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Prosthoblissus primigenius n. gen., n. sp., holotype AMNH JZC-Bu186: dorsal oblique habitus.

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The earliest chinch bug (Hemiptera, Blissidae): A new genus from mid-Cretaceous Kachin amber

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ABSTRACT

The earliest known fossil of the chinch bug family Blissidae Stål, 1862 is described and figured from a macropterous male preserved in mid-Cretaceous Kachin amber of northern Myanmar. *Prostobliissus primigenius* n. gen., n. sp. is noteworthy for the putatively plesiomorphic retention of open procoxal cavities, a character state shared with a swath of arguable early-diverging extant genera. It is distinguished from those genera based on a unique combination of plesiomorphic and apomorphic character states, as well as from *Eobliissus gallicus* Garrouste, Schubnel & Nel, 2019, the prior earliest fossil of the family. This occurrence extends the age of the family from the early Eocene to the middle Cretaceous, greatly revising available calibration points for crown-group Blissidae.

KEY WORDS
Cenomanian,
Heteroptera,
Lygaeoidea,
Myanmar,
palaeobiodiversity,
new genus,
new species.

RÉSUMÉ

La première punaise velue (Hemiptera, Blissidae) : un nouveau genre de l'ambre crétacé moyen du Kachin. Le plus ancien fossile connu de la famille Blissidae Stål, 1862 est décrit et illustré à partir d'un mâle macroptère préservé dans l'ambre de Kachin du Crétacé moyen, dans le nord du Myanmar. *Prostobliissus primigenius* n. gen., n. sp. est remarquable pour sa potentielle rétention de plésiomorphies, avec des cavités procoxales ouvertes, un état de caractère partagé avec un ensemble de genres actuels dont la divergence précoce est discutable. Il se distingue de ces genres par une combinaison unique d'états de caractères plésiomorphes et apomorphes, ainsi que d'*Eobliissus gallicus* Garrouste, Schubnel & Nel, 2019, le plus ancien fossile de la famille. Cette occurrence étend l'âge de la famille du début de l'Éocène au milieu du Crétacé, révisant considérablement les points de calibration fossiles utilisables pour le groupe-couronne des Blissidae.

MOTS CLÉS
Cénomanien,
Heteroptera,
Lygaeoidea,
Myanmar,
paléobiodiversité,
genre nouveau,
espèce nouvelle.

INTRODUCTION

Blissidae Stål, 1862, or chinch bugs, are a small family of Lygaeoidea Schilling, 1829 (Heteroptera: Pentatomomorpha), with about 53 extant genera and more than 420 extant species (Schuh & Weirauch 2020). Blissid species are distinctive among the superfamily for their specialized feeding on sap, rather than seeds, and for typically living between leaf sheaths and breeding solely on monocots (Slater 1976). The family is found throughout the world, although there is a concentration of their diversity in the tropics. While many species of the genus *Blissus* Burmeister, 1835 can be pestiferous, the species *Blissus leucopterus* (Say, 1832) and *B. insularis* Barber, 1918, both native to North America (from southern Canada into Central America), are particularly injurious to turf grass and grain crops (Sweet 2000). For much of their taxonomic history, blissids were considered a specialized subfamily of Lygaeidae (e.g. Slater 1979), but since the groundbreaking phylogeny of Henry (1997), the group has been accorded familial rank. Indeed, estimations of phylogeny among Lygaeoidea are currently robust, with morphological and molecular analyses converging on a largely congruent suite of relationships (Henry 1997; Liu *et al.* 2019). It is challenging, however, to provide solid estimates of clade divergence owing to a dearth of reliable calibration points for many families, and this is certainly the case for Blissidae.

The fossil record of Blissidae is scant and restricted to three occurrences, all comparatively modern with respect to presumed antiquity of lygaeoid families. Hitherto the records of Blissidae as fossils were confined to the Cenozoic. Two fossils are of dubious taxonomic attribution, *Ischnodemus rottensis* Statz & Wagner, 1950 from the Upper Oligocene of Rott, Germany (Statz & Wagner 1950) and putative species of the same genus, *Ischnodemus* sp., from the Lower Miocene of Izarra, Spain (Ortuño & Arillo 1997). The sole amber fossil is that of *Eoblissus gallicus* Garrouste, Schubnel, & Nel, 2019 from the Lower Eocene amber of Oise, France (Garrouste *et al.* 2019).

Herein we report the earliest occurrence of chinch bugs, from a unique, brachypterous individual in mid-Cretaceous Kachin Amber, doubling the previous earliest age of a fossil in the family. The new fossil documented here is described as a new genus and species, and provides a significant calibration point for understanding the timing of diversification for these specialized bugs.

