

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@easyasp.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

Accepted 23.ii.2016.

Published online at www.senckenberg.de/arthropod-systematics on 03.vi.2016.

Editor in charge: Christian Schmidt.

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; RYVKIN 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 *Duocalcar 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 & GRIMALDI 2014). The only putative omaliine in this list, *Pseudolestea insinuans* Schaufuss, 1890, has never been revised since its original description by SCHAUFUSS (1890). The diagnosis of *Pseudolestea* 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 *Pseudolestea* with two omaliine genera (he wrote: “Dieser Staphyline [*Pseudolestea*] hat etwa die Form einer *Leesteua*, ist aber schmaler und nähert sich dadurch mehr im Habitus einem *Boreaphilus*”), we cannot be even sure that *Pseudolestea* in fact represents an omaliine. Another omaliine known from the Baltic amber is the genus *Eusphalerum* reported by HIEKE & PIETRZENIUK (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 Omaliinae 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 Omaliinae 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-SR μ CT), 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 *Phyllodrepa antiqua*,

for examination of the ventral side of the body fully concealed by non-transparent milky substance common in Baltic amber fossils. The microtomographic 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 μ m (distance sample-detector 30 mm, range angle 180°) and 1.75 μ m (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 VGSTUDIOMAX 2.1 of Volume Graphics (<http://www.volumegraphics.com/en/products/vgstudiomax.html>). Microtomographic 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

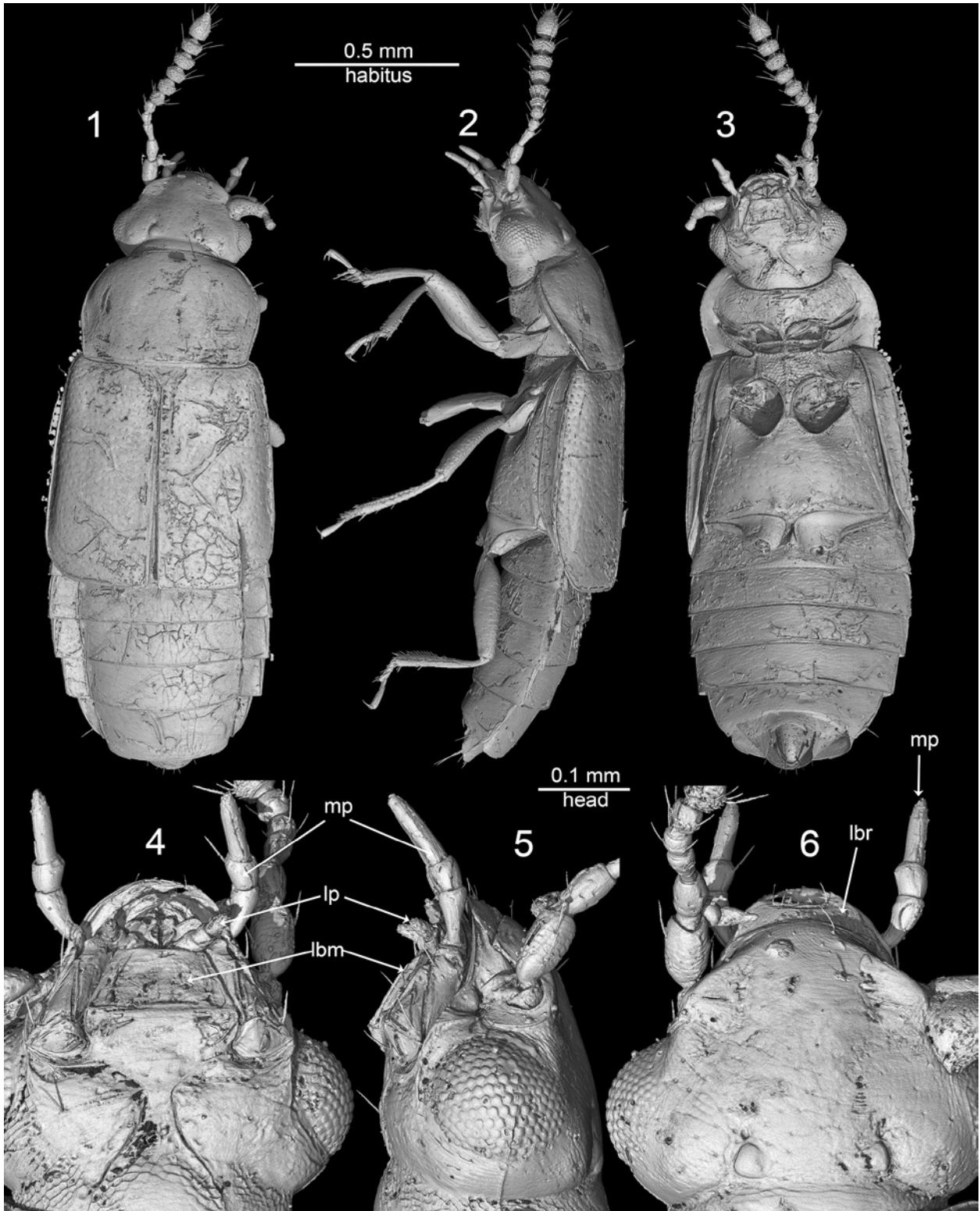
Tribe Omaliini MacLeay, 1825

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. Henningsen 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. Henningsen date: 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.



