

AN AQUATIC WATER SCAVENGER BEETLE IN EARLY MIOCENE AMBER FROM THE DOMINICAN REPUBLIC (COLEOPTERA: HYDROPHILIDAE)

MARTIN FIKÁČEK^{1, 2} and MICHAEL S. ENGEL^{3, 4}

¹*Department of Entomology, National Museum, Kunratice 1,
CZ-148 00 Praha 4, Czech Republic*

²*Department of Zoology, Faculty of Science, Charles University in Prague, Viničná 7,
CZ-128 44 Praha 2, Czech Republic; e-mail. mfikacek@gmail.com*

³*Division of Entomology (Paleoentomology), Natural History Museum, and
Department of Ecology & Evolutionary Biology, 1501 Crestline Drive - Suite 140,
University of Kansas, Lawrence, KS 66049-2811, USA; e-mail: msengel@ku.edu*

⁴*Division of Invertebrate Zoology (Entomology), American Museum of Natural
History, Central Park West at 79th Street, New York, NY 10024-5192, USA*

Abstract.— We describe a fossil hydrophilid beetle *Anacaena paleodominica* **sp. nov.** from the Early Miocene amber of the Dominican Republic, which is the only definitive amber inclusion of the family Hydrophilidae documented. The species belongs to the Recent *Anacaena suturalis* species group known from the Nearctic, Neotropical, and Australian regions. The fossil demonstrates that representatives of the species group may already have been widespread and common by the Early Miocene, and indicates a possible Miocene/post-Miocene extinction of the aquatic insect fauna on the island of Hispaniola.



Key words.— Dominican amber, Coleoptera, Hydrophilidae, *Anacaena*, island, extinction.

INTRODUCTION

The beetle family Hydrophilidae comprises 3335 Recent species distributed world-wide (Hansen 1999, Short & Fikáček 2011) and inhabiting a wide spectrum of habitats from truly aquatic through semiaquatic and hygropetric to completely terrestrial. Especially the aquatic taxa are rather frequent in the fossil record – ca. 150 fossil hydrophilid species are described (Fikáček, unpubl. data.), even though the ongoing revision of fossil hydrophilids reveals a rather high percentage of misidentified taxa (e.g., Fikáček *et al.* 2010, 2011).

Surprisingly, all data concerning fossil hydrophilid beetles has been based on compression fossils and no amber inclusions have hitherto been described in detail. Amber inclusions of hydrophilid beetles have

merely been listed without further details from Baltic, Dominican, Mexican and Bitterfeld ambers (see Table 1 for references), and are also infrequently identified as such in various collections. Unfortunately, a portion of these records seem to be based on misidentifications with other families of small body size and semiglobular appearance and hydrophilids seem therefore to be really quite rare as amber inclusions. At present, we are only aware of three specimens from Baltic amber (Komarek, personal communication; Fikáček *et al.*, in prep.) and of a single specimen from Dominican amber. The Dominican specimen is studied in detail herein – it is perhaps the same specimen referred to by Poinar & Poinar (1999), or at the very least is the same species from which their record of the genus *Anacaena* in Dominican amber was derived.

MATERIAL AND METHODS

The fossil specimen was examined using an Olympus SZX16 binocular microscope. Photographs were taken either using a Nikon D1x digital camera attached to an Infinity K-2 long-distance microscope lens or a Nikon Coolpix P6000 camera attached to the aforementioned Olympus microscope. As it is impossible to see all preserved details of the specimen in one view, each drawing includes those characters observable when the specimen is examined in several positions and from different lightings.

The comparison with modern specimens is based on material deposited in the collection of the Division of Entomology, University of Kansas Natural History Museum, Lawrence, USA and the entomological collection of the National Museum, Prague, Czech Republic. Morphological terminology follows Komarek (2004), and diagnostic characters for Neotropical *Anacaena* are adopted from the taxonomic revision of Recent species undertaken by Komarek (2005).

TAXONOMY

Order **Coleoptera** Linnaeus, 1758

Family **Hydrophilidae** Latreille, 1802

Anacaena paleodominica sp. nov.

