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## Maternal care by Early Cretaceous cockroaches

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Most cockroaches produce a special capsular structure, the ootheca, to enclose eggs for protection and maternal brood care. However, the origin and early evolution of the cockroach ootheca is poorly known, attributable to a lack of fossil evidence from the Mesozoic. Here, we report the earliest known cockroach fossil possessing an internally partitioned ootheca: *Piniblattella yixianensis* Gao, Shih & Ren sp. nov. is described from the mid Early Cretaceous Yixian Formation of China. The ootheca of this species measures 46–62% of its body length, contains 60–70 eggs, and exhibits the oviparity B reproduction mode, similar to that of the extant ectobiid and blattid cockroaches. In conjunction with several isolated ootheca specimens preserved in the mid-Cretaceous Myanmar amber (Burmite), we infer that the cockroach reproductive mode using the complete oothecate structure occurred during or before the mid Early Cretaceous. Maternal care associated with the oothecate condition in these Cretaceous cockroaches added a unique and major life-history trait, later resulting in true viviparity. This new life-history trait providing maternal protection and care may have been a key factor in the subsequent evolutionary diversification and ecological expansion of modern cockroach lineages.

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**Keywords:** oviparity; Dictyoptera; Blattaria; Isoptera; Mantodea; *Piniblattella*

### Introduction

Parental care is a beneficial behaviour adopted by many extant animals that augments growth rates and is associated with enhanced offspring survival (Lukas 2013; Vršanský *et al.* 2016). Insects employ several methods to protect their young (Suzuki 2013), such as provisioning food for immatures, hiding or covering eggs before abandonment, and guarding eggs after oviposition. A few recent studies have documented the role of parental care in the insect fossil record. For example, Peñalver *et al.* (2012) reported two species of pollinating thrips from Early Cretaceous amber of Spain that could be an example of early parental care. Cai *et al.* (2014) concluded that carcass-burying carrion beetles from the Middle Jurassic of China were comparable to taxa from earliest Cenomanian Myanmar amber (Burmite) as early examples of elaborate biparental care in insects. Wang *et al.* (2015) documented, also from Myanmar amber, fossil evidence for brood care provided by a scale-insect species. Although various levels of biparental and uniparental care were present among

several insect lineages during the Early Cretaceous and probably earlier (Poinar & Danforth 2006; Barden & Grimaldi 2016; Engel *et al.* 2016), virtually nothing is known of such behaviour among cockroach taxa during this time interval. Cockroaches with oothecae were postulated to have originated in the Early Jurassic (Vršanský *et al.* 2002a; Vršanský & Ansoerge 2007; Barna 2014). Additionally, the origin of parental care in cockroaches is an important issue because comparisons of cockroach parental behaviour have been made with the closely related termites or Isoptera (Nalepa & Lenz 2000; Djernæs *et al.* 2015). However, recent evidence indicates that Isoptera are a derived clade within the eusocial cockroaches (Inward *et al.* 2007; Vršanský 2010), suggesting that the more basally positioned cockroach clade of interest here, Ectobiidae, evolved parental care independent of and earlier than Isoptera.

Dictyoptera (Martynov 1925; Hennig 1981) is a super-order comprising conventionally the three insect orders of Blattodea (cockroaches), Mantodea (mantids) and Isoptera (termites) (Misof *et al.* 2014; Djernæs *et al.* 2015;

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but see Inward *et al.* 2007 for an alternative view). Most extant cockroach and mantid taxa produce a special egg-capsule structure, commonly called the ootheca, to enclose their eggs (Gullan & Cranston 2014). Mantid females lay eggs surrounded by a frothy foam which hardens into a leathery case that also is called an ootheca. By contrast, cockroaches produce a relatively hardened ootheca that extends posteriorly from abdominal terminalia encasing two rows of elongate, ovate eggs (McKittrick 1964; Roth 1970) (Fig. 1J). The similar structure of oothecae occurring in two orders of Dictyoptera is considered to be homologous by many (Nalepa & Lenz 2000). Structurally, the cockroach ootheca is an egg-containing capsule that is tanned and leathery in consistency, and contains internal partitions between eggs that are represented externally as furrowed linear depressions on the oothecal surface ending at the lateral oothecal margin to form a distinctive keel (Roth 1968; Bell 1981; Bell *et al.* 2007). Oothecae of cockroaches and mantids provide protection for eggs and offspring involved in predator avoidance and are able to survive under inclement environmental conditions until first-instar nymphs establish independent life habits (Roth & Willis 1957; Roth 1970, 2003; Bell *et al.* 2007).

The origin and early evolution of cockroach oothecae remain poorly known, as oothecae are rarely preserved in the fossil record, including deposits of Cenozoic age (Vršanský 1999a). Grimaldi & Engel (2005) illustrated an ectobiid cockroach that bore an ootheca lodged in its abdominal terminalia, from the Lower Cretaceous Crato Formation of Brazil, dated at ~115 Ma (Martill & Heimhofer 2007; Barling *et al.* 2015). Hörnig *et al.* (2013) presented photographs of two cockroach fossils with evident oothecate structures, also recovered from the Crato Formation. These three Brazilian specimens are presently the earliest definite record of fossil oothecae, although they have not been formally described or placed in their taxonomic contexts. Later, Lee (2016) described 981 specimens of fossil cockroaches from the Crato Formation, and assigned them to 11 taxa. The aforementioned fossil cockroaches with oothecae from the Crato locality should be *Piniblattella limai* (Pinto & Purper 1986; Lee 2016). Several obscure fossils reported from Palaeozoic deposits were presumed to be oothecae, but these occurrences are now considered fragments of other organisms (Sellards 1904; Rasnitsyn & Quicke 2002). A few fossils of potential mantid oothecae have been reported from mid-Cretaceous (earliest Cenomanian) Myanmar amber (Grimaldi *et al.* 2002). Several other isolated possible cockroach oothecae have been mentioned from the Late Cretaceous Coniacian stage, ~88 Ma, of Kyzyl-Kum in Central Asia (Nessov 1995; Rasnitsyn & Quicke 2002), the lower–middle Eocene (~48 Ma) Green River Formation of Wyoming, USA (Brown 1957), the middle Eocene

