



## Blind life in the Baltic amber forests: description of an eyeless species of the ground beetle genus *Trechus* Clairville, 1806 (Coleoptera: Carabidae: Trechini)

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### Abstract

The first eyeless beetle known from Baltic amber, *Trechus eoanophthalmus* **sp. n.**, is described and imaged using light microscopy and X-ray micro-computed tomography. Based on external characters, the new species is most similar to species of the Palaearctic *Trechus* sensu stricto clade and seems to be closely related to the Baltic amber fossil *T. balticus* Schmidt & Faille, 2015. Due to the poor conservation of the internal parts of the body, no information on the genital characters can be provided. Therefore, the systematic position of this fossil within the megadiverse genus *Trechus* remains dubious. The occurrence of the blind and flightless *T. eoanophthalmus* **sp. n.** in the Baltic amber forests supports a previous hypothesis that these forests were located in an area partly characterised by mountainous habitats with temperate climatic conditions.

**Key words:** fossil species, new species, Eocene, MicroCT, palaeoecology

### Introduction

Fossils of the ground beetle genus *Trechus* Clairville, 1806 preserved in Baltic amber have been reported in a number of checklists on amber inclusions during the last hundred years (Klebs 1910, Bachofen-Echt 1949, Larsson 1978, Spahr 1981, Keilbach 1982, Hieke & Pietrzeniuk 1984, Alekseev 2013). However, the first representative of this genus was not described at the species level until recently: *Trechus balticus* Schmidt & Faille, 2015. This species also represents the first obligatory wingless ground beetle known from Baltic amber characterised by markedly shortened metepisternae.

The Eocene Baltic amber forests covered a large area between the Scandinavian Shield in the west and the Ural mountains in the east, and was considered to be situated in the tropical and subtropical zone of the Eocene (55–35 Mya, Weitschat & Wichard 2010). However, based on the discovery of a number of extratropically distributed insect groups in Baltic amber, some authors have suggested the presence of a temperate climate, at least regionally, within the area of the Baltic amber forests, e.g., along slopes of higher elevated areas (Ander 1942, Kohlman-Adamska 2001, Schmidt & Faille 2015). With respect to the discovery of the wingless amber fossil *Trechus balticus*, this assumption is further supported by the fact that all extant *Trechus* species, which are obligatory wingless, occur exclusively in mountainous regions.

In this paper we describe the second wingless species of the genus *Trechus* from Baltic amber. The finding of this new species provides further support to the aforementioned hypothesis of higher elevated areas within the Baltic amber forest. In addition, this fossil represents the first eyeless beetle species known from the Paleogene.

### Material and methods

Due to particularities of the preservation of the fossil (see Preservation status below, for details), description and

figuring of the diagnostic characters are based on the negative imprint of the original beetle body on the inclusion wall. The fossil was studied and imaged using light microscopy and X-ray micro-computed tomography (micro-CT). For light microscopy analyses, we used a Leica M205-C stereomicroscope with a Leica DFC450 digital camera, a motorised focussing drive, and a Leica KL 2500 LED 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 Xradia MicroXCT-200 X-ray imaging system (Carl Zeiss Microscopy GmbH, Pleasanton, USA) under phase contrast (40 KV, 8 W) using the 4x detector (11 s, 4.15 µm pixel size).

Tomography projections were reconstructed by using XM Reconstructor software (Carl Zeiss Microscopy GmbH), resulting in image stacks (TIFF format). All scans were performed using Binning 2 (summarizing 4 pixels, resulting in noise reduction) and subsequently reconstructed with Binning 1 to prevent information loss. Volume rendering of image stacks was performed by using Amira 5.6.0 software (FEI Visualization Science Group, Burlington, USA) using the "Volren" or "Voltex" function. Colour maps were set to "Gray", and the histograms were adjusted to individual image stack's properties. Additionally, parts not related to the specimen were segmented and masked in the volume visualization. The same applies for certain parts of the specimen to enhance the visibility of diagnostic features. The image stacks have been deposited in MorphDBase ([www.morphdbase.de/?P\\_Michalik\\_20160201-M-7.1](http://www.morphdbase.de/?P_Michalik_20160201-M-7.1)). Micro-CT scanning did not provide sufficient resolution to image fine structures such as small setae, hairs, mandibular dentition, and micro sculpture of the body surface.

Measurements of the fossil specimen were taken as follows: Body size was quantified by the standardized body length, i.e., the sum of: (1) the distance from apex of right mandible in closed position to cervical collar, (2) the median length of pronotum, (3) the distance from base of scutellum along suture to apex of left elytron. The width of the head, of the pronotum, and of the elytra was measured at their widest points. The width of the pronotal apex was measured between the tips of the apical angles, the width of the pronotal base was measured between the tips of the laterobasal angles.

### ***Trechus eoanophthalmus* sp. n.**

Figs. 1–13

Holotype. Male in Baltic amber; size of piece approximately 17.0 x 15.6 x 8.6 mm (irregularly cut, Fig. 7), No. 452 in the collection F. Eichmann, Hannover, Germany (likely to be later deposited at the Geologisch-Paläontologisches Museum, University of Hamburg, Germany).

**Preservation status.** The specimen is markedly shrunken with its exoskeleton, which is completely dissociated from the inclusion wall. The latter represents the negative imprint of the beetle body and is visible in most portions. Detached parts of the original beetle exoskeleton, e.g., the distorted right elytron, which moves freely in the cavity of the amber piece, and the shrunken legs, are visible under optical microscope and could be imaged in detail using micro-CT (Figs 8–11). This particular condition of preservation is probably the result of the embedding of an immature and thus teneral specimen whose exoskeleton collapsed after the resin was cured.

