A RARE DIVING BEETLE FROM BALTIC AMBER: HYDROTRUPES PROMETHEUS NEW SPECIES REVEALS FORMER WIDESPREAD DISTRIBUTION OF THE GENUS (COLEOPTERA, DYTISCIDAE)

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ABSTRACT—A new species in the extant genus, Hydrotrupes Sharp, H. prometheus n. sp., (Coleoptera, Dytiscidae) is described from Baltic amber (Eocene) based on examination of a single female specimen. This description represents one of a limited number of diving beetle taxa described from fossiliferous amber and is currently the oldest known fossil assigned to Agabinae. Based on this specimen Hydrotrupes during the Eocene suggests that the current disjunct distribution of living Hydrotrupes species occurring in western North America and eastern China is a relict of former widespread distribution in the northern continents. Considering the age of this fossil and its similarity to living members of the genus Hydrotrupes, the conservation of morphology in this lineage of diving beetles is notable. Key morphological characters of the new species are illustrated, and the significance of this discovery for understanding Agabinae evolution and the biogeography of this previously hypothesized trans-Beringian lineage is discussed.

INTRODUCTION

AQUATIC INSECTS would seem to be unlikely candidates for fossilization in amber as tree resins are associated with terrestrial habitats, and for the most part, many aquatic insect groups occur infrequently in amber. However, the frequency of these occurrences varies dramatically between amber deposits, and Wichard et al. (2009) recently reported that aquatic insects comprise nearly 25% of the animal inclusions in Baltic amber. This is especially notable because of the extensive number of fossil amber deposits worldwide, Baltic amber includes the largest number of fossil insect taxa discovered to date. Schmidt and Dilcher (2007) studied tree resin inclusions in a modern swamp forest, and their investigation suggests a simple explanation, at least in part, for this phenomenon. Their research indicates that subaqueous tree resins trapped aquatic organisms, which are likely to become embedded particularly in the case of highly motile animals such as aquatic beetles, and changing water levels allowed for solidification of the resin that once solidified may easily become redeposited or covered by sediment (Schmidt and Dilcher, 2007). Diving beetles (Dytiscidae) are a family of adephagan beetles with approximately 3,800 extant species worldwide (Nilsson, 2001), constituting one of the more diverse and prominent groups of aquatic Coleoptera and are often, depending on the species and habitat, a very abundant element of the local aquatic fauna. Dytiscids are far from the most commonly reported inclusions of aquatic insects in amber (Wichard et al., 2009) and are not among the most frequently encountered beetles in general from worldwide amber deposits (Hieke and Pietrzeniuk, 1984), yet dytiscid adults and larvae are reported from amber by several authors (Berendt, 1845; Grimaldi and Engel, 2005; Handlirsch, 1908; Helm, 1896; Keilbach, 1982; Larsson, 1978; Poinar, 1992; Poinar and Poinar, 1999; Spahr, 1981a, 1981b; Weidner, 1958; Weitschat and Wichard, 1998, 2010; Wichard and Weitschat, 1996; Wunderlich, 1986) though many of these refer to the same specimens. Examples of the unusual inclusion of water beetles in amber can also be found in the distantly related water scavenger beetles (Hydrophilidae); Ficáček and Engel (2011) reported several such occurrences as well as diving beetle fossils misidentified as hydrophilids, highlighting the importance of reassessing the identification of fossils from historical studies. The first diving beetle species described from amber was Glesseria rostrata Koch and Berendt, 1845 of a putative dytiscid larva, and yet only recently were dytiscid taxa first described from adults from amber, beginning with Copelatus aphroditae Balke, 2003 in Miller and Balke, 2003 and C. predavetereus Miller, 2003 in Miller and Balke (2003), followed more recently by Hydroporus castengroehni Balke et al., 2010.

