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First extinct species of the genus *Holoparamecus* (Coleoptera: Merophysiidae: Holoparamecinae) from Eocene amber deposits

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Taxonomy, new species, Coleoptera, Merophysiidae, *Holoparamecus*, Bitterfeld amber, Baltic amber, Paleogene, Tertiary

Abstract. *Holoparamecus* (*Blumenus*) *hoffeinsorum* Reike & Alekseev sp. nov. and *H*. (*Blumenus*) *paschalis* Reike & Alekseev sp. nov., two fossil representatives of the family Merophysiidae, are described on the basis of specimens from Bitterfeld and Baltic amber. The newly described species are illustrated and compared with related extant representatives of the genus. Phase-contrast synchrotron microtomography was used for the first time to study a member of this family. New combinations and synonymy, as well as a check-list and identification key are proposed for the species included in the subgenus *Blumenus* Belon.

INTRODUCTION

The genus *Holoparamecus* Curtis, 1833 comprises 48 currently described species worldwide (Rücker 2018) and is divided into seven subgenera: *Holoparamecus* s. str.; *Blumenus* Belon, 1887; *Calyptobium* Aubé, 1843; *Microparamecus* Dajoz, 1967; *Neoparamecus* Dajoz 1975; *Tocalium* Motschulsky, 1867; and *Tomyrium* Reitter, 1880. The subgenus *Blumenus* was originally described as genus, but was later transferred by Belon (1902) to become a subgenus of *Holoparamecus*. The subgenus *Blumenus* includes five known recent species: *Holoparamecus gabrielae* Rücker, 2003 (described from Mexico), *H. johnsoni* Rücker 1981 (described from Brazil), *H. lanatus* Rücker, 1985 (described from Indonesia, Sumatra), *H. pumilus* Sharp, 1902 (described from Mexico), and *H. villiger* (Belon, 1887) (described from South America, Brazil).

Arriaga-Varela et al. (2018) recently reported the existence of a genus that is externally similar and closely related to *Holoparamecus* in the present-day Neotropical Region (i.e., *Rueckeria* Arriaga-Varela, Tomaszewska, Huo & Seidel, 2018). The systematic position of *Holoparamecus* and its near relations is not fully resolved at the moment: the group has been

given generic status within the subfamily Merophysiinae in Endomychidae (Tomaszewska 2000; Rücker & Löbl 2007; Shockley et al. 2009a; Robertson et al. 2015), or it has been treated as a separate subfamily among the Merophysiidae (e.g., Rücker 2018). The latter taxonomic opinion has been commonly used within the past 60 years and was applied in the last monographic revision of the group, so it has been followed in our paper. Future studies on the phylogeny of the group will be required in order to determine whether the subfamilies Merophysiinae and Holoparamecinae really should have independent status, or whether they belong to Endomychidae as proposed in most recent publications.

The first representatives of the genus *Holoparamecus* in Baltic amber were mentioned by Klebs (1910). The genus has been also listed from Baltic amber by subsequent authors (Handlirsch 1925; Bachofen-Echt 1949; Larsson 1978; Shockley & Alekseev 2014; Alekseev 2017), but no species have been described. Furthermore, no fossil records from Bitterfeld amber or from other Lagerstätten have been published for this genus. Only one extinct Merophysiinae representative, *Cretaparamecus tarsalis* Tomaszewska, Slipiński, Bai & Zhang, 2018, has been described from the lowermost Cenomanian Burmese amber (Tomaszewska et al. 2018), which makes the genus the oldest currently known for the group.

The Recent species within the genus *Holoparamecus* are distinguishable based upon the size and presence of the eyes, the shape of the antennal club, the numbers of antennal segments (sometimes there is a difference between males and females), the number of antennal club segments (1 or 2), the pronotal bordering (present or absent), the body form (habitus more or less egg-shaped in outline), and the male genitalia. The use of synchrotron X-ray microtomography for internal structures hidden within the amber inclusions could provide the relevant comparison points with modern congeners, and is especially useful for the correct subgeneric placements of Baltic amber inclusions (see e.g., Reike et al. 2017).

The current work began as an effort to reassess the old "*Holoparamecus*" reports from the European Eocene, and provide a thoroughly illustrated description (which is necessary for understanding the evolution and distributional history of the group). In the present paper, two new species of *Holoparamecus* are described and illustrated from Bitterfeld and Baltic amber, complete with features of male genitalia. Phase-contrast synchrotron microtomography was used to study a member of this genus for the first time. Fossil representatives of the group from European Eocene amber are formally described for the first time. Observations made herein highlight the close relationship between the recently proposed genus *Rueckeria* (discovered in 2018) and *Holoparamecus* in a broad sense on a global scale, and suggest that these similarities should be pointed out for further discussion (see Rücker 2018). Clarification of the current systematics within the genus *Holoparamecus* was an additional product of our research.

