

# Chrysidid wasps (Hymenoptera: Chrysididae) from Cretaceous Burmese amber: Phylogenetic affinities and classification

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## ABSTRACT

Representatives of chrysidid wasps are described for the first time from inclusions in Late Cretaceous Burmese amber. Five new genera and new species are described and illustrated: †*Auricleptes nebulosus* gen. et sp. nov., †*Azanichrum pilosum* gen. et sp. nov., †*Bohartiura glabrata* gen. et sp. nov., †*Burmasega ammirabilis* gen. et sp. nov., and †*Miracorium tetrafoveolatum* gen. et sp. nov. We coded 49 morphological characters for species representing the subfamilies Amiseginae, Loboscelidiinae, Cleptinae and Chrysidinae. The cladistic analysis recovered the following relationships: Cleptinae + (†*Auricleptes* + (†*Burmasega* + (†*Miracorium* + ((Loboscelidiinae + Amiseginae) + ((†*Azanichrum* + †*Bohartiura*) + (†*Palaeochrum* Krombein + (extant Chrysidinae)))))). In light of the cladistic results, we discuss the implications of characters for the interpretation of phylogenetic relationships within the family, and explore the main morphological changes occurred during the diversification of the chrysidid wasps.

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## 1. Introduction

The diversity of Cretaceous insects revealed by inclusions in Burmese amber has increased considerably in recent years (e.g. Ross et al., 2010; Grimaldi, 2016; Guo et al., 2017; Ross, 2017). Many of the described taxa have no counterparts in the extant fauna, with some of them exhibiting very unique morphologies (e.g. Engel et al., 2016; Perrichot et al., 2016; Barden et al., 2017; Rasnitsyn et al., 2017).

In Hymenoptera, much of the diversity is represented by families with extant descendants, although 12 of the 37 recorded families constitute extinct lineages (compiled from Ross, 2017, with modifications). Among the stinging Hymenoptera (Aculeata), 13 families have representatives in Burmese amber, with a single family—Formicidae—containing almost half of the described species (20 of 50 named species). In Chrysoidea, the 12 described species belong to the families Bethyridae, Dryinidae, Embolemidae and Falsiformicidae (*Burmomyrma* is most likely a falsiformicid, and not a formicid as proposed originally by Dlussky (1996), and the two putative Scolebythidae described recently by

Cockx and McKellar (2016) probably do not belong in this family; Melo, unpubl. data).

Up to now, chrysidid wasps have not been reported from Burmese amber. Chrysididae are a diverse group mostly composed of parasitoid and cleptoparasitic wasps distributed worldwide. The clade is divided into four main groups: (1) the Cleptinae, which parasitize prepupal larvae of sawfly wasps; the clade composed of the pan-tropical (2) Amiseginae and (3) Loboscelidiinae, both containing parasitoids specialized on eggs of phasmatodean walking sticks; and (4) the colorful clade composed of the chrysidine cuckoo wasps, which are specialized cleptoparasites attacking primarily other solitary aculeate hymenopterans (Kimsey and Bohart, 1991).

The oldest fossils assigned to the family are dated from the Late Cretaceous amber of Canada (Canadian amber; Campanian) (Evans, 1969; McKellar and Engel, 2014), Siberia (Taimyr amber; late Cenomanian and Santonian) (Evans, 1973; Krombein, 1986), and France (Charentese amber; late Cenomanian) (Cockx et al., 2016). Other taxa assumed to be closely related to the living groups are known from the Eocene amber deposits of the Baltic region (Brues, 1933; Krombein, 1986), Russia (Kaliningrad) (Bischoff, 1916), and Ukraine (Rovno) (Perkovsky and Rasnitsyn, 2013); and taxa from the early Miocene from the Dominican Republic (Engel, 2006).

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A few Cenozoic compression fossils are also known from different localities worldwide (Giebel, 1862; Förster, 1891; Cockerell, 1907; Bischoff, 1916).

Cuckoo wasps of the subfamily Chrysidinae have not previously been recorded from the Cretaceous period. The earliest record of the group is from Baltic amber inclusions of the Eocene (Brues, 1933; Krombein, 1986). Modern Chrysidinae are distributed worldwide with greatest diversity in arid areas. Only members of the Cleptinae and Amiseginae have been described from Cretaceous amber. The Cleptinae are represented by three fossil genera from the Late Cretaceous: †*Procleptes* Evans, 1969 (3 spp.) from Canada (McKellar and Engel, 2014); the monotypic †*Hypocleptes rasnitsyni* Evans, 1973 from Siberia; and †*Sphaerocleptes neraudeai* Cockx et al., 2016 from France. Based on morphological similarities these taxa have been considered as closely related to the extant genus *Cleptes* Latreille, 1802 (sensu Kimsey and Bohart, 1991). Living Cleptinae comprise species of *Cleptes* occurring in the Holarctic region (with a single known representative from the Neotropics), and *Cleptidea* Mocsáry, 1904, a genus restricted to the tropical areas of the Neotropical region. The Amiseginae are represented by two monotypic genera from the Late Cretaceous and Eocene, respectively: †*Protamisega kathanga* Evans, 1973 from Siberia (Taymir amber) and †*Protadelphe aenea* Krombein, 1986 from Baltic amber. Several recent studies on the modern fauna of Amiseginae from the Oriental region have demonstrated how limited is our knowledge about the diversity of this group (Kimsey, 1986a, 1990, 1995, 2005, 2011, 2014a, b; Kimsey et al., 2013, 2016). The same holds for the extinct fauna, since a large number of the chrysidid inclusions in Burmese amber apparently represent undescribed amisegine taxa (Lucena and Melo, unpubl. data).

In this paper, we present the first record of Chrysididae in inclusions of Burmese amber from the Upper Cretaceous with descriptions of five new genera and species. We discuss the phylogenetic affinities of the new taxa and explore the main morphological changes that occurred in the evolution of the clade. We also present new morphological characters and discuss their implications for the classification and interpretation of the phylogenetic relationships among subfamilies and tribes of Chrysididae.

## 2. Material and methods

### 2.1. Preparation of specimens and morphological study

The studied amber pieces came from the Hukawng Valley, near Tanai, Kachin state, in northern Myanmar (a map of the fossil locality can be found in Kania et al., 2015: fig. 1). Burmese amber has been dated as originating in the early Cenomanian, at about 99–98 Ma (Shi et al., 2012). The pieces are deposited in the Department of Zoology (DZUP) of the Universidade Federal do Paraná (UFPR) under care of the second author. In order to have a better view of the inclusions at least one surface of each piece was trimmed with a precision diamond-wire saw (Well model 3032-4, USA) and/or ground with wet emery paper in a rotary polisher (Aropol model VV200PU, Brazil) at the facilities of UFPR's Microscopy Center. Final polishing was carried out in the same rotary polisher using aluminum oxide (grits of 1 and 0.3 µm).

Inclusions were studied using a Leica M125 stereomicroscope. Photographs were taken using a Leica DFC295 camera attached to the stereomicroscope. Images were improved using Zerene Stacker® software to combine multiple images then enhanced with Adobe Photoshop®. Morphological terminology follows that of Kimsey and Bohart (1991). The abbreviations F, S and T are employed for flagellomeres, metasomal sterna, and metasomal terga, respectively. MOD refers to the diameter of the mid ocellus.

### 2.2. Cladistic analysis

We performed a cladistic analysis of Chrysididae with a matrix of 49 characters (Table 1). Among those, 17 characters are newly proposed and 32 were taken from Table 8 of Carpenter (1999), which is a revision of the morphological studies originally carried out by Bohart and Kimsey (1982), Kimsey (1986b), and Kimsey and Bohart (1991). We excluded Carpenter's characters 9 and 21, because they are only informative when including representatives of Allocoeliini (not sampled in our study). In order to reflect the actual conditions observed in the studied taxa, we re-interpreted characters 12, 28 and 33 of Carpenter (1999). His character 12 (pronotal pit) actually conflates two distinct morphological conditions observed within the Amiseginae (see Table 1: characters 16 and 17; see also Kimsey and Bohart, 1991: 75). Carpenter's character 28 (metasomal spiracles) was also divided into two distinct characters, because the position of the spiracles in the metasomal terga is variable and reflect distinct character conditions (characters 40 and 41 in Table 1). We also changed his character 33 (ovipositor tube), since the number of metasomal segments composing the ovipositor tube varies among the chrysidids. In Cleptinae and Amiseginae, the tube is composed of segments V–VIII; in Chrysidini, Elampini and Parnopini, it is composed of segments IV–VII; and in Allocoeliini it is composed of segments III–VII (Kimsey and Bohart, 1991: 34–35; see character 47 in our Table 1).

In addition to the fossil taxa herein described, we included in our analyses the previously described fossil †*Palaeochrum* Krombein, 1986 (Eocene, Baltic amber) and representatives of extant groups of Chrysididae (Table 2). We included †*Palaeochrum* because it is supposed to be an Elampini (Krombein, 1986), which has raised questions concerning the morphological evolution in the chrysidine clade. The characters for this taxon were coded based on the original description presented by Krombein (1986). We also included 15 terminal species representing the four major extant chrysidid groups (Table 2): Cleptinae (3 spp.), Loboscelidiinae (1 sp.), Amiseginae (4 spp.), and Chrysidinae (Chrysidini 3 spp.; Elampini 3 spp.; and Parnopini 1 sp.).