Figs. 1–7

Type locality and age. Dominican amber (Dominican Republic, Early Miocene [Burdigalian] in age, ca. 19 Ma). The age of Dominican amber has been confused in the literature with ages ranging from the Eocene to the Miocene. Current evidence supports an Early Miocene origin for Dominican amber (e.g., Iturralde-Vinent, 2001; Iturralde-Vinent & MacPhee, 1996, 1999; Grimaldi & Engel, 2005; Penney 2010), an age that correlates well with the more modern character of the included fauna relative to truly Paleogene deposits (e.g., Grimaldi 1995; Engel 2001; Penney 2010).

Type material. Holotype: AMNH DR-10-778 (piece of amber containing the hydrophilid specimen described herein and also some additional specimens of Diptera). Deposited in the American Museum of Natural History, New York.

Description. Body length 1.4 mm, body width ca. 0.8 mm, length/width ratio ca. 1.7. Head dark brown, darker than pronotum, with very inconspicuous paler preocular patches; pronotum dark brown medially, becoming gradually paler laterad, lateral portions largely pale reddish brown; elytra dark brown except for slightly paler sutural interval.

Head. Compound eyes rather large in dorsal view, indistinctly protruding laterad, not emarginate

anteriorly. Antennae with nine antennomeres, antennomere IX elongate, slightly longer than wide. Maxillary palpus short and stout, palpomere II longest, strongly swollen distally, palpomere III short, palpomere IV indistinctly shorter than palpomere II. Mentum transverse. Tentorial pits distinct, minute, gular suture diverging posteriad.

Thorax. Anterior and posterior corners of pronotum rounded, pronotal punctation fine and sparse. Prosternum ecarinate medially, lateral aperture of procoxa open but very narrow. Mesoscutellar shield small, triangular. Elytron with very distinct sutural stria in posterior two-thirds; elytral punctation coarse, consisting of punctures much coarser and more densely arranged than on pronotum; all punctures of same size, some of them arranged in irregular series, punctation between these series irregular. Epipleuron wide anteriorly, strongly narrowing towards level of metacoxae. Metaventricle flat.

Legs. Procoxae globular, each bearing several spines ventrally; profemur with distinct tibial groove, densely pubescent on dorsal surface; protibia with stout spines along lateral surface and on apex; protarsus with five tarsomeres, protarsomeres I–IV subequal in length, protarsomere V longest. Mesofemur densely pubescent on ventral surface; mesotibia with long spines along lateral surface and on apex; mesotarsus with mesobasitarsomere shortest, mesotarsomere II longest and subequal to mesotarsomeres III–V combined. Metafemur with dense pubescence restricted to basolateral portion only; metatibia with several long spines distally; metatarsus about as long as metatibia, metabasitarsomere shortest, metatarsomere II longest, metatarsomeres III–V subequal in length. Meso- and metatarsus bearing swimming hairs. Pretarsal claws small, arcuate.

Abdomen with five visible ventrites, ventrite I ecarinate medially. Sternite VIII with sparsely arranged long setae on posterior margin. Aedeagus with pointed parameral apices.

Generic placement. The new species may be assigned to the hydrophilid genus *Anacaena* on the basis of the following characters: (1) body weakly convex, elongate oval; (2) antenna with loosely-segmented antennal club; (3) prosternum ecarinate; (4) hypomeron without defined antennal grooves; (5) procoxae contiguous; (6) all femora bearing dense hydrophobic pubescence; (7) abdomen with five ventrites; (8) elytron with deeply impressed sutural stria, but without other longitudinal striae. By the general habitus and small body size, the fossil also resembles the hydrophilid genera *Notionotus* and *Paracymus* (both occurring in the Neotropical region), but may be distinguished from them as follows: *Notionotus* differs by the absence of the sutural stria on the elytron, while *Paracymus* differs in at least a partly carinate