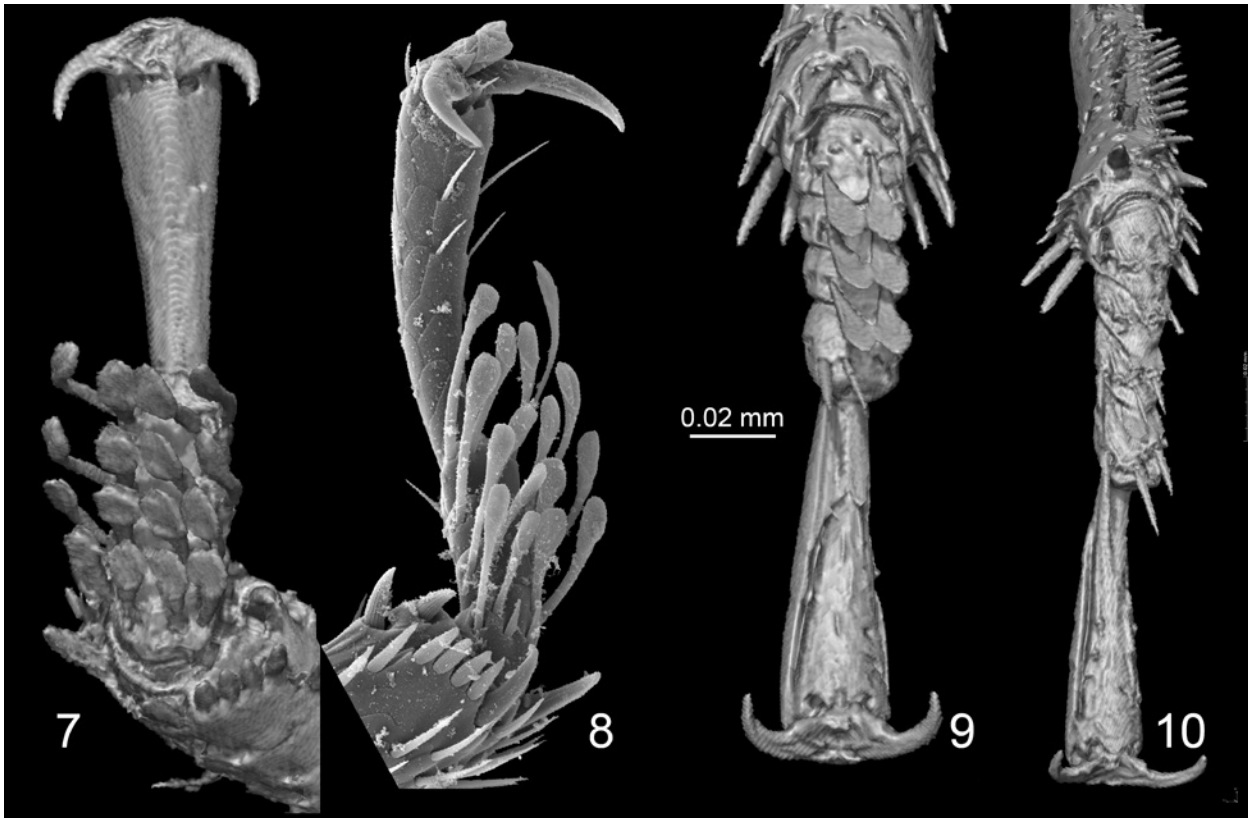
Figs. 1–6. *Paraphloeostiba electrica* sp.n. 1: Habitus, dorsal view. 2: Habitus, lateral view. 3: Habitus ventral view (without the legs). 4: Head and mouthparts, ventral view. 5: Head and mouthparts, lateral view. 6: Head and mouthparts, dorsal view. – **Abbreviations:** lbm: labium; lbr: labrum; lp: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

