

Revision of Bethylinae from Dominican amber, with description of a new genus (Hymenoptera, Bethyliidae)

Diego N. Barbosa¹, Gabriel A. R. Melo¹

¹ *Laboratório de Biologia Comparada de Hymenoptera, Departamento de Zoologia, Universidade Federal do Paraná, Cx. postal 19020, 81531-980, Curitiba, PR, Brazil*

Corresponding author: Gabriel A. R. Melo (garmelo@ufpr.br)

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Abstract

Fossil species of bethyline wasps from Dominican amber are revised. Based on a cladistic analysis of female morphological data we recognize a new genus and species, †*Crassibethylus dominicanus* **gen. et sp. nov.**, which came out as sister group of the clade *Odontepyris* + *Prosierola*. We also transfer to Bethyliidae a fossil taxon originally described in Sclerogibbidae, placing †*Pterosclerogibba* Olmi as a new junior synonym under *Goniozus* Förster, in the new combination †*Goniozus antiquus* (Olmi). Additionally, the third species of Bethylinae known from Dominican amber, †*Goniozus respectus* Sorg, is diagnosed and illustrated with color images of the holotype. An identification key to the species of Bethylinae from Dominican amber is provided.

Keywords

Aculeata, aptery, Chrysoidea, Lepidoptera, Miocene

Introduction

Bethylinae have their diversity represented by 540 species distributed into 11 genera, and recorded around all zoogeographical regions (Azevedo et al. 2018; Ramos and Azevedo 2020). Their fossil diversity is represented by 20 species distributed in seven genera, †*Cretabethylus* Rasnitsyn, from Russia, Transbaikalia; *Eupsenella* Westwood, from Baltic, Oise French, and Rovno amber; *Goniozus* Förster, from Baltic, Rovno, Mexican and Dominican amber; *Lytopsenella* Kieffer, from Baltic and Rovno amber;

†*Nucifrangibulum* Cockx, McKellar & Perrichot, from Charentese French amber; *Prosierola* Kieffer, from Baltic amber; and *Sierola* Cameron, from Baltic, Rovno and Zhangpu amber (Azevedo et al. 2018; Brazidec and Perrichot 2022, in press).

The females of Bethylinae are idiobiont ectoparasitoids mostly of lepidopterous mature larvae. The majority of host records are based on species of *Goniozus*, and according to Hardy and Blackburn (1991) and Bentley et al. (2009) they have gregarious life histories and exhibit a subsocial behavior with maternal care and defense of the developing brood. The males of Bethylinae, as in the other bethylid wasps, emerge before their sibling females and have the capacity to inseminate all of them, the sex ratio being female biased with a low degree of variation (Khird et al. 2014).

In Bethylinae, there is a reduced sexual dimorphism, thus being easy to establish sex associations in most groups. The genera belonging to Bethylinae are recognized based on the following combination of characteristics: antenna with 10 or 11 flagellomeres; mandible thick, short, with four sharp apical teeth; clypeus extending posterad into frons, with clypeal carina strongly outcurved in profile; dorsal pronotal area with posterior margin outcurved medially; legs with tarsal claws bifid and strongly angled; forewing with first abscissa of vein Rs+M tubular, minimally as a stub; sting with posterior area of second valvifer with anterior slender projection (Azevedo et al. 2018; Barbosa et al. 2021).

The phylogenetic relationships within Bethylinae have received the attention from previous studies conducted by Sorg (1988), Polaszek and Krombein (1994), Terayama (1995), Carpenter (1999), De Ploëg and Nel (2004) and Ramos and Azevedo (2020). The latter investigation avoided some of the shortcomings of the former studies, using a broader representation both in terms of geographic distribution and morphological diversity within the subfamily. Ramos and Azevedo's (2020) results recovered three main clades: *Lytopsenella* + *Eupsenella*; *Odontepyris* + *Prosierola*; "*Goniozus*" + (*Sierola* + (*Afrobethylus* + *Bethylus*)). There is good support for the monophyly of the constituent genera in Bethylinae, except for *Goniozus*.

In the present work we revise the fauna of Bethylinae known from Dominican amber. Our starting point was an intriguing fossil inclusion that at first sight suggested a female sclerogibbid wasp due to its distinctly swollen profemora. Further study revealed that instead it represented a Bethylinae, showing many features in common with *Odontepyris* and *Prosierola*, and which is described here as new genus. During our investigations we also concluded that †*Pterosclerogibba antiqua*, a Dominican amber fossil described by Olmi (2005) in Sclerogibbidae, represents a bethyline wasp as well.