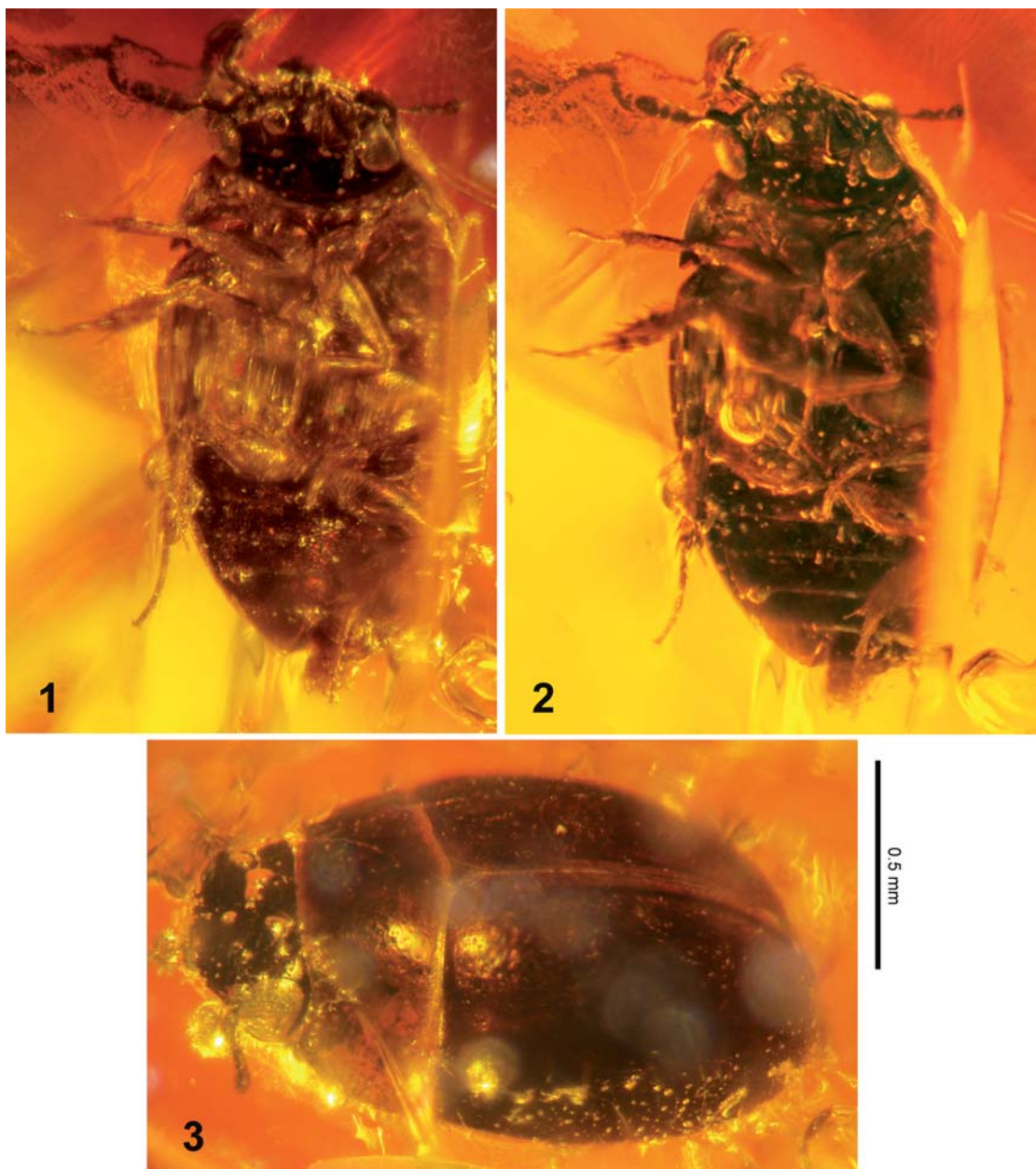
Table 1. List of published records of the Hydrophiloidea preserved as amber and copal inclusions (only primary references included).