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

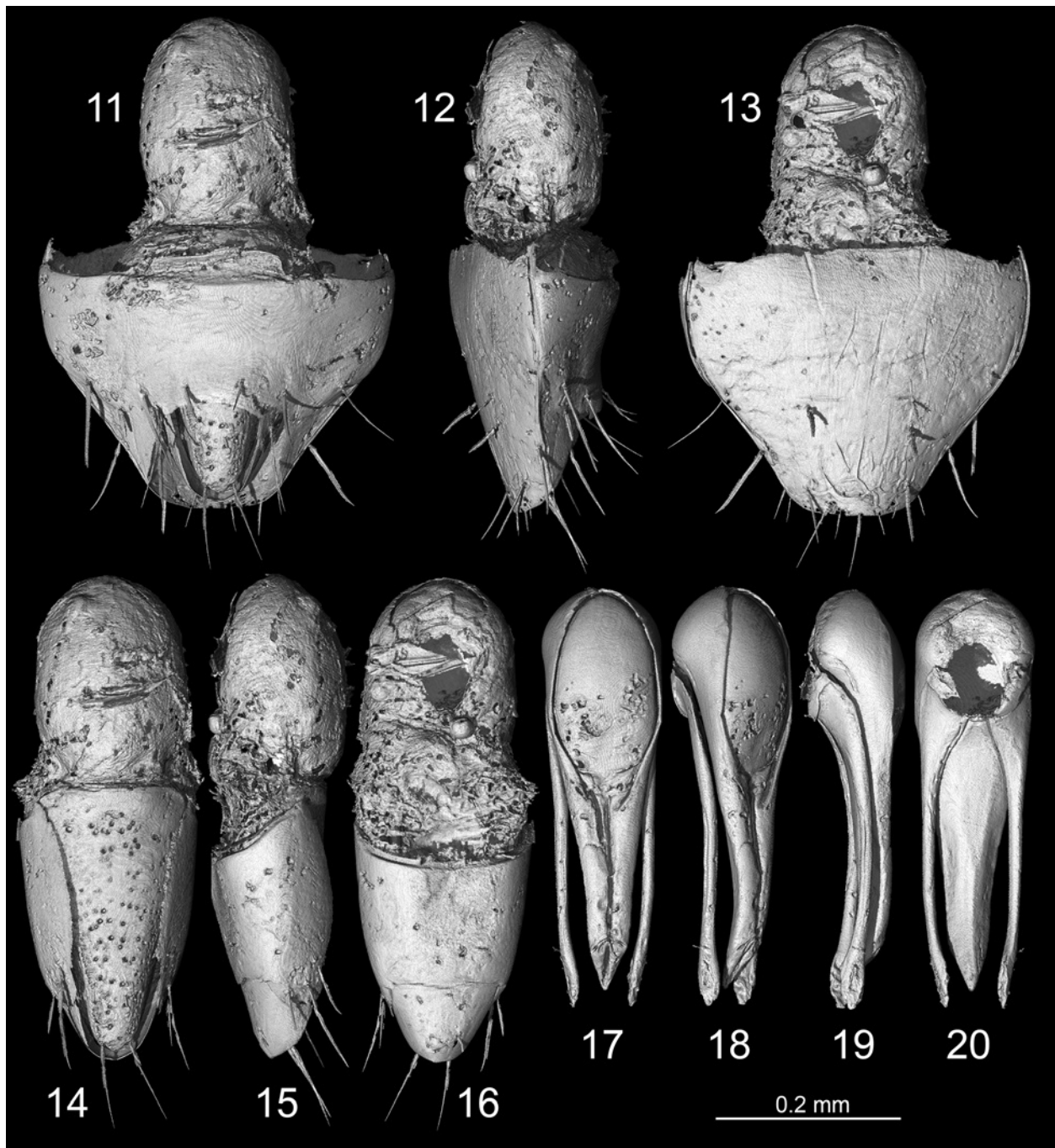


Figs. 7–10. *Paraphloeostiba*, tarsi. **7:** *P. electrica* sp.n., protarsus. **8:** *P. gayndahensis* (MacLeay), protarsus. **9:** *P. electrica* sp.n., mesotarsus. **10:** *P. electrica* sp.n., metatarsus. (7, 9, 10 by PPC-Sr μ CT; 8 by SEM)

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 \times as long as wide, enlarged toward apex, 2.5 \times as long as 3, palpomere 3 almost 2 \times as wide as base of 2, palpomere 4 parallel-sided, sharpened in the apical fifth of its length, 4 \times as long as wide, 3.5 \times as long and 0.3 \times 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 \times as long as wide, 2 smaller, 1.5 \times as long as wide, 3 subconical, 1.5 \times as long as wide, 4–5 subquadrate, 6–9 transverse, 10 almost twice as wide

as long, 11 1.5 \times 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 \times 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



Figs. 11–20. *Paraphloeostiba electrica* sp.n., male terminalia. **11:** Abdominal segment VIII, ventral view. **12:** Abdominal segment VIII, lateral view. **13:** Abdominal segment VIII, dorsal view. **14:** Abdominal segments IX and X, ventral view. **15:** Abdominal segments IX and X, lateral view. **16:** Abdominal segments IX and X, dorsal view. **17:** Aedeagus, ventral view. **18:** Aedeagus, ventro-lateral view. **19:** Aedeagus, lateral view. **20:** Aedeagus dorsal view. (Pictures by PPC-SrμCT)

