

Revision of the fossil species of *Thaumatodryinus* Perkins from Dominican amber, with a new combination and description of a new species (Hymenoptera, Dryinidae)

André L. Martins¹, 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)

Academic editor: Michael Ohl | Received 17 August 2020 | Accepted 30 September 2020 | Published 30 October 2020

<http://zoobank.org/ED8D2D07-C038-4429-B5FF-1011D2B48907>

Citation: Martins AL, Melo GAR (2020) Revision of the fossil species of *Thaumatodryinus* Perkins from Dominican amber, with a new combination and description of a new species (Hymenoptera, Dryinidae). Journal of Hymenoptera Research 79: 77–88. <https://doi.org/10.3897/jhr.79.57686>

Abstract

The fossil species of *Thaumatodryinus* from Dominican amber are studied, and the first revision is presented with a key to the known taxa. We recognize three species, *T. miocenicus* Olmi, 1995, *T. priscus* (Olmi, 1998), **comb. nov.** and *T. fuscescens* **sp. nov.** The current classification of the genus and relationships between fossil and living species are discussed. Comments on the host records for *Thaumatodryinus* are presented.

Keywords

Aculeata, Chrysidoidea, Miocene, Thaumatodryinae, wasps

Introduction

In recent years, a significant number of species of Dryinidae have been described from different fossiliferous deposits (Olmi et al. 2014; Guglielmino et al. 2018; Perkovsky et al. 2019). Currently, 73 extinct species of Dryinidae are known from amber inclu-

sions and rock impressions (Olmi et al. 2014; Guglielmino et al. 2018; Perkovsky et al. 2019, 2020a,b; Martins and Melo 2019; Martynova et al. 2020; Olmi et al. 2020). The Dominican amber is the third largest deposit in number of fossil dryinid species (Kachin Burmese amber in first with 33 species and Baltic amber in second with 22 species), with a total of 14 species of the following genera: *Aphelopus* Dalman, *Dryinus* Latreille, *Harpactosphexion* Haupt and *Thaumatodryinus* (Olmi et al. 2014; Perkovsky et al. 2019, 2020a,b; Martynova et al. 2019).

Thaumatodryinae is a small subfamily of Dryinidae, known to attack nymphs of the auchenorrhynchous Flatidae (Guglielmino et al. 2013). This subfamily has an almost worldwide distribution, being absent only from the Palearctic region. A single genus is recognized, *Thaumatodryinus* Perkins, with 32 described species, of which only *T. miocenicus* Olmi 1995 has been described from a fossil inclusion (Olmi and Virla 2014; Olmi and Xu 2015; Olmi et al. 2019).

Olmi (1984) proposed the subfamily Thaumatodryinae for the type-genus *Thaumatodryinus* Perkins, but a few years later he transferred *Thaumatodryinus* to the subfamily Dryinae and sunk Thaumatodryinae under the latter (Olmi 1993). The resurrection of Thaumatodryinae was proposed by Tribull (2015), after her molecular phylogenetic studies having showed that *Thaumatodryinus* does not belong in Dryinae. Morphological support for this hypothesis was obtained more recently by Martins (2018). His phylogenetic hypothesis also corroborated an independent position for *Thaumatodryinus* outside of the clade composed of Dryinae plus Gonatopodinae.

In this study, we contribute for the knowledge of Dryinidae by reviewing the fossil species of *Thaumatodryinus* from Dominican amber and propose a new species for the genus. Furthermore, the status of *Dryinus priscus* Olmi, 1998 is reinterpreted based on our comparative morphological study.

Materials and methods

The amber pieces studied here are deposited in the Department of Zoology, of the Universidade Federal do Paraná, Curitiba, Brazil (DZUP) and in the American Museum of Natural History, New York, USA (AMNH). The inclusions have been obtained from amber fossiliferous Miocene deposits in the Dominican Republic. 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).

Morphological terminology follows Olmi and Virla (2014); specific terms used for integumental sculpture, follows Olmi and Virla (2014) and Harris (1979); we adopted Brothers's (2011) terminology for the forewing venation. The term rhinaria (*sensu* Olmi 1984) is interpreted herein as equivalent to “ADOs”, Antennal Dorsal Organs (*sensu* Riolo et al. 2016). The diagnosis for the previously described species was prepared based on the original descriptions and redescrptions by Olmi (1995, 1998) and Olmi and Virla (2014), complemented by notes taken by the first author during his visit to the AMNH.

