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Corentin Jouault. A new species of thorny lacewing (Neuroptera: Rhachiberothidae: Paraberothinae) from mid-Cretaceous Burmese amber with novel raptorial foreleg structure. *Proceedings of the Geologists' Association*, 2022, 133 (1), pp.32-39. 10.1016/j.pgeola.2021.11.001 . insu-03445490

HAL Id: insu-03445490

<https://insu.hal.science/insu-03445490>

Submitted on 30 Nov 2021

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A new species of thorny lacewing (Neuroptera: Rhachiberothidae: Paraberothinae) from mid-Cretaceous Burmese amber with novel raptorial foreleg structure

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Abstract: A new species, namely *Astioberotha coutreti* sp. nov., of the thorny lacewing subfamily Paraberothinae, is described and figured from a complete individual preserved in mid-Cretaceous amber from Tanai, northern Myanmar. *Astioberotha coutreti* sp. nov. preserves nearly all the diagnostic characters of this subfamily, and differs from the type species of the genus *Astioberotha* owing to the fore femur with one long basal spine and 34 additional smaller spines: protibia bearing five distal spines; probasitarsus with two spines on inner edge located near mid-length; forewing with numerous maculation spots; intra-RP crossvein between RP3 and RP4 present (4rp3-rp4). *Astioberotha coutreti* sp. nov. together with the recent description of several other Paraberothinae from the mid-Cretaceous Burmese amber, are used to discuss the paleobiogeography of the subfamily.

Keywords: Insecta, Cenomanian, Paleodiversity, Systematic

1. Introduction

The Rhachiberothidae, also known as thorny lacewings, are easily recognizable within the Neuroptera because of their raptorial forelegs (the only other extant neuropteran family with raptorial legs is the Mantispidae but the two families are distinguishable on the basis of the elongation of the pronotum relative to the insertion of the anterior legs; see discussion part below). The fossil subfamily Mesithoninae also displays raptorial forelegs but has no extant representative (Markarkin et al., 2012; Khramov, 2013; Liu et al., 2015). It was sometimes raised at a family level or considered either as a subfamily of Rhachiberothidae or of Mantispidae (Mesithoninae = Mesomantispinae). The next step to clarify its placement will be to investigate its position using phylogenomic analyses.

Considering the Rhachiberothidae without the Symphrasinae, only 13 species within three genera of Rhachiberothidae are described, while these are relatively numerous in the fossil record and especially during the Cretaceous (e.g., Aspöck and Aspöck, 1997; Makarkin, 2015; Oswald, 2019; Nakamine et al., 2020). In addition to their particular morphology, modern taxa show a restricted distribution to the sub-Saharan area (Aspöck and Aspöck, 1997). If the subfamily Symphrasinae is integrated in the Rhachiberothidae as suggested by Ardila-Camacho et al. (2021), the diversity of the family is increased, but, more important, the Cretaceous diversity of the Rhachiberothidae (including Symphrasinae) is extended by four species (*Archaeosymphrasis pennyi*, *Habrosymphrasis xiai*, *Haplosymphrasites zouae*, *Parasymphrasites electrinus*) (Lu et al., 2020; Shi et al., 2020).

The patent advances linked to the new techniques of phylogenetic analysis and molecular sequencing, have made it possible to clarify the placement of Rhachiberothidae since they have long been considered to be enigmatic and were formerly considered as a subfamily of Berothidae due to venation characters (Tjeder, 1959; Makarkin and Kupryjanowicz, 2010). A family rank has

been proposed for the Rhachiberothidae by Aspöck and Mansell (1994) and is now followed in most of recent works (Engel et al., 2018; Winterton et al., 2018). However, the affinities between (Rhachiberothidae + Berothidae + Mantispidae) and the rest of the Neuroptera remain uncertain. In fact, Winterton et al. (2018: figs. 1, 4) showed that this monophyletic clade occupies a position of early diverged clade with respect to the clade (Chrysopoidea + Myrmeleontoidea) while Vasilikopoulos et al. (2020: figs. 1, 2) found the Chrysopoidea grouped with the (Berothidae + Mantispidae) within a monophyletic clade (note that Rhachiberothidae are not integrated in the analyses of Vasilikopoulos et al., 2020). These differences of relationships with other mantispoid families are not only recorded in phylogenomic analyses since even before the development of these techniques the relationships of rachiberothids with other families were uncertain. In fact, they were previously considered to be the sister lineage of Berothidae (Aspöck and Mansell, 1994; Aspöck et al., 2001, 2012), or of the Mantispidae (Liu et al., 2015; Engel et al., 2018). Recently, a molecular phylogenetic study suggested that Mantispidae would occupy a position of early diverged lineage with respect to a more inclusive clade (Rhachiberothidae + Berothidae) (Song et al., 2019). Here I follow the family status of the Rhachiberothidae as proposed in Winterton et al. (2018).

Due to their presence in many amber deposits, the Rhachiberothidae appears to be speciose during the Cretaceous period and widely distributed in the northern hemisphere (Nakamine et al., 2020: fig. 16). Their fossil record was recently restudied and discussed following the discovery of several Paraberothinae in Burmese amber (Nakamine et al., 2020). Herein, a new species of Paraberothinae is described and figured from the Kachin mid-Cretaceous Burmese amber.

2. Material and methods

The amber piece containing the specimen comes from the deposits of Noiye 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 *Astioberotha coutreti* sp. nov. (Figs. 1-3) is complete and well-preserved. The amber piece was polished to facilitate the observation of the specimen using a grinder polisher (Buehler EcoMet 30), and a thin silicon carbide sanding paper (grit size = 7000). 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 software.

