A–I – Mordellistenini, Baltic amber. A–D – *Baltistena longistrigata* sp. nov., holotype, PřFUK69: A – habitus; B – hypopygium; C – hind leg; D – head and pronotum laterally. E–I – *Baltistena hoffeinsorum* sp. nov., holotype, PřFUK92: E – habitus; F – hind legs; G – metatarsomere IV and serrate pretarsal claws; H – hypopygium; I – eye. Scale bars: A, F – 0.5 mm; B – 0.15 mm; C, D, H – 0.2 mm; E – 0.8 mm; G – 0.05 mm; I – 0.3 mm.



Figs 8. A–F – Mordellistenini, Baltic amber, *Baltistena concava* sp. nov., holotype, PřFUK93: A, B – habitus; C – eye; D – head with antenna and thorax; E – hypopygium; F – protarsomeres IV and V and serrate pretarsal claws. Scale bars: A, B – 0.8 mm; C, E – 0.2 mm; D – 0.3 mm; F – 0.1 mm.

posterior edge. Metakatepisternum absent. Pretarsal claws without visible teeth. Tip of pygidium with setae similar to those on rest of pygidium.

Lengths (in mm): pronotal disc = 0.8, elytra = 2.4, mesotibia = 2.0, metatarsomere I = 0.5, pygidium = 1.35.

Etymology. The species name refers to the remarkably long lateral combs on metatibia; adjective.

Differential diagnosis. Among Eocene Mordellistenini this species is unique in terms of its long and strongly oblique tibial combs (excluding preapical one). Among the extant genera with penultimate pro- and mesotarsomeres emarginated or bilobed and similar long and oblique metatibial combs are the monotypic African *Fahraeusiella* Ermisch, 1953, worldwide distributed *Glipostenoda* Ermisch, 1950, *Mordellistenoda* Ermisch, 1941 from the Oriental and Australian Realm, *Morphomordellochroa* Ermisch, 1969 with two African species, and *Xanthomorda* Ermisch, 1969 from Africa and Papua New Guinea. However, the comb formula and shape and length of the combs of *Baltistena longistrigata* sp. nov. are different from species of the above-mentioned genera depicted in Ermisch (1941b, 1950b, 1953, 1969), Franciscolo (1958) and Shiyake (1997). For more affinities and differences from the above-mentioned genera the obscured mouthparts and antennae of the holotype (if preserved) have to be investigated using microtomography.

Baltistena hoffeinsorum sp. nov.

(Figs 7E–I, 10C)

Type material. Holotype: PřfUK92, obtained from Jonas Damzen (original number JDC8781): Baltic amber.

Description. Head subglobular, frons continuously convex, posterior edge of eye near posterior margin of head, elytra convex, metacoxae broad, comb formula 6//5/3/0/0, pygidium long. Main characters: Antenna 3.25× as long as width of eye, basal antennomere robust, flagellomeres cylindrical, antennomere IX and X 3.0× as long as wide apically, antennomere XI 2.3× as long as wide. Structure of maxillary palpi, notably ultimate palpomere, indiscernible. Eyes rather coarsely facetted. Interfacetal setae present, distinctly shorter than diameter of facets. Form of scutellum indiscernible (dorsal view not available). Basal side of pronotum indiscernible (dorsal view not available). Elytra 2.7× as long as pronotal disc. Protarsomere I about 1.1× as long as remaining tarsomeres combined, tarsomere IV deeply dilated. Protibia seems to be shallowly curved in lateral view. Mesotarsomere IV deeply dilated. Mesotibia about 1.3× as long as respective tarsus. Metatibia with six very short transverse combs. Metatibia with two subequally long spurs, about as long as 3/4 of metatarsomere I. Metatarsomere I with five short transverse combs, metatarsomere II with three short combs, tarsomeres III and IV without combs. Pygidium 3.1× as long as hypopygium. Anterior edge of metanepisternum 2.0× as long as its posterior edge, ventral edge 4.0× as long as its posterior edge. Metakatepisternum fully developed; suture between metakatepisternum and metaventrite straight, metacoxal margin distinctly concave ventrally. Pretarsal claws distinctly dentate. Tip of pygidium with setae similar to those on remaining parts of pygidium.

Lengths (in mm): pronotal disc = 1.1, elytra = 3.0, mesotibia = 0.8, metatarsomere I = 0.6, pygidium = 1.4.

Etymology. The species name is given in honour of Christel and Hans Werner Hoffeins, outstanding German paleoentomologists; noun in apposition.

Differential diagnosis. Eyes finely faceted with short setae, penultimate pro- and mesotarsomeres deeply dilated, antennomeres long, narrow and cylindrical, antennomeres I–III 2× as long as wide, antennomeres IV–VII indiscernible, antennomeres VIII–X 3.5× as long as wide, antennomere XI 5× as long as wide. This species can be distinguished from other Eocene species using the key below. More characters, notably of the palpomeres and genitalia, need to be observed for a better comparison with extant genera with deeply dilated penultimate pro- and mesotarsomeres.

Baltistena concava sp. nov.

(Figs 8A–F, 10D)

Type material. Holotype: PřfUK93, obtained from Jonas Damzen (original number JDC9819): Baltic amber.

Description. Head subglobular, frons continuously convex, posterior edge of eye near posterior margin of head, elytra convex, metacoxa broad, comb formula 6//4/3/2/0, pygidium long. Main characters: Right antenna well visible, length ratios of antennomeres as follows: 2-1.6-1-1.25-5.8-6.25-5.8-5.8-5.8-5.8-7.5, basal antennomere robust, flagellomeres cylindrical and slightly wider apically, antennomeres V–X about 2.7× as long as wide, antennomere XI 3.75× as long as wide. Structure of maxillary palpi not discernible. Eyes with small facets. Interfacetal setae present. Form of scutellum not observable. Form of basal side of pronotum not observable. Elytra 3.0× as long as pronotal disc. Protarsomere IV deeply dilated. Structure of protibia indiscernible. Mesotarsomere IV deeply dilated. Mesotibia 1.1× as long as mesotarsus. Right metatibia with six combs, left metatibia with one additional rudimentary cluster of dark scale-like setae on the most proximal position visible. Two subequal tibial spurs on metatibia present, outer one half as long as inner one. Metatarsomere I with four short transverse combs, metatarsomere II with three short combs, metatarsomere III with two longer and more oblique combs and metatarsomere IV without combs. Pygidium 2.4× as long as hypopygium. Anterior edge of metanepisternum 2.15× as long as posterior edge, ventral edge 4.15× as long as posterior edge. Metakatepisternum fully developed; suture between metakatepisternum and metaventrite slightly concave, middle of metacoxal margin distinctly concave. Pretarsal claws long with few short and widely spaced teeth. Tip of pygidium with ring of few, long, distinct, black scale-like setae.