MATERIAL AND METHODS

Two new species are described on the basis of five specimens from Baltic and Bitterfeld amber. The material examined is deposited in the following collections:

CCHH private collection of Christel and Hans Werner Hoffeins (Hamburg, Germany), later the specimens will be deposited at the Senckenberg Deutsches Entomologisches Institut (Müncheberg, Germany) as part of the institute's amber collection;

CVIA private collection of Vitalii Alekseev (Kaliningrad, Russia), later the specimen will bedeposited in the Paleontological Institute, Russian Academy of Science (Moscow, Russia) for permanent preservation;

GPIH Geological-Palaeontological Institute and Museum of Hamburg University (Hamburg, Germany), as collection of Carsten Gröhn;

HPR private collection of Hans-Peter Reike (Moritzburg, OT Boxdorf, Germany), later the specimen will be deposited at the collection of the Senckenberg Naturhistorische Sammlungen (Dresden, Germany) [MTD];

WRCN private collection of Wolfgang H. Rücker (Neuwied, Germany);

All photographs were taken using a Nikon SMZ 745T stereomicroscope equipped with a Nikon DS-Fi1 digital camera. Extended depth of field at high magnifications was achieved by combining multiple images from a range of focal planes using Zerene Stacker 1.04 software. The resulting figures were edited using Adobe Photoshop CS8.

The pieces of amber were scanned using synchrotron X-ray microtomography at the tomography station on the electron storage ring BESSY II, Helmholtz-Zentrum Berlin (Görner et al. 2001). Compared to conventional X-ray sources, synchrotron X-ray radiation allows for high-resolution measurements in phase contrast mode. This method is helpful for specimens that contain light elements (for example carbon), and improves the image contrast after the reconstruction of the 3D volume.

The tomography of the amber was performed using 2200 projections and an exposure time of 3 s. The energy of the synchrotron X-ray beam was set to 19 keV using a multilayer Si-W monochromator. The magnification was adjusted to a spatial resolution of 1.1 µm, using a 20 µm-thick CdWO4 scintillator and a pco400 camera (4008 × 2672 pixel). In order to obtain phase information we increased the distance between the sample and the scintillator to 50 mm. The reconstruction of the 3D volume was done using the software Octopus (Vlassenbroeck et al. 2007) and analyzed by the software Volume Graphics (VG) Studio MAX afterwards.

SYSTEMATIC PALAEONTOLOGY

Family Merophysiidae Seidlitz, 1872
Subfamily Holoparamecinae Seidlitz, 1888
Genus *Holoparamecus* Curtis, 1833
Subgenus *Blumenus* Belon, 1887

Remarks. The species under consideration belong to the subfamily Holoparamecinae within Merophysiidae based on a combination of the following characters: (1) hind coxae widely separated, (2) abdomen with 5 visible ventrites, (3) antennal insertions located under the margin of the head, (4) trochanters elongate.

The following characters support attribution to the genus *Holoparamecus*: (1) antennae more than eight-segmented, (2) elytra with one distinct sutural stria. The new species, *H. hoffeinsorum* Reike & Alekseev sp. nov., has a 10-segmented antenna in both sexes with the antennal club consisting of only one segment. Therefore, it evidently belongs to

the subgenus *Blumenus* Belon, 1887. The second species under description, *H. paschalis* Reike & Alekseev sp. nov., is represented by the female only. An indisputable subgeneric assignment was impossible in the case; however, the species was placed in the same subgenus provisionally.

Holoparamecus (*Blumenus*) *hoffeinsorum* Reike & Alekseev sp. nov.
(Figs. 1-2, 5-10, 12, 13)

Type strata. Bitterfeld amber (holotype), Eocene.

Type locality. Germany, Sachsen-Anhalt, Goitzsche (Bitterfeld-Wolfen).

Type material. Holotype: "AWI-132" (♂), adult. Complete beetle is included in a small, transparent amber piece (measurements: 12 × 12 × 5 mm) and preserved without supplementary fixation. Ventral side of the beetle is obscured by a "milky" opacity. Syninclusions: fagacean trichomes, one mite specimen, tiny pieces of dirt; (CVIA) (Figs. 1-2, 9).

Paratype: "117-1" (♀), adult. Complete beetle, included in small-sized yellow amber piece embedded in a block of GTS polyester resin with approximate dimensions of 15 × 10 × 3 mm. The specimen is clearly visible in dorsal and ventral aspect. Syninclusions: fagacean trichomes; (CCHH), (Figs. 5-6).

Paratype: "211-3" (♀), adult. Complete beetle, included in small-sized yellow amber piece embedded in a block of GTS polyester resin with approximate dimensions of 14 × 8 × 4 mm. The specimen is clearly visible in dorsal and ventral aspect. Syninclusions: absent; (CCHH), (Figs. 7-8, 10).

Paratype: "1186" (♀), adult. Complete beetle in a small, transparent amber piece (measurements: 10 × 8 × 5 mm) and preserved without supplementary fixation. Ventral side of the beetle is obscured by a dense "milky" opacity. Syninclusions: fagacean trichomes, one Nematocera (Diptera) specimen; (GPIH), (Fig. 12).