Reference	Original identification	Comments
Baltic amber (middle Eocene)		
Motschulsky (1856)	small hydrophilids by Spahr (1981).	The record is based on the collection of Prof. F. A. Menge from Gdańsk (Poland), and was incorrectly interpreted as a record of the genus <i>Hydrophilus</i>
Klebs (1910)	? <i>Cercyon</i> sp.	Klebs' collection was later included into the collection of the Königsberg Museum (today Kaliningrad) which was destroyed during World War II. A small part survives today in the University in Göttingen (see Ritzkowski 1990 below) and singletons are possibly present in several other museums (some seen in the Museum of Comparative Zoology at Harvard University, some should be in the Natural History Museum in London).
Williamson (1932)	Hydrophilidae, Georissidae	List of families is based on the Klebs' compilation of the insects deposited at that time in the collection of the Königsberg Museum which was mostly destroyed during World War II (see also the notes by Klebs (1910) and Ritzkowski (1990)).
Bachofen-Echt (1949)	<i>Cercyon</i> sp.	Bachofen-Echt's collection is not present in the Naturhistorisches Museum Wien, nor at the University of Vienna, and is generally considered to be lost.
Andréé (1951)	<i>Cercyon</i> sp.	The record may be merely a citation of previous records by Klebs (1910) and/or Bachofen-Echt (1949).
Katinas (1971)	Hydrophilidae	Most probably just a citation of previously published records.
Ritzkowski (1990)	Hydrophilidae	List of the specimens being originally a part of the collection of the Königsberg Museum and deposited at present at the University of Göttingen. The list is evidently based on recent identification, not the original Klebs' determinations. All specimens listed as Hydrophilidae were reexamined by us, and none of them belongs to the Hydrophiloidea [most of them belong to a species of Tenebrionoidea (?Anthicidae, ?Salpingidae), a few belong probably to Coccinellidae and Phalacridae].
Kubisz (2000)	<i>Cercyon</i> sp.	Megasternini sp., currently studied in detail by the authors.
Bitterfeld amber (middle Eocene)		
Dunlop (2010)	Hydrophilidae	Not examined.
Dominican amber (Early Miocene)		
Wu (1997)	Hydrophilidae (photos F389, F390)	Specimen on Fig. F-389: Dytiscidae; specimen on Fig. F-390: surely not Hydrophilidae, possibly also Dytiscidae.
Poinar & Poinar (1999)	<i>Anacaena</i> sp.	Record possibly based on the specimen described herein as <i>Anacaena paleodominica</i> sp. nov.
Mexican amber (Early Miocene)		
Solorzáno-Kraemer (2007, 2010)	Hydrophilidae (<i>Anacaena</i> sp.)	Single specimen sent to M.F. by M. Solorzáno-Kraemer in 2008 belonged to Phalacridae.
Copal (subfossil)		
Gistl (1831) [Brazilian copal, age unknown]	<i>Sphaeridium melanarium</i> Gistl (1831)	Generic placement of this species is dubious as only one very characteristic species of <i>Sphaeridium</i> is living in the Neotropics today; if the species is really a hydrophilid, then the short description would rather match some species of the tribes Coelostomatini or Megasternini. The Gistl collection should be present in the Zoologische Staatssammlung in München (Germany), but the specimens can not generally be located or identified there (e.g., Jelínek & Audisio 2009). The copal specimen was wholly extracted from the resin by boiling in rosemary oil according to Gistl (1831) and Leonhard & Bronn (1833).
Hiura & Miyatake (1974) [Japanese copal, Pleistocene]	Hydrophilidae	Not examined.

prosternum and the absence of dense hydrophobic pubescence on the femora.

Differential diagnosis. The new species resembles three Recent Neotropical species, *A. attigua* d'Orchymont, 1942, *A. hirsuta* Komarek, 2005, and *A. suturalis* (LeConte, 1866), in the combination of the following characters: (1) antennae with nine antennomeres; (2) antennomere IX slightly longer than wide; (3) procoxa with several spines; (4) dense pubescence of metafemur reduced to anterobasal portion; (5) apices of parameres pointed; and (6) meso- and

metatarsomeres with long swimming hairs [short in *A. attigua*]. It differs from *A. hirsuta* by the absence of elytral pubescence and short elongate body, from *A. attigua* by the pronotum largely pale laterally, much smaller body size and presence of long setae on meso- and metatarsus, and from *A. suturalis* by the much less elongate body, laterally paled pronotum, elytra with coarse and partly subserially arranged punctures and procoxae with long spiniform setae [slightly longer but not spiniform setae may be present in *A. suturalis*]. Although some Recent species,



