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A MESOZOIC SPECIES OF *ANOTYLUS* (COLEOPTERA, STAPHYLINIDAE, OXYTELINAE) FROM LIAONING, CHINA, WITH THE EARLIEST EVIDENCE OF SEXUAL DIMORPHISM IN ROVE BEETLES

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ABSTRACT—A new species of the staphylinid subfamily Oxytelinae is described and figured from a series of well-preserved compression fossils of the Yixian Formation (Early Cretaceous), Beipiao City, Liaoning Province, northeastern China. The species is placed in the recent genus *Anotylus* Thomson, 1859 based on typical morphological features for the genus as well as secondary sexual characters. The strong projection of the anterior pronotal angles is a feature also possessed by males of several recent Neotropical taxa in the genus. This is the earliest fossil rove beetle with clearly demonstrable sexual dimorphism.

INTRODUCTION

THE SUBFAMILY Oxytelinae is one of the more ancient groups of Staphylinidae yet its species diversity today constitutes less than 5% of that of the family. The monophyly of Oxytelinae is well supported by adult tergite IX divided longitudinally (not unique) with anterior mesal margins fused to tergite X and a pair of glands opening at the base of the tergite IX halves (Thayer, 2005). According to Herman (2001), Oxytelinae includes exactly 2,000 named, extant species and is worldwide. Within the subfamily a relatively low percentage of the named species belong to the putatively ancient tribes Euphaniini, Coprophilini, and Planeustomini (altogether less than 100 species), while the majority are members of Blediini and Oxytelini (sensu Makranczy, 2006). In the tribe Oxytelini there are three important lineages: the *Carpelimus* group of genera, the *Thinobius* group of genera, and those genera that formed the Oxytelini in the sense of earlier authors (*Anotylus* being the most species rich of them). The analysis in the aforementioned work focuses on the *Carpelimus* group, while the hypotheses about the phylogenetic relationships of *Anotylus* and related genera have not changed much, except *Anotylus* and *Oxytelus* are now better characterized (which involves synonymy of several previously valid generic names). The majority of the species in this lineage are either in *Anotylus* (most diverse in the Neotropics) or *Oxytelus* (most diverse in tropical Africa).

In addition to the previously described extinct genera, *Mesoxytelus* Tichomirova, 1968, *Turgaphloeus* Ryvkin, 1990, and *Morda* Ryvkin, 1990, two further extinct genera have been described: *Dolichoxenus* with one species, *Dolichoxenus newtoni*, from early Miocene (Burdigalian) amber of the Dominican Republic (Engel and Chatzimanolis, 2009) and *Sinoxytelus*, with three species: *Sinoxytelus euglypheus, S. breviventer*, and *S. longisetosus* from the Early Cretaceous Yixian Formation (Yue et al., 2010). Both genera were placed in the tribe Oxytelini. Herein, some very well-preserved specimens of compression fossils, collected from the Yixian Formation (Early Cretaceous) at a site near Chaomidian Village, Beipiao City, Liaoning Province in northeastern China, are documented. The material represents a new species belonging to the subfamily Oxytelinae. Based on the current state of our knowledge and from the observable features in the fossil series, the species is best assigned to the genus *Anotylus*. Here we describe this new taxon and discuss its phylogenetic significance.

These specimens are from the Yixian Formation (Early Cretaceous) of Chaomidian Village, Beipiao City, Liaoning Province, China. The Chaomidian fossil bearing strata are mainly of lacustrine origin intercalated with volcanic rocks (Ren et al., 1995). They consist of mainly gray-green thin tuffaceous siltstone and muddy siltstone, producing insects, plants, conchostracans, bivalves, sturgeon, etc. (Ren et al., 1997). The fossil bearing bed is 3 m thick and located in an unknown horizon within the Yixian Formation. The age of Yixian Formation is still controversial. But Early Cretaceous (Swisher et al., 1999; Li et al., 2001; Pang et al., 2002) seems more plausible than Late Jurassic (Ren et al., 1997; Zheng et al., 2003) or Late Jurassic to Early Cretaceous boundary (Zhang et al., 2008). The Yixian Formation yielded many well preserved fossils such as dinosaurs (Chen et al., 1998), mammals (Hu et al., 1997; Luo, et al., 2007), angiosperms (Sun et al., 1998) and different kinds of insects: Mecoptera (Ren et al., 2009), Ephemeroptera (Huang et al., 2007), Odonata (Zhang et al., 2008), Diptera (Ren, 1998), Hemiptera (Yao et al., 2007) and Coleoptera (Yue et al., 2011; Chang et al., 2010).

