Zootaxa 4869 (2): 281–289
https://www.mapress.com/j/zt/

Article

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

https://doi.org/10.11646/zootaxa.4869.2.8
http://zoobank.org/urn:lsid:zoobank.org:pub:60042C2C-46F1-4980-BFBE-BE92B5BE63A5

The first new genus of the tribe Hypulini Seidlitz (Coleoptera: Melandryidae) described from late Eocene Baltic amber

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Abstract

A new extinct monotypic genus of the false darkling beetles, *Madelinia gedanoposita* **gen.** et **sp. nov.**, is described and illustrated based on an inclusion in Baltic amber. The new taxon from a northern European Eocene forest is compared with the morphologically similar extant beetles as well as fossil melandryid beetles found in Baltic amber. The specimen establishes that the tribe Hypulini dates back to at least the Eocene and represents the first fossil genus of the group described. The composition of the tribe is discussed, and its present-day geographic distribution is mapped.

Key words: Tenebrionoidea, Cenozoic, Paleogene, fossil resin, new taxa

Introduction

Currently, the family Melandryidae is represented by approximately 60 genera and 420 described species and is distributed worldwide (Nikitsky & Pollock 2010). The family is divided into two subfamilies: Osphyinae (two tribes, Conopalpini and Osphyini) and Melandryinae (eight tribes, Anisoxiellini, Dircaeini, Hypulini, Melandryini, Orchesiini, Serropalpini, Xylitini, and Zilorini), with the last subfamily having several genera now treated as *incertae sedis*, e.g. East Asian and North American genera *Microtonus*, and *Symphora* (Nikitsky & Pollock 2010). The systematic relationships among false darkling beetles are not well-documented for recent representatives. As Dr. Darren A. Pollock noted, "the tribal classification of the subfamily Melandryinae seems inadequate and probably artificial" (Pollock 2002), and the commonly used diagnostic features for tribal limits are weak and imprecise. The Holarctic tribe of interest, Hypulini, consists of four extant genera with 25 species (*sensu* Nikitsky & Pollock 2008). The genera *Hypulus* Paykull (Europe—2 spp., North America—2(?) spp., Asia—6 spp.), *Marolia* Mulsant (Europe—3 spp., North Africa—1 sp.), *Neogonus* Hampe (Europe—5 spp., Asia—1 sp.), and *Nipponomarolia* Miyatake (Asia—5 spp.) are recognized.

The oldest geological record of the family Melandryidae is *Archaeoxylita zherichini* Nikitsky 1977 from Lower Cretaceous (Santonian) Taimyr amber (Nikitsky 1977). The biodiversity of the family Melandryidae described from Eocene Baltic amber at present consists of 11 extinct species, assigned to seven genera of at least three tribes (Orchesiini, Dircaeini, and Serropalpini) within the subfamily Melandryinae. The presence in Baltic amber of a representative of the second subfamily, Osphyinae, is mentioned by Larsson (1978). One other fossil species, *Orchesia* (*Orchestera*) *rasnitzyni* Nikitsky, 2011, described from Rovno amber (Nikitsky 2011), is also reported from Baltic amber. Three known fossil species (all belonging to extinct monotypic genera, *Abderina* Seidlitz, 1898, *Electroabdera* Alekseev, 2014 and *Quasianisoxya* Alekseev, 2015) combine features of different lineages, are morphologically intermediate and therefore of doubtful tribal placement, only originally and tentatively placed in Serropalpini and in Dircaeini. Historically, several additional taxa at the generic level of Melandryinae were mentioned by Klebs (1910); among them—first reported from Baltic amber—was a probable representative of the tribe Hypulini (in Klebs' paper literally "bei *Hypulus*"). Subsequent lists and reviews only cited Klebs' data, and no descriptions or even additional reports have been published on Hypulini in Baltic amber for over 100 years.

Accepted by E. Ruzzier: 9 Oct. 2020; published: 2 Nov. 2020

In this paper, we formally describe and illustrate the first fossil representative of Hypulini from late Eocene Baltic amber. The new melandryid taxon is compared with the morphologically close extant and fossil representatives, expanding our knowledge about the evolution of the tribe and the family.

Material and methods

The amber piece MAIG 6692 containing the holotype is deposited in the Museum of Amber Inclusions (Muzeum Inkluzji w Bursztynie), Department of Invertebrate Zoology and Parasitology, Faculty of Biology, University of Gdańsk, Poland.

