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A new cockroach, with bipectinate antennae, (Blattaria: Olidae fam. nov.) further highlights the differences between the Burmite and other faunas

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Abstract: Only a few families have been recognized in the 320 million year history of cockroaches. The 31st one, represented by monotypic *Ol xiai* sp. n. from the Myanmar amber is described here. It inhabited lowland forest near the shore. It possesses several unique morphological features including bipectinate antennae, round terminal palpomeres, sophisticated forewing shape with broken R and CuP forming a distinct unsclerotised area and with RS branched to both sides, and a huge foretibial spur. The new genus also displays several putatively apomorphic reductions (short antennae, rudimental femoral terminal spine, short pronotal chaetae, minor arolia, short palps). Synapomorphies with early ant-nest parasites (short antennae, dense pronotal setosity, irregular spacing of wing veins, indication of maculated colouration) suggest an origin from Blattidae or ancestral Mesoblattinidae during the Early Cretaceous. No plesiomorphies are apparent. An attached mite documents a phoresy on males. A syninclusion of a coccoid male is not ecologically informative at the given state of knowledge.

Key words: fossil insect; amber cockroach; Late Cretaceous; new family; bipectinate antenna

Introduction

Cockroaches are generally considered to be a conservative group of organisms and surprisingly this is, at least partly, met by a high extinction rate since their origination rate is apparently comparable to that of beetles (Nicholson et al. 2015). As a result, in fossil records of cockroaches we see evidence of bursts of genera and species, but over the approximately 320 million year history of the order we know of only 30 valid cockroach families (Vršanský & Bechly 2015; Bai et al. 2016). It came about as a surprise to discover the first indigenous cockroach family in the history of the order, namely from the Myanmar amber Lagerstätte. The modified mouthparts and forelegs displayed by the new family suggest a highly specialized way of life and might also indicate that it originated from ant-parasite cockroaches or their ancestors. The discovery contributes to the numerous unusual insects that inhabited ancient forests of Myanmar.

Material and methods

The source area of the Myanmar amber cockroach fossils was described in detail by Šmídová & Lei (2017). The sample referred to here is deposited in the Lingpoge Amber Museum in Shanghai (F.Y. Xia, curator) under identification number BA17100. The visibility of structures in photographs (8–50 layers) was enhanced using all-surface (Adobe Photoshop 11 selective colour adjustment and “unsharp mask” functions). The drawing was based on the photographs and made using Corel Draw X. Wing nomenclature follows the earliest significant venation concept by Comstock & Needham (1898).

Systematic palaeoentomology

Order Blattaria Latreille, 1810
Superfamily Blattoidea Latreille, 1810
Olidae fam. n.

Type genus. *Ol* gen. n. herein designated and by monotypy.

