

**Palaeotanyrhina exophthalma gen. et sp. nov.
(Palaeotanyrhinidae fam. nov.) (Reduvioidea: Hemiptera)
in mid-Cretaceous Burmese amber**

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Palaeotanyrhina exophthalma gen. et sp. nov.
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in mid-Cretaceous Burmese amber

GEORGE POINAR JR., ALEX E. BROWN & PÉTER KÓBOR

Abstract

Palaeotanyrhina exophthalma gen. et sp. nov. is described in a new family, Palaeotanyrhinidae fam. nov., (Reduvoidea: Hemiptera) in mid-Cretaceous Burmese amber. Diagnostic characters of *Palaeotanyrhina exophthalma* gen. et sp. nov. include large stalked eyes, an extended head, a 4-segmented labium that reaches the tip of the abdomen and an extremely short, vertical first segment, ocelli on a synthlipsis tubercle between the eyes, forewing membrane lacking veins, a 3-3-3 tarsal formula and fossula spongiosa on the fore tarsi.

Key words: Mid-Cretaceous; Burmese amber; Palaeotanyrhinidae; Reduvoidea; Hemiptera.

1. Introduction

Burmese amber has supplied scientists with a wealth of invertebrate, vertebrate and plant fossils, showing examples of the range of life that existed in this mid-Cretaceous forest. The Reduvoidea is one of the hemipteran lineages that has been previously reported in these deposits (POINAR 2018). Based on a cladistic analysis, the present fossil also has features of the Reduvoidea, such as a length greater than 5 mm, ocelli positioned on an elevated disc just behind the eyes, non-raptorial forelegs, 3-segmented tarsi and “fossula spongiosa” on the fore tarsi (LENT & WYGODZINSKY 1979). However, other features, such as the long labium that surpasses the sulcus, the venation of the forewing, the bulging eyes and shape of the head and antennomeres are unique characters of this specimen. Since the fossil cannot be placed in any modern family of the Reduvoidea, it is described in a new extinct family, the Palaeotanyrhinidae nov.

2. Material and methods

The specimen originated from the Noije Bum 2001 Summit Site mine excavated in the Hukawng Valley and located southwest of Maingkhwan in Kachin State (26°20'N, 96°36'E) in Myanmar. Based on paleontological evidence, this site was dated to the late Albian of the Early Cretaceous (CRUICKSHANK & KO 2003), placing the age at 97 to 110 Ma. A more recent study using U-Pb zircon dating determined the age to be 98.79 ± 0.62 Ma or at the Albian/Cenomanian boundary (SHI et al. 2012). Nuclear magnetic resonance (NMR) spectra and the presence of

araucaroid wood fibers in amber samples from the Noije Bum 2001 Summit Site indicate an araucarian tree source for the amber (POINAR et al. 2007). Observations and photographs were made with a Nikon SMZ-10 R stereoscopic microscope and Nikon Optiphot compound microscope with magnifications up to 800 X. Helicon Focus Pro X64 was used to stack photos for better depth of field. Characters and terms presented by SCHUH & SLATER (1995) and SCHUH et al. (2009) were used in the present study. Measurements were performed on scaled photos using ImageJ software.

The characters observed suggest that this aberrant new true bug belongs to infraorder Cimicomorpha. To discuss its placement within the infraorder, a cladistic analysis was performed based on the morphological dataset by SCHUH et al. (2009). From among the 73 characters included in the character matrix 33 were observable in *Palaeotanyrhina*. Missing characters are mostly internal structures or obscure features, and thus cannot be studied in an amber inclusion. However, it must be noted that even fragmentary morphological data acquired from fossils improves morphological phylogenies and provide the basis to form and test hypotheses on relationships among taxa or evolutionary scenarios (EDGEcombe 2010; KOCH et al. 2021).

Parsimony analysis was performed using TNT 1.1 software (GOLOBOFF et al. 2008) under equal weights. Analysis was composed using traditional search strategy. All characters were treated as non-additive. Characters were optimized on a strict consensus of 60 equally parsimonious trees using “fast optimization” in WinClada (NIXON 2002).

