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Discovery of the pincer wasp Thaumatodryininae (Hymenoptera, Dryinidae) in Burmese amber, with description of a new genus and the first phylogenetic analysis of the subfamily

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Abstract

Thaumatodryininae is a small subfamily of Dryinidae, known to attack nymphs of auchenorrhynchous Flatidae (Hemiptera). Only one genus is recognized, *Thaumatodryinus* Perkins, with 35 species including fossil and extant taxa. Currently, the oldest record for the genus is from Baltic amber. Here, we present the first record of Thaumatodryininae from mid-Cretaceous Burmese amber with the description of *†Thaumatorrhinos athrix* **gen. et sp. nov.**, derived from the first phylogeny for this subfamily based on morphological characters. The placement of *†Thaumatorrhinos* **gen. nov.** in Thaumatodryininae and the phylogenetic relationships of this subfamily within Dryinidae are discussed.

Keywords

Cladistic analyses, Chrysidoidea, fossil, mid-Cretaceous, phylogeny, morphology

1. Introduction

Knowledge about the fossil fauna of insects preserved in amber has increased considerably in recent years, especially those from mid-Cretaceous Burmese amber, from Kachin, Myanmar (Ross 2021). This amber deposit, with an estimated age between 99–98 Mya (Shi et al. 2012), has revealed a number of unique insect groups and many of those, belonging to Hymenoptera, turned out to be key elements for our understanding of the phylogenetic relationships among the main lineages of Chrysidoidea (e.g. Lucena and Melo 2018; Zhang et al. 2018; Martynova et al. 2019; Melo and Lucena 2020; Olmi et al. 2020).

Chrysidoid wasps of the family Dryinidae are popularly known as pincer wasps due the chelate fore legs of the females. They use these pincers to hold their larval hosts, which all belong to Auchenorrhyncha (Hemiptera) (Guglielmino et al. 2013; Martins and Domahovski 2017a,b; Martins et al. 2020, 2021; Virla et al. 2023). It is one of the largest families of Chrysidoidea with about 1,924 spe-

cies described in 17 subfamilies and 53 genera (Olmi et al. 2014, 2019, 2020, 2022; Martins et al. 2020, 2021; Perkovsky et al. 2019, 2020a,b; Martins and Melo 2019, 2020; Martynova et al. 2020; Martins 2022, 2023; Martins and Perioto 2021; Martins and Domahovski 2022). About 90 fossil species of dryinids preserved as rock impressions and as inclusions in different amber deposits (Lebanese, Mongolia, Taimyr, Burmese, Canada, France, Baltic, Mexican and Dominican amber) are known (Ponomarenko 1975; Olmi 1995; Olmi et al. 2010, 2014, 2022; Martins and Melo 2019, 2020).

Although there are many taxonomic studies dealing with the family Dryinidae, only a few phylogenetic studies have been published, as by Carpenter (1999), Tribull (2015), and Branstetter et al. (2017). These studies used different groups and approaches, whether morphological, molecular or phylogenomic, and in all of them Dryinidae were recovered as a monophyletic group. Up to now, Tribull's (2015) study was the most representative investigation of the relationships within Dryinidae and her hypotheses provided support for recognizing Thaumatodryininae as a subfamily distinct from Dryininae.

Thaumatodryininae are one of the smallest subfamilies of Dryinidae, with 35 described species placed in the single genus *Thaumatodryinus* Perkins (Martins and Melo 2020; Brazidec and Perrichot 2023). It has an almost worldwide distribution, being absent only from the Palearctic region, and is known to attack nymphs of the auchenorrhynchous Hemiptera of the family Flatidae (Guglielmino et al. 2013; Martins and Melo 2020). One of the diagnostic characters of *Thaumatodryinus* is the presence of rhinaria on flagellomeres 3–8 accompanied by long and delicate setae, whose length is longer than the diameter of the flagellomere (Martins and Melo 2020). These sensory structures are present only on the antennae of females belonging to Apodryininae, Dryininae, Gonatopodinae, and Thaumatodryininae, and seem to be involved in host location (Olmi 1984; Riolo et al. 2016). Additional characters for the recognition of this genus are the bulging hemispherical compound eyes, the vertex with a convex contour in frontal view, and the elongated claw of the pincer with a simple apex, lacking subapical teeth.

Fossil species of Thaumatodryininae have been described from Baltic, Dominican, and Mexican ambers (Olmi 1984; Olmi and Bechly 2001; Olmi and Virla 2014; Olmi et al. 2019; Martins and Melo 2020; Brazidec and Perrichot 2023). Brues (1923, 1933) described three fossil species in *Thaumatodryinus* from Baltic amber, which were transferred to †*Harpactosphecion* Haupt (1944) by Olmi and Bechly (2001). While †*H. filicornis* (Brues 1923) and †*H. gracile* (Brues 1933) indeed belong in †*Harpactosphecion*, we believe that †*T. deletus* Brues should be maintained in *Thaumatodryinus* (Martins and Melo, unpubl. results), therefore representing a legitimate record of this genus in Baltic amber.

We provide herein the first record of Thaumatodryininae in mid-Cretaceous Burmese amber, represented by a new genus and species. The placement of the new taxon is corroborated by the first phylogenetic investigation, based on morphological data under an exemplar approach, involving a broad sample of dryinid representatives and providing a series of newly proposed characters.

2. Material and methods

2.1. Taxonomic study

The studied amber piece came from the Hukawng Valley, near Tanai, Kachin state, in northern Myanmar, whose age has been estimated to be around 99–98 Mya (Shi et al. 2012). The piece is deposited in the Departament of Zoology, Universidade Federal do Paraná, Curitiba, Brazil (DZUP). In order to have a better view of the inclusion,

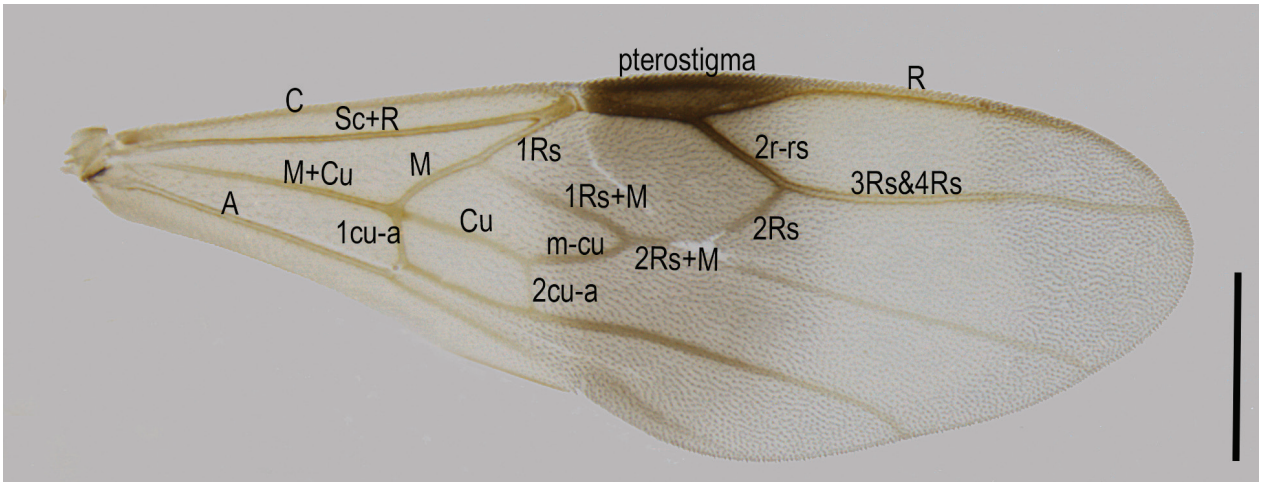

Figure 1. Terminology used for the fore wing venation, based on the wing of *Thaumatodryinus macilentus* Perkins (Dryinidae, Thaumatodryininae). Legends: C = costa; Sc+R = subcosta+radius; M+Cu = media+cubitus; A = anal; M = media; 1Rs = 1st radial sector; 1cu-a = 1st cubital–anal; Cu = cubitus; 1Rs+M = 1st radial sector+media; m-cu = medial–cubital; 2cu-a = 2nd cubital–anal; 2Rs+M = 2nd radial sector+media; 2Rs = 2nd radial; 2r-rs = 2nd radial–radial sector; 3Rs&4Rs = 3rd and 4th radial sector; Scale bar = 1mm.

Table 1. List of terminal taxa of Dryinidae (Hymenoptera, Chrysidoidea) used in the phylogenetic analysis. Country of origin (or fossil deposit) and acronyms of the depository institutions are indicated.

Subfamilies	Species	Country/ Deposit	Institution
Aphelopinae	*Aphelopus trinitatis*	Brazil	DZUP
Aphelopinae	*Crovettia barbara*	Brazil	DZUP
Anteoninae	*Anteon elianeae*	Brazil	DZUP
Anteoninae	*Deinodryinus pseudoamoenus*	Brazil	DZUP
Anteoninae	*Lonchodryinus tricolor*	Brazil	UEFS
Bocchinae	*Bocchus* sp.	Brazil	DZUB
Conganteoninae	*Conganteon walkerense*	South Africa	DZUP
Thaumatodryininae	*Thaumatodryinus koebelei*	Australia	DZUP
Thaumatodryininae	*Thaumatodryinus macilentus*	Brazil	DZUP
Thaumatodryininae	†*Thaumatodryinus fuscescens*	Dominican amber	DZUP
Thaumatodryininae	†*Thaumatorrhinos athrix*	Burmese amber	DZUP
Gonatopodinae	*Gonatopus cubensis*	Brazil	DZUP
Gonatopodinae	*Neodryinus albosignatus*	Brazil	UFES
Gonatopodinae	*Pareucamptonyx paranaensis*	Brazil	DZUP
Dryininae	*Gonadryinus* sp.	Brazil	MZSP
Dryininae	†*Harpactosphecion* sp.	Dominican amber	DZUP
Dryininae	*Dryinus bolivianus*	Brazil	UFES
Dryininae	*Dryinus bocainanus*	Brazil	DZUP
Dryininae	*Dryinus constans*	Brazil	MZSP
Dryininae	*Dryinus ruficeps*	Brazil	UFES
Dryininae	*Dryinus magnificus*	Brazil	CZMA
Dryininae	*Dryinus catarinae*	Brazil	UEMG

Institutional abbreviations: CZMA – Coleção Zoológica do Maranhão, Caxias, Maranhão, Brazil – Dr. Francisco Limeira-de-Oliveira; **DZUB** – Coleção Entomológica da Universidade de Brasília, Brasília, Distrito Federal, Brazil – Dr. Antônio J. C. Aguiar; **DZUP** – Coleção Entomológica Pe. Jesus Santiago Moure, Universidade Federal do Paraná, Curitiba, Paraná, Brazil – Dr. Gabriel A. R. Melo; **MZSP** – Museu de Zoologia da Universidade de São Paulo, São Paulo, São Paulo, Brazil – Dr. Carlos R. F. Brandão; **UEMG** – Universidade do Estado de Minas Gerais, Passos, Minas Gerais, Brazil – Dra. Sônia L. Modesto-Zampieron and Dr. Juliano F. Nunes; **UEFS** – Universidade Estadual de Feira de Santana, Feira de Santana, Bahia, Brazil – Dr. Freddy B. Quijano and Dr. Sérgio Andena; **UFES** – Universidade Federal do Espírito Santo, Vitória, Espirito Santo, Brazil – Dr. Marcelo T. Tavares. †Indicate fossil species.

the piece was manually trimmed with a jewellery saw and ground with wet emery paper (grit sizes of 800 to 3000). Final polishing was obtained using a sanding sponge pad (grit size of 5000), followed by rubbing in a soft cloth.