Most parts of the negative imprint of the beetle body were visible in detail using a light microscope (see, e.g., microsculpture of head, Fig. 3, protibial groove, Fig. 6). However, since the amber piece was polished only from two sides lateral to the inclusion (Fig. 7) a view directly from dorsad and ventrad of the beetle is not possible due to refractions. The mouth parts are surrounded by dirt particles and therefore, the basal portion of mandibles, maxillae and mentum could not be examined using light microscopy (only the apical part of mandibles and apical segments of the palpi were visible, Figs. 3). In addition, the results of micro-CT imaging showed that the imprint of the inclusion was destroyed on the ventral surface of head (Fig. 11) and therefore, diagnostic characters of the mentum could not be reconstructed.

**Syninclusions.** Apart from several dirt particles, no syninclusions are preserved in the amber piece.

**Description.** Body length: 4.4 mm.

Colour: Colour of body surface undeterminable.

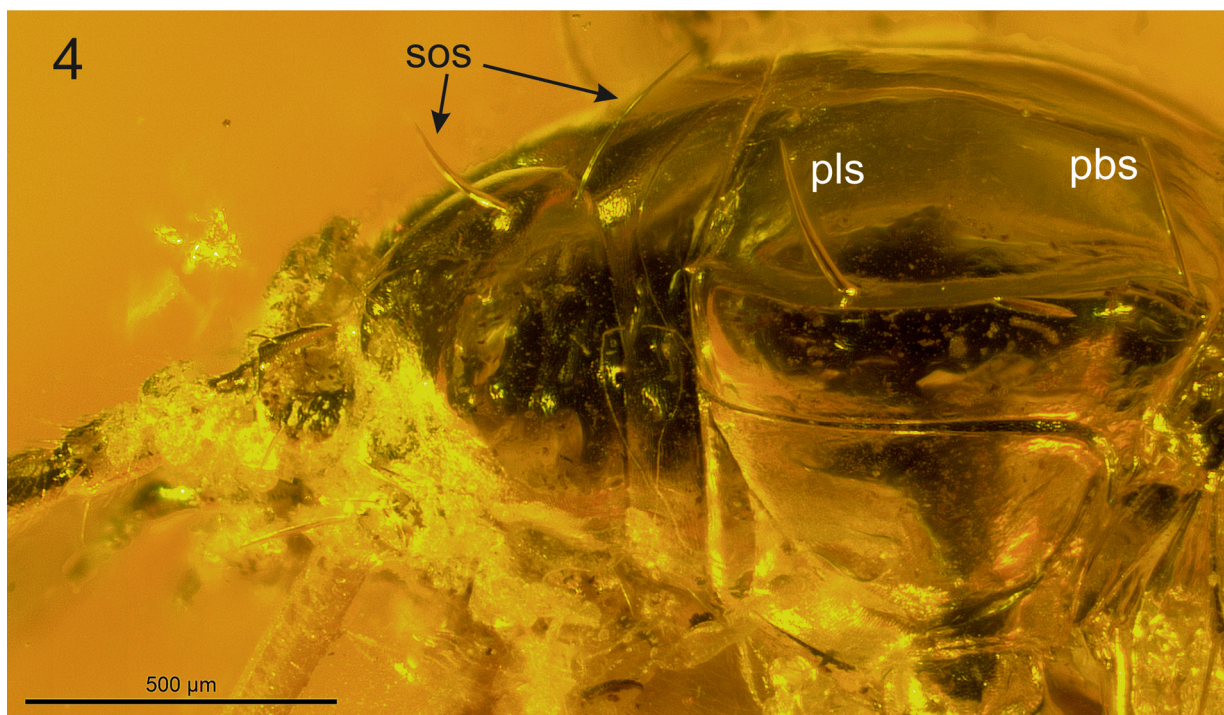
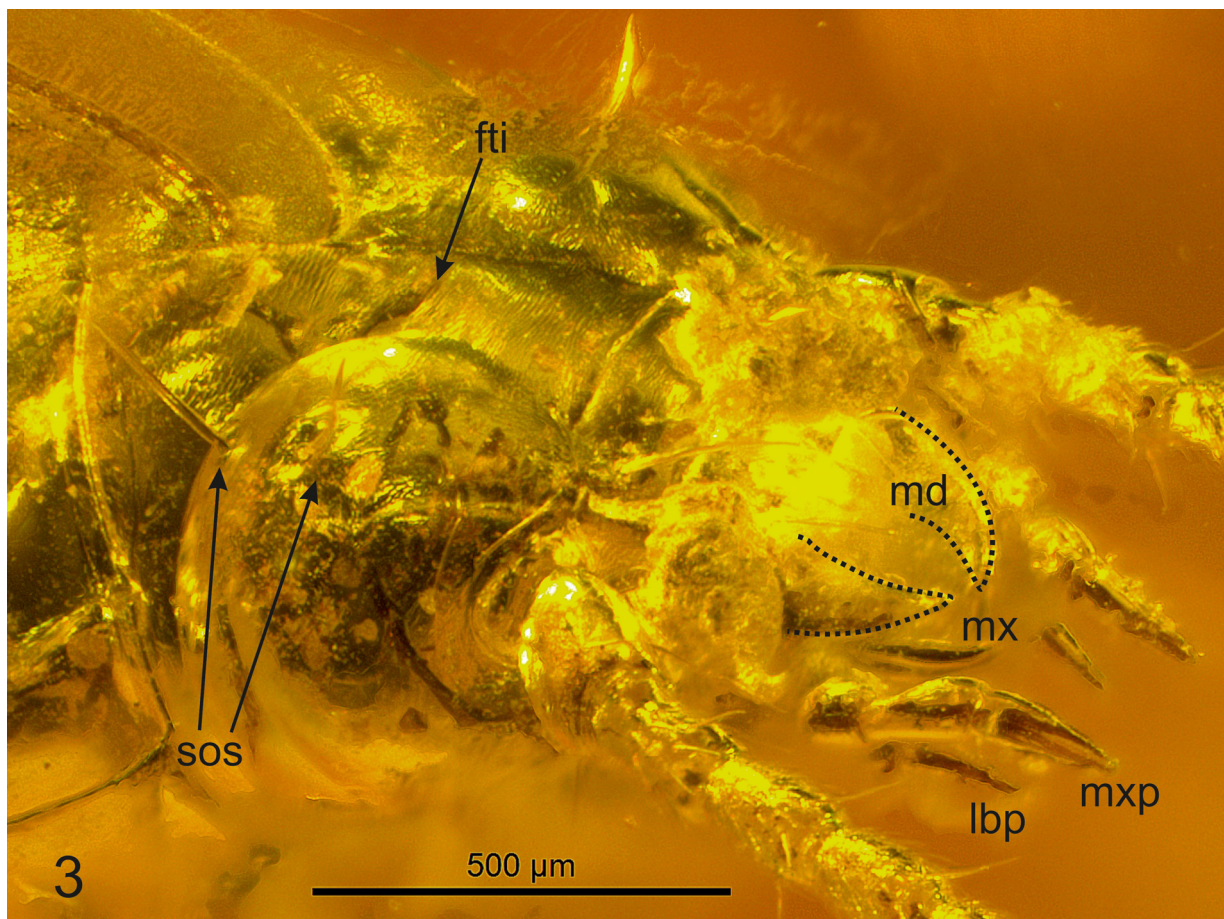
Microsculpture: Clypeus and frons with slightly engraved markedly transverse meshes, neck with larger and less transverse meshes (Fig. 3). Discs of pronotum and elytra with very fine and weakly impressed transverse meshes (visible under magnification > 150 x), appearing polished under lower magnifications.