Outgroups were represented by *Trigonalys* Westwood (Trigonalidae), *Plumarius* Philippi (Plumariidae) and *Apenesia* Westwood (Bethyldidae). For the purpose of this study, we consider that it is not necessary to have a larger number of outgroup terminals, since the monophyly of Chrysididae is well supported in many phylogenetic studies (e.g., Day, 1979; Carpenter, 1986, 1999; Brothers and Carpenter, 1993; Brothers, 1999, 2011; Ronquist et al., 1999; Branstetter et al., 2017). We aim to evaluate here the phylogenetic position of the representatives of the extinct fauna among the main clades of Chrysididae and how the morphological characters are informative for supporting the clades. Trees were rooted between *Trigonalys* and the other analyzed species in accordance with recent molecular phylogenetic hypotheses for Hymenoptera (Branstetter et al., 2017; Peters et al., 2017).

The morphological characters were assembled into a matrix using the software Winclada (Nixon, 2002). We used the same treatment as Carpenter (1999) for his multistate characters (additive and non-additive). The data matrix was analyzed under implied weighting (with the default  $k = 3$ ) as implemented in the software TNT (Goloboff et al., 2003, 2008a), version 1.5 (Goloboff and Catalano, 2016). 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., 2008b; Goloboff, 2014). For comparative purposes, an equal weight analysis was also carried out in TNT. Character state transformations were visualized using Winclada under an unambiguous optimization scheme, with unsupported branches collapsed.

**Table 1**

List of morphological characters used in the phylogenetic analysis. Characters taken from [Carpenter \(1999\)](#) are marked with a “(C)”. Multistate characters are treated as additive, except when indicated. Character length and indices (steps: ‘L’; consistency index: ‘Ci’, and retention index: ‘Ri’) based on the strict consensus of [Fig. 6](#). Those marked with [A] represent autapomorphies.

1. Maxillary palp: six (0); five (1); four (2); two (3). [non-additive] [L:3, Ci:100, Ri:100].
2. Scapal basin (C): absent (0); present (1). [L:1, Ci:100, Ri:100].
3. Front: indistinct, not elongated (0); elongated (1). [L:3, Ci:33, Ri:66].
4. Frontal sulcus: absent (0); present (1). [L:2, Ci:50, Ri:75].
5. Malar sulcus (C): absent (0); present (1). [L:2, Ci:50, Ri:75].
6. Mandible form: apical margin truncate (0); apical margin pointed (1). [L:1, Ci:100, Ri:100].
7. Mandible, subapical teeth: four (0); three (1); two (2); one (3); none (4). [non-additive] [L:3, Ci:100, Ri:100].
8. Antennal position (C): inserting low on face (0); inserting midface (1). [L:3, Ci:33, Ri:0].
9. Genal carina (C): absent (0); present (1). [L:2, Ci:50, Ri:87].
10. Pre-occipital carina (C): absent (0); present (1). [L:1, Ci:100, Ri:100].
11. Transfrontal carina (C): absent (0); present (1). [L:2, Ci:50, Ri:75].
12. Cervical projection (C): absent (0); present (1). [A].
13. Tongue (C): flat short (0); protruding, long and slender (1). [L:1, Ci:100, Ri:100].
14. Pronotum (C): quadrate, short collar (0); narrowed, long collar (1). [L:3, Ci:33, Ri:66].
15. Pronotal lobe (C): adjacent to tegula (0); separated from tegula (1). [L:2, Ci:50, Ri:90].
16. Posteromedial pronotal pit, situated on the pronotal dorsum (re-interpreted from [Carpenter \(1999\)](#)): absent (0); present (1). [A].
17. Pronotal lobe pit, situated at origin of the pronotal lobe (re-interpreted from [Carpenter \(1999\)](#)): absent (0); present (1). [L:1, Ci:100, Ri:100].
18. Longitudinal sulcus of pronotum: absent (0); present (1). [L:3, Ci:33, Ri:66].
19. Transverse sulcus of pronotum: absent (0); present (1). [L:4, Ci:25, Ri:57].
20. Prosternum (C): exposed (0); obscured by propleuron (1). [L:4, Ci:25, Ri:57].
21. Prothorax (C): freely moveable (0); fused to mesothorax (1). [A].
22. Tegular clip (C): absent (0); present (1). [A].
23. Tegula (C): covering forewing base (0); covering both wing bases (1). [L:2, Ci:50, Ri:0].
24. Mesopleuron, scrobal sulcus (C): short, shallow, oblique (0); broad, horizontal (1); broad pit (2); absent (3) [non-additive]. [L:9, Ci:33, Ri:25].
25. Epimeral plate (C): absent (0); present (1). [A].
26. Scutellar lobe (C): absent (0); present (1). [L:1, Ci:100, Ri:100].
27. Metapleural carina (C): absent (0); present (1). [L:1, Ci:100, Ri:100].
28. Metanotum, size: much reduced (0); as long as or slightly shorter than mesoscutellum (1); distinctly longer than mesoscutellum (2). [L:3, Ci:66, Ri:85].
29. Metanotum, surface: unmodified (0); deeply foveate (1); with shallow lateral foveae and elevated disk (2); spoon-like (3); mucronate (4); pulvinate (5) [non-additive]. [L:7, Ci:57, Ri:50].
30. Propodeal spiracles: dorsal (0); latero-ventral (1). [L:2, Ci:50, Ri:87].
31. Propodeal dorsal surface: long (0); short, shelf-like (1); absent (2). [L:4, Ci:50, Ri:87].
32. Tarsal claw (C): unidentate (0); more than one tooth (1); simple (2). [non-additive]. [L:5, Ci:40, Ri:57].
33. Wing venation reduction (C): not extreme (0); extreme, pterostigma, C, cu-a and hindwing veins absent (1). [A].
34. Forewing, RS + M (C): originating near base of M (0); originating near apex of M (1). [L:2, Ci:50, Ri:50].
35. Number of enclosed cells on forewing: ten (0); seven (1); six (2); five (3); four (4); three (5); one (6). [non-additive]. [L:7, Ci:85, Ri:50].
36. Costal cell: broad (0); narrow (1). [L:2, Ci:50, Ri:66].
37. Female terga (C): six (0); four (1); three (2); two (3). [L:3, Ci:100, Ri:100].
38. Male terga (C): seven (0); five (1); four (2); three (3); two (4). [L:5, Ci:60, Ri:84].
39. Metasomal sterna (C): convex (0); concave or flat (1). [L:1, Ci:100, Ri:100].
40. Metasomal tergum I, spiracle (re-interpreted from [Carpenter \(1999\)](#)): not on laterotergite (0); on laterotergite (1). [L:1, Ci:100, Ri:100].
41. Metasomal terga II and III, spiracles (re-interpreted from [Carpenter \(1999\)](#)): not on laterotergites (0); on laterotergites (1). [L:2, Ci:50, Ri:85].
42. Tergum III (C): evenly curved (0); with subapical pit row or traces (1). [L:1, Ci:100, Ri:100].
43. Tergum III rim (C): smooth (0); dentate or angulate (1); thickened, with denticles and foveae (2) [non-additive]. [L:2, Ci:100, Ri:100].
44. Sternum II spots (C): absent (0); present (1). [L:1, Ci:100, Ri:100].
45. Metasomal sterna, plates: undivided (0); divided (1). [L:1, Ci:100, Ri:100].
46. Digitus (C): lobate (0); elongate (1); absent (2) [non-additive]. [L:3, Ci:66, Ri:75].
47. Ovipositor tube, shape, segments V–VIII (re-interpreted from [Carpenter \(1999\)](#)): large and robust (0); needle-like (1). [L:1, Ci:100, Ri:100].
48. Sting: long, well-sclerotized (0); reduced, soft (1). [L:2, Ci:50, Ri:66].
49. Hosts (C): Lepidoptera or Coleoptera prepupae (0); sawfly prepupae (1); Phasmida eggs (2); Aculeata (3); [non-additive]. [L:3, Ci:100, Ri:100].

### 3. Systematic paleontology

Order Hymenoptera Linnaeus  
 Superfamily Chrysidoidea Latreille  
 Family Chrysididae Latreille  
 Subfamily *Incertae sedis*

Genus †*Auricleptes* gen. nov.

LSID: urn:lsid:zoobank.org:act:A03291CF-362D-4DA3-AD4F-6F9E6293C3D0

Type species. †*Auricleptes nebulosus* sp. nov.

**Diagnosis.** Metanotum distinctly longer than mesoscutellum; propodeal lateral process largely lobulate, “ear-like”; sting long, curved and well-sclerotized; mesoscutum with strong preaxillar carina; lateral margin of pronotum delimited by sharp produced carina; dorsal surface of propodeum short, “shelf-like”; pronotum intersected by strong medial longitudinal sulcus and anterior transverse groove; mesopleuron with distinct transverse scrobal sulcus.

**Description. Head:** front not protruded; posterior margin well excavated; eye protuberant; scapal area slightly convex, with strong longitudinal sulcus from antennal sockets towards median ocellus; facial carinae absent; least ocular distance wide, as long as scapal length; inner ocular margins subparallel, slightly convergent above, divergent below; gena indistinct, without carina; antennal insertion adjacent to clypeal margin; clypeus apparently very short; antenna composed of eleven cylindrical flagellomeres; scape long, stout; relatively long pedicel, as long as F3. **Mesosoma:** prosternum exposed, not reduced or hidden. Pronotum collar-shaped, longer than broad, intersected by strong medial longitudinal and anterior transverse sulci; anterior area declivitous, constricted at the head insertion; lateral lobe well developed and reaching tegula, without pits; lateral margin delimited by sharp produced carina; posterior margin evenly rounded to mesoscutum. Notauli deeply impressed, lateral area of mesoscutum protruded, largely lobulate; preaxillar carina strongly produced; parapsidal lines discretely marked anterolaterally; mesoscutellar lobe absent.

