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Palaeoleptus burmanicus n. gen., n. sp., an Early Cretaceous shore bug (Hemiptera: Palaeoleptidae n. fam.) in Burmese amber

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ABSTRACT

Palaeoleptus burmanicus gen. et sp. nov. (Hemiptera: Leptopodomorpha: Palaeoleptidae fam. nov.) is described from Early Cretaceous Burmese amber. The fossil is characterized by nearly completely coreaceous wings with only a small membranous area at the distal tip, and a unique wing venation consisting of eight closed cells, including four obliquely orientated toward the embolar wing margin and two large vertically-positioned cells extending nearly to the apical wing margin. Additional characters are large, compound eyes, three pairs of cephalic trichobothria, four antennal segments all similar in texture, spines on the profemur, ocelli positioned on a tubercle and a rostrum extending to the mesocoxae, with the second segment bearing four pairs of spines. The female fossil contains an asymmetrical subgenital plate orientated toward the left side of the body, indicating a side-by-side mating behavior as occurs in extant Leptopodomorpha.

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1. Introduction

The Leptopodomorpha consists of four families of predatory Hemiptera, the Aepophilidae, Saldidae, Leptopodidae and Omaniidae (Schuh and Slater, 1995). Of these, the Saldidae (shore bugs) are the most familiar since aside from their world-wide distribution, many species occur in large numbers along various bodies of fresh and salt water (Polhemus, 1976, 1985; Péricart, 1990).

With the exception of the aepophilids, the Leptopodomorpha are noted for their large, protruding compound eyes, small to medium size (most under 5 mm), dark color, presence of ocelli, hemelytra with a well-developed membrane in macropterous (fully winged) forms, longish legs bearing spines and/or setae and a welldeveloped rostrum not extending beyond the metacoxae. A fossil Leptopodomorpha in Burmese amber with a combination of characters found in extant saldids, leptopodids and omaniids, as well as a unique wing venation not previously noted in extant or extinct members of the group, is described here.

2. Materials and method

The amber piece containing the fossil is roughly oval in outline, measuring 16 mm in length by 12 mm in width by 3 mm

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deep. Observations, drawings, and photographs were made with a Nikon SMZ-10 R stereoscopic microscope and Nikon Optiphot compound microscope with magnifications up to $700\times$. The amber was obtained from a mine first excavated in 2001, in the Hukawng Valley, southwest of Maingkhwan in Kachin State ($26^{\circ}20'$ N, $96^{\circ}36'$ E) in Burma (Myanmar). This new amber site, known as the Noije Bum 2001 Summit Site, was assigned to the Lower Cretaceous, upper Albian, on the basis of paleontological evidence (Cruickshank and Ko, 2003), placing the age at 97 to 110 Ma. 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 (possibly *Agathis*) tree source for the amber (Poinar et al., 2007).

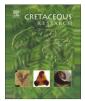
The specimen is well preserved and complete except for missing the tarsi of the first and second right legs (Figs. 1,2).

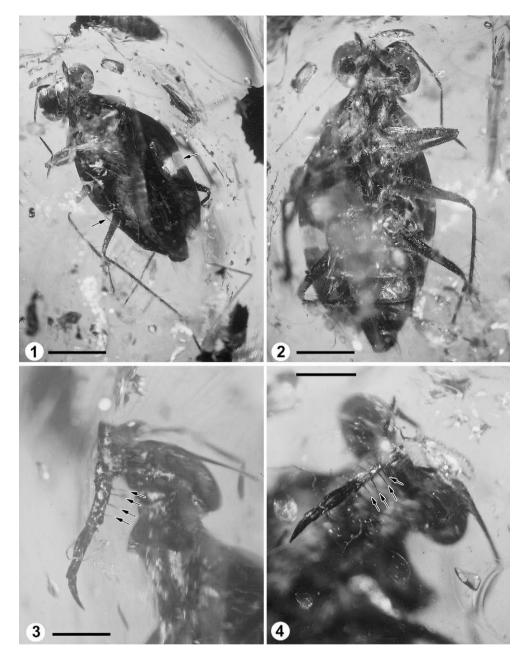
3. Systematic palaeontology

Order Hemiptera Series Leptopodomorpha Palaeoleptidae Poinar fam. nov. *Type genus: Palaeoleptus* gen. nov.