MATERIAL AND METHODS

The holotype is embedded in a piece of yellow Kachin amber, which originated from amber mines around Noiye Bum Hill, Hukawng Valley (26°29'N, 96°35'E), Kachin State, Myanmar (refer to Grimaldi & Ross, 2017, for a detailed map). Radiometric data based on zircons from volcanic clasts found within the amber-bearing sediments and taphonomic analysis of pholadids have established an Early Cenomanian age (98.79 ± 0.62 Ma) (Shi *et al.* 2012; Smith & Ross 2017). Some ammonites found in the amber-bearing bed and within the amber itself corroborate an

either latest Albian or earliest Cenomanian age (Cruickshank & Ko 2003; Yu *et al.* 2019), with the convergence of these multiple sources of data strongly indicating a fauna from just after the Albian–Cenomanian boundary. The specimen was obtained legally, well prior to 2017 (Engel 2020), and is deposited in the American Museum of Natural History (AMNH) under accession number AMNH JZC-Bu294.

The specimen was studied using Nikon SMZ25 and Leica M205C stereomicroscopes and photographed with a Nikon ZII camera. Photographs were exported in NEF format and processed with Nikon NX Studio software. All images were digitally stacked photomicrographic composites of several individual focal planes, which were obtained using Helicon Focus 6.7 software. All measurements were obtained with ImageJ software and recorded in millimeters. Morphological terminology follows Schuh & Weirauch (2020) and taxonomic attribution follows those synapomorphies for and within Lygaeoidea from Henry (1997) as well as the extensive generic accounts for Blissidae by Slater (1979) and Henry & Dellapé (2024). Given that the genus proposed herein is currently monotypic we have provided an extensive generic description that largely characterizes the genus and species, with more minor specific details summarized in the specific account.

SYSTEMATIC PALAEOLOGY

Class INSECTA Linnaeus, 1758
Order HEMIPTERA Linnaeus, 1758
Suborder HETEROPTERA Latreille, 1810
Superfamily LYGAEOIDEA Schilling, 1829
Family BLISSIDAE Stål, 1862

Prosthoblissus n. gen.

(Fig. 1)

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TYPE SPECIES. — *Prosthoblissus primigenius* n. sp.

ETYMOLOGY. — The new generic name is a combination of the Ancient Greek *πρόσθεν* (*prósthēn*, meaning, “before” or “earlier”) and *Blissus* Burmeister, 1835 (itself from Ancient Greek *βλίσσω* / *blíssō*, meaning, “to steal honey from the hive”), type genus of Blissidae. The gender of the name is masculine.

DIAGNOSIS. — The new genus can be distinguished from all extant and extinct Blissidae by the following combination of characters (refer also to Discussion, *infra*): ocelli absent; rostrum exceptionally short, extending merely to procoxae; meso- and metasterna not grooved; procoxal cavities open; femora incrassate, particularly profemur; all femora mutic; protibia bispinose, apically opposite spur; metatarsomere II with a pair of spines; macropterous, oblique apical margin of corium slightly convex; apical margin of abdominal tergum III spiculate.

DESCRIPTION

Body

Relatively slender and elongate, dorsoventrally compressed (as preserved); integument non-pruinose and generally dark matt as preserved except pronotum and mesonotum shiny