Materials and methods

Examined material

The amber piece containing the fossil inclusion that prompted this study is deposited in the Department of Zoology, of the Universidade Federal do Paraná, Curitiba, Brazil (DZUP). It is from Miocene deposits from the Dominican Republic and was obtained from a dealer established in USA. Additional institutions containing

Dominican amber taxa mentioned in the text are as follows: GPCO, George Poinar's collection, Department of Entomology, Oregon State University, Corvallis, USA; SGN, Senckenberg Gesellschaft für Naturforschung, Frankfurt, Germany. Dominican amber has been estimated to be around 15–20 million years old, from the Burdigalian, in the Early Miocene (Iturralde-Vinent and MacPhee 2019).

Terminology

Morphological terminology follows mainly Huber and Sharkey (1993), including for wing venation, except for some terms taken from Lanes et al. (2020). Those related to the integument follow Harris (1979).

Identification

We used the key proposed by Azevedo et al. (2018) for genus-level identifications. The species were identified through comparison with original descriptions in Sorg (1988) and Olmi (2005), and with illustrations in Martynova et al. (2019) and Perkovsky et al. (2020).

Phylogenetic analysis

In order to establish the phylogenetic position of the bethyline taxon under investigation, we used Ramos and Azevedo's (2020) matrix for females, keeping their same selection of in-group and outgroup taxa (see Suppl. material 1). The two additional bethyline taxa treated here were not included in the analysis because we were not able to directly examine them.

The tree searches followed all parameters used by Ramos and Azevedo (2020). For choice of concavity value (K) we used the TNT script setk.run, proposed by Salvador Arias (Instituto Miguel Lillo, Argentina). Tree visualization and character optimization were carried out in Winclada 1:00:08 (Nixon 2002).

Specimen illustrations

The specimen images were obtained by a LEICA DFC295 digital camera, and the stacking was carried using the software Zerene Stacker. The figures were prepared in GIMP (2.10.18). The images of the type specimen of †*Goniozus respectus* Sorg were provided by the depositary institution.

Results

Phylogenetic relationships

The implied weighting analysis, under $K=13.3$, resulted in six most parsimonious trees, whose strict consensus is shown in Fig. 1 (complete tree with all taxa shown as Suppl. material 2). The monophyly of the subfamily Bethylinae, as well as all

