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Two new genera and species of tiger beetles from Baltic amber (Coleoptera: Carabidae: Cicindelinae)

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Abstract. Two fossil tiger beetle species (Coleoptera, Carabidae, Cicindelinae) are described from Eocene Baltic amber using light microscopic and X-ray microscopic techniques. Both species are considered representatives of the subtribe Iresina Rivalier, 1971 due to the shared combination of character states: glabrous head, six labral and four suborbital setae, and glabrous pronotum. *Palaeopronyssiformia groehni* Wiesner, Will, and Schmidt, **new genus**, **new species**, is characterized by a glabrous and furrowed head with six labral setae, large eyes, presence of two supraorbital setae on each side, mandibles with two teeth of the incisor region, and a glabrous and furrowed pronotum. *Palaeoiresina cassolai* Wiesner, Will, and Schmidt, **new genus**, **new species**, is characterized by a unicolored, undentated labrum, mandibles with two teeth of the incisor region, glabrous head with six labral setae, two clypeal setae, two supraorbital setae on each side, and a glabrous pronotum, mesepisternum, mesepimeron, and metepisternum. The species described here represent the only known tiger beetle fossils preserved in Baltic amber.

Key Words. Taxonomy, new genus, new species, X-ray microscopy

Introduction

Amber is the fossilized resin from ancient trees. This aromatic resin can drip from and ooze down trees, as well as fill internal fissures, trapping debris such as seeds, leaves, feathers and insects. The Baltic region of Europe is home to the largest known deposit of amber, called Baltic amber.

There are five published records of fossil tiger beetles preserved in Baltic amber (35–50 Mya) (Standke 2008). The first was a purported specimen of *Odontochila*, mentioned by Brullé (1839) from the collection of the Musee d'Histoire Naturelle, Dijon. However, this specimen was subsequently studied by Horn (1907: 461) and determined to be instead an extant species, *Pogonostoma chalybaeum* Klug, 1835 that was preserved in recent Copal.

Second was a beetle from the collection of the Museum für Naturkunde, Berlin, which was determined by Horn (1906) to be either a *Tetracha carolina* (Linné, 1766) or a closely related species. Nearly a century thereafter, this specimen was studied in more detail (Röschmann 1999). He concluded that it was a species closely related to but not identical with *T. carolina*. Although he indicated he was preparing a formal redescription of it as a new species (Röschmann 1999: 208), this rediscription was never published. Unfortunately, this specimen disappeared without a trace from the collection of the

Naturkundemuseum in the late 1990s (Christian Neumann, Museum für Naturkunde, Berlin, pers. comm.). The exact identity of this fossil remains unknown.

The third specimen was mentioned by Larsson (1978: 109) from the collection of the Copenhagen Museum. He wrote: "*a* Collyris *or a form very related to this. … A study of the piece was rendered somewhat difficult by extensive opacities, but the general body build of the animal, together with the completely clear regions around the head and prothorax as well as front legs, mouth parts and antennae, established the determination mentioned as certain.*" But this specimen was also lost without a trace in the 1970s (Lars Vilhelmsen, Natural History Museum of Denmark, Copenhagen, pers. comm.).

The fourth specimen was originally identified as a "Cicindelinae" by Weitschat and Wichard (1998: 157), but subsequent examination showed it not to be a member of Cicindelinae but instead a member of the Carabidae tribe Lebiini.

The fifth specimen was only included as a photograph of a Cicindelidae by Gröhn (2015: 265), and was subsequently loaned to one of us (JW).

A sixth fossil specimen was acquired by the Essig Museum of Entomology (EMEC) and accessioned to the University of California, Museum of Paleontology (accession number UCMP 5068). In 2011 the specimen was sent as a loan to Fabio Cassola (Roma) and he prepared a preliminary study in which he determined it was an undescribed genus and species. However, his work was cut short as he passed away before the study could be completed and left only a draft manuscript.

Currently, the latter two specimens are the only available tiger beetle fossils preserved in Baltic amber. The details of their anatomy and descriptions of these fossils based on our observations are presented here.

Materials and Methods

The two fossil Cicindelinae specimens preserved in Eocene Baltic amber are from the coastal area of the southeastern Baltic Sea. *P. groehni* is deposited in Geologisch-Palaeontologisches Institut of University, Hamburg, Germany. *P. cassolai* is deposited deposited in the University of California, Museum of Palaeontology, Berkeley, CA, U.S.A. The specimens were studied and imaged using light microscopy and micro-CT. The methods and technology used were described in detail in a previous work by Schmidt et al. (2016). Micro-CT scans were performed under phase contrast (40 KV, 8 W) using a 4× detector (10 s, 4.15 µm pixel size) and 10× detector (30 s, 1.89 µm pixel size).

Body size was quantified by a standardized body length, the sum of: (1) the median length of the head, (2) the length of pronotum, (3) the length of elytra. The length of the head was measured dorsally from the base of labrum to the base of the pronotum; the width of the head was measured across the widest point including compound eyes. The width of the labrum, pronotum and elytra were measured at their widest points. The length of the labrum was measured at its maximum extension in the center. The length of the pronotum was measured along its median line. The width of the pronotal apical margin was measured between the tips of the lateroapical angles, and the width of hind angles of the pronotal base between the tips of the laterobasal angles. The length of elytra was measured from the most anterior point of the elytral humerus to the apex of the right elytron.

Results

Palaeopronyssiformia Wiesner, Will, and Schmidt, **new genus**

Type species. *Palaeopronyssiformia groehni* Wiesner, Will, and Schmidt, new species.

Description. Body length: 11.4 mm in the type specimen.