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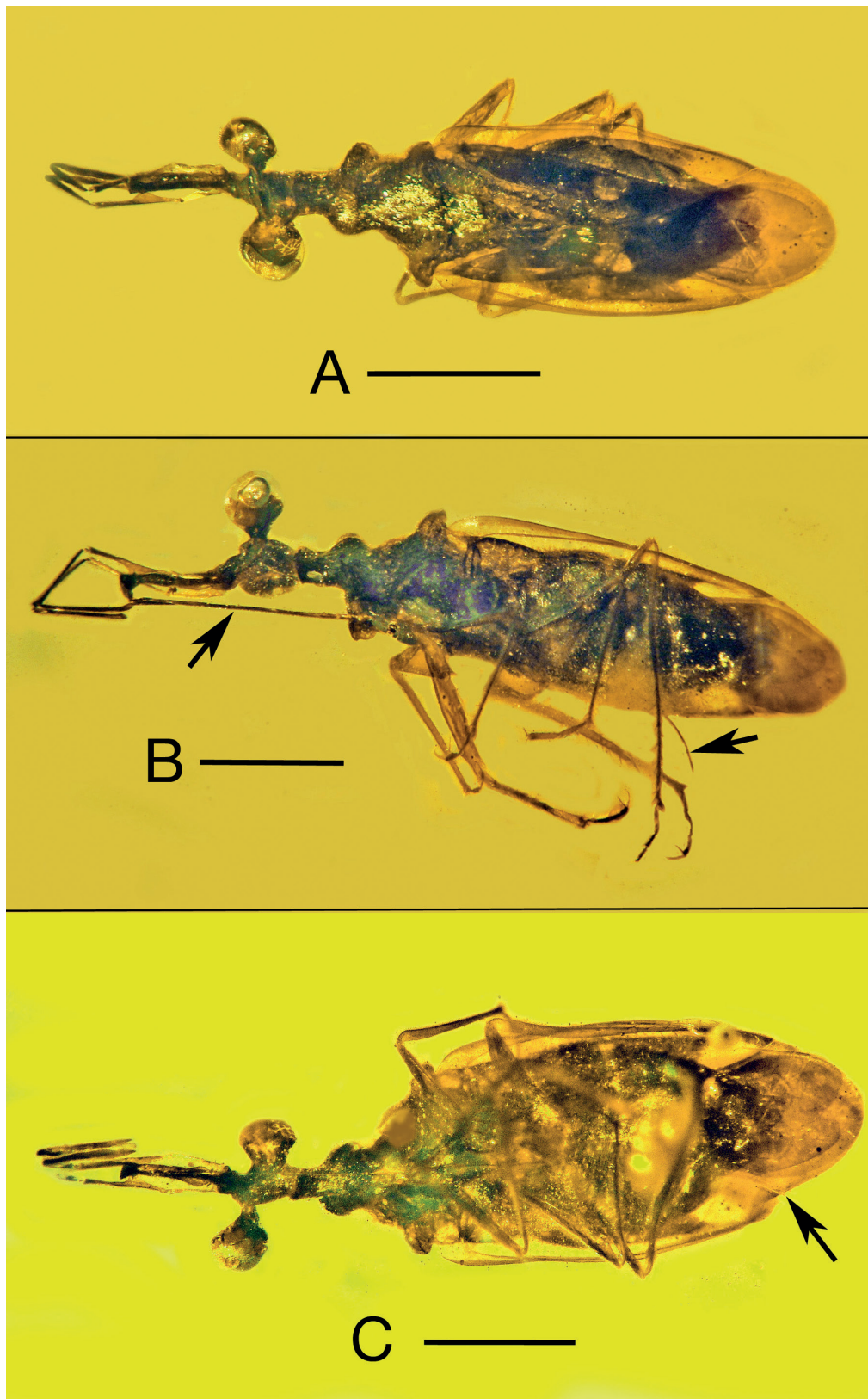


Fig. 1. Holotype of *Palaeotanyrhina exophthalma* gen. et sp. nov. in Burmese amber. **A** – Dorsal view. Bar = 1.5 mm. **B** – Lateral view. Arrow shows tip of labium. Bar = 1.2 mm. **C** – Ventral view. Arrow shows tip of labium. Bar = 1.3 mm.

3. Systematic paleontology

Order Hemiptera LINNAEUS, 1758

Suborder Heteroptera LATREILLE, 1810

Infraorder Cimicomorpha THOMAS & FROESCHNER, 1988

Superfamily Reduvioidea MCGAVIN, 1993

Family Palaeotanyrhinidae POINAR, BROWN & KÓBOR nov.

LSID Zoobank for family: urn:lsid:zoobank.org:pub:B543DE37-8F7D-4234-8CCC-1C263FF40623

Type genus: *Palaeotanyrhina* POINAR, BROWN & KÓBOR nov.

Diagnosis: General habitus ovoid. Head conspicuously elongate, bilobate with shortly stylate, enlarged compound eyes; ocelli situated on synthlipsis disc posteriad to eyes. Antennae tetramerous; antennomere II bearing triangular flange medially. Labrum triangular, hook-shaped; anteriorly inserted labium tetramerous, extremely long (extending to tip of abdomen) with labiomere I conspicuously minute. Pronotum trilobate, subdivided into a collar, anterior and posterior lobes. Hemelytron with differentiated clavus-corium and membrane; clavus narrow, corium with simplified venation, membrane without observable venation. Fore femora moderately incrassate; fore tibiae with fossula spongiosa; tarsal formula 3-3-3.

Genera included: Type genus only.

Genus *Palaeotanyrhina* POINAR, BROWN & KÓBOR nov.

LSID Zoobank for genus: urn:lsid:zoobank.org:act:604CA5CA-0055-477F-BB54-F4A26260CA8C

Etymology: The generic name is from the Greek “palaios” = old, the Greek “tanyo” = stretched out, and the Greek “rhinos” = beak in reference to the extended head and long labium of the fossil.

Type species: *Palaeotanyrhina exophthalma* POINAR, BROWN & KÓBOR sp. nov.

Diagnosis: Small insect (~7.0 mm) with conspicuously elongate head and labium; clypeus with lateral triangular flanges subbasally. Antennomere II with triangular flanges medially. Eyes large, moderately stylate. Coloration generally dark except semi-hyaline hemelytron and light-colored femora and tibiae.

Palaeotanyrhina exophthalma

POINAR, BROWN & KÓBOR gen. et sp. nov.