Wing venation is adapted from Nakamine et al. (2020). The amber piece is housed in the Geological Department and Museum of the University of Rennes, France (IGR). It was legally obtained and donated to the institute. Wing venation abbreviations are as follows: A1–A3, first to third anal vein; CuA, anterior cubitus; CuP, posterior cubitus; MA and MP, anterior and posterior branches of media; RA, anterior radius; RP, posterior sector; ScP, subcosta posterior.

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3. Systematic Paleontology

Order Neuroptera Linnaeus, 1758

Superfamily Mantispoidea Leach, 1815

Family Rhachiberothidae Tjeder, 1959

Subfamily Paraberotherinae Nel et al., 2005

(for a summary of the rhachiberotherid fossil diversity see Nakamine et al., 2020: tab. 1).

Genus *Astioberotha* Nakamine et al., 2020

Included species: *Astioberotha falcipes* (type species); *Astioberotha coutreti* sp. nov.

***Astioberotha coutreti* sp. nov.**

(Figs 1-3)

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Etymology. The specific epithet is a patronym honoring my friend Baptiste Coutret for his 24th birthday. The specific epithet is to be treated as a noun in a genitive case.

Material. A nearly complete adult, partly invisible due to cracks, preserved in a ca. 13 mm × 11 mm × 6 mm flattened, clear yellow, transparent amber piece; holotype specimen accession number IGR.BU-047, is housed in the amber collection of the Geological Department and Museum of the University of Rennes, France (IGR).

Diagnosis. Fore femur with one long basal spine and 34 additional smaller spines along outer edge, no diminution of spine length between base and middle of fore femur. Protibia bearing on ventral edge, five distal slightly curved spines directed toward apex, no proximal spines. Probasitarsus with two spines on inner edge located near mid-length (lacking spine or spine-like setae on second to fifth tarsomeres). Forewing with numerous elongate oval maculation spots present near crossveins and near dichotomies of RP and MA; intra-RP crossvein between RP3 and RP4 present (4rp3-rp4).

Description. Body. Length ca. 4.70 mm as preserved (measured from vertex to apex of abdomen). Head. Vertex with dense fine setae. Mandibles simple without differentiated tooth. Eyes large, protruding laterally. Antennae cracked; scape slightly elongate, about three as long as width; pedicel ca. 0.4 times length of scape; both covered with fine dense setae; flagellum moniliform, antennae with more than 50 flagellomeres, all with scattered fine setae. Pronotum ca. 0.80 mm long, elongate, slightly narrower than maximum width of head, covered with fine, long setae. Mesothorax ca. 0.66 mm long and metathorax ca. 0.57 mm long.

Procoxa elongate nearly as long as profemur, slightly narrowed distally. Protrochanter elongate, ca. 0.36 mm long. Profemur long, ca. 0.75 mm, slightly broadened, covered with dense fine setae on surface, with spines of variable lengths forming two rows on ventral edge, only slightly curved distally. Protibia long, ca. 0.91 mm, slender, covered with fine setae on dorsal and lateral edges, with a single row of five spines regularly spaced and located distally on internal edge. All protarsomeres covered with fine setae; probasitarsus longest, with two spines located slightly before mid-length and few thin setae on inner edge; lengths of tarsomeres from base to apex (in mm) 0.31, 0.07, 0.06, 0.05, 0.08; claws curved.

Mesocoxa stout and conical. Mesotrochanter elongate, slightly upcurved. Mesofemur long, ca. 1.13 mm, slender, covered with dense long setae. Mesotibia long, ca. 1.33 mm, slender, covered with dense long setae, several long stronger setae; all mesotarsomeres covered with fine setae; first tarsomere the longest; lengths of tarsomeres from base to apex (in mm) 0.53, 0.16, 0.08, 0.06, 0.07; claws small, curved.

Metacoxa similar to mesocoxa. Metatrochanter elongate, slightly upcurved. Metafemur long, ca. 1.20 mm, slender, covered with dense long setae. Metatibia long, ca. 1.87 mm, slender, covered with dense long setae, several long stronger setae. all metatarsomeres covered with fine setae; first tarsomere the longest; lengths of tarsomeres from base to apex (in mm) 0.55, 0.16, 0.08, 0.6, 0.9; claws small, curved.

Forewing hyaline, elongate-ovoid, ca. 5.21 mm long, ca. 2.08 mm wide. Trichosors present along whole wing margin; thin setae sparsely present on dorsal and ventral surfaces of longitudinal veins, but absent on crossveins. Costal space slightly broader in the apical part of the lower third of the wing; about half of subcostal veinlets once forked. ScP fused with RA in apical third. Subcostal space with proximal crossvein (1scp-r) located well before R fork. RP divided into four branches; RP1 deeply forked; 4rp3-rp4 present before RP4 dichotomy. Two ra-rp crossveins present; 2ra-rp located between origin of RP3 and RP4; 3ra-rp located after RP1 and RP2 fork between RP1 and