MATERIAL AND METHODS

The type specimens of the new species are deposited in the Key Laboratory of Insect Evolution and Environmental Changes, Capital Normal University in Beijing, China. They were examined using a Leica MZ12.5 dissecting microscope. Photos of fossils were taken with a digital camera attached to a Leica M165C microscope. SEM images were taken of uncoated specimens with a Hitachi S-2600 N scanning electron microscope. We follow the systematic arrangement of Oxytelinae proposed by Makranczy (2006).

SYSTEMATIC PALEONTOLOGY

Family STAPHYLINIDAE Latreille, 1802
Subfamily OXYTELINAE Fleming, 1821
Tribe OXYTELINI Fleming, 1821
Genus ANOTYLUS Thomson, 1859
ANOTYLUS ARCHAICUS new species
Figure 1

Diagnosis.—Trilobed surface impression on scutellum with median lobe elongate and probably open behind, lateral lobes rounded, not elongate; mandible strong; anterior angles of pronotum strongly modified, with extension, showing sexual dimorphism.

Description.—Moderately sized (7.9–10.6 mm) in length. Body weakly pubescent, almost bare. Temples distinct. Pronotum slightly wider than long. Elytra parallel-sided.

Head capsule broad, about as wide as long, with slightly indicated posterior angles, base of head retracted under pronotum so that neck constriction, if present, not visible. Compound eyes large, slightly larger than temples. Gular sutures separated, gula diverging anteriad and posteriad before reaching submentum and basal margin of head, respectively. Mandibles elongate and strong, with broader basal part, gradually narrowing apicad, slightly curved, with sharp apex. Labrum slightly transverse. Antennal insertions at sides of frons, seemingly with distance between them longer than distance from either insertion to margin of compound eye. First segment of antenna slightly longer than second segment, second segment about two times longer than third segment, segments IV–X similar to each other in shape and size, last segment obtuse.

Pronotum much wider than long, widest before middle. Anterior angles of pronotum obtuse and posterior angles sharp (with a slight concavity anteriad of angle) in most specimens (paratypes). On holotype, supposedly a male, anterior pronotal angles projected ahead by about one-seventh of pronotal length, sides of pronotum and projection gently curved; traces of this can also be seen on one side of a more poorly preserved paratype (by comparison, similar features can be observed in the recent taxa in Makranczy, 2011, figs. 5, 11 but most prominently on figs. 18, 25). Scutellum (Fig. 1.5) with a trilobed impression (cf. figs. 35–37 in Hammond, 1976 and figs. 7, 13, 20, 27 in Makranczy, 2011), bluntly pointed posteriorly, lateral lobes more stout, rounded, median lobe elongate, open behind.

Legs long and slender, anterior legs about as long as posterior legs; pro- and mesocoxae moderately large, conical, contiguous; tibiae with distinct and arranged double spine rows (apparent on a mesotibia on female paratype, Fig. 1.3); metacoxae large, transversely triangular; tarsi short, tarsal segments not clear.

Elytra about 1.5 times longer than pronotum, without apparent puncture-rows, elytra relatively oblong, their lateral contours slightly diverging posteriad, with smooth poorly distinct humeral angles and obtuse sutural angle; epipleural part not visible. Elytral surface without striae or punctuation.

Abdomen oblong and wide, not parallel-sided but narrowing towards apex, second sternite fully developed, first sternite completely absent. At least segments III–V with two pairs of paratergites, tergites III–VII, each, with one basal carina and pair of curved basolateral ridges; tergite IX consisting of two triangular lateral sclerites.

Measurements (in mm; holotype data follows range in parentheses): Body length (bl) = 7.9–10.6 (9.4); head length (hl) = 1.1–1.4 (1.2); head width (hw) = 1.1–1.5 (1.3); pronotum length (pl) = 1.3–1.7 (1.3); pronotum width (pw) = 1.7–2.1 (1.9); elytral length (el) = 1.7–2.2 (1.9); elytral width (ew) = 2.2–2.6 (2.4).

Etymology.—The Latin word (adapted from Greek) ''archaicus'' means ''ancient.''

Type.—Holotype: CNU-COL-LB2008260PC (male) (Figs. 1.1–2 and with pronotum magnified on Figs. 1.6–1.7). Paratypes: male: CNU-COL-LB2008078; female: CNU-COL-LB2008073, CNU-COL-LB2008089, CNU-COL-LB2008081, CNU-COL-LB2008091, CNU-COL-LB2008111, CNU-COL-LB2008072, CNU-COL-LB2008305 (Fig. 1.5), CNU-COL-LB2008105, CNU-COL-LB2008100PC (Figs. 1.3, 1.4); undetermined: CNU-COL-LB2008070, CNU-COL-LB2008079, CNU-COL-LB2008076.

