



Article Fossil History of Ambrosia Beetles (Coleoptera; Platypodidae) with Description of a New Genus from Dominican Amber

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Abstract: The fossil record of ambrosia beetles is summarized and a new genus and species in the subfamily Mecopelminae, *Gongyloceria dominicana* **gen. et sp. nov.** is described. The new genus differs from the extant genus *Mecopelmus* Blackman, 1944, possessing weakly elongated tarsi, finely faceted eyes, a scape not reaching the posterior margin of the eye, coarsely sculptured pronotum and elytra, and a larger body size. It is the first Miocene record of the Mecopelminae. The genus *Xyleborites* Wickham, 1913, **placem. n.** is transferred from the Scolytidae to the Platypodidae. A list of the fossil Platypodidae, including a key to the subfamilies and tribes of ambrosia beetles, is presented. *Xyleborites* longipennis Wickham, 1913 and *Gongyloceria dominicana* **sp. nov**. may have been related to Paullinieae recorded from the late Eocene and the early Miocene of North and Central America. Distribution maps with fossil records for ambrosia beetles are included.

Keywords: Curculionoidea; new taxa; species diversity; trophic links; fossil records



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1. Introduction

Platypodidae, one of the groups of Curculionoidea, has more than 30 genera and 1400 species in the modern fauna [1]. There are a number of tribes, some of which have specific hosts. For instance, members of the Schedlariini feed on xylem of *Bursera* (Burseraceae), while the Mecopelmini feed on phloem of *Serjania* (Sapindaceae) [2]. Imagoes and larvae of Tesserocerinae and Platypodinae develop on fungi in woody tunnels [1]. The females of many of these species have mycetangia for the transfer of spores and fungal hyphae.

Morphologically, the Platypodidae are quite uniform, being cylindrical beetles with short, often modified antennae. The female forehead is often characterized by dense hairs; geniculate antennae with fused club segments; elytra, usually with a modified, often armed cavities; modified legs with enlarged procoxae; flattened femora; tibia, usually with rugae; and long narrow tarsi.

The family status was adopted by Wood [3] and Bright [4] with modifications by Thompson [5]. The family consists of three subfamilies: Mecopelminae, Tesserocerinae, and Platypodinae. The subfamily Mecopelminae was previously named Coptonotinae; however, after the exclusion of the genus *Coptonotus* Chapuis, 1869 from ambrosia beetles [5], the name of this platypodine group was changed. It differs from other groups by having the posterior margin of the prosternum straight or weakly curved in the pleural area [3]. It includes two tribes, the Mecopelmini and Schedlariini [3,4]. The subfamily Tesserocerinae with the tribes Diapodini, Tesserocerini, and Platytarsulini is characterized by separate maxilla, lacinia, and galea [3]. The subfamily Platypodinae with one tribe differs from other groups in having maxillae, with the lacinia and galea combined into one mesal element [3].

Paleontological records of platypodids are quite rare (except for the tribe Tesserocerini in New World Miocene amber) but occur in mid-Cretaceous Burmese amber, as well as in amber from the late Eocene of Europe and North America and the Miocene of Central America, Africa, and Asia [6–16]. The study of fossils is important for understanding the phylogeny of this group.

The purpose of the present study is to describe new platypodid taxa from Dominican amber and to show the diversity, fossil records, modern distribution, and possible food preferences of members of this family.

2. Materials and Methods

The studied specimens are deposited in the Poinar amber collection maintained at Oregon State University, Corvallis, OR, USA (PACO); Harvard University, Museum of Comparative Zoology, Cambridge, MA, USA (MCZ); and the Institute of Systematics and Ecology of Animals, Siberian Branch, Russian Academy of Sciences, Novosibirsk.

Observations and photographs of *Gongyloceria dominicana* sp. n. were made with a Nikon SMA-10R stereoscopic microscope and a Nikon Optiphot microscope with magnifications up to 600X. Helicon Focus Pro X54 was used to stack photos for better clarity and depth of field. Photographs of modern ambrosia beetles were taken using a Zeiss Stemi 2000-C dissecting stereomicroscope, and photos of *Xyleborites longipennis* were taken using a Leica M165C binocular microscope.

