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Manuel Brazidec, Vincent Perrichot. Thaumtodryinus (Hymenoptera: Dryinidae) in time: A new record from the Miocene of southwestern Mexico. *Journal of South American Earth Sciences*, 2023, 128, pp.104460. <10.1016/j.jsames.2023.104460>. <insu-04132407>

HAL Id: insu-04132407

<https://insu.hal.science/insu-04132407v1>

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PII: S0895-9811(23)00271-7

DOI: <https://doi.org/10.1016/j.jsames.2023.104460>

Reference: SAMES 104460

To appear in: *Journal of South American Earth Sciences*

Received Date: 25 May 2023

Revised Date: 15 June 2023

Accepted Date: 15 June 2023

Please cite this article as: Brazidec, M., Perrichot, V., *Thaumatomydryinus* (Hymenoptera: Dryinidae) in time: A new record from the Miocene of southwestern Mexico, *Journal of South American Earth Sciences* (2023), doi: <https://doi.org/10.1016/j.jsames.2023.104460>.

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***Thaumatomydryinus* (Hymenoptera: Dryinidae) in time: a new record from the Miocene of southwestern Mexico**

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Abstract

Miocene Dryinidae are relatively well-known compared to other Chrysidoidea families. But most taxa (16 out of 17 described species) derive from the amber mines of the Dominican Republic. Here, a new fossil species of Dryinidae, *Thaumatomydryinus cotyi* sp. nov., is described and figured from the early to middle Miocene of Totolapa (Mexico), and compared to more or less contemporaneous Dominican species. *Thaumatomydryinus cotyi* sp. nov. is noteworthy characterized by the testaceous body, the tridentate mandibles, the clypeal anterior margin outcurved, the pronotum striate rugose, the mesopleuron and propodeum areolate rugose, and the propodeum shorter than high. We also propose an up-to-date key to the subfamilies of Dryinidae and summarize the fossil fauna from Totolapa, a deposit hitherto less studied than the coeval amber from Simojovel.

Keywords: Chiapas amber; taxonomy; fossil record; Insecta; Chrysidoidea; Thaumatomydryinae

1. Introduction

Within the Dryinidae, dubbed pincer wasps, the third largest family of Chrysidoidea, *Thaumatodryinus* Perkins, 1905 is a mid-sized genus, with 33 recognized species. The extant fauna comprises 30 species, of almost worldwide distribution (Xu et al., 2009; Olmi and Virla., 2014; Olmi et al., 2019), the genus being apparently absent from the Palearctic region. The fossil record is exclusively of Miocene age, the three species deriving from the highly-fossiliferous amber mines of the Dominican Republic and having been recently revised by Martins and Melo (2020). Additionally, one female of the recent *Thaumatodryinus dentatus* Benoit, 1954 has been recorded from the subfossil resin of Madagascar (Olmi et al., 2019), found to be not older than a few hundred years, hence the term ‘Defaunation Resin’ (Delclós et al., 2020; Solórzano-Kraemer et al., 2020). Data on host-parasite association for *Thaumatodryinus* are scarce but the few records assume a parasitoid habit on nymphs of Auchernorrhyncha (the ground plan for the Dryinidae) of the family Flatidae (Guglielmino et al., 2013). An exceptional flatid nymph parasitized by a dryinid larva was found in Dominican amber (Olmi, 1995). However, the limited taxonomic knowledge on thylacia (the protective sac formed by the cast larval skins and protruding out of the host body), and considering that Flatidae are also attacked by *Gonatopus* Ljungh, 1810 and *Neodryinus* Perkins, 1905 (Guglielmino et al., 2013), it is not possible to ensure that the larva belongs to *Thaumatodryinus*.

Thaumatodryinus was placed in its own, monotypic subfamily, the Thaumatodryininae, by Olmi (1984) and then subsequently synonymized under the Dryininae (Olmi, 1993). Tribull (2015), in a molecular phylogenetic study of the Dryinidae, proposed a resurrection of the Thaumatodryininae, which was later corroborated from morphological data by Martins (2018), so this subfamily is now commonly accepted (e.g., Barthélémy and Olmi, 2019; Olmi et al., 2019, 2020). The defining synapomorphy for the genus and subfamily is the presence,

in females, of tufts of four long setae on flagellomeres 3–8 (one tuft on F3–F7, two tufts on F8) (Xu et al., 2013).

In this study, we expand the fossil record of *Thaumatomyrmex* by describing a new species based on a female specimen, from the Miocene of Totolapa (Chiapas, Mexico). Although the fossiliferous potential of the Chiapas amber has been known for more than six decades, the Chrysidoidea—and more generally Hymenoptera, still receive limited attention. So far, *Dryinus palaeomexicanus* Olmi, 1995 was the only dryinid species described from Chiapas amber, from Simojovel (Olmi, 1995).

2. Material and methods

The specimen studied here derived from a mine owned by the Ramirez family along the Río Salado, in Totolapa, State of Chiapas, southwestern Mexico (see map in Durán-Ruiz et al., 2013: fig. 1). This amber is less known than that from Simojovel, located approximately 60 km northward of Totolapa. However, both have been assigned to the same variety, the Simojovelite, due to identical chemical composition. (Lambert et al., 1989; Riquelme et al., 2014). The Simojovel amber typically occurs in the the Mazantic shale and Balumtum sandstone formations, dated early to middle Miocene. The amber-bearing strata in Totolapa have been correlated with the latter two formations so we assume here a similar age (ca. 23–15 Ma) for Totolapa amber (e.g., Perrilliat et al., 2010; Durán-Ruiz et al., 2013; Riquelme and Menéndez-Acuña, 2017; Hegna et al., 2020). The piece was bought to the Ramirez family by M. David Coty (France) in 2007, after collection on their property and offered for study to the authors in March 2023. To avoid any discrepancies, we donate the specimen to the paleontological collection of the Museo de Paleontología de la Facultad de Ciencias (FCMP), Universidad Nacional Autónoma de México, as the specimen hardly falls in the frame of the guidelines of the Mexican government on the exportation and property of fossils collected on

the territory. The piece has been carefully prepared using a grinder polisher (Buehler MetaServ3000) with thin silicon carbide sanding papers, in order to obtain as many views as possible of the specimen. Stacks of raw images of several focal planes were obtained using a Leica DMC4500 camera attached to a Leica M205C stereomicroscope and subsequently digitally compiled using Helicon Focus 6.7. The specimen was additionally observed using a Leica M80 stereomicroscope. The figures were composed using the Adobe Illustrator CC2019 and Photoshop CC2019 software, and the details of the body have been redrawn from sketch drawings made with a camera lucida attached to the stereomicroscope. The morphological and surface sculpturing nomenclatures follow Olmi et al. (2019). The term ‘ADOs’ (= Antennal Dorsal Organs) is here used in the sense of Riolo et al. (2016). It corresponds to the term “rhinaria” sensu Olmi (1984). Main measurements and indices are used as follows: POL = minimum distance between the inner edges of the lateral ocelli; OL = minimum distance between the inner edges of the lateral ocellus and the median ocellus; OOL = minimum distance from the outer edge of the lateral ocellus to the eye inner margin; OPL = minimum distance from the posterior edge of a lateral ocellus to the occipital carina; TL = minimum distance from the posterior edge of eye to the occipital carina; F = flagellomere. The ImageJ 1.53 software was used for measurements (Schneider et al., 2012).

