

Praeblattella aliciae sp. nov. from Cretaceous Myanmar amber indicates a transition of the Mesoblattinidae towards the Ectobiidae

Jan Hinkelman^{1,*}¹* Croatian Geological Survey, Sachsova 2, 10000 Zagreb, Croatia; (corresponding author: jhinkelman@hgi-cgs.hr)doi: 10.4154/gc.2026.07
Original scientific paper

Abstract

The cockroach *Praeblattella* VRŠANSKÝ, 2003 is a cosmopolitan genus recorded from the Mesozoic localities of Japan, Mongolia, the Russian Federation, South Korea, Thailand, Myanmar, Kazakhstan, Mongolia, India and USA, ranging in age from the Oxfordian to the Campanian (Late Jurassic to Late Cretaceous). Until now, two species were described from the amber of Cretaceous age, from North Myanmar *Praeblattella patrickmuelleri* ŠMÍDOVÁ in ŠMÍDOVÁ, BRUTHANSOVÁ & HAIN, 2024 and *Praeblattella continuosa* ŠMÍDOVÁ in ŠMÍDOVÁ, BRUTHANSOVÁ & HAIN, 2024. A new species from Myanmar amber, *Praeblattella aliciae* sp. nov. is described here, with characteristic pale forewing longitudinal colouration (including distinct dark maculae) and a venation scheme typical for the genus. The geographic distribution of *Praeblattella* fossil specimens is also given. Due to its high level of preservation in amber, this new species expands the fossil record and contributes to a better understanding of the morphology of this cockroach genus. It is unique in revealing characteristics transitional to its descendant family, the Ectobiidae.

Keywords: Fossil insect, Cretaceous, cockroach

Article history:

Manuscript received: October 1, 2025

Revised manuscript accepted: March 13, 2026

Available online: May 18, 2026

1. INTRODUCTION

Mesoblattinidae HANDLIRSCH, 1906, an extinct cosmopolitan cockroach family with a range from the Hettangian to the Cenomanian (Lower Jurassic to Upper Cretaceous) (HUBER, 1974; KADDUMI, 2007; ENGEL & PÉREZ-DE LA FUENTE, 2012; VRŠANSKÝ & MAKHOUL, 2013; ŠMÍDOVÁ & LEI, 2017; ŠMÍDOVÁ, 2020), is characterized by a mostly conservative morphology, including forewings with parallel margins, regular and overall reduced venation, varying space between forewing veins and indistinct intercalaries, a straight RS vein, 2–4 branched Sc and a branched A (VRŠANSKÝ & ANSORGE, 2007; WEI & REN, 2013; ENGEL & PÉREZ-DE LA FUENTE, 2012). Although members of this family are commonly found in sedimentary rocks (SO et al., 2021; ZHANG et al., 2023; KOVÁČOVÁ, 2023; VRŠANSKÝ, 2020, 2024; VRŠANSKÝ et al., 2025), in recent years their fossil record expanded to the North Myanmar amber (HINKELMAN, 2019, 2021a, b; HINKELMAN & VRŠANSKÁ, 2020; KOVÁČOVÁ, 2023; ŠMÍDOVÁ et al., 2024), Lebanese amber (VRŠANSKÝ, 2004b), French amber (VRŠANSKÝ, 2009) and Russian Taymyr amber (VRŠANSKÝ, 2019).

North Myanmar amber is known for its exceptionally well preserved and diverse floral and faunal remains of Cretaceous age (98 Ma) with around 2,989 species described, the majority being insects (ROSS, 2025). It is estimated that there are ca. 4,000 cockroach specimens available from Northern Myanmar amber alone (VRŠANSKÝ & WANG, 2017; Fig. 1).

The fossil record of the extinct cockroach genus *Praeblattella* VRŠANSKÝ, 2003 ranges from the Oxfordian to the Cenomanian (Middle Jurassic to Upper Cretaceous).

The palaeogeographical distribution, limited to eastern Laurasia, is a consequence of fossil bias (Fig. 4), as undescribed species also occurred in India, Botswana and the USA.

Specimens of *Praeblattella* have been found in Cretaceous localities such as Baissa, Russia (VRŠANSKÝ, 1997), Bon Tsaagan Nuur, Mongolia (VRŠANSKÝ, 2003), Kitadani, Japan (OYAMA et al., 2022), Jinju, South Korea (VRŠANSKÝ et al., 2025), Thailand (KOVÁČOVÁ, 2023), Viliuy, Russia (VRŠANSKÝ et al., 2024) and the Myanmar amber (ŠMÍDOVÁ et al., 2024), as well as Jurassic localities in Tasgorosay, Kazakhstan (MAJTANÍK & KOTULOVÁ, 2023) and Bakhar, Mongolia (VRŠANSKÝ, 2020). The type specimen *Praeblattella ponomarenkoi* was described by VRŠANSKÝ (2003) from the Lower Cretaceous (Barremian) locality at Bon Tsaagan Nuur (Mongolia).

Praeblattella aliciae sp. nov., described here, is the third representative of *Praeblattella* from the Myanmar amber described so far (Figs. 2 a–d, 3 a–b). The species is characterized by its unique forewing colouration with thick cross-veins and coloured main veins, characteristic of this genus. Additionally, the cercus is preserved in great detail as well as a unique deformation/fusion of a forewing vein. *P. aliciae* expands the Myanmar amber cockroach record to 73 genera and 106 species (ROSS, 2025).

2. MATERIALS AND METHODS

The studied amber specimen containing an adult female cockroach (CGS-AMB-001) is in the collection of the Croatian Geological Survey (HGI-CGS). The specimen originates from 98.8±0.6 Ma (early Cenomanian) old amber from the Hukawng