Lengths (in mm): pronotal disc = 1.0, elytra = 2.9, mesotibia = 1.0, metatarsomere I = 0.6, pygidium = 1.8.

Etymology. The species name refers to the concave shape of the frontal edge of the metacoxa; adjective.

Differential diagnosis. This peculiar beetle is characterized by short antennomeres I–IV and extremely prolonged cylindrical antennomeres V–XI, concave anterior metacoxal margin, and dilated pro- and mesotarsomeres IV.

It is difficult to determine its generic affinities. In terms of the shape of its antennae and penultimate pro- and mesotarsomere it resembles *Mordellistena virginica* Steury & Steiner, 2020 from the USA, which, however, differs in almost straight anterior metacoxal margin (Steury & Steiner 2020: fig. 7C). The inclusion of *M. virginica* in *Mordellistena* is contrary to the definition of this genus, because Ermisch (1950a) put *Mordellistena* into the Mordellistenini group of genera with pro- and mesotarsomeres apically truncate, which is not the case in *M. virginica*. Thus, the generic placement of *M. virginica* must be reconsidered, but this is outside the scope of this contribution.

The antenna is also similar to that depicted for *Mordellistena erythroderes* Hill, 1922 from Queensland, Australia (Hill 1922), but the poor description of this Australian species prevents further comparison and verification of its generic placement.

Another taxon sharing the same antennal structure and shape of penultimate pro- and mesotarsomeres with *B. concava* sp. nov. is the genus *Pulchrimorda* Ermisch, 1968 from Southeast Asia, notably *P. tamdaoensis* Horák & Farkač, 2017 and *P. fusca* Horák & Farkač, 2017 (Horák & Farkač 2017). The male antennae in both species are almost identical with those of *B. concava* sp. nov., but in species of *Pulchrimorda* the eyes are glabrous, while in *B. concava* sp. nov. interfacetal setae are present.

Baltistena brevispina sp. nov.

(Figs 9A–F, 10E)

Type material. Holotype: PřfUK95, obtained from Jonas Damzen (original number JDC4109): Baltic amber.

Description. Head subglobular, frons continuously convex, posterior edge of eye near posterior margin of head, elytra convex, metacoxa broad, comb formula 7//6/2/0/0, pygidium long. Main characters: Both antennae almost completely visible, length ratios of antennomeres: 2-1.3-1-1.3-2-1.6-1.3-1.6-1.6-1.6-2.3, basal antennomere robust, flagellomeres cylindrical with both margins almost parallel. Structure of maxillary palpi indiscernible. Eyes with small facets. Interfacetal setae present. Form of scutellum indiscernible (dorsal view not available). Basal side of pronotum indiscernible (dorsal view not available), posterior angles of pronotal disc sharply pointed. Elytra about 3.7× as long as pronotal disc. All protarsomeres cylindrical, straight, length ratios: 4-3-1.8-1.4-1.5. Protibia seemingly shallowly curved in lateral view. Mesotarsomere IV straight. Mesotibia longer than respective tarsus. Metatibia with seven short transverse combs. Two subequal tibial spurs on metatibia, outer one half as long as inner one. Metatarsomere I with six short transverse combs, metatarsomere II with two short combs, tarsomeres III and IV without combs. Pygidium 2.2× as long as hypopygium. Anterior edge of metanepisternum 1.6× as long as its posterior edge, ventral edge 3.0× as long as posterior edge. Metakatepisternum fully developed, suture between metakatepisternum and metaventrite almost parallel with metacoxal margin. Pretarsal claws with two or three widely spaced teeth. Tip of pygidium with very short black scale-like setae.

Lengths in mm: pronotal disc = 1.2, elytra = 3.3, mesotibia = 1.1, metatarsomere I = 0.75, pygidium = 1.7.

Etymology. The species name refers to the short spiniform setae on the ventral edge of metatibia.

Differential diagnosis. This species is characterized by truncated pro- and mesotarsomere IV, antennomeres I–IV combined shorter than antennomeres V–VII combined, antennomere IV shorter than antennomere V, eyes small with small facets, posterior angles of pronotal disc sharp and suture between metakatepisternum and metaventrite almost parallel with metacoxal margin. Characters of *Baltistena brevispina* sp. nov., including the shape of antennomeres, with some reservations fit the definition of the genus *Mordellistena* (s. str.), particularly the *M. pumila* or *M. pentas* species-group. Ermisch (1963: 16) defines the *M. pumila* species-group as follows: antennomere IV shorter than antennomere V, metatibia with 3–4 short combs, metatarsomere I with 2–5 short combs, metatarsomere II with only two similar combs (unlike the *M. pentas* species-group where three combs are present on metatarsomere II). In *Baltistena brevispina* sp. nov. the number of combs is, however, slightly different (see description above).

Baltistena atronigra sp. nov.