Figs. 1–3, 4A–C, 5

LSID Zoobank for species: urn:lsid:zoobank.org:act:29BD3079-D08C-4D7A-A700-D4EB3C19AE35

Etymology: The specific epithet is taken from the Greek “exophthalmos” = protruding eyes.

Holotype (male): Deposited in the Poinar amber collection maintained at Oregon State University under accession number He-4-39.

Type locality: Hukawng Valley southwest of Maingkhwan in Kachin State (26°20'N, 96°36'E), Myanmar.

Diagnosis: Small male insect (~7.0 mm) with conspicuously elongate head and labium; clypeus with lateral triangular flanges subbasally. Antennomere II with triangular flanges medially. Eyes large, moderately stylate. Coloration generally dark except semi-hyaline hemelytron and light-colored femora and tibiae.

Included species: Type species only.

Description of holotype: Body ~7.0 mm in length, well-preserved and nearly complete, with only the tip of the right metatarsus missing. Coloration. Body generally of darkish coloration with hemelytra semi-hyaline, femora and tibiae appear to be ochraceous.

Head correct, bilobate with a minute, inconspicuous postoccipital region. Vertex subdivided by transversal postocular constriction. Compound eyes large, spherical, shortly stylate; eye stalks erect. Ocelli situated on protruding, synthlipsis disc posteriad to compound eyes, appearing to be divided by short longitudinal incision medially. Frons trapeziform, separated from both vertex and clypeus by shallow transversal furrows. Antenniferous tubercles well-developed, visible in dorsal view. Antennomeres covered with dense, decumbent pubescence, length of setae subequal to diameter of antennomeres. Antennomeres I–III subcylindrical, antennomere IV rather fusiform; antennomere I shortest, antennomere II with triangular flanges medially, antennomere IV longest; ratio of antennomeres: 1 : 1.44 : 1.21 : 1.53. Clypeus conspicuously elongate with triangular flanges subbasally, labrum and labium inserted on anterior surface. Labrum triangular, apex hook-shaped with sensory papilla. Labium tetramerous with labiomeres I, II and IV short, labiomere III conspicuously elongate; labiomere I appears to be obscured by labrum; apex of labium with extended maxillae and mandibula, reaching apex of abdomen.

Thorax. Pronotum trilobate with lateral margins finely carinate; subdivided into collar, anterior and posterior lobe by transversal constrictions. Collar subcylindrical, length to width: 1 : 1.30. Anterior lobe bulbous with pronotal callosities separated by a thin, longitudinal furrow. Posterior lobe appears to be densely punctate except for raised, angulate humeral edges. Scutellum triangular, medially elevated without conspicuous median carina. Mesothoracic wing with differentiated clavus-corium and membrane, i.e., hemelytron; venation simplified. Clavus narrow, more sclerotized than rest of the corium. Corium divided by vein M+R in two closed cells. Veins Sc and C running close to each other, forming a narrow exocorium, adjoining subapically anteriorly to corial margin. Membrane without distinct venation. Metathoracic wings obscured by hemelytra. Integument of thoracic pleurites and sternites appear to be densely punctate. Peritreme and evaporatorium of metathoracic scent efferent apparatus unobservable. Mesosternite with labial groove between mesocoxae. Femora fusiform. Fore femora moderately incrassate compared to mid and hind femora. Tibiae subcylindrical, integument with dense, decumbent pubescence; fore tibiae with fossula spongiosa apically that continues to the terminus of the tarsus (Fig. 4C), hind tibiae appear to be armed with spur-like process apically. Tarsomere I shortest, tarsomere III longest. Pretarsus with simple, evenly curved claws.

Abdomen. Abdominal tergites obscured by wings, abdominal sternites with dense pubescence.

Measurements (in mm): Total body length: 6.89; length of head: 1.45; width of head: 1.45; diameter of eyes: 0.73; distance between ocelli: 0.16; length of antennomeres I–IV: 0.41–0.71–0.59–0.77; (labiomeres partly obscured, not possible to measure); length of pronotum: 1.35; width of pronotum: 1.27; length of scutellum: 0.63; width of scutellum: 0.87.

