A New Tytthonyx LeConte (Coleoptera: Cantharidae) from Dominican Amber, with Notes on Diagnostic Characters of West Indian Cantharids with Short Elytra

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Source: The Coleopterists Bulletin, 76(4) : 577-583

Published By: The Coleopterists Society

URL: https://doi.org/10.1649/0010-065X-76.4.577

The Coleopterists Bulletin 76(4): 577–583. 2022.

A New *Tytthonyx* LeConte (Coleoptera: Cantharidae) from Dominican Amber, with Notes on Diagnostic Characters of West Indian Cantharids with Short Elytra

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Abstract

Tytthonyx milleri Ivie, Fanti, and Ferreira, **new species** (Cantharidae, Tytthonyxini) is described from Miocene Dominican amber. The new species is compared with the other two described fossil taxa of the genus, as well as two additional, undescribed Dominican amber cantharid species, and their morphology is discussed. A comparison of extant and fossil *Tytthonyx* LeConte and *Caccodes* Sharp is given.

Keywords: soldier beetle, paleoentomology, Miocene, Elateroidea

DOI.org/10.1649/0010-065X-76.4.577
Zoobank.org/urn:lsid:zoobank.org:pub:88AEA250-3D9E-40D3-B393-32C4FB04DAF3

Introduction

The Cantharidae have over 5,100 named species (Delkeskamp 1977; Kazantsev and Brancucci 1997; Ramsdale 2002; Zhang *et al.* 2018). The cantharid fauna of the West Indies remains poorly described, the last review of the extant fauna being the very out-of-date Leng and Mutchler (1922). Many species have been described since then, and the fauna now stands at over 150 described species, with many awaiting descriptions (M. A. Ivie, unpublished data). Most of this increase was due to the work of Walter Wittmer (1991a, b, 1992, 1998, etc.) with smaller additions by Pic (1928, 1938), Zayas (1988) and Constantin (2012). Of the known fauna, 52 extant species are described from Hispaniola (Perez-Gelabert 2020). The Hispaniolan country of the Dominican Republic is rich in amber fossils, with many described species of Coleoptera (Perez-Gelabert 2020). Four fossil Cantharidae have been described from Dominican amber: *Tytthonyx geiseri* Poinar and Fanti, 2016, *Tytthonyx stadili* Fanti and Damgaard, 2019, *Silis hegnai* Fanti and Pankowski, 2021, and *Silis curleri* Fanti and Pankowski, 2021, while Wu (1997: fig. F, 408–409) reported and illustrated two further members of the family. Recently, the authors discovered another amber specimen of Cantharidae, which is herein described and compared with other known members of this group.

Materials and Methods

The specimen herein studied and described arrived a few years ago in the MAI laboratory at Montana State University, where it was cleaned and

polished to get a good view of the inclusion. For photographs, the specimen was completely submerged in olive oil. After photos, the specimen was further worked to be able to discern characters of the mandibles and pronotum. Photos were taken using a Canon 6D DSLR using the lens MP-E 65 mm and a Stackshot™ automated macro rail for focus stacking. Images were processed with Zerene Stacker software version 1.04. Enhancements to digital images were made in Adobe Photoshop CC 2021 and the final plate was prepared using Adobe Illustrator CC 2021. The specimen will be permanently deposited in the Amber Collections of the American Museum of Natural History, New York, NY, USA (AMNH), but is currently housed in the West Indian Beetle Fauna collection at Montana State University, Bozeman, MT, USA (WIBF 049821). Dominican amber is currently referred to the Late Early/Middle Miocene, roughly 15–20 million years ago (Iturralde-Vinent 2001; Iturralde-Vinent and MacPhee 1996, 2019; Solórzano Kraemer 2007). Nomenclature of wing venation follows Brancucci (1980) to facilitate comparison with existing literature.

Results

Family Cantharidae Imhoff, 1856
Subfamily Silinae Mulsant, 1862
Tribe Tytthonyxini Arnett, 1962
Genus *Tytthonyx* LeConte, 1851
Subgenus *Tytthonyx* LeConte, 1851

Tytthonyx (*Tytthonyx*) *milleri* Ivie, Fanti, and Ferreira, new species

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Fig. 1

Type Specimen. Holotype: female, in Dominican amber, accession no. WIBF 049821.

