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Two new fossil species of Omaliinae from Baltic amber (Coleoptera: Staphylinidae) and their significance for understanding the Eocene-Oligocene climate

ADRIANO ZANETTI¹, MICHEL PERREAU *-² & ALEXEY SOLODOVNIKOV³

¹ Museo Civico di Storia Naturale, Lungadige Porta Vittoria 9, I-37129 Verona, Italy; Adriano Zanetti [zanet@easypas.it] — ² Université Paris Diderot, Sorbonne Paris Cité, IUT Paris Diderot, case 7139, 5, rue Thomas Mann, F-75205 Paris cedex 13 France; Michel Perreau * [michel.perreau@univ-paris-diderot.fr] — ³ Department of Entomology, Zoological Museum, Natural History Museum of Denmark, Universitetsparken 15, Copenhagen 2100, Denmark; Alexey Solodovnikov [asolodovnikov@snm.ku.dk] — * Corresponding author

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Abstract

Two fossil species, Paraphloeostiba electrica sp.n. and Phyllodrepa antiqua sp.n. (Staphylinidae, Omaliinae), are described from Baltic amber. Their external and relevant internal structures are illustrated using propagation phase contrast synchrotron microtomography. The palaeobiogeography of the two genera, the thermophilous Paraphloeostiba, the temperate Phyllodrepa, as well as palaeoenvironment of the amber forest are discussed in light of the new findings.

Key words

Omaliini, Eusphalerini, synchrotron microtomography, temperate, thermophilous.

1. Introduction

With more than 60,000 described living species (SOLODOVNIKOV et al. 2013) Staphylinidae (rove beetles) is the most speciose family of Coleoptera, presently divided into 32 subfamilies. Among them the subfamily Omaliinae is moderately large (about 1,500 described species) and one of the oldest rove beetle groups, known since the Mesozoic (TIKHOMIROVA 1968). The presence of a pair of ocelli on the vertex of the head is the most characteristic omaliine feature since the ocelli occur only in a few other staphyliniform beetle families (THAYER 1985A; LESCHEN & BEUTEL 2004). Other characters which are classically distinctive for the Omaliinae within Staphylinidae are tarsal formula 5-5-5, procoxal cavities opened behind, well-developed prosternal and postprocoxal processes, abdominal intersegmental membranes with brick-wall-like pattern, patches of wing folding, microtrichia on some abdominal tergites, as well as some features of genitalia (THAYER 1985A; PERIS et al. 2014). To date, 17 Mesozoic fossil species, mostly compression fossils that are thought to belong to Omaliinae have been reported: 13 from the Jurassic and 4 from the Cretaceous (TIKHOMIROVA 1968; RYKIN 1985, 1990; HERMAN 2001; CHATZIMANOLIS & ENGEL 2011; CHATZIMANOLIS et al. 2012; Cai & Huang 2013; PERIS et al. 2014). But their systematic positions, especially tribal or generic assignment within the subfamily, are still uncertain. Among them only Duo-calcar geminum Peris & Thayer, 2014 from Cretaceous amber, studied by the same techniques used in this paper, is to be considered as a reliably identified extinct Mesozoic taxon. Many more amber preserved fossils of rove
beetles are known from the Cenozoic. In particular, 82 species of Staphylinidae were described from Baltic amber (40–50 mya), belonging to Aleocharinae (8), Omaliinae (1), Oxyporinae (1), Paederinae (5), Pselaphinae (33), Scydmaeninae (19), Staphylininae (2), Steninae (9), and Tachyporinae (4) (Chatzimanolis & Engel 2011; Parker & Gremali 2014). The only putative omaline in this list, Pseudolesteua insinuans Schaufuss, 1890, has never been revised since its original description by Schaufuss (1890). The diagnosis of Pseudolesteua in the original description is insufficient for its unambiguous identification, but contains enough information to rule out any close affinity of that fossil with the two new species described here. Based on Schaufuss (1890), who only pointed to some habitus resemblance of Pseudolesteua with two omaline genera (he wrote: “Dieser Staphylina [Pseudolesteua] hat etwa die Form einer Les­teua, ist aber schmäler und nähert sich dadurch mehr im Habitus einem Boreaphilus”), we cannot be even sure that Pseudolesteua in fact represents an omaline. An­other omaline known from the Baltic amber is the genus Eusphalerum reported by Hieke & Pietrzyńuk (1984) based on material identified by E. Reitter. It was reported as an undescribed species of Anthobium, the genus name wrongly used for the current Eusphalerum until the middle of the last century (Tottenham 1949). As a result, two species that we are describing here are the first reliably recorded fossil Omalinae from Baltic amber. Because the groups they belong to are systematically complex and require examination of characters difficult to observe with light microscopy, we used propagation phase contrast synchrotron microtomography for detailed study of the specimens.