* Corresponding author

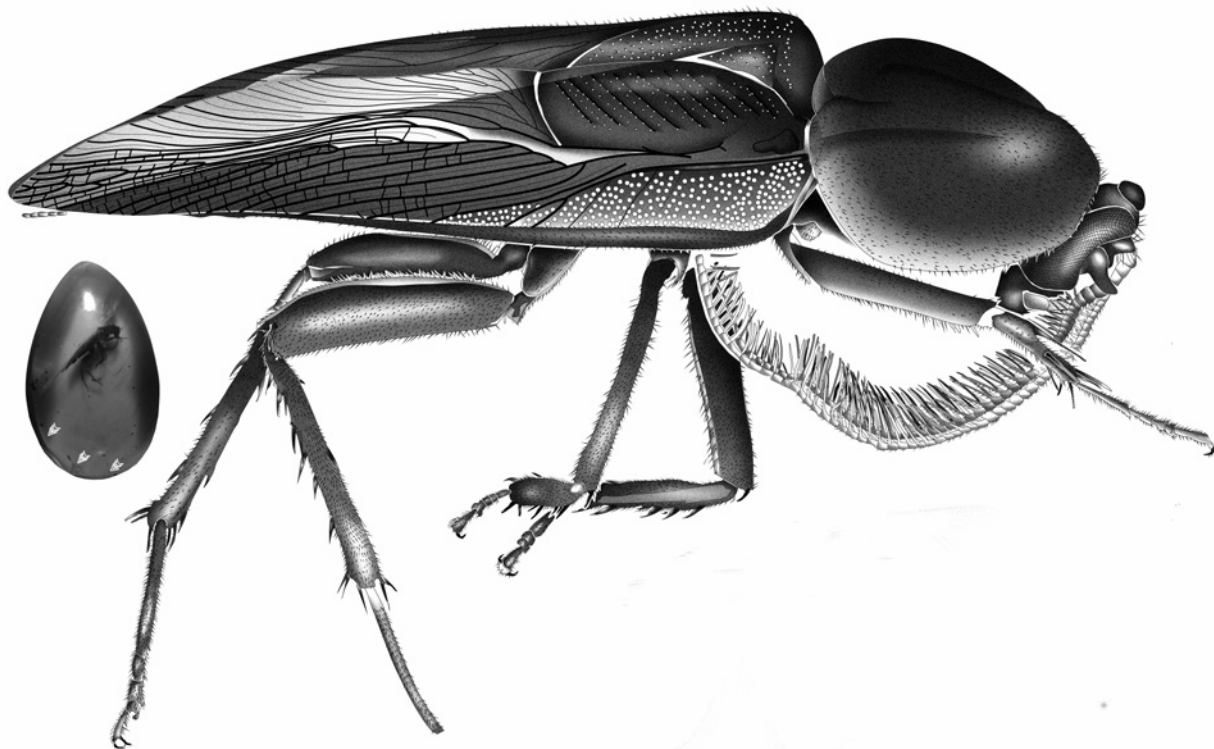


Fig. 1. A Dinosaur-aged cockroach *Ol xiai* sp. n. from Myanmar amber, representing the new family Olidae. Note unique bipectinate antenna. Total specimen length 15.7 mm. Original line-drawing. Three triple arrows show amber layers.

Description. As for species.

Differential diagnosis. The representatives of the family differ from most cockroaches in reduced femoral spine, extremely elongated medial foretibial spur and bipectinate antennae. It differs from the stem family Blattidae in having lateral ocelli covered by “roofs”, pectinate antennae, elongated body, reduction of terminal femoral spine, forewing veins irregularly spaced forming an area between R and M/CuA/CuP, irregular sclerotisation and in having a distinct scutellum.

***Ol* gen. n.** (Figs 1, 2)

Type species. *Ol xiai* sp. n., by monotypy.

Description. As for species.

Derivation of name: after *ol* (Santali language for writing). This combination of letters also alluded to typing of zero and one (01) which is a common abbreviation for optical lithography. Gender masculine.

Differential diagnosis. None due to monotypy. Suggested generic characters are lateral extensions on antenna; long, oval terminal palpomere, very narrow body and wings and only slightly irregular venation.

***Ol xiai* sp. n.**

Description. Medium-size, strongly sclerotised, entirely black cockroach (very large among those preserved in Myanmar amber) with overall body length 15.7 mm (as preserved) (Figs 1, 2A).

Head with very strong layer of chitin, hard and melanised, dark black, hypognathous, elongated

(length/width ca. 1.6/2.7 mm), ca. 2.5 mm deep. Eyes comparatively narrow, only slightly protruding beyond head outline. Lateral ocellus lentiform medium-size round covered with distinct roof-like sheaths. Central ocellus invisible. Labial palps not observed, maxillary palps extremely short (together all 4 or 5 segments ca. 0.7 mm long) with terminal palpomere rounded ca. 0.2 mm in diameter. Antenna short (only about a half body length), bipectinate, with ca. 60 segments (Fig. 2F). Base of each segment (maximum length 0.17 mm) somewhat widened anteriorly. Width of flagellum base max. 0.083 mm. Two, max. 0.95 mm long and 0.039 mm wide (shorter towards apex), movable extensions on each (except basal 4 segments) of the antennomere. Some extensions have lateral secondary, extremely small (0.052 mm) up to six spines on each side, probably representing sensillae. Scape (highly specialized, allowing antenna to fold down), pedicel (undifferentiated) and a basal antennomere without extensions. Neck short (not as long as in *Manipulator*).

Pronotum nearly transversal, with indistinct paranaotolia (4.4/ca. 3 mm), black, hard, sclerotized and melanised, densely covered with extremely short but strong and apparently colored (black) sensilla chaetica. Scutellum very distinct, long and wide (ca. 2/ca. 1.7 mm).