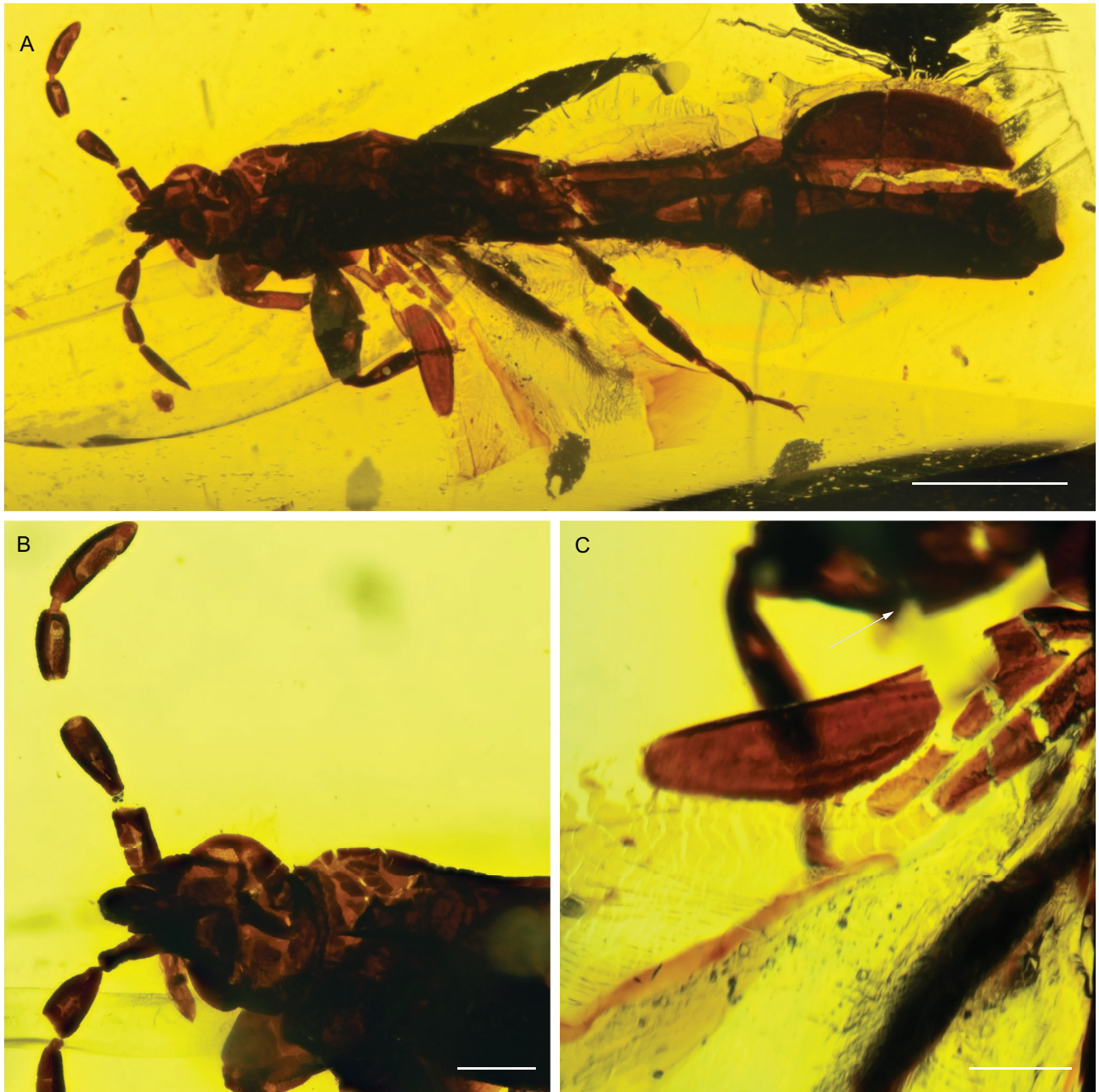


FIG. 1. — *Prosthoblissus primigenius* n. gen., n. sp., holotype AMNH JZC-Bu186: **A**, dorsal oblique habitus; **B**, detail of head and anterior part of pronotum; **C**, detail of hemelytral corium; arrow points to a transverse fracture of profemur in background. Scale bars: A, 1 mm; B, 0.25 mm.

(other areas may have been shining in life but are altered taphonomically – darkened, partially cleared in some places, and quite fragmented; likewise integument could have had pruinose areas in life with the powdery granulations obliterated by the resin but, where evident, the complete absence of minute spicules on the integument suggests that these areas were truly not pruinose).

Head

Not declivitous, projecting forward, slightly longer than maximum breadth, with short, broad collar posterior to

compound eyes; compound eyes hemispherical, protruding; ocelli absent; tylus longer than juga, extending to nearly $0.75 \times$ length of antennomere I; genal tusks absent; buccula narrow, short, not extending beyond jugum, rounded and not dilated apically; labium short, extending to anterior of prosternum.

Pronotum

About as long as wide (slightly distorted as preserved, slightly longer than wide as preserved but medial compression of pronotum means a precise measurement of width as in life impossible to determine; likely as long as wide in life); in-

tegument largely and smooth, shining, not microspiculate, with faint transverse striae posteriorly. Mesoscutellum longer than wide, apex acutely rounded; meso- and metasterna not grooved.

Hemelytron

Macropterous, membrane well-developed (extended and broken at edge of amber but sufficiently broad and extensive at that point of cutoff to indicate that its extension would likely have covered most of abdominal segments and at least base of segment IV but almost certainly not surpassing abdominal apex), hyaline and clear (as preserved), membrane without cells; corium weakly punctate, apex rounded (rather than tapering to point on anterior wing margin), oblique apical-posterior margin slightly convex; clavus about 0.5 × length of corium, narrow.