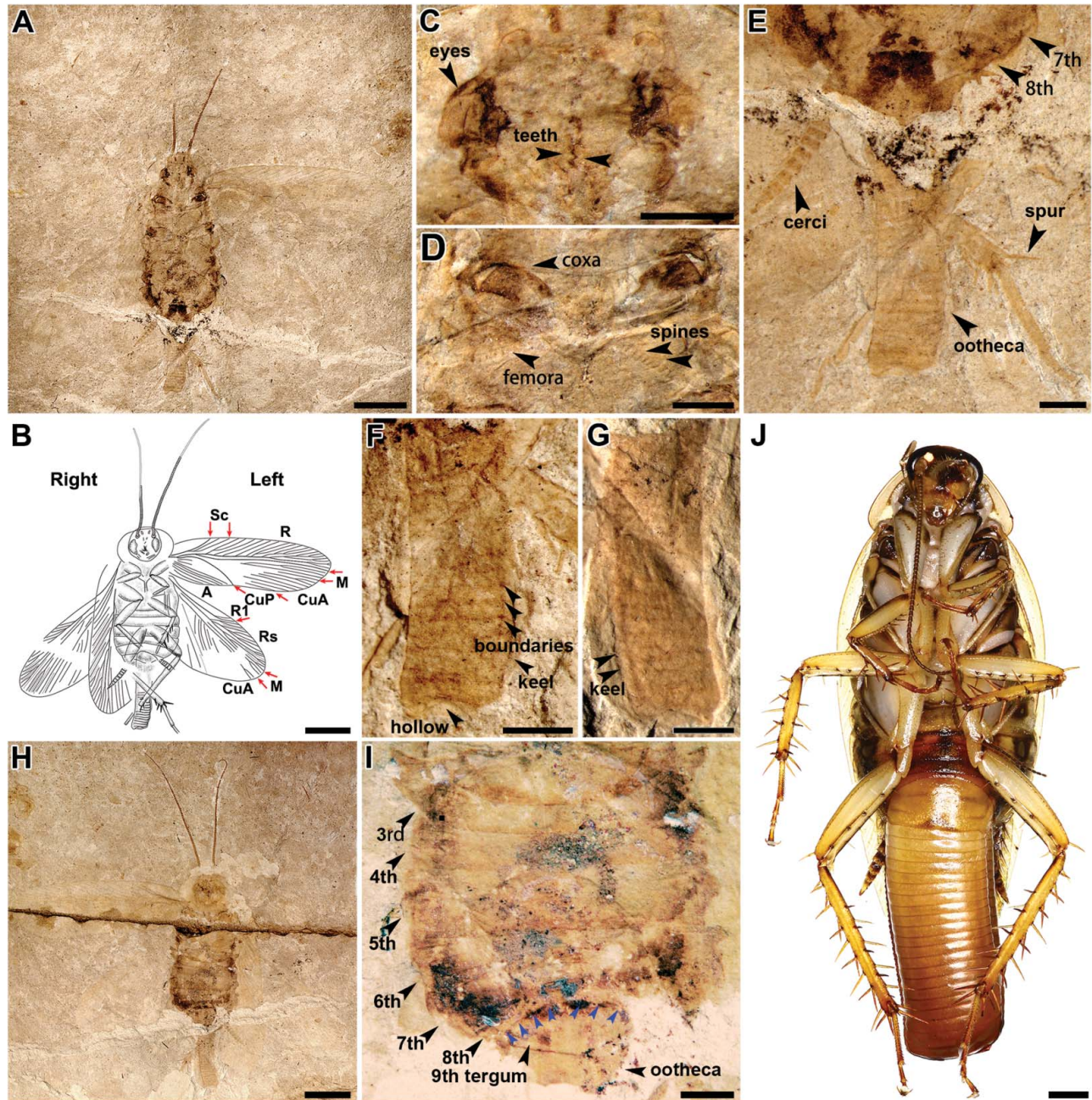
(~47 Ma) Geiseltal of Messel, Germany (Haupt 1956), and the late Eocene Bembridge Marls of the Isle of Wight, UK (Anisyutkin *et al.* 2008; Ross & Self 2014).

Here, we describe *Piniblattella yixianensis* Gao, Shih & Ren sp. nov., based on six oothecate cockroach specimens from the mid Early Cretaceous Yixian Formation, latest Barremian (125 Ma), at the Huangbanjigou locality near Beipiao City, Liaoning Province, north-eastern China (Swisher *et al.* 1999; Zhou *et al.* 2003). After an examination of about 5000 fossil cockroach specimens from this locality housed at the Capital Normal University, six specimens were identified with oothecae. In addition, seven similar but isolated amber cockroach oothecae were collected from the earliest Cenomanian,  $98.79 \pm 0.62$  Ma, Myanmar amber (Shi *et al.* 2012; Cohen *et al.* 2013; Ross 2015), located at the northern limits of Noije Bum village, south-west of the town of Tanai in the Hukawng Valley, Kachin Province, northern Myanmar (Cruickshank & Ko 2003). The oothecae from these two localities greatly increase the breadth of morphological characters available and enhance understanding of the Mesozoic evolution of cockroach reproduction and maternal care.

## Material and methods

All fossil cockroach specimens with oothecae from compression deposits described in this report were collected from the Yixian Formation at Huangbanjigou Village, near Beipiao City, western Liaoning Province, north-eastern China. The age of this locality is dated as  $124.6 \pm 0.1$  Ma (Swisher *et al.* 1999; Zhou *et al.* 2003), equivalent to the latest Barremian Stage of the mid Early Cretaceous (Zhou *et al.* 2003). The Jehol Biota is noted for its exceptional preservation of diverse plants, pterosaurs, dinosaurs, birds and mammals, and its rich fauna of diverse insects (Chang 2008; Ren *et al.* 2010). Palaeoenvironmental reconstructions of the Yixian Formation based on stratigraphical and sedimentological analyses indicate the dominance of extensive freshwater lacustrine deposits that lack known fluvial and deltaic sediments (Sun *et al.* 1998).

Specimens from Myanmar amber that bear isolated oothecae originated from deposits associated with lignite deposits. The Myanmar amber locality is located at the north end of the village of Noije Bum (approximately  $26^{\circ}15'N$ ,  $96^{\circ}34'E$ ), about 18 kilometres south-west of the town of Tanai in the Hukawng Valley of Kachin Province, northern Myanmar (Cruickshank & Ko 2003). The age of Myanmar amber is considered to be  $98.79 \pm 0.62$  Ma (earliest Cenomanian), close to the Early–Late Cretaceous boundary (Shi *et al.* 2012; Ross 2015).



**Figure 1.** Holotype of *Piniblattella yixianensis* Gao, Shih & Ren sp. nov., CNU-BLA-LB2013800p/c (part and counterpart), from the Lower Cretaceous Yixian Formation of north-eastern China. **A**, habitus of the specimen (part slab) in ventral view; **B**, overlay line drawing of **A**; **C**, head; **D**, forelegs; **E**, terminalia; **F**, ootheca; **G**, ootheca of the specimen (counterpart slab), under direct, oblique lighting from the right; **H**, habitus of the specimen (counterpart slab) in dorsal view; **I**, abdominal part of **H**; the blue arrows show the connecting position between ootheca and abdomen; the abdominal segments from 3<sup>rd</sup> to 8<sup>th</sup> are indicated; **J**, extant cockroach, *Blattella bisignata* Wattenwyl, 1893, in ventral view, with ootheca showing a typical oviparity B mode of reproduction. Scale bars: A, B, H = 4 mm; C–G, I, J = 1 mm.