Occurrence.—Early Cretaceous; fossils were collected from Yixian Formation, a site near Chaomidian Village, Beipiao City, Liaoning Province, northeastern China.

Discussion.—The new fossil rove beetle species described here can be placed in the extant subfamily Oxytelinae based on the following characters: presence of a fully developed sternite II; antennal insertion at sides of frons; abdomen with two paratergites per segments. The following characters support placement of *Anotylus archaicus* n. sp. in Oxytelini: abdomen with complete sternum II, hence seven complete sterna can be counted. Oxytelini currently contains 23 genera (see list in Makranczy, 2006, p. 99) with the additions of two genera by Engel and Chatzimanolis (2009) and Yue et al. (2010). The fossils described herein are complete enough to allow a placement in *Anotylus*. There are some important characters missing or not visible, as usual for compression fossils, but the following combination of characters support placement of *A. archaicus* in *Anotylus:* basolateral ridges missing on tergite II; mesotibiae with distinct and arranged double spine rows. The type of scutellar impression, which is an important character for the identification of *Anotylus*, cannot be seen clearly in most specimens but at least in one paratype and partly in the holotype it is distinctly trilobed and resembles an *Anotylus*-type impression. Furthermore, the broad inner laterosclerites suggest relationship to several extant *Anotylus* species possessing this feature (e.g., those in former *Oxytelopsis* Fauvel, 1895).

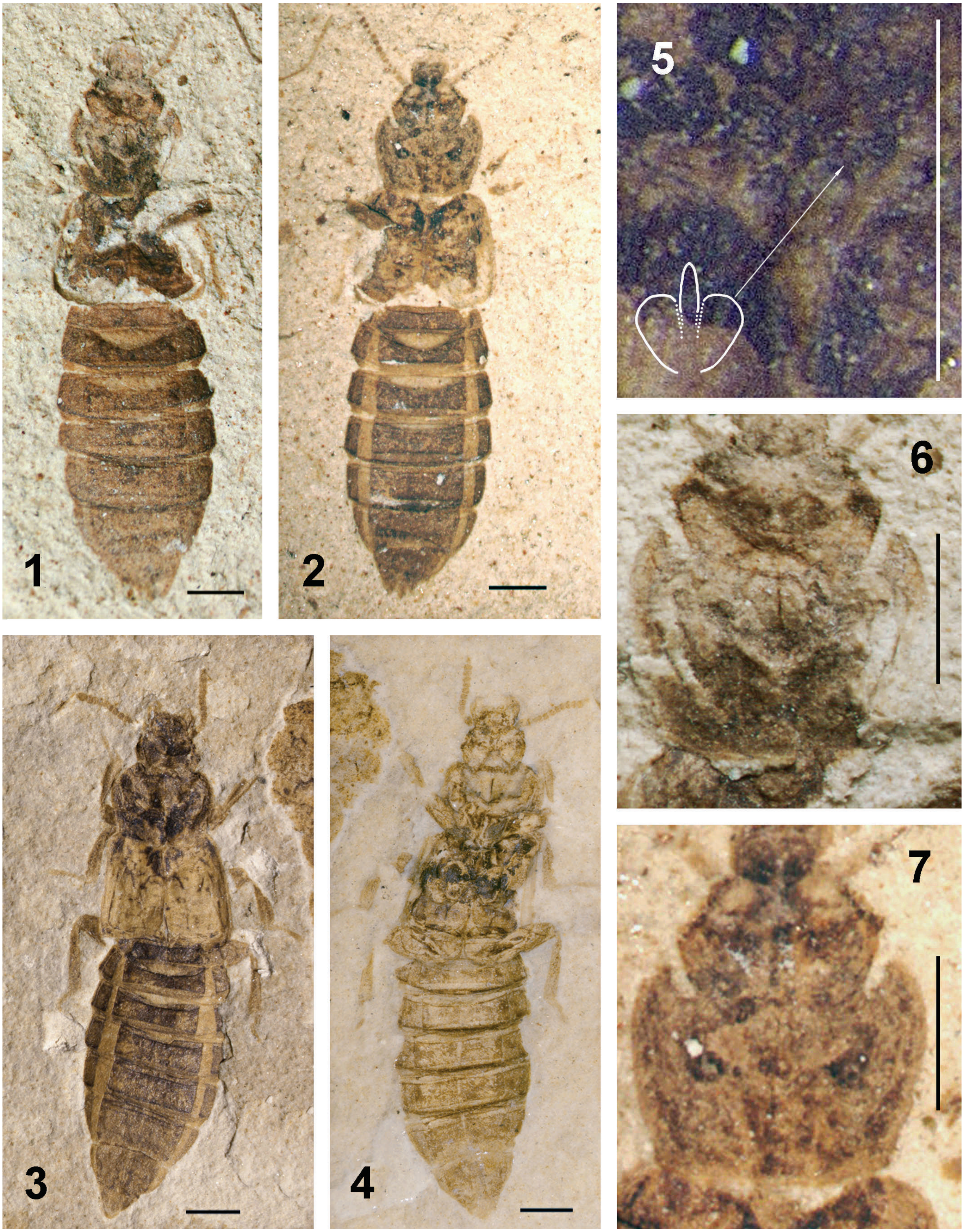
The placement into *Anotylus* unavoidably involves a statement of antiquity for this genus. It is without doubt that *Anotylus* appeared very early in the history of the subfamily, although it is likely to have gained its current, overwhelming diversity in the last 4 to 5 million years, similar to most other mega-diverse staphylinid lineages, especially the Aleocharinae (Ashe, personal commun., 2005).