**Table 2**  
Morphological data matrix. The symbol “?” stands for missing data; “-” for inapplicable characters; “\$” for polymorphisms. The subset of polymorphisms are: *Trigonalys melanoleuca* [1,2], *Adelpho hyalophora* [1,2,4], and *Stilbum cyanurum* [3,4].

| Species                             | Characters  |            |             |            |            |
|-------------------------------------|-------------|------------|-------------|------------|------------|
|                                     | 1–10        | 11–20      | 21–30       | 31–40      | 41–49      |
| <i>Trigonalys melanoleuca</i>       | 000000\$100 | 0000000001 | 0003000000  | 0000000100 | 00000?–0   |
| <i>Plumarius</i> sp.                | 0000002100  | 0000000001 | 0003000000  | 0001100000 | 000000–00  |
| <i>Apenesia</i> sp.                 | 0010000000  | 0000000000 | 0002000020  | 000–500000 | 000002–00  |
| † <i>Auricleptes nebulosus</i>      | 10010?7000  | 00?1000110 | 000100020?  | 100–511?0? | ?0000?00?  |
| † <i>Burmasega ammirabilis</i>      | 1111112000  | 00?1000011 | 000100010?  | 1001311?0? | ?0000?00?  |
| † <i>Miracorium tetrafoveolatum</i> | 1100012000  | 00?1000010 | 000300011?  | 120–50?10? | ?0000????  |
| <i>Cleptes fritzi</i>               | 1001002000  | 0001000010 | 0003000120  | 0000511100 | 000000011  |
| <i>Cleptidea mutilloides</i>        | 1001002000  | 0001000110 | 0003000120  | 000–511100 | 000000011  |
| <i>Cleptidea xanthomelas</i>        | 1001002000  | 0001000110 | 0003000120  | 0000511100 | 000000011  |
| <i>Loboscelidia</i> sp.             | 1110014100  | 0100000001 | 1110000001  | 201–6–1100 | 000001112  |
| <i>Adelpho hyalophora</i>           | 2110115000  | 0000001011 | 0001000021  | 000–511100 | 100001112  |
| <i>Amisega aeneiceps</i>            | 2110114000  | 0000101001 | 0003000001  | 000–511100 | 100001112  |
| <i>Amisega semiflava</i>            | 2110114000  | 0000101001 | 0003000001  | 000–511100 | 100001112  |
| <i>Duckeia cyanea</i>               | 2110114000  | 0000111001 | 0003000001  | 000–511100 | 100001112  |
| † <i>Azanichrum pilosum</i>         | 11000?7010  | 10?0000010 | 000100115?  | 120121?11? | ?000?????  |
| † <i>Bohartiura glabrata</i>        | 11000?7010  | 10?1000000 | 000300110?  | 100–511?1? | ?0000?–1?  |
| † <i>Palaeochrum diversum</i>       | ?000012010  | 00?010000? | 000?70?10?  | 120151?21? | ?00??????? |
| <i>Elampus gayi</i>                 | 1100012010  | 0010100000 | 0000001140  | 210–512310 | 001011–13  |
| <i>Hedychrum neotropicum</i>        | 1100012000  | 0010100000 | 0003001100  | 2001512310 | 000011–13  |
| <i>Holopyga iheringia</i>           | 1100012010  | 0010100000 | 0000001100  | 2101512310 | 000011–13  |
| <i>Parnopes grandior</i>            | 3100013010  | 0010100100 | 0013101141  | 2201512211 | 102012–13  |
| <i>Chrysis intricata</i>            | 1100013011  | 1010100100 | 0001011101  | 2201312311 | 111111–13  |
| <i>Caenochrysis parvula</i>         | 1100013011  | 1010100100 | 0001011101  | 2201312311 | 111111–13  |
| <i>Stilbum cyanurum</i>             | 1100013011  | 1010100100 | 00010111\$1 | 2201412311 | 111111–13  |

Mesoscutellum two-thirds as long as mesoscutum; dorsum without sulcus or foveae, at the same dorsal plane as mesoscutum. Metanotum longer than mesoscutellum; dorsum flattened, without sulcus or foveae, with some indistinct lateral sculpture; dorsal limit slightly below that of mesoscutellum; dorsomedial junctures linear between mesoscutum-mesoscutellum, and mesoscutellum-metanotum. Mesopleuron round anteriorly, ecarinate, with distinct transverse scrobal sulcus medially; posterior area deflected with sharp margins. Tibial spur formula 1–2–2; tarsal claws with a single preapical tooth; hind femur enlarged dorsoventrally. Fore wing with three enclosed cells: costal, medial and sub-medial; *Rs* long, roundly curved towards costal margin almost enclosing the marginal cell; *M* diverging from *M+Cu* at *1cu-a*; *R1* longer than stigma; most other veins nebulous. Dorsal surface of propodeum short, “shelf-like”, indistinctly carinate marginally; posterior surface with distinct medial ridge in dorsal view; lateral propodeal process largely lobulate, “ear-like”. **Metasoma**: metasomal petiole absent; four exposed terga; ovipositor apparatus partially exposed; sting long, sclerotized, slightly curved; metasomal sterna convex. **Taxonomic remarks**. †*Auricleptes* gen. nov. superficially resembles representatives of Cleptinae, but it is readily distinguished by a combination of distinctive though not unique traits, such as: pronotum intersected anteriorly by a transverse groove and longitudinally by a medial sulcus (both absent in †*Hypocleptes*, †*Sphaerocleptes* and †*Procleptes*; variable in extant Cleptinae); dentate tarsal claws (reduced or edentate in †*Procleptes*); and the long, curved and well-sclerotized sting (reduced in extant Cleptinae; unknown in †*Procleptes*, †*Hypocleptes* and †*Sphaerocleptes*). Moreover, the flattened metanotum, longer than mesoscutellum (metanotum shorter than mesoscutellum in *Cleptes*, *Cleptidea*, †*Hypocleptes* and †*Procleptes*, and with posterior convexity projecting posteriorly over propodeum in †*Sphaerocleptes*), and the propodeal lateral process large and lobulate (differently shaped in †*Procleptes*, *Cleptes* and *Cleptidea*; short and round in †*Hypocleptes* and †*Sphaerocleptes*) are unique to this taxon. **Etymology**. The genus name is a combination of words derived from the Latin *auris* (“ear”, noun), referring to the large “ear-shaped”

lateral processes of the propodeum, and *cleptes*, meaning “thief”, as used for the extant genus *Cleptes*. The name is masculine.

†*Auricleptes nebulosus* sp. nov.

LSID: urn:lsid:zoobank.org:act:5AA91D20-68AE-4E4F-8C6B-33789C3FF8FB  
(Fig. 1A–D)

**Description**. Holotype female. Approximate body length: 3.0 mm. **Head**: head dark; antennae brown; eyes with abundant short, sub-erect setae; ocelli set dispersed in a triangle at the median front, inserted in small depressions; lateral ocelli closer to ocular orbit than to each other; malar space longer than F1 length; F1 slightly longer than F2; F2–F11 subequal in length. **Mesosoma**: pronotum and mesoscutum dark; mesoscutellum and metanotum brown; coxae, trochanters and femora dark; tibiae and tarsi with a lighter color; anterior basitarsus with numerous long spines on the inner surface; anterior tibial spur distinctly long; wings hyaline with light brown veins; forewing membrane entirely setose. **Metasoma**: metasoma dark; metasomal sterna with short erect setae. **Integumental sculpture**: integument mostly smooth, but with some wrinkles on the head and terga perhaps due to compression; dorsum of mesosoma finely punctate.

**Type material**. Holotype female, in amber piece DZUP 027632 (Bur-244). The specimen is well preserved, but the body is somewhat flattened and with some distorted parts, in particular the antennae.

**Etymology**. The species name is a Latin adjective, meaning “obscure”, in reference to the phylogenetic affinities of this taxon.

Subfamily *Incertae sedis*

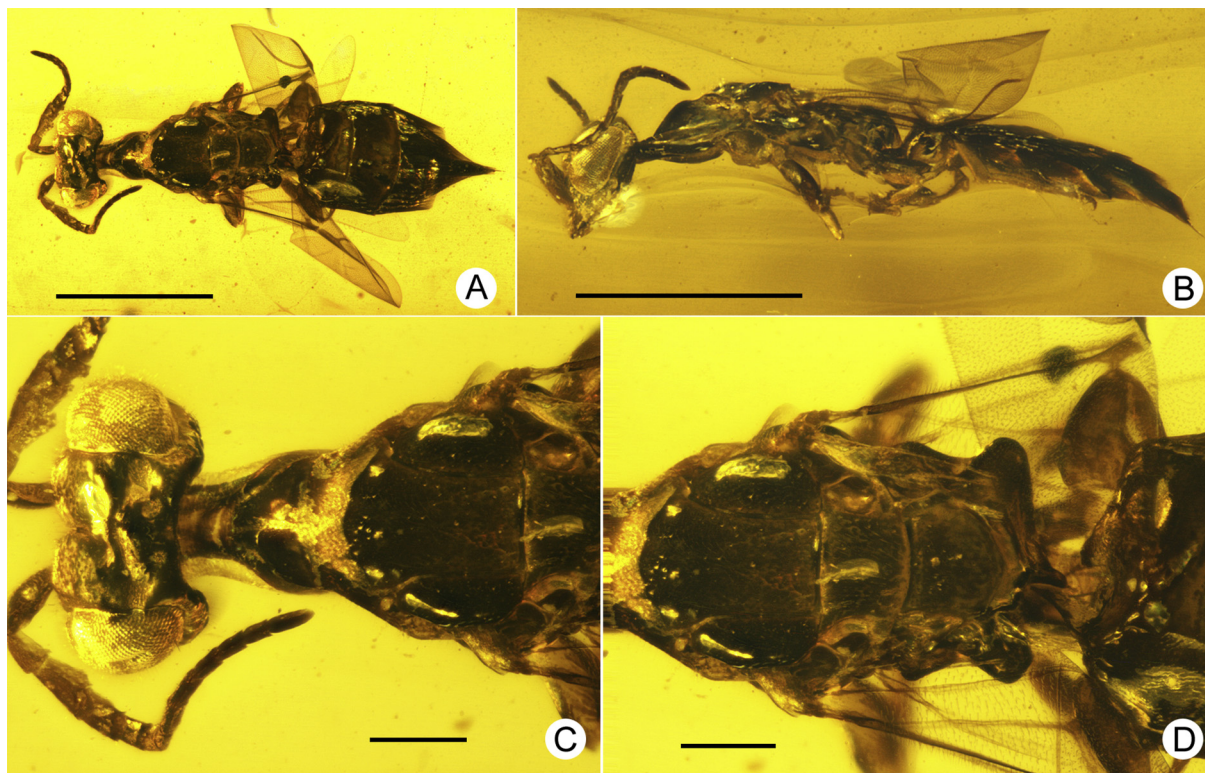
Genus †*Burmasega* gen. nov.