All materials described in this paper are housed in the Key Lab of Insect Evolution and Environmental Changes, College of Life Sciences, Capital Normal University, Beijing, China (CNU). The specimens were examined under a Leica MZ 16.5 dissecting microscope, and photographs

were taken with a digital camera system connected to this microscope. In some compression specimens, ethanol (95%) was applied to wet the specimen surface to improve photographic clarity and contrast. Line drawings were prepared using CorelDraw X7 and Adobe Photoshop CC 2015.

## Systematic palaeontology

Order **Blattaria** Latreille, 1810

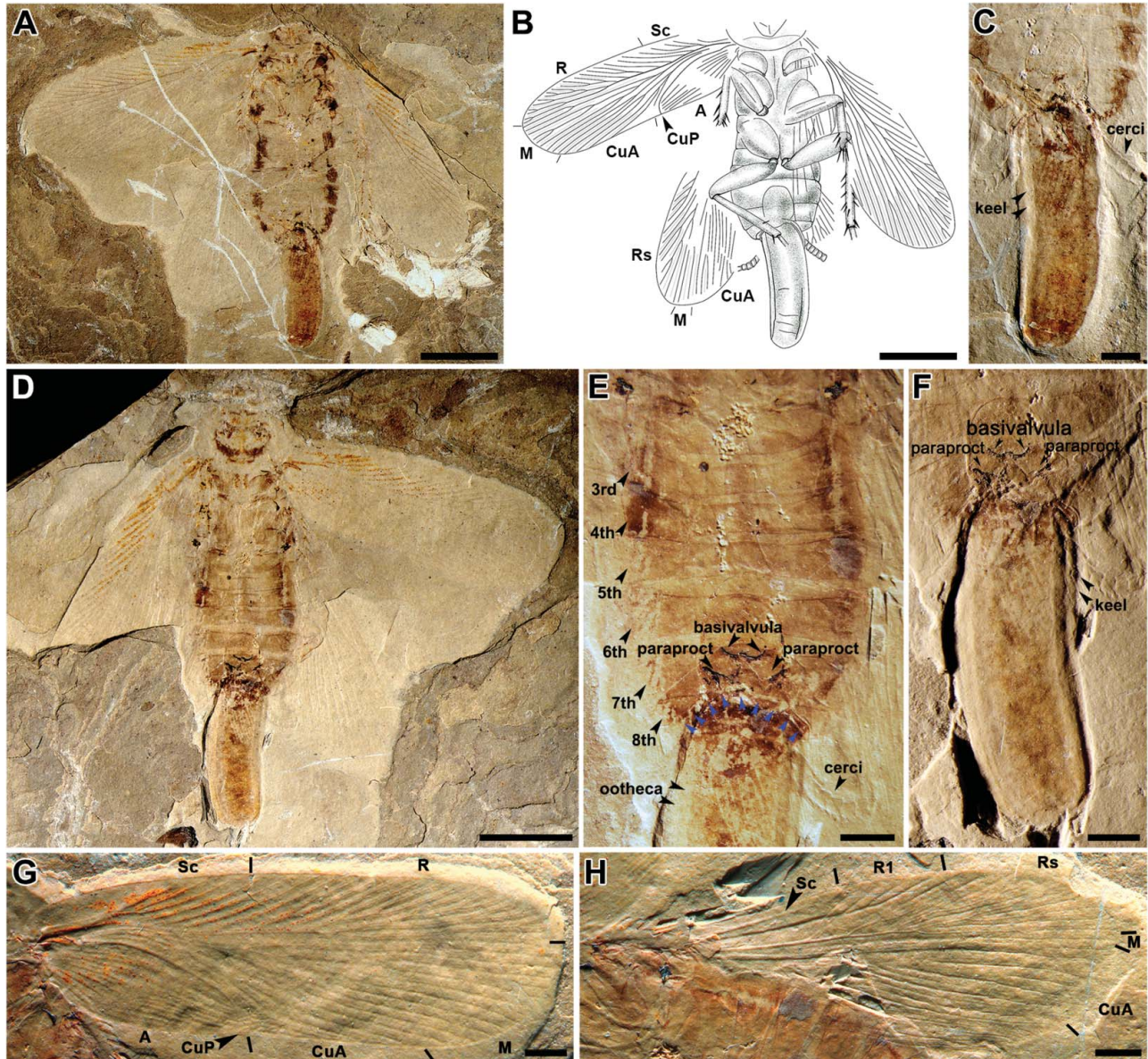
Family **Ectobiidae** Brunner von Wattenwyl, 1865

Genus ***Piniblattella*** Vršanský, 1997

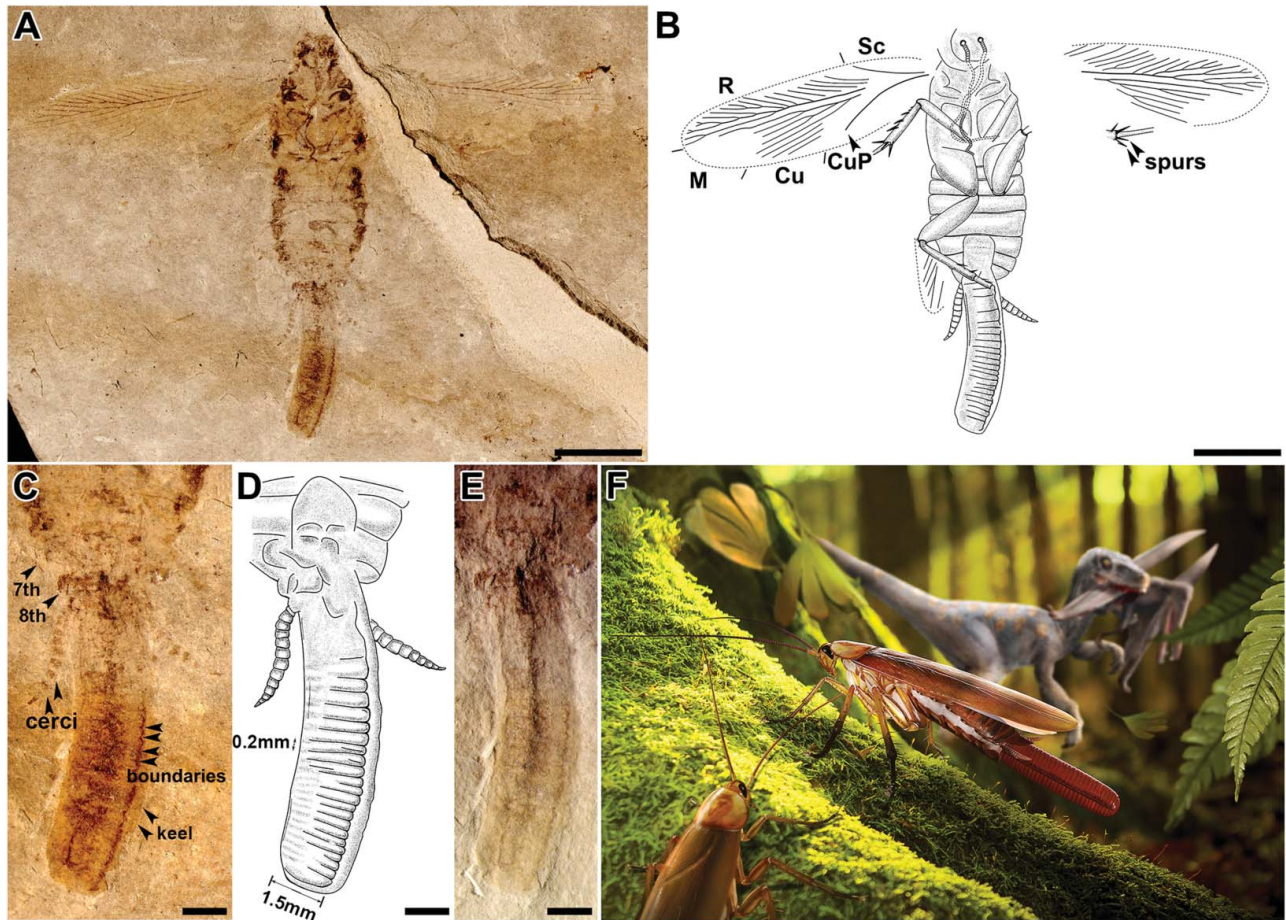
***Piniblattella yixianensis*** Gao, Shih & Ren sp. nov.  
(Figs 1–4)