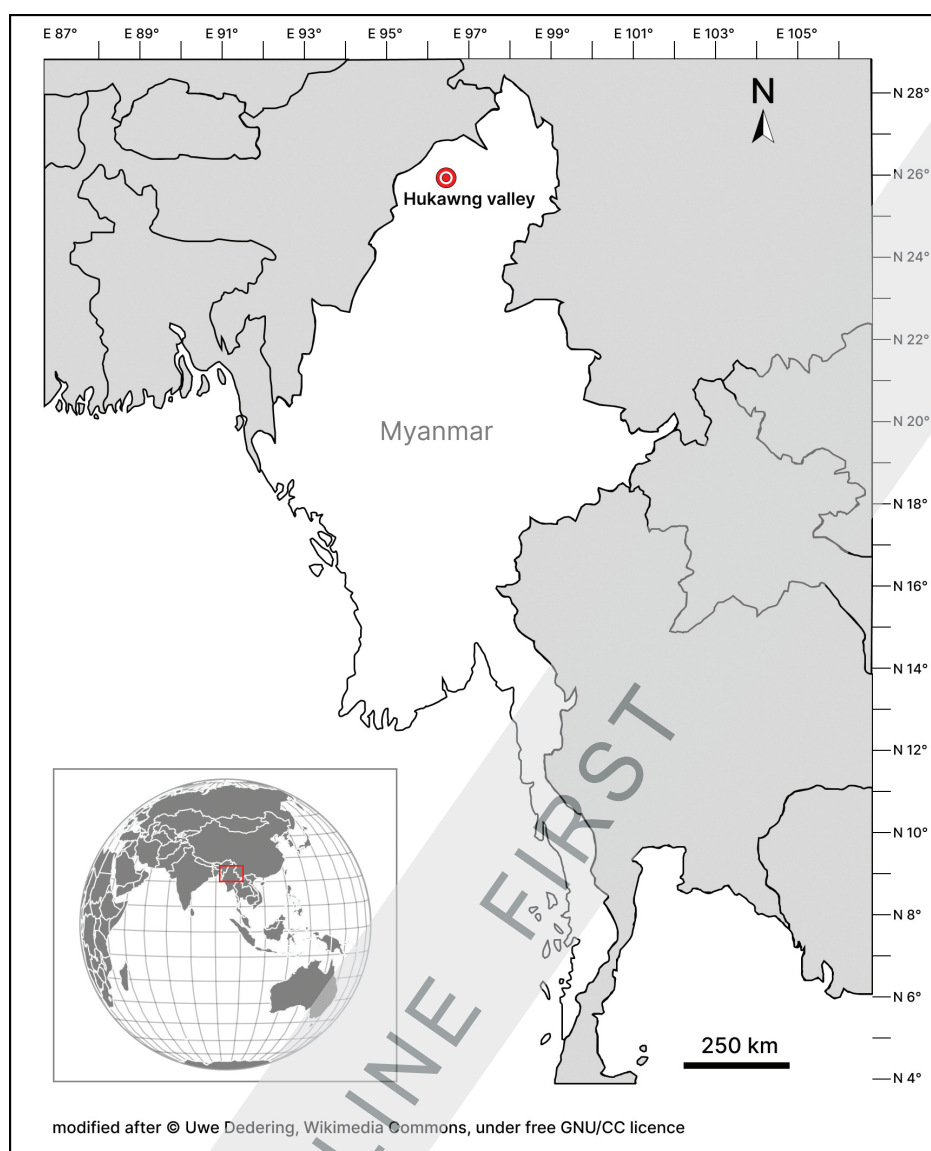


Figure 1. Map of Myanmar with the highlighted locality of the Hukawng Valley amber mine, from which the amber sample originates.

valley, Kachin, Myanmar (26°20'N, 96°36'E; Fig. 1) (SHI et al., 2012; KANIA et al., 2015). The specimen was studied using an AmScope 7X-45X Magnification Trinocular Zoom Stereo Microscope and photographed with an AmScope MU Series 18.0MP camera. CombineZP stacking software and Figma software were used for stacking and stitching individual photographs into one high resolution photograph. The photographs were subsequently edited in Adobe Photoshop CS5 (Fig. 2). Digital drawings of the specimen were made using Figma software (Fig. 3). The specimen and its minute anatomical details were measured with the help of a micrometer scale. Additionally, a palaeogeographic map was constructed in order to show the distribution of *Praeblattella* fossils at their respective localities (Fig. 4).

The wing venation scheme was based on the system established by COMSTOCK & NEEDHAM (1898) and recently revised by LI et al. (2018), with the following abbreviations: RFW – Right forewing, LFW – Left forewing, HW – Hind wing, A – Anal sector, C – Costa, Sc – Subcosta, RS – Radius Sector, M – media, CuA – Anterior cubitus, CuP – Posterior Cubitus.

3. Systematic Palaeontology

Suborder Blattaria Latreille, 1810 *sensu* KLASS & MEIER, 2006

Superfamily Blattoidea LATREILLE, 1810

Family Mesoblattinidae HANDLIRSCH, 1906

Type genus: *Mesoblattina* GEINITZ, 1880

Composition: *Aporoblattina* SCUDDER, 1886; *Actinoblattulla* HANDLIRSCH, 1906; *Artitocoblatta* HANDLIRSCH, 1906; *Austroblattula* TILLYARD, 1919; *Archimesoblatta* VRŠANSKÝ, 2003; *Blattidium* WESTWOOD, 1854; *Basiblattina* ZHANG, 1997; *Brachymesoblatta* VRŠANSKÝ, 2003; *Breviblattina* VRŠANSKÝ, 2004a; *Cuniculoblatta* HINKELMAN, 2021b; *Durdlestoneia* HANDLIRSCH, 1906; *Fusoblatta* HONG, 1980; *Gondwablatta* VRŠANSKÝ, 2004b; *Hongaya* HANDLIRSCH, 1908; *Hispanoblatta* MARTÍNEZ-DELCLÓS, 1993; *Jingyuanoblatta* LIN, 1982; *Jinjublatta* VRŠANSKÝ, LEE, SOHN, VRŠANSKÁ, JANG & NAM, 2025; *Kulmbachiellon* KUHN, 1938; *Kedysia akokolvek* VRŠANSKÝ & KOUBOVÁ,