RA. M basally approaching R, divided into media anterior (MA) and media posterior (MP); one aberrant crossvein (4ma-mp) present. Two r-m crossveins present; 2rp-ma located slightly distal to RP and MA origin; 4rp-ma located between RP4 and MA. Cu divided into CuA and CuP; one crossvein (2cua-cup) present between stem of CuA and anterior branch of CuP. One 1m-cua crossvein present located before M fork and reaching CuA. Two mp-cua crossveins present; 1mp-cua between stem of MP and CuA; 3mp-cua between MP and anterior branch of CuA. Three anal veins present: A1, A2 and A3; A3 not conspicuous (maybe simple). One cu-a crossvein (1cup-aa) present between stem of CuP and A1. One a-a crossvein (1a1-a2) present between stem of A1 and A2. Hind wing hyaline, elongate-ovoid, ca. 5.02 mm long, ca. 1.93 mm wide. Trichosors present on wing margin; thin setae sparsely present on dorsal and ventral surfaces of longitudinal veins, but absent on crossveins. Costal space narrowed; subcostal veinlets poorly preserved. ScP fused with RA in basal part of apical third of wing. Subcostal space without crossvein. RP divided into five branches; intra- RP crossvein (4rp4-rp5) present. Two ra-rp crossveins present; 2ra-rp located between RP4 and RP5 origin; 3ra-rp located after dichotomy of RP1 and RP2. M divided into MA and MP; one crossvein (4ma-mp) present. Two rp-m crossveins present; 1rp-m located near stems of RP and M; 4rp-ma located between RP5 and MA. Origin of Cu unclear; CuP pectinately branched with at least eight simple branches; one crossvein (2cua-cup) present. One mp-cu crossvein present; 3mp-cua located between MP and CuA. Anal veins present, A1, A2, and A3 forked.

Abdomen. Not clearly nor fully visible due to some amber cracks; elongate-ovoid, slightly compressed laterally, slightly thinner anteriorly, with moderately scattered setae; six sternites and tergites visible. Terminalia not visible (hidden in an amber crack).

4. Discussion

4.1. Systematic placement

At first sight, the Rhachiberothidae resembles superficially Mantispidae or Berothidae. In the present discussion, the subfamily Symphrasinae is not treated as belonging to the Mantispidae despite a recent and valuable work on the Mantispoidea (Ardila-Camacho et al., 2021) mostly because a confirmation using molecular data or, at a broader scale, genomic data is needed. The character allowing to quickly separate the Rhachiberothidae (Symphrasinae excluded) from the Berothidae is the presence of developed raptorial forelegs in the first family. Moreover, the elongation of the pronotum relative to the position of the forelegs (before insertion or after) allows to differentiate the thorny lacewing from the mantidflies, in fact the pronotum is elongated posteriorly to forelegs in Mantispidae (Aspöck and Mansell, 1994). Therefore, the fossil studied here is undoubtedly attributed to the Rhachiberothidae.

The Rhachiberothidae is today divided into two valid subfamilies, the Paraberotherinae and the Rhachiberothinae. The Paraberotherinae can be separated from Rhachiberothinae based on the presence of at least two (and usually numerous) spines on the inner edge of the protibia, and the absence of the vein 2scp-r on the forewing (Nakamine et al., 2020). Makarkin (2015) proposed a series of characters allowing to distinguish the Cretaceous Paraberotherinae (list recently revised by Nakamine et al., 2020: 1152). Most of the characters (nine of the 11 characters) in this list are visible on the fossil studied: (1) small body size (forewing 2.9–5.4 mm long) (Fig. 1.); (2) antennal scapus long to very long (ca. three times longer than wide) (Fig. 2A, D); (3) forelegs raptorial (Figs. 1, 2B, 3B); (4) five protarsomeres (Figs. 2B, 3B); (5) at least two spines present on the inner edge of the protibia (synapomorphy) (Figs. 2B, 3B); (6) subcosta posterior (ScP) and radius anterior (RA) fused distally in both fore- and hind wings (Figs. 1, 3A, C); (7) 2scp-r absent on forewing (Figs. 1, 3A, C); (8) 1rp-m straight in the hind wing (here slightly curved due to the preservation in amber) (Figs. 1, 3A, C); and (9) CuP present in the hind wing (Figs. 1, 3A, C). Thus the fossil described here is placed with confidence in the subfamily Paraberotherinae.

4.2. In deep comparison with fossil genera of the subfamily Paraberotherinae

The presence or absence of crossveins (e.g., 4rp3-rp4) is highly variable in Cretaceous Rachiberothidae. Therefore, a comparison based on this character is provided but a stronger support is accorded to the configuration of forelegs.

The specimen described above can be distinguished from the six paraberotherine genera *Albertoberotha*, *Creagroparaberotha*, *Eorhachiberotha*, *Raptorapax*, *Stygioberotha*, and *Uranoberotha*, by the length of scape (three times as long as maximum width, contra 5–10 times width in these genera) (Engel, 2004; McKellar and Engel, 2009; Petrulevičius et al., 2010; Makarkin, 2015; Nakamine et al., 2020).

The specimen also differs from *Albertoberotha* in having a forewing with RP1 forked with anterior and a posterior branches (vs. with only one branch); 4rp3-rp4 present (vs. absent); 1m-cua present (vs. absent); 3mp-cua present (vs. absent); 2cua-cup present (vs. absent) (McKellar and Engel, 2009: figs 1, 3-4). The forelegs of the studied fossil and of *Albertoberotha* strongly differ owing to the presence of numerous spines (24) along the tibia of *Albertoberotha* while only five spines are recorded in the new specimen presented in this study. The tarsal configuration also differs due to the presence of only two spines on the probasitarsus (located near mid-length) while spines are recorded on first and second tarsomeres in *Albertoberotha* (McKellar and Engel, 2009: 116). Additionally, 5-6 spine like setae *plus* a distal one are recorded on the probasitarsus of *Albertoberotha* while there is only two of them and no distal seta in the new fossil. *Albertoberotha* has only 27 flagellomeres while the new fossil has more than 49 flagellomeres (Nakamine et al., 2020: table 1). Some of these differences of character states treated individually may fall in the intrageneric range of variability but the combination of all of them excludes affinity of the present fossil with the genus *Albertoberotha*.