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

Figs. 17–20, elongate, basal bulb not distinctly demarcated 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 monogeneric 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 Omaliini, 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 electrica*, formed by 4 regular rows of modified setae where the external ones are enlarged and curved at apex (clavate adhesive setae according to SMETANA 1986 or disco-setae according to STORK 1980) and the internal ones are leaf-shaped, is characteristic for this genus. STEEL (1955) described and illustrated very similar setation in the genus *Xanthonomus* Bernhauer, 1926, which is also a member of Omaliini and includes two species, *X. latus* Steel, 1955 from Malaysia and *X. toxopeanus* Bernhauer, 1926 from Indonesia. Later, STEEL (1960) reported a similar state in his new genus *Paraphloeostiba*. Despite the similarity in tarsal setation, the external characters of *Xanthonomus* such as lack of paratergites on segments III–VI, habitus, and the shape of maxillary palpi allow us to exclude attribution of our fossil specimen to this genus. In addition to other characters listed above, the shape of the modified tarsal setae of the new fossil species is very similar to living *Paraphloeostiba* (Fig. 8). It is noteworthy that the genus *Xylostiba* Ganglbauer, 1895, which is close to *Paraphloeostiba*, has normal setae. It is also remarkable that clavate adhesive setae usually occur only in male Coleoptera (e.g. in *Anthobium atrocephalum* (Gyllenhal,

1827), *Prosopaspis* Smetana, 1986, *Pycnoglypta* Thomson, 1858, and *Micralymma* Westwood, 1838) (SMETANA l.c., STORK l.c., THAYER 1985b), but in the case of *Paraphloeostiba*, they are present in both sexes, though more strongly developed in males. It should be noted that the mesoventrite of the amber fossil has a vestigial median carina that is a character state present in *Omalium* and related genera. Other characters including the shape of maxillary palpi in *P. electrica* do not fit the genus *Omalium* Gravenhorst, 1802 and its allies. Moreover, at least in one of the species of *Paraphloeostiba*, namely *P. gayndahensis* (MacLeay, 1871), the mesoventrite is somewhat elevated in the middle too. Overall, the inclusion of this new fossil omaliine species in the extant genus *Paraphloeostiba* seems strongly supported and, therefore, *Paraphloeostiba electrica* is hypothesized as its first extinct representative. It is most similar to *Paraphloeostiba solomonensis* Steel, 1960.

Finally, our extensive examination of the morphology of the Omaliinae taxa triggered by the study of *P. electrica* reveals a blurred border between the tribes Omaliini and Eusphalerini and therefore casts doubts on their reciprocal monophyly. The aedeagus of *P. electrica* is a “basic” Omaliinae type, with simple basal bulb, median lobe and simple parameres. The only peculiar modification is the elliptical plate on the ventral surface. 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.), *Omaliomimus* 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 unsclerotized (e.g., Fig. 28). We observed this pattern in *Acrolocha* Thomson, 1858, *Acrulia*, *Acruliopsis* Zerche, 2003, *Dialycera* Ganglbauer, 1895, *Dropephylla* Mulsant & Rey, 1880, *Hapalaraea* Thomson, 1858, *Hypopycna* 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 (LARSSON 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 (Feno-Sarmatia in SZWEDO & SONTAG 2013) that produced the Baltic amber resin. This evidence from such group like Staphylinidae, 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 (LARSSON 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, LARSSON (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 palaeoclimate 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., SZWEDO & SONTAG 2013), such combination of temperate and thermophilic taxa calls for reduced seasonality of temperature in tem-

perate regions during the Eocene (ARCHIBALD & FARRELL 2003) as one of the possible explanations. Naturally all paleoclimatic 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