This published work and its new nomenclatural act are registered in ZooBank with the following LSID (reference): urn:lsid:zoobank.org:pub:570EBDE5-D105-4FA8-AD71-7484FDAB2CA4

3. Key to the subfamilies of Dryinidae (modified from: Olmi and Bechly, 2001; Olmi and Guglielmino, 2012; Olmi et al., 2014, 2019, 2020)

♀♀ (unknown in Apoaphelopinae, Burmadryininae)

1. Protarsus not chelate ... 2

- Protarsus modified into chela ... **4**
2. Fore wing with [C], [R] and [1Cu] cells enclosed by tubular veins, pterostigma slender (more than $3 \times$ longer than wide) ... †**Archaeodryininae**
Fore wing with only [C] and/or [R] cells enclosed by tubular veins, pterostigma thick (less than $3 \times$ longer than wide) ... **3**
3. Head hypognathous, frons and clypeus without strong median carina ... **Aphelopinae**
Head prognathous, frons and clypeus with strong median carina ... **Erwiniinae**
4. Apterous, ocelli absent ... **5**
Macropterous, micropterous or apterous, ocelli present ... **6**
5. Prothorax fused with the mesothorax, except mobile prepectus... **Apodryininae**
Prothorax not fused with the mesothorax ... **Plesiodryininae**
6. Chela composed of protarsomere 5 + arolium + tarsal claws opposed to basal lobe of protarsomere ... †**Raptodryininae**
Chela composed of protarsomere 5 opposed to one enlarged tarsal claw ... **7**
7. Chela without a rudimentary claw ... **8**
Chela with a rudimentary claw ... **10**
8. Mesotibia without spurs, occipital carina absent ... **Transdryininae**
Mesotibia with one spur, occipital carina present ... **9**
9. Protochanter long and slender, pronotal disc swollen ... †**Palaeoanteoninae**
Protochanter short and broad, pronotal disc flat ... **Anteoninae**
10. Mesotibia without spurs ... **Gonatopodinae**
Mesotibia with one spur ... **11**
11. Macropterous, fore wing with only [C] and [R] cells enclosed by tubular veins ...
Conganteoninae
Macropterous, micropterous or apterous, fore wing with [C], [R] and [1Cu] cells enclosed by tubular veins ... **12**
12. Lateral regions of prothorax continuous with mesopleuron, epicnemium concealed ...
Bocchinae
Lateral regions of prothorax not continuous with mesopleuron, epicnemium distinct ... **13**
13. Protochanter short and broad (less than $2 \times$ longer than wide) ... †**Protodryininae**
Protochanter long and slender (more than $3 \times$ longer than wide), composed of slender stalk and widened apex ... **14**
14. Antenna with tufts of long setae on flagellomeres 3–8 ... **Thaumatomydryininae**
Antennae without such setae on flagellomeres 3–8 ... **Dryininae**

♂♂ (unknown in Archeodryininae, Erwiniinae, Palaeoanteoninae, Plesiodryininae, Protodryininae, Raptodryininae, Transdryininae)

1. Macropterous, fore wing with only [C] cell enclosed by tubular veins, occipital carina complete ... **2**
Macropterous, brachypterous, micropterous or apterous, fore wing with at least [C] and [R] cells enclosed by tubular veins (if only [C] cell opened, the occipital carina is absent) ... **3**
2. Fore wing with 2r-rs&Rs and pterostigma present, other veins (except C and Sc+R) not even indicated, hind wing without dark medial longitudinal stripe ... **Aphelopinae** (part.)
Fore wing with 2r-rs&Rs present, pterostigma absent, M and Cu indicated by dark stripes, hind wing with dark medial longitudinal stripe ... **Apoaphelopinae**

3. Macropterous, fore wing with [C] and [R] cells enclosed by tubular veins, occipital carina complete ... **4**
Macropterous, brachypterous, micropterous or apterous, fore wing with [C], [R] and [1Cu] cells enclosed by tubular veins, sometimes [R] and [1Cu] fused, (if only [C] cell closed, the occipital carina is absent) ... **5**
4. Flagellomere 1 more than 3 × as long as wide ... **Conganteoninae**
Flagellomere 1 less than 3 × as long as wide ... **Aphelopinae** (part., a few males of *Crovettia*)
5. Fore wing with [R] and [1Cu] fused, forming one cell ... †**Burmadryininae**
Macropterous, brachypterous, micropterous or apterous, fore wing with [R] and [1Cu] cells clearly delimited (if only [C] cell closed, the occipital carina is absent) ... **6**
6. Mandible never with intermediate rudimentary tooth, usually four teeth getting larger from anterior to posterior one, or four teeth of different length ... **7**
Mandible with 1–4 teeth, quadridentate mandible always with rudimentary tooth ... **8**
7. Fore wing with poststigmatal abscissa of R1 as long or longer than pterostigma ...
Thaumatodryinae
Fore wing with poststigmatal abscissa of R1 shorter than pterostigma or absent ...
Anteoninae
8. Lateral regions of prothorax continuous with mesopleuron, epicnemium concealed ...
Bocchinae
Lateral regions of prothorax not continuous with mesopleuron, epicnemium distinct ... **9**
9. Mesosternum distinct, not fused with mesopleuron ... **Apodryininae**
Mesosternum fused with mesopleuron, indistinct ... **10**
10. Occipital carina present, either complete or incomplete, dorsal process of paramere absent ... **Dryininae**
Occipital carina absent (if present and complete, the dorsal process of paramere is present) ... **Gonatopodinae**

4. Systematic palaeontology

Superfamily Chrysidoidea Latreille, 1802

Family Dryinidae Haliday, 1833

Subfamily Thaumatodryininae Olmi, 1984

Genus *Thaumatodryinus* Perkins, 1905

Thaumatodryinus cotyi sp. nov.

Figs. 1, 2, 3

LSID (species): urn:lsid:zoobank.org:act:203DE9BD-4995-483D-9275-D0EAD497A35A

Material. Holotype number FCMP-1562, a nearly complete female, missing left flagellomeres 2–8, apex of wings, apex of left fore and midlegs, and apex of hind legs.