2. Material and methods

Four pieces of Baltic amber, each with one inclusion of Staphylinidae Omalinae belonging to the Zoological Museum, Natural History Museum of Denmark, Copenhagen (ZMUC) were tentatively identified by V. Puthz as Eusphalerum sp. This paper deals with two of these specimens, referenced as ZMUC-900029 and ZMUC-900027. The other two, referenced as ZMUC-900028 and ZMUC-900026 (with an additional old handwritten label “Baltic amber” and a recent printed label, with “Staphylinidae Liban, 1941–43 Kobmand Tidemand M.M.”), are still under study [according to Lars Vilhelmsen, ZMUC amber collection curator, “Liban” on the label has no relation to Lebanon or Lebanese amber].

External and internal structures are illustrated using propagation phase contrast synchrotron microtomography (PPC-SRμCT), which allows a complete virtual dis­section of specimens in a non-destructive way (Taffor­eau et al. 2006; Perreau & Tafforeau 2011). This tech­nique was particularly useful for the study of genitalia in both specimens, and, in case of Phyllobrepa antiqua, for examination of the ventral side of the body fully con­cealed by non-transparent milky substance common in Baltic amber fossils. The micromorphic scans of the samples were performed on beamline ID19 of the Eu­ropean Synchrotron Radiation Facility (ESRF, Grenoble, France). Scans were performed with a monochromatic X-ray beam at the energy of 15 keV using a multilayer monochromator. The CCD detector was a FreLoN HD2k (fast read-out low noise) with 2048×2048 pixels. Two resolutions were used: 0.678 μm (distance sample-de­ctor 30 mm, range angle 180°) and 1.75 μm (distance sample-detector 70 mm, range angle 360°). 1999 pro­jections were acquired for each scan and performed by continuous rotation to blur out details located outside the field of interest (far from rotation center and generally undesired) in order to decrease their contribution to the noise of the final reconstructed slices (Lak et al. 2008). Tomographic reconstructions were made using inhouse software of ESRF. Segmentations of selected structures were made with the software VGSTUDIO MAX 2.1 of Volume Graphics (http://www.volumegraphics.com/en/products/vgstudiomax.html). Micromorphic data linked to these specimens (original slices and processed data) and used for the present analysis are publicly available on the ESRF online paleontological database http://paleo.esrf.eu.

Habitus pictures in Figs. 33–35 were photographed on a Visionary Digital system, using Adobe Lightroom (Adobe Systems Inc. 2006–09).

3. Systematics

Order Coleoptera Linnaeus, 1758
Family Staphylinidae Latreille, 1802
Subfamily Omaliinae MacLeay, 1825
Tribe Omaliini MacLeay, 1825

Genus Paraphloeostiba Steel, 1960

Paraphloeostiba electrica sp.n.

Figs. 1–7, 9–20, 32–34

Material. Holotype ♀: as inclusion in a piece of amber 9 mm × 5 mm × 2.5 mm in size, with one aphid as syninclusion, in paper envelope with the following 3 handwritten labels: “Staphylini­dae Thysanoptera (?)” [crossed out in pencil] C.V. Henninges 1-5 1967”; “Eusphalerum spec. det. Puthz 1974”; “Eusphalerum sp. det. Solodovnikov 2007”, inserted in transparent plastic envelope with the following printed label: “SNM Amber Collection/ZMUC-900029/ Class: Insecta/ Order: Coleoptera/ Family: Staphylini­dae/ Eusphalerum sp/ Baltic Amber/ Leg. C.V. Hennings 1-5.1967/ Dep. ZMUC”, the following handwritten label: “MP018” (reference of ESRF scan), and the following printed label (red): “Paraphloeostiba electrica n. sp. Zanetti, Perreau and Solodovnik­ov, 2014 HOLOTYPE”. The holotype is deposited in the ZMUC.
Type locality. Baltic amber.