Morphological terminology follows Olmi and Virla (2014); specific terms used for integumental sculpture, follow Olmi and Virla (2014) and Harris (1979); we adopted Brothers's (2011) terminology for the fore wing venation, with some modifications (Fig. 1). The term "rhinaria" (sensu Olmi 1984) is interpreted herein as equivalent to "ADOs" = Antennal Dorsal Organs (sensu Riolo et al. 2016). The classification adopted for the species groups in *Dryinus* follows Martins (2018).

In the description of the genus and species and in the character descriptions the following abbreviations are used: **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; **POL** – refers to the minimum distance between the inner edges of the lateral ocelli; and **TL** – refers to the minimum distance from the posterior edge of the eye to the occipital carina. The measurements provided for ocellar ratio, antennomeres, and the fore-leg articles represent relative values.

The inclusions were studied using a Leica M125 stereomicroscope. Color images of †*Thaumatorrhinos athrix* **gen. et sp. nov.** were obtained by a LEICA DFC295 digital camera. Image stacking was done using the software Zerene Stacker 1.04 Built T2021-08-28-1410. The figure plates were prepared using Adobe Photoshop (version CS6).

2.2. Phylogenetic analysis

The cladistic analyses were based on a matrix of 100 characters and 22 terminal taxa (Table 1 and Table S1), including extant and fossil species from Dominican and Burmese amber. Most characters were taken from the female morphology, as the taxonomy of the family is mostly based on this sex. For those characters involving the male morphology, we coded them based on genus-level groundplans; for taxa in which the males are unknown, the terminal was left with missing data. The characters, all from the external morphology of the adult wasps, were numbered according to their respective tagma, from anterior to posterior (head, mesosoma, and metasoma). We used a question mark (?) for missing information, and a hyphen (–) was assigned to inapplicable states.

Outgroups were chosen from different genera belonging to more basal subfamilies of Dryinidae for which we had available material (Anteoninae, Aphelopinae, Bocchinae, and Conganteoninae). Representatives of the more derived subfamilies, Gonatopodinae and Dryininae, were included in the ingroup in order to test the position of the new genus and the monophyly of Thaumatodryininae (Table 1).

The characters and their states were assembled in a matrix, subsequently converted to a text file, and then formatted as a Nona file. Multistate characters were treated as non-additive (Fitch 1971). The heuristic searches for the most parsimonious trees were conducted in TNT v.1.6 (Goloboff and Morales 2023), using the following specifications in the analyses: space for 99999 trees in memory; traditional tree search; random seed 0; 1000 replications; TBR algorithm; 10 trees saved per replication. Analyses were carried out under implied weights (with the default k = 3) as implemented in TNT. Parsimony analyses under implied weights are advocated to improve phylogenetic resolution for resolving conflict between characters in favor of those exhibiting a lower degree of homoplasy (Goloboff 1993; Goloboff et al. 2008; Goloboff 2014). Support for the branches was estimated through symmetric re-sampling (Goloboff et al. 2003), also in TNT v.1.6 (traditional tree search – TBR = 1000 replications; 10000 re-sampling replications). Both the optimization of the characters and the visualization of the cladograms were done in the software Winclada 1.00.08 (Nixon 2002), with only unambiguous changes shown. In the topologies analyses, the value of symmetric resampling was considered above 15%. For comparative purposes, an equal-weight analysis (Fig. S1) was also carried out in TNT. Trees were rooted between Anteoninae and the clade containing Conganteoninae + Bocchinae + Aphelopinae, based on an unpublished reanalysis of Tribull's (2015) dataset.

3. Results

In this study we present the first phylogenetic analysis for Dryinidae, based on morphological data under an exemplar approach, combining fossil and extant taxa and using a set of newly proposed characters from all body regions. The cladistic analysis was based on a matrix of 100 characters and 22 terminal taxa (Table 1 and Table S1): 36 from the head; 60 from the mesosoma, and four from the

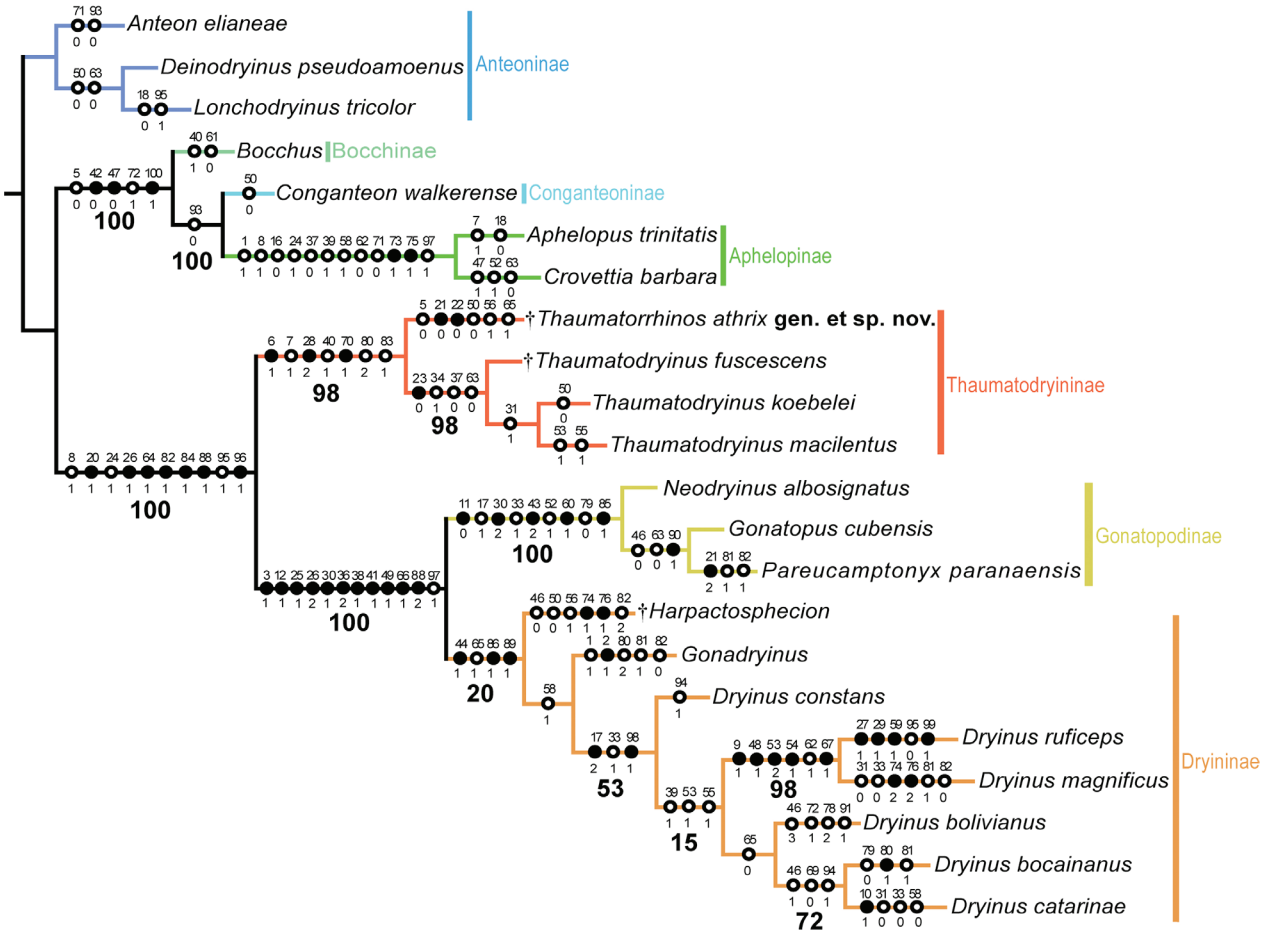

Figure 2. Most parsimonious tree resulting from a cladistic analysis under implied weighting (k = 3) of 100 morphological characters and 22 terminal taxa, focusing in Thaumatodryininae (Hymenoptera, Dryinidae). Character-state transformations are shown under unambiguous optimization, depicted as solid (unique transformations) and empty circles (reversals or multiple transformations). Branch support indicated for the major clades is derived from symmetrical resampling.

metasoma. Most of the characters apply to females; when specific to males, these are indicated as such. We assembled a dataset with 100 characters, of which only 14 (indicated in the respective character comment) had been used previously (Carpenter 1999), showing how incipient is our current knowledge of the relationships within Dryinidae based on morphology. Among these characters, 81 were coded as binary and 19 as multistate. For each character, the number of steps (L), consistency index (ci), and retention index (ri), as found in the weighted analysis, are provided. Those indicated as non-informative by the analyses do not have ci and ri values.

3.1. List of characters

Head

1. Maxillary palpomeres, number: (0) six; (1) five; (2) four. (L: 2; ci: 50; ri: 50). This character corresponds partially with character 15 of Carpenter (1999).

