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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* is at least 40 million years old. The occurrence of *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 all 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 subaquatic 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); Fikáček 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. predaveterus* Miller, 2003 in Miller and Balke (2003), followed more recently by *Hydroporus carstengroehni* 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. chinensis* 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 a erect a new species of *Hydrotrupes*.

Photographs of the only known specimen of the species described herein are hosted at the website Anders Leth

FIGURE *1*—*Hydrotrupes prometheus* n. sp., ZMUC00036776, female holotype; habitus in posterodorsal aspect with amber piece lying flat.

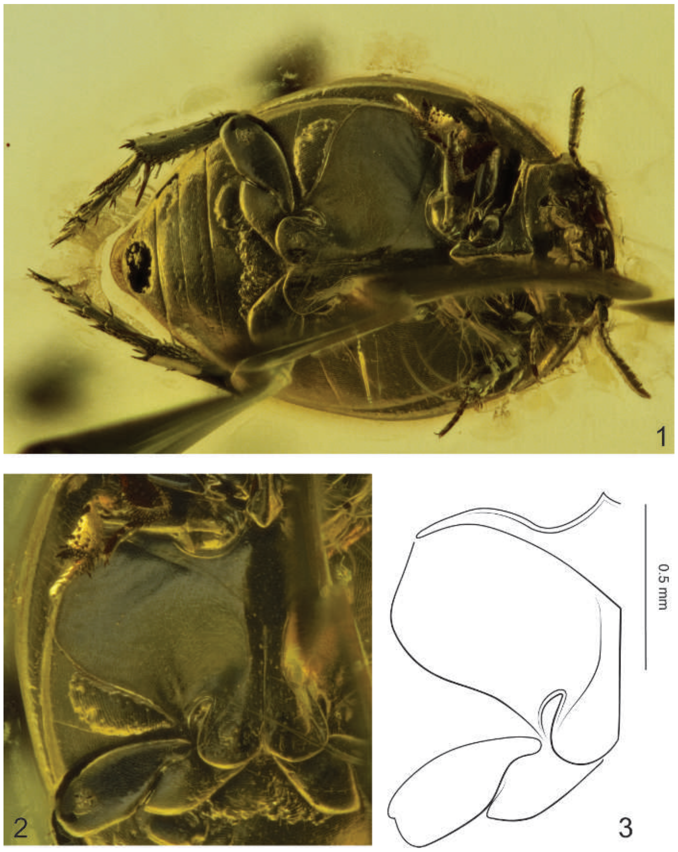

FIGURE *2*—*Hydrotrupes prometheus* n. sp., ZMUC00036776, female holotype: *1*, ventral habitus; *2*, close-up of pterothorax, ventral aspect; *3*, left half of metaventrite, metacoxa, metatrochanter, and metafemur.

Damgaard (www.amber-inclusions.dk). 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,