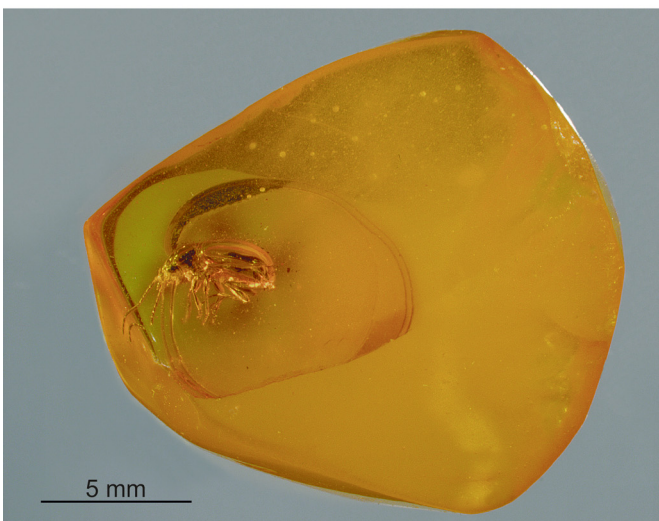
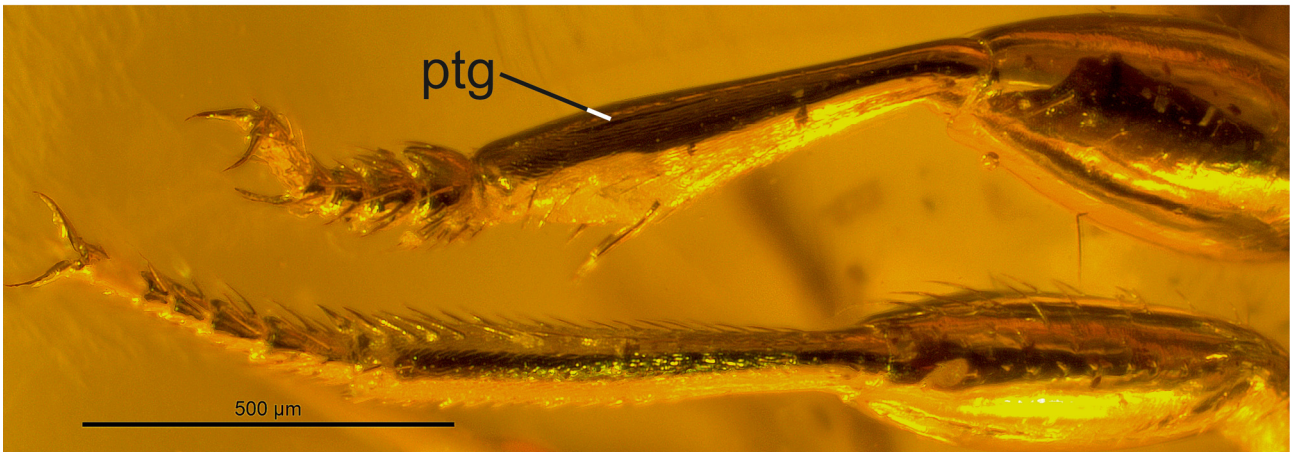
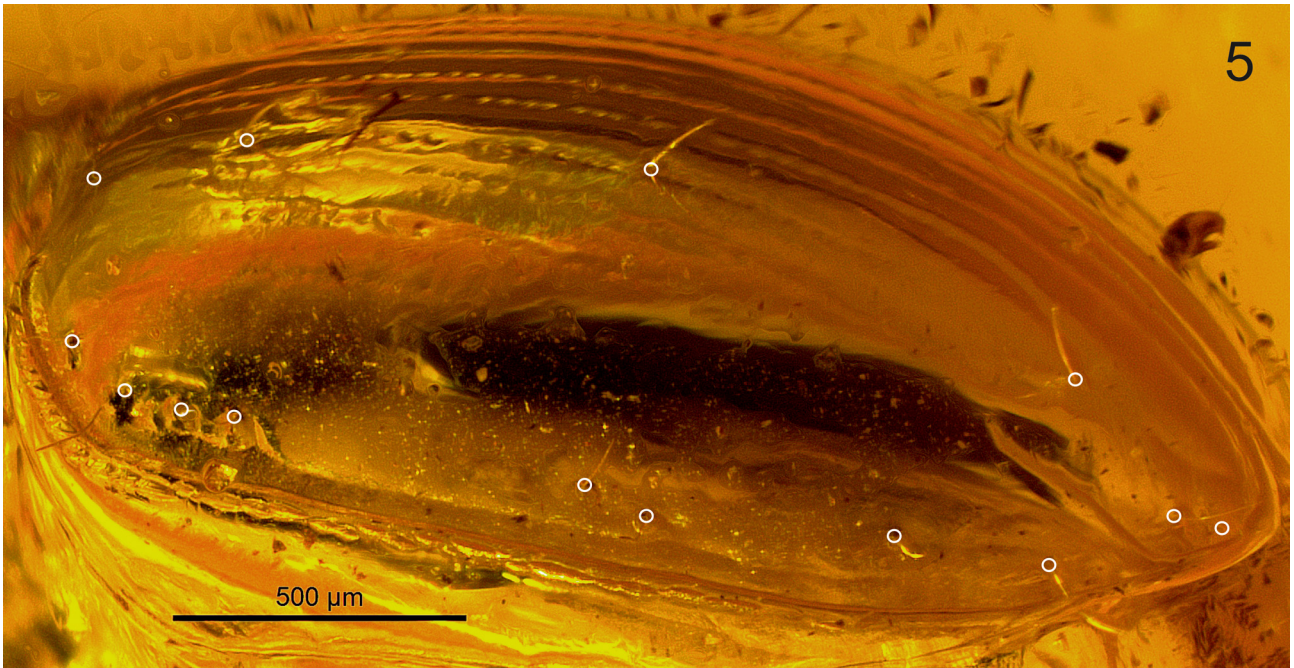
**FIGURES 1–2.** *Trechus eoanophthalmus* sp.n., holotype. Fig. 1, left lateral aspect. Fig. 2, right lateral aspect.