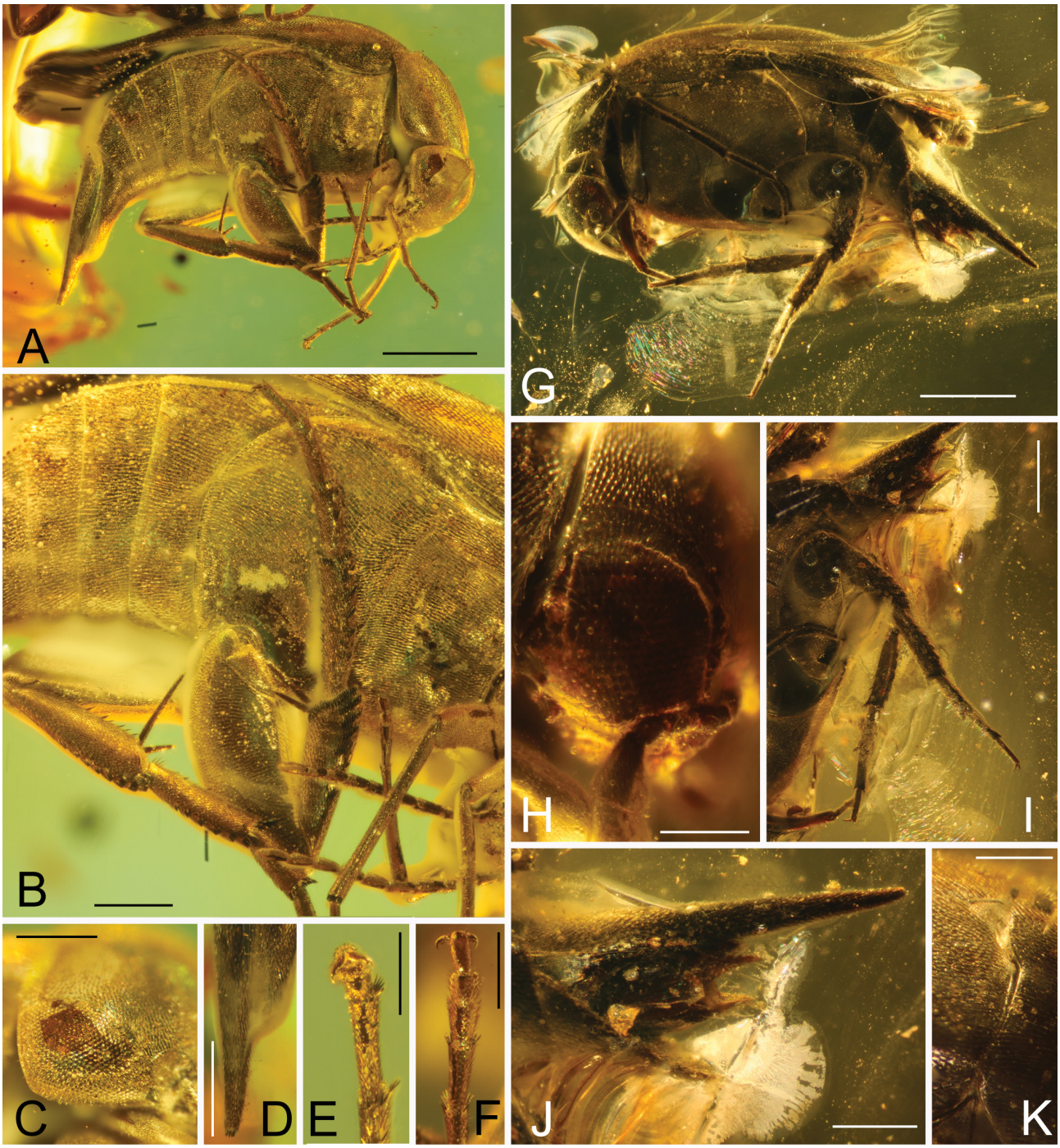
(Figs 9G–K, 10F)

Type material. Holotype: PřfUK108, obtained from 'vermiculosis' – Poland: Baltic amber.

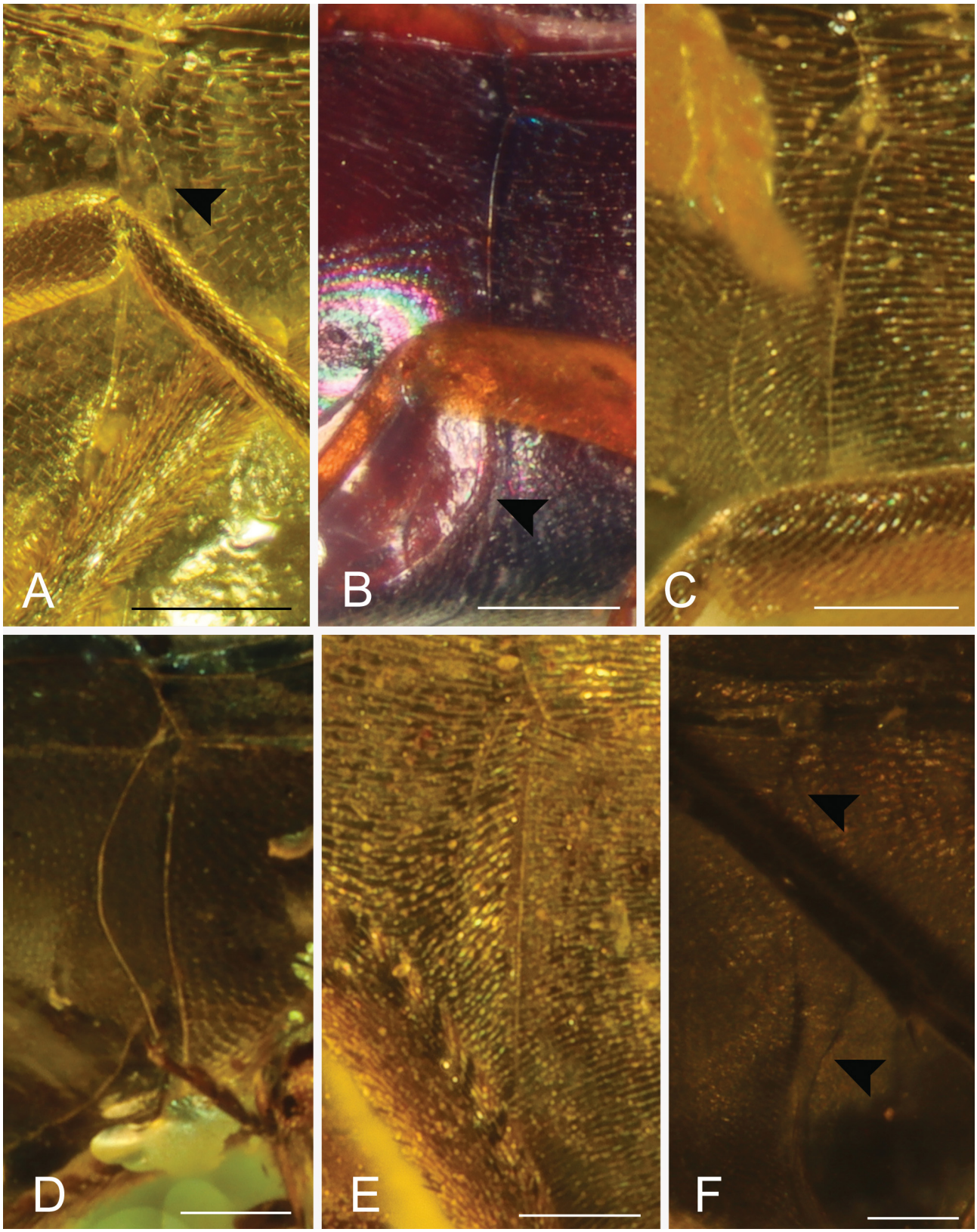
Description. Head subglobular, frons continuously convex, posterior edge of eye near posterior margin of head, elytra convex, metacoxae broad, comb formula 5//5/?/?/?, pygidium long. Main characters: Only right antenna almost complete, but poorly visible because of distortion; four basal antennomeres short and cylindrical; antennomere V as long as preceding two, with distal edge distinctly wider; antennomere IX almost cylindrical with apex slightly wider, antennomeres X and XI cylindrical. Maxillary palpomere IV small, malleiform (bean-shaped). Facetes moderatelly sized. Long interfacetal setae present. Form of scutellum indiscernible (dorsal view not available). Basal side of pronotum indiscernible (dorsal view not available), posterior angles of pronotal disc obtuse. Elytra about 3.5× as long as pronotal disc. Protarsomeres cylindrical, straight, length ratios not measurable. Shape of protibia not discernible. Mesotarsomere IV cylindrical, straight. Mesotibia as long as respective tarsus. Metatibia with five long transverse combs. Two subequal tibial spurs inserted on metatibia, but their length not measurable. Metatarsomere I with five long transverse combs, metatarsomeres II with two short combs, tarsomeres III–IV poorly visible. Pygidium 2.5× as long as hypopygium. Metanepisternum partly hidden behind middle leg. Metakatepisternum fully developed, suture between metakatepisternum and metaventrite straight, metacoxal margin distinctly concave ventrally. Pretarsal claws with distinct sharp long teeth. Tip of pygidium with setae similar to those on rest of pygidium.

