Balticeler kerneggeri gen. nov., sp. nov., an enigmatic Baltic amber fossil of the ground beetle subfamily Trechinae (Coleoptera, Carabidae)

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http://zoobank.org/0D454AFB-9C31-42C3-A5B9-CD9E256C1F41

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Abstract

Balticeler kerneggeri **gen. nov.**, **sp. nov.**, is described based on six fossil specimens preserved in Eocene Baltic amber and imaged using light microscopy and X-ray micro-computed tomography. Based on certain characters observed in the fossil species it is considered a "middle grade" Carabidae, outside of the large family Harpalinae (as it possesses a scrobal seta, the lack of which is a synapomorphy of that subfamily), but possessing four synapomorphies that indicate *Balticeler* belongs to a large clade of carabids including Harpalinae (anisochaetous Grade B antennal cleaner, conjunct mesocoxae, closed procoxal cavities, and a well-developed external lobe of the metepimeron). This remarkable beetle has several striking features, including lack of externally-visible sexually dimorphic characters, lack of lateral borders on the pronotum, and very long and thin mandibles and maxillae. In combination, these states are unique within Carabidae. We consider the presence of a dorsally completely open aedeagal median lobe as a synapomorphy of the fossil species with the subfamily Trechinae, a pubescent and relatively long second antennomere and a 4+2+2 pattern of umbilicate setae as synapomorphies of the supertribe Trechitae, and a quadrisetose clypeus as a synapomorphy with the Trechitae clade Bembidarenini + Trechini sensu Maddison et al. (2019). As it lacks a synapomorphy of Bembidarenini + Trechini, we propose that it is a member of the stem group of that clade.

Key Words

Introduction

In recent years, paleontological knowledge of ground beetle has increased rapidly. This became possible due to the availability of numerous well-preserved fossil species in Baltic and Burmese Amber on the one hand, and due to the application of non-invasive high-resolution investigation techniques to amber inclusions such as X-ray microscopy on the other (Schmidt et al. 2019; Beutel et al. 2020). Based on previously described fossils from Eocene Baltic amber (50–44 Ma; Wolfe et al. 2009) it appears evident that the carabid fauna of the mid Paleogene period had a modern appearance with occurrence of several species belonging to recent genera, e.g., *Bembidion* Latreille (Schmidt and Michalik 2017), *Calathus* Bonelli (Ortuño and Arillo 2009),

Coptodera Dejean (Gamboa and Ortuño 2015), *Limodromus* Motschulsky (Schmidt 2015), and *Trechus* Clairville (Schmidt et al. 2016). However, the fossil treasures of amber deposits are far from being comprehensively investigated. Many of the ground beetle genera mentioned in the earlier catalogues of amber fossils (e.g., Klebs 1910; Bachofen-Echt 1949; Larsson 1978; Spahr 1981; Keilbach 1982) have not been investigated using modern methods. For instance, based on the catalogues mentioned above, the genus *Nebria* Bonelli was noted as being preserved in Baltic amber; however, based on micro-CT analyses it was shown that all of the available nebriine amber fossils belong to an extinct lineage which is more closely related to the genera *Leistus* Frölich and *Nippononebria* Uéno (Schmidt et al. 2019). For additional ground beetles described from Baltic amber

close relationships to modern genera remain unclear, e.g., the cliviine fossil *Dyschiriomimus* Yablokov-Khnzorian and the tachyine fossil *Tarsitachys* Erwin (Yablokov-Khnzorian 1960; Gamboa and Ortuño 2015). In this study, we document the presence of an additional carabid species in the pre-Palearctic fauna of the Eocene period which is known to us from six fossils preserved in Baltic amber; this species is exceptional in its external shape, and has no close relatives in the modern fauna.

Materials and methods

This study is based on six fossil specimens preserved in pieces of Eocene Baltic amber (see below for details). This fossil material originated in the coastal area of the southeastern Baltic Sea.

The specimens were studied and imaged using light microscopy and micro-CT. For light microscopy analyses, we used a Leica M205-C stereomicroscope with a Leica DFC450 digital camera, a motorized focusing drive, and a cold-light source with a polarizing filter system on a three-armed gooseneck. Images were subsequently processed with Leica LAS application software and enhanced with Corel DRAW Graphics Suite X5.

Micro-CT scans were performed with a ZEISS Xradia 410 Versa X-ray imaging system operating with ZEISS Xradia Scout-and-Scan Control System v.11.1 (Carl Zeiss X-Ray Microscopy, Pleasanton, USA) using the 4× objective lens. Scan settings used are shown in Table 1. Tomography projections were reconstructed by using Reconstructor Scut-and-Scan v.11.1 software (Carl Zeiss Microscopy GmbH), resulting in image stacks (TIFF format). Volume rendering of image stacks was performed by using Amira 6.1 software (FEI Visualization Science Group, Burlington, USA) using the "Volren", "Volume Rendering" and "Segmentation" functions.

Measurements and proportions: The measurement features in Amira Software was used and applied to the X-ray scanning results of the negative imprint of the fossil on the inclusion wall. The length of the head was measured from apex of clypeus to a point on midline at level of posterior margin of compound eye. The width of the head was measured across the widest portion including compound eyes. The length of the pronotum was measured from apical margin to basal margin along midline. The width of the pronotum and the width of each elytron were measured at their widest points (in dorsal aspect). The width of the pronotal apical margin was measured between the tips of the front angles. The width of the pronotal base was measured between the tips of the hind angles. The length of each elytron was measured along the midline from the apex of scutellum to the apex of the respective elytron. The length of the femur and the aedeagal median lobe were measured across their longest distances.

Body length is given as standardized body length (SBL), which equals the sum of the lengths of the head, pronotum, and the longer elytron.

Ratios were presented as follows: pronotal width to head width (PW/HW); width to length of pronotum (PW/PL); width of pronotum to width of pronotal base (PW/PWb); width of pronotal base to width of pronotal apical margin (PWb/PWa); width of elytra to width of pronotum (EW/PW); length of the longer elytron to width of elytra (EL/EW); length of the longer elytron to length of the longer femur (EL/FL); length of the longer elytron to length of the aedeagal median lobe (EL/AedL).

Results and taxonomy

The six specimens are documented in Figs 1–35, as well as in the description, below. Measurements are recorded in Tables 2, 3.

### *Balticeler* Schmidt & Maddison, gen. nov.

http://zoobank.org/A33BE760-1C69-4DE3-BEE5-E2168C3CCCA2

Type species. *Balticeler kerneggeri* sp. nov.

Description. Diagnosis: Small, markedly shiny ground beetle (due to reduced microsculpture on body surface), with nearly cylindrical body shape (Figs 11–14); pronotal marginal borders absent, very slender mandibles and maxillae, and with basal protarsomeres in male not widened.

Head: Slender in its anterior part, robust from level of eyes towards base, with disc markedly convex, base broad and neck constriction absent (Figs 1, 15). Mandibles and maxillae notably long and slender, teeth on mandibular internal margin small, not prominent, markedly shifted basally, mandibular scrobe with seta (Fig. 17). Labrum with apical margin very slightly concave, with six setae

Table 1. MicroCT scan settings.

	holotype	paratype 1	paratype 2	paratype 3	paratype 4	paratype 5
voltage [V]	40	45	40	40	40	40
power [W]	8	8	8	8	8	8
object lens	4	4	4	4	4	4
lens filter	none	none	LE3	none	none	none
cam binning	2	2	2	2	2	2
distance to source [mm]	90	102	80	90	120	100
distance to detector [mm]	70	17	60	102	80	40
vertical stitch	none	2×	none	none	none	none
voxel size [µm]	3.79	2.4	3.85	3.16	4.02	4.81
exposure time [sec]	40	26	30	20	25	20
number of images/segment (scanning radius)	2401 (360°)	2501 (360°)	1201 (180°)	2401 (360°)	2401 (360°)	2201 (360°)
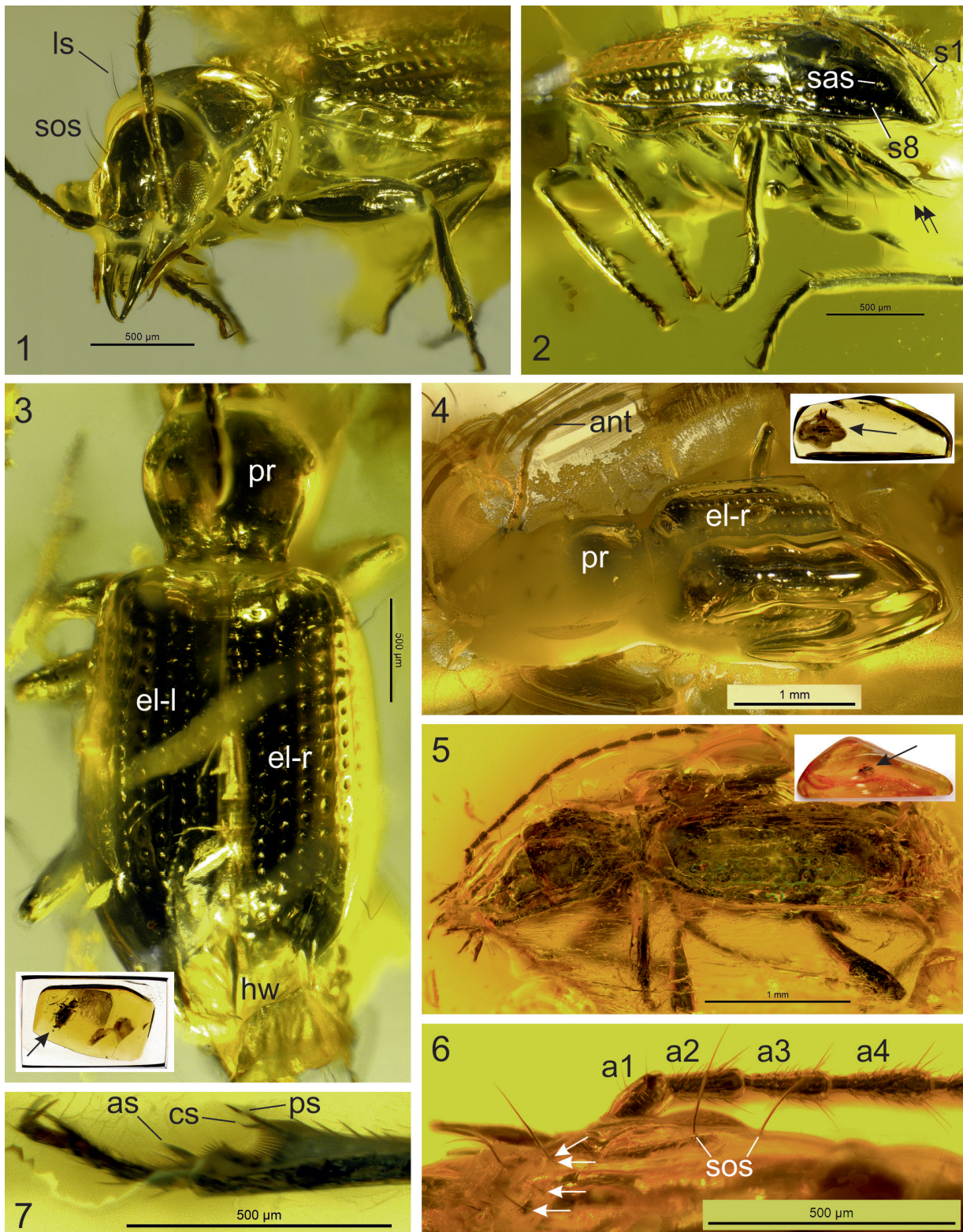
Figures 1–7. *Balticeler kerneggeri* gen. nov., sp. nov., light microscopic images of the holotype (coll. Kernegger 235; **1–3**), paratype 1 (OSAC 000-2900006; **4**), paratype 2 (coll. Groehn 8234; **5–7**); the enclosed photographs in **3–5** show the general view of the respective amber pieces, with arrows pointing to the respective location of the carabid fossil. **1.** Frontolateral view of the fossil specimen. **2.** Posterolateral view of the fossil specimen (the arrows point to the two setae on left side of abdominal segment VII). **3–5.** Dorsal (**3, 4**) respectively left dorsolateral view (**5**) of the fossil specimens. **6.** Head, left dorsolateral view (the white arrows point to the insertions of the four clypeal setae). **7.** Right protarsomeres and anterior part of tibia with antenna cleaner, anterior surface. Abbreviations: **a1–a4** – antennomeres 1–4; **ant** –antenna; **as** – protibial anterior spur; **cs** – clip setae of antenna cleaner; **el-l** – left elytron; **el-r** – right elytron; **hw** – hind wing; **ls** – pronotal lateral seta; **pr** – pronotum; **ps** – protibial posterior spur; **s1, s8** – 1st resp. 8th elytral stria; **sas** – subapical seta of elytra; **sos** –supraorbital seta.