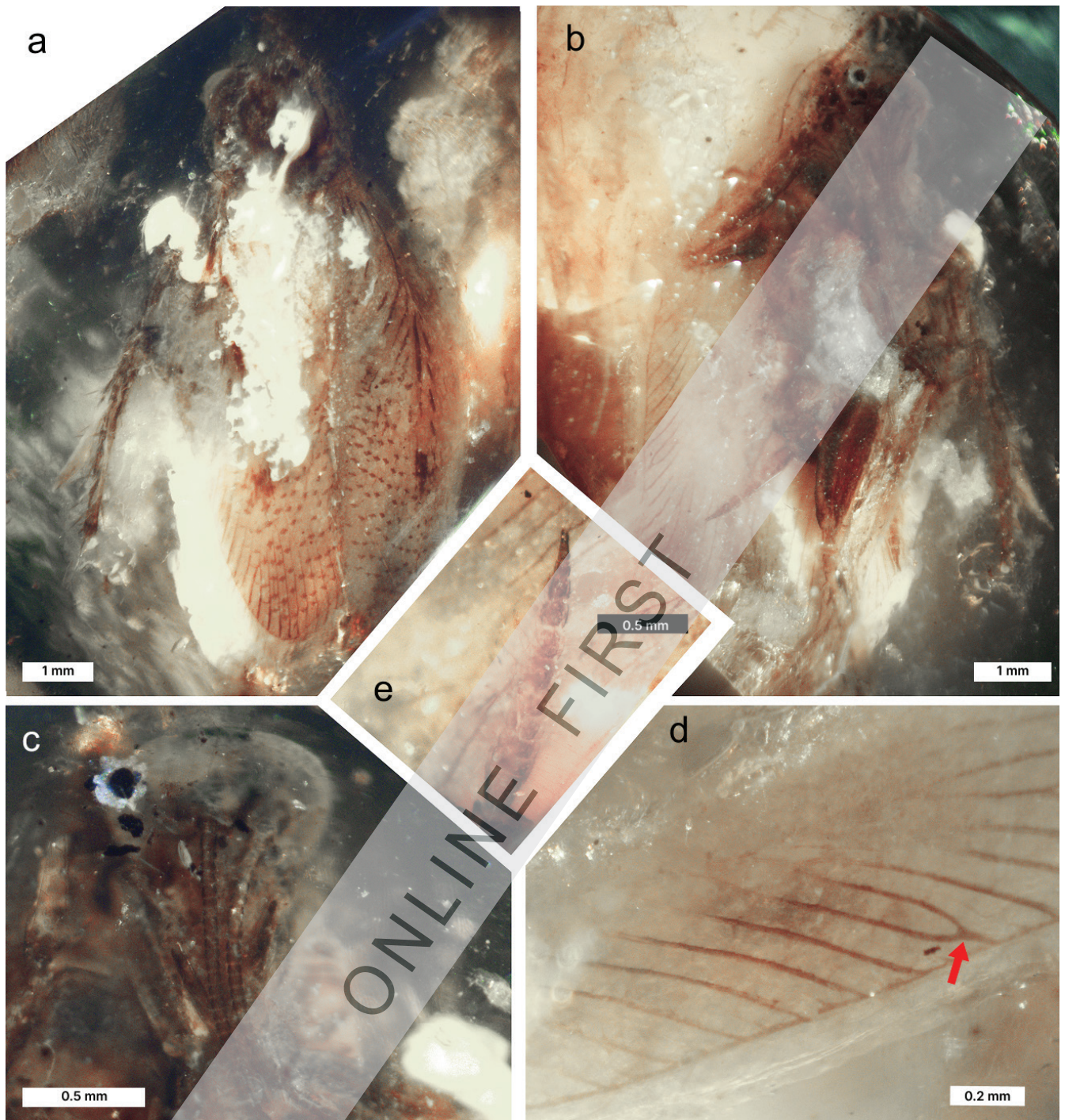


Figure 2. *Praeblattella aliciae* sp. nov. (a) Dorsal view; (b) Ventral view; (c) Detailed view of the head; (d) Detail of fused forewing vein; (e) Detailed view of the cercus

2025; *Lithoblatta* HANDLIRSCH, 1906; *Laiyangia* GRABAU, 1923; *Malmoblattina* HANDLIRSCH, 1906; *Mesoblattellina* MENDES, 2000; *Mongolblatta* VRŠANSKÝ, 2004a; *Mieroblattina* VRŠANSKÝ & MAKHOUL, 2013; *Mesoblatta* HINKELMAN in HINKELMAN & VRŠANSKÁ, 2020; *Meloblatta* VRŠANSKÝ in VRŠANSKÝ, VRŠANSKÁ, VASILENKO, PUŠKELOVÁ & BIROŇ, 2021; *Nipponoblatta* FUJIYAMA, 1974; *Nogueroblatta* MARTÍNEZ-DELCLÒS, 1993; *Nymphoblatta* VRŠANSKÝ & GRIMALDI in VRŠANSKÝ, 2004b; *Otazka* VRŠANSKÝ in VRŠANSKÝ, VRŠANSKÁ, VASILENKO, PUŠKELOVÁ & BIROŇ, 2021; *Pareinoblatta* HANDLIRSCH, 1906; *Praeblattella*

VRŠANSKÝ, 2003; *Pulchellablatta* MARTINS-NETO & GALLEGO in MARTINS-NETO, MANCUSO & GALLEGO, 2005; *Perlucipecta* WEI & REN, 2013; *Rithma* GIEBEL, 1856; *Rhaetoblattina* HANDLIRSCH, 1908; *Raptoblatta* DITTMANN, HÖRNIG, HAUG & HAUG, 2015; *Schambeloblattina* HANDLIRSCH, 1906; *Stantoniella* HANDLIRSCH, 1907; *Stenotegmina* LIN, 1982; *Summatiblatta* LIN, 1986; *Sivis* VRŠANSKÝ, 2009; *Spinaeblattina* HINKELMAN, 2019; *Turoniblatta* VRŠANSKÝ, 2004b.

Stratigraphic range: Hettangian – Campanian (Lower Jurassic – Upper Cretaceous)

Geographic range: Cosmopolitan with occurrences from the “subtropical” forest beyond the ancient polar circle (Yakutia, Taimyr, Khabarovsk, Magadan and Chukotka; Arctic circle deposits within the Russian Federation), as well as from warm temperate localities in Siberia (Chernovskie Kopi, Baissa, Viliuy, Khetana; deposits within the Russian Federation) and the tropical locality of Myanmar (VRŠANSKÝ, 2019; VRŠANSKÝ et al., 2024; HINKELMAN, 2019, 2021a, b; HINKELMAN & VRŠANSKÁ, 2020).

Genus *Praeblattella* VRŠANSKÝ, 2003

Composition: *P. elegans* (VRŠANSKÝ, 1997); *P. dichotoma* VRŠANSKÝ, 2003; *P. ponomarenkoi* VRŠANSKÝ, 2003; *P. zrnko* VRŠANSKÝ, 2003; *P. jurassica* VRŠANSKÝ, 2020; *P. arcuata* OYAMA, YUKAWA & IMAI, 2022; *P. inexpecta* OYAMA, YUKAWA & IMAI, 2022; *P. krzeminski* KOVÁČOVÁ, MAJTANÍK & QUICKE, 2023; *P. solus* MAJTANÍK in MAJTANÍK & KOTULOVÁ, 2023; *P. patrickmuelleri* ŠMÍDOVÁ in ŠMÍDOVÁ, BRUTHANSOVÁ & HAIN, 2024; *P. borealis* VRŠANSKÝ & KOVÁČOVÁ in VRŠANSKÝ, KOVÁČOVÁ, VASILENKO, PÁLKOVÁ, NAGY, KOSNÁČ, VIDLIČKA & MARTIN, 2024; *P. continuosa* ŠMÍDOVÁ in ŠMÍDOVÁ, BRUTHANSOVÁ & HAIN, 2024; *P. Decolor* VRŠANSKÝ, LEE, SOHN, VRŠANSKÁ, JANG & NAM, 2025; *P. tinctoria* VRŠANSKÝ, LEE, SOHN, VRŠANSKÁ, JANG & NAM, 2025; *P. aliciae* sp. nov. and undescribed species from New Jersey amber (VRŠANSKÝ, 2004b), Kota Formation (India; ENGEL & PÉREZ-DE LA FUENTE, 2012) and Botswana (RAYNER et al., 1998).

