A new coleopterous family Wabbelidae fam. nov. (Coleoptera: Cucujoidea) from Baltic amber (Cenozoic, Paleogene, Eocene)

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An unknown peculiar beetle from Tertiary Baltic amber, Wabbel cerebricavus gen. et sp. nov. designated to a new family, is described and illustrated. The new family, Wabbelidae fam. nov., is diagnosed and assigned to the superfamily Cucujoidea. The new family can be identified by the thick moniliform antennae, modified (deeply concave) frons and vertex, longitudinally strigose pronotum with pair of basal grooves, wide gula with complete gular sutures, pentamerous non-lobed tarsi, seriate punctuation of elytra, and dorsally non-flattened body.

Key words: taxonomy, fossil resin, new family, Polyphaga, Cucujiformia

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INTRODUCTION

Baltic amber is comparatively young (as compared with inclusions from Burmese, Lebanese, Spanish, and other Cretaceous amber deposits) and includes almost modern insect fauna at the family level. The most dramatic changes in insect fauna took place before Cainozoic (Zherikhin 1978), the last major extinction of insects was in the early Cretaceous, and the rate of extinct lineages of family rank from Eocene is low.

New insect families from Baltic amber were established in different orders. At least fifteen insect families are known: Protoxenidae in Strepsiptera (Pohl et al. 2005), Weitschatiidae in Hemiptera (Koteja 2008), Ogmomyidae in Trichoptera (Wichard 2013), Elektraphididae in Homoptera, Catastylidae and Palpigeridae in Collembola (according to Zherikhin 1970), Babidae in Ephemeroptera (Kluge et al. 2006), Yantarocentridae in Trichoptera (Ivanov & Melnitsky 2016), Hoffeinsmyiidae in Diptera (Michelsen 2009), and Paleomelittidae (Engel 2001), Pelecinopteridae (Zherikhin 1970), and Electrotomidae (Rasnitsyn 1977) in Hymenoptera. Three new coleopteran families were described based on the material from Baltic amber: (1) Berendtimiridae, a family with the monotypic genus Berendtimirus Winkler, 1987; (2) Electrapatidae, at present considered to be of the tribe Electrapatini Iablokoff-Khnzorian, 1962, belonging to the family Schizopodidae LeConte, 1859; (3) Circaeidae
In the present paper the description of a new enigmatic taxon of beetles discovered in Baltic amber is provided. The inclusion cannot be assigned to any extant family and therefore is placed in a new genus and new family based on a combination of peculiar external morphological characteristics.

MATERIAL AND METHODS

The examined material for the study consists of a single specimen (holotype) originating from the private collection of Christel and Hans Werner Hoffeins (Hamburg, Germany) [CCHH]. The holotype will be deposited in the collection of Senckenberg Deutsches Entomologisches Institut in Müncheberg (Germany) [SDEI]. The amber piece was prepared manually and embedded in a block of polyester resin (Hoffeins 2001). Photographs were taken with a Zeiss AxioCamICc 3 digital camera mounted on a Zeiss Stemi 2000 stereomicroscope. Measurements were taken with the ocular micrometer of the stereomicroscope. Reconstructions were based on free-hand drawings made during the examination of the original specimen. Figures were edited using Adobe Photoshop CS8 software.

SYSTEMATIC PALAEONTOLOGY

Genus Wabbel gen.nov.

Type species. Wabbel cerebricavus sp. nov.

Composition. The new genus is monotypic, represented by the type species only.


Derivatio nominis. The generic name of new taxon is derived from the word “Wabbel” (or “Wabel”), i.e. “beetle” in the low Prussian dialect of German language.

Note: Unfortunately, morphology of genitalia, wings venation, and wing folding are not accessible in the studied fossil specimen and cannot be seen.

Wabbel cerebricavus sp. nov. (Figs. 1-6)

Material examined. Holotype No. 1615-4 [CCHH], imago, sex unknown. Inclusion in a small yellow amber piece, embedded in a block of GTS polyester resin measuring 10 x 9 x 6 mm. Syninclusions are absent.