near apical margin (Fig. 1). Clypeus with two primary setae on each side (Fig. 15). Anterior and posterior tactile supraorbital setae present (Figs 1, 15, 16); suborbital seta absent. Furrows on head disc shallow, very short, terminating posteriorly at level of anterior supraorbital setae (Figs 1, 15). Eyes moderately large, moderately protruded laterally; tempora short, about quarter of eye length, very slightly wrinkled towards the neck (Figs 15, 16). Antennae moderately slender, pubescent beginning from second antennomere; pedicellus about as long as scapus and third antennomere (Fig. 3). Ligula long and slender, with apex pointed, partly fused with paraglossae, latter distinctly protruded apically (Fig. 19); chaetotaxy of ligula not visible with the methods we used. Mentum with median tooth simple, with one pair of sharply defined pits; mentum and submentum separated by distinct suture; mentum with one pair of tactile setae laterally of apical tooth, submentum with two pairs of tactile setae in normal position (Fig. 18). Terminal maxillary and labial palpomeres about as long as penultimate palpomere, with shape slightly conical (Fig. 1); penultimate maxillary palpomere glabrous; penultimate labial palpomere glabrous except for two long setae in middle.

Prothorax: Small, subcordate, with disc markedly convex, and with apical, basal and lateral borders absent (Figs 13, 14, 20; in CT images from some angles, such as that shown in Fig. 20, the shrunken exoskeleton and the negative imprint of the beetle on the inclusion wall may give the impression of existing border lines); anterior margin straight with lateral angles rounded, not protruded anteriorly; basal margin slightly convex in middle and with outer sixth markedly shifted anterad; laterobasal angles moderately large, obtuse, very slightly protruded laterally; anterior lateral seta situated near anterior end of second pronotal third, posterior seta situated at basal angle (Figs 8, 20). Median line on pronotal disc deep between anterior and posterior transverse impressions, absent near apex and base; anterior transverse impression distinct, complete; posterior transverse impression broad, marked by three large pits medially, and small, irregularly impressed laterobasal grooves laterally (Fig. 20). Prosternum coarsely punctate (Figs 12, 22); prosternal process short, widened towards truncated posterior margin (Fig. 22); procoxal cavities closed externally.

Pterothorax: Elytra in dorsal view moderately ovate to sub-parallel, much broader than pronotum, with sides very slightly narrowed towards broad humerus (Figs 3, 8, 11, 26, 29, 36, 38, 41), in lateral and frontal or caudal views markedly convex towards disc, such that hind body is almost circular in cross-section (Figs 9, 13, 14, 21, 28, 30, 37, 39, 40, 42). Basal border absent from base of 5th stria inwards (Fig. 11). Parascutellar stria abbreviated, connected with the first stria, parascutellar tactile seta present, situated at base of second stria (Fig. 11). Striae 1–9 slightly impressed in anterior 4/5 but markedly accented by rows of large and deeply engraved punctures (Figs 3, 8–11, 21, 29, 36, 41); punctures gradually less

deep from anterior 1/9 towards base and posterior quarter towards apex, latter smooth beside the deeply engraved 1st and 8th striae, with recurrent stria absent and subapical setiferous pore "isolated" (the seventh and the internally adjacent striae are invisible) (Figs 2, 21); intervals convex on elytral disc, flat near elytral base and apex. Three discal setae present on each elytron; all are connected to the third stria, with anterior one located near end of anterior elytral 5th, second located slightly anterior of elytral middle, and posterior one located slightly posterior of elytral 2/3 (Figs 9, 11). Umbilicate series consists of eight setae distinctly separated into three groups (Fig. 14): humeral group (four setae, with posterior one slightly more distant than setae 1–3), medial group (two setae, located distinctly behind elytral middle), subapical group (two setae). Elytral subapical plica present (Fig. 21). Hindwings fully developed. Mesoventrite and metaventrite near anterior margin coarsely punctate (Figs 12, 22); mesocoxal cavities conjunct; mesepimeron wide, metanepisternum long and slender, external lobe of metepimeron well developed (Fig. 22).

Legs moderately robust, short (Fig. 12). Protibia with antenna cleaner anisochaetous Grade B (Hlavac 1971), with basal portion of cleaning channel flat, extending basad far beyond insertion of the clip setae, and with insertion of posterior spur very slightly distad of that of the clip setae (Figs 24, 25); protibial external surface smooth, without longitudinal groove, and with apicolateral surface obliquely excised (Fig. 23). Basal protarsomeres of males not dilated, not uniquely dentate (Fig. 23). Fifth tarsomeres of all legs ventrally smooth, without setae. Mesocoxa with one seta at external margin; metacoxae laterally not extended to elytral epipleuron, trisetose, with both the external setae distinctly removed from the coxal ridge; metatrochanter with a single seta (Fig. 22).

Abdomen: Smooth beside primary setation: segments IV–VI with a single, VII with two pairs of setae near apical margin (Fig. 2).

Male genitalia: Shape of the parameres of Trechitae type, nearly symmetrical, in general structure similar to parameres of Patrobini, markedly large, each with a long and slender apical apophysis which is more strongly sclerotized on its internal margin, with a large and almost discoidal middle portion, and with a heavily sclerotized basal portion (Figs 32a–d, 35a); chaetotaxy and membranous parts (e.g., those which probably connect apical and medial portions of the parameres externally) not recognizable. Median lobe moderately long and slender, in lateral view slightly sinusoidal in apical third (Figs 32a, 33, 34a), in dorsal view with its distal portion very slightly bent to the right (Figs 32c, d, 34b); apical lamella well-developed, almost as broad as median lobe. Dorsal surface of median lobe completely open: basal and apical ostia broadly connected across the dorsal median lobe surface, with separated lateral lobes of median lobe basal bulb (Figs 32b, c).