In the description and diagnosis the following abbreviations were used: POL, refers to the minimum distance between the inner edges of the lateral ocelli; OL, refers to the minimum distance between the inner edges of the lateral ocellus and the median ocellus; OOL, refers to the minimum distance from the outer edge of the lateral ocellus to the eye inner margin; OPL, refers to the minimum distance from the posterior edge of a lateral ocellus to the occipital carina; and TL, refers to the minimum distance from the posterior edge of eye to the occipital carina. The measurements provided for ocellar ratio, antennomeres and for the fore leg articles represent relative values.

Study of the inclusions was carried out in a Leica M125 stereomicroscope. Color images of *Thaumatomyrmex fuscescens* sp. nov. were obtained by a LEICA DFC295 digital camera, and those of *T. miocenicus* Olmi and *Dryinus priscus* Olmi by a Nikon DS-Ri2 using NIS-Elements D–Z-series 11*. Image stacking was carried using the software Zerene Stacker. The figure plates were prepared using Adobe Photoshop (version Cs6).

Systematic paleontology

Family Dryinidae Haliday, 1833

Subfamily Thaumatomyrmecinae Olmi, 1984

Genus *Thaumatomyrmex* Perkins, 1905

Type species. *Thaumatomyrmex koebelei* Perkins, 1905, by monotypy.

Diagnosis. Among living and fossil dryinids, the species of *Thaumatomyrmex* can be recognized by the following combination of characters: mandible with four teeth in both sexes, teeth progressively larger from anterior to posterior ends along cutting edge; outer surface of mandible with a distinct basal sulcus, extending from the anterior to the posterior condyle; mid portion of anterior margin of clypeus straight or convex; occipital carina complete in fossil taxa and in males of most living species, females of many living taxa with incomplete carina; maxillary and labial palpomeres in proportion 6:3; antenna filiform in both sexes; flagellomeres 3–7 of female with single set of rhinaria on its mid length, flagellomere 8 with two sets of rhinaria along its length; rhinaria on flagellomeres 5–8 each with four long setae, two at each side; pronotum saddle-shaped and crossed by strong transverse impression at central portion, pronotal lobe reaching tegula; anterior margin of mesoscutellum with a foveate groove; fore wing with 2r-rs shorter than 3Rs&4Rs; female with tarsal claw simple and with basal expansion, male with bifid claw, without basal expansion; apex of 3rd tarsomere of fore leg with variable number of thick bristles in female; chela with rudimentary claw, enlarged claw with one row of lamellae and two subapical teeth laterally on outer surface; female hind coxa with a distinct basal projection ventrally; dorsal and posterior surfaces of propodeum convex; tibial spur formula for both sexes 1/1/2.

Key to species of *Thaumatomydryinus* from Dominican amber (females only)

- 1 Eyes hemispherical, about $1.1\times$ longer than wide; maximum head width about $1.9\times$ distance between inner margins of tegulae; antenna with 1st flagellomere as long as 2nd (Fig. 1); POL more than $3\times$ OL; OOL about $6\times$ OPL; lower margin of clypeus straight; pronotum with rugose marks on lateral border of the transverse impression; mesoscutum granulate; notauli percurrent; anterior margin of mesoscutellum with a narrow row of small foveae, not with a groove *Thaumatomydryinus fuscescens* sp. nov.
- Eyes slightly longer, about $1.3\text{--}1.4\times$ width; maximum head width about $1.7\times$ distance between inner margins of tegulae; proportion between 1st and 2nd flagellomeres variable; POL shorter than $2.5\times$ OL; OOL about $5\times$ OPL; lower margin of clypeus convex; pronotum surface mostly granulate; sculpture of mesoscutum variable; notauli not extending along entire length of mesoscutum; anterior margin of mesoscutellum with a groove 2
- 2 Antenna with 1st flagellomere shorter than 2nd (Fig. 2); POL $2.3\times$ OL; mesoscutum reticulate rugose; notauli extending for approximately half of mesoscutum length; anterior margin of mesoscutellum with a foveate narrow groove; propodeum short, distinctly shorter than high in lateral view *Thaumatomydryinus miocenicus* Olmi
- Antenna with 1st flagellomere almost as long as 2nd (Fig. 3); POL $2\times$ OL; mesoscutum granulate; notauli extending for approximately 0.7 of mesoscutum length; anterior margin of mesoscutellum with a broad, shallow groove; propodeum distinctly long, about as long as high in lateral view *Thaumatomydryinus priscus* (Olmi) comb. nov.

† *Thaumatomydryinus fuscescens* sp. nov.

