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***Cretonthophilus tuberculatus*, a remarkable new genus and species of hister beetle (Coleoptera: Histeridae) from Cretaceous Burmese amber**

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The early history of the beetle family Histeridae is still very obscure. In part this results from difficulty resolving phylogenetic relationships at deeper levels (Caterino & Vogler, 2002; McKenna *et al.*, 2015a). But it is also partly a result of a sparse and poorly documented fossil record (Chatzimanolis *et al.*, 2006). Here we describe a new genus and species of fossil histerid from Burmese amber (~99 mya), which helps to address both of these problems.

Although histerid fossils have been reported from a variety of fossil localities and strata, relatively few have been adequately described. Until recently, the earliest described species of Histeridae was *Onthophilus intermedius* Handschin (1944) from the Oligocene phosphorites of Quercy, France (23–28 mya). A number of other taxa have been reported from more recent amber (*Trypanaeus hispaniolus* Chatzimanolis *et al.* (2006), early to mid-Miocene—15–20 mya—Dominican amber) or limestone fossils (e.g. numerous *Hister* spp. from mid-Miocene—13 mya—deposits at Öhningen; Heer, 1862). While fossil histerids have been noted from older deposits, such as the Eocene Florissant shales (34 mya; Scudder, 1886) and Baltic amber (37.7 mya; Swedo & Sontag, 2009), little has been adequately described. Chatzimanolis *et al.* (2006) therefore remarked, “*In particular, it should be hoped that definitive Mesozoic histerids will be discovered, particularly in Cretaceous ambers, as such taxa might contribute most greatly to our understanding of early histerid evolution.*” The first such discovery was the recent description of *Pantostictus burmanicus* Poinar and Brown (2009) from Burmese amber (99 mya), which pushed the fossil record for the family significantly earlier.

Here we describe as a second Mesozoic record for the family a new genus and species of Histeridae that is of the same Middle Cretaceous age as *Pantostictus burmanicus*, but is highly distinct morphologically. This new specimen resembles modern Onthophilinae, but exhibits a number of distinctive characteristics. This fossil pushes the origin of the Histeridae considerably earlier, showing that not only had the family arisen by this time, but it had diversified considerably.

Methods

To protect the small amber piece with the tiny fossil beetle inclusion during preparation, the specimen was embedded in a block of two-part polyester resin (GTS, VossChemie, Germany). Then the specimen was ground and polished with a polishing machine (LaboPol-4, Struers, Willich, Germany) using wet silicon carbide abrasive papers (grain sizes grit 220 to 4000). The microphotographs have been made with an Olympus DP71 digital camera on an Olympus SZX16 microscope and with a Leica DFC490 digital macro camera on a Leica Z16-Apo microscope with Leica Application Suite V3.8 software for focus stacking. The images have been processed with Photoshop CS5 software.

Systematic Paleontology

Family: Histeridae Gyllenhal, 1808

Subfamily: Onthophilinae MacLeay, 1819

***Cretonthophilus* n. gen.**

Type species. *Cretonthophilus tuberculatus* n. sp.

Diagnosis. This genus shares many superficial sculpturing characters with various extant genera of Onthophilinae, including the carinae of the frons, pronotum, and elytra. However, it differs substantially from any genus in the form and

placement of the hypomeral antennal cavities, which are deeply excavate and extend posterad beyond the hypomeral midpoint. In all modern members of Onthophilinae the antennal cavities lie further forward, immediately under the anterolateral corners, and the antennae themselves curve laterad or up to 180 degrees such that the apex of the club is exposed anteriorly. Further, the distinct sutures separating the apical three antennomeres are not seen in any modern Onthophilinae, which all have the club completely fused, with at most annular series of setae marking former antennomere boundaries. The prolonged, apically emarginate prosternal lobe is unique in this group, and nearly in the family, although it does vary somewhat in various subordinate groups.

Etymology. The genus is named for its geological origin as well as its similarity to modern *Onthophilus* Leach.

***Cretonthophilus tuberculatus* Caterino, Wolf-Schwenninger & Bechly, n. sp.**

Type material. Holotype SMNS BU-162 (old no. F2787/Bu/CJW), deposited at the State Museum for Natural History in Stuttgart, Germany; a complete beetle of undetermined sex, preserved in a small and clear piece of Middle Cretaceous amber from Myanmar, without syninclusions. The sole specimen is remarkably well preserved, with all body parts intact, although the thorax and head are slightly distended. Some fracturing of the matrix at the posterior end of the body obscures some details of the elytral apices and pygidia, and a few small air bubbles slightly obscure some details of the ventrites.