Diagnosis (Based on VRŠANSKÝ, 2003 and ŠMÍDOVÁ et al., 2024): Small to medium sized cockroaches characterized by a hypognathous or opisthognathous head, vaulted pronotum with colouration and dorsoventrally flattened body. Females possess a very short and bivalvate, externally protruding ovipositor. Males are distinguished by having small tergal glands. The forewing Sc vein can be simple or have 2–4 branches, RS may be differentiated within R. R is straight overall; M can vary in the number of branches, but generally there are 4–5. CuA more or less contains three branches and is slightly sigmoidal. Hindwing R differentiates into R1 and RS, while M is usually simple or with 2–3 branches. CuA can have multiple blind branches and the CuP is simple. One of the distinguishing features of *Praeblattella* is the unique “pale” longitudinal colouration of the forewing in the shape of dark bands surrounding the main veins and cross-veins.

Praeblattella aliciae sp. nov.

(Figs. 2 a–e, 3 a–b)

Zoobank code: 4130FA03-22FF-4117-B76D-B60BEB6961E8

Derivation of name: *aliciae* is derived from the name Alicia, spouse of the author.

Types: Holotype: CGS-AMB-001; length 9 mm, width 4.3 mm (Figs. 2 a–e, 3 a–b).

Type locality and stratum: Lower Cenomanian amber bearing deposits of the Hukawng valley, Kachin, Myanmar.

Material: One specimen (holotype).

Differential diagnosis: *P. aliciae* differs from all other *Praeblattella* species in the colouration of the forewing which alongside the characteristic “pale” colouration, has two distinct irregular dots or “maculae” on both wings. The pronotal colouration appears in the form of an irregular dark pattern as opposed to *P. patrickmuelleri* where it has a triangular shape. Forewing intercalaries are not coloured to the degree seen in *P. tinctoria* or completely absent colouration as in *P. jurassica*. From *P. decolor* it differs in the colouration of the forewing, completely missing in the former species. *P. dichotoma* has richer venation in the M area with 7–9 veins and the R area with 18–25 veins, while *P. aliciae* has 5–6 in the M area and ca. 13 in R. *P. zrnko* is missing colouration from the basal anterior part of R, which is not the case in *P. aliciae*. The overall venation in *P. aliciae* is not as rich as in *P. elegans* which, as an example, has M with up to 12–22 veinlets. Although *P. aliciae* has two distinct irregular dots or “maculae” on both wings, they differ from the distinct dark colouration restricted to the central area of the forewing, as seen in *P. krzeminski*. The pronotum in *P. aliciae* appears more oval when compared to *P. ponomarenkoi* where it is more transverse, while the Sc is branched with three veins (simple in *P. aliciae*).

Autapomorphies: Forewing colouration contains distinct two dark-coloured dots on both wings. This is also a synapomorphy with the recently described *Kedysi akokolvek* VRŠANSKÝ & KOUBOVÁ, 2025 from the Myanmar amber as well as some Ectobiid cockroaches. Anterior veins are more strongly coloured, especially the R vein.

Character of preservation: An almost fully preserved adult cockroach. Maxillary palps, labial palps, mandibles and other mouth parts are indistinct. Legs are partially preserved (left foreleg, right midleg and partial hindlegs). Left hindfemur only partially visible.

Description (based on the holotype): Adult small cockroach, 9 mm long and 4.3 mm wide (Figs. 2 a–e, 3 a–b). Body dorsoventrally flattened, pale in colour. Head standard in size, hypognathous (1.09 mm long and 0.94 mm wide). Sensilla on head are indistinct. Eyes are large and reniform 0.77 mm long and 0.47 mm wide, with comparatively small ocular facets (0.01 mm in diameter). Pronotum is translucent, paranotalia are obscured, but possibly present, overall flat and oval, 2.3 mm wide and 2.21 mm long. Head is only slightly overhanging the pronotum. The pronotum with a unique coloured pattern in the form of thick and irregular, dark vertical stripes, connecting in the lower part, similar to roschach ink blots. Sensilla on the pronotum indistinct. Antenna is filiform, moderately thin, and partially preserved, pointed downwards. Proximal segments of the antenna are conical. The right antenna with 21 conical antennomeres as preserved, 1.81 mm long (antennomeres 1–21 length 0.18 / 0.14 / 0.11 / 0.09 / 0.09 / 0.07 / 0.06 / 0.07 / 0.05 / 0.05 / 0.06 / 0.08 / 0.09 / 0.07 / 0.06 / 0.06 / 0.07 / 0.12 / 0.08 / 0.09 / 0.12). Left antenna with 16 conical antennomeres as preserved, 1.57 mm long (antennomeres 1–16 length 0.10 / 0.12 / 0.15 / 0.15 / 0.08 / 0.10

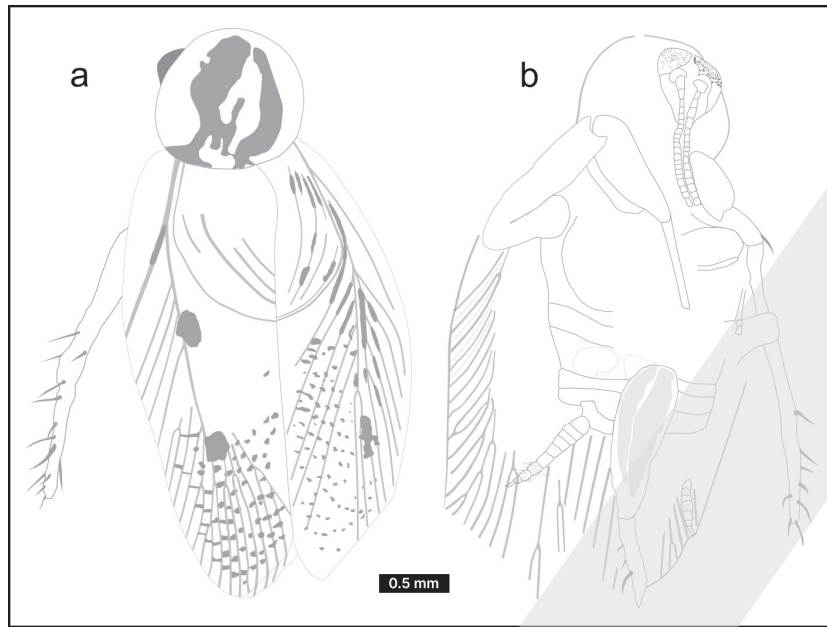


Figure 3. Digital drawings of *Praeblattella aliciae* sp. nov. (a) Dorsal view; (b) Ventral view