<http://zoobank.org/48DD7867-AB75-4443-9346-B7DF4A35C982>

Figure 1

Diagnosis. *Thaumatomydryinus fuscescens* sp. nov. is characterized by the body predominantly testaceous, except head and part of pronotum and remainder of mesosoma black; eyes hemispherical, about $1.1\times$ longer than wide; maximum head width about $1.9\times$ distance between inner margins of tegulae; frontal line present; mid portion of clypeus with anterior margin straight; antenna with 1st flagellomere as long as 2nd; POL $3.2\times$ OL; OOL about $6\times$ OPL; occipital carina complete; notauli percurrent, extending from anterior to posterior margins of mesoscutum.

Description. Female holotype (Fig. 1A–F). Approximate body length: 4.1 mm. **Color.** Head black, except mandible, clypeus and antenna testaceous (Fig. 1A–D); pronotum black, except dorsal-posterior surface brown (Fig. 1B); mesosoma black; legs testaceous, except pro- and metafemur with middle portion darkened (Fig. 1); fore wing with one transverse darkened band; metasoma testaceous. **Pubesence.** Head with short setae (Fig. 1A–C); antenna with setae; eye glabrous (Fig. 1C); pronotum



Figure 1. †*Thaumatotdryinus fuscescens* sp. nov., female holotype. **A** habitus, dorsal view **B** right antenna, dorsal view **C** head and mesosoma, antero-ventral view **D** head and mesosoma, dorsal view **E** apical portion of flagellum, with details of flagellomeres 5–8 **F–G** Apical portion of fore leg, with details of the chela. Scale bars: 2 mm (**A**), 0.5 mm (**B**), 0.5 mm (**C–D**), 0.3 mm (**E–G**).

with fine and erect setae (Fig. 1B); mesosoma with conspicuous erect setae (Fig. 1B); propodeum with erect setae; metasoma with more conspicuous erect pilosity on last tergum. **Integumental sculpture.** Head finely granulated (Fig. 1A–C); frontal line in the form of a low carina and apparently complete, not visible near mid ocellus; malar sulcus well-marked; mandible with a marked groove at the base; pronotum granulate, except by rugosity on lateral portions of transverse impression; mesoscutum granulate;

notauli complete; mesoscutellum rugulose, its anterior margin with a narrow row of small foveae, not with a groove; mesopleuron rugose; metapleuron reticulate-rugose; propodeum reticulate rugose. **Structure and proportions.** Vertex convex, except by ocellar triangle slightly elevated. Ocellar ratio: POL = 16; OL = 5; OOL = 25; OPL = 4; TL = 9. Antennomeres in following proportions: 35: 15: 45: 45: 60: 65: 55: 23: 27: 25. Eye hemispherical, about $1.1\times$ longer than wide; maximum head width about $1.9\times$ distance between inner margins of tegulae; occipital carina complete; mid portion of clypeus with anterior margin straight; maxillary palpomeres elongated; malar space about as long as basal width of mandible; notaulus complete (Fig. 1B). Head longer than pronotum (60:55); mesoscutum longer than mesoscutellum and metanotum shorter than propodeum. Fore wing with three cells closed by pigmented tubular veins; vein abscissa 3Rs&4Rs longer than 2r-rs (65:30). Dorsal surface of propodeum distinctly longer than posterior surface (50:45); mesopleuron with a groove in the central region. Articles of fore leg (Fig. 1E–F) in the following proportions: 54 (coxa): 50 (trochanter): 63 (femur): 80 (tibia), 46: 8: 15: 34: 50 (tarsomeres 1–5), and 46 (enlarged claw). Segment 3 of protarsus with four long bristles and segment 4 with five long bristles. Chela (Fig. 1E–F) and enlarged claw with two subapical teeth and one row of about 26 lamellae. Segment 5 of protarsus with two rows of at least 40 lamellae; distal apex with group of approximately seven long lamellae.

Remarks. *Thaumtodryinus fuscescens* sp. nov. is more similar to the extant Neotropical fauna than to the other two species found in the Dominican amber. It has in common with some of the living species a convex vertex and slightly elevated ocellar triangle, straight lower clypeal margin, complete occipital carina, percurrent notauli and anterior margin of mesoscutellum with a narrow row of small foveae. Among the fossil species studied here, *T. fuscescens* sp. nov. is more similar to *T. miocenicus* and differs from *T. priscus* by the head shape with eyes protuberant on the lateral side, frontal line present and ratio of OL short than TL. The new species differ from *T. miocenicus* and *T. priscus* by the granulated integument of the head; clypeus with lower margin straight; 1st flagellomere as long as 2nd; hemispherical-shaped eyes; and percurrent notauli. The chela of *T. fuscescens* is closed and for this reason it is not possible to determine the number of lamellae in the enlarged claw and in the 5th tarsomere.