Type strata: Baltic Amber. Upper to mid-Eocene.
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Type locality: Baltic Sea coast, Yantarny settlement [formerly Palmnicken], Sambian (Samland) peninsula, Kaliningrad region, Russia.

Diagnosis. As stated for the new genus (vide supra).

Description. Habitus. Total body length 4.2 mm, maximal body width 1.6 mm. Elongate-ovate, moderately convex dorsally and subflattened ventrally, entirely black.

Head. Subquadrate; prognathous, not retracted into pronotum, finely punctate, not constricted behind eyes. Frons and vertex exceptionally deep concave, forming a hole in the basal median third of head. Clypeus dull, longitudinally triangular with angle directed basally, sharply separated, slightly convex. Gular sutures well
separated, entire; gula wide, smooth. Genae projecting forwards, knobbed in front of eyes. Temples 2.5 x longer than diameter of eye, bearing a brush of long, dense, brown hair. Compound eyes small, round, entire, without interfacetal setae, not prominent, coarsely facettated (in each eye about 50 facets). Maxillary palps 4-segmented; first and third palpomeres short and transverse; second palpomere longitudinal and 3 x longer than palpomere 1 or 3; terminal palpomere cylindrical, apically rounded, being the longest. Ratio of palpomeres 1:3:1.4. Antennal insertions exposed in dorsal view; distantly in front of eyes; separated from each other by a distance narrower than the distance between eyes, but wider than the first antennomere length. Antenna with 11 freely articulating antennomeres, moniliform, nearly uniform in width, thick, not flattened, extending to elytral basis. Scape conical, pedicel and antennomeres 3-9 slightly transverse, antennomere 10 subquadrate, antennomere 11 slightly longitudinal, truncate. All antennomeres with irregularly long (sometimes longer than length of segment), thick, black, sparse, semierect hairs.

Thorax. Pronotum transverse (in dorsal view about 0.69 times as long as its median length), slightly narrower than elytral base, finely bordered laterally and basally. Anterior margin straight, posterior margin gradually arcuate; lateral margins weakly rounded. Posterior angles rectangular, anterior angles slightly protruding forwards, rounded. Pronotal surface covered with irregular, dense and coarse punctures medially; with rased punctures laterally. Pronotal pubescence long, accumbent, brown; directed forwards in anterior margin. Pronotum longitudinally stribose in apical and central part (nearly 20 fine keels); with two symmetrical, deep, longitudinal, tear-shaped grooves basally. Procoxa separated. Prosternal process slightly extended beyond procoxal cavities, elongate, gradually dilated apically, truncate, wider than the shortest procoxal diameter. Notosternal suture complete. Hypomeron with dense, large, and rounded punctures. Prosternum in front of coxal cavities with fine lines directed forward and accumbent long hairs. The ratio of lengths of prothorax to mesoventrite to metaventrite to abdomen is 4.5:1.0:4.5:11.5. Metaventrite without transverse suture, distinctly shorter than the prothorax and mesoventrite combined. Metepimeron meeting anterior angle of ventrite 1. Scutellar shield strongly transverse, pentagonal with rounded angles. Elytra evenly convex; elongate oval in dorsal outline; concealing abdominal apex; separately rounded apically; with widely flattened lateral margins and apices; finely punctate; shiny. Elytral punctures small, bearing short hairs, arranged in striae, shallower on disc, becoming confused apically. Each elytron with 18 rows of fine punctures (formed by strial and interstrial punctuation equal in size), 4 rows in basal third with distinctly enlarged 8-10 punctures bearing erect hairs, 4 x as long as interval between strial punctures. All elytral intervals flat. Epipleura well developed, wide, reaching apex, without cavities. Metathoracic wings fully developed, partially exposed in the holotype specimen.

Abdomen. With five visible, similarly articulated, finely and densely punctured, finely pubescent ventrites. Relative lengths (medially) of ventrites 1, 5 equal to 3.5-1.7-1.7-1.5-3.0. Intercoxal process of abdominal ventrite 1 widely triangular and acute. The first ventrite is approximately as long as the second when measured without process. Femoral lines absent.