Type horizon and age. Lower Eocene – Lower Oligocene.

Measurements. Length of head (from apex of clypeus to neck): 0.30 mm; maximal width of head on level of the eyes: 0.43 mm; length of pronotum: 0.39 mm; maximal width of pronotum: 0.55 mm; length of elytral suture: 0.64 mm (from tip of scutellum); width of elytra: 0.70 mm; length from apex of clypeus to apex of elytra: 1.40 mm; total body length (from apex of clypeus to the

Figs. 1–6. *Paraphleostiba electrica* sp.n. 1: Habitus, dorsal view. 2: Habitus, lateral view. 3: Habitus ventral view (without the legs). 4: Head and mouthparts, ventral view. 5: Head and mouthparts, lateral view. 6: Head and mouthparts, dorsal view. – *Abbreviations*: lbm: labium; lbr: labrum; lp: labial palp; mp: maxillary palp. (Pictures by PPC-SrμCT)
apex of abdomen, with extended abdomen): 2.00 mm.

**Coloration.** The specimen appears black and shiny, with mouthparts, legs, and apex of abdomen slightly paler, brown.

**Description. Head.** Labrum inserted below clypeus, which is not separated from frons, emarginate medially with a couple of setae near the emargination, narrower than apical margin of clypeus. Clypeus apically rounded. Maxillary palpomere 2 about 2 × as long as wide, enlarged toward apex, 2.5 × as long as 3, palpomere 3 almost 2 × as wide as base of 2, palpomere 4 parallel-sided, sharpened in the apical fifth of its length, 4 × as long as wide, 3.5 × as long and 0.3 × as wide as palpomere 3 (Figs. 4–6). Labial palpomeres 1–3 stout, progressively narrowed (Fig. 4). Gular sutures closest at level of midpoint of eyes (Fig. 4). Eyes prominent, with medium-size ommatidia (Fig. 6), infraorbital carina and stripes at the internal margin of the eyes not visible, temples rather long (1/2 of eye length), convex. Punctuation of head superficial and rather sparse, distance between punctures approximatively equal to their diameter [directly observed by optical stereomicroscope], microsculpture not visible, depressions below antennae scarcely evident, ocelli large and prominent, ante-ocellar impressions (dorsal tentorial pits) clearly visible. Antennae short, antennomere 1 1.5 × as long as wide, 2 smaller, 1.5 × as long as wide, 3 subconical, 1.5 × as long as wide, 4–5 subquadrate, 6–9 transverse, 10 almost twice as wide as long, 11 1.5 × as long as wide with conical apex, 4–11 with long setae. **Prothorax.** Pronotum transverse (width/length ratio = 1.5), widest at middle, anterior margin narrower than posterior, lateral margins rounded in anterior two thirds, almost rectilinear, somewhat sinuate in posterior third, anterior angles entirely rounded, posterior angles somewhat obtuse, scarcely rounded. Surface convex, punctuation rather dense and regular on apparently glossy surface [directly observed by optical stereomicroscope], posterior angles without clear depression, pubescence not visible. Scutellum triangular, acute at apex, wider at base than long. Elytra scarcely elongate (ratio of length of elytra from scutellum to apex / combined width of elytra at apex of scutellum = 0.9), scarcely dilated at apex, apex truncate, punctuation dense and coarse (visible on anterior half of left elytron) (Fig. 1). Legs with unmodified femora and rectilinear tibiae. Procoxal cavities transverse, contiguous along the median line, prosternal process narrowed. Mesoventrite sculptured, with a scarcely developed median carina, mesocoxal cavities rounded, separated by mesoventral process (Fig. 3). Metaventrite wide, trapezoidal, 1.7 × as wide as long, sparsely punctured and scarcely sculptured, metacoxae contiguous. Metathoracic wings well developed, everted and clearly visible in the inclusion, however not well stretched to see wing venation and omitted from the tomographic illustrations for clarity. **Abdomen** flat, paratergites well developed (two per segment, on segments III–VII). Tergites visible from IV. (III covered
by elytra), with scarcely visible microsculpture (Fig. 1), wind-folding patches not visible. Abdominal tergite III with a transversal groove without setae (Fig. 32). Sternites with more evident transverse microsculpture, sternite VIII deeply emarginate. Apex of abdomen as in Figs. 11–13. Sternite IX clearly punctured (Figs. 14–16).