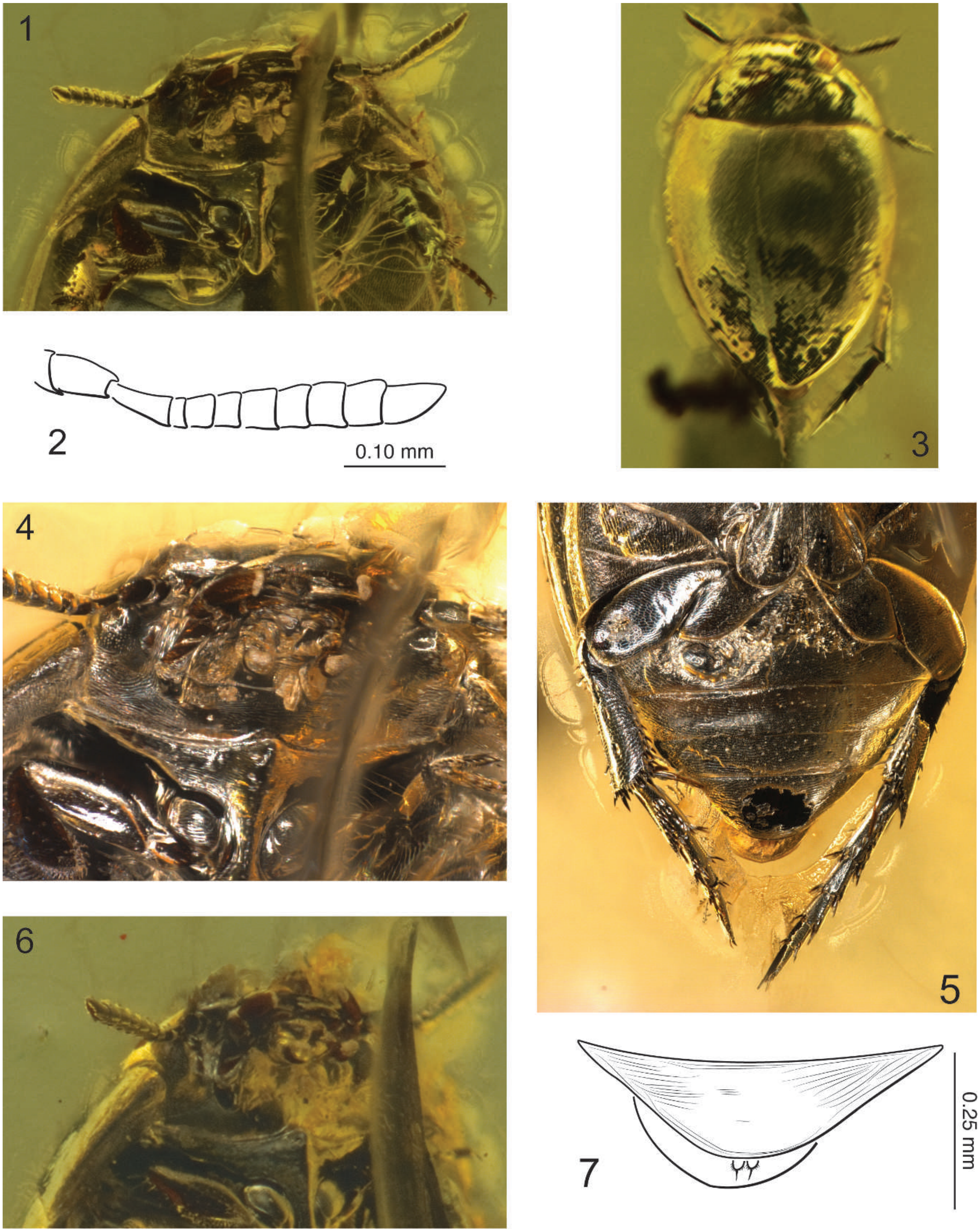

FIGURE 3—*Hydrotrupes prometheus* n. sp., ZMUC00036776, female holotype: *1*, head and prothorax, ventral aspect; *2*, left antenna, ventral aspect; *3*, dorsal habitus; *4*, close-up of head and prothorax, ventral aspect; *5*, close-up of hind legs and abdomen, ventral aspect; *6*, ventral right oblique of *4* with different lighting; *7*, abdominal ventrite VII, pygidium, and apices of gonocoxae, ventral aspect.

