Zootaxa 4337 (3): 413–422
http://www.mapress.com/j/zt/

Article

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

https://doi.org/10.11646/zootaxa.4337.3.6
http://zoobank.org/urn:lsid:zoobank.org:pub:4F937323-3789-420A-A4FD-E2783EFF4761

First fossil representatives of Pharaxonothinae Crowson (Coleoptera: Erotylidae): indirect evidence for cycads existence in Baltic amber forest

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Abstract

A new species of Erotylidae, *Cycadophila* (*s. str.*) *mumia* **sp. nov.**, the first fossil representative of the subfamily Pharaxonothinae, is described and illustrated from Eocene Baltic amber. A second closely related specimen is reported but not described as new due to poor preservation in amber. The occurrence of representatives of the Recent cycad-specialized genus in Baltic amber can indirectly indicate the presence of their host plants (Cycadales: Cycadophyta: Cycadopsida) in the Eocene amber forest.

Key words: pleasing fungus beetle, fossil resin, Paleogene, Tertiary

Zusammenfassung

Eine neue Art der Erotylidae, *Cycadophila* (*s. str.*) *mumia* **sp. nov.** wird als erster fossiler Vertreter der Unterfamilie Pharaxonothinae aus dem Baltischen Bernstein des Eozäns beschrieben und abgebildet. Ein zweites Exemplar dieser Unterfamilie, das einer weiteren neuen Art angehört, wird gemeldet jedoch wegen mangelnder Erhaltung nicht beschrieben. Das Fund der heutzutage mit der Palmfarne engverbundene Gattung kann indirekt auf die Existenz der Käferfutterpflanzen (Cycadales: Cycadophyta: Cycadopsida) in europäische Eozäner Bernsteinwald deuten.

Schlüsselwörter: Pilzkäfer, fossiles Harz, Paläogen, Tertiär

Introduction

Fossil records of the subfamily Pharaxonothinae Crowson, 1952 (Erotylidae), as reported in the literature (Węgrzynowicz 2002; Lyubarsky & Perkovsky 2017a), are unknown. Recently described erotylids from Eocene Baltic, Bitterfeld and Rovno ambers (Alekseev 2014; Lyubarsky & Perkovsky 2012, 2017a, 2017b; Lyubarsky *et al*. 2016) were placed in Erotylinae Latreille, 1802 (*Triplax contienensis* Alekseev, 2014), Languriinae Crotch, 1873 (*Serramorphus rasnitsyni* Lyubarsky & Perkovsky, 2017), and Xenoscelinae Ganglbauer, 1899 (*Xenochimatium rovnense* Lyubarsky & Perkovsky, 2012; *Warnis tvanksticus* Lyubarsky, Perkovsky & Alekseev, 2016; *Xenophagus popovi* Lyubarsky & Perkovsky, 2017).

The present paper brings the total number of described erotylid species from European succinites to six. The first fossil representative of Pharaxonothinae and the first extinct species of the genus *Cycadophila* Xu, Tang & Skelley, 2015 is described and illustrated from Baltic amber.

Material and methods

Three fossil specimens were examined during the current study:

Accepted by M. Gimmel: 15 Sept. 2017; published: 19 Oct. 2017

- two specimens (No. 280-4 and No. 578-1) from the private collection of Christel and Hans Werner Hoffeins (Hamburg, Germany) [CCHH]. The holotype (No. 280-4) will be deposited in the collection of Senckenberg Deutsches Entomologisches Institut (Müncheberg, Germany) [SDEI]. The amber piece with holotype was prepared manually and embedded in a block of polyester resin (Hoffeins 2001). The piece No. 578-1 is currently not embedded in artificial resin. Photographs were taken using a Zeiss AxioCamICc 3 digital camera mounted on a Zeiss Stemi 2000 stereomicroscope.
- one specimen (No. 043) from the private collection of Andris Bukejs [CAB], maintained at Institute of Life Sciences and Technologies, Daugavpils University (Daugavpils, Latvia). The amber piece was prepared manually and preserved without supplementary fixation. Observations of this specimen was made using a Nikon® SMZ 745T stereomicroscope. The photographs were taken using a Nikon® SMZ 745T stereomicroscope with Nikon® DSFi1 digital camera. Extended depth of field at high magnifications was achieved by combining multiple images from a range of focal planes using Helicon Focus 6.0.1 software.