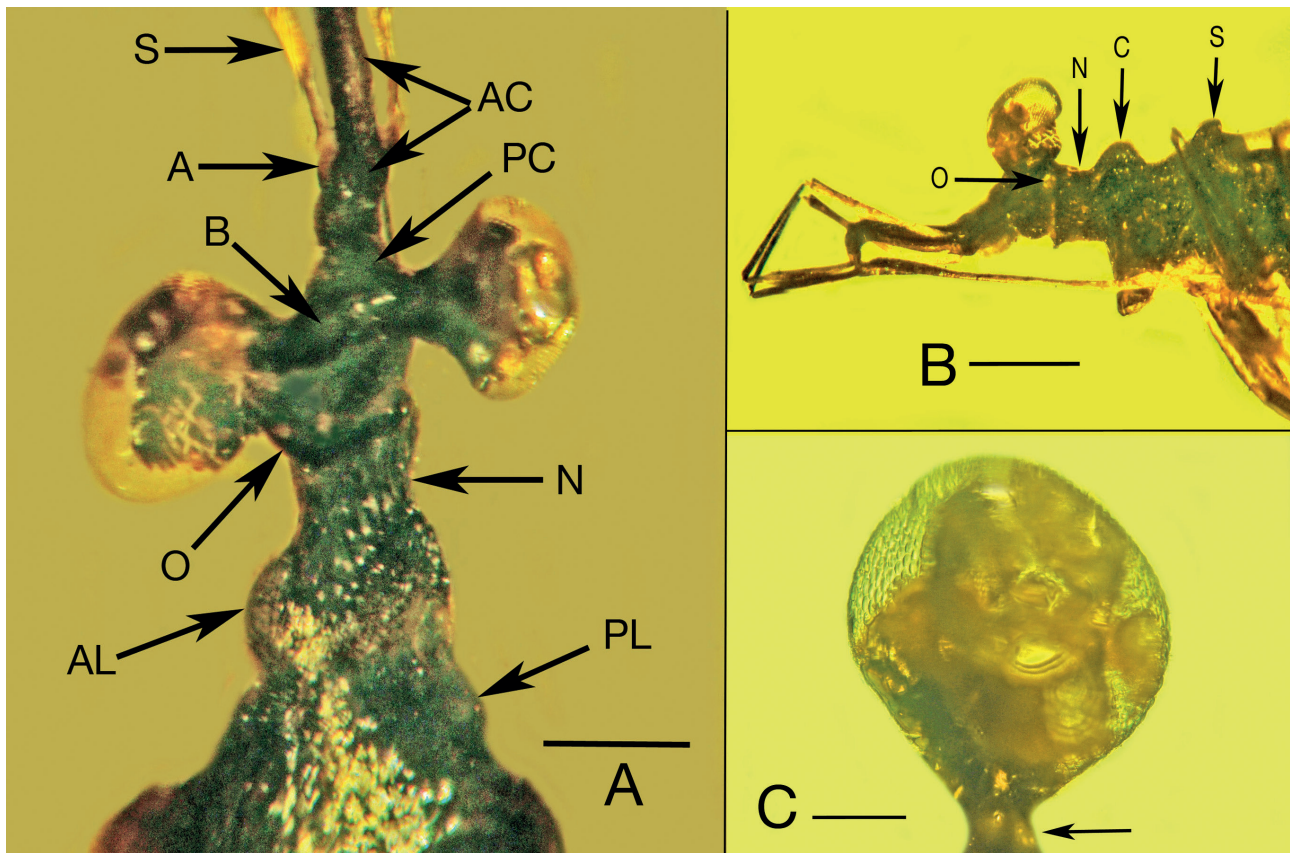


Fig. 2. Holotype of *Palaeotanyrhina exophthalma* gen. et sp. nov. in Burmese amber. **A** – Dorsal view of head. A = Antenniferous tubercle; AC = anterior clypeus; AL = anterior lobe of pronotum; B = synthlipsis bridge; N = neck or collar; O = ocellar tubercle; S = scape; PC = posterior clypeus and frons; PL = posterior lobe of pronotum. Bar = 0.5 mm. **B** – Lateral view of head. C = pronotal callus; N = neck or collar; O = ocellus (ocellar tubercle distorted to lower left side); S = scutellum. Bar = 1.1 mm. **C** – Lateral view of eye. Arrow shows basal stalk. Bar = 0.2 mm.

4. Discussion

Palaeotanyrhina exophthalma gen. et sp. nov. displays an amalgamation of exoskeletal structures which are characteristic of various heteropteran groups. One of the most notable of these character states, the bilobate head, is characteristic to the infraorder Enicocephalomorpha (WYGODZINSKY & SCHMIDT 1991; GRIMALDI 1993, SPANGENBERG et al. 2013). In this case it is coupled with a conspicuous head extension similar to the genus *Proboscidopirates* VILLIERS, 1958 (e.g., BAŇAŘ et al. 2015, figs. 1–3, 5). The simplified venation of the mesothoracic wing, is also to be observed in an enicocephalomorph genus, *Alienates* BARBER, 1953 (WYGODZINSKY & SCHMIDT 1991). However, the mesothoracic wing is homogeneous in Enicocephalomorpha [hemelytron is bipartite (clavus+corium and membrane) in *Palaeotanyrhina*] and tarsal formula 1-1-1 in Enicocephalomorpha (tarsal formula 3-3-3 in *Palaeotanyrhina*). This suggests that *Palaeotanyrhina* has

a closer relationship with “modern” heteropteran groups. In the extensive phylogenetic analysis of SCHUH et al. (2009), the monophyly of Cimicomorpha was supported by the anteriorly inserted labium, this character state can also be observed in *Palaeotanyrhina* gen. nov. Furthermore, fossula spongiosa occurs in several predaceous cimicomorph taxa, an elongate head is observed in e.g., the triatomine genera *Eratyrus* and *Rhodnius* (Reduviidae: Triatominae) and an example of an elongate labiomere III coupled with shortened labiomeres I–II and IV is present in the enigmatic reduviid family Velocipedidae (VAN DOESBURG 2004). Considering the above, we regard *Palaeotanyrhina* to be an aberrant extinct lineage of Cimicomorpha. To test this hypothesis, we performed a phylogenetic reconstruction based on the morphological characters included in the matrix of SCHUH et al. (2009). An exhaustive search under equal weights resulted in 60 equally parsimonious trees (L = 295, CI = 37, RI = 82), from which a strict consensus was estimated (Fig. 6).