The diagnosis of *Creagroparaberotha* was recently revised (Nakamine et al., 2020: 14) and numerous differences are recorded between the new specimen described in this paper and the genus *Creagroparaberotha*. The protibia of *Creagroparaberotha* has numerous (> 12) ventral spine-like setae, covering entire length (vs. five in our specimen and located distally) (Nakamine et al., 2020: fig 9b). The probasitarsus of *Creagroparaberotha* bears slightly curved spine on its dorsal edge while the new fossil has two conspicuous spines on probasitarsus. The configuration of femoral spines also greatly differs with three major spines protruding from edge of profemur while there is no such configuration in the fossil described and illustrated in the study. Therefore, affinity with this genus is refuted.

The genus *Eorhachiberotha* was only figured with a drawing of wings and of foreleg (Engel, 2004). Aside from the scape length, the new specimen differs from this genus owing to the presence of spines on probasitarsus (vs. absent in *Eorhachiberotha*) but also due to the profemur bearing numerous spines (vs. few spines, maybe 15). Additionally, the wing venation of both specimens greatly differs with numerous crossveins present in the specimen described in this paper while the wing venation of *Eorhachiberotha* appears to be simpler (e.g. 4rp3-rp4, 4rp-ma, 4ma-mp absent). Additionally, the type species of *Eorhachiberotha* has 30 flagellomeres while the new specimen has more than 49 flagellomeres. These differences are enough to not attribute the specimen to this genus.

Raptorapax displays a unique configuration of forelegs with profemora and protibia, bearing numerous spines, and resembling to rakes or whalebone (Petrulevičius et al. 2010: plates 1-2) while the configuration of the forelegs of the new fossil is more simple (only with five distal spines on protibia but with a strong and conspicuous basal spine on profemur absent in *Raptorapax*). Additionally, the type species of *Raptorapax* has 29 flagellomeres while the new specimen has more than 49 flagellomeres. Even in the wing venation of *Raptorapax* is not well preserved the differences mentioned previously are sufficient to not place the new specimen in this genus.

The genus *Stygioberotha* was recently created (Nakamine et al., 2020: 11) and the following characters were proposed to separate it from other Rachiberothidae: profemur bearing two long spines each on the proximal and distal position of ventral edge (only one long spine is recorded near profemur base in the fossil described above); protibia bearing four long slightly curved hooked spines towards apex on the distal area of ventral ridge (here the difference is only the number: four vs. five); protarsus: all tarsomeres lack spine or spine-like setae (two spine-like setae are visible in the probasitarsus of the new specimen); forewing with only one anal vein present (the other anal veins are maybe present but not preserved in the type species of *Stygioberotha*, therefore I do not consider their presence on the specimen described in the systematic paleontology section as a difference); hind wing with RP divided into four branches (vs. five in the specimen figured here), anal vein absent (see comment for the forewing). Additionally, the type species of *Stygioberotha* has 37 flagellomeres while the new specimen has more than 49 flagellomeres. If the wing venation of the type specimen of *Stygioberotha* and that of the specimen described above are superficially similar the configuration of the forelegs greatly differs and falls outside the range of intrageneric variability.

Nakamine et al. (2020) also created the genus *Uranoberotha* and proposed the following characters as diagnostic of the genus: protibia with single row of 22 proximally inclined spines regularly spaced on external ventral edge (vs. only five spines present on the distal part in the new specimen). Probasitarsus: 5–7 small spine-like setae on external ventral edge and one long curved spine distally (vs. only two located near mid-length). Forewing hyaline (vs. with conspicuous collocated dots); subcostal veinlets simple (vs. most of them forked). Additionally, the type species of *Uranoberotha* has 42 flagellomeres while the new specimen has more than 49 flagellomeres. These differences prevent a placement in the genus *Uranoberotha*.

The new fossil can be discriminated from *Acanthoberotha*, *Alboberotha*, *Chimerhachiberotha*, *Kujiberotha*, *Paraberotha*, and *Spinoberotha* on the basis of the numbers of spines on protibia

(15 in *Acanthoberothes*, 24 in *Alboberothes*, at least six in *Kujiberothes*, 12 in *Paraberothes*, and much numerous but not counted in *Chimerhachiberothes* and *Spinoberothes* vs. five) (Whalley, 1980; Nel et al. 2005; Nakamine and Yamamoto, 2018; Nakamine et al., 2020).

Furthermore, it can be differentiated from *Acanthoberothes* owing to its protibia with only five distal spines (vs. at least 15 spines in *Acanthoberothes*); probasitarsus with only two spines located near midlength (vs. 9–10 spine-like setae on external edge and one slightly curved claw-like spine at apex); forewing with a coloration pattern (vs. hyaline). Note that the initial diagnosis of *Acanthoberothes* indicates that the hind wings have a RP divided into four branches (Nakamine et al., 2020: 4) while the drawing of the type species indicates five branches (Nakamine et al., 2020: fig. 3). The difference between the new fossil and this genus are sufficient to not place it in the genus *Acanthoberothes*.

The genus *Alboberothes* was described based on a specimen from French Cretaceous amber (Nel et al., 2005). The preservation of the specimen does not allow an indeep comparison but the configuration of the forelegs differs at least owing to the 24 spines on protibia (Nakamine et al., 2020: tabl. 1) while only five are recorded on the new fossil. Additionally, one spine like seta is present on probasitarsus of *Alboberothes* (Nakamine et al., 2020: tabl. 1) while two of them are present in the new fossil.

The new fossil differs from *Chimerhaberothes* Nel et al., 2005 at least in lacking an enlarged fore femur (Nel et al., 2005: fig. 11), in having numerous spines along outer edge of fore femur; five conspicuous spines along inner edge of tibiae; probasitarsus with two spines located slightly near it mid length. These differences are indicators of two distinct genera and do not fall within the range of possible intrageneric variability.