Procoxal cavities

Open posteriorly, separated mesally by simple prosternal projection; femora incrassate, mutic (including profemur; one profemur damaged and broken transversely at about midlength, with ventral portion of break artificially pulled open, not to be confused with profemoral armature: Fig. 1C); protibia bispinose apically, with thin, longitudinal brush of setae on apical quarter; tibiae not flattened or armed along outer edges; metatarsomere II with a pair of spines.

Abdomen

Elongate, slender (apical segments artificially appearing widened owing to splitting of integument and splaying of sclerites); apical margin of tergum III spiculate; abdominal spiracles II and III dorsal, spiracles IV–VI likely dorsal as well (refer to Discussion, *infra*); sterna unarmed.

Prosthoblissus primigenius n. sp. (Fig. 1)

[urn:lsid:zoobank.org:act:4BEA3DAA-C80A-476D-87BD-17AC0DABAE40](https://doi.org/10.21203/rs.3.rs-3111111/v1)

TYPE MATERIAL. — **Holotype.** Myanmar • Specimen almost complete, with the rostrum, forewings, and the abdomen in a 1.2 × 0.7 × 0.4 cm subrectangular piece of amber; Kachin amber, Noiye Bum Hill, Hukawng Valley, Kachin State; 26°29'N, 96°35'E; unnamed formation, earliest Cenomanian; AMNH JZC-Bu186.

TYPE LOCALITY. — Kachin amber, Noiye Bum Hill, Hukawng Valley (26°29'N, 96°35'E), Kachin State, Myanmar.

ETYMOLOGY. — The specific epithet is the Latin adjective *primigenius*, meaning, “firstborn”, “original”, or “primitive”.

DIAGNOSIS. — As for the genus.

DESCRIPTION

Male

As for genus with following minor additions. Adult: Total body length 5.9 mm (apex of tylus to apical margin of distalmost abdominal segment); body elongate; head length 0.78 mm (apex of tylus to posterior margin), maximum width across

compound eyes 0.65 mm; interocular distance 0.34 mm; antennomere lengths (I–IV) 0.29 mm, 0.29 mm, 0.23 mm, 0.35 mm, respectively. Pronotal mediolongitudinal length 0.79 mm, medial width 0.77 mm; mesoscutellum mediolongitudinal length 0.53 mm, basal width 0.47 mm.

Integument dark brown to black as preserved, lighter brown in areas where integument partially cleared (likely completely black in life). Integument largely glabrous, with exceptionally sparse, short, erect setae. Pronotum smooth and shining, without rugosity or visible punctation, with faint transverse striations in posterior third, with shallow, narrow, mediolongitudinal furrow; faint, small, paramedial calli anteriorly on either side of furrow. Mesoscutellum with sparsely scattered, faint, shallow punctures, otherwise seemingly smooth. Hemelytral corium with faint, shallow punctures; corium and clavus dark brown (as preserved) except a couple of transverse clear bands. Abdominal terga and sterna, where evident, impunctate.

DISCUSSION

The current fossil can be assigned to Lygaeoidea based on the presence of incrassate profemora (lost in more derived lygaeoid lineages) and absence of cells on hemelytral membrane, which are synapomorphies of the superfamily (*sensu* Henry 1997). In addition, the short bucculae that do not extend beyond the tylus and are narrowed anteriorly is consistent with a blissid, although males in some derived genera have apomorphically long and expanded bucculae (Slater 1979). Unfortunately, most characters for subordinate groups within the superfamily are derived from the abdominal spiracles, which are mostly unobservable in the fossil given its preservation. The spiracles of segments II and III are certainly dorsal and it seems that there is a faint indication of a dorsally positioned spiracle on segment IV, all of which are consistent with Blissidae. The spiracles of IV–VI are certainly not located ventrally as that portion of the sterna is distinct but the lateral connexival portion of the abdomen is damaged and that of segments V and VI is particularly fragmented. This implies that they were dorsal in placement but this is by inference rather than observation. Regardless, aside from the presence of the aforementioned character states the fossil also shares with Blissidae the rather flattened body, fusiform apical antennomere (IV), large and nearly squarish pronotum, and weakly punctate hemelytra (Henry 1997; Schuh & Weirauch 2020). Relationships among genera of Blissidae were explored by Slater (1979) and more recently by Henry & Dellapé (2024), although for a reduced set of genera with closed procoxal cavities. Considerable work on the inner phylogeny of Blissidae remains to be undertaken, and ideally incorporating the two key fossil genera: *Eoblissus* and *Prosthoblissus* n. gen. The new genus can be distinguished rather easily from the only other amber-fossil blissid, *E. gallicus* in Eocene Oise amber. Of particular significance, in *P. primigenius* n. gen., n. sp. the profemora are mutic (vs armed with six denticles ventrally in *E. gallicus*), the rostrum does not extend much beyond anterior margin of the prosternum (extending to mesocoxae

in *E. gallicus*), and the antennomeres are comparatively short and thickened (unusually elongate and almost filiform in *E. gallicus*). The holotype of *E. gallicus* also has a particularly well-developed hemelytron, the membrane of which clearly extends beyond the abdominal apex.