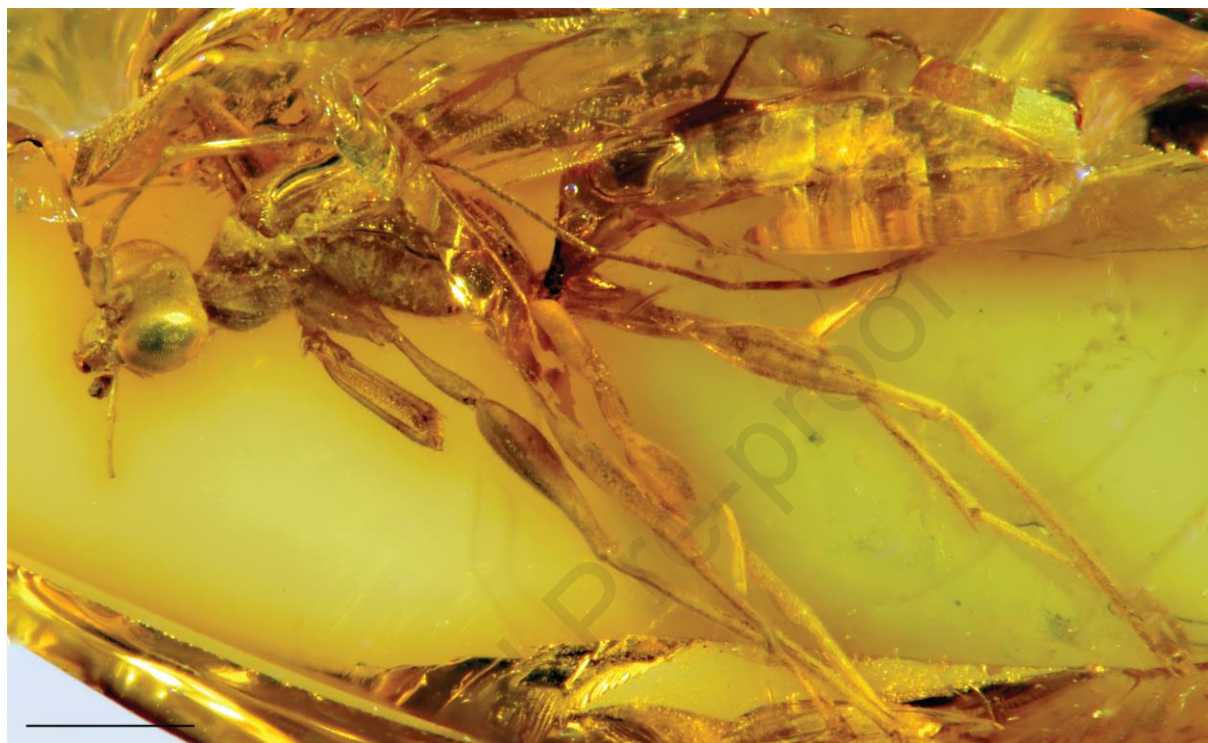


Figure 1. *Thaumatotryinus cotyi* sp. nov., holotype female FCMP-1562, habitus in laterodorsal view. Scale bar = 1 mm.

Etymology. This species is named after David Coty, who allowed the study of the specimen through his generous donation, this way contributing to advances in the knowledge of the Totolapa amber. The specific epithet is to be treated as a noun in a genitive case.

Diagnosis (Female). Body predominantly testaceous (Fig. 1). Pronotum striate rugose; mesoscutum granulate; mesopleuron reticulate rugose (Fig. 3A, B). Frontal line present, touching median ocellus (Figs. 2A, 3A); vertex inconspicuously convex; compound eye $1.4 \times$ as long as wide (Fig. 3A); F1 $0.79 \times$ F2 length; F4 longest; F7 $1.06 \times$ F8 length; anterior clypeal margin outcurved (Figs. 2A, 3A); malar space long; mandible tridentate (Figs. 2B,

3C); occipital carina complete; occiput moderately excavated. Pronotum shorter than head; notaulus complete (Figs. 2A, 3A, B); mesoscutellum anteriorly with marked groove; propodeum shorter than high in lateral view (Fig. 2A).

Type locality. Río Salado Mine, Totolapa, State of Chiapas, southwestern Mexico.

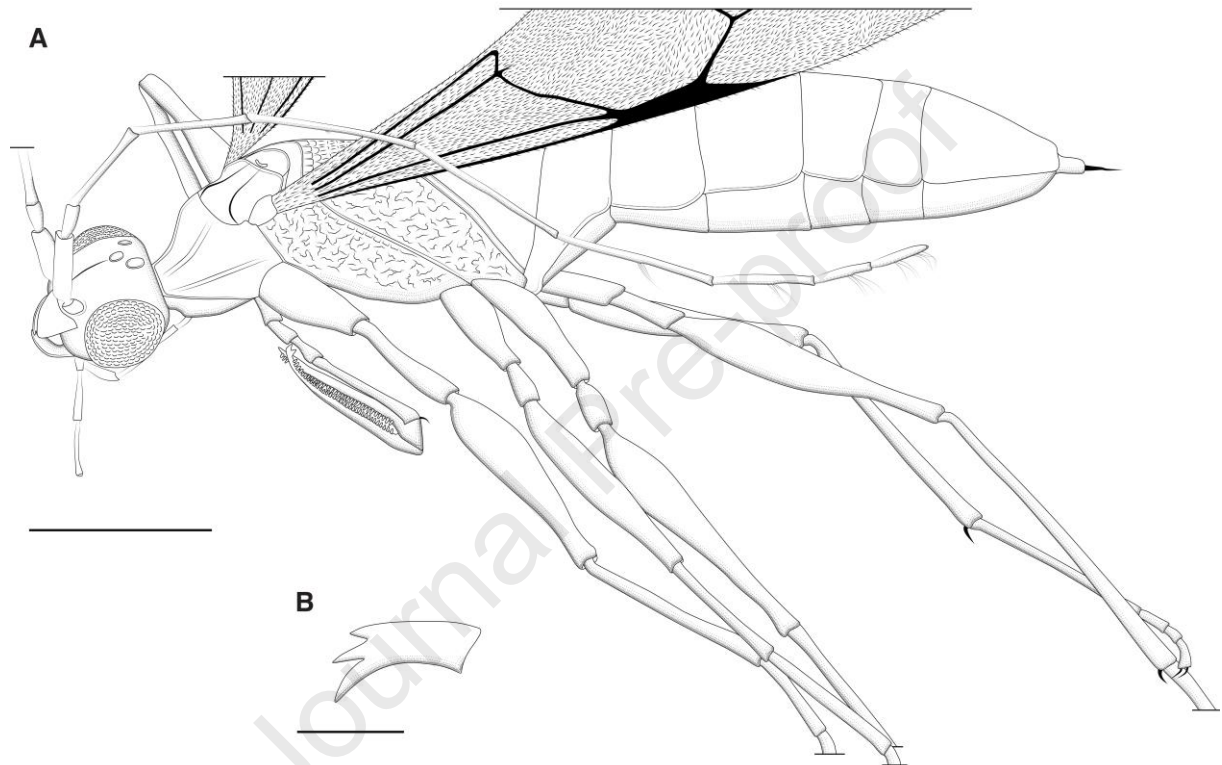


Figure 2. Line drawing of *Thaumatotryinus cotyi* sp. nov., holotype female FCMP-1562; A. habitus in laterodorsal view, B. left mandible in frontal view. Scale bars: A = 1 mm, B = 0.25 mm.

