PETER VRŠANSKÝ

Late Mesozoic cockroaches s.l. from the Karabastau Formation in Kazakhstan

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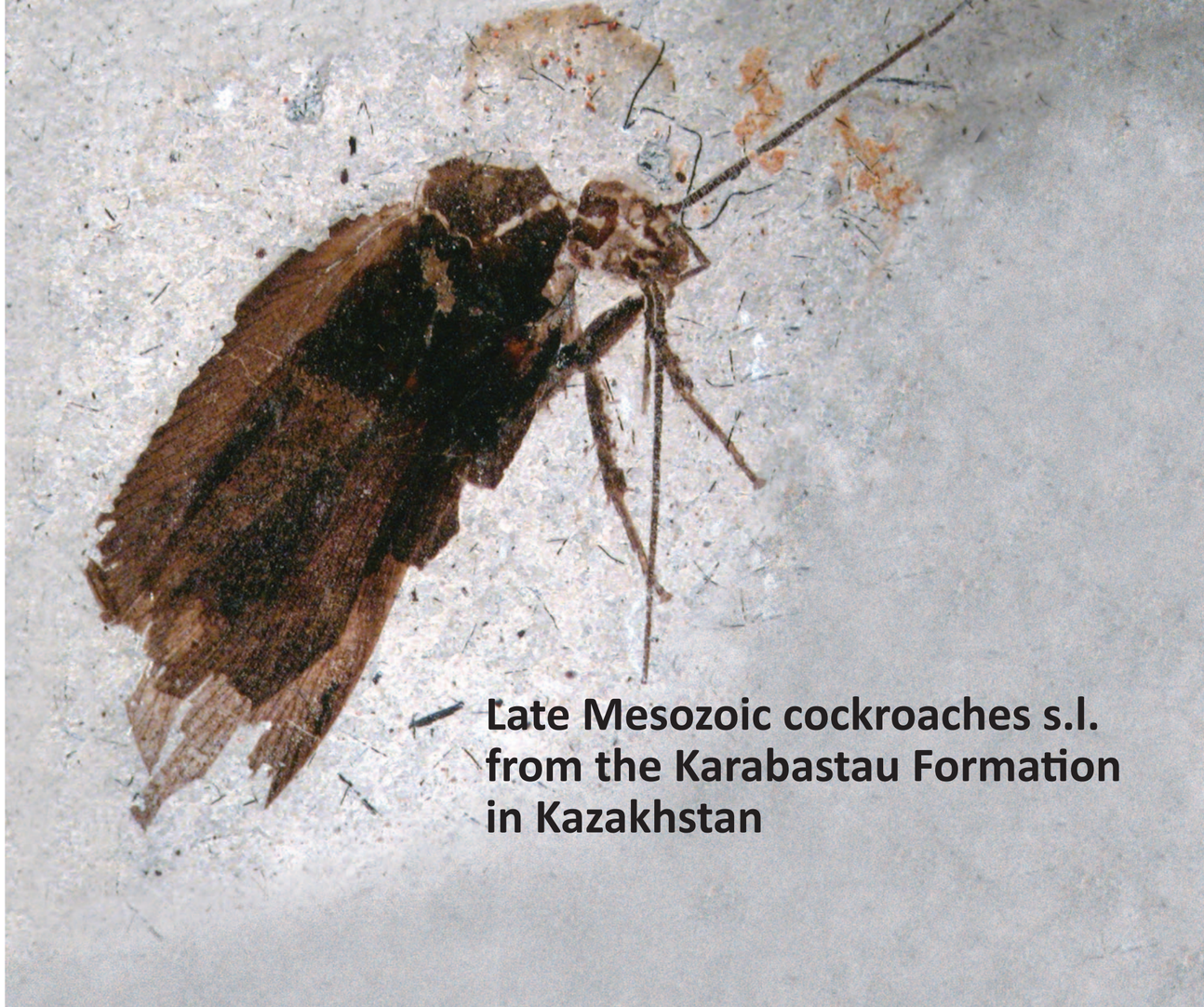

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Nikto nevie. Ten kto vie, toho to nezaujíma.

(“Nobody knows. Who knows is not interested.” Zuzana V. 2019, Smolenice)

…a response of my friend to an accommodation request in a congress centre…

I would like to express this primitive and epic work to the memory of my examples, my intellectual models, Ἐμπεδοκλῆς, 老子, عمر خيام and Immanuel Kant. **Bearing in mind their possible capabilities, I was attempting to reach their heights independently on them, as a teen. Instead, my fate resulted in 30 years of studying Kazakhstan cockroaches. This pointing reality is aimed at a single gained wisdom: there are no animal-human stars hanging freely in outer space. They did not originate there. To each of them there are firm stairways, just untrustily long. To this small lantern of this book, there are 2,539 single steps of roughly 55,000 I already have made before and of 110,000 total possible ones. The stars of these gigants are still as remote as in the beginning, but the distinct stairs are clearly recogniseable leading from here to them now. It worth this work (seeing them).**

What is right may properly be uttered even twice. Ἐμπεδοκλῆς (Empedocles)

Name that can be named is not that name anymore 老子 (Lao-c´)

And make the writer on a fairer leaf. Inscribe our names, or quite obliterate! **عمر خيام** (Omar Khajjám)

Do not erect a name without a sound reason, do not omit a name without a significant reason.
Immanuel Kant

These Big 4 also created the history greatest mistakes, which goes side by side. Thus I also dedicate this 30 years of work to fairly open-minded and non-aligned future followers of the unbiased pure, unequivocal and independent truth (if any).

Please recover the global forest.

Running title: Karatau cockroaches s.l.

LATE MESOZOIC COCKROACHES S.L. FROM THE KARABASTAU FORMATION IN KAZAKHSTAN

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Bratislava 2024-07-21
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Press-release: **Within 315-million-years of life on Earth and cockroach existence on land, the Karabastau of Kazakhstan is the most diverse fossil site, with three thousands Jurassic cockroach specimens and 95 species traced evolutionary patterns in non-parallel detail. Data specifically comprise morphological details and coloration variabilities and also wing mutations are discussed. The paleoenvironment reveals a rainforest-like ecosystem formed by diverse, multietage conifer trees, interconnected by-fungi, and with a complex structure of predators, parasites, endosymbionts and several pollinators. The most diverse known conifer biome was lacking (only) advanced flowers, grasses and eusocial mammals. The study might help in global forest recovery.**

ABSTRACT: **The here established Global Contemporary Nature Reference Point (GCNRP8) of history's richest fossil site, namely the Karabastau Formation in Kazakhstan, reveal the first systemic comparison with modern terrestrial non-marine ecosystems and also with all Mesozoic Lagerstätten. It is find closest to paleogeographically adjacent Laurasian Bakhar and coeval Gondwanan Kota. An unequivocally "tropical" biome was found here based on the recorded palaeoflora and fauna, suggesting that it was fully structured, interconnected by fungi, in multietage forests with multiply tree levels including a canopy, moss and shrub levels, and likely rarely comprising early angiosperms, but lacking advanced ones such as grasses. A fully established foodchain was found here that included predators, parasites, parasitoids, commensals and endosymbionts. Nearly half of the insect families represent extant clades. Cockroaches (forming 9.7 % of all insects) with the earliest known praying mantodean, a termite, umenocoleoid, operamid, manipulatorid, blaberid and the earliest corydiid are formally described along with 95 cockroach species (73 new; n= 2,539 classified) of possibly Kimmeridgian Upper Jurassic age (supported by plants, palynology, and tectonics). Taphonomy with 18.8 % of articulated adults and 7.3 % immature individuals suggest short pre-depoisitional transport and splashing of living insects from banks – localities Galkino and Mikhailovka slightly differ intuitively, but not statistically. Forewing variability performed for 14 species reveal Coefficient of variability ranges CV 7.42-17.5 % (7.42-12.07 % for four statistically significant sets) independent on the species size (ave= 14.5 mm). Extremely rare mutations reveal lowest ever rate (1.6 % of specimens). Network analysis is found irrelevant for forewings only – topology is intuitively correct (due to similarity), but clade supports decrease with increased robustness, while complex (including body) dataset reveals intuition-identical topology and statistical supports for most major clades. On the basis of this locality and time interval, restricted family-level diversification rate of indigenous cockroach families is fastest among all insects (0.6 per 1 Ma). First systemic approach with disentangled structure of evolution found its phenetic and phylogenetical (origins and radiations of taxa and life-forms separately) aspects acting highly independently. Unique genera in Karatau evolved more quickly than unique forms (diversification rates 2.01/0.69 per 1 Ma), also accelerated in Karatau compared with general ratio 0.13 per 1 Ma. Otherwise extremely rare *Eye* forewing form present in 9 genera and 18 species is a reliable evidence for an "ecosystem fashion". Significant advance in evolutionary theory shifts the main phylogeny hypothesis as a process of (1) a "constructive capillary compensation" (organising-to-complexity) – (2) "adaptive" stabilisation — (3) "explosive reduction ring" radiations concept, open now for testing along taxonomic spectra. Hopefully the study will help in global forest recovery.**

Keywords: Fossil insects, Blattodea, Mesozoic, evolution, systematics, phylogenetics

Illustrations: 165; outlines: 283; charts: 48; photographs: 996; tables: 30; CT:2; SEM: 11



SUMMARY

Cockroaches belong to one of the most numerous terrestrial fossils with 110,000 collected specimens, and evaluation of main Lagerstätten is still incomplete (with 13/29 examined sites), highlighting their vast contribution to past ecosystems (knowledge). The greatest fossil assemblage of cockroaches is described here from the sediments of the Karabastau Formation in Kazakhstan from a possible Kimmeridgian Upper Jurassic age (supported by insects, plants, pollen and tectonics). The assemblage consists of 73 new and 22 already established species. Among 2,539 classified cockroach specimens (659 were indetermined from a total 3,198), constituting 9.7 % of all collected insects, dominant were Caloblattinidae (n= 261; 10.3 %), Blattulidae (n= 745; 29.3 %), predatory Raphidiomimidae (n= 508; 20 %) and Liberiblattindiae (n= 791; 31.15 %). Blaberidae (n= 5; 0.2 %), Mesoblattinidae (n= 55; 2.17 %), Fractaliidae (n= 1), golden beetle-like Latiblattidae (n= 86; 3.39 %), predatory Manipulatoridae (n= 5; 0.2 %), Corydiidae (n= 1), eusocial Socialidae (n= 1), Operamidae fam.n. (n= 7; 0.28 %), predatory mantid Lovecidae fam.n. (n= 8; 0.32 %), beetle-like Umenocoleidae (n= 1) and holoptic Skokidae (n= 6; 0.24 %) were rare. Fuziidae and Chresmodidae were absent. Blaberidae, Umenocoleidae, Fractaliidae, Manipulatoridae, Corydiidae, Socialidae have their first appearance (FOD) in Karatau, Kazakstan, while Latiblattidae, Lovecidae, Operamidae, Skokidae are indigenous to this locality (with both FOD and LOD). FOD/indigenous/LOD ratio reveal a strongly asymmetrical value 13/21/1 among a total 48 genera. The first systemic approach disentangled structure of evolution phenetic and phylogenetical aspects (origins and radiations of taxa vs forms separately) acting highly independently. Local genus/form diversification rates extracted from differences from the predecessing cockroaches of (GCNRP7) Daohugou reveal highly differing rates 2.01 and 0.69 (comparable with 0.6 for families) per 1 Ma respectively, which is, nevertheless, highly accelerated diversification rate compared with a general form ratio of 0.13 per 1 Ma in cockroaches. Otherwise extremely rare Eye forewing form present in 9 genera and 18 species is a reliable evidence for an "ecosystem fashion".

Dominant species were the blattulids *Blattula brevicaudata* Vishniakova, 1968 (n= 418), *B. rectinervosa* Vishniakova, 1971 (n= 153); and the liberiblattinids *Aktassoblatta fusca* Vishniakova, 1971 (n= 535), *Memento mori* (n= 110) and *Ano ona* (n= 92). *The d*iversity index 3.241/7.407 (SW/Hulbert); the genus indigousness was 43.8 %. The most dominant species and the most diverse genus are indigenous – a pattern observed also in other sites and confirming Reduction ring theory. Cohorts recorded eudominant decomposers; predatory manipulatorids, lovecids, diverse liberiblattinids, blattulids and raphidiomimids (1+1+27+15+22= 66 spp.; n= 3+9+791+745+508= 2,056); golden-beetle-like latiblattids (4 spp., n= 55); aquatic (1 sp.; n= 1 and 47 larvae); brachypterous (n=?1), presumed beetle-like pollinator (n= 1) and presumed liberiblattinid pollinators (1 sp., n= 6 and 1 larva). The high partition of sophistically colored individuals and taxa indicate a wet and complex environment. 10.42 % (10) of cockroach species posses monochromatic coloration, 25.53 % (24) sophisticated coloration, which is the highest partition in any known fossil assemblage supporting acceleration of insect lifeforms in Karatau. Six species have entirely transparent forewings. Ecologically remarkable

are the dominant *Blattula rectinervosa*, the rare *Asioblatta punctata* and *Rhipidoblatta triky,* which might serve as food for birds or pterosaurs (preserved together in a single regurgite). *Blattula brevicaudata, B. microscopica, Chuanblatta stalosa* and *Aktassoblatta fusca* were discovered in diverse putative fish coprolites and regurgites. Traces of predation are visible as broken legs and bitten fore- and hindwing apexes. Variability revealed indicate very similar per centual values in all species, contributing to the proposed variability trends over time, and at the same time reveling similar values in a single locality over the cockroach spectra – on similar phylogenetical stage (CV= 7.42/10.12 (*B. microscopica* F/H); 7.8/9.62 (*B. rectinervosa* F/H); 8/9.38 (*B. brevicaudata* F/H); 8.31/15.19 (*A. ona* F/H); 8.63/13.86 (*A. chorevei* F/H); 10.3/11.33 (*A. bavsa*); 9.29 (*D. triocella*); 12.07/21.79 (*A. fusca* F/H); 13.2 (*C. stalosa*); 14.17 (*F. casovec);* 14.88 *(Olzmazg si);* 14.98 (*F. storozhenkoi*); 15.54 (*L. lativalvata*); 17.05 (*M. mori*)). Wing deformities representing deleterious mutations were extremely rare (n= 57; 1.6 %) suggesting a balanced ecosystem - high competition exceptionally favouring well flying groups can be excluded by short predepositional transport and occurrence of non-flying immature individuals and also non-flying adults. Forewing sizes ranges between 2.5 and 36 mm (with an average of 14.5 mm). Wing areas reveal average 38.63 veins on 56.3 mm^2 and 0.69 veins per 1 mm^2; R^2= 0.69 for forewings and 25.46; 34.65; 0.74; R^2= 0.56 for hindwings. Besides a different forewings shape of the umenocoleid (somewhat similar to a hindwing), the shape analysis does not reveal separation of any taxa (not even species). Numerous species of very similar Blattulidae might represent evidence for two different asynchronous assemblages represented in collections (but not more due to homogenous fish fauna). Comparing cockroaches from Karatau with other Late Jurassic sites, it is advanced in evolutionary aspect, suggesting J3-K2 transitional stage, with specialized liberiblattinids, umenocoleids, caloblattinids and blattulids and also with post-127Ma-Diversification-Point taxa (mantodeans, umenocoleoids, termites, corydiids and blaberids), only ectobiids are missing. This is coevally consistent with the proposed stratigraphic indications of the J3-K1 age. Paleogeographically nearly half of the Karabastau cockroaches are indigenous, otherwise they are typically pan-Laurasian with links to Gondwana represented solely by *Cameloblatta* (North Korea and the North Myanmar amber) and *Liberiblattina* (found also in Kota, India). Relation with other localities confirms close links with Bakhar and Daohugou and also Yixian.

This exceptional material allowed for significant advance in evolutionary theory shifts the main hypothesis as a process of (1) a "constructive capillary compensation" (organising-to-complexity) – (2) "adaptive" stabilisation – (3) "explosive reduction" radiations/diversification concept. Also mass mutations are proved in the general scheme ouwing evolution evidence independent on morphology and coloration.

Gut content reveals a mixed detritivorous diet for the studied liberiblattinids, caloblattinids and mesoblattinids, and carnivory for lovecids, manipulatorids and raphidiomimids on the basis of chitins of insect exosceletons.

Network analysis is found irrelevant for forewings only (supports decrease with increased robustness 82-51 as 32.4-13.68 %), while complex local dataset (including bodies) reveal intuition-identical topology (due to here-revealed similarity) and statistical supports for most major clades. Mantodea, Umenocoleoidea, Skokidae and Blattulidae excluding more basal groups are being ingroups of Liberiblattinidae in this local dataset - derived from Raphidiomimidae with Manipulatoridae and Caloblattinidae (and Latiblattidae as ingroup). Judging only on the basis of this locality, the diversification rate of cockroaches at family level is the fastest among all insects.

Taphonomy of most of the 35 non-biased Karatau collections was strongly favoured (non-biased by collecting) towards complete individuals (900 adults/1281 FW/633 HW/186 immature individuals), which in combination with complete immature stages mostly suggest short pre-depoisitional transport and drowning of insects from the lake/river banks. Locallties Galkino and Mikhailovka, which differ by fish taphonomy and in insects slightly intuitively, did not differ statistically.

After Messel Gruße (GCNRP1), Baltic amber (GCNRP2), North Myanmar amber (GCNRP3), Lebanon amber (GCNRP4), Crato (GCNRP5), Yixian (GCNRP6) and Baissa (GCNRP7) sediments, Karabastau is established here as the Global Contemporary Nature Reference Point (GCNRP8), before Daohugou as the last GCNRP9 with occurrence of rather completely preserved non-marine ecosystems.

The paleoenvironment reveals a rainforest-like, unequivocally "tropical" biome, which was fully structured, interconnected by fungi in multietage forests with multiply tree levels including a canopy, moss and shrub levels, probably with rare early angiosperms, but possibly lacking advanced angiosperms such as grasses, and eusocial mammals. Nearly halve of the insect families represent still living clades. Fully established foodchain included predators, parasites, parasitoids, commensals and endosymbionts.

Discrepancy with Karatau botanical (macrofossil and pollen) record is caused taphonomically – rich flora already occurred in the predecessing Daohugou and evidence is also rising for records of true flowers and fruits in the Early Jurassic.

Hopefully the study will help in global forest recovery.

ESTABLISHED TAXA:

Aktassoblatta fusca Vishniakova, 1971
= Palaeovia praecarnia Vršanský, 2008 syn.n.
Aktassoblatta pullata Vishniakova, 1971
Asioblatta punctata Vishniakova, 1968
Blattula brevicaudata Vishniakova, 1968
Blattula rectinervosa Vishniakova, 1971
Cameloblatta variegata Vishniakova, 1973
Decomposita triocella Vršanský, 2008
Falcatusiblatta karatavica (Vishniakova, 1968) comb. Liang et al. (2018)
= Rhipidoblattina karatavica Vishniakova, 1968
Fractalia aristovi Vršanský in Vršanský et al. (2021)
Hydrokhoohydra aquabella Vršanský in Vršanský et al. (2019)
Karatavoblatta longicaudata Vishniakova, 1968
Kazachiblattina asiatica (Vishniakova, 1968) comb. Vršanský (2002)*= Artitocoblatta asiatica* Vishniakova, 1968
Latiblatta lativalvata Vishniakova, 1968
Liberiblattina ihringovae Vršanský, 2002
Pseudomantina nigroalba Vršanský in Vršanský et al. (2021)
Raphidiomima chimaera Vishniakova, 1973
Raphidiomima cognata Vishniakova, 1973
Rhipidoblatta fusca Vishniakova, 1968
= Srdiecko tri Vršanský, 2008 syn.n.
Rhipidoblatta brevivalvata Vishniakova, 1968
Rhipidoblattina maculata Vishniakova, 1968
Rhipidoblattinopsis latitergata Vishniakova, 1968
Skok svaba Vršanský, 2007

FORMALISED TAXA:

Ano mal sp.n.
Ano ona sp.n.
Ano naslosa sp.n.
Ano palindrom sp.n.
Ano si sp.n.
Ano tak sp.n.
Akinisia chorevei gen. et sp.n.
Aposema gigantenna gen. et sp. n.
Asvab bavsa gen. et sp.n.
Blattula ahanaha sp.n.
Blattula druha sp.n.
Blattula fragilia sp.n.
Blattula gracilicosta sp.n.
Blattula microscopica sp.n.
Blattula nebude sp.n.
Blattula summa sp.n.
Caloblattina laesis sp.n.
Cameloblatta stress sp.n.
Chuanblatta stalosa sp.n.
Cretaholocompsa karatauensis sp.n.
Decomposita apicata sp.n.
Decomposita basquatirgis sp.n.
Decomposita pentavisia sp.n.
Decomposita tristriata sp.n.
Divocina polnoci sp.n.
Elisama prelistama sp.n.
Elisamoides sediomasle sp.n.
Falcatusiblatta casovec sp.n.
Falcatusiblatta disrupta sp.n.
Falcatusiblatta storozhenkoi sp.n.
Falcatussiblatta tooold sp.n.
Falcatussiblatta zaloha sp.n.
Fosilia tubuliovipositorica gen. et sp.n.
Hra nice sp.n.
Katatychi symptosi gen. et sp.n.
Liadoblattina crassivenata sp.n.
Latiblatta osud sp.n. (Latiblattidae fam.n.)
Liberiblattina cunicula sp.n.
Liberiblattina cipka sp.n.
Liberiblattina kontrapunktata sp.n.
Liberiblattina kontravenata sp.n.
Liberiblattina liberiblattina sp.n.
Liberiblattina luminanala sp.n.
Liberiblattina nenicom sp.n.
Liberiblattina oddajsami sp.n.
Liberiblattina paleontologica sp.n.
Liberiblattina zokamuvypadli sp.n.
Lovec pratiena gen. et sp.n. (Lovecidae fam.n.)
Makacka akcakam gen. et sp.n.
Makacka akmacaka gen. et sp.n.
Maloval hlavolam gen. et sp.n.
Manipulator olim sp.n.
Macaroblattula velipsespilev sp.n.
Memento mori gen. et sp.n.
Mesoblattina etarakan sp.n.
Miniblattina inflatica sp.n.

Morphna una sp.n.
Okienkula ojedinela gen. et sp.n.
Okruhliak samoodpovedaniesi gen. et sp.n.
Olzmasg zi gen. et sp.n.
Operam monita gen. et sp.n. (Operamidae fam.n.)
Operam simpla sp.n.
Operam testudina sp.n.
Perlucipecta liangiae sp.n.
Rhipidoblatta matriky sp.n.
Rhipidoblatta matrikarky sp.n.
Rhipidoblatta triky sp.n.
Rhipidoblatta trimestre sp.n.
Rhipidoblatta trika sp.n.
Rhipidoblattina dmitrievi sp.n.
Sivis lukashevichiae sp.n.
Sociala borat sp.n.
Spono spono sp.n.