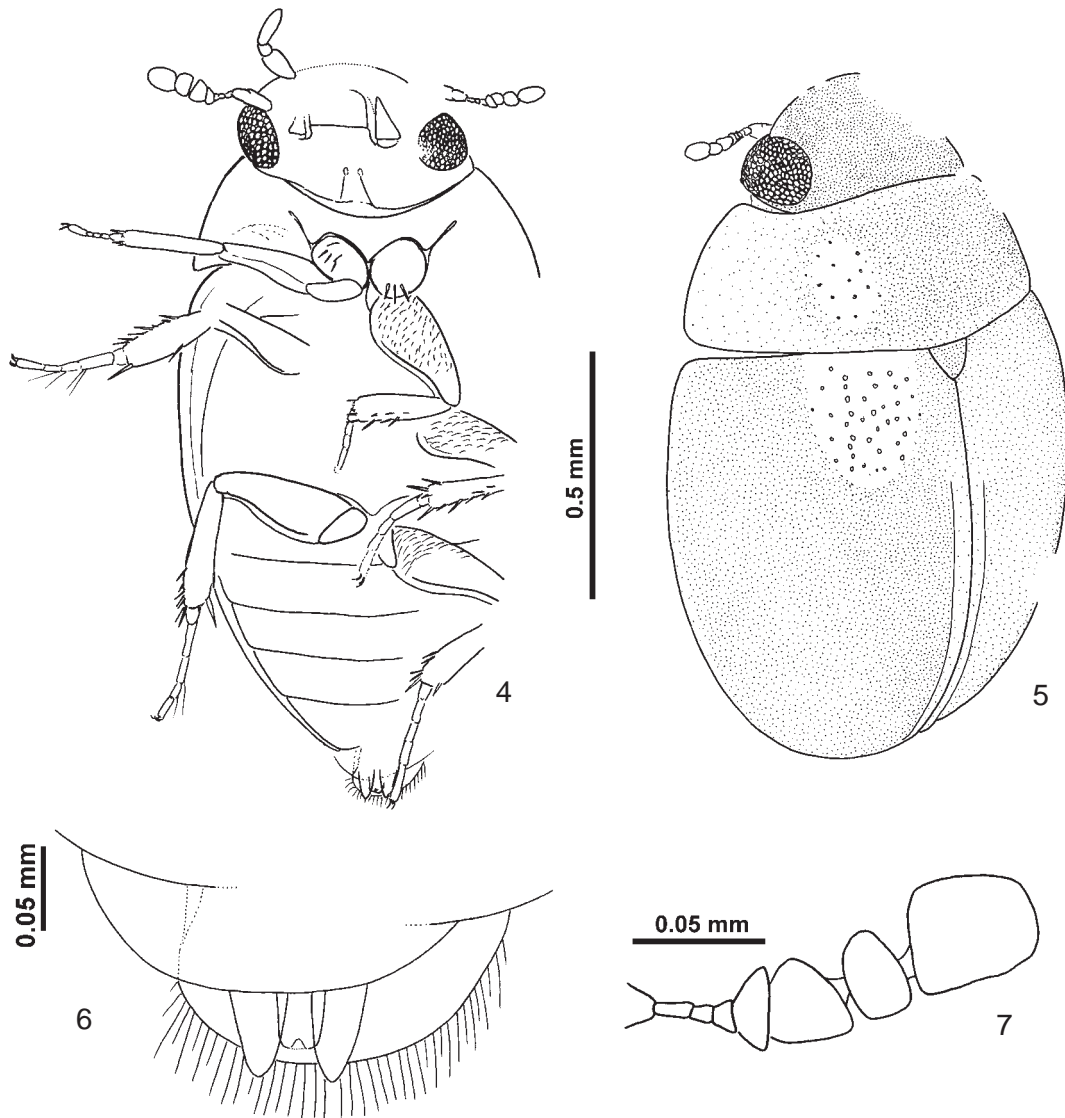
Figures 1–3. *Anacaena paleodomínica* sp. nov., holotype. (1–2) ventral view using two different forms of lighting; (3) dorsolateral view. Scale bar refers to all photos.

especially *A. suturalis*, are quite variable in some characters (especially in body size and dorsal body punctuation in *A. suturalis*; Komarek 2005), the new species seems not to fit the range of variability of any of the aforementioned species and may easily be distinguished from them by the characters listed above. All of these characters along with the great antiquity of the specimen therefore justify assignment of the amber specimen to the new species, *A. paleodominica* sp. nov.