Head. Markedly broad due to large, hemispherical protruded eyes (Fig. 2). Mandibles with two teeth of the incisor region (Fig. 8). Labrum 1.5 times wider than long, with six setae near apical margin and five teeth in middle of apical margin; the central tooth is distinctly shorter than the lateral teeth, the internal latero-apical teeth are longest (Fig. 7). Antennae filiform, probably extending posterior behind

elytral shoulders. Maxillary palpus with three visible palpomeres (the basal one is invisible). Apical palpomere presumably two times longer than the following palpomere, third palpomere stouter than the apical two, all sparsely setose. Labial palpus with two slender palpomeres, the basal one densely covered with long setae, 2.5 times longer than apical palpomere (Fig. 9–11). Frons, vertex and orbital plates densely covered with rather deep furrows (Fig. 2, 6.) Two supraorbital setae each side (Fig. 2, 6); setae on clypeus could not be found. Vertex steeply slanted towards front,

Pronotum. Moderately small and slender, only slightly longer than broad, with maximum width slightly before middle, and with apical margin distinctly broader than basal margin (Fig. 12). Anterior margin distinctly convex in middle; lateral margin unbordered throughout, slightly sinusoidal with middle part convex, anterior lateral angles distinctly protruded laterally, and intermediate parts (levels of anterior and posterior transverse furrows) concave. Basal margin probably nearly straight with laterobasal angles slightly obtuse, rounded at tip, not protruded laterally. Disc in anterior ¾ with moderately engraved dense transverse furrows both sides of median line (Fig. 2, 12). Anterior and posterior transverse grooves broad and moderately deep, with intermediate part distinctly globose.

Elytra. Elongated-ovate, with maximum width slightly before the apical third, not fused. Shoulders broad, obtuse angulate with humerus rounded; lateral margin slightly but distinctly concave before middle. Chaetotaxy and patterns of micro- and macrosculpture could not be imaged.

Legs. Slender, of usual cicindelid shape, last tarsomeres with two small claws apically (Fig. 3).

Etymology. The name is composed of the prefix Palaeo (Greek palaios = ancient) and the name of the genus *Pronyssiformia,* whose female labrum it resembles.

Diagnosis. As the ventral and lateral sides of the fossil are not visible (see Preservation status of the type specimen below), the incorporation into the phylogeny of the subfamily Cicindelinae is hypothetical. The glabrous head with six labral and four suborbital setae and the obviously glabrous pronotum are indicators for the membership of subtribe Iresina Rivalier, 1971. Within this subtribe, the shape of the labrum most resembles the female of *Pronyssiformia excoffieri* (Fairmaire, 1897), a monotypic genus from China, from which it differs by the large eyes, the presence of two suborbital setae instead of one posterior only and the furrows on head and pronotum.

Remarks. Rivalier (1971: 137) distinguished the subtribe Prothymina Horn, 1910 by the number of labial setae. The presence of only four setae made it distinctly different from the subtribe Iresina Rivalier, 1971, which exhibited six or more labial setae. Bouchard et al. (2011: 103) proposed the older name Dromicina Thomson, 1859 as replacement name for Prothymina. Genus *Pronyssiformia* Horn, 1929 was included by Horn in the subtribe Prothymina, which had been omitted by Rivalier (1971). And in fact, this genus would not fit with Rivalier's key (1971: 137), as it has 6 labral setae and would therefore key out as a member of subtribe Iresina, where it should be placed near *Distipsidera* Westwood, 1837.

Palaeopronyssiformia groehni Wiesner, Will, and Schmidt, **new species**
(Fig. 1–12)

Holotype. Female in Baltic amber; size of amber piece approximately 44 x 24 x 7 mm, irregularly cut, with GPIH collection number 4924, coll. Gröhn no. 8155, Holotype *Palaeopronyssiformia groehni*, des. Wiesner, Will, and Schmidt, 2017. Deposited in Geologisch-Palaeontologisches Institut of University Hamburg (GPIH, now CeNak, Centrum für Naturkunde, collection of Carsten Gröhn), Hamburg, Germany (Fig. 5).

Preservation status. A clear piece of amber, crossed by several fracture lines. A large flow line runs through almost the entire amber piece and adjoins the embedded Cicindelinae fossil laterally and dorsally, and therefore, the lateral aspect of the fossil cannot be viewed using light microscopy, and structures on dorsal surface of elytra are not visible (Fig. 1). In addition, the entire ventral surface is densely covered by milky coating (Fig. 4). The right protarsi, the left mesotarsi, and the right metatarsi reach to the surface of the amber piece and are thus lost; the apical part of the left hindleg is broken

away and preserved in the same piece of amber 20 mm at the side of the beetle (Fig. 3). Probably as a result of microbial processes during embedding of the beetle in the resin most parts of its body give insufficient contrasts in the micro-CT analyses, which is particularly apparent on the ventral surface of the prothorax and the abdomen. However, most details of diagnostic importance of the external morphology of the head and pronotum as well as the outline of the elytra were reconstructed based on both, light and X-ray microscopic analyses.

Syninclusions. A small Diptera dorsal of the Cicindelinae fossil (Fig. 1), stellate hairs and other tiny plant remains, several dirt particles.

Description. See diagnosis and description chapters of the monotypic genus above.

Body length. 11.4 mm.

Color. Difficult to identify due to the possibility of preservation artifacts. Dorsal surface of head and pronotum seemingly rufescent-brown, with some metallic luster. Color of elytra and ventral surface of body unrecognizable.

Head. 1.4 times wider than pronotum. Frons with eight deeply engraved long and additional 4–5 shorter transverse furrows, vertex with 2–3 transverse furrows, orbital plates with 7–8 long and deeply engraved longitudinally furrows; latter continuing towards disc with additionally diagonally furrows which are directed to the center of disc (Fig. 2, 6).

Pronotum. Presumably 1.05 times longer than wide, with basal margin approximately 0.8 times as broad as apical margin (note that the pronotal basal margin is hardly recognizable in the fossil).