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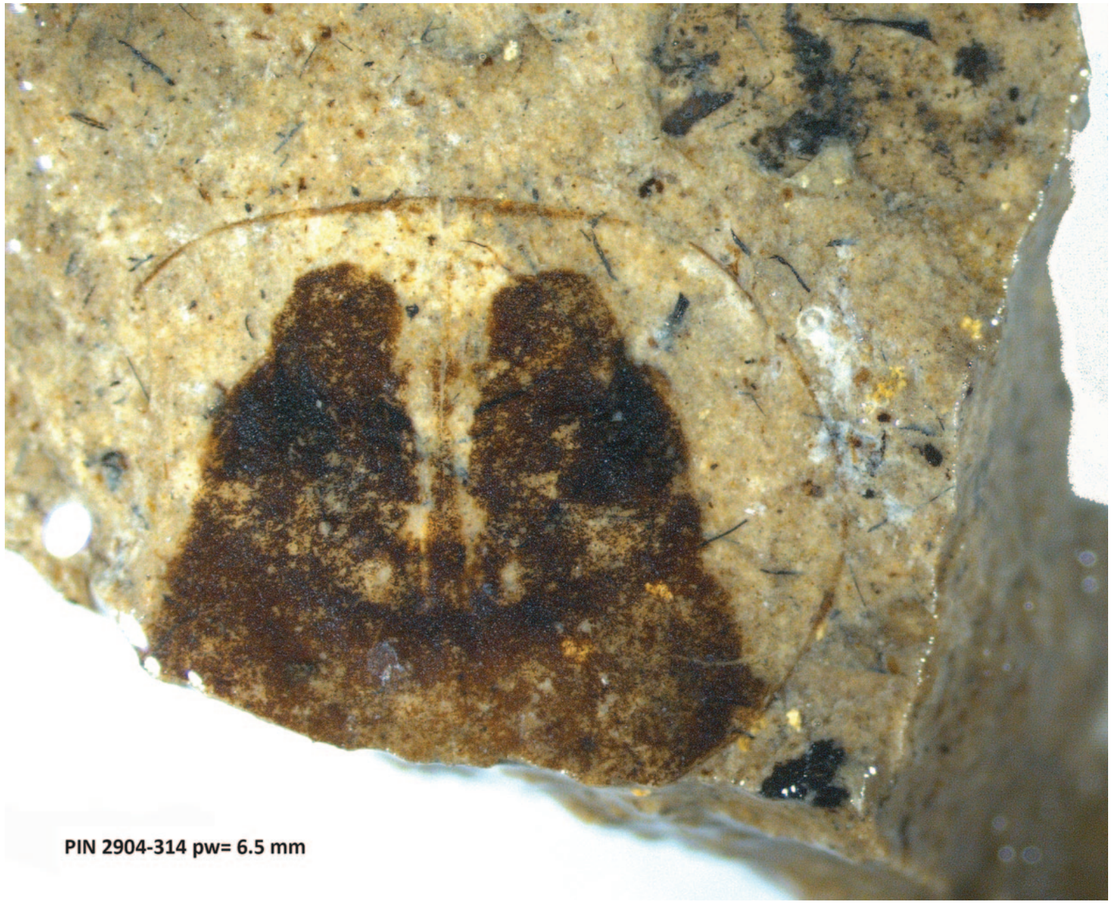


STRUCTURE OF THE BOOK

Over a thousand visual representations inevitably lures most of the nature lovers, naturalist and even researchers. In this respect it would be more logical to include general conclusions and chapters with global relevance first. Nevertheless, this is due to taxonomical principles impossible – results cannot be discussed prior the formal establishement of respective taxa.

Nevertheless, the most general conclusions regarding ecosystems are placed in the very beginning (green bookmark).

It includes also Philosophical conclusion, marked with empty bookmark. As I expect most readers do not have a quantum physics fundament, I recommend to skip this chapter or postpone it at the end of the reading.

Consequently, the taxonomy part is in the very actual beginning. For non-specialist I recommend to skip the whole taxonomical part (with red bookmark).

Follows the blue-bookmark part relevant to all entomologist and green bookmark part second part possibly interesting to all biologist.

Final gray bookmark label is for the systemic conclusions which might be relevant for multidisciplinary readership.

Please let me introduce this epos about ancient cockroaches by citing the funeral speech of our former president:

“Death is like a life. But totally different.“



INTRODUCTION TO KARABASTAU COCKROACHES

Introduction to a similar study of fossil cockroaches was performed in December 2020 (Vršanský 2020), so here only an amendment is presented.

From that time, in 2021, huge cockroach s.s. collections were additionally evaluated (Anisyutkin and Perkovsky 2021; Hinkelman 2021ab; Chen et al. 2021ab; Li and Huang 2021; Liang et al. 2021; Luo et al. 2021; Oyama et al. 2021; So and Won 2021abc; So et al. 2021; Sendi 2021ab, 2024ab; Schneider et al. 2021; Šmídová 2021; Šmídová et al. 2021, 2024; Song et al. 2021; Taniguchi et al. 2021; Vršanský et al. 2021abcde, Wappler and Vršanský 2021; Vršanský and Kazimírová 2023 and citations therein), allowing for more general evolutionary patterns to be identified, discovered and catalogised, exemplifying huge collection and study potential for stratigraphy, phylogeny, variability, diversity and ecology of ancient biotas and understanding of living ones.

These papers from 2021 progressed in revealing probably the most bizzare cockroach in the history (*Laticephalana*), first two brachypterous fossils (*Cuniculoblatta, Cercoula*), the most abundant fossil cockroach in history (*Chuanblatta,* n= 655 in a single collection at CNU Beijing with more specimens still being located within other governmental and private institutions in China), new localities in Germany, North Korea, U.S.A and Algeria, earliest representatives of respective families, most primitive termite, metallic cockroach and many others. In total, 48 new species of fossil cockroaches s.l. were formalised in 2021.

They were followed with 20 new species s.s. erected in 2022 (Qiu 2022; Li and Huang 2022; Correia et al. 2022; Vršanský et al. 2022ab; Szabó et al. 2022; Poinar 2022; Káčerová and Azar 2022; Hinkelman 2022; Kováčová 2022; Vršanský and Sendi 2022) particularly with first rainbow insect with photonic crystals, new Jurassic sites in Kazakhstan and Thailand and in 2023 monographed Lebanese amber (Sendi et al. 2023ab, see also Vršanský and Kazimírová 2023; Anisyutkin and Perkovski 2023; Zhang et al. 2023; Barna et al. 2023; Majtaník and Kotulová 2023; Kováčová 2023; Kováčová et al. 2023; Liang et al. 2023).

The Jurassic has vast collections, including ~20,000 specimens that remain formally unevaluated (Handlirsch 1906, Vršanský and Ansorge 2007, Vršanský 2008), with certain Karabastau cockroaches already surveyed (Vishniakova 1971, 1973; Vršanský 2009, Liang et al. 2018, 2019, Vršanský et al. 2019, 2021e). Jurassic cockroaches were described by Germar (1839); Heer (1852, 1964, 1965); Giebel (1856); Oppenheim (1888); Brauer et al. (1889); Haughton (1924); Hong (1980, 1983, 1997); Lin (1978, 1982, 1985, 1986); Handlirsch (1939); Bode (1953); Fujiyama (1974); Whalley (1985); Zhang (1986); Wang (1987); Martynova (1951); Ren et al. (1995); Hong & Xiao (1997); Martin (2010) and Kováčová et al. (2023).

These fossil represent the same insect order of cockroaches s.str. (Vršanský et al. 2009), with cosmetical differences from living representatives. Nevertheless, most of them are from “another world” revealing the central ocellus and extremely long externally protruding ovipositor of females. It is hypothetised here that this ovipositor has laid eggs into the hardened prescursors of ootheca (Vishniakova 1968) as evidenced with the presence of oocytes

within extremely narrow tube of ovipositor (Vršanský et al. 2021a, Sendi 2021a).

Aim of the present study was to systematically describe more than 3,000 cockroach fossils from the locality Karatau in Kazakhstan, compare it with the other described and undescribed taxa from the Jurassic and Cretaceous periods and evaluate their ecological, stratigraphical and phylogenetical contexts. It is surprising that Karabastau had an extremely high diversity, and these nearly exclusively conifer forests are comparable to those extant anhiosperm-dominated rainforests.

Some recent general evolutionary patterns were confirmed, some were newly discovered and were presented here.

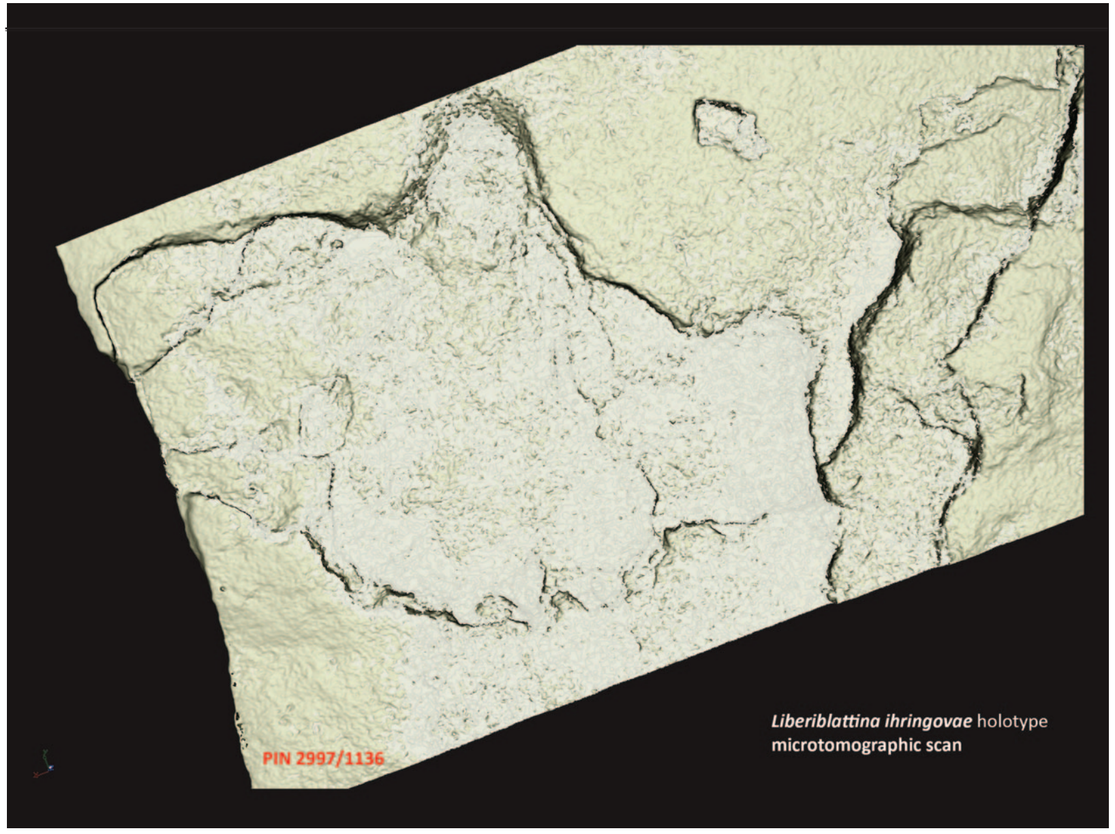
MATERIAL AND METHODS

Material (n= 3,198) catalogised cockroaches among ca. 30,000 collected insects (additional 26 excluded from the Blattaria collection; several additional specimens are under the same numbers as two or more impressions) was collected by the Paleontological Institute of the Russian Academy of Sciences (formerly UdSSR) in 1910-20 (M.A. Vedeniapin, the head of the expedition, collection 204, n= 8; V.D. Prinada, the head of the expedition to Galkino, collection 965, n= 63; N.V. Shabarov, the head of the expedition, collection 1789, n= 210, collection 2452, n= 808; A.I. Turutanova-Ketova, the head of the expedition, collection 5211, n= 6, collection 2231, n= 65, collection 2335, n= 100, collection 2465, n= 84); in 1936 (R.F. Gekker, the head of the expedition, collection 124, n= 10, the head of expeditions); in 1937 (B.B. Rohdendorf, the head of the expedition, collection 197, n= 291); 96 insects were collected by Middle Asiatic Institute; in 1962-1965 (A.G. Sharov, the head of the expedition to Mikhailovka; 1962: collection 2066, n= 3892; 1963: collection 2239, n= 2597; 1964: collection 2384, n= 1335; 1965: collection 2554, n= 1250).

Photographs were made using a Leica binocular lens with a Nikon pix. camera manually attached to the right ocular. Some of the photographs were manually combined.

Drawings represent re-drawn photographs checked under the microscope for venation details. Some of them were adjusted for coloration using ADOBE Photoshop (legal, whole-surface modifications). Wing nomenclature follow the Comstock-Needham system (1898-1899).

Abbreviations used: Sc- subcosta, R- radius, RS- radius sector, M- media, Cu- cubitus (CuA- anterior, CuP- posterior), A- anal veins, CW- cross-veins, IC- intercalary veins, f- forewing, ff- both forewings, h- hindwing, hh- both hindwings, p- pronotum, c- isolated clavus, l- length (in photograph it means the total length of specimen), w- width. FOD- First occurence, LOD- Last occurrence. GCNRP- Global Contemporary Nature Reference Point.



Abbreviations for localities: G – Galkino; M – Mikhailovka; K – Karabastau; O1 – outcrop 1; 02 – outcrop 2.

The study of the specimens was performed during 2005-2011 in the Arthropoda Laboratory, PIN RAS.

For phylogenetic analysis(figps. 597-602), I computed the most parsimonious trees (see discussion paragraph parsimony analysis) in PAUP* 4.0b8 (Swofford 2003) using a heuristic search, 10 random additional taxon replicates, the accelerated transformation optimization algorithm (ACCTRAN), as well as the three bisection-reconnection branch-swapping (TBR) algorithm. Characters were treated as unordered and unweighted. A 50 % majority-rule consensus tree was constructed from most parsimonious trees found during the heuristic search. Branching reliability was assessed by the bootstrap method with 1,000 replicates. A phylogenetic network is constructed in SplitsTree 4 (neighbour-net algorithm – Bryant and Moulton 2004) with bootstrap analysis (1,000 replicates) in effect.

Ordination analysis and similarity analysis (figs. **)** were performed using PAST.

Shape analysis (see Stroka 2023) were made using SHAPE, which uses Fourier analysis (Kuhl and Giardina 1982), and principal components (ChainCoder, CHC2NEF, ChcViewer, NefViewer, PrinComp a PrinPrint) (Iwata and Ukai 2002) The ChainCoder program extracts object outlines from digital images and stores the relevant information as a chain code (Freeman, 1974). Black and white images are processed by ChainCoder 8-bit quantization and stored as a chain code. The area of the object was also measured and recorded. The ChcViewer program is used to display the resulting file. The Chc2Nef program provides normalized EFA from chain-coded contours. The EFA coefficients are calculated by discrete Fourier transformation of the chain-coded contour (Kuhl and Giardina, 1982). The EFA coefficients are then normalized to be invariant with respect to magnitude, rotation, and initial point, a procedure based on the first harmonic ellipse (Kuhl and Giardina, 1982). Coefficients can also be normalized using a procedure based on the furthest point of the contour from its centroid. If these normalization methods do not help in assigning biological meaning to the contour shape, the coefficients can also be normalized using manual contour alignment. The NefViewer program is used to display the result. The PrinComp program performs a principal component analysis of the EFA coefficients. The normalized EFA coefficients still cannot be used directly as shape characteristics because the number of coefficients is generally very large and the morphological meaning of each coefficient is difficult to interpret separately. Principal component analysis is effective for summarizing information about the variation contained in the coefficients (Rohlf and Archie, 1984). PrinComp performs principal component analysis based on the variance and covariance matrix of the coefficients. The PrinComp program performs a principal component analysis of the EFA coefficients. Visualization is performed using the procedure proposed by Furuta et al. (1995). First, the EFA coefficients are calculated, with the score for a particular principal component equal to the mean plus or minus twice the standard deviation, that is, the square 27 root of the component's eigenvalue, and the remaining component scores are zero. Then, the shape of the contour for each condition can be reconstructed from the calculated coefficients by inverse Fourier transformation.

SEM investigation (at Division of microstructure of surfaces and interfaces, Institute of Materials and Machine Mechanics, Slovak Academy of Sciences) of the uncoated specimens observed in a SEM Jeol 6610 with SEI detector (JEOL Ltd., Tokyo, Japan). EDX detector Oxford X-max 50 mm2 (Oxford Instruments plc, Abingdon, United Kingdom) was used for chemical analysis of samples.

MicroCT imaging 3D microtomographic images were made using an Xradia MicroXCT system (Zeiss X-Ray Microscopy) with a tungsten microfocus X-ray source and variable secondary optical magnification. Mode= MO. Scans were made with an anode voltage setting of 160 kV and 90 µA with an exposure time of 750 ms for projection images every 0.20° over a half-rotation. Projections= 1,800. Using the 4X scintillator-objective and 2 k×2 k projection images without camera-pixel binning, scans were made of 3.3–3.5 mm regions of the sample with 1.7 or 1.8 µm pixels. Tomographic slices were reconstructed with the Xradia XMReconstructor software, and 3D images were exported as TIFF stacks with isotropic voxel sizes of 30 µm. No filter used. Images were analysed using VG Studio MAX 2.1 software.

UNIDENTIFIABLE SPECIMENS:

<u>Specimens excluded from the order (as these specimens were catalogised as Blattaria, it is most probable that it originally contained a cockroach, which was damaged during deposition, or an error occurred during the first, field lens-based inspection and examination; n= 26):</u> 2904/765; 2231/24; 2239/145; 2384/24±, 171, 316, 337, 630; 2452/77, 378, 500, 597, 623; 2997/4252± , 4260±, 4272±, 4274, 4313, 4320, 4356, 4375, 44?3, 4876, 4307, 4254±, 5071.

<u>Cockroaches incertae sedis (n= 661):</u>

Incertae sedis complete specimens (n= 152; if both, forewing and a hindwing was preserved, it is consider for a "complete" specimen; complete specimen means an adult):

- **Incertae sedis complete specimens family incertae sedis (<u>n= 15</u>):** 2066/45, 179=186, 488; 2384/198; 2452/402±; 2511/96; 2784/84,630, 2257; 2997/34,105, 189, 1397, 1677±, 4295.
- **Caloblatttinidae complete specimens (<u>n= 107</u>, disproportionally high partition of indetermined complete specimens result from the collection methodics – complete specimen is frequently collected also under weak preservation state, while badly preserved isolated part doubtfully will be even noticed in the field; unfortunately excellently preserved guts with contents occur on indeterminable specimens):** 1789/217 **G;** 2039/51; 2066/133, 223 (f= 20 mm), 291, 309, 437, 486, 437; 2231/63; 2239/154, 172, 187, 258±, 1678; 2384/29, 58, 61, 65± (male tergal glands), 196, 1114; 2452/121, 124, 144, 348, 379, 398, 401, 404, 407, 360, 954, 982±; 2554/3, 5, 6, 7, 30, 37, 38, 42, 176, 459; 2784/733, 777, 794, 899, 921, 930; 962, 1016; 2904/87 (with long ovipositor), 298, 329, 328, 336, 3217, 331,



319±, 325, 316, 333, 185, 206, 213, 220, 303±, 1899, 1900; 2997/64, 65, 67, 71, 72, 82±, 91, 141±, 164±, 165 (gut content 7.5 mm), 262, 263, 1134±, 1153±, 1173 (f= 11mm), 1175, 1195, 1202 (gut content), 1239, 1290, 1313, 1325, 1326, 1343, 1557, 1574, 1578 (gut content*), 1586±, 1624±, 1699, 1900, 4372, 4395, 4974, 4407, 4420, 4292, 4299.

- **Blattulidae complete specimens (n= 7):** 2066/48, 107, 127, 368, 371, 373, 497±.
- **Liberiblattinidae complete specimens (n= 13):** 1789/70 **G;** 2066/169; 2554/10, 63, 81; 2784/953; 2904/305, 379; 2997/96, 1282 (f= 9 mm), 1344, 1437±, 4278.
- **Raphidiomimidae complete specimens (n= 10):** 2066/357 (l= 7.6 mm); 2239/196, 245, 269; 2384/38, 281 (w= 1.8 mm); 2554/167; 2904/22± (f= 14 mm, ?Liadoblattina), 26±, 361 (with gut).

Incertae sedis forewings (n= 122):

- **Incertae sedis forewings family incertae sedis (n= 28,** this does not mean here are new families hidden – certain groups are so homoplasic that weakly preserved forewing does not allow discrimination, such as colored Liberiblattinidae and Raphidiomimidae from other superfamilies. I do not expect a hidden new family in the material): 1789/75 ; 2066/79, 159±, 210, 221 (l= 14 mm), 233=229, 226=326 (331), 230, 286, 399; 2239/156; 2384/ 82; 2554/89, 117, 144 (l= 14 mm), 159 (l= 22 mm), 170, 193, 197; 2784/658; 2904/14±, 15±, 16±, 20, 45±, 53±; 2997/1236, 1304.
- **Caloblattinidae forewings (n= 75):** 1789/66 **G,** 216 **G;** 2066/75, 193, 217, 243±, 265, 267, 275±, 340, 342, 353, 354±, 381, 392, 439, 514; 2231/21, 30; 2239/254; 2335/56; 2452/79; 2465/903 (not included in the table); 2554/119±, 127, 137, 138, 162, 172, 194, 1317±; 2784/643±, 675, 674, 679, 731, 779, 820, 878, 993, 8475; 2904/174, 250, 263, 270, 299, 300, 309, 1859, 1869, 1880, 1901, 1902; 2997/199±, 1140, 1188, 1262, 1265, 1275, 1277, 1291, 1299, 1301, 1372, 1408, 1559, 1562, 1566, 1587±, 1593, 1590, 1690, 2817, 4288, 4289.
- **Raphidiomimidae forewings (n= 6):** 2554/15, 124, 190; 2997/69, 172, 4306,
- **Liberiblattinidae forewings (n= 12):** 2066/62; 2239/88, 93, 97; 2384/ 129 (l= 13 mm), 1117; 2465/ 978; 2784/ 760±; 2997/ 117, 258 (l= 17 mm), 1148±, 4413.
- **Blattulidae forewings (n= 1):** 2066/161c.

Incertae sedis isolated clavi (n= 16; number of isolated is disproportionally low in this unselectively collected assemblage; nevertheless, there are some, which means at least limited conditions occurred allowing for long term (over a month) stay in water): 147/167 (l= 7 mm); 2066/364 (l= 7 mm), 369, 376, 494 (l/w= 6/ 2.5 mm); 2452/635 (l= 4 mm); 2904/247 (l= 9mm), 1894 (?Liadoblattina); 2997/271, 1205, 1224, 1229, 1286, 1368, 1621 (l= 3.7 mm), 1697 (l= 6 mm).

Incertae sedis hindwings (n= 109):

- **Incertae sedis hindwings family incertae sedis (n= 20)**: 1789/71 **G,** 80 **G,** 84 **G,** 926 (l= 17 mm) **G;** 2066/141, 187±, 236, 237, 239, 252, 435; 2335/16, 49; 2554/145; 2784/659, 934; 2904/174; 2997/204 (l= 13 mm), 1222, 2808 (*), 4373.
- **Caloblattinidae hindwings (n= 54):** 2066/178, 211, 215, 220, 243, 297, 344, 305, 310, 361, 378, 383, 395, 438±, 454, 465; 2239/267, 270, 279, 288±, 375; 2452/129, 235, 1567; 2554/41, 182, 186, 183; 2784/727 (l= 15mm), 775, 780, 988; 2904/135, 154, 159, 168, 173, 249, 256, 257, 1182 (l= 11 mm), 1883; 2997/47, 98±, 1183, 1214, 1271 (l= 9 mm!!!), 1280, 1287, 1331, 1352 (l= 13 mm), 1371, 1418 (l= 24 mm), 1670.
- **Liberiblattinidae isolated hindwings (n= 33):** 167/99 M, 156; 1789/63 (l= 9 mm: 1.4+3.3.4+blind) **G;** 2066/77, 251, 397; 2452/45 (h= 8 mm)(not included in the table); 2554/193 (l= 18 mm);



2784/722, 736, 798 (l= 7-8 mm: 3+8.5.7+), 850, 880, 917, 941, 958, 2268; 2904/165, 362, 411, 412; 2997/92, 1256, 1297, 1302 (l= 8.5 mm), 1305, 1320 (l= 12 mm), 1330, 1335, 1339, 1341, 1363, 4419.