Reconstructions were based on free-hand drawings made during examination of the original specimen. Figures were edited using Adobe Photoshop CS8 software. Measurements were taken using an ocular micrometer of a stereomicroscope (expressed in millimeters).

The following literature sources were used for the generic attribution and comparison with recent taxa: Chaves & Genaro (2005), Franz & Skelley (2008), Leschen (2003), Pakaluk (1988), Xu *et al*. (2015) and Skelley *et al*. (2017).

Systematic Palaeontology

Superfamily Cucujoidea Latreille, 1802

Family Erotylidae Latreille, 1802

Subfamily Pharaxonothinae Crowson, 1952

Genus *Cycadophila* Xu, Tang & Skelley, 2015

Note. The specimens considered here were assigned to the subfamily Pharaxonothinae based on a combination of the following visible external morphological characters: (1) lateral pockets on the mentum present; (2) tarsal shelf of tarsomere 5 absent; (3) metepisternal ctenidium absent; (4) antennal insertion hidden in dorsal view; (4) anterior angles of pronotum poorly developed; (5) mesometaventral articulation monocondylic; (6) ventrite 1 without subcoxal lines. According to Leschen (2003), the above mentioned combination of characters (especially possession of distinct lateral pockets on the mentum) can distinguish these specimens from the habitually similar representatives of the subfamily Xenoscelinae. However, characters not visible or that require dissection are needed to unequivocally confirm placement in the Pharaxonothinae.

Within the Pharaxonothinae, these fossils were assigned to the genus *Cycadophila* based on: (1) large eyes that encroach upon head ventrally; (2) 11-segmented antennae with a 3-segmented antennal club not flattened; (3) pro- and mesocoxal cavities open; (4) supraocular stria present, not extending posteriorly beyond eyes; (5) pronotal callosity absent; (6) elytra glabrous with non-impressed rows of punctures; (7) pronotum with narrow basal sulci; (8) submentum separated from gula by transverse impression (submental-gular suture); (9) 5-segmented tarsi with tarsomeres 1–3 pubescent ventrally with long, fine, dense, distally directed setae, not lobed beneath.

According to the up-to-date key of Skelley *et al*. (2017), the studied extinct specimens can be assigned to the subgenus *Cycadophila* Xu, Tang & Skelley, 2015 due to (1) lateral pronotal carinae narrow in lateral view, and (2) protibia without stout setae along lateral margin. Several morphological characters (e.g. head swollen dorsally; clypeus convex in lateral view; ventral interocular distance 0.58× head width; pronotal surface near anterior angles slightly impressed; pronotal lateral carinae parallel most length; elytra without colour patterns) allow placement of these specimens in the extant *nigra* species group. This placement is tentative and not irreproachable at the moment, because the shape of the prosternal process is not clear due to the position of the legs, and anterior pronotal angles are not sharply angulate as is typical for the *nigra* species group.

***Cycadophila* (*s. str.*) *mumia* sp. nov.**
(Figs 1–9)

Type material. Holotype: No. 280-4 [CCHH], adult, sex unknown. Beetle inclusion in a small amber piece embedded in a block of GTS-polyester resin with dimensions 13 × 7.5 × 6 mm. Syninclusion: one specimen of Sciaridae (Diptera: Nematocera).

Paratype: No. 043 [CAB], adult, sex unknown. Complete beetle included in a small, yellow subquadratic amber piece with approximate dimensions 19 × 18 × 5 mm and weight 1.2 g. Mouthparts and ventral side of the specimen obscured by "milky" opacity. Syninclusions: one stellate trichome, and few small gas vesicles.

Type strata. Baltic amber, mid-Eocene to Upper Eocene.

Type locality. Yantarny settlement (formerly Palmnicken), Sambian (Samland) Peninsula, the Kaliningrad region, Russia.

Etymology. The specific epithet is derived from the medieval Latin, meaning "mummy, an embalmed corpse". It is a noun in apposition.