In contrast to the fossil genus *Sinoxytelus* Yue, Zhao and Ren, 2010 which was collected at the same locality, *A. archaicus* possesses the following differences: labrum broad, much longer and wider; mandible stronger; anterior angles of pronotum showing sexual dimorphism, pronotum widest before middle; tibiae much stronger.

DISCUSSION

Anotylus archaicus is represented by some reasonably well-preserved and complete specimens. This is the earliest and best documented fossil record for *Anotylus.* Some locations of younger fossil records of *Anotylus gibbulus* Eppelsheim, 1878 are mentioned in the literature from the British Isles (Pleistocene) and one also from Toronto, Ontario, Canada (Pleistocene). Those with precise age information are: Four Ashes, Staffordshire England (38,500 ± 1,100 B.P.); Staffordshire, England (in excess of 44,000 B.P.); and Brandon Wood, Warwickshire, England (early Wolstonian age) (Hammond et al., 1979). Regarding these fossil occurrences, it is notable that the current distribution of this recent species (from the Caucasus through Central Asia to the Far East) shifted considerably from the known fossil locations.

The genus *Anotylus* is today cosmopolitan. It contained almost 400 described species at the time of the last catalog (Herman, 2001) with the current center of diversity in the Neotropics where purportedly more than 80% of the species are still undescribed. This diversity is immediately evident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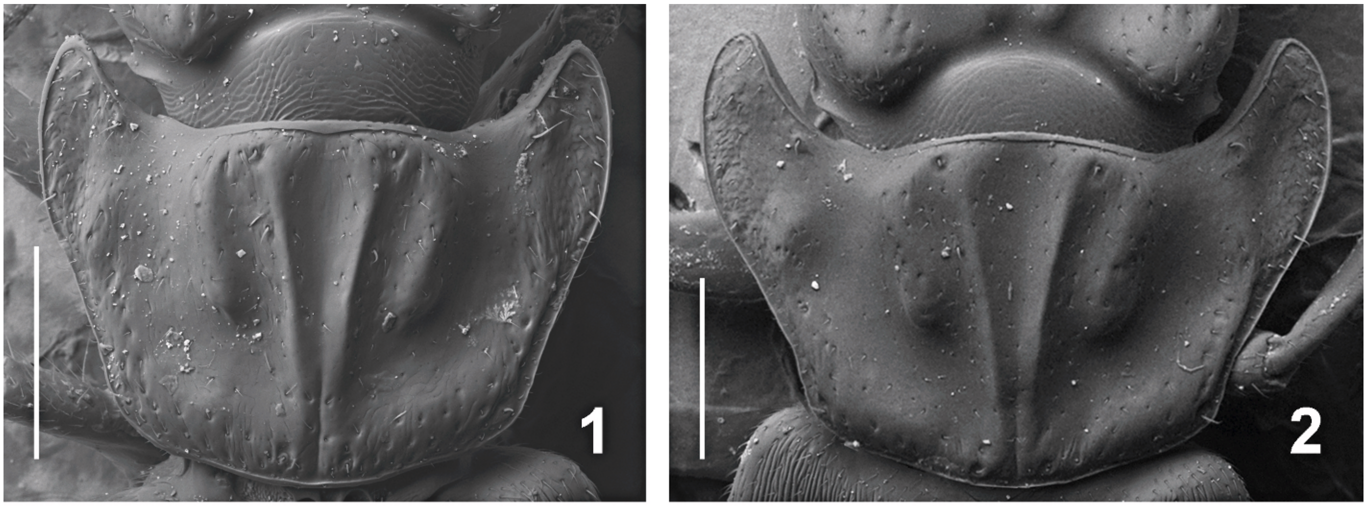