Type Locality. Dominican Republic: Cordillera Septentrional.

Type Horizon. Late Early/Middle Miocene; 15–20 million years ago (mya), probably close to 16 mya. La Toca Formation.

Etymology. The species is named after the late Richard Stuart Miller (1945–2021). Rich's interests were mainly focused on "cantharoids", most strongly on Lycidae and Lampyridae, and his extensive collection was donated to the Montana Entomology Collection at Montana State University.

Diagnosis. The generic placement of the species is discussed below. Currently, four other species of short-elytra cantharids are known from Dominican amber, two of which have been described: *T. geiseri* and *T. stadili*. *Tytthonyx milleri* can be separated from *T. stadili* by its smaller size (2.8 mm in *T. milleri* and 6.0 mm in *T. stadili*) and the flavous color (*T. stadili* has a black face, elytra, venter, and basal eight antennomeres). *Tytthonyx milleri* has somewhat stronger serration of antennomeres 3–5 and a convex head (almost flat in *T. stadili* although this character state is possibly an artifact of preservation) (Fanti and Damgaard 2019). From *T. geiseri*, which is similar in size, it is quite different (see Discussion below). The easiest way to distinguish them is by the length of the antenna, which is as long as the body in *T. milleri* and longer than the body in *T. geiseri*. The form of the pronotum is also distinctly different, being more rounded anterolaterally (square in *T. geiseri*) (Poinar and Fanti 2016). These characters are all potentially somewhat related to the different sexes of the types, but exceed the variation seen in most modern species.

Description. Female (based on the wide last abdominal ventrite), adult, alate, entirely flavous. Body length *ca.* 2.8 mm. Head completely exposed, elongate, narrowed behind the eyes, convex medially, pubescent and shallowly punctate. Eyes round, inserted laterally. Frontoclypeal region (face) constricted by antennal insertions near front of eyes, with a transverse depression between antennal insertions and a widened frontal margin, frontal margin nearly straight, slightly concave. Mandibles long, broad basal to the median strong retinaculum, thereafter long, thin, falciform. Maxillary palp 4-segmented; first palpomere robust, short; second elongate, cylindrical; third robust, intermediate in length between first two; fourth globular, apically pointed. Labial palp 3-segmented; terminal palpomere globular and apically pointed. Antenna with 11 antennomeres, serrate; relatively short, reaching *ca.* midpoint of abdomen; scape stout, club-shaped; antennomere 2 filiform, about two-thirds length of first; antennomeres 3–8 (especially 4–7) serrate, subequal in length; antennomere 9 slightly serrate; antennomeres 10–11 filiform with terminal antennomere rounded at apex; all antennomeres pubescent. Pronotum transverse, surface slightly convex, pubescent, shallowly punctate, slightly wider than head, corners round, anterior and posterior margins and lateral beads strongly bordered, sides irregular and slightly enlarged near the anterior margin, lacking secretory pore. Elytra very short, reaching base of first ventrite; slightly dehiscent apically, apices round; setae short. Hind wings fully developed, surpassing last abdominal tergite; costal margin with series of dark bristles; radial cell open; r-m connected at both ends; Mr apparently narrowly erased at base; M_{3+4} complete; cubital vein not visible. Ventrites transverse, pubescent, last ventrite wide. Legs long, slender; pro- and mesocoxae conical; trochanters elongate and offset, rounded apically; femora and tibiae cylindrical, straight; with small,