- **Raphidiomimidae isolated hindwings (n= 2):** 2997/ 4193, 4355.

Incertae bodies (n= 37)

- **Bodies incertae sedis families (n= 9):** 2239/292; 2554/21, 26 (long ovipositor), 27, 108; 2904/1881; 2997/1579, 1641, 1629.
- **Bodies Caloblattinidae (n= 25):** 2066/34, 94, 200, 205; 2231/29, 62; 2335/15; 2452/352; 2784/759, 794 body, 2267, 2270 (ovipositor), 633, 757 (ovipositor); 2904/400; 2997/198±, 1185, 1575, 1661 (opvipositor), 1662 (ovipositor), 4086 (cuticle), 4243, 4244 (ovipositor), 1696 (ovipositor), 1720± (ovipositor).
- **Bodies Liberiblattinidae (n= 3):** 2239/321; 2384/160, 165.

Incertae legs (n= 68): 1789/223 **G;** 2066/52, 85± (broken), 102, 117, 121±, 138, 139±, 167, 335, 349, 359, 417±, 453, 456, 457, 461; 2239/293± (9.5mm femur) 294, 295±, 296± (10.5 mm tibia), 297±, 298, 299, 300, 301, 302±, 303= 308, 305, 306, 307, 309 (l= 8.5 mm), 311, 312, 314, 315±; 2335/59; 2384/1113, 1115, 1118= 1121; 1120±; 2452 336, 5171 (pathology); 2465/935; 2554/116, 154; 2784/709, 730, 924; 2904/38, 384, 385, 386, 387, 388, 389, 390, 391, 392, 393, 394; 2997/219, 1678±, 1680, 1681, 1683, 1684, 4285, 4342.

Incertae pronota (n= 6): 2066/188; 2239/191±; 2384/1286; 2784/273, 939; 2904/314.

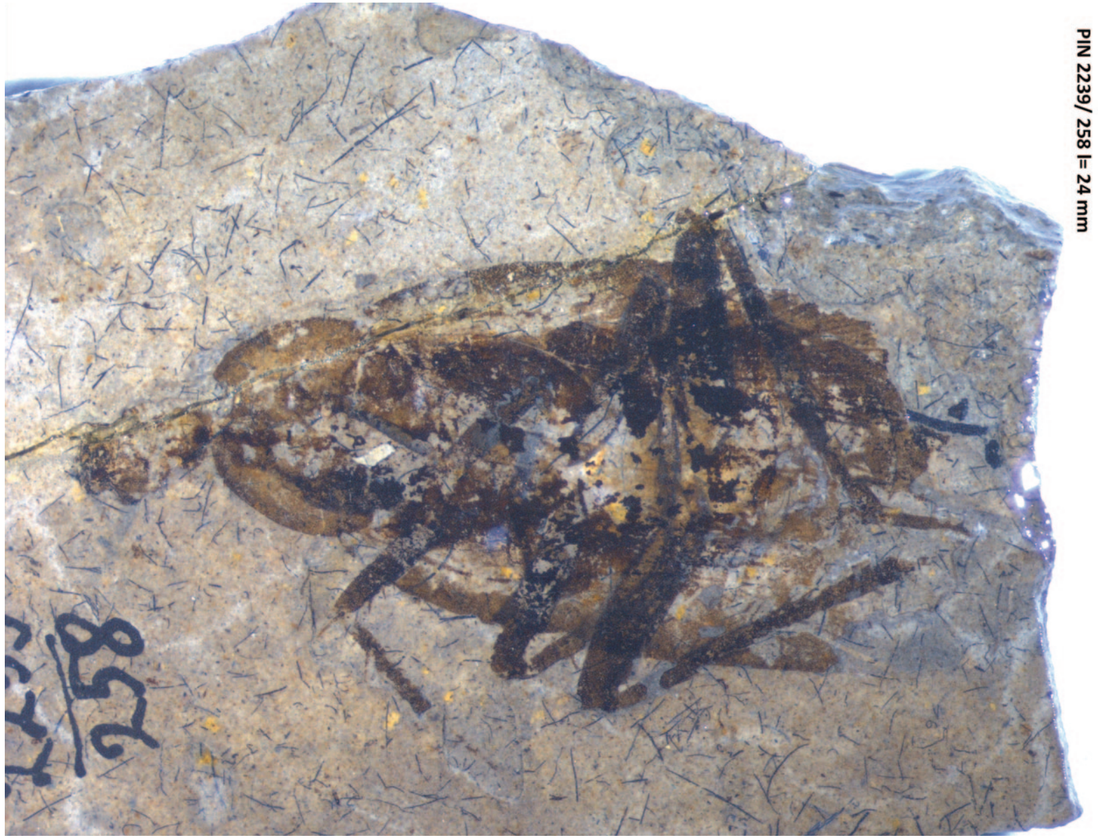
Incertae head (n= 1) 2239/249± (29 mm up to the antenna tip).

Unspecified fragments (n= 64)

- **Unspecified fragments family incertae sedis (n= 48,** consider that in minor fragments it is mostly impossible to discern Caloblattinidae and Raphidiomimidae, but also some fragments among small Liberiblattinidae and Blattulidae): GEOLCOM 5; 145/167 M; 167/303 M, 313; 2231/32; 2239/74, 86, 93, 224, 171, 190, 192, 204, 361; 2384/41, 69, 87, 107; 2452/78, 296=396, 489, 893; 2465/906, 917, 933; 2554/168, 172, 174; 2784/662; 2904/4, 204, 360, 372; 2997/27, 193, 243, 760, 1217, 1219, 1241, 1281, 1360, 1359, 1428, 1979±, 4273±, 4350, 4357.
- **Unspecified fragments Liberiblattinidae (n= 15):** 2039/29, 39, 45; 2239/194, 223; 2335/26, 71; 2384/52, 110; 2452/70, 383, 660, 658; 2997/94, 4943.
- **Unspecified fragments Raphidiomimidae (n= 1):** 2452/341.

Incertae sedis

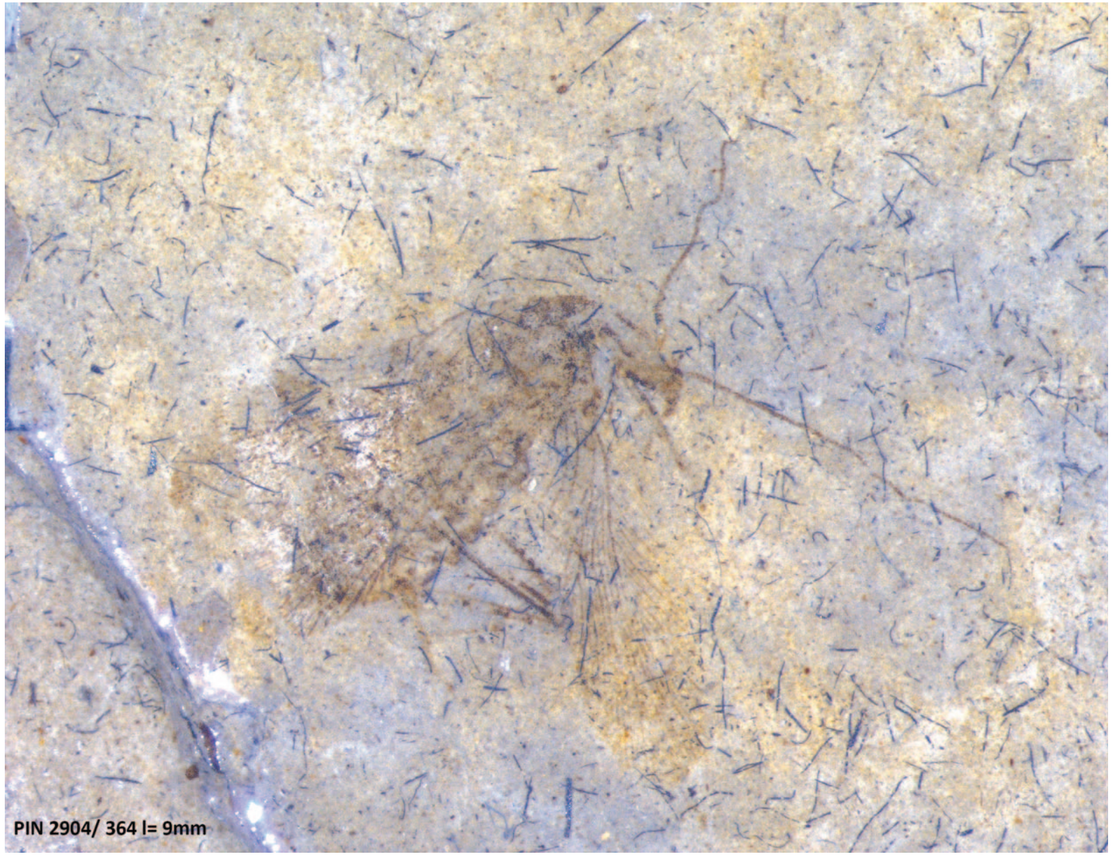
26 unidentified cockroaches and 659 cockroaches incertae sedis are huge numbers requiring attempt of explanation. Up to 261 of them are represented by Caloblattinidae. This is caused by high conservativeness of this family combined with numerous similar species occurring in eudominant genera such as *Rhipidoblatta*. As a result, numerous even rather well-preserved fragments are impossible to determine. Also, it is apparent that some unidentified species occur within the incertae sedis material, as apparently some small species (f= 11-13 mm) occur here unformalised among identifiable material. Considerable low proportions of isolated clavi (under 3 % of all material), suggests that most of the material did not underwent a pre-depositional transport and stayed in open water for a minimum time (3 weeks at most – see also Duncan et al. 2003). At the same time it is a direct evidence for rare stay longer in the same waterbody (for that rare 16 isolated clavi). For comparison, this ratio is usually doubled (6.1 % in the only complexly evaluated Bakhar). Taphonomical reasons for not collecting isolated clavi might be excluded due to very low number of disarticulated wings without clavus.
24 isolated legs also suggest a high fidelity of collections as isolated legs are usually either not preserved or not collected.



PIN 2239/ 258 l= 24 mm

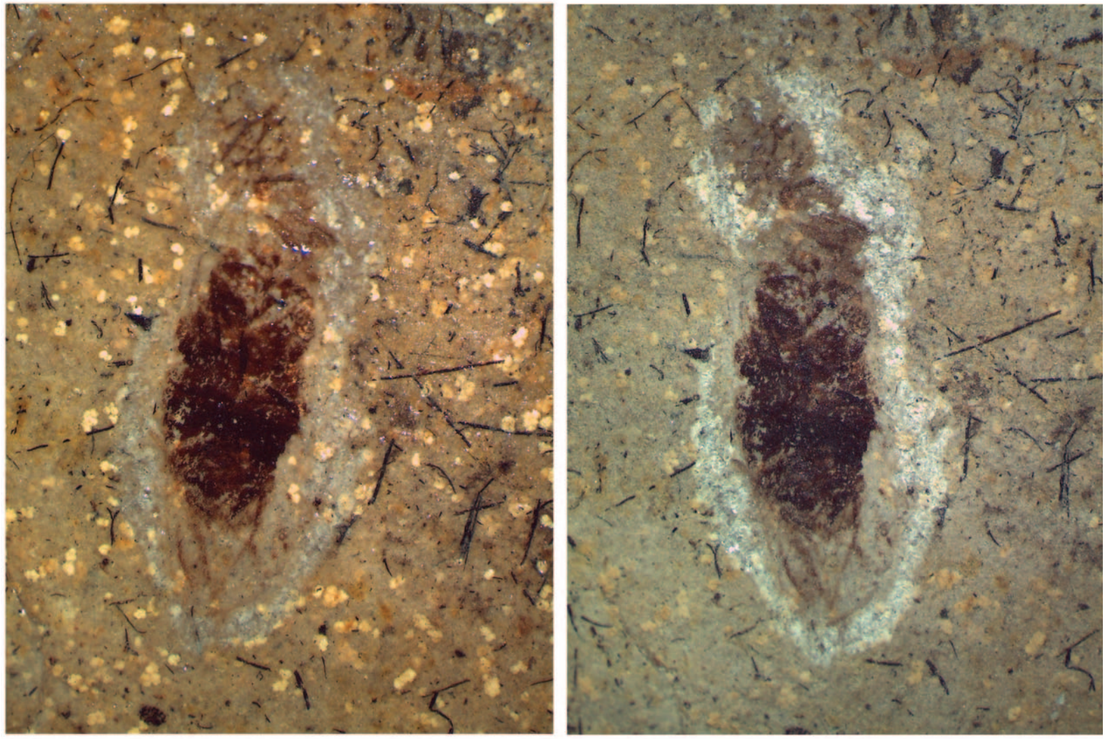


PIN 2384/240 l= 15 mm


PIN 2904/ 364 l= 9mm

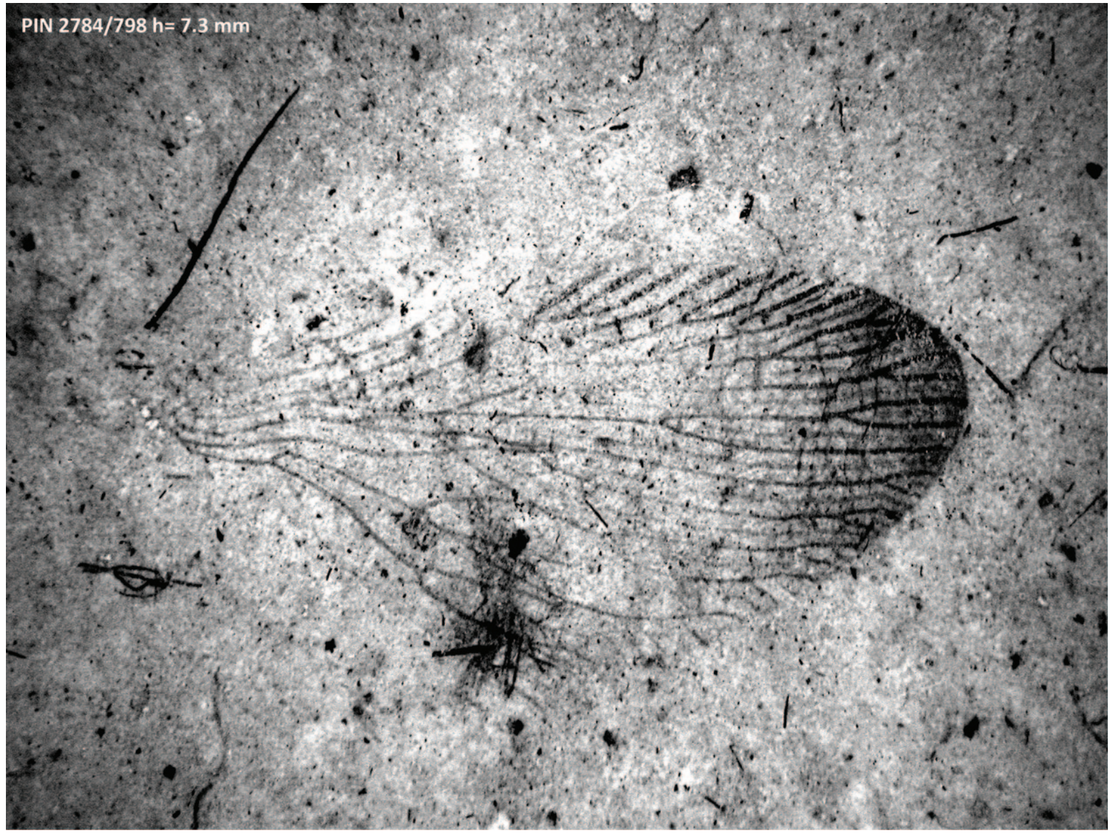

PIN 2904/ 364 l= 9 mm





PIN 2384/ 281 w= 1.8 mm


PIN 2452/45 h= 8 mm


PIN 2784/798 h= 7.3 mm

Proportion of unidentified isolated hidwings (n= 109) compared to unidentified isolated forewings (n= 120) is adequate taking into consideration much more difficult determination of hindwings. In this respect 150 unidentified complete specimens might sound disrupting, but complete specimens are frequently collected also in weak preservation condition so a high number is expected. It does not mean, and I do not expect a new family hidden in this indetermined material, mostly it reflects similarity of sophistically-colored representatives of Caloblattinidae, Liberiblattinidae and Raphidiomimidae, and habitus similarity of small Liberiblattinidae and Blattulidae (impossible to discriminate on weak specimens). The same holds true for unidentified fragments which rarely allows discrimination among Caloblattinidae and Raphidiomimidae.

Good indicator for reliability of diversity values is that several species (*L. crassivenata, S. spono, M. velipsespilev, O. ojedinela, P. nigroalba, O. simpla, A. naslosa, A. palindrom, L. cipka, L. luminanala, L. kontravenata, L. kontrapunctata, L. cunicula, H. nice, E. sediomasle*) are identified exclusively on the basis of very small fragments. Taking into consideration small fraction of fractioned insects, this is a rather high amount of species (15.5 %) – an indication that within IS, few hidden species occur at most. To decline too high optimism resulting from this figure, it must be noted that all these species possessed characterised and/or unique coloration making their identification simpler. At least 2 additional species are present (small raphiodiomimid figp. 37; big Mesoblatta-like caloblattinid with huge ovipositor figps. 67, 71).

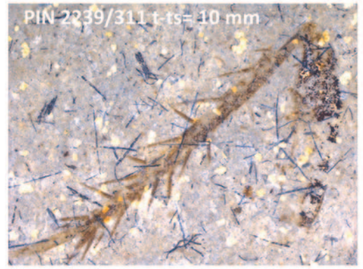
Immature specimens (n=86 unidentified; some of the immatures are additionaly categorized within their species such as the presumed (semi)aquatic ones or *Blattula brevicaudata*):

The immature cockroaches belong to rather rare fossils in the sedimenteary record (while their occurrence in amber is common) due to the preservation mostly of flying winged adult individuals. Nevertheless, due to frequent (rain etc.) splashing and lake and mare inflows, they sporadically occur in all major *Lagerstätten.* The proportion of immature individuals is low also in Karabastau (n= 186/3,192 all material, i.e., 5.8 %, under 3 % among indetermined material). Specially categoised are larvae (n= 47) of *Hydrokhoohydra aquabella,* which is a presumed (semi)aquatic species and its high abundance is thus of different nature. Splashing of larvae might equivocally be explained by their predominantly small size – a possible reason for rather high occurrence of larvae of eudominant *Blattula brevicaudata,* while other possibility is its near-shore habitat and/or much higher abundance of earlier stages, or combined. This process is rather a contribution to the general procedure of burying as most of the dominantly flying winged adults apparently fall into the light trap the waterbody represented.
Long transportation can be excluded also for larvae as they are mostly completely articulated.
Size partition of immature individuals reveals predominance of earliest instars (see Vršanský 1997), with a remarkable occurrence of very large raphidiomimid larva. Nearly 20 mm long specimens without wings possibly representing immatures are also preserved with a gut content (figps. 574-575). On the other hand, taking into consideration naturally higher partition of imamature individuals above adults, surprising is their absence from the coprolites. This is a supporting evidence provided for these coprolites belong to an in-flight insect-feeding pterosaur.
Systematically, all taxonomic spectrum appears covered by larvae. Besides from common Blattulidae (more species) and Liberiblattinidae (several species), Caloblattinidae, Raphidiomimidae and Skokidae also occur.