Forewing moderately elongated (12.5/ca. 5 mm), strongly modified, sclerotised in the basal part including most of the clavus. Veins standardly thick, intercalaries diverse (as wide as main veins in the radial area, less distinct in medial field). Two deformities (sensu Vršanský 2005; Vršanský et al. 2017) occur: a fusion

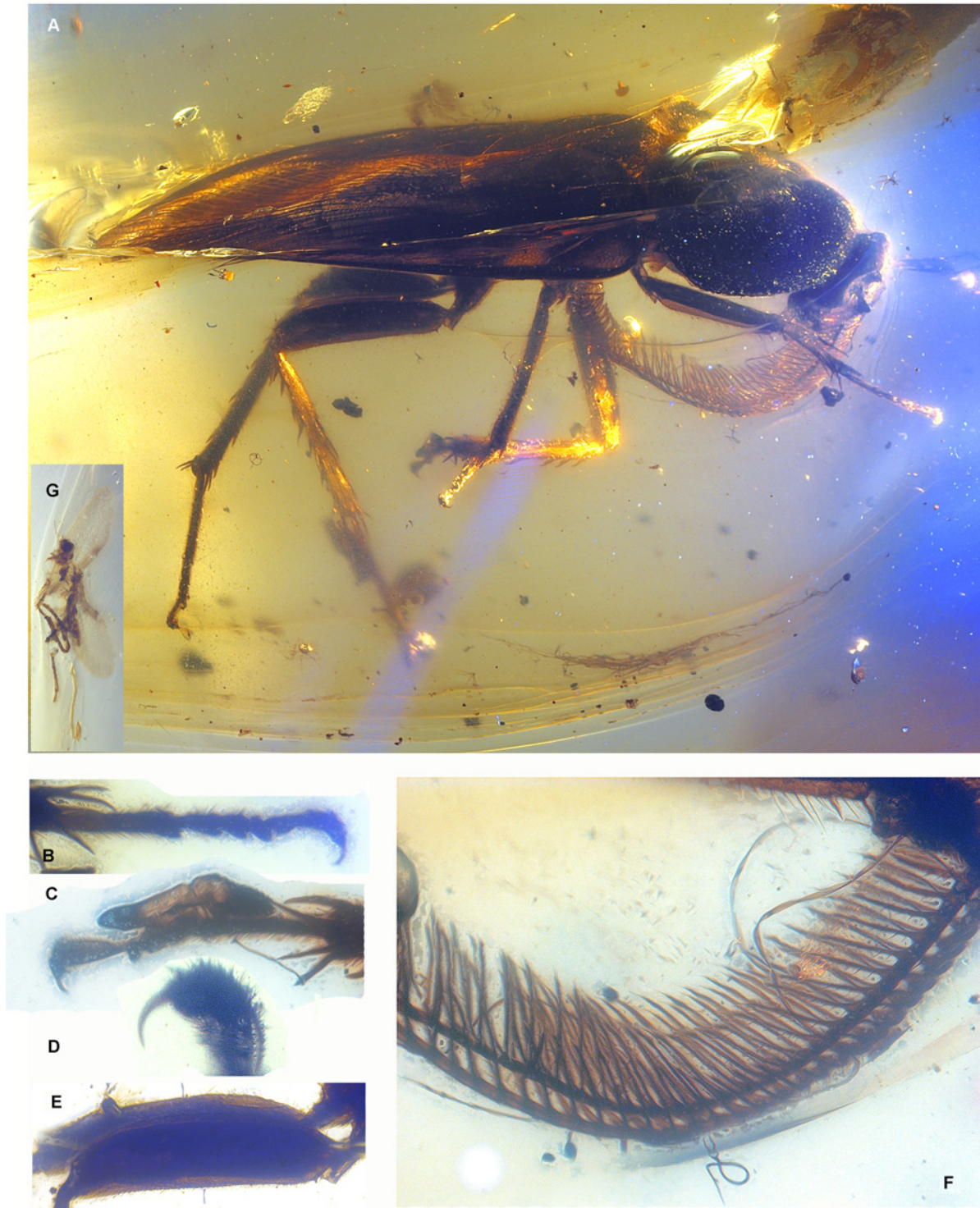


Fig. 2. A Dinosaur-aged cockroach *Ol xiai* sp. n. from Myanmar amber, representing the new family Olidae. A: Right lateral view on complete specimen – 15.7 mm long; B: Fore tarsus 1.95 mm long; C: A phoretic mite attached to right hind tarsus – 1.67 mm; D: Left middle claw 0.2 mm wide; E: hind femora L3.50–R3.53 mm long; F: bipectinate antennae with lateral extensions up to 0.95 mm long; G: Male coccid as syninclusion overall length including penis 2 mm.