Elytra. 1.7 times longer than wide.

Etymology. Named after Carsten Gröhn, Glinde, Germany, discoverer of this remarkable Baltic amber fossil.

Differential diagnosis. Presently, *Tetracha* cf. *carolina* is the only Eocene Cicindelinae species identified to species level. *Palaeopronyssiformia groehni* new genus, new species, differs from *T. carolina* by the shape of labrum and pronotum. The labrum of *T. carolina* has four setae only and four short marginal teeth, the pronotum has its maximum width nearly behind the head, the anterior corners of pronotum are more advanced than the anterior margin of prosternum. For comparison with *Palaeoiresina cassolai* new genus, new species, see description of the latter, below.

Palaeoiresina Wiesner, Will, and Schmidt, **new genus**

Type species. *Palaeoiresina cassolai* Wiesner, Will, and Schmidt, new species.

Description. Body length: 8.8 mm in the type species.

Head. Moderately broad with eyes rather small, moderately protruded. Mandibles with two teeth of the incisor region, teeth of left mandible longer (Fig. 18). Labrum markedly short, 3.8 times wider than long, with apical margin simple, slightly convexly produced in middle, undentated, with six setae, (Fig. 17). Antennae filiform. Labial palpus with two palpomeres, the basal one sparsely setose, presumable 1.2 times longer than apical palpomere. Maxillary palpus with two visible sparsely setose palpomeres, basal two palpomeres invisible (Fig. 19). Frons and vertex smooth or almost so, supraorbital area densely covered with longitudinal furrows. Two supraorbital setae each side; clypeus with a single seta each side (Fig. 17). Vertex shallowly slanted towards front.

Pronotum. Approximately as long as wide, its maximum width distinctly before the middle, with base almost as broad as apical margin; latter nearly straight with lateroapical angles fully rounded, not protruded. Side margin convex in middle, slightly notched at level of anterior transverse groove, concave at level of posterior transverse groove, finely bordered (border line disappeares near apex). Basal margin moderately convex, distinctly and broadly bordered, with laterobasal angles markedly bent anterior, latter slightly obtuse, rounded at tip, slightly protruded laterally. Disc covered with

distinct furrows on the plate. Anterior and posterior transverse grooves moderately deep, intermediate part distinctly globose (Fig. 19).

Elytra. Elongated-ovate, with maximum width at the beginning of the apical third, not fused. Shoulders broad, with humerus suggestively obtuse angulate; lateral margin almost straight before widest point. Anterior part of elytra densely punctured, near anterior margin sparsely covered with setae (Fig. 13; posterior part of elytra is lost in the fossil specimen).

Legs. Slender, of usual cicindelid shape, last tarsomeres with two small claws apically, three basal tarsomeres of protarsi widened.

Etymology. The name is composed of the prefix Palaeo (Greek palaios = ancient) and the name of the subtribe Iresina.

Diagnosis. As the ventral side of the fossil is not visible (see Preservation status of the type specimen below), determination of its systematic position within Cicindelinae is as difficult as in the preceding described species. The glabrous head with six labral and four suborbital setae, the two clypeal setae and the obviously glabrous pronotum, mesepisternum, mesepimeron, and metepisternum (as visible) are indicators for the membership in the subtribe Iresina Rivalier, 1971. Given its total body length and the sculpture of its surface it somewhat resembles species in the genus *Rhytidophaena* Bates, 1891, which is distributed along foothills on the southern slopes of the Himalaya from Pakistan to China. However, the fossil differs markedly by unicolored, undentated labrum, mandibles with two teeth of the incisor region and presence of setae on clypeus.

Palaeoiresina cassolai Wiesner, Will, and Schmidt, **new species**
(Fig. 13–20)

Holotype. Male in Baltic amber; size of amber piece approximately 20 x 18 x 7 mm, irregularly cut, deposited in the University of California, Museum of Palaeontology, Berkeley, CA, specimen number UCMP404030, locality number UCMP IP15208 (Fig. 14).

Preservation status. The embedded fossil borders to the surface of the amber piece so that posterior parts of elytra and abdomen, parts of the left hindleg, and the right antenna, are lost (Fig. 14–16). Several flow lines run through the amber piece and therefore, particularly the ventral parts of the embedded Cicindelini fossil cannot be viewed using light microscopy (Fig. 14). As observed in the previously described Baltic amber inclusion, this fossil exposes few parts of the beetle body for adequate contrasts in the micro-CT analyses and is probably a result of microbial processes during embedding of the beetle in the resin. However, most details of diagnostic importance of the external morphology of the head and pronotum as well as the outline of the anterior part of the elytra were reconstructed based on a combination of the light and X-ray microscopic analyses.

Syninclusions. One tiny Diptera, stellate hairs, several tiny dirt particles.

Description. See diagnosis and description chapters of the monotypic genus above.

Body length. 8.8 mm.

Color. Head, pronotum and elytra seemingly unicolored rufescent-brown, with metallic luster all over.

Head. 1.1 times wider than pronotum. Supraorbital area densely covered with 8–10 moderately deep engraved longitudinal furrows, latter continuing towards disc with few additionally short diagonally furrows (Fig. 13, 17).

Pronotum. 1.01 times longer than wide, with apical margin 1.02 times broader than basal margin.

Elytra. 1.7 times longer than wide.

Etymology. This species is dedicated in honor of the world-renowned tiger beetle specialist, Fabio Cassola of Rome, who passed away on January 14, 2016, at the age of 77. His lifelong passion for tiger

beetles leaves us with a legacy of 203 publications that he authored or co-authored, a body of work that is an extraordinarily important contribution to the knowledge of this group.