Hydrotrupes Sharp, 1882 is a genus of black, moderately small diving beetles of which only a single species, H. palpalis Sharp, 1882 from western North America was known since its description until Nilsson (2003) described a second species from eastern China, H. chinesis Nilsson, 2003, based on a single male collected in a residual rock pool from a mostly dried up stream. The new species placed in this genus, which is so far only known from the female holotype, is presumed extinct. Species determinations within much of Agabinae, including Hydrotrupes, depend largely on examination of the male genitalia, particularly shape and setation of the lateral lobes and features of the median lobe. The only known specimen of the new species is an adult female, and despite not having access to this character system, features of the habitus, the prosternal process, and the antennae have been shown to be useful in species recognition within Hydrotrupes (Nilsson, 2003) as well as the use of the relative width of the metaventral wing (the lateral process of the metaventrite) within Agabinae taxonomy (e.g., Larson, 1989). The new species described herein appears to possess an external character state combination sufficient to separate it from extant species (see below), and based on the high level of observable detail, even color and microsculpture, the biogeography of known, living members of the genus, and the rarity, and therefore significance, of the specimen, it seems appropriate to erect a new species of Hydrotrupes.

Photographs of the only known specimen of the species described herein are hosted at the website Anders Leth
The main goal of this study is the description of a new species of Hydrotrupes from Baltic amber with a discussion of its importance for understanding the evolution of the group and its significance for evaluating current biogeography in light of historical biogeography.

MATERIALS AND METHODS
Measurements and preparation of material.—The amber piece was examined following the recommendations proposed by Grimaldi (1993), and the whole amber piece containing H. prometheus was placed in a tray and submerged in glycerin before examination. The beetle is at approximately a 45° angle to the widest surface of the amber piece and an attempt was made to correct for this when imaging the specimen. Measurements were taken with an ocular scale on a Wild M5 dissecting microscope, and the scale was calibrated with a Wild stage micrometer. Stretching and compression of the amber, as well as optical distortion, lead to unavoidable inaccuracy in measurements. Nevertheless, the beetle is intact with the elytra closed (Fig. 1) and the following measurements are also provided as ratios to give an indication of shape. Measurements include: 1) total length (TL); 2) greatest width (GW); 3) greatest length of metafemur (ML); 4) greatest length of metatrochanter (RL); 5) shortest distance across metaventral wing (WV); and 6) width of metacoxal plate along same line as WV (WC, Fig. 4.4) (WV and WC following [Larson, 1989]).

Illustrations.—All illustrations were initially made using a drawing tube on a Wild M5 dissecting scope. These were then scanned, and line drawings were created digitally based on the initial drawings.

Material.—The Baltic amber specimen was examined from the personal amber collection of Anders Leth Damgaard (ALDC, A.L. Damgaard), and the holotype is housed in the ALDC, Denmark for safekeeping to be eventually deposited in the Zoological Museum, University of Copenhagen (ZMUC, A. Solodovnikov). The holotype is catalogued with the ZMUC with the following database number: ZMUC00036776. Specimens of Hydrotrupes palpalis were examined from the University of Arizona Insect Collection (UAIC, W. Moore), the Santa Barbara Museum of Natural History (SBMNH, M.S. Caterino), and the senior author’s personal research collection (RAGC, R. A. Gómez). Also, the single known specimen of H. chinensis was not examined for this investigation.

SYSTEMATIC PALEONTOLOGY
Order COLEOPTERA Linnaeus, 1758
Family Dytiscidae Leach, 1817
Subfamily Agabinae Thomson, 1867
Tribe Agabini Thomson, 1867
Genus Hydrotrupes Sharp, 1882
Hydrotrupes prometheus new species
Figures 1–3