/ 0.06 / 0.06 / 0.06 / 0.09 / 0.09 / 0.11 / 0.09 / 0.12 / 0.09 / 0.10). Scape is conical in shape, 1.18 mm long and 1.12 mm wide. Pedicle similar in size to rest of antennomeres, 0.12–0.14 mm long. Legs are cursorial/strong. Frontcoxae are small, 0.95 mm long and 0.47 mm wide. Forefemur is short when compared with mid and hindfemora, 1.08 mm long and 0.38 mm wide, lacking strong armament. A large terminal femoral spine is preserved, 0.31 mm long and curved. Foretibia only partially visible. Midfemur long, 1.91–1.81 mm long and 0.53–0.56 mm wide, with ca. 5 short and delicate spurs, the one closest to the

tibia curved. Terminal femoral spines indistinct. Tibia partially visible only on left midleg, and apparently thin. Right hindfemur longest, 2.25 mm long and 0.72 mm wide, with strong carination present and lacking strong armament. Terminal femoral spine indistinct. Hindtibia thick, 0.20 mm, with strong spines up to ca. 0.36 mm long. Left hindfemur only partially visible. Terminal femoral spine obscured. Hindtibia comparatively long, 2.64 mm long and 0.20 mm wide. Spines on hindtibia very long and strong, 0.38 mm. Forewings are long and fully developed, ellipsoidal in shape. Left forewing

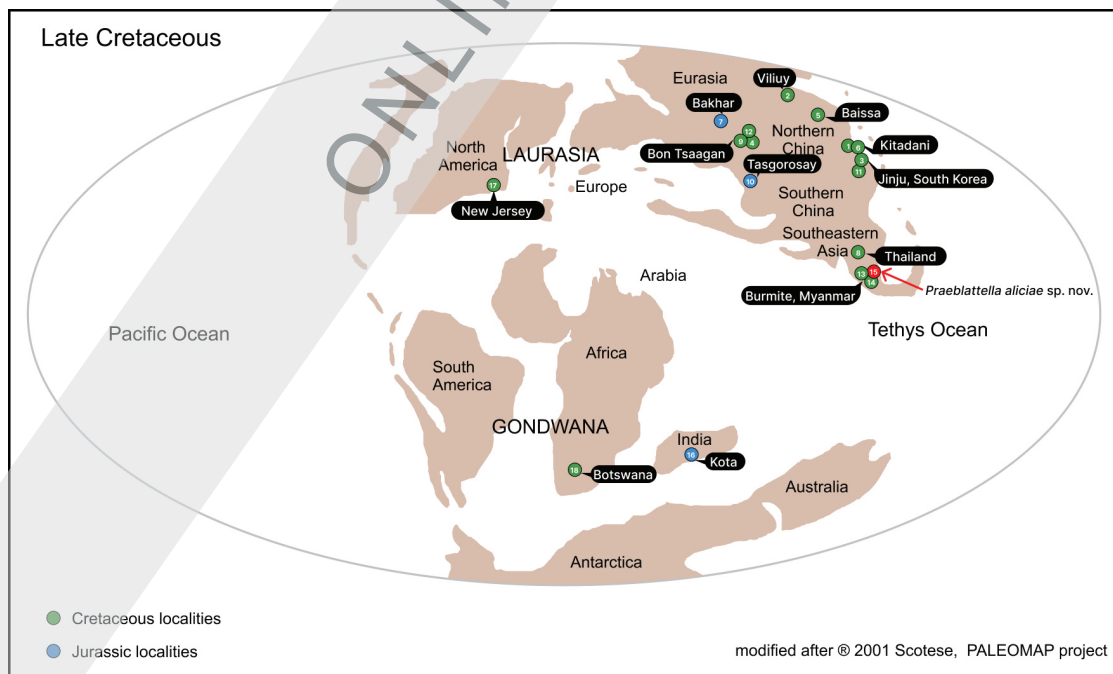


Figure 4. Late Cretaceous palaeogeographic map showing the distribution of *Praeblattella* fossils at the respective localities. Numbers indicate the following species: 1. *Praeblattella arcuata*; 2. *Praeblattella borealis*; 3. *Praeblattella decolor*; 4. *Praeblattella dichotoma*; 5. *Praeblattella elegans*; 6. *Praeblattella inexpecta*; 7. *Praeblattella jurassica*; 8. *Praeblattella krzeminski*; 9. *Praeblattella ponomarenko*; 10. *Praeblattella solus*; 11. *Praeblattella tinctoria*; 12. *Praeblattella zrnko*; 13. *Praeblattella patrickmuelleri*; 14. *Praeblattella continuosa*; 15. *Praeblattella aliciae* sp. nov.; 16. Undescribed specimen from Kota (India); 17. Undescribed specimen from New Jersey amber; 18. Undescribed specimen from Botswana

7.13 mm long and 2.32 mm wide, right forewing 7.05 mm long and 2.24 mm wide. Colouration on the surface of the wing in the form of dark bands surrounding veins and cross-veins. Dark bands form 2 distinct small, irregular maculae/dots, 0.32–0.52 mm in diameter. Forewing veins are distinct, ca. 0.06 wide. Intercalaries are present but not distinct as main veins. Due to colouring, the cross-veins appear thick (0.06 mm), forming distinct colouration patterns. Sc is simple and thick (0.06 mm). RS is well developed and comb-like, with 13 simple branches at wing margin (some main veins of RS display branching).

Some veins display mutations such as a fused RS. R and M veins are placed very closely together. R1 is simple, M comparatively narrow with 5–6 branches at wing margin. CuA shows three simple branches. CuP is not strongly curved, nor sigmoidal. Anal area is comparatively large with simple veins (coloured); ca. four visible but probably more are present. Hindwings are obscured. In total, four tergal segments of the abdomen can be seen, the rest is indistinct. Subgenital plate is only partially visible. Sensilla on subgenital plate is indistinct. Cercus is massive and segmented, slightly curved. Right cercus contains 10 cercomeres (1–10 length 0.21 / 0.11 / 0.10 / 0.13 / 0.15 / 0.20 / 0.16 / 0.15 / 0.10 / 0.15 mm; width 0.25 / 0.29 / 0.26 / 0.22 / 0.17 / 0.16 / 0.16 / 0.12 / 0.09 / 0.03 mm). Cercal sensilla appear dense and short, ca. 0.14 mm long.