Differential diagnosis. This species differs from the above described *Palaeopronyssiformia groehni* new genus, new species, by its much smaller size, the short undentated labrum and the smaller eyes. It differs from *Tetracha* cf. *carolina*, another Cicindelinae species described from Baltic amber, by the shape of the labrum and pronotum. The labrum of *T. carolina* has four setae only and four short marginal teeth, the pronotum has its maximum width close to its anterior edge, the anterior corners of pronotum are more advanced than the anterior margin of prosternum.

Conclusions

The Eocene of Northern Europe had a notable diversity of tiger beetle lineages. Representatives of three Cicindelinae subtribes and four genera are known from Baltic amber deposits to date: Collyridina (spec. near *Collyris*, Larsson 1978), Iresina (*Palaeopronyssiformia groehni,* new genus, new species, *Palaeoiresina cassolai,* new genus, new species); Megacephalina (*Tetracha* cf. *carolina*, Röschmann 1999). In the recent world fauna, close relatives of the Baltic amber Cicindelinae fossils are distributed in North and South America (*Tetracha*), in East and South East Asia (*Collyris*), and in South America, Reunion, Mauritius, India, East and South East Asia, and Australia (Iresina) (Wiesner 1992; Erwin and Pearson 2008). Faunal connections of the Eocene Northern Europe with the modern warm-temperate and subtropical North America and South East Asia are well known (see literature review in Alekseev 2017). All Baltic amber fossil lineages of Cicindelinae presently known are now absent from the recent fauna of Europe and the Western Palearctic (except for Megacephalina, which is represented by *Grammognatha euphratica* (Latreille and Dejean, 1822) from the Mediterranean coasts, Asia Minor, Central Asia, and India).

While representatives of Collyridina are arboreal hunters (Naviaux 1995), and *Tetracha* species are found on open ground or areas with sparse vegetation (Erwin and Pearson 2008), the habitat preferences of the two species described here are difficult to ascertain. Recent species of tribe Iresina are associated with various habitats such as open ground or in forests where they are known to use different sized tree trunks as a substrate for hunting prey (Lawton 1972). Accordingly, we hypothesize that *Palaeopronyssiformia groehni,* new genus, new species, *Palaeoiresina cassolai,* new genus, new species, were also dwellers of the Baltic amber forest floor, which would have had open areas created by riparian corridors, erosional areas on steep slopes, and clearings created by fallen trees.

Acknowledgments

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Figure 1. *Palaeopronyssiformia groehni,* new genus, new species, light microscopic image of the holotype, dorsal aspect.