Etimology. The species is named in reference to its overall dark coloration, from the Latin *fuscus*, dark, dusky, and *-escens*, beginning of, becoming.

Type material. Holotype female, in amber from the Dominican Republic (piece DZUP Dom-018). According to the amber dealer, it is probably from La Toca or Los Cacaos mine, in Santiago de los Caballeros.

†*Thaumtodryinus miocenicus* Olmi, 1995

Figure 2

Thaumtodryinus miocenicus Olmi, 1995: 263. Female holotype. Dominican Republic: amber from unknown mine, probably El Valle mine (AMNH, examined).

Extended diagnosis. Female holotype, 5.6 mm (see fig. 1–2 in Olmi (1995) and fig. 140 in Olmi and Virla (2014)). *Thaumatotdryinus miocenicus* is easily recognized by the following combination of characters: black head, except antenna brown to dark brown; mesosoma mostly black; legs and metasoma apparently brown. Antenna with dense and short setae. Head slightly convex, granulated; upper frons and vertex with pilosity; occiput slightly excavated and densely hairy; frontal line present but apparently incomplete in holotype (complete in paratype Do-4066-M); mid portion of clypeus with anterior margin convex. Mesoscutum reticulate rugose; notauli incomplete, reaching approximately half the length of mesoscutum; mesoscutellum reticulate rugose, hairy and shorter than mesoscutum; anterior margin of mesoscutellum with a foveate narrow groove; metanotum reticulate rugose, shorter than scutellum. Propodeum apparently reticulate

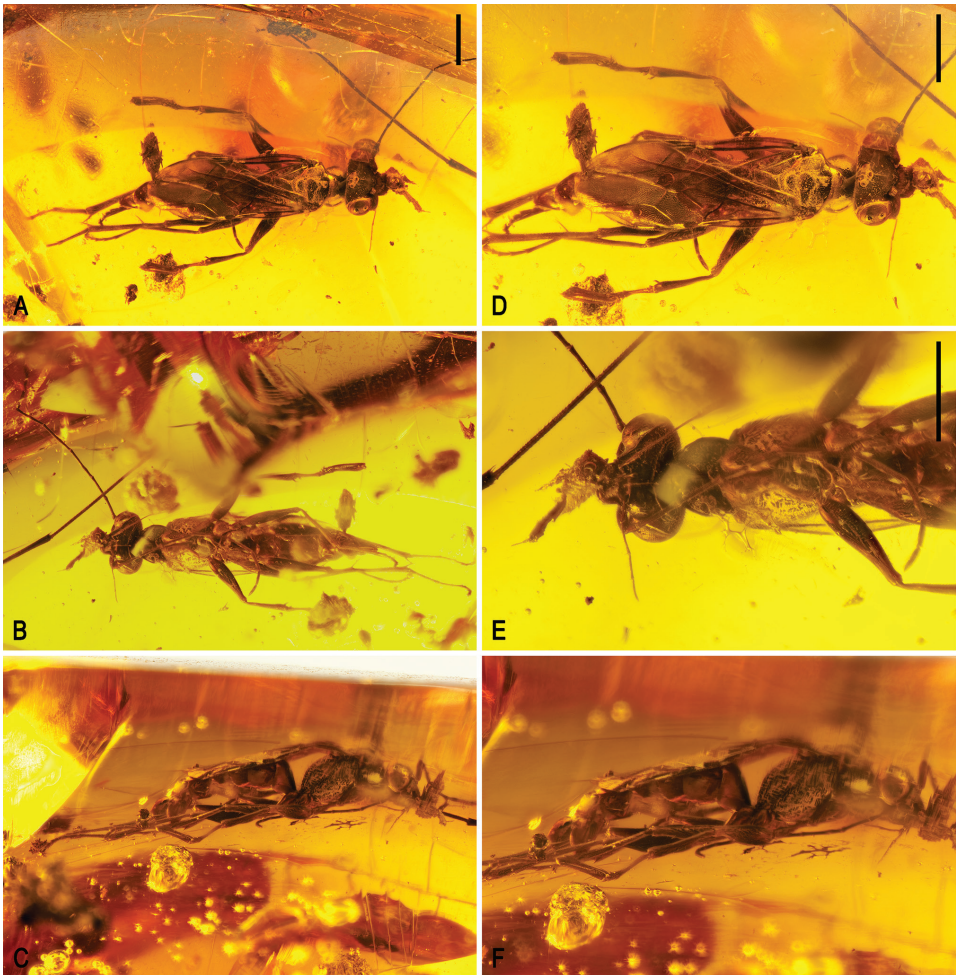


Figure 2. † *Thaumatotdryinus miocenicus* Olmi, 1995, female holotype. **A** habitus, dorsal view **B** habitus, ventral view **C** habitus, lateral view **D** habitus, dorsal view **E** head and mesosoma, ventral view **F** habitus, lateral view. Scale bars: 1 mm (**A–C**), 1 mm (**D, F**), 1 mm (**E**).