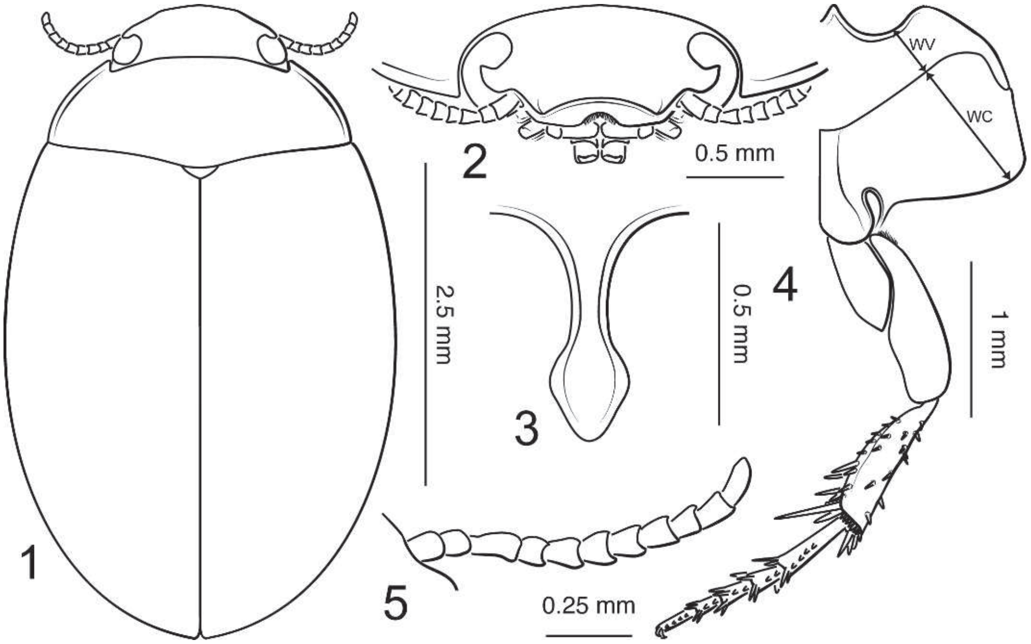

FIGURE *4*—*Hydrotrupes palpalis* Sharp, 1882 morphology (CBP0061335): *1*, male dorsal habitus; *2*, male head and anterior third of pronotum, anterior aspect; *3*, prosternal process, ventral aspect; *4*, left half of metaventrite and hind leg showing measurements taken of metaventral wing width (WV) and metacoxal width (WC); *5*, right male antenna, dorsal aspect.

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 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). 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 irregularly rugulose, rugulae more conspicuous laterally (Fig. 3.5, 3.7). Pro- and mesolegs short and robust, pro- and mesotibiae expanded apically and heavily spined, mesotibia longer than protibia. Metaleg with femur moderately short and broad, metafemur without setal row and groove near anteroapical angle; metatrochanter very large (ML/RL=1.28); metatibia slender, heavily spined; anterior metatibial spur large, more than twice as large as posterior metatibial spur; metatarsomeres straight, not lobed (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 mesotarsomeres 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.

Holotype.—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 swimming hairs (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 prosternum and prosternal 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 Miller and Perkins (2012) listed above is modified to reflect this.

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 aphroditae* (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 hygropetric 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).

Morphology and systematics of Hydrotrupes.—Based on this discovery, *Hydrotrupes* is certainly an old lineage of diving beetles and is at least 40 million years old. Interestingly, despite the tremendous age of this specimen and the historical and current biogeography of the group, the morphology of *H. prometheus* (Figs. 1–3) is strikingly similar to recent members of the genus (Fig. 4). It appears to be a dytiscid genus with rather limited morphological diversity between the recent species (Miller and Perkins, 2012; Nilsson, 2003), and this fossil provides historical evidence that this morphological homogeneity has been conserved for a long period of time. Another notable example of long morphological stasis drawn from Dytiscidae is *C. aphroditae* (Eocene), which closely resembles modern species with a presumably derived character state (presence of elytral striae) for the genus (Miller and Balke, 2003). The relevance of the group's morphological stasis is that the lineage's acquisition of its very characteristic adult generic autapomorphies (e.g., the reduction of natatory setae in both sexes [Fig. 3.5], the short and robust labial palpi [Fig. 3.6], etc.) must have occurred before or during the Eocene. The phylogenetic position of *Hydrotrupes* has been a subject of interest for many years (e.g., Alarie et al., 1998; Beutel, 1994; Miller, 2001; Ribera et al., 2008) and has been challenging to infer because of the group's divergent morphology within the larger Agabinae and the attention that has been paid to a plesiomorphic character state (Balke et al., 2005), the absence of a mandibular sucking channel in the larva (Beutel, 1994; Roughley, 2000), which is present in the vast majority of diving beetles, has perhaps contributed to the diversification of certain clades of Dytiscoidea when present (Balke et al., 2005; Beutel et al., 2013), and of course, is a character state 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 *Agametrus* Sharp, 1882, *Andonectes* Guéorguiev, 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 the lineage's divergent morphology is likely due to selection pressure for specialization in hygropetric habitats.