We used previous reports from the literature and collection data to show modern distributions and localities of fossil forms.

Morphological terminology follows that of Lawrence et al. [17].

Nomenclatural actions introduced in the present work are registered in ZooBank (www.zoobank.org) under LSID urn:lsid:zoobank.org:pub: AC7D809C-6EE1-488E-AA3D-1F76E3133DAB.

3. Results

Description of New Fossil Taxa of Platypodidae

Superfamily: Curculionoidea Latreitte, 1802.

Family: Platypodidae Shuckard, 1840.

Subfamily: Mecopelminae Thompson, 1992.

Tribe: Mecopelmini Thompson, 1992.

Genus: Gongyloceria Legalov and Poinar, gen. n.

urn:lsid:zoobank.org:act:60281641-BDCA-41DB-9B40-5C61C87C1586

Type species: Gongyloceria dominicana Legalov and Poinar, sp. n.

Diagnosis: Its body is subcylindrical, dark, more than five mm in length, covered with sparse short setae. Its head is as wide as its pronotum; its rostrum is reduced; it has finely faceted large eyes large; quite a narrow forehead; has a geniculate antennae with a three-segmented funicle; and its scape does not reach the posterior margin of its eye. Its antennal club is formed of fused segments without sutures; furthermore, it possesses a pronotum with laterally compressed sides and a densely punctuate disk; an elytra with convex declivity; an elytral interstriae narrower than striae; a laterally straight posterior margin of prosternum; narrowly separated procoxal cavities; a narrow metaepisternum; a metacoxal cavity length: subequal, fused first and second ventrites; a third ventrite shorter than the second; an enlarged procoxae; metacoxal cavities not strongly encroaching on the first ventrite; laterally compressed femora, flattened tibiae with mucro and spines on the lateral margin; elongated tarsi, shorter than tibiae; a first tarsomere longer or subequal to its second and third tarsomeres; and third tarsomere conical.

Etymology: The genus is formed from the Greek "gongylos", which means ball or sphere, and the Greek word "keraia", which means antenna regarding its ball-shaped segmentless antennae.

Notes: This genus belongs to the family Platypodidae based on the head as wide as the pronotum with reduced rostrum, antennal club without sutures, long first tarsomere, laterally straight posterior margin of the prosternum, metacoxal cavities not strongly encroaching on first ventrite, second ventrite subequal to third ventrite, and narrow third tarsomere. The posterior margin of the prosternum being laterally straight indicates that the fossil belongs to the subfamily Mecopelminae. The metacoxal cavities not strongly encroaching on the first ventrite, the second ventrite subequal to the third ventrite, the protibia without costate rugas, the narrow and conical third tarsomere, the three-segmented antennal funicle, and the elytra with convex unarmed declivities place this genus in the tribe Mecopelmini.

Comparison: *Gongyloceria* differs from the genus *Mecopelmus* Blackman, 1944 from Panama in having weakly elongated tarsi, finely faceted eyes, a scape not reaching the posterior margin of the eyes, a coarsely sculptured pronotum and elytra, and a larger body size. It is distinguished from the genus *Xyleborites* Wickham, 1913 from the Eocene of the Florissant by its coarsely sculptured pronotum and elytra, and larger body size. The new genus differs from the Mexican genus *Schedlarius* Wood, 1957 by the straight posterior margin of the prosternum, its metacoxal cavities not strongly encroaching on the first ventrite, second ventrite subequal to the third ventrite, protibia without costate rugas, its narrow and conical third tarsomere, antennal funicle with three segments, and unarmed elytral declivity.