**Etymology.** The generic name compounds the geographical term "Balticum" which is the origin of the
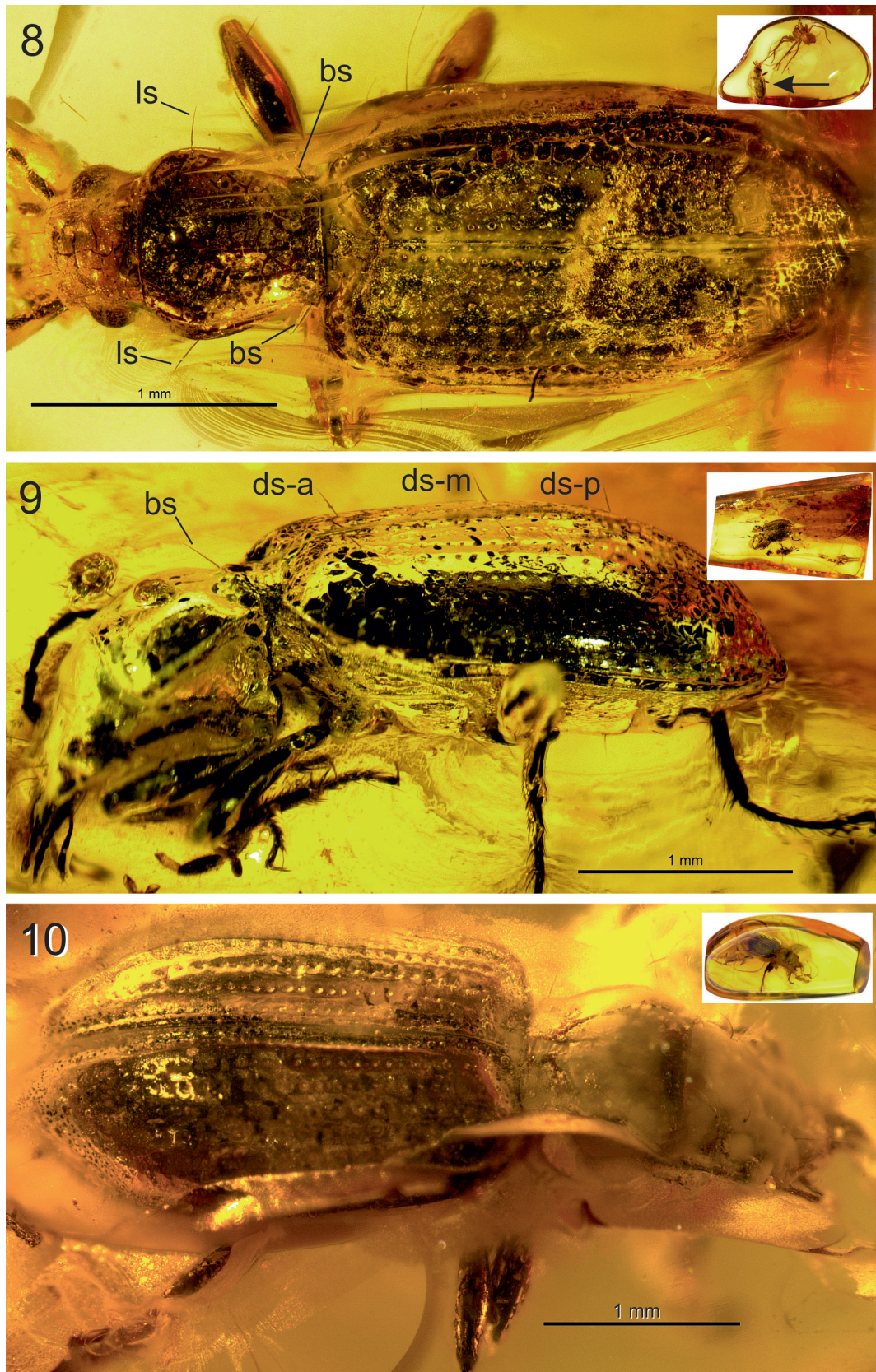
Figures 8–10. *Balticeler kerneggeri* gen. nov., sp. nov., light microscopic images of the paratype 3 (OSAC 000-2900387; **8**), paratype 4 (OSAC 000-2900600; **9**), paratype 5 (coll. Sciaky; **10**); the enclosed photographs show the general view of the respective amber pieces, with arrow in **8** pointing to the location of the carabid fossil. **8.** Dorsal view. **9.** Left lateral view. **10.** Right dorsolateral view. Abbreviations: **bs** – pronotal basal seta; **ds-a, ds-m, ds-p** – anterior, medial respectively posterior discal seta on right elytron; **ls** – pronotal lateral seta.
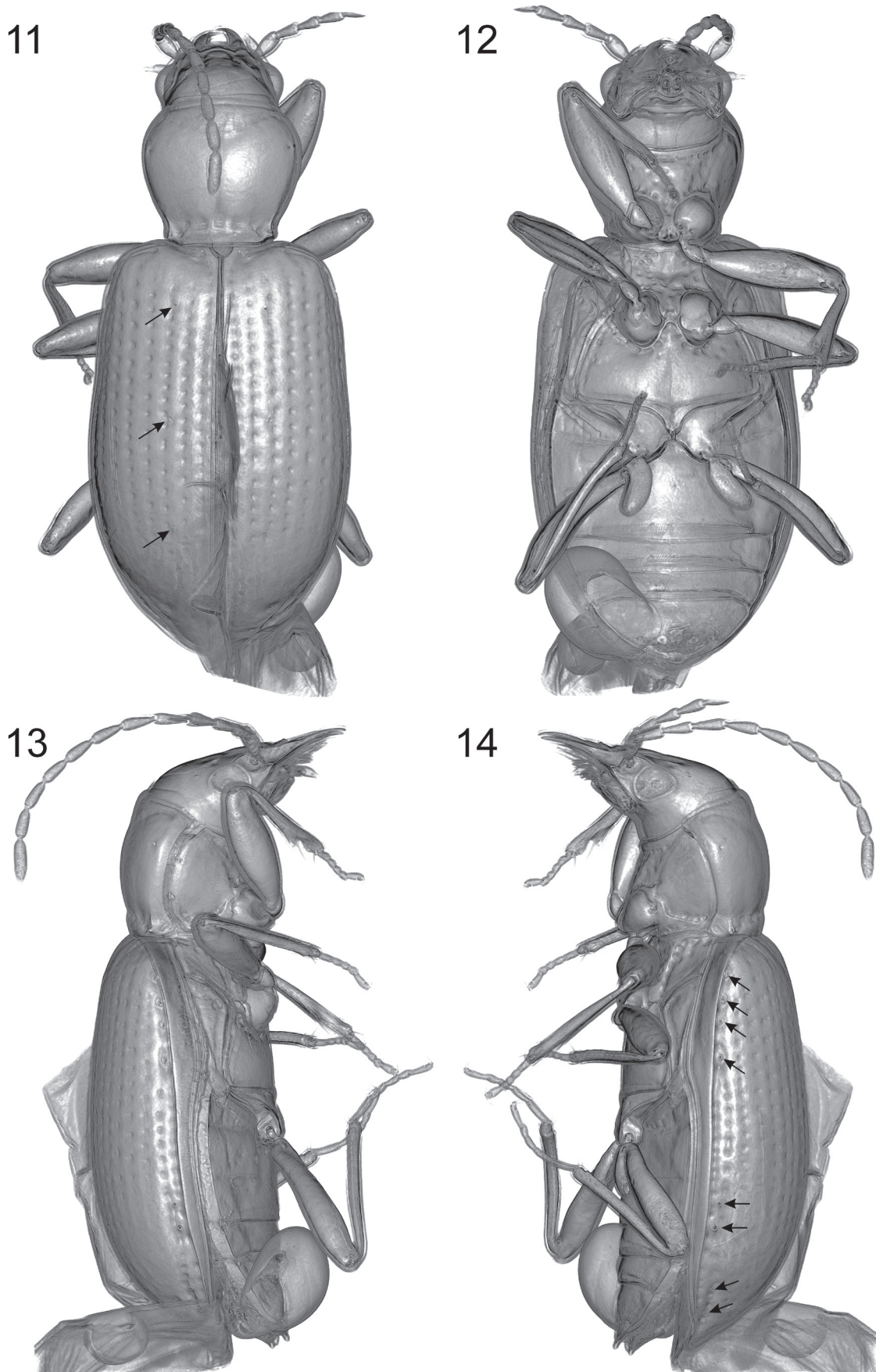
Figures 11–14. *Balticeler kerneggeri* gen. nov., sp. nov., volume rendering of the holotype. **11.** Dorsal aspect (the black arrows point to the positions of the discal seta on left elytron). **12.** Ventral aspect. **13.** Right lateral aspect. **14.** Left lateral aspect (the black arrows point to the positions of the seta of the umbilicate series on left elytron).

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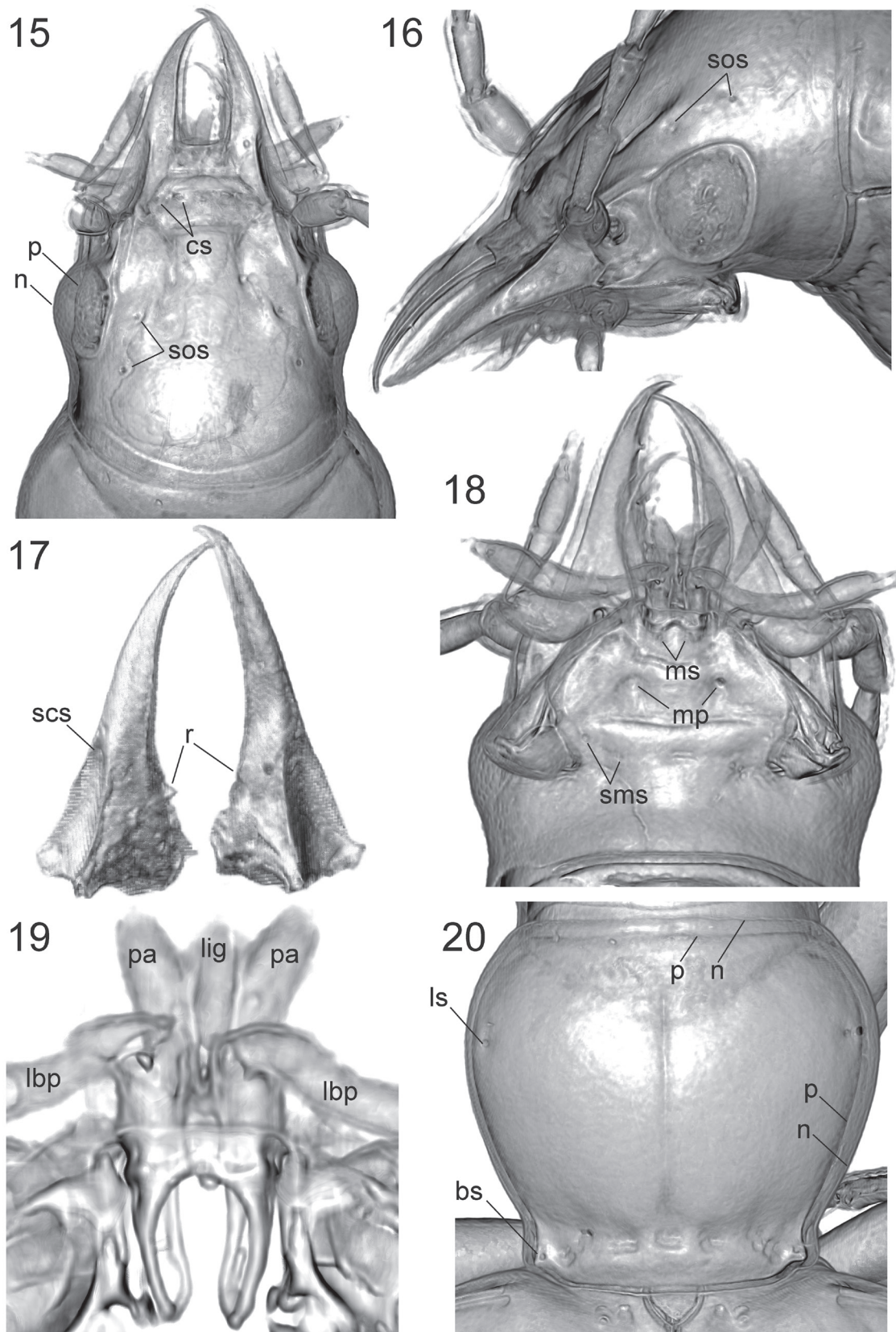
Figures 15–20. *Balticeler kerneggeri* gen. nov., sp. nov., volume rendering of the holotype. **15.** Head, dorsal aspect. **16.** Head, left lateral aspect. **17.** Mandibles, dorsal aspect. **18.** Head, ventral aspect. **19.** Labium, ventral aspect. **20.** Pronotum, dorsal aspect. Abbreviations: **bs** –pronotal basal seta; **cs** – clypeal setae; **lbp** – labial palpomeres; **lig** – ligula; **mp** – mentum pits; **ls** – pronotal lateral seta; **ms** – setae of mentum; **n** – negative imprint of the specimen on the inclusion wall; **p** – shrunken exoskeleton of the fossilized specimen (= positive); **pa** – paraglossae; **r** – retinacle of mandibular teeth; **scs** – scrobal setae of mandibles; **sms** – setae on submentum (only right side is shown); **sos** – supraorbital setae.