The genus *Kujiberothes* was described from the Upper Cretaceous Kuji amber and represent an important discovery outside other widely studied deposits. The wing venation of the holotype specimen is partial, challenging the comparison of the wing venations, but the raptorial forelegs are

relatively well preserved (Nakamine and Yamamoto, 2018). Apparently, the femur of *Kujiberothera* possesses three spines protruding in length from other spines (Nakamine and Yamamoto, 2018: fig. 3C-D) while there is no such spines in the new fossil specimen. Similarly, the probasitarsus of *Kujiberothera* bears nine small spine-like setae on external ventral ridge while there is only two of them located near mid-length in the new specimen (Nakamine and Yamamoto, 2018: 113). An indeep comparison is not possible but it seems very unlikely that the specimen described in this paper belongs to the genus *Kujiberothera*.

The genus *Paraberothera*, like the genus *Raptorapax*, has a profemora and a protibia bearing numerous spines that resembling to rakes or whalebone (Whalley, 1980). The similarity between these two genera may indicate close phylogenetic relationships. This structure strongly differs from the one of the specimen described above and combined with the lack of numerous crossveins in forewing (Whalley, 1980: fig. 6) prevent the placement of the new fossil in this particular genus.

The genus *Spinoberothera* is really strange owing to its mid and hind-legs raptorial, with long spines on femora and tibiae (Nel et al., 2005) is condition alone prevent assignation of the new specimen to this genus. Furthermore, the new fossil differs from *Spinoberothera* due to its forewings with a coloration pattern (vs. hyaline in *Spinoberothera*); most of crossveins in the costal field forked (vs. simple); numerous crossveins present i.e. 4rp3-rp4, 4rp-ma, 4ma-mp, 3mp-cua (vs. absent) (Nel et al., 2005: fig. 14). The configuration of the foreleg with femora with ca. 10 long and strong spines disposed into two rows of on inner edge, four long spinous setae on outer lateral edge, and several long setae on outer edge greatly differ from that of the new fossil (Nel et al., 2005: 70). The latter has long and strong basal spines and 34 additional conspicuous spines. The configuration of the tibiae bearing numerous sharp spines on their inner edge disposed in two rows differs from that of the new fossil possessing only five distal strong spines and few setae on inner edge. In the initial description of *Spinoberothera* there is no mention of the presence of spines on probasitarsus (only

numerous setae) while two distinct spines are present in the new fossil. All these differences clearly show that the new fossil can not be attributed to the genus *Spinoberotha*.

The new fossil can be distinguished from *Retinoberotha* in having a vein 1rp-m in hind wing (while absent from *Retinoberotha*). However, it is possible that this vein was present but not mentioned nor preserved. Apparently, the veins 2ra-rp and 4rp3-rp4 in forewing are also absent in *Retinoberotha* while present in the new specimen. The forewing of the new fossil differs from that of *Retinoberotha* owing to the presence of a conspicuous coloration pattern (vs. absent). The hind wing venation also differs on both specimens due to the absence of 1rp-m (Schlüter, 1978: figs. 36, 38) but this absence is maybe only due to the non-observation of the vein while hypothetically present. The poor preservation of the forelegs of *Retinoberotha* is challenging to compare the new fossil material with this genus (Schlüter, 1978: fig. 37). Therefore, even if the comparison of the foreleg structures is not possible I prefer to not attribute the new fossil to this genus.

Similarly, the genus *Scoloberotha* can be hypothetically differentiated from the new specimen owing to the absence of a vein 1rp-m in hind wing (while present in the new fossil) (Engel and Grimaldi, 2008). However, this absence is maybe due to the conservation. The configuration of forelegs of *Scoloberotha*, apparently with numerous strong setae on the outer edge of the tibia (Engel and Grimaldi, 2008: fig. 45), differs from that of the new fossil. The profermur of *Scoloberotha* superficially resembles that of the new fossil (Fig. 3B; Engel and Grimaldi, 2008: fig. 46). On the other hand, the hind wing venation is very different with 1scp-r and the crossveins in the radial, medial and cubital fields absent (vs. present in the new fossil) (Fig. 3C; Engel and Grimaldi, 2008: fig. 46). The forewing of *Scoloberotha* also lacks coloration patten (Engel and Grimaldi, 2008: 32) while it is present in the new fossil; and apparently lacks outer gradate crossvein (here corresponding to 4rp3-rp4, 4rp-ma, 4ma-mp, 3mp-cua) while they are present in the new fossil. The protibia of *Scoloberotha* bears three distal spines (Engel and Grimaldi, 2008: 32) while five of them are recorded in the new specimen. No indication is given for the presence or absence of probasitarsus

spines. If the coloration pattern and the absence of one or two crossveins fall inside the range of intrageneric variability, the total absence of crossvein and the forelegs with numerous strong setae on the outer edge of the tibia (while absent in the new specimen) seem to indicate that the new fossil does not belong to the genus *Scoloberotha*.

The new specimen can be distinguished from *Rhachibermissa* based on the wing venation. In fact, the new fossil has a RP divided into four branches in forewing and five branches in hind wing, whereas RP has three branches in fore- and hind wings in *Rhachibermissa* (Engel & Grimaldi, 2008); 2ra-rp is present in both wings (vs. absent in *Rhachibermissa*); nearly all the costal crossveins are forked (vs. nearly all simple in *Rhachibermissa*); coloration pattern of forewings greatly differs owing to the presence of spots while *Rhachibermissa splendida* has diffuse coloration along branches (Grimaldi, 2000). The forelegs configuration of *Rhachibermissa* is also different from that of the new fossil owing to the absence of a strong basal spine, protibia with four distal spines (vs. five), probasitarsus short (vs. long), tarsomeres one to three with a spine (while only the probasitarsus of the new fossil bears two spines) (Grimaldi, 2000: fig. 17). These differences fall outside of the intrageneric variability and the attribution of the new fossil to the genus *Rhachibermissa* is not possible.