The resulted topology corresponds to the morphology-only analysis of SCHUH et al. (2009, fig. 4), with terminal branches of the Miridae clade. The clade Reduvioidea (Pachynomindae + Reduviidae) was considered monophyletic, supported by three non-homoplasious transformations: one antennal pedicellar trichobothria present (9: 1), abdominal spiracles on sternum adjacent to discrete laterotergite (44: 1) and paired pseudospermathecae situated on ectodermal portion of median oviduct (66: 1). Contrastingly, on the tree of SCHUH et al. (2009) Reduvioidea was supported by a single non-homoplasious character (9: 1). Including a single fossil record has improved the support of the clade, which agrees with the conclusions of EDGECOMBE (2009) and KOCH et al. (2021).

Palaeotanyrhina was nested within the Reduvioidea clade as a basal taxon in all resulting trees. *Palaeotanyrhina* was also diagnosed by two homoplasious transformations: labial groove present on thoracic sternum (13: 1) and costal/ M-R veins extending to apex of corium on anterior wing margin (36: 1). In addition, *Palaeotanyrhina* displays a set of characters which are to be considered unique in terms of the superfamily Reduvioidea, e.g., extremely elongate head, stylate eyes, ocelli situated on protruding synthlipsis disc and triblobate pronotum with well-developed collar.

Considering the above, Palaeotanyrhinidae fam. nov. was erected to accommodate this new monotypic genus that represents an extinct, aberrant lineage of Redu-

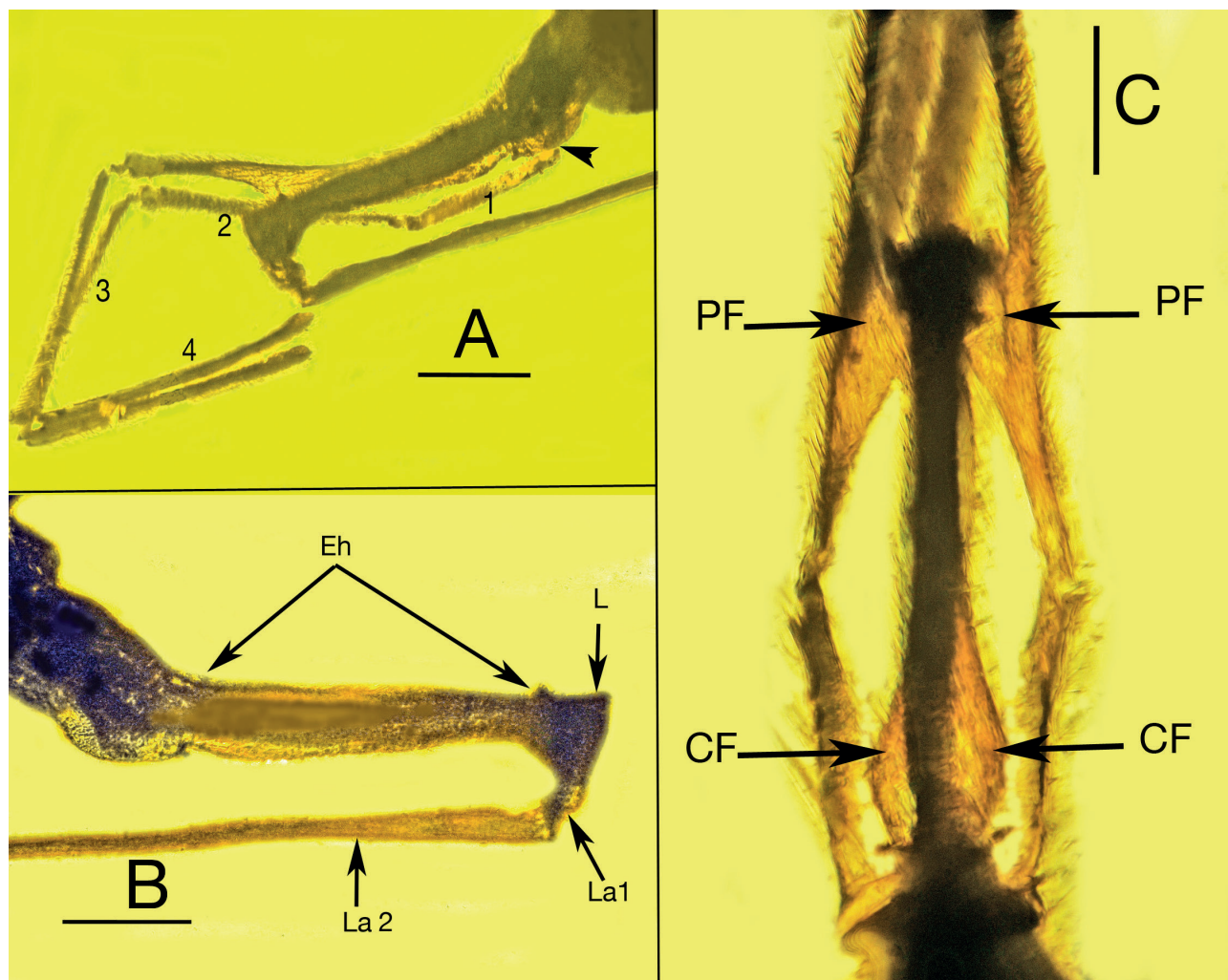


Fig. 3. Holotype of *Palaeotanyrhina exophthalma* gen. et sp. nov. in Burmese amber. **A** – Antennae. Arrowhead shows insertion point. Numbers refer to segments. Bar = 0.3 mm. **B** – Extended head (Eh); L= labrum; La1= first labial segment. La2= second labial segment. Bar = 0.4 mm. **C** – Dorsal view of extended head and antennomeres. CF= clypeal flanges; PF = protruding flanges. Bar = 180 µm.