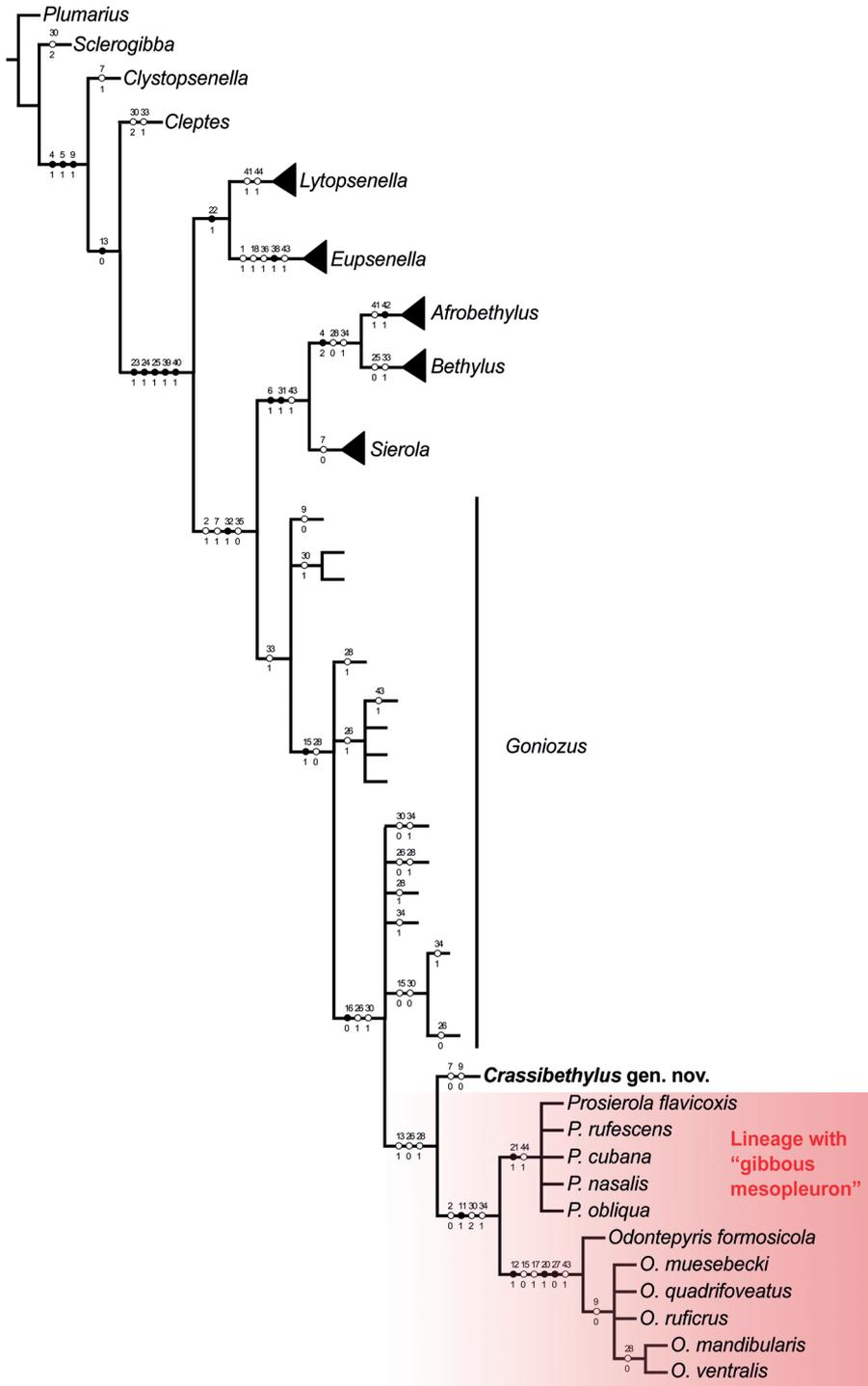


Figure 1. Simplified cladogram of the relationships within the bethylid subfamily Bethylinae; strict consensus of six most parsimonious trees under implied weighting. Original data matrix from Ramos and Azevedo (2020), for species represented by female specimens. See text for further details.

clades retrieved by Ramos and Azevedo (2020), were also recovered here. Additionally, the fossil bethyline under investigation came out as sister-group of the clade *Prosierola* + *Odontepyris*, supported by the mesoscutellar groove present as sulcus (character 13:1), ventral carina of metasomal petiole straight (26:0) and forewing vein 2Cu present (28:1). The fossil taxon was supported by two transformations: maxillary palp with four articles (7:0) and prosternum smaller than area of procoxa (9:0). Moreover, the clade *Prosierola* + *Odontepyris* was supported by four transformations: frontal unsculptured streak present (2:0), gibbous mesopleuron (11:1), forewing with vein 1Rs longer than M (30:2) and Rs+M shorter than 1Rs (34:1). *Prosierola* was supported by two transformations: propodeum with a pair of conspicuous anterior pits on the propodeal disc (21:1) and distal region of dorsal area of the tergite 9 enlarged (44:1). And *Odontepyris* was supported by six transformations: mesopleuron with a dentate process (12:1), metapostnotum not marked dorsally as a smooth triangular area (15:0), median metapostnotal carina present (17:1), propodeum with a pair of pits in basal outer portion (20:1), forewing bula absent (27:0) and proximal margin of first valvifer angled (43:1).

Although we did not code the fossil bethyline under investigation as possessing a gibbous mesopleuron, it has a considerably swollen mesopleuron, therefore reinforcing its similarity to the clade *Prosierola* + *Odontepyris*. Also, it shares with *Prosierola* the posterior margin of the pronotum slightly produced backward medially (8:1). Considering its unique position and close relationship with *Prosierola* and *Odontepyris*, we propose a new fossil genus to accommodate this Dominican amber bethyline.

Taxonomy

Order Hymenoptera Linnaeus, 1758

Superfamily Chrysidoidea Latreille, 1802

Family Bethylidae Haliday, 1839

Subfamily Bethylinae Haliday, 1839

† *Crassibethylus* gen. nov.