Legs. Moderately developed. Trochantins not visible. Pro- and metacoxal cavities closed, mesocoxal cavities open. All coxae separated: procoxae separated by a distance slightly wider than the minimal procoxal diameter by the prosternal process; mesocoxae narrowly separated; meso-metaventral junction without metaventral knob; metacoxae separated by a distance approximately 2 x the coxal diameter with wide triangular process of ventrite 1. Procoxae transverse, 2 x as long as wide; mesocoxae nearly round. Metacoxae transverse, do not extend laterally to meet the elytra.
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Fig. 3. *Wabbel cerebricavus* gen. et sp. nov. Head and pronotum.

Fig. 4. *Wabbel cerebricavus* gen. et sp. nov.: A - Abdomen, thorax and head ventrally; B - Meso-, metathorax and abdomen (schematically).
Trochanters of all legs large, completely separating femora and coxae. Femora subflattened, simple. Tibiae slightly shorter than femora; with longitudinal keels; pubescent; shortly setose apically, without crenulation, denticles, or spines. Tarsomeres lobed. Tarsi shorter than tibiae, pubescent below. Length of apical tarsomere subequal to combined length of tarsomeres 2-4; tarsomeres 1-4 cylindrical, almost equal in size. Tarsal claws equal in size, thin, simple, length about one third of apical tarsomere.

Derivatio nominis. The specific epithet refers to the very peculiar concave form of frons and vertex. It is formed after the Latin “cerebrum” (brain, brainpan) and “cavus, -a, -um” (empty, hollow, concave).

The new genus exhibits a unique combination of characteristics warranting its recognition as a new family. Further investigations by X-ray micro-computed tomography (micro-CT) could help to study internal features in this specimen and may add data on the systematic placement of the taxon. If additional conspecific or congeneric specimens will be found in Baltic amber material in the future, this can be useful for understanding the position of the taxon in the system of Coleoptera, too. At the moment, it is proposed to establish the new family Wabbelidae fam. nov. based upon the monotypic genus Wabbel gen. nov. and to place this family in the system as follows:

Order Coleoptera Linnaeus, 1758
Suborder Polyphaga Emery, 1886
Series Cucujiformia Lameere, 1938
Superfamily Cucujoidea Latreille, 1802
Family Wabbelidae fam. nov.

Type genus. Wabbel gen. nov.

Composition. The new family is proposed for one generic group only, consisting of the one new species Wabbel cerebricavus sp. nov. from Baltic amber.

Description. The new family includes one genus and one species as described above in detail. The list of the most important (Leschen et al. 2005) characteristics can be summarized as follows: Body form oblong, head prognathous, metacoxae not meeting edges of elytral epipleura, metepimeron meeting anterior angle of ventrite 1, metaventrite shorter than prothorax and mesoventrite combined, tarsi not lobed, tarsal formula 5-5-5, metaventrite without transverse suture, basal ventrite free, antennal insertions not concealed, protibiae simple (without crenulation, denticles, or spines), procoxal cavities closed, mesocoxal cavities open, metacoxal cavities closed, procoxae strongly transverse, head without subocular antennal grooves, elytra not truncate and concealing abdominal apex, ventrite 1 without femoral lines, pronotum without sublateral carinae, elytra without ridges, antennae 11-segmented with antennal club indistinct, epipleuron without deep cavity, procoxal cavities without narrow lateral slits, prosternal process wider than the shortest diameter of a procoxal cavity, head without postocular constriction, genae projecting forward, elytral punctuation seriate, mesocoxal cavities narrowly separated.

Diagnosis. First ventrite undivided by metacoxae and prothorax without notopleural sutures. These findings suggest placement of Wabbelidae fam. nov. in the suborder of Polyphaga, excluding a relationship of the new taxon to Rhysodidae (fairly similarly thick moniliform antennae, 5-segmented tarsi, small eyes, dorsal surface of head with grooves and lobes). Not strongly projecting procoxae exclude a possible membership of Staphylinoidea with similarly formed tarsi and antennae. The appendages’ morphology (antennae, legs) and some other habitual characteristics (e.g. elytral punctuation) do resemble those of the families Jacobsoniidae Heller, 1926 and Ptinidae Latreille, 1802 from the series Bostrichiformia.
Figure 5. *Wabbel cerebricavus* gen. et sp. nov. Habitus dorsally, reconstruction.