Diagnosis. Large, protruding compound eyes; antennal segments similar in texture; ocelli positioned on tubercle; pre-ocellar spots present; second rostral segment bearing four pairs of spines;







Figs. 1–4. Palaeoleptus burmanicus. 1, Dorsal view of holotype. Arrows show wing bands. Scale 1.3 mm. 2, Ventral view of holotype. Scale 922 µm. 3, Lateral view of rostrum, Arrows show spines on second segment (opposite set of spines hidden from view). Scale 440 µm. 4, Dorsal view of rostrum showing 4 pairs of spines on second rostral segment. Arrows show one of each pair. Scale 500 µm.

forewing nearly completely coreaceous except for small membranous area at distal border; wing venation consisting of eight closed cells including four obliquely orientated toward embolar wing margin and two large vertically-positioned cells extending nearly to apical wing margin.

Genus Palaeoleptus Poinar gen. nov.

Type species. Palaeoleptus burmanicus gen. nov., sp. nov.

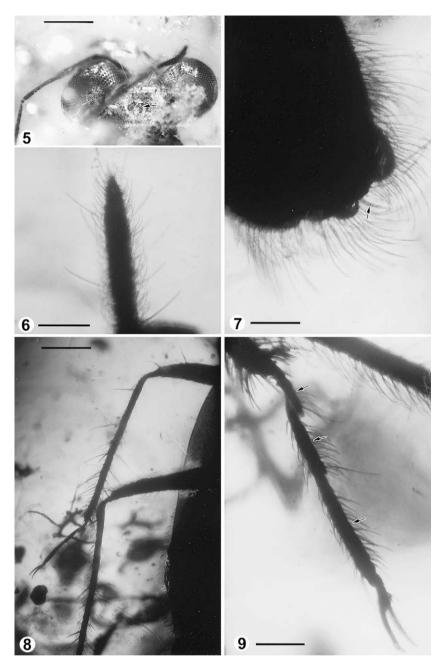
Description. Characters as indicated in family diagnosis; three pairs of cephalic trichobothria; antennal segments all similar in diameter and pubescence; four-segmented rostrum of medium length with tip extending to base of mesocoxae; anterior femur bearing spines.

Diagnosis. The predominately tegminal wings and unique wing venation separate *Palaeoleptus* from all extant and extinct macropterous Leptopodomorpha.

Palaeoleptus burmanicus Poinar sp. nov. Figs. 1–11

Material. Holotype (E5) in Burmese amber deposited in the Buckley amber collection, Florence, Kentucky. Specimen available for study by contacting RB.

Description. As for family and genus; macropterous female; length, 5.3 mm; greatest width, 2.3 mm; color black-ochraceous with antennae and rostrum brownish-ferruginous; white band on each wing.

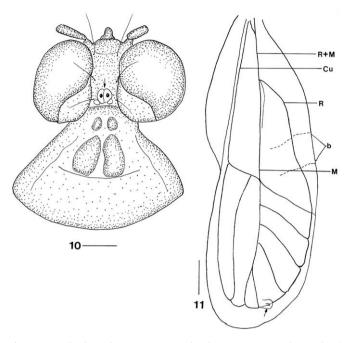


Figs. 5–9. *Palaeoleptus burmanicus.* 5, Dorsal view of head showing ocellar tubercle (arrow). Note different sizes of ommatidia. Scale 510 μm. 6, Tip of fourth antennomere showing long and short setae. Scale 88 μm. 7, Asymmetrical genital plate (ventral view). Arrow shows tip of ovipositor. Scale 136 μm. 8, Left middle and hind leg showing spines on tibiae. Scale 447 μm. 9, Three-segmented tarsus (arrows) and straight claws. Scale 117 μm.

Head. Length along median line, 1.5 mm; bearing three pairs of cephalic trichobothria, one pair at base of compound eyes, another adjacent to ocellar tubercle and third near base of clypeus; compound eyes large, silvery, protruding, rounded on top, flattened on lower surface, extending posteriorly slightly beyond pronotal collar; with few short setae on outer border; eye length, 765 μ m, width, 617 μ m; ommatidia numerous, varying in size depending on location; largest ommatidia (greatest dimension, 32 μ m) on anterior portion of eye; smallest ommatidia (greatest dimension, 13 μ m) on posterior portion of eye; interocular space forward, 297 μ m, at mid-eye, 459 μ m, posteriorly, 297 μ m; ocelli located on tubercle between compound eyes; preocellular spots located just lateral and posterior to ocellar tubercle; antennae 4- segmented, length antennomeres, first, 351 μ m, second, 946 μ m; third, 675 μ m, fourth,

557 μ m; antennomeres, especially the terminal three, with dense, short setae ranging from 24 μ m to 34 μ m in length and sparse long setae ranging from 68 μ m to 107 μ m in length; rostrum medium in length, 4- segmented, first segment mostly covered by labrum, lengths of segments, first, 111 μ m; second, 444 μ m; third, 445 μ m; fourth, 278 μ m; second segment bearing four pairs of spines; median channel between mesocoxae considered as reception point for tip for rostrum.