Lengths (in mm): pronotal disc = 0.85, elytra = 3.0, mesotibia = 0.9, metatarsomere I = 0.6, pygidium = 1.3.

Etymology. The species name refers to the dull black colour of the body; adjective.



Figs 9. A–K – Mordellistenini, Baltic amber. A–F – *Baltistena brevispina* sp. nov., holotype, PřFUK95: A – habitus; B – hind leg; C – eye; D – hypopygium; E – middle leg; F – fore leg. G–K – *Baltistena atronigra* sp. nov., holotype, PřFUK108: G – habitus; H – eye; I – hind legs; J – hypopygium; K – base of pronotal disc and scutellum. Scale bars: A – 1.0 mm; B – 0.4 mm; C, J – 0.3 mm; D, I – 0.5 mm; E, F – 0.15 mm; G – 0.8 mm; H, K – 0.2 mm.



Figs 10. A–F – Metakatepisternum: A – *Baltimorda*, undescribed species A, PřfUK71. B – *Palaeostena eocenica* (Kubisz, 2003), PřfUK107. C – *Baltistena hoffeinsorum* sp. nov., holotype, PřFUK92. D – *Baltistena concava* sp. nov., holotype, PřFUK93. E – *Baltistena brevispina* sp. nov., holotype, PřFUK95. F – *Baltistena atronigra* sp. nov., holotype, PřFUK108. Scale bars: 0.2 mm.

Table 2. Comparison of *Baltistena atronigra* sp. nov. with extant genera of Mordellistenini.

Mordellistenini with truncate pro- and mesotarsomere IV	Prominent generic character(s) of respective genus/subgenus	Difference in *Baltistena atronigra* n.sp.
Mordellistena (s. str.) Costa, 1854	finely faceted eyes	roughly faceted eyes
Mordellistena (*Pseudomordellina* Ermisch, 1952)	finely faceted eyes	roughly faceted eyes
Mordellistena (*Mordellokoiles* Franciscolo, 1952)	finely faceted eyes	roughly faceted eyes
Mordellina (s. str.) Schilsky, 1908	outer metatibial spur absent	both metatibial spurs present
Mordellina (*Pseudomordellistena* Ermisch, 1951)	at least the most distal metatibial comb long and strongly oblique	all metatibial combs transverse
Gymnostena Franciscolo, 1950	eyes glabrous	eyes with interfacetal setae
Mordelloxena Franciscolo, 1950	eyes glabrous, pygidium reduced	eyes with interfacetal setae, pygidium developed
Mordellistenula Stchegoleva-Barovskaya, 1930	eyes glabrous, head compressed dorso-ventraly	eyes with interfacetal setae, head convex, semi-globular
Uhligia Horák, 1990	eyes glabrous, head compressed dorso-ventraly	eyes with interfacetal setae, head convex, semi-globular
Mordellochroa Emery, 1876	eyes glabrous	eyes with interfacetal setae
Mordellistenochroa Horák, 1982	eyes glabrous	eyes with interfacetal setae
Tolidostena Ermisch, 1942	eyes glabrous	eyes with interfacetal setae

Differential diagnosis. This species is characterized by truncated pro- and mesotarsomere IV, antennomeres I–IV combined shorter than antennomeres V–VII combined, antennomere IV cylindrical, half the length of antennomere V, antennomere V robust, distinctly broader apically, maxillary palpomere IV small malleiform (bean-shaped), eyes with large facets with long interfacetal setae, posterior angles of pronotal disc obtuse, suture between metakatepisternum and metaventrite straight, metacoxal margin distinctly concave ventrally, combs short and transverse, complete comb formula indiscernible. For its features differing from the 12 extant genera and subgenera with truncated pro- and mesotarsomere IV see Table 2.

Rovnostena new collective group

Diagnosis. A collective group name (ICZN 1999) established to accommodate species of the family Mordellidae, tribe Mordellistenini described from Eocene Rovno amber from Ukraine. No type species is designated in accordance with article 13.3.2. of ICZN (1999).

Etymology. The name is composed of the words Rovno and suffix -*stena* (a form often used in nomenclature of the family). Feminine gender.

Rovnostena ponomarenkoi (Odnosum & Perkovsky, 2009) comb. nov.

Glipostena ponomarenkoi Odnosum & Perkovsky, 2009: 1095. Holotype: ♀, Rovno amber.