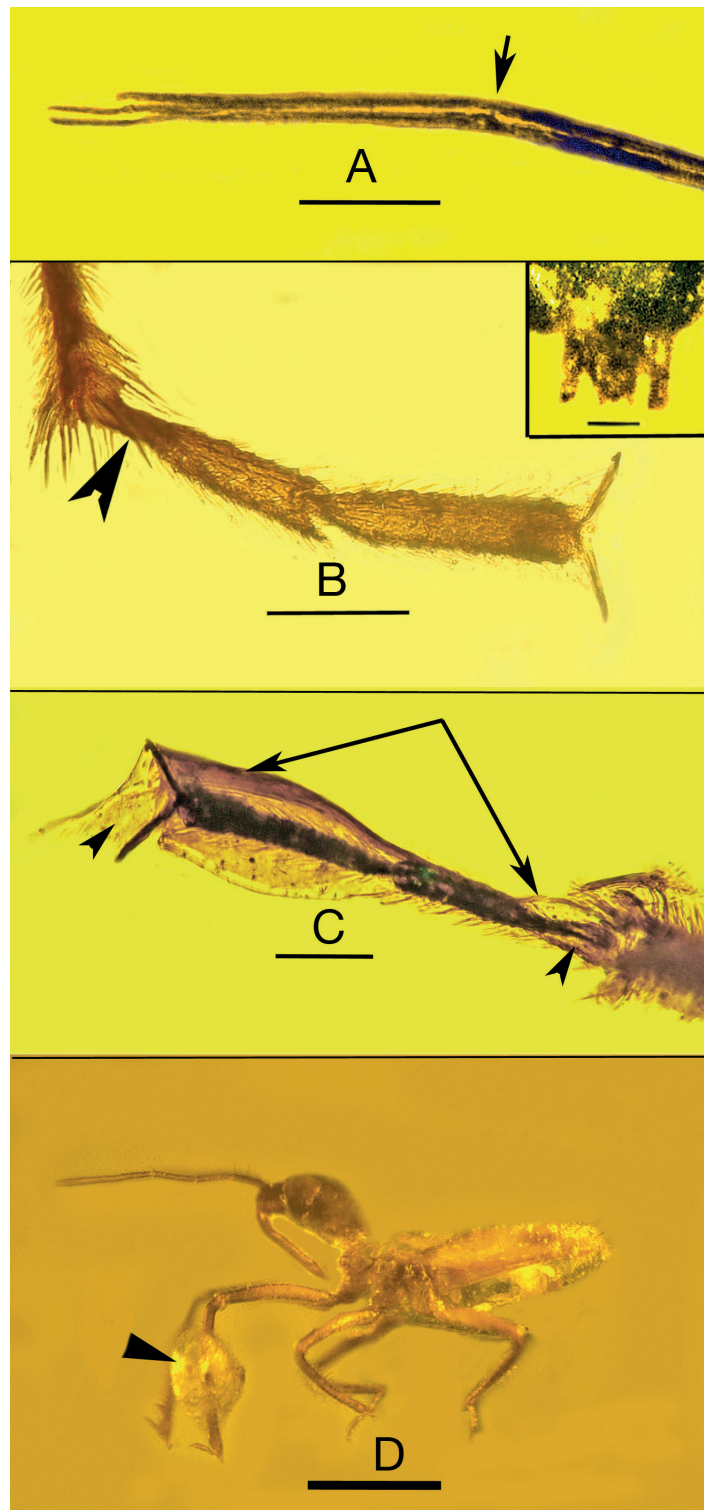


Fig. 4. A–C – Holotype of *Palaeotanyrhina exophthalma* gen. et sp. nov. in Burmese amber. **A** – Tip of labium. Note two extended maxillary stylets and short mandibular stylet. Arrow shows joint between segments. Bar = 148 μ m. **B** – Mesotarsus. Arrowhead shows short first tarsomere. Bar = 0.2 mm. Insert shows pygophor. Bar = 0.1 mm. **C** – Strap-like cover (arrows) enclosing fossula spongiosa on protarsus. Right arrowhead shows short first tarsomere. Left arrowhead shows released secretion from fossula spongiosa. Bar = 0.2 mm. **D** – A reduviid (specimen HE-4-21 deposited in the Poinar amber collection maintained at Oregon State University) in Dominican amber that has applied resin to its fore tibia (arrowhead). Bar = 1 mm.