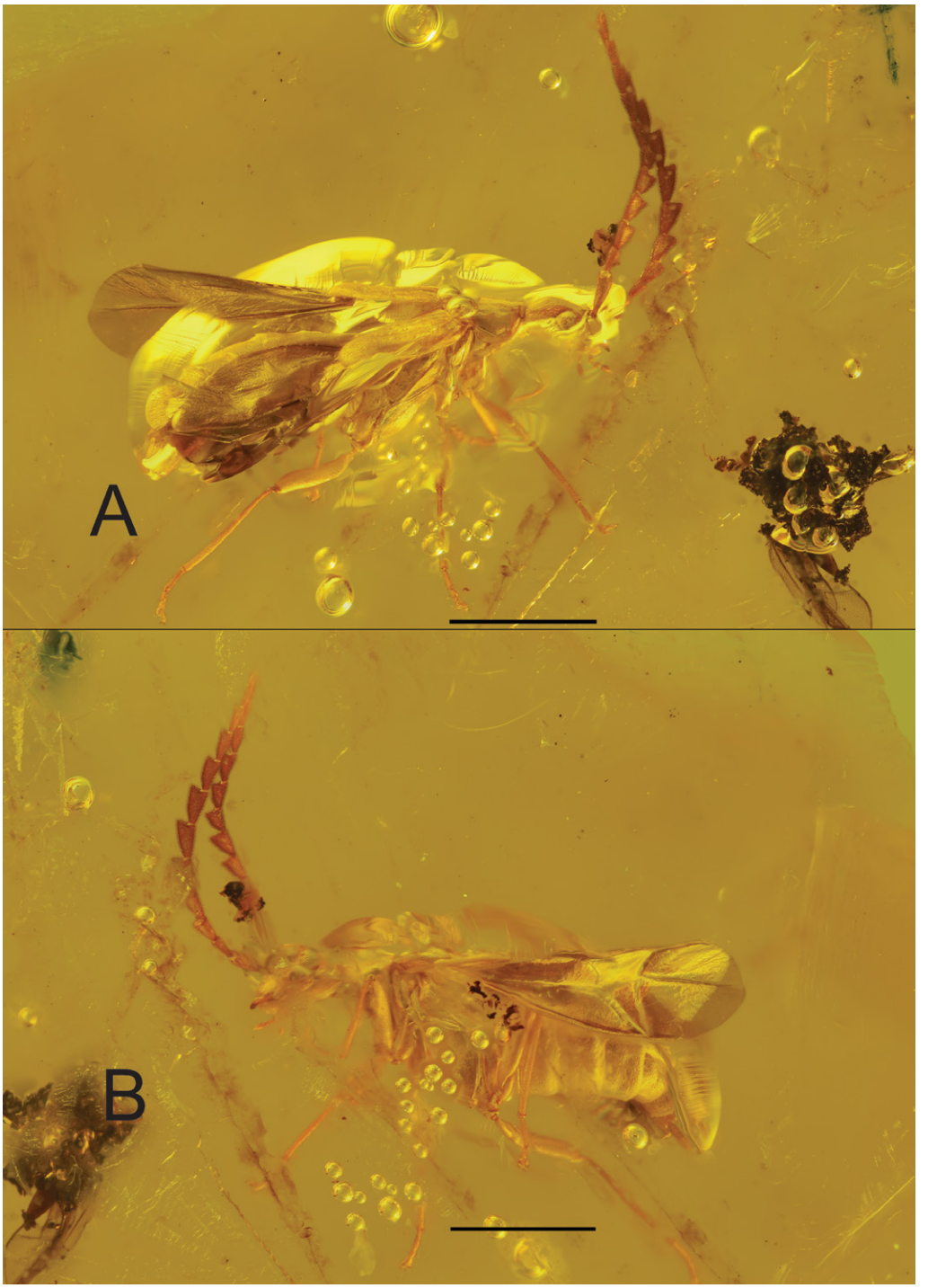

Fig. 1. *Tytthonyx* (*Tytthonyx*) *milleri*, **new species** in Dominican amber. Holotype (WIBF 049821). A) Right lateral view, scale bar = 1.0 mm, B) Left lateral view, scale bar = 1.0 mm.

fine apical spur on pro- and metatibiae, slightly stouter on mesotibia. Tarsal formula 5-5-5; metatarsus with first tarsomere elongate and thin, the second tarsomere about one-third length of first, third tarsomere small, fourth very short and strongly bilobed, fifth tarsomere slender, subequal to second; claws simple and minute. Male unknown.

