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Corentin Jouault: Conceptualization, Data curation, Investigation, Methodology, Visualization, Writing - original draft, Writing - review & editing. Vincent Perrichot: Data curation, Investigation, Writing - original draft, Writing - review & editing. André Nel: Supervision, Data curation, Investigation, Writing - original draft, Writing - review & editing.
New flat wasps from mid-Cretaceous Burmese amber deposits highlight the betylid antiquity and paleobiogeography (Hymenoptera: Chrysidoidea)

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Abstract

Examination of Hkamti and Tanai Burmese ambers reveals two new genera and species of †Lancepyrinae: \textit{Protopyris myanmarensis} Jouault & Nel gen. et sp. nov. and \textit{Burmapyris azevedoi} Jouault, Perrichot & Nel gen. et sp. nov. \textit{Protopyris} Jouault & Nel gen. nov. is the first Bethylidae described from amber of the Hkamti deposit (lower Albian, mid-Cretaceous) in Myanmar. These specimens provide useful clues to understand the paleobiogeographic evolution of the †Lancepyrinae, since they are only predated by genera described from Lebanese and Spanish amber. These new taxa suggest a major paleobiogeographic scenario, since Burmese amber was probably produced on an island that separated from Gondwana during the Late Jurassic to Early Cretaceous. It thus suggests a possible earlier origin for the †Lancepyrinae, and thereby for the Bethylidae, in the Late Jurassic to earliest Cretaceous.

Key words. Hkamti amber, Bethylidae, †Lancepyrinae, paleobiogeography, Abian
The †Lancepyrinae are a small extinct bethylid subfamily, originally described from Barremian Cretaceous Lebanese amber (Azevedo and Azar, 2012). Members can be easily distinguished from related taxa mainly by having fore wing venation with an unusual combination of closed lanceolate cell 2R1, tubular and well-pigmented vein Rs+M, and angled vein Rs&M (Azevedo and Azar 2012).

Later, this work was supplemented by the additions of Ortega and Engel (2013) and Engel et al. (2016), with descriptions of further lancepyrine genera and species, challenging the constant presence of a tubular Rs+M vein. †Lancepyrinae were hitherto known only by five species from Lebanese, Spanish, and Taimyr amber (Evans, 1973; Azevedo and Azar, 2012; Ortega-Blanco and Engel, 2013; Engel et al., 2016), but remained unknown from the Burmese amber biota. As for the other bethylid fossil subfamilies, we do not have a record of behavior or clue to understand †Lancepyrinae biology (Azevedo et al., 2018).

Recently, two phylogenies have been proposed to investigate the relationships between Bethylidae subfamilies (Jouault et al., 2020a; Colombo et al., 2020). However, if their results do not record †Lancepyrinae at exactly the same position, both recover them as an early diverging lineage among Bethylidae. In Jouault et al. (2020a: fig 6), they fall as a part of separate radiation (†Lancepyrinae + †Protopristocerinae) sister group of the clade (Mesitiinae + Pristocerinae + Epyrinae + Scleroderminae); while Colombo et al. (2020: fig 1B) recorded them as sister group to the clade (Mesitiinae + †Elektroepyrinae + Pristocerinae + Epyrinae + Scleroderminae + †Protopristocerinae). It is therefore probable that new phylogenies will be necessary to clarify this placement, above all a molecular phylogeny updating the results of Carr et al. (2010).

Herein, we describe the first records of †Lancepyrinae from two Cretaceous Burmese amber deposits, and we discuss their placement and the implication on the paleobiogeographic history of the subfamily.

**Material and methods**
The amber piece containing the type of *Protopyris myanmarensis* gen. et sp. nov. derives from the deposits of Hkamti site (about 80 km southwest of the Angbamo site), Hkamti District, Sagaing Region, Myanmar, see detailed map in Zheng et al. (2018: supplementary figure 2) or in Xing and Qiu, (2020: fig. 1). Zircon U-Pb analyses established an early Albian age (109.7 ± 0.4 Ma) for Hkamti amber, based on zircon analyses of clastic deposits at the surface (Xing & Qiu, 2020). The paleobiota from this deposit is almost unknown, with only one ostracod and one Diapriidae described to date (Xing et al., 2018; Jouault et al., 2020b). The amber piece containing the type of *Burmapyris azevedoi* gen. et sp. nov. derives 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 earliest Cenomanian age (98.79 ± 0.62 Ma) for Kachin amber, based on zircons from volcanic clasts 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 specimens were examined and photographed using a Leica MZ APO stereomicroscope equipped with a Canon EOS 5D Mark II camera. All images are digitally stacked photomicrographic composites of several individual focal planes, which were obtained using HeliconFocus 6.7. The figures were composed with Adobe Illustrator CC 2019 and Adobe Photoshop CS19 software. The specimens are housed in the amber collection of the Geological Department and Museum (IGR) of the University of Rennes, France. We follow the nomenclature, classification, and terminology for morphological features of the body and wing venation of Azevedo et al. (2018).