Preparation of the amber specimen for examination and photography was performed by Mr. Marius Veta (Palanga, Lithuania). The amber piece was cut and polished to allow a better view of the inclusion. Photographs were taken using a Canon DSLR camera with a macro lens. Extended depth of field at high magnifications was achieved by combining multiple images from a range of focal planes using a focus stacking software, Helicon Focus.

Measurements were made using an ocular micrometer in a stereoscopic microscope. Reconstructions were made based on free-hand drawings during examination of the original specimen. All images were edited using Adobe Photoshop® CS8 software.

The following sources were used for the generic attribution and comparison with extant and extinct taxa and for morphological terminology: Seidlitz (1898), Nikitsky (1992), Pollock (2002), and Nikitsky & Pollock (2010). Specimens collected by the first author in the Kaliningrad region, including both recent European representatives of *Hypulus* Paykull, 1798 [*H. quercinus* (Quensel, 1790) and *H. bifasciatus* (Fabricius, 1792)] as well as representatives of other melandryid tribes, were also used for morphological comparison with the corresponding groups.

Systematic Paleontology

Family Melandryidae Leach, 1815

Subfamily Melandryinae Leach, 1815

Tribe Hypulini Seidlitz, 1875

Genus *Madelinia* gen. nov.

Type species: *Madelinia gedanoposita* **sp. nov.**, here designated.

Diagnosis. *Madelinia* **gen. nov.** (Figs. 1–3) is assigned to the tribe Hypulini within Melandryinae based on the following combination of characters: (1) procoxae contiguous; (2) claws simple; (3) antennae 11-segmented; (4) base of pronotum closely associated with the base of elytra (not loosely laying over it as in Melandryini); (5) head well visible from above (not vertically oriented as in Serropalpini); (6) elytra elongated, narrowly ovate; elytral punctation irregular and elytral vestiture depressed (in contrast to Zilorini); (7) lateral edges of pronotum not fully margined; (8) metatibia comparatively long (in contrast to Orchesiini); (9) metatibial spurs comparatively short (in contrast to Orchesiini and Serropalpini); (10) penultimate tarsomere of all legs lobed.

The new genus can be distinguished from all other described extant Hypulini of the Northern Hemisphere by the following set of characters: (1) hind wings present, macropterous (in contrast to the wingless genera *Marolia* and *Nipponomarolia*); (2) scutellum visible (in contrast to *Nipponomarolia*); (3) pronotal base distinctly margined (in contrast to *Hypulus*); (4) pronotum with distinct basal triangular depressions (in contrast to *Marolia* and *Neogonus*); (5) pronotal base slightly narrower than elytral base (in contrast to distinctly narrower pronotal base in *Nipponomarolia* and *Neogonus*); (6) pronotum laterally margined at one third of posterior angles only (in contrast to *Marolia*); (7) elytra uniformly dark colored (in contrast to the elytra with color pattern in *Hypulus* and *Marolia*); (8) metatarsomere 1 not shorter than one half of metatibia (in contrast to *Neogonus*).

Madelinia **gen. nov.** strongly resembles the European *Marolia* and the Holarctic *Hypulus*, but does not fully

correspond to either extant genus, and therefore is placed into a new genus within the tribe. This new genus from Baltic amber can be easily distinguished from other Melandryinae described from Baltic amber using the combination of the abovementioned "tribal" characters 1, 4, 5, 7–9, as well the "generic" characters 3–6.

Note. Due to the "milky" opacity in the amber obscuring part of the specimen, the sutures of the head, the pro- and mesothorax, the precise length of the epipleura, the form of distal labial palpomere, detail of the mouthparts, and the form of the eye margins (incised anteriorly or not) were impossible to examine. Also, the genitalia remained internal and were not studied in the specimen.

Etymology. The name of the new genus, *Madelinia*, is of feminine gender. It is named after Madeline Pankowski (Rockville, Maryland, USA), sister of the second author, who donated this amber inclusion to the Museum of Amber Inclusions for further scientific study and preservation.

Remarks. The new genus is monotypic, represented by the type species only. Therefore, the generic description considerably overlaps that of the species.

Madelinia gedanoposita sp. nov.

(Figs. 1–3)

Material examined. Holotype: No. 6692 [MAIG], adult, sex unknown. Complete beetle inclusion in a transparent, yellow piece of amber with dimensions 16×7×5 mm (weight 0.6 g) without any further fixation. The complete beetle with a partially exposed apex of its metathoracic wing is well preserved, but its forebody is not perfectly visible: Parts of the head and thorax on the ventral side are covered by a milky or opaque amber layer. Organic syninclusions are represented by stellate fagacean trichomes.