Remarks: *P. aliciae* sp. nov. can be placed within *Praeblattella* based on its almost identical venation scheme characteristic for the type species *Praeblattella ponomarenkoi* VRŠANSKÝ, 2003 with a simplified Sc, richly branched but almost straight RS, M with ca. 5–6 veins at wing margin and CuA with 3 veins. The unique “pale” colouration of forewing, with dark bands covering the main veins and cross-veins, is a characteristic on the level of genus.

Occurrence: Known only from the lower Cenomanian of the Hukawng valley.

4. Discussion and conclusion

The newly described *P. aliciae* is placed within *Praeblattella* due to basically identical venation on the forewings. The Sc is simplified, RS is richly branched while M contains 5–6 veins. CuA has characteristic three veins and is slightly sigmoidal. The most prominent character of *Praeblattella* is the unique “pale” longitudinal colouration of the forewing, containing dark bands that cover the main veins and cross-veins. Such a forewing colouration, although not present in all species of the genus, is a characteristic of *Praeblattella*. A similar type of colouration can be seen in another extinct cockroach species from the Myanmar amber, *Bubosa poinari* ŠMÍDOVÁ, 2020. In the latter species, it has been suggested that such a colouration pattern was likely a camouflage on the leaf and dirt substrate (ŠMÍDOVÁ, 2020). The same holds true for the *P. aliciae* described herein. The extinct ectobiid cockroach *Neoblattella nechapetomu* VRŠANSKÝ, SENDI & AZAR in SENDI, VRŠANSKÝ & AZAR (2023) also has small black dots on the forewing, while veins Sc, stem of R and CuP are strongly coloured, similar to those in *P. aliciae*. Modern equivalents of such forewing colouration can best be observed

in certain species of *Ectobius* such as *Ectobius lapponicus* LINNAEUS, 1758 or *Ectobius kholisi* VRŠANSKÝ, ORUŽINSKÝ, BARNA, VIDLIČKA & LABANDEIRA, 2014, which also display coloured bands around veins and small dark dots or maculae on both wings. Moreover, the approximated R and M veins in the forewing of *P. aliciae* are also characteristic for *Ectobius* and other advanced Ectobiidae. The mentioned similarities of *P. aliciae* with *N. nechapetomu* and modern ectobiids further strengthens the idea that the major cockroach family Ectobiidae polyphyletically derived from the extinct Mesoblattinidae, which was previously proposed by VRŠANSKÝ & KOUBOVÁ (2025).

The fused vein documented in this described new species (Fig. 2d) is an example of a deformity or change in the regularity of venation. Such wing venation deformities usually appear as fusion of one vein to another (such is the case in newly described *P. aliciae*), mutual fusion of two veins, loss of a branch, veins not terminating at the wing margin, cross-veins with additional branches, blind veins with unfinished growth and even wide/lentiform veins resembling loops (VRŠANSKÝ, 2005; VRŠANSKÝ et al., 2017). An increased deformation pattern documented for Cretaceous cockroaches has been associated with significant diversifications at regular intervals (VRŠANSKÝ et al., 2017), however, within burmite deformities appear extremely rarely (VRŠANSKÝ, 2025).

Praeblattella aliciae represents the 15th species of this genus, and the 3rd species found in the Myanmar amber, and as such, contributes to a better knowledge of the diversity and geographical distribution of this remarkable, extinct cockroach genus.

Acknowledgment

I thank Ivona IVKIĆ FILIPOVIĆ (Croatian Geological Survey) for providing the AmScope 7X-45X Magnification Trinocular Zoom Stereo Microscope for making photographs of the specimen and two anonymous reviewers for their work, advice and valuable suggestions which improved this manuscript. This work was partially supported by the Croatian Science Foundation under the project number HRZZ IP-2024-05-1687.

References

- COMSTOCK, J.H. & NEEDHAM, J.G. (1898): The wings of insects.— The American Naturalist, 33, 117–126. <https://doi.org/10.1086/276766>
- DITTMANN, I.L., HÖRNIG, M.K., HAUG, J.T. & HAUG, C. (2015): *Raptoblatta waddingtonae* n. gen. et n. sp.— an Early Cretaceous roach-like insect with a mantodean-type raptorial foreleg.— Palaeodiversity, 8, 103–111.
- ENGEL, M.S. & PÉREZ-DE LA FUENTE, R. (2012): A new species of roach from the Jurassic of India (Blattaria: Mesoblattinidae).— Journal of the Kansas Entomological Society, 85, 1–4. <https://doi.org/10.2317/JKES110524.1>
- FUJIYAMA, I. (1974): A Liassic Cockroach from Toyora, Japan.— Bulletin of the National Science Museum, Tokyo, Ser. 17(4), 311–314.
- GEINITZ, F.E. (1880): Der Jura von Dobbertin in Mecklenburg und seine Versteinerungen.— Zeitschrift der Deutschen Geologischen Gesellschaft, 32, 510–535.
- GIEBEL, C.G. (1856): Die Insecten und Spinnen der Vorwelt mit steter Berücksichtigung der lebenden Insekten und Spinnen.— Die Fauna der Vorwelt, 2, 1–511.