Age. Early to middle Miocene, ca. 23–15 Ma.

Description. Female, body length 5.89 mm.

Colour. Body testaceous except castaneous petiole and mandibular teeth.

Pubescence. Head covered with fine, short setae; compound eye glabrous; mandibles surrounded by a few long setae (ca. one third of mandibular basal teeth); antenna with uniform short pubescence; flagellomeres 3–7 with one tuft of four long setae located at midpoint of flagellomere; flagellomere 8 with two tufts of four long setae, respectively located apically of first third and second third of flagellomere. Mesosoma with fine, dense setae; mesosomal setae at most twice the length of head setae. Legs with fine, short setae; protarsomeres 2–3 with thick, long setae, about as long as protarsomere 3.

Integumental sculpture. Head finely granulated; frontal line present and complete; malar sulcus conspicuous, extending from eye toward base of mandible; mandible with sulcus at base. Pronotum granulate medially, striate rugose laterally; mesoscutum granulate; mesopleuron, metapleuron and propodeum reticulate rugose; metasoma smooth.

Structure and measurements. Length of head, from anteriormost point of clypeus to occipital carina = 0.73 mm. Vertex almost flat, only moderately convex. Ocellar triangle slightly elevated. Ocellar ratio: POL = ca. 0.12 mm; OL = ca. 0.08 mm; OOL = 0.15 mm; OPL = 0.07 mm; TL = 0.04 mm. Frons flat or slightly convex. Compound eye bulging, oval, about $1.4 \times$ as long as wide. Antenna elongate, filiform, posteriorly reaching metasomal tergite 6; torulus distinctly elevated and directed upward; scape cylindrical, $3 \times$ as long as median width (length 0.30 mm); pedicel somewhat conical, base slightly narrower than apex, about twice as long as median width (length 0.15 mm); length of flagellomeres: F1 = 0.50 mm, F2 = 0.63 mm, F3 = 0.94 mm, F4 = 0.99 mm, F5 = 0.81 mm, F6 = 0.57 mm, F7 = 0.34 mm, F8 = 0.32 mm; F8 tapering at apex; ADOs present at least on flagellomeres 4–8. Clypeus somewhat triangular, with anterior margin outcurved. Malar space longer than basal width of mandible. Mandible thick, tridentate, teeth decreasing in length ventrodorsally. Palpal formula 6–3, maxillary palpomeres elongate, posteriorly reaching procoxae. Occipital carina present, complete. Occiput shallowly excavated.

Length of mesosoma, from anteriormost point of pronotum to propodeal foramen = 2.03 mm.

Pronotum saddle-shaped, $0.87 \times$ head length, pronotal lobe reaching tegula. Mesoscutum shorter than pronotum, longer than mesoscutellum. Notaulus complete, converging posteriorly. Mesoscutellum anteriorly with conspicuous reniform groove. Metanotum shorter than propodeum. Propodeum shorter than high in lateral view, dorsal surface shorter than posterior surface.

Fore wing hyaline, micropubescent, with apex not preserved; length of preserved part = ca. 2 mm; [C], [R] and [1Cu] cells closed by tubular veins C, Sc+R, M+Cu, A, 1Rs&1M and 1cu-a; 1Cu spectral; pterostigma long and narrow, about $5 \times$ as long as wide; poststigmatal abscissa of R1 present, shorter than pterostigma; 2r-rs tubular, $1.6 \times$ as short as pterostigma; short apical stub of 2Rs present at intersection of 2r-rs and 3Rs, tubular.

Protrochanter long and slender, widened apically, longer than procoxa. Profemur swollen.

Protibia long and slender, longer than profemur. Probasitarsomere longer than protarsomeres 2–3 combined. Protarsomeres 2–3 about as long as wide. Protarsomere 4 slightly shorter than probasitarsomere. Chela composed of protarsomere 5 opposed to enlarged tarsal claw.

Rudimentary claw present. Protarsomere 5 longer than protarsomere 4, with one row of about 30 lamellae and two subapical teeth. Enlarged claw with two rows of about 40 lamellae and two subapical teeth. Mesofemur slender. Metafemur more swollen than mesofemur. Tibial spurs formula 1-1-2.