2. Labial palpomeres, number: (0) three; (1) two. (L: 1). This character corresponds partially with character 16 of Carpenter (1999).

3. Mandible, number of teeth (male): (0) four; (1) three. (L: 1; ci: 100; ri: 100). — State (1) applies to the genus *Dryinus* Latreille (Dryininae) as well as to the genera of Gonatopodinae (*Gonatopus* Ljungh, *Neodryinus* Perkins and *Pareucamptonyx* Olmi). Species of *Dryinus* and *Gonatopus* exhibit strong sexual dimorphism. We examined a significant number of male specimens and found that the number of teeth in the mandible is constant. In this study, it is assumed that all genera of these two subfamilies have the same number of teeth. This character corresponds partially with character 14 of Carpenter (1999).

4. Mandible, shape of teeth (female): (0) long, spaced apart from each other, mandible relatively robust in shape; (1) with progressive sizes, lower tooth longer than the others. (L: 2; ci: 50; ri: 88). — State (0) applies to Anteoninae, Aphelopinae, Bocchinae, Conganteoninae, and Thaumatodryininae. Although members of Aphelopinae, Bocchinae, and Conganteoninae have the second tooth reduced (see next character), the other teeth are relatively long and placed far apart from each other. State (1) applies to Dryininae and Gonatopodinae, in which the teeth are of increasing sizes from the upper to the lower one.

5. Mandible, size of second tooth (female): (0) reduced, reaching approximately one-half of the size of the third tooth (Fig. 5A); (1) subequal in size or longer. (L: 2; ci: 50; ri: 75). — We count the mandibular teeth from the lower to the upper one, the second tooth being the one right above the apical, lowermost tooth. The reduced second tooth in Dryinidae is described by Olmi & Virla (2014) as a rudimentary mandibular tooth. State (0) applies to Aphelopinae, Conganteoninae, Bocchinae, and †*Thaumatorrhinos* **gen. nov.**

6. Mandible, curvature: (0) continuous, slightly curving towards apex (convex shape); (1) abruptly curved near base, making almost a right angle (Figs 4A, 5A). (L: 1; ci: 100; ri: 100). — State (1) is exclusive to Thaumatodryininae while state (0) applies to the remaining genera of Dryinidae. In taxa that received state (1) the mandible has a distinct basal portion, with a depressed surface in relation to the apical portion.

7. Epistomal suture, position in relation to the antennal alveolus: (0) in contact; (1) separated by at least half the diameter of the antennal alveolus. (L: 2; ci: 50; ri: 75).

8. Clypeus, anterior condyle of mandible in relation to antennal alveolus: (0) situated outside the outer margin of the alveolus (wide clypeus); (1) aligned with the outer margin of the alveolus (narrow clypeus). (L: 2; ci: 50; ri: 75). — State (0) applies to *Anteon* Jurine, *Bocchus* Ashmead, *Conganteon* Benoit, *Deinodryinus* Perkins and *Lonchodryinus* Kieffer.

9. Clypeus, apical margin shape: (0) without recess; (1) with a medial recess. (L: 1; ci: 100; ri: 100). — State (1) applies to the species of *Dryinus* belonging to the *magnificus* and *ruficeps* groups. This character corresponds partially with character 10 of Carpenter (1999).

10. Clypeus, apical margin in relation to base of mandible: (0) margin not projected and not covering the base of the mandible when closed; (1) margin projected and covering the base of the mandible when closed. (L: 1). — State (1) applies only to species of *Dryinus* of the *catarinae* group.

11. Genal bridge, medial surface: (0) convex throughout, accompanying the curvature of the eyes; (1) medially flat, convexity following the curvature of the eyes restricted to the sides. (L: 1; ci: 100; ri: 100). — State (0) applies only to Gonatopodinae.

12. Genal bridge, length in relation to mandibular basal width: (0) shorter or equal; (1) longer. (L: 1; ci: 100; ri: 100). — State (1) is related to the prognathism present in Gonatopodinae and Dryininae. The elongation of the genal bridge and the direction of the buccal apparatus facing forward causes the genal bridge to become longer than the width of the base of the mandible.

13. Malar space, length in relation to mandibular basal width: (0). shorter; (1) longer. (L: 3; ci: 33; ri: 75).

14. Antennal rim (border of antennal alveolus): (0) poorly developed, as high as one-half of the basal diameter of scape; (1) well developed, about as high as the basal diameter of scape. (L: 2; ci: 50; ri: 83). — The basal diameter of the scape is measured distal to the radicle.

15. Scape, angulation between radicle and main shaft (male): (0) almost forming a right angle; (1) aligned. (L:

1; ci: 100; ri: 100). — State (0) is found only in males of Anteoninae, in which the main shaft of the scape is inserted in the radicle at an angle close to 90 degrees.

16. Scape, length in relation to pedicel: (0) up to 2 × its length; (1) more than 2× its length. (L: 3; ci: 33; ri: 50). — State (0) applies to *Aphelopus*, *Crovettia* and Thaumatodryininae, except for †*Thaumatodryinus fuscescens*.

17. Flagellomeres, length of the 1st: (0) subequal to second flagellomere (0.8–1.2 × its length); (1) 1.3–2 × as long as second flagellomere; (2) above 2 × as long as second flagellomere. (L: 5; ci: 40; ri: 72).

18. Flagellomeres, width: (0) homogeneous, flagellomeres with uniform diameters; (1) increasing in diameter distally, flagellum somewhat clavate. (L: 5; ci: 20; ri: 42). — State (0) applies to *Lonchodryinus*, in Anteoninae, Aphelopinae, Conganteoninae, and Thaumatodryininae. State (1) applies to *Bocchus* (Bocchinae), *Anteon*, *Deinodryinus* (Anteoninae), Gonatopodinae and Dryininae (except for †*Harpactosphecion* and *Gonadryinus*, which have state (0)).

19. Flagellomeres, thickening: (0) starting at the 2nd flagellomere; (1) starting at the 3rd flagellomere; (2) starting at the 4th flagellomere. (L: 4; ci: 25; ri: 0). — This character only applies to terminals that received state (1) in the previous character.

20. Rhinaria, occurrence: (0) absent; (1) present**.** (L: 1; ci: 100; ri: 100). — The rhinaria are grooves with a sensory function accompanied by internal and/or external bristles, generally seen on flagellomeres 3–8. State (1) applies to Gonatopodinae, Dryininae and Thaumatodryininae. This character corresponds partially with character 5 of Carpenter (1999).

21. Rhinaria, distribution: (0) present on all flagellomeres (Fig. 5B); (1) present on the 3rd to the 8th flagellomere; (2) present only on the three distal flagellomeres. (L: 2). — This character and the following apply only to taxa that received state (1) in the preceding character. State (0) applies to †*Thaumatorrhinos* **gen. nov.** (Thaumatodryininae); state (1) applies to Gonatopodinae (except *Pareucamptonyx*) and Dryininae, and state (2) applies only to *Pareucamptonyx*.

22. Rhinaria, location on flagellomeres: (0). occupying the entire length of the flagellomeres (Fig. 5B); (1) located in the basal third and reaching up to the median length of the flagellomeres; (2) located in the apical third of the flagellomeres. (L: 2; ci: 100; ri: 100). — State (0) applies only to †*Thaumatorrhinos* **gen. nov.** State (1) applies to *Thaumatodryinus* and state (2) applies to Gonatopodinae and Dryininae.

23. Rhinaria, setation: (0) with long bristles exceeding the diameter of the flagellomere; (1) bristles absent or rhinaria accompanied by short setae less than the diameter of the flagellomere. (L: 1; ci: 100; ri: 100). — State (0) applies to *Thaumatodryinus*, in which each flagellomere has four long setae, one pair at each end of each rhinarium.

24. Compound eye, groove along outer orbit: (0) present; (1) absent. (L: 2; ci: 50; ri: 75). — This groove is continuous with that present in the malar space, differentiating itself by being wider and bordering the entire outer eye orbit and reaching up to the inner margin of the compound eye. State (0) applies to the genera of Bocchinae, Conganteoninae and Anteoninae.

25. Compound, eye, ommatidia: (0) with uniform diameter; (1) frontal facets of the lower third about 2 × as large as the dorsal and latero-posterior facets. (L: 1; ci: 100; ri: 100). — State (1) applies to Gonatopodinae and Dryininae.

26. Compound eye, location on head: (0) occupying the anterior portion of the dorsal region of the head; (1) occupying the lateral region of the head (Figs 4A, 5A); (2) occupying the entire dorsal region of the head and parallel to the vertex. (L: 2; ci: 100; ri: 100). — State (0) applies to Anteoninae, Aphelopinae, Bocchinae and Conganteoninae, in which the genal bridge is reduced and the vertex has a larger extension, causing the eye to be restricted to the anterior portion. State (1) applies to Thaumatodryininae, in which the genal bridge and the vertex have approximately the same length, causing the eyes to be displaced laterally, while state (2) applies to Gonatopodinae and Dryininae, in which the genal bridge is elongated and almost parallel to the vertex, causing a displacement of the buccal apparatus to the anterior region, characterizing a prognathous condition, while the eyes occupy almost the entire surface.

27. Upper frons, relation to eye surface: (0) in the same plane or at a slightly lower level; (1) at a distinctly lower level. (L: 1). — An upper frons at a distinctly lower level compared to the eye surface is found in Gonatopodinae and Dryininae. This seems to result from a bulging of the compound eyes in these lineages, in which the eyes are projected from the head laterally and their surface does not form a continuous plane with the frons surface.

28. Vertex, in relation to upper limit of eyes (head in frontal view): (0) approximately in the same plane; (1) in a lower plane, with a concave profile; (2) in an upper plane, with a distinctly convex profile. (L: 5; ci: 40; ri: 75). — The surface of the upper frons and vertex of the species in the *ruficeps* group of *Dryinus* is in a distinct lower plane compared to the eyes and has a strongly concave profile.

29. Mid ocellus, position in relation to lateral ocelli: (0) placed not far apart, OL 0.5–1.5 × POL; (1) placed far apart, OL at least 2 × POL. (L: 1). — State (1) is closely associated with the excavated vertex in *Dryinus*.