Main measurements and abbreviations used are as follows: length of fore wing (LFW); length of head, mandibles excluded (LH); width of head (WH); width of frons (WF); height of eye (HE); length of eye (LE); 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).
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Systematic paleontology

Class Insecta Linnaeus, 1758
Order Hymenoptera Linnaeus, 1758
Superfamily Chrysidoidea Latreille, 1802
Family Bethylidae Haliday, 1839
Subfamily †Lancepyrinae Azevedo and Azar, 2012

Genus Protopyris gen. nov. Jouault & Nel
Figs 1-2
urn:lsid:zoobank.org:act:8C12080A-83F2-48D3-AC6D-7C92DA4C6710

Type species. Protopyris myanmarensis sp. nov. Jouault & Nel

Etymology. The genus name is a combination of the Greek « prótos » meaning ‘primitive’ and the generic name Epyris, commonly used as a stem for many bethylid genera. Gender masculine.

Diagnosis. Body depressed; mandibles dentate with four(?) teeth along masticatory margin and one long apical tooth; clypeus reduced, not projecting; antennae with 11 flagellomeres; scape less than twice as long as pedicel; notauli conspicuous; fore wing venation developed, with cells C, R, 1Cu, 1M, and 2R1 delimited by tubular veins; M and cu-a veins aligned; 2Cu not clearly delimited; 2R1 opened at apex; pterostigma narrow, elongate; propodeum rectangular and not spinose; legs with slightly enlarged femora.

Protopyris myanmarensis sp. nov. Jouault & Nel
Holotype: Specimen identifier IGR.BU-015 (a nearly complete specimen, with right antenna destroyed, in a rectangular piece of amber measuring $5 \times 4 \times 1.5$ mm).

Etymology. Named after the originating country of the amber piece, Myanmar. The specific epithet is to be treated as an adjective in the genitive case.

Locality and horizon. Hkamti site, Hkamti District, Sagaing Region, Myanmar; lower Albian (ca. 110 Ma), mid-Cretaceous.

Diagnosis. As for the genus.

Description. Sex unknown; body ca. 2.10 mm long, depressed, almost smooth and not strongly foveolate; wings clear, setose, LFW 1.25 mm. LH 0.50 mm; WH 0.53 mm; WF 0.31 mm; LE 0.25 mm; OOL 0.15 mm; WOT ca. 0.12 mm; DAO 0.03 mm; VOL 0.11 mm. Head sub-quadrate, not pubescent, with small dorsal median depression, finely punctate but not sculptured; mandible projecting forward, ca. 0.12 mm long, dentate, apparently with four equal, sharp, small teeth along masticatory margin and one longer apical tooth; only two maxillary palpomeres visible (but certainly more are present); flagellomeres with cylindrical cross-section; measurable antennomere lengths (in mm) scape 0.11 mm, pedicel 0.07 mm, F1 ca. 0.03 mm, F2 ca. 0.03 mm, F3 0.05 mm, F4 to F10 sub-equal to equal ca. 0.06 mm (all flagellomeres compressed due to preservation, thereby useful width measurements not provided); occipital carina slightly marked; posterior head margin nearly straight with small median concavity; compound eye without microsetae, closer to mandibular insertion than posterior to head margin; ocellar triangle nearly equilateral, with two posterior ocelli slightly more distant from each other than from anterior.