Description. Body elongate subparallel-sided (Fig. 1), darkly rufescent, with strong dorsal elytral and pronotal carinae, and lateral pronotal tubercles (Figs. 1, 3); most surfaces appearing weakly encrusted with debris.

Dimensions (of holotype, in mm). Total (pronotal-elytral) length: 1.7; maximum (elytral) width: 1.05; pronotal length: 0.6; maximum pronotal width: 0.9; elytral length: 0.95; lengths of prosternum, mesoventrite, metaventrite, first visible abdominal sternite: 0.52, 0.2, 0.28, 0.25; lengths of protibia, mesotibia, metatibia: 0.42, 0.48, 0.51.

Head: frontal disk depressed at middle but strongly carinate (Fig. 5), as follows: with acute, slightly longitudinal dorsomedian tubercle; complete suborbital carina; prominent carina along anterior edge of eye; and strong, anteriorly convergent epistomal carinae; labrum about one-half width of distance between eyes, strongly protuberant, bisetose on lower surface; mandibles apically acute, sides concave; ventral mouthparts barely visible. Antennae deeply inserted beneath frontal carinae, at side of frons, adjacent to and just below midpoint of eye; scape (Figs. 4, 5) rather short, narrow, carinate along anterior edge, in repose resting below antero-ventral margin of eye; pedicel cylindrical, about one-third length of scape; antennomeres 3–8 shorter, globose; antennal club setose, comprising three antennomeres, with row of short setae in distinct, complete periarticular grooves.

Dorsum: Lacking obvious scales or setae; prothorax narrowed to front, with deeply pentalobate lateral margins; dorsal disk longitudinally carinate, with incomplete lateral and sublateral basal carinae and paired, incomplete median anterior carinae rising to form acute tubercles at anterior margin. Scutellum visible, small, subquadrate; elytra with prominent humeral lobes, and three prominent dorsal carinae, more strongly elevated posterad, corresponding to the intervals between the 5th and sutural, the 3rd and 4th, and the inner subhumeral and 1st dorsal elytral striae; also with weak epipleural carina; dorsal striae appear foveate. Propygidium obscured by matrix fracturing; pygidium flat to slightly concave, fully operculate, folded beneath.