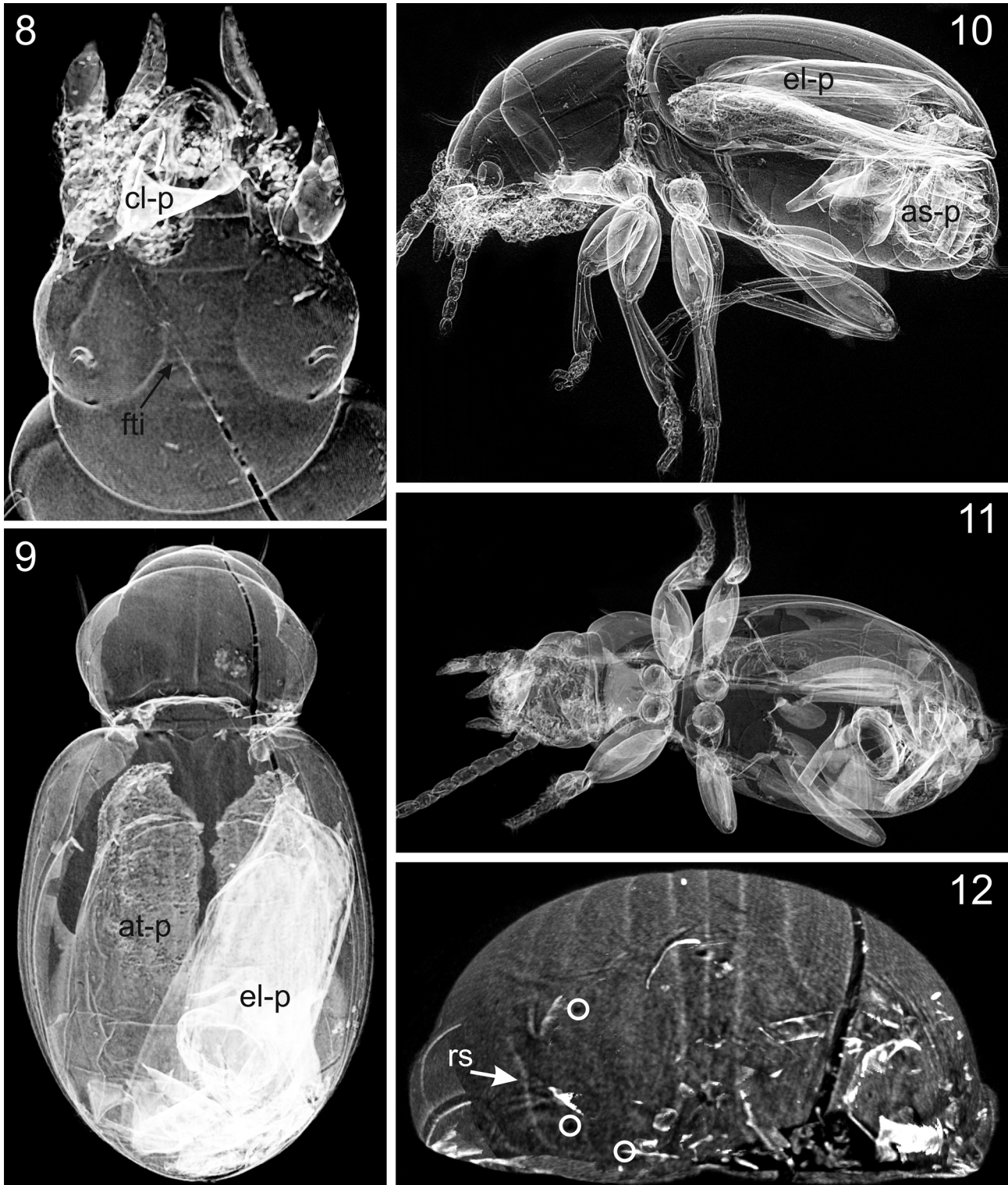


**FIGURES 3–4.** *Trechus eoanophthalmus* sp.n., holotype. Fig. 3, head (view at an angle from right above), showing markedly transverse micro-meshes on frons, and moderately transverse meshes on neck. For better visualization, the outline of the right mandible is indicated by a dotted line. Fig. 4, head and pronotum, left lateral aspect. Abbreviations: fti = frontal transverse impression; lbp = labial palpus; md = mandible; mx = maxilla; mxp = maxillary palpus; pbs = pronotal basolateral seta; pls = pronotal lateral seta; sos = supraorbital setae.



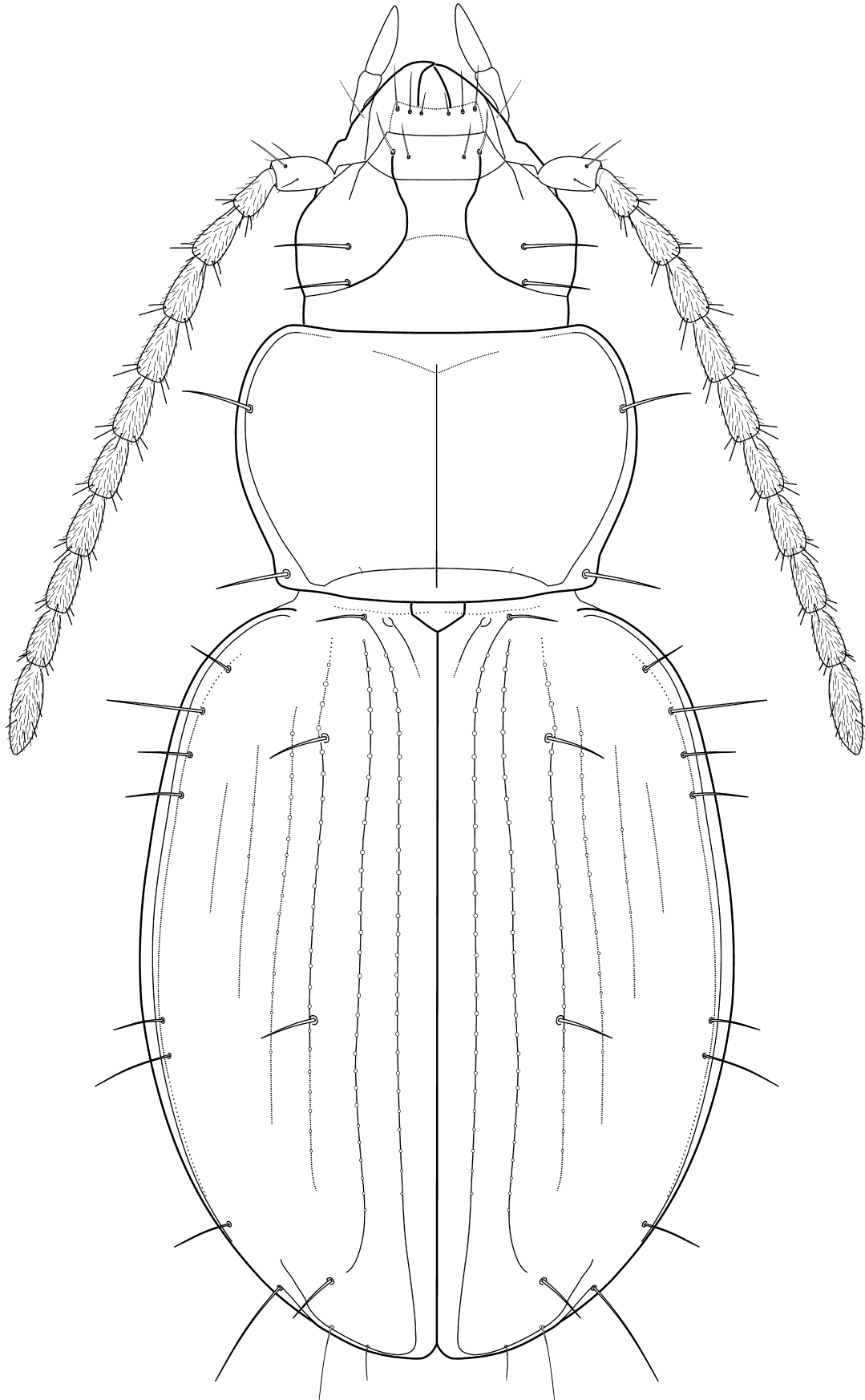


**FIGURES 5–7.** *Trechus eoanophthalmus* sp.n., holotype. Fig. 5, left elytron (the insertions of the setae are marked by white circles). Fig. 6, left foreleg and middle leg, dorsal view. Fig. 7, general view of the fossil with contours of the amber piece. Abbreviation: ptg= protibial dorsolateral groove.



**FIGURES 8–12.** *Trechus eoanophthalmus* sp.n., holotype; MicroCT images. Fig. 8, negative imprint of head, dorsal view. Fig. 9, negative imprint of elytra and pronotum, dorsal view, and deformed right elytron and abdominal tergites in the cavity of the inclusion. Fig. 10, negative imprint of the inclusion with deformed remains of the beetle body in the cavity of the inclusion, left lateral view. Fig. 11, same, ventral view. Fig. 12, apical portion of elytra (negative imprint), caudal view (the insertions of the setae of the apical triangle are marked by white circles). Abbreviations: as-p = abdominal sternites (deformed positive); at-p = abdominal tergites (deformed positive); cl-p = clypeus (deformed positive); el-p = right elytron (deformed positive); fti = frontal transverse impression; rs = recurrent stria.