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22

23 **24**

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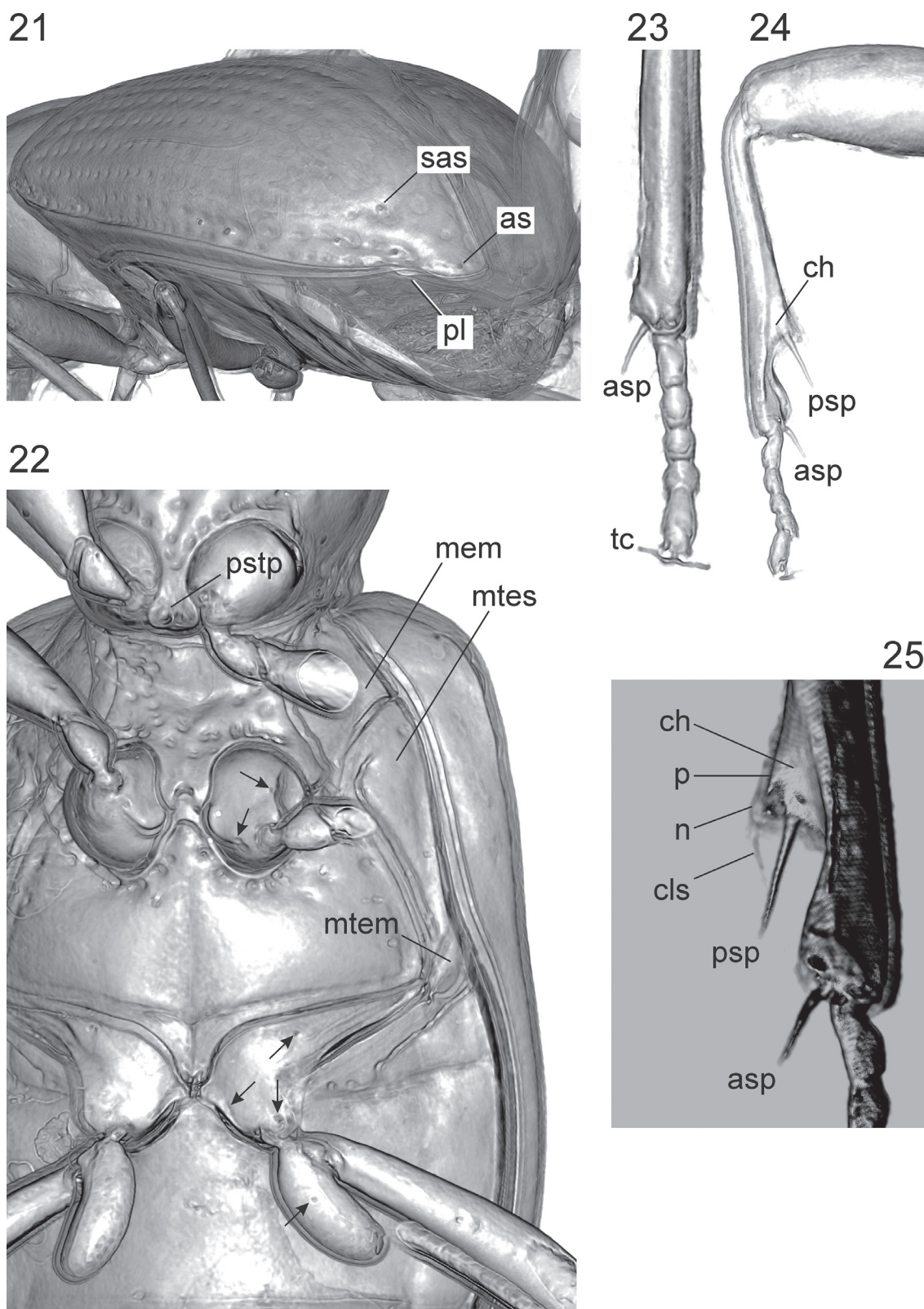
Figures 21–25. *Balticeler kerneggeri* gen. nov., sp. nov., volume rendering of the holotype. **21.** Elytra and abdomen, left lateral aspect. **22.** Ventral aspect of median part of body showing pro-, meso- and metasterna; the arrows point to the insertions of the setae on mesocoxa, metacoxa and metatrochanter. **23.** Tarsomeres and apical portion of tibia of left proleg, view from dorsad. **24.** Left proleg, view from anterad. **25.** Antenna cleaner of left proleg, view from posterad (note that in the fossilized specimen the clip setae are preserved only in the negative imprint of the beetle body on the inclusion wall). Abbreviations: **as** – apical seta of elytra; **asp** – protibial apical spur; **cls** – clip setae; **mem** – mesepimeron; **mtem** – external lobe of metepimeron; **mtes** – metanepisternum; **n** – negative imprint of the tibia on the inclusion wall; **p** – shrunken exoskeleton of the fossilized tibia (= positive); **pl** – epipleural apical plica of elytra; **psp** – protibial apical spur; **pstp** – prosternal process; **sas** – subapical seta of elytra; **tc** – tarsal claws.

amber where the new fossil lineage is preserved, and the Latin verb "celare" (concealing), and therewith refers to the specific circumstance that an odd lineage of ground beetles is hidden in Baltic amber.

Balticeler kerneggeri Schmidt & Maddison, sp. nov.
http://zoobank.org/32A6F70E-6731-490D-B563-73F3F79695B0

Type material. *Holotype*: Male in Baltic amber, Coll. Friedrich Kernegger in the Centrum of Natural History, Hamburg (CeNak), with collection number "GPIH 04897, coll. Kernegger 1995/235". Size of the amber piece approx. 13 × 7 × 7 mm, irregularly cut, embedded in synthetic resin (Hoffeins 2001) (Fig. 3).

Preservation status: The amber is clear but pervaded by few flowlines dorsally of the embedded beetle fossil. The fossil is partly covered by milky coating on the ventral side of the body. The exoskeleton of the specimen and its negative imprint on the inclusion wall is well preserved and could therefore be visualized in detail using micro-CT (Figs 11–14). In contrast, the aedeagus is poorly preserved inside the fossilized beetle body: it is strongly shrunken and deformed and therefore, its original shape and structure could not be determined.

Syninclusions: None.

Paratype 1: Male in Baltic amber, deposited in the Oregon State University Collection, with specimen number OSAC_0002900006. Size of the amber piece approx. 21 × 8 × 4 mm, irregularly cut (Fig. 4).

Preservation status: The embedded beetle fossil is almost completely surrounded by flowlines. Head and prothorax are additionally covered by milky coating. Therefore, only small parts of the beetle body are visible using light microscopy (Fig. 4). The exoskeleton of the fossil and its negative imprint on the inclusion wall are moderately well preserved and could therefore be imaged using micro-CT, but the head capsule is partly shrunken and displaced into the prothorax (Figs 26–28). The aedeagus is rather well preserved inside the fossilized beetle body and could therefore be imaged using micro-CT in most details (Figs 27, 28, 32, 33, 35); its external shape particularly near base, including the lateral lobes of the median lobe basal bulb, seem somewhat deformed (Fig. 33), probably because the fossil specimen was embedded during an immature stage of its development; the apical apophysis of the right paramere is only partly preserved (Fig. 32d).

Syninclusions: None.

Paratype 2: Male in Baltic amber, Coll. Carsten Gröhn in the collection of the Geological-Palaeontological Institute of the University of Hamburg (GPIH), now in the Centrum of Natural History, Hamburg (CeNak), with collection number "GPIH 5044, coll. Gröhn 8234". The amber piece was nearly triangularly cut with an edge length of about 33, 26, and 16 mm, and with width of 5 mm (Fig. 5).

Preservation status: The amber is clear; large flowlines are attached to the left lateral side of the embedded beetle.

The ventral surface of the beetle body is partly covered by milky coating. Antenna, legs, and dorsal surface of head are clear and thus well visible using light microscopy (Figs 6, 7). The skeleton of the fossil beetle specimen together with its aedeagus is moderately well preserved and could therefore be imaged using micro-CT (Figs 29–31); however, the basal portion of the aedeagus is partly decayed so that the parameres are preserved only with the more strongly sclerotized median parts (Fig. 34 a, b).

Syninclusions: 1 stellate hair, few dust particles.

Paratype 3: Specimen of unknown sex in Baltic amber, deposited in the Oregon State University Collection, with amber piece number OSAC_AMB0000387. According to the dealer (Marius Veta, Palanga) from whom the amber was purchased, this is most likely Baltic amber from the Yantarni mine, but there is a slight chance that it is Rovno amber. Size of the amber piece approx. 14 × 8 × 2 mm, irregularly cut (Fig. 8).

Preservation status: The amber is clear but the ventral surface of the embedded beetle is completely covered by milky coating. Flowlines within the amber extend to each lateral side of the fossil. Most parts of the legs and the tip of the abdomen were abraded during polishing process and are thus lacking. Therefore, only the dorsal side of the beetle body is visible using light microscopy (Fig. 8). The negative imprint of the fossil on the inclusion wall has low contrast in the X-ray analyses and therefore, certain details of external morphology could not be imaged and the sex of the specimen could not be assessed (Figs 36, 37).

Syninclusions: One spider.