Diagnosis.—As noted by Nilsson (2003) in his diagnosis of H. chinensis, Hydrotrupes species are morphologically similar,
Figure 3—Hydrotripes prometheu sp. n., ZMUC00036776, female holotype: 1, head and prothorax, ventral aspect; 2, left antenna, ventral aspect; 3, dorsal habitus; 4, close-up of head and prothorax, ventral aspect; 5, close-up of hind legs and abdomen, ventral aspect; 6, ventral right oblique of 4 with different lighting; 7, abdominal ventrite VII, pygidium, and apices of gonocoxae, ventral aspect.
which also applies to the new species described herein, and as with many genera within Agabinae (Ribera et al., 2004), *Hydrotrupes* is a rather morphologically homogenous group. The new species shares numerous morphological character states with both *H. chinensis* and *H. palpalis*, and the most apparent differences between the species seem to be body shape and size, antennal shape, the shape of the prosternal process, the relative width of the metaventral wing, and the morphology of the male genitalia, particularly the apex of the median lobe and setation of the lateral lobes.

Body: members of *Hydrotrupes* are relatively small, broadly oval diving beetles, and *H. prometheus* is currently the smallest known species in the genus (TL=2.31 mm). *Hydrotrupes chinensis* (TL=4.3 mm; Nilsson, 2003) and *H. palpalis* (TL=3.3–4.2 mm; Miller and Perkins, 2012) are both larger in total length. Proportionally, the body is robust (TL/GW=1.57; Fig. 3.3) and most similar to *H. chinensis* (TL/GW=1.59) and narrower than *H. palpalis* (TL/GW=1.7–1.8; Fig. 4.1).

Metaventral wing: the metaventral wing of *H. prometheus* is very narrow (WC/WS=6.0; Fig. 2) and narrower than all other known *Hydrotrupes* species. The metaventral wing of extant *Hydrotrupes* species is moderately broad (Fig. 4.4), (WC/WV=1.7–2.2 in *H. palpalis* (Miller and Perkins, 2012) and (WC/WV=2.65) in *H. chinensis* (Nilsson, 2003).

Prosternal process: the prosternal process of *H. prometheus* is short and broad (Figs. 2.1, 2.2, 3.1), a character state which it shares with the North American species, *H. palpalis* (Fig. 4.3). The prosternal process of *H. chinensis* differs in being slightly narrower and more elongate apically.

Antenna: the antennomeres of the female holotype of *H. prometheus* are expanded (incrassate) and short (Fig. 3.1, 3.2), more robust than the antennomeres of both sexes of *H. palpalis*, of which the male is sexually dimorphic with slightly flattened antennomeres in dorsal aspect (Fig. 4.5), and the male antennomeres of *H. chinensis*, which is known only from the male holotype (Nilsson, 2003).

**Description.**—Measurements (in mm): TL=2.31; GW=1.47; ML=0.50; RL=0.39; WS=0.08; WC=0.48; TL/GW=1.57; ML/RL=1.28; WC/WV=6.00.

Body broadly ovoid, robust; lateral outline between pronotum and elytra continuous in dorsal aspect; lateral margins of pronotum broadly and evenly curved; lateral margins of elytra broadly curved (Figs. 1, 2.1, 3.3); dorsally moderately convex, ventrally nearly flat (Fig. 2.1). Coloration black throughout, dorsum of head and pronotum appearing darker than elytra, antennae and palpi dark brown.

Dorsum, particularly of the head and pronotum, partially obscured by trapped air, visible sculpture of pronotum and elytra comprised of large irregular meshes (Fig. 1). Eyes small in size, anterior margin of eye deeply emarginate (Fig. 3.3); antennae short and robust (Fig. 3.2). Maxillary and labial palpomeres short, apical palpomeres broad (Fig. 3.4, 3.6), each with two nearly round sensorial fields that are approximately contiguous medially, apical labial palpomere distinctly short and subquadrate, penultimate palpomere cup-shaped (Fig. 3.6). Pronotal bead broad, increasing in width anteriorly; posterior angles of pronotum obtuse. Elytral epipleuron broad anteriorly, abruptly and evenly narrowed medially, slender posteriorly (Fig. 2.1). Prosternum anteromedially slightly projecting anteriorly, anteriorly broadly rounded; prosternum laterally beaded; prosternal process short and broad, broadly rounded apically (Fig. 2.1, 2.2). Metaventrite with anteromedian emargination shallow; without distinct microsculpturing; metaventral wing distinctly narrow (WC/WV=6.0), apically slender and short (Fig. 2.2). Surface of metacoxal plate with conspicuous microsculpturing consisting of very narrow, longitudinally oriented sculpticells that broaden anteromedially; metacoxal plate medially slightly narrowed; lobes of metacoxal processes large, broadly rounded posteriorly, without distinct incisions along posterior margin (Fig. 2.1, 2.2, 3.5); metacoxal lines curved, weakly divergent anteriorly, strongly divergent posteriorly without contacting the hind margin of the metacoxal processes, (Fig. 2.2, 2.3). Abdominal ventrites