Type strata. Baltic amber from Eocene amber-bearing *Blaue Erde* deposits (mostly Bartonian age, as interpreted for extinct Central European resin-producing forests according to Bukejs *et al*. 2019).

Type locality. "Primorskoe" mine, Yantarny settlement (formerly Palmnicken), Sambian (Samland) Peninsula, Kaliningrad Region, Russia.

Diagnosis. As stated above, for the new genus.

Description. *Body* elongated, slightly convex dorsally; dark, unicolorous. Dorsal surface evenly punctured and covered with fine, decumbent, conspicuous pubescence.

Measurements: Body length approximately 5.8 mm (measured laterally, head obliquely directed as preserved), maximum body width 1.8 mm (elytra postmedially); head length about 0.6 mm; pronotal length about 1.0 mm, maximum pronotal width 1.2 mm; elytral length 4.5 mm.

Head. Compound eyes weakly convex, without intrafacetal setae; ommatidial facets distinct and fine (as large as punctures on anterior part of pronotum). Terminal maxillary palpomere cultriform, 2.5 times as long as penultimate palpomere. Antennae 11-segmented, filiform, reaching posteriorly to humeri, with short pubescence. Antennomeres 3–10 conically elongated, all almost uniform in size, about 3 times as long as wide; pedicel cylindrical, about 2 times as long as wide; scape and antennomere 11 slightly wider than other antennomeres; scape rounded; antennomere 11 ovoid, pointed apically, about 1.5 times as long as antennomere 10.

Thorax. Pronotum transverse, 1.2 times as wide as long, widest at middle. Pronotal base narrower than elytra at humeri. Anterior margin of pronotum slightly rounded; posterior margin bisinuate; lateral pronotal margins gradually narrowed toward the anterior from the middle. Lateral pronotal carina present, discernible in lateral view in one-third of pronotal length basally. Anterior angles rounded; posterior angles pronounced, pointed, acute. Pronotal disc slightly convex, uneven, with pair of shallow symmetrical depressions at middle. Basal impressions distinct, comparatively deep, triangular, reaching one-fourth of pronotal length. Pronotum densely punctate, distance between punctures equal to 0.5 times diameter of one puncture. Punctures with decumbent fine long hairs directed toward the posterior, as long as 2.0–3.0 times diameter of one puncture.

Elytra elongate, widest behind the middle, with distinct humeri and separately rounded elytral apices. Elytral disc slightly convex; dorsal surface evenly and irregularly punctate and pubescent. Pubescence decumbent, long; distance among punctures equal to 0.5–2.0 times diameter of one puncture (denser at the base, sparser posteriad). Hind wings present. Scutellar shield transverse, 1.6 times as wide as long, oval, matte. Elytral epipleura narrow, widest basally and then gradually narrowed toward the posterior.

FIGURES 1–2. *Madelinia gedanoposita* **gen.** et **sp. nov.**, holotype, No MAIG 6692, habitus: 1) dorsal view; 2) right lateral view. Scale bars represent 1.0 mm.