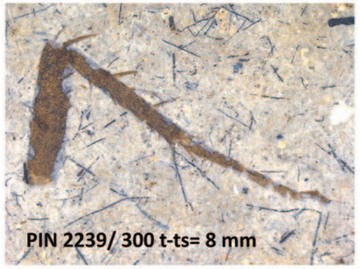
- **Immatures Caloblattinidae sp. incertae sedis (n= 15):** 2239/317 (w= 1.5mm), 332 (w= 1.7 mm), 325 (l= 3.8



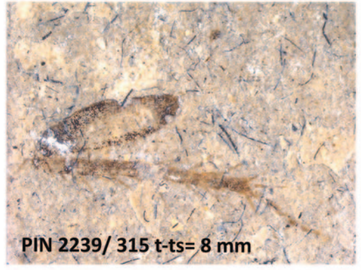
Incertae sedis leg


PIN 2239/311 t-ts= 10 mm

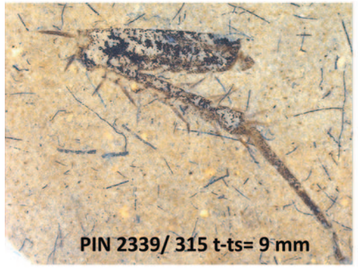

PIN 2239/ 309 t-ts= 8.5 mm


PIN 2239/ 300 t-ts= 8 mm


PIN 2239/ 298 t-ts= 6 mm


PIN 2239/ 315 t-ts= 8 mm

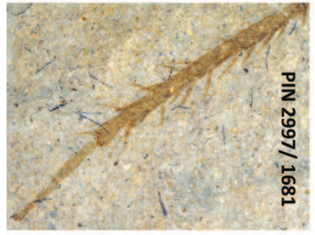

PIN 2239/299 t-ts= 7 mm


PIN 2339/ 315 t-ts= 9 mm

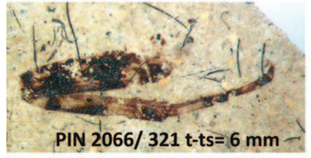

PIN 2384/ 1113 t-ts= 18 mm
238


PIN 2384/1118=1121 t= 6 mm

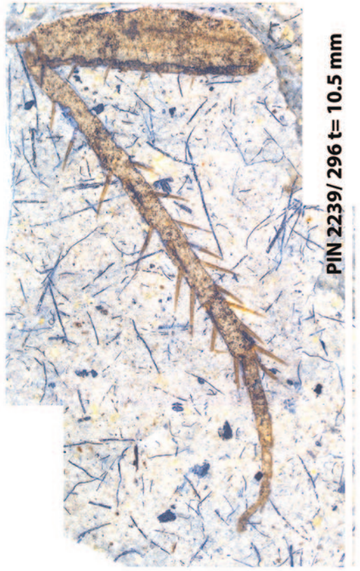

PIN 2066/ 85 BROKEN


PIN 2997/ 1681


PIN 2239/ 293 f= 9.3 mm


PIN 2066/ 321 t-ts= 6 mm


PIN 2997/ 1683 t-ts= 14 mm


PIN 2239/ 296 t= 10.5 mm




PIN 2239/294 t-ts= 9 mm

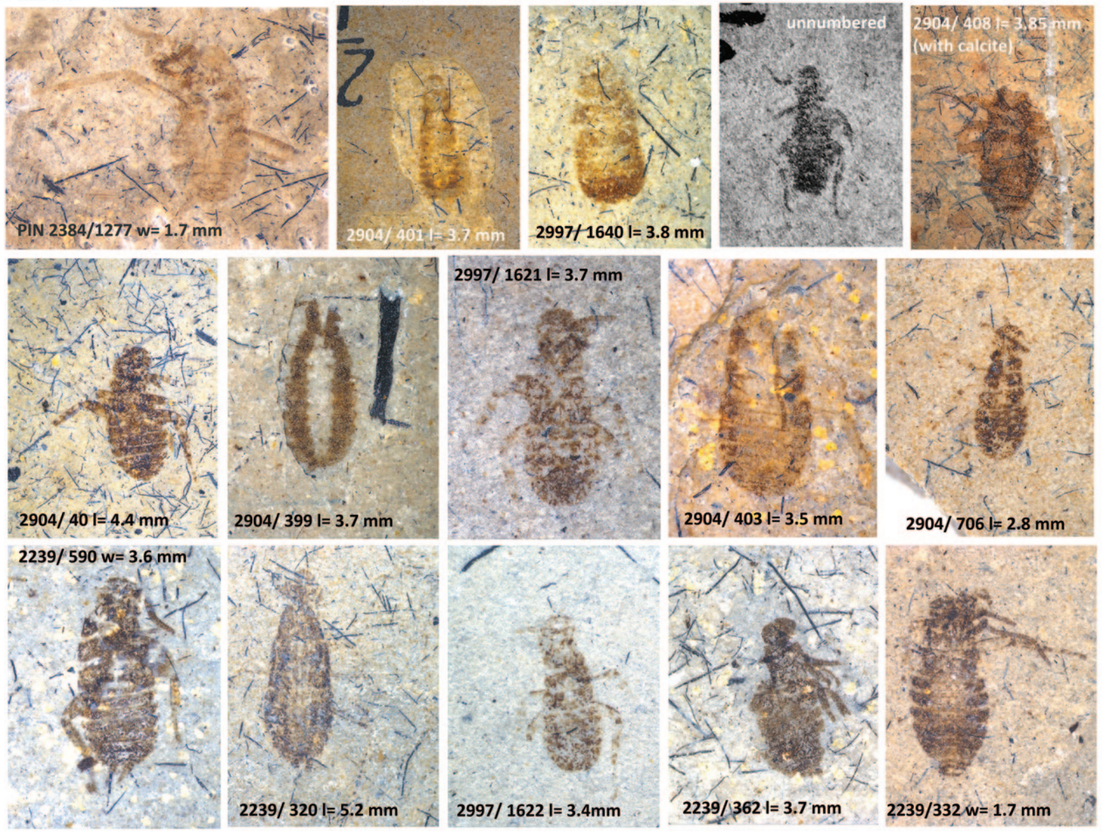

PIN 2066/ 343 l= 7 mm

mm), 362± (l= 3.7 mm); 2784/642±, 855 (l= 2.8 mm); 2904/302, 404, 408; 2997/1626 (w= 1.8 mm), 1627, 1634 (w= 2.8 mm), 1637, 1652, 1676

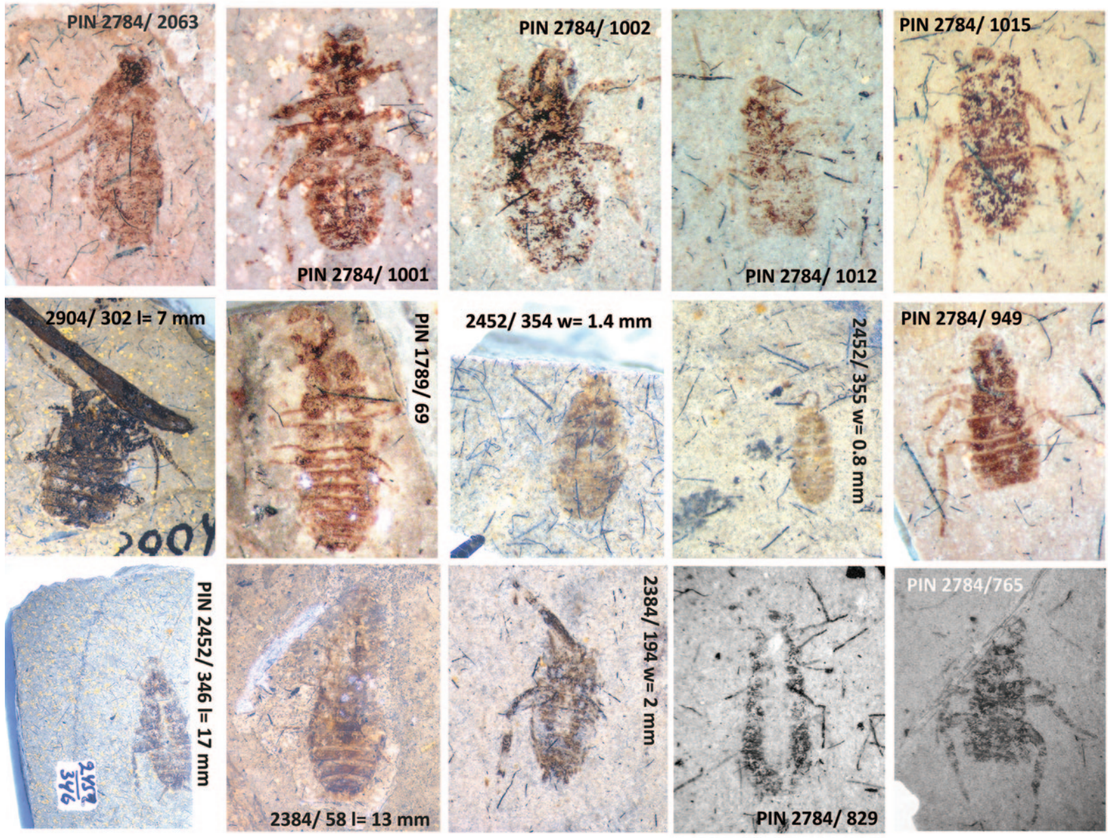
- **Immatures Raphidiomimidae sp. incertae sedis (n=10):** 1789/69 **G;** 2066/498 (w= 1.8 mm); 2239/343 (l= 4 mm); 2384/58 (l= 13 mm); 2554/999 (w= 1.3 mm); 2904/401, 406; 2997/1172, 1648 (l= 3 mm), 1659 (l= 2.6 mm)
- **Immatures Mesoblattinidae sp. incertae sedis (n= 1):** 2904/403
- **Immatures Blattulidae sp. incertae sedis (n= 15)** 2239/319 (w= 1 mm), 335 (w= 1.5 mm), 365 (l= 3.6 mm), 367 (l= 2.6 mm), 369 (w= 0.9 mm); 2452/554; 2554/150; 2784/1004; 2904/230, 395, 398; 2997/4242 (l= 5 mm), 4339 (l= 3.3 mm), 4426 (l= 3.4 mm), 4427 (w= 1.1 mm)
- **Immatures fam. incertae sedis (n= 45):** 1789/76 (w= 3.5 mm) **G;** 2066/63, 190 (l= 10 mm); 2239/239± (w= 3 mm), 324 (l= 4.2 mm), 328 (w= 1.5 mm), 336, 368; 2384/60 (w= 3.8 mm), 197 (l= 3 mm); 1277 (w= 1.7 mm); 2452/239, 346 (l= 17 mm; w= 6 mm), 354 (w= 1.4 mm); 2554/86, 109, 120; 2784/652, 654 (l= 3.6 mm), 742 (w= 1 mm), 857 (l= 2.6 mm), 860 (w= 1.5 mm), 868, 870 (l= 3.3 mm), 883, 884, 856, 1002 (l= 5 mm), 1015 (w= 1.4 mm), 2063 (l= 6 mm; w= 2 mm); 2904/34 (w= 3.5 mm); 2997/1381, 1622 (l= 3.4 mm), 1631, 1633, 1636, 1644 (w= 1.3 mm), 1650 (l= 3.5 mm), 1653, 1654 (l= 2.5 mm), 1663 (w= 3 mm), 4334 (w= 1 mm), 4337 (= 1.8 mm), 4340± (l= 5.8 mm), 4341± (l= 5.2 mm)

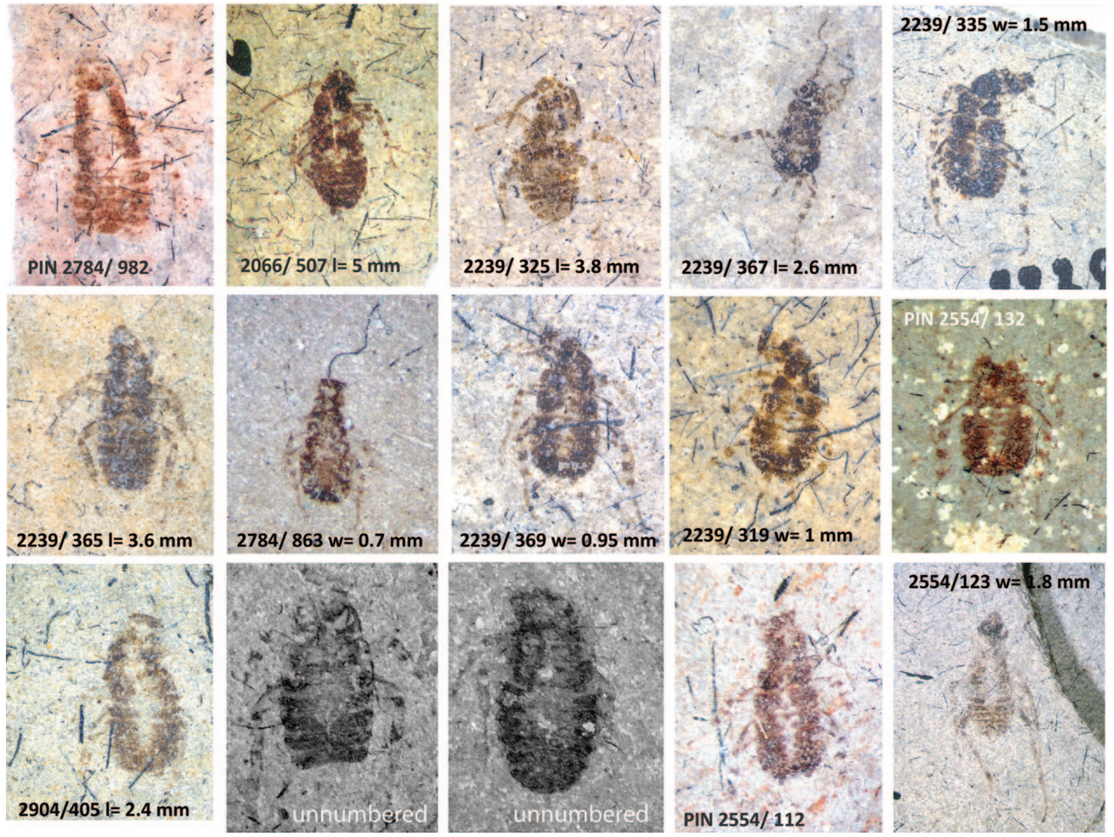
NUMBER (IN)COMPATIBILITIES

In such consistent material collected by numerous diverse expeditions and collectors, some problems with numeration occurred. Several numbers are repeated, in some cased the same number has been given to four different specimens. Additional problem might have occurred with samples representing positive and negative imprints. This, predicting that some different numbers might be given to the same (±) specimen, might exemplify the specimen numbers biasing most common species, where such “miss” is more probable. Among 2,539 classified specimens (897 photographed), 174 are identified with both polarities. Additional (24/48) specimens were binded two numbers within the same individual. Thus possibly exemplification resulting from relabelling the same positive and negative specimens might hypothetically reach a maximum of 399 specimens checked only initially. Additionally rare or unique specimens must be also excluded (over 50 %), so taking into consideration small percentage of the both sides collected in species where all specimens were documented (only 202 among all classified specimens – 8 %), the repeating and exaggeration of collection in this cause was minimal.



Immature individuals


PIN 2784/ 2063
PIN 2784/ 1001
PIN 2784/ 1002
PIN 2784/ 1012
PIN 2784/ 1015
2904/ 302 l= 7 mm
PIN 1789/ 69
2452/ 354 w= 1.4 mm
2452/ 355 w= 0.8 mm
PIN 2784/ 949
PIN 2452/ 346 l= 17 mm
2384/ 58 l= 13 mm
2384/ 194 w= 2 mm
PIN 2784/ 829
PIN 2784/765


PIN 2784/ 982
2066/ 507 l= 5 mm
2239/ 325 l= 3.8 mm
2239/ 367 l= 2.6 mm
2239/ 335 w= 1.5 mm
2239/ 365 l= 3.6 mm
2784/ 863 w= 0.7 mm
2239/ 369 w= 0.95 mm
2239/ 319 w= 1 mm
PIN 2554/ 132
2904/405 l= 2.4 mm
unnumbered
unnumbered
PIN 2554/ 112
2554/123 w= 1.8 mm



Alcohol reveals sediment transparency

METASTUDY

SELF-REFLECTION OF THE PRESENT STUDY

According to the extent of study which lasted 30 years I am including a short self-reflection of the performed work, possibly helpful for teachers and students about to conduct a study of similar extent (in any group).
It might seems that a 3,000-sample collection is not that huge, as I experienced a lot of studies with a level-higher number of samples of living specimens. Nevertheless, lack of any systematical background, lack of any (taxonomical or any other) system, lack of taxonomic revisions and a total lack of any keys resulted in a titanic amount of a research performance.
Degree of incertainty was too high. Similar degree was already performed on Bakhar, with 1,178 specimens, these, nevertheless comprised mostly forewings. Here a separate evaluation was needed for forewings, hidwings and often also for diverse body and head structures. And then, surely to combine data into a complex picture of morphotypes within a (newly established) system.

As at the beginning, even the most fundamental cockroach taxonomics was not resolved, looking at the world most comparative collection was natural, taking into consideration the complete preservation of specimens representing the only complete specimens within several families.

It is a virtue of my Russian hosts to introduce the collection in consequent phases, since knowing the total amount of the collection in the very beginning, I will definitely disagree to undergo the complete detailed systematical evaluation (perspective of 30 years of work on a fossil cockroach to a teenager might not work every time).
Nevertheless, taking into consideration inevitability of the evaluation of this collection in the general knowledge of the cockroach morphology, at least partial results were performed from the very beginning.
In the very first stages (1994), I selectively evaluated few interesting samples (Vršanský 2008a,b) and get aquainted with unpublished materials of V.N. Vishniakova. Later I studied her excellent published works (see introduction).

Especially important was initial check of the complete specimens of families Raphidiomimidae, Caloblattinidae, Liberiblattinidae, Umenocoleidae, Blattulidae and Mesoblattinidae s.str., which, although unpublished till now, allowed me to perform systematical analyses of numerous other localities and also to access new gross groups at other sites.
Notice that the best preserved specimens of abovementioned families (and also only sedimentary Fractaliidae, Operamidae, Latiblattidae, Skokidae and also Lovecidae and Socialidae) are present here. Recognising 31 families in the 320 Ma history of the (sub)order worldwide, this number has no equivalent in other localities furthermore supported with the earliest umenocoleid.

Systematical approach in evaluation started in 2005 with survey of ca. 500 specimens. At this stage I estimated ca. 60 species present in the collection. After survey of ca. 1,500 specimens my estimation of species diversity raised to 100 species. After all collection was surveyed and documented, estimation was established to 110 species. Neverteheless, only after systematical evaluation and catalogisation of all photo-

graphs and drawings into species (in December 2021), concerning the intraspecific variability, the number of species was established at 60! This might look strikingly similar to the first estimate, nevertheless, the concept of the species and species (and its contents) itself were entirely different.

Moreover after finding several new taxa among the collection the total number raised to 72. It is rather important concern drawing into attention a complete lack of intuition in such vast data with too many incertainties. Consequent 83, 138, 152 and 83 % difference in estimated number of species is disrupting. On the basis of overall evaluation, variability simply turned much higher than expected in one group and lower in another.

The most problematic specimens evaluated at the very end unequivocally reveal presence of “obscure” Blaberidae (unknown from the Jurassic, and known from the Cretaceous only since Šmídová (2021; see also Oyama et al. 2021) and also Umenocoleidae (the only Jurassic record) and Lovecidae (the only Jurassic true mantis), and also putative Socialidae (the record of Jurassic eusociality supported with unpublished data from Kota and possibly Chernovskie Kopi – Barna 2014, Vršanský and Aristov 2014). These final records significantly influence also the paleogeography.

Nevertheless, the total number of species terminated in 95!!! And this happened in the very terminate phasis (and greatly contributed with studying and concerning the Vishiakovas species at the very end).

Thus the style of this study might appear highly uneffective. Performing the same study now, it will barely take me to conduct the study of the same quality more than five calendar years. Nevertheless, due to incertainity of general knowledge 30 years ago, such consequent study was the only possible way.

I did not have the possibility to study the types established by Vishniakova (unavailable, at the exhibition), but her documentation was excellent enough to concern her species and establish additional material to them, in this study.

The huge partition of incertae sedis specimens also reflects problems of study as these specimens were marked as such during the survey stage of the study. Having had the possibility to survey them now again, I were surely determine part of them (possibly up to 15 % of them) to the presently established species.

Second Möby-stripe hologram side of the truth is that another reference point (GCNRP) was discovered since the beginning of the study, namely North Myanmar amber. Without seeing that collection (of burmite) it would also be impossible to evaluate the present collection. And it was performed only in 2021-22, 23 and 24.

It might become sound disturbing or demotivating, but I am not going to evaluate anymore collection of such extent, but will happily provide all my experience, expertise and advice to any student anywhere. In the matter of fact the release today I consider the peak of my research career aimed at considering truth. It was terribly hard, and at the same time simple, and adventurous pleasure.

I only hope the gigantic amount of this study will not scare students similarly as the huge work of Klass (2003) scared me so that I was able to study his gigantic contribution only after having 30-years of experience with the group. Thus I tried to separate aspects of the gained knowledge into several levels starting at pure aestethic, ending in prolification of whole lineages and significant changes in the general view of evolution as a principle, not restricted to organic world.

Welcome in my epos about cockroaches from Karabastau.

PRACTICES IN ORIGINAL FOSSIL COCKROACH RESEARCH PUBLICATIONS

Also, due to the amount of performed investigations, I am exploiting possibility of this monograph to include a self-reflection of the whole working group. I do not mean my working team, but all fossil cockroach specialists.

I am not about to analyse the research data and correctness of performed analysis/ses as it is too premature to make a report on active experts and inactive experts are simply death or too old and the field, thanks to them shifted significantly. Besides Martynov (1937) and Bekker-Migdysova (1961), I mean predominantly V.N. Vishniakova, whose study this my work prolongs. Also I do not tread J. Schneider as he performs studies on Palaeozoic cockroaches related to conclusions on evolution of Mesozoic and living cockroaches only marginally – due to huge and highly improbable and thin Early Triassic bottleneck.

Also I will not analyse my own research efforts and I let this feedback to anybody else that is interested and informed. From the same reason I will touch my own working research group in Slovakia only marginally.

So in this chapter I focus solely on the formal side of evaluations, because due to frontier position of the cockroach palaeoo-entomology in the field – self-reflection is absolutely unevitable for further progress. Fossil cockroach specialists did a huge advance (158 fossil species described during the 5-year period 2018-2022), which clearly delimit the positive perspective. And there is also a huge space for improvements.

I Photodocumentation of the fossil cockroaches – macroscopic side – does not need a special attention, because in the past years, the photographs are satisfactory, which concerns all authors. Due to availability of frontier equipment in nearly all countires, there cannot be claimed any objection. Standard in journals publishing research on fossil cockroaches are set high enough. I think all authors spend time enough for detailed documentations and this comprise details as well. So photographic docummentaion of stuctures used in classical mnorphological character analyses are sufficient (photos in this work were made before 2011 in a very provisory conditions).

II 3D photodocumentation of the fossil cockroaches is much more rare if not absent. Calalogised are only two such studies (Hörnig et al. 2018, see also Vršanský et al. 2018). Under the condition of a serious illustration it might appear ineffective to provide sedimentary compression in 3D. Nevertheless, study on bugs (Vršanský et al. 2015) reveal extremely important information hidden in third dimension even of visually totally planar sedimentary fossils. Thus I urge each member of the team to provide 3D documentation of the sedimentary fossil they now evaluate (I provide here a single 3D documented fossil, which is the sole one I still posses for study). Even more sophisticated is the situation with amber. Basically till now, not a single fully valid 3D picture was obtained from any amber cockroach (neither any other organism). Fortunately at least a partial 3D extraction was possible for *Anaplecta* in 2014 related to a Keyence pres-

entation for a high-scholl competition SUMACO 2015 from Chiapas amber (Barna et al. 2019). Similar partial 3D pictures were obtained from Baltic amber immatures (Hörnig et al. 2016). There is a huge space for this improvement, as it is rather simple and accessible.

III Illustrations of fossil cockroaches belong to the frontier documentation source for any fossils. Inside our group I must mention hyperrealistic pencil drawings of I Koubová (Koubová and Mlynský 2020, Vršanský et al. 2019, 2023b), nearly autistic ink drawings by T Mlynský and my own 115,000-vector drawing of Teyia (both Vršanský et al. 2018). I am also fully satisfied with minimally simplified illustrations within my whole group (L Podstrelená in Podstrelená and Sendi 2018) and by L Šmídová in Czech Republic (Šmídová 2020, 2021; Šmídová et al. 2021, 2024), J Káčerová (Sendi et al. 2023) and J-H Liang in China (Liang et al. 2019, 2021). In contrast to previous years, when papers lacking illustrations were accepted also in hi-profile journals (providing nothing-saying commented photographs only), last publications of basically all authors contain at least pictograms. I must stress that photographs without explanatory drawings worth nothing. Even specialists are unable to recognize most of the structures provided by other authors and non-specialists are simply lost. Of a special value are scientific reconstructions provided by L. Šmídová and J Káčerová (Sendi et al. 2023, Vršanský et al. 2023a, Šmídová et al. 2024).

IV 3D surface sediment measurements are also insufficiently performed, although were shown to reveal data complementary to 3D photographs. They are very simply possible to perform and reveal extremely interesting results (see Nel et al. 2014; Vršanský et al. 2018).

V measurements of areas is virtually lacking too. Wing areas are data only partially dependent on other morphological measurements (Oružinský and Vršanský 2017), but still such measurements are rare (Hinkelman 2022, Vršanský et al. 2022a, Kováčová 2022).
VI measurements of coloration are entirely independent on other morphological data as coloration, as it is shown in this work, evolve nearly entirely independently on morphological characters. It is being used since two years ago (Kováčová 2022, Hinkleman 2022).

VII Shape analyses are lacking in the analyses completely. My team elaborated the methodology slowly (Luo et al. 2022). Shape is frequently a character-independent trait.

VIII ST/CT with phase contrast is now also routinely available in advanced countries. It has been widely used on the amber samples (Vršanský et al. 2012, 2021, 2023a; Vršanský 2009, 2019; Bai et al. 2016; Sendi et al. 2020b; Luo et al. 2021, 2022; Šmídová et al. 2024), but more effort need to be performed on the sedimentary fossils (Sendi et al. 2022a). CT was performed here for *Liberiblattina ihringovae* holotype and reveals surface details including venation (figg. 25).