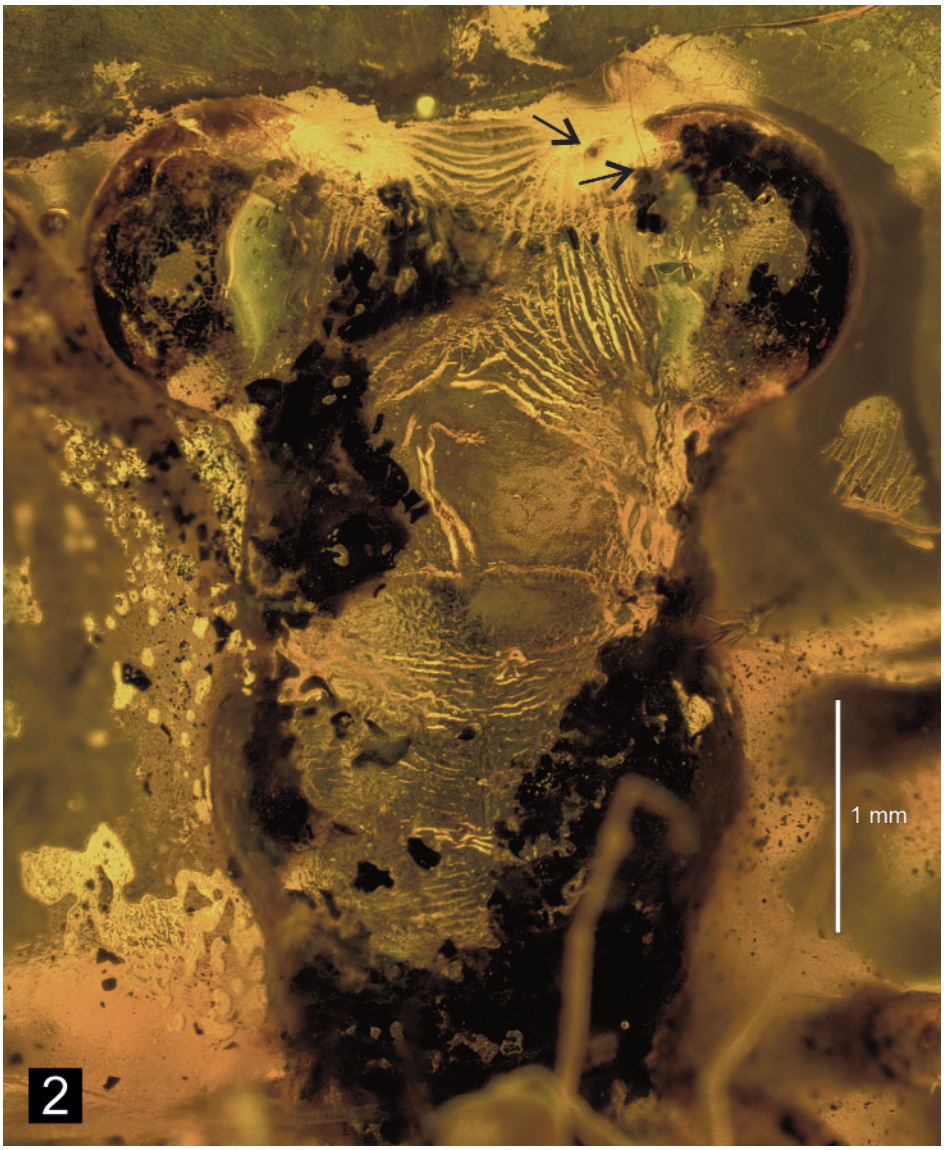
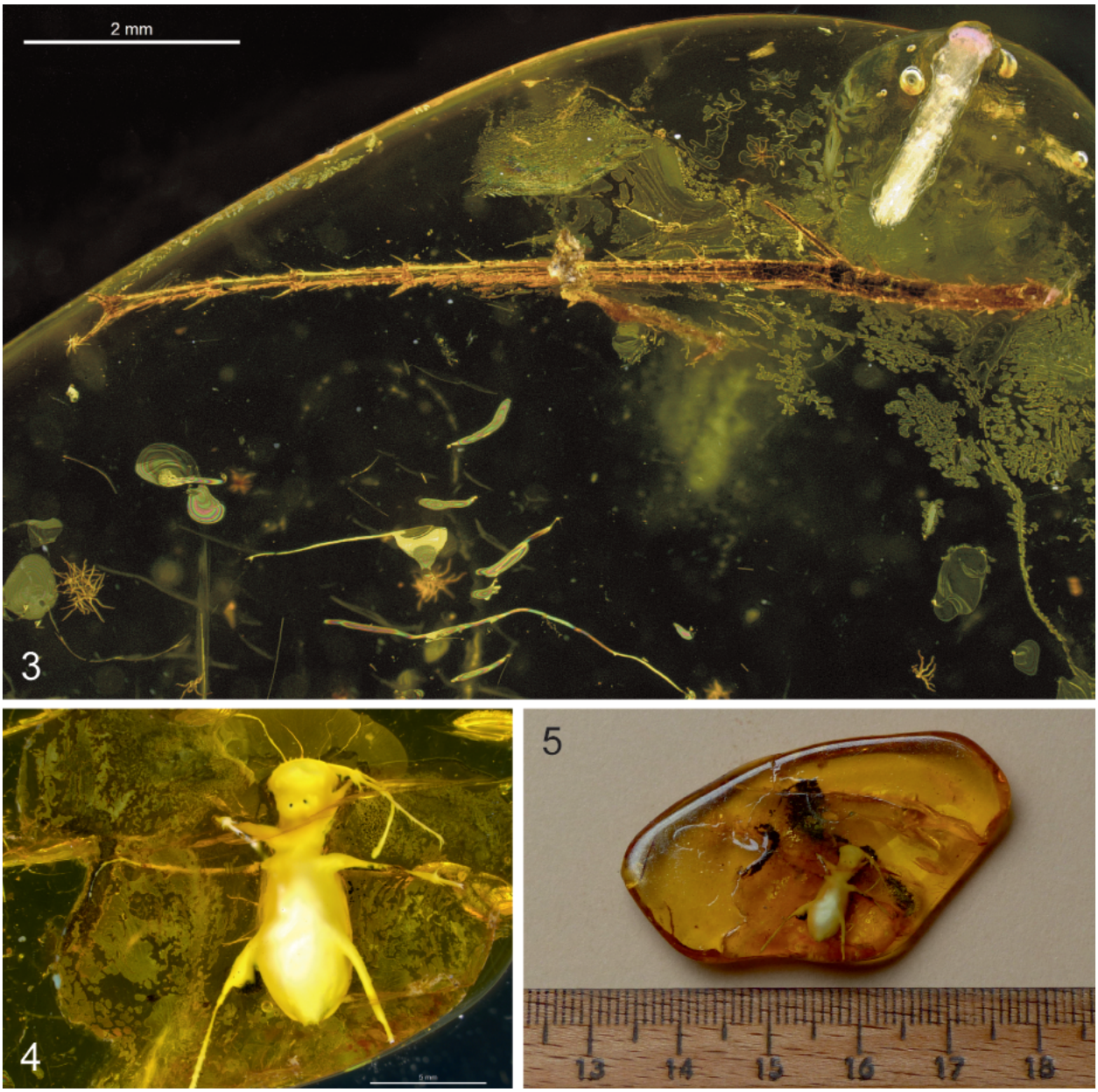
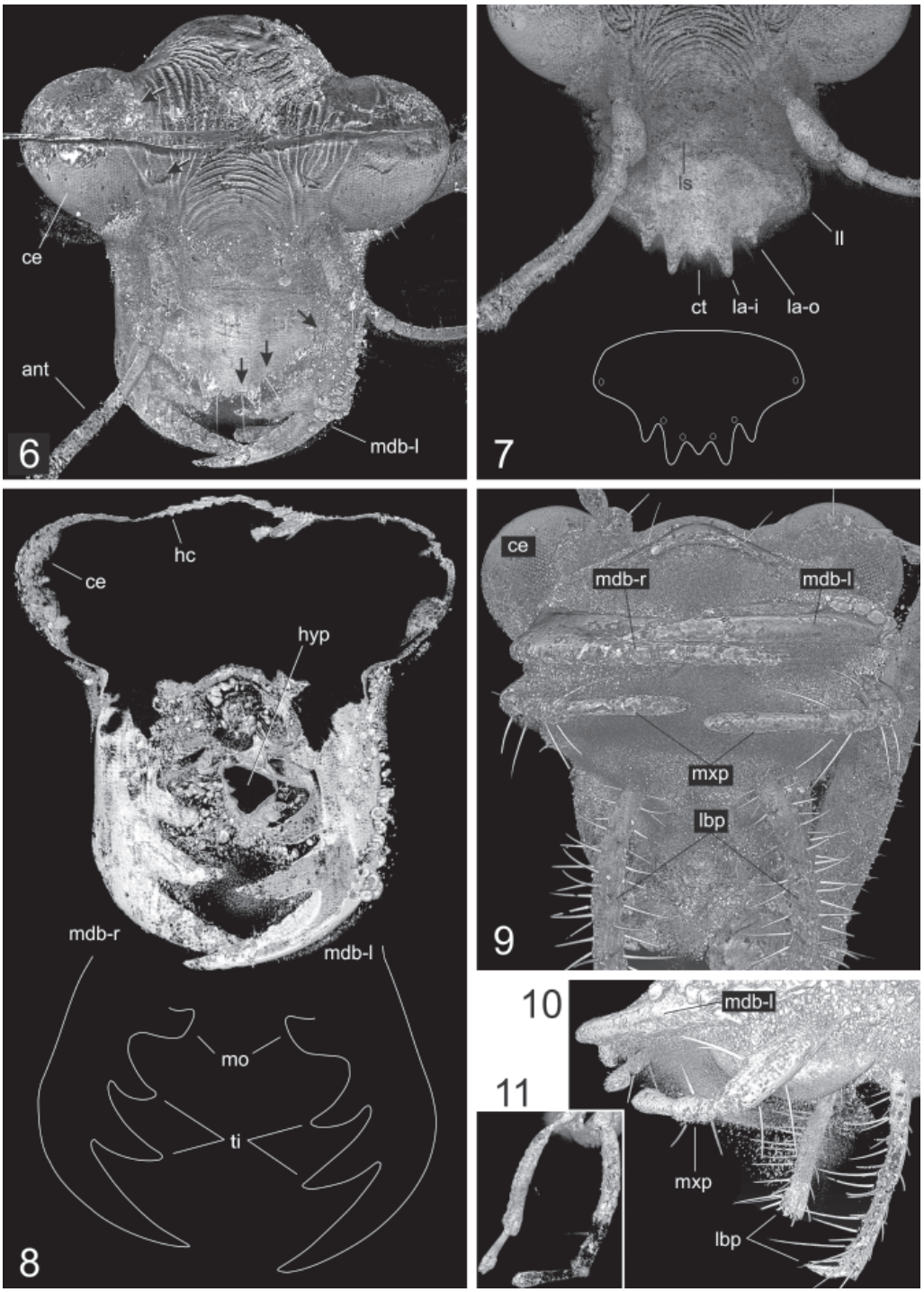