**Diagnosis.** Unlike *Piniblattella vitimica* (Vishniakova, 1964) and *P. minuta* Vršanský, 1997, the new species has

forewings with Sc 3-branched and a lower number of veins (forewing 11–15 mm long, R with 18–19 vein endings, M at most nine-branched and with a total of 33–36 endings from Sc to CuA). Unlike *P. sharingolensis* Vršanský, 2005, known essentially from a hind wing only, the new species has hind wing M straight with a terminal fork (Vršanský 2005). *Piniblattella yixianensis* differs from *P. limai* (Pinto & Purper, 1986) in Sc three-branched and more endings of R in forewing; the latter has Sc bifurcated and R 8–11 branches (Pinto & Purper



**Figure 2.** Paratype of *Piniblattella yixianensis* Gao, Shih & Ren sp. nov., CNU-BLA-LB2013729p/c (part and counterpart), from the Lower Cretaceous Yixian Formation of north-eastern China. **A**, habitus of the specimen (part slab) in ventral view; **B**, overlay line drawing of **A**; **C**, ootheca under direct oblique light from the right; **D**, habitus of the counterpart specimen in dorsal view; **E**, abdominal part of **D**, the blue arrows showing the connecting position between ootheca and abdomen; **F**, ootheca of the counterpart specimen under direct, oblique lighting from the right; the abdominal segments from 3<sup>rd</sup> to 8<sup>th</sup> are indicated; **G**, **H**, forewing and hind wing. Scale bars: **A**, **B**, **D** = 4 mm; **C**, **E**–**H** = 1 mm.



**Figure 3.** Paratype of *Piniblattella yixianensis* Gao, Shih & Ren sp. nov., CNU-BLA-LB2013736, from the Lower Cretaceous Yixian Formation of north-eastern China. **A**, habitus of the paratype specimen in ventral view; **B**, overlay line drawing of **A**; **C**, terminalia of the abdomen of **A**; **D**, overlay line drawing of **C**; **E**, ootheca under direct, oblique lighting from the right; **F**, reconstruction of *P. yixianensis* sp. nov.; artwork by Dr Chen Wang. Scale bars: **A**, **B** = 4 mm; **C**–**E** = 1 mm.

1986; Lee 2016). *Piniblattella yixianensis* can be distinguished from *P. magna* Lee, 2016, by the smaller body size, smaller pronotum and shorter antennae (Lee 2016).

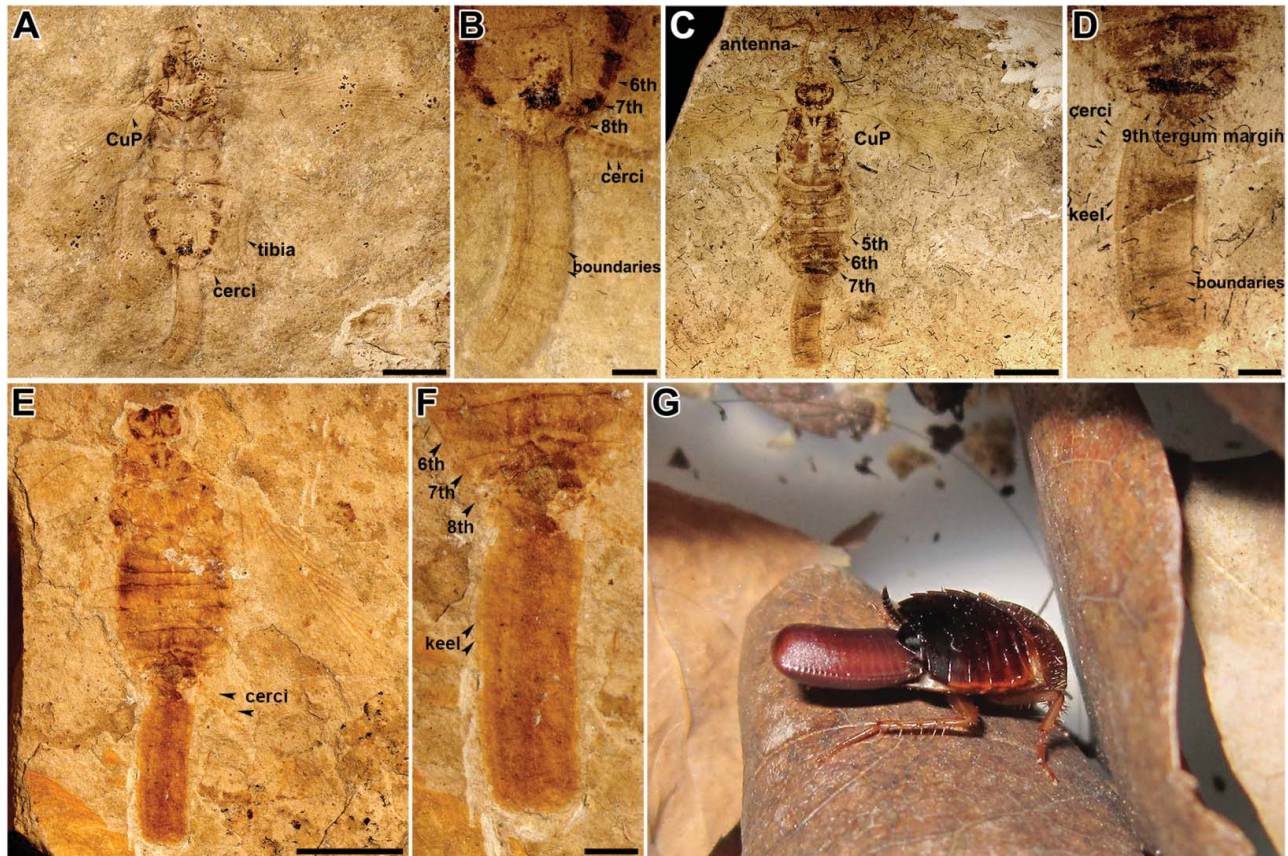
**Derivation of name.** The specific epithet derives from the Yixian Formation.