Paratype 4: Specimen of unknown sex in Baltic amber, deposited in the Oregon State University Collection, with amber piece number OSAC_AMB0000600. Size of the amber piece approx. 13 × 8 × 5 mm, cut into an approximately trapezoidal form (Fig. 9).

Preservation status: The amber is pervaded by numerous air bubbles on the right side to the embedded beetle fossil; the latter is well visible from dorsal, left lateral and ventral sides using light microscope (Fig. 9), but the head and thorax are covered by milky coating ventrally. The stone was very likely altered by autoclaving in order to reduce milky coating; this is evident from the blackened appendages of the beetle which are slightly deformed (particularly tibiae and tarsi), and from one of the synincluded Collembola which has a roasted appearance (for the effect of autoclaving on amber fossils see Hoffeins 2012). Very probably as a consequence of autoclaving, the negative imprint of the fossil on the inclusion wall has low contrast in the X-ray analyses; certain details of external morphology could thus not be imaged, and the genital armatures are not preserved (Figs 38–40).

Syninclusions: One rove beetle (Staphylinidae), one springtail (Collembola), remains of a second springtail.

Paratype 5: Specimen of unknown sex in Baltic amber, ex collectio Riccardo Sciaky (Milano), now preserved in the Museum für Naturkunde Berlin, with specimen number MB.I.8614. Size of the amber piece approx. 10 × 5 × 5 mm, polished into a somewhat bean-shaped piece (Fig. 10).
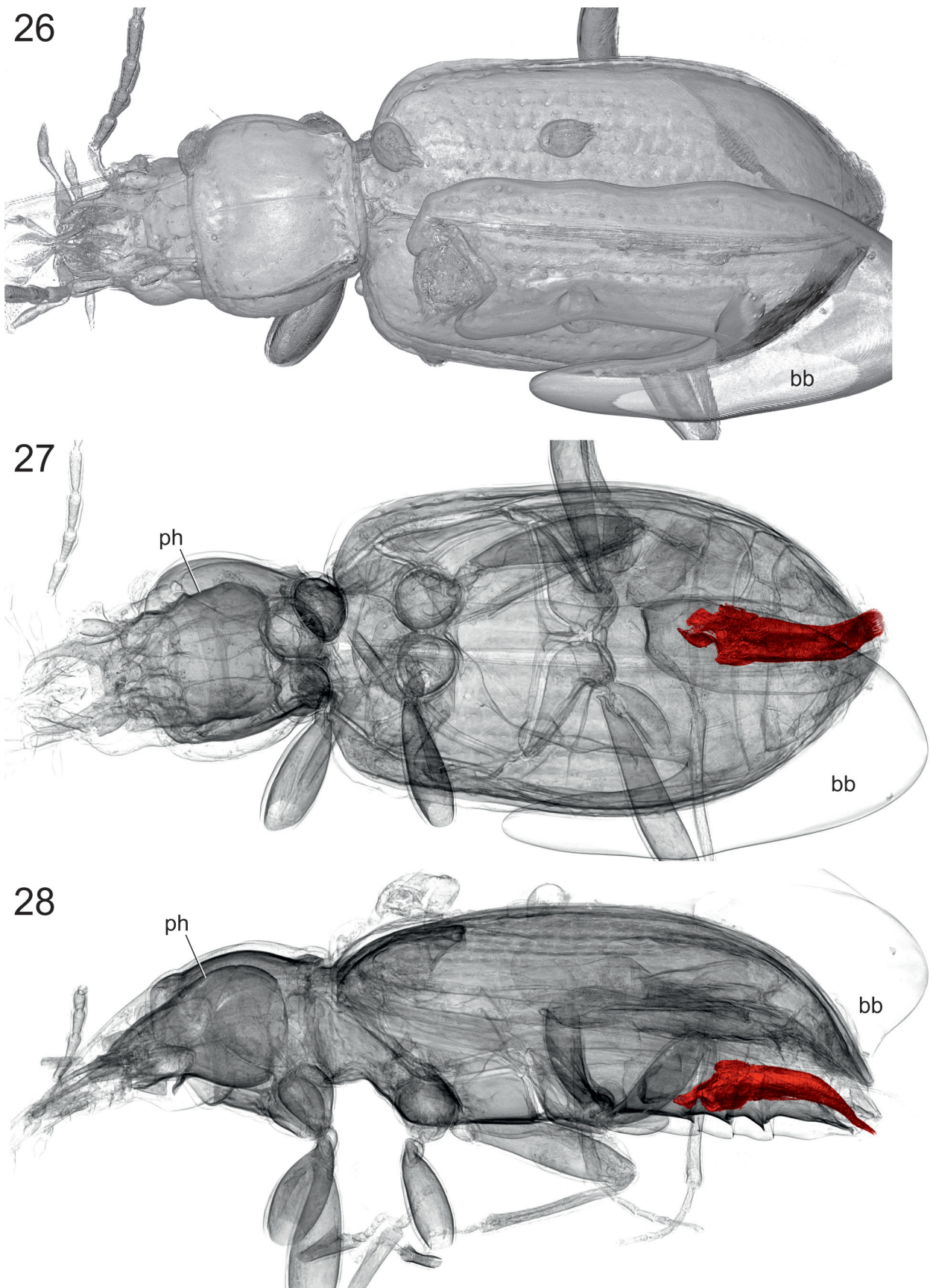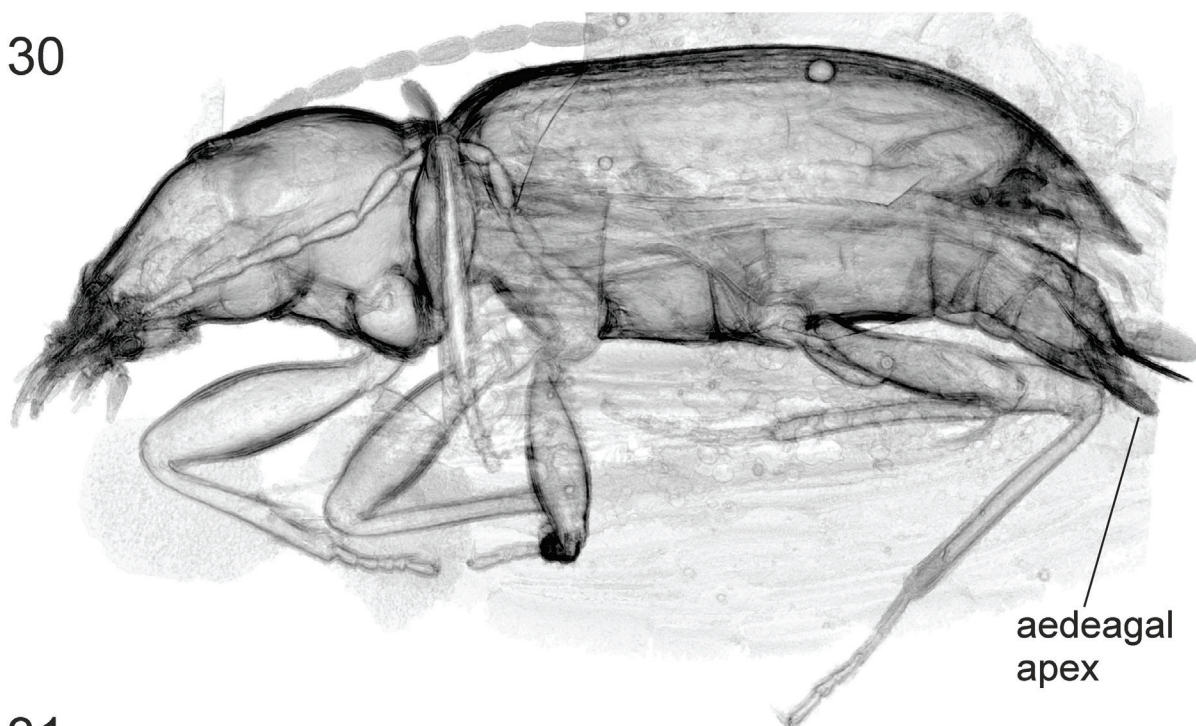
Figures 26–28. *Balticeler kerneggeri* gen. nov., sp. nov., volume rendering of the paratype 1 (OSAC 000-2900006) using different grey scales. **26, 27.** Dorsal aspect. **28.** Right lateral aspect. The aedeagus (highlighted by red colour) was separated by the segmentation function of Amira software in **27** and **28**. Abbreviations: **bb** – air bubble attached to the left posterior part of the beetle body; **ph** – shrunken and posteriorly displaced head capsule of the fossil specimen.
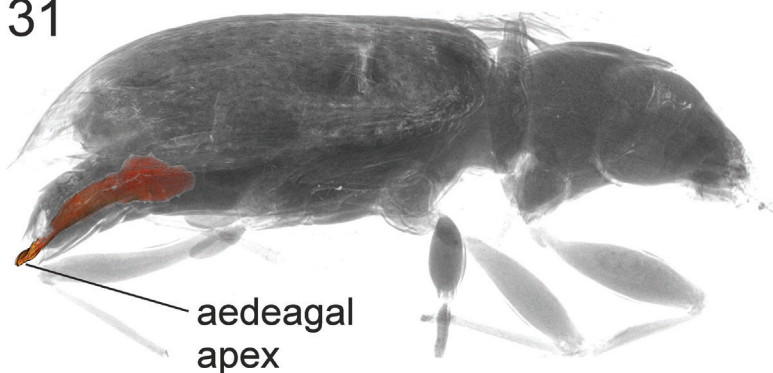
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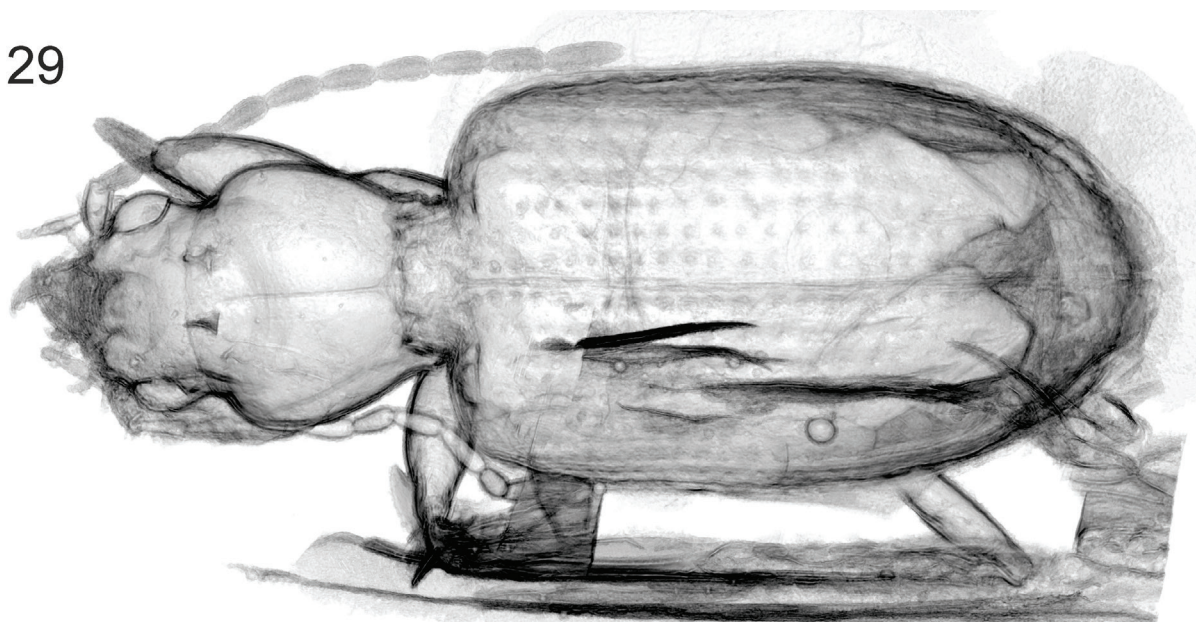
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aedeagal
apex