LSID: urn:lsid:zoobank.org:act:AA27D9BA-7E18-4838-A93F-A659398E18EE

Type species. †*Burmasega ammirabilis* sp. nov.

**Diagnosis**. Metanotum as long as mesoscutellum; mesopleuron partially bisected by scrobal sulcus connected to anterior deep drop-shaped fovea; pronotum with anterior transverse groove





**Fig. 1.** †*Auricleptes nebulosus* Lucena & Melo, gen. et sp. nov. (A) Habitus dorsal; (B) habitus lateral; (C) dorsal view of pronotum; (D) dorsal view of metanotum and propodeum. Scale bars: A–B: 0.5 mm. C–D: 0.2 mm.

extending laterally towards mesopleuron; lateral pronotal margin with strong pre-marginal sulcus forming a lamellar edge; metasomal T1–T2 with strong anterolateral carina; fore wing with five enclosed cells; scapal basin excavated; propodeal lateral process with distinct lamellar edge from the apex towards posterior margin of propodeum; posterior margin of metasomal sterna convex; ovipositor tube robust with long, well-sclerotized, sting.

**Description. Head:** front well developed; eye bulging; occipital carina short, partially developed at the supra-posterior angulation of eye; lateral gena ecarinate; head without posterior angulation; vertex without median ridge; least ocular distance wide, as long as the scapal length; ocelli set in compact triangle; scapal basin concave, with medial longitudinal groove from antennal sockets towards median ocellus; malar areas convergent below, shorter than half eye height; malar sulcus present; malar space short, less than F3 length; inner ocular margin subparallel, slightly divergent above; antennal insertion adjacent to clypeal margin; clypeus very short. Antenna with long stout scape, relatively long pedicel, as long as F3, and 11 subequal cylindrical flagellomeres; F4–F11 with distinct ventral sensory areas. Maxillary and labial palpi composed respectively of five and three articles; mandible tapering apically, well sclerotized, with two subapical teeth. **Mesosoma:** prosternum reduced, partially hidden under propleuron. Pronotum collar-shaped, longer than broad, with anterior declivitous area and marked anterior transverse groove; anterior area furrowed transversely and constricted at head insertion; lateral lobe well developed and reaching tegula, without pits; lateral margin with pre-marginal sulcus forming a lamellar edge; posterior margin evenly rounded to the mesoscutum. Notauli deeply marked; parapsidal lines discrete. Mesoscutellar lobe absent; mesoscutellum two-thirds as long as mesoscutum; dorsum slightly convex, without sulcus or foveae; dorsal limit at same plane as mesoscutum. Mesopleuron ecarinate, unarmed, deflected posteriorly; with anterior

deep drop-shaped fovea; partially bisected by transverse scrobal sulcus. Metanotum as long as mesoscutellum; dorsum without sulcus or foveae; dorsal limit slightly below plane of mesoscutellum. Tibial spur formula 1-2-2; tarsal claws with single sub-medial perpendicular tooth; hind coxa enlarged; hind femur enlarged dorsoventrally. Fore wing with complete venation for the group, five enclosed cells: costal, medial, submedial, discoidal and subdiscoidal. *Rs* curved towards costal margin almost enclosing marginal cell, fading gradually distally. Propodeum partially obscured by wings; dorsal surface apparently short; lateral process pointed and sharp (lateral view), with distinct lamellar edge at lateral margin from apex of process towards posterior margin of propodeum. **Metasoma:** metasomal petiole absent. Four exposed terga; lateral margin of T1 with strong carina extending along anterolateral margin of T2. Sterna convex; posterior margins of plates convex. Ovipositor apparatus partially exposed; tube apparently robust, with relatively long, curved and well-sclerotized sting.

**Taxonomic remarks.** The new taxon is superficially similar to Amiseginae, sharing the characteristic reduced prosternum, which is partially obscured by propleuron, the well-developed front, and presence of malar sulcus. †*Burmasega* gen. nov. differs from extant and extinct amisegines by a combination of distinctive though not unique traits, as such: the long metanotum, as long as the mesoscutellum (short in several extant New World amisegines, and in †*Protamisega* and †*Protadelphe*); the short malar space, shorter than F3 length (much longer in most extant amisegines, and in †*Protamisega* and †*Protadelphe*); the complete wing venation with five enclosed cells (with three or fewer enclosed cells in extant Amiseginae, †*Protamisega*, and †*Protadelphe*); the mesopleuron partially bisected by the scrobal sulcus connected to an anterior deep drop-shaped fovea (variable in extant Amiseginae, absent in †*Protamisega*, and †*Protadelphe*); the long, curved and sclerotized

sting (reduced in extant Amiseginae, unknown in †*Protamisega* and †*Protadelphe*); and the anterolateral pronotum with a strong pre-marginal sulcus forming a lamellar edge (variable in extant Amiseginae, absent in †*Protamisega* and †*Protadelphe*).

**Etymology.** The generic name combines the words *Burma*, referring to the country from which the amber originated, and *-sega*, a suffix widely used in the taxonomy of Amiseginae. The name is feminine.

†*Burmasega ammirabilis* sp. nov.

LSID: urn:lsid:zoobank.org:act:1DD68F7F-BB21-4A41-A3C4-4E398A24B3DB

(Fig. 2A–C)

**Description.** Holotype female. Approximate body length: 3.8 mm.

**Head:** integument finely sculptured; lateral gena smoothly sculptured, without distinct carina or processes, narrowed above; with some elongated setae; F1 longer than length of F2+F3; F2–F11 subequal in size; ocular setae not discernible at 100× magnification. **Mesosoma:** integument finely sculptured; short, suberect, sparse silvery setae on dorsum, especially on pronotum and mesoscutum; propleuron and fore coxa with some elongated setae; anterior basitarsus with numerous short setae on the inner surface; hind tibia with condensed erect setae on outer surface; forewing membrane entirely setose; *M* diverging from *M*+*Cu* slightly before *1cu-a*; short *M* after discoidal cell; *R*1 as long as tubular portion of *Rs*. **Metasoma:** integument finely sculptured; terga with short, suberect, sparse silvery setation on marginal areas.

**Type material.** Holotype female, in amber piece DZUP 027633 (Bur-015). Small, fully winged, well preserved specimen. Coloration indistinct; wings hyaline with brown veins; tarsi light brown. Specimen located at the margins of the small amber cabochon.

**Etymology.** The species name is a Latin adjective for “admirable, wonderful”.

Subfamily *Incertae sedis*

Genus †*Miracorium* gen. nov.

LSID: urn:lsid:zoobank.org:act:2277DFE6-E65B-4F65-AC2A-3910476316ED

Type species. †*Miracorium tetrafoveolatum* sp. nov.

**Diagnosis.** Scapal basin well excavated; head without genal, facial and pre-occipital carinae; pronotum longer than broad, with anterior declivitous narrowed area, and marked anterior transverse groove; anterolateral margin of pronotum somewhat membranous; metanotum with an anterior pair of medial deep foveae followed by a pair of even larger and deeper posterolateral foveae; dorsal surface of propodeum “shelf-like”; fore wing with broad costal cell; tarsal claws simple, edentate.

**Description.** **Head:** front somewhat flattened frontally; eye protuberant; occipital carina absent; vertex without crest or median ridge; facial carinae absent; least ocular distance wide, longer than scapal length; ocelli set in triangle on vertex; scapal basin well excavated, occupying much of facial area; malar areas strongly convergent below; inner ocular margins convergent at ocellar area, strongly divergent below at malar area; lateral gena indistinct; gena smoothly sculptured, without carinae or processes; malar space longer than 2.5× F1; antennal insertion adjacent to clypeal margin; clypeus very short. Antenna with 11 short flagellomeres, somewhat flattened; scape long, stout; pedicel shorter than F1. Maxillary palpus with five articles. Mandible short, well-sclerotized, with two preapical teeth. **Mesosoma:** pronotum