Comments on identification. According to Ermisch (1941b), the genus *Glipostena* belongs to the group of genera that are defined by 'Der Halsschild weniger breit als lang' [= the pronotum slightly wider than long], while in *G. ponomarenkoi,* according to its description, the pronotum is 1.7–1.8× wider than long, that is, much wider than cited by Ermisch (1941b). In the comparison by Odnosum & Perkovsky (2009), this species shares with *G. sergeli* from Baltic amber 'short lateral ridges taken not more than one third of the hind tibia width and parallel to its apical margin', which according to the authors 'sharply differentiate' *G. ponomarenkoi* from recent species that have long ridges that reach the middle of the hind tibia and are not parallel with the apical margin (see, e.g., Ermisch 1941b: fig. 13; Ermisch 1952: fig. 21; Franciscolo 2000: figs 1, 2). The comb formula for species of *Glipostena* is usually 4//2/1/1/0 or rarely 3–5//3/1/1/0 (Franciscolo 1999), while in *G. ponomarenkoi* it is 6//5/4/3/0. The shape of maxillary palpomeres, an important generic character of *Glipostena*, is not described for this fossil.

In summary, *G. ponomarenkoi* differs from all extant *Glipostena* in terms of three important generic characters. Therefore, its assignment to this extant genus is not accepted and this species is transferred to *Rovnostena* new collective group.

A key to Mordellistenini from Baltic and Rovno Eocene amber

1 Pro- and mesotarsomere IV truncated at apex. 2
– Pro- and mesotarsomere IV more or less emarginated at apex. 3
2 Postero-lateral angles of pronotal disc sharp, suture between metakatepisternum and metaventrite almost parallel with metacoxal margin. .... ***Baltistena brevispina* sp. nov.**
– Postero-lateral angles of pronotal disc obtuse, suture between metakatepisternum and metaventrite straight, metacoxal margin distinctly concave ventrally. .... ***Baltistena atronigra* sp. nov.**
3 Metatibial combs long and strongly oblique. .... ***Baltistena longistrigata* sp. nov.**
– Metatibial combs short, more or less parallel with apical margin of tibia. 4
4 Dorsal edge of pygidium straight, antennomere XI with parallel margins. 5
– Dorsal edge of pygidium slightly but distinctly convex, antennomere XI with one margin emarginated half way along its length. ... ***Baltistena ultima* sp. nov.**
5 Pygidium more than 3.0× as long as hypopygium. .. 6
– Pygidium less than 2.8× as long as hypopygium. 7
6 Suture between metakatepisternum and metaventrite almost parallel with metacoxal margin, comb formula

3(+2)//3/1/0/0, pygidium 3.1× as long as hypopygium. ..... ***Baltistena aurata* sp. nov.**
– Suture between metakatepisternum and metaventrite straight, metacoxal margin distinctly concave especially ventrally, comb formula 6//5/3/0/0, pygidium 3.1× as long as hypopygium. ..... ***Baltistena hoffeinsorum* sp. nov.**
7 Metatarsomeres III and IV without combs. 8
– Only metatarsomere IV without combs. 9
8 Antennomeres III and IV combined 1.5× as long as antennomere V, comb formula 7(+1)//4/2/0/0. ..... ***Palaeostena eocenica*** (Kubisz, 2003)
– Antennomeres III and IV combined as long as antennomere V, comb formula 5//5/3/0/0. ..... ***Baltistena amplicollis*** (Ermisch, 1941)
9 Elytra about 3.7–4.1× as long as pronotal disc. 10
– Elytra about 2.5–3.1× as long as pronotal disc. 11
10 Antennomeres III and IV combined as long as antennomere V, comb formula 7//5/3/2/0. ..... ***Baltistena sergeli*** (Ermisch, 1943)
– Antennomeres III and IV combined 1.25× as long as antennomere V, comb formula 6//4/3/2/0. ..... ***Baltistena korschefskyi*** (Ermisch, 1941)
11 Antennomeres IX and X relatively short, 1.4 or 2.0× as long as wide. 12
– Antennomeres IX and X relatively long, 2.5 or 3.1× as long as wide 13
12 Antennomeres IX and X ca. 1.4× as long as wide, comb formula 5//4/3/2/0. ..... ***Baltistena soror*** (Ermisch, 1941)
– Antennomeres IX and X ca. 2.0× as long as wide, comb formula 6//5/4/3/0. ..... ***Rovnostena ponomarenkoi*** (Odnosum & Perkovsky, 2009)
13 Antennomeres IX and X ca. 2.5× as long as wide, comb formula 7//3/2/2/0. ..... ***Baltistena antiqua*** (Ermisch, 1941)
– Antennomeres IX and X ca. 3.1× as long as wide, comb formula 6//4/3/2/0. ..... ***Baltistena concava* sp. nov.**

Note. *Baltistena goeckei* (Ermisch, 1941) cannot be included in this key as the holotype has been lost. The comb formula in this species according to its description is 5//4/3/0/0, which tentatively indicates it is distinct from the other five species with metatarsomeres III and IV without combs (i.e., *P. eocenica*, *B. amplicollis*, *B. aurata* sp. nov., *B. hoffeinsorum* sp. nov., and *B. ultima* sp. nov.).

Part II. Specimens preserved as compression fossils in Eocene and Oligocene shales

The *Petrimordella* new collective group is established without subfamilial affinity for all the compression fossils of Eocene and Oligocene Mordellidae described so far, because based on their descriptions, it is not possible to determine their generic and tribal placements or whether they are new species. Reasons for each new combination with *Petrimordella* nov. are explained separately under each species. The collective genus name allows preservation of all available species names for eventual cataloging purposes. If future investigations reveal characters allowing their proper generic placement, their generic status might be reconsidered. However, considering the mode and low quality of the preservation of taxonomically important characters of Mordellidae this is highly unlikely.

Mordellidae incertae sedis

Petrimordella new collective group

Diagnosis. A collective group name according to ICZN (1999), established to accommodate species of the family Mordellidae preserved as compression fossils in Eocene and Oligocene matrices. If other mordellids from Palaeocene or Miocene shales are recorded in the future, the utilization of this generic name will be automatically extended to include these species. No type species is designated in accordance with the article 13.3.2. of ICZN (1999).

Etymology. The name is composed of the latinized Greek noun *petra* (a stone) and the generic name *Mordella*. Feminine gender.

Petrimordella lapidicola (Wickham, 1909) comb. nov.

Mordella lapidicola Wickham, 1909: 130. Holotype: Middle Eocene, Florissant Formation, Colorado, USA.