Mesosoma with dorsum smooth, not roughly sculptured; femora slightly thickened, tibia thin, tarsal claws simple; tibial spur formula 1-2-2; arolium present; notauli well-marked, posteriorly convergent; parapsidal furrows weak; metanotum developed medially and overlapping mesoscutellum posteriorly; metapsectal-propodeal complex rectangular, not foveolate, with marginal carinae and no
posterior spines; posterior margin of propodeum straight. Fore wing covered with microtrichiae and bordered with small microtrichiae; elongated with apical margin gently rounded; anterior border not angularly incurved anterior to pterostigma; veins C, Sc+R, A, R1, Rs, Rs+M, 2r-rs&Rs, M+Cu, M, cu-a, Cu and cells C, R, 1Cu, 1M and 2R1 present; M and cu-a veins aligned; cell 2Cu open, virtually enclosed by spectral vein; cell 2R1 distally opened; Rs+M prolonged as a spectral vein originating from 1M at level of pterostigma base; pterostigma long and narrow; prestigmal abscissa of R1 conspicuous. Hind wing with only veins C and Sc+R, hamuli uncountable.

Metasoma with short petiole; six tergites present, T1 reduced, T2 enlarged, all tergites convex, partly covering sternites; sting not preserved (apical part of metasoma destroyed); length of clearly visible tergites: T1 0.26 mm, T2 0.15 mm, T3 ca. 0.15 mm, more distal tergites impossible to measure because of bent metasoma.

Genus *Burmapyris* gen. nov. Jouault, Perrichot & Nel

Figs 3-4

 urn:lsid:zoobank.org:act:A627B4D5-35BB-48F5-B198-A2721DDB01D1

*Type species*. *Burmapyris azevedoi* Jouault, Perrichot & Nel sp. nov.

*Etymology*. The generic epithet is a combination of ‘Burma’ referring to Burmese amber and the generic name *Epyris*, commonly used as a suffix for many bethylid genera. Gender masculine.

*Diagnosis*. Female (sting visible) with body weakly depressed; mandibles heavily dentate with five(?) sharp teeth along masticatory margin, with apical tooth longer and stouter; clypeus triangular and slightly projecting; antennae stout, with 11 flagellomeres; scape nearly twice as long as pedicel; notauli conspicuous; fore wing venation developed, with cells C, R, 1Cu, and 2R1 delimited by tubular veins; M and cu-a veins aligned; pre- and post-stigmal R1 abscissae present; 1M and 2Cu not clearly delimited; 2R1 opened at apex; pterostigma short, wide in apical one-third of length; hind wing with four hamuli; propodeum rectangular and not spinose; legs with slightly enlarged femora.
Burmapyris azevedoi sp. nov. Jouault, Perrichot & Nel

urn:lsid:zoobank.org:act:9EE1F4FE-9B6C-43AB-8C2A-823D4A48F0E1

Holotype: Specimen identifier IGR.BU-016 (complete female, in a rectangular piece of amber measuring 5 × 4 × 2 mm).

Etymology. The specific epithet is a patronym honoring Dr. Celso O. Azevedo, a world authority in Bethylidae taxonomy. The specific epithet is to be treat as a noun in a genitive case.

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

Diagnosis. As for the genus.

Description. Female (sting slightly visible); body ca. 2.5 mm long, almost smooth and not strongly foveolate; wings clear and setose, LFW at least 1.50 mm (bent). LH 0.57 mm; WH 0.53 mm; WF 0.31 mm; HE 0.18 mm; LE ca. 0.25 mm; OOL 0.15 mm; WOT ca. 0.15 mm; DAO 0.05 mm; VOL ca. 0.12 mm. Head slightly longer than wide, not pubescent, without dorsal median depression, sculpture apparently absent; mandible bent downward and slightly curved backwards, ca. 0.18 mm long; only four maxillary palpomeres visible (but certainly more numerous); flagellomeres with cylindrical cross-section; measurable antenomere lengths (in mm): scape ca. 0.15 mm, pedicel 0.08 mm, F1 to F7 ca. 0.12 mm, F8 to F10 ca. 0.11 mm, F11 0.18 mm; occipital carina conspicuous; posterior head margin curved; compound eye without microsetae, closer to mandibular insertion than to posterior head margin; ocellar triangle nearly equilateral, situated posteriorly on head, with two posterior ocelli slightly more distant from each other than from anterior.