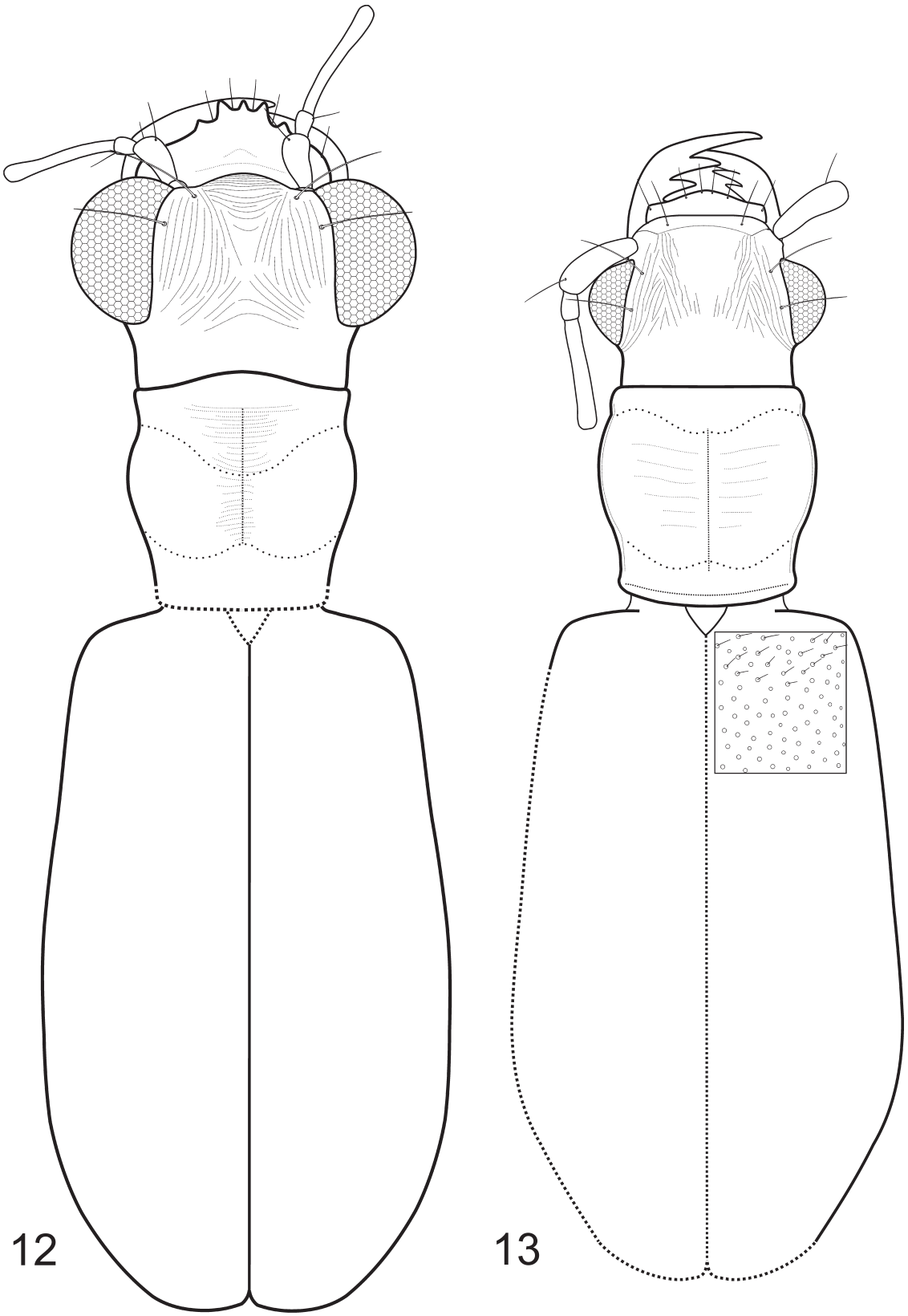
Figure 2. *Palaeopronyssiformia groehni,* new genus, new species, holotype, light microscopic image of head and pronotum, dorsal aspect; the arrows point to the insertions of the supraorbital setae.