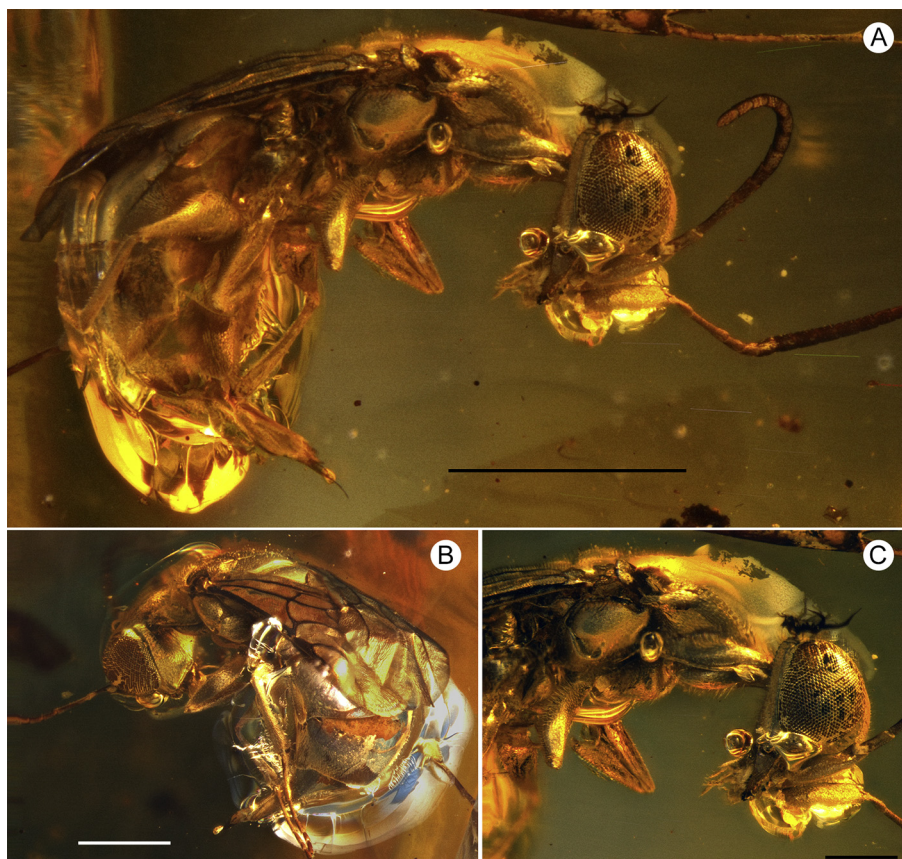


Fig. 2. †*Burmasega ammirabilis* Lucena & Melo, gen. et sp. nov. (A) Habitus lateral; (B) postero-oblique view; (C) lateral view of head and mesosoma. Scale bars: A: 0.5 mm. B–C: 0.1 mm.



longer than broad, with anterior declivitous narrowed area, and marked anterior transverse groove; lateral lobe well developed and reaching tegula; dorsum without longitudinal sulcus; anterolateral margin membranous; posterior margin evenly rounded to the mesoscutum. Notauli deeply impressed; parapsidal lines marked posterolaterally. Mesoscutellar lobes absent; mesoscutellum two-thirds as long as mesoscutum; dorsum slightly convex, without sulcus or foveae, dorsal limit below dorsal plane of mesoscutum. Metanotum as long as mesoscutellum, dorsal limit below dorsal plane of mesoscutellum; with pair of anterior medial small deep foveae followed by pair of even deeper and larger posterolateral foveae. Dorsomedial junctures linear between mesoscutum-mesoscutellum, and mesoscutellum-metanotum. Mesopleuron ecarinate, unarmed posteriorly, without episternal or scrobal sulcus; scrobe well-marked posteriorly. Tibial spur formula 1-2-2; tarsal claws edentate, with enlarged basal area. Fore wing with reduced venation for the group, three enclosed cells: costal, medial and submedial; costal cell relatively broad; Rs evenly curved towards costal margin almost enclosing marginal cell; M diverging from M+Cu slightly before cu-a; R1 as long as M. Dorsum of propodeum very short, “shelf-like”, with distinct longitudinal crests forming irregular foveae in dorsal view; lateral propodeal process small, somewhat blunt. **Metasoma:** metasomal petiole absent. Five exposed terga. Sterna convex, undivided medially; S5 very short, “flap-shaped”. **Taxonomic remarks.** The metanotum in chrysidids tends to provide informative characters to identify taxa in many living groups. Chrysidinae taxa, such as *Elampus* Spinola, *Parnopes* Latreille, *Philoctetes* Abeille de Perrin as well as many lineages in Amiseginae and Cleptinae, are readily diagnosed by specializations in this sclerite. The set of foveae on the metanotum of †*Miracorium* gen.

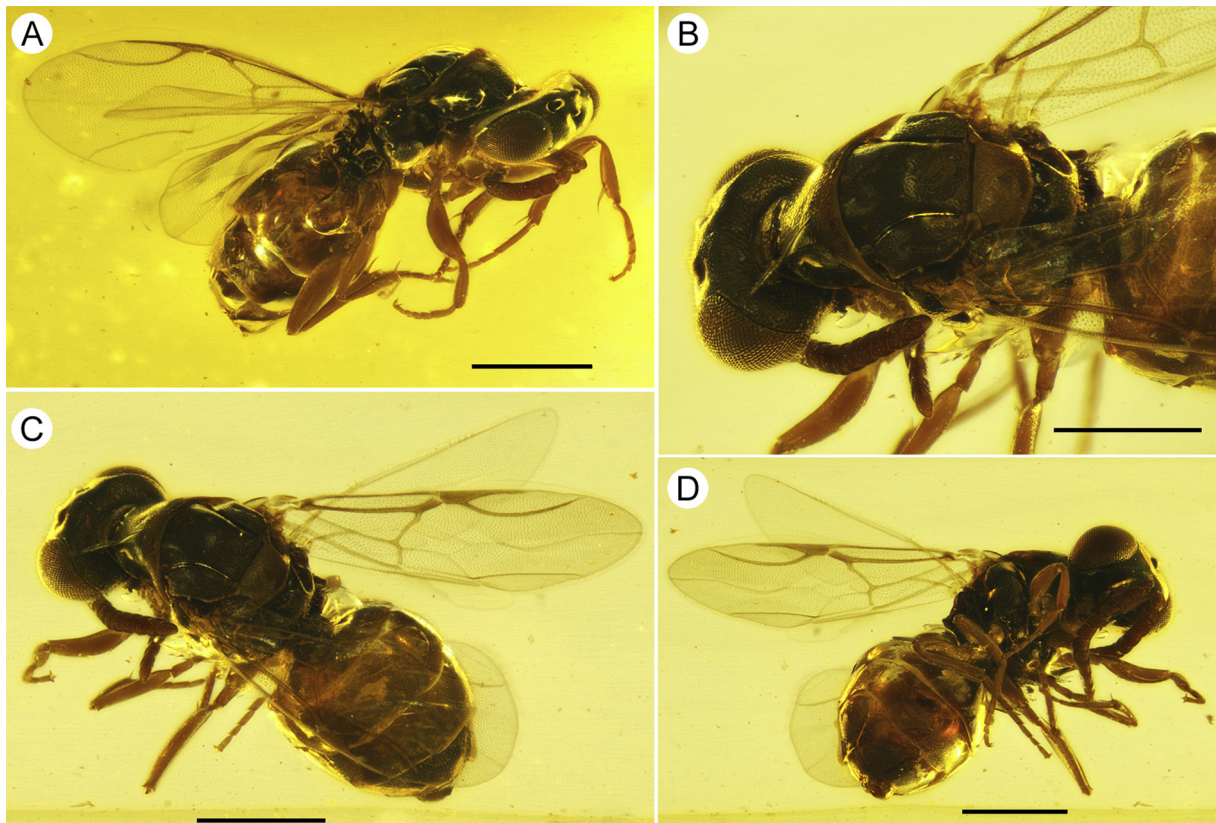
nov. is unique for this taxon. As far as we know no other chrysidid have this configuration. Living species of *Cleptidea* (Cleptinae) present some modifications of the metanotum with shallow marginal depressions and elevated disk, which superficially resembles that of †*Miracorium*, however these superficial similarities are not structurally the same.

**Etymology.** The genus name is a combination of words derived from Latin, *mirus* (adjective) for “admirable, wonderful”, and *corium* (noun, gender neuter) for “skin”, referring to the well preserved, apparently colorful integument.

†*Miracorium tetrafoveolatum* sp. nov.

LSID: urn:lsid:zoobank.org:act:8D5AD406-F2CF-4064-B500-581F8D2140FE  
(Fig. 3A–D)

**Description.** Holotype male. Approximate body length: 2.0 mm. **Head:** integument finely sculptured, with tiny, shallow, sparse punctures; lateral ocelli closer to ocular margin than to each other; ocular setae not discernible at 100× magnification; flagellomeres short, stout, subequal in size. **Mesosoma:** integument finely sculptured; dorsum of mesosoma and mesopleuron predominantly punctulate, interspaces shiny. Forewing with disconnected tubular Cu1; most veins spectral; membrane setose; tegula small, semitransparent. Hind tibia with condensed erect setae on outer surface. **Metasoma:** finely sculptured; S2 posterior margin straight, S3–S4 posterior margins somewhat convex. **Coloration:** head and mesosoma predominantly darkened, with some metallic shine; metasoma light, luteous, some metallic shine marginally on terga and sterna; posterolateral margin of pronotum light colored, differing from rest of pronotum; mesoscutellum light, pale, distinct from the rest of mesosoma; wing membrane hyaline, veins light



**Fig. 3.** †*Miracorium tetrafoveolatum* Lucena & Melo, gen. et sp. nov. (A) Habitus lateral; (B) dorsolateral view of mesosoma; (C) habitus dorsal-oblique view; (D) habitus ventral-oblique view. Scale bars: A, C, D: 0.5 mm. B: 1 mm.



brown. **Vestiture:** indistinct, short, suberect, sparse setation on dorsum, especially on mesosoma.

**Type material.** Holotype male, in amber piece DZUP 027634 (Bur-273). Small, complete, fully winged, well preserved specimen.

**Etymology.** The species name combines the words *tetra* (adjective), meaning “four”, and *foveola* (noun), in reference to the foveae on the metanotum.

Subfamily Chrysidinae Latreille

Tribe *Incertae sedis*

Genus †*Azanichrum* gen. nov.

LSID: urn:lsid:zoobank.org:act:3F14C87A-A490-4FF5-A454-078DB3F6C316

Type species. †*Azanichrum pilosum* sp. nov.