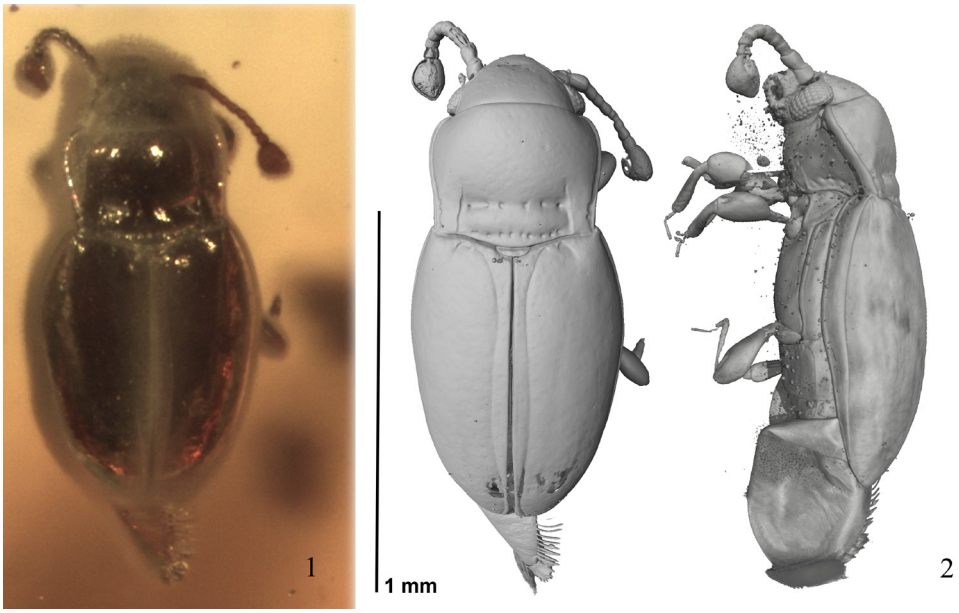
Paratype: "No. 24" (sex unknown), adult. Complete beetle in a small, transparent amber piece (measurements: 13 × 11 × 5 mm) and preserved without supplementary fixation. Ventral side of the beetle is obscured partially by a dense "milky" opacity. Syninclusions: fagacean trichomes, tiny pieces of dirt; (HP)], (Fig. 13).

Remark. In contrast to the holotype, all paratypes originate from Baltic amber of Yantarny settlement (formerly Palmnicken) in Sambian (Samland) Peninsula of the Kaliningrad region (Russia). Four examined specimens are recognized here as one single species.

Description. Holotype: body length 1.2 mm, maximum width 0.54 mm. Body entirely dark brown; elongate, convex dorsally and moderately convex ventrally. Head, pronotum and elytra appear glabrous (but they bear extremely fine and very short, erect setae). Inconspicuous short pubescence for some specimens visible at magnifications above 120×.

Head transverse, evenly convex dorsally; covered with very fine punctures, interspaces between punctures wider than one puncture diameter. Compound eyes large, convex with moderately large and distinct facets; distance between eyes nearly equal to 9× transverse diameter of compound eye. Tempora absent. Antennal insertions located under the margin of head slightly before anterior edge of eyes. Antennae 10-segmented, 0.36 mm long. Scape cylindrical, as long as antennomere 2; antennomere 2 wider than antennomere 3, and 1.5× longer than antennomere 3; antennomere 3 is 1.2× as long as antennomere 4; antennomere 4 is as long as antennomere 5; antennomere 6-9 are as long as wide. Antennal club one-segmented, about 1.2× as long as wide.

Pronotum 0.25 mm long and 0.38 mm wide, broadly rounded, transverse (approximately 0.66× as long as wide). Pronotal disc convex, with moderately sloping sides. Pronotum



Figs. 1-2. *Holoparamecus hoffeinsorum* Reike & Alekseev sp. nov., holotype "AWI-132" (CVIA): 1- photo, dorsal view; 2- phase-contrast synchrotron microtomography renderings (BESSY II, Helmholtz-Zentrum, Berlin), dorsal and lateral views.

slightly narrowed anteriad and posteriad, widest in the anterior third of its length; with one gradual impression limited at sides by two longitudinal sulci and provided with row of foveate punctures posteriorly. Surface of pronotum covered with very fine punctures (similar to punctures on head), distance between punctures more than one puncture diameter. The pronotal base with transverse row of distinct foveate punctures. Lateral pronotal margins rounded, bordered, non-crenulate. Anterior and posterior pronotal margins simple, not bordered. Posterior angles nearly right-angled. Scutellar shield strongly transverse, impunctate.

Pro-, meso- and metaventrites smooth, covered with very fine punctures; distance between punctures larger than two diameters of each point. Pro- and mesocoxae nearly globose, separated by distance almost equal to transverse coxal diameter. Metacoxae elongate, transverse, about 2.5× as wide as long, separated by distance approximately equal to transverse coxal diameter. Metepisternum narrow, with nearly straight lateral margins, about 8× as long as wide.

Elytra 0.65 mm long and 0.54 mm wide (maximum width, both elytra measured together), about 1.21× as long as combined width, oval, convex, widest within anterior third of length, shiny. Base of elytra about as wide as pronotal base. Humeral calli developed. Elytral punctures irregular, very fine (similar to punctures on pronotum), distance between punctures more than one puncture diameter. Sutural stria sharply defined, complete (reaching apical margin of elytra), with two curved indentations anteriorly. Metathoracic wings fully developed, partially exposed in holotype, and bearing fringe of setae distally.

Abdomen with five visible ventrites; smooth. Ventrite 1 longest, punctured like pro-, meso- and metaventrites. Ventrites 2-5 covered with distinctly smaller and sparser punctures than ventrite 1. Relative length ratios of ventrites 1-5 equal to 7-2-2-2-3.

Legs moderately long and narrow. Trochanters elongate. Femora spindle-shaped, thickest at middle and about 2× as wide as tibiae. Tibiae slender, with tibiae and femora approximately equal in length. Tibiae about 2× as long as tarsi. Tarsi with three simple subcylindrical tarsomeres. Tarsomeres 1 and 2 subequal in length; ventral process of pro- and mesotarsomere elongated; tarsomere 3 about 1.4-2.0× longer than tarsomeres 1-2 combined. Claws simple, small and thin.