Jacobsoniidae can be recognized by a minute, narrowly elongate body, an elongate prothorax, lack of a visible scutellum, and a markedly elongate metaventrite (at least 2.5 x as long as mesoventrite), combined with a relatively short abdomen and extremely slender metepisterna, which are potential synapomorphies of the family (Löbl & Burekhardt 1988; Lawrence & Leschen 2010; Bi et al. 2015; Cai et al. 2016). Additionally, all known modern Jacobsoniidae have antennal insertions concealed from above and a pronotal disc without paired basal impressions (Lawrence & Leschen 2010). The characteristics of *Wabbel* gen. nov. representing Wabbelidae fam. nov., i.e. comparatively short metaventrite, distinct transverse scutellum, metepisterna not slender, abdomen not shortened, paired pronotal impressions, and dorsally exposed antennal insertions, exclude the beetle from the systematical vicinity of apparently similar Jacobsoniidae.
In addition, *Wabbel* gen. nov. is similar to some members of the subfamily Ptininae by the widely separated metacoxae without coxal plates, by the open mesocoxae, by the hidden trochanters, by the long femora, by the non-clubbed antennae, by the legs with pentamerous tarsi and the terminal tarsomere being the longest, by the separation of procoxae by prosternal process (present in numerous genera of spider-beetles), and by the triangular clypeal form. The reasons to exclude the Ptinidae from possible groups to which the new taxon can be assigned are the following: *Wabbel* gen. nov. has a large head with long temples and gula, whereas Ptininae have a head moderately deflexed downwards and constricted in pronotum (Mynhardt & Philips 2013); in Ptininae the antennal insertions are closely together between eyes (Belles 1978; Philips 2000), whereas the antennal insertions in *Wabbel* gen. nov. are moderately wide, separated from each other and from eyes; *Wabbel* gen. nov. has prothoracic lateral margins, whereas in ptinids such structure is absent (Mynhardt & Philips 2013); in Ptininae the first 3 ventrites are connate while ventrite 4 is often reduced (Philips 2000), whereas the new taxon has basal ventrites with complete sutures and nearly equal in length; in contrast to the newly described taxon, ptinids have open procoxal cavities (Philips 2000). To the author’s opinion, the attempt to assign the new genus to Jacobsoniidae or Ptininae (Ptinidae) would destroy the modern concepts of these taxa. The new genus has a highly specialized head, whereas specialization in ptinids (and, possibly, in the whole bostrichoid lineage) is connected with different pronotal modifications. The trend towards integration of the head and prothorax in a single unit in Ptininae and the apparent absence of such integration in *Wabbel* gen. nov. are an important obstacle to evolutionary relation. The antennal form in Ptininae and Jacobsoniidae distinctly varies between the genera (moniliform in *Sarothrias*, distinctly clubbed in *Derolathrus* and *Saphophagus*) and species of one genus (e.g., *Polyplocotes* Westwood 1869 has antennae with compressed, widened, or reduced segments in different species). A similar antennal form may be observed in several unrelated coleopteran myrmecophiles while the number and form of antennal segments may vary within one genus (Lawrence & Reichardt 1969; Bell & Philips 2009). Thus, such characters are not of paramount importance. The more important dissimilarities between Wabbelidae fam. nov., Ptinidae, and Jacobsoniidae are listed above.

The not concealed head without a median ocellus, not excavated metacoxae without vertical posterior face, absent metacoxal plates, not approximated antennal insertion, not truncate elytra, tarsal formula 5-5-5, simple claws, well-developed intercoxal process of first abdominal ventrite, and long antennae allow for tentatively placing *Wabbel* gen. nov. among Cucujoidea.

This superfamily includes 25 recent families and remains difficult to characterize owing to the phenotypic heterogeneity exhibited in this group. There are no characteristics that unite all the families of Cucujoidea as the superfamily is characterized by the following combination of features only (Robertson et al. 2015): Adults with procoxal cavities internally open (mostly), tarsal formula 5-5-5 in female and 5-5-5 or 5-5-4 in male animals (rarely 4-4-4). However, it has not been possible to definitely assign the taxon to any known family of the superfamily.