of RS branch to another RS branch near wing apex and fusion of Medial branch to another M branch at the same dichotomisation system, near wing center. Cross-veins common. Costal area with cup like tubercles and holes resembling (but not identical, cups are incompletely formed such like in *Diplopteridae* – see

Anisyutkin 2007; Li & Wang 2015; Vrřanský et al. 2016) to *bunky* of *Umenocoleidae* (see also Lee 2016). Costa extremely strong, ca. 0.2 mm wide in the widest point near basis. Costal area wide (ca. 1.2 mm), Sc thus short and dichotomized with 5 veins meeting margin (some side branches reticulating rather than dichotomizing).

R with RS reaching apex, covering nearly a half of the wings width. R1 broken, forming unsclerotised area between R and M/CuA/CuP, with 6 simple and long, nearly straight veins; RS is branched to both sides of the stem, with 10 veins at margin. Distances among R1 veins regular, RS irregular (dense venation, with one vein fusion as a deformity). Media regular, with extremely long, nearly straight simple branches (7 meet margin, also with one vein fusion). CuA again irregular, with two main stems, amounting to 12 veins at margin. CuP sharply cut with irregular area forming an unsclerotised abovementioned area. Anal veins simple, visible as rough punctuation in a completely hardened clavus; nearly identical structures represent intercalaries. Hindwing membranous, transparent, fully developed, subequal to forewing in length (terminate at the same position, forewing is thus slightly longer), membranous, transparent.

Legs cursorial, very strongly sclerotised, densely covered with sensilla and modified surface (sclerotised punctuation). Carination dense, spurs very short. All three pairs of coxae free, ?/1.32/1.8 mm long and comparatively strong. Fore trochanter free, nearly 1 mm long. Fore femur (length/width 2.62/0.54 mm) with two subterminal short spines (right one, the left one possess a series of extremely short, rudimentary, but wide spines), tibia short (1.59/0.22 mm) with about 10 up to 0.45 mm long spurs. One additional unique, huge spur (0.9 mm long) is also present. Tarsi 5-segmented (0.88/0.3/0.22/0.18/0.55 mm), totally 1.95 mm long and 0.16 mm wide (Fig. 2B). Claw symmetrical, strong, 0.23 mm long, arolium only about 0.15 mm in diameter, minute pulvilli also present. Mid coxa strong, 1.32 mm long, trochanter comparatively short (1.04 mm), mid femur without spurs, tibia (R2.96 – L3.39 mm) strongly carinated with short (0.36 mm) spines. Mid tarsi very short and wide (1.67/0.14 mm). Terminal tarsomere 0.48 mm long, claw 0.2 mm long (Fig. 2D). Hind trochanter long (0.61 mm) and wide. Hind femur moderate (3.50/1.00 mm), without carination (Fig. 2E). Terminal spine nearly completely reduced. Hind tibia long and strong 1.59/0.22 mm), left tarsi long (tarsomeres 1–5 length 1.63 – 0.34 – 0.29 – 0.26 – 0.66 mm) but narrow (length/width 2.98/0.19 mm), with pulvilli modified into hook-like extensions. *Itts*-region not observed, although tarsi are visible.

Body long and thin, completely overlapped with the wings. Cerci with 11 segments, long (1.7 mm), basal cercomeres long (ca. 0.4 mm), two terminal cercomeres very short. Cercal sensilla numerous but short from below (dorsal side not observable). Two styli symmetrical, long, located close to each other (measurements are unavailable), unsegmented.

Holotype. A complete adult male. **Type locality.** Hukawng, Myanmar. **Type horizon.** Cenomanian Upper Cretaceous.

Derivation of name. After Fangyuan Xia, who makes huge effort for promoting science on Myanmar amber.

Character of preservation. A complete adult (one of about 4,000 collected Myanmar amber cockroach individuals).