rugose and short, distinctly shorter than high in lateral view; fore wing overlapped in holotype and color not visible, but in paratypes, fore wing with one dark transverse band beneath pterostigma. Ocellar ratio: POL= 7; OL= 3; OOL= 10; OPL= 2; TL= 3. Antennomeres in following proportions: 14:7:22:24:34:20:19 (flagellomere 8–10 not visible). Eye somewhat elongate, about 1.3× longer than wide; maximum head width about 1.7× distance between inner margins of tegulae. Pronotum shorter than head (16:37). Mesoscutum longer than pronotum (20:16). Fore wing with 2r-rs shorter than 3Rs&4Rs. Fore leg segments in following proportions: 30 (coxa): 15 (trochanter): 40 (femur): 43 (tibia): 22 (1th tarsomere): 3 (2nd tarsomere): 7 (3rd tarsomere): 22 (4th tarsomere): 36 (5th tarsomere); 5th tarsomere longer than enlarged claw and with two rows of at least 30 lamellae; distal apex with group of approximately three long lamellae; enlarged claw with two subapical teeth and one row of 29 lamellae. Propodeum short, distinctly shorter than high in lateral view, with dorsal surface shorter than posterior surface (45:50).

Remarks. While in the original description Olmi (1995) mentioned that the mandibles are “not distinctly visible”, Olmi and Virla (2004) stated that the mandibles are “tridentate”. We could not clearly see the condition in the type material but consider more likely that *T. miocenicus* has quadridentate mandibles as in all other *Thaumatomyrmex*. When the mandibles are closed, it is quite hard to observe the tooth closer to the clypeus, giving the impression that the mandibles are tridentate.

Examined material. Female holotype, in amber from the Dominican Republic: amber from an unknown mine (probably El Valle mine) DR-99-146 HT (AMNH). Two paratype females: same locality label as holotype, DR-99-147 PT and DR-99-148 PT (AMNH).

†*Thaumatomyrmex priscus* (Olmi, 1998), **comb. nov.**

Figure 3

Dryinus priscus Olmi, 1998: 77. Female holotype. Dominican Republic: amber from unknown mine, probably El Valle mine (AMNH, examined).

Extended diagnosis. Female holotype, 4.0 mm (see fig. 55 in Olmi 1998). *Thaumatomyrmex priscus* is easily recognized by the body testaceous, except by the dark petiole and mesoscutellum apparently black or brown. Antenna with dense and short setae and rhinaria present in flagellomeres 3–8. Head slightly convex, apparently granulated; eye somewhat bulging; frontal line absent; mid portion of clypeus with anterior margin convex. Pronotum granulated; mesoscutum granulated, notauli incomplete, reaching approximately 0.7 of mesoscutum length; mesoscutellum shorter than mesoscutum, with sculpture not clearly evident; anterior margin of mesoscutellum with broad, shallow groove; metanotum shorter than mesoscutellum, with indistinct sculpture; propodeum reticulate rugose and distinctly long, about as long as high in lateral view. Ocellar ratio: POL= 5; OL= 2.5; OOL= 10; OPL= 2; TL= 3. Antennomeres in following proportions: 9:5:20:19:23:27:20:15:10:12. Eye elongated, about 1.4× longer than wide; maxi-