IX Photodocumetations of cockroach microstructures is still entirely unsatisfactory, although sensillae are ocassionally preserved in sediments and regulary in amber. In spite of the presentation of microstructures as an independent source of information a long time ago (Vršanský 2001), the first special study was performed recently (Tanigushi 2021). The reason for rarity of such study is the destructive character of such performance. Therefore we also perform this analysis only in structures close to surface and not systematically, because till recently no amber material was available in sufficient amout to allow for sections. But other groups are missing this approach entirely, and I would like to stress that at least surface is routinely accessible for standar microscopes with lenses up to 100x magnification. Moreover now the record of Myanmar amber is abundant enough to be opened for cutting.

X Parasites of cockroaches were rarely documented, although were apparently common. Aggressive parasitism of a mite was documented on burmite *Magniocula*

paradoxona, and mites were observed on *Teyia branislavi, Meilia jinghjanae, Pabuonqed eulna* and phoretic pseudoscorpion of *Stavba* sp. (Vršanský et al. 2018, 2019ac, 2022b). *Nematodes* were recently also discovered on two indetermined burmite cockroaches (Luo et al. 2023). A putative parasitic fungus occurs on a cockroach from Lebanon amber (Sendi et al. 2023b).

XI Other interractions were studies only sporadically, and exclusively in amber. Burmite contains peculiar feeding of an adult *Manipulator* on a moth and a feeding of a millipede on the *Manipulator* (unpublished). A burmite corydiid larva (possibly Magniocula) occurrs within a fern sporangium (Poinar 2021). Predation of an ant to the alienopterid was also documented (Barden et al. 2020).

XII Ontogenetic errors are restricted to documentation of 4-segmented tarsi though to be a result of ontogenetical error (but see Vršanský 2002, Li and Huang 2022, Vršanský et al. 2022b).

XIII Mutations of wings are locally independent source of information (Vršanský 2005; Vršanský et al. 2017) and fortunately is concerned in vast majority of modern works on fossil cockroaches of all ages.

XIV Trace fossils are fortunately rising in analyses, although they are not regularly contained in descriptions and/or formalized. Several cockroach samples contain coprolites (Vršanský et al. 2013, 2019; Greppi et al. 2023), but frequent isolated coprolites also occur. I am also not treating here the isolated ocurrences of ootheca, sometimes (I think correctly) regarded for trace fossils (Anisyutkin and Rasnitsyn 2008; Hinkelman 2019; Cariglino et al. 2020; Gao et al. 2019; Sendi 2021; Šmídová et al. 2024). The precise description of mantis-like ootheca (Li and Huang 2019), allowed to understand the injecting the oocytes (see also Vršanský et al. 2021, Sendi 2021) into precursors of true ootheca, without the keel and without surface calciumoxalate crystals – a hypothesis of Vishniakova (1968). Also trace fossils can be potentially regarded as fossilized sperm (Poinar 2023).

XV Reversed trace fossils contain cockroaches in coprolites of putative birds, pterosaurs and possibly fish. Cockroaches are most common content of these coprolites, and studied only twice (Ansorge 1998, Vršanský 2003a). Suprisingly, also after passing digestive tract they can be classified within respective species with a high confidence.

XVI Gut content is a separate category studied only in few species, in amber only in *Pozabudnutie antiquorum* (Vršanský et al. 2022). In sedimentary record this possibility is frequent, although reported extremely sporadically, mostly in predators (Liang et al. 2009, 2021) and without details in Fuziidae (Vršanský et al. 2009). They were also common in Baissa (Vršanský 1998).

XVII Syninclusions are obligatory part of any publication, which should reveal a context data for cockroach assemblages in the remote future. This part is virtually missing in most of the publications (but see Sendi 2024), although in early stages, it requires only general habitus photgraphs of adjacent syninclusions and syncompressions. I urge authors or to document synocurrences in the earliest stages, to avoid lack of these data such as in the present publication, when I have no more possibility to restudy the material for syncompressions. Moreover the present as well as basically all other material was cut of “redundant” parts, so it is important to document syninclusions /syncompressions directly in the field, during the collection.

XVIII destructive studies are also mostly required to reval symbiosis while ocassionally it is possible to document gut (or on fecalia) endosymbionts including bacterians directly from the the surface (Poinar 2009, Hinkelman and Vršanská 2020; Kováčová 2023). Unfortunately, only these three works refer to this unique opportunity.
XIX Virus infection was also documented

(Vršanský et al. 2019c).

XX Container analysis (analysis of the geological carrier or fossil medium) using modest sedimentological and spectroscopical data is also rising, and reveal important data of the environment and/or resin source tree. How important they are was revealed on classification of the sole assemblage among Myanmar amber data (Vršanský et al. 2022b) or establishing environmental conditions in Tasgorosay sediments (Majtaník and Kotulová 2022; Vršanský et al. 2024).

XXI Knowledge of references basically trigerred the reason for providing this chapter. The citation politics is what is discrediting the whole field, and document the absence of unbiased, free and democratic science in all parts of the word, including U.S.A. and the core of EU (I am native EU citizen) – the countries which consider themselves the most democratic. Selective referencing is totally unacceptable in my view, and its amount in the contemporary cockroach research is devastating. In total, only a fraction of relevant (and definitely known to the authors) literature is cited in studies of fossil cockroaches. Not even all works regarding cockroaches from the same locality are referenced.
Papers are frequently rejected on the basis of subjective alternative opinion (fully valid, which nevertheless, should be subjected to the same criticism), frequently not giving competing teams chance to express their opinion which they hold.
Social networks often contain opinion that some people should not have chance to publish at all.
Papers are frequently hold and/or postponed more than a year in redactions, preventing to express opinion, data and their interpretation if they differ from oponents and/or leaders. The field look more like applying of power of authorities than free(will) research. Sincerely, I barely can hold my question why these people entered science if they do not accept the opposite opinion. For science, the judge is the only one: the time. Let it in effect.
I am using the same place for explicitely declaring that I am using all references which I am aware of and the lack of anything relevant in referencing is my purely technical, idiosyncratic fault and/or error, conscious or unconscious. I excuse myself for any.
I am personally sure that any political, economical and/or religional interests discredits any deep research potential, which, nevertheless, cannot be the cause for restricting people of other opinion and/or philosophy from gaining their own results and paving their own research way. In this respect, my countries are very non-democratic in insisting on democracy in research. I am strictly holding this (democratic) way, but I am not influencing others to follow. Freedom, democracy and free science cannot be protected. They can only be enabled.
I am strict active atheist actively eliminating all beliefs, trusts, visions, constructions, gods and goddesses and religions spontaneously emerging in my head (P. Vršanský: Evolutionary Ethics of Active Atheism, in preparation), and I am sure that this is the only way ahead in frontier advanced thoughtforms and research. But I will never insist of anybody following this (terribly difficult) way, the more to discredit directly opposite way in performing scientific research methods. Anybody is free in science, guilty or not.

RECOMMENDATION FOR FUTURE STUDENTS

As I have already declared, material is not available for me anymore so I was unable to finish several topics.

First of all I recommend attempting of categorization of incertae sedis specimens into a now firmly established system. I feel dominance will not be influenced, just slightly more precise data obtained. I do not expect more than 5-10 new species in the incertae sedis material as I documented and evaluated all what seems different to me at that time. Most of incertae material results from numerous related species within the locality.

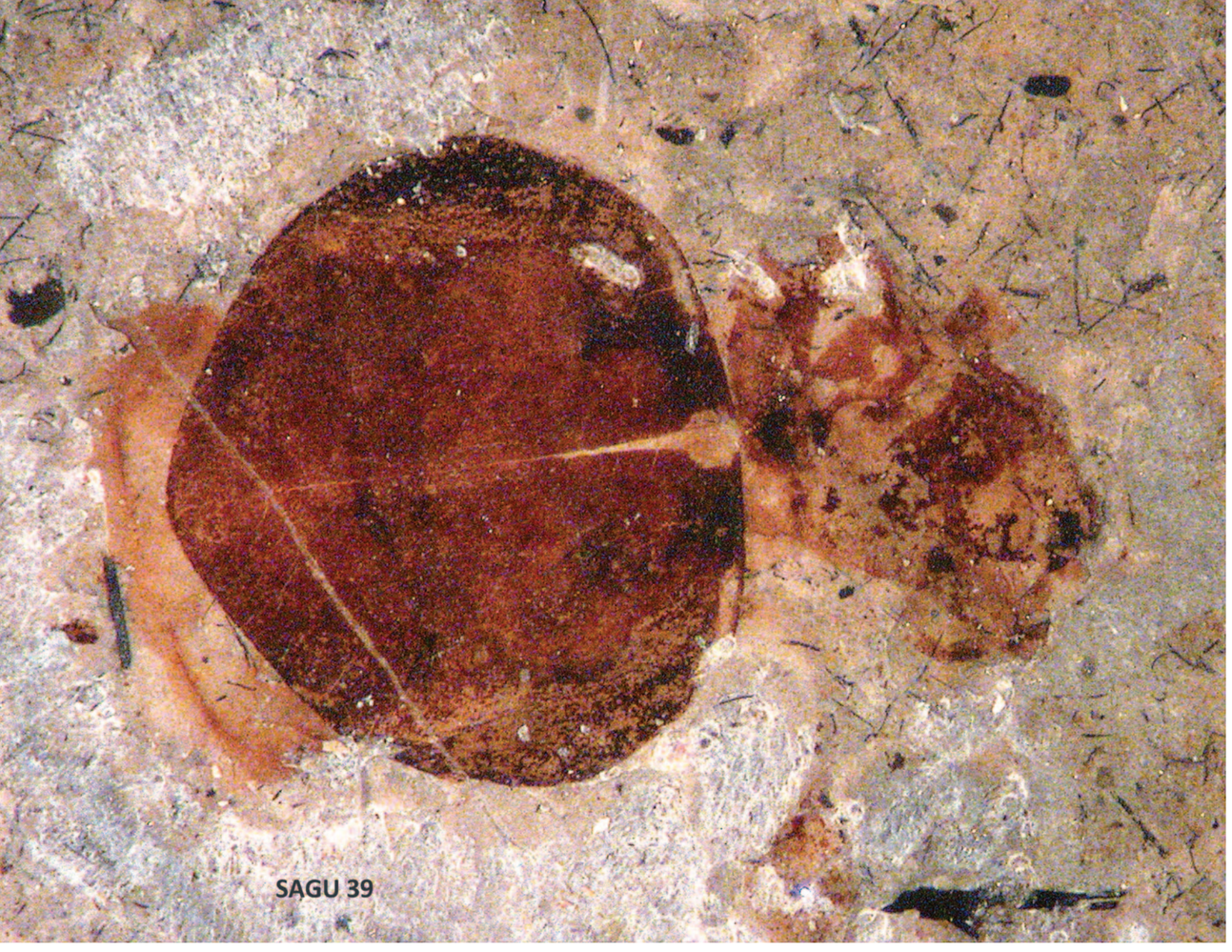
Important unfinished study is the study of the gut contents with scanning electron microscopy (SEM). Numerous species contain gut content and all of them were attempted to document photographically (and under alcohol) in the present study, so important inferences were gained and main trophic relations established. Nevertheless, SEM documentation can reveal precisely the source of food of these ancient cockroaches.

Important and possible is also detailed sedimentological analysis of the different-looking samples which will surely reveal rather different sedimentary conditions within both Galkino and Mikhailovka.

The ongoing is study of burned wood along cockroach specimens, which will be published in a separate publication.

I also recommend to more detaily study 3D profiles of these compression fossils to establish degree of planarity of the sample. As already revealed third dimension hidden also in entirely planary (to human naked eye) samples, this can reveal the real 3-dimension appearance necessary for reconstructions of these cockroaches.

Finally I strongly suggest to give 4-digit or more-digit numbers to the specimens as in the case of vast collections, 3-digit numbers are present in huge quantitites.



PHILOSOPHY

This should likely be the end of the study, nevertheless I also included it in the very beginning to demonstrate additional frameworks of my thinking. All are purely rational and even in places they seem unconventional, they are extracted from my love with quantum physics and advanced math. I am sure this part will discredit myself in purely technical manner, but to understand this performance fully – it is essential.

Virtual reality is the world observed here and in the most of palaeontological works. It is the world we actually see in shared subjective perceptions. Most of us can exchange nearly same impulses so this reality is also objective to some degree. And actually it is a virtual reality as this world apparently do not exist and will not exist anymore.

Due to modifications of the space-time it is philosophically also not fully certain that these lost worlds form our past entirely or even in a limited degree (due to space-time modifications the (modified) past influencing present) can differ from "actual" past.
Numerous animals and humans can recognise pasts as entities, and they cannot discriminate this past as differing from the presence substantially. From the relativity perspective it is a part of totally in-time static space-time. To me personally it has taken this 30 years to recognise that this specific past is totally different from the presence, and I hope I can mediate this objective reality to anyone frankly. So one can see this whole world contained in this book is an illusion. Simply said: it is the (totally different) past.
Nevertheless, as over 1,000 photographs and artworks might stimulate complex and complete perception, they might potentially form a residuum of the same living past (moment), but they can also represent organisms which died in remote places and remote times and never met together (nor specimens neither their species). So we must be cautious putting them together in a causal relation, understand "the reality" (similarly as two wild animals we see at once in a forest might never see each other throughout their lives – instead we classify them within a same percepted forest).
How convincing virtual reality of the past can be is exemplified with the North Myanmar amber, roughly representing a transparent cube of 1,000 cubic meters (m^2) from the age of dinosaurs. Nevertheless it is still unclear how long this cube have been depositing. If up to 50 million years as suggested recently (Vršanský et al. 2019, 2022, 2023; Hinkelman and Vršanská 2020, Hinkelman 2022), than the probability of meeting any two individuals except those one preserved within each other is close to zero. Karatau sediments with insects and vertebrates might provide a similar level of illusion. This is necessary to keep in mind reconstructing the objective reality of this past. Error in such a case would be cosmetical (real with high probability near-identical sister species), nevertheless, philosophically different from the perceived ones.

Quantum modification of the past. This lead us to the interpretations of the (mostly visual) perceptions, which might be even more intriguing. According to the quantuum theory, even the simplest experiment (diafragma) is observer-dependent. Observing a reality we are changing it. It is obscure how this projects into the real macroscopic life (which is the case here), but the present civilisation is in this respect fully "quantum", as pure passive watching of internet (not only advertise-

ments) changes our own reality substantially. Basically by observing (watching) we permanently cause collapsing of the quantum functions of the macroworlds. Recently it has been proposed that the function spontaneously collapses anyway, but what about "watching" collapses projected to the past?

AI is serving us sequences which we did not requested or asked (we are not even able to reconstruct or understand them) and thus modifies our own reality seriously- not only in offering advertisement products. How this relates to the fossilised cockroach? Can we change the (very remote) past by observing it? Definitely yes. How? Lets disregard the fact that each palaeobiologist see the fossil imprint differently and focus on interpretation. Such work changes our imagination not only of the specific past, but also relations within the past and principles which ruled the past. This way we modify our predictions fot the future. Moment? This is direcly modifying the future, present but also the past! As the winner is the one (system) with the best reconstruction, it is the same system that reconstructed the past. It will be most probably a system with the best perception of the past, but not necessarily and the more not unequivocally real. So yes, recognising this as a past reality to some degree, we are changing it. It can happen that only organism knowing the past (reading this book) is the one that will survive and thus have the past at the end.

This is a perfect point for explaining the quantum logic at geological macroscale. "1" is the ecosystem as it was. "0" is how this book would like without Vedeniapin, Prinada, Shabarov, Turutanova-Ketova, Gekker, Rohdendorf, Sharov, and many others. Unit of quantum information is a three-dimensional (not more dimensional) sphere or better said doonut (toroid). In a line it is clear that this ecosystem is simply insufficiently known. La–teral declinations might result from biased views, from errors and also from future modifications.

So the past and future is present here in one place, waiting to be connected by the observer, similarly as living organisms with different evolutionary tempo (such as ferns with orkhids and/or with their pollinators) can be interconnected by viruses.

Evolution. The property which we perceive as a (long-term, sometimes qualitative) change is most commonly referred as the evolution. In Einstein's 4D hypothetical universum this is a pure statics, and only thanks to Quantuum hypothesis there is a real (at least matematical) space for any change, although it is extremely difficult to imagine and define it in essence and measure in reality. Nevertheless, in this work I perceive nature as really changing and also I have no other choice as human can only perceive thing that change in time (it means space extracted from time at least to some degree). Dealing with one specific group extracted (and appearing changing) in time, I will focus on space they inhabit within their cases and their environments. Thus, to quantify this (contextually morphological) processes, I access 9 different and rather independent datasets here revealed for cockroaches, each adressed in a separate paragraphs. Surprising parallel with the new approaches in quantum theory is the ***hypothesis of constructive capillary compensation/ explosive radiation reduction rings*** resemble holographic projections operating coevally in 2D and in 3D at the same time- reduction ring is 2D in a morphospace and 3D in genospace at the same time.

Paleontology cycles and bridges static space-time into a dynamic one, but mostly it strightens and untangles the deforrmed space-time. We transmit the quantum observer from the past to the present and vice versa.....The empty central part of donut shape of the knowledge in addition to "1 and also 0" coevally represents "non-1" and "non-0".

(1) Classical phylogeny- this is most commonly used (morphological) set and in this work it is adopted in a classical sence, although over a hundred plain (not in combinations or distributional ones) characters are adressed for the first time here. **(2) Shapes**- represent complementary and rather independent data on classical (numerical) morphology. It is being frequently used in some other arthropods (banally in ostracods) but the first complex shape evaluation of any insect-cockroach locality is presented here. **(3) Coloration and life forms** - this is, as we will see, a largely underestimated dataset basically representing phenetical similarity and dissimilarity which is nearly entirely independent on phylogeny (and e.g., on venation) as practically all families can reach all life forms and coloration given them enough space and time. It nevertheless, represent a frontier data for environment for the phylogeny itself and must be studied with maximum care. Karabastau cockroaches enabled a first progress in this respect here. **(4) Variability** - cockroaches are among few (if not the only one) groups that reveal species (or what we consider for species) variability in a sufficient number of species (and specimens) to reveal global patterns. **(5) Mutations** - expressed vein deformities rather sophisticatedly fixed to environmental properties represent unique cockroach datasets, independent of small phylogenetical changes. **(6) Microstructures** - counter-intuitively, the smallest structures are at the same time most conservative and represent independent data from classical macromorphology. Unfortunately the Karabastau record, although representing the most complexly preserved cockroaches, is practically lacking preserved microstructures. This is surprising as other groups at the sites, often preserved along with cockroaches, such as flies, possess microstructures normally. Thus this source is mentioned here only marginally. **(7) Temporal and (paleo)geographical distribution,** context of their genera - although focused on context of studied species and threating them only indirectly through ocurrences of their higher ranks, sometimes reveal direct information on adaptability and (behavioural) characters allowing to access diverse (or the only one) environments. **(8) Containers/carriers/media with taphonomy** - although very rarely, also carriers/containers (sediments, coal, amber) can reveal important characteristics of species. In the case of Karabastau, this is mostly irrelevant as the sediment is largely uniform and disallows separation of species based on sediment type (due to physical inaccessibility of material). What is attempted to access is to separte the whole collection by collecting numbers and collectors. **(9) Syncompressions**- directly identify species which ocurred with high probability in the same ecosystem. Unfortunately during the specimen inspections, these were not taken into consideration and are not threated in this study. I leave this important and responsible work for the Karabastau next generation student.

More specifically, this (and following from it already performed studies) work seriously changes a technical perception of a change (evolution) itsef. Reduction as the only way to evolve and specialize in abovemention hypothesis of constructive capillary compensation/explosive reduction rings was largely (along with the North Myanmar amber and Daohugou among fossil sites) based on observations provided here. It follows constructive evolution is possible only episodically with gross changes synchronised along the taxonomic spectrum. All the rest in basically a reduction, which can result in specialisation if the source taxon is modest enough. In addition to explaining high diversity in tropics largely independent on temperature but dependent entirely on reduction potential of the primary producers and thus on photosynthesis efficiency (Vršanský et al. 2017, 2019, 2021), this brings also a major explanation for the success of sexual reproduction, as in sexually reproducting organisms, there are two possible sources of reduction (there are always two winners), and moreover, even once reduced taxon might return to the original state due to (if) heterogamic state. So change is better (returning) (more robust sensu Wagner 2005, 2007) in two. Literally, when reduction rules, and now we see it rules. Apparenly since today, two are enough since multichannel (with more than 2 sexes) reproduction is rare.



PIN 2784/687

FEELINGS

I also feel responsible to briefly comment also my feelings touching these stones, these geological carriers, these cockroach remains, these messengers of the past.

On the one side these conserves of ancient animals represent their death corpses and each of them represent natural or unnatural failure of a respective individual. Sincerely, this point of view I recognised only during writing this chapter. And lead me to corrections about the mutation rates as modified cockroaches might have entered the fossil record with higher probability. Empathy.

It might not appear as the right approach. Nevertheless, I always saw see a living beings behind them and I have tried to reconstruct their active habits first. This leads to the feeling of being a part of the virtual reality, which the past (and past forests) represents. Anyways it has something to do with the present and many feeling are analogical to remembering meetings and encounters with living cockroaches (free of allergens after fossilisation). Only writing these passages I am trying to imagine them having them in hands and observe them directly.

Only consequently I tried to understand the burial patterns, which empathites me with the past aquatic environment of a past rivers and the source lake, where they have fallen during the flight, with insect predators and cadaverivores inside.

I am not sure that this is a good idea and a better approach. Nevertheless, it is a different approach. I appreciate alternatives. The forest do too.

To shift this further I offered a sample also to the hands of a sensible, the most sensitive person I know. And trust me, I understand that I personally, in spite of the former words, did not feel anything remarkable compared to that person which these samples lead near-agony and into a trance.

I must explicitely declare that the history of cockroaches with their million years lasting duties to the ecosystem are yet more important that human contribution to the forest and I deeply feel it like this. They are more important than us. Lets try to equalise.