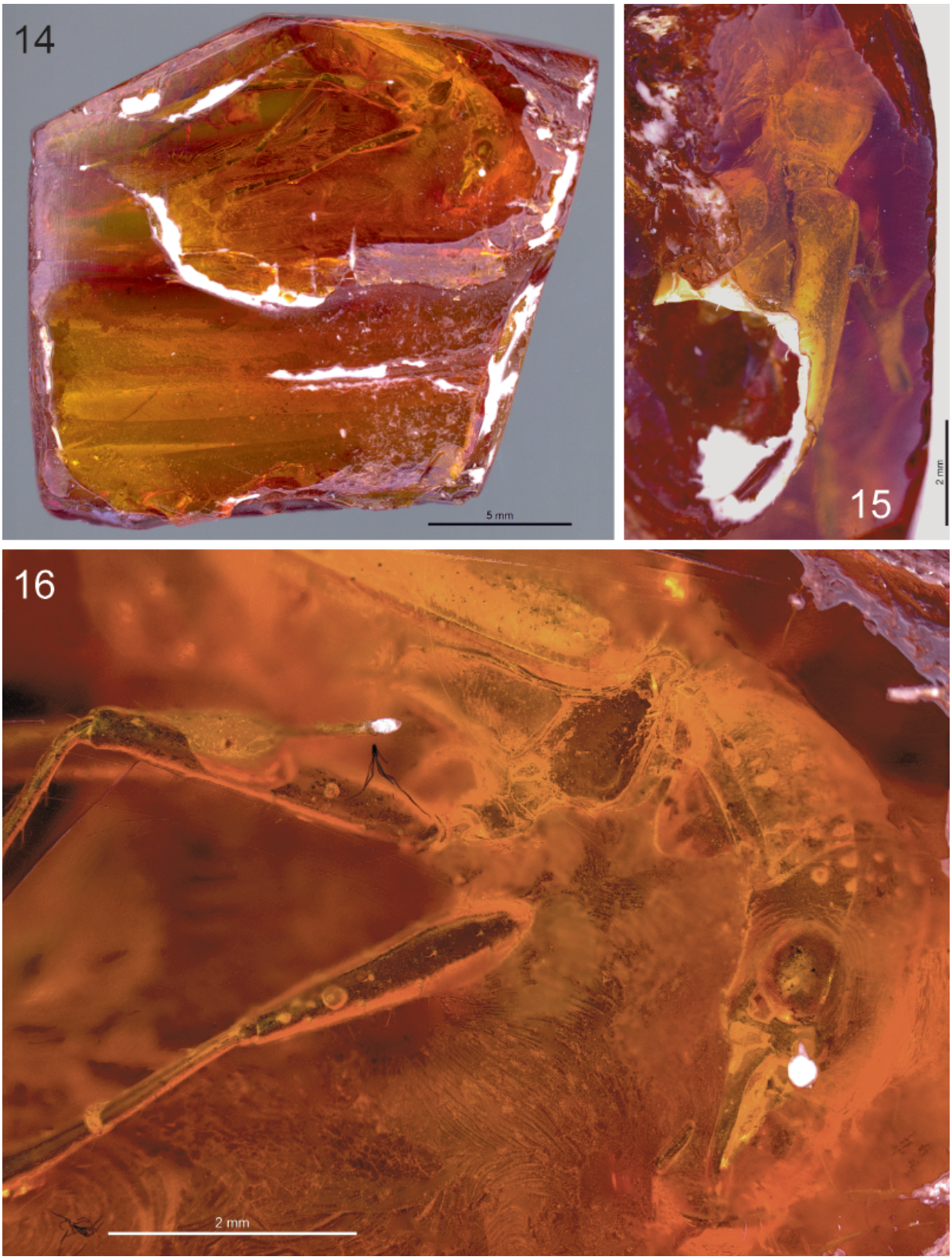
Figures 3–5. *Palaeopronyssiformia groehni,* new genus, new species, light microscopic image of the holotype. **3)** Terminal part of left hind leg broken away from the specimen (preserved near the left corner of the amber piece as shown in fig. 5), and several stellate hairs (syninclusions) mainly near bottom of this photo. **4)** Ventral aspect of body; latter is fully covered by milky coating. **5)** General view with contours of the amber piece.