**FIGURE 13.** *Trechus eanophthalmus* sp. n., reconstruction of the external shape in dorsal view. Since the labrum is only hardly visible in the fossil specimen, the assumed shape is indicated by a dotted line.

Head: Length 1.09 mm, short and robust, notably broad near base (Fig. 8). Mandibles of normal length for *Trechus* (mandibular dentition and chaetotaxy of the mandibular groove could not be reconstructed). Labrum with three pairs of setae (shape of the labral apical margin could not be displayed). Clypeus with two pairs of setae in normal position. Shape of apical segments of maxillary and labial palpi as in *Trechus* sensu stricto. Eyes completely reduced (Figs 1–4, 8). Tempora, frons, orbital and supraorbital areas smooth, markedly convex, with supraorbital furrows deep, complete, and almost uniformly bent on disc (Figs 3–4); frons with a slight but distinct transverse impression (Figs 3, 8); two supraorbital setae present and in normal position for *Trechus*. Antennae moderately short, with scapus rather robust (length 0.17 mm; length/width = 1.31; 1.3 times broader than pedicellus), and with pedicellus and third antennomere of the same length (0.16 mm) and shape.

Prothorax: Pronotum markedly transverse (width/length = 1.54), length 0.82 mm, 1.39 times broader than head, broadest in middle, with sides evenly rounded in anterior 5/6 and straight before the small but well developed laterobasal angles; basal margin 1.25 times broader than apical margin. Disk markedly convex, smooth (Fig. 4). Anterior margin almost straight, very finely beaded in outer third, smooth in middle, with apical angles very slightly protruded, rounded. Posterior margin not beaded, moderately convex in middle, slightly incised before outer quarters; laterobasal angles small, not shifted anteriorly, almost rectangular, not protruded laterally. Median longitudinal impression distinct, somewhat deeper near base, disappearing near apex; anterior transverse impression very fine, smooth; posterior transverse impression deep and linear, smooth, laterobasal foveae indistinct; pronotal base convex between laterobasal foveae and side margin. Lateral gutter moderately narrow throughout, very slightly widened towards base, smooth. Both lateral and laterobasal setae present, with the lateral seta located at apical third of pronotum. Proepisternum and prosternal process glabrous and smooth, latter without margin.

Pterothorax: Elytra markedly convex on disc (Figs. 1–2, 10), in dorsal view short-ovate (Fig. 9), length 2.49 mm, length/width = 1.21, widest near their mid-length, moderately wider than pronotum (width of elytra/width of pronotum = 1.20), glabrous beside normal setation. Humeral angles fully rounded, basal groove absent. Parascutellar stria and parascutellar seta present. First stria complete, second stria disappearing near apex, third and fourth striae distinctly finer impressed than inner striae, disappearing near base and apex, fifth and sixth striae indistinct, seventh and eighth striae absent; inner striae finely punctated apart from the apical fifth of elytra (Figs. 5, 13). Each elytron with two discal setae in third stria, and with preapical seta, situated at apical eighth of elytra, almost equally as close to the apical margin as to the suture of elytra (Figs 5, 12). Recurrent stria extending towards the reduced fifth stria anteriorly, moderately long, almost straight, with front end situated slightly anterior of the level of the preapical seta (Fig. 12). Setae of umbilicate humeral series close to the elytral margin, with posterior three setae equidistant from each other, and with first seta slightly more distant from second (Figs. 5, 13). The two setae of the medial group of the umbilicate series far removed from the preapical group (Figs. 5, 13). Epipleura long, nearly reaching the apex. Metepisternum short, glabrous and smooth, with outer margin 1.2 times longer than anterior margin.

Abdomen: Abdominal sternites V–VII and anal sternite each with one (male) pair of setae near apical margin; surfaces smooth, without hairs or micropunctures.

Legs: Moderately short, robust, all femora unmodified; protibia straight and moderately dilated towards apex, glabrous on their anterior surface, with a short and very fine longitudinal groove on external surface (Fig. 6). Basal two protarsomeres moderately dilated (Fig. 6).

Male genitalia: Could not be located within the collapsed abdominal portion of the exoskeleton.

**Etymology.** The name of the new species is a combination of “eo”, derived from the Eocene epoch when the beetle was fossilized, and “anophthalmus” (= eyeless), derived from a combination of the Greek words “a(n)” = without, and “ophthalmos” = eye.

**Relationships.** *Trechus eoanophthalmus* sp. n. shares all diagnostic features with the previously described *T. balticus* placing the new fossil species either in the main *Trechus* clade sensu Faille *et al.* (2013) or in the Nearctic lineage *Microtrechus* Jeannel, 1927 (see discussion in Schmidt & Faille 2015): shape of mandibles normal; orbital area glabrous, with deep furrows semicircularly separating well developed supraorbital region from frons and neck; two supraorbital setae present; apical segment of maxillary palpus as long as the penultimate, at base almost as broad as apex of penultimate segment, and at apex regularly conically pointed; pronotum and elytra glabrous; pronotum with posterior transverse impression and laterobasal foveae linear and sharply limited towards the convex disc, with one anterolateral and one laterobasal setae each side; elytra with basal groove absent, and with



two discal setae; recurrent sutural stria forming a deep carina directed towards the end of the fifth stria; apical triangle present, setae of humeral group situated close to the elytral margin, setae of medial group well separated from the preapical group; apical portion of protibia glabrous on external surface.