**Legs** (Fig. 2) similar in shape, tibiae approximately as long as femora, profemora somewhat sinuate, meso- and metafemora rectilinear. All tibiae rectilinear, only protibiae very feebly curved, intermediate with some spines at the external margin, posterior with a fringe of long setae at internal margin, and a few spines externally. All tarsi with tarsomere 5 longer than 1–4 combined, ventral surface of pro- and mesotarsi 1–4 with modified setae, arranged in 4 rather regular longitudinal rows (Figs. 7, 9), the two external rows formed by long strongly enlarged setae, curved in the apical portion, the two internal rows formed by shorter leaf-shaped setae. Metatarsus with a few normal setae (Fig. 10), some setigerous pores seem to be present, some setae could be lost. **Aedeagus** as in

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Fig. 17–20, elongate, basal bulb not distinctly delimited from the apical part, median lobe apically somewhat carinate in dorsal (parameral) view, apex acute but not pointed at the tip, parameres thin, enlarged at apex, apical setae not evident. Basal bulb in ventral view with a large elliptical plate clearly separated from the rest of the integument.

**Etymology.** From the Greek ηλεκτρικός, “of the amber”.

**Discussion.** The type specimen of this new species was previously identified as *Eusphalerum* sp. of the monogenic tribe Eusphalerini. This genus, despite its high trophic specialization (the adults live on flowers and feed on pollen), is difficult to identify morphologically. Among other Omaliinae, the unique distinctive character of Eusphalerini is the broadened tarsomeres 1–4 with dense ventral setae. The general body shape of the fossil specimen recalls *Eusphalerum*, but the setation of tarsi is quite different and remarkable, with 4 rows of modified setae, at least in pro- and mesotarsi. As *Eusphalerum* has to be excluded, the characters, mostly the shape of tarsi with tarsomere 5 longer than tarsomeres 1–4 combined and the presence of a transversal groove on the abdominal tergite III (Thayer 1992; Newton & Thayer 1995) even if setae are missing probably after diagenesis, suggest that the specimen belongs to Omaliini. Within Omaliinae, considering characters reported for the European representatives (Zanetti 1987, 2012): sides of pronotum not crenulate; palpomere 4 (apical) narrower than 3; antennomere 6 wide; head and pronotum not opaque; very long maxillary palpomere 4, this fossil can be placed in *Paraphloeostiba* Steel, 1960. Other explored characters, especially considering non-European genera (setation of tarsi, morphology of aedeagus, shape of mesosternum), also support such generic placement. Actually, the setation of protarsi and mesotarsi of *Paraphloeostiba* elec- 
trica (Smetana, 1986) and the integument. Probably this is an apomorphic feature present in several genera of the tribe, but that has not been yet reported in Omaliini. We observed it in a recent species of *Paraphloeostiba* (P. gayndahensis), and in such genera as Carcinocephalus Bernhauer, 1903, Crymus Fauvel, 1904, “Nesomalium” helmsi (Cameron, 1945) (to be included in a new genus, Thayer pers. comm.), Omalium Jeannel, 1940, Omalium, Phloeonomus Heer, 1839, Phloeostiba Thomson, 1858, and Xylostiba. In many other Omaliini genera the basal bulb of the aedeagus is encased by a single sclerotized piece, with only the ventral median line un sclerotized (e.g., Fig. 28). We observed this pattern in Acrolocha Thomson, 1858, Acrulia, Acruliopsis Zerche, 2003, Dialycera Ganglbauer, 1895, Droephylla Mulsant & Rey, 1880, Hapalaraeae Thomson, 1858, Hypocyna Mulsant & Rey, 1880, Phyllodrepa Thomson, 1859, Prosopaspis Smetana, 1987, and Pycnoglypta Thomson, 1858. Such a shape of the ventral surface of the basal bulb is also characteristic for Eusphalerini, a tribe that is scarcely supported by morphological evidence. A phylogenetic analysis is needed to ascertain the status of this tribe, and to assess the value of observed character states.