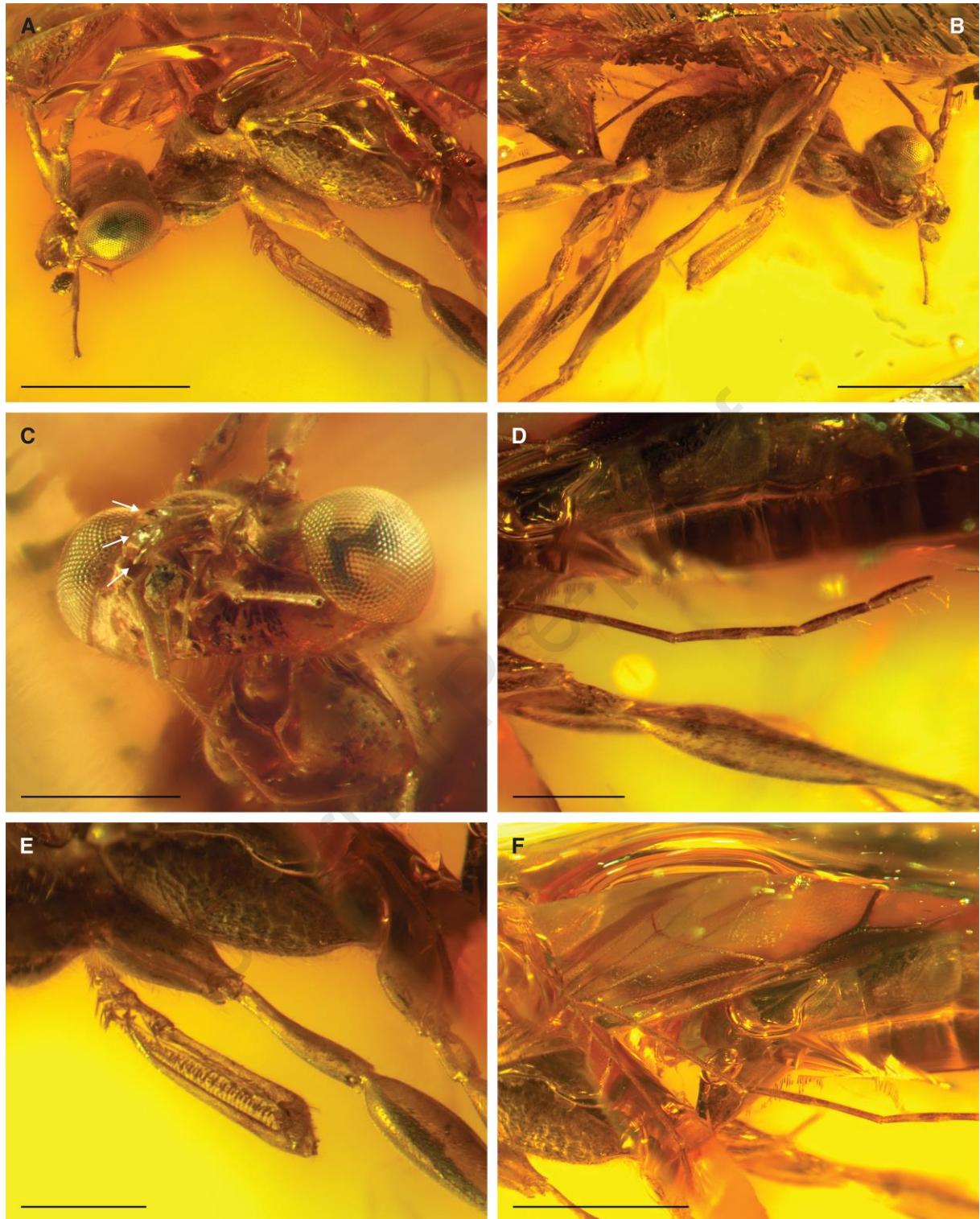


Figure 3. *Thaumatotdryinus cotyi* sp. nov., holotype female FCMP-1562; A. head and mesosoma in left laterodorsal view, B. head and mesosoma in right lateroventral view, C. head in frontal view (arrows: mandibular teeth), D. flagellomeres 5–8, E. right chela, F. basal half of fore wing. Scale bars: A, B, F = 1 mm, C–E = 0.5 mm.

Length of metasoma, excluding sting = 3.13 mm. Seven segments visible. First segment (length 0.84 mm), conical, narrowing towards propodeal foramen. Following segments regularly decreasing in length, except segment 6, about as long as segment 2. Sting exerted.

5. Key to the fossil species of *Thaumatomyrmex* (modified from Martins and Melo, 2020)

1. Compound eyes hemispherical, about $1.1 \times$ as long as wide, anterior margin of clypeus straight, mesoscutum-mesoscutellar articulation with a narrow row of small foveae ... *Thaumatomyrmex fuscescens* Martins and Melo, 2020 [Dominican amber]

Compound eye elongate, more than $1.3 \times$ as long as wide, anterior margin of clypeus outcurved, mesoscutum-mesoscutellar articulation with a groove ... **2**

2. Pronotum striate rugose, notauli percurrent ... *Thaumatomyrmex cotyi* sp. nov. [Mexican amber]

Pronotum mostly granulate, notauli not extending along entire length of mesoscutum ... **3**

3. Antenna with flagellomere 1 shorter than flagellomere 2, POL $2.3 \times$ OL, mesoscutum reticulate rugose, notauli extending for approximately $0.5 \times$ mesoscutum length, anterior margin of mesoscutellum with a foveate narrow groove, propodeum short, distinctly shorter than high in lateral view ... *Thaumatomyrmex miocenicus* Olmi, 1995 [Dominican amber]

Antenna with flagellomere 1 almost as long as flagellomere 2, POL $2 \times$ OL, mesoscutum granulate, notauli extending for approximately $0.7 \times$ mesoscutum length, anterior margin of mesoscutellum with a broad, shallow groove, propodeum distinctly long, about as long as wide in lateral view... *Thaumatomyrmex priscus* (Olmi, 1998) [Dominican amber]

6. Discussion

The specimen is easily recognizable as a member of the Thaumatomyrmecinae, owing to the presence of tufts of four long setae on flagellomeres 3–8 (Fig. 3D; present although hardly distinguishable on flagellomeres 3–4, as directed toward the specimen and hidden by cracks in the amber), which is their best defining feature. It also displays most of the diagnostic characters of the subfamily, namely the reduced fore wing venation, the palpal formula 6:3, the protarsomere 3 with a few thick setae, the protarsus chelate with a rudimentary claw, the pronotal tubercle reaching the tegula, the occipital carina complete (in all extinct females) or

the tibial spurs formula (Olmi et al., 2019; Martins and Melo, 2020). But our specimen exhibits a novel pattern for the subfamily, in the configuration of the mandibles. Indeed, all known living thaumatodryinine species possess quadridentate mandibles, whereas the mandibles can clearly be seen as tridentate here (Figs. 2B, 3C; on the left mandible, right mandible obscured under the clypeus). The mandibles of the fossil *Thaumatodryinus miocenicus* Olmi, 1995 have also been interpreted as tridentate by Olmi and Virla (2014). Subsequent restudy of the original material by Martins and Melo (2020) did not allow for a clear assessment of the number of teeth. The latter authors pointed out that the mandible configuration is difficult to observe because obscured by the clypeus and considered ‘likely’ that *T. miocenicus* actually has mandible with four teeth. Subjecting the type specimen to a μ CT-scan would be beneficial to further investigate and statute on the configuration of the mandible. As for now, we cannot rule out the possibility that some extinct thaumatodryinines possessed tridentate mandibles before the arising of the modern quadridentate lineage. Despite this variation, we assign our fossil to the genus *Thaumatodryinus*.

It is not surprising to record a specimen of *Thaumatodryinus* in Chiapas amber. The genus today widely occurs in Central America and Mexico (Olmi and Virla, 2014) and extends northwards until Virginia (Krombein, 1952). Furthermore, three species (*T. priscus*, *T. fuscescens*, and *T. miocenicus*) are recorded from the early Miocene of Dominican Republic (Olmi, 1995, 1998; Martins and Melo, 2020). Mexican and Dominican ambers are considered of somewhat similar ages (Solórzano-Kraemer, 2007), produced in comparable environments by trees of the genus *Hymenaea* (Poinar and Brown, 2002; Solórzano-Kraemer, 2010), and share a large number of genera (Rosse-Guillevic et al., 2022: appendix 1). *Thaumatodryinus* is the second dryinid genus found in both Mexican and Dominican ambers, after *Dryinus* Latreille, 1804 (e.g., Currado and Olmi, 1983; Olmi, 1995; Olmi et al., 2011).