30. Occipital carina, extent (male): (0) complete; (1) restricted to the vertex; (2) absent. (L: 2; ci: 100; ri: 100). — State (0) applies to Anteoninae, Aphelopinae, Bocchinae, Conganteoninae and *Thaumatodryinus*. For Dryininae, especially *Dryinus*, state (1) applies since all studied specimens exhibit the occipital carina restricted to the vertex. For specimens of Gonatopodinae, state (2) is considered since a significant number of specimens of *Gonatopus* were studied and all lack an occipital carina. This character corresponds partially with character 7 of Carpenter (1999).

31. Occipital carina, extent (female): (0) complete; (1) restricted to the vertex, behind the ocelli, or absent. (L: 5; ci: 20; ri: 55). — State (0) applies to Anteoninae, Aphelopinae, Bocchinae, and Conganteoninae and fossil species of Dryininae and Thaumatodryininae (except extant *Dryinus* from the *catarinae* and *magnificus* groups). State (1) applies to extant species of *Thaumatodryinus* (Thaumatodryininae), Gonatopodinae, and Dryininae.

This character corresponds partially with character 6 of Carpenter (1999).

32. Occipital carina, form (female): (0) elevated and with short perpendicular carinae forming a trabecular band; (1) low and without perpendicular carinae. (L: 2; ci: 50; ri: 85). — State (0) applies to Anteoninae, Aphelopinae, Bocchinae and Conganteoninae. State (1) applies to Thaumatodryininae, Gonatopodinae, and Dryininae.

33. TL region (female): (0) present; (1) absent. (L: 4; ci: 25; ri: 50). — TL is considered as the minimum distance from the posterior edge of an eye to the occipital carina, and this region is present in more basal groups of Dryinidae, such as in all Anteoninae, Aphelopinae, Bocchinae, and Conganteoninae, as well as in some Thaumatodryininae and Dryininae.

34. TL region, surface (female): (0) flat, continuous with the apex; (1) posteriorly inclined towards the occipital region. (L: 2; ci: 50; ri: 66). — State (1) applies when the occipital carina is displaced below the vertex.

35. TL region (male): (0) present; (1) absent. (L: 1; ci: 100; ri: 100). — The TL region is present only in males of Anteoninae, Aphelopinae, Bocchinae, Conganteoninae and Thaumatodryininae. The male specimens of Dryininae and Gonatopodinae lack this region, and the posterior margin of the eye abuts the occipital region.

36. Head, shape of posterior region (female): (0) strongly concave, fitting with the pronotum, gena, and vertex distinctly differentiated from occipital region (Figs 4C, 5B); (1) flat, gena narrow and continuous with occipital region; (2) central portion concave, vertex sunken, genal region little differentiated and distinctly convex; (3) central portion concave and continuous with vertex, gena distinctly differentiated from occipital region. (L: 5; ci: 60; ri: 91). — State (0) applies to Anteoninae, Aphelopinae, Bocchinae, Conganteoninae and †*Thaumatorrhinos* **gen. nov**. State (1) applies to *Thaumatodryinus*, state (2) to Gonatopodinae, and state (3) to Dryininae.

Mesosoma

37. Pronotum, length in relation to mesoscutum: (0) less than 1 ×; (1) equal to or greater than 1 ×. (L: 2; ci: 50; ri: 75).

38. Pronotum, shape in lateral view: (0) plane or concave; (1) convex, disc raised. (L: 1; ci: 100; ri: 100). — The dorsal portion of the pronotum in Dryinidae when elevated and convex is referred to as "disc" by Olmi & Virla (2014). State (0) applies to *Bocchus* and *Thaumatodryinus*.

39. Pronotum, transverse impression: (0) present; (1) absent. (L: 2; ci: 50; ri: 83). — State (1) applies to species of the *autumnalis*, *bocainanus* and *catarinae* species groups in the genus *Dryinus*.

40. Pronotum, transverse impression location: (0) near the anterior margin; (1) at the central portion. (L: 2; ci: 50; ri: 75).

41. Pronotum, lower lateral margin: (0) extending ventrally, forming ventral corners; (1) not extending ventrally, without ventral corners and forming a straight margin. (L: 1; ci: 100; ri: 100). — State (0) applies to the subfamilies Anteoninae, Aphelopinae, Bocchinae, Conganteoninae and Thaumatodryininae. State (1) applies to the species of Gonatopodinae and Dryininae.

42. Pronotum, posterior portion in relation to mesoscutum: (0) juxtaposed to the mesoscutum; (1) overlapping the anterior region of the mesoscutum medially. (L: 1; ci: 100; ri: 100). — State (0) applies to Aphelopinae, Bocchinae, and Conganteoninae.

43. Pronotum, in relation to anterior margin of mesoscutum: (0) occupying the entire margin and pronotal lobe reaching tegula; (1) occupying most of the anterior margin and pronotal lobe not reaching tegula; (2) restricted to the central region, with a reduced pronotal lobe, and with a strangulated appearance. (L: 3; ci: 66; ri: 90). — State (0) applies to Anteoninae, Aphelopinae, Bocchinae, Conganteoninae and Thaumatodryininae. State (1) applies to Dryininae (except †*Harpactosphecion*). State (2) applies to Gonatopodinae.

44. Pronotum, posterior margin sculpture: (0) with a smooth laminar area; (1) with a rugose area. (L: 1; ci: 100; ri: 100).

45. Pronotum, posterior margin: (0) lacking a carinate groove; (1) with a carinate groove. (L: 3; ci: 33; ri: 0). — State (0) applies to *Gonadryinus* and *Dryinus* of the *constans* and *magnificus* species groups.

46. Pronotum, sculpture: (0) smooth; (1) granulate; (2) smooth and crossed by several carinae; (3) rugose. (L: 11; ci: 27; ri: 61).

47. Prepectus: (0) not visible, apparently fused to the pronotum; (1) externally visible, separate from the pronotum. (L: 2; ci: 50; ri: 50). — State (0) applies to the specimens of Aphelopinae (except *Crovettia*), Bocchinae and Conganteoninae, while state (1) applies to Anteoninae, Dryininae, Gonatopodinae, and Thaumatodryininae.

48. Prepectus, lateral surface: (0) flat; (1) depressed, forming a well-defined groove. (L: 1; ci: 100; ri: 100). — State (1) applies to *Dryinus* species of the *magnificus* and *ruficeps* groups.

49. Ventral surface of prepectus: (0) independent lateral sclerites, separated from one another ventrally by remainder of the mesopleura; (1) lateral sclerites extending ventrally and fused medially. (L: 1; ci: 100; ri: 100). — State (0) of this character applies to Aphelopinae, Bocchinae and Conganteoninae (although the pronotum is fused to the prepectus in these subfamilies, we consider that these groups have this condition), Anteoninae and Thaumatodryininae. State (1) applies to Dryininae and Gonatopodinae, in which the prepectus is fused ventrally and their halves are not separated by the remainder of the mesopleura.

50. Acetabular carina: (0) present; (1) absent. (L: 5; ci: 20; ri: 20). — The acetabular carina, located in the ventral region of the mesopleuron, provides a reinforcement of the body wall.

51. Anterior medial region of the mesoscutum: (0) without differentiation; (1) strongly convex and with smooth integument. (L: 2; ci: 50; ri: 88).

52. Notauli: (0) present; (1) absent. (L: 2; ci: 50; ri: 66). — State (1) of applies to *Crovettia*, and also to the females of Gonatopodinae because of the fusion of their mesosomal structures.

53. Notauli format: (0) in groove; (1) in the form of a different sculpture; (2) in the form of a carina. (L: 3; ci: 66; ri: 83).

54. Notauli location in relation to the convex and smooth area of the mesoscutum: (0) parallel to the smooth area; (1) interrupted in the smooth region. (L: 1; ci: 100; ri: 100). — This character applies only to Dryininae. State (0) applies to species of *Dryinus* of the groups *autumnalis*, *bocainanus*, *catarinae* and *constans*, *Gonadryinus* and †*Harpactosphecion*. State (1) applies to the species of *Dryinus* species of groups *magnificus* and *ruficeps*.

55. Notauli in relation to the mesoscutum: (0) percurrent; (1) not percurrent. (L: 4; ci: 25; ri: 50). — State (0) is attributed when the notauli occupy the entire length of the mesoscutum, that is, when they are considered complete.

56. Ratio of the smallest distances between the notauli in the anterior and posterior portions of the mesoscutum (female): (0) less than three; (1) equal to or greater than three. (L: 2; ci: 50; ri: 0). — State (1) of this character is considered when the notauli almost completely converge in the posterior portion of the mesoscutum and, it applies to †*Thaumatorrhinos* **gen. nov.** (Thaumatodryininae) and †*Harpactosphecion* (Dryininae).

57. Ratio of the smallest distances between the notauli in the anterior and posterior portions of the mesoscutum (male): (0) less than three; (1) equal to or greater than three. (L:0). — State (0) applies to Dryininae and state (1) is to Gonatopodinae. Due to the strong sexual dimorphism present in *Dryinus* (Dryininae) and *Gonatopus* (Gonatopodinae), which makes it almost impossible to propose sex associations based on external morphology, we assume that all *Dryinus* males exhibit the condition (0) and all *Gonatopus* males as well as *Pareucamptonyx* and *Neodryinus* (Gonatopodinae) have the state (1).

58. Anterior margin of mesoscutellum: (0) with a wide groove and several foveae; (1) with a narrow, straight, and deep groove. (L: 3; ci: 33; ri: 71).

59. Metanotum, dorsal surface: (0) flat; (1) protruding. (L: 1). — The metanotum has a flat surface when its surface is continuous with the mesoscutellum. State (1) applies to *Dryinus* species in the *ruficeps* group.

60. Relative length of metanotum: (0) at least equal to half or longer than mesoscutellum length; (1) shorter than half the mesoscutellum length. (L: 1; ci: 100; ri: 100).

61. Propodeum, shape: (0) dorsal surface of the propodeum separated from the posterior surface by a well-marked edge, the two surfaces practically forming a right angle; (1) dorsal surface of the propodeum continuous with the posterior surface, giving the propodeum a smoothly convex profile in lateral view. (L: 3; ci: 33; ri: 77).

62. Propodeum, ratio between height and length: (0) equal to or greater than one; (1) less than one. (L: 5; ci: 20; ri: 55).