Differential diagnosis. *Cycadophila mumia* **sp. nov.** differs from extant species of the subgenus in the following combination of characters: submental-gular suture with deep depression (similar to *Cycadophila abyssa* Skelley, Xu & Tang, 2017 and *C. cyclochasma* Skelley, Xu & Tang, 2017); comparatively smaller body length (about 3.8 mm); strongly transverse pronotum (length to width ratio 0.6); pronotal anterior margin curved, sinuate behind eye; supraocular stria long, reaching anterior inner angle of eye; body unicolorous ochraceous or dark brown without dark maculation along elytral suture; posterior portion of hypomera strigose.

Description. Holotype. Body elongate, oval, weakly convex, apparently glabrous dorsally; unicolorous ochraceous. Body length 3.75 mm, maximum body width 1.5 mm; pronotal length 0.78 mm, maximum pronotal width 1.3 mm; elytral length 2.8 mm.

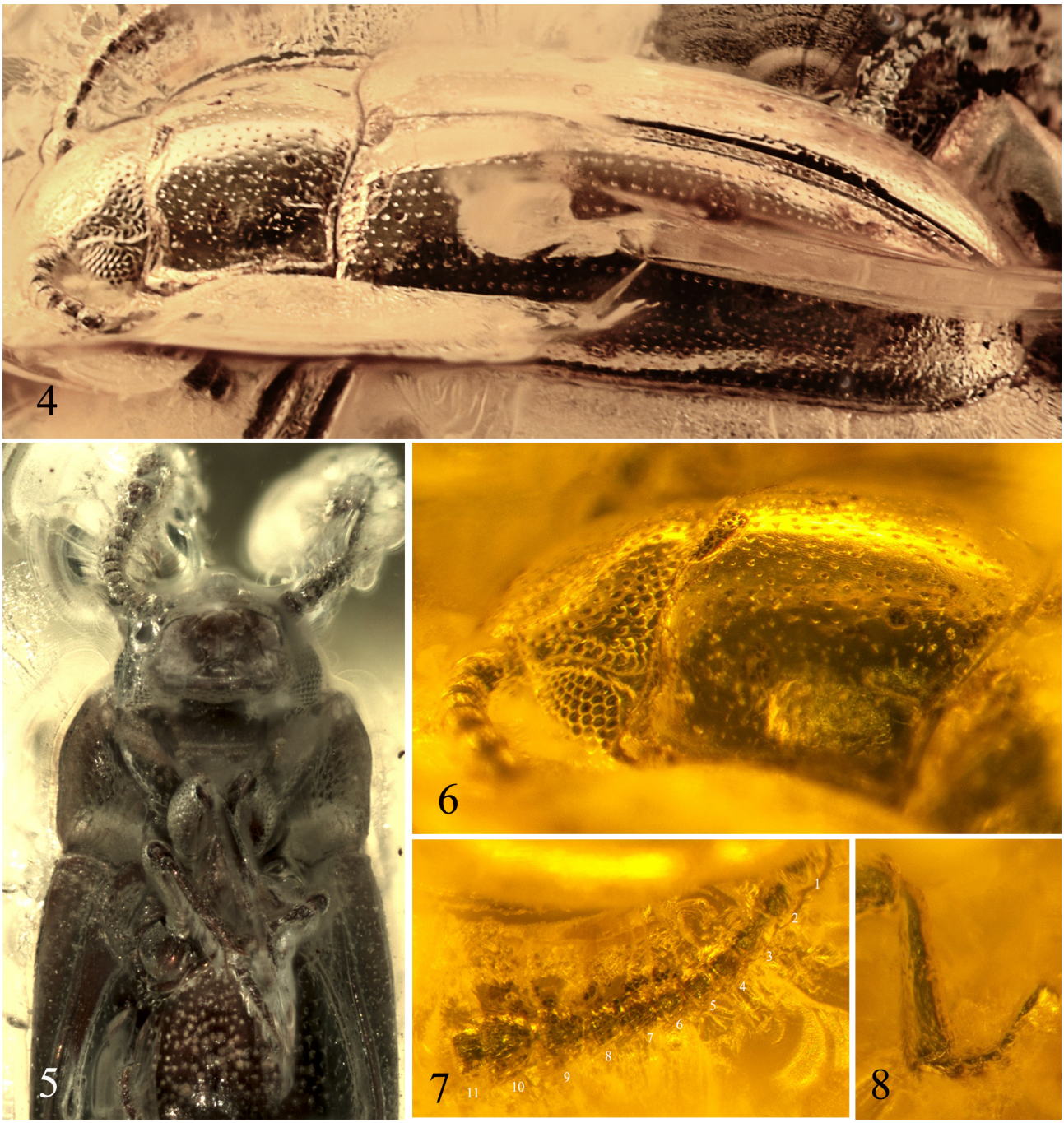
Head. Eyes prominent, coarsely faceted (10–11 facets in longitudinal axis), wide ventrally in relation to dorsal width; interfacetal setae not apparent. Dorsal interocular distance/ head width ratio 0.83; ventral interocular distance/ head width ratio 0.58. Clypeus convex, rounded apically. Supraocular stria present, long (reaching anterior inner angle of eye). Frons slightly convex. Vertex and transverse occipital ridge (vertexal line) not discernible in holotype because posterior portion of head retracted into pronotum. Punctation on frons rather dense (distance between punctures equal to 1.0–1.5× diameter of one puncture), becoming fine and sparse toward clypeus; clypeus punctures become finer and sparser toward apical margin where they disappear. Terminal maxillary and labial palpomeres almost equal in shape and size, elongate, mucronate, as wide as and no less than twice longer than penultimate palpomeres. Mentum subtriangular, rounded apically, impressed, with two symmetrical lateral pockets. Submentum distinctly punctate, separated from gula by transverse, dumbbell-shaped, deep impression. Antennae 11-segmented with 3-segmented club oval in cross section; relatively short and robust, extending to base of pronotum, bearing small setiferous punctures. Scape and pedicel cylindrical; antennomeres 3–4 almost as long as wide; antennomeres 5–8 slightly conical; antennomeres 9–10 transverse; antennomere 11 rounded. Relative length ratios of antennomeres 1–11 equal to 9:8:6:6:5:5:5:5:8:9:8.