Comments on the original description. Uninformative description was provided. It is proposed by the author that this species 'can be distinguished from any others which may be discovered in these shales by the comparative measurements.'

Petrimordella florissantensis (Wickham, 1912) comb. nov.

Mordellistena florissantensis Wickham, 1912: 33. Holotype: Middle Eocene, Florissant Formation, Colorado, USA.

Comments on the original description. Uninformative description. Compared with *Mordella lapidicola* Wickham, 1909 but described in *Mordellistena*, therefore its tribal placement is doubtful. From the line drawing (Wickham 1912: Plate II, fig. 16) it is not evident that this beetle belongs to Mordellidae.

Petrimordella smithiana (Wickham, 1913) comb. nov.

Mordellistena smithiana Wickham, 1913: 21. Holotype: Middle Eocene, Florissant Formation, Colorado, USA.

Comments on the original description. No informative characters were described, except for measurements and the shape of body. It is proposed that 'Legs wanting, except a small portion of one of the hind pair that shows no characters of importance.' As the presence and numbers of combs on metatibia and metatarsomeres are essential for identification of Mordellistenini, the tribal placement of this fossil is doubtful.

Petrimordella nearctica (Wickham, 1914) comb. nov.

Mordellistena nearctica Wickham, 1914a: 268. Holotype: Middle Eocene, Florissant Formation, Colorado, USA.

Comments on the original description. The description including line drawing is uninformative and only indicates: 'Hind leg with stout and short femur and tibia, tarsus not

defined.' Doubtful tribal placement (see above).

***Petrimordella protogaea* (Wickham, 1914) comb. nov.**

Mordellistena protogaea Wickham, 1914a: 269. Holotype: Middle Eocene, Florissant Formation, Colorado, USA.

Comments on the original description. Description and line drawing are uninformative. Hind legs are not described as they are not present in this fossil. Doubtful tribal placement (see above).

***Petrimordella scudderiana* (Wickham, 1914) comb. nov.**

Mordellistena scudderiana Wickham, 1914a: 268. Holotype: Middle Eocene, Florissant Formation, Colorado, USA.

Comments on the original description. Description and line drawing are uninformative as they only indicate that: 'Legs lacking except one belonging to the hind pair, which has a moderately thickened femur.' Doubtful tribal placement (see above).

***Petrimordella inundata* (Wickham, 1914) comb. nov.**

Tomoxia inundata Wickham, 1914b: 488. Holotype: Middle Eocene, Florissant Formation, Colorado, USA.

Comments on the original description. Uninformative description. From the line drawing (Wickham 1914b: Plate 15, fig. 5) it is not evident that this beetle belongs to Mordellidae.

***Petrimordella stygia* (Wickham, 1914) comb. nov.**

Mordella stygia Wickham, 1914b: 489. Holotype: Middle Eocene, Florissant Formation, Colorado, USA.

Comments on the original description. Uninformative description, differential diagnosis is based on size only. From the line drawing (Wickham 1914b: Plate 15, fig. 6) it is not evident that this beetle belongs to Mordellidae.

***Petrimordella priscula* (Cockerell, 1924) comb. nov.**

Mordella priscula Cockerell, 1924: 11. Holotype: Lower Eocene, Green River Formation, Colorado, USA.

Comments on the original description. Uninformative description based on size and colour. The differential diagnosis is based on comparison of genera *Mordellistena* and *Mordella*, therefore the tribal placement of this species and its generic identity are doubtful.

***Petrimordella indata* (Statz, 1952) comb. nov.**

Mordella indata Statz, 1952: 3. Syntypes: 2 specimens, Oligocene (Chattian), Rott-am-Siebengebirge, Germany.

Comments on the original description. Description is moderately detailed, but erection of the species is apparently based on the sole fact that it is a fossil and therefore must be a new species, and thus there is no differential diagnosis or comparison with other species. Tribal or generic identity cannot be established.

***Petrimordella nigrapilosa* (Statz, 1952) comb. nov.**

Mordella nigrapilosa Statz, 1952: 4. Holotype: Oligocene (Chattian), Rott-am-Siebengebirge, Germany.

Comments on the original description. The description of this species is of the same style as in *Mordella indata* and thus neither tribal nor generic identity can be established.

***Petrimordella oligocenica* (Nel, 1985) comb. nov.**

Stenalia oligocenica Nel, 1985: 120. Holotype: Oligocene (Rupelian), Alpes de Haute-Provence, Cereste, France.

Comments on the original description. According to the pictures provided, this is a poorly preserved fossil. The description is based on measurements. The tarsal formula is incorrectly proposed as 4-4-5 (unknown among Coleoptera) instead of the usual 5-5-4 pattern in Tenebrionoidea. As the metanepisternum is neither described nor figured, it is impossible to attribute the fossil to Stenaliini, because the shape of this sclerite is the character that differentiates Stenaliini from other tribes (Franciscolo 1957a).

***Petrimordella rasnitsyni* (Odnosum & Perkovsky, 2016) comb. nov.**

Isotrilophus rasnitsyni Odnosum & Perkovsky, 2016: 610. Holotype: Lower Eocene, Green River Formation, Colorado, USA.

Comments on the original description. The text is extremely short and contains only information on the general shape of the head, eye, metanepisternum, pronotum and elytra, which is insufficient for determining the specific, generic and tribal identity of this specimen. The differential diagnosis is based mainly on the shape of metanepisternum, without any explanation why this character is considered to be of specific and not of generic or sexual value. For comments on taxonomic value of this structure see Discussion below.

Discussion

Diversity of Eocene Mordellidae

Post-Cretaceous fossil Mordellidae are described from various Eocene and Oligocene shales in France, Germany and USA, and after the inclusions preserved in Eocene Baltic and Rovno amber. Presence of Mordellidae is corroborated also from Miocene amber from the Dominican Republic (Wu 1997) and Mexico (Sólorzano Kraemer 2010), but there are no published descriptions. The monotypic *Asiamordella furvis* Hong, 2002 from the lower Eocene Fushun amber (China) (Hong 2002) is no longer considered to be a member of Mordellidae (Batelka & Prokop 2023).