LIberiblattina hindwing with wood

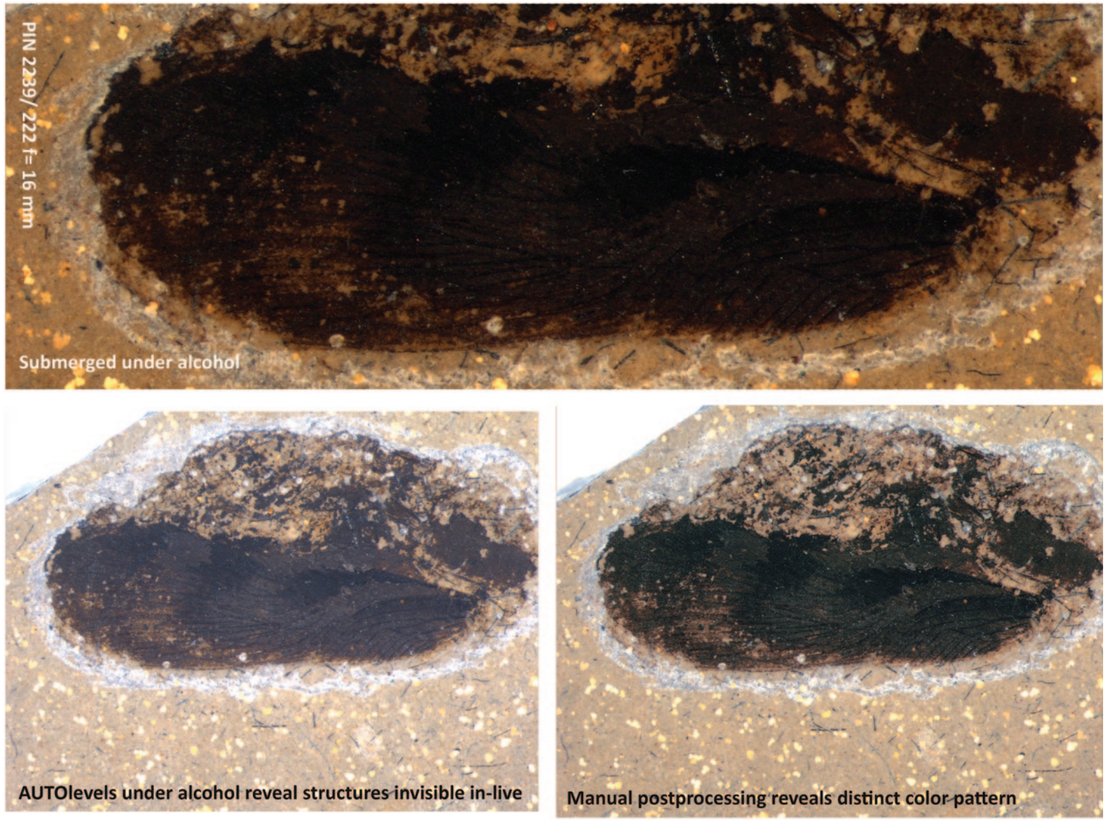
GEOLOGICAL SETTINGS AND ENVIRONMENTS

Geographically, all localities were excellently characterised by Gekker (1948). They a re located in Karatau Ridge (Syr-Darynsk) in South Kazakhstan NE and ENE from Chimkent, river Borolday, right inflow of Arisa in the Ters Basin. It further spread in more than 40 km and is exposed in 4 main sites of Mikhailovka, Galkino, Karabastau s.str. and Chugarchak. The site (Galkino) was discovered by A. A. Anickovič (GEORAZVEDKA) in 1921, and Mikhailovka and Chugurchak later by E.A. Falkova and V.G Muchin respecively in 1925 and 1923. The lake was similar in appearance with the Lake Baikal, with steep rocky slopes, with banks fromed with Paleozoic limestones, conglomerates, dolomites, sandstones and marls, and with mouting rivers (Doludenko and Orlovskaya 1976).

STRATIGRAPHY

Geologically, Orlovskaya (1971) characterises profiles as alternation of conglomerates, sandstones, argillites and limestone and fine laminated dolomites (so called fish-shale). It unequivocally represents a freshwater deposits (with freshwater fauna) and likely a continental lake, although a marine influence has not beed definitely excluded (Gekker 1948). Jurassic loose sediments are finely laminated and soily laminated, laminated sandstones, and dolomites. The total profile reaches 2 km, with Horizon 1 represented with sand conglomerates (up to 1,000 m thick) and coal (up to 500 m) with ferns, ginkgoes, nilsonians, benettites and gymnospems. Horizon 2 contain laminated sandstones (up to 400 m) and scorpulous shales and sandstones (up to 250 m). Horizon 3 represents an alternation of conglomerate/sandstones with fine-laminated bituminous shale containing insects (possibly up to 100 m). Horizon 4 represents hidden crystalline limestones and marls (up to 50 m).

So the maximum span of the insectiferous profile might span as much as 100 m, but much restricted span, only in range of centimeters was also proposed (see Gekker 1948). Martynov and Rohdendorf (personal communication to Gekker 1948) both noted insects restricted to 2-3 cm layers within respective beds. Generally,



the most productive “paper shales” span only 10-20 cm, which does not exclude episodic-only deposition of the whole profile with insects.

Seasonality of deposition also cannot be excluded (Gorizdro-Kulchitskaja 1932). Stratigraphy is well established- it is predecessed by Toguz Formation and followed by Balabugon Formation lacking flora (Doludenko and Orlovskaya 1976). Based on the stratigraphic position and similarity of palynological characteristics, the Karabastau Formation is clearly comparable with the Chagabulak Formation of Western Kazakhstan (Kirichkova and Doludenko 1996). In Bosingen, the Akshabulak Formation may be exposed (Buvalkin et al. 1988, 1989), which may be an age analogue of the Karabastau Formation of the Karatau Ridge (Kirichkova and Doludenko 1996).
Lithology was studied in detail by Gekker (1948). Karabastau Formation was established by Buvalkin (1968).

Thus, Kimmeridgian age is supported by tectonics, insects and pollen (pollen does not exclude the possibility of terminal Callovian age, which is, nevertheless, not concordant with insect, and cockroach in particular, data).

CONTEXT OF INSECTS

Martynov (1925) and Rohdendorf (1938) suggested extremely high insect specialisation (by extinct groups, inlcuding some Palaeozoic relics), higher than in living forms, a similar postulate to that of the cockroaches and wasps from burmite (Vršanský and Bechly 2015, Vršanský and Wang 2017, Ohmkuhnle and Rasnitsyn 2018).;

EDNA fossil insect database (active 2024-05-03; updated 10th June 2022) records 888 insect species in Karabastau, of which 37 were synonimised. Disregarding cockroaches, among 479 insect genera, 155 families, only eleven (Aenigmephemeridae, Ansorgiidae, Archocyrtidae, Eomyidae, Juragomphidae, Malmopsyllidae, Mesophantasmatidae, Palaeophoridae, Tanyderophrynidae, Tipulopleciidae, Scaphocoridae) were indigenous to Karatau. This is a peculiar situation, as additional three families (Latiblattidae fam.n., Operamidae fam.n., Skokidae) are represented by “conservative” cockroaches – usually cockroaches have a conservative morphology.

Another peculiar context is associated with the presence of the still living families. Of 155 families from Karabastau, 66 families of nearly all orders are still living (Acroceridae, Anaxyelidae, Anisopodidae, Anthribidae, Berothidae, Bethylonymidae, Bittacidae, Buprestidae, Carabidae, Cephidae, Cerophytidae, Chaoboridae, Chironomidae, Chrysomelidae, Chrysophidae, Coniopterygidae, Coreidae, Corixidae, Cupedidae, Dytiscidae, Elateridae, Empididae, Eostratiomyiidae, Eumastacidae, Gomphidae, Gryllidae, Gyrinidae, Heloridae, Hybosoridae, Hydraenidae, Ithyceridae, Mantispidae, Miridae, Mega-

lodontesidae, Megalyridae, Mesopentacoridae, Micropterigidae Nannochoristidae, Naucoridae, Nemestrinidae, Limoniidae, Locustopsidae, Lygaeidae, Nabidae, Nemonychidae, Notonectidae, Ommatidae, Osmylidae, Prophalangopsidae, Psychopsidae, Rhagionidae, Roproniidae, Scarabaeidae, Siricidae, Staphylinidae, Tanyderidae, Tenebrionidae, Tettigarctidae, Trachypachidae, Trichoceridae, Trogossitidae, Xyelidae, Xylophagidae, Xyelotomidae, Xyelydidae, Xylomyidae). Additionally, here determined (rare) Blaberidae and Corydiidae are also still living.

Peculiar it is because it reveals that nearly a halve of the Karabastau entomofauna was fully modern. Nevertheless, only 20 % of "conservative" Karabastau cockroach families (and only 0.23 % of specimens) were modern.

According to this indicator (restricted to Kartau context), the diversification tempo of cockroaches is higher than that of beetles, hymenopteras and/or flies i.e., highest – supported also with the former inference of indigenous families (which definitely cannot be explained by higher extinction rates). Higher extinction rates might explain lower partition of modern families only. It is very likely that this parameter is caused with a single element, namely the expansion of (unknown) egg parasites as at K/Pg all external ovipositor-bearing cockroaches except Alienopteridae without true modern ootheca went extinct. This is one of the most enigmatic transition as it affected all decomposing as well as all predatory cockroaches (except true mantodeans).

None record relates to an extinct order.

RECENT ADVANCE IN INSECTS

Strange organs have been discovered on hind legs of scorpionfly males (Novokshonov 1996) and gut content of *Aboilus* grasshoppers include clumps of *Classopollis* pollen grains (Krassilov et al. 1997). Interesting inference is that anaxyelid complex at Daohugou is even more diverse than at Karatau (Kopylov et al. 2020), possibly making Daohugou a site with comparative complexity. Currently a lepidopteran *Pima karatauensis* Tsvetkov, 2020 (Lepidoptera: Pyralidae, Phycitinae), *Arkadiserphus leleji* Rasnitsyn, 2021 (a hymenopteran genus known from burmite), *Karataulius martae* Sukatsheva et Sinithenkova, 2023, *Archiphilopotamus expectatus* Sukatsheva et Sinithenkova, 2023, *Juraphilopotamus inopinatus* Sukatsheva et Sinithenkova, 2023 (Trichoptera: Necrotauliidae, Philopotamidae), *Tipunia* (Diptera, Tipulidae), *Cretapsychops skywalkeri* Khramov et Chemakos, 2022 (Neuroptera: Psychopsidae), were erected (Tsvetkov 2020, Rasnitsyn 2021, Sukatsheva and Sinithenkova 2023, Kopec et al. 2023).





ALL FAUNA FROM KARATAU

Terrestrial vertebrate fauna is typical Mesozoic, with turtle *Yaxartemys longicaudata* (Xinjiangchelyidae); anurognathid insectivorous pterosaurs *Batrachognathus volans,* pterodactylomorph *Sordes pilosus;* an atoposaurid crocodylomorph *Karatausuchus sharovi;* protofeathers of *Praeornis sharovi;* a paramacellodid lizard *Sharovisaurus karatauensis;* and stem-group salamander *Karaurus sharovi* (Vedenjapin 1936, Gekker 1948, Skutchas 2013, *Sordud pilosus* Sharov1971).

Important fish studied by Gekker (1948) reveal a clearly differing taphonomical situation at Galkino and Mikhailovka, with different degree of cummulation of dominant fish. At the same time, impoverished and shared fish fauna (with only 5 species – see Gekker 1948 for *Coccolepis* Agassiz, 1843, *Pholidophorus* Agassiz, 1832 and *"Galkinia"*) might suggest that the diversity of cockroaches is real – if the span of the lakes would be larger, it would become reflected in change in taxonomic composition of fish. It furthermore (n= 1823) suggest a rather small waterbody. Generally fish are rarely found along with insects (Gekker 1948), but a complete *Rhipidoblatta ?tri* was preserved with a complete fish skeleton. Remarkably, fish species are found always isolated, even when found in masses – these mass agglomerations were, nevertheless formed post-mortem and does not reflect mass ocurrences of fish (Gekker 1948).

Molluscs were rare and small suggesting shallow water and warm (which influenced decay of insects), rapidly evaporating (Brick 1925) water inlfluenced to a high degree by the winds and waves (orienting dead fish in one direction): to sum up it strongly suggest a hard (Ca-Mg) freshwater reservoir, nevertheless, the marine influence could not be definitely excluded- the banks were sharp (no sandy beaches) and surrounded by dolomite and limestone mountains (Gekker 1948).

FLORA FROM KARATAU

In contrast to Martynov (1925), who established a separate Zoogeographical Province for Karatau, flora entirely belongs to Euro-Sinic paleofloristic area, while the Siberian one was shifted much northern (Kirichkova and Doludenko 1996). More specifically (Doludenko and Orlovskaya 1976) to the Middle-Asian Povince of Indo-European Paleofloristic Region. First flora was reported by Romanovskij (1878). Dolomite flora was found identical to Jurassic of Gondwanan India; while coal typical for lowland wetlands (Doludenko and Orlovskaya 1976).

Karabastau complex is characterized with dominance of conifer trees of the family Cheirolepidiaceae (*Pagiophyllum, Brachyphyllum* – both possibly representing the same genus but with numerous, up to 17-20 species in Karatau), benetittes (*Ptilophyllum, Otozamites*), cycasses (*Paracycas, Cycadites*) and ferns *Stachypteris* (Orlovskaya 1971). Kimmeridgian age of this paleofloristic region was confirmed by palynology, although terminal Callovian age cannot be excluded on the basis of pollen (Sakulina 1968, 1971; Muraklovskaja 1968).

Totally, there are 180 plant species recorded in Karatau (Doludenko and Orlovskaya 1976). Conifers were represented with 17-20 species, ferns in low abundance (*Clathopters, Coniopteris, Cladophlebis, Stachypterus*), few czekanowskias (*Phoenicopsis, Czekanowskia* (Turutan-Ketova 1929, 1930, 1936, 1950, 1963)), some ginkgoes (5 genera), numerous benetitttes, cycasses and gymnosperms.

Nevertheless, only 8 species pass from the Early Jurassic, 37 appears from the MIddle Jurassic Borolsay, and 62 in Karabastau in this up to 35 Ma lasting flora (of which Karabastau might be short-living) - remarkable finds comprise leaf of *Otozamites* turkestana Turutanova-Ketova, 1929; 80 cm long, cones and winged seeds *Pityospermum* (Doludenko and Orlovskaya 1976).

Palynology is in strong disagreement with macrofossils (absence of benetittes, czekanovskias, gingoes, and cycasses), suggesting that benettites might be entomophilous (Krassilov 1973). *Classopolis* covers 95-100 % (5 species), *Dicassites* 2 %, 6 others and 8 spores also occurred. Proposed entomophyli for Classopolis is probably false, and they were anomophilous due to high abundances (Doludenko and Orlovskaya 1976).

Both plants and pollen were apparently deposited without transport near banks. The homogenity (also of pollen) suggest that the impoverished flora is not preferentially preserved (more rigid leaves), supported also by the presence of fine insects. Nevertheless, thuth is that a single cockroach was preserved along with a wood (figp. 62) and no-one with a leaf.

The greatest lesson the flora provides is unequivocal warm xeric climate it indicates, suggesting a forest zone of rised platforms and with occurrence of xeromorphs, which was explained by aridification (Strachov 1960) and/or by physiologically dry flora (Doludenko and Orlovskaya 1976).
On the other side, insects (and cock-

roaches analysed here in particular) unequivocally indicate warm and wet environment (Rohdendorf 1968).

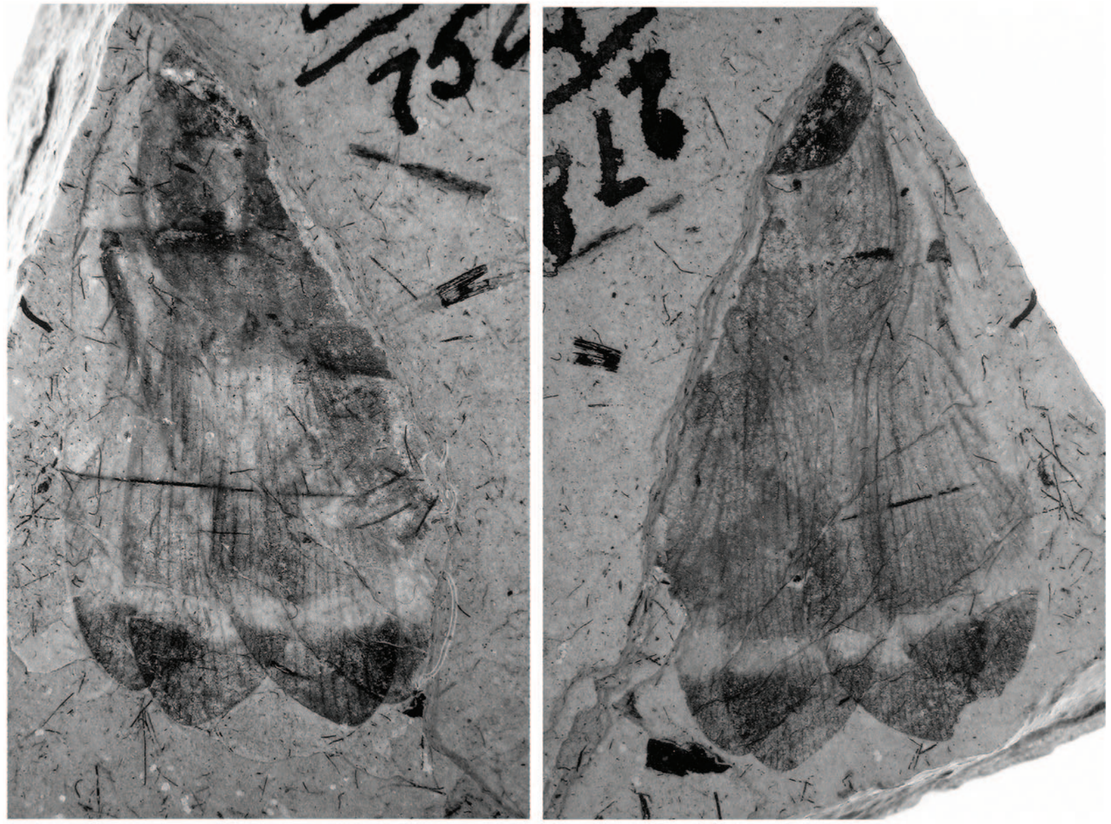
There are only three possible explanations: (1, highly improbable) insects and cockroaches in particular were all different from living clades and were xerothermous; (2, rather improbable but most probable among these three possibilities) insects were, in spite of fine preservation transported from elevated wet mountaneous environments; (3, improbable, proposed as one of opportunities by Doludenko and Orlovskaya 1976) Plants were selectively preserved favouring xeromorphs. (4) Possible is also episodic preservation of plants and their dissolving in "insect" strata – this hypothesis was, nevertheless, not tested.

All thing being equal, the complexity of the ecosystems of Karatau is evidenced in the predecessing Daohugou biota, where 32 genera of macrofossils (Na et al. 2017) and 87 different palynomorph species (Na et al. 2015) occurred and the list will be further enriched in the future. Furthermore, the evidence is also rising for the ocurrences of angiosperm flowers and fruits in the Middle, and even Early Jurassic (Chen et al. 2020, Han et al. 2023). Thus it cannot be definitively excluded that *Maloval* is an angiosperm pollinator and that the extreme Karatau diversity is partially caused with the early radiation of angiosperms.

STRATIFICATION OF THE FOREST

The fauna unequivocally evidences dense forest cover. The performed fire analysis (unpublished) with several different burning temperatures document stratification of the forest in separate etages including the moderately tall, tall and also canopy level top tall trees. The shrub layer was also fully formed. The grass level was missing, but the erosion was partially halted by mosses and fungi/bacterian-generated gells. The fungal interconnection (and possibly with mucous bacterial gells) was also likely formed (see below). These forests, extant rainforests analogues, were among the most difverse (and also conifer-based) ecosystems of the history, comparable only to burmite.





Decomposita triocella

ENVIRONMENT

This is surely the most important factor in structuring phylogeny of any subordinated groups, such as cockroaches. Nevertheless, the Karatau is insufficiently known to directly evaluate conditions threat on cockroaches to force their evolution. Moreover, generally the influence of environment is inaccessible for study at the present state of knowledge. Lack of detrimental mutations and huge diversity suggest that the environment was extremely competitive, balanced and complex.

GLOBAL ECOSYSTEM

The very disturbing situation with the cockroach diversity higher than in modern rainforests is supported also on the basis of dominant beetles (55.5 %; only 5 specimens per species in average) and hymenopterans (1.8 %; ca. 200 spp.). There are several dozens of genera among nearly all orders represented by multiple species evidencing either a higher diversity or a presence of more assemblages. Genera with most numerous species are within hymenopterans, coleopterans, dipterans and othropterans (*Symphytopterus* (12 spp.), *Leptephialites* (11), *Aboilus* (11), *Codemus* (10), *Hypnomorphus* (14), *Bethylonymellus* (16) and *Brachycleistogaster* (12)).

It might be argued that earlier researchers did tend to describe species rather than consider intraspecific variability. Nevertheless, the amber record of burmite confirm presence of numerous sibling species (see Rasnitsyn 2007, Jiang et al. 2024). Thus the current state (of numerous species) must be taken very seriously until the contrary was validated. Numerous here well-established cockroach species in several independent lineages partially support this (approach).

While Gekker (1948) suggested warm and wet climate with diverse plants, wetlike and also with xeromorphic elements, on the basis of diverse odonatans, ephemeras, plecopterans, phasmatodeans, cockroaches, homopteras and neuropterans, Panfilov (1968) suggested unequicovally “tropical” climate.
On the other side, raphidiopteran and mecopteran high diversity today indicate rater a moderate zone, which was interpreted as due to absence of birds and ants as top predators (Panfilov 1968). This leads author to compare the Karatau climate to Monsoon of the India (changing of dry and wet periods).
Here analysed cockroaches, with aposematic forms also unequivocally indicate “tropical” (not “subtropical”) ecosystem.



RESULTS

SYSTEMATIC PALAEONTOLOGY

System:

Mantides Latreille, 1802
- Mantides Latreille, 1802
  - Lovecoidea superfam.n.
    - Lovecidae fam.n.
      - *Lovec pratiena* gen. et sp.n
  - Termitina Latreille, 1802
    - Socialioidea Vršanský, 2010
      - Socialidae Vršanský, 2010
        - *Sociala borat* sp.n.
  - Blattaria Latreille, 1810
    - Blattoidea Latreille, 1810
      - Mesoblattinidae Handlirsch, 1908
        - *Mesoblattina etarakan* sp.n.
        - *Perlucipecta liangiae* sp.n.
        - *Sivis lukashevichiae* sp.n.
      - Blaberidae Saussure, 1864
        - *Morphna una* sp.n.
    - Corydioidea Saussure, 1864
      - Corydiidae Saussure, 1864
        - *Okruhliak samoodpovedaniesi* gen. et sp.n.
        - *Cretaholocompsa karatauensis* sp.n.
    - Raphidiomimoidea Vishniakova, 1973
      - Raphidiomimidae Vishniakova, 1973
        - *Cameloblatta stress* sp.n.
        - *Cameloblatta variegata* Vishniakova, 1973
        - *Decomposita apicata* sp.n.
        - *Decomposita basquatirgis* sp.n.
        - *Decomposita pentavisia* sp.n.
        - *Decomposita triocella* Vršanský, 2008
        - *Decomposita tristriata* sp.n.
        - *Divocina polnoci* sp.n.
        - *Falcatusiblatta casovec* sp.n.
        - *Falcatusiblatta disrupta* sp.n.
        - *Falcatusiblatta karatavica* (Vishniakova, 1968)
          = *Rhipidoblattina karatavica* Vishniakova, 1968
        - *Falcatusiblatta storozhenkoi* sp.n.
        - *Falcatussiblatta tooold* sp.n.
        - *Falcatussiblatta zaloha* sp.n.
        - *Chuanblatta stalosa* sp.n.
        - *Liadoblattina crassivenata* sp.n.
        - *Olzmasg zi* gen. et sp.n.
        - *Raphidiomima chimaera* Vishniakova, 1973
        - *Raphidiomima cognata* Vishniakova, 1973
        - *Rhipidoblattina dmitrievi* sp.n.
        - *Rhipidoblattina maculata* Vishniakova, 1968

Caloblattinidae Vršanský et Ansorge in Vršanský (2000)
- *Aposema gigantenna* gen. et sp. n.
- *Asioblatta punctata* Vishniakova, 1968
- *Caloblattina laesis* sp.n
- *Karatavoblatta longicaudata* Vishniakova, 1968
- *Rhipidoblatta brevivalvata* Vishniakova, 1968

Rhipidoblatta fusca Vishniakova, 1968
= *Srdiecko tri* Vršanský, 2008 syn.n.
Rhipidoblatta matriky sp.n.
Rhipidoblatta matrikarky sp.n.
Rhipidoblatta trika sp.n.
Rhipidoblatta triky sp.n.
Rhipidoblatta trimestre sp.n.
Rhipidoblattinopsis latitergata Vishniakova, 1968

Latiblattidae fam.n.
Latiblatta lativalvata Vishniakova, 1968
Latiblatta osud sp.n.
*Fosilia tubulioviposito*rica gen. et sp.n.