63. Posterior surface of propodeum: (0) without longitudinal carinae; (1) with two longitudinal carinae. (L: 4; ci: 25; ri: 57). — State (1) refers to a pair of longitudinal carinae, each one associated with the foramen of the posterior coxae and which are considered here as reinforcement carinae.

64. Protrochanter, its length in relation to its maximum width: (0) up to 2.9 × its width; (1) greater than 3 × its width. (L: 1; ci: 100; ri: 100). — State (0) applies to the species of Anteoninae, Aphelopinae, Bocchinae, and Conganteoninae. State (1) applies to Thaumatodryininae, Gonatopodinae, and Dryininae (although the species of *Dryinus* of the *bocainanus* group have a ratio less than 3,

the terminal representing this group was here attributed this state). This character corresponds partially with character 24 of Carpenter (1999).

65. Protrochanter, its length in relation to the maximum pronotum length: (0) shorter or equal; (1) longer. (L: 3; ci: 33; ri: 60).

66. Protrochanter, shape of the apical region: (0) straight; (1) with a distinct curvature. (L: 1; ci: 100; ri: 100). — The protrochanter is considered straight when it does not present a curvature in its distal part, which in Dryininae and Gonatopodinae is quite variable.

67. Degree of curvature of the protrochanter apical region: (0) with a slight curvature; (1) with a sharp curvature in the apical region. (L: 1; ci: 100; ri: 100). — This character applies to the species that possess condition (1) of the previous character. State (0) applies to Gonatopodinae (*Gonatopus*, *Neodryinus*, and *Pareucamptonyx*) and *Dryinus* of the species groups *autumnalis*, *constans*, *bocainanus* and *catarinae*. State (1) applies to *Dryinus* of the species groups *magnificus* and *ruficeps*.

68. Relative length of profemur in relation to the protrochanter: (0) more than 4 × as long; (1) 2–2.4 × as long; (2) less than 2 × as long. (L: 4; ci: 50; ri: 85).

69. Relative length of profemur in relation to its maximum width: (0) shorter than 3 ×; (1) longer than 3 ×. (L: 4; ci: 25; ri: 50). — State (0) applies to Anteoninae, Aphelopinae (except *Aphelopus*), *Dryinus* species from the *catarinae* and *bocainanus* groups. State (1) applies to specimens of *Aphelopus* (Aphelopinae), *Conganteon* (Conganteoninae), remaining Dryininae, Gonatopodinae, and Thaumatodryininae.

70. Apex of the 3rd protarsomere: (0) without differentiated bristles longer than tarsomere; (1) with two or three bristles longer than the diameter of the tarsomere (see fig.1G in Martins & Melo 2020). (L: 1; ci: 100; ri: 100). — State (0) of this character applies to the other subfamilies and state (1) to Thaumatodryininae.

71. Articulation of 4th protarsomere on 3rd: (0) tightly articulated, tarsomeres juxtaposed and with the same diameter; (1) 3rd tarsomere with a smaller diameter than 4th, the latter apparently partially loose and hanging from the former. (L: 2; ci: 50; ri: 50).

72. Ratio of the 1st protarsomere length in relation to the 5th: (0) smaller; (1) equal or greater. (L: 2; ci: 50; ri: 75). — State (1) applies to specimens of Aphelopinae, Bocchinae, Conganteoninae, and *Dryinus* species of the *autumnalis* group.

73. Chela: (0) present; (1) absent. (L: 1; ci: 100; ri: 100). — State (1) applies to females of Aphelopinae. This character corresponds partially with character 25 of Carpenter (1999).

74. Apex of the 5th protarsomere in relation to the other tarsomeres: (0) reaches the 3rd tarsomere; (1) reaches the 2nd tarsomere; (2) reaches the 1st tarsomere. (L: 3; ci: 66; ri: 0). — State (2) applies to *Dryinus* of the *magnificus* group.

75. Protarsomere "hooks": (0) present; (1) absent. (L: 1; ci: 100; ri: 100). — These "hooks" are projections of the tarsomere integument, forming a blade with a set of bristles at its apex.

76. Location of "hooks" on protarsomeres: (0) located on the 2nd and 3rd tarsomeres; (1) located only on the 3rd tarsomere; (2) located only on the 1st tarsomere. (ci: 3; ri: 66; ri: 0). — State (0) applies to Anteoninae, Bocchinae, Conganteoninae, Dryininae (except for *Dryinus* species of the *magnificus* species group), Gonatopodinae and Thaumatodryininae. State (2) applies to *Dryinus* species of the *magnificus* group. State (1) applies to †*Harpactosphecion*; although the hook is coming out of the third protarsomere it overlaps the second.

77. Rudimentary claw of the chela: (0) absent; (1) present. (L: 1; ci: 100; ri: 100). This character corresponds partially with character 29 of Carpenter (1999).

78. Setae on the inner margin of the enlarged claw, number: (0) with only one; (1) with a series of setae; (2) setae absent. (L: 4; ci: 50; ri: 50). — State (0) applies to Anteoninae and *Bocchus* (Bocchinae). State (1) applies to Dryininae, Gonatopodinae and Thaumatodryininae. State (2) applies to *Conganteon* (Conganteoninae) and *Dryinus* species of the *autumnalis* group (Dryininae). This character corresponds partially with character 26 of Carpenter (1999).

79. Shape of the setae on the enlarged claw: (0) short, thin, and with a tapered apex, differing from the lamellae of the 5th protarsomere; (1) longer and thicker, commonly with an enlarged apex, and similar to the lamellae of the 5th protarsomere. (L: 2; ci: 50; ri: 66). — This character applies only to terminals coded as (0) and (1) in the preceding character. State (0) applies to specimens of Gonatopodinae and species of *Dryinus* (Dryininae) of the *bocainanus* group. State (1) applies to Thaumatodryininae, Gonatopodinae, and to the remaining Dryininae.

80. Apex of enlarged claw (I): (0) without foliaceous lamella; (1) with a foliaceous lamella; (2) with an elongated lamella about 1.5 × the length of the others. (L: 5; ci: 40; ri: 66). — State (1) applies only to *Dryinus* species of the *bocainanus* group (Dryininae).

81. Apex of the enlarged claw (II): (0) with tooth (pointed); (1) blunt or rounded. (L: 4; ci: 25; ri: 0). — State (1) applies to the *Dryinus* of the *bocainanus* group, to *Gonadryinus*, and *Pareucamptonyx*. This character corresponds partially with character 28 of Carpenter (1999).

82. Apex of the enlarged claw (III): (0) without subapical tooth; (1) with one subapical tooth; (2) with two subapical teeth. (L: 6; ci: 33; ri: 60). — State (0) applies to the specimens of Anteoninae, Bocchinae, Conganteoninae, *Pareucamptonyx* (Gonatopodinae), *Gonadryinus* and the group *magnificus* in *Dryinus* (Dryininae). State (1) applies to *Gonatopus* and *Neodryinus* (Gonatopodinae) and the other groups of *Dryinus*. State (2) applies only to *Thaumatodryinus* and †*Harpactosphecion*.

83. Tooth at the apex of the enlarged claw: (0) straight; (1) with a curvature and its dorsal surface flattened. (L: 2; ci: 50; ri: 75). — State (1) applies to Thaumatodryininae and *D. catarinae*.

84. Tarsal claw of the median and posterior legs, shape: (0) with a sharp curvature; (1) with a smooth, open curve. (L: 1; ci: 100; ri: 100). — State (0) applies to Anteoninae, Aphelopinae, Bocchinae and Conganteoninae, while the state (1) applies to Dryininae, Gonatopodinae and Thaumatodryininae.

85. Mesotibial spur: (0) present; (1) absent. (L: 1; ci: 100; ri: 100). — State (1) is a synapomorphy of Gonatopodinae. This character corresponds partially with character 30 of Carpenter (1999).

86. Position of metacoxal foramen: (0) in the ventral region of mesosoma; (1) displaced dorsally towards the posterior surface of the propodeum. (L: 1; ci: 100; ri: 100). — State (1) applies to Dryininae, although *Dryinus caraibicus* exhibits a somewhat intermediate condition. This character deals with the relative position of the foramina of the posterior coxae in relation to the ventral region of the metepisternum.

87. Dorsal margin of metacoxa: (0) without carina; (1) with carina. (L: 3; ci: 33; ri: 60). — State (0) is applied to Anteoninae, *Thaumatodryinus* (Thaumatodryininae), Gonatopodinae and Dryininae. State (1) applies to Aphelopinae, Bocchinae, Conganteoninae, and †*Thaumatorrhinos* **gen. nov.** (Thaumatodryininae).

88. Inner ventral margin of metacoxal base: (0) without carina or expansion; (1) with a well-developed lamella or a lamelliform lobe; (2) with a low short carina. (L: 2; ci: 100; ri: 100). — State (0) applies to Aphelopinae, Conganteoninae, Bocchinae and Anteoninae. State (1) is applied to Thaumatodryininae. State (2) applies to Gonatopodinae and Dryininae.

89. Propodeal orifice, shape: (0) circular; (1) elliptical, much wider than high. (L: 1; ci: 100; ri: 100).

Wings

90. Wings: (0) present; (1) absent. (L: 1; ci: 100; ri: 100).

91. Dark transverse bands on fore wing: (0) present (Fig. 1); (1) absent. (L: 6; ci: 16; ri: 37). — State (0) applies to the species of Anteoninae (*Anteon* and *Deinodryinus*), Dryininae (*Dryinus*), Gonatopodinae (*Neodryinus*) and Thaumatodryininae.

92. Number of transverse bands on fore wing: (0) one; (1) two. (L: 1; ci: 100; ri: 100).

93. Pterostigma, shape of inner margin: (0) semicircular; (1) elongated (Fig. 1). (L: 2; ci: 50; ri: 66). — The pterostigma is considered semi-circular when its inner margin is a segment of a circle.

94. Divergence between veins M and Cu in fore wing: (0) coinciding with cu-a; (1) apical to cu-a. (L: 2; ci: 50; ri: 50).

95. Vein 3Rs&4Rs in relation to 2r-rs, length: (0) shorter or equal; (1) longer (Figs 1, 3E). (L: 3; ci: 33; ri: 66). This character corresponds partially with character 3 of Carpenter (1999).