**Palaeobiogeography.** Presently, the genus *Paraphloeostiba* is known from 30 recent species distributed in (sub)tropics, mostly of the Oriental, Ethiopian and Pacific biogeographic regions: India, Ceylon, southeastern Asia, Mariana Islands, Solomon Islands, New Hebrides, Norfolk Island, Australia, the Seychelles and Fiji (Herman 2001). Undescribed species are known from high mountains of central China. One of the species, *P. gayndahensis* (MacLeay, 1871), described from Australia
and later recorded from Lord Howe Island (Steel 1960), is now adventive in several regions and distributed almost worldwide. *Paraphloeostiba* is one of the very few thermophilic genera of Omaliinae, most of the recent members of the subfamily being distinctly temperate (Tikhomirova 1973). Finding an extinct member of *Paraphloeostiba* in Baltic amber, a fossil resin that originated in northern Europe (Larsen 1978) from the piece collected in Denmark is very interesting. First, it shows that the distribution of this genus in the past was wider than present and consistent with the pattern recorded for many other beetles and insects with known Baltic amber fossils (Weitschat & Wichard 2010; Alekseev 2013). Usually the formerly wider distributions of thermophilic taxa are correlated to palaeoclimate, whereby temperate regions including northern Europe were significantly warmer and mild during most of the Eocene even at high latitudes, because of the greenhouse effect (Huber & Caballero 2011). The climate became colder and more seasonal at the Eocene-Oligocene boundary, with corresponding shifts or contraction of distributions thermophilic insect taxa (Archibald & Farrell 2003) that are now restricted to (sub)tropical areas. Second, a new record of a clearly thermophilic rove beetle amber fossil genus contributes additional evidence towards a better knowledge about the palaeoenvironment of the forest in Paleo-Europe (Fennoscandia in Szwebo & Sontag 2013) that produced the Baltic amber resin. This evidence from such group like Staphylinae, that is a rather landscape-dependent family comprising lineages of diverse ecological specializations, is very valuable, because neither the original source area nor age of origin of the Baltic amber is certain (Larsen 1978; Alekseev 2013).

Much of this uncertainty of origin and age is associated with both complex ways of amber (re)deposition and the composite nature of the fossil entomofauna preserved in Baltic amber, which is still only fragmentarily known. Multiple and rather remote collecting locations for the Baltic amber pieces, and various other evidence including a combination of temperate and thermophilic taxa in various Baltic amber inclusions identified from a limited number of insect groups, have contributed to uncertainty about the palaeoenvironmental conditions, place and time of the Baltic amber origin. For example, Larsen (1978) suggested that the Baltic amber found in Denmark was formed in a different area compared to the Baltic amber found in the Gulf of Gdańsk in Poland. The mix of thermophilic and temperate insect faunal elements in the Baltic amber, noted long ago, was either attributed to the special paleoclimate features of the amber forest (Wheeler 1910), or, with respect to notable climate cooling at the Eocene-Oligocene boundary, was associated with (and contributes to) uncertainty about the Baltic amber place and age of origin. According to Alekseev (2013), age estimates vary from Lower Eocene to Lower Oligocene. Assuming the hypothesis of the single place/time of origin of the Baltic amber (e.g., Szwebo & Sontag 2013), such combination of temperate and thermophilic taxa calls for reduced seasonality of temperature in temperate regions during the Eocene (Archibald & Farrell 2003) as one of the possible explanations. Naturally all paleoclimatologic reconstructions inferred from the ecological preferences of recent species assume ecological niche conservatism within lineages, which may not always be the case. Only special studies exploring a gradient of ecological preferences of a given lineage in the context of its phylogeny could prove or reject such assumptions. Such studies do not exist for any group of rove beetles because neither adequate phylogenies, nor detailed ecological information have been generated for them. Therefore, we are left only with speculations. Nevertheless, it seems noteworthy that one of the only two omaliines reliably known from Baltic amber belongs to *Paraphloeostiba*, which is – exceptionally – thermophilic in this mainly temperate subfamily. In accordance with other sources of data, it points to distinctly warm palaeoclimatic conditions of the Paleocene-Eocene amber forest of Europe. It also calls for future evolutionary studies of ecological preferences in Omaliinae.

Genus Phyllodrepa Thomson, 1859

*Phyllodrepa antiqua* sp.n.