*Trechus eanophthalmus* **sp. n.** is distinguished from *Microtrechus* by two dilated male protarsomeres. Thus, the new species is most likely a representative of the main *Trechus* clade sensu Faille *et al.* (2013). However, phylogenetic studies have shown that the genus *Trechus* sensu auctorum is a non-monophyletic assemblage (see Faille *et al.* 2010, 2011, 2013). In addition, the phylogenetic positions of many of the non-European lineages need still to be investigated. Like in the previously described Baltic amber fossil *T. balticus*, phylogenetically important genital characters could not be revealed in *T. eanophthalmus* **sp. n.** due to the poor preservation of the internal parts of its body. Consequently, the systematic position of *T. eanophthalmus* **sp. n.** within the mega-diverse genus *Trechus* remains dubious. Nevertheless, it seems very likely that the Eocene fossil species, *T. balticus* and *T. eanophthalmus* **sp. n.**, are closely related and may thus represent members of the same (extinct?) branch within *Trechus* sensu lato. This hypothesis is based on two derived character states, which are potential synapomorphies of the two fossil species: i) microsculpture of pronotum and elytra consist of very fine very weakly impressed transverse meshes; ii) elytral striation markedly reduced laterally and apically. However, since these character states are also present in some of the extant *Trechus* species, this hypothesis needs further testing based on a more extensive fossil data set.

A particular character of the fossil *T. eanophthalmus* **sp. n.** is the complete reduction of the compound eyes. Within the extant world fauna of Trechini a huge number of anophthalmous and microphthalmous species are described, and their diversity is particularly rich in the southern parts of the Western Palaearctic (e.g., Jeannel 1928, Casale & Laneyrie 1982, Casale *et al.* 1998). It has been shown, however, that different degrees of eye reduction evolved several times independently at least within *Trechus* sensu lato (Casale 2011, Faille *et al.* 2010, 2011, 2013, 2014). Therefore, “eyelessness” as present in the fossil *T. eanophthalmus* **sp. n.** is likely not an indication for a close relationship with any of the extant eyeless Trechini lineages.

**Differential diagnosis.** The Baltic amber fossil species *Trechus balticus* is the only trechine beetle known from Paleogene deposits to date (Schmidt & Faille 2015). *Trechus eanophthalmus* **sp. n.** is easily distinguished from the latter by the completely reduced eyes, larger and more robust body, broader lateral gutter of pronotum, and the presence of a fine groove on external surface of the protibia. *Trechoides fasciatus* Motschulsky, 1856 is another Baltic amber fossil with uncertain taxonomic position within Carabidae, and its holotype specimen was very probably lost (Schmidt & Faille 2015). Comparison has thus to be based on the few characters given in the original description. *Trechus eanophthalmus* **sp. n.** is distinguished from the latter taxon by the much larger body size (almost three times longer), the reduced eyes, and the apically rounded elytra.

### Biogeographical and palaeoecological implications

With respect to the extant fauna, the megadiverse genus *Trechus* sensu lato is characterised by strictly extra-tropical distributional patterns. All species are adapted to warm temperate or colder climatic conditions. Outside the Holarctic, occurrences of *Trechus* are limited to high altitudes of the East African mountains. The affinities of this genus are under debate as shown by Faille *et al.* (2013), but its putative close relatives inhabit temperate climatic zones as well (e.g., *Anophthalmus* Sturm, 1844, *Duvalius* Delarouzee, 1859). Thus, it seems likely that the extinct species, *T. eanophthalmus* **sp. n.** and *T. balticus*, were also adapted to temperate climate conditions. This hypothesis seems particularly interesting in the light of the paleoclimate in the region of the Baltic amber producing forests. It was assumed that these forests occurred in the paratropical to subtropical zone of the Eocene (Weitschat & Wichard 1998, 2010). However, the co-occurrence of tropical and temperate biota in Baltic amber deposits first noted by Wheeler (1910) raised doubt on this hypothesis (see detailed discussion by Archibald & Farrell 2003; herein referred to as “Wheeler's dilemma”). In fact, it seems more likely that low temperature seasonality with milder winters may cause the presence of clearly thermophilic organisms in the higher latitudes during the Eocene, but not necessarily tropical or subtropical climate (Archibald & Farrell 2003).

An alternative hypothesis for this phenomenon of Paleogene biogeography was first proposed by Ulmer (1912) and more extensively discussed by Ander (1942). Based on the presence of a number of fresh-water insects adapted to creeks and fast flowing waters in small streams, these authors concluded that a part of the amber forests were

mountainous. Consequently, in her graphic reconstruction of the Baltic amber forest, Kohlman-Adamska (2001) showed long mountain slopes with tropical vegetation in the valleys and cold adapted vegetation in the higher altitudes. The mountain hypothesis was recently re-discussed by Schmidt & Faille (2015) based on the discovery of the flightless Baltic amber fossil *T. balticus*. This species is to be considered a montane species because most, if not all, of the recent flightless *Trechus* species occur exclusively in mountainous regions. Consequently, Schmidt & Faille (2015) assume the existence of high elevated areas within the large region that was covered by the Baltic amber forests. Our data on the flightless and eyeless *T. eoanophthalmus* sp.n. provide further support for this hypothesis. While eye reduction in Trechini is often combined with a slender body shape as a result of the adaptation to the hypogean environment (Jeannel 1928, Casale *et al.* 1998), eyelessness and a more compact body might indicate an epiedaphic mode of life. With respect to the extant fauna, epiedaphic eyeless Trechini ground beetles are, for example, known from the Caucasus and described within the *Nannotrechus* complex (Belousov 1998) and from the cloud forests of the Himalayas and Eastern Tibet and described within the genus *Duvalioblemus* Deuve, 1995 (Uéno & Zhao 1997, Belousov & Kabak 2003, Deuve 2014, unpublished data of J.S.). These enigmatic beetles occur in the upper soil layers and can be found even under small stones and rotting tree trunks. Another example is the blind and epiedaphic Caelostomini genus *Caecocaelus* Straneo, 1949 from the mountains of East Africa. Assuming that *T. eoanophthalmus* sp.n. had a similar lifestyle, it is therefore not unlikely that this blind beetle was once trapped by a clump of resin lying on the ground near the trunk base of an amber producing tree.