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Figs 2, 3

Type species. † *Crassibethylus dominicanus* sp. nov.

Diagnosis. Maxillary palp with four articles; prosternum shorter than area of procoxa; pro- and metafemora strongly swollen, profemur lenticular-shaped, about 0.6× as wide as long; posterior margin of pronotum slightly produced backward medially; mesoscutellar groove present as a narrow sulcus; forewing vein 2Cu present; insertion of metacoxae displaced anteriorly between mesocoxal insertion; ventral carina of metasomal petiole straight.

Description. Female. Head. Head as long as wide; antenna with 11 flagellomeres; clypeus with median clypeal carina continuous with frontal carina, lateral lobe not evident; anterior margin of frons projected anteriorly. Eye large, occupying most of lateral

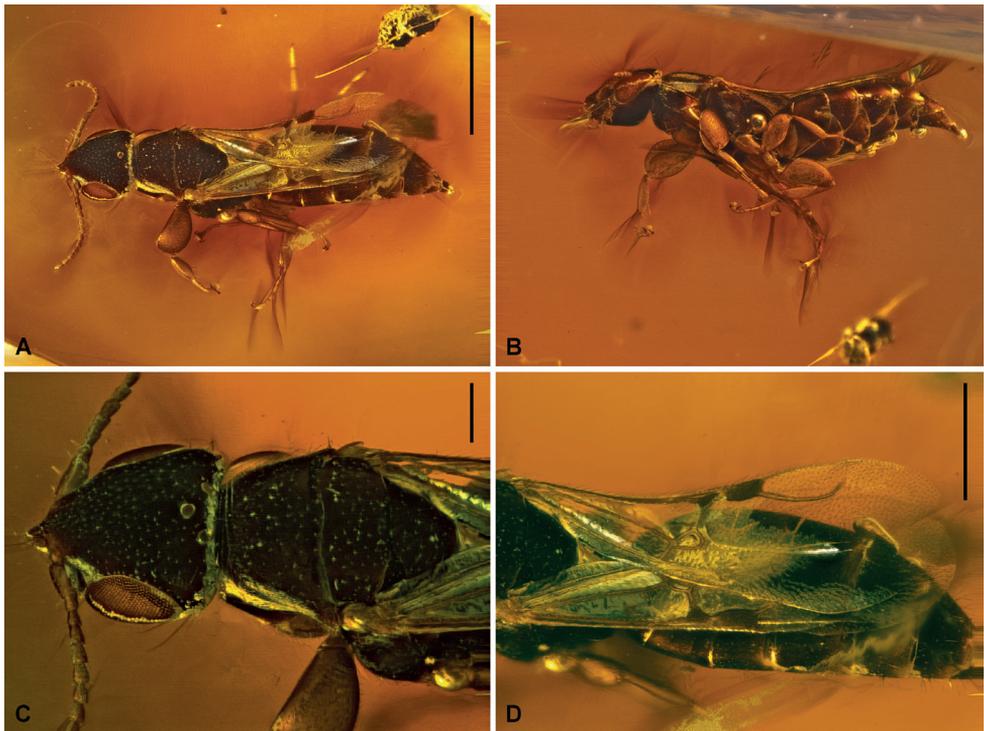


Figure 2. †*Crassibethylus dominicanus* gen. et sp. nov. Female holotype **A** dorsal habitus **B** lateral habitus **C** head and mesosoma, in dorsal view **D** wings and metasoma, in frontal view. Scale bars: 1 mm (**A**); 0.2 mm (**C**); 0.5 mm (**D**). **A, B** at same scale.

portion of head. Ocelli located close to vertex crest; anterior angle of ocellar triangle obtuse. Vertex straight. **Mesosoma.** Pronotum with dorsal pronotal area longer than mesoscutum, its posterior margin slightly produced backward medially. Mesoscutum without notaulus; parapsidal signum absent. Mesoscutellar groove as a narrow sulcus, lacking enlarged lateral pits. Metapectal-propodeal complex coriaceous; metapostnotum indistinct, apparently without metapostnotal median carina and metapostnotal-propodeal suture; posterior transverse carina present. Mesopleuron somewhat swollen in dorsal view, coriaceous, not sculptured; mesopleural pit shallow. Prosternum relatively large, somewhat rhombic-shape. **Wings.** Forewing with costal cell conspicuous; second radial cell closed, short, almost triangular; length of vein Rs2 as long as vein M2; length of vein Rs2+M2 as long as vein 1Rs2; stigma well developed, bula present. **Legs.** Pro- and metafemora strongly swollen, profemur lenticular-shaped, about 0.6× as wide as long. Insertion of metacoxae displaced anteriorly between mesocoxal insertion. Tarsal claws strongly curved, with a large basal expansion. **Metasoma.** Sting with 3vv narrow and long.