The new fossil specimen differs from the genus *Micromantispa* (Shi et al., 2015; Nakamine et al., 2020) owing to protibia bearing two or three spines on the distal area of ventral ridge, covered with thick prostrate setae on dorsal edge (vs. five); probasitarsus elongate, with two spine-like setae on ventral edge and one long spine on the end (vs. only with two spine-like setae on ventral edge); second protarsomere bearing one spine at the end (vs. absent): forewing hyaline (vs. with conspicuous coloration pattern), elongate-oval; RP divided into four branches, intra-RP crossvein between RP3 and RP4 present. Hind wing hyaline, ovoid; basal crossvein between RP and M present. These differences prevent attribution of the new fossil to the genus *Micromantispa*.

The new specimen is at first sight similar to *Astioberotha*. However, it differs from *Astioberotha* by possessing a profemur without reduction of the lengths of spines (between the base and the middle of profemur); a protibia with five distal spines (vs. two or three) and not possessing proximal spines (vs. two present); tarsomeres two to four without spines (vs. with two short spines in *Astioberotha*); intra-RP crossvein (4rp3-rp4) in forewing present (absent in *Astioberotha*); numerous maculation spots present near crossveins and near dichotomies of RP and MA (only one maculation spot present near 2m-cu in *Astioberotha*) (Nakamine et al., 2020). According to the illustration of the profemur of *Astioberotha* (Nakamine et al., 2020: fig. 4b), the reduction or gap between the basal spines and the spines in the middle of the profemur is not so important since the spines are present but smaller maybe broken or used. The configuration of the protibia and the number of spines fall into the intrageneric range of variability.

Given the detailed comparisons proposed above the new fossil specimen seems to resemble mostly to the type species of *Astioberotha* but differs from the latter owing to the characters proposed in the diagnosis.

4.3. Paleobiogeographical implications

As discussed in many recent articles, the Cretaceous biota of Burmese amber appears to benefit from late inputs from Laurasian fauna (e.g. Jouault, 2021) and early inputs from Gondwana fauna (e.g. Poinar, 2019) prior to its separation from the South-east of Gondwana and its migration through the Meso-Tethys Ocean (Seton et al., 2012). Distribution of extant and extinct Rachiberothidae may suggest that rachiberothids have colonized the West Burma block (WBB) when it was close to Laurasia (during the late Cretaceous, Westerweel et al., 2019) or they would have colonized the WBB before it separated from Gondwana (during the Early Jurassic, Seton et al., 2012; Van Hinsbergen et al., 2012). If the hypothesis of the presence of rachiberothids on Gondwana during the Early Jurassic is preferred, then modern populations could be relics of ancient Gondwana popu-

lations. To confirm this hypothesis, it becomes urgent to document complete Gondwanan assemblages of insects, for example those of the Congolese Cretaceous amber (Bouju and Perrichot, 2020), of the Orapa, or of the Crato formation (Ribeiro et al., 2021).

The main implication of such paleobiogeographical implications will be the modification of the assumed age of the family Rachiberothidae. In fact, if the Rachiberothidae were present on the Gondwana before its break-up and before the separation of the WWB from the Gondwana, this would suggest that the family would be older than previously thought. If a population was present on the Gondwana and has colonized the WWB, the Rachiberothidae would have appeared at least before 125 Ma during the earliest Cretaceous or maybe during the late Jurassic. In fact, during the early Jurassic, the WWB 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. Geological evidence suggests that the WWB separated from the Gondwana after or at about 125 Ma, but remained relatively nearby until ca. 120 Ma (e.g. Metcalfe, 1990, 1996; Scotese, 2014). Later, it was isolated geographically during the mid-Cretaceous (Westerweel et al., 2019) for more than 20 Ma (Heine et al., 2004; Seton et al., 2012; Jouault et al., 2021a).

Interestingly, several neuropteran lineages (e.g. Araripeneurinae, Babinskaiidae) is already known from both the formation of Crato and from the Burmese amber (e.g. Lu et al., 2019; Ngô-Muller et al., 2020) and other genera of Hymenoptera are shared between the two deposits (e.g. *Cuoriosivespa* in Jouault et al., 2021b), it can therefore be expected that similar discoveries will be made soon for the Rachiberothidae. These discoveries highlight that a paleofaunal link between WWB and Gondwana has existed and that origin of part of the WWB fauna was supplemented by fauna from the Gondwana. These discoveries also suggest that the hypothesis suggesting an older age for the Rachiberothidae, is likely.

5. Conclusion

Despite the numerous recent discoveries of rachiberothids in the Cretaceous amber of Burma, their diversity still seems to be underestimated. It would also seem that slightly older deposits (Hkamti, Myanmar) can provide important fossils to better understand the past diversity of Neuroptera and particularly of the Rachiberothidae and Berothidae. The description of *Astioberotha coutreti* sp. nov. and the record of numerous other raptorial foreleg configurations in mid-Cretaceous rachiberothids suggest that they may have specialized on certain types of prey. If observations on their ecology and biology are few (for extant species), future direct evidences of predation in amber will be hopefully found and thus provide novel evidences on the biology of these insects.

Acknowledgements

I am grateful to the two anonymous reviewers for their valuable comments and precisions provided in early draft and review of the paper. I also thank Dr. Caroline Buttler for managing the article during the editing process. This work is part of the Ph.D. project of Corentin Jouault on the « Impact des interactions biotiques et paléo-événements sur la diversification des insectes Neuroptera ».