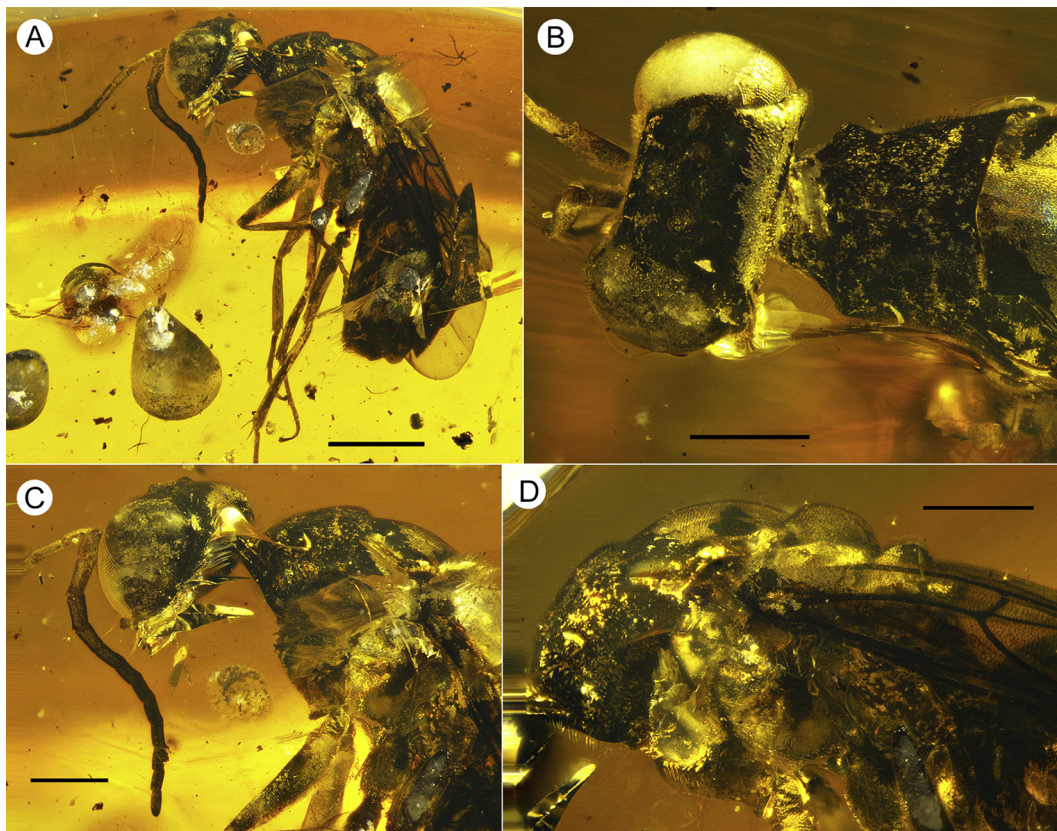
**Diagnosis.** Disc of metanotum and mesoscutellum strongly swollen; pronotum with anterolateral process; genal carina well-developed; *Cu1* unusually long; five exposed metasomal terga; tarsal claws simple; head with transverse frontal carina.

**Description.** **Head:** somewhat flattened frontally; preoccipital carina absent; eye bulging; scapal basin excavated, occupying much of facial area; transverse frontal carina produced between facial hollow and frontal area; ocelli set in a compact triangle in middle of front, inserted in shallow depressions; least ocular distance wide, longer than scapal length; inner ocular margin convergent medially, divergent at ocellar area; lateral gena narrow, about 0.5× MOD; genal carina produced from mandible socket to vertex; malar space short, about 1× MOD; antennal insertion adjacent to clypeal margin; antenna with 11 relatively long cylindrical flagellomeres; scape long, stout; pedicel shorter than F3. Maxillary and labial palpi composed respectively of five and three articles, subequal in size.

**Mesosoma:** pronotum longer than broad, with anterior strong declivitous narrowed area, with marked anterior transverse groove; anterolateral margin with distinct process; posterolateral lobe well developed and reaching tegula; dorsum without longitudinal sulcus; posterior margin evenly rounded to the mesoscutum. Notauli marked by thin line; parapsidal lines marked posterolaterally. Mesoscutellar lobe absent; mesoscutellum about one-third as long as mesoscutum, disc strongly swollen; dorsal limit at the same plane as mesoscutum. Metanotum shorter than mesoscutellum, strongly swollen on disc; dorsal limit slightly below dorsal plane of mesoscutellum; dorsomedial junctures between mesoscutum-mesoscutellum, and mesoscutellum-metanotum convex, narrowed laterally. Mesopleuron ecarinate, unarmed; deflected posteriorly, with strong scrobal sulcus dividing mesopleuron submedially. Tibial spur formula 1-2-2; tarsal claws edentate. Fore wing with complete venation, apparently with six enclosed cells: costal, marginal, medial, submedial, discoidal and subdiscoidal; *Rs* evenly curved towards costal margin enclosing marginal cell; *M* diverging from *M+Cu* at *cu-a*; *Cu1* unusually long, ending near distal margin. Dorsal surface of propodeum short, “shelf-like”, with distinct longitudinal crests forming irregular enclosures in dorsal view; lateral process well developed, pointed.

**Metasoma:** metasomal petiole absent. Five exposed terga, laterotergites present; T2 longer than T1+T3 combined. Sternal surface flat to slightly concave.

**Taxonomic remarks.** The raised, pulvinate mesoscutellum and metanotum are unique to the new taxon. The unusually long T2 would suggest affinities with †*Palaeochrum*, but it seems to be convergent, since this character-state is observed also in many other non-related groups of Elampini and Chrysidini. †*Azanichrum* gen. nov. is distinguished from †*Palaeochrum* also based on the



**Fig. 4.** †*Azanichrum pilosum* Lucena & Melo, gen. et sp. nov. (A) Habitus lateral; (B) dorsal view of pronotum; (C) lateral view of head; (D) lateral view of mesosoma. Scale bars: A: 1 mm. C–D: 0.5 mm.



lateral process of the pronotum (absent in †*Palaeochrum*), and the complete forewing venation (reduced in †*Palaeochrum*).

**Etymology.** The genus name is a combination of the Greek words  $\alpha\zeta\alpha\nu\omega$ , meaning “to dry”, and  $\chi\rho\omicron\alpha$ , “color of the skin”, here in the form of the suffix *-chrum*, which has been widely used for elampine taxa. The name is neuter.

†*Azanichrum pilosum* sp. nov.

LSID: urn:lsid:zoobank.org:act:49A9606D-EF88-44B3-AF8F-5210790F2C78

(Fig. 4A–D)

**Description.** Holotype male. Approximate body length: 5.1 mm.

**Head:** scapal basin apparently setose; flagellomeres with relatively long setae ventrally, F1–F3 slightly longer than F4–F11. Ocular setae not discernible at 100× magnification. **Mesosoma:** pronotum and mesoscutum with some apparently polished areas. Posterolateral margin of pronotum with stout short suberect brown setae (dorsal view). Anterior basitarsus with numerous spines on inner surface; hind tibia with condensed erect setae on outer surface; short erect setae on propleuron and anterior coxa; forewing membrane entirely setose. **Metasoma:** integument finely puncticulate. **Coloration:** body apparently dark greenish, with some metallic shine on mesoscutum and mesopleuron; flagellomeres dark; wings hyaline, with dark veins.

**Type material.** Holotype male, in amber piece DZUP 027635 (Bur-095). Medium-sized, fully winged, well-preserved specimen. It is situated on the margin of the large cabochon and the apical portions of the mid and hind left legs have been removed during grinding. Syninclusions include some plant debris, a fly and an auchenorrhynchous nymph.

**Etymology.** The species name is derived from Latin *pilosum* (adjective), meaning “hairy”, in reference to the distinct pilosity on the pronotum.

Subfamily Chrysidinae Latreille

Tribe *Incertae sedis*

Genus †*Bohartiura* gen. nov.

LSID: urn:lsid:zoobank.org:act:F82347E6-A27E-4319-9D7A-1F1A48609791

Type species. †*Bohartiura glabrata* sp. nov.

**Diagnosis.** Median ocellus set in a profound depression connected to scapal hollow; least ocular distance short, narrower than scapal length; inner ocular margin strongly convergent above at ocellar

area; genal carina present; mesoscutum with bulging lobulate lateral area.

**Description.** **Head:** somewhat flattened frontally; genal carina produced from mandibular socket towards vertex; occipital carina absent; eye bulging; scapal basin deeply excavated, occupying much of facial area; ocelli set in a compact triangle close to vertex; median ocellus set in a deep depression connected to scapal hollow; least ocular distance short, narrower than scapal length; inner ocular margin strongly convergent above ocellar area, divergent below; antennal insertion adjacent to clypeal margin; antenna with 11 cylindrical flagellomeres; scape long and stout; pedicel as long as F3; maxillary palpus with five articles, distal very short. **Mesosoma:** pronotum longer than broad, with anterior declivitous narrowed area; lateral lobe well developed and reaching tegula; dorsum without longitudinal sulcus; posterior margin evenly rounded to mesoscutum; anterolateral margin ecarinate, with pre-marginal sulcus forming a lamellar edge. Notauli deeply impressed; lateral area somewhat lobulate. Mesoscutellum convex, dorsal limit at same plane as mesoscutum. Metanotum convex, shorter than mesoscutellum, at same plane as mesoscutellum. Anterior mesopleuron carinate; mesopleuron without transverse sulcus, with distinct scrobe, deeply marked posteriorly. Tibial spur formula 1-2-2; tarsal claws with single sub-basal perpendicular tooth. Wings with reduced venation, forewing with three enclosed cells: costal, medial and submedial; incomplete discoidal cell; Rs curved towards costal margin almost enclosing marginal cell; tegula reduced, semitransparent. Dorsum of propodeum short, “shelf-like”; lateral propodeal process short, pointed. **Metasoma:** metasoma with four exposed terga, laterotergites present; sternal surface apparently convex or flat.