Liberiblattinidae Vršanský, 2002
Ano mal sp.n.
Ano ona sp.n.
Ano naslosa sp.n.
Ano palindrom sp.n.
Ano si sp.n.
Ano tak sp.n.
Akinisia chorevei gen. et sp.n.
Aktassoblatta fusca Vishniakova, 1971
= *Palaeovia praecarnia* Vršanský, 2008 syn.n.
Aktassoblatta pullata Vishniakova, 1971
Hra nice sp.n.
Hydrokhoohydra aquabella Vršanský
in Vršanský et al. (2019a)
Katatychi symptosi gen. et sp.n.
Kazachiblattina asiatica (Vishniakova, 1968) comb.
Vršanský (2002)
= *Artitocoblatta asiatica* Vishniakova, 1968
Liberiblattina cunicula sp.n.
Liberiblattina cipka sp.n.
Liberiblattina ihringovae Vršanský, 2002
Liberiblattina kontrapunktata sp.n.
Liberiblattina kontravenata sp.n.
Liberiblattina liberiblattina sp.n.
Liberiblattina luminanala sp.n.
Liberiblattina nenicocom sp.n.
Liberiblattina oddajsami sp.n.
Liberiblattina paleontologica sp.n.
Liberiblattina zokamuvypadli sp.n.
Makacka akcakam gen. et sp.n.
Makacka akmacaka gen. et sp.n.
Memento mori gen. et sp.n.
Miniblattina inflatica sp.n.

Skokidae Vršanský, 2007
Skok svaba Vršanský, 2007

Manipulatoridae Vršanský et Bechly, 2015
Manipulator olim sp.n.

Blattuloidea Vishniakova, 1982
Blattulidae Vishniakova, 1982
Asvab bavsa gen. et sp.n.
Blattula ahanaha sp.n. 6mm s pterostigmou
Blattula brevicaudata Vishniakova, 1968
Blattula druha sp.n.
Blattula fragilia sp.n.
Blattula gracilicosta sp.n.
Blattula microscopica sp.n.
Blattula nebude sp.n.
Blattula rectinervosa Vishniakova, 1971
Blattula summa sp.n.
Elisama prelistama sp.n.
Macaroblattula velipsespilev sp.n.
Okienkula ojedinela gen. et sp.n.
Pseudomantina nigroalba Vršanský
in Vršanský et al. (2021)
Spono spono sp.n.

Umenocoleoidea Chen et Tan, 1973
Umenocoleidae Chen et Tan, 1973
Maloval hlavolam gen. et sp.n.

Fractaliidae Vršanský et Hinkelman
in Vršanský et al. (2021)
Fractalia aristovi Vršanský in Vršanský et al. (2021)

Operamidae fam.n
Operam monita gen. et sp.n.
Operam simpla sp.n.
Operam testudina sp.n.

Order Mantides Latreille, 1802 (p. 270)

= Termitina Latreille, 1802 (p. 293)= Blattaria Latreille, 1810= Blattodea Brunner von Wattenwyl, 1882
= Dictyoptera Latreille, 1829
= Chresmoda Germar, 1839
= Alienoptera Bai et al. 2016= Aethiocarenodea Poinar et Brown, 2017

Type genus and species: *Mantis religiosa* Linnaeus, 1758.

Composition: cockroaches, mantodeans, termites, chresmodids, umenocoleids/ alienopterids.

Stratigraphic range: Pennsylvanian- living
Geographic range: Cosmopolitan

In this concept, Isoptera Brullé, 1832 are considered for one lineage of eusocial cockroaches (Inward et al. 2007), Mantodea Burmeister, 1838 are considered for one of the ten different predatory cockroach lineages (Vršanský et al. 2019) and Alienoptera Bai et al. 2016= Aethiocarenoda Poinar et Brown, 2017 are considered for mimicking cockroaches of the superfamily Umenocoleoidea Chen et Tán, 1973 (Vršanský et al. 2018, 2021 which is considered for Blattaria s.str.). *Chresmoda* Germar, 1839 are considered for water-skimming cockroaches (Vršanský 2020, on the basis of burmite species with multi-segmented cerci and modified corydioid-like head).

Remark: In spite of risking the lost of confidence among readers in the first paragraph, I decide to follow the time priority and use order of Mantides for the whole group of cockroaches (and termites, alienopterids and chresmodids). I follow the same principle as for term Blattaria originally used by Latreille for cockroaches at the level of families applied at that time (Latreille 1810). Nevertheless, Latreille (1802) applied the same principle 8 years before to establish groups of termites, and 23 pages above also for mantodeans. Thus in this book and in my following works (if any), I will be using “Mantides” as the order for cockroaches and all its direct descendants. And Termitina Latreille, 1802 for strict termites.

Diagnosis: Insects with “incomplete” metamorphosis, originally winged, forewing with clavus (rarely reduced), cerci segmented (rarely secondarily simple), tarsi 5- segmented (rarely 3 or 4- segmented).



Suborder Mantides Latreille, 1802 (p. 270) = Mantodea Burmeister, 1838

(paradoxically subordinated under superfamily Raphidiomimoidea Vishniakova, 1973 and also more strictly under Liberiblattinidae Vršanský, 2002)

= Mantodea Burmeister, 1838

Type genus and species: *Mantis religiosa* Linnaeus, 1758.

Composition: Juramantidae, Baissomantidae, Cretomantidae, Jantarimantidae, Santanmantidae; Eumantodea.

Stratigraphic range: Upper Jurassic- living
Geographic range: cosmopolitan (beyond polar circles during Cretaceous)

Remarks: Order should be a major cathegory, nevertheless, mantodean split from the "corydioid" cockroaches (Liberiblattinidae) and thus are at the same time subordinated to minor rank of Raphidiomimoidea.
Systematic remarks. Formally, this problem was already solved (Vršanský et al. 2019), but to remind, mantodeans are only one of at least ten predatory cockroach groups, some of which are even more spectacular than true mantodeans, and thus mantodeans cannot have order of their own (unless orders will be erected for the each of the other nine groups). Other predatory groups are 1) certain Phyloblattindae; 2) whole Mutoviidae; 3) certain Blattulidae; 4) certain Liberiblattinidae; 5) whole Manipulatoridae; 6) whole Eadiidae; 7) *Raptoblatta waddingtonae* (Mesoblattinidae); 8) certain Caloblattinidae; 9) whole Raphidiomimidae.
Generally the results are consistent with molecular data besides the fact that most lineages were extinct and thus not prone to the analysis (see the phylogenetical part how absence of taxa and/or data modifies the structure of networks).

Diagnosis (modified after Vršanský et al. 2019): predatory corydioid cockroaches usually with raptorial forelegs, elongated forewing SC, pseudovein and posteriorly branched A.

Superfamily Lovecidae
Family Lovecidae fam.n.

Type genus: *Lovec* gen.n. described below, and my monotypy.

Differential diagnosis: Differs from Eumantodea in having forewing Sc not entrirely elongate and in having R in more or less original state. Juramantidae and Santanmantidae have modified A towards longer and more straight branches (Vršanský 2002; Grimaldi 2003; Hörnig et al. 2013). Baissomantidae have more derived A without standard branchings and terminal dichotomisations are replaced with reticulations (Gratchev and Zherikhin 1993; Demers-Potvin et al. 2021). Cretomantidae and Jantarimantidae (also *Ambermantis*) have more specialized, robust forelegs (Cretomantidae with short tibia).
Autapomorphies: blind branches of A1. All unique and new characters (raptorial



Lovec pratiena

legs, elongated wings, extremely elongated and narrow Sc, pseudovein) are no autapomorphies as these are shared as mantid synapomorphies

Description: as for species.

Systematical remarks: The present taxon can be categorized within mantodeans on the basis of pseudovein, long branched forewing Sc and raptorial legs. It can be derived directly from the Liberiblattinidae basing on elongated Sc and extremely curved R. The coloration and character of branches is most similar to *Elisamoides Vršanský, 2004*. *Liberiblattina* Vršanský, 2002 has normal forelegs and conspicuous coloration. *Kazachiblattina* Vršanský, 2002, has much shorter wing and Sc, and normal cursorial legs with short tibia. *Gurvanoblatta* Vishniakova, 1986 also has much shorter Sc, and secondarily branched posteriormost CuA. *Brachymesoblatta* Vršanský, 2003 is much smaller with wider wing, reduced venation and tertiary branched veins. *Eublattula* Handlirsch, 1939 as a basalmost taxon of the family has much shorter wing and Sc. *Kurablattina* Martin, 2010 is a basal unspecialised taxon with wide wings. *Miniblattina* Sendi, 2021 is a miniaturised taxon derived from unmodified *Stavba* Vršanský et Vršanská in Vršanský et al. (2019c). *Hydrokhoohydra* Vršanský in Vršanský et al. (2019a) and *Cryptoblatta* Sendi et Azar in Vršanský et al. (2019a) are aquatic specialists. *Entropia* Vršanský, Liang et Ren, 2012 and *Ano* Vršanský, 2020 are basal standard unmodified liberiblattinids. *Leptolythica* Vršanský, 2008 is very similar in habitus, but has short antenna and does not have raptorial legs.

Genus *Lovec* gen.n.

Type species: *Lovec pratiena* sp.n., by monotypy.

Description. Costal fieled extremely narrow, Sc simplified and elongated. R short, strongly curved, RS not differentiated. M and CuA expanded; CuP sharply curved; A1 with blind branches, other A branched. And as for type species.

Derivation of name: after *lovec* (Slavic for hunter).

Lovec pratiena sp.n.

(figps. 81, 83)

Holotype: PIN 2904/334. A complete winged adult female.

Type locality: Mikhailovka, Karatau, Kazakhstan.

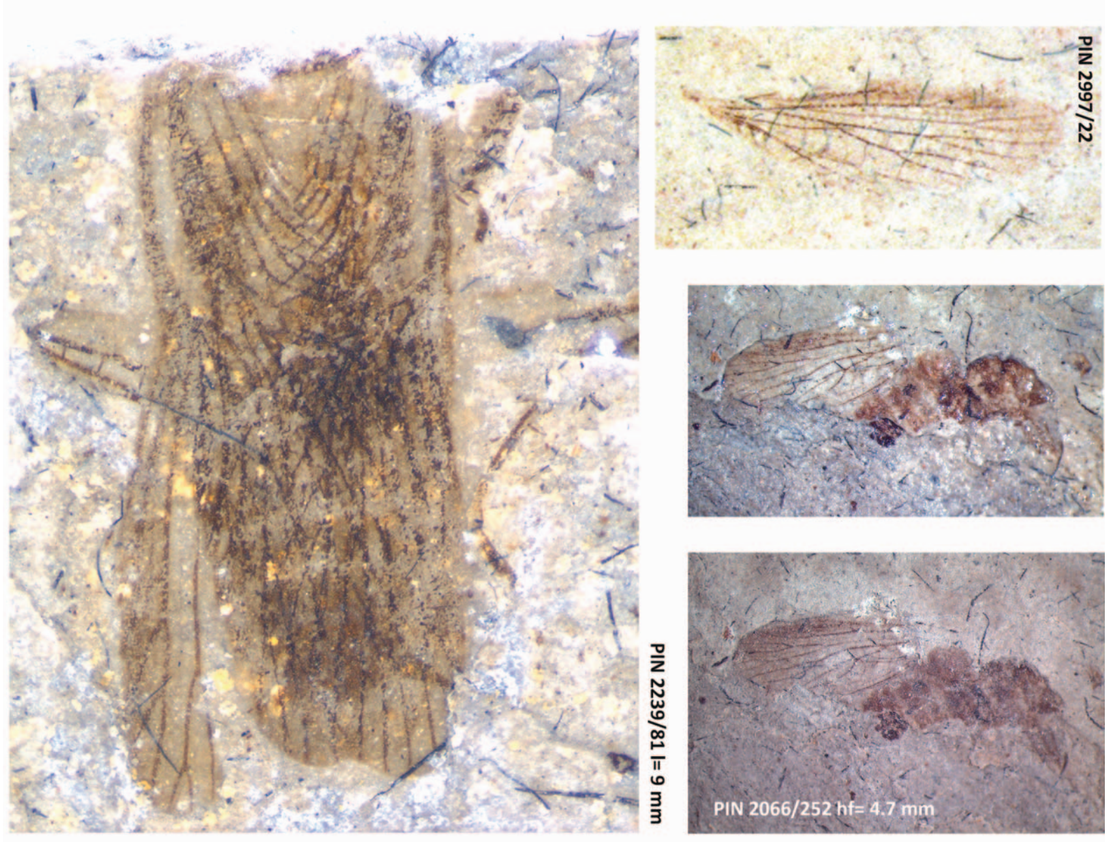
Type horizon: Kimmeridgian Upper Jurassic, Karabastau Formation.

Additional material. PIN 2066/252 (hindwing, body and foreleg); 2239/81 (l= 9 mm); 2904/49 (f= 8 mm; both forewings with both fore legs), 1856 (complete specimens); 2904/1874, 147 (h= 8 mm), 162; 2997/22 (h= 5.5mm)(hindwings). The same locality as the type.

Diagnosis. Head very large, globular, nearly as wide (2.3 mm) as only slightly prolonged pronotum with paranotalia and central posterior extension (3/2.9 mm). Forewing length 8-9 mm. Costal field extremely narrow, with simplified and elongated Sc, ocassionally richly branched, with short and long offshots. R with 6-8 mostly simple branches. Due to extreme shortening, the so-called RS not differentiated, but the pre-terminal vein is branched. M with 5-6 veins at margin. CuA with 6-9 veins at margin; CuP sharply curved; A branched, A1 with 2 blind branches, total A with 7-11 veins at margin. Forewing pale in costal space, but dark in part of radius, rest of the wing pale.

Hindwing extremely short (5.5-8 mm) when compared with the forewing (because of its terminally shifted articulation – both wings at the same level during the repose), with very strong but short Sc reaching only 1/3 of the wing length. Radial veins also very strong, R1 and RS dstinctly separated (3+ 4-5). M strong, with 2-5 veins meeting margin CuA with dichotomised conservative 5 branches (possibly 4 in in 2997/22). CuP simple, connected with CuA with net of sigmoidally curved cross-veins. A1 with up to 6 short rami. Cross-veins in the hindwing are resttricted to connections of RS with M (3-5) and within CUA (2-5).

Fore coxa extrelemy elongated, free, femur with two rows of spines; tibia long, with terminal spurs. Foreleg probably



monochromatic dark. Mid and hind-femora pale, with dark longitudinal stripe. Body narrow, cerci multisegmented, short and wide (0.67/ 0.22 mm).

Remarks: By analogy with the Middle Jurassic carnivorous cockroaches *Divocina* (Raphidiomimidae) and *Pseudomantina* (Blattulidae), which are presumed as nocturnal, identical habits are presumed for the present species. Homoplasies include the composition of gut with very small fragments of chitin, and characteristic coloration with dark fore and hindwings, but with narrow pale anterior margin of obscure optical function.

It is notable that the single significant Jurassic mantis (*Juramantis* is possibly basal-most Cretaceous) is extremely small and nocturnal. Thus it can be natural that predecessors of mantodeans were also nocturnal. Moreover noctural is also the abovementioned *Divocina* (no other nocturnal predators are known from the type locality Daohugou) and also predatory cockroach *Eadia aidae* (Eadiidae) is dark and their nocturnal habits could not be excluded.

Another important character shift to be observed on the present specimen is the transformation of blind rami of CuA, i.e., regular veins into sigmoidally curved cross-veins. At least in this case it is clear the origin of the cross-veins.

Even more intriguing is the apparent origination of the pseudovein, a structure known from mantodeans and liberiblattinid cockroaches. Pseudovein is apparently modified from the blind anteriormost branch of forewing A1 and the adjacent cross-vein. This structure (anteriorly branched A1 as well as pseudovein) is known nowhere else but in the Liberiblattinidae (*Ano*) and mantodeans.

All specimens represents almost ideally symmetrical individual (M 5/ 6; CuA 9/ 8; 9/ 11; R 8/ 8), which is in deep contrast with the variability (specimens are deeply different) of the species (and the family Liberiblattinidae in general). Other representatives of this family display the same pattern. The lack of correlation between the variability and symmetry is obscure, but extremely interesting.

A similar fossil (WAM 08.116 after Martin 2010) is present in the ?Lower Jurassic sediments of Mintaja in Australia, attributed to *Elisamoides cantabillingensis* Martin, 2010. It has the same size and a very similar coloration with typical pale stripe along clavus, to the present fossil, but venation characteristic for the genus *Elisamoides*, which further supports this genus to be ancestral for *Lovec* and all mantodeans. Nevertheless, the venation differs from *Lovec* in having characteristic doubled M. Additional linkeage to the ancient Liberiblattinidae is the indication of subapical pale macula

Remarkable is also a very distinct long carbonised filament protruding from the mouthparts of the present specimen, found also at least in 5 different specimens of diverse Blattaria from the locality.

Mutations: Apparent deformity of A1, namely 2 blind anterior branches fusing with CuP become fixed and are observed in both visible parts of the all three preserved specimens and on both wings (PIN 2239/81, 2904/49, 334). These deformities are not counted into the total number of detrimental mutations as in the clavus they have protective function with little influence to the aerodynamics. Nevertheless, this is an extremely important observatrion as it directly confirms these mantodeans belong to the same lineage and most probably to a single population.

Derivation of name*: pratiena* is after *pra* (Slavic for ancient) and derived from *tieň* (Slavic for shadow).

Character of preservation: Five complete specimens (2 disarticulated); 4 hindwings.

Taphonomy: Most specimens are represented with isolated damaged and disarticulated hindwings, and also complete specimens are greatly dissarticulated. Complete specimens are also partially disarticulated and damaged. Combined with the presence of a complete holotype with articulated cerci this suggest a preburial predation and short pre-depositional transport.

Suborder Termitina Latreille, 1802 (p. 293)

(subordinated under the superfamily Corydioidea Saussure, 1864)

= Isoptera Brullé, 1832

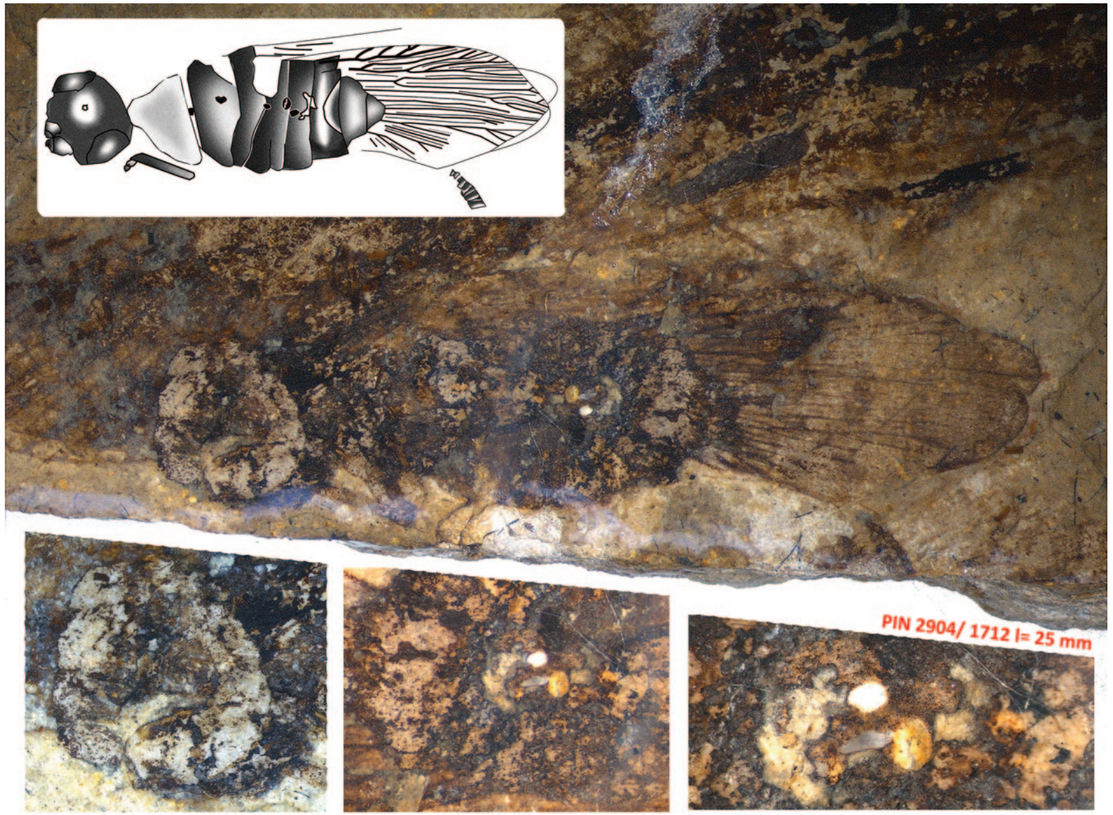
Type genus: *Termes* Linnaeus, 1758.

Composition: Socialidae Vršanský, 2010; ?Cryptocercidae Handlirsch, 1925; Pabuonqedidae Vršanský et al., 2019; Cratomastotermitidae Engel et al., 2009; Mastotermitidae Desneux, 1904; Euisoptera Engel et al., 2009.

Stratigraphic range: Upper Jurassic- living
Geographic range: Cosmopolitan (except polar regions, absent beyond polar circles even during Cretaceous)

Diagnosis: Eusocial insects that are classified at the taxonomic rank of infraorder Isoptera, or alternatively as epifamily Termitoidae, within the order Blattaria (along with cockroaches, alienopterids, mantodeans and chresmodids). Termites were once classified in a separate order from cockroaches, but recent phylogenetic studies indicate that they evolved from cockroaches, as they are deeply nested within the group, and the sister group to wood eating cockroaches of the genus *Cryptocercus*, which might itself appear a termite (Inward et al. 2007; Vršanský et al. 2018, 2019d; Vršanský 2020; Wikipedia active 2022-05-22).

Remarks: After careful examination I decide to place Socialidae directly within termites. In spite of the lacking unequivocal evidence for the breaking cleavage sutura, according to my opinion, the evidence is strong enough for this controversial placement. Arguments are 1) pale body of the type species (indirect evidence – also cave species can be transparent); 2) long palps serving for communication (indirect evidence – also presumably unsocial *Manipulator* has long palps); 3) here presented evidence for the small body (autapomorphy of termites); 4) large head (indirect evidence, also social *Melyroidea*-group has huge head, but also some miniaturized species); 5) sharply ascending radial veins (indirect evidence- autapomorphy of temites, but rarely homoplasically occur in some derived taxa, never in the Mesozoic or Paleozoic); 6) here presented skewing of veins forming secondary reticulations and fusions (autapomorphy of all termites except Pabuonqedidae); 7) short probasitarsus (autapomorphy of termites); 8) fontanelle (termite autapomorphy). Taking into consideration strong need for total evidence and potentially rough response of opponents, I anyway think the evidence is strong enough. It is more safe than ignoring these records.



Family Socialidae Vršanský, 2010

Type genus and species: *Sociala perlucida* Vršanský, 2010. Archingeay amber; Albian.

Composition: Type. And species described here.

Stratigraphic range: Upper Jurassic (FOD) – Upper Cretaceous
Geographic range: Laurasian

Diagnosis (after Vršanský 2010; relevant parts not based on upreserved forewing): Head wider than pronotum with large eyes. Pronotum campaniform. Body small. Wings triangular. Legs delicate.