Paleobiology. The presence of the swimming hairs on the meso- and metatarsi indicates that *A. paleodominica* sp. nov. was probably an aquatic species, as are modern representatives of the *A. suturalis* group to which it belongs.

DISCUSSION

Anacaena paleodominica sp. nov. described above is a member of the *A. suturalis* species group represented in the Recent fauna by five species in the New World: *Anacaena attigua* d'Orchymont, 1942 (Peru), *A. hirsuta* Komarek, 2005 (Central America), *A. schoedli* Komarek, 2005 (Central America), *A. solstitialis* (Kirsch, 1873) (widely distributed from Mexico to southern Brazil), and *A. suturalis* LeConte, 1866 (widely distributed from Canada to Argentina) (Komarek 2005). In addition, the Australian species *Anacaena nitens* (Gentili, 1993) from Queensland seems to be closely related as it shares some characters with the species of the *suturalis* group (i.e.,



Figures 4–7. *Anacaena paleodominica* sp. nov., holotype. (4) ventral view; (5) dorsolateral view; (6) detail of partly everted aedeagus; (7) detail of antennomeres II–IX.

elongate body shape, subserially arranged elytral punctures, swimming hairs on meso- and metatarsi; Komarek 2007), although the sister relationships of *A. nitens* and *A. suturalis* were not unambiguously supported in the phylogenetic analysis undertaken by Komarek & Beutel (2007). If the definition of the group including *A. nitens* proposed by Komarek (2007) is correct, then it is evident that the group should date back to at least the Early Eocene when Australia and South America were last connected (Sanmartín & Ronquist 2004, see also Fikáček & Short 2010). The presence of *A. paleodominica* sp. nov. in the Early Miocene of the Caribbean is congruent with this scenario, and suggests that the fauna of the *suturalis* group was common and widely distributed by that time in what was to become Central America.

At present, there is only a single species of *Anacaena*, *A. suturalis*, occurring in the Caribbean (recorded from the Dominican Republic and Jamaica; Komarek 2005). The species is currently very widespread, inhabiting various kinds of aquatic habitats from southern Canada to Argentina. Although knowledge of the Caribbean fauna is possibly biased by low collecting effort, the presence of a separate species during the Early Miocene may indicate Miocene/post-Miocene extinctions of the aquatic fauna of the island of Hispaniola (similar extinction is well documented for the semi-aquatic bugs (Heteroptera: Gerrromorpha); Damgaard 2008). Hispaniola was never connected with the mainland and the “island effect” therefore cannot be responsible for the loss of species diversity. During the Miocene, southern Hispaniola was subsided into the ocean before reconstituting later in the epoch, while a combined central Hispaniola-Puerto Rico landmass remained above sea level during this same timeframe. Had the fossil species been restricted to the southern Hispaniola landmass in the Early Miocene, then its extinction could also have been brought about by a failure to disperse to surrounding landmasses in the latest part of the Early Miocene (Iturralde-Vinent & MacPhee 1999). Modern *A. suturalis* is very likely a more recent invasion of the West Indies via Central America and Jamaica.

As it was mentioned in the introduction, *A. paleodominica* is the first amber inclusion of a hydrophiloid beetle described in detail and one of a very few amber inclusions of the superfamily known to the authors (published records are not considered as they are frequently based on misidentified specimens, see Table 1). The rarity of hydrophiloid beetles in amber is slightly surprising, as inclusions representing many other insect groups inhabiting standing water are known, even though infrequent (e.g., Wichard *et al.* 2009). The absence of the terrestrial species seems to be easier to explain as most of these species occur in microhabitats such as leaf litter and herbivore

excrements, which makes their capture in tree resins unlikely. However, many modern representatives of the terrestrial subfamily Sphaeridiinae are common in decaying or fermenting fruits, and a series of *Dactylosternum hydrophiloides* (MacLeay, 1825) was recently collected in fermenting tree sap in Laos (J. Hájek, pers. comm.). Based on these data, we assume that hydrophiloid beetles may be rather infrequent as amber inclusions, but are possibly also largely overlooked, partly for the small body size of many species (e.g., *A. paleodominica* is merely 1.4 mm long!) and partly owing to their similarity with many other groups of Coleoptera.

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