Figs. 21–31, 35


Type locality. Baltic amber.

Type horizon and age. Lower Eocene – Lower Oligocene.

Measurements. Length of head (from apex of clypeus to neck): 0.36 mm; maximal width of head: 0.50 mm; length of pronotum: 0.47 mm; width of pronotum: 0.63 mm; length of elytral suture: 0.75 mm (from the tip of scutellum); width of elytra: 0.95 mm; length from clypeus to apex of elytra: 1.50 mm; total length (from apex of clypeus to the apex of abdomen, with extended abdomen): 2.45 mm. Coloration. Only dorsal surface is accessible for light microscopy since the ventral side of inclusion is covered with thick cloud of milky substance. Dorsally specimen appears black and shiny.

Description. Head. Eyes large, occupying most of sides of head, with medium-size ommatidia, separated from vertex by two ridges extending posterad from antennal insertions. Maxillary palpomere 2 about 2 × as long as wide, 2 × as long as 3, palpomere 3 conical, as long as wide, about as wide as 2, palpomere 4 somewhat longer...
than 2 as wide as 3, progressively sharpened towards apex. Labial palpi scarcely visible. Gular sutures closest at level of posterior margin of eyes. Infraorbital carina scarcely prominent, very close to the eye. Temples short, strongly convergent posterad, as long as 1/5 of eye length. Ocelli large, ante-ocular depressions (dorsal tentorial pits) large, rounded and close to ocelli, impressions below antennae large and superficial. Punctuation
superficial, sparse and irregular, almost absent in front of eyes. Microsculpture not visible. Antennae with antennomere 1 globose, as long as wide, 2 subquadrate, small, 3 subconical, 1.5 × as long as wide, 4 – 5 subquadrate, 6 – 10 transverse and progressively enlarged, 10 twice as wide as long, 11 twice as long as wide, conical at apex.

**Prothorax.** Pronotum 1.2 × as wide as head, convex, with two superficial longitudinal impressions in posterior half, moderately transverse (width/length ratio = 1.3), widest slightly in front of middle, anterior angles obtuse, not marked, posterior angles marked, feebly obtuse, lateral margins finely crenulate, mostly in posterior

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**Figs. 32–35.** 32: *Paraphloeostiba electrica* sp.n.: abdominal tergite III with a transversal groove (arrow). 33: *P. electrica* sp.n. habitus dorsal view. 34: *P. electrica* sp.n. habitus ventral view. 35: *Phyllodrepa antiqua* sp.n. habitus dorsal view.
half (Fig. 24), rectilinear in front of posterior angles, anterior margin scarcely narrower than posterior; punctuation similar to that of head, more regular, microsculpture not visible, depression near posterior angles shallow and indistinct. Scutellum triangular, rounded at apex, wider than long. Elytra 1.2 × wider than pronotum, weakly elongate (ratio of length of suture/combined width of elytra = 1.05), weakly enlarged posteriorly, punctuation similar to that of pronotum, weakly coarser. Procoxal cavities contiguous along median line, prosternal process narrowed. Mesoventrite punctate, without median carina, mesocoxal cavities separated by process of mesoventrite. Metaventrite wide, trapezoidal, 1.5 × as wide as long, sparsely punctured, metacoxae contiguous. Metathoracic wings well developed, everted and nearly visible in the inclusion, omitted from the tomographic illustrations for clarity. **Abdomen** flat, paratergites (two per segment, on segments III – VII) well developed. Ter- gites visible from III (partially covered by elytra), with scarcely visible microsculpture and decumbent pubescence, VIII emarginate in the middle. Groove of tergite III not clearly visible. Wing-folding patches not visible. Stermites superficially punctured, emargination of VIII not visible. **Legs** (Figs. 22, 23) similar in shape, tibiae approximately as long as femora, almost rectilinear, femora rectilinear. All tibiae rectilinear, only protibiae very feebly curved, mesotibiae with some spines on external side. All tarsi with tarsomere 5 somewhat longer than 1–4 combined, ventral surface with normal setae (Figs. 25–27). **Aedeagus** as in Figs. 28–31, basal bulb enlarged with ventral surface sulcate in the middle, apex of median lobe narrow, bent with respect to basal bulb, parameres enlarged at base, curved in the middle and not expanded at apex.