The new family Wabbelidae fam. nov. is compared with all families of the superfamily in consecutive order as the new taxon obviously differs from: Passandridae by the open mesocoxal cavities and by the not parallel-sided body form; Helotidae by the metaventrite without transverse complete suture and by the transverse procoxae; Nitidulidae, Kateretidae, and Monotomidae by the absence of an antennal club and by not exposing the pygidium; Laemophloeidae by the pronotum without sublateral carinae and by elytra without longitudinal ridges;
Protocucujidae by the simple non-lobed tarsomeres;
Smicripidae by the 5-segmented tarsi;
Silvanidae by the absence of lobed tarsomeres and by the transverse fore coxae;
Sphindidae by the absence of an antennal club and by a tubercle or cavity on the mandible;
Cyclaxyridae by the elonget, not strongly convex body and by the absence of a deep cavity on the epipleuron;
Hobartiidae by the non-clubbed antennae;
Tasmosalpingidae, Lamingtoniidae, and Phloeostichidae by the closed procoxal cavities;
Cucujidae by the markedly convex dorsal surface;

Cavognathidae by the absence of narrow lateral slits on the procoxal cavities, the frons without deep pits, and the closed procoxal cavities;
Myraboliidae by the absence of slits on the procoxal cavities, the body form not flattened and parallel-sided, and the non-3-segmented club;
Agapythidae by the prosternal process wider than the shortest diameter of a procoxal cavity and by the head without a postocular constriction;
Priasilphidae by the narrowly separated meso-coxal cavities, the abdomen with free ventrites, and the seriate punctuation of the elytra;

Cryptophagidae by the open meso-coxal cavities, the transverse procoxae, the moniliform antennae, and the seriate elytral punctuation;
Phalacridae by the elonget, not strongly convex body, the moniliform antennae, and the simple (non-toothed) claws;
Erotylidae by the non-clubbed antennae;
Boganiidae by the mandibles without setose cavities on the dorsal side and by the all-simple tarsomeres (non-lobed ventrally);
Cybocephalidae by the not rounded body, the non-lobed tarsomeres, and the 5-segmented tarsi.

According to Bouchard et al. (2011), the superfamily Cucujoidea Latreille, 1802 includes two families that are also extinct: Parandrexidae Kirejtshuk, 1994 and Sinisilvanidae Hong, 2002. The position of Sinisilvanidae within Silvanidae is considered unclear (according to its original description probably within the subfamily Silvaninae sensu stricto) by Kirejtshuk (2011). The Mesozoic family Parandrexidae (as diagnosed by Soriano et al. 2006) differs from newly described Wabbelidae fam. nov. by the subfiliform antennae (moniliform in

Fig. 6. Wabbel cerebricavus gen.et sp.nov. Forebody ventro-laterally: (1) compound eye [small]; (2) gula [wide]; (3) gular sutures [complete]; (4) notosternal suture [complete]; (5) pronotal border [present]; (6) procoxae [transverse, i.e. longer than wide]; (7) prosternal process [wide]; (8) hypomeron; (9) protrochanter; (10) elytral epipleuron
Wabbelidae), the long mandibles, the long palpomeres, the narrowly separated and flat coxae, and the 4-segmented tarsi.

Wabbelidae fam. nov. can readily be distinguished from other Cucujoidea by the following unique combination of characteristics: (1) thick moniliform antennae without distinct 3-segmented club, (2) modified (deeply concave) frons and vertex, (3) longitudinally strigose pronotum with pair of basal grooves, (4) wide gula with complete and well-separated gular sutures, (5) pentamerous non-lobed tarsi with first tarsomere equal to the second, (6) seriate punctuation of elytra, and (7) dorsally non-flattened body.

Taken separately, these characteristics are not unique and occur in several taxa of modern beetles. However, the complex of the characteristics listed above is unique for the superfamily. It allows assuming that Wabel gen. nov. is a representative of a formerly unknown taxon, whose rank is equal to other families of Cucujoidea.