Thorax. Pronotum evenly convex, transverse, 1.7× as wide as long, widest in the middle with narrow longitudinal sulcus posterolaterally, located at half distance between midline and lateral margin, sulci as long as one-fourth of pronotal length. Lateral margins slightly arcuate, widely bordered; anterior margin slightly arcuate, narrowly bordered; posterior margin bisinuate, narrowly bordered. Anterior angles weakly developed, obtusely rounded; posterior angles almost rectangular. Pronotal punctation fine and sparse, distance between punctures equal to 2.0–5.0× diameter of one puncture.

Elytra elongate-oval, about 1.8× as long as wide combined, 3.6× as long as pronotum; without marginal line at base (with only weak rudiment in humeral area); with impressed sutural impunctate stria in apical one-third of elytral length. Elytral punctures fine (about as large as pronotal punctures) and dense, forming non-impressed striae on disc and confused laterally. Scutellary striole shortened, extending to one-fourth of elytral length. Interstriae flat, with row of extremely fine secondary punctures. Epipleura well developed, extending to elytral apex. Scutellar shield distinctly transverse, pentagonal with rounded angles, twice wider than long; scutellar surface not visible because of structure of amber. Hind wings not visible.

Prosternum and anterior portion of hypomeron punctured, posterior portion of hypomeron strigose. Procoxal process expanded beyond procoxal area. Procoxal cavities open externally. Mesoventrite sparsely punctured.

FIGURES 1–3. *Cycadophila mumia* **sp. nov.**, holotype, habitus: 1—dorsal view; 2—ventral view; 3—lateral view. Scale bar = 1 mm.



FIGURES 4–8. *Cycadophila mumia* **sp. nov.**: 4—habitus, dorso-lateral view, paratype; 5—details of forebody, ventral view, holotype; 6—head and pronotum, dorso-lateral view, paratype; 7—antenna, paratype; 8—protibia and tarsus, paratype. Not reproduced to the same scale.