To understand the faunistic assemblage of Eocene and Oligocene Mordellidae, precise descriptions and differential diagnoses are needed. Regrettably, these are not available so far. There are no taxonomic studies revising supposedly congeneric extant and Eocene and Oligocene species. Because of the scant data on fossil specimens, comparisons with extant 'relatives' by specialists on this family are lacking. On the other hand, those who study fossil material tend to put Eocene and Oligocene species into extant genera. The only exception is Kubisz (2001, 2003) who established new genus group taxa for the Baltic Mordellini and Mordellistenini species he described.

As demonstrated in the Systematic part, the suggested phylogenetic affinity of Eocene species to extant genera in

all previous descriptions is based on incorrect or misleading arguments. There are at least five species of Mordellini and 15 species of Mordellistenini recorded from Baltic and Rovno amber deposits, all but *Baltistena brevispina* sp. nov. with uncertain affinity to extant genera. However, the number of described species is only a fragment of the diversity of Eocene Mordellidae in the western part of the Palaearctic. Almost every specimen we obtained was unique and differed from those previously described. In addition, there are also at least two possibly undescribed but imperfectly preserved Mordellistenini (PřfUK67 and 68) in our collection. Based on the material listed in this study and the diversity in the Klebs and Copenhagen collections documented by Larsson (1978), there are more specimens of Mordellistenini (39) than Mordellini (27 specimens).

Disparity of Baltic Mordellidae

All presently known specimens are of the modern wedge-shaped, a more or less convex body, with expanded metacoxae and a prolonged pygidium. Extant Mordellidae are, however, much more diverse in terms of the shape of head, antennae, legs and the ultimate abdominal segments, especially in the tropics. Superficial similarity of Baltic Mordellidae may be a result of convergence caused by natural forces in Eocene Baltic forests. Close examination of the morphology of the Baltic species reveals unique combinations of characters, even though not all characters are usually observable. Selected taxonomically important characters are commented on and evaluated below.

Eye. Size of cornea lenses of ommatidia ('facets') is noted by various researchers of Mordellidae as an important character at the generic level. In Mordellistenini genera the facets vary in size from 'small' (e.g., in *Scaphiostena* Horák, 1994 – Horák 1994) and 'medium' (e.g., in *Mordellistenoda* (Shiyake 1997), to 'large' (e.g., in *Jenisia* Horák, 2008 – Horák 2008) and 'very large' (diameter 0.040 mm) in *Glipostena* (Franciscolo 1999). Franciscolo (1962b) has found that in members of *Mordellistena* they do not exceed 0.015 mm in diameter, while in *Mordellina* Schilsky they are never smaller than 0.022. It is difficult to measure and compare small convex structures embedded in amber, but in some of the newly described species of Mordellistenini where the facets can be counted and the eyes can be measured, differences among species can be documented. In the five new species the diameter of facets is as follows: *Baltistena longistrigata* sp. nov. and *B. brevispina* sp. nov. 0.018 mm, in *B. atronigra* sp. nov. 0.020 mm, in *B. concava* sp. nov. 0.022 mm, and in *B. hoffeinsorum* sp. nov. 0.025 mm. This is similar to the size of facets reported for extant Mordellistenini, e.g., 0.020 mm in *Mordellina* Schilsky (Tsuru 2011) and 0.022 mm in *Mordellistena* (Franciscolo 1991). There is a need for a comparative study of eyes of extant genera.

Maxillary palpomere IV. Because the head of Mordellidae is deflexed, the palpi of fossils are usually hidden. The shape of maxillary palpomere IV is documented for seven species only. There are two morphotypes in Baltic Mordellidae: securiform palpomere with apical cavity, i.e., type A1 sensu Franciscolo (1957a), which is visible in *Baltistena korschefskyi*; malleiform terminal palpomere (bean-shaped as in species of *Mordellochroa* Emery, 1876), i.e., type C1 sensu Franciscolo (1957a) reported in *Palaeostena eocenica* (Kubisz 2003), *Baltistena amplicollis*, *B. soror*, *B. sergeli* and *B. aurata* sp. nov., and in *Baltimorda* sp. (SDEI-Amb-000635). Because of the limited number of samples any evaluation is premature, but it is noteworthy that in extant Mordellidae palpomere IV is much more diverse in shape and sometimes remarkably modified (Franciscolo 1957a).

Shape of tarsomeres. Ermisch (1950a, paragraphs 65 and 72) established two groups of genera in Mordellistenini, differing in the shape of the penultimate tarsomere of their first two pairs of legs. Among the genera with truncated pro- and mesotarsomere IV Ermisch placed for example the genera *Mordellistena* and *Mordellochroa*, among those with emarginated and dilated pro- and mesotarsomere IV for example *Falsomordellistena* and *Glipostena*. The second type of pro- and mesotarsomere IV is present in all Eocene Mordellistenini except *Baltistena brevispina* sp. nov. and *B. atronigra* sp. nov. that have truncated tarsomeres. More attention should be paid to this character if incorrect differential diagnoses are to be avoided, as it was the case in Ermisch (1941a).

Tibial and tarsal combs. A preapical comb on the metatibia is recorded in all detailed descriptions of inclusions in Eocene amber. In Mordellistenini various comb formulas are documented. Number of combs on metatibia vary from 5 to 8, whereas on metatarsomeres there are always fewer. In some species of Mordellistenini there are no combs present on metatarsomere III and IV, while in others they are absent only on the ultimate one. In the majority of species, the combs are short and more or less parallel with the apical margin of metatibia, with the exception of *Baltistena longistrigata* sp. nov. in which combs are much prolonged and strongly oblique along almost the whole length of the tibia. The comb formula for the specimens examined was similar only for *Baltistena korschefskyi* and *B. concava* sp. nov., but it is noteworthy that on rare occasions the number of combs may differ slightly on the left and right sides. The comb formula should only be used for identification in combination with other characters.

Pretarsal claws. The claws in both informally described Mordellini appear simple, without visible traces of teeth or protuberances. According to Ray (1939), dentate claws are present in all Neotropical Mordellidae. Dentate claws are also depicted in numerous studies by Franciscolo on various Mordellini, e.g., *Neocurtimorda* Franciscolo, 1949 (Franciscolo 1949), *Yakuhananomia* Kôno, 1935 (Franciscolo 1951), *Mordellopalpus* Franciscolo, 1955 (Franciscolo 1955). Franciscolo (1980: 209) states: 'Ray and myself have often used claw structure (form, denticulations) for identification purposes; in all genera so far examined claws are dentate; only *Mordellistena arabyssa* Francisc. (1956A: 467) is known to have very feebly dentate claws…'. The first mordellid reported with simple claws, i.e., with their inner edge smooth without any denticulation or serration, was the monotypic *Stenomordellaria* Ermisch, 1950 from New Zealand, a genus

revised by Franciscolo (1980). The absence of teeth on claws of some Baltic Mordellini is thus quite enigmatic. This character has neither been mentioned nor figured in descriptions of Eocene mordellids so far.