Aedeagus simple, 0.15 mm long and 0.05 mm wide (Fig. 9), internal structures not visible.

Female genitalia (paratype "211-3" (CCHH) see Fig. 10).

Variability. Paratypes (Figs. 5-8, 10, 12, 13). Body length: "1186" (GPI) - 1.26 mm, "117-1" (CCHH) - 1.06 mm, "211-3" (CCHH) - 1.01 mm, "24" (HPR) - 1.20 mm. Otherwise, all paratypes are similar in all visible morphological characters to holotype. Paratype "211-3" has undetermined mite underneath elytra (Fig. 8).

Differential diagnosis. Examination of genital features is necessary for adequate placement of a species within *Holoparamecus*. Intersexual differences in antennomere numbers are known for representatives of the genus. It was shown by virtual dissection, that both sexes of the new species uniformly possess 10-segmented antennae. The antennal club consists of only one enlarged segment, leading to placement of the new species in the subgenus *Blumenus* Belon, 1887.

New species from Baltic amber clearly differs from *H. gabrielae, H. pumilus* and *H. johnsoni* in having eyes (the Recent species mentioned are eyeless). Two other Recent species, *H. lanatus* and *H. villiger*, can be easily distinguished from the new species by the long hairs on the elytra (whereas the dorsum of *H. hoffeinsorum* Reike & Alekseev sp. nov. is inconspicuously pubescent). Additionally, *H. hoffeinsorum* Reike & Alekseev sp. nov. differs from *H. lanatus* and *H. villiger* in the body shape and in the form of male genitalia.

Note. The newly described species is found in Bitterfeld and in true Eastern (Sambian) Baltic amber. The differences in body size between specimens (intraspecific variation consists 1.01-1.26 mm) have no species-specific value, therefore all specimens were considered conspecific and assigned to a single extinct species herein.

Etymology. The epithet of the new species is dedicated to the collectors of most specimens of the type series and outstanding experts in amber inclusions Christel and Hans-Werner Hoffeins.

Holoparamecus (*Blumenus*) *paschalis* Reike & Alekseev sp. nov.
(Figs. 3-4, 11)

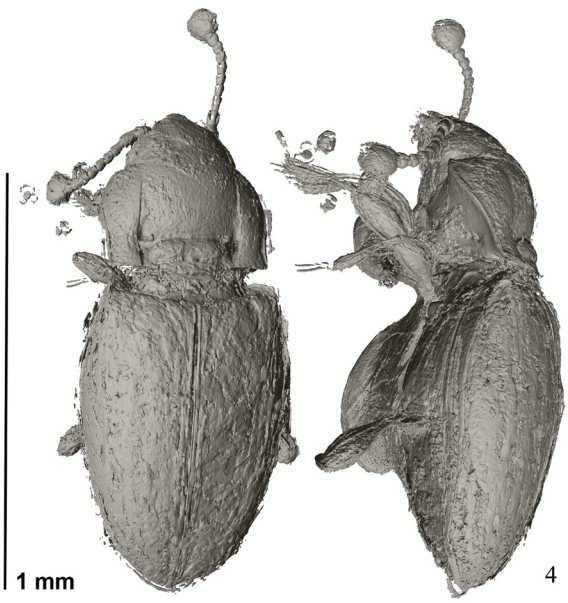
Type strata. Baltic amber, Eocene.

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

Type material. Holotype: "747-6 (♀), adult. Complete beetle, included in small-sized yellow amber piece embedded in a block of GTS polyester resin with dimensions of 15 × 10 × 5 mm. The specimen is clearly visible in dorsal aspect, ventral side of the beetle is obscured by a "milky" opacity. Syninclusions: absent; (CCHH - now HPR), (Figs. 3-4, 11).

Description. Holotype: body length 1.14 mm, maximum width 0.51 mm. Body entirely dark brown; elongate, convex dorsally and moderately convex ventrally. Head, pronotum and elytra appear glabrous and hairless. No pubescence visible at magnifications up to 120×.

Head transverse, evenly convex dorsally; covered with very fine punctures, interspaces between punctures wider than one puncture diameter. Compound eyes large, convex with moderately large and distinct facets; distance between eyes nearly equal to 9× transverse diameter of compound eye. Tempora absent. Antennal insertions located under margin of head, slightly before anterior edge of eyes. Antennae 10-segmented, 0.32 mm long. Scape cylindrical, as long as antennomere 2; antennomere 2 wider than antennomere 3, and 1.2× longer than antennomere 3; antennomere 3 is 1.4× as long as antennomere 4; antennomere



Figs. 3-4. *Holoparamecus paschalis* Reike & Alekseev sp. nov., holotype, "747-6" (CCHH - now HPR): 3- photo, dorso-lateral view; 4- phase-contrast synchrotron microtomography renderings (BESSY II, Helmholtz-Zentrum, Berlin), dorsal and lateral views.

4 is as long as antennomere 5; antennomere 6-8 are as long as wide, antennomere 9 is 1.6× wider than long. Antennal club one-segmented, about 1.2× as long as wide.

Pronotum 0.3 mm long and 0.4 mm wide, broadly rounded, transverse (approximately 0.75× as long as wide). Pronotal disc convex, with moderately sloping sides. Pronotum slightly narrowed anteriad and parallel posteriad, widest in middle of its length; with one gradual impression limited at sides by two longitudinal sulci and without row of foveate punctures posteriorly. Surface of pronotum covered with very fine punctures (similar to punctures on head), distance between punctures more than one puncture diameter. Pronotal base with transverse row of four distinct foveate punctures. Lateral pronotal margins rounded, bordered, non-crenulate. Anterior and posterior pronotal margins slightly bordered. Posterior angles nearly right-angled. Scutellar shield strongly transverse, impunctate.