- GRABAU, A.W. (1923): Cretaceous fossils from Shantung.– Bulletin of the Geological Survey of China, 5, 143–181.
- HANDLIRSCH, A. (1906–1908): Die Fossilen Insekten und die Phylogenie der Rezenten Formen, parts V–VII.– Ein Handbuch für Palaontologen und Zoologen, 1364.
- HINKELMAN, J. (2019): *Spinaeblattina myanmarensis* gen. et sp. nov. and *Blattoothecichnus argenteus* ichnogen. et ichnosp. nov. (both Mesoblattinidae) from mid-Cretaceous Myanmar amber.– Cretaceous Research, 99, 229–239. <https://doi.org/10.1016/j.cretres.2019.02.026>
- HINKELMAN, J. (2021a): *Mongolblatta sendii* sp. n. (Mesoblattinidae) from North Myanmar amber links record to Laurasian sediments.– Palaeontographica Abteilung A: Palaeozoology – Stratigraphy, 321, 81–96. <https://doi.org/10.1127/pala/2021/0105>
- HINKELMAN, J. (2021b): *Cuniculoblatta breviaolata* gen. et sp. n., the second case of brachyptery from Cretaceous North Myanmar amber.– Palaeontographica Abteilung A: Palaeozoology – Stratigraphy, 321, 97–107. <https://doi.org/10.1127/pala/2021/0104>
- HINKELMAN, J. & VRŠANSKÁ, L. (2020): A Myanmar amber cockroach with protruding feces contains pollen and a rich microcenosis.– The Science of Nature, 107, 13. <https://doi.org/10.1007/s00114-020-1669-y>
- HONG, Y.C. (1980): New genus and species of Mesoblattinidae (Blattodea, Insecta) in China.– Bulletin Chinese Academic Geological Science, Series VI, 1/2, 49–60.
- HUBER, I. (1974): Taxonomic and Ontogenetic studies of Cockroaches (Blattaria).– University of Kansas 568 Science Bulletin, 50, 233–332.
- KADDUMI, H.F. (2007): Amber of Jordan. The Oldest Prehistoric Insects in Fossilized Resin.– Eternal River Museum of Natural History, Amman, 298 p.
- KANIA, I., WANG, B. & SZWEDO, J. (2015): *Dicranoptycha* Osten Sacken, 1860 (Diptera, Limoniidae) from the earliest Cenomanian Burmese amber.– Cretaceous Research, 52, 522–530. <https://doi.org/10.1016/j.cretres.2014.03.002>
- KLASS, K.D. & MEIER, R.A. (2006): A phylogenetic analysis of Dictyoptera (Insecta) based on morphological characters.– Entomologische Abhandlungen, 63, 3–50.
- KOVÁČOVÁ, Z. (2023): New cockroach (Insecta: Blattaria) from North Myanmar amber.– Biologia, 78, 1679–1693. <https://doi.org/10.1007/s11756-022-01295-1>
- KOVÁČOVÁ, Z., MAJTANÍK, M. & QUICKE, D.L.J. (2023): Possibly Oxfordian (Upper Jurassic) cockroach assemblage (Insecta: Blattaria) from the Phra Wihan Formation in Thailand.– Biologia, 78, 1433–1446. <https://doi.org/10.1007/s11756-022-01294-2>
- KUHN, O. (1938): Drei neue Insekten aus dem Mesozoikum von Bayern.– Paläontologische Zeitschrift, 20, 318–320.
- LATREILLE, P.A. (1810): Considérations générales sur l'ordre naturel des animaux composant les classes des crustacés, des arachnides, et des insectes, avec un tableau méthodique de leurs genres, disposés en familles.– Chez F. Schoell, Paris, 444 p.
- LI, X.R., ZHENG, Y.H., WANG, C.C. & WANG, Z.Q. (2018): Old method not old-fashioned: parallelism between wing venation and wing-pad tracheation of cockroaches and a revision of terminology.– Zoomorphology, 137, 519–533. <https://doi.org/10.1007/s00435-018-0419-6>
- LIN, Q.B. (1982): Insecta.– In: Palaentological Atlas Of Northwest China: Shaanxi, Gansu, Ningxia, 3. Geological Publishing House, Beijing, 70–83.
- LIN, Q.B. (1986): Early Mesozoic fossil insects from South China.– Palaeontologica Sinica B, 170, 1–112.
- LINNAEUS, C. (1758): Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Editio decima, reformata. Tomus I.– Laurentii Salvii, Stockholm, 824 p.
- MAJTANÍK, M. & KOTULOVÁ, J. (2023): Insect J3–K1 assemblage from Tasgorosay in Kazakhstan was dominated by cockroaches.– Biologia, 78, 1565–1584. <https://doi.org/10.1007/s11756-022-01307-0>
- MARTÍNEZ-DELCLÓS, X. (1993): Blátidos (Insecta, Blattodea) del Cretácico Inferior de España. Familias Mesoblattinidae, Blattulidae y Polipbagidae.– Boletín Geológico y Minero, 104, 516–538.
- MARTINS-NETO, R.G., MANCUSO, A. & GALLEGO, O.F. (2005): The Triassic Insect Fauna from Argentina. Blattoptera from the Los Rastros Formation (Bermejo Basin), La Rioja Province.– Ameghiniana, 42/4, 1–21.
- MENDES, M. (2000): Novas baratas (Insecta, Blattodea) da Formação Santana, Cretáceo Inferior do nordeste do Brasil “New cockroaches (Insecta, Blattodea, Blattidae) from the Santana Formation, Lower Cretaceous, Northeastern Brazil.”– Revista da Universidade de Guarulhos: Série Geociências, 5/6, 25–35.
- OYAMA, N., YUKAWA, H. & IMAI, T. (2022): New cockroach assemblage from the Lower Cretaceous Kitadani Formation, Fukui, Japan.– Palaeontographica Abteilung A: Palaeozoology – Stratigraphy, 321, 37–52. <http://dx.doi.org/10.1127/pala/2021/0112>
- RAYNER, R.J., BAMFORD, M., BROTHERS, D.J., DIPPENAAR-SCHOEMAN, A., MCKAY, I.J., OBERPRIELER, R.G. & WATERS, S.B. (1998): Cretaceous fossils from the Orapa Diamond Mine.– Palaeontologia Africana, 33, 55–65.
- ROSS, A. (2025): Supplement to the Burmese (Myanmar) amber checklist and bibliography, 2024.– Palaeoentomology, 8, 12–28. <https://doi.org/10.11646/palaeoentomology.8.1.4>
- SCUDDER, S.H. (1886): A review of Mesozoic cockroaches.– Memoirs of the Boston Society of Natural History, 3, 439–484.
- SENDI, H., VRŠANSKÝ, P. & AZAR, D. (2023): Jordanian–Lebanese–Syrian cockroaches s.s. from Lower Cretaceous amber – Monograph.– Biologia, 78, 1447–1541. <https://doi.org/10.1007/s11756-023-01357-y>
- SHI, G., GRIMALDI, D.A., HARLOW, G.E., WANG, J., WANG, J., YANG, M., LEI, W., LI, Q. & LI, X. (2012): Age constraint on Burmese amber based on U–Pb dating of zircons.– Cretaceous Research, 37, 155–163. <http://dx.doi.org/10.1016/j.cretres.2012.03.014>
- SO, K.S., WON, C.G., RI, C.J., JON, S.H. & JU, I.Y. (2021): A new species of *Spinaeblattina* Hinkelman, 2019 (Insecta, Blattaria, Mesoblattinidae) from the Lower Cretaceous of Paektho-Dong, Sinuiju, Democratic People's Republic of Korea.– Paleontological Journal, 55, 910–912. <https://doi.org/10.1134/S0031030121080086>
- ŠMÍDOVÁ, L. (2020): Cryptic bark cockroach (Blattinae: *Bubosa poinari* gen. et sp. nov.) from mid-Cretaceous amber of northern Myanmar.– Cretaceous Research, 109, 104383. <https://doi.org/10.1016/j.cretres.2020.104383>
- ŠMÍDOVÁ, L. & LEI, X.J. (2017): The earliest amber-recorded type cockroach family was aposematic (Blattaria: Blattidae).– Cretaceous Research, 72, 189–199. <https://doi.org/10.1016/j.cretres.2017.01.008>
- ŠMÍDOVÁ, L., BRUTHANSOVÁ, J. & HAIN, M. (2024): The ootheca-bearing cockroach *Praeblattella* indicates primitive external egg retention in the Cretaceous.– Palaeontographica Abteilung A, 327. <https://doi.org/10.1127/pala/2024/0146>
- TILLYARD, R.J. (1919): Mesozoic Insects of Queensland. No. 6 Blattoidea.– Proceedings of the Linnean Society of New South Wales, 44, 358–382.
- VRŠANSKÝ, P. (1997): *Piniblattella* gen. nov. – the most ancient genus of the family Blattellidae (Blattodea) from the Lower Cretaceous of Siberia.– Entomological Problems, 28/1, 67–79.
- VRŠANSKÝ, P. (2003): Unique assemblage of Dictyoptera (Insecta – Blattaria, Mantodea, Isoptera) from the Lower Cretaceous of Bon Tsagaan Nuur in Mongolia.– Entomological Problems, 33, 119–151.
- VRŠANSKÝ, P. (2004a): Transitional Jurassic/Cretaceous Cockroach assemblage (Insecta, Blattaria) from the Shar-Teg in Mongolia.– Geologica Carpathica, 55, 457–468.
- VRŠANSKÝ, P. (2004b): Cretaceous Gondwanian Cockroaches (Insecta: Blattaria).– Entomological Problems, 34, 49–54.
- VRŠANSKÝ, P. (2005): Mass mutations of insects at the Jurassic/ Cretaceous boundary?– Geologica Carpathica, 56, 473–781.
- VRŠANSKÝ, P. (2009): Albian cockroaches (Insecta, Blattida) from French amber of Archingeay.– Geodiversitas, 31, 73–98. <https://doi.org/10.5252/g2009n1a7>