Metasoma

96. Flap of tendon on tergum I: (0) small and narrow, its width distinctly less than 0.5 × the width of the propodeal orifice; (1) well-developed, distinctly wide (at least as wide as 0.5 × the width of the propodeal orifice). (L: 1; ci: 100; ri: 100). — The flap on tergum I is well developed in Thaumatodryininae, Gonatopodinae and Dryininae. There is some variation in shape, especially in Gonatopodinae.

97. Lateral portions of tergum I: (0) without a flexion line; (1) with a basal flexion line extending to the spiracle. (L: 2; ci: 50; ri: 87).

98. Ventral region of the first metasomal segment: (0) basal portion of sternum I (petiole) in the same plane as the rest of the sclerite; (1) basal portion of the sternum I forming a strong angle in relation to the surface of the rest of the sclerite. (L: 1; ci: 100; ri: 100).

99. Pale yellow (whitish) crossbands on metasomal terga: (0) absent; (1) present. (L: 1). — State (1) applies only to species of *Dryinus* of the *ruficeps* group.

100. Apex of sternum VI in relation to tergum VI: (0) sclerite with sides extending dorsally forming a high channel to accommodate the stinger apparatus. (1) sclerites not extending dorsally and not forming a channel. (L: 1; ci: 100; ri: 100). — State (1) applies to Aphelopinae, Bocchinae and Conganteoninae.

3.2. Phylogenetic relationships

The phylogenetic analysis under implied weighting resulted in one most parsimonious tree shown in Fig. 2 and Fig S2 with acctran otimization, with L = 227; Ci = 52; Ri = 79. Thaumatodryininae was recovered as a monophyletic

group and sister group of a clade composed of the subfamilies Gonatopodinae and Dryininae, with strong support of symmetric resampling (100%). This major clade was supported by seven unique transformations, which can be interpreted as synapomorphies: flagellomeres with rhinaria (20:1); compound eye with frontal facets of the lower third about 2 × as large as the dorsal and latero-posterior ones (26:1); protrochanter longer than 3 × its width (64:1); apex of the enlarged claw with one subapical tooth (82:1); tarsal claws of the middle and posterior legs forming a smooth, open curve (84:1) metacoxal base with a well-developed lamella or a lamelliform lobe (88:1); flap of tendon on tergum I well-developed, distinctly wide (at least as wide as 0.5 × the width of the propodeal orifice) (96:1); and three homoplastic transformations: anterior condyle of the mandible, in relation to the antennal alveolus, aligned with the outer margin of the alveolus (narrow clypeus) (8:1); lack of groove along outer orbit (24:1); fore wing with 3Rs&4Rs longer than 2r-rs (95:1) (Figs 1, 3E).

Our phylogenetic results placed the Burmese taxon, described here as a new genus and species, †*Thaumatorrhinos athrix* **gen. et sp. nov.** (see below), as sister group to *Thaumatodryinus* (represented here by three species, the fossil †*T. fuscescens* from Dominican amber; *T. koebelei*, the type species of the genus, from Australia; and *T. macilentus* from the Neotropical region). The Thaumatodryininae clade (Fig. 2) has a support of 98% in the symmetric resampling and three unique transformations optimized in this branch: mandible (Fig. 3D) with an abrupt curve near base, making almost a right angle (6:1); vertex (Figs 3A, C, 4A, 5B) with a distinctly convex profile (28:2); and 3rd protarsomere (Fig. 4B) without differentiated bristles longer than tarsomere (70:1). Four homoplastic transformations also provide support for the clade: antennal alveolus (Fig. 5A) separated from the epistomal suture by at least half of alveolus diameter (7:1); pronotum with transverse impression located at its mid length (40:1); apex of the enlarged claw with a lamella about 1.5 × the length of the others (80:2); and tooth at the apex of the elongated claw without a curvature and its dorsal surface flattened (83:1). The phylogenetic hypothesis recovered here, with Thaumatodryininae apart from Dryininae, agrees with the phylogenetic results obtained by Tribull (2015) from molecular data.

The genus †*Thaumatorrhinos* **gen. nov.** was supported by two unique transformation: rhinaria (Figs 4C, 5B) present on flagellomeres 1–8 (21:0) and rhinaria occupying the entire length of the flagellomeres (22:0); and four homoplastic transformations: second apical tooth of the mandible reduced (Fig. 5A), reaching approximately 0.5 × the size of the third tooth (5:0); acetabular carina present (50:0); distance between the notauli in the anterior portion of the mesoscutum at least 3 × distance in posterior portion (56:1); protrochanter longer than the maximum length of the pronotum (65:1).

Thaumatodryinus, represented here by three species, was supported by 98% in the symmetric resampling and by one unique transformations: rhinaria with long and delicate setae exceeding the diameter of the flagellum (23:0) (see fig. 1E in Martins and Melo 2020); and three homoplastic transformations: TL surface tilted posteriorly towards the occipital region (34:1) (see figs 1B, D in Martins and Melo 2020); pronotum shorter than mesoscutum length (37:0); posterior surface of propodeum without pair of longitudinal carinae (63:0). The relationship between the extant species *T. koebelei* and *T. macilentus* was supported by one homoplastic transformation: occipital carina restricted to its dorsal portion (31:1).

Additional results recovered here involve the monophyly of the group containing Dryininae and Gonatopodinae, supported by 100% in the symmetric resampling. Gonatopodinae was represented here by three genera (*Neodryinus* Perkins considered the sister-group of *Gonatopus* Ljungh plus *Pareucamptonyx* Olmi) and Dryininae by three genera (*Dryinus* Latreille, *Gonadryinus* Olmi and †*Harpactosphecion* Haupt). Also, the results confirm the synonymy indicated in Martins (2018) of *Megadryinus* Richards under *Dryinus*, represented here by *D. magnificus* (Richards).

3.3. Systematic paleontology

Order Hymenoptera Linnaeus, 1758
Superfamily Chrysidoidea Latreille, 1802
Family Dryinidae Haliday, 1833
Subfamily Thaumatodryininae Olmi, 1984

Genus †*Thaumatorrhinos* gen. nov.

https://zoobank.org/84401471-B73C-49CB-9324-5A8F5E640D44

Type species. †*Thaumatorrhinos athrix* **sp. nov.**

Diagnosis. Head with convex vertex; occipital carina complete; frontal line absent; rhinaria present on all antennal flagellomeres and occupying most of flagellomere length; clypeus with mid portion of anterior margin straight; mandible with four teeth, second one shorter than the others (rudimentary); pronotum crossed by strong transverse impression; notauli complete and converging posteriorly; fore wing stigmal vein with 3Rs&4Rs longer than 2r-rs; propodeum with dorsal surface shorter than posterior surface, the latter with two longitudinal carinae.

Description. ***Head*****:** (Figs 3A, B, 4C) with vertex convex; TL surface (Figs 3A, C, 4C, 5B) very long, about as long as OOL; occipital carina (Figs 3C, F, 5B) complete and well developed; eye (Figs 3B, D, 4A, 5A) located on lateral side of the head; antenna (Fig. 3A, B) filiform and with rhinaria (Figs 4C, D, 5B) on all flagellomeres, rhinaria extending almost along entire length of flagellomere and without long setae; mid portion of anterior margin of clypeus (Fig. 5A) straight; mandible (Figs 3D, 4A) with long base and apex with four teeth, the second subapical

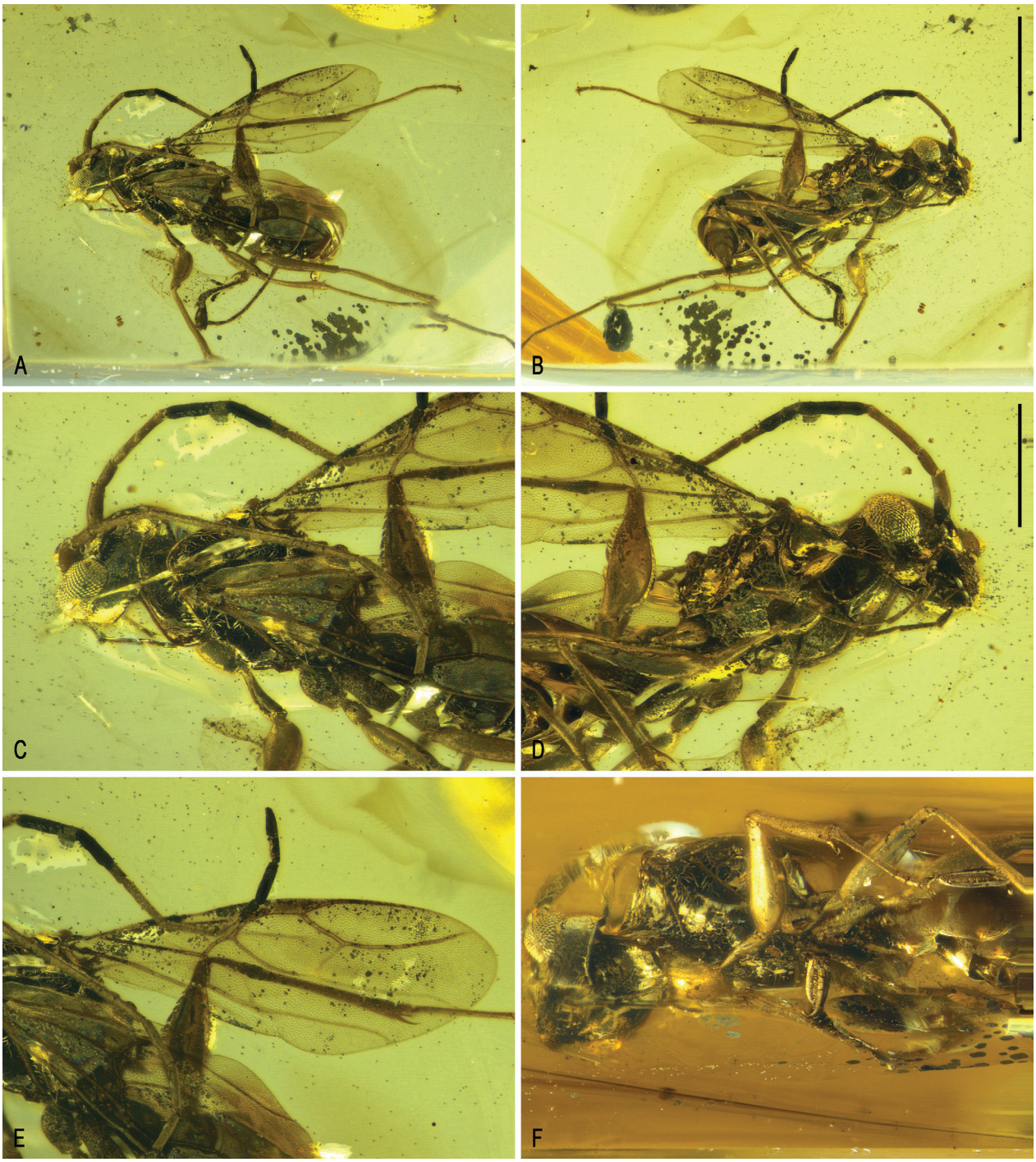

Figure 3. †*Thaumatorrhinos athrix* **gen. et sp. nov. A** Habitus, dorso-lateral view; **B** habitus, ventro-lateral view; **C** head and mesosoma, dorso-lateral view; **D** head and mesosoma, ventro-lateral view; **E** fore wing; **F** head and mesosoma, ventral view. Scale bars: 1 mm (A, B); 0.5 mm (C–F).