Structure and details of pro-, meso- and metaventrites not visible.

Elytra 0.69 mm long and 0.51 mm wide (maximum width, both elytra measured together), about 1.35× as long as combined width, oval, convex, widest within anterior third of length, shiny. Base of elytra about as wide as pronotal base. Humeral calli developed. Elytral punctures irregular, very fine (similar to punctures on pronotum), distance between punctures more than one puncture diameter. Sutural stria sharply defined, complete (reach apical end of elytra), with two embayments anteriorly. Metathoracic wings fully developed, bearing fringe of setae distally.

Abdomen with five visible ventrites; structure and details not visible. Ventrite 1 longest. Relative length ratios of ventrites 1-5 equal to 5.5-2-2-2-2.

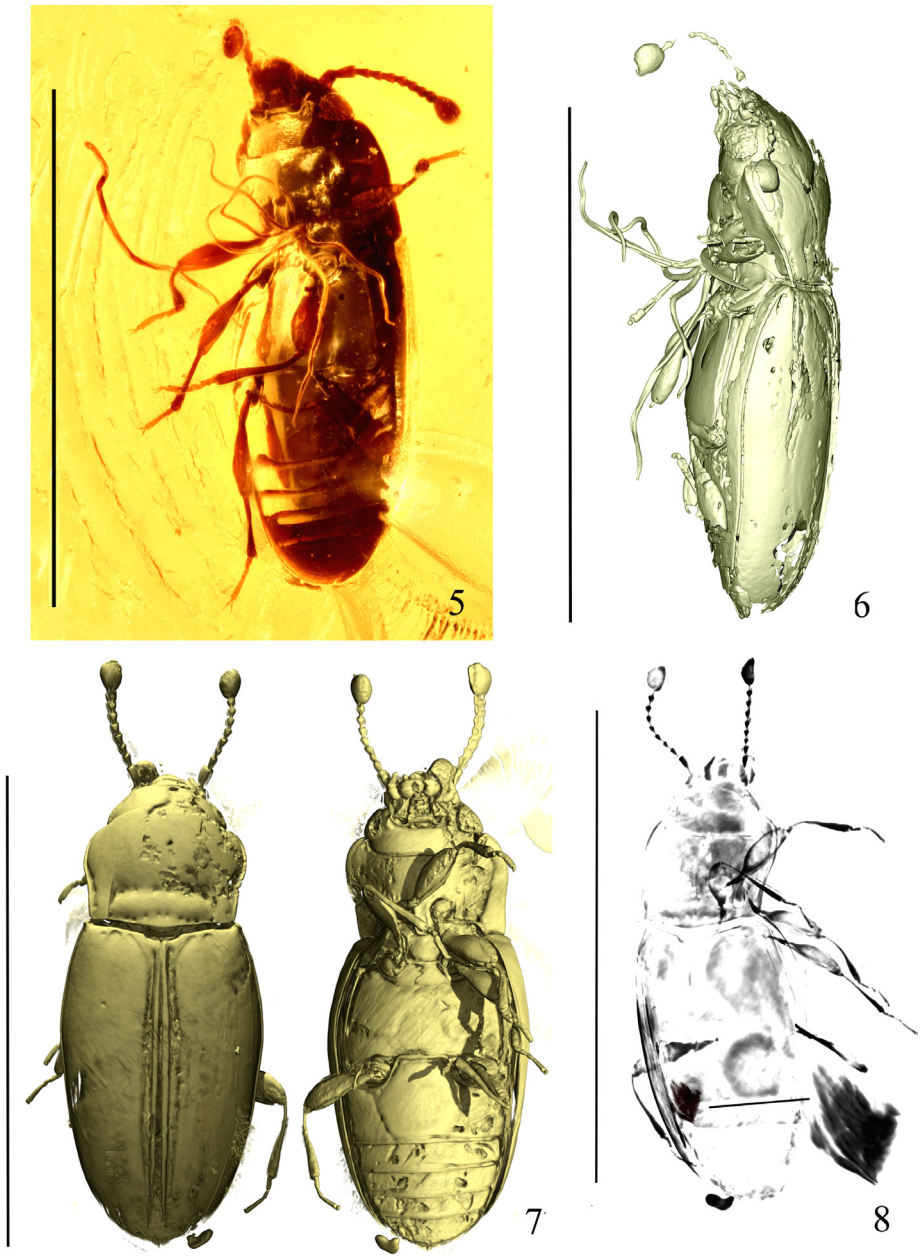
Legs moderately long and narrow. Trochanters elongate, nearly thickest at middle and about 2× as wide as tibiae. Tibiae slender, with tibiae and femora approximately equal in length. Tarsi with three simple subcylindrical tarsomeres. Tarsomeres 1 and 2 subequal in length; ventral process of pro- and mesotarsomere elongated; tarsomere 3 about 1.4-1.8× longer than tarsomeres 1-2 combined. Claws simple, small and thin.

Female genitalia detailed in Fig. 11.