Beside the difference in the mandibular configuration, our specimen differs from the three other fossil species as follows: eye oval vs. hemispherical, F1 shorter than F2 vs. as long, anterior margin of clypeus outcurved vs. straight, vertex almost flat vs. convex, mesoscutellum with a groove vs. a row of foveae, dorsal surface of propodeum shorter than posterior surface vs. distinctly longer (*T. fuscescens*); body light brown vs. mainly black, F1 distinctly shorter than F2 vs. slightly shorter, pronotum slightly shorter than head vs. twice as short, mesoscutum granulate vs. reticulate rugose, notauli complete vs. incomplete (*T. miocenicus*); frontal line present vs. absent, F1 distinctly shorter than F2 vs. about as long, F7 longer than F8 vs. shorter, notauli complete vs. incomplete, dorsal surface of propodeum shorter than posterior vs. as long (*T. priscus*). Therefore, we propose the new species *Thaumatodryinus cotyi* sp. nov. for this fossil.

The new species enriches the fossil fauna of Totolapa, as well as the Miocene record for the Dryinidae and the Chrysidoidea. Amber from Totolapa has only been recently confirmed to be similar to that of Simojovel, the ‘typical’ Chiapas amber (Durán-Ruiz et al., 2013; Riquelme et al., 2014). And despite being known for about 40 years (Bryant, 1983), only a few inclusions of arthropods, fungi and bacteria have been described to date (Table 1), comparatively to the richer Simojovel fauna (e.g., Solórzano-Kraemer, 2010; Rosse-Guillevic et al., 2022: appendix 1). Miocene-aged Dryinidae are rather diverse, with 18 species recorded, which is twice more than the Bethyloidea, the second chrysoid family in terms of species from this period. The four other families are only sporadically found throughout the various deposits around the globe (Brazidec and Perrichot, 2023: Table 1). Describing new Miocene chrysoids will be crucial to decipher the distributional pattern of the genera during the last major climate optimum (the Mid-Miocene Climatic Optimum) and before the establishment of the modern fauna.

Table 1. Synopsis of organic amber inclusions deriving from the locality of Totolapa.

Order	Family	Genus	Species	Reference
Actinomycetales	Thermomonosporaceae	<i>Thermomonosporopsis</i>	<i>T. chiapasensis</i> Breton et al., 2014	Breton et al., 2014
	?	? <i>Micromonospora</i>	<i>Micromonospora</i> sp.	Breton et al., 2014
	?	? <i>Streptosporangium</i>	<i>Streptosporangium</i> sp.	Breton et al., 2014
	?	<i>Scopaeopsis</i>	<i>S. verticillata</i> Breton et al., 2014	Breton et al., 2014
	-	-	Actinomycetales sp.	Breton et al., 2014
Burkholderiales	-	<i>Melanothrix</i>	<i>M. mexicana</i> Breton et al., 2014	Breton et al., 2014
Fungi	-	-	Fungi spp.	Breton et al., 2014
Archaeognatha	Meinertellidae	<i>Neomachilellus</i>	<i>N. ezetaelenesis</i> Riquelme et al., 2015	Riquelme et al., 2015
Blattodea	Termitidae	<i>Nasutermes</i>	<i>Nasutermes</i> sp.	Coty et al., 2014
Coleoptera	Artematopodidae	<i>Electribius</i>	<i>E. palaeomexicanus</i> Wu et al., 2015	Wu et al., 2015
	Curculionidae	<i>Caulophilus</i>	<i>C. ayotzinapa</i> Barrios-Izás and Coty, 2016	Barrios-Izás and Coty, 2016
Diptera	Dolichopodidae	<i>Medetera</i>	<i>M. totolapa</i> Bickel and Solórzano-Kraemer, 2016	Bickel and Solórzano-Kraemer, 2016
		<i>Systemus</i>	<i>Systemus</i> sp.	Bickel and Solórzano-Kraemer, 2016
	Psychodidae	<i>Succinarisemus</i>	<i>S. totolapensis</i> Coty et al., 2013	Coty et al., 2013
	Scatopsidae	<i>Psectrosciara</i>	<i>P. fossilis</i> Nel and Coty, 2016	Nel and Coty, 2016
	Stratiomyidae	<i>Electrothopomyia</i>	<i>E. saltensis</i> Coty and Nel, 2013	Coty and Nel, 2013
			<i>E. tzotzili</i> Coty and Nel, 2013	Coty and Nel, 2013
Hemiptera	Ceratocombidae	<i>Leptonannus</i>	<i>L. miocenicus</i> Azar et al., 2010	Azar et al., 2010

	Tingidae	<i>Leptopharsa</i>	<i>L. tacanae</i> Coty et al., 2015	Coty et al., 2015
Hymenoptera	Bethyridae	<i>Bakeriella</i>	<i>B.nanyhela</i> Brazidec and Perrichot, 2022	Brazidec and Perrichot, 2022
		<i>Goniozus</i>	<i>G. cotyi</i> Brazidec and Perrichot, 2022	Brazidec and Perrichot, 2022
		<i>Solepyris</i>	<i>S. electromexicanus</i> Brazidec and Perrichot, 2022	Brazidec and Perrichot, 2022
	Dryinidae	<i>Thaumatomyrmex</i>	<i>Thaumatomyrmex cotyi</i> sp. nov.	This study
	Formicidae	<i>Azteca</i>	<i>Azteca</i> sp.	Durán-Ruiz et al., 2013 ; Coty et al., 2014
		<i>Camponotus</i>	<i>Camponotus</i> sp.	Durán-Ruiz et al., 2013
		<i>Forelius</i>	<i>Forelius</i> sp.	Durán-Ruiz et al., 2013
		<i>Neivamyrmex</i>	<i>Neivamyrmex</i> sp.	Coty et al., 2014
Araneae	Salticidae	<i>Maevia</i>	<i>Maevia eureka</i> Riquelme and Menéndez-Acuña, 2017	Riquelme and Hill, 2013; Riquelme and Menéndez-Acuña, 2017
		-	Salticidae spp.	Riquelme et al., 2021
Pseudoscorpionida	Chthoniidae	<i>Tyrannochthonius</i>	<i>Tyrannochthonius</i> sp.	Judson, 2016

Acknowledgments

We warmly thank David Coty for the donation of his material and discussion on the mining and geology of the deposit. We are in debt to Manuel and Heriberto Ramirez and their

whole family, owners and miners of the Río Salado Mine, for allowing David Coty's collecting on their property. We also thank Dr. Mónica M. Solorzano-Kraemer (Senckenberg Research Institute, Germany) and Dr. Francisco Sour Tovar (Universidad Nacional Autónoma de México) for advice and help with the final repository of the studied material. We express our gratitude to the Editor-in-Chief of Journal of South American Earth Sciences, Dr. Francisco J. Vega, for his guidance throughout the submission process as well as to two anonymous reviewers for their useful comments. This work is part of Manuel Brazidec Ph.D. project on "The role of greenhouses on the diversification and evolution of chrysidoid wasps".