Articulation between meso- and metaventrite monocondylic. Mesocoxal cavities open. Mesepimeron and mesepisternum with dense and coarse punctures. Metaventrite slightly convex, with small, sparse punctures, distance between punctures equal to 2.0–4.0× diameter of one puncture. Mesocoxal lines absent. Metaventrite with distinct transverse row of small punctures (about 15 punctures) along metacoxal cavities; and with central longitudinal fine line (discrimen), apparent in basal half. Metepisternal ctenidium absent.

Legs short and robust**.** All coxae distinctly separated, pro- and mesocoxae semiglobular, metacoxae transverse, elongate-oval. Coxae, femora and tibiae finely and densely punctate. Femora fairly robust, compressed laterally, with slightly concave, glabrous surface ventrally to receive tibiae. Tibiae gradually dilated to apex, with apical fringe of short and narrow spinules. Tarsi pentamerous. Tarsomeres 1–3 not lobed beneath, pubescent ventrally with long, fine, dense, distally directed setae. Tarsomeres 1–4 cylindrical; tarsomere 4 slightly shorter than tarsomere 3; onychium about as long as tarsomeres 3–4 combined. Onychia paired, simple.

Abdomen. With five visible, similarly articulated ventrites; covered with fine setigerous punctures, distance between punctures 1.5–3.0× diameter of one puncture. Ventrite 1 without subcoxal lines. Intercoxal process of abdominal ventrite 1 narrowly rounded. Relative length (medially, including intercoxal process) ratios of ventrites 1–5 equal to 30:17:17:15:20.

Paratype. Body length 3.6 mm, dark brown. Head with narrow ridge located posteriorly to eye (its medial portion hidden under anterior margin of pronotum); this character is interpreted by us as the lateral portions of a transverse occipital ridge (vertexal suture). Scutellar shield densely covered with small punctures, protibiae more distinctly dilated apically than in holotype; otherwise similar in all visible morphological characters to holotype.