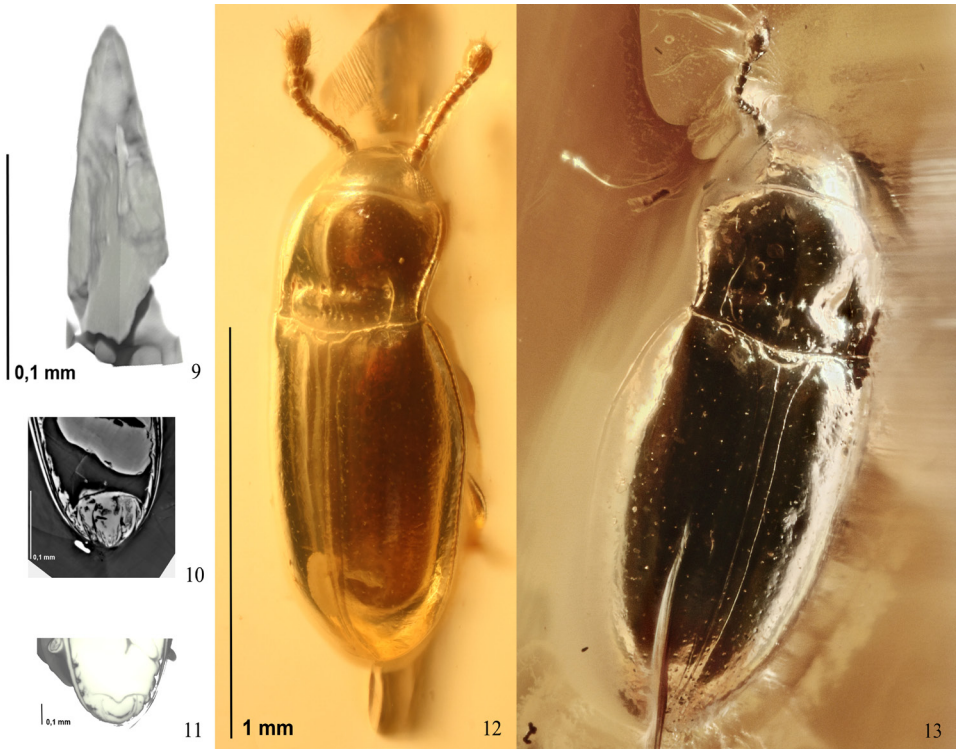
Differential diagnosis. The antennal club consists of only one enlarged segment, and the beetle has 10-segmented antenna, which leads to placement of the new species in the subgenus *Blumenus* Belon, 1887.

The new species from Baltic amber clearly differs from *H. gabrielae, H. pumilus* and *H. johnsoni* in having eyes (the Recent species mentioned are eyeless). Two other Recent species, *H. lanatus* and *H. villiger*, can be easily distinguished from the new species based on the long hairs on the elytra (whereas the dorsum of *H. paschalis* Reike & Alekseev sp. nov. is shiny). *H. paschalis* Reike & Alekseev sp. nov. differs from *H. hoffeinsorum* Reike & Alekseev sp. nov. in the shape of the pronotal impression, the elytral pubescence and the form of the antenna.

Etymology. The specific epithet “paschalis” is the subjective derived from the Latin word “pascha” (Easter, Resurrection Sunday), referring to the “resurrection of beetle from the dead”, to the time of species description (April 2019), and to the egg-shaped form and colour of the beetle (like an Easter egg).



Figs. 5-8. *Holoparamecus hoffeinsorum* sp. nov., paratypes: 5- paratype "117-1" (CCHH), ventrolateral habitus; 6- paratype "117-1" (CCHH), phase-contrast synchrotron microtomography renderings (BESSY II, Helmholtz-Zentrum, Berlin); 7- paratype "211-3" (CCHH), phase-contrast synchrotron microtomography renderings (BESSY II, Helmholtz-Zentrum, Berlin): lateral and ventral views; 8- paratype "211-3" (CCHH), habitus phase-contrast synchrotron microtomography renderings (BESSY II, Helmholtz-Zentrum, Berlin): undetermined mite under the elytra (the black line indicate its position). Scale bars = 1 mm.



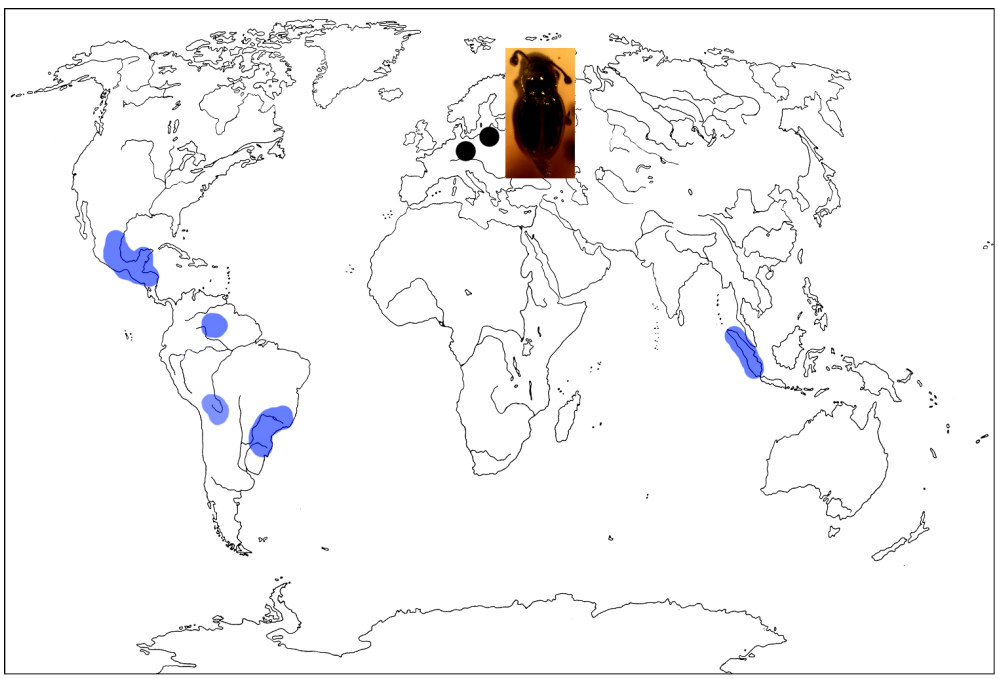
Figs. 9-13. *Holoparamecus* spp.: 9- *H. hoffeinsorum* Reike & Alekseev sp. nov., aedeagus in ventral view, "AWI-132"; 10- *H. hoffeinsorum* Reike & Alekseev sp. nov., female genitalia, paratype "211-3" (CCHH); 11- *H. paschalis* Reike & Alekseev sp. nov., female genitalia, holotype "747-6" (CCHH - now HPR); 12- *H. hoffeinsorum* Reike & Alekseev sp. nov., paratype"1186" (GPIH), habitus in dorsolateral view; 13- *H. hoffeinsorum* Reike & Alekseev sp. nov., paratype"24" (HPR), habitus in dorsal view.