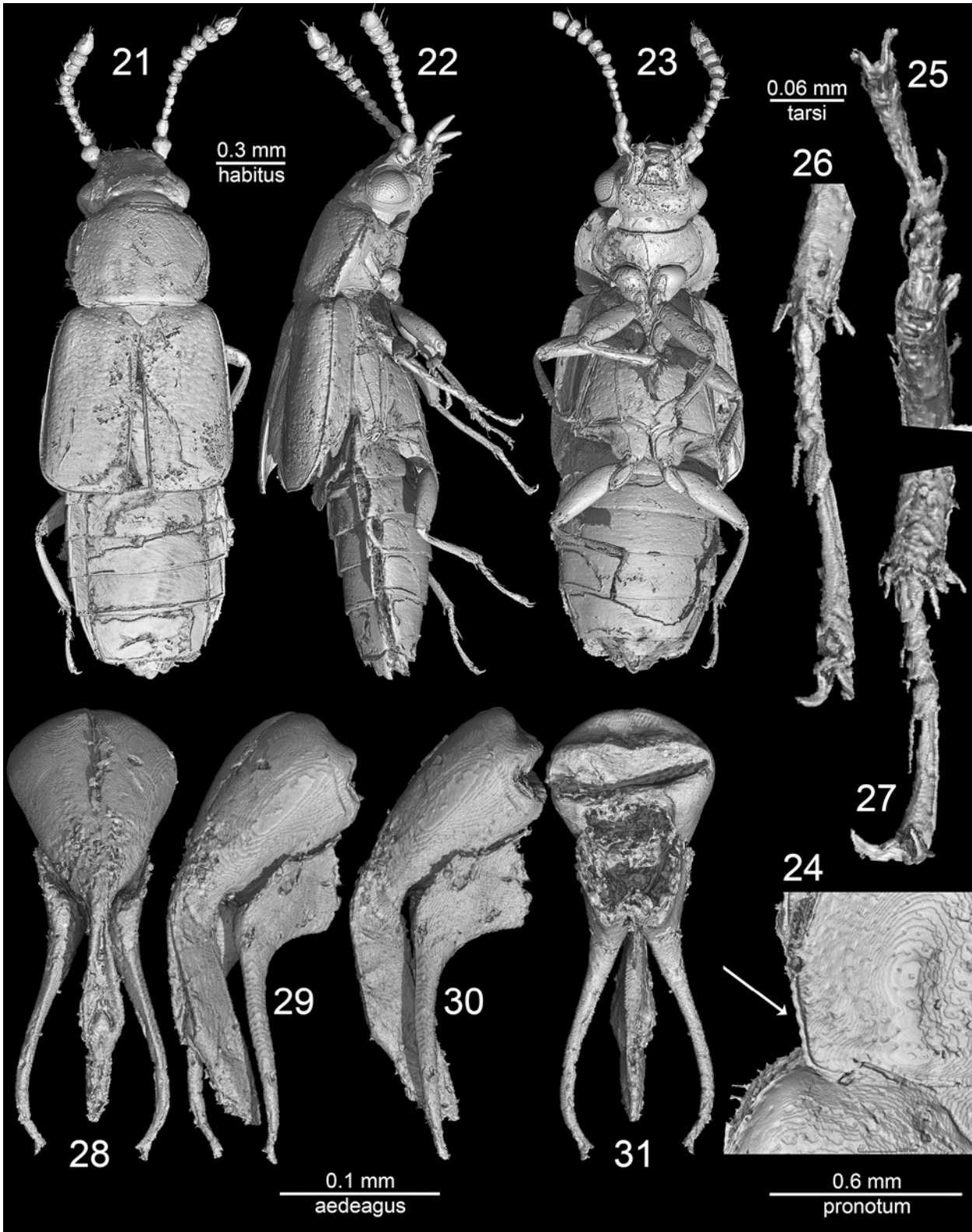
Material. Holotype: ♂, as inclusion in a piece of amber, 6 mm × 4 mm × 4 mm size, in paper envelope with three handwritten labels: “Staphylinidae C.V. Henningsen 3-5 1967”; “Eusphalerum spec. det. Puthz 1974”; “Eusphalerum sp. det. Solodovnikov 2007”, inserted in transparent plastic envelope with the printed label: “SNM Amber Collection/ZMUC-900027/ Class: Insecta/ Order: Coleoptera/ Family: Staphylinidae/ *Eusphalerum* sp./ Baltic Amber/ Leg. C.V. Henningsen date: 3.5.1967/ Dep. ZMUC”, the handwritten label: “MP020” [reference of ESRF scan], and the printed label [red]: “*Phyllodrepa antiqua* 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): 0.36 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.