- VRŠANSKÝ, P. (2019): Santonian cockroaches from Yantardakh amber (Russia: Taimyr) differ in dominance.– *Palaeoentomology*, 002, 297–307. <http://dx.doi.org/10.11646/palaeoentomology.2.3.15>
- VRŠANSKÝ, P. (2020): Cockroaches from Jurassic sediments of the Bakhar Formation in Mongolia.– *Cham*, Switzerland, Springer Nature, 91 p.
- VRŠANSKÝ, P. (2024): Late Mesozoic cockroaches s.l. from the Karabastau Formation in Kazakhstan.– *Amba Projekty*, 14, 1–700.
- VRŠANSKÝ, P. (2025): Family diagnosis and paleogeography extended by asymmetrically deformed burmite liberiblattinid.– *Biologia*, 80, 937–947.
- VRŠANSKÝ, P. & ANSORGE, J. (2007): Lower Jurassic cockroaches (Insecta: Blattaria) from Germany and England.– *African Invertebrates*, 48, 103–126.
- VRŠANSKÝ, P. & KOUBOVÁ, I. (2025): *Kedysi akokolvek* gen. et sp. n. (Mantides: Mesoblattinidae; burmite) further complicates transition pattern towards Ectobiidae evidences.– *Palaeontographica: Abteilung A*, 331/4–6, 97–109.
- VRŠANSKÝ, P. & MAKHOUL, E. (2013): *Mieroblattina pacis* gen. et sp. n. – Upper Cretaceous cockroach (Blattida: Mesoblattinidae) from Namoura limestone of Lebanon.– In: AZAR, D., ENGEL, M.S., JARZEMBOWSKI, E., KROGMANN, L., NEL, A. & SANTIAGO-BLAY, J. (eds.): *Insect Evolution in an Ambiferous and Stone Alphabet*. Leiden: Brill, 165–172. https://doi.org/10.1163/9789004210714_012
- VRŠANSKÝ, P. & WANG, B. (2017): A new cockroach, with bipectinate antennae (Blattaria: Olidae fam. nov.) further highlights the differences between the Burmite and other faunas.– *Biologia*, 72, 1327–1333. <https://doi.org/10.1515/biolog-2017-0144>
- VRŠANSKÝ, P., ORUŽINSKÝ, R., ARISTOV, D., WEI, D.D., VIDLIČKA, L. & REN, D. (2017): Temporary deleterious mass mutations relate to originations of cockroach families.– *Biologia*, 27, 886–912. <https://doi.org/10.1515/biolog-2017-0096>
- VRŠANSKÝ, P., ORUŽINSKÝ, R., BARNA, P., VIDLIČKA, L. & LABAN-DEIRA, C.C. (2014): Native *Ectobius* (Blattaria: Ectobiidae) from the early Eocene Green River Formation of Colorado and its reintroduction to North America 49 million years later.– *Annals of the Entomological Society of America*, 107, 28–36. <https://doi.org/10.1603/AN13042>
- VRŠANSKÝ, P., VRŠANSKÁ, L., VASILENKO, D.V., PUŠKELOVÁ, L., BIRON, A. (2021): An isolated Cretaceous analogue of Madagascar on the Adria-Turkey microcontinent indicated by fossils in Brezina, Algeria.– *Palaeontographica Abteilung A: Palaeozoology – Stratigraphy*, 321, 19–35. <https://doi.org/10.1127/pala/2021/0107>
- VRŠANSKÝ, P., KOVÁČOVÁ, Z., VASILENKO, D.V., PÁLKOVÁ, H., NAGY, Š., KOSNÁČ, D., VIDLIČKA, E. & MARTIN, S.K. (2024): Systematics of Mesozoic 'Arctic' polar cockroaches.– *Biologia*, 80, 51–77. <https://doi.org/10.1007/s11756-024-01814-2>
- VRŠANSKÝ, P., LEE, S.B., SOHN, J., VRŠANSKÁ, L., JANG, J. & NAM, G.S. (2025): Jinju cockroaches.– *Amba Projekty*, 15, 1–174.
- WEI, D.D. & REN, D. (2013): Completely preserved cockroaches of the family Mesoblattinidae from the Upper Jurassic-Lower Cretaceous Yixian Formation (Liaoning Province, NE China).– *Geologica Carpathica*, 64, 291–304. <https://doi.org/10.2478/geoca-2013-0021>
- WESTWOOD, J.O. (1854): Contributions to fossil entomology.– *Quarterly Journal of the Geological Society*, 10, 378–396.
- ZHANG, H.C. (1997): Early Cretaceous insects from the Dalazi Formation of the Zhixin basin, Jilin Province, China.– *Palaeoworld*, 7, 75–103.
- ZHANG, Y., CHEN, L., WANG, Z., FANG, J. & LUO, C. (2023): A new cockroach (Blattaria: Mesoblattinidae: Spinaeblattina) from the Lower Cretaceous Laiyang Formation of China.– *Cretaceous Research*, 156, 105808. <https://doi.org/10.1016/j.cretres.2023.105808>

ONLINE FIRST