tooth (Fig. 5A) rudimentary; maxillary and labial palpi with, respectively, 5 and 3 palpomeres. — ***Pronotum*:** saddle-shaped and crossed by strong transverse impression at central portion; notauli complete and strongly converging posteriorly. — ***Fore wing*:** (Fig. 3A–D) hyaline and stigmal vein with 3Rs&4Rs longer than 2r-rs (Fig. 3E), almost reaching the wing apical margin; veins Rs+M, 2Cua and 3Cu present; divergence between M and Cu veins coinciding with cu-a (Fig. 3E). — ***Protarsomere*:** Apex of 3rd protarsomere (Fig. 4B) with 4 long setae; chela (Fig. 4B) with rudimentary claw; enlarged claw with one row of lamellae and apex reaching inner margin of 5th protarsomere; apex of enlarged claw pointed and without lateral teeth; tibial spur formula 1/1/2. Propodeum with two longitudinal carinae on posterior surface.

Etymology. The genus is named after its peculiar rhinaria, from the Greek *thaumatos* (wonder, marvel) and *rhinos* (of the nose or snout). The name is feminine.

Remarks. †*Thaumatorrhinos* **gen. nov.** is closely related to *Thaumatodryinus* and its placement in Thaumatodryin-

inae is supported by the head with convex vertex leaving the compound eyes located on the sides of the head; antenna with filiform flagellomeres; base of the mandible with a flat area; pronotum with transverse impression located at its mid length; and apex of 3rd protarsomere (Fig. 4B) with four long setae. However, it differs from *Thaumatodryinus* by the mandible with three large teeth and one shorter rudimentary tooth (Fig. 5A); antenna with rhinaria on all flagellomeres and occupying about their entire extension (Fig. 5B); occipital carina complete (Fig. 5B); notauli percurrent and indicated as deep sulci; apex of enlarged claw forming a gentle curvature in relation to the main shaft, lateral teeth absent; dorsal surface of propodeum separated from its posterior surface by a well-marked edge, the two surfaces practically forming a right angle; and posterior surface of propodeum with a pair of longitudinal carinae.

†*Thaumatorrhinos athrix* sp. nov.

https://zoobank.org/446AB7B2-DB62-4EF3-B6D9-379631561C4D

Figs 3A–F, 4A–D, 5A, B

Type material. Holotype female, in amber piece DZUP Bur-398. The specimen is well preserved and complete.

Locality and age. Hukawng Valley, near Tanai, Kachin state, in northern Myanmar. Cenomanian, 99–98 million years ago, middle Cretaceous.

Etymology. We named the species after its bare rhinaria, from the Greek *athrix* (without hair).

Diagnosis. Same as for the genus.

Description. Female holotype (Figs 3, 4 and 5). Approximate body length: 2.12 mm. — **Color:** Head (Figs 3A–C, 4A, C) dark brown, except antenna, clypeus and mandible (Fig. 3D) testaceous; eye (Fig. 3A–C) gray; pronotum black, except lateral sides testaceous; mesosoma (Fig. 3D, F) black; legs (Fig. 3A, B) testaceous; fore wing (Fig. 3E) hyaline; metasoma (Fig. 3B) brownish testaceous. — **Pubescence:** Mostly fine and short. — **Integumental surface:** Head (Figs 3C, 4A) mostly smooth and partially punctate; pronotum smooth, except for transverse carinae; remainder of mesosoma mostly smooth, except for distinct carinae on mesopleuron (Fig. 3D); propodeum with coarse areolation formed by anastomosing carinae. — **Structure and proportions:** Vertex (Figs 3A, C, 4A,

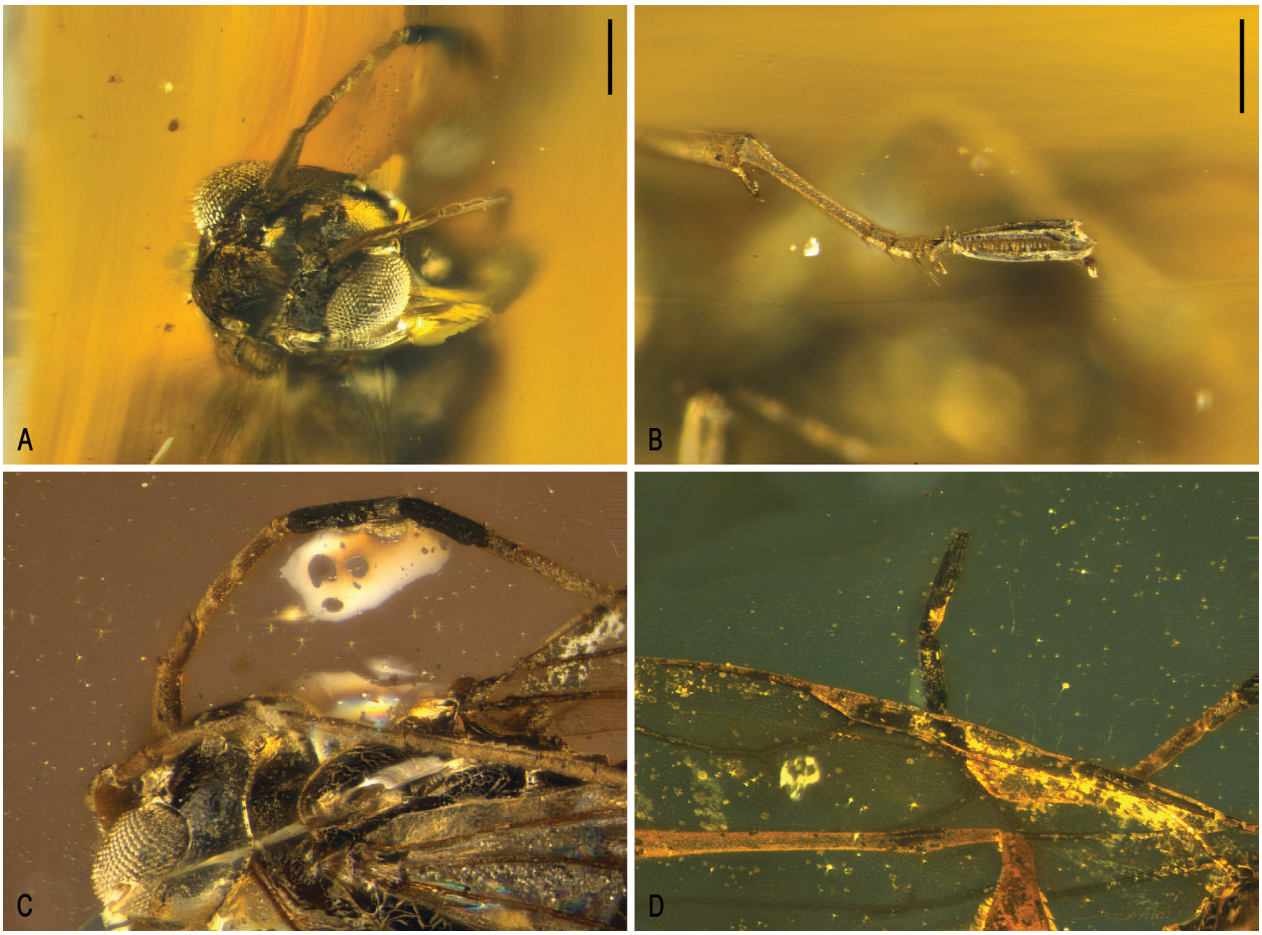

Figure 4. †*Thaumatorrhinos athrix* **gen. et sp. nov. A** Head, frontal view; **B** protarsomeres and chela; **C** head and part of mesosoma, dorsal view and details of flagellomeres with rhinaria. **D** flagellomeres 7–8 with details of rhinaria. Scale bar: 0.2 mm; B–D at the same scale.