Metanepisternum. The shape of the metanepisternum may differ greatly in length and height. In *Baltimorda*, undescribed species B (PřfUK94), it is much longer and narrower than in *Baltimorda*, ?undescribed species A (PřfUK71) (see Systematic part above). However, this sclerite is neither described nor figured for '*Mordella*' *scheelei*, *Succimorda rubromaculata*, '*Mordellaria*' *friedrichi* and '*Tomoxia*' *succinea*, making it impossible to compare them with the undescribed Mordellini mentioned in this study. Description of the metanepisternum is also lacking for all previously described Baltic Mordellistenini. The shape of the metanepisternum is an important character at the tribal level (Franciscolo 1957a: 238), generic level (Franciscolo 1987), or is considered sexually dimorphic (Franciscolo 2000) and should not be omitted in future taxonomic studies. Its taxonomic importance in Mordellidae needs to be evaluated.

Metakatepisternum (Figs 10A–F). A narrow and slightly curved sclerite delimits the metacoxae from the metaventrite in some species, whereas it externally disappears along with metacoxa in others. This structure is depicted as delimited from metaventrite by a 'transverse suture on the metasternal plate' in extant *Glipodes dietrichi* Franciscolo, 1962 (Conaliini) by Franciscolo (1962a). There is no other description of this structure or its suture in nearly 190 taxonomical studies on Mordellidae. Surprisingly, a separate metakatepisternum is not rare in Eocene Mordellidae in both tribes: it is well visible in *Baltimorda*, ?undescribed species A (PřfUK71), *Baltistena hoffeinsorum* sp. nov., *B. concava* sp. nov., *B. brevispina* sp. nov., and *B. atronigra* sp. nov., and partially so on the ventral half of *Palaeostena eocenica* (PřfUK107). This taxonomically important character is rarely commented on by taxonomists, although it is clearly visible in some figures of recently described species, e.g., Steury & Steiner (2020: fig. 7C; 2021: fig. 23 right). The metakatepisternum is also clearly visible in many common European species, e.g., *Mordellistena neuwaldeggiana* (Panzer, 1796). Its taxonomic potential in Mordellidae needs further study.

Tip of pygidium. The examination of the pygidium (tergite VII) of specimens using light microscopy revealed three distinct morphotypes. In *Baltistena aurata* sp. nov., *B. concava* sp. nov., and *B. ultima* sp. nov., the end bears a ring of long, distinct, black scale-like setae similar to those forming combs on the hind legs, whereas the rest of the setation on the pygidium is pale. A ring of indistinct, very short black scale-like setae is visible in *Baltistena brevispina* sp. nov., *Palaeostena* and *Baltimorda*, undescribed species B. In *Baltistena atronigra* sp. nov., *B. hoffeinsorum* sp. nov., *B. longistrigata* sp. nov. and *Baltimorda*, ?undescribed species A, apparently no apical setae are present. The pygidium plays an important role in jumping in Mordellidae (Reuter 1995). It is likely that the presence of distinct caudal scale-like setae relates to their escape strategy and it should be noted by taxonomists.

Eocene and Oligocene compression fossils

To describe a new species of Mordellidae based only on measurements or colour (both undoubtedly affected by mineralogical processes) or because it is the only known fossil of its family from the respective strata lacks scientific credibility. Editors of scientific journals should reject such descriptions although these may be conformed with formal requirements, as they are uninformative and misleading. The collective group name *Petrimordella* nov. introduced above, allows the scientific community to record, with a particular species name, information on the presence of the respective Mordellidae in the particular fossil strata (but it may not always be a mordellid), and thus avoid contamination of the extant taxonomic units (e.g., genera or tribes) by unfounded speculations and incorrect conclusions.

Conclusion

All 12 descriptions of Eocene and Oligocene compression fossils have no taxonomic justification at the generic and tribal levels. Eleven species described from Eocene amber by previous authors were misplaced in the extant genera. The tendency to put Eocene and Oligocene Mordellidae into an extant genus obscures possible important differences (see for example the Comments on identification under *Palaeostena eocenica* or *Rovnostena ponomarenkoi*). The situation is even more complicated by the fact that the male genitalia of extant species are as a rule used as an important feature for identification, both at generic and species levels, but genitalia of fossil Mordellidae have not been studied. Due to the combination of incorrect descriptors and neglected important delimiting characters, fossil Mordellidae were ignored by taxonomists and students of paleobiogeography, paleodiversity and evolution of beetles. To untangle the record of fossil Mordellidae and to document it in a transparent way will undoubtedly be an endless and challenging task. This was highlighted by the case of 'the first fossil tumbling flower beetle-type larva', which was placed in Mordellidae, but recently correctly identified as a symphytan Hymenoptera (Batelka & Engel 2022), and by the evaluation of the systematic placement of the Eocene *Asiamordella* Hong, 2002, which might belong to Ripiphoridae but not to Mordellidae (Batelka & Prokop 2023).

There are many specimens of Mordellidae in Baltic amber collections in public institutions. Bao et al. (2018) reports 39 specimens in Gdańsk University (including their types), Larsson (1978) 25 specimens in the Klebs collection (Albertus University in Königsberg, Germany) and 18 in the amber collection at the University of Copenhagen. In the collection used in the current study there are 27 specimens including previously described species. That is a total of 108 specimens. It is likely that there are also several hundred specimens in various institutions, all of which should be examined before any conclusions about the diversity of this group in Eocene forests in Europe are drawn. Single descriptions lacking the taxonomic context of other Eocene and extant species are no longer desirable. Collective groups should be used instead of unfounded first reports of supposed extant genera.

It is hoped that this study will stimulate a more comprehensive approach to the study of Eocene species of this family and detailed comparison with their possible extant relatives. The results indicate that it is likely that the majority of Eocene species from Baltic and Rovno amber do not belong to extant genera in the West Palaearctic, but probably represent a specific fauna with unknown affinities with extant species.

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