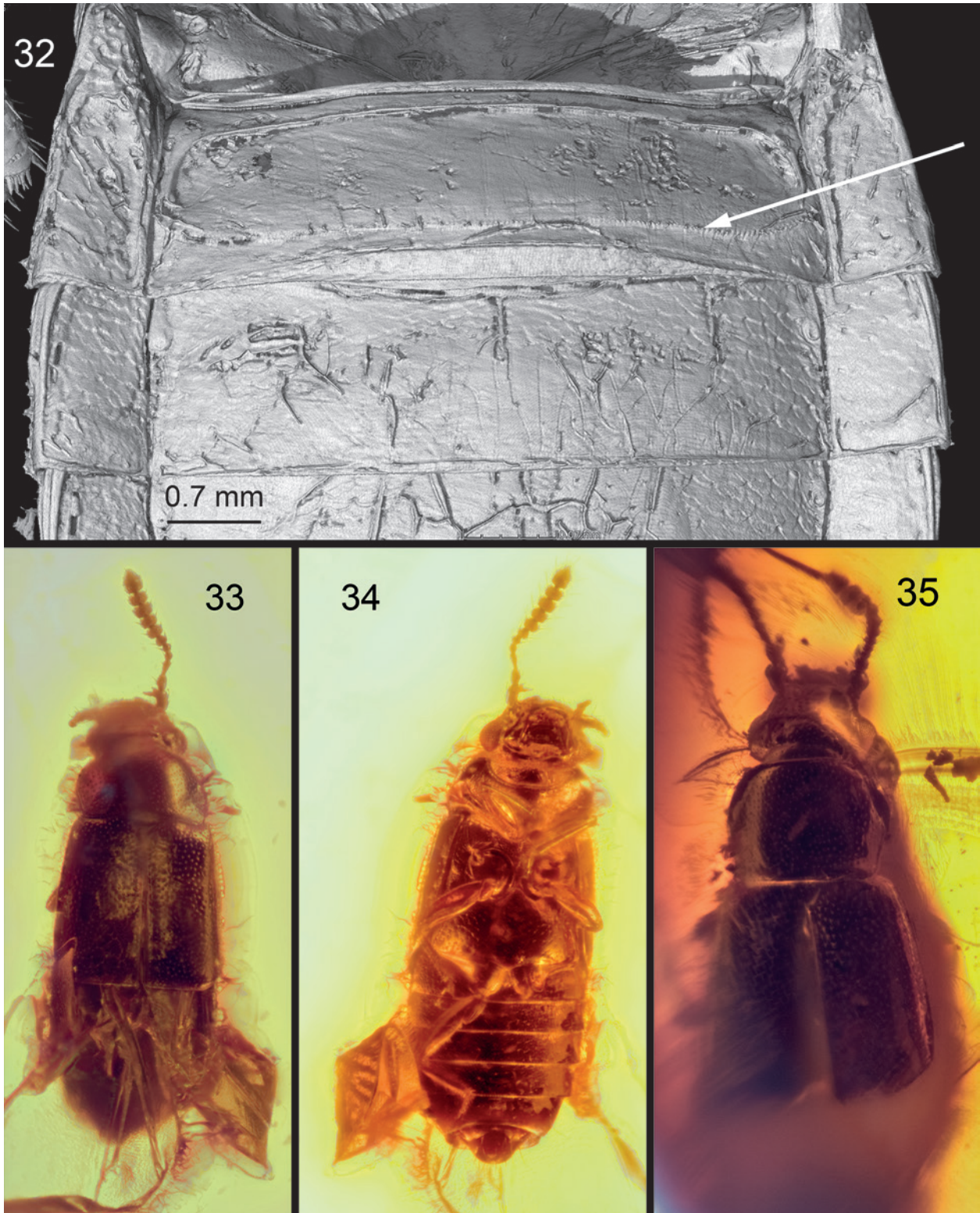
Description. Head. Eyes large, occupying most of sides of head, with medium-size ommatidia, separated from vertex by two ridges extending posterad from antennal insertions. Maxillary palpomere 2 about 2 × as long as wide, 2 × as long as 3, palpomere 3 conical, as long as wide, about as wide as 2, palpomere 4 somewhat longer



Figs. 21–31. *Phyllodrepa antiqua* sp.n. 21: Habitus, dorsal view. 22: Habitus, lateral view. 23: Habitus, ventral view. 24: Pronotum, lateral margin (arrow shows the crenulation). 25: Protarsus. 26: Mesotarsus. 27: Metatarsus. 28: Aedeagus, ventral view. 29: Aedeagus, latero-ventral view. 30: Aedeagus, lateral view. 31: Aedeagus, dorsal view. (Pictures by PPC-SrμCT)

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-ocellar depressions (dorsal tentorial pits) large, rounded and close to ocelli, impressions below antennae large and superficial. Punctuation



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.

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, $1.5 \times$ 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 $1.2 \times$ 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

half (Fig. 24), rectilinear in front of posterior angles, anterior margin scarcely narrower than posterior; punctation 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 $1.2 \times$ wider than pronotum, weakly elongate (ratio of length of suture/combined width of elytra = 1.05), weakly enlarged posterad, punctation 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, $1.5 \times$ as wide as long, sparsely punctured, metacoxae contiguous. Metathoracic wings well developed, everted and well visible in the inclusion, omitted from the tomographic illustrations for clarity. **Abdomen** flat, paratergites (two per segment, on segments III–VII) well developed. Tergites 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. Sternites 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 acarinate mesoventrite, 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 antecellar 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 Transbaikalia 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.

Palaebiogeography. 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 palaebiogeographic 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, *Paraphloeostiba* is a rare termophilous member of the subfamily, while *Phyllodrepa* is a more typical temperate. As discussed above with respect to *Paraphloeostiba*, 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.