FIGURE 2—Pronota of *Anotylus deboeri* Makranczy, 2011 males, a recent Neotropical species of *Anotylus* in the Snow Entomological Collection, Division of Entomology, University of Kansas. *1,* ''minor'' male (Paratype) from PANAMA, Chiriquí Prov.; *2,* ''major'' male (holotype) from PANAMA, Panamá Prov. Scale = 0.3 mm.

when insect collections from the Neotropical region are examined. Some of the most unusual oxytelines live in the Neotropics and some of them are possibly myrmecophiles. Interestingly, *A. archaicus* shares features of these rather specialized modern beetles, similar to *Sinoxytelus* Yue, Zhao and Ren, 2010, including one unique character with *Mimopaederus* Cameron, 1936 (exclusively found on Rapa Island, Southern Australs): a longitudinal midline keel on the base of the second abdominal sternite which is best visible in transparent preparation (cf. fig. 72, Makranczy, 2006). A supposed myrmecophile fossil genus *Dolichoxenus* Engel and Chatzimanolis, 2009 from Dominican amber is similar to the recent taxon, *Jerozenia* Herman, 2003 which is only known from tropical Africa. It is therefore apparent that these lineages went through considerable diversification and the current centers of their diversity (or occurrences) lie far from the known fossil locations, perhaps owing to numerous climate changes, continental drift, and our incomplete knowledge of the staphylinid fossil record.

One of the most striking characteristics of most species in *Oxytelus* and *Anotylus* is sexual dimorphism. The most widespread secondary sexual character is the macrocephaly, i.e., the males with enlarged temples, usually apparent as larger and wider heads and extended postocular area. Moreover, there are cephalic horns in many species of *Anotylus*. In a few Neotropical species the pronotal anterior corners of males are strongly modified, usually extended anteriorly and enlarged (Fig. 2.1, 2.2). The expression of these features is not equal in all male specimens. For this reason the terms ''major males'' (Fig. 2.2) and ''minor males'' (Fig. 2.1) are in use. Major males have variably developed sexual characters, with minors being more female-like (Hammond, 1976). Female specimens are difficult to associate with their male counterparts, primarily because they are lacking species-specific features. Moreover, it is possible that several similar species may be present in any given sample, especially those from traps left out for extended periods of time like flight intercept traps (FIT). Four species were recently described with their holotypes purported to be males of sexually dimorphic taxa. Only one of them, *Anotylus deboeri* Makranczy, 2011, is represented by a pair of males. The paratype of this species is a ''minor'' male and thus a proof of sexual dimorphism as such specimens are much closer to females in morphology. The pronotal shape (Fig. 2.1) is more normal and the projections in the anterior pronotal corners are less developed, as opposed to the holotype of that species (Fig. 2.2) with twice as large projections in the anterior pronotal corners. The presence of this character state in a fossil is the earliest evidence of sexual dimorphism in staphylinid beetles and it further supports the attribution to *Anotylus,* as out is unique among oxytelines in possessing this feature.

Sexual dimorphism has been reported rarely for fossil beetles. The hypothesized earliest sexual dimorphism among arthropods is in the Ordovician trilobite *Ampyx* (Knell and Fortey, 2005). For beetles, there are some reports of slight morphological differences between specimens that are interpreted as sexual dimorphism distinguishing the genders, e.g., the click beetle *Paradesmatus baiae* Chang et al.,2009 from the Middle Jurassic (Chang et al., 2009); however, in this case there is no detailed elaboration demonstrating that the feature is attributed only to sexual dimorphism rather than another reason. Therefore, *A. archaicus* is the earliest clearly demonstrable evidence of sexual dimorphism among Mesozoic Coleoptera.

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FIGURE 1—*Anotylus archaicus* n. sp., photographs of holotype and paratypes. *1, 2,* holotype, CNU-COL-LB2008260PC; *3, 4,* paratype, CNU-COL-LB2008100PC; *5,* scutellum of paratype CNU-COL-LB2008305, arrow from outline sketch to same part of object; *6, 7,* holotype, head and pronotum enlarged. Scale = 1 mm.

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