Mesosoma with dorsum smooth, not roughly sculptured; femora slightly thickened, tibia thin, tarsal claws simple; tibial spur formula 1-2-2; arolium present; notauli well-marked, slightly posteriorly convergent; parapsidal furrows weak; metanotum developed medially and overlapping mesoscutellum posteriorly; metapental-propodeal complex rectangular, not foveolate, with marginal carinae and no posterior spines; posterior margin of propodeum straight. Fore wing covered with mi-
crotrichiae and bordered with small microtrichiae, with apical margin gently rounded; anterior border not angularly incurved anterior to pterostigma; veins C, Sc+R, A, R1, Rs, Rs+M, 2r-rs&Rs, M+Cu, M, cu-a and cells C, R, 1Cu, and 2R1 present; M and cu-a veins aligned; cell 2Cu and 1M open, virtually enclosed by spectral vein; cell 2R1 distally opened; Rs+M long and prolonged as a spectral vein originating from 1M after pterostigma apex; pre- and post-stigmal abscessae of R1 conspicuous. Hind wing with only veins C and Sc+R, and 4 hamuli.

Metasoma with short petiole; apex interiorized, but six tergites visible, T1 reduced, T2 enlarged, all tergites convex, partly covering sternites; sting not preserved; length of clearly visible tergites: T1 0.43 mm, T2 0.27 mm, T3 0.22 mm, T4 ca. 0.12 mm, other tergites not measurable since interiorized.

Key to genera of †Lancepyrinae (modified from Azevedo et al., 2018):

1. Fore wing with Rs+M vein conspicuous and tubular .................................................. 2
   – Fore wing with Rs+M vein apparently absent, weak or spectral ........................................ 5

2. Fore wing with 2R1 cell closed ............... Lancepyris Azevedo & Azar, 2012 (Ain Dara amber, Lebanon)
   – Fore wing with 2R1 cell opened .......................................................................................... 3

3. Fore wing with a short pterostigma and Rs+M vein short (not enclosing 1M cell or reaching apex of pterostigma) .............................................. Archaepyris Evan, 1973 (Taimyr amber, Russia)
   – Fore wing with an elongate pterostigma and Rs+M long (enclosing 1M cell or reaching apex of pterostigma) .................................................................
4. Rs+M long, continuing after 1M cell, 1M cell not fully enclosed by tubular veins .......................... *Burmapyrus* Jouault, Perrichot & Nel gen. nov. (Kachin amber, Myanmar)

- Rs+M short, only cancelling 1M cell, 1M cell fully enclosed by tubular veins ........................................... *Protopyris* Jouault & Nel gen. nov. (Hkamti amber, Myanmar)

5. Fore wing with cu-a vein postfurcal with M vein ................................. *Zophepyris* Engel et al., 2016 (Peñacerrada amber, Spain)

- Fore wing with cu-a vein aligned or antefurcal with M vein ................................................................. 6

6. Fore wing with 2r-rs&Rs vein arising on distal half of pterostigma .......................... *Cretepyris* Ortega-Blanco & Engel, 2013 (Peñacerrada amber, Spain)

- Fore wing with 2r-rs&Rs vein arising on basal half of pterostigma ................................................................. *Liztor* Ortega-Blanco & Engel, 2013 (Peñacerrada amber, Spain)

**Discussion**

**Systematic placement and phylogenetic hypothesis**

Following the key to superfamilies proposed in Goulet and Huber (1993), our specimens key out in Chrysidoidea because of their pronotum being more than half as long as their mesoscutum, and their metasomal terga 1 and 2 having very weak constriction at their junction dorsally and laterally or with no constriction at all. Following the key to Chrysidoidea families in Goulet and Huber (1993), they key out in Bethylidae because of their antenna with 10 or 11 flagellomeres, the presence of wings, their profemora not enlarged or swollen, metasoma with six or seven exposed
terga, pronotum touching tegula, and prognathous heads. Additionally, our specimens could be confused with Scolebythidae but differ from the latter in having a pronotal anterior flange rendering propleura visible in dorsal aspect; the propleura closely situated so that the prostrenum is not large, exposed, and diamond-shaped; and the protrochanter inserted ventrally on procoxa (Engel and Grijmaldi, 2007). Our specimens also differ from †Chrysobythidae at least in lacking a shallow medial line on head (vs. present in †Chrysobythidae); in having the clypeus more or less triangular (vs. raised as a convex, somewhat squared lobe), the fore wing with a reduced number of closed cells (vs. six enclosed cells) and the cells 1R1 and 2R1 open (Melo and Lucena, 2020).