Discussion

Generic Placement of *Tytthonyx* (*Tytthonyx*) *milleri* among Other Fossils. The generic and even subfamilial placement of all the amber species is problematic. The two long-elytra species placed in *Silis* Charpentier have been discussed by Fanti and Pankowski (2021), and as pointed out there, further study will probably show that none of the Neotropical species are congeneric in a phylogenetic sense with the Holarctic members of that genus. The two short-elytra genera common on Hispaniola and the surrounding region that are in contention for the amber species are the siline *Tytthonyx* (19 extant species on Hispaniola; Perez-Gelabert 2020) and the malthinine *Caccodes* Sharp (seven extant species on Hispaniola; *loc. cit.*). Numerous undescribed species of both genera are known from Hispaniola (MAI, unpublished). The only keys that seem to include these latter two genera in a modern context are those of Ramsdale (2002), which is limited to the small Nearctic fauna, and Constantin (2018), who gave two keys limited to the fauna of French Guiana (FG) [Note: Constantin (2018) included keys in both French and English, and we have relied on the English versions]. Ramsdale (2002) distinguished *Tytthonyx* and *Caccodes* by the degree of antennal serration. This character is not useful outside the US mainland, as violations occur in both genera from the West Indies and elsewhere.

Constantin (2018) gave two keys that distinguished these genera—but specifically for the species found in FG. No claim to extra-limital generality of these characters was made or implied. Only one *Tytthonyx* species was in FG, so his keys were very narrowly defined for that particular genus, and characters used for both genera are not valid when extended into the West Indies and other regions. He used the slender vs. thicker antenna, relative length/width of antennomeres 3–4, length and shape of the temples, and size to distinguish the genera. However, similar to Ramsdale's (2002) key, these do not universally hold outside the FG fauna, and none can be used for the West Indian species, including the amber specimen at hand.

Tytthonyx are placed in the Tytthonyxini, a monogeneric tribe endemic to the New World. The tribe was "provisionally placed '*incertae sedis*' in the Silinae" by Brancucci (1980: 215) in the last revision of the higher classification of the family. In his brief discussion of Tytthonyxini, he distinguished the group from the core Silinae by the short elytra that reach only the second or third abdominal segment, and the reduced venation of the hind wing with an open radial cell, the cubital vein erased at the base, and a series of large bristles on the costal margin, all of which are peculiarities specific to the Malthininae and not found in any species of Silinae. Other non-Silinae characters shared with *Malthinus* Latreille (Malthinini) were the mandibles with a retinaculum and the fourth segment of the maxillary palpi globose. When comparing *Tytthonyx* with the genus *Caccodes*, he noted that the pronotum was similar but free of any secretory pore on the margins. This single obscure mention of this pore may give the only universal character outside the genitalia to convincingly distinguish *Tytthonyx* from *Caccodes*.

No concise and clear definition exists for *Caccodes* as a worldwide whole. Besides the brief mention of a pore on the *Caccodes* pronotum in the diagnosis of *Tytthonyx*, Brancucci (1980) did not define it. Other characters mentioned by Wittmer (1980) included the pronotum wider than long and with a curved anterior pronotal angle, which do not hold up, and were abandoned later. A few years later, he characterized *Caccodes* by the unique form of the male genitalia (Wittmer 1986), which seems consistent in the material examined by us.

Most species of *Caccodes* seem to have filiform or very weakly serrate antennae, but as noted above, this is not universal in the genus where relatively strong serrations are known, and *Tytthonyx* have antennae ranging from simple to strongly pectinate. Brancucci (1980) relied heavily on genitalic characters to distinguish the subfamilies/tribes and used them to place these genera of tiny animals (see Brancucci 1980 for details). In the end, it seems that the main non-genitalic character that can distinguish these genera is the presence or absence of a secretory pore at the anterior end of the lateral margin of the pronotum.

The species described herein has a retinaculum on the mandible, a globular last maxillary palpomere, an open radial cell and bristles on the costal margin of the hindwing, all agreeing with the characters given by Brancucci (1980) for *Tytthonyx*. As noted above, these are not specifically helpful in distinguishing between *Caccodes* and *Tytthonyx*, as the former is shared by both genera, and the wing characters have not been studied in *Caccodes*. To address this last issue, paratypes of *Caccodes iviei* Wittmer and other congeners in the West Indian Beetle Fauna Project collection at Montana State University were examined and share the same wing character states as those in *Tytthonyx*. Thus, these characters do not help with generic placement either.

Luckily, after reworking our specimen, the lateral margin of the pronotum is clearly visible on our specimen, and no pore is present, allowing us to place *T. milleri* with some certainty. This character is likewise visible in *T. stadili* and allows us to confirm that generic placement as well.