Gongyloceria dominicana Legalov and Poinar, **sp. n.** (Figures 1 and 2)

LSIDurn:lsid:zoobank.org:act:19BCF70E-8351-4336-8D0D-04E97597CDF8

Description: Its body is black-brown, with a length of 5.1 mm. Its integument is covered with sparse semierect setae. It possesses a densely punctated spherical head. Its eyes are large and finely faceted. Its frons are about 0.8 times as long as eye width, weakly convex, and densely punctate without setae. Its temples are quite short, and its antennae geniculate. Its scape is about 3.2 times as long as wide at the apex, and about 1.2 times as long as the second-fourth antennomeres combined, not reaching the posterior margin of the eye. The second–fourth antennomeres are conical. The second antennomere is about 1.1 times as long as wide at the apex, and about 0.3 times as long as—and about 0.7 times as narrow as—the scape. The third antennomere is about 0.8 times as long as wide at the apex, while it is about 0.6 times as long as—and slightly narrower than—the second antennomere. The fourth antennomere is about 0.6 times as long as wide at the apex, and about 1.1 times as long as—and about 1.4 times as wide as—the third antennomere. The club is about 1.3 times as long as wide in the middle, about 3.4 times as long as—and about 1.7 times as wide as—the fourth antennomere, and it is equal in length to the second–fourth antennomeres combined. The pronotum is about 1.6 times as long as wide at the apex, 1.4 times as long as wide in the middle, and about 1.2 times as long as wide at the base. Its disk is weakly convex and densely punctate. The intervals between punctures are subequal to their diameters. Elytra subcylindrical, 1.6 times as long as pronotum, about 1.7 times as long as wide at base and in middle, and about 2.3 times as long as apical fourth. The elytra sides are subparallel. The elytral interstriae are convex and narrow, narrower than the width of striae, and coarsely punctate. The striae are deep and wide, with a row of large points. The elytral declivity is convex. The procoxal portion of the prosternum is 0.5 times as long as the procoxal cavity length. The postcoxal portion of the prosternum is very short. The procoxal cavities are narrowly separated, while the mesocoxal cavities are quite widely separated. The metaventrite is weakly convex, about 2.3 times as long as the metacoxal cavity length, while densely punctate. The metanepisternum is about 10 times as long as it is wide in the middle, and it is also finely punctate. The abdomen is weakly convex and densely punctuate. The first ventrite is subequal to the metacoxal cavity length. The second ventrite is subequal to first ventrite. The third ventrite is about 0.7 times as long as the second ventrite. The fourth ventrite is about 0.6 times as long as the third ventrite. The fifth ventrite subequal to the third and fourth ventrites combined. The tarsi are quite long. The procoxae are enlarged. The mesocoxae are rounded and widely separated. The femora are laterally compressed, weakly clavate, and transverse rugose. The profemora are about 3.0 times as long as wide in the middle. The metafemora are about 4.5 times as long as wide in the middle. Tibiae are almost straight, flattened, with terminal mucro and three spines on the lateral margin. Protibia are about 3.0 times as long as wide in the middle. Metatibia

are about 3.7 times as long as wide in the middle. Tarsi are elongated. The first tarsomere is long-conical. The second and third tarsomeres are conical. The fourth tarsomere is small. The fifth tarsomere is elongated. The claws are free and long. Protarsi are slightly shorter than the protibiae. Metatarsi are 0.7 times as long as metatibiae. Protarsi: the first tarsomere is about 4.3 times as long as wide at the apex; the second tarsomere is about 1.7 times as long as wide at the apex, and about 0.4 times as long as, and slightly wider than, the first tarsomere; the third tarsomere is about 2.1 times as long as wide at the apex, 1.2 times as long as, and subequal in width to, the second tarsomere; the fifth tarsomere is about 6.8 times as long as wide at the apex, 2.5 times as long as, and about 0.8 times as narrow as, the third tarsomere, while it is about 1.4 times as long as the second and third tarsomeres combined. Metatarsi: the first tarsomere is about 2.4 times as long as wide at the apex; the second tarsomere is about subequal in length and width, and is about 0.6 times as long as, and about 1.3 times as wide as, the first tarsomere; the third tarsomere is about 1.5 times as long as wide at the apex, and about 1.2 times as long as, and about 0.8 times as narrow as, the second tarsomere; the fifth tarsomere is about 4.1 times as long as wide at the apex, and about 1.7 times as long as, and about 0.6 times as narrow as, the third tarsomere, while it is about 0.9 times as long as the second and third tarsomeres combined.



Figure 1. *Gongyloceria dominicana* sp. nov., holotype—Dominican amber: (**A**) dorsal view; (**B**) ventral view; (**C**) lateral view.