31

aedeagal
apex

Figures 29–31. *Balticeler kerneggeri* gen. nov., sp. nov., volume rendering of the paratype 2 (coll. Groehn 8234) using different grey scales. **29.** Dorsal aspect. **30.** Left lateral aspect. **31.** Right lateral aspect (downsized visualization with respect to **30**) to show position of aedeagus (separated using the segmentation function of Amira software and highlighted by red colour) in the beetle body.
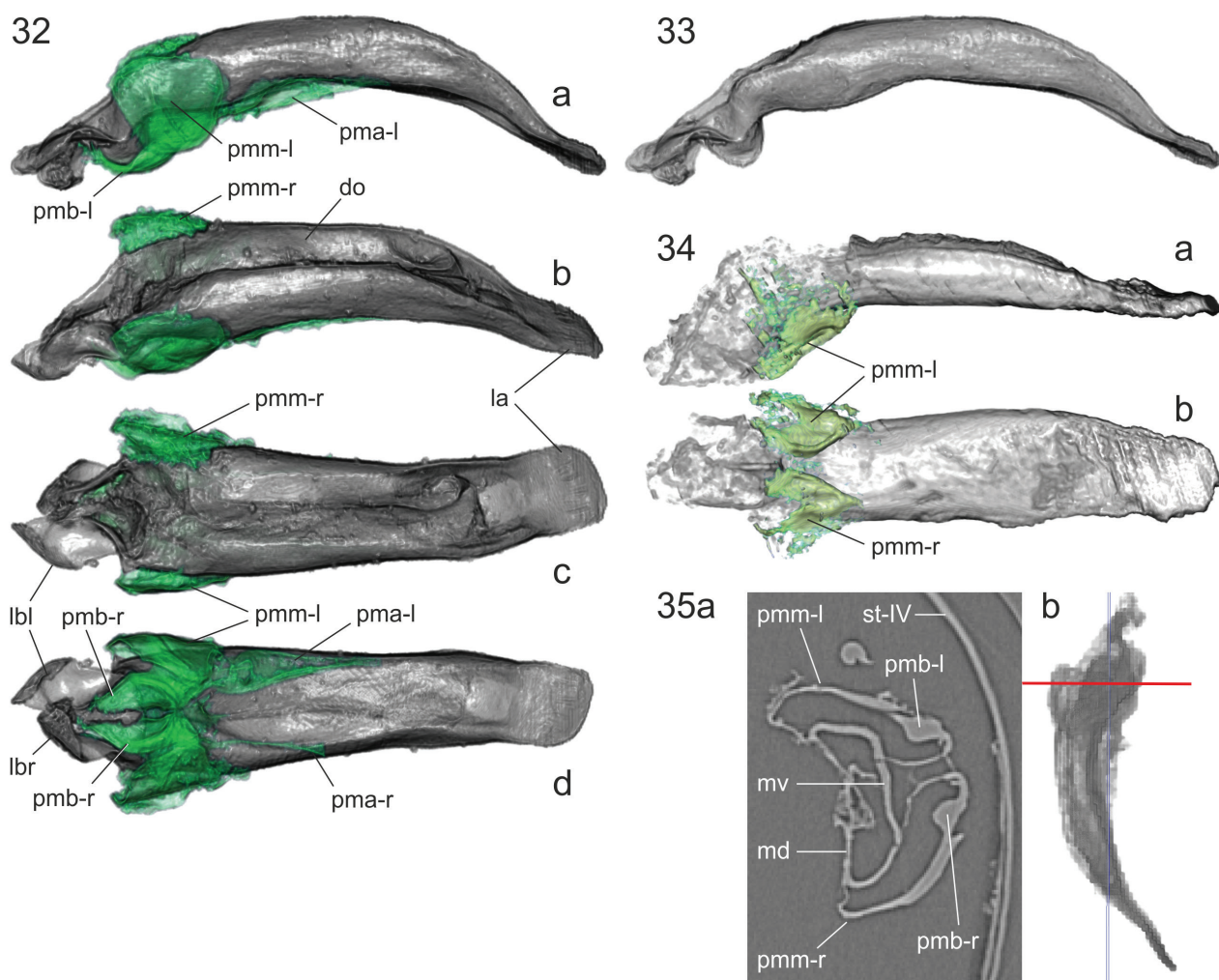
Figures 32–35. *Balticeler kerneggeri* gen. nov., sp. nov., volume rendering of the aedeagus of paratype 1 (OSAC 000-2900006) (**32, 33**) and paratype 2 (coll. Groehn 8234) (**34**), and transverse sections through the abdomen with aedeagus of paratype 1 (**35**). **32a, 33, 34a.** Left lateral view. **32b.** Left dorsolateral view. **32c.** Dorsal view. **32d, 34b.** Ventral view. The parameres were separated using the segmentation function of Amira software and highlighted by green colour in **32** and **34**. The position of the selected slice in **35a** is shown as a red line in **35b** which illustrates the aedeagus in right lateral view. Abbreviations: **do** – dorsal opening (= dorsally connected basal and apical ostia); **la** – apical lamella of aedeagus; **lbl, lbr** – left resp. right lobe of median lobe bulb; **md** – membranous dorsal surface of the median lobe; **mv** – ventral surface of the median lobe; **pma-l** – apical apophysis of the left paramere; **pma-r** – preserved remain of the apical apophysis of the right paramere; **pmb-l, pmb-r** – basal part of the left respectively right paramere; **pmm-l, pmm-r** – discoidal middle portion of the left respectively right paramere; **st-IV** – sternit IV.

Preservation status: Rather poor; head and ventral surface of the beetle fossil are completely covered by milky coating; in addition, flow lines of the amber surrounding the specimen (Fig. 10). The negative imprint of the fossil on the inclusion wall has moderate low contrast in the X-ray analyses (Figs 41, 42), and the genital armatures are not preserved.

Syninclusions: None.

Description. Color: All specimens appear unicolored dark throughout, markedly shiny. No metallic reflection is visible.

Microsculpture: Head, pronotum and elytra with very finely impressed very small transverse meshes (visible at magnifications of > 80×).

Measurements and proportions, given as mean (min–max values):

Standardized body length 3.43 (3.01–3.77) mm.
PW/HW = 1.24 (1.21–1.28).
PW/PL = 1.09 (1.02–1.13).
PW/PWb = 1.39 (1.33–1.46).
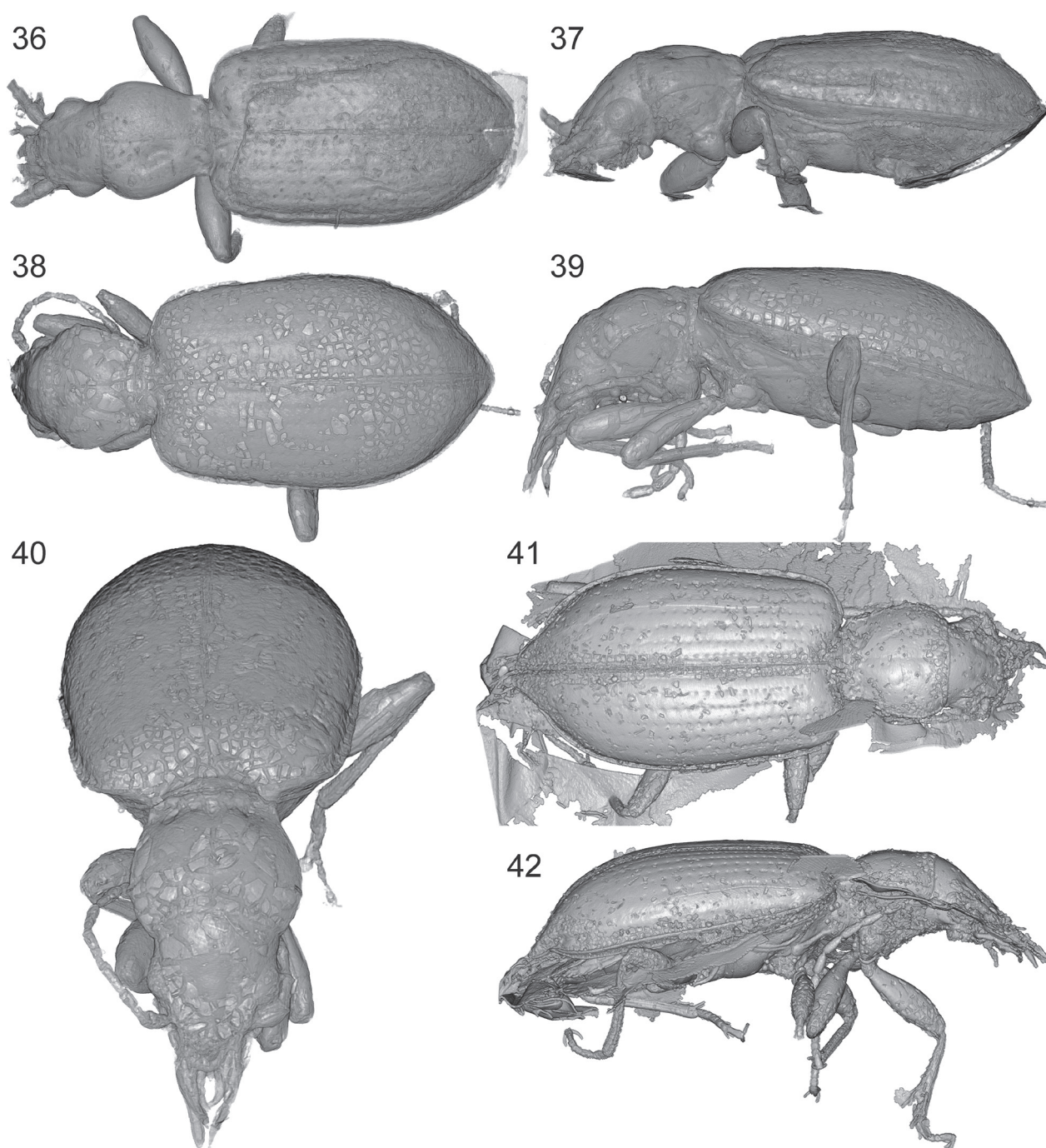PWb/PWa = 1.03 (0.97–1.08).
EW/PW = 1.66 (1.60–1.77).
EL/EW = 1.55 (1.50–1.59).
EL/FL = 2.18 (2.13–2.21).
EL/AedL = 2.36, 2.63 (paratypes 1, 2).