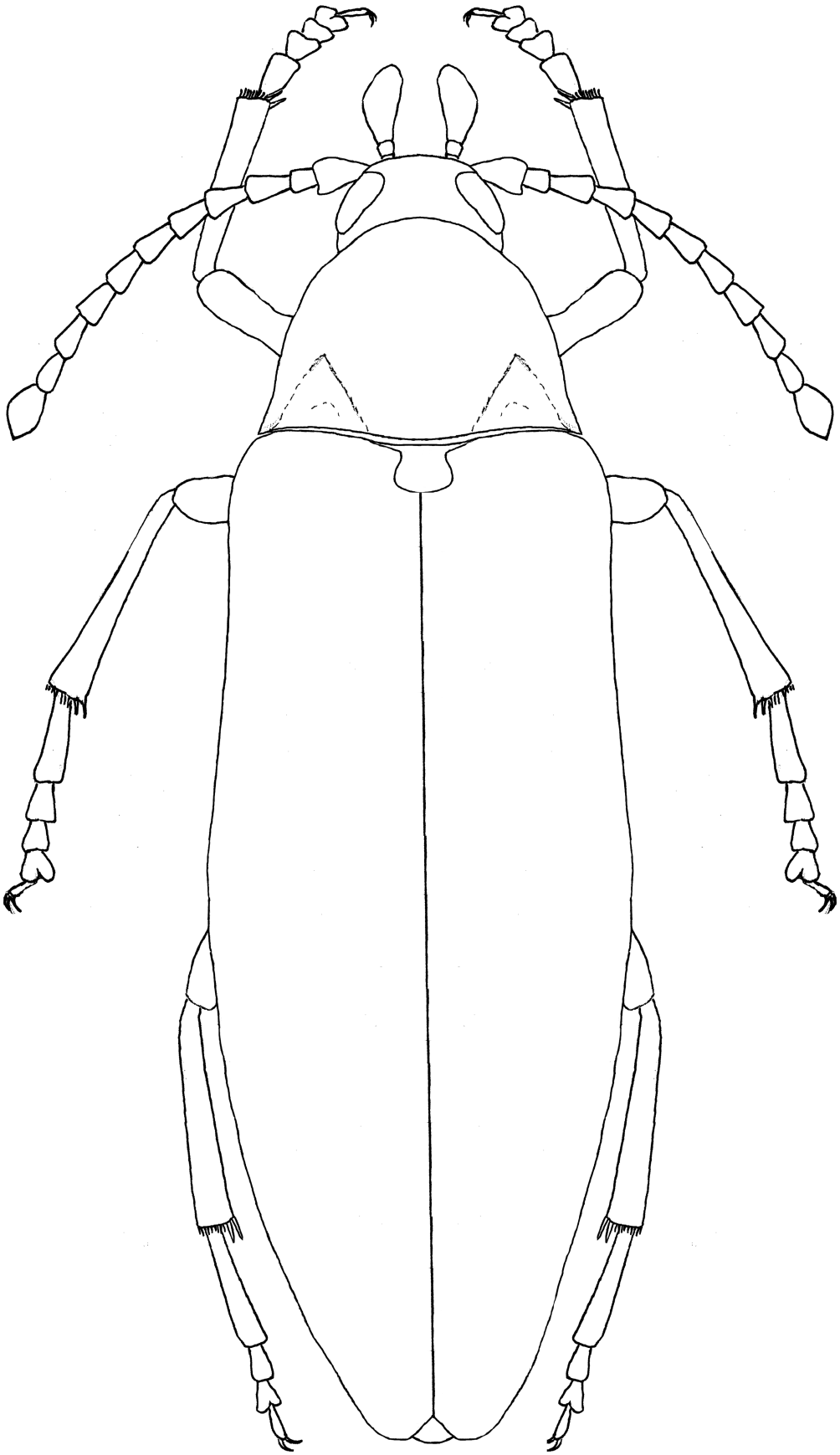

FIGURE 3. Reconstruction of *Madelinia gedanoposita* **gen.** et **sp. nov.** from Baltic amber: habitus, dorsal view. Body length approximately 5.8 mm.

Legs slender. Procoxae contiguous. Meso- and metacoxae narrowly separated. Femora weakly flattened. Tibiae straight, subequal in length to femora, finely punctate and setose, with two short spurs of equal length on the inner angle apically. Metatibial spurs about 0.5 times as long as tibial width at apex, slightly serrate at inner side. Tarsi 5-5-4. Penultimate tarsomere of all legs lobed. Protarsomere 2–4 widened, transverse. Tarsal claws simple, symmetrical. Ratio of metatarsomere lengths 4.0: 1.0: 0.7: 1.0.

Abdomen with five visible abdominal ventrites. All ventrites finely punctate and shortly pubescent. Ratio of lengths of ventrites 1–5 2.5: 2.5: 2.0: 1.0: 1.0 (medially).

Etymology. The specific epithet *gedanoposita* is a compound Latin adjective formed from "Gedanum" (the Latin name of Gdańsk) and "positus, -a" (placed, deposited), meaning "deposited in Gdańsk."

Discussion

Notes on the Hypulini composition and limitation. The tribe Hypulini is not a stable systematic group with strict limits and its composition has evolved over the past two centuries based on the interpretations of different authors. The tribe was first created by Seidlitz (1875) and updated in his subsequent work (Seidlitz 1898). According to Seidlitz (1898), the "Hypulina" group included seven genera: *Drances* Champion, 1889; *Symphora* LeConte, 1866; *Hypulus* Paykull; *Neogonus* Hampe; *Marolia* Mulsant; *Zilora* Mulsant, 1856; and *Euryzilora* Lewis, 1895. Two genera, *Zilora* and *Euryzilora*, now represent a separate tribe Zilorini Nikitsky, 2007 (Nikitsky 2007; Nikitsky & Pollock 2010), while the genus *Symphora* as well as the genera *Microtonus* LeConte, 1862 and *Hira* Hayashi, 1960 are treated as *incertae sedis* within Melandryidae (Nikitsky & Pollock 2010). The genus *Nipponomarolia* Miyatake, 1982, with five Japanese species described at the end of the 20th century (Nikitsky & Pollock 2008), was added to the tribe relatively recently (Miyatake 1982). *Doxozilora* Broun, 1909, a monotypic genus endemic to New Zealand, with the single representative *D. punctata* Broun, 1909, resembles a representative of the tribe Hypulini in several details. However, the genus cannot be placed in the tribe due to a number of features, such as its appendiculate tarsal claws (Broun 1909), and is "of unclear systematic position" (Nikitsky & Pollock 2010).