It is challenging to make a complete comparison with extant genera in the absence of data from the genitalia and nymphs, as well as some other characters such as the presence or absence of pruinosity, although it generally appears that the insect is non-pruinose throughout. Nonetheless, the open procoxal cavities excludes a rather large number of genera. Slater (1979) postulated that the character-state of closed procoxal cavities was uniquely derived, with those genera retaining open procoxal cavities forming a grade to a “closed” clade. If this polarity is continually borne out by future phylogenetic analyses, then the retention of such open cavities in the fossil reported here is intuitively pleasing given its age. Among those genera with open procoxal cavities, *Heteroblissus* Barber, 1954 and *Praetorblissus* Slater, 1966 are multispinose, while in *Macchiademus* Slater & Wilcox, 1973, *Barrerablissus* Brailovskiy, 2015, and some species of *Capodemus* Slater & Sweet, 1972 and *Dimorphopterus* Stål, 1872, there is at least a single spine, if not two. In *Prosthoblissus* n. gen. the profemur is mutic. From those mutic species of *Capodemus* and *Dimorphopterus* the fossil genus differs in the weakly convex corial margin (straight to concave in these genera). In *Macchiademus* the ocelli are present, albeit small, while *P. primigenius* n. gen., n. sp., clearly lacks ocelli. In addition, the protibiae is terete and not flattened and expanded, as in *Geoblissus* Hidaka, 1959. The seemingly non-pruinose mesoscutellum would further aid the distinction of *Prosthoblissus* n. gen. from these latter genera. In *Praeblissus* Barber, 1949 and *Caveloblissus* Slater & Wilcox, 1968 the rostra are more elongate, extending to the metacoxae or mesocoxae, respectively (Henry & Dellapé 2024). The tylus and juga lack spines and the body is elongate, thereby excluding the genus *Talpoblissus* Slater & Wilcox, 1973. *Tympanoblissus* Dellapé & Minghetti, 2020, *Howdenoblissus* Štys, 1991 and *Cundinablissus* Brailovskiy, 2022 are wholly apterous but the large profemoral spine of *Tympanoblissus* also distinguishes it from the fossil, while the presence of ocelli in *Cundinablissus* also differs from that of *Prosthoblissus* n. gen. The remaining extant genera with open procoxal cavities (e.g. *Aulacoblissus* Slater, 1986, *Napoblissus* Brailovskiy & Barrera, 2012, *Hasanobochrus* Ghauri, 1982) all have some degree of profemoral spination, which stands in stark contrast to the mutic profemur of *P. primigenius* n. gen., n. sp. Lastly, differing from all of these genera, *P. primigenius* n. gen., n. sp. has the apical margin of tergum III spiculate and the apex of the protibia bispinose, putative autapomorphies of the fossil, while the former character is unmodified in *Eoblissus* and all extant genera and the latter character-state is absent in *E. gallicus* and at least most genera with open procoxal cavities.

While there remains much to be discovered regarding the evolutionary history and past diversity of chinch bugs, the new genus provides a key minimum age of 99 Ma for calibrating the family in estimates of divergence times for Lygaeoidea.

The fossil not only attests to the antiquity of Blissidae but provides further evidence of the Early Cretaceous diversification of lygaeoid bugs.

CONCLUSION

Here we report a remarkable new fossil that significantly extends the geological history of chinch bugs, family Blissidae. Overall, the fossil record of Lygaeoidea is quite heterogeneous, although the lineage seemed to diverge during the Late Jurassic (Liu *et al.* 2019). Such a divergence estimation is congruent with reported occurrences of lygaeoids from the Late Jurassic and Early Cretaceous (Hong 1980; Popov 1986, 1990), but the taxonomic attribution of most of these fossils is questionable. The first fossils that can be accurately attributed are from Eocene Oise and Baltic ambers. The new fossil genus and species, *P. primigenius* n. gen., n. sp., aside from encompassing a unique combination of character states, reinforces the notion that lygaeoids diverged at the end of the Jurassic or in the Early Cretaceous, such that crown-group Blissidae would be present by the mid-Cretaceous. The current fossil thus represents a key calibration point for all future phylogenetic estimations of relationships among Lygaeoidea and within Blissidae.

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