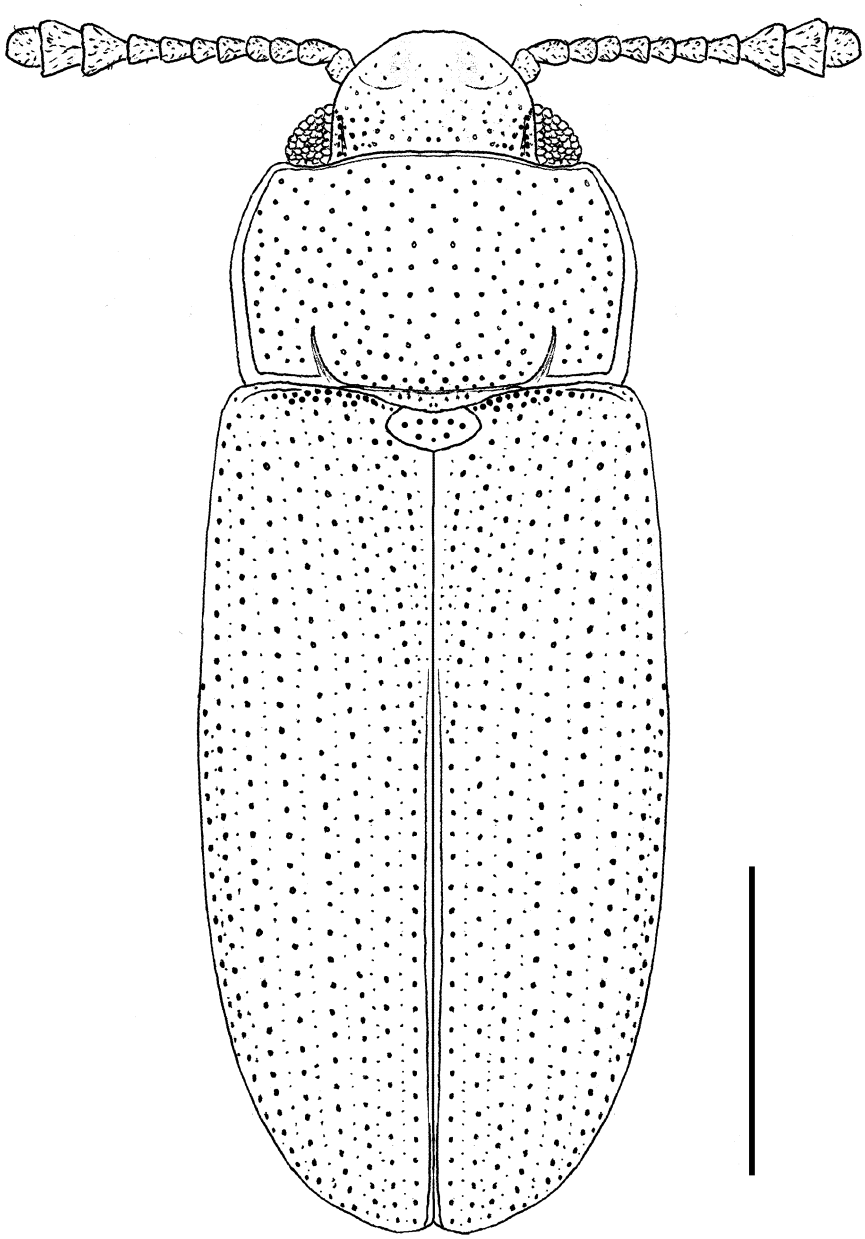


FIGURE 9. *Cycadophila mumia* **sp. nov.**, reconstruction of habitus, dorsal view. Scale bar = 1 mm.

Fossil record of Erotylidae

Pharaxonothinae gen. indet.

(Figs 10–11)

Material examined. Specimen No 578-1 [CCHH], adult, sex unknown; Baltic amber, Yantarny, Kaliningrad region, Russia. Almost complete beetle (left metatarsomeres 2–5 lost) embedded in medium-sized, elongate, transparent, orange amber piece with approximate dimensions 35 × 14 × 6 mm. Body length of beetle is 3.3 mm. Syninclusions are represented by one fragment of Nematocera (Chironomidae?) and numerous small detritus particles. The amber piece was apparently subjected to thermal and high-pressure processing in an autoclave, based on what is evident from characters mentioned by Hoffeins (2012). The right side of elytra and pronotum is fragmented and destroyed, the right antenna is partially disintegrated and the head (especially clypeal and frontal area) is strongly deformed. The dark monochrome body colour of the specimen may also be a result of the discolouration during "improving" of the amber piece.

Note. The specimen belongs to an undescribed species of Pharaxonothinae, either to *Pharaxonotha* or to the morphologically close *Cycadophila*. It differs from *C. mumia* **sp. nov.** in the finely bordered elytral base, acute anterior pronotal angles, smaller body size, elytral punctation in rows laterally, and dark body colour. The main characters of the subfamily and *Pharaxonotha* (*sensu lato*) (e.g. glabrous body; elytra with non-impressed punctate rows and shortened scutellary striole; pro- and mesocoxal cavities open; narrow pronotal posterolateral sulci; abdomen without metacoxal lines; 11-segmented antennae with a 3-segmented antennal club not flattened; transverse scutellar shield; tarsal formula 5-5-5) are clearly visible on the specimen. The beetle is probably not conspecific with *Cycadophila mumia* **sp. nov.**, but it cannot be named and formally described at present due to poor preservation.

FIGURES 10–11. Undescribed representative of Pharaxonothinae in Baltic amber, specimen No. 578-1 [CCHH]: 10—habitus, dorso-lateral view; 11—habitus, lateral view. Scale bar = 1 mm.

Discussion

Cycadales (Cycadophyta: Cycadopsida) are one of the oldest groups of insect-pollinated seed plants (Labandeira 2000, 2010), that originated during the Permian and were very abundant during the Jurassic period (Renner 2011). The most ancient (Middle Jurassic, 174–163 Ma) pollinator of cycads probably belongs to Boganiidae (Liu *et al.* 2017).