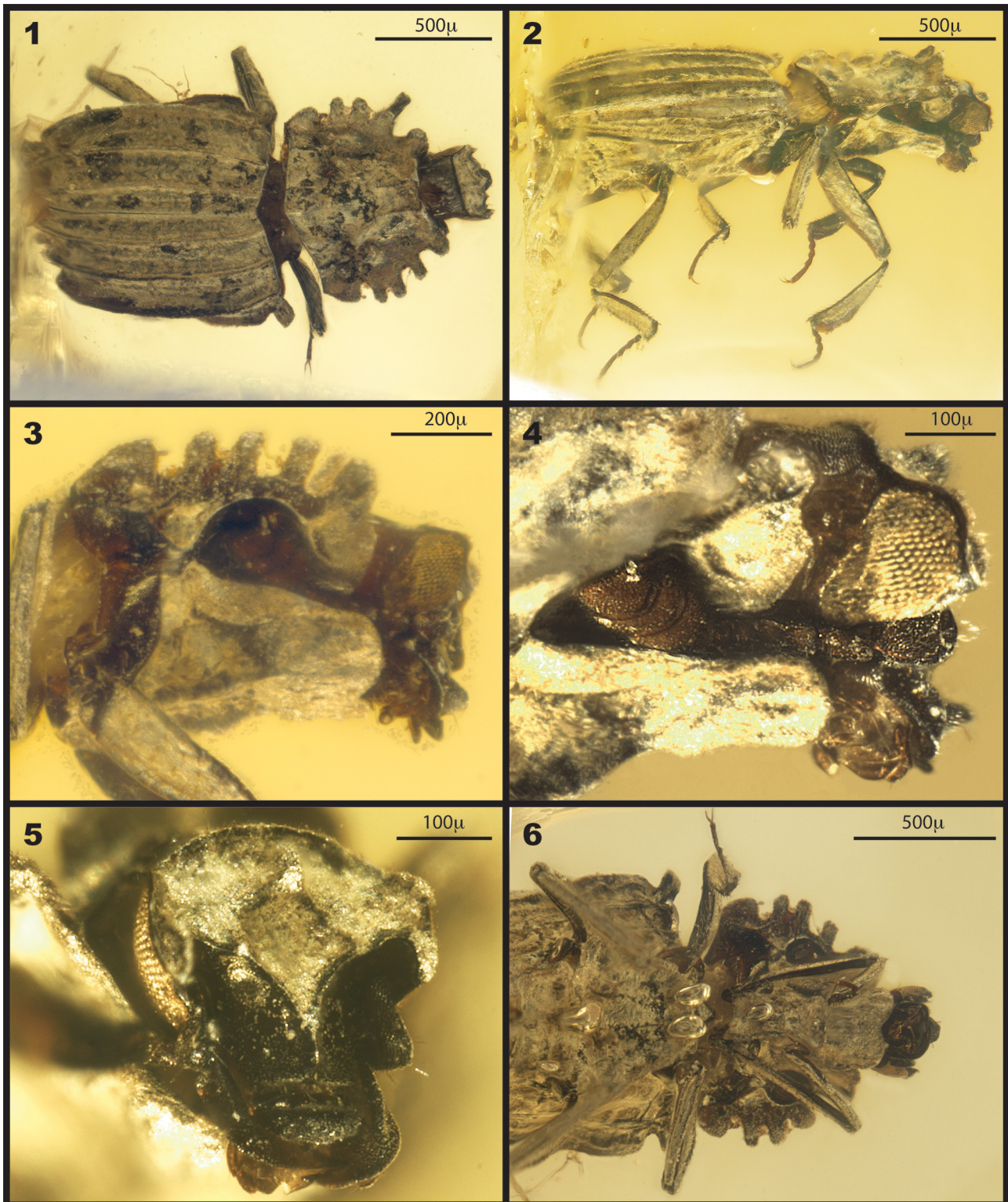
Sterna: Prosternal keel slightly emarginate at posterior margin, weakly depressed (Figs. 3, 6), with longitudinal carinae slightly convergent anterad, reaching prosternal lobe, ending freely; prosternal lobe strongly produced, flat, apically emarginate, with prominent lateral alae slightly concealing antennal cavities, funicular groove broad; antennal cavities large, with well-defined margins all around, extending posterad just beyond midpoint of hypomeron, not completely closed posterad, with a notch laterad the procoxa.

Mesoventrite with prominent, acute anterior projection (inserting beneath, and not identical in shape to prosternal emargination; Fig. 6) and shallow anterolateral emarginations; disk apparently with small paired setose pits; metaventrite with paired setose pits near posterior margin; little else of surface sculpturing distinct, though some weak carinae and foveation are evident. First abdominal ventrite with paired setose pits mediad metacoxae; subsequent abdominal ventrites with single series of large punctures.

Legs: Procoxa globular, not strongly transverse; profemur narrowed toward apex, with weak groove on inner margin for reception of the protibia, and few recumbent setae along outer margin toward apex; protibia widened to apex, with distinct protarsal groove present along midline of distal one-third, lacking strong apical spurs, but with stout spines scattered along weakly rounded outer margin, and more densely toward apex of inner margin; tarsi 5-5-5; protarsomeres 1–4 similar in length, each with apical pair of ventral setae; protarsomere 5 about twice as long as preceding tarsomeres, lacking ventral setae; protarsal claws identical, evenly curved, about half as long as ultimate tarsomere. Meso- and metathoracic legs similar, femora narrow, elongate, tapered slightly to base and apex, weakly grooved on inner margins;

tibiae somewhat abruptly widened from base, subparallel-sided to apex, flat, lacking obvious tarsal grooves, with series of stout setae along inner margins and single distinct apical spine at inner apex; tarsi rather elongate, with tarsomeres 1–4 subequal and bearing apical pair of ventral setae, ultimate tarsomere twice as long and lacking setae, bearing pair of evenly curved claws.

Sex not determinable, because genitalia are not visible.



FIGURES 1–6. Photographs of holotype specimen SMNS BU-162 from Cretaceous Burmese amber. **1.** Dorsal view. **2.** Lateral view. **3.** Lateral view of prothorax, showing antennal cavity. **4.** Lateral view of head and antenna. **5.** Anterior view of head. **6.** Ventral view of thoracic ventrites.