For individual measurements and proportions see Tables 2, 3.

Figures 36–42. *Balticeler kerneggeri* gen. nov., sp. nov., volume rendering of the paratype 3 (OSAC 000-2900387) (**36, 37**), paratype 4 (OSAC 000-2900600) (**38–40**), paratype 5 (coll. Sciaky) (**41, 42**). **36, 38, 41.** Dorsal aspect. **37, 39.** Left lateral aspect. **40.** Dorso-frontal aspect. **42.** Right lateral aspect.

Table 2. Measurements [μm].

	holotype	paratype 1	paratype 2	paratype 3	paratype 4	paratype 5
length of head	432	n. a.	429	427	464	464
width of head	695	n. a.	686	644	701	728
length of pronotum	787	826	814	725	794	858
width of pronotum	865	932	831	776	900	925
pronotal apical width	595	646	566	552	668	655
pronotal basal width	614	700	568	542	651	698
length of left / right elytron	2172 / 2147	2376 / 2384	2130 / 2124	1927 / 1937	2340 / 2356	2445 / 2455
width of left / right elytron	707 / 715	742 / 753	699 / 648	617 / 624	785 / 770	817 / 820
length of left / right metafemur	973 / 992	n. a.	956 / 1002	n. a.	1077 / n. a.	1078 / 1113
length aedeagus	n. a.	908	901	n. a.	n. a.	n. a.

Table 3. Body length and proportions.

	holotype	paratype 1	paratype 2	paratype 3	paratype 4	paratype 5
Standardized body length [mm]	3.39	n. a.	3.37	3.01	3.61	3.77
PW/HW	1.24	n. a.	1.21	1.21	1.28	1.27
PW/PL	1.10	1.13	1.02	1.07	1.13	1.08
PW/PWb	1.41	1.33	1.46	1.43	1.38	1.33
PWb/PWa	1.08	1.08	1.00	0.98	0.97	1.07
EW/PW	1.64	1.60	1.62	1.60	1.73	1.77
EL/EW	1.53	1.59	1.58	1.56	1.52	1.50
EL/FL	2.19	n. a.	2.13	n. a.	2.19	2.21
EL/AedL	n. a.	2.63	2.36	n. a.	n. a.	n. a.

Derivation of species epithet. The species epithet is given in honor of Friedrich Kernegger, Hamburg, who found a piece of amber bearing a fossilized specimen of this extraordinarily interesting species more than 25 years ago.

Discussion

Evidence that *Balticeler* is a middle-grade carabid

The new fossil genus and species *Balticeler kerneggeri* appears to be a member of a paraphyletic collection of lineages sometimes called "middle-grade" Carabidae. The evidence for this comes from the presence of synapomorphies in *Balticeler* that group it with so-called higher carabids, i.e., the subfamily Harpalinae, combined with the lack of a derived characteristic that would place it within crown-Harpalinae. Four character states present in *Balticeler* that are derived within Carabidae are:

(i)　　antennal cleaner anisochaetous Grade B (Hlavac 1971);
(ii)　　mesocoxae conjunct (Bell 1967; Beutel 1992);
(iii)　procoxal cavities externally closed (Bell 1967; Beutel 1992);
(iv)　external lobe of metepimeron well developed (Beutel 1992).

These derived states indicate that *Balticeler* is more closely related to Harpalinae than are those lineages that are sometimes called "basal-grade" carabids, i.e., those with plesiomorphic states for these four characters.

The character state plesiomorphic within Carabidae that indicates *Balticeler* is not a member of crown Harpalinae is:

(v)　　seta in mandibular scrobe present (Maddison et al. 1999).

Evidence that *Balticeler* is a genus of Trechinae

Within the middle-grade carabids, our evidence suggests that *Balticeler* is a member of the subfamily Trechinae sensu Maddison et al. (2019) (= Trechinae + Patrobinae

in sense of previous authors, but without Lissopogonini). We propose the following as derived character states that help place *Balticeler* within Trechinae:

(vi)　dorsal surface of aedeagal median lobe open, unsclerotized [a proposed autapomorphy of Trechinae]
(vii)　clypeus quadrisetose [a proposed synapomorphy of Bembidarenini + Trechini]
(viii)　antennomere 2 pubescent [a proposed autapomorphy of Trechitae]
(ix)　pedicellus about as long as scapus [a proposed autapomorphy of Trechitae]
(x)　　umbilicate series of setae arranged in a 4+2+2 pattern [a proposed autapomorphy of Trechitae]

These characters are discussed in turn, below.

One of the primary characteristics that supports the placement of *Balticeler* in Trechinae is the surface of the aedeagal median lobe, which is not sclerotized dorsally and thus completely open between the basal and apical ostia and, thus, the lobes of median lobe basal bulb are free (Fig. 23). Within carabid groups characterized by character states i–v listed above, a completely open dorsal surface of the aedeagal median lobe is only present in Patrobini, Bembidarenini and two basal clades of Trechini (in the paraphyletic Trechodina). Based on a multigene analysis of Trechinae, Patrobini was identified as the sister group to the supertribe Trechitae, which includes all other Trechinae (Maddison et al. 2019). Within Trechitae, Bembidarenini was identified as the sister group of Trechini. The phylogenetic tree inferred from molecular data suggests that a dorsally open aedeagal median lobe is an autapomorphic character of Trechinae, and that it was secondarily closed at least twice in the evolution of Trechitae: once in the ancestor of the Trechina stem group, and a second time in the ancestor of the Clade B1 stem group of Maddison et al. (2019) which includes Anillini, Bembidiini, Pogonini, Tachyini, Sinozolini, and Zolini. If so, *Balticeler* might be considered a crown or stem group member of the subfamily Trechinae in the sense of Maddison et al. (2019).

This view is further supported by an additional character state observed in the fossil specimens which makes it more likely that *Balticeler* represents a member of Trechitae: the clypeus is quadrisetose, with two primary setae on each side. This character state is also developed in Bembidarenini and Trechini (absent only in *Omalodera* Blanchard; Arnaud Faille, pers. comm. 2021), but absent

in all other Trechinae. If a quadrisetose clypeus represents a synapomorphic character state of Bembidarenini and Trechini, as seems probable, the likewise quadrisetose *Balticeler* could therefore be considered a member of the Bembidarenini + Trechini clade. We present as a working hypothesis that the quadrisetose clypeus represents a derived character state within both Trechinae and Trechitae, and that it evolved in the stem lineage of a clade comprising *Balticeler* + Bembidarenini + Trechini.

A quadrisetose clypeus is likewise developed in two other groups of middle-grade Carabidae, the genus *Psydrus* LeConte (Psydrini) and Gehringiini, neither of which are closely related to Trechitae (Maddison et al. 2019). Of the three genera within Psydrini, only *Psydrus* has a quadrisetose clypeus (*Nomius* Castelnau and *Laccocenus* Sloane have a bisetose clypeus); the quadrisetose clypeus is presumably derived within Psydrini. If a quadrisetose clypeus was an indication of a relationship with psydrines, it would suggest a sister group relationship to *Psydrus* itself. A quadrisetose clypeus is present in both *Gehringia* Darlington (based upon Darlington 1933; Deuve 2005, and the specimens we have examined) and *Afrogehringia* Baehr, Schüle, and Lorenz (based upon the two specimens we have examined). The third genus of gehringiine, *Helenaea* Schatzmayr and Koch (1934) appears to have only two setae on the anterior margin of the clypeus based upon available descriptions (e.g., Deuve 2005), but given the sister group relationship between *Afrogehringia* and *Helenaea* (Baehr et al. 2009), and the modified clypeus of *Helenaea*, this is likely a secondary loss.

Psydrines and gehringiines, however, differ from *Balticeler* in a number of aspects that speak against the potential relationship suggested by the setation of the clypeus. Both groups differ from *Balticeler* in having a very small or absent outer lobe of the metepimeron and by a dorsally closed aedeagal median lobe base. In addition, if *Balticeler* were the sister group of *Psydrus*, one would predict that it would have eight setae along the apical margin of the labrum (a synapomorphy of *Psydrus* and *Nomius*). Psydrini also lack an elytral plica, as well as having a unique position of the posterior spur of the antennal cleaner, which is distinctly distad of the clip setae, characteristics one would expect *Balticeler* to share if it were the sister to *Psydrus*. In addition to the metepimeral shape and aedeagal structure, gehringiines differ from *Balticeler* by the underlapping of elytral edges, apically truncate elytra, and by the metacoxa which laterally extends to elytral epipleuron, although these are all likely derived characters of gehringiines and don't exclude the possibility that *Balticeler* is the sister group to the tribe.