DISCUSSION

Systematic notes. An interesting and thoroughly figured paper providing a revision of Neotropical beetles related to *Holoparamecus* was recently published (Arriaga-Varela et al. 2018). Six new species were described: one of them was assigned to the genus *Lycoperdinella* Champion, 1913 and five were placed into the new genus *Rueckeria* Arriaga-Varela, Tomaszewska, Huo & Seidel, 2018. However, the generic placement of these beetles should be corrected. The genus *Holoparamecus* varies in different characters and includes quite heterogeneous species, arranged in seven subgenera. A key to the known subgenera of *Holoparamecus* (adopted after Dajoz 1975) is provided below:

Fig. 14. Specimen compared with holotype of extant *H.* (*Blumenus*) *villiger* (Belon, 1887), dorsal view (photo: W. H. Rücker).

Fig. 15. Distribution of extant species belonging to the subgenus *Blumenus* Belon (blue area) and Eocene fossil records in Bitterfeld and Baltic amber (black dots).



(1) Antennal club consists of only one segment 2
- Antennal club consists of two segments 3
(2) Antenna 9-segmented in both sexes ..... *Microparamecus* Dajoz, 1967
- Antenna 10-segmented in both sexes ..... *Blumenus* Belon, 1887
(3) Antenna 9-segmented (male) or 10-segmented (female) ..... *Holoparamecus* s. str. Curtis, 1833
- Antennae of male and female have more antennal segments 4
(4) Antenna10-segmented in male and 11-segmented in female ..... *Tocalium* Motschulsky, 1867
- Antenna 11-segmented in both sexes 5
(5) Elytron with sutural line strongly reduced ..... *Tomyrium* Reitter, 1880
- Elytron with sutural line distinct and well-developed 6
(6) Sutural line long (reaching at least apical third of elytron ..... *Calyptobium* Aubé, 1843
- Sutural line shorter than two thirds of elytral length ..... *Neoparamecus* Dajoz, 1975

The morphological characteristics mentioned as distinctive genus-level characters in Arriaga-Varela et al. (2018) for the genus *Rueckeria* also occur in the different *Holoparamecus* species within the subgenus *Blumenus* Belon, 1887 and cannot separate the recently erected genus from the subgenus *Blumenus*. Characters such as "bordered pronotal margins" are also present in taxa such as *H. baliensis* Reike, 2018, or *H. villiger* (Belon, 1887); postcoxal lines on the ventrite are known in *H. baliensis* Reike, 2018; and a 10-segmented antenna is typical for all representatives of the subgenus *Blumenus*. Apparently, the character states connected with "pronotal margin", "form of terminal antennomere", "postcoxal lines", and "humeral denticle" can gradually vary and should be used maximally for intra-generic diagnostic goals in Holoparamecinae and related beetles.

Additionally, the photo of a specimen compared with the holotype of *H*. (*Blumenus*) *villiger* (Belon, 1887) (coll. WRCN, det. Johnson, 1980, comp. with holotype by Rücker, 2006) showed the well-developed crenulation of pronotal margins (Fig. 14). This character (i.e., more or less strongly developed crenulation) is mentioned as a genus-level feature for the separation of *Holoparamecus*, *Rueckeria* and *Lycoperdinella* (Arriaga-Varela et al. 2018). However, the representatives of *Blumenus* can also possess such crenulation. Moreover, the identity of *L. boliviensis* Arriaga-Varela, Tomaszewska, Huo & Seidel, 2018 and *Holoparamecus villiger* should be reassessed (details below).

Based on the explanations above, it seems to be relevant to conclude:

1. The genera *Rueckeria* and *Lycoperdinella* should be synonymized with the subgenus *Blumenus.*

2. *Lycoperdinella boliviensis* is conspecific with *Holoparamecus* (*Blumenus*) *villiger*, and these species should be synonymized. The drawing and the description of *Holoparamecus* (*Blumenus*) *villiger* Belon 1887 in Dajoz (1975) includes many errors compared with the holotype. Within the description of Belon (1887) nothing is written on the number of eye-facetts or about the structure of the pronotal margin etc. The studied specimen has well-developed wings and eyes, long pubescence on the elytra and well-developed crenulation of pronotal margins.