Type locality and horizon. Hukawng Valley (exact outcrop among the various amber mines in this valley is unknown, because the specimen was acquired from a trader), Kachin State, northern Myanmar (Burma); Burmese amber (Burmite), lowermost Upper Cretaceous, earliest Cenomanian, 98.79 ± 0.62 mya based on U-Pb dating of zircons from the rind of unprocessed amber (Shi *et al.*, 2012).

Etymology. The species name refers to the prominent tubercles of the head and pronotum, particularly.

Discussion

Placement of this new species to higher taxon within the family is difficult. It shares obvious similarities with Onthophilinae, and *Onthophilus* in particular. However, it also exhibits a number of distinctive, and likely plesiomorphic characters that would seem to preclude placement in any modern subfamily. In particular, having the three antennomeres of the antennal club distinctly separated by sutures is a plesiomorphy seen only in *Anapleus* (less clearly in *Dendrophilus*, where the antennomeres appear fused along the midline), and nowhere within modern Onthophilinae. More complicated is the problem that Onthophilinae itself has not been established as monophyletic by any autapomorphies, and has been considered by some authors to be polyphyletic (e.g. Kovarik, 1994).

Prosternal morphology has provided much of the basis for histerid classification in the past, so these characters of the new taxon are particularly worth exploring. *Cretonthophilus* exhibits very deep and well defined, mid-hypomeral antennal cavities. In extant Histeridae, the antennal cavities are either poorly developed, with the antennae simply concealed beneath the protibiae (Abraeinae, Dendrophilinae and Sapriniinae) or are well defined, occurring in the anterolateral corners of the hypomeron, concealed ventrally by lateral extensions of the prosternal lobe known as alae (Onthophilinae, Tribalinae, and others). The antennal cavities in *Cretonthophilus* are intermediate in some ways, clearly well defined, but sitting rather posterad from the anterior corners, and deeply excavated rather than concealed by alae. The prominent prosternal lobe complicates the interpretation, since its anterior extension makes the cavities appear to be more posterior than they really are. However, the orientation of the antenna, extending more or less posteriorly into the cavity emphasizes the point; in modern forms, where the antennal cavity lies under the anterior corner of the hypomeron, the funicle is typically curved such that the apex of the club points nearly anteriorly. Our interpretation is that this represents an early stage of the evolution of this well developed and 'alate' type of antennal cavity, with the cavity independent of protibial shielding, but with prosternal closure still weak.

The conspicuous body sculpturing has some commonalities with extant forms, but some unique elements as well. Development of three prominent elytral carinae is shared with a number of *Onthophilus* spp. and *Epiechinus* spp. (Helava, 1978; Ôhara, 1986, 1994), as well as species of *Peploglyptus* LeConte (Caterino, 2004). This would seem a potentially strong synapomorphy, except that it appears unlikely that its sharing even among the extant genera is indicative of close relationship, with both morphological (Kovarik, 1994) and molecular data (Caterino, unpublished) separating *Peploglyptus* from other Onthophilinae. It is also not yet clear that the condition is identical in all these extant taxa with regard to exactly which intervals are elevated. Pronotal carinae, particularly the paired median carinae developed as anterior tubercles in *Cretonthophilus*, are also common to various *Onthophilus* and *Epiechinus* spp., as is the median frontal tubercle, and it would almost have to be the case that these are symplesiomorphic or convergent to some degree as well. Resolution of these questions will be greatly aided by a better understanding of relationships among these similar but diverse extant genera.

For now it seems best to place *Cretonthophilus* as the most basal genus within Onthophilinae, as it likely falls among the diverse taxa it now contains, while retaining a unique plesiomorphic antennal club. If, as seems likely, this subfamily is divided further, this placement will ensure that *Cretonthophilus* is considered in any future phylogenetic analyses of the group. Considering the characters discussed above, there are some quite different alternative phylogenetic possibilities. Its position may be along a stem leading to some subgrouping of onthophiline genera (perhaps, given the similar ventral pits, those related to *Epiechinus*). On the other hand, particularly considering the plesiomorphic antennal club, placement along a stem lineage basal to the entirety of the extant family also seems possible.

Aside from their common age and provenance, *Cretonthophilus* shows no substantial similarity to *Pantostictus burmanicus* Poinar and Brown, which remains unplaced to subfamily. The presence of two such distinctive and derived forms indicates that Histeridae originated considerably earlier. At the same time, if the Histeridae split from the other Histeroidea ~120 mya as recent analyses indicate (McKenna *et al.*, 2015b), then a rapid early diversification must be assumed.

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