Phylogenetically annotated character list:

- Head hypognathous – **plesiomorphy** (at the level of order Blattaria)
- Eyes large – **plesiomorphy** (at the level of order Blattaria)
- Lateral ocelli present – **plesiomorphy** (at the level of order Blattaria; in numerous taxa this trait is homoplasically reduced)
- Lateral ocelli with covering sheaths – **autapomorphy** (this unusual trait is homoplasically present in Manipulatoridae)
- Central ocellus absent – **synapomorphy** (absent also in some extinct Blattidae, all extinct Ectobiidae and all living cockroaches)
- Antennae bipectinate – **autapomorphy** (dense spines on antenna are known in some undescribed Myanmar amber cockroaches, and also in living *Pseudothyrocera*, but truly pectinate antenna are unknown apart from the new species)
- Antennae short – **synapomorphy** (shared with Cretaceous ant-nest fixed blattids; in numerous living taxa this trait is homoplasically present)
- Antennal flagellum widened – **synapomorphy** (with an undescribed Blattidae from the Myanmar amber)
- Maxillary palps short, with terminal palpomere modified to a round flat disk – **autapomorphy**
- Labial palps either entirely reduced or detached – **unknown**
- Neck not extremely elongated – **plesiomorphy** (at the level of order Blattaria; extremely long neck is autapomorphy of *Manipulator*)
- Pronotum transversal – **plesiomorphy** (at the level of order Blattaria; elongated pronotum rarely occurs in advanced Late Carboniferous cockroaches, and also in primitive blattids such as in *Protagonista*)
- Pronotum densely setose – **synapomorphy** (with Cretaceous ant-nest associated blattids; this character frequently occurs in living Polyphagidae)
- Pronotum trichiae shorter than antennal width – **autapomorphy** (perhaps reduced)
- Pronotum basally with roof-like extension – probably **autapomorphy** (this character occurs widely among living cockroaches)
- Paranotalia present – **plesiomorphy** (at the level of order Blattaria)
- Scutellum present – **autapomorphy** (this trait appears homoplasically in most taxa that have hardened forewings)
- Forewings overlapping – **plesiomorphy** (at the level of order Blattaria, homoplasically this trait is frequently reduced)
- Left FW is under – **undiagnostic form**
- Vein deformities present among two RS veins and within M veins – **undiagnostic displays of a temporary deleterious mutation**
- Folding sutura visible (left forewing) – **autapomorphy**