Two additional non-Palaearctic genera, included in the tribe by Seidlitz (1898) and later included based on the original description, namely *Drances* from central Mexico, and *Diegoa* Fairmaire, 1899 from the northern Madagascar, deserve mention here. These taxa definitely should not be included in the tribe based on recent assessments and without detailed study of the holotypes, because:

1. The original description of *Diegoa picta* Fairmaire, 1899: 486–487, the sole representative of the corresponding genus *Diegoa*, affirms the following, according to the author (Fairmaire 1899): "Cet insecte présente une grande ressemblance avec plusieurs *Marolia* de l'Amérique du Nord, notamment les *M. fulminans* et *Holmbergi*." [Translation: This insect is very similar to *Marolia* from North America, especially *M. fulminans* and *Holmbergi.*] According to present-day North American works, the species *Hypulus fulminans* LeConte 1859 is conspecific with *Prothalpia holmbergi* (Mannerheim, 1852) (see Pollock 2015), which is included in the tribe Melandryini (Pollock 2002). As a result, "*Marolia*" *sensu* Fairmaire is *Prothalpia* LeConte, 1862 and the placement into the tribe or even comparison of *Diegoa* Fairmaire with the tribe Hypulini was formally never made. Unfortunately, the original description of the beetle provides few details to help distinguish the genus ["la tète plus large, les yeux plus gros et plus saillants, les palpes maxillaires plus courts, à dernier article plus court et obliquement tronqué"; i.e., "pronotum wider, eyes larger and protruding, the maxillary palpi shorter and the last palpomere shorter and obliquely truncate"]. Thus, the attribution to a certain tribe is not possible and the genus should be treated as genus *incertae sedis*, at least within the subfamily Melandryinae (or the family) pending additional study of the holotype.

2. In the original description of the monotypic genus *Drances* Champion, 1889 with one species included, *D. angustatus*, it is stated (Champion 1889-1893): "*Drances* is perhaps nearest allied to *Symphora*." The differences from our fossil beetle can be easily discerned from the description (e.g., last maxillary palpomere securiform, total body length 4.3 mm, eyes deeply emarginated, etc.). However, the tribal placement of *Drances* is not clear, and its position *incertae sedis* within the subfamily Melandryinae, along with the genus *Symphora* as well, seems to be the most logical conclusion before a detailed re-description of the beetle.

The specimen described in the current paper establishes that the tribe Hypulini, restricted to the present-day Holarctic realm, dates to at least the Eocene. It also confirms the presence of the tribe in the Western Palaearctic in the Paleogene. The Hypulini, as well the whole family, needs a worldwide revision based on a modern phylogenetic

analysis. The newly described species, as well as the fossil melandryid taxa described in the past, should be helpful when the tribe and related genera are analyzed more closely and the establishment of a new subfamily, tribe or subtribe within the family may be necessary.

Notes on the distribution of the tribe in the present-day world. The global distribution of the false darkling beetle genera placed into the tribe Hypulini is mapped in Fig. 4. The northern limits of the distribution in eastern North America, Europe and the Far East almost coincide with the northern distribution limits of oak, *Quercus* L. (see Denk *et al*. 2017). The northernmost point of the present-day Hypulini distribution belongs to the widest-distributed European species *Hypulus quercinus* and is situated in the Scandinavian Peninsula at approximately 61˚N (Ehnström & Axelsson 2002). Four genera placed in the Hypulini have a chain-like distribution in the present-day world with three "concentrations" of the genera in the Palaearctic. These three areas, each with two sympatric Hypulini genera, are situated in southern Europe (genera *Hypulus* and *Marolia*), in central Asia (*Hypulus* and *Neogonus*) and in Japan (*Hypulus* and *Nipponomarolia*). The areas of the highest species diversity are situated in Japan (eight species) and in southern Europe (Italy, Switzerland, France, and Greece—four species). Only two species of the tribe (both from the genus *Hypulus*) inhabit the present-day Sambian Peninsula of the Kaliningrad region.