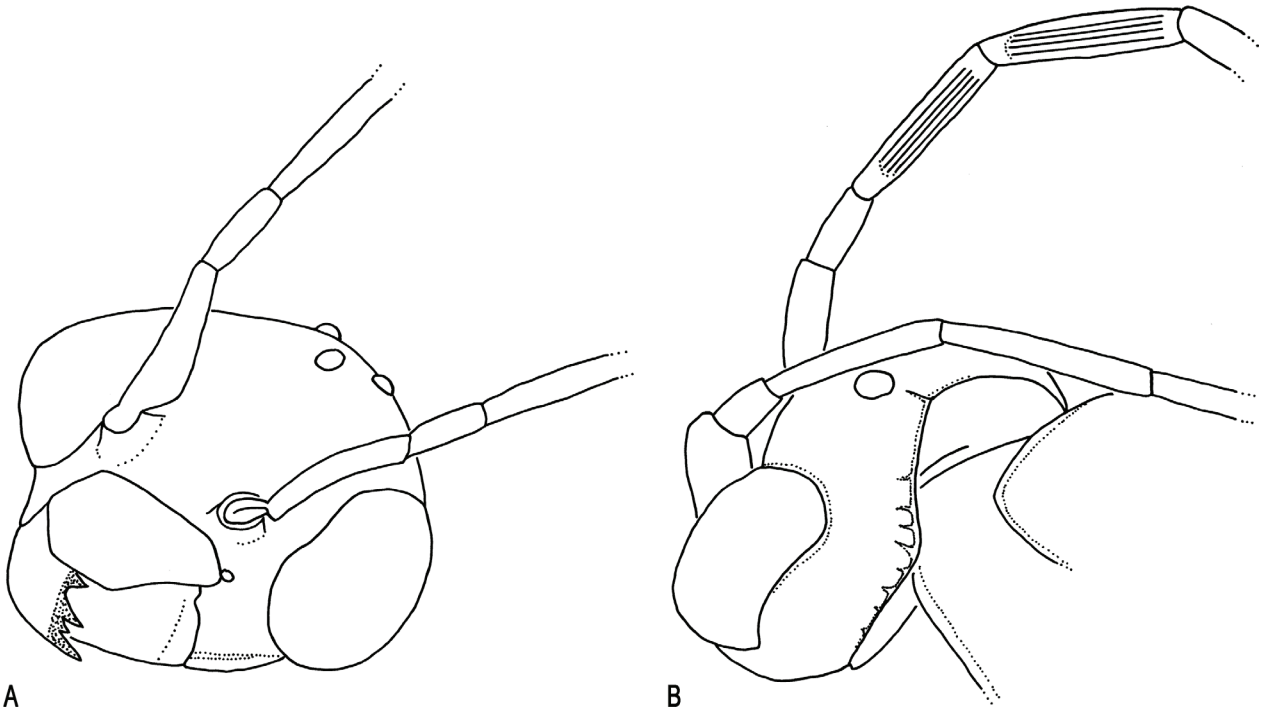

Figure 5. †*Thaumatorrhinos athrix* **gen. et sp. nov. A** Head, frontal view; **B** head, dorsal view.

C, 5B) convex, except for slightly elevated ocellar triangle. Ocellar ratio: **OL** = 5; **POL** = 9; **OPL** = 7; **OOL** = 13; **TL** = 12. Surface of **OPL** with a carina on each side behind the posterior ocelli. Antennomeres in following proportions: 24:12:28:30:27:27:25:20:17:25. Antenna with rhinaria on flagellomeres 1–8 and occupying about entire extension of flagellomere (Fig. 5B). Occipital carina (Figs 3A, C, F, 4C) complete and well developed, with short and sparse perpendicular carinae (Fig. 5B) forming a trabecular band. Dorsal surface of propodeum distinctly shorter than posterior surface (15:30); posterior surface with a pair of long longitudinal carinae. Fore leg (Fig. 3E) in the following proportions: 25 (coxa): 28 (trochanter): 63 (femur): 65 (tibia), 30: 6: 8:27: 30 (tarsomeres 1–5), and 26 (enlarged claw). Claws of meso and meta legs without basal expansion; apex of protarsomere 3 (Fig. 4B) with four long bristles and apex of protarsomere 5 with two long lamellae; apex of enlarged claw pointed, without lateral teeth and with one large lamella; enlarged claw and protarsomeres 5 with lamellae (measurements could not be taken because the chela is closed).

Remarks. Same as for the genus.

Key to the genera of *Thaumatodryininae*

1 Mandible with four large, subequal teeth; antenna with rhinaria on flagellomeres 3–8 and located in basal third of sclerite; occipital carina variable, complete or incomplete; notauli variable, but never indicated as deep sulci; pointed apex of enlarged claw forming an almost right angle with the main shaft and provided with two subapical teeth; dorsal surface of propodeum continuous with its posterior surface, giving it a convex profile in lateral view; posterior surface of propodeum without longitudinal carinae ..... ***Thaumatodryinus*** **Perkins 1905**

– Mandible with three large teeth and one smaller rudimentary tooth (Fig. 5A); antenna with rhinaria on all flagellomeres and occupying about their entire extension (Fig. 5B); occipital carina complete (Fig. 5B); notauli percurrent and indicated as deep sulci; apex of enlarged claw gently curved in relation to the main shaft, lateral teeth absent; dorsal surface of propodeum separated from its posterior surface by a well-marked edge, the two surfaces practically forming a right angle; posterior surface of propodeum with a pair of longitudinal carinae .... †***Thaumatorrhinos*** **gen. nov.**

4. Discussion

Thaumatodryininae were recovered as a monophyletic group and placed distantly from Dryininae, a result that corroborates the hypothesis presented by Tribull (2015) using molecular data. The placement of Thaumatodryin-

inae as a clade apart from Dryininae was strongly supported by the data. Our analyses also allowed the positioning of a mid-Cretaceous amber fossil, described here as †*Thaumatorrhinos* **gen. nov.**, in Thaumatodryininae and coming out as sister group of *Thaumatodryinus*, previously the only genus recognized in this subfamily. Therefore, we expand the scope of the subfamily by adding a new lineage, which exhibits a series of plesiomorphic features when compared to *Thaumatodryinus*. The discovery of †*Thaumatorrhinos* **gen. nov.** revealed that Thaumatodryininae can be considered an independent lineage at least since the mid-Cretaceous, thus being much older than the previously assumed Eocene age (Martins and Melo 2020).

This new fossil also allowed us to refine the scenario involving the evolution of the rhinaria, a remarkable feature present on the female antennae of some dryinid subfamilies (Olmi 1984). The term rhinaria was introduced by Olmi (1984: 19–20) to refer to the fine grooves on the flagellomeres. They represent specialized sensory organs, apparently involved in host finding, and their ultrastructure has been investigated by Riolo et al. (2016), who renamed them as "antennal dorsal organs". The condition of the rhinaria in †*Thaumatorrhinos* **gen. nov.** resembles that observed in Gonatopodinae and Dryininae, except for being present also on the two basal-most flagellomeres and for extending along the entire length of the flagellomeres. Since the rhinaria in †*Thaumatorrhinos* **gen. nov.** (and for that matter in Gonatopodinae and Dryininae as well) lack the characteristic long setae seen in *Thaumatodryinus*, we can conclude that the latter genus has an apomorphic condition.

Placement of †*Thaumatorrhinos* **gen. nov.** in Thaumatodryininae is strongly supported by the following characters: mandible with abrupt curvature near the base, making almost a right angle; vertex with a distinctly convex profile; 3rd protarsomere with differentiated bristles longer than the tarsomere; antennal alveolus separated from the epistomal suture by at least half of the alveolus diameter; pronotum with transversal impression located at its mid length. Despite that, †*Thaumatorrhinos* **gen. nov.** exhibits many features that clearly separates it from *Thaumatodryinus*, justifying its recognition as a distinct genus.

Possession by †*Thaumatorrhinos* **gen. nov.** of a small, "rudimentary" tooth in the mandible is also observed in the subfamilies Aphelopinae, Bocchinae, and Conganteoninae. Character optimization indicated independent gains of this condition in the two lineages (see Fig. 2, character 5:0). Although being a slightly less parsimonious explanation, the condition in †*Thaumatorrhinos* **gen. nov.** could also represent a retained plesiomorphy, with the more derived condition seen in *Thaumatodryinus*, with four progressively enlarged teeth, having evolved independently from that seen in Gonatopodinae and Dryininae.

Currently, several fossil species belonging to different groups of Dryinidae have been described from different fossil deposits, mainly from Burmese amber (Martynova et al. 2019, 2020; Martins and Melo 2019, 2020; Perkovsky et al. 2019; Tribull et al. 2020; Olmi et al. 2020, 2021, 2022; Wang et al. 2021), especially taxa belonging to Dryininae. Although they have not been included in our phylogenetic analyses, a series of unequivocal characters support the position of †*Thaumatorrhinos* **gen. nov.** in Thaumatodryininae, and not in Dryininae, such as: mandible with abrupt curvature near the base, making almost a right angle; vertex with a distinctly convex profile; 3rd protarsomere without differentiated bristles longer than the tarsomere; antennal alveolus separated from the epistomal suture by at least half of the alveolus diameter; pronotum with transversal impression located at its mid length; apex of the enlarged claw with a lamella about 1.5x the length of the others; and tooth at the apex of the elongated claw not curved with a flattened dorsal surface. Additional characters differentiating †*Thaumatorrhinos* **gen. nov.** from other extinct genera of Dryininae, such as †*Hybristodryinus* Engel, are the presence of rhinaria in all flagellomeres; fore wing with vein 3Rs&4Rs much longer than 2r-rs and reaching apex of wing; and the tibial spur formula 1:1:2.

Our results reinforce the importance of fossils for improving our understanding of the evolutionary history of different insect groups, in particular of Dryinidae. These records, together with the study of the extant fauna and using phylogenetic tools, have made it possible to correctly position, interpret and reinterpret different characteristics present in these lineages and to understand the evolutionary history of the family.

5. Declarations

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Competing Interest: The authors have declared that no competing interests exist.

Authors' contributions: GARM obtained the piece preserved in amber. ALM and GARM planned, prepared, and designed the study. GARM made the drawings. ALM did the photography, constructed the characters, performed the cladistic analyses, and described the new taxa. ALM and GARM wrote the manuscript, discussed the results, and revised the manuscript. Both authors have read and approved the final version of the manuscript.

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Supplementary Material 1

Figures S1, S2

Authors: Martins AL, Melo GAR (2024)
Data type: .pdf
Explanation notes: Figure S1. Consensus tree under parsimony analysis with equal weighting of characters (8 trees; 237 steps; Ci = 50; Ri = 77). — **Figure S2.** Most parsimonious tree resulting from a cladistic analysis under implied weighting (k = 3) of 100 morphological characters and 22 terminal taxa, focusing on Thaumatodryininae (Hymenoptera, Dryinidae). Character-state transformations are shown under acctran optimization, depicted as solid (unique transformations) and empty circles (reversals or multiple transformations). Branch support indicated for the major clades is derived from symmetrical resampling.

Link: https://doi.org/asp.82.e106734.suppl1

Supplementary Material 2

Table S1

Authors: Martins AL, Melo GAR (2024)
Data type: .pdf
Explanation notes: Matrix of morphological characters and states used for the phylogenetic analyses.

Link: https://doi.org/asp.82.e106734.suppl2