Etymology. The genus name is an allusion to the strongly swollen profemora, from Latin *crassus*, thick, fat, stout, and *Bethylus*, the type genus of Bethylinae.

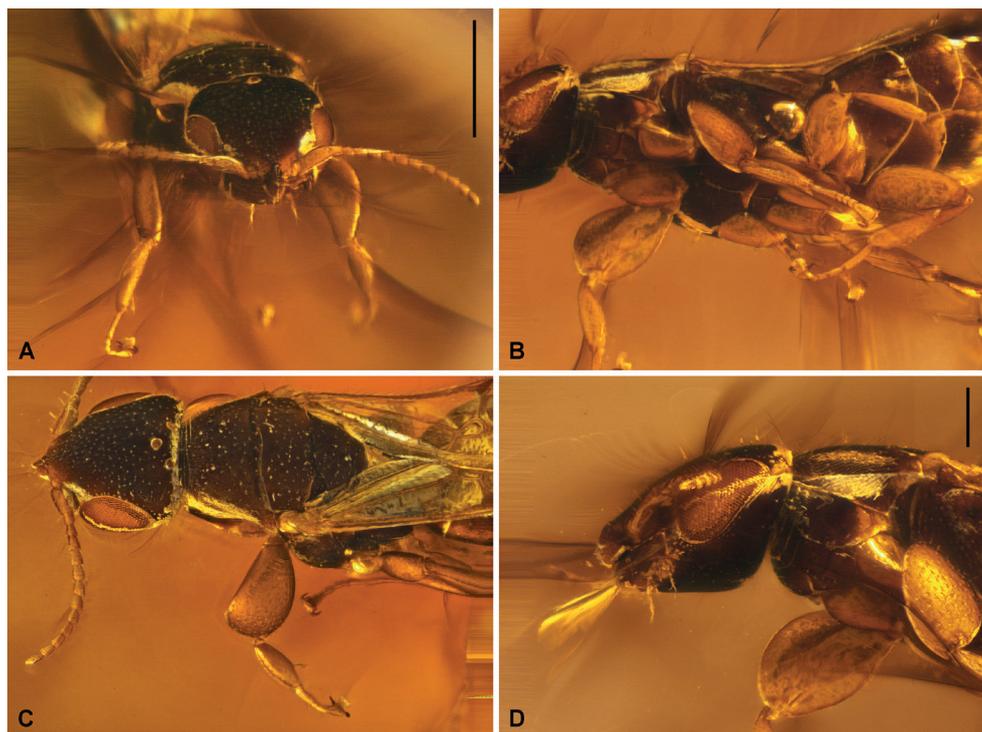


Figure 3. †*Crassibethylus dominicanus* gen. et sp. nov. Female holotype **A** head, in frontal view **B** mesosoma, in lateroventral view **C** head and mesosoma, in dorsal view **D** head and protorax, in lateroventral view. Scale bars: 0.5 mm (**A**); 0.2 mm (**D**). **A–C** at same scale.

†*Crassibethylus dominicanus* sp. nov.

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Figs 2, 3

Type material. *Holotype* female, amber inclusion from the Dominican Republic (DZUP Dom-024). Specimen complete and very well preserved. Syninclusions: one small spider and a springtail.