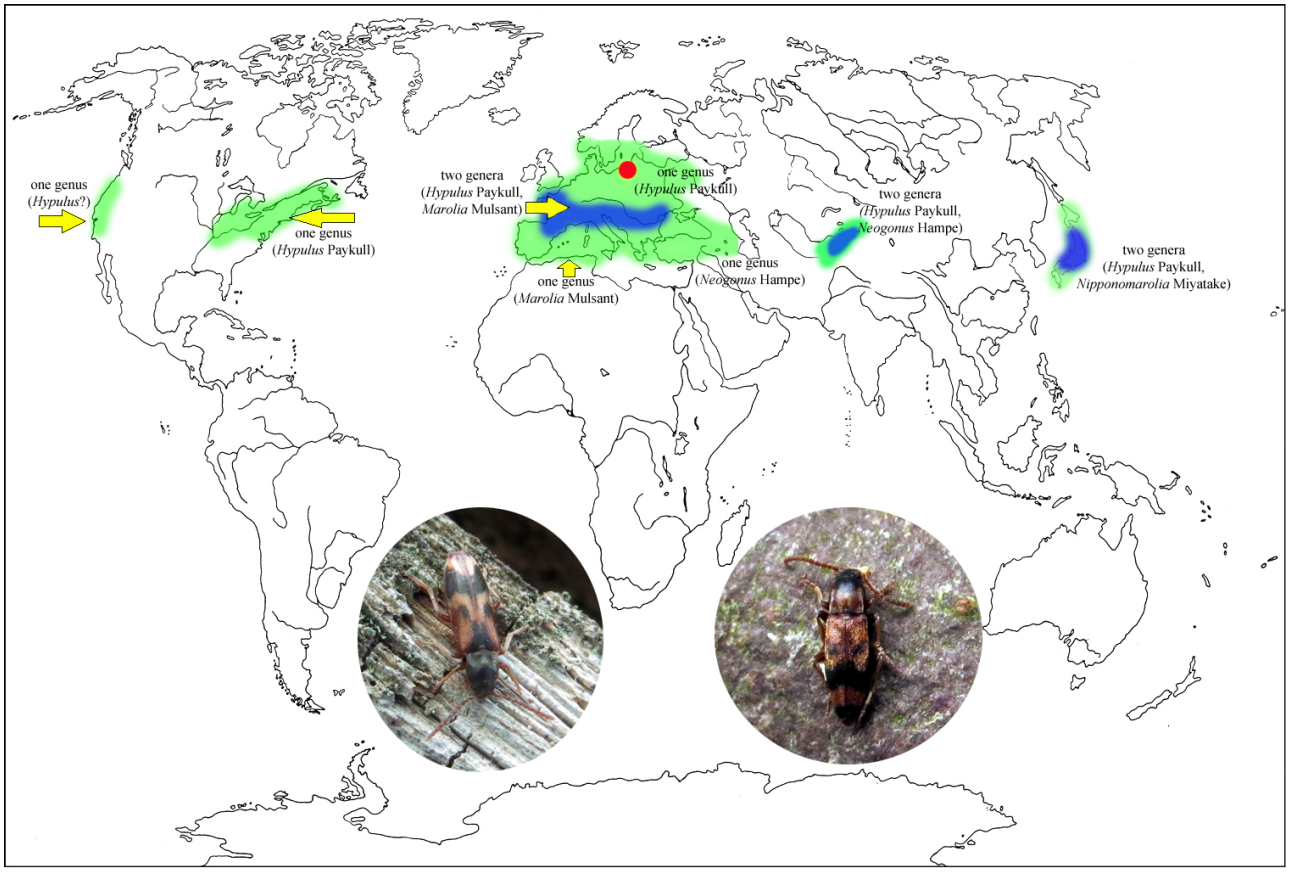

FIGURE 4. Distribution and generic diversity of the tribe Hypulini in the present-day world (green area—distribution area of one genus; blue area—area of sympatric distribution for two genera), and locality of Eocene *Madelinia gedanoposita* **gen.** et **sp. nov.** (red dot). In the round photos are shown two extant representatives of the genus *Hypulus* from the Sambian Peninsula (Kaliningrad region), *H. quercinus* and *H. bifasciatus*.