4. Acknowledgments

We are indebted to Paul Tafforeau (ESRF) and Carmen Soriano for the algorithmic reconstruction of the tomographic scans. Many thanks to Karin Wolf Schwenninger (Staatliches Museum für Naturkunde, Stuttgart) for the SEM picture. Dagmara Żyła (ZMUC) is sincerely acknowledged for the critical reading of the final version of the manuscript and Richard Leschen for useful suggestions. We are very thankful to Margaret Thayer and to an anonymous reviewer for their critical comments that led to the better final version of the paper, and in particular for the helpful information on *Acruliopsis* and *Prosopaspis*. Finally, Line Kræmer (ZMUC) is sincerely acknowledged for taking digital habitus photos of the amber specimens. This work was funded by ESRF under the experiments n°EC530 and LS2248, and by the scientific society “Speofauna” (Paris, France).

5. References

- ADOBE SYSTEMS INC. 2006–2009. Adobe Photoshop Lightroom 2, version 2.6. – Adobe Systems Incorporated, San Jose, USA.
- ALEKSEEV V.I. 2013. The beetles (Insecta: Coleoptera) of Baltic amber: the checklist of described species and preliminary analysis of biodiversity. – *Zoology and Ecology* **23**(1): 5–12. <http://dx.doi.org/10.1080/21658005.2013.769717>.
- ARCHIBALD B., FARRELL B.D. 2003. Wheeler’s dilemma. – *Acta Zoologica Cracoviensia* **46** (suppl. Fossil Insects): 17–23.
- CAI C.-Y., HUANG D.Y. 2013. *Sinanthobium daohugouense*, a tiny new omaliine rove beetle (Coleoptera: Staphylinidae) from the Middle Jurassic of China. – *The Canadian Entomologist* **145**: 496–500.
- CHATZIMANOLIS S., ENGEL M.S. 2011. A new species of *Diochus* from Baltic amber (Coleoptera, Staphylinidae, Diochini). – *ZooKeys* **138**: 65–73.
- CHATZIMANOLIS S., GRIMALDI D.A., ENGEL M.S., FRASER N.C. 2012. *Leehermania prorova*, the earliest staphyliniform beetle, from the Late Triassic of Virginia (Coleoptera: Staphylinidae). – *American Museum Novitates* **3761**: 1–28.
- HERMAN L.H. 2001. Catalog of the Staphylinidae (Insecta: Coleoptera). 1758 to the end of the second millennium. – *Bulletin of the American Museum of Natural History* **256**: 4218 pp.
- HIEKE F., PIETRZENIUK E. 1984. Die Bernstein-Käfer des Museum für Naturkunde, Berlin (Insecta, Coleoptera). – *Mitteilungen aus dem Zoologischen Museum in Berlin* **60**: 297–326.
- HUBER M., CABALLERO R. 2011. The early Eocene equable climate problem revisited. – *Climate of the Past* **7**: 603–633.
- LAK M., NÉRAUDEAU D., NEL A., CLOETENS P., PERRICHOT V., TAFFOREAU P. 2008. Phase contrast X-ray synchrotron imaging: opening access to fossil inclusions in opaque amber. – *Microscopy and Microanalysis* **14**: 251–259.
- LARSSON S.G. 1978. Baltic amber - a palaeobiological study. – *Entomograph* **1**: 192 pp.
- LESCHEN R.A.B., BEUTEL R.G. 2004. Ocellar atavism in Coleoptera: plesiomorphy or apomorphy? – *Journal of Zoological Systematics and Evolutionary Research* **42**(1): 63–69.
- NEWTON A.F., THAYER M. 1995. Protopselaphinae new sub-family for *Protopselaphus* new genus from Malaysia, with a phylogenetic analysis and review of the Omaliine Group of Staphylinidae including Pselaphidae (Coleoptera). Pp. 219–320 in: PAKALUK J., SLIPINSKI S.A. (eds): *Biology, Phylogeny, and Classification of Coleoptera: Papers Celebrating the 80th Birthday of Roy A. Crowson*. – Muzeum i Instytut Zoologii PAN, Warszawa.
- NEWTON A.F., THAYER M.K., ASHE J.S., CHANDLER D.S. 2000. 22. Staphylinidae Latreille, 1802. Pp. 272–418 in: ARNETT R.H., THOMAS M.C. (eds), *American Beetles Volume 1, Archostemata, Myxophaga, Adephaga, Polyphaga: Staphyliniformia*. – CRC Press, Boca Raton, FL. xv + 443 pp.
- PARKER J., GRIMALDI D.A. 2014. Specialized myrmecophily at the ecological dawn of modern ants. – *Current Biology* **24**: 2428–2434.
- PERIS D., THAYER M.K., NÉRAUDEAU D. 2014. Oldest Omaliini (Coleoptera: Staphylinidae: Omaliinae) discovered in the opaque Cretaceous amber of Charentes. – *Annals of the Entomological Society of America* **107**(5): 902–910.
- PERREAU M., TAFFOREAU P. 2011. Virtual dissection using phase-contrast X-ray synchrotron microtomography: reducing the gap between fossils and extant species. – *Systematic Entomology* **36**: 573–580.
- RYVKIN A.B. 1985. Zhuki semeistva Staphylinidae iz Iury Zabai-kal’ia. – *Trudy Paleontologicheskogo Instituta, Akademia Nauk SSSR* **211**: 88–91. [in Russian]
- RYVKIN A.B. 1990. Semeistvo Staphylinidae Latreille, 1802. Pp. 52–66 in: RASNITSYN A.P. (ed.), *Pozdne-Mezozoiskie nasekomye vostochnogo Zabaikal’ia*. – *Trudy Paleontologicheskogo Instituta, Akademia Nauk SSSR* **239**: 1–222. [in Russian]
- SCHAUFUSS L.W. 1890. Eine Staphylinidengattung aus dem baltischen Bernsteine. – *Entomologische Nachrichten* **16**(5): 69–70.
- SOLODOVNIKOV A., YUE Y., TARASOV S., REN D. 2013. Extinct and extant rove beetles meet in the matrix: Early Cretaceous fossils shed light on the evolution of a hyperdiverse insect lineage (Coleoptera: Staphylinidae: Staphylininae). – *Cladistics* **29**: 360–403.
- STEEL W.O. 1955. Notes on the Omaliinae (Col. Staphylinidae). 7. The genus *Xanthonomus* Bernhauer. – *The Entomologist’s Monthly Magazine* **91**: 275–278.
- STEEL W.O. 1960. Three new Omaliinae genera from Asia and Australasia previously confused with *Phloeonomus* Thomson. – *Transactions of the Royal Entomological Society of London* **112**(7): 141–172.
- STORK N.E. 1980. A scanning electron microscope study of tarsal adhesive setae in the Coleoptera. – *Zoological Journal of the Linnean Society* **68**: 173–306.
- SZWEDO J., SONTAG E. 2013. The flies (Diptera) say that amber from the Gulf of Gdańsk, Bitterfeld and Rovno is the same Baltic amber. – *Polish Journal of Entomology* **82**(4): 379–388.
- TAFFOREAU P., BOISTEL R., BOLLER E., BRAVIN A., BRUNET M., CHAÏMANEE Y., CLOETENS P., FEIST M., HOSZOWSKA J., JAEGER J.J., et al. 2006. Applications of X-ray synchrotron microtomography for non-destructive 3D studies of paleontological specimens. – *Applied Physics A, Materials Science, Processing* **83**: 195–202.
- THAYER M. 1985a. *Micralymma marinum* (Stroem) in North America: biological notes and new distributional records (Coleoptera: Staphylinidae). – *Psyche* **92**(1): 49–55.
- THAYER M. 1985b. The larva of *Brathinus nitidus* Leconte and the systematic position of the genus (Coleoptera: Staphylinidae). – *The Coleopterist Bulletin* **39**(2): 174–184.