Following the key to subfamily of Azevedo et al. (2018), Protopyris gen. nov. and Burmapyris gen. nov. key out in †Lancepyrinae because of their developed wings; the fore wings with Rs+M vein tubular and straight, at least as stub, with at most six closed cells; the clypeus not projecting backward onto frons; and the tarsal claws slightly curved. Following the key to genera of †Lancepyrinae of Azevedo et al. (2018), Protopyris gen. nov. keys out near Archaepyris Evans, 1973 because of the fore wing with Rs+M vein conspicuous and tubular, and 2R1 cell opened. However, Protopyris gen. nov. differs from Archaepyris in having an elongate fore wing, an elongate pterostigma, 1M cell conspicuous and closed, 2Cu cell virtually delimited by spectral veins, and M and cu-a veins aligned. Unfortunately, Evans (1973) did not provide extensive illustrations as for the other species he described. Thus, it is difficult to make a full comparison with our specimen. Following the key to genera of †Lancepyrinae of Azevedo et al. (2018), Burmapyris gen. nov. also keys out near Lancepyris because of the fore wing with Rs+M vein conspicuous and tubular and 2R1 opened, but it differs from the latter in having a fore wing with a long and wide pterostigma, a tubular Rs+M, 1M and 2Cu cells closed by conspicuous spectral veins, M and cu-a veins aligned, and R1 poststigmal present. Both new genera differ from each other in having the body respectively depressed vs. weakly depressed, and different fore wing venations (see. Figs 1,2C,3,4D).
Rasnitsyn (1969, 1980), proposed a general trend among various hymenopteran lineages consisting in the miniaturization, reduction of venation, enlargement of the pterostigma, and reduction of number of antennal flagellomeres. The reduction of wing venation has been recently investigated in two bethylid subfamilies (viz. †Holopsenellinae and Scleroderminae) by Jouault et al. (2020a), in accordance with Rasnitsyn’s observations. Thereby, by comparing the age and the wing venation of the new species described herein and previously described genera, it is possible to infer some phylogenetic placement of Protopyris gen. nov. and Burmapyris gen. nov. (Fig. 5) and to propose a hypothetic phylogeny of the †Lancepyrinae. Lancepyris and Protopyris display a relatively more complete and complex wing venation than other representatives, with numerous closed cells. Thereby, it is likely that they diverged earlier than other lancepyrine wasps (Fig. 2C) (Azevedo et al., 2018: fig 92D). This hypothesis is also supported by their age, in fact, Lancepyris is the oldest record of the subfamily, which would be congruent with a relatively ‘basal’ position in the †Lancepyrinae. Proposing relationships between the other taxa is more complicated since the differences in venation are reduced. However, Zophepyris and Burmapyris share a tubular Rs+M vein (Fig. 4D) (Azevedo et al., 2018: fig 92F), not recorded in other ‘advanced’ genera (viz. Liztor, Archaepyris, Cretepyris), suggesting that they could be closely related. Liztor, Archaepyris, and Cretepyris all have closed R and 1Cu cells (Azevedo et al., 2018: figs 92A,B,C,E), but only Liztor has a reduced 2r-rs&Rs vein while Archaepyris and Cretepyris display an elongated and tubular 2r-rs&Rs vein. Thereby, we assume that these two genera could be closely related to each other than to Liztor, which could be the sister group of (Archaepyris + Cretepyris) since the rest of their wing venations is similar.