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 autapomorphies. 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) was hypothesized by Nilsson (2003) to be one of a plethora of examples of a trans-Beringian disjunction of a non-marine animal lineage (Sanmartín et al., 2001), comparable to the distribution of another lineage of Hydradephaga, Amphizoidae, as well as other polyphagan water beetle clades (see Nilsson, 2003). This Pacific intercontinental disjunction is a very common biogeographic phenomenon that is displayed in many groups of plants (Li, 1952; Thorne, 1972; Wu, 1983; Hong, 1993; Wen, 1999), but the western North America eastern Asia disjunction is certainly not as prevalent among plants as the repeated disjunction between eastern North American and eastern Asia (Wen, 1999) that is also displayed in a species group of agabine diving beetle (Nilsson, 1997). As the name suggests, trans-Beringian disjunctions are thought to be the result of dispersal via the Bering land bridge (Sanmartín et al., 2001; Wen, 1999) and range restriction of formerly widespread temperate forests in the Northern Hemisphere in the Tertiary (Wen, 1999). However, the disjunct distribution of modern *Hydrotrupes* (Fig. 5.1) appears to be a relict of former widespread distribution of the genus, considering *H. prometheus* occurred in the Baltic region during the Eocene (Fig. 5.2), and currently there are no known *Hydrotrupes* species from the western Palearctic region. It seems reasonable then that *Hydrotrupes* historically occurred throughout the northern continents and was more diverse, and that its present day distribution is the result of global climate changes (e.g., cooling of the Northern Hemisphere in the Tertiary) and extinction events. Another reasonable conclusion based on the age of Baltic amber is that *Hydrotrupes* may have originally been widespread in the Palearctic and migrated to North America via the Thulean Bridge (Sanmartín et al., 2001), which was accessible until 50 Myr and is considered to have been one of the most important exchange routes of temperate fauna in the early Eocene, when the climate warmed dramatically (McKenna, 1983). Nevertheless, the occurrence of *Hydrotrupes* in the Baltic region in the Eocene broadly challenges the previous hypothesis that the modern trans-Beringian disjunct distribution of the genus resulted from passage across the Pacific with the Beringian land bridge (Nilsson, 2003). This contradictory example instead provides a cautionary tale on the interpretation of the biogeographic pattern of a taxon that is currently distributed in eastern China and western North America as having originated from a trans-Beringian disjunction.

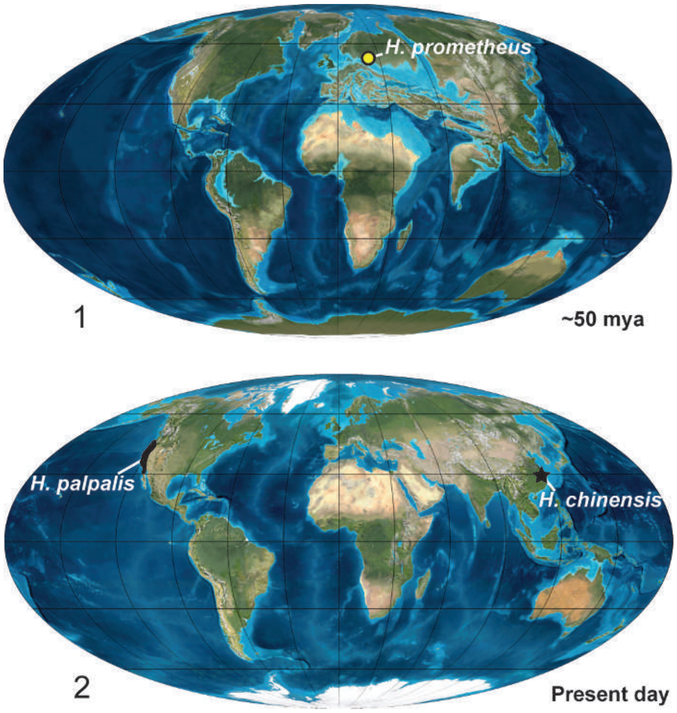

FIGURE 5—*Hydrotrupes* Sharp, 1882 distribution on paleogeographic maps drawn by Ron Blakely (http://www2.nau.edu/rcb7): *1*, *H. prometheus* n. sp., Eocene; *2*, *H. chinensis* Nilsson, 2003 and *H. palpalis* Sharp, 1882, present day.

