

A Lacewing Bug, *Paleoanomala aptenus* gen. et sp. nov. (Hemiptera: Tingidae), in Mid-Cretaceous Burmese Amber

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ABSTRACT

A female lacewing bug in mid-Cretaceous Burmese amber is described as *Paleoanomala aptenus* gen. et sp. nov. (Tingidae: Hemiptera). This specimen is small and flightless and has partially fused hemelytra. The dorsum is covered with areoles formed by large dark punctures. The reduced eyes, lack of ocelli, and a flattened body suggest that this specimen lived in a stable, protected habitat. It is proposed that the precursor of *Paleoanomala* was macropterous with functional wings, however, the suture separating the original hemelytra is now partially fused and not capable of separation.

ARTICLE HISTORY

Received 13 May 2020
Revised 20 May 2020
Accepted 1 June 2020

KEYWORDS

Burmese amber
Hemiptera
Lacewing
Mid-Cretaceous amber
Myanmar
Tingidae

Introduction

Lace or lacewing bugs (Hemiptera: Tingidae) are an ancient cosmopolitan group with a wide range of morphological shapes and feeding sites. They are herbivores and most are free-living and feed on the foliage of angiosperms, both dicots and monocots. Some are found in flower galls where they feed on pollen while others are subterranean and feed on the roots of angiosperms. Many species are host specific, feeding on a single species or genus of plants and when populations build up, plant damage can result. While damage to crops and flowers is not frequently noted, some

tingids have been used as biological control agents of weeds. For example, *Teleonemia scrupulosa* Stål, the lantana lace bug, was introduced from Central America, via Fiji, to Australia to control lantana (Gross & Cassis, 1991). Species of *Acalypta* Westwood (Fig. 1) develop on mosses and are capable of delivering a painful “sting” when removed from leaves of *Racomitrium* sp. (Poinar, 2019). All extant flightless members of the family Vianaididae (Tingoidea) appear to be myrmecophilous inquilines, even though they are phytophagous (Comstock, 1950; Schuh & Slater, 1995). The

specimen described below is the first fossil flightless member of the Tingioidea.

Materials and methods

The specimen originated from the Noiye Bum 2001 Summit Site mine excavated in the Hukawng Valley in 2001 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 Mya. A more recent study using U-Pb zircon dating determined the age to be 98.79 ± 0.62 Mya 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 Noiye 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.



Fig. 1. Extant nymph of *Acalypta* sp. recovered from a moss (*Racomitrium* sp.) in Oregon. Scale bar = 0.8 mm (Photo by G. O. Poinar, Jr.).

Results

Order Hemiptera

Superfamily Tingioidea Laporte, 1833

Family Tingidae Laporte, 1833

Subfamily Tingiometrinae Heiss, Golub & Popov, 2000 (extinct)

Genus *Paleoanomala* gen. n.

LSID: urn:lsid:zoobank.org:pub:58EB69C1-C9BA-4B2D-972A-C4EF7830FA2C

Diagnosis: Flightless female with fused hemelytra; body small, dorsum punctate, with areoles outlined by large dark punctures; eyes reduced, ocelli absent; head somewhat elongated, antelocular portion slightly longer than postocular portion; clypeus swollen and rounded at tip; labium 4-segmented, its apex reaching posterior margin of middle coxa; dorsum of head with antelocular transverse row of four large tubercles and two additional intra-ocular tubercles; antennal segment 2 longer than first segment, segment 4 setose; scutellum exposed moderately large; abdominal sterna 2-5 separate.

Type species: *Paleoanomala aptenus* gen. et sp. nov.

Etymology: Generic name from the Greek “palaios” = old and the Greek “anomalos” = deviating from the general rule, irregular.

Diagnosis: as for type genus (monotypic)

LSID: urn:lsid:zoobank.org:act:9C1D451F-D5C4-46DC-81AD-BAD21F72E84C

Type material: Accession number B-He-36 deposited in the Poinar amber collection maintained at Oregon State University.

Etymology: Specific epithet is from the Greek “apten” = unable to fly.