Thorax. Covered with sparse but fairly long, erect setae throughout; pronotum transverse, unarmed, with straight anterior border, edges covered by compound eyes; lateral margins smooth, rounded at base; posterior margin concave, partly covering scutellum; posterior lobes greatly reduced; medial area anterior to pronotal furrow with two sets of paired calli (anterior pair small,



Figs. 10–11. *Palaeoleptus burmanicus.* 10, Head and pronotum. Arrow shows tubercle with ocelli. Scale 316 μ m. 11, Fore wing venation. R = radius, M = media, Cu = cubital, b = area of white wing band. Arrow shows modification on wing apex that could function to accommodate grasping apparatus of male. Scale 430 μ m.

posterior pair large); length pronotum along midline, 1.08 mm; width pronotum at base, 1.78 mm; scutellum large, length, 783 µm; width at anterior border, 540 µm; legs long, slender; coxae and trochanters well developed, with following coxal lengths, procoxa, 652 μm, mesocoxa, 347 μm, metacoxa, 522 μm; all femurs approximately equal in thickness and bearing spines (six on forefemur) and dense coating of setae; femur lengths, profemur, 1.30 mm, mesofemur, 1.52 mm, metafemur, 1.74 mm; all tibia bearing long spines and dense coating of setae; metatibia more than twice length of protibia; tibial lengths, protibia, 1.09 mm, mesotibia, 1.52 mm, metatibia, 2.61 mm; tarsal formula 3-3-3, tarsal lengths, tarsomere l, 145 µm; tarsomere ll, 218 µm, tarsomere lll, 315 µm; claws simple, straight, length, 170 µm; wings tegminal except for membranous area distal to terminal cells; dark except for white band extending partially across corium; wing length, 4 mm; cuneus absent; clavus and claval suture distinct; clavus with dark spots but lacking punctures; wings covering abdomen except for exposed genital plate; wing venation consisting of eight closed cells, including four obliquely orientated toward embolar wing margin and two large vertically-positioned cells extending nearly to apical wing margin; expanded button-like structure at tip of fourth oblique cell.

Abdomen. Dark brown to black, covered with setae, especially dense along lateral borders and on subgenital plate; length abdomen, 3.22 mm; seven segments clearly visible, terminal segment with asymmetrical subgenital plate directed toward left side of body; ovipositor slender, partially transparent, partly extruded from subgenital plate (extruded portion, 68 μm); spiracles not observed.

Etymology. Palaeo is from the Greek "palaeo" for old and leptus is from the Greek "leptos" for small, thin. The specific epithet "burmanicus" refers to the type locality.

Type locality. Amber mine in the Hukawng Valley, southwest of Maingkhwan in Kachin Sate (26°20'N, 96°36'E), northern Myanmar (Burma).

4. Discussion

Schuh and Slater (1995) list four families in the Leptopodomorpha, the Saldidae, Aepophilidae, Leptopodidae and Omaniidae. Placement of *Palaeoleptus* in a separate family is based on its unique forewing venation, as well as its combination of characters preventing its placement in any of the above four families. The series of eight closed cells, with four obliquely orientated toward the embolar wing margin and two large vertically-positioned cells extending nearly to wing tip is a configuration not present on any extant Leptopodomorpha.

Even without the unique wing characters, it would be difficult to place *Palaeoleptus* in any extant family of the Leptopodomorpha. While omaniids have tegminal forewings, they are coleopteroid in form and lack closed cells. Also, all extant omaniids are under two mm in length. The Aepophilidae contains a single species greatly modified due to its life style of living in rock crevices in the intertidial zone. It has greatly reduced eyes, no ocelli, and reduced padlike forewings. Macropterous saldids and leptopodids normally have a distinct forewing membrane (Schuh and Slater, 1995; Polhemus, 1985; Péricart, 1990). *Palaeoleptus* shares some features with both of these groups. The rostral and profemur spines of *Palaeoleptus*, as well as the ocelli positioned on a tubercle, are characteristic of leptopodids, yet the latter group have a short rostrum never surpassing the forecoxae, a deeply punctured clavus and only up to four closed cells in the forewing.