The subgenus *Blumenus* Belon, 1887 within *Holoparamecus* Curtis, 1833 currently includes two extinct species and 11 extant species. New combinations resulting from the proposed new generic synonymy for *Rueckeria* and *Lycoperdinella* and transfer of species into *Blumenus* are also listed below.

LIST OF THE SPECIES PLACED IN THE SUBGENUS *BLUMENUS* BELON, 1887, IN ALPHABETIC ORDER

Type species: *Holoparamecus* (*Blumenus*) *villiger* (Belon, 1887)

1. *H.* (*B.*) *gabrielae* Rücker, 2003 (Mexico)
2. *H. (B.) hoffeinsorum* Reike & Alekseev **sp. nov.** (Europe: Bitterfeld and Baltic amber)
3. *H.* (*B.*) *inecol* (Arriaga-Varela, Tomaszewska, Huo & Seidel, 2018) **comb. nov.** (Mexico)
4. *H.* (*B.*) *johnsoni* Rücker 1981 (Brazil)
5. *H.* (*B.*) *lanatus* Rücker, 1985 (Indonesia: Sumatra)
6. *H.* (*B.*) *nigrileonis* (Arriaga-Varela, Tomaszewska, Huo & Seidel, 2018) **comb. nov.** (Mexico)
7. *H.* (*B.*) *ocelotl* (Arriaga-Varela, Tomaszewska, Huo & Seidel, 2018) **comb. nov.** (Mexico)
8. *H. (B.) paschalis* Reike & Alekseev **sp. nov.** (Europe: Baltic amber)
9. *H.* (*B.*) *puma* (Arriaga-Varela, Tomaszewska, Huo & Seidel, 2018) **comb. nov.** (Mexico)
10. *H.* (*B.*) *pumilus* Sharp, 1902 (Mexico)
11. *H.* (*B.*) *skelleyi* (Arriaga-Varela, Tomaszewska, Huo & Seidel, 2018) **comb. nov.** (Mexico)
12. *H.* (*B.*) *subcaecus* (Champion, 1913) **comb. nov.** (Guatemala)
13. *H.* (*B.*) *villiger* (Belon, 1887) [= *Lycoperdinella boliviensis* Arriaga-Varela, Tomaszewska, Huo & Seidel, 2018 **syn. nov.**] (Brazil, Bolivia)

Below we propose a new, simplified identification key for all currently known species of the subgenus *Blumenus*.

(1) Eyeless species ..... *B. gabrielae, pumilus* and *B. johnsoni*
- Species with eyes developed 2
(2) Elytra with long erect pubescence ..... *B. villiger*, *B. lanatus* and *B. subcaecus*
- Elytral pubescence short or indistinct 3
(3) Transverse pronotal basal impression with deep and large punctures 4
- Transverse pronotal basal impression without deep and large punctures 5
(4) Longitudinal pronotal sulci short, not reaching pronotal middle ..... *B. hoffeinsorum*
- Longitudinal pronotal sulci longer than pronotal mid-length ..... *B. puma*
(5) Longitudinal pronotal sulci three-quarters of pronotal length 6
- Longitudinal pronotal sulci less than three-quarters of pronotal length ..... *B. nigrileonis*, *B. skelleyi* and *B. inecol*
(6) Lateral pronotal margins distinctly crenulate ..... *B. ocelotl*
- Lateral pronotal margins non-crenulate ..... *B. paschalis*

Ecological and distributional notes. The distribution of the subgenus *Blumenus* is mapped in Fig. 15. The reports of extant species belonging to the subgenus (Belon 1887; Sharp 1902; Rücker 1981, 1985, 2003; Arriaga-Varela et al. 2018) are restricted to Neotropical (Brazil, Bolivia, Mexico) and Oriental (Sumatra) Regions. The new record of *Holoparamecus* (*Blumenus*) *hoffeinsorum* Reike & Alekseev sp. nov. and *H.* (*Blumenus*) *paschalis* Reike & Alekseev sp. nov. from Baltic and Bitterfeld amber indicates the presence of the subgenus in the Palaearctic Region during the Eocene. The occurrence of this taxon, which apparently prefers warm and humid tropical climate in its recent distribution, in Baltic amber supports

the inference of higher thermal values prevailing during the times of "amber forest" growth in Eocene Europe (Alekseev & Alekseev 2016; Bukejs et al. 2016). However, it is hard to evaluate the phylogenetic value of the characters used within the current *Holoparamecus* subgeneric classification. Single characters, such as a similar antennal structure in very distantly distributed (Sumatra and Brazil!), tiny, and insufficiently studied species could also be the result of simple convergent adaptation in different evolutionary lineages. The distributional vectors in the past and any conclusions concerning the subgenera of *Holoparamecus* can only be hypothesized with great caution given our current knowledge. However, the Neotropical affinity of the newly described species from Baltic amber appears to be better supported.

Extant *Holoparamecus* species are typically mycetophagous, mostly feeding on spores and hyphae of micro-fungi. The representatives of the genus inhabit leaf litter and bird nests, while some species feed on the molds of stored grains (Shockley et al. 2009b), or may be associated with bat guano (Rücker 2003). For the fossil species, a similar biology in the Eocene forest habitats can be assumed (i.e., dwelling in forest litter and soil, and perhaps also tree holes or subcortical spaces under loosened bark).

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