Description. *Holotype.* *Female.* Body length 3.2 mm; forewing 1.95 mm long. **Color.** Wings clear hyaline; antenna, mandible, palpi, tegula, legs, and wing venation light castaneous; metasoma castaneous; head and mesosoma dark castaneous. **Head.** Head as long as wide in dorsal view, triangular-shaped in both frontal and lateral views. Mandible narrow and evenly wide along its extension. Clypeus with median lobe rounded, well projected; median carina well developed, continuous with frontal carina; lateral lobe inconspicuous. Antenna with flagellar pubescence sparse, with few outstanding erect setae; scape 3.0× longer than pedicel; pedicel as long as first flagellomere; flagellomeres subequal in length. Eye not protruding, elliptical, large, and glabrous; area between anterior margin of eye and demarcation of median clypeal lobe clearly

concave. Frons coriaceous and finely punctate. Posterior ocelli close to vertex crest; anterior angle of ocellar triangle obtuse; anterior ocellus aligned with upper tangent of eyes. Vertex crest straight, sparse thick setae at corner. Hypostomal carina straight. **Mesosoma.** Pronotum wider than long, coriaceous and finely punctate; anterior corner angled. Metapectal-propodeal complex with lateral marginal carina. **Wings.** Forewing with R2 cell longer than 1Cu2 cell; only one longitudinal flexion line present, not forming rectangular area. **Metasoma.** About 2.3× longer than wide, polished, whole surface glabrous. Genitalia with 3vv narrow and longer than wide.

Male. unknown.

Etymology. The specific epithet *dominicanus* is an allusion to the Dominican Republic, country from the where the amber piece originated.

Goniozus Förster

Goniozus Förster, 1856: 95. Type species: *Bethylus claripennis* Förster, 1851.

Parasierola Cameron, 1883: 197. Type species: *Parasierola testaceicornis* Cameron, 1883.

Progoniozus Kieffer, 1905: 105. Type species: *Perisemus floridanus* Ashmead, 1905.

Parasierola Kieffer, 1914: 533. Type species: *Parasierola gallicola* Kieffer, 1905.

†*Pterosclerogibba* Olmi, 2005: 186. Type species: †*Pterosclerogibba antiqua* Olmi, 2005, syn. nov.

Remarks. *Goniozus* Förster is the second most speciose genus in Bethylinae, being composed by 174 described species, three of them representing fossil taxa, two from Baltic amber and one from Dominican amber (Azevedo et al. 2018). Its species are distributed around all zoogeographic regions. The taxonomic efforts for this genus are represented by a species revision for the Nearctic region (Evan, 1978), in which nine species groups were recognized; and a species revision for the Sino-Japanese region (Terayama 2006). The latest phylogenetic work for this group, published by Ramos and Azevedo (2020), included the largest representation of the diversity within *Goniozus*, and retrieved it as a paraphyletic group, a result also found here. Based on this result, Ramos and Azevedo (2020) reinforced the necessity to further investigate its constituent groups in order to better delimit the genus, based on the morphological evidence.

The fossil fauna of Dominican amber is interpreted here as containing two species of *Goniozus*. In addition to †*G. respectus*, described by Sorg (1988), we also transfer the taxon †*Pterosclerogibba antiqua*, described by Olmi (2005) as a sclerogibbid wasp, to *Goniozus* (see below).

†*Goniozus antiquus* (Olmi) comb. nov.

†*Pterosclerogibba antiqua* Olmi, 2005: 186. Female holotype. Dominican Republic: amber from La Toca mine (GPCO, not examined).

Diagnosis. Antenna, tibia, and tarsi light castaneous; head and mesosoma castaneous; metasoma dark-castaneous to nearly black. Head longer than wide, not punctured; clypeal carina strong, but not extending over frons; antenna relatively short, apical portion moniliform; malar space as long as eye length; eye small, without pilosity; ocellar triangle with a right anterior angle; vertex concave, apparently without thick setae. Mesosoma without conspicuous setae; posterior margin of dorsal pronotal area concave posteriorly; mesoscutum shorter than dorsal pronotal area, not punctured, notaulus absent; mesopleuron not gibbous; mesoscutellum as long as mesoscutum, not punctured; metapectal-propodeal complex as long as mesonotum. Forewing with clearly developed pterostigma, venation apparently reduced. Proleg with a swollen femur, almost 2.0× longer than wide, metafemora not distinctly swollen. Metasoma without visible setae; sting curved downward.