Type locality: Myanmar (Burma), state of Kachin, Noiye bum 2001 Summit Site amber mine in the Hukawng Valley, SW of Maingkhwan (26°20'N, 96°36'E).

Diagnosis: as for genus (by monotypy).

Paleoanomala aptenus gen. et sp. nov.

Description: The specimen is complete (Figs. 2-10).



Fig. 2. Dorsal view of *Paleoanomala aptenus* gen. et sp. nov. in Burmese amber. Scale bar = 0.7 mm.

Head (Fig. 5): Posterior portion of head broader than anterior portion; eyes small, barely protruding laterally, positioned roughly in middle of head; ocelli absent; antennae 4-segmented, second antennal segment longest, 3.4 x as long as first, third, and fourth segments that are much more slender than first two; terminal antennomere distinctly setose, with setae longer than segmental diameter; labium 4-segmented, apex extending to the anterior margin of the metasternum.



Fig. 3. Ventral view of *Paleoanomala aptenus* gen. et sp. nov. in Burmese amber. Scale bar = 0.7 mm.

Thorax (Figs. 2,5,7): Pronotum bilobed, widest posteriorly, with paranota expanded; basal margin

of pronotum wider than V-shaped anterior margin, overlapped by scutellum; median carina distinct; lateral carinae somewhat obscured, separating paranotum from disk of pronotum. Pro-, meso- and metasternum separated by transverse sutures. Metanotum fused with first abdominal segment. Legs long and slender, femora and tibiae cylindrical; tarsi two-segmented, claws thin, pulvilli not discernible.

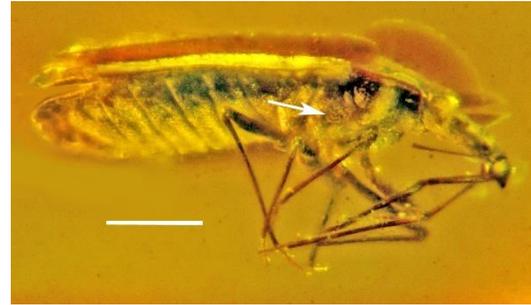


Fig. 4. Lateral view of *P. aptenus* gen. et sp. nov. in Burmese amber. Arrow shows metathoracic gland opening. Scale bar = 0.7 mm.

Abdomen (Figs. 2-5, 7-10): Disc ovate, covering apex of abdomen, dorsum punctate, reticulately sculptured over entire area, with areoles bordered by large dark tubercles; lateral margins with exposed connexium bearing setose outer cell margins. First five abdominal segments separate, subequal, ranging from 160- 190 μ m in width. Hypocostal lamina with an indistinct row of small areolae extending only to end of 5th abdominal segment; sternites I-VI separated; sternite VI fused with sternite VII which shows a median and 2 (1+1) lateral posteriorly directed projections.

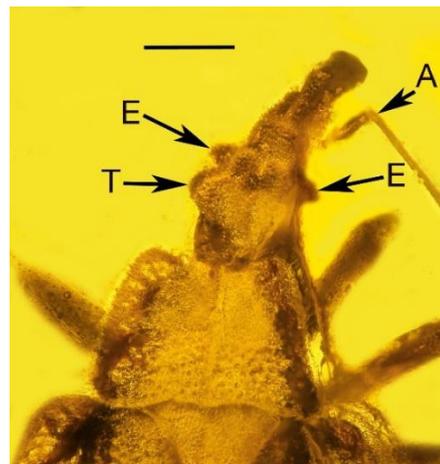


Fig. 5. Eyes (E), antenna (A) and one of four postocular tubercles (T) of *Paleoanomala aptenus* gen. et sp. nov. in Burmese amber. Scale bar = 222 μ m.

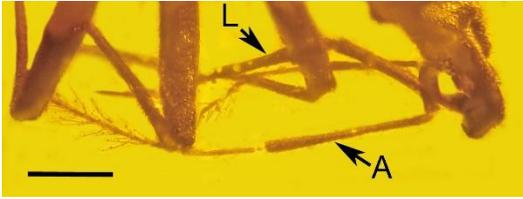


Fig. 6. Labium (L) and antenna (A) of *Paleanomala aptenus* gen. et sp. nov. in Burmese amber. Scale bar = 200 μ m.