The proposed phylogenetic position of *Balticeler* within Trechitae and the Bembidarenini + Trechini clade is difficult to verify due to a striking autapomorphy of the fossil taxon: the basal protarsomeres of *Balticeler* are not sexually dimorphic. Because of the absence of any modifications on the male protarsomeres, they lack the tooth-like prolongation on the outer apical margin. Uniquely dentate basal protarsomeres of males is currently the only known morphological synapomorphy of adults of the supertribe (Maddison et al. 2019). However, a female-like shape of male protarsomeres is also present in at least some Trechina (e.g., *Aphaenops* Bonvouloir, Jeannel 1928). The phylogenetic position of *Aphaenops* deeply nested within subtribe Trechina is strongly supported by additional morphological and molecular data (Jeannel 1928; Faille et al. 2010), and in that group the lack of sexual dimorphism and subsequent loss of dentate male protarsomeres is surely a derived state within Trechitae. We propose that the female-like protarsomeres in male *Balticeler* represent a similar secondary loss.

Balticeler shares with Trechitae the derived state of a pubescent antennal base. Pubescence begins from the second (*Balticeler*, Bembidiini, Tachyini, Zolini, the genus *Chaltenia* Roig-Juñent and Cicchino within Sinozolini) or first antennomere (all other Trechitae except Pogonini). Pubescence begins from the third or fourth antennomere in Pogonini, Patrobini and in all other members of the middle-grade carabids examined (including 15 genera of Moriomorphini, *Lissopogonus* Andrewes, and 11 genera of Broscini), except for those taxa that are either generally pubescent (e.g., *Cymbionotum* Baudi, *Apotomus* Illiger, brachinines) or have additional setae in many places of the body (all three genera of Psydrini). The smooth antennal base in Pogonini could represent a reversal since this group clusters within Clade B1 Trechitae of Maddison et al. (2019).

The pedicellus is markedly slender and about as long as the scapus in *Balticeler* and all other Trechitae except Bembidiini, Tachyini, Zolini, some Pogonini, and very few Trechini (e.g., *Aphaenops queffeleci* Cabidoche, some *Pachydesus* Motschulsky, *Sporades* Fauvel, *Trechisibius* Motschulsky, *Trechosia* Jeannel, Arnaud Faille, pers. comm. 2021). We view this as a derived character state within middle-grade carabids. Outside of Trechitae, all of the middle-grade carabids we have examined have a pedicellus no longer than 0.7 of the length of the scapus, which is similar in length to those trechites in Clade B1 of Maddison et al. (2019) that have a shorter pedicellus. We propose that the shorter pedicellus in some but not all members of Clade B1 is due to reversal.

Reduction of the number of setae in the umbilicate series and consequent separation into three or two groups was repeatedly evolved in many different groups of Carabidae. The 4+2+2 pattern, however, is observed only in Trechitae, and we consider it an autapomorphy of the group. Beside the fossil *Balticeler*, this pattern occurs in Bembidarenini, Trechini, Bembidiini, Tachyini, some Sinozolini and Anillini. In Lovriciina, the number of umbilicate setae is reduced further. One or more additional setae in the umbilicate series are observed in other species of Trechitae with larger adults. Pogonini possess an almost-continuous umbilicate series similarly to that found in the Trechitae sister group Patrobini. It is therefore likely that the 4+2+2 pattern evolved in the Trechitae stem group and was subsequently modified in some terminal groups.

Evidence that *Balticeler* is a stem Bembidarenini + Trechini

Within Trechitae, we propose that *Balticeler* is a member of the stem group of Bembidarenini + Trechini, and thus the sister group of the two recent lineages of this clade. Evidence for it being a member of the stem group rather than the crown group comes from lack of an apomorphy that *Balticeler* should possess if it were within crown Bembidarenini + Trechini. All four genera of Bembidarenini, as well as all genera of Trechini we have examined (including members of all Trechodina subgroups, including the *Trechobembix* assemblage sensu Maddison et al. 2019, and various Trechina) possess a single long suborbital seta in approximately the same position on each side. Some other groups of Trechinae possess a scattering of short setae suborbitally (including, for example, some *Bembidion* Latreille, some *Sinechostictus* Motschulsky, *Orzolina* Machado, *Phrypeus* Casey, some Anillini), but lack a bilaterally symmetrical pair of long setae in that region. Similar scattered short setae in the suborbital region are also present in several non-Trechitae tribes, including the three genera of Psydrini and brachinines. The only other species of Trechinae we have seen with a single long suborbital seta are within two groups: many species of the subtribe Tachyina (including species of *Meotachys* Erwin, *Nothoderis* Boyd and Erwin, *Paratachys* Casey, *Pericompsus* LeConte, *Tachyta* Kirby, and *Tachyura* Motschulsky), and a few members of Pogonini [e.g., *Sirdenus grayii* (Wollaston)]. We have confirmed the lack of a long suborbital seta in Zolini (based on an examination of eight genera, including *Pterocyrtus* Sloane), Sinozolini (all three genera), four genera of Pogonini, Anillini (six genera examined, including *Nesamblyops* Jeannel), Xystosomina (five genera examined), all eight genera of Bembidiini, and Patrobini (15 genera examined, including *Platidiolus* Chaudoir). Outside of Trechinae a single long suborbital seta is lacking in the 15 genera of Moriomorphini examined, all three genera of Psydrini, as well as *Gehringia*, *Lissopogonus*, Broscini, Melaenini, and in all other tribes outside of Harpalinae we have examined (with Nototylini, Mantichorini, and Protopaussini being the only tribes outside of Harpalinae we have not examined). The only lineage of carabids outside of Trechinae that possesses a single long suborbital seta at a fixed position that we know of is the subtribe Pericalina, a lebiine group deeply nested within the large subfamily Harpalinae. Thus, it appears that the suborbital seta is derived within Trechitae. Although it has arisen more than once in Trechitae, the lack of a suborbital seta in *Balticeler* provides evidence against it being a member of crown Bembidarenini + Trechini. In addition, *Balticeler* lacks two apomorphies that place it outside of the phylogenetically diverse tribe Trechini: (1) *Balticeler* lacks Trechini-like supraorbital furrows, and (2) it lacks a recurrent stria on the elytron.

In addition, *Balticeler* can be reasonably excluded from the crown groups of other described tribes of Tre-chitae. From crown Anillini, Bembidiini, or Tachyini, it can be excluded because of the lack of subulate apical palpomeres. There is evidence that it is not a member of crown Sinozolini, as it lacks a bifid tooth on the mentum. Similarly, it appears to not be a member of crown Pogonini, as it lacks the larger number of umbilical setae present in that group.

Evidence for and against *Balticeler* being a Promecognathini or Scaritinae

There are two alternative placements of *Balticeler* which should be considered, based upon some similarities it shares with two other groups of Carabidae: within Prome-cognathini or its stem group, and within Scaritinae or its stem group.

Balticeler shares two distinctive apomorphies with *Promecognathus* Chaudoir: (i) long, thin, straight mandibles; (ii) lack of external sexual dimorphism, with unmodified male protarsomeres and with the last visible abdominal sternite with two pairs of setae (rather than one pair typical of males). Similarly long and thin mandibles are present in some other carabid groups (e.g., Lovriciina and some trechines), and thus this character state is homoplastic. Males having the last visible abdominal sternites with two pairs of setae, as is typical in females, also occur in the intertidal *Bembidion* subgenus *Desarmatocillenus* Netolitzky (Sasakawa 2007). However, *Promecognathus* has plesiomorphic states in two thoracic characters that indicate it is not part of the middle-grade of carabids, in contrast to *Balticeler*: *Promecognathus* (i) has disjunct mesocoxae, and (ii) lacks an externally visible lobed metepimeron. In addition, *Promecognathus* lacks all of the apomorphies mentioned above that *Balticeler* shares with Trechitae.

As with *Promecognathus*, *Balticeler* shares with most scaritines unmodified male protarsomeres, and with the scaritine tribe Dyschiriini, as well as many species of Clivinini and Scaritini, the last visible abdominal sternite with two pairs of setae in males. Long and thin mandibles are present in some lineages of Clivinini, e.g., *Camptidius* Putzeys, *Camptodontus* Dejean, *Climax* Putzeys, and *Stratiotes* Putzeys. In external shape, with its subcylindrical pronotum and hind body, *Balticeler* is particularly similar to species of Dyschiriini. In addition, several species of *Dyschirius* Bonelli (incl. *Dyschiriodes* Jeannel) share the reduced pronotal marginal border and elytral basal border with *Balticeler* (but not the long and thin mandibles). However, scaritines are characterized by at least two notable synapomorphies which *Balticeler* lacks: (i) the protibia is markedly modified as an adaptation to the fossorial way of life, with large tooth-like expansions laterally and apically; (ii) the insertion of the antenna, if viewed from above, is overlapped by a lateral extension of the frontal plate. Because both these character states are lacking in *Balticeler* the latter is unlikely to belong in

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crown scaritines. In addition, as mentioned for *Promecognathus*, scaritines have plesiomorphic states in two thoracic characters that indicate they are not part of the middle-grade of carabids: (i) disjunct mesocoxae, and (ii) lack of an externally visible lobed metepimeron.

Conclusions

Balticeler as a member of a new tribe?

The placement of *Balticeler* within Trechitae as a member of the stem lineage of Bembidarenini + Trechini is only moderately well supported. All of the character states that suggest this placement are homoplastic, with the derived state having evolved several times within Carabidae, or lost within some group of trechites. Placement of *Balticeler* as a member of stem Bembidarenini + Trechini and the evidence against *Balticeler* being within any other living tribe either within or outside of Trechitae would require, should we feel compelled to place *Balticeler* within a tribe, the creation of a new monobasic tribe to house it. However, for the moment we prefer to leave *Balticeler incertae sedis* within the classification of Trechitae, outside of any existing tribe. Creating a new tribe for *Balticeler* now would set a precedent that could lead to the creation of many tribal-level taxa should additional lineages of various stem groups of Trechitae be discovered in amber deposits, especially Burmese amber. We prefer a more cautious approach, in which new family group names are created when the evidence for their distinctiveness is sufficiently strong to make them moderately stable as new stem lineages are discovered. Once the amber fauna is better known, or the morphological studies of Trechinae provide stronger evidence for the placement of *Balticeler*, a more stable and complete tribal classification can be devised.

Acknowledgements

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