**Figure 4—** *Hydrotrupes palpalis* Sharp, 1882 morphology (CBP0061335): 1, male dorsal habitus; 2, male head and anterior third of pronotum, anterior aspect; 3, prostatic process, ventral aspect; 4, left half of metaventrite and hind leg showing measurements taken of metaventral wing width (WV) and metacoxal width (WC); 5, right male antenna, dorsal aspect.
irregularly rugulose, rugulae more conspicuous laterally (Fig. 3.5).
Metatibia and metatarsus nearly without natatory setae, ventral surface lacking natatory setae, very sparse natatory setae along dorsal surface of metatibia and metatarsus; tarsal claws of all legs small and simple, subequal in length. The gonocoxae are slightly extruded; apices of gonocoxae narrowly rounded and setose, with elongate setae apically among several other shorter setae (Fig. 3.7). The female pro- and mesotarsi are slender and lack ventral adhesive setae (Fig. 3.1). Although the male is not known, it is likely that the male pro- and mesotarsomerites I–III are broader and possess ventral adhesive setae like male H. palpalis.

Etymology.—This species is named after the Greek Titan Prometheus who gave mankind fire for the scientific value of this specimen and because of the golden yellow glow of the amber piece.

Hydrotrupes.—ZMUC00036776: female in Baltic amber piece stored in a sealed plastic storage bag labeled “Baltic amber/Dytiscidae.” On a label fixed to the outside of the plastic bag: “HOLOTYPE: Hydrotrupes prometheus R.A. Gómez and A.L. Damgaard, 2013” (red printed label with double black line border). The piece is light yellow and clear and measures approximately 3 cm at its longest, 2 cm at its widest, and 1 cm at its tallest. The beetle is surrounded laterally by slight aberrations in the amber resulting from the beetle’s struggle to escape, particularly on both sides of the metatarsi, which can be mistaken for a predatory setae (Fig. 1), and the beetle ventrally lies below a shallow interrupted crack on the surface of the piece (Fig. 2.1). In addition to the beetle, the amber piece includes several “Sternhaare” or stellate hairs, which are putative minute parts of oak trees and are characteristic of Baltic amber (Weitschat and Wichard, 1998) in close proximity to the specimen, unidentified debris, and a mite.

Occurrence.—Baltic amber, Eocene, Lithuania. More specific locality data are not currently known. Based on current evidence, the geological age of Baltic amber has recently been dated to be ca. 40–55 million years old (e.g., Michelsen, 2000; Ritzkowski, 1997; Weitschat and Wichard, 1998).