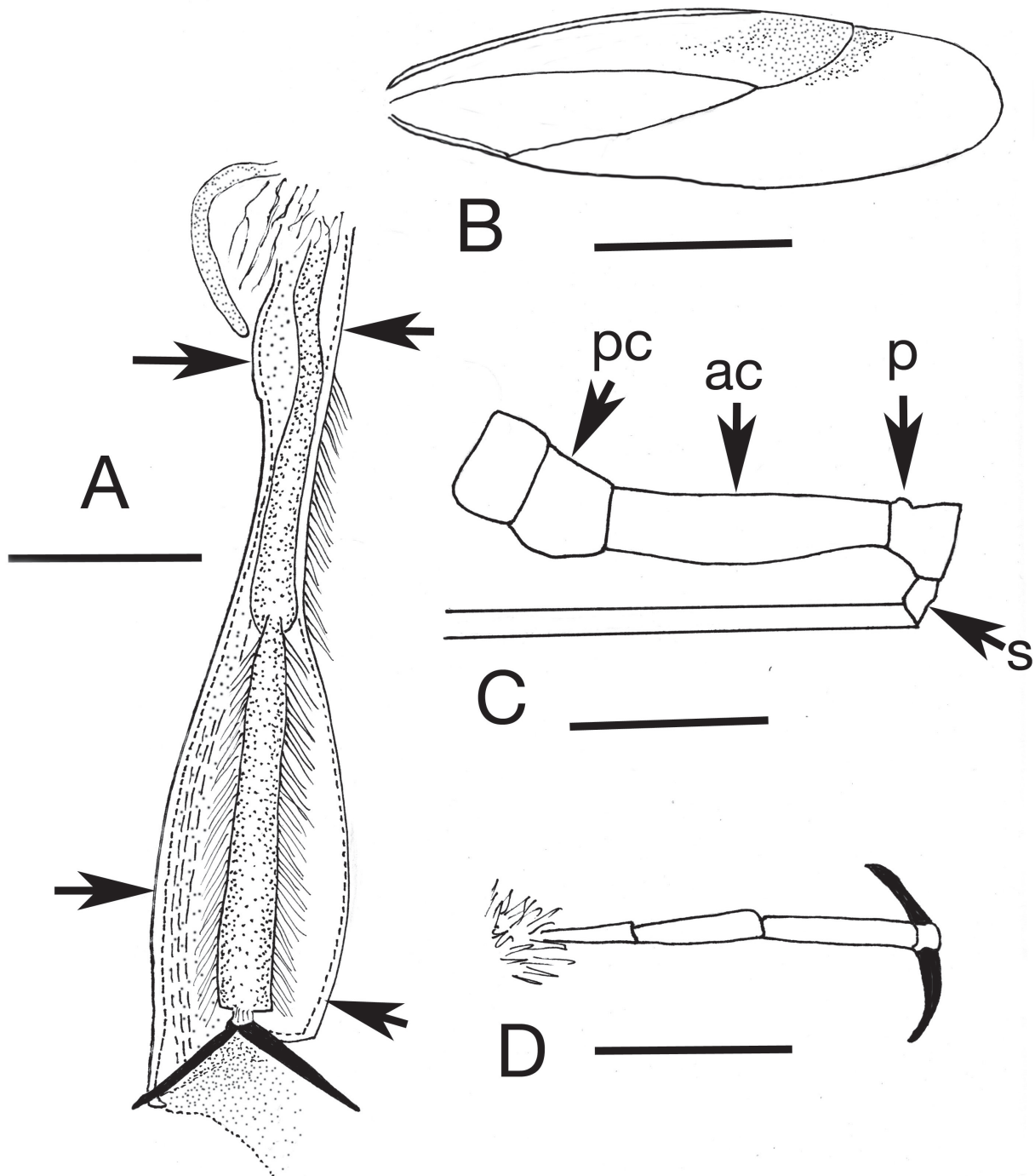


Fig. 5. Features of holotype of *Palaeotanyrhina exophthalma* gen. et sp. nov. in Burmese amber. **A** – Fossula spongiosa on protarsus. Arrows show borders of sheath that encloses protarsus. Bar = 56 μ m. **B** – Forewing. Note two large closed cells on corium, a cloudy area on the embolium possibly representing a greatly reduced pterostigma and the absence of a claval commissure. Bar = 1.4 mm. **C** – Anterior portion of head; ac = elongated anterior portion of head; p = sensory papilla on labrum; pc = posterior portion of head; s = first segment of labium; Bar = 0.4 mm. **D** – Metatarsus. Bar = 300 μ m.