**Taxonomic remarks.** †*Bohartiura* gen. nov. most closely resembles †*Palaeochrum*. The new taxon is readily distinguished by distinct morphological traits absent in †*Palaeochrum*, such as: median ocellus inserted in a deep depression; and dentate tarsal claws.

**Etymology.** The genus is named after Richard M. Bohart, eminent hymenopterist who contributed to the modern foundations in the taxonomy and systematics of the chrysidid wasps. The name is feminine.

†*Bohartiura glabrata* sp. nov.

LSID: urn:lsid:zoobank.org:act:3AA41B17-6B00-49D2-9582-43F807574FF5

(Fig. 5A–B)

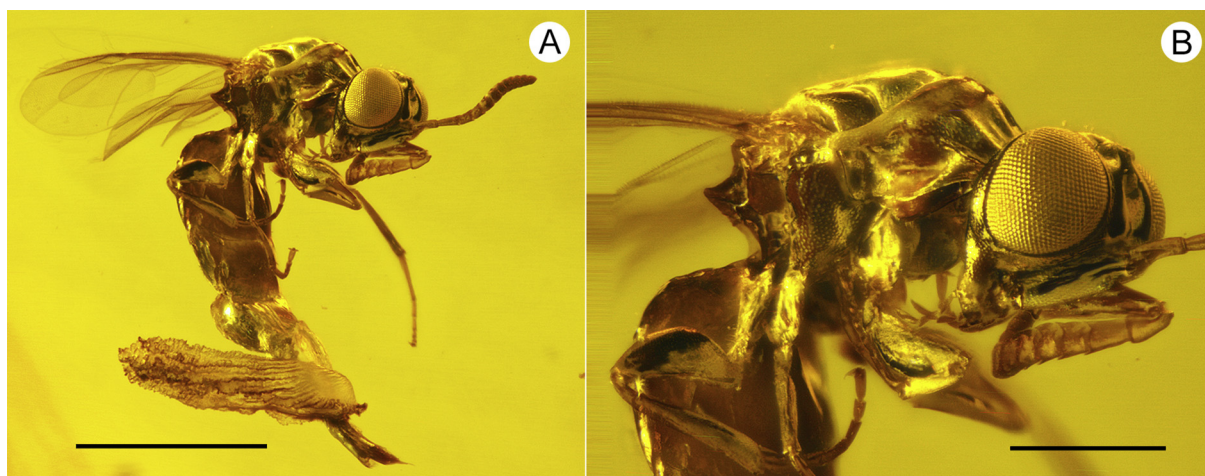


Fig. 5. †*Bohartiura glabrata* Lucena & Melo, gen. et sp. nov. (A) Habitus lateral; (B) head antero-lateral-oblique view. Scale bars: A: 0.5 mm. B: 1 mm.

**Description.** Holotype female. Approximate body length: 2.5 mm. **Head:** lateral ocelli implanted in shallow depressions; malar space longer than F1 length; upper genal area short; F1 slightly longer than F2; F2–F11 subequal in size. **Mesosoma:** some striate marks may be compression artifacts. **Metasoma:** anterolateral margins of T1–T2 carinate. **Coloration:** body integument apparently greenish or dark, with some metallic shine preserved on mesosoma; scape greenish; flagellomeres brownish; pronotum with light brownish margin posterolaterally; wings hyaline with dark veins; metasoma light brown reddish, with some metallic shine preserved on terga. **Vestiture:** apparently much reduced, especially on dorsum; wings entirely setose; ocular setae not discernible at 100× magnification. **Integumental sculpture:** finely punctate; pronotum and metasoma with striate marks, though we are interpreting these as artifacts, since legs and antennae show strong compression as well. **Type material.** Holotype female, in amber piece DZUP 027636 (Bur-038). Small, fully winged specimen, somewhat distorted by compression. It died with the apex of the metasoma stretched and with a large vesicle everted (perhaps the venom sac). The large cabochon also contains five nematoceran flies.

**Etymology.** The species name is derived from Latin *glabra* (adjective) for “hairless”.

#### 4. Phylogenetic relationships

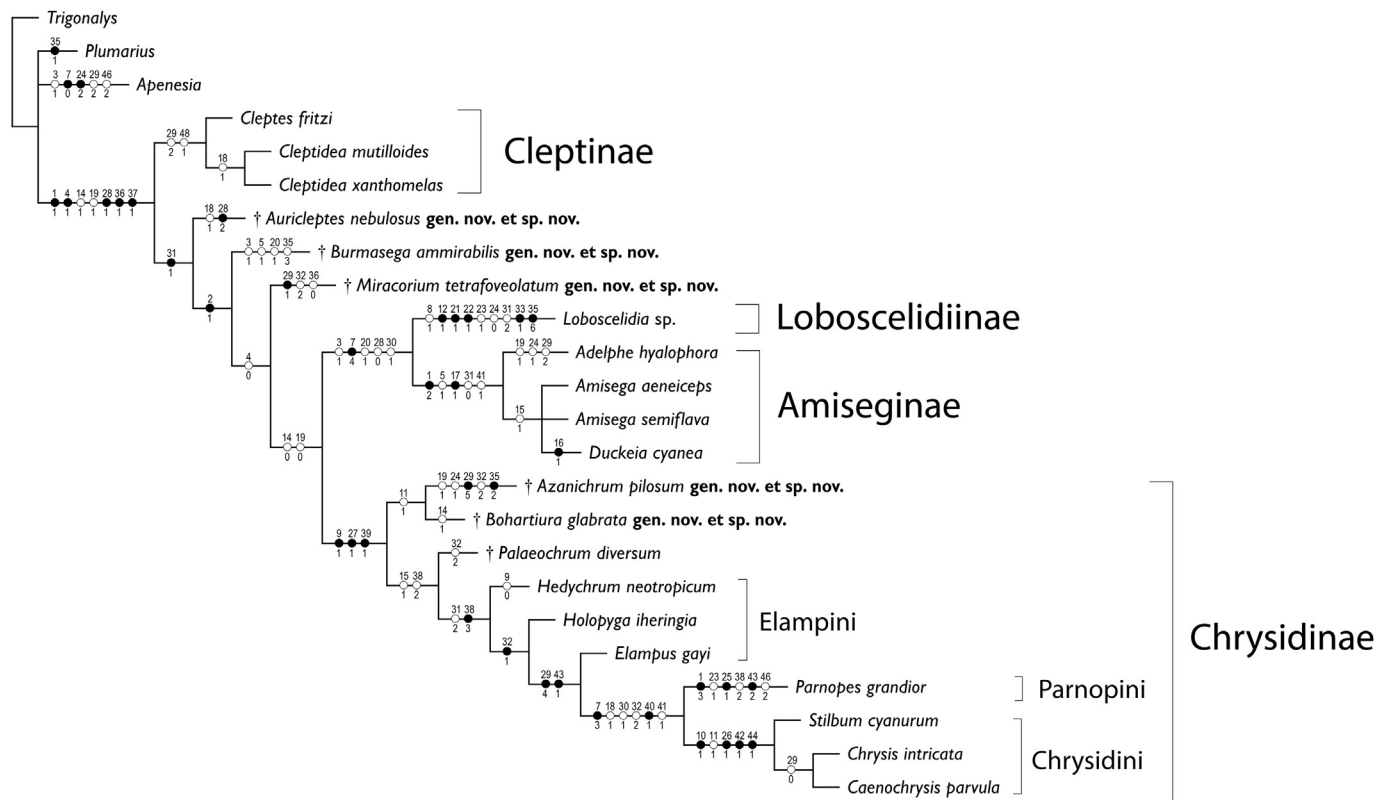
The implied weighting analysis resulted in two most parsimonious trees (L: 115–116, CI: 63, RI: 82), whose strict consensus is shown here as Fig. 6. All major extant groups were recovered as monophyletic as in Carpenter (1999), except for the Elampini. Focusing on the phylogenetic position of the fossil taxa herein

described, we found that †*Azanichrum* and †*Bohartiura* formed a clade, which consistently came out as sister-group of the Chrysidinae, including †*Palaeochrum*. This positioning was supported by three non-homoplastic character transformations (Fig. 6). By contrast, †*Auricleptes*, †*Burmasega* and †*Miracorium* did not exhibit close relationships with any of the extant subfamilies and came out as a grade between the Cleptinae and the clade formed by (Loboscelidiinae + Amiseginae) + Chrysidinae. Considering the weak support for the intervening branches, these relationships are most likely the result of a morphological character set insufficient for a proper resolution (see Discussion below). As expected, the equal weighting analysis returned a larger number of trees (L = 115, CI = 63, RI = 82), whose consensus is poorly resolved (Fig. S1). Therefore, the discussion of the relationships and of the character transformations supporting them is based on the implied weighting results.

#### 5. Discussion

##### 5.1. †*Auricleptes*

At a first glance †*Auricleptes* resembles extant Cleptinae and is characterized for having a combination of distinctive and plesiomorphic characters. The intersections on the pronotum resemble that of living forms *Cleptidea* Mocsáry, but the unusually long metanotum, and the large lobulate “ear-like” lateral processes of the propodeum are unique for †*Auricleptes*. Similar to that observed in †*Burmasega*, †*Auricleptes* also has a well-sclerotized, relatively long, and apparently functional sting. Living forms of Cleptinae are known to be parasites on prepupal larvae of sawfly wasps. They have a robust ovipositor apparatus, with the sting acting more as an



**Fig. 6.** Strict consensus of the two most parsimonious trees resulting from a cladistic analysis under implied weighting of 49 characters from representatives of extinct and extant chrysidids. Character state transformations are depicted as solid (unequivocal changes) and empty (reversals or multiple changes) circles; only unambiguous transformations are shown. Unsupported branches were collapsed.



egg guide than as a weapon or defensive structure (see Kimsey and Bohart, 1991: 35). Assuming that the long and well-sclerotized sting was functional in these extinct groups, there were at least two independent losses of the functional sting in the chrysidid evolution: (1) in the Cleptinae lineage, and (2) in the ancestor of the clade composed of Amiseginae + Loboscelidiinae and the extant Chrysidinae, since this character condition is unknown in other extinct Chrysidinae taxa.