Figure 2. *Gongyloceria dominicana* sp. nov., holotype—Dominican amber: detail of head and lateral view.

Material examined: Holotype—PACO # 92, Dominican amber. Etymology: The species epithet indicates the place of origin of the fossil. Genus: *Xyleborites* Wickham, 1913, placem. n. (Figure 3) *Xyleborites longipennis* (Wickham 1913)—Florissant

Remarks: This beetle was described in the family Scolytidae as being closely related to *Xyleborus* Eichhoff, 1864 [18]; however, it was subsequently placed in Scolytidae incertae sedis [2]. The very large eyes and narrow forehead, head not hidden by pronotum, and the base of its elytra without granules places the fossil in the Mecopelminae.



Figure 3. *Xyleborites longipennis*, holotype, body, lateral view, Florissant: (**A**) without alcohol; (**B**) with alcohol.

Key to subfamilies and tribes of Platypodidae

Posterior margin of prosternum laterally straight (Figure 1C) or weakly curved in pleural area (Figure 4I). (Mecopelminae).
 Posterior margin of prosternum laterally strongly curved in pleural area (Figure 4H)
 Posterior margin of prosternum laterally straight (Figure 1C). Metacoxal cavities not

strongly encroaching on first ventrite. Second ventrite longer or subequal to third ventrite. Protibia without costate rugas. Third tarsomere narrow and conical. Three-segmented antennal funicle. Elytra simple, with convex unarmed declivity...... Mecopelmini



Figure 4. Platypodidae spp.: (**A**) *Platytarsulus* sp., abdomen, arrow shows first ventrite; (**B**) *Crossotarsus* sp., abdomen, arrow shows first ventrite; (**C**) *Schedlarius mexicanus* Dugès, 1886, habitus, dorsal view, arrow shows elytral declivity; (**D**) *Platytarsulus* sp., mouthpart, arrow shows maxilla; (**E**) *Diapus* sp., prosternum; (**F**) *Tesserocerus* sp., prosternum, arrow shows posterior margin; (**G**) *Treptoplatypus severini* Blandford, 1894, mouthpart, arrow shows mesal element; (**H**) *Spathidicerus thomsoni* Chapuis,

1865, prosternum, arrow shows posterior margin; (I) *Schedlarius mexicanus*, head and prosternum, lateral view, arrow shows elytral declivity. Scale bars 0.5 mm for (**A**,**B**,**D**,**F**), 1.0 mm for (**C**,**E**,**H**,**I**), 0.2 mm for (**G**).

List of the fossil Platypodidae Subfamily: Palaeotylinae Poinar, Vega and Legalov, 2020; Genus: Palaeotylus Poinar, Vega and Legalov, 2020; *P. femoralis* Poinar, Vega and Legalov, 2020—Burmese amber [19]; Subfamily: Mecopelminae Thompson, 1992; Tribe: Mecopelmini Thompson, 1992; Genus: Xyleborites Wickham, 1913, placem. n.; X. longipennis Wickham, 1913—Florissant [18]; Genus: Gongyloceria Legalov and Poinar, gen. n.; Gongyloceria dominicana Legalov and Poinar, sp. n.—Dominican amber; Subfamily: Tesserocerinae Strohmeyer, 1914; Tribe: Tesserocerini Strohmeyer, 1914; Genus: Eoplatypus Peris, Solórzano Kraemer, and Cognato, 2017; E. jordali Peris, Solórzano Kraemer, and Cognato, 2017—Baltic amber [11]; Genus: Cenocephalus Chapuis, 1865; C. aniskini Legalov, 2020—Baltic amber [7]; *C. hurdi* Schedl, 1962—Mexican amber [9]; C. quadrilobus Schedl, 1962—Mexican amber [9]; C. succinicaptus Schedl, 1962—Mexican amber [9]; *C. tenuis* Peris and Solórzano Kraemer, 2015—Mexican amber [14]; *C. antillicus* Bright and Poinar, 1994—Dominican amber [12]; *C. antiques* Bright and Poinar, 1994—Dominican amber [12]; *C. biconicus* Bright and Poinar, 1994—Dominican amber [12]; C. exquisitus Bright and Poinar, 1994—Dominican amber [12]; C. quasiexquisitus Davis and Engel, 2007—Dominican amber [13]; *C. rhinoceroide*(Schawaller, 1981)—Dominican amber [10]; *C. senectus* Bright and Poinar, 1994—Dominican amber [12]; *C. spinatus* Bright and Poinar, 1994—Dominican amber [12]; *C. josephi* Legalov and Pankowski, in lit.—Ethiopian amber [16]; Genus: Chaetastus Nunberg, 1953; *Ch. Samsockorum* Legalov and Pankowski, in lit.—Ethiopian amber [16]; Genus: Tesserocerus Saunders, 1837; T. simojovelensis Peris and Solórzano Kraemer, 2015—Mexican amber [14]; *T. primus* Bright and Poinar, 1994—Dominican amber [12]; Tribe: Diapodini Strohmeyer, 1914; Genus: *Diapus* Chapuis, 1865; D. resinae Solórzano-Kraemer and Cognato, 2022—Zhangpu amber [15]; D. ethiopicus Solórzano-Kraemer and Cognato, 2022-Ethiopian amber [15]; Platypodidae incertae sedis; Genus: *Platypodidarum* Kohring and Schlueter, 1989; *P. ferrarae* Kohring and Schlueter, 1989—Sicilian amber [20]; Genus: ? Platypus Herbst, 1793; "P." maravignae Guerin-Meneville, 1838—Sicilian amber [21].