Remars: transparent body is highly unlikely to preserve in sediments, and the present species was apparently sclerotized.

Sociala borat sp.n. (figp. 86)

Holotype: PIN 2904/1712 (l= 25 mm). A complete winged reproductive adult, possibly Queen.
Type locality: Mikhailovka, Karatau, Kazakhstan.
Type horizon: Kimmeridgian Upper Jurassic, Karabastau Formation.

Differential diagnosis: Differs from the type species in large size and massive sclerotization and in lacking short apical foretibial spurs..
Description: Big, melanized, dark "termite" amounting to 25 mm of total length from head to the end of hindwings, with small body (9.1/ 6.5 mm). Head large, globular (ca. 4.2/ 4.6 mm), uncovered by the pronotum, with large round unmelanised eyes 2.4-0.1 mm, widely (2.4 mm) separated. Mandible very wide and very short (L 1.2/ 1.6; R 0.9/ 0.8 mm), even more sclerotized than rest of the body. Fontanella present 0.26 mm in diameter.
Pronotum campaniform (2.9/ 4.8 mm) possibly transparent, in distal part very narrow (0.9 mm).
Body wide, but extremely short, terminal sternal margins sharply curved, ovipositor outer valves not protruding if present (sex unknown, presumed reproductive female, possibly Queen). Cerci multisegmented, long (2.4/ 0.7 mm as preserved), with 8 segments preserved, totally probably amounting to more than 11, cercomeres heterogenous
Forewing 17.4 mm longwith distinct melanised costa, R ascenting in sharp angle, sharp apex posed anteriorly, wing triangular. Hindwing shorter than forewing, in repose all wings reach the same position, sharpened at centally posed apex, very wide. Costa distinct, Sc straight, simple, Strong R1 stem with strong terminally dichotimised veins (5 at margin) differentiated from strong RS (7), which also dichotomises terminally. M is impossible to discriminate from CuA (base unpreserved), together these systems count up to 15 long straight veins at margin plus additional blind branches (other than posteriormost CuA) – in these systems regularity of veins in absent. CuP seems to have 2 branches, A1 in remigium with short blind branches.
Forefemora and tibia tiny (3/ 0.4 mm), cursorial (if active at all), forebasitarsus very short (0.4/ 0.4 mm). Spurs including the terminal femoral spur absent.
Systematical remarks: The specimen can be categorized within wider Dictyoptera on the basis of multisegmented cerci and liberiblattinid type of venation with massive intercalaries. More specifically it is placed within Socialidae on the basis of unique campaniform pronotum, huge head and in lacking forefemoral spurs (also apical spur is missing in both taxa).

While the extremely small body and tiny delicate legs directly suggest eusocial organization and placement within Eutermites, I preferred to place this taxon only within Socialidae.
Sharply curved tergal and sternal margins suggest corydioid s.l. origin.
Remarks: Unidentifiable pollen grains and/or fungi preserved throughout the diffestive track suggest at least opportunistic pollivory and/or fungivory. Yellow colored inclusions divided by half directly represent pollen. It cannot be excluded this diet was a primary diet shift leading to social life. Notably also other eusocial cockroaches of the *Melyroidea*-group, shifted diet (towards algaevory) – see Hinkelman et al. (2021). If we evidence specialized pollivore or a generalist opportunistic eating pollen prior burial is unclear. Nevertheless, mouthparts are specialized, shortened and massive.
Mutations: The preserved specimen contain numerous wing deformations. There are terminal irregular dichotomisations of R1, RS, M and also CuA – i.e., in all venial systems except simple Sc and CuP (A invisible). Also there are interminated veins of CuA and suddenly lost width (but prolonging further in narrowed width) RS1. The pattern observed has two possible explanations or a combination of them, either it is an evidence for the mutations resulting from the diversification point, but more probably it is a resulting from fligt restricted to the nuptial one.
Derivation of name: *borat* is after Borat comedy.
Character of preservation: one completely articulated winged adult.
Taphonomy: a single specimen suggest a rarity or incidental flight from more remote area – full articulation suggest burial near the source waterbody and no or short pre-depositional transport.
Syncompression: A large winged insect, possibly an odonatan.

Suborder Blattaria Latreile, 1810 s.str.

(i.e., without Isoptera, Mantodea and Chresmoda

= Blattariae Latreille, 1810
= Dermatoda, Blattaedes Billberg, 1820
= Blattina MacLeay, 1821
= Blattae Charpentier, 1825
= Blattaria Burmeister, 1829
= Blattidae Stephens, 1829
= Blattina, Blattites Newman, 1834
= Cursoria, Blattidae Westwood, 1839
= Blattinae Swainson et Shuckard, 1840
= Blattoidea Fieber, 1851
= Cursoria, Blattina Fischer, 1853
= Orthoptera, Cursoria Gerstaecker, 1863
= Blattodea Brunner von Wattewyl, 1882
= Neoblattariae Scudder, 1895
= Blattidi Acloque, 1897
= Blattoidea Handlirsch, 1903
= Blattacea Sallards, 1904
= Blattidea Burr, 1910
= Palaeoptera Crampton, 1915
= Blattoides Crampton, 1916
= Blattoida Crampton, 1920
= Blattoptera Bey-Bienko, 1960 (list from Princis 1962 up to here)
= Alienoptera Bai et al., 2016 (according to Vršanský et al. 2018)
=Aethiocarenodea Poinar et Brown, 2017 (according to Vršanský et al. 2018)



Superfamily Blattoidea Latreile, 1810

Statigraphic range: Earliest Jurassic (Connecticut, U.S.A.)- still living
Geographic range: cosmopolitan

Composition: Blattidae Latreille, 1810; Mesoblattinidae Handlirsch, 1906

Remarks: The present concept threat this family as representing advanced, modern crown cockroaches which possess cockroach (modern) ootheca with keel, either primitive long in some Mesoblattinidae (the same is Cryptocercidae) or advanced in Blattidae and other Mesoblattinidae as in *Praeblattella* Vršanský, 2003. They do not rotate it.

Family Mesoblattinidae Handlirsch, 1906

Type genus and species: *Mesoblattina protypa* Geinitz, 1880. Dobbertin, Germany; Early Jurassic.

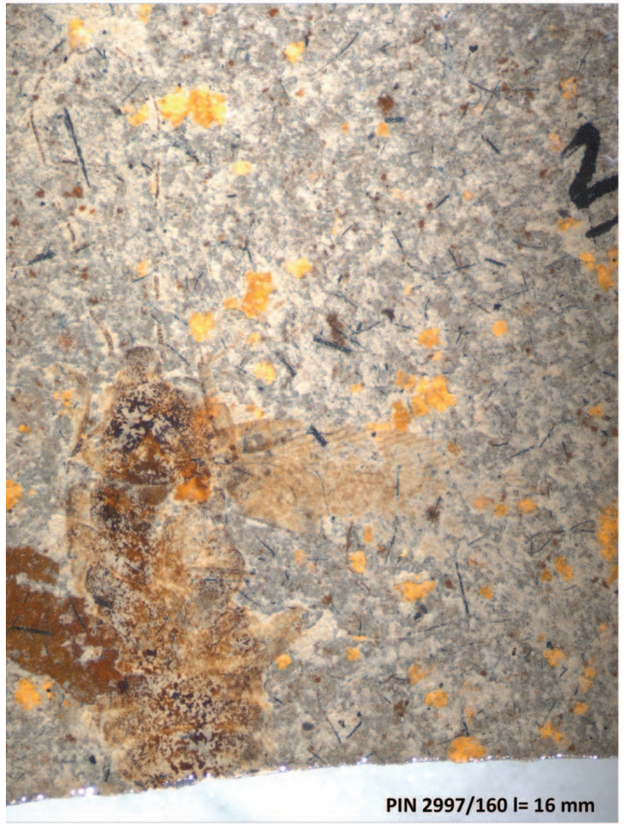
Diagnosis (after Vršanský and Ansorge 2007): Medium-sized cockroaches, plesiomorphically with short external ovipositor, with generally reduced and regular venation (with exception of area between bases of M and R) without branchlets, and with dense venation present in apical parts of R and M in forewing. Forewings with more or less parallel borders, without distinct intercalaries. A without numerous reticulations; venation of Cu and M, with exception of the first stem, regular; R straight; Sc two- to four-branched. Hindwing with simple Sc; R1 and RS differentiated; M with up to 5 branches; CuA secondarily branched and with additional blind branches; CuP simple.

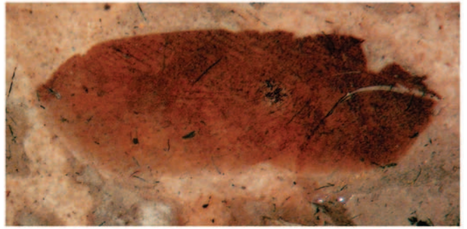
Composition: *Mesoblattina* Geinitz, 1880; *Artitocoblatta* Handlirsch, 1906; *Hispanoblatta* Martínez-Delclós, 1993; *Archimesoblatta* Vršanský, 2003; *Breviblattina* Vršanský, 2004a; *Mongolblatta* Vršanský, 2004a; *Gondwablatta* Vršanský, 2004b; *Nymphoblatta* Vršanský et Grimaldi in Vršanský, 2004b; *Sivis* Vršanský, 2009; *Perlucipecta* Wei et Ren, 2013; *Raptoblatta* Dittmann et al., 2015; *Spinaeblattina* Hinkelman, 2019; *Mesoblatta* Hinkelman, 2020; *Cuniculoblatta* Hinkelman, 2021, and an undescribed genus from Orapa.

Stratigraphic range: earliest Jurassic – terminal Cretaceous
Geographic range: cosmopolitan

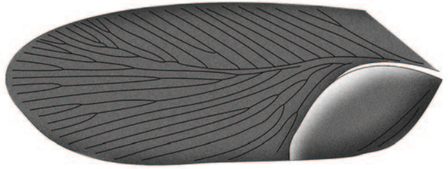
Genus *Mesoblattina* Geinitz, 1880

Type species: *Mesoblattina protypa* Geinitz, 1880. Dobbertin, Germany; Early Jurassic.





PIN 2554/176 f= 13.5 mm





Mesoblattina etarakan

Composition: undescribed species from Zhouangzi and Kota (and possibly in Swiss Schambelen according to Handlirsch 1906). Other species plafed in this genus do not belong to this genus.

Stratigraphic range: Early Jurassic – Late Cretaceous
Geographic range: cosmopolitan

Diagnosis (after Vršanský and Ansorge 2007): Forewings coriaceous, well sclerotised, with strictly parallel borders; Sc simple; R very straight, not distinguished into R and RS, with simple branches (apical branches are the exception); A not branched up to the apical third, clavus very short. Local irregularities of venation present.

Mesoblattina etarakan sp.n.
(figp. 91)

Holotype: PIN 2554/176 (f= 13.5 mm). A completely articulated forewing.
Type locality: Mikhailovka, Karatau, Kazakhstan.
Type horizon: Kimmeridgian Upper Jurassic, Karabastau Formation.

Additional material: PIN 2997/152=160 (completely articulated individual - with antenna; l= 16 mm); 2904/55 (completely articulated forewing). The same locality as the type.

Differential diagnosis: Differs from its (also unpublished) congeners in being significantly larger, nearly as twice as long as the type species.
Autapomorphies: close approximation of R and M stems.
Desription: Moderately large cockroach (very large within the family), with body length ca. 16 mm. Head robust, vely large, nearly 2.6 mm wide, monochromatically dark and with pale big (1/ 0.8 mm) eyes. Antenna moderately long and thin (ca. 16/ 0.14 mm), multisegmented, with over 100 antennomeres.
Pronotum wide, with fully developed paranotalia, 2.6/ 5.7 mm, dark, possibly with maculation and pale anterior later margins.
Forewing ca. 13.5 mm long and 4.8 mm wide, monochromatically dark, probably brown, without maculation (unlike possibly pronotum and body). Margins parallel, venation regular (except R-M area), intercalaries and cross-veins not visible, probably absent. Costa if present then thin, costal area rather wide, with branched Sc (2-5). R sigmoidal, short, with RS indicated, totally with 20 veins meeting margin (holotype). M expanded, with numerous derived dichotomization of up to 6th order, runs parallel and very close to R stem, with 14 veins at margin. CuA with 3 main stems (8 vein at margin). Clavus very short, arcuate, curving out of the straight posterior margin line, with numerous anal veins, which are branched.
Body wide.
Forelegs comparatively long, forefemur 3.3/ 0.6 mm, with terminal femoral spure; foretibia 0.6 mm long, tarsus up to 1.3 mm long.
Remarks: Thes species can be categorized withing Mesoblattinidae on the basis of regular venation except for the R-M area (It is notable that irregularity in this area is conservatively retained, and while in most species of the family this area is expanded, here this area is shrinked, so irregularity is retained in both possible modes.). All species within family differ in not having monochromatic forewing. Another monochromatic genus is *Mongolblatta* Vršanský, 2004 with more regular venation and direct forewing contures.
It is impossible to trace relations within the genus *Mesoblattina* in spite of the present species being more younger.
Derivation of name: *etarakan* is after *electronic tarakan* (Russian for a cockroach).
Character of preservation: one complete specimen, two isolated completely articulated forewings (with clavus).
Taphonomy: Due to complete articulation the species lived in approximity of source waterbody, with no or short pre-depostional transport. Apparenly rare (or rarely flying) species.

Genus *Perlucipecta* Wei et Ren, 2013

Type species: *P. aurea* Wei et Ren, 2013. Yixian, China. Early Cretaceous.

Composition. Besides the type species, *P. vrsanskyi* Wei et Ren, 2013 (Yixian), *P. santanensis* Lee, 2016 (Crato).

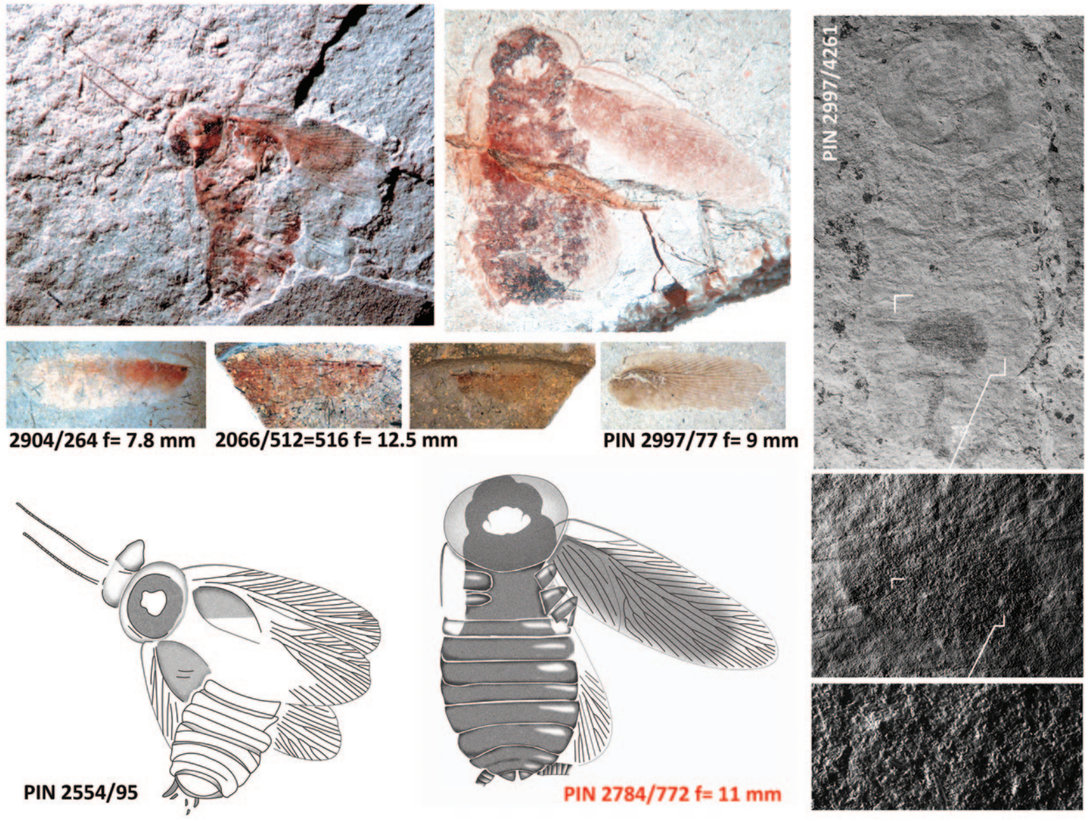
Diagnosis (after Wei and Ren 2013): assigned to the family Mesoblattinidiae based on the following features: branched forewing Sc; hindwing simple Sc, Rs differentiated, simplified M, CuA with secondarily branched veins and blind rami. It differs from all the other representatives of the family by the following features: expanded venation with retained intercalaries and distinct cross-veins; large size; facultative simplification of hindwing M.

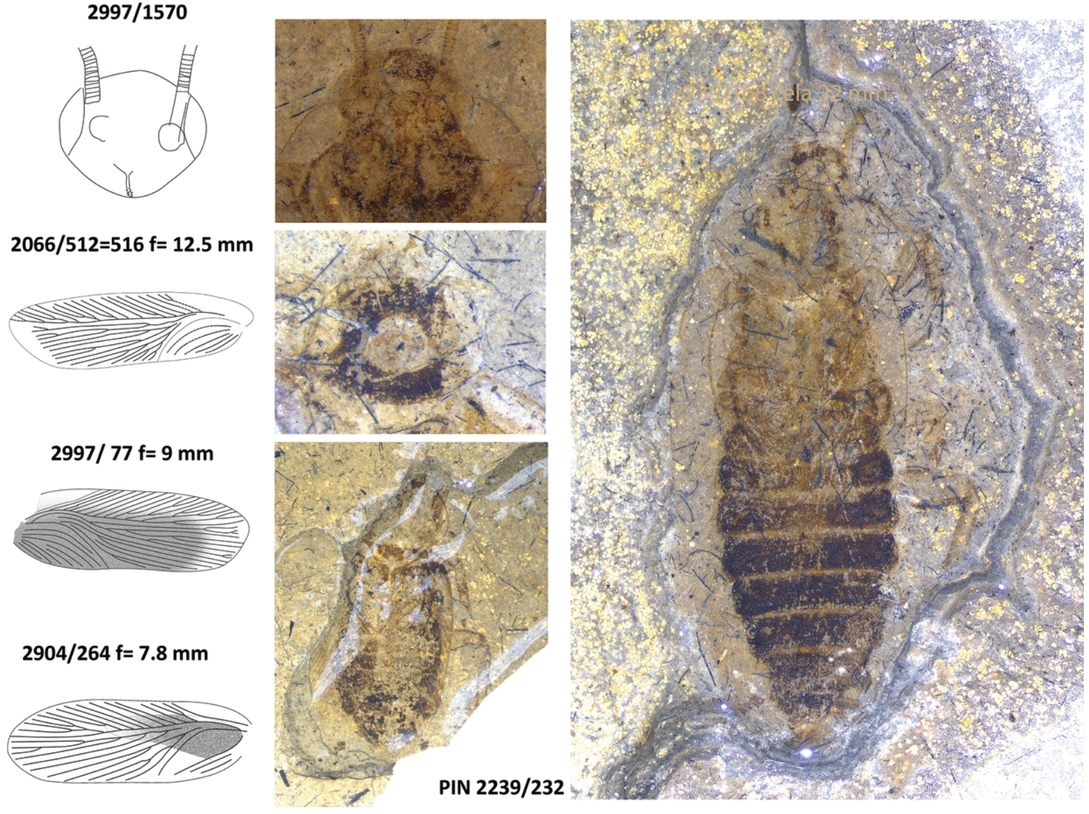
Perlucipecta liangiae sp.n.
(figps. 94-95)

Holotype: PIN 2784/772. A complete female.
Type locality: Mikhailovka, Karatau, Kazakhstan.
Type horizon: Kimmeridgian Upper Jurassic, Karabastau Formation.

Additional material: PIN ?/193; 2066/406; 2231/20; 2239/232±; 2554/2±, 95, 153; 2904/294, 297, 301, 311; 2997/1164±, 1552±, 1570, 4261± (body with gut content) (complete specimens); PIN 167/314; 2066/60, 178±, 393, 512=516 12.5mm; 2239/184, 230±; 2554/14, 22; 2784/768; 2904/194, 199; 260, 264±; 2997/77, 1179, 1215, 1318, 1424, 1429, 1538 (isolated forewings); 2239/329 (w= 1.2 mm); 2452/375; 2997/1640 (immature individuals). The same locality as the type.

Differential diagnosis: Differs from type locality (Yixian) representatives of the genus in having central dark and pale center coloration of the pronotum and from P. santanensis in having smaller, more globular, less prolonged head.
Description: Head globular, very small about 3 mm wide. Mandibles black, small. Pronotum only slightly transversal (2.8/ 3.5mm) with distinct paranotalia and central dark coloration with the very center pale. Wing intercalaries indistinct. Forewing 7-14 mm long and ca. 3.4 mm wide; with dark coloration restricted to central parts (costal field is pale). Sc 3-5; R 12-20 (RS indistinct and possibly restricted to terminal 3 veins); M 5-12; CuA 5-10; CuP reaching a third of the wing length; A 7-8. Hind wing slighly smaller than forewing, with wide remigium. Sc simple, RS differentiated (11); Media simple or with 2 veins. CuA rich, with at least 11 veins at margin, some branches are secondarily branched. Body 3.6 mm wide. Three basal segments straight, about 1.6 mm long, posterior segments carved, last segment fluently carved and vaulted, undivided.
Remarks. Gut (figp. 94) contains a small (0.14/0.02 mm) needle-like strongly carbonized particles, which apparently represent undigested fragments of plants. Two immatures determined based on the wide abdomen characteristic for the Mesoblattinidae represent (categorized in this species by exclusion from other two species within this family, based on size) evidence that the species occurred near the shore and thus have high burial potential. In this light, the rarity of adults means the whole family was actually extremely rare in the source area.
The present species might actually belong to two separate species as in the Yixian Formation, differing in size and coloration is only statistical and the morphology differ only in male tergal glands. Stratigraphic differences of two species from Karatau are indistinct if any (more common species occurs in all collections except for 2384 where less abundant species occur in 3 specimens, which is insignificant).
Derivation of name: After Dr. Jun-Hui Liang, my favourite student.
Character of preservation: 16 complete specimens, 21 isolated single forewings, 3 immature individuals.
Taphonomy: Complete specimens suggest short or no pre-depositional transport. Lacking of hindwings is obscure.


PIN 2997/4261
2904/264 f= 7.8 mm
2066/512=516 f= 12.5 mm
PIN 2997/77 f= 9 mm
PIN 2554/95
PIN 2784/772 f= 11 mm


2997/1570
2066/512=516 f= 12.5 mm
2997/ 77 f= 9 mm
2904/264 f= 7.8 mm
PIN 2239/232

Genus *Sivis* Vršanský, 2009

Type species: *S. odpo* Vršanský, 2009
Type locality: Archingeay, France
Type horizon: Albian Late Cretaceous Archingeay amber

Composition. Besides the type species, *S. tykadlo* Kováčová, 2023 (North Myanmar amber), undescribed species from Spanish amber. Possible congenery with *Nymphoblatta* Vršanský et Grimaldi in Vršanský (2004) cannot be definitely excluded.