The previously described taxa †*Hypocleptes* Evans 1973, †*Procleptes* Evans 1969 and †*Sphaerocleptes* Cockx et al., 2016 were originally placed in Cleptinae, apparently related to the living group *Cleptes* Latreille. However, Cleptinae as a whole lacks distinctive shared characters (see also Kimsey and Bohart, 1991: 44), which prevents a precise phylogenetic arrangement for them. Extant *Cleptidea* and *Cleptes* are both structurally conservative groups regarding their morphological diversity, and as a consequence most of the diagnostic characters used to distinguish groups are based primarily on coloration and sculpturing of the integument (e.g., Kimsey, 1981, 1986b; Móczár, 1997a,b, 1998, 2001). The Cleptinae was supposed to be monophyletic based on the derived character-state of the pronotum and specialization of the parasitic life-history (see results of Carpenter, 1999). The biology of the extinct taxa is hardly accessible based solely on morphology, and the assumed derived condition of the narrowed, furrowed and long collar-shaped pronotum of Cleptinae may be rather plesiomorphic, since it is manifest in other non-related chrysidid groups. Some other fossils of Chrysididae seem to have this long collar-shaped pronotum, usually with interchangeable, submedial, transverse sulcus and/or furrowed by grooves as observed in †*Auricleptes*, †*Burmasega* and †*Hypocleptes*.

The short, shelf-like, dorsal surface of the propodeum found in †*Auricleptes* (also present in other extinct chrysidid taxa) contrasts remarkably to the condition seen in the groups assigned to Cleptinae, which have a long dorsal plane of propodeum and a typical short metanotum. Given the distribution of character-states observed in †*Auricleptes*, supported also by the cladistic analysis, we consider †*Auricleptes nebulosus* as *incertae sedis* within Chrysididae (Fig. 6).

A comprehensive taxon sampling with detailed comparative morphological study of all fossil taxa and representatives of extant groups is necessary to address properly the issues of: 1) whether Cleptinae holds itself as monophyletic, 2) the interrelationships of groups assigned to Cleptinae, including extinct taxa originally assigned to this subfamily, and 3) to which group †*Auricleptes* is most closely related.

## 5.2. †*Burmasega*

†*Burmasega* has some of the most typical diagnostic characters of Amiseginae, as such: (1) presence of the malar sulcus; (2) front protruded; (3) elongated female F1; and (4) reduced prosternum, partially obscured by the propleuron (Kimsey and Bohart, 1991). Despite this, the new taxon lacks some of the other characters interpreted as synapomorphic for the Amiseginae, as the pronotal pits, situated posteromedially on the pronotal dorsum and laterally at the base of the pronotal lobe. In our cladistic analysis, †*Burmasega* was recovered in a relatively basal position, as the sister-group of the clade composed of †*Miracorium* and (Loboscelidiinae + Amiseginae) + Chrysidinae (Fig. 6).

One of the most distinguishing morphological structures shared by all Amiseginae is the typical needle-like ovipositor (present also in Loboscelidiinae). †*Burmasega* lacks this, having in its place an apparently generalized and more robust ovipositor tube, with long, curved, and well-sclerotized sting. This may suggest a non-specialized parasite habit contrasting with that for the extant Amiseginae. Modern Amiseginae (and perhaps the Loboscelidiinae

too) are known as specialized parasitoids on walking stick eggs (Kimsey and Bohart, 1991; Baker, 2016). Other extinct taxa, as †*Protamisega* and †*Protadelphe* both share the typical needle-like ovipositor with the extant Amiseginae, but there is no clear indication to which groups they are more closely related phylogenetically. Based on the typical needle-like ovipositor, we are assuming that †*Protamisega* and †*Protadelphe* are closer to the extant lineages than from †*Burmasega*, but further comparative morphological studies are needed to address this issue properly. Kimsey and Bohart (1991) presented the most comprehensive though yet preliminary study for the Amiseginae, which included only representatives of the extant groups. Phylogenetic affinities among Amiseginae taxa are quite difficult to address once our basic knowledge about the diversity of this clade, both living and fossil, is yet far from complete. Additionally, some of the characters traditionally interpreted as uniform among the Amiseginae (e.g., characters herein re-interpreted: 1, 15, 39, and 40; see also Kimsey and Bohart, 1991) actually exhibit variable conditions within this group and must be thoroughly and carefully re-evaluated.

## 5.3. †*Miracorium*

†*Miracorium* retains some of the character-states interpreted as plesiomorphic: (1) five exposed metasomal terga in males; (2) pronotum longer than broad, with the posterolateral lobe reaching the tegula; (3) absence of mesoscutellar lobe; (4) propodeum with short dorsal surface; (5) absence of genal, transfrontal and occipital carinae; (6) absence of metapleural carina; and (7) convex metasomal sterna. At the same time, it exhibits characters found in typical extant Chrysidinae, as such: (1) head with distinct scapal basin; (2) apical margin of mandibles tapering; and (3) simple tarsal claws. This combination of characters is reflected in our cladistic analyses, with †*Miracorium* coming out as an early-diverging lineage and forming the sister-group of the clade composed of Loboscelidiinae + Amiseginae and Chrysidinae (Fig. 6).

The simple tarsal claws of †*Miracorium* suggest phylogenetic affinities with extant forms of Chrysidinae, such as Parnopini and Chrysidini (*sensu* Kimsey and Bohart, 1991; Carpenter, 1999). However, based on our results, edentate tarsal claws originated at least four times: (1) in †*Miracorium*, (2) in †*Azanichrum*, (3) in †*Palaeochrum*, and (4) in the ancestor of Parnopini + Chrysidini. When considering additional taxa not sampled in the present study, the number of teeth in the claws shows an even higher degree of homoplasy.

## 5.4. Chrysidinae *sensu lato*

The Chrysidinae are interpreted here in a broader scope to include the newly described fossil taxa †*Azanichrum* and †*Bohartiura*. Their close relationship is supported by three non-homoplastic synapomorphies: (1) the genal carina; (2) the metapleura carina; and (3) the concave metasomal sterna. Possession of a transfrontal carina supports the clade †*Azanichrum* + †*Bohartiura*, but this character is also present in Chrysidini (and in some unusual Amiseginae and Elampini not sampled here) and must be interpreted with some caution. We consider premature to propose a new tribal classification for these Chrysidinae for the moment, since their interrelationships is not yet satisfactorily understood. †*Azanichrum* is unique in having a pulvinate mesoscutellum and metanotum, and the forewing with six enclosed cells. Other distinctive but not exclusive characters found in this taxon are: the lateral process of the pronotum; the transverse groove on the anterior declivity of pronotum; and the simple tarsal claws.

†*Bohartiura* superficially resembles †*Palaeochrum*, but the female of the latter is unknown, as well as the male of †*Bohartiura*.

Given the geographical and temporal divergences between them it is unconvincing that †*Bohartiura* would be such an extreme dimorphic female of †*Palaeochrum*. Sexual dimorphism is variable in the Chrysidinae and seems to be phylogenetically unstable. Some unrelated groups show remarkable morphological dimorphism, as in some groups of Allocoeliini and the Parnopini, but it is inconsistently exhibited in the Elampini and Chrysidini. Furthermore, †*Bohartiura* has dentate tarsal claws and its pronotal lobe is adjacent to the tegula, contrasting with the edentate claw and the pronotal lobe separated from the tegula exhibited by †*Palaeochrum*. The reduction in the number of metasomal terga of †*Palaeochrum* indicates a closer phylogenetic relationship of this taxon with the clade of the extant Chrysidinae than with other extinct taxa. In the most parsimonious scenario, the reduction of external segments of the metasoma in Chrysidinae occurred in the ancestral lineage of †*Palaeochrum* + extant Chrysidinae, with four metasomal terga in males (retained in Parnopini), but which have subsequently changed in Chrysidini and Elampini, both with three exposed segments in males and females, and reached its extreme in Allocoeliini with only two exposed terga in both males and females. These external reductions most likely were followed by internal specializations as seen in the living groups of Chrysidinae (e.g. Kimsey, 1992), and may have had significant importance along the diversification of the cuckoo wasps clade. According to Krombein (1986), †*Palaeochrum* would be positioned in Elampini, based on general similarities of habitus, but †*Palaeochrum* lacks synapomorphies exhibited by the living taxa, such as: (1) lack of dorsal surface of the propodeum; and (2) reduction on the male metasomal terga. Our results, however, place this extinct taxon as sister-group of the extant Chrysidinae (Fig. 6).

## 6. Conclusions

Based on the interpretation of previously described fossil groups and the evidence brought by the new fossils herein described, we extend the classification proposed by Kimsey and Bohart (1991) to include the extinct chrysidid groups, shedding light in some of the morphological characters interpreted as landmarks along the evolution of Chrysididae wasps. Our results also provide a phylogenetic basis for future revisions of some taxa with problematic placement in Chrysididae (e.g. extinct taxa assigned to Cleptinae and Amiseginae), and it will be useful for a better understanding of the evolution of the chrysidid wasps. The phylogenetic affinities of these groups are particularly difficult to properly address, since the terminal species used herein are intended to represent the morphological diversity found in the main lineages to which they are phylogenetically related. A study with comprehensive taxon sampling in consonance with review of other previously described fossil taxa is necessary to improve our knowledge on the morphological patterns in the evolutionary history of Chrysididae.

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## Appendix A. Supplementary data

Supplementary data related to this article can be found at <https://doi.org/10.1016/j.cretres.2018.03.018>.