- THAYER M. 1992. Discovery of sexual wing dimorphism in Staphylinidae (Coleoptera): “*Omalius*” *flavidum*, and discussion of wing dimorphism in insects. – Journal of New York Entomological Society **100**(4): 540–573.
- TIKHOMIROVA A.L. 1968. Zhuki-stafilinidy Iuri Karatau. Pp. 139–154 in: ROHDENDORF B.B. (ed.), Iurskie nasekomye Karatau, Akademiia Nauk SSSR, Otdelenie obshei biologii. – Moskva, Izdatel'stvo Nauka. [in Russian]
- TIKHOMIROVA A.L. 1973. Morfoekologicheskiye osobennosti i filogenez Stafilinid (s katalogom fauny SSSR) [Morpho-ecological features and phylogenesis of Staphylinidae]. – Akademiia Nauk SSSR, Moscow. [in Russian]
- TOTTENHAM C.E. 1949. The generic names of the British Staphylinidae with a check list of the species. Part 9. – Pp. 345–466 in: The Generic Names of British Insects. – London, Royal Entomological Society of London.
- WEITSCHAT W., WICHARD W. 2010. Baltic Amber. Pp. 80–115 in: PENNEY D. (ed.), Biodiversity of Fossils in Amber from the Major World Deposits. – Siri Scientific Press, Manchester.
- WHEELER W.M. 1910. Ants; their structure, development and behavior. – Columbia University Press, New York.
- ZANETTI A. 1987. Fauna d'Italia XXV, Coleoptera Staphylinidae Omaliinae. – Calderini, Bologna. xii + 472 pp.
- ZANETTI A. 2012. Omaliinae – Proteininae – Micropeplinae – Pseudopsinae. Pp. 49–127, 321 in: ASSING V., SCHÜLKE M. (eds), Die Käfer Mitteleuropas Band 4 Staphylinidae (exklusive Aleocharinae, Pselaphinae und Scydmaeninae). 2. Auflage. – Spektrum Akademischer Verlag, Heidelberg.