A different problem exists for *T. geiseri*. The pronotum is described as "quite transverse" which would point to *Caccodes*, but in fact it is close to quadrate. This is, however, not useful to decide the question of generic placement. The lateral margin of the pronotum is not clearly visible to confirm this, but in figure 7 of Poinar and Fanti (2016) what could be a secretory pore is evident in the front left angle of the pronotum in the correct position to be the *Caccodes* condition. Through the courtesy of George Poinar, we were able to study four new photos of the holotype, but the clarity of the amber laterad the critical area does not allow a good view. Unfortunately, the specimen is not available for loan and exactly what is represented in this image is impossible to discern from the photos. The new photos allow a view of the long temples and the globular last maxillary palpomere with a pointed tip, which also hint at *Caccodes*, but are not enough to decide the question. Reexamination of the specimen will be required to support or refute the generic placement. As the specimen is not currently available, we will simply point out that *T. geiseri* may in fact be generically misplaced.

The two specimens in Wu (1997) are likewise impossible to place with certainty. If they could be located, with further study they could prove to be much better specimens for description, as the genitalia may even be visible. The shape and antennae resemble *Caccodes* but as stressed above, these are not enough to place them. Should anyone discover the whereabouts of the Wu material, we would be grateful to hear of it.

Even after the generic confusion has been addressed, the species status of the specimen under study is uncertain. Proper species determinations in these groups are totally dependent on examination of the genitalia. Extreme variation in color, and sexual dimorphism, are common, and poorly preserved, faded fossils without well-visible characters are functionally named as individuals rather than biological taxa as they lack normally used species-level characters. The ongoing assumption that amber specimens may properly be named as new if no other amber species are described in the group is both intellectually lazy and biologically invalid. Extant taxa that also occur in Dominican amber are well known (Ferreira *et al*. 2022; Keller and Skelley 2019; Tarasov *et al*. 2016) and so an assumption of novelty based only on the fact that the specimen is a fossil is never warranted. Comparison with a selection of extant species with what is visible on the specimen studied here makes the generic placement of the specimen herein described difficult. Descriptions are better supported if incorporated into studies of the extant fauna of Hispaniola (*e.g.*, Ferreira and Ivie 2017; Hopp and Ivie 2009; Lawrence *et al*. 2014; Woodruff 2002) and it is hoped this will become the norm rather than the exception.

Subfamily Placement of *Tytthonyx*. Extant species of *Tytthonyx* appear morphologically unchanged from the basic form seen in amber over the past 16–20 million years. As discussed above, the genus belongs to the monogeneric tribe Tytthonyxini, placed *incertae sedis* in the Silinae, but with references to the Malthininae (Brancucci 1980; Ramsdale 2002; Wittmer 1991a, 1992). On the other hand, Hsiao *et al.* (2021) recently suggested that the placement of Tytthonyxini within Silinae *sensu* Brancucci (1980) should be rejected, and that it be elevated to subfamily status and placed sister to Malthininae. The study cited characters of the hind wing with a fully open radial cell and a short median recurrent vein, and enlarged gonostyli that are fused to the coxites (Hsiao *et al.* 2021), but no taxonomic changes were formally made in their study. While the discovery of *T. milleri* does not bring any further data to support this discussion, we hope that its description will promote the inclusion of further specimens of this lineage in higher-level phylogenies and future morphological studies of the family Cantharidae.

Acknowledgments

MAI thanks Michael Geiser for discussions on characters, and George Poinar for photos of the holotype of *T. geiseri*. MAI also thanks the many funders, collaborators and field and lab helpers who helped develop the collections that made this work much better. The donation of the Alistair S. Ramsdale and Richard S. Miller collections by their respective families is gratefully acknowledged. Two helpful anonymous reviewers also deserve our thanks for comments and ideas that led to us improving the manuscript. This project has received funding from the European Union's Horizon 2020 research and innovation programme under the Marie Sklodowska-Curie grant agreement No. 101018841 (postdoctoral fellowship of Vinicius S. Ferreira). This is a contribution of the Montana Agricultural Experiment Station.

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(Received 19 March 2022; accepted 10 September 2022. Publication date 20 December 2022.)