4. Fossil Ambrosia Beetles Review

The systematic position of the Platypodidae is debated. Some authors [2–7,19,22–29] consider this group as an independent family similar to bark beetles. On the basis of cladistic morphological and molecular genetics, it was proposed that the Platypodidae was a subfamily of Curculionidae [30–33]. Unfortunately, which group of weevils gave rise to the Platypodidae has not been shown using morphological characteristics. Based on

molecular data [34–36], the stem group resemble members of the Dryophthorinae. This is questionable because the Dryophthorinae is a very specialized group with pronounced apomorphies (fifth tarsomere with claws widely separated by dermal lobes, mouthparts with prementum positioned in mouth cavity, rostrum with pleurostomal, a deep sinus, first and second ventrites fused, tibiae with large unci and two bunches of setae at apex, etc.), which are absent in ambrosia beetles. In our opinion, one of the main distinguishing features are free first and second ventrites, which in all weevils are always fused. Other important features of Platypodidae were provided by Morimoto and Kojima [28]. It appears that the most likely ancestors of the Platypodidae are the Ithyceridae, a diverse Early Cretaceous group that gave rise to the Curculionidae, Brentidae, and Scolytidae. The Ithyceridae are characterized by non-fused first and second abdominal ventrites, a feature that could have been passed on to their descendants.

In modern fauna, ambrosia beetles are mainly distributed throughout the tropics and subtropics [1,2]. A few species live in temperate latitudes, reaching north to England in Europe, British Columbia (Canada) in North America, and south to Argentina and New Zealand (Figure 5). However, the distribution of various groups of the family differs. The widespread Platypodinae occupies an area that coincides with the distribution of the family (Figure 5). Relictual groups, such as Schedlariini and Mecopelmini, have survived only in Central America—the former in Mexico and the latter in Panama. The subfamily Tesserocerinae is tropical to subtropical (Figures 6-8). The oldest Platypodidae is Palaeotylus *femoralis*, which has been found in mid-Cretaceous Burmese amber [19]. However, it is poorly preserved, which led to doubts about its systematic position and the suggestion that it is a representative of the Zopheridae [37]. However, extant and Burmese amber Zopheridae [38–43] differ greatly from *Palaeotylus*. There are no other Platypodidae fossils from either the early or late Cretaceous [6,44]. Modern groups of Platypodidae appear in Tertiary amber, with impressions in late Eocene Baltic amber and Florissant deposits. Representatives of the tribe Tesserocerini are found in Baltic amber (Figure 6); however, they are very rare, with only three specimens recovered [7,11]. They have not been found in Rovno amber [7,8]. The oldest representative of the subfamily Mecopelminae is described from the terminal Eocene of the United States. Oligocene fossils of Platypodidae are unknown [8].