Because the dispersal ability of these beetles is very low, diversification seems more likely achieved in nearly stable environments, which is present in mountains of lower latitudes. The drastic Quaternary temperature changes are well-known to have caused regional extinctions and multiple range shifts of more than 1000 km for species with high dispersal power at least in the higher latitudes (e.g., De Lattin 1967, Lang 1994, Elias 2010). However, in middle and lower latitudes, mountain slopes were long enough that temperature changes may have been compensated by vertical range shifts and the species could survive *in situ*. In Europe, the glacial refuges of temperate plants and animals were located along the Alps south of the so-called Holdhaus-line known for a long time as “Massifs de Refuge” (Chodat & Pampanini 1902, Holdhaus 1906, 1954); this has been recently supported by investigations of a comprehensive data set on flightless ground beetles including a phylogeographical analysis by Drees *et al.* (2010). For Southeast Asia, Schmidt *et al.* (2011) calculated Last Glaciation Maximum vertical range shifts of only 450–700 m for local endemic high alpine *Trechus* species in South Tibet. Consequently, with respect to the recent fauna, high mountains of middle and lower latitudes are rich in species with very low dispersal power, such as tiny wingless epiedaphic Trechini, while these species are absent in northern parts of the Holarctic. Although during the Eocene the climate was generally much warmer than today, drastic temperature changes were likely and could have occurred in the Baltic amber forests in Northern Europe (up to 6°C between 55–35 Mya, see Zachos *et al.* 2001). Consequently, multiple climate change driven faunal turnover can also be assumed for the Eocene and may have particularly impacted on the lowlands, whereas mountain ranges within the amber forests may have presented a relatively stable environment for the evolution of the blind, wingless ground beetles, e.g. *T. eoanophthalmus* sp.n.

Up to today, no clear information for certain altitudes of the land surface in the different portions of Northern Europe during the Paleogene exist. The reasons for this are mainly i) the lack of sediments, which allow a proper investigation of erosional processes and dating of landforms for important areas such as the Fennoscandian Shield (Rudberg 1983), and ii) the fact that the region of the Baltic amber producing forests was completely covered by the Quaternary ice sheets with strong transformation of the preglacial landforms as a result (see Aseev *et al.* 1983, Rudberg 1983). However, the high diversity of planation surfaces and related outcrops in Scandinavia as well as the existence of monadnocks in different parts the Fennoscandian shield (see overview in Rudberg 1983) suggest rather high preglacial relief dynamics for this area. In this respect the presence of an apparently montane ground beetle fossil species in the Baltic amber deposits may be of particular interest for geosciences.

The hypothesis of a locally mountainous Eocene North Europe suggests the contemporaneous coexistence of tropical and temperate habitats along mountain slopes, which is widely developed in modern mountains in the lower latitudes. For example, in parallel of the Central and Eastern Himalaya a broad transition zone is developed, reaching from approx. 1500 to 2500 m a.s.l. This zone includes both, thermophilic Oriental and cold adapted Palaearctic elements of the ground beetle fauna (unpublished data collection of J.S.). With respect to the above discussed milder winter hypothesis of Archibald & Farrell (2003), it is noteworthy that the southern slopes of the



Himalayan mountain arc are influenced by a seasonal climate (see Mieke 1991, for details). Last but not least, the hypothesis of a rather mountainous Eocene North Europe leads inevitably to the additional assumption that a significant quantity of resin was transferred down-slope by the fast running streams, which may have resulted in an accumulation of fossil bearing amber pieces originating from different altitudes. Latter processes might reflect the divergences of the climatic adaptations of the Baltic amber biota as it is suggested by various authors based on the fossil evidence.

## Conclusions

Due to the insufficient preservation and resulting absence of phylogenetically important male genital characters of *T. eoanophthalmus* sp.n., the taxonomic position of the new fossil species within *Trechus* sensu lato cannot be assessed with certainty. However, the striking similarity to extant species of the *Trechus* sensu stricto clade makes it likely that the extinct *T. eoanophthalmus* and the similar *T. balticus* are representatives of the stem lineage of the latter group. The investigation of additional fossil material with better preservation condition may help to solve this important problem in Trechini paleontology.

The finding of eyeless and flightless representatives of the genus *Trechus* sensu lato in Baltic amber deposits is, however, a clear hint that the edaphic fauna of that genus could have been already species diverse during the Eocene. Thus, additional *Trechus* species in Baltic amber (and thus also in Bitterfeld and Rovno ambers) can be expected to be present in the Paleogene fauna of North Europe. This becomes even more obvious considering the small distributional areas due to the very low dispersal ability of tiny wingless *Trechus* species. With respect to the vast area covered by Baltic amber producing forests, the contemporary existence of a number of closely related allopatrically distributed wingless *Trechus* species is highly probable. However, the contemporary existence of the Eocene species preserved in Baltic amber can hardly be verified today. Since the Baltic amber forest has produced resin over a long period of approx. 10–20 Ma, the occurrence of chronospecies can be expected, in particular because the Eocene included periods of relative drastic climate changes (see Zachos *et al.* 2001) and thus the possibility of multiple faunal turnovers. The latter could have resulted in temporary success of different *Trechus* lineages at different times.

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