- phy** (homoplastic throughout the numerous representatives of the order with hardened wings)
- FW shape with sigmoidal curvature – **autapomorphy** (derived shape of more or less normally developed forewing is unknown in Mesozoic cockroaches and mantodeans and is characteristic for advanced cockroaches and mantodeans, simple oval shape predominates)
 - Distance between veins is not constant – **autapomorphy** (this character is plesiomorphic at the level of the order and characteristic for Palaeozoic cockroaches, but here it is an apparent autapomorphy as this character is not present in any post-Triassic group except for relic *Irreblattia*; homoplasically also frequently occurs in modified living cockroaches and Mantodeans)
 - FW locally (clavus and basal part of the cubital, medial and partially in costal areas) fully sclerotised – **autapomorphy** (homoplasically occurs in numerous cockroach lineages, but in known fossil representatives the forewing, where sclerotised is sclerotised totally – see Umenocoleoidea)
 - FW Costa wide – **autapomorphy** (homoplasically present in all Umenocoleoidea except *Jantaropterix* and *Cratovitisma*)
 - FW costal area with deep cup-like punctuation – **autapomorphy** (homoplasically frequently present in living lineages of Blattidae, Blaberidae and Corydiidae)
 - FW Sc short – **plesiomorphy** (at the level of “*Voltziablatta*-group”; this character is modified in all described Liberiblattinidae as elongated, but some derived Liberiblattinidae have it short – this character disqualifies Liberiblattinidae as a possible stem)
 - FW Sc wide – **plesiomorphy** (at the level of earliest Mesoblattinidae)
 - FW Sc branched – **plesiomorphy** (at the level of order Blattaria)
 - FW R sigmoidally curved – **plesiomorphy** (at the level of Phylloblattidae)
 - FW R broken, forming along with broken clavus an irregular unsclerotised area between these two systems and M – **autapomorphy**
 - FW R branches simple – **synapomorphy** (with Mesozoic Blattidae)
 - FW RS differentiated – **plesiomorphy** (at the level of order)
 - FW RS branched to both sides – **autapomorphy** (this character frequently occur in living cockroaches and also mantises, but is unknown in any Mesozoic group)
 - FW M rich – **plesiomorphy** (at the level of order)
 - FW M branches long and straight – **synapomorphy** (with early Blattidae, homoplasically commonly occurring in all living cockroach lineages)
 - FW CuA divided into 2 main branches – **plesiomorphy** (at the level of Liberiblattinidae)
 - FW CuA richly branched – **plesiomorphy** (at the level of order)
 - FW clavus nearly whole completely sclerotized on both tegmina – **autapomorphy** (a separate control of sclerotisation of a part of the wing is present only in one wing on the overlapped side of some living cockroaches)
 - FW A formed as tuberculate punctuations – **autapomorphy** (this character homoplasically occurs in Cenozoic *Morphna*)
 - FW A simple – **plesiomorphy** (at the level of advanced Mesoblattinidae, i.e. also in earliest Blattidae and Ectobiidae)
 - Legs cursorial – **plesiomorphy** (at the level of order Blattaria)
 - General composition of legs (numerous characters, free coxae, strong femur with few spines, carinated tibia, 5-segmented tarsi) characteristic for cockroaches – **plesiomorphies** (at the level of order Blattaria)
 - Terminal femoral spur (all pairs) nearly entirely reduced – **autapomorphy**
 - Huge foretibial spur present – **autapomorphy**
 - Pulvilli present – **synapomorphy** (at the level of earliest Liberiblattinidae and all living cockroaches, mantises and termites; homoplasically this trait is reducing in numerous taxa)
 - Hind pulvilli with extensions – **autapomorphy**
 - Hind pulvillus extension of 4th tarsomere hooked – **autapomorphy**
 - *Itt sclerite* absent – **autapomorphy** (unless just un-preserved or invisible)
 - Arolium present – **synapomorphy** (or Liberiblattinidae and all modern cockroaches, with frequent exceptions of reduction)
 - Arolium small – **synapomorphy** with earliest known Blattidae (*Balatronis*)
 - Body very narrow – **synapomorphy** with undescribed Cretaceous ant-nest fixed blattids
 - Abdomen with distinct and regular segmentation – **plesiomorphy** (at the level of order Blattaria)
 - Cerci long – **plesiomorphy** (at the level of order Blattaria)
 - Cerci 11-segmented (cerci with few segments, like 11 are symplesiomorphic at the level of Mesoblattinidae, but this character is homoplastic also in certain Umenocoleidae and Alienopteridae, down to 7 segments)
 - First cercomere very long – **autapomorphic** (this trait homoplasically occur among representatives of Umenocoleoidea, in some undescribed extinct Mantodea, but not in their relatives Eadiidae, Manipulatoridae and directly ancestral liberiblattinid genera)
 - Very long cerci – **synapomorphic** with Blattidae (homoplasically in *Jantaropterix* and Nocticolidae)
 - Cercal sensillae rather short also from ventral side – **plesiomorphy** (at the level of order Blattaria)
 - Styli present – **plesiomorphy** (at the level of order Blattaria; in living cockroaches this trait is frequently homoplasically lost or reduced on one of both sides)
 - Styli unsegmented **autapomorphy** (this trait homoplasically occurs along taxonomical spectrum, but styli of extinct cockroaches were segmented)

- Styli 2 – **synapomorphy** (at the level of Mesoblattinidae)
- Styli symmetrical – **plesiomorphy** (at the level of order Blattaria, in living cockroaches, styli are frequently asymmetrical)

Discussion

The type specimen was preserved in a rather large piece of amber (5.5/3.2/1.5 mm), making evaluation of specimen difficult which was further hampered by the amber's yellow to yellow-orange hue. Three distinct, about 10 mm thick, perpendicular to the major axis layers within the amber piece suggest the amber was situated for a considerable time on the tree trunk before it hardened and originally was a part of a big resin piece. The amber is clear and contains almost no other inclusions, only seed particles, a phoretic mite (1.5 mm long) (Fig. 2C) and a male coccid (Fig. 1G, ecologically insignificant).

The combination of fully developed hindwing and forewing with cross-veins indicates that individuals used flight several times during their life.

Systematical remarks. Although the species is highly derived with some unique character states, it can be categorized within the Dictyoptera based on its hypognathous head, flagellate antenna, pronotum with parnotalia, forewing with characteristic venation (short Sc, comb-like R+RS, M and CuA branched, CuP forming clavus with A), carinated legs, 5-segmented tarsi and multisegmented cerci. A distinct clavus, terminal femoral spine and a hypognathous head are order-specific though some cockroaches have secondarily lost the hypognathous head condition. It can be further included in Blattoidea on the basis of hindwing veer-like pleating. We treat this superfamily here as containing stem Mesoblattinidae Handlirsh, 1906 and also their other descendants, Ectobiidae (relation of these 3 families is now under consideration) and also Blaberidae (independently descending directly from Mesoblattinidae).