Figure 5. Distribution of Platypodidae.



Figure 6. Distribution of Tesserocerini. Fossil records: green spheres—Mexican amber, red spheres—Dominican amber, light blue sphere—Baltic amber, pink sphere—Ethiopian amber, blue sphere—Tanzanian copal.

Platypodidae are highly diverse in the Miocene. A rich fauna occurs in early Miocene Dominican and Mexican amber [10,12–14]. In total, 14 species belong to the extant genera *Cenocephalus* and *Tesserocerus* of the tribe Tesserocerini. Modern species of these genera are absent in Western India today [45]; however, *Cenocephalus* occurs in Costa Rica and further south, and *Tesserocerus* is found in Mexico [45] (Figure 6). An extinct genus of the subfamily Mecopelmimae is described in the present work. Representatives of Platypodidae are known from early Miocene Ethiopian amber [15,16]. These are species of the genera *Cenocephalus*, *Chaetastus* [16], and *Diapus* [15]. The first two belong to the tribe Tesserocerini (Figure 6), and the third to the tribe Diapodini (Figure 7). Species from the genera *Chaetastus* and *Diapus* are now distributed in tropical Africa; however, they do not reach as far north as Ethiopia [45]. Diapodini species are also found in Chinese Zhangpu amber [15] (Figure 7). The genus *Diapus* is found in southwestern China but is absent from Fujian [46].



Figure 7. Distribution of Diapodini. Fossil records: pink sphere—Ethiopian amber, light blue sphere—Zhangpu amber.

A representative of the Platypodidae, probably belonging to the tribe Platytarsulini, was recorded from Sumatran amber [47,48] (Figure 8). Two species of Platypodidae of unclear taxonomy have been described from Sicilian amber [20,21]. The Platypodidae of Miocene ambers belong to the subfamily Mecopelmimae and the tribes Tesserocerini and Diapodini of the subfamily Tesserocerinae. There are no reliable records of the most diverse and abundant subfamily Platypodinae in the Miocene. The subfamily Tesserocerinae is more primitive and older than the Platypodinae, which is confirmed by paleontological data. Tesserocerini diversity was higher in the Miocene, and they probably replaced Platypodinae; thus, no representatives of this tribe are now known from Hispaniola, and only six species of Platypodinae have been recorded [49]. Reliable finds of Platypodinae occurred in late Quaternary Colombian, Tanzanian [50,51], and Holocene Madagascar copals. *Chaetastus* from Tesserocerini was recorded from Tanzanian copal [52] (Figure 6). It can be assumed that the formation of the modern fauna of Platypodidae did not occur earlier than the Pliocene–Pleistocene.



Figure 8. Distribution of Platytarsulini. Fossil record: green sphere—Sumatran amber.

The trophic relationships of the Eocene and Miocene ambrosia beetles are difficult to determine due to the wide range of food plants associated with modern representatives [2]. It has been suggested that they were pre-angiosperms [11,14]. However, *Mecopelmus zeteki* Blackman, 1944 is a monophage on *Serjania* [2] of the tribe Paullinieae from the family Sapindaceae, and we can assume the same trophic links apply to the fossil representatives of Mecopelminae. The first finds of representatives of the tribe Paullinieae (including *Serjania*) were from the early Eocene of the USA [53–57]; however, the systematic positions of these remains were undetermined [58]. Pollen resembling *Serjania*, *Paullinia*, and *Cardiospermum* were reported from the late Eocene of Panama [59,60]. Diversification of the crown group Paullinieae in the tropics is assumed to be in the early Miocene [58]. It is likely that the new species developed from *Serjania* spp. or a related genus. *Xyleborites longipennis* could have developed on representatives of Paullinieae, which were noted in the Florissant [61].

5. Conclusions

Ambrosia beetles have been known since the late Cretaceous. The appearance of modern Platypodidae lineages occurred in tropical forests in the Eocene [62]. The subfamily Tesserocerinae was dominant in the Miocene. There are no reliable pre-Quaternary records of the now dominant Platypodinae. Their diversification apparently occurred only recently.

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