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Figure caption

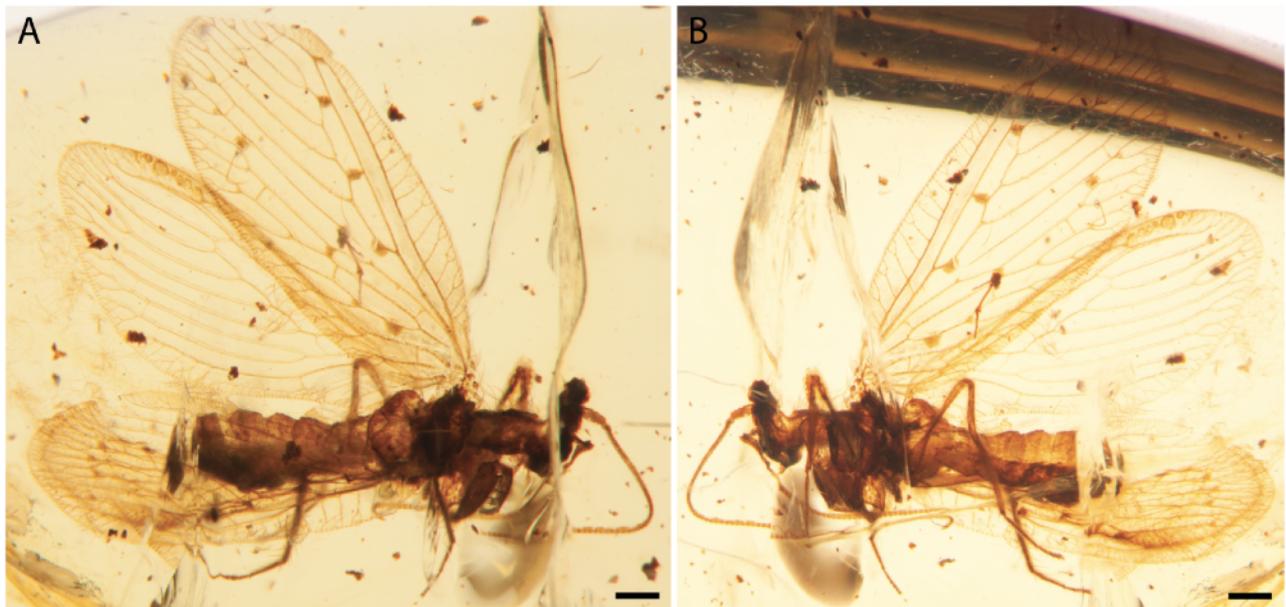


Figure 1. *Astioberotha coutreti* sp. nov. holotype IGR.BU-047. A: Habitus in dorsal view; B: Habitus in ventral view. Scale bars equal 0.5 mm.