Notes on the presumed variability of the fossil. The extant adult representatives of the externally similar genus *Hypulus* from Europe can significantly (approximately 1.5 times) vary in body length, with the body size of an adult probably depending on the feeding regime of the larva. The available collection material from the Kaliningrad region shows the fluctuations in body lengths 4.5–6.5 mm in *H. bifasciatus* (14 adult specimens measured), and 4.0–6.6 mm in *H. quercinus* (10 specimens measured). The secondary sexual dimorphic characters in *Hypulus* are not pronounced; however, the comparatively wider protarsi and slightly narrower elytra are typical for males. A similar variability in an extinct taxon can be expected.

Notes on the presumed paleoecology of the fossil species. Modern representatives of Hypulini are associated

with dead wood (white or brown rots) of deciduous trees, primarily with *Quercus*, *Fagus* and *Aesculus* (Fagaceae), but also with *Corylus*, *Carpinus* and *Alnus* (Betulaceae), as well as *Crataegus* and *Malus* (Rosacea) (Seidlitz 1898; Ehnström & Axelsson 2002; Nikitsky & Pollock 2010; Recalde Irurzun & Pérez-Moreno 2011; Hörren 2015; Tamutis *et al*. 2019). Adults of Hypulini are mostly crepuscular and nocturnal, usually occurring along the forest floor on logs and twigs infested by fungi, and not forming any aggregations. For the fossil species, a similar biology can be assumed, and the association of *Madelinia gedanoposita* **gen.** et **sp. nov.** with non-coniferous (fagacean or betulacean) and non-resiniferous host trees is also probable, based upon the modern biology of the Palaearctic genera. The rarity of this beetle group in amber could be the result of these ecological peculiarities, and this specimen could be classified as an "incidental catch."

We anticipate that continued detailed documentation of the beetles in Baltic amber will not only be useful for a better understanding of the evolutionary history of the biosphere during the early Cenozoic, but also for the precise reconstruction of the "Baltic amber forest" paleoecosystems. Furthermore, the study of beetles from Baltic amber (and, of course, other fossils) will continue to help us close the gaps in our knowledge of present-day faunas, allowing us to better understand modern biodiversity and ways to protect it.

Acknowledgements

The authors are sincerely grateful to Madeline and Mark Pankowski (Rockville, Maryland, USA) for donating this amber specimen to science, Dr. Elżbieta Sontag (MAIG, Gdańsk, Poland) for the loan of interesting material for study, and to Mr. Marius Veta (Palanga, Lithuania) for granting us permission to use his excellent photographs in the paper. We also want to express our gratitude to Dr. Ondřej Konvička (České Budějovice, Czech Republic) and to Dr. Darren A. Pollock (Portales, New Mexico, USA) for their kind help with literature sources, as well as to Dr. Pollock and the editor for their valuable suggestions that improved our manuscript.

The study of V.I.A. was done with the support of the state assignment of IO RAS (Theme No. 0149–2019–0013).

References

Broun, T. (1909) LIII—Descriptions of new genera and species of New Zealand Coleoptera (continued from p. 233.). *The Annals and Magazine of Natural History*, 3 (17), 385–415.
https://doi.org/10.1080/00222930908692601

Bukejs, A., Alekseev, V.I. & Pollock, D.A. (2019) Waidelotinae, a new subfamily of Pyrochroidae (Coleoptera: Tenebrionoidea) from Baltic amber of the Sambian peninsula and the interpretation of Sambian amber stratigraphy, age and location. *Zootaxa*, 4664 (2), 261–273.
https://doi.org/10.11646/zootaxa.4664.2.8

Champion, G.C. (1889–1893) Heteromera (part). *In*: Godman, F.D. & Salvin, O. (Eds.), *Biologia Centrali-Americana. Insecta. Coleoptera. Vol. IV. Part 2*. R.H. Porter, London, pp. 1–494.

Denk, T., Grimm, G.W., Manos, P.S., Deng, M. & Hipp, A.L. (2017) An updated infrageneric classification of the oaks: review of previous taxonomic schemes and synthesis of evolutionary patterns. *In*: Gil-Pelegrín, E., Peguero-Pina, J.J. & Sancho-Knapik, D. (Eds.), *Oaks Physiological Ecology. Exploring the Functional Diversity of Genus Quercus*. Springer, Cham, pp. 13–38.
https://doi.org/10.1101/168146

Ehnström, B. & Axelsson, R. (2002) *Insektsgnag i bark och ved*. ArtDatabanken, SLU, Uppsala, 512 pp.

Fairmaire, L. (1899) Matériaux pour la faune coléoptérique de la région Malgache. *Annales de la Société Entomologique de France*, LXVIII, 466–507.
https://doi.org/10.5962/bhl.part.8623

Hörren, T. (2015) Erstnachweis des Düsterkäfers *Marolia variegata* (Bosc d'Antic, 1791) für Deutschland im Unteren Moseltal (Col., Melandryidae). *Die Mitteilungen der Arbeitsgemeinschaft Rheinischer Koleopterologen, Bonn*, 25, 3–6.