Measurements: Holotype: Body length from clypeus to apex of abdomen 2.6 mm; head length, 588 μ m; eye diameter, 72 μ m; length of postocular portion eye, 226 μ m; length of anteocular portion 340 μ m; length of antennae 1.1 mm, length of antennal segments I / II / III / IV = 120 / 410 / 230 / 360 μ m, respectively; length of labium segments, I / II / III / IV = 350 / 230 / 230 / 180 μ m, respectively; pronotum length, 420 μ m; pronotum width, 600 μ m; scutellum length, 350 μ m; scutellum width, 385 μ m; length abdomen, 1.8 mm; width abdomen, 1.5 mm; length profemora, 620 μ m; length protibia, 620 μ m; length mesofemora, 620 μ m; length mesotibia, 570 μ m; length metafemur, 790 μ m; length metatibia, 790 μ m.

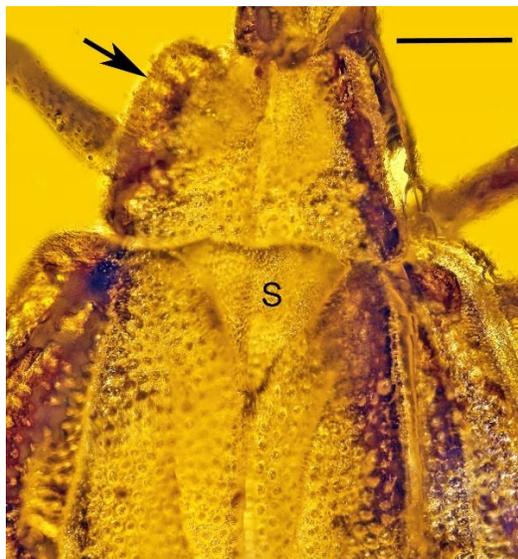


Fig. 7. Dorsal view of pronotum and scutellum (S) of *Paleanomala aptenus* gen. et sp. nov. in Burmese amber. Arrow shows paranotum. Scale bar = 230 μ m.



Fig. 8. Dorsal view of abdominal disc of *Paleanomala aptenus* gen. et sp. nov. in Burmese amber. Arrows show fused portions of the central suture. Scale bar = 310 μ m.

Comments: While the holotype is placed in the subfamily Tingiometrinae based on the shape of the head, it also possesses some features of the subfamily Vianaididae (Shuh & Slater, 1995). These include the flightless coleopteroid body, reduced eyes, absent ocelli, moderately large exposed scutellum, and second antennal segment larger than the first. However, abdominal sterna II-V are fused in the Vianaidinae and they are separate in the fossil. Also, the shape of the body and head of the fossil differ from those of the wingless forms of Vianaididae.

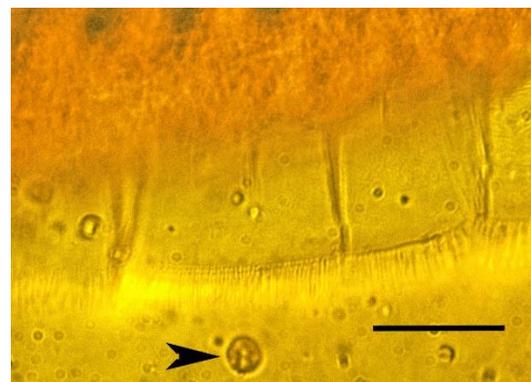


Fig. 9. Connexium with straight, short setae along the border of *Paleanomala aptenus* gen. et sp. nov. in Burmese amber. Arrow shows pollen grain. Scale bar = 50 μ m.



Fig. 10. Terminal abdominal sternites of *Paleanomala aptenus* gen. et sp. nov. in Burmese amber. Scale bar = 240 μ m.