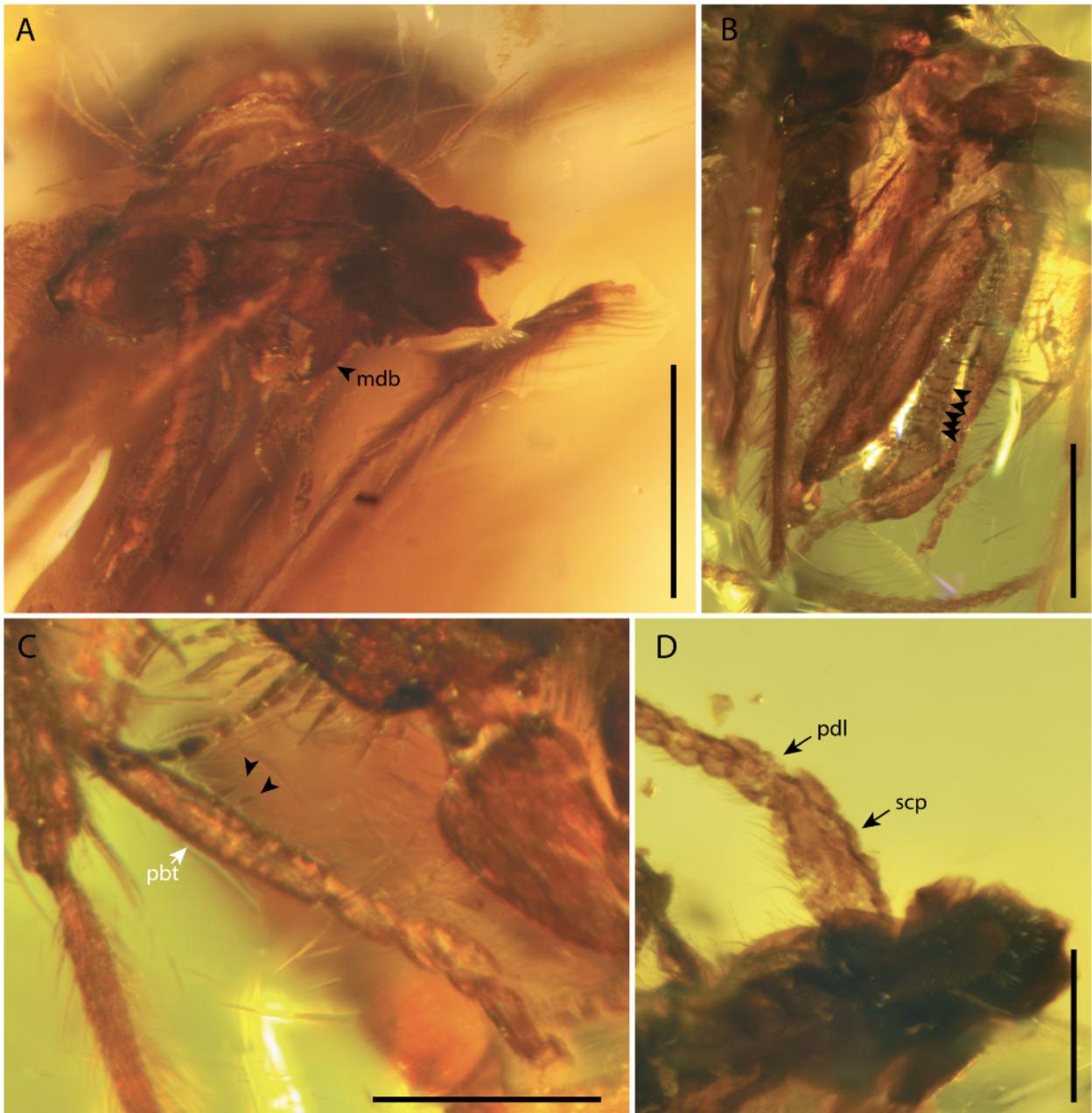


Figure 2. Detailed view of *Astioberotha coutreti* sp. nov. holotype IGR.BU-047. A: Head in full face view; B: Right foreleg with black arrow pointing inner tibial spines; C: Left probasitarsus with black arrow pointing inner spines; D: Head in ventral view. Scale bars equal 0.5 mm (A, B); 0.25 mm (C, D). mdb = mandible; pbt = probasitarsus; scp = scape; pdl = pedicel.

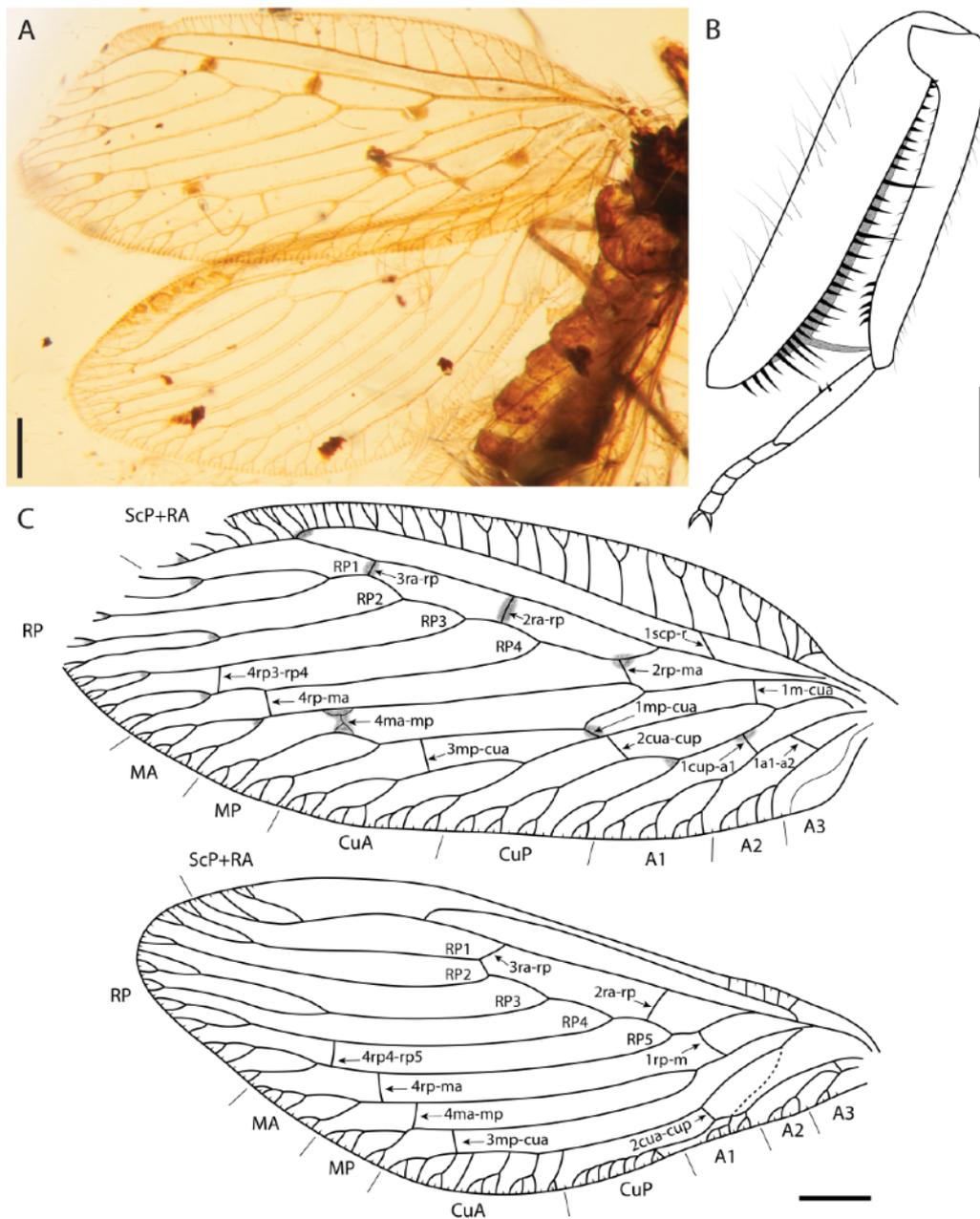


Figure 3. *Astioberotha coutreti* sp. nov. holotype IGR.BU-047. A: Wings in dorsal view; B: Line drawing of distal part of foreleg; C: Line drawing of wing venation with name of veins labelled. Scale bars equal 0.5 mm (A, C); 0.25 mm (B).