Klebs, R. (1910) Über Bernsteineinschlüsse im Allgemeinen und die Coleopteren meiner Bernsteinsammlung. *Schriften der Physikalisch-ökonomischen Gesellschaft zu Königsberg*, 51 (3), 217–242.

Larsson, S.G. (1978) *Baltic amber—a palaeobiological study. Vol. 1.* Scandinavian Science Press Ltd., Klampenborg, 192 pp.

Miyatake, M. (1982) A new genus and two new species of the tribe Hypulini from Japan (Coleoptera, Melandryidae). *Transactions of the Shikoku Entomological Society*, 16 (1–2), 29–35.

Nikitsky, N.B. (1977) Two new genera of false darkling beetles (Coleoptera, Melandryidae) from Upper Cretaceous. *Paleonto-*

logical Journal, 2, 140–143. [in Russian]
Nikitsky, N.B. (1992) Family Melandryidae. *In*: Ler, P.A. (Ed.), *Key to Insects of the Far East of the USSR. Vol. III. Coleoptera. Part 2.* Nauka, St. Petersburg. pp. 435–474, 659. [in Russian]
Nikitsky, N.B. (2007) New taxa of the hairy fungus beetles and false darkling beetles (Coleoptera, Mycetophagidae, Melandryidae). *Byulleten' Moskovskogo Obshchestva Ispytateley Prirody Otdel Biologicheskiy*, 112 (4), 58–62. [in Russian]
Nikitsky, N.B. (2011) New species of the genus *Orchesia* Latr. from the Upper Eocene (Coleoptera: Tenebrionoidea). *Paleontological Journal*, 5, 82–84.
https://doi.org/10.1134/S003103011105008X
Nikitsky, N.B. & Pollock, D.A. (2008) Melandryidae. *In*: Löbl, I. & Smetana, A. (Eds.), *Catalogue of Palaearctic Coleoptera. Vol. 5. Tenebrionoidea*. Apollo Books, Stenstrup, pp. 64–72.
Nikitsky, N.B. & Pollock, D.A. (2010) Melandryidae. *In*: Leschen, R.A.B., Beutel, R.G. & Lawrence, J.F. (Eds.), *Handbook of Zoology. Vol. 2. Coleoptera, Beetles. Morphology and Systematics (Elateroidea, Bostrichiformia, Cucujiformia partim)*. Walter de Gruyter GmbH & Co, Berlin, pp. 520–533.
Pollock, D.A. (2002) 100. Melandryidae Leach 1815. *In*: Arnett, R.H. Jr., Thomas, M.C., Skelley, P.E. & Frank, J.H. (Eds.), *American Beetles. Vol. 2. Polyphaga: Scarabaeoidea through Curculionoidea.* CRC Press, Boca Raton, pp. 417–422.
Pollock, D.A. (2015) Lectotype designations in Tetratomidae, Melandryidae, Boridae and Mycteridae, based on material in the Museum of Comparative Zoology, Harvard University (Coleoptera: Tenebrionoidea). *Insecta Mundi*, 0427, 1–15.
Recalde Irurzun, J.I. & Pérez-Moreno, I. (2011) Elementos para el conocimiento de los melándridos y tetratómidos del norte de España y actualización del catálogo de especies ibéricas (Coleoptera: Tenebrionoidea: Melandryidae, Tetratomidae). *Boletín de la Sociedad Entomológica Aragonesa (S.E.A.)*, 49, 309–319.
Seidlitz, G. (1875) *Fauna Baltica. Die Käfer (Coleoptera) der Ostseeprovinzen Russlands*. H. Laakmann, Dorpat, 102 pp.
Seidlitz, G. (1898) Melandryidae. *In*: Erichson, W.F. (Ed.), *Naturgeschichte der Insecten Deutschlands. Erste Abtheilung. Coleoptera. Fünfter Band. Zweite Hälfte*. Nicolaische Verlags-Buchhandlung, Berlin, pp. 365–680.
Tamutis, V., Ferenca, R. & Pollock, D.A. (2019) Faunistic review of Tetratomidae and Melandryidae (Coleoptera: Tenebrionoidea) in Lithuania with an annotated checklist of the species. *Zootaxa*, 4668 (2), 183–206.
https://doi.org/10.11646/zootaxa.4668.2.2