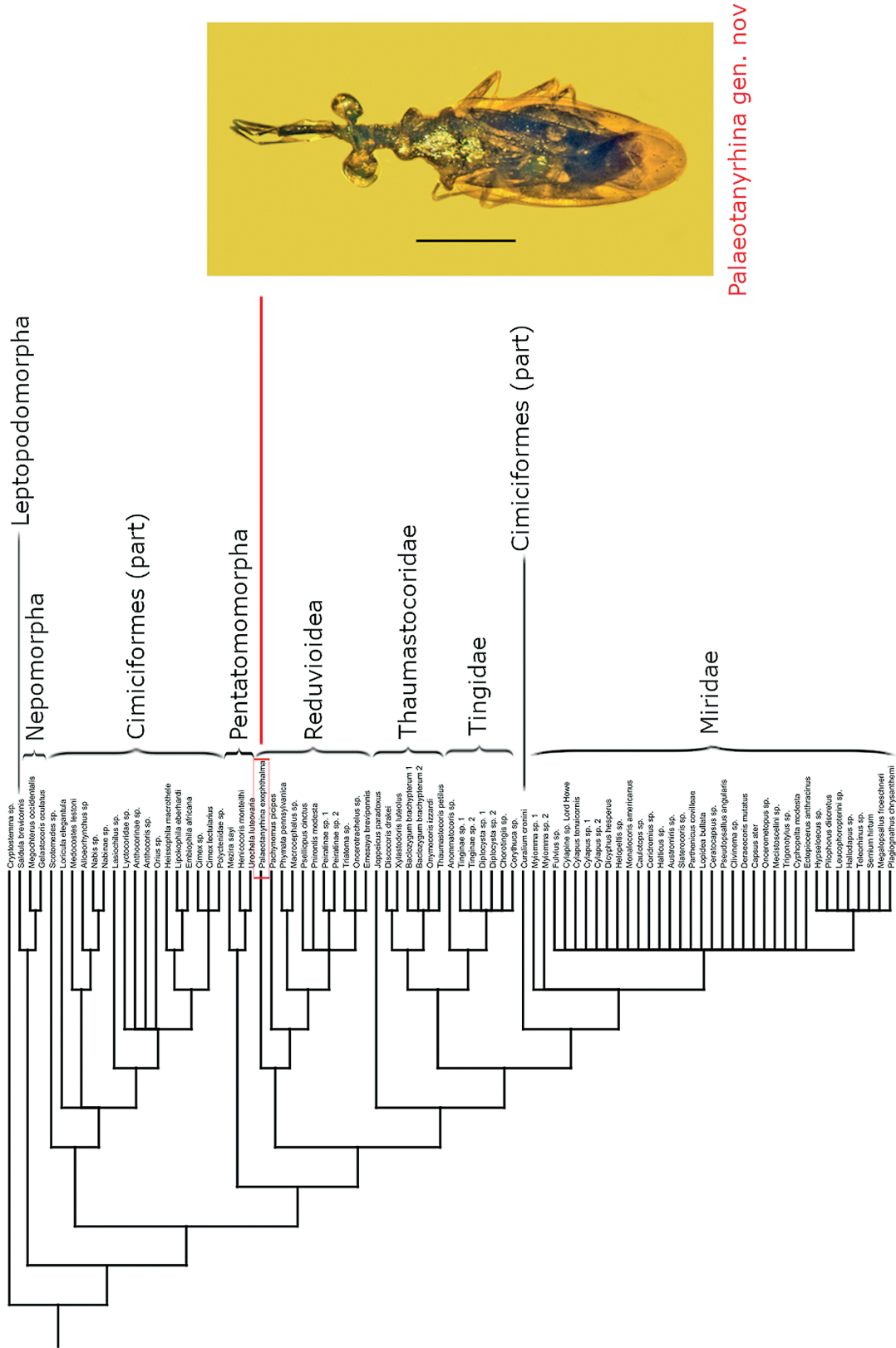


Fig. 6. The placement of *Palaeotanyrhina* gen. nov. within the infraorder Cimicomorpha. Strict consensus of 60 equally parsimonious trees resulted by traditional search under equal weights in TNT 1.1 software.

vioidea. Further elucidation on its relationship within the superfamily and the evolutionary significance of *Palaeotanyrhina* awaits further phylogenetic analysis involving other known fossil reduvioid true bugs and an improved character matrix.

In Figs. 4C and 5A, a sheath enclosing the fore tarsus can be observed. Considering its position and contents, it may contain a gluey substance associated with sticky trap predation (STP), a predation method which can be observed in extant reduviid subfamilies Harpactorinae and Bactrodinae (AVILA-NÚÑEZ et al. 2017). Adhesive fluid used to trap prey can be of endogenous or exogenous origin (ZHANG & WEIRAUCH 2013). The former can be observed in the tribe Harpactorini where the bugs possess a specialized dermal gland that secretes the fluid, while in the latter case the insect harvests the sticky substance from plants and purposely coats its legs and other body parts as occurs in “resin bugs” (Reduviidae: Harpactorinae: Apiomerini) (Fig. 4D). While on *Palaeotanyrhina*, this phenomenon is clearly endogenous and shows the ancient nature of this predation method, suggesting that *Palaeotanyrhina* was a predaceous true bug most likely feeding on smaller arthropods.

5. Conclusions

Here, we report an aberrant new true bug, *Palaeotanyrhina exophthalma* gen. et sp. nov. from mid-Cretaceous Burmese amber. This monotypic new genus displays an amalgamation of characters attributed to various heteropteran groups. A careful study of the exoskeletal features suggests that *Palaeotanyrhina* is a representative of infraorder Cimicomorpha. To determine its placement, a phylogenetic analysis was performed which concluded that this new aberrant true bug should be assigned to the superfamily Reduivoidea, and since its characters are unique in terms of the superfamily, a new family, Palaeotanyrhinidae nov., should be erected to accommodate it. The observation of traces suspected to be an adhesive substance combined with the presence of fossula spongiosa suggest that *Palaeotanyrhina* was a predator feeding on smaller arthropods.

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