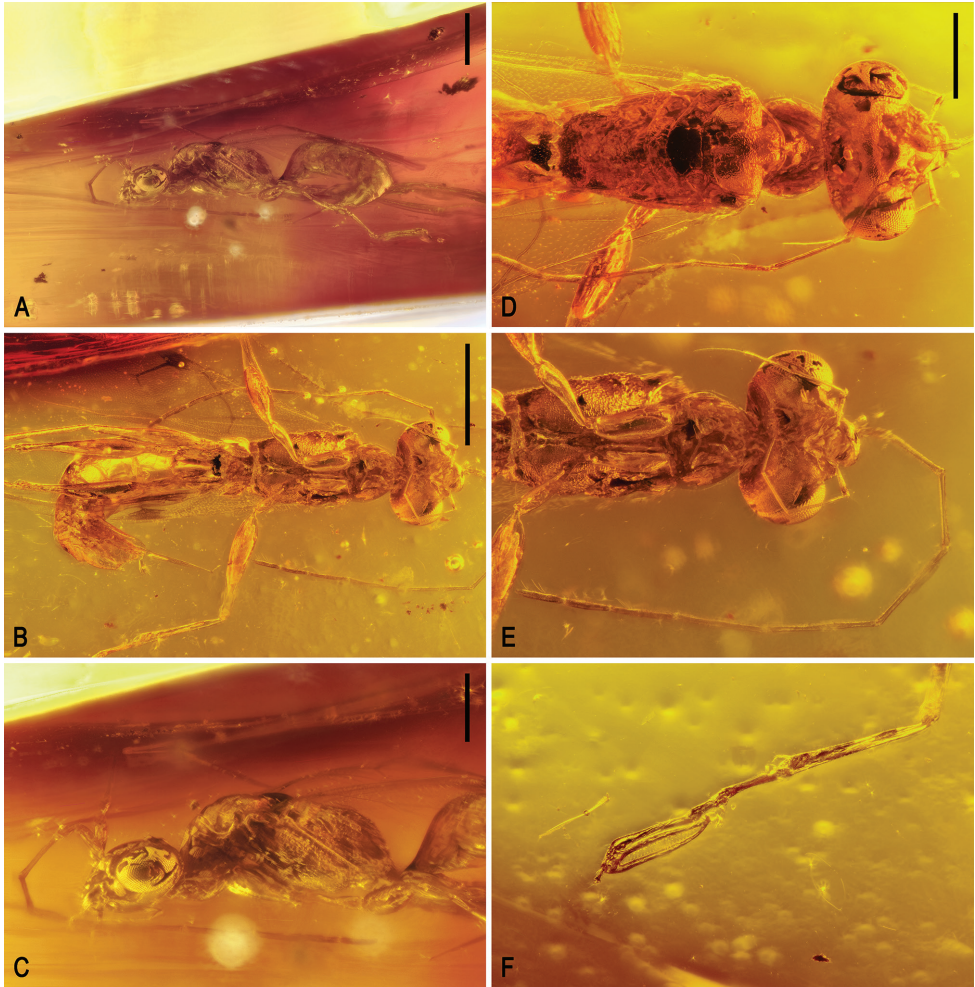


Figure 3. †*Thaumatotdryinus priscus* (Olm, 1998), female holotype. **A** habitus, lateral view **B** habitus, ventral view **C** head and mesosoma, lateral view **D** head and mesosoma, dorsal view **E** head and mesosoma, ventral view **F** apical portion of fore leg, with details of the chela. Scales: 1 mm (**A**), 1 mm (**B**), 0.5 mm (**C**), 0.5 mm (**D–F**).

num head width about $1.7\times$ distance between inner margins of tegulae; pronotum shorter than head (15:26); mesoscutum as long as pronotum (16:15). Fore wing with one dark transverse band and vein 2r-rs shorter than 3Rs&4Rs (11:21). Fore leg segments in following proportions: 19 (coxa): 20 (trochanter): 45 (femur): 30 (tibia): 11 (1th tarsomere): 4 (2nd tarsomere): 6 (3th tarsomere): 21 (4th tarsomere): 31 (5th tarsomere); 5th tarsomere slightly longer than enlarged claw (31:27) and with two rows of numerous lamellae (exact number hard to observe); enlarged claw apparently with one subapical tooth and with one row of numerous lamellae (exact number hard to observe). Propodeum distinctly long, about as long as high in lateral view, dorsal surface as long as posterior surface.

Remarks. This species was originally described in the genus *Dryinus* by Olmi (1998) and redescribed as such by Olmi and Virla (2014), but this taxon belongs in *Thaumatodryinus* since it exhibits all the diagnostic features of the genus, including the characteristic long setae on flagellomeres (see Fig. 3). Furthermore, we have noticed that the specimen illustrated by Olmi and Virla (2014: 254) representing *Dryinus priscus* Olmi does not correspond to the holotype. The inclusion shown in their Plate 100 corresponds to a species of *Harpactosphecion* Haupt, which can be easily recognized by the long and distinctly curved, fore trochanter, and the thin flagella.

Examined material. Female holotype, in amber from Dominican Republic: amber from an unknown mine (probably El Valle mine) DR-14-341 (AMNH).