**Material.** Holotype: CNU-BLA-LB2013800p/c (part and counterpart), female, nearly complete specimen (Fig. 1). Paratypes: CNU-BLA-LB2013729p/c (Fig. 2), CNU-BLA-LB2013736 (Fig. 3), CNU-BLA-LB2013730 (Fig. 4A, B), CNU-BLA-LB2013702 (Fig. 4C, D) and CNU-BLA-LB2013651 (Fig. 4E, F).

**Occurrence.** Yixian Formation, mid Early Cretaceous, latest Barremian, c. 125 Ma (Swisher *et al.* 1999).

**Description. Holotype.** Body length 13.1 mm, excluding ootheca (Fig. 1A, B, H); forewing length 15.0 mm; head round, covered by pronotum (2.9 mm high and 5.0 mm wide), the latter transversely elliptical in shape (wider than long); antenna with over 80 antennomeres

and about 14.0 mm long as preserved (Fig. 1H). Eyes semicircular in shape, three ocelli arranged as equilateral triangle; chewing mouthparts partly visible, mandible with at least three incisors on the right and two visible on the left, with overlapping right and left incisiform teeth (Fig. 1C). The mesonotum and metanotum nearly as wide as pronotum, about 5.0 mm at the widest point and 3.0 mm high together. Legs with coxae not flattened. Foreleg relatively short and thin, front femur (c. 2.11 mm) longer than front coxa (c. 1.63 mm), longer than foretibia (c. 1.35 mm as preserved), bearing only a row of spines on the outside (at least nine visible), spines approximately equal in length (Fig. 1D); spines found on the middle femur (c. 2.90 mm) but absent on hind femur (c. 3.57 mm as preserved), hind tibia (c. 5.68 mm) much longer than middle one (c. 2.64 mm) and possessing several long and stiff spurs around the apex, the longest one measuring nearly 0.8 mm long (Fig. 1A, E). Abdomen with eight identifiable segments in ventral view, the 5th segment widest and the 6th, 7th and 8th segments tapering towards



**Figure 4.** Paratypes of *Piniblattella yixianensis* Gao, Shih & Ren sp. nov., from the Lower Cretaceous Yixian Formation of north-eastern China. **A, B**, CNU-BLA-LB2013730 in ventral view. **C, D**, CNU-BLA-LB2013702 in dorsal view. **E, F**, CNU-BLA-LB2013651 in dorsal view. **G**, natural habitus of an extant cockroach, *Episymphloe* sp., with a conspicuous ootheca. Scale bars: A, C, E = 4 mm; B, D, F = 1 mm.

the terminal of abdomen. The 8th segment very short, wrapping the ootheca so that its posterior margin curves (shown by blue arrows in Fig. 1I), while the posterior margin of the 9th tergum projects as a triangle, covering the ootheca (Fig. 1I) (a similar structure is shown in Fig. 4C, D in CNU-BLA-LB2013702). A pair of cerci (c. 2.13 mm as preserved) extending from the abdominal terminalia above the base of the ootheca (Fig. 1E), with 10 cercomeres, the 5th and 6th cercomeres widest and distally acuminate (Fig. 1E). Forewing with a total of 35 vein endings from Sc to CuA; Sc three-branched; R vein multi-

branched with 19 endings and the basal branches simple; vein M with nine branches reaching the wing margin. CuP strongly curving at the basal part, but relatively straight at the terminus. Hind wing, M straight with a terminal fork (Fig. 1A, B).

Ootheca slightly curved, but basal part invisible due to poor preservation; nearly 5.0 mm in length as preserved (excluding missing basal part) and widest part about 1.5 mm (Table 1). Many transverse sulci indicate the boundaries between eggs, and constitute nearly equal divisions within the ootheca (Fig. 1E–G), the surface

**Table 1.** Ootheca data for cockroach specimens from the mid Lower Cretaceous Yixian Formation of China. Measurements in mm.

Specimen	Body length, minus ootheca	Length of ootheca as preserved	Width of ootheca at widest point	Length ratio of ootheca/body	Length of forewing
CNU-BLA-LB2013800p	13.1	> 5.0 <sup>a</sup>	1.5		15.0
CNU-BLA-LB2013729p	12.3	6.7	2.4	0.55	12.9
CNU-BLA-LB2013736	12.4	7.1	1.9	0.57	12.3
CNU-BLA-LB2013730	13.6	6.3	1.6	0.46	12.2
CNU-BLA-LB2013702	13.4	6.1	2.2	0.46	13.4
CNU-BLA-LB2013651	10.9	6.8	2.0	0.62	–

<sup>a</sup> Ootheca is missing its basal part.

expressions of divisions slightly bending inside and around the left margin, the distance between adjacent lineations about 0.2 mm. An obvious indentation occurs at the distal aspect of the ootheca (Fig. 1F, G).

**Paratypes.** Five paratypes with body 10.9–13.6 mm in length, forewing 11.0–13.0 mm long, ootheca about 6.1–7.1 mm long and 1.6–2.4 mm wide, length ratio of ootheca to body about 0.46–0.62 (Table 1; Figs 2–4). Detailed descriptions of these paratypes are as follows.