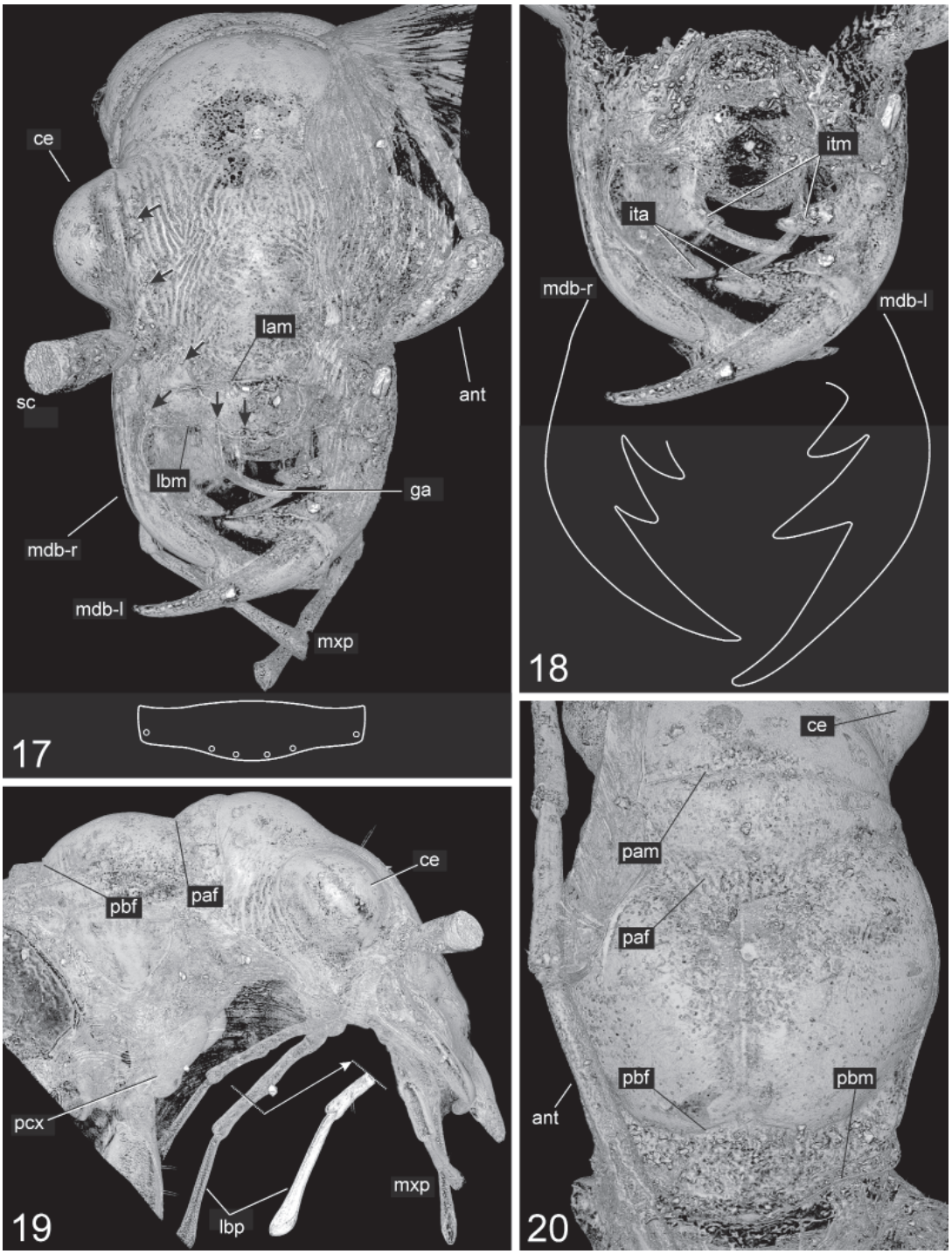
Figures 6–11. *Palaeopronyssiformia groehni,* new genus, new species, volume rendering of the holotype. **6)** Head, frontal aspect; the black arrows point to the insertions of the supraorbital setae and the labral setae. **7)** Anterior part of head with labrum; the reconstructed contour line of labrum is shown below (the white circles represent the pores of the six labral setae). **8)** Frontal section through head with mandibles; the reconstructed contour line of the apical portion of mandibles is shown below. **9)** Head, ventral aspect. **10)** Anterior part of head showing palps; note that the terminal labial palpomeres are not shown due to limited scanning sector. **11)** Labial palpomeres; note that based on this scanning results most setae show too low contrast and can thus not be imaged. Abbreviations: ant: antenna; ce: compound eye; ct: central tooth of labrum; hc: head capsule; hyp: hypopharynx; la-e: external latero-apical tooth of labrum; la-i: internal latero-apical tooth of labrum; lbp: labial palps; ll: lateral lobe of labrum; mdb-l: left mandible; mdb-r: right mandible; mo: molar; mxp: maxillary palps; ti: teeth of the incisor region.



Figures 12–13. Simplified reconstructions of the general habitus of the holotypes. The probable respective outlines of those parts of the body which could not be visualized are marked as dotted lines. **12)** *Palaeopronyssiformia groehni,* new genus, new species. **13)** *Palaeoiresina cassolai,* new genus, new species.



Figures 14–16. *Palaeoiresina cassolai,* new genus, new species, light microscopic image of the holotype. **14)** General view with contours of the amber piece. **15)** Dorsal view; the amber piece is broken together with the apical portion of the elytra and makes a hole into the beetle's abdomen. **16)** Lateral view of the anterior portion of body.



Figures 17–20. *Palaeoiresina cassolai,* new genus, new species, volume rendering of the holotype. **17)** Head, frontal aspect (the black arrows point to the insertions of the supraorbital setae, the clypeal seta and the labral setae); the reconstructed contour line of the labrum is shown below (the white circles represent the pores of the six labral setae). **18)** Anterior part of head with mandibles; the reconstructed contour line of the apical portion of mandibles is shown below. **19)** Anterior part of body with head and prothorax, right lateral view; the right apical palpomere of labium is shown based on an additional scan. **20)** Pronotum, dorsal aspect. Abbreviations: ant: antenna; ce: compound eye; ga: galea; ita: anterior tooth of incisor region of mandibles; itm: median tooth of incisor region; lam: anterior margin of labrum; lbm: basal margin of labrum; lbp: labial palps; mdb-l: left mandible; mdb-r: right mandible; mxp: maxillary palps; paf: anterior transversal furrow of pronotum; pam: pronotal apical margin; pbf: posterior transversal furrow of pronotum; pbm: pronotal basal margin; pcx: procoxa; sc: antennal scape.