Discussion

Adult Hemiptera exhibit a variety of wing polymorphism (pterygopolymorphism), including macroptery (complete wings), stenoptery (complete but narrowed wings), brachyptery (short, abbreviated wings), microptery (vestigial wings) and aptery (no wings). The partially fused central suture extending the length of the abdominal disc in the fossil indicates that the predecessor of *Paleanomala aptenus* gen. et sp. nov. had separate hemielytra. Thus, the fossil represents a transitional stage of a macropterous lineage that is in the process of losing its wings and becoming apterous. The condition of the fossil also could be considered as an extreme form of brachyptery, although the condition of the hind wings, if present at all, is unknown as they are unobservable. Whether macropterous forms of *Paleanomala aptenus* gen. et sp. nov. existed concurrently is unknown.

The causes of apterism in Tingidae have been little discussed, even though most members of the Vianaididae, a mainly Neotropical group that appear to be associated with ants, are wingless (Kormilev, 1955; Gross & Cassis, 1991; Schuh & Slater, 1995; Golub & Popov, 2000; Montemayor & Carpintero, 2007).

It is interesting to compare the condition in *Paleanomala aptenus* gen. et sp. nov. with widespread polyphyletic aptery in the Aradidae (Hemiptera). All apterous species of Aradidae are considered to have evolved from macropterous lineages. Some apterous species still retain a scutellum, as in macropterous forms, while in other wingless aradids, wing pads appear in late instars, but disappear in adults (Usinger, 1950). Apterism in aradids and tingids is presumed to arise with the disuse of wings, probably

accompanied by shifts to new habitats (Lamarckian concept) (Usinger, 1950).

The present fossil shows that the transition from macroptery to aptery was occurring in tingids by the mid-Cretaceous.

A number of Tingidae have been described from Burmese amber, including *Spinitingis ellenbergeri* and *Burmacader multivenosus* (Heiss & Guilbert, 2013), *Tingiometra burmanica* (Heiss et al., 2015), *Burmacader lativentris* (Heiss & Guilbert, 2018), *Paraphatnomacader huarongcheni* (Guilbert & Heiss, 2019a), *Tingiphatnoma bispinosa* (Guilbert & Heiss, 2019b), *Tingiphatnoma andreneli* (Maksoud et al., 2019), *Tingiphatnoma suchorskii* (Heiss & Guilbert, 2019), and *Tingiometra pankowskii*, *T. secunda*, and *T. yuripopovi* (Golub & Heiss, 2020). While quite diverse in morphological features, all of the above specimens have functional wings, which separate them from *Paleanomala aptenus* gen. et sp. nov.

Several trinucleate pollen grains are adjacent to the specimen (Fig. 11). These grains closely resemble trinucleate angiosperm pollen depicted by Brewbaker (1967) (Fig. 1). The assumingly vegetative nucleus is the largest of the three. The two small fertilization nuclei are considered to be the egg nucleus and the endosperm nucleus. It is possible that these pollen grains are from flowers of the food plant of *Paleanomala aptenus* gen. et sp. nov.

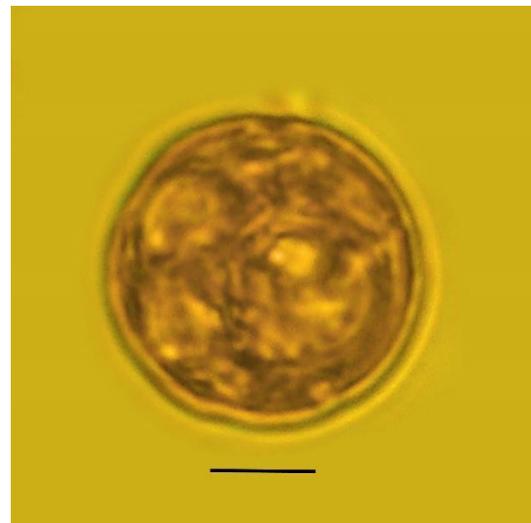


Fig. 11. Detail of the trinucleate pollen grain shown in Fig. 9. Scale bar = 6 μ m.

Acknowledgements

The authors thank Ernst Heiss for help with obtaining literature and Ken Chambers for discussions on pollen morphology.

Conflict of interest statement

The authors declare no conflict of interest.

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