CNU-BLA-LB-2013729p/c (Fig. 2). Female, with part (Fig. 2A) and counterpart (Fig. 2D). Head poorly preserved, almost round, 2.5 mm wide by 2.1 mm high, extending beyond the pronotum, with transparent edges, the latter ovoidal in shape; dimensions at least 4.4 mm wide perpendicular to median body axis and 3.0 mm along median body axis. Eyes nearly triangular in shape, three ocelli visible. Thorax without visible details. Legs not clear, femur of the mid-leg about 2.68 mm, that of hind leg about 3.59 mm. The mid-leg tibia (*c.* 2.47 mm as preserved) and hind leg tibia (*c.* 3.83 mm as preserved) covered with robustly hardened spines, displaying dark brown colour. Abdomen slightly broader than thorax; the 5th segment widest and longest, the 8th segment connecting to ootheca, forming a curve at its posterior margin (indicated in Fig. 2E by blue arrows); external genitalia originating from the 6th segment; basivalvula divided into two parts, each semicircular in shape, making a slight sinus at their connecting position; paraproct evidently divided as left and right halves (Fig. 2E, F). Cercus with eight cercomeres visible, tapering to an evident terminus. Ootheca hardened and intact, no indication of boundaries (boundaries are the external demarcations on the oothecal surface that define internal partitions between eggs); apical part nearly round. Oothecal internal boundaries present (Fig. 2E, F). Forewing (Fig. 2G, H) length 13.0 mm, lacking discernible markings; 36 veins intercepting wing margin from Sc to CuA veins. Sc vein relatively short with three branches; R vein stem nearly straight, only slightly bending at basal part, with 19 branches reaching wing margin; M vein with nine branched veins; CuP vein clearly thicker than other veins and strongly curved at apical part. Hind wing Rs vein (Fig. 2H) with many branches; M vein simple.

CNU-BLA-LB-2013736 (Fig. 3). Female, only body present, forewings and external genitalia well preserved. Head *c.* 2 mm along median body axis and 1.6 mm perpendicular to median body axis; eyes nearly ovoidal; antenna over 6 mm long and tapering to its apex. Details of thorax unclear; coxa of hind legs slightly flattened, about 2.40 mm as preserved. The femur of mid-leg about 2.65 mm as preserved, and that of hind leg about 3.16 mm. Tibia (*c.* 2.35 mm) of the middle legs possessing many hardened spines, mainly on the outside; top several spurs (robust spines) *c.* 1 mm long, with radiating

projections. Tibia (*c.* 3.02 mm as preserved) of the hind legs having several spurs on the inner side. Abdomen with the 4th and 5th segments demonstrably wider and longer along medial axis than others; both sides of abdomen infused with dark colour. Two cerci (*c.* 2.73 mm as preserved) protruding from abdomen, each bearing over 11 cercomeres, the 6th or 7th cercomeres widest, the apical two cercomeres sharply tapering. Ootheca slightly curved; about 7.1 mm along medial axis, the longest ootheca among all six cockroach specimens. Oothecal boundary lines between two eggs evident and easily recognizable; expressed as external linear demarcations on the oothecal surface, the distance between two successive boundaries *c.* 0.2 mm (Fig. 3C, D); cases enclosing each egg almost symmetrically arranged crosswise in the capsule, forming a notched edge along the ootheca. Two rows of eggs converging and forming a relatively smooth keel along the lateral side of the ootheca; keel and edge of egg case *c.* 0.3 mm (Fig. 3C–E). Wings poorly preserved. Forewing 12.4 mm in length, R vein with 19 branches reaching wing margin, M vein with nine vein endings.

CNU-BLA-LB2013730 (Fig. 4A, B). Female, only body present, wings and ootheca nearly completely preserved; details not clearly discernible. Head structure not clear, protruding from pronotum; the latter about 4 mm in width. Thorax somewhat narrower than abdomen; abdomen evidently tapering from 6th to 8th segments, the 8th segment very short. Hind legs with coxa slightly flattened, *c.* 2.5 mm long and 1.6 mm wide at the widest point; femur *c.* 3.1 mm long and 0.8 mm wide at widest point; tibia about 3.5 mm long, covered with many spines. Other legs unclear. Forewing 13.0 mm in length, R vein with 18 branches, each branch reaching to wing margin, M vein with eight vein endings. Sc4 vein branched; CuP vein sharply curving towards the apex, demonstrably thicker than other veins. Each cercus (*c.* 2.5 mm) of eight visible cercomeres, tapering towards the apex. Ootheca gradually thickening from base (*c.* 1.22 mm wide) to the apex (*c.* 1.55 mm wide).

CNU-BLA-LB2013-702 (Fig. 4C, D). Female in dorsal view; hind wing and legs not evident. Head *c.* 2.4 mm in width; minimally protruding from pronotum, the latter nearly spherical in shape; 4.3 mm wide and 3.0 mm along median body axis. Antennae about 5.50 mm in length. Mesothorax clearly narrower than metathorax, *c.* 4.6 mm at the widest point. Abdomen with 4th segment widest, but each segment nearly equal in height except for 8th one. The 9th tergum slightly covering ootheca and forming a triangular posterior margin based on an impression line (Fig. 4D). Cerci (*c.* 2.61 mm) nearly rectilinear, tapering apically, over 12 cercomeres. Ootheca slightly curved, the lateral keel border displaying minor notches (Fig. 4D). Forewing (12.7 mm in length) with Sc vein three-branched; R vein with 18 branches reaching the margin of wing, M vein with no more than eight vein endings; anal



wing region occupying nearly half of wing width; CuP vein slightly bent near middle part, almost disappearing towards apex (Fig. 4A).

CNU-BLA-LB-2013651 (Fig. 4E, F). Female in ventral aspect; poorly preserved, with only hind wings present; part of head evident; details of body not discernible. Forewing 11.5 mm in length, with R vein bearing 18 branches, M vein with six vein endings; CuP vein nearly linear. Abdomen with the 5th and 6th segments distinctly wider and longer than other segments, the 7th and 8th segments very short. Cerci about 2.38 mm in length, 12 cercomeres visible. Ootheca slightly curved at the basal part, the front margin reaching the boundary of the 7th abdominal segment; details not clear.

**Remarks.** Family-level systematics of extant cockroaches is based principally on molecular sequence data and genitalia morphology; it is difficult to assign fossil species to an extant family due to the lack of well-preserved genitalia characters. Evangelista *et al.* (2017) suggested that the valvate subgenital plate of females should be used as a diagnostic character for *Piniblattella*, since the venation pattern of cockroaches includes many plesiomorphic and homoplastic characters (Rehn 1951; Klass 2001; Ross 2012). Unfortunately, no traces of a valvate subgenital plate were found in *Piniblattella yixianensis* sp. nov. Because of these extenuating circumstances, we tentatively assign the new species to Ectobiidae and to the genus *Piniblattella* based on its similarity to the type species of this genus. The principal similarities are a long, parallel-sided forewing with strongly pigmented radius and very short foretibia. Blattellidae Karny, 1908 has been commonly used in the literature, but Ectobiidae Brunner von Wattenwyl, 1865, has nomenclatural priority. Phylodromiidae Brunner von Wattenwyl, 1865 and Plectopterinae McKittrick, 1964 are synonyms. We excluded *Piniblattella altera* Vršanský, 1997 and *P. elegans* Vršanský, 1997 from comparison because they have been transferred to other genera (Vršanský 2003).