Remarks.—Hydrotrupes adults can be separated from other dytiscid genera based on the following: 1) the eye with the anterior margin deeply emarginate; 2) the scutellum exposed in dorsal aspect with the elytra closed; 3) the elytra together apically rounded; 4) the pronotum and proventricle process in approximately the same plane in lateral aspect; 5) the metacoxal lines broadly separated from metacoxal suture medially; 6) the labial palpi relatively short with the apical palpomere broad and subquadrate; and 7) natatory setae strongly reduced on legs (Miller and Perkins, 2012). This species can be placed within Hydrotrupes based on the presence and examination of all of the aforementioned characters. Here we note that H. chinensis possesses a dorsal fringe of natatory setae on the metatibia and metatarsus (Nilsson, 2003), and the wording of character 7 of and mesotarsi (Nilsson, 2000). The systematic position of Hydrotrupes is presently in question present (Balke et al., 2005; Beutel et al., 2013), and of course, is a characteristic feature that cannot be verified in H. prometheus presently. The systematic position of Hydrotrupes remains unresolved, but a recent phylogeny of Dytiscidae inferred from molecular sequence data (Ribera et al., 2008) supports a close relationship between Hydrotrupes and the ‘austral agabines’ of the Platynectes Régimbart, 1879 group, an informal grouping of genera that also includes Agametris Sharp, 1882, Andonectes Géorgiev, 1971, and Leuronectes Sharp, 1882 (Nilsson, 2000), and the clade that includes these taxa is part of an unresolved polytomy near the basal node of Dytiscidae. Ribera et al. (2008) argue that the unusual features of Hydrotrupes are either autapomorphies in the case of the reduction in swimming hairs and the robust labial palpi or a derived reversal in the case of the absence of a larval mandibular channel, and that

Discussion

The occurrence of diving beetles in amber.—Due to the high level of detail preserved in this Baltic amber specimen, this species can be unambiguously assigned to Hydrotrupes and therefore, Agabinae based on the current classification of Dytiscidae (Nilsson, 2001), as nearly all external characters that are informative in grouping in addition to other characters are clearly visible. This Baltic amber diving beetle inclusion is interesting for a number of reasons. Firstly, H. prometheus is currently the oldest known Agabinae fossil as the previous oldest known agabine fossil occurred in the Oligocene (Nilsson, 2001). In addition to this, it is one of the oldest fossil diving beetles that can be unambiguously placed in an extant subfamily (Nilsson, 2013). The other two fossils in this category, both of which are also known from Baltic amber, are Copelatus aphrodites (Copelatinae) and Hydroporus carstengroehni (Hydroporinae). Now it is known that members of three of ten extant subfamilies of diving beetles were present in Paleogene Europe, representing the first (Hydroporinae, about 2100 extant species), second (Copelatinae, about 650 species), and fourth (Agabinae, about 400 species) most diverse subfamilies (Nilsson, 2013). This taxon from the Eocene is important to future studies focusing on Agabinae evolution and, possibly, the evolution of the hydropetric syndrome (see below) as well as being useful for calibrations derived from fossil data. The only other described diving beetle fossil placed in a living clade is Hydroporus petrefactus Weyenberg, 1869 from the Jurassic of Bavaria (Nilsson, 2001), but its classification within Dytiscidae, much less Hydroporinae, has been called into question (e.g., Prokin and Ren, 2010).
the lineage’s divergent morphology is likely due to selection pressure for specialization in hygropetric habits.

The investigation of the historical biogeography of Agabinae by Ribera et al. (2004) inferred from mitochondrial sequence data did not sample Hydrotrupes, however, their molecular clock analyses support the diversification of the main lineages within Agabinae having occurred during the late Eocene, which is consistent with current thinking on the age of Baltic amber and therefore, this inclusion. However, this is perhaps best viewed as a minimal possible age of the group. The age of Agabinae, or more conservatively, perhaps the clade that includes Hydrotrupes and members of the Platynectes group, may indeed date back further than the late Eocene. The challenge presented by fossils is that they offer extremely valuable data on the first occurrence of a distinctive morphological trait, but these appearances do not necessarily closely follow lineage divergence (Magallón, 2004). This inherent uncertainty between the timing of these two events has a profound effect on the accuracy of dating lineages, and Magallón (2004) suggests that first fossil appearance documents a distinctive feature once it has already become abundant rather than when it originated. Therefore, perhaps the origin of the Hydrotrupes lineage is earlier than the late Eocene because of the time required for the Hydrotrupes lineage to diverge from stem members of the Hydrotrupes–Platynectes group clade and attain its distinctive morphology in abundance, particularly its autopomorphies. In addition, the time required for the Hydrotrupes–Platynectes group lineage to diverge from other clades of diving beetles would also suggest that this lineage may be considerably older than the late Eocene. An alternative hypothesis is that these lineages radiated rapidly in the early Cenozoic, with Hydrotrupes diverging from other clades early on and rapidly acquiring a distinctive morphology that was maintained for millions of years. This is certainly speculative and cannot be directly confirmed because of the imprecise dating of Baltic amber, but it offers hypotheses for future studies to test.