The rostrum reaching beyond the procoxae and the uniform nature of all four antennomeres of *Palaeoleptus* are features of saldids, however saldids have unarmed rostrums that reach at least to the base of the metacoxae and the ocelli are not positioned on tubercles (Polhemus, 1976, 1985; Horvath, 1911; Cobben, 1985; Péricart, 1990; Schuh and Slater, 1995).

Palaeoleptus also differs from fossil representatives of the Leptopodomorpha. *Salda exigua* Germar and Berendt (1856) from Eocene Baltic amber has only three closed cells in the forewing membrane, the rostrum extends only to the front coxae and the antennal length is greater than half the body length. *Leptosalda chiapensis* Cobben (1971) from Oligocene-Miocene Mexican amber is only 1.45 mm in length, has a short rostrum with segments 2–4 subequal in length and the rostral tip does not extend beyond the anterior coxae. The Oligocene genus *Oligosaldina* Statz and Wagner (1950) has a distinct membrane with only four closed cells. The Miocene species, *Propentacora froeschneri* (Lewis, 1969), contains five closed cells in the wing membrane, but the corial vein continues between the third and fourth membrane cells and there are no vertical wing cells.

The Cretaceous family Mesolygaeidae Zhang is characterized by small eyes, a large pronotum that extends well over the scutellum and wings with a different cell arrangement from those of Palaeoleptus (Zhang, 1991). The Jurassic genus Saldonia Popov (1973, 1985) in the Archegocimicidae Handlirsch, 1906 (Carpenter, 1992; Rasnitsyn and Quicke, 2002) consists of two species of compression fossils (S. rasnitsyni Popov and S. sibirica Popov) from Eastern Siberia. While Saldonia has a completely different venational pattern from Palaeoleptus, some of the wing cells of Saldonia are directed towards the embolar margin as in Palaeoleptus. However, in Saldonia, there are 11-12 closed tegminal cells, whereas in Palaeoleptus, there are only eight closed cells. In addition, veins R and M are fused between 37% and 40% of the total wing length in Saldonia while in Palaeoleptus, these veins are only fused for 20% of the total wing length. Other differences between Saldonia and Palaeoleptus are the presence of a terminal membrane in the latter genus and the absence of any membrane in Saldonia, separated ocelli positioned flat on the vertex in Saldonia and adjacent ocelli positioned on a tubercle in *Palaeoleptus*, compound eyes separated by a distance greater that their width in *Saldonia* but separated by a distance less than half the eye width in *Palaeoleptus* and an extremely short rostrum in *Saldonia*, barely reaching to the procoxae, while the rostrum in *Palaeoleptus* extends to the mesocoxae.

The Palaeoleptidae represents a basal group of the Leptopodomorpha positioned between the Saldidae and Leptopodidae. It represents what we have previously characterized as a chimera (fossils with diagnostic morphological features found in two or more present day groups) (Poinar and Poinar, 2008). After examining numerous fossils from Burmese amber, it is obvious that the Early Cretaceous was a period when genetic plasticity was great, species radiated extensively both structurally and behaviorally and the partitioning of habitats was continually changing. Another Burmese amber "chimera" was the dipteran, *Dacochile microsoma* Poinar and Brown (2006) with characters of two extant families, the Tanyderidae and Psychodidae (Bruchomyiinae).

The asymmetrical genital plate directed to the left side of the body suggests that *Palaeoleptus* practiced side by side mating with the male positioned on the left side of the female. Side by side mating occurs in extant members of the Leptopodomorpha and the same left-directed genital plate occurs in female Saldidae (Schuh and Slater, 1995; Polhemus, 1985). The button-like modification of the wing apex at the tip of oblique cell 4 (Fig. 11) appears to be part of the normal wing structure and not an artifact. While a corresponding feature could not be located on any described member of the Leptopodomorpha, it possibly functioned to accommodate the grasping apparatus of the male during copulation. In some saldids, the female has an embolar notch or a cluster of short setae near the middle of the wing margin that pairs with the male grasping apparatus during mating (Polhemus, 1985).

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