Paleobiogeographic implications

Correlation between paleogeography and fossil record often provided interesting hypotheses on taxa antiquity. The Burma Terrane, where the amber was initially produced, displays an interesting geological and paleobiogeographic history allowing consistent hypothesis on origin and antiqui-
ty of taxa composing the Burmese amber Biota. In fact, during the Early Jurassic, the Terrane was located near the Australian block in East Gondwana (van Hinsbergen et al., 2012; Seton et al., 2012) and separated from East Laurasia (Asian region) by the Mesotethys Ocean. In addition, the extant Pacific islands (Malaysia, Papua, Borneo, etc.) did not yet exist (Neall and Trewich, 2008), making it almost impossible to transfer wildlife from East Laurasia to the East Gondwana (Australia and Burmese Terranes). Following this period, the Burmese Terrane began to break away from the Australian block to go north (as for the Indian block) to the Asian region between the Late Jurassic and the Early Cretaceous (Heine et al., 2004; Heine and Müller, 2005). The Burma Terrane is supposed to have been separated from the Gondwana after 125 Ma ago, but close to its margin ca. 120 Ma ago (Metcalfe, 1990, 1996; Scotese, 2014; Westerweel et al., 2019). Later, it was isolated geographically and occupied an island position in the Tethys Ocean between Asia and the Indian block during the mid-Cretaceous (Westerweel et al., 2019) for more than 20 Ma (Heine et al., 2004; Seton et al., 2012). It is very likely that the stem group of the Bethylidae was already present on the Burma Terrane before its complete separation from Gondwana, ca. 125-120 Ma ago, since we already have fossil record of the family in Lebanese amber during the Barremian (Fig. 6) (Azevedo and Azar, 2012). The record of lancepyrine wasps in Lebanese and Spanish amber (in southern Laurasia), respectively located in the central part of the southern Tethyan margin and the western Tethyan margin (Peris et al., 2016: fig. 1), suggests that the †Lancepyrinae were already diversified along the western Tethys. However, the record of Protopyris gen. nov. and Burmapyris gen. nov. on the Burma Terrane suggests that the †Lancepyrinae had also conquered the eastern Gondwana before the break-up of the Burma Terrane. Ezcurra and Agnolin (2012: fig. 2) proposed the paleogeographic Eurogondwana model, according to which Gondwanan lineages could colonize Laurasia and North America via an Apulia microplate from 145 to 99 Ma, prior to continental drift. This scenario is in accordance with the presence of other †Lancepyrinae in Spain and Lebanon during the Early Cretaceous (Azevedo and Azar, 2012; Ortega-Blanco and Engel, 2013; Engel et al., 2016). The record of Archaepyris in Taimyr amber (Late Cretaceous) (Evans, 1973) may also indicate that the
†Lancepyrinae already colonized the eastern Laurasia during the mid-Cretaceous. According to this peculiar geological history, it is very likely that the †Lancepyrinae and, therefore the Bethylidae, arose before the break-up of the Burma Terrane from South-East Gondwana, indicating at least an Early Cretaceous (or even Late Jurassic) origin for the family.

Conclusion

Both new genera described herein are the first †Lancepyrinae described from Burmese amber and Protopyris myanmarensis gen. et sp. nov. is the first Bethylidae described from the lower Albian Hkamti amber. These discoveries highlight the underestimated diversity of bethylid wasps in Burmese biota. The peculiar palaeogeographic history of the Burma Terrane provides evidence for the antiquity of the †Lancepyrinae and, therefore, of the entire Bethylidae family. It is likely that the Bethylidae arose during the earliest Cretaceous, before the Gondwana breakup, and maybe during the Late Jurassic. It stands to reason that a morphological- and molecular-based phylogeny with time divergence estimates has becomes a necessity for our understanding of this family.

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References


Rasnitsyn, A.P., 1969. The origin and evolution of Lower Hymenoptera. Transactions of the Paleontological Institute, Academy of Sciences of the USSR 123, 1–196 [In Russian].


Figure captions.

Figure 1. *Protopyris myanmarensis* sp. nov. Jouault & Nel, holotype IGR.BU-015. Photographs of habitus. A: Dorsal view. B: Ventral view. Scale bars: 0.5 mm.

Figure 2. *Protopyris myanmarensis* sp. nov. Jouault & Nel, holotype IGR.BU-015. A: Mesosoma. B: Head. C: Wing. D: Line drawing of fore wing with vein and cell nomenclature (cell names in bold). Scale bars: 0.25 mm (A,B); 0.5 mm (C).

Figure 3. *Burmapyris azevedoi* sp. nov. Jouault, Perrichot & Nel, holotype IGR.BU-016. Photographs of habitus A: Right view. B: Left view. Scale bars: 0.5 mm.
Figure 4. *Burmapyris azevedoi* sp. nov. Jouault, Perrichot & Nel, holotype IGR.BU-016. A: Head in left view. B: Mesosoma. C: Wings (with hamuli indicated by black arrows). D: Line drawing of fore wing with vein and cell nomenclature (cell names in bold). Scale bars: 0.25 mm.

Figure 5. Hypothetical phylogeny of Lancepyrinae with affixed geological time scale.

Figure 6. Global paleogeographic reconstruction for the mid-Cretaceous (100 Ma) period, showing distribution of Lancepyrinae; modified from Global Paleogeography and Tectonics in Deep Time © 2016 Colorado Plateau Geosystems Inc., localities of amber-producing forests after Westerweel et al. (2019).
Declaration of interests

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