In the most recent key to cucujoid families (Leschen et al. 2005), Wabel cerebricavus (and correspondingly Wabbelidae fam. nov.) runs to couplet 31, Priasilphidae/Agapythidae, having occiput without stridulatory files. Insertion of a couplet “31a” at this point would separate Wabbelidae:

31a. Antennae moniliform, frons and vertex deeply concave ......................................................... Wabbelidae
-Antennae clubbed, head without deep grooves or concavity..................................................... 31

DISCUSSION

The new taxon may represent a highly modified form with special adaptation associated with inquilinous habits. Such myrmecophilous beetles are always a problem to taxonomists. Many beetle families originally proposed to comprise such inquilines no longer qualify (Lawrence & Reichardt 1969). Antennal, leg, and body shape modifications as well as hairs are known for different groups of myrmecophilous beetles (Parker 2016). So, surprisingly, the pronotal form (lobes and grooves) of the recent Southern African myrmecophilous pinine genus Diplocotidus Péringuey, redescribed by Bell & Philips (2008), is fairly similar to the unique form of the head of our new taxon. Externally similar and, possibly, functionally equivalent forms of the forebody could arise only convergently in these beetles. Elongation of the clypeus, protection of mouthparts, and reduction of body hairs or scales, so that the surface appears shiny, probably represent adaptations associated with myrmecophilous habits (Lawrence & Reichardt 1966; Philips & Mynhardt 2011) as similar trends are found in Paussidae, clavigerine Pselaphidae, several representatives of Dacoderinae (Salpingidae), different and non-related groups of Ptininae (Diplocotes, Diplocotidus, Gnostus, Fabrasia etc.), and other inquilines. Some other superficially similar beetle groups (Rhysodidae, Jacobsoniidae) are mentioned in the diagnosis of the family. The way of life of the fossil taxon remains unknown as the factors explaining such striking head morphology are left to speculation.

The accurate dating of Baltic Tertiary amber is a debatable question: Either Lower Oligocene [Rupelian, 33.9 - 28.1 Ma], Upper Eocene [Priabonian, 38.0 - 33.9 Ma], or Lower Eocene [Ypresian-Lutetian, 56.0 - 41.3 Ma] is estimated as the time of amber forest existence by different authors (Ritzkowski 1997; Jaúoszyñski & Perkovsky 2016; Vitali & Daamgard 2016). The support of distinct branches of science should be used for final conclusions. So, Vitali & Damgaard (2016) supposed Early Oligocene as the age of Baltic amber origin, because of the predominance of temperate taxa of cerambycid beetles in the Baltic amber fauna. According to the opinion of the authors, the Eocene of Northern Europe was warmer than the Oligocene, and biota of temperate Asian areas could only immigrate after the drying of
the Turgai strait, which had taken place between Eocene and Oligocene. However, geological data contradict this hypothesis. According to Baraboshkin et al. (2007), continental Asia had a northern land connection with Fennosarmatia in Bartonian and Priabonian. Therefore, the faunal migrations may have taken place much earlier than in Oligocene. Moreover, the width of the narrow Turgai gate of Turgai strait span about 250 km in Ypresian (Baraboshkin et al. 2007). Such distance over water was surely not an insurmountable obstacle for taxa possibly transported by floating wood during millions of years. A similar direct migration route across narrow sea straits from Fennosarmatia to Northern America via Britain and Greenland during Eocene (and earlier) can be easily assumed, too. The absence of climatic and wide geographical barriers between all land parts of the Northern Hemisphere in Eocene should have resulted in the mixed and more or less homogeneous insect fauna of the whole area. The effectiveness of isolation of southern continents (considering north/south directed sea currents and atmospheric circulations) for insect migrations could be questioned, too. With regard to this question, the paper of Graham (2006) is of interest since it deals with possible causes for the similarity of modern-day biodiversity between the Caribbean and Africa. Arguments stating that the age of Baltic amber as a fossilized Oligocene resin based on faunal peculiarities only and neglected the geological data concerning the sedimentation of amber and palaeo-geographic data from the Eocene, can thus be rejected.

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