**Etymology.** From the Latin *antiquus*, “ancient”.

**Discussion.** The fossil can be excluded from Coryphiini by the shape of the maxillary palpi (distal palpomere not much smaller than preceding one), from Anthophagini by the length of its distal metatarsomere, and from Eusphalerini by the partially crenulate pronotum margins, the lack of expanded tarsomeres 1–4 on all tarsi, and the shape of the aedeagus. The shape of the hind tarsi matches that present in Omaliini. And the characters such as: frons and vertex not elevated, the apical and subapical maxillary palpomeres having the equal width, presence of long elytra, an acarine mesoventre, and hind tarsus at least 3/5 as long as hind tibia (Newton et al. 2000; Zanetti 1987), place the species in the lead to the *Phyllodrepa* complex, now composed of several genera (*Phyllodrepa* Thomson, 1859, *Dropephylla* Mulsant & Rey, 1880, *Dialycera* Mulsant & Rey, 1880, and *Hapalaraea* Thomson, 1858, Zanetti l.c.). The new species shares small body size with the members of the genus *Dropephylla*, but differs from the latter by the presence of ante- ocellar impressions. Despite the small size, the habitus and other characters (head with two impressions between the base of antennae, sides of pronotum not concave in front of posterior angles, posterior legs not modified in male) place the new species into the genus *Phyllodrepa*, even though it has crenulate pronotal margins, an unusual character for this genus which is also present in the genera *Dialycera* and *Hapalaraea*. The arched median lobe in lateral view of the new species (Fig. 30) is present both in *Phyllodrepa* and *Dropephylla*, e.g. *Phyllodrepa nigra* (Gravenhorst, 1806) and *Dropephylla vilis* (Erichson, 1840) (Zanetti 2012). This pattern, inter alia, raises doubts about the monophyly of the genus *Phyllodrepa* as currently defined. These observations and the poor systematic knowledge of the non-Palaearctic fauna of the *Phyllodrepa* complex, make the generic assignment of this fossil species to *Phyllodrepa* only provisional. Two extinct Mesozoic genera *Eophyllodrepa* Ryvkin, 1985 and *Daidromus* Ryvkin, 1990, described from Jurassic of Transbaicaia in Russia have been mentioned as similar to the genus *Phyllodrepa* (Ryvkin 1985, 1990). *Phyllodrepa antiqua*, however, differs well from both of them as follows: from *Eophyllodrepa* in smaller body size (3.5 mm in *Eophyllodrepa*), in relatively shorter sutural area of elytra, in antennae more sharply enlarging apicad, in lacking lateral invaginations on elytra, and in not so distinctly developed emarginations on the preapical abdominal sternites in males; from *Daidromus* in smaller body size (3.4 mm in *Daidromus*), lacking clear longitudinal striae on head disk anterior to ocelli, shape of pronotum with more rounded lateral sides, and in shape of antennae with distinct apical club.

**Palaeobiogeography.** Although Herman (2001) reports nearly global distribution of the extant members of the genus *Phyllodrepa* (then including also *Dropephylla*), real distribution of the genus is confined to Holarctic, and montane regions of northern India and Nepal only. This is because extra-Holarctic species do not in fact belong to *Phyllodrepa* (Margaret Thayer, pers. comm.), a situation still very common for many rove beetle ‘genera’ that were based on European type species and accumulated numerous ‘exotic’ species at the early stages of entomological explorations without subsequent revision. In such restricted sense the genus *Phyllodrepa* is strongly temperate. Since the non-Palaearctic members were not recently revised, and there is no phylogenetically sound concept of the *Phyllodrepa* complex, any palaeobiogeographic interpretation of this species from Baltic amber here tentatively identified as a species of *Phyllodrepa*, is premature. It is however a very interesting fact that among two genera of Omaliinae here detected from Baltic amber, *Paraphloeoestiba* is a rare termophilous member of the subfamily, while *Phyllodrepa* is a more typical temperate. As discussed above with respect to *Paraphloeoestiba*, such puzzling mixture of termophilous and temperate elements is at the heart of discussions about place, time and palaeoenvironment of Baltic amber. In this context and assuming ecological niche conservatism, Omaliinae is a very promising group for exploring the palaeoenvironmental conditions of the Cenozoic amber forests.
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5. References

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