The diversity of diving beetles as with many lineages of aquatic Coleoptera is highest in the tropics (Jäch and Balke, 2008) as is the diversity of some of the subfamilies of Dytiscidae such as the Copelatinae, most species of which occur in wet tropical forests worldwide. However, this isn't applicable in the case of the Agabinae, whose members are most diverse in the Holarctic, with few species groups of predominately north temperate clades and a small number of species poor genera occurring 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 regions in addition to a few eastern Palearctic 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 Agnolín (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 Palearctic via the Atlantogea biogeographical paleoprovince to the Neotropical region would have required passage through the African continent (Ezcurra and Agnolín, 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 Agnolín, 2012).

Paleoecology.—It is well known that adults and larvae of *Hydrotrupes* occur in hygropetric habitats (Alarie et al., 1998; Beutel, 1994; Miller and Perkins, 2012; Roughley, 2000), which are those habitats where a thin film of water flows over a rock surface, and diving beetles are fairly diverse among hygropetric beetles worldwide (Miller and Perkins, 2012). This Baltic amber specimen may be the first known hygropetric diving beetle fossil according to the principal of behavior fixity, which suggests that the behavior, ecology, and climatic preferences of fossil organisms can be inferred based on similarities with their modern congeners (Boucot and Poinar, 2010). *Hydrotrupes prometheus* is very morphologically similar to extant *Hydrotrupes* species and is most divergent morphologically in antennal shape and metaventral wing width in relation to the width of the metacoxal plate. Ribera et al., (2003) listed morphological features characteristic of hygropetric diving beetles including robust and short antennae and appendages (Figs. 2.1, 3.1, 3.2) as well as a reduction in swimming hairs (Fig. 3.5), but whether these shared features in presumed extinct and extant *Hydrotrupes* species is conclusive evidence of a hygropetric palaeobiology of *H. prometheus* is not entirely obvious. Specimens of the extant species, *H. palpalis*, for example, have been collected from hygropetric habitats as well as less specialized aquatic habitats (Miller and Perkins, 2012) and adults can be abundant along terrestrial shoreline habitats, among sand bars more frequently than gravel bars (Hering, 1998). Miller and Perkins (2012) suggested that *H. palpalis* may not be exclusively hygropetric for these reasons, which could perhaps apply to *H. prometheus* and might also be a plausible explanation for its occurrence in amber. In addition, recent close relatives of *Hydrotrupes*, species in the genus *Platynectes*, for example, are largely rheobiontic (Balke, 2005), excluding an undescribed species from hygropetric habitats in Venezuela (Miller, personal commun., 2013), often inhabiting tropical forest streams (Hendrich and Balke, 2000), which could support a more generalist aquatic paleoecology of *H. prometheus* in Baltic forests.

If the habitat requirements of *Hydrotrupes* historically were not hygropetric, then it may be the case that *Hydrotrupes* survived as a relictual lineage by invading these hygropetric habitats, which Spangler and Steiner (2005) report may have existed at the edges of rivers or ponds for millions of years. If accepted, this would indicate that *Hydrotrupes* was outcompeted by other aquatic Coleoptera in less specialized freshwater habitats in the Northern Hemisphere. This general hypothesis has been applied as the basis for the unusual, relictual distribution of the primitive carrion beetles (Agyrtidae), which are restricted to north temperate areas aside from a single genus endemic to New Zealand (Newton, 1997). Newton (1997) proposed that agyrtids survived unspecialized only in regions never colonized by members of the more 'modern' carrion beetles (Silphidae) such as New Zealand, and in areas colonized by silphids, agyrtids survived by invading specialized habitats (underground fungi). The recently described dytiscoid family, the cliff water beetles (Aspidytidae), is seemingly restricted to hygropetric habitats and displays an amphitropical distribution, being recorded from collecting sites in South Africa and China (Ribera et al., 2002; Balke et al., 2003). The question is whether this is indicative of a very relictual distribution or an artifact of the under sampling of hygropetric habitats worldwide. Numerous new taxa have been discovered from hygropetric habitats worldwide (see Miller and Perkins, 2012 for a review of hygropetric Coleoptera), including new families such as the previously mentioned Aspidytidae and Meruidae (Spangler and Steiner, 2005), and Miller and Perkins (2012) suggest that as these habitats are more comprehensively sampled, it is likely that many new hygropetric taxa remain to be discovered based on current rates of discovery.

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