Discussion

All fossil species of Thaumatodryinae are currently known only from Dominican amber. Species described originally in *Thaumatodryinus* from Baltic amber by Brues (1923, 1933) have been all transferred to *Harpactosphecion*, a distantly related fossil genus belonging to the Dryininae (Olmi 1984; Olmi and Bechly 2001). These two genera resemble each other in their general morphology, having elongated, slender bodies and long antennae and legs. Among many differences, they can be easily set apart by details of their antennae: while the flagella of *Harpactosphecion* lack conspicuous pilosity and the first two flagellomeres are distinctly longer than the 3rd, *Thaumatodryinus* possesses distinctly long setae projecting from all rhinaria and their first two flagellomeres are about as long as the 3rd.

We document here the presence of three species of *Thaumatodryinus* in Dominican amber. Two of them, *T. fuscescens* sp. nov. and *T. miocenicus*, resemble the extant species in their protuberant and hemispherical eyes, and a more compact propodeum. *Thaumatodryinus priscus* is more divergent, possessing more elongated eyes and a longer propodeum. In general, it has a more slim, elongated body and this might have contributed to its interpretation as a *Dryinus* by Olmi (1998). Also, the amber piece containing the holotype has been further polished after the original description, allowing for a better view of the inclusion, as can be seen in the photographs provided here.

As far as it is known, species of *Thaumatodryinus* attack only the fulgoroid family Flatidae and host records are known for four species of *Thaumatodryinus* from the Australian, Nearctic, Neotropical and Oriental regions (Guglielmino et al. 2013). They have been reared from six species belonging to five different genera of Flatidae (Guglielmino et al. 2013). The fossil record of Flatidae is scanty and the oldest records are from the Paleocene of Argentina and China (Szwedo and Stroiński 2013). Additional more recent records include a nymph preserved in Dominican amber and parasitized by a dryinid larva (Olmi 1995). This could represent a larva of *Thaumatodryinus*, although this cannot be stated with certainty considering that Flatidae are also attacked by three other dryinid genera, *Gonatopus* Ljungh and *Neodryinus* Perkins (Gonatopodinae), and *Dryinus* (Dryininae) (Guglielmino et al. 2013).

Acknowledgements

We would like to thank James Carpenter and David Grimaldi for granting access to the collections under their care and for their kind help during ALM's visit to the American Museum of Natural History (AMNH). We also thank Brunno Rosa for taking photographs of the type material of the fossil species deposited in the AMNH collection. The visit of ALM to the AMNH was made possible through an AMNH's Collection Study Grant. This work was also supported by the Conselho Nacional de Desenvolvimento Científico e Tecnológico – CNPq by grants 151827/2019-2 to ALM and 309641/2016-0 to GARM.

References

- Brothers DJ (2011) A new late Cretaceous family of Hymenoptera, and phylogeny of the Plu-mariidae and Chrysidoidea (Aculeata). *ZooKeys* 130: 515–542. <https://doi.org/10.3897/zookeys.130.1591>
- Guglielmino A, Olmi M, Bückle C (2013) An updated host-parasite catalogue of world Dryinidae (Hymenoptera: Chrysidoidea). *Zootaxa* 3740: 1–113. <https://doi.org/10.11646/zootaxa.3740.1.1>
- Guglielmino A, Olmi M, Marletta A, Speranza S (2018) Discovery of the first species of *Dryinus* Latreille (Hymenoptera: Dryinidae) from Burmese amber. *Zootaxa* 4394 (3): 443–448. <https://doi.org/10.11646/zootaxa.4394.3.10>
- Haliday AH (1833) An essay on the classification of the Parasitic Hymenoptera of Britain, which correspond with the *Ichneumones minuti* of Linnaeus. *The Entomological Magazine* 1: 259–273.
- Harris RA (1979) A glossary of surface sculpturing. *Occasional Papers in Entomology* 28: 1–31.
- Martins AL, Melo GAR (2019) The oldest confirmed fossil of Bocchinae (Hymenoptera, Dryinidae), with description of a new species of *Bocchus* Ashmead from Baltic amber. *Historical Biology*. <https://doi.org/10.1080/08912963.2019.1613392>
- Martins AL (2018) Sistemática do gênero *Dryinus* Latreille (Hymenoptera, Dryinidae): relações filogenéticas entre os grupos de espécies da região neotropical e revisão da fauna brasileira. PhD Dissertation. Universidade Federal do Paraná (Curitiba).
- Martynova KV, Zhang Q, Olmi M, Müller P, Perkovsky EE (2020) Revision of the genus *Dryinus* Latreille (Hymenoptera: Dryinidae) from mid-Cretaceous Kachin (Myanmar) amber. *Cretaceous Research* 106 (2020) 104–217. <https://doi.org/10.1016/j.cretres.2019.104217>
- Olmi M (1984) A revision of the Dryinidae (Hymenoptera). *Memoirs of the American Entomological Institute* 37(I–XII): 1–1913.
- Olmi M (1993) A new generic classification for Thaumatodryininae, Dryininae and Gonatopodinae, with descriptions of new species (Hymenoptera Dryinidae). *Bollettino di Zoologia agraria e di Bachicoltura Ser. II*, 25: 57–89.
- Olmi M (1995) Dryinids and emblemidids in amber (Hymenoptera Dryinidae et Emblemididae). *Redia* 78: 253–271.
- Olmi M (1998 [“1997”]) New Emblemididae and Dryinidae (Hymenoptera Chrysidoidea). *Frustula Entomologica* 20 (33): 30–118