The taxon shares characters with some derived, parasitic Cretaceous Blattidae, notably the setated pronotum, narrow body and venation characters (distinct coloured cross-veins, long branches, branched Sc – this character is frequent in living cockroaches but is absent in fossil forms). Cercus is characteristic also for primitive Mesoblattinidae (usually 9 or 10 segments, see Wei & Ren 2013), which is nevertheless, most probably a regress or adaptation related to perception (antenna is also strongly modified). Nevertheless, also the ancient Blattidae have this type of cercus with about 11 segments (while the basal cercomere is unique). Styli are also characteristic for Blattidae. Forewing with extremely long and more or less straight branches is typical for the early Blattidae while sclerotisation is unique. Derivation directly from Blattidae and not from Mesoblattinidae is suggested with the structure of the costal area with punctuation and

rather richly branched Sc with untrue branches (reticulating). Also the widened campaniform bases of flagellum are present exclusively in some undescribed Cretaceous Blattidae currently under evaluation.

Morphologically, the bipectinate antennae, nearly entirely reduced terminal femoral spurs, reduced palp and round terminal palpomere, very long forefemoral spine and sclerotised clavus/near-clavus area are unique autapomorphies (without homoplasies). Short antennae, narrow body and dense setation of pronotum and some other parts are symplesiomorphies with undescribed ant-nest fixed Cretaceous blattids (these characters were absent in Mesozoic forms).

Combination of these states allowed us to erect a new family and derive it directly from the Early Cretaceous Blattidae (within Blattoidea). While it is hardly possible to specify the origin time of the new family, it is clear that it happened coevally or after origin of the Blattidae probably in the Early Cretaceous. Due to recent proof for the in-cycles origination of cockroach major and aberrant taxa, it is very probable that the origination time corresponds to the K1 origination peak (see Vršanský et al. 2017) at 126–128 Ma. Nevertheless, prove for this group is absent prior to K2, although similar pre-adaptations are known in an undescribed blattid from Early Cretaceous Syrian amber. Several characters are obscurely found reduced (narrow body, short antenna, short palps, setation of pronotum, chaetica on forewings, terminal femoral spine).

Ecologically, the species was apparently rare in the amber forest source area and also no nymphs displaying antennal or other morphology have been found. Rare preservation does not automatically mean their actual rarity, nevertheless, the comparative sample size (about 4,000 collected cockroaches in Myanmar amber) might present an indication. Specimen was preserved in a large pieces of amber which likely means the source area was a near-shore amber producing forest (close to post-fluvial deposition). Although no definitive conclusions can be made, it is probably that the species was ecologically associated with ants, as the source of the family were the ancient Blattidae, all of them found to be related directly to ants including true ant parasites or indirectly as *Balatronis* with aposematic coloration related to ant alert allomones (Šmídová & Lei 2017; Sendi & Azar 2017). This is supported with narrow body, short antenna and also dense setation of the pronotum and legs, all as strong plesiomorphies at the level of earliest blattids from Myanmar amber (while hard sclerotisation including legs is autapomorphic, but possibly also related to protection against ants). Interesting is also the attachment of a mite to the left mid tarsus. The presence of this unique morphotype in the Myanmar amber only increases the known disparity between the cockroaches in this past forest, compared to those living in other and current rainforests. The cause for this phenomenon is unknown. Some authors, for example Szwedó (2009), on the basis of herbivores, link these differences to the differentiated dendroflora of the ancient forest which was not dominated by angiosperm.

The occurrence of extremely derived cockroaches outside Burmite is unknown. Apart from the diversity, this fauna display far more bizarre cockroach forms than in all living rainforest cockroach faunas taken together. In addition to the aberrant new species Burmite includes strange predatory forms in 6 separate cockroach lineages including true mantodeans (Vršanský & Bechly 2015; Delclos et al. 2016), aberrant pollinators (Bai et al. 2016), beetle-like forms (Ross et al. 2010), possibly poisonous species (Šmídová & Lei 2017), still undescribed mole-like species as well as eusocial cockroaches. Bizarre forms were present also in other insect orders, such as dancing damselfly (Zheng et al., 2017), caddisfly with bipectinate antennae (Wichard & Wang 2017), and unicorn ants (Perrichot et al. 2016).

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