References

- Azar, D., Nel, A., Coty, D., Garrouste, R., 2010. The second fossil ceratocombid bug from the Miocene amber of Chiapas (Mexico) (Hemiptera: Ceratocombidae). *Annales de la Société entomologique de France* 46, 100–102. <https://doi.org/10.1080/00379271.2010.10697642>
- Barrios-Izás, M., Coty, D., 2016. A new fossil species of *Caulophilus* Wollaston, 1854 (Coleoptera: Curculionidae: Cossoninae) from Mexican amber. *The Coleopterists Bulletin* 70, 177–179. <https://doi.org/10.1649/072.070.0126>
- Barthélémy, C., Olmi, M., 2019. Checklist of Dryinidae and Sclerogibbidae (Hymenoptera, Chrysidoidea) from Hong Kong. *Zootaxa* 4615, 529–548. <https://doi.org/10.11646/zootaxa.4615.3.7>
- Bickel, D.J., Solórzano-Kraemer, M.M., 2016. The Dolichopodidae (Diptera) of Mexican amber. *Boletín de la Sociedad Geológica Mexicana* 68, 11–21.
- Brazidec, M., Perrichot, V., 2022. The first flat wasps (Hymenoptera: Bethyridae) from Miocene Mexican amber. *Journal of South American Earth Sciences* 116, 103838. <https://doi.org/10.1016/j.jsames.2022.103838>

- Brazidec, M., Perrichot, V., 2023. Two new chrysidoid wasps (Hymenoptera: Bethyridae, Chrysididae) from mid-Miocene Zhangpu amber. *Palaeoworld*.
<https://doi.org/10.1016/j.palwor.2022.11.003>
- Breton, G., de Lourdes Serrano-Sánchez, Vega, F.J., 2014. Filamentous micro-organisms, inorganic inclusions and pseudo-fossils in the Miocene amber from Totolapa (Chiapas, Mexico): taphonomy and systematics. *Boletín de la Sociedad Geológica Mexicana* 66, 199–214.
- Bryant, D.D., 1983. A recently discovered amber source near Totolapa, Chiapas, Mexico. *American Antiquity* 48, 354–357. <https://doi.org/10.2307/280456>
- Coty, D., Nel, A., 2013. New fossil Pachygastrinae from Mexican amber (Diptera: Stratiomyidae). *Annales de la Société entomologique de France* 49, 267–272.
<https://doi.org/10.1080/00379271.2013.845473>
- Coty, D., Aria, C., Garrouste, R., Wils, P., Legendre, F., Nel, A., 2014. The first ant-termite syninclusion in amber with CT-scan analysis of taphonomy. *PLoS ONE* 9, e104410.
<https://doi.org/10.1371/journal.pone.0104410>
- Coty, D., Garrouste, R., Nel, A., 2015. The first lace bug from Chiapas amber (Totolapa, Mexico) (Hemiptera: Tingidae). *Annales de la Société entomologique de France* 50, 286–290. <https://doi.org/10.1080/00379271.2014.982024>
- Coty, D., Salamé, Y., Nel, A., Azar, D., 2013. A new psychodid fly from Mexican amber (Diptera; Psychodidae). In: Azar, D., Engel, M.S., Jarzembowski, E., Krogmann, L., Nel, A., Santiago-Blay, J. (Eds.), *Insect Evolution in an Amberiferous and Stone Alphabet*. Brill, Leiden, pp. 13–25.

- Currado, I., Olmi, M., 1983. Primo reperto di Driinide fossile in ambra della Repubblica Dominicana (Hymenoptera, Dryinidae). Bollettino del Museo Regionale di Scienze Naturali Torino 1, 329–334.
- Delclòs, X., Peñalver, E., Ranaivosoa, V., Solórzano-Kraemer, M.M., 2020. Unravelling the mystery of "Madagascar copal": Age, origin and preservation of a Recent resin. PLoS One, 15, e0232623. <https://doi.org/10.1371/journal.pone.0232623>
- Durán-Ruiz, C., Riquelme, F., Coutiño-José, M., Carbot-Chanona, G., Castaño-Meneses, Ramos-Arias, M., 2013. Ants from the Miocene Totolapa amber (Chiapas, Mexico), with the first record of the genus *Forelius* (Hymenoptera, Formicidae). Canadian Journal of Earth Sciences 50, 495–502. <https://doi.org/10.1139/cjes-2012-0166>
- Guglielmino, A., Olmi, M., Bückle, C., 2013. An updated host-parasite catalogue of the world Dryinidae (Hymenoptera: Chrysidoidea). Zootaxa 3740, 1–113. <http://dx.doi.org/10.11646/zootaxa.3740.1.1>
- Hegna, T.A., Lazo-Wasem, E.A., Serrano-Sánchez, M.d.L., Barragán, R., Vega, F.J., 2020. A new fossil talitrig amphipod from the lower early Miocene Chiapas amber documented with microCT scanning. Journal of South American Earth Sciences 98, 102462. <https://doi.org/10.1016/j.jsames.2019.102462>
- Judson, M.L.I., 2016. Pseudoscorpions (Arachnida, Chelonethi) in Mexican amber, with a list of extant species associated with mangrove and *Hymenaea* trees in Chiapas. Boletín de la Sociedad Geológica Mexicana 68, 57–79.
- Krombein, K.V., 1952. Preliminary annotated list of the wasps of Westmoreland State Park, Virginia, with notes on the genus *Thaumatodryinus* (Hymenoptera: Aculeata). Transactions of the American Entomological Society 78, 89–100.

- Lambert, J.B., Frye, J.S., Lee Jr., T.A., Welch, C.J., Poinar Jr., G.O., 1989. Analysis of Mexican amber by Carbon-13 NMR Spectroscopy. *Archeological Chemistry* 4, 381–388. <https://doi.org/10.1021/ba-1988-0220.ch021>
- Martins, A.L., 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).
- Martins, A.L., Melo, G.A.R., 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>
- Nel, A., Coty, D., 2016. A fossil dung midge in Mexican amber (Diptera: Scatopsidae). *Palaeontologia Electronica* 19.2.22A: 1–6. <https://doi.org/10.26879/633>
- Olmi, M., 1984. A revision of the Dryinidae (Hymenoptera). *Memoirs of the American Entomological Institute* 37, 1–1913.
- Olmi, M., 1993. A new generic classification for Thaumatodryininae, Dryininae and Gonatopodinae, with descriptions of new species (Hymenoptera Dryinidae). *Bolletino di Zoologia agraria e di Bachicoltura* 25, 57–89.
- Olmi, M., 1995. Dryinids and emblemidids in amber (Hymenoptera Dryinidae et Emblemididae). *Redia* 78, 253–271.
- Olmi, M., 1998. New Emblemididae and Dryinidae (Hymenoptera Chrysidoidea). *Frustula Entomologica* 20, 30–118.
- Olmi, M., Bechly, G., 2001. New parasitic wasps from Baltic amber (Insecta: Hymenoptera: Dryinidae). *Stuttgarter Beiträge zur Naturkunde Serie B* 306 1–58.