- Olmi M, Virla EG (2014) Dryinidae of the Neotropical region (Hymenoptera: Chrysidoidea). *Zootaxa* 3792 (1): 1–534. <https://doi.org/10.11646/zootaxa.3792.2.1>
- Olmi M, Xu Z (2015) Dryinidae of the eastern Palearctic region (Hymenoptera: Chrysidoidea). *Zootaxa* 3996 (1): 1–253. <https://doi.org/10.11646/zootaxa.3996.1.1>
- Olmi M, Perkovsky EE, Martynova KV, Contarino M, Bückler C, Guglielmino A (2020) An important intermediate step in the evolution of pincer wasps: an extraordinary new type of chela from mid-Cretaceous Burmese amber (Hymenoptera, Dryinidae). *Cretaceous Research* 111 (104420): 1–13. <https://doi.org/10.1016/j.cretres.2020.104420>
- Olmi M, Xu Z, Guglielmino A (2014) Descriptions of new fossil taxa of Dryinidae (Hymenoptera: Chrysidoidea) from Burmese amber (Myanmar). *Acta Entomologica Musei Nationalis Pragae* 54(2): 703–714.
- Olmi M, Copeland RS, Noort SV (2019) Dryinidae of the Afrotropical region (Hymenoptera, Chrysidoidea). *Zootaxa*, 4630 (1): 001–619. <https://doi.org/10.11646/zootaxa.4630.1.1>
- Perkovsky EE, Olmi M, Müller P, Martynova KV (2019) A review of the genus *Hybristodryinus* Engel, 2005 (Hymenoptera, Dryinidae) from mid-Cretaceous Burmese amber, with a discussion on its phylogenetic significance. *Cretaceous Research* 99 (2019) 169–189. <https://doi.org/10.1016/j.cretres.2019.01.023>
- Perkovsky EE, Olmi M, Vasilenko DV, Capradossi L, Guglielmino A (2020a) First *Bocchus* Ashmead (Hymenoptera: Dryinidae) from Upper Eocene Rovno amber: *B. schmalhauseni* sp. nov. *Zootaxa* 4819 (3): 544–556. <https://doi.org/10.11646/zootaxa.4819.3.6>
- Perkovsky EE, Olmi M, Müller P, Capradossi L, Vasilenko D, Guglielmino A (2020b) A review of the Palaeoanteoninae (Hymenoptera: Dryinidae), with description of the first species from Kachin (Myanmar) amber and comments on its phylogenetic significance. *Cretaceous Research* 116 (104582): 1–8. <https://doi.org/10.1016/j.cretres.2020.104582>.
- Poinar GO (1992) *Life in Amber*. Stanford University Press, Stanford, 350 p.
- Riolo P, Isidoro N, Ruschioni S, Minuz RL, Bin F, Romani R (2016) Anatomy of the Antennal Dorsal Organ in female of *Neodryinus typhlocybae* (Hymenoptera: Dryinidae): a peculiar sensory structure possibly involved in perception of host vibration. *Journal of Morphology* 277: 128–137. <https://doi.org/10.1002/jmor.20485>
- Szwedo J, Stroiński A, Lin QB (2013) Discovery of a Flatidae planthopper (Hemiptera: Fulgoromorpha) in the Paleocene of northern Tibet and its taxonomic and biogeographic significance. *Geodiversitas* 35 (4): 767–776. <https://doi.org/10.5252/g2013n4a2>
- Tribull CM (2015) Phylogenetic relationships among the subfamilies of Dryinidae (Hymenoptera, Chrysidoidea) as reconstructed by molecular sequencing. *Journal of Hymenoptera Research* 45: 15–29. <https://doi.org/10.3897/JHR.45.5010>