## Discussion

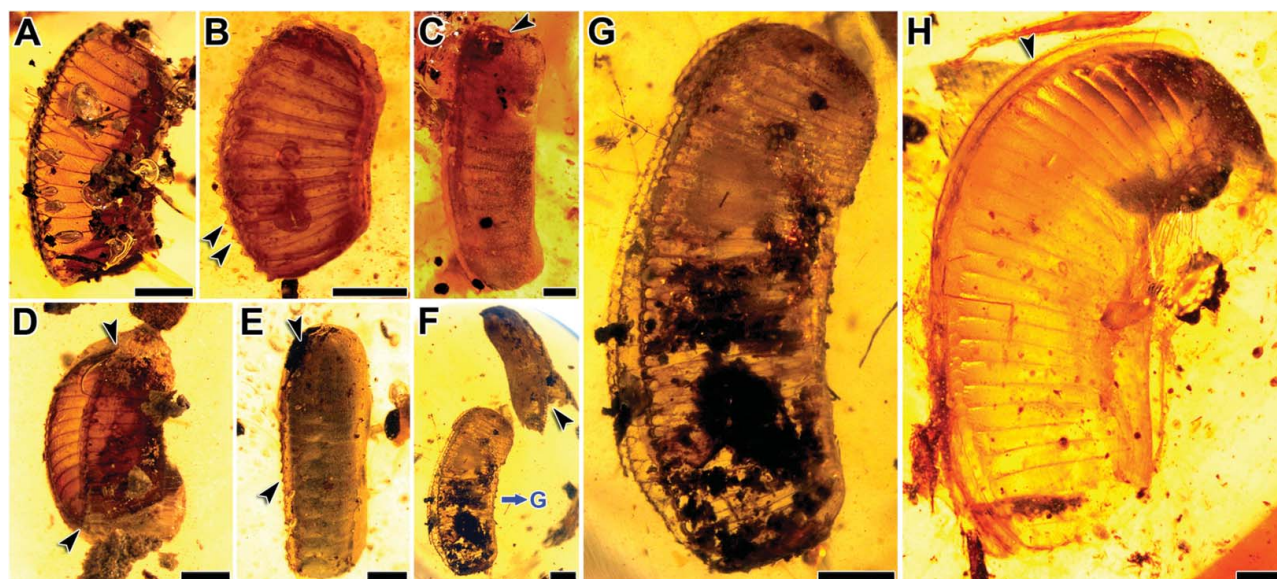
### Structure of Cretaceous oothecae and modes of reproduction

*Piniblattella yixianensis* sp. nov. had a conspicuous and intact ootheca that originated from a short, truncate, mostly internal ovipositor that provided structure, such as egg partition lineations, during oothecal development. In particular, both CNU-BLA-LB2013800p/c (Fig. 1) and CNU-BLA-LB2013736 (Fig. 3) exhibit visible egg-partition lineations on the oothecal surface. The oothecae of these specimens are of different lengths, most likely due to the missing basal part of the ootheca in CNU-BLA-LB2013800p/c. Size measurements for individual eggs

for the two specimens are virtually the same, and the eggs are somewhat less than 0.2 mm in width (Fig. 3D). It is reasonable to infer that the oothecae of *P. yixianensis* also enclosed two rows of eggs, similar to those of extant cockroaches. Specimen CNU-BLA-LB2013800p/c (Fig. 1) has a tubiform ootheca characterized by ensheathed, horizontally arranged eggs and an apical indentation of the ootheca (Fig. 1F), providing morphological features identical to extant cockroaches. Compared with the oothecae of extant cockroaches (Roth 1968; Roth & Willis 1954), and based on the lengths ranging from 6.1 to 7.1 mm for the oothecae of the five paratype specimens (Table 1), we estimate that *P. yixianensis* sp. nov. had 60 to 70 eggs.

Based on Roth's hypothesis (Roth & Willis 1954, 1957), the modes of reproduction in extant cockroaches with oothecae are divided into four types (Roth 2003). The first type is a condition wherein the ootheca is partly connected to the abdominal terminalia and is shed shortly after its formation (oviparity A). The second type is an ootheca that is carried externally until the eggs hatch and nymphs are discharged (oviparity B). For these two types of ovoviviparity A and ovoviviparity B, the ootheca resides inside the abdomen and is not externally evident. As all specimens of *P. yixianensis* sp. nov. bear oothecae that display a relatively underdeveloped and unornamented keel and are firmly attached to the cockroach's abdominal terminalia, we suggest that *P. yixianensis* had a reproductive mode of oviparity B. In addition, all examined specimens of *P. yixianensis*, except for CNU-BLA-LB2013729p/c which is not well preserved, have oothecae with a left-positioned lateral keel. The third and fourth types of Roth's (Roth & Willis 1954, 1957) reproductive modes are very limited in their phylogenetic distribution and are not germane to the following discussion.

After examining more than 10,000 fossil cockroach specimens in the CNU fossil collections, representing several major clades from the late Middle Jurassic Jiulongshan Formation, no oothecate cockroaches or isolated oothecae were discovered. These cockroach specimens belong to lineages bearing external needle- or sword-shaped ovipositors (Vršanský 1997; Vršanský *et al.* 2009; Liang *et al.* 2012). In the CNU fossil collection of approximately 5000 cockroaches from the mid Early Cretaceous Yixian Formation, only six oothecate specimens were collected and are described in this contribution. Our findings predate by 10 million years the aforementioned three cockroaches with oothecae from the Crato Formation of Lower Cretaceous from Brazil (~115 Ma) (Grimaldi & Engel 2005; Hörnig *et al.* 2013; Lee 2016). We found several isolated cockroach oothecae (Fig. 5) from earliest Cenomanian Myanmar amber (99 Ma) (Cruickshank & Ko 2003; Shi *et al.* 2012). These two assemblages of oothecae show significant structural diversity, with lengths ranging from 3.5 to 13.0 mm, and widths from 1.8 to 4.7 mm (Table 2).



**Figure 5.** Oothecae from mid-Cretaceous Myanmar amber. **A**, CNU-BLA-MA2015-102; **B**, CNU-BLA-MA2015-104, showing a row of distinct and well-regulated protrusions along the oothecal keel; **C**, CNU-BLA-MA2015-101 exhibiting a hole at the terminus; **D**, CNU-BLA-MA2015-105, displaying cracks along the oothecal keel; **E**, CNU-BLA-MA2015-109; **F**, CNU-BLA-MA2015-108, showing two oothecae within a single amber piece; the upper one displaying a cracked area on the keel; **G**, enlargement of the lower ootheca in **F**, exhibiting a clear zipper-like structure along the keel; **H**, CNU-BLA-MA2015-107 showing relatively smooth keel structure. Scale bars = 1 mm.