Biogeographic relevance of H. prometheus.—Hydrotrupes as noted previously, is currently known from two recent species, one western North American species, H. palpalis (California and Oregon, U.S.A. reaching as far south as northern Baja California, Mexico [Gómez, unpublished data]), and one eastern Asian species, H. chinensis (Anhui, China). This present day Pacific intercontinental disjunction (Fig. 5.1) appeared to be a relict of former widespread distribution of the genus, is that 50 mya. However, this is not applicable in the case of the Agabinae, whose members are most diverse in the Holartic, with few species groups of predominately north temperate clades and a small number of species present in the Southern Hemisphere (Nilsson, 2000, 2001; Ribera et al., 2004). The close relationship between Hydrotrupes and the “austral agabines” of the Platynectes group (Ribera et al., 2008) presents an intriguing problem of biogeography. Members of the Platynectes group are most diverse in the Southern Hemisphere and are seemingly absent from the African continent. All but one of the genera included in the group are Neotropical (Nilsson, 2000, 2001, 2013) and the most widespread and diverse genus, Platynectes, includes members known from the Neotropical, Australian, and Oriental lineages. THE FIGURE 5.—Hydrotrupes Sharp, 1882 distribution on paleogeographic maps drawn by Ron Blakely (http://www2.nau.edu/rob7/): 1, H. prometheus n. sp., Eocene; 2, H. chinensis Nilsson, 2003 and H. palpalis Sharp, 1882, present day.
regions in addition to a few eastern Paleartic species from China and Japan (Nilsson, 2013). Is the close relationship between Hydrotrupes and members of the Platynectes group, the historically widespread distribution of Hydrotrupes in the northern continents, and the minimal possible age of this lineage evidence for a classical Laurasia and Gondwana vicariant event between these two clades or a dispersal event? Gondwana began to separate from Laurasia in the Early–Middle Jurassic (ca. 180 mya), and given that dytiscids were not common in the Early Cretaceous (Beutel et al., 2013; Grimaldi and Engel, 2005) but were certainly present by 150 mya (Grimaldi and Engel, 2005), it seems unlikely that the current distribution of these particular diving beetle lineages was the result of a classical Laurasia and Gondwana vicariant scenario, without the Hydrotrupes–Platynectes group lineage being exceptionally earlier than the Eocene. However, if we consider Hydrotrupes a member of a more inclusive, historically Gondwanan lineage, which is a possibility, that was present in the Laurasian territories in the Paleogene then perhaps, the Late Cretaceous–Paleogene biogeographic pattern through the Atlantogea biogeographical paleoprovince proposed recently by Ezcurra and Agnolin (2012) is a reasonable hypothesis for the origin of the clade that includes Hydrotrupes and members of the Platynectes group. One conspicuous problem with this hypothesis when applied to these taxa is that dispersal from the Paleartic via the Atlantogea biogeographical paleoprovince to the Neotropical region would have required passage through the African continent (Ezcurra and Agnolin, 2012), a region from which no members of the Platynectes group of genera nor Hydrotrupes are currently known (Nilsson, 2013). However, the group’s apparent absence in Africa does not guarantee its historical absence, and if this pattern is accepted, then dispersal from South America to Australia was still possible via Antarctica up until the end of the Cretaceous (Ezcurra and Agnolin, 2012).

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