Remarks. Olmi (2005) described †*Pterosclerogibba antiqua* as the first fully winged female of Sclerogibbidae, and postulated that this species has a great importance for evolutionary studies of the family. However, the photographs of the holotype provided in Martynova et al. (2019: 1797) and Perkovsky et al. (2020: 3) clearly indicate to us that it represents a Bethylidae. The following features, which according to Azevedo et al. (2018) are useful for the identification of bethylid wasps, can be observed in the holotype: head elongate, depressed, and prognathous; clypeus with vertical carina extending between antennae; antenna placed close to the clypeus and with 11 flagellomeres in both sexes; clypeus partially covered by antennal base; occipital carina present and complete; dorsal pronotal area always present and at least as long as wide; mesoscutum-mesoscutellar suture always represented either by sulcus or pits, or both; metapostnotum well developed and invading propodeum; propleuron covered by pronotal collar in dorsal view; mesopleural pit always present centrally or nearly so; forewing with pterostigma present and well developed. Moreover, additional features observed in the holotype of †*Pterosclerogibba antiqua* indicate that it belongs to Bethylinae, as follows: head triangular-shaped, in lateral profile; swollen profemur; and strongly curved tarsal claws. Although both Olmi (2005) and Martynova et al. (2019) outlined what they interpreted as the wings, these represent small cracks in the amber around the inclusion. The true wings are folded over the specimen, as can be seen in Perkovsky et al. (2020).

Within Bethylinae, Olmi's species can be accommodated in *Goniozus* based on its general morphology and especially for lacking diagnostic features found in other genera of Bethylinae. Considering that *Goniozus*, as currently defined (see Ramos and Azevedo 2020), represents a paraphyletic assemblage, future work should focus in better positioning †*Goniozus antiquus* among the many species groups found within this genus.

†*Goniozus respectus* Sorg

Fig. 4

†*Goniozus respectus* Sorg, 1988: 86. Female holotype. Dominican Republic: amber from unknown mine (SGN, examined through photographs).

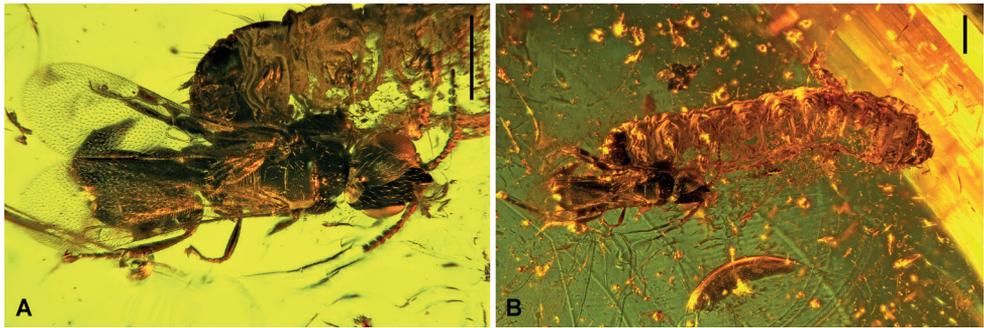


Figure 4. †*Goniozus respectus* Sorg. Female holotype **A** dorsal habitus **B** view of the amber inclusions, showing the female holotype and a microlepidopteran larva (putative host). Scale bars: 0.5 mm.

Diagnosis. Antenna, clypeus and legs light castaneous; head and mesosoma dark-castaneous nearly black. Head as long as wide, sparsely punctured; antenna with flagellomeres with large sensilla, distinctly moniliform; malar space shorter than eye length; eye large, without pilosity; ocellar triangle with anterior angle obtuse; vertex straight, with few scattered setae. Mesosoma setae as long as head setae; posterior margin of dorsal pronotal area concave; mesoscutum shorter than dorsal pronotal area, punctured, notaulus absent; mesoscutellum as long as mesoscutum, punctured; metanotum with metascutellum visible; metapectal-propodeal complex longer than mesonotum, lateral marginal carina of the metapectal-propodeal complex present. Forewing with clearly developed pterostigma, 1M2 cell, Rs2 vein not reach margin. Legs with profemur almost 3.0× longer than wide, metafemora not distinctly swollen. Metasoma with setae slightly longer than those on mesosoma.

Remarks. The species was described by Sorg (1988) based on a single female specimen. In addition to the description, the author also illustrated the head and forewing. We were able to study this taxon based also on color photographs kindly provided by Dr. Solórzano Kraemer. As already emphasized by Sorg (1988), the wasp is preserved together with a microlepidopteran larva (see Fig. 4). Considering that all Bethylinae are known to parasitize larvae of Lepidoptera, except for the unusual *Goniozus* attacking *Microstigmus* wasps (Melo and Evans 1993), one can deduce that the larva entombed together with †*Goniozus respectus* likely represents its host.