Myanmar amber oothecae are divided generally into two groups based on egg number. In the first group, each ootheca encompasses fewer than 40 eggs (Fig. 5A–E), whereas in the second group each ootheca houses more than 60 eggs (Fig. 5F–H). The widths of individual eggs among these oothecae vary considerably, ranging from 0.2 to 0.6 mm (Table 2). Specimens CNU-BLA-MA2015104 (Fig. 5B), CNU-BLA-MA2015101 (Fig. 5C) and CNU-BLA-MA2015109 (Fig. 5E) clearly exhibit serrated protrusions along the lateral oothecal border. The appearance of specimen CNU-BLA-MA2015105 (Fig. 5D) suggests that the ootheca could have been opened laterally along the keel during eclosion for the nymphs to emerge. This condition is also demonstrated by the particularities of the upper oothecal surface in specimen CNU-BLA-MA2015108 (Fig. 5F).

### Evolutionary significance of the Cretaceous cockroaches with oothecae

These new results from several Cretaceous biotas suggest that oothecae were involved in protection of eggs and nymphs and were commonly adopted by cockroaches during the Early Cretaceous, though oothecae were supposed to have been present from the earliest Jurassic (Vršanský *et al.* 2002a; Vršanský & Ansoerge 2007; Cohen *et al.* 2013; Barna 2014). In addition, it was during this same time interval that several crown cockroach clades initially appeared in the fossil record (Vršanský 2000, 2010; Vršanský *et al.* 2002b; Grimaldi & Engel 2005), such as species within the *Piniblattella* Vršanský, 1997 (Ectobiidae) and *Vitisma* Vršanský, 1999b (Blattidae) lineages (Šmídová & Lei 2017; Sendi & Azar 2017), both recovered from the Early Cretaceous of Transbaikalia in Russia

**Table 2.** Cockroach ootheca data from the mid-Cretaceous Myanmar amber. Measurements in mm.

Figure	Specimen ID no.	Length of ootheca	Width of ootheca	Number of eggs	Width of egg
Fig. 5A	CNU-BLA-MA2015102	~4.24	~2.18	~30	~0.27
Fig. 5B	CNU-BLA-MA2015104	~3.53	~2.20	~22	~0.30
Fig. 5C	CNU-BLA-MA2015101	~8.32	~2.92	~26	~0.60
Fig. 5D	CNU-BLA-MA2015105	~4.77	~1.86	~34	~0.28
Fig. 5E	CNU-BLA-MA2015109	~6.50	~2.52	~26	~0.50
Fig. 5G	CNU-BLA-MA2015108	~7.20	~2.86	> 60	~0.21
Fig. 5H	CNU-BLA-MA2015107	~13.00	~4.64	> 60	~0.40

(Vršanský 1997, 1999a). These species presumably had oothecae, but no oothecae have been found directly connected to a known body fossil (Vršanský 1997, 1999b). Two major groups of Dictyoptera, the diverse termites and mantids, are also described from these and other Cretaceous strata (Ren *et al.* 1995; Vršanský 2002, 2008; Grimaldi 2003; Hörnig *et al.* 2013; Vršanský & Aristov 2014; Engel *et al.* 2016). However, Mesozoic fossil records lack definitive oothecae or egg capsules of mantids. One interpretation of this interesting absence is that soft tissues, such as the pliable egg capsules of mantids, are difficult to preserve physically as compression fossils or in the chemical environment of amber (McNamara *et al.* 2010).

Palaeozoic ‘roachoids’, stem-group representatives of Dictyoptera, first appeared during the Early Pennsylvanian, and are considered to be one of the most ancient of extant insect clades (Jarzembowski 1994, 2008; Grimaldi & Engel 2005). Pennsylvanian roachoids possessed elongate external ovipositors that assumed two basic forms (Schneider *et al.* 2004; Schneider & Werneburg 2006). The first ovipositor morphotype was needle-shaped structures that bore circular cross sections. The second morphotype consisted of sword-shaped forms that were laterally flattened and lenticular in cross section. These ovipositor morphotypes and their modifications indicate a variety of egg-laying strategies (Vršanský 1999a; Labandeira 2006). By contrast, extant Dictyoptera (Figs 1J, 4G) have very short, blunt, internally deployed and modified ovipositors for producing and carrying oothecae (Roth & Willis 1954; Roth 1970). Based on several phylogenetic studies, it appears that extant lineages of Dictyoptera are generally considered to have arisen during the Early Cretaceous or possibly earlier, in the Jurassic (Djermæs *et al.* 2012, 2015; Misof *et al.* 2014; Legendre *et al.* 2015). Although fossil mantids currently have not been documented from the Jurassic, raphidiomimid cockroaches have been reported from the Early Jurassic to mid-Cretaceous. Mesozoic ‘roachoid’ raphidiomimids, with short and wide ovipositors, are considered to be predatory based on their head modifications, specialized mouthparts, and forelegs that bore two rows of sharp spines on the forefemur and foretibia, indicating convergent or parallel evolution between Mesozoic ‘roachoids’ and mantises (Grimaldi & Engel 2005; Liang *et al.* 2009). Therefore, it is likely that Palaeozoic ‘roachoids’ with long ovipositors survived the end-Permian extinctions, and subsequently diversified during the Triassic, Jurassic and Early Cretaceous (Vršanský 2002, 2005); while several clades of crown cockroaches with very short ovipositor started to emerge during or before the Middle Jurassic.

### Potential driving forces for the development of cockroach oothecae

Contemporaneously with the emergence of several landmasses in Eastern Asia (Ren *et al.* 2010), palaeobotanical

and sedimentological evidence indicates that seasonal climatic fluctuations between semiarid and mesic conditions were present for the Jehol Biota, as represented in the Yixian Formation (Zhou *et al.* 2003). This context of fluctuating palaeoenvironments as documented in the Jehol Biota likely was a driving force for the evolution of the cockroach ootheca as a useful device for protection of their young. It is suggested that the diversification of many co-existing, potential predators, especially birds, feathered dinosaurs, pterosaurs, early mammals and especially large predaceous insects, might have played an important role as a key driving force for cockroach inconspicuousness that was afforded by the adoption of oothecae (Fig. 3F). Such a retreat would be consistent with oothecal structures such as in the mid Early Cretaceous *P. yixianensis* sp. nov., similar to extant cockroaches possessing oviparity B reproduction mode. These findings highlight that cockroach maternal care, such as oothecal carriage and egg protection until hatching, was adopted during or by the Early Cretaceous. The oothecate condition was a more efficient reproductive mode than contemporaneous and earlier styles of direct egg laying via elongate piercing or slashing ovipositors. Such structural advances may have been among the key factors that set the stage for the evolutionary diversification and current ecological success of cockroaches.

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