- Olmi, M., Guglielmino, A. A contribution to the knowledge of Dryinidae from Late Eocene Baltic amber (Hymenoptera: Chrysidoidea), with description of new subfamily, Protodryininae subfam. nov. *Zootaxa* 3351, 15–26.
<https://doi.org/10.11646/zootaxa.3351.1.2>
- Olmi, M., Virla, E.G., 2014. Dryinidae of the Neotropical region (Hymenoptera: Chrysidoidea). *Zootaxa* 3792, 1–534. <http://dx.doi.org/10.11646/zootaxa.3792.1.1>
- Olmi, M., Copeland, R.S., van Noort, S., 2019. Dryinidae of the Afrotropical region (Hymenoptera, Chrysidoidea). *Zootaxa* 4630: 1–619.
<https://doi.org/10.11646/zootaxa.4630.1.1>
- Olmi, M., Guglielmino, A., Vollaro, M., 2011. Revision of fossil species of *Dryinus* belonging to *constans* group, with description of a new species (Hymenoptera: Dryinidae). *Zootaxa* 2981, 43–55. <https://doi.org/10.11646/zootaxa.2981.1.4>
- Olmi, M., Perkovsky, E.E., Martynova, K.V., Contarini, M., Bückle, 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* 11, 104420. <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, 703–714.
- Perrilliat, M.C., Vega, F.J., Coutiño, M.A., 2010. Miocene mollusks from the Simojovel area in Chiapas, southwestern Mexico. *Journal of South American Earth Sciences* 30, 111–119.
<https://doi.org/10.1016/j.jsames.2010.04.005>
- Poinar, G.O. Jr., Brown, A.E., 2002. *Hymenaea mexicana* sp. nov. (Leguminosae: Caesalpinioideae) from Mexican amber indicates Old World connections. *Botanical*

Journal of the Linnean Society 139, 125–132. <https://doi.org/10.1046/j.1095-8339.2002.00053.x>

Riolo, P., Isidoro, N., Ruschioni, S., Minuz, E.L., Bin, F., Romani, R., 2016. Anatomy of the Antennal Dorsal Organ in female of *Neodryinus thyphlocybae* (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>

Riquelme, F., Hill, D.E., 2013. Insights into amber salticids from the Neogene of Middle America, with the first report of Marpissinae (Araneae: Salticidae) from the Chiapas amber. *Peckhamia* 106, 1–5.

Riquelme, F., Menéndez-Acuña, M., 2017. Miocene spider *Maevia eureka* nov. sp. (Araneae: Salticidae). *PeerJ* 5, e3614. <https://doi.org/10.7717/peerj.3614>

Riquelme, F., Menéndez-Acuña, M., Yoval-Martínez, I., 2021. Jumping spiders (Araneae: Salticidae) from Miocene Mexican amber. *Palaeodiversity* 14, 5–13. <https://doi.org/10.18476/pale.v14.a2>

Riquelme, F., Montejo-Cruz, M., Luna-Castro, B., Zuñiga-Mijangos, L., 2015. Fossil jumping-bristletail from the Chiapas amber: *Neomachilellus* (*Praeneomachilellus*) *ezetaelenensis* sp. nov. (Microcoryphia: Meinertellidae). *Neues Jahrbuch für Geologie und Paläontologie* 275, 93–106. <https://doi.org/10.1127/njgpa/2015/0453>

Riquelme, F., Ruvalcaba-Sil, J.L., Alvarado-Ortega, J., Estrada-Ruiz, E., Galicia-Chávez, Porras-Múzquiz, H., Stojanoff, V., Siddons, D.P., Miller, L., 2014. Amber from México: Coahuilite, Simojovelite and Bacalite. *MRS Proceeding* 1618, 169–180. <https://doi.org/10.1557/opl.2014.466>

- Rosse-Guillevic, S., Peñalver, E., Hammel, J.U., León, A., Solórzano-Kraemer, M.M., 2022. The genus *Plecia* (Diptera: Bibionidae) in middle Miocene Dominican amber. *Historical Biology*. <https://doi.org/10.1080/08912963.2022.2067755>
- Schneider, C.A., Rasband, W.S., Eliceiri, K.W., 2012. NIH Image to ImageJ: 25 years of image analysis. *Nature Methods* 9, 671–675. <https://doi.org/10.1038/nmeth.2089>
- Solórzano-Kraemer, M.M., 2007. Systematic, palaeoecology, and palaeobiogeography of the insect fauna from Mexican amber. *Palaeontographica Abteilung A* 282, 1–133. <https://doi.org/10.1127/pala/282/2007/1>
- Solórzano-Kraemer, M.M., 2010. Mexican amber. In: Penney, D. (Ed.), *Biodiversity of Fossils in Amber from the Major World Deposits*. Siri Scientific Press, pp. 42–56.
- Solórzano-Kraemer, M.M., Delclòs, X., Engel, M.S., Peñalver, E., 2020. A revised definition for copal and its significance for palaeontological and Anthropocene biodiversity-loss studies. *Scientific Reports*, 10, 19904. <https://doi.org/10.1038/s41598-020-76808-6>
- Tribull, C.M., 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>
- Wu, H., Coty, D., Ding, M., 2015. First artematopodid beetle in Mexican amber and its biogeographic implications (Coleoptera, Artematopodidae). *Alcheringa: An Australasian Journal of Palaeontology* 39, 508–513. <https://doi.org/10.1080/03115518.2015.1041306>
- Xu, Z., Olmi, M., He, J., 2009. A taxonomic revision of the Oriental species of *Thaumatomyia* Perkins, with descriptions of two new species from P. R. China (Hymenoptera: Dryinidae). *Zootaxa* 2175, 19–28. <https://doi.org/10.11646/zootaxa.2175.1.2>

Xu, Z., Olmi, M., He, J., 2013. Dryinidae of the Oriental region (Hymenoptera: Chrysidoidea). *Zootaxa* 3614, 1–460. <https://doi.org/10.11646/zootaxa.3900.1.1>

Highlights

- Description of the first species of *Thaumatodryinus* in Miocene Chiapas amber (Mexico)
- *Thaumatodryinus* is the second Dryinidae genus common for Mexican and Dominican ambers
- *Thaumatodryinus cotyi* sp. nov. has a unique tridentate configuration of the mandibles
- The fossil fauna from Totolapa is at least as diverse as that of Simojovel but under-investigated

Declaration of interests

☒ The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

☐ The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: