A new protopristocerine wasp (Hymenoptera: Bethylidae) from the mid-Cretaceous Burmese amber

Corentin Jouault, Manuel Brazidec

A new protopristocerine wasp (Hymenoptera: Bethylidae) from the mid-Cretaceous Burmese amber

Corentin Jouault [1,2,3]*, Manuel Brazidec [2]

[1]Institut de Systématique, Évolution, Biodiversité (ISYEB) Muséum national d'Histoire naturelle, CNRS, Sorbonne Université, EPHE, Université des Antilles, CP50, 57 rue Cuvier 75005 Paris, France; jouaultc0@gmail.com; https://orcid.org/0000-0002-3680-5172

[2]Univ. Rennes, CNRS, Géosciences Rennes, UMR 6118, F-35000, Rennes, France

[3]CNRS, UMR 5554 Institut des Sciences de l'Évolution de Montpellier, Place Eugène Bataillon, 34095, Montpellier, France

*Corresponding author: jouaultc0@gmail.com

ABSTRACT

Ramageoptera platycephala gen. et sp. nov., a new protopristocerine wasp, is described and figured from a female individual preserved in mid-Cretaceous amber from Tanai, northern Myanmar. *Ramageoptera platycephala* gen. et sp. nov. shows most of the known characters used to circumscribe the extinct sub- family Protopristocerinae, and highlights the putative status of stem-Pristocerinae that may occupy the Protopristocerinae. *Ramageoptera platycephala* gen. et sp. nov. is unique among the Protopristocerinae, at least, for possessing a flat and square shaped head; eyes glabrous and small; mandibles with four conspicuous sharp teeth; antenna with short scape;

forewing with Rs + M vein absent; vein M straight; cell 2R1 distally opened; cell 1Cu closed, sub-equal to R cell; cell 2Cu open.

RÉSUMÉ

Ramageoptera platycephala gen. et sp. nov., une nouvelle guêpe protopristocerine est décrite et illustrée sur la base d'une femelle préservée dans l'ambre Cénomanien de Tanai, Myanmar du nord. *Ramageoptera platycephala* gen. et sp. nov. possède la plus part des caractères utilisés pour circonscrire la sous-famille éteinte Protopristocerinae et souligne le status hypothétique de groupe souche des Pristocerinae que pourraient occuper les Protopristocerinae. *Ramageoptera platycephala* gen. et sp. nov. est unique parmi les Protopristocerinae car elle possède une tête plate et carrée, des yeux glabres et petits, des mandibules avec quatre dents acérées sur la marge masticatrice, des antennes avec un scape court, une aile antérieure avec la veine Rs + M absente, la veine M droite, la cellule 2R1 ouverte distalement, la cellule 1Cu fermée et sub-égale à la cellule R, la cellule 2Cu ouverte.

Keywords: New taxa; Mesozoic; Fossil record; taxonomy

Mots clés : Nouveau taxon, Mésozoïque, registre fossile, taxonomie

1. Introduction

The family Bethylidae, often called flat wasps due to their flat body, are relatively speciose today but their past diversity remains underestimated, especially for the Cretaceous, despite this time interval being crucial to understand the evolutionary history of the clade. Indeed, at least twenty unpublished morpho-species are currently known from the Cretaceous deposits of Myanmar but to date undescribed (C.J. pers. obs.). To this is added an unprecedented and relatively little documented fauna in the amber of the Eocene Oise amber (e.g. Perrichot and Nel, 2008; Falières

and Nel, 2019), and an entirely new fossil fauna that remains to be described in the Miocene amber of Zhangpu (Wang et al., 2021) or Totolapa (C.J. pers. obs.). This undescribed diversity challenges the comprehension of the diversification of the Bethylidae, prevents a global phylogenetic analysis and blurs the time divergence estimates within the family. Also, it appears that the compression or imprint fossils are less suitable for the study of Bethylidae due to their coarser preservation making it difficult to observe key criteria such as the shape of the prosternum (e.g. Orapa: Brothers and Rasnitsyn, 2003). Nevertheless, several new extinct flat wasp genera have been recently described from Cretaceous deposits (e.g. Colombo et al., 2021; Jouault et al., 2021a). Here we add a new protopristocerine genus from the Burmese amber, contributing to increase the knowledge of the Cretaceous diversity of Bethylidae.

Recently, two morphological phylogenies have been proposed to investigate the relationships between the bethylid subfamilies (Colombo et al., 2020; Jouault et al., 2021b). But their results do not record Protopristocerinae at the same position. In Jouault et al. (2021b: fig 6), they group with the Lancepyrinae to form a clade sister to (Mesitiinae + Pristocerinae + Epyrinae + Scleroderminae); while Colombo et al. (2020: fig 1B) recorded them as sister lineage to the clade Epyrinae. It is therefore probable that new phylogenies, using total-evidence, shall be necessary to clarify their relationships within the Bethylidae.

2. Material and methods

The amber piece containing the specimen comes from the deposits of Noije Bum in the Hukawng Valley (26° 29′ N, 96° 35′ E), Kachin State, northern Myanmar (see detailed map in Grimaldi and Ross, 2017: fig. 2). Radiometric data established an early Cenomanian age (98.79 ± 0.62 Ma) for Kachin amber, based on zircons from volcanic clastes found within the amber-bearing sediments (Shi et al., 2012). Some ammonites found in the amber-bearing bed and within amber corroborate a late Albian–early Cenomanian age (Cruickshank and Ko, 2003; Yu et al., 2019). The holotype of

Ramageoptera platycephala gen. et sp. nov. is a well-preserved female with apex of right antenna damaged. The specimen was examined and photographed with a Leica MZ APO with an attached Canon EOS 5D Mark II camera. All images are digitally stacked photomicrographic composites of several individual focal planes, which were obtained using Helicon Focus 6.7. The figures were composed with Adobe Illustrator CC2019 and Photoshop CC2019 softwares. The amber piece is housed in the Geological Department and Museum of the University of Rennes, France (IGR).

The nomenclature and classification follow Azevedo et al. (2018). Main measurements and indices used are as follow: length of forewing (LFW); length of head, measure from vertex to apex of clypeus (LH); width of head above eyes (WH); width of frons (WF); height/width of eye (HE); ocello-ocular line (OOL); width of ocellar triangle (WOT); diameter of anterior ocellus (DAO); vertex-ocular line (VOL). The nomenclature of integument sculpture follows Harris (1979).

Published work and nomenclatural acts are registered in ZooBank (http://www.zoobank.org/, last access: 12 November 2021), with the following LSID (reference): urn:lsid:zoobank.org:pub:6267A922-1209-4AE5-AF2C-CABE2A153E98.

3. Systematic paleontology

Order Hymenoptera Linnaeus, 1758

Superfamily Chrysidoidea Latreille, 1802

Family Bethylidae Haliday, 1839

Subfamily Protopristocerinae Nagy, 1974

Genus *Ramageoptera* gen. nov.

urn:lsid:zoobank.org:act:0DAF1E06-072D-41BC-A145-6C19B945E384

Type species. *Ramageoptera platycephala* sp. nov.

Etymology. The genus name is a combination of the surname of Thibault Ramage (friend of C.J.) and the ancient Greek πτερά (pterá) used to form words relating to wings. Gender feminine.

Diagnosis. Female fully winged; head flat and square-shaped; eyes glabrous and small (i.e. not occupying entire lateral surface of head); mandibles with four conspicuous sharp teeth; antenna with short scape (Figs. 1 and 2A); neck present between head and mesosoma; prosternum large, trapezoidal (Fig. 2A); metanotum developed medially and overlapping mesoscutellum posteriorly (sensu Azevedo et al., 2018); well-developed notauli; tiny parapsi- dal furrows (Fig. 2B); posterior margin of metapectal—propodeal complex with a distinct ridge but lacking postero-lateral spine; legs thickened; forewing with Rs + M vein absent; vein M straight (not forming a sigmoidal curve with cu-a); cell 2R1 distally opened; cell 1Cu closed, sub-equal to R cell; cell 2Cu open (Fig. 3D).

Ramageoptera platycephala sp. nov.

Figs. 1-3

urn:lsid:zoobank.org:act:0E236FDE-55C8-493D-B93A-C442E6D4F0CC

Holotype. Specimen identifier IGR.BU-050 (a nearly complete specimen, with right antenna damaged, in a piece of amber measuring 7 × 4 × 5 mm).

Etymology. The specific epithet refers to the flat head of the species and is combination of the ancient Greek πλατύς (platús) and Latin *cephalus* referring to the head. The specific epithet is to be treated as an adjective.

Locality and horizon. Noije Bum Hill, Hukawng Valley, Kachin State, Myanmar; upper Albian to lower Cenomanian, mid-Cretaceous.

Diagnosis. As for the genus (*vide supra*).

Description. Female; body ca. 3.62mm long, depressed, not strongly foveolate, pubescent; LFW: 1.83mm; wings setose. LH: 0.71 mm; WH: 0.50 mm; WF: 0.09 mm; HE: 0.14 mm; OOL: 0.37 mm; WOT: 0.11 mm; DAO: 0.04 mm; VOL: 0.06 mm. Head pubescent, postero-lateral corners rounded, substrigulate; mandible with four strong and acute teeth; five visible maxillary palpomeres, three visible labial palpomeres; clypeus small, apically truncate, with a median concavity; antenna with

11 cylindrical flagellomeres; length of antennomeres (in mm): scape 0.14 mm, pedicel 0.09, F1 0.06, F2 0.05, F3 0.06, F4 0.06, F5 0.06, F6 0.07, F7 0,07, F8 0.07, F9 0.07, F10 0.06, F11 0.08; apical flagellomere tapering toward apex; occipital carina present; eyes glabrous; ocellar triangle sub-equilateral.

Mesosoma with dorsum smooth, not roughly sculptured; prosternum large, trapezoidal with anterior margin the longest side; notauli well-marked, no apparent sculpturing between them; parapsidal furrows very weak; metanotum developed medially and overlapping mesoscutellum posteriorly; metapectal- propodeal complex smoothly aerolate, with distinct transverse anterior (apparently smooth, i.e. without posterior projection) and metapostnotal median ridges, metapostnotal lateral area smoothly areolate-rugose, transverse posterior margin ridge like (i.e. ridge present between propodeal declivity and metapostnotum); propodeal declivity concave, without strong sculpture; legs moderately thickened, fore legs with femur ca. 0.33 mm long, conspicuously swollen, tibia ca. 0.31 mm long, basitarsus ca. 0.12 mm long, second tarsomere ca. 0.05 mm long, third ca. 0.04 mm long, fourth ca. 0.03 mm long, fifth ca. 0.09 mm long, tarsal claw ca. 0.05mm long, calcar present and bifid; mid legs with femur ca. 0.21 mm long, slightly swollen, tibia ca. 0.24 mm long, basitarsus ca. 0.12 mm long, second tarsomere ca. 0.07 mm long, third ca. 0.05 mm long, fourth ca. 0.02 mm long, fifth ca. 0.08 mm long; hind legs with femur ca. 0.40 mm long, conspicuously swollen, tibia ca. 0.41 mm long, basitarsus ca. 0.21 mm long, second tarsomere ca. 0.09 mm long, third ca. 0.07 mm long, fourth ca. 0.06 mm long, fifth ca. 0.11 mm long; tarsal claw with a small preapical tooth; arolium well-developed. Forewing covered and bordered with small setae; anterior border not angularly incurved anterior to pterostigma; costal vein present; pterostigma wider at 2r-rs&Rs base; 2r-rs&Rs long and as strongly developed as other veins, originating distad pterostigma midlength; 1-RS&1-M slightly curved; Cu present as a stub; cu-a strong, originating distad meeting point of 1-RS&1-M and Cu; A stub present after cu-a and A meeting point; 2R1 cell present, open

apically; cells R and 1Cu closed; no basal stub of Rs + M; poststigmal abscissa of R1, ghost vein, not clearly visible; several unpigmented veins present on wing membrane.

Metasoma with short petiole; seven tergites, T2 enlarged, convex, partly covering sternites; sting visible, straight at least 0.17 mm long, i.e. visible part; lengths of tergites (heights cannot be determined): T1 0.28mm, T2 0.23mm, T3 0.33mm, T4 0.33mm, T5 0.25 mm, T6 0.2 mm; T7 ca. 0.1 mm.

Remark. The apparent carina or ridge visible in the middle of frons (from base of clypeus to anterior ocelli) is the result of a crack in amber and not a real structure (Fig. 3A).

4. Discussion

Following the key to superfamilies proposed in Goulet and Huber (1993), the new specimen keys out in Chrysidoidea because of the pronotum being more than half as long as the mesoscutum, and the metasomal terga 1 and 2 having no constriction at all. Following the key to Chrysidoidea families in Goulet and Huber (1993), it keys out in Bethylidae because of the antenna with 11 flagellomeres, the presence of wings, the profemora not enlarged or swollen, metasoma with seven exposed tergites, pronotum touching tegula, and prognathous head. However, it is important to mention that the keys in Goulet and Hubert (1993) are proposed for extant Hymenoptera and not include fossil taxa. To prevent misplacement, we also compared the new specimen with the other fossil families known from the mid-Cretaceous Burmese amber.

Burmese amber chrysidoid fauna encompasses several extant families (e.g. Bethylidae, Chrysididae, Scolebythidae) but also the extinct families Chrysobythidae and Plumalexiidae (Brothers, 2011; Melo and Lucena, 2020). The new fossil can be differentiated from the Scolebythidae in having a well-developed pronotal anterior flange rendering propleura invisible in dorsal aspect; the protrochanter inserted ventrally on procoxa (Engel and Grimaldi, 2007). Note that some scolebythids have protrochanter inserted normally on procoxa (Engel et al., 2013: fig. 4).

However, it is interesting to mention that the prosternum is not concealed between procoxae as in most of other bethylids (see a few exceptions like *Bethylus* Latreille, 1801, *Megaprosternum* Azevedo, 2006 and *Solepyris* Azevedo, 2006): this feature would be reminiscent of the Scolebythidae but it differs from scolebythid prosternum in not being diamond-shaped and in having the propleura not closely situated. The new fossil differs from the Chrysobythidae at least in having the clypeus more or less triangular (vs. raised as a convex, somewhat squared lobe), the forewing with a reduced number of closed cells (vs. six enclosed cells) and the cells 1R1 and 2R1 open (Melo and Lucena, 2020).

Among the Bethylidae, the new specimen would key out in the Pristocerinae following the key to the extant subfamilies of Bethylidae proposed in Azevedo et al. (2018) because of the following characters: winged (macropterous, micropterous, brachypterous); forewing with Rs+M vein absent; metanotum developed medially and overlapping mesoscutellum posteriorly.

Recently, the subfamily Elektroepyrinae was created to accommodate the genus *Elektroepyris* described from Ypresian Oise amber (Perrichot and Nel, 2008; Colombo et al., 2020). The new fossil cannot be attributed to this subfamily, at least, owing to its eye large but smaller than frons width (vs. longer than frons width in Elektroepyrinae); frons not strongly coriaceous; anterior ocellus clearly posteriad supra-ocular line (vs. anteriad supra-ocular line); forewing with vein Cu present (vs. absent) and A short (vs. long). The Protopristocerinae, not included in the key proposed by Azevedo et al. (2018), greatly resembles the Pristocerinae but is supported by the following characters: antenna with 11 flagellomeres; forewing fully developed with 2R1 cell opened apically, 1Cu cell much longer than R cell, pterostigma elongated and narrow; legs moderately thickened; second metasomal segment enlarged; metasomal sterna unarmed (Azevedo et al., 2018). To date, there is no clear character allowing an accurate separation between the Pristocerinae and the Protopristocerinae. Previous works argued that the character 1Cu cell longer than cell R is putatively an apomorphy supporting the Protopristocerinae (e.g., Azevedo et al., 2018). However,

this condition is not found in all the Protopristocerinae (Falières and Nel, 2019; Jouault et al., 2020) challenging its utility to subfamily level diagnosis. Therefore, most of the species currently placed in the Protopristocerinae result from the character fully winged female (vs. apterous in Pristocerinae) as initially used to define the subfamily (Nagy, 1974). The presence of both a sting and seven tergites shows that the new specimen is a female, thus the presence of wings allows us to place it in the Protopristocerinae. Additionally, the new fossil displays heavily toothed mandibles, this character being found in male Pristocerinae but also in female Protopristocerinae (Falières and Nel, 2019: figs. 2A, B). In view of the characters discussed above and the retention of the fully wing female (plesiomorphy), the subfamily Protopristocerinae is poorly supported and may constitute a stem group of the Pristocerinae.

Currently, the Protopristocerinae encompasses five fossil genera: *Protopristocera* Brues, 1923, *Bethylopteron* Brues, 1933, *Bethylitella* Cockerell, 1917, *Gynopteron*, Falières and Nel, 2019, and *Cretapristocera* Jouault et al., 2021. The new fossil differs from the genus *Protopristocera* at least due to its eyes not pubescent (vs. pubescent in *Protopristocera*), lacking a second discoidal cell large and oblong (vs. present), having thickened legs (Brues, 1923). Our fossil differs from *Bethylopteron* owing to the shape of its head i.e. flat and squared (vs. rounded in *Bethylopteron*), ocelli of normal size (vs. extremely large), notauli present (vs. absent), and in having a different configuration of wing venation (i.e. no basal vein (= 1-RS&1-M) curved inward nor forming a sigmoid curve with the interstitial nervulus (= cu-a)) (Brues, 1933). The genus *Bethylitella* is poorly illustrated or described and requires revision. However, it differs from the new species owing to the different configuration of the masticatory margin of the mandibles i.e. with five small teeth (vs. four sharp teeth in the new specimen), the head rounded (vs. flat), and the wing venation. *Bethylitella* seems to have a reduced venation, differentiating it from *Ramageoptera* gen. nov. (Cockerell, 1917: fig. 6). We cannot place the new fossil in *Gynopteron* owing to its head conspicuously flattened (vs. quite rounded), neck present (vs. absent, i.e. not distinct space between anterior surface of pronotum

and occiput), small eyes located in anterior half of head (vs. large occupying nearly all lateral surface of head in *Gynopteron*) (Falières and Nel, 2019). Finally, it differs from *Cretapristocera*, at least in having mandibles with numerous teeth (vs. saber-shaped with one tooth in *Cretapristocera*), short scape (vs. long), forewing with cell 1Cu closed (vs. open) (Jouault et al., 2021). Therefore, we create a new genus to accommodate the specimen.

Jouault et al. (2021) proposed a key to the genera of Protopristocerinae. *Ramageoptera* gen. nov. should be accommodated in this key as follow:

1. Antenna with 13 antennomeres with short scape; forewing venation usually developed but sometimes reduced …… 2

- Antenna with 12 antennomeres, scape elongated; forewing venation always reduced (Cenomanian: Myanmar) ..... *Cretapristocera*

2. Head elongated with small eyes …..…….. 3

- Head almost globose with large eyes ……..… 5

3. Mandibles with four large teeth along masticatory margin……..…. *Ramageoptera* gen. nov.

- Mandibles with numerous shorter teeth along masticatory margin ……. 4

4. Legs with pro- and meta-femora clearly thickened; forewing cell 2R1 open …..…… *Bethylitella*

- Legs, except pro-femora, only slightly thickened; forewing cell 2R1 almost closed ….……. *Protopristocera*

5. Notauli well-developed, parapsidal furrow weak (Eocene: Oise amber) …… *Gynopteron*

- Notauli weak, parapsidal furrow well-visible (Eocene: Baltic amber) ……. *Bethylopteron*

5. Conclusion

Amber from northern Myanmar provides once again novel insights into the paleodiversity of flat wasps during the Cretaceous. The description of *Ramageoptera platycephala* gen. et sp. nov. increases the diversity of the protopristocerine wasps documented from the Cenomanian Burmese

amber and strengthens the hypothesis suggesting that the Protopristocerinae are stem-Pristocerinae, only mostly differentiated owing to the winged females (plesiomorphy). If the bethylid fossil record continues to grow, it seems obvious that a phylogeny integrating the whole fossil diversity at a genus level will be needed to clarify the classification and estimate times of divergence among the various clades.

Disclosure of interest

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

Acknowledgment

We thank the editor Prof. Didier Néraudeau for the invitation to contribute to this volume and for its advice during the publication process. We thank Prof. André Nel (MNHN) for his corrections on the first version of the manuscript. We are grateful to Prof. Alexandr P. Rasnitsyn and to an anonymous reviewer for their insightful comments and suggestions. This work was contributed by Corentin Jouault during its Ph.D. project on the « Impact des interactions biotiques et paléo-évènements sur la diversification des insectes Neuropterida » and is a part of Manuel Brazidec Ph.D. project on the « Le rôle des optimums climatiques sur la diversification et l'évolution des guêpes chrysidoïdes ».

References

Azevedo, C.O., Alencar, I.D.C.C., Ramos, M.S., Barbosa, D.N., Colombo, W.D., Vargas, J.M.R., Lim, J., 2018. Global guide of the flat wasps (Hymenoptera, Bethylidae). Zootaxa 4489, 1-294. https://doi.org/10.11646/zootaxa.4489.1.1.

Brothers, D.J., 2011. A new Late Cretaceous family of Hymenoptera, and phylogeny of the Plumariidae and Chrysidoidea (Aculeata). ZooKeys 130, 515–542. https://doi.org/10.3897/zookeys.130.1591

Brothers, D.J., Rasnitsyn, A.P., 2003. Diversity of Hymenoptera and other insects in the Late Cretaceous (Turonian) deposits at Orapa, Botswana: a preliminary review. African Entomology 11, 221–226.

Brues, C.T., 1923. Some new fossil parasitic Hymenoptera from Baltic amber. Proceedings of the American Academy of Arts and Sciences 58, 327–346. https://doi.org/10.2307/20025999

Brues, C.T. (1933a) The parasitic Hymenoptera of the Baltic amber. Part I. Bernstein-Forschungen 3, 4–172.

Cockerell, T.D.A., 1917. Arthropods in Burmese amber. American Journal of Science, (4) 44, 360–368. https://doi.org/10.2475/ajs.s4-44.263.360

Colombo, W.D., Perkovsky, E.E., Azevedo, C.O., 2020. Phylogenetic overview of flat wasps (Hymenoptera, Bethylidae) reveals Elektroepyrinae, a new fossil subfamily. Palaeoentomology 3, 269–283. https://doi.org/10.11646/palaeoentomology.3.3.8

Colombo, W.D., Perkovsky, E.E., Waichert, C., Azevedo, C.O., 2021. Synopsis of the fossil flat wasps Epyrinae (Hymenoptera, Bethylidae), with description of three new genera and 10 new species. Journal of Systematic Palaeontology 19, 39–89. https://doi.org/10.1080/08912963.2020.1733551

Cruickshank, R.D., Ko, K., 2003. Geology of an amber locality in the Hukawng Valley, northern Myanmar. Journal of Asian Earth Sciences 21, 441–455. https:// doi.org/10.1016/S1367-9120(02)00044-5.

Engel, M.S., Grimaldi, D.A., 2007. Cretaceous Scolebythidae and phylogeny of the family (Hymenoptera: Chrysidoidea). American Museum Novitates 3568, 1-16. http://hdl.handle.net/2246/5859.

Engel, M.S., Ortega-Blanco, J., McKellar, R.C., 2013. New scolebythid wasps in Cretaceous amber from Spain and Canada, with implications for the phylogeny of the family (Hymenoptera: Scolebythidae). Cretaceous Research 46, 31–42. http://dx.doi.org/10.1016/j.cretres.2013.09.003

Falières, E., Nel, A., 2019. The first representative of the extinct flat wasp subfamily Protopristocerinae (Insecta: Hymenoptera, Bethylidae). Palaeoentomology 002, 322–326. https://doi.org/10.11646/palaeoentomology.2.4.4

Goulet, H., Huber, J.T., 1993. Hymenoptera of the world: an identification guide to families. Agriculture Canada, Ottawa, Ontario, p. 680.

Grimaldi, D.A., Ross, A.J., 2017. Extraordinary Lagersta€tten in amber, with particular reference to the Cretaceous of Burma. In: Fraser, N.C., Sues, H.D. (Eds.), Terrestrial Conservation Lagersta€tten: Windows into the Evolution of Life on Land. Dunedin Academic Press, Edinburgh, pp. 287–342.

Jouault, C., Perrichot, V., Nel, A., 2021a. New flat wasps from mid-Cretaceous Burmese amber deposits highlight the bethylid antiquity and paleobiogeography (Hymenoptera: Chrysidoidea). Cretaceous Research 123, 104772. https://doi.org/10.1016/j.cretres.2021.104772

Jouault, C., Ngô-Muller, V., Pouillon, J.-M., Nel, A., 2021b. New Burmese amber fossils clarify the evolution of bethylid wasps (Hymenoptera: Chrysidoidea). Zoological Journal of the Linnean Society 191, 1044–1058. https://doi.org/10.1093/zoolinnean/zlaa078

Melo, G.A.R., Lucena, D.A.A., 2020. †Chrysobythidae, a new family of chrysidoid wasps from Cretaceous Burmese amber (Hymenoptera, Aculeata). Historical Biology 32, 1143-1155. https://doi.org/10.1080/08912963.2019.1570184

Nagy, C.G., 1974. A new bethylid subfamily allied to Protopristocerinae. Bolletino de Societa Entomologica Italiana 106, 126–129.

Perrichot, V., Nel, A., 2008. Eocene bethylid wasps from French amber (Hymenoptera: Bethylidae). Neues Jahrbuch für Geologie und Paläontologie 248, 91–101. https://doi.org/10.1127/0077-7749/2008/0248-0091

Shi, G.-H., Grimaldi, D.A., Harlow, G.E., Wang, J., Yang, M.-C., Lei, W.-Y., Li, Q.-L., Li, X.- H., 2012. Age constraint on Burmese amber based on U-Pb dating of zircons. Cretaceous Research 37, 155–163. https://doi.org/10.1016/j.cretres.2012.03.014.

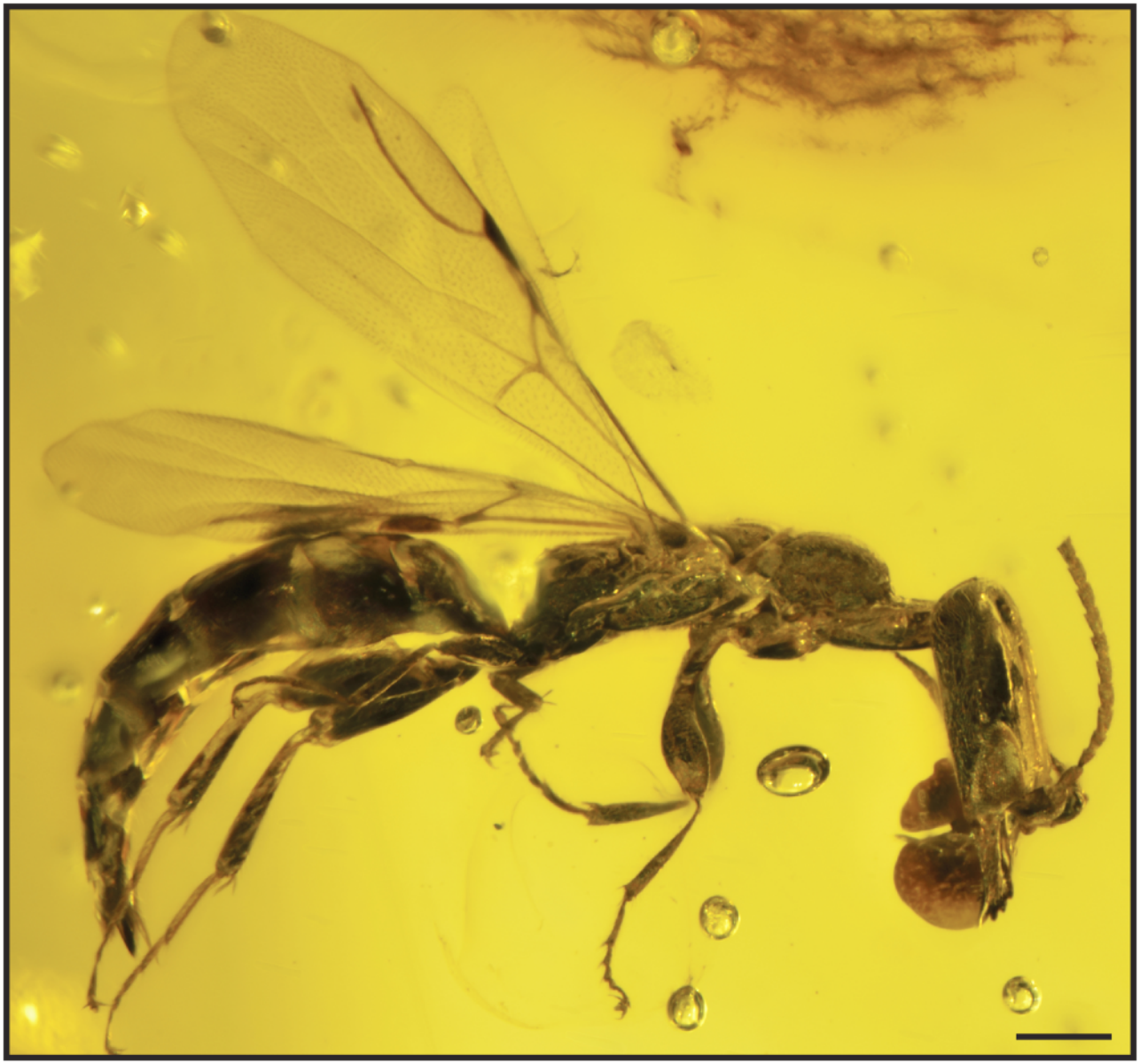
Wang B, Shi G, Xu C, Spicer R, Perrichot V, Schmidt AR, Feldberg K, Heinrichs J, Chény C, Pang H, et al. 2021. Zhangpu biota reveals the richest Cenozoic rainforest biome. Science Advances 7:eabg0625. https://doi.org/10.1126/sciadv.abg0625

Yu, T.-T., Kelly, R., Mu, L., Ross, A., Kennedy, J., Broly, P., Xiai, F.-Y., Zhang, H.-C., Wang, B., Dilcher, D., 2019. An ammonite trapped in Burmese amber. Proceedings of the National Academy of Sciences of the United States of America 116, 11345–11350. https://doi.org/10.1073/pnas.1821292116.

Figure captions

Fig. 1. *Ramageoptera platycephala* gen. et sp. nov., holotype IGR.BU-050. Habitus in right-lateral view. Scale bar: 0.25 mm.

Ramageoptera platycephala gen. et sp. nov., holotype IGR.BU-050. Habitus en vue latérale droite. Barre d'échelle : 0,25 mm.



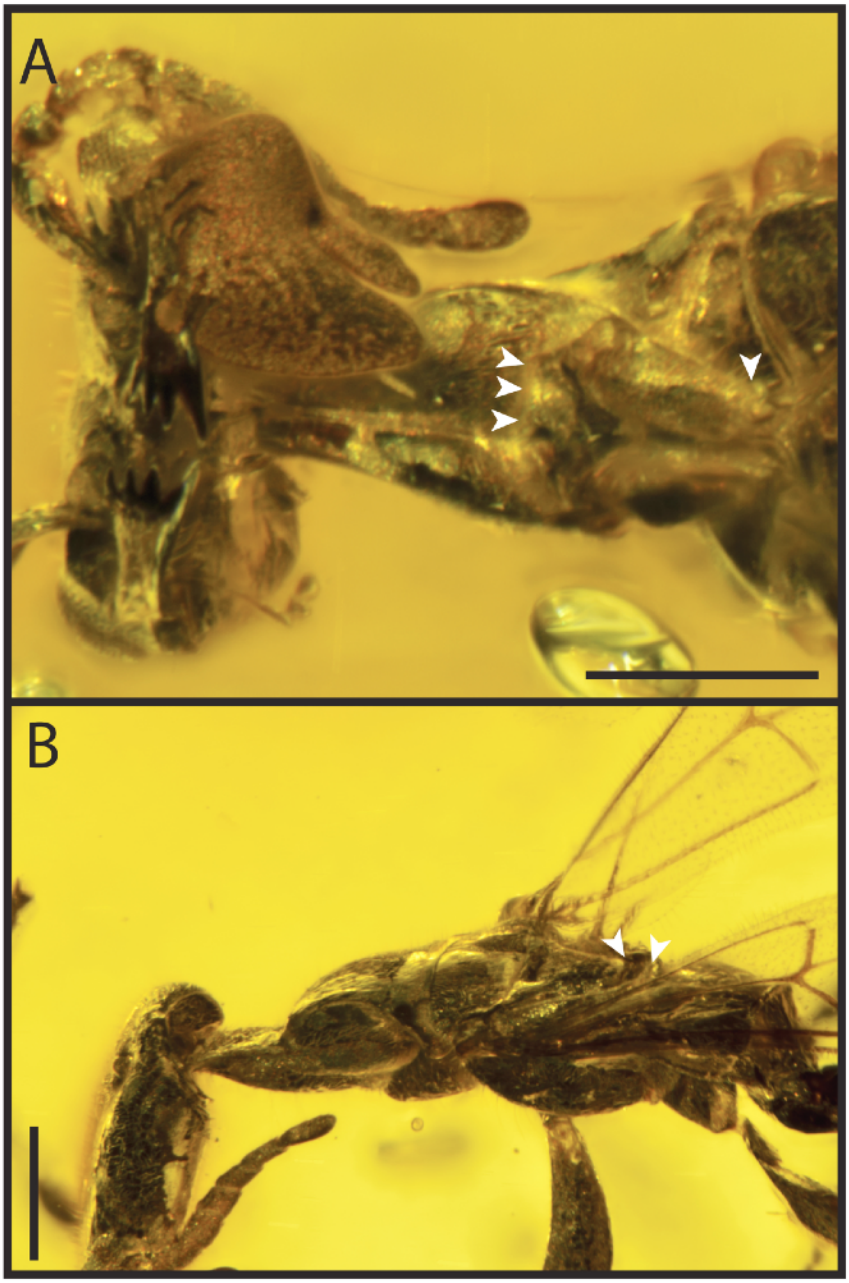


Fig. 2. *Ramageoptera platycephala* gen. et sp. nov., holotype IGR.BU-050. A. Detailed view of prosternum (arrows pointing anterior margin of prosternum and insertion of protrochanter on procoxa). B. Dorsolateral view of mesosoma (arrows pointing metanotum developed medially and overlapping mesoscutellum posteriorly). Scale bars: 0.25 mm.

Ramageoptera platycephala gen. et sp. nov., holotype IGR.BU-050. A. Vue détaillée du prosternum (les flèches indiquent la marge antérieure du prosternum et l'insertion des protrochanter sur les procoxa). B. Vue dorso-latérale du mésosoma (les flèches indiquent le métanotum développé médialement et superposant le mésoscutellum à l'arrière). Barres d'échelle : 0,25 mm.

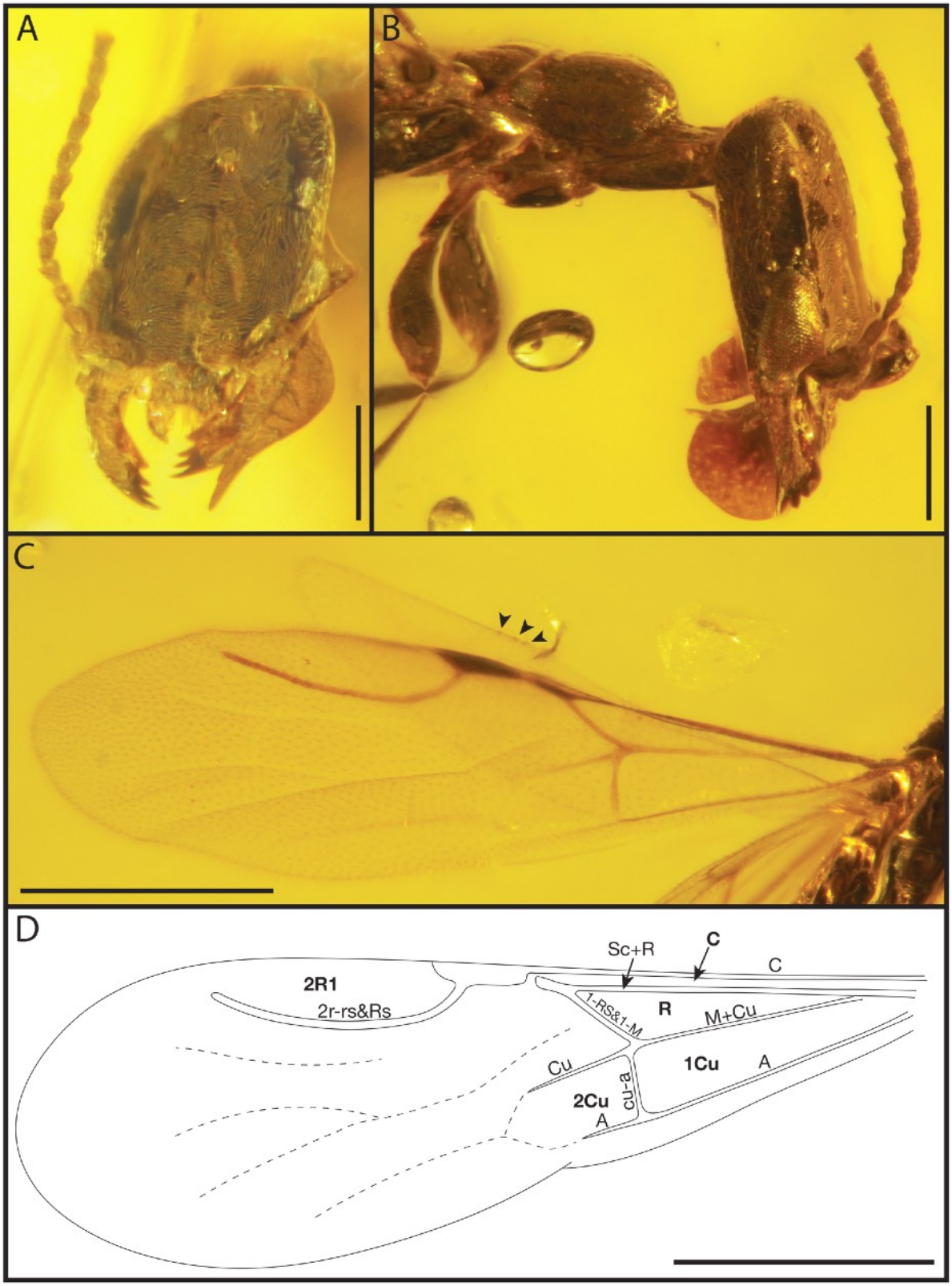


Fig. 3. *Ramageoptera platycephala* gen. et sp. nov., holotype IGR.BU-050. A. Head in full face view. B. Anterior part of mesosoma and head in right lateral view. C. Microphotograph of wings

(arrows pointing the three hamuli). D. Interpretative line drawing of forewing venation with names of cells and veins labelled. Scale bars: 0.25 mm (A, B); 0.5 mm (C, D).

Ramageoptera platycephala gen. et sp. nov., holotype IGR.BU-050. A. Tête en vue frontal. B. Partie antérieure du mésosoma et de la tête en vue latérale de droite. C. Microphotographie des ailes (les flèches indiquent les trois hamuli). D. Dessin interprétatif de la nervation de l'aile antérieure avec les noms de cellules et des nervures indiqués. Barres d'échelle : 0,25 mm (A, B) ; 0,5 mm (C, D).