Key to the species of Bethylinae from Dominican amber

- 1 Profemur and metafemur strongly swollen, profemur about 0.6× as wide as long; mesopleuron swollen; insertion of metacoxae displaced between mesocoxae..... †*Crassibethylus dominicanus* gen. et sp. nov.
- Profemur and metafemur not as swollen, profemur much less than 0.6× as wide as long; mesopleuron not swollen; metacoxae inserted posteriorly to mesocoxal insertion..... 2 (*Goniozus*)

- 2 Head longer than wide, with malar space as long as eye length; eye small; ocellar triangle with anterior angle right; vertex concave; notauli absent; metapectal-propodeal complex as long as mesonotum; profemur almost 2.0× longer than wide..... †*G. antiquus* (Olm)
- Head as long as wide, with malar space shorter than eye length; eye large; ocellar triangle with anterior angle obtuse; vertex straight; mesoscutum with notauli; metapectal-propodeal complex longer than mesonotum; profemur almost 3.0× longer than wide..... †*G. respectus* Sorg

Discussion

The discovery of an enigmatic bethylid wasp in Dominican amber has provided us with an opportunity to reassess the taxa currently known from this fossil deposit. The inclusion of the new fossil in the dataset assembled by Ramos and Azevedo (2020) recovered its sister-group relationship with the clade *Odontepyris* + *Prosierola*, a position supported by some unequivocal morphological features present in these three lineages. In addition to these characters, their phylogenetic affinity is also reinforced by the morphology of the mesopleuron. The clade *Odontepyris* + *Prosierola* is notable for their swollen mesopleuron, giving it a “gibbous” appearance in dorsal view (see Ramos and Azevedo 2020). Although we did not code †*Crassibethylus* gen. nov. as having a swollen mesopleuron, it has a condition reminiscent of that seen in species of *Odontepyris* and *Prosierola*. These three taxa have a broad mesosoma, with the foramina of their mesocoxae placed considerably apart from each other. It is possible that the mesopleuron in this group became enlarged to accommodate the musculature associated with the mesocoxae.

Our phylogenetic results also shed light on the age and biogeography of the *Odontepyris* + *Prosierola* clade. While the species of *Odontepyris* are distributed in the Old World, being presently recorded from the Afrotropical, Australian, Oriental and Palearctic regions, *Prosierola* is restricted to the New World, including the Greater Antilles (Azevedo et al. 2018). The discovery of †*Crassibethylus* gen. nov. and its placement as sister to *Odontepyris* + *Prosierola* could indicate a New World origin for the entire group. Improved resolution of the biogeographic pattern, however, will require further study of the relationships involving the species groups in *Goniozus*.

Although recognition of a new taxon at genus level in Bethylinae does not solve the paraphyletic condition of *Goniozus*, we think that simply subsuming *Odontepyris* and *Prosierola* (and for that matter †*Crassibethylus* gen. nov. as well) within *Goniozus* is not a reasonable solution to the problem. These taxa have distinct morphologies and occupy distinct regions of the globe. Future work on Bethylinae should focus on establishing the limits of the species groups within *Goniozus*, so that a new genus-level classification could be proposed on more solid ground. There are already some genus-group names available, currently synonymized under *Goniozus*, that could be reinstated for some of these lineages.

It is also important to call attention to additional contributions of our work to the understanding of the evolution within Sclerogibbidae. The removal of †*Pterosclerogibba* from Sclerogibbidae to Bethylidae, placed here as a synonym of *Goniozus*, makes the fauna of Sclerogibbidae known from Dominican amber restricted to †*Probethylus poinari*, a taxon described from an apterous female and exhibiting a condition similar to that found in the extant species (Olmí 2005). Therefore, presence of fully developed wings in female sclerogibbid wasps is restricted to those taxa known only from the Cretaceous (see Perkovsky et al. 2020).

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Supplementary material 1

Character matrix

Authors: Diego N. Barbosa, Gabriel A. R. Melo

Data type: Morphological (Excel spreadsheet)

Explanation note: Morphological character matrix.

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Supplementary material 2

Phylogenetic tree

Authors: Diego N. Barbosa, Gabriel A. R. Melo

Data type: (PDF file)

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