Primitive beetles of the family Erotylidae are among the most frequently reported extant coleopteran pollinators of cycads in tropical and subtropical areas (Pakaluk 1988; Leschen 2003; Chaves & Genaro 2005; Leschen & Buckley 2007; Franz & Skelley 2008; Suinyuy *et al*. 2009; Radha & Singh 2014; Valencia-Montoya *et al*. 2017). Of all beetle genera known to pollinate cycads (mostly Curculionidae, Belidae, Boganiidae, Erotylidae and Nitidulidae), *Pharaxonotha* is considered to be one of the most important in the New World based on the fact it has been associated at least with four Recent cycad genera of the family Zamiaceae: *Zamia*, *Dioon*, *Microcycas*, and *Ceratozamia* (Tang 1987; Vovides 1991; Chaves & Genaro 2005; Xu *et al*. 2015; Skelley *et al*. 2017). For some cycad populations, *Pharaxonotha* can be considered the primary and sole pollinator (Franz & Skelley 2008; Valencia-Montoya *et al.* 2017). Cycads offer food, protection, and breeding sites for the beetles, which mate and lay their eggs on the microsporophylls where the larvae develop, feeding on male sporangia tissue and male cone rachis (Valencia-Montoya *et al*. 2017). With the exception of the saprophagous *Pharaxonotha kirschii* Reitter, 1875, all five other described New World representatives of the genus are mutualistic pollinators of a cycad, e.g. *Ph. floridana* (Casey, 1890), *Ph. clarkorum* Pakaluk, 1988, *Ph. confusa* Pakaluk, 1988 and *Ph. portophylla* Franz & Skelley 2008 feed on *Zamia* spp. while *Ph. esperanzae* Chaves & Genaro 2005 feeds on male cones of *Microcycas* (Pakaluk 1988; Chaves & Genaro 2005; Franz & Skelley 2008).

The recently described (Xu *et al*. 2015) and revised (Skelley *et al*. 2017) Asian genus *Cycadophila*, closely related to *Pharaxonotha*, represents a generally similar trophic role. The genus *Cycadophila* includes 21 extant species divided into two subgenera: *Strobilophila* (5 spp.) and *Cycadophila* (16 spp.) (Skelley *et al*. 2017). Among representatives of the nominate subgenus, there are species with known associations with cycads (7 spp.), as well as those with no precise host data (9 spp., among them 6 spp. with presumed cycad association). All described species of the subgenus *Strobilophila* are cycad associated. Known host plants belong to the genus *Cycas* (Cycadaceae): several species develop in male cones (microsporophylls) and adults of some other species are reported to feed on pollen (Xu *et al*. 2015; Skelley *et al*. 2017).

Concerning Cycadales in Baltic amber, Caspary (1881) reported on the new species *Zamites sambiensis* in Cycadaceae and *Phyllites lancilobus* in Cycadaceae or Proteaceae, and Caspary & Klebs (1906) mention *Zamiophyllum sambiense* (Caspary). But the determination was not confirmed, and no additional fossils have been found since and thus the record is considered to be doubtful. However, cycads placed in Zamiaceae did exist during the Eocene of Europe (Kvaček & Manchester 1999), Oligocene and lower Miocene (Kvaček 2014).

Cycadophila mumia **sp. nov**. represents the oldest fossil record of this genus and also the subfamily Pharaxonothinae. The trapping of different species of *Pharaxonotha*-like beetles in Baltic amber can indirectly indicate a possibility of the presence of cycads, which are the presumed host plant for a majority of adults and their larvae in the Recent fauna. However, considering the existence of a related saprophagous *Pharaxonotha kirschii* and several *Cycadophila* with a possibly non-cycad-associated mode of life (such as *C. torquata* Skelley, Xu & Tang, 2017 and *C. convexa* Skelley, Xu & Tang, 2017), the undisputed occurrence of cycads in the Eocene Baltic amber forest can be confirmed by palynological analysis only.

Acknowledgements

The authors are sincerely grateful to Christel and Hans Werner Hoffeins (Hamburg, Germany) for the loan of the material, suggestion and comments in improving the manuscript, and to Dr. Pavel I. Alekseev (Saint-Petersburg, Russia) for providing photographs. We are very grateful to anonymous reviewers for their valuable comments and corrections to an earlier version of this manuscript. Special thanks are given to Dr. Matthew L. Gimmel (Santa Barbara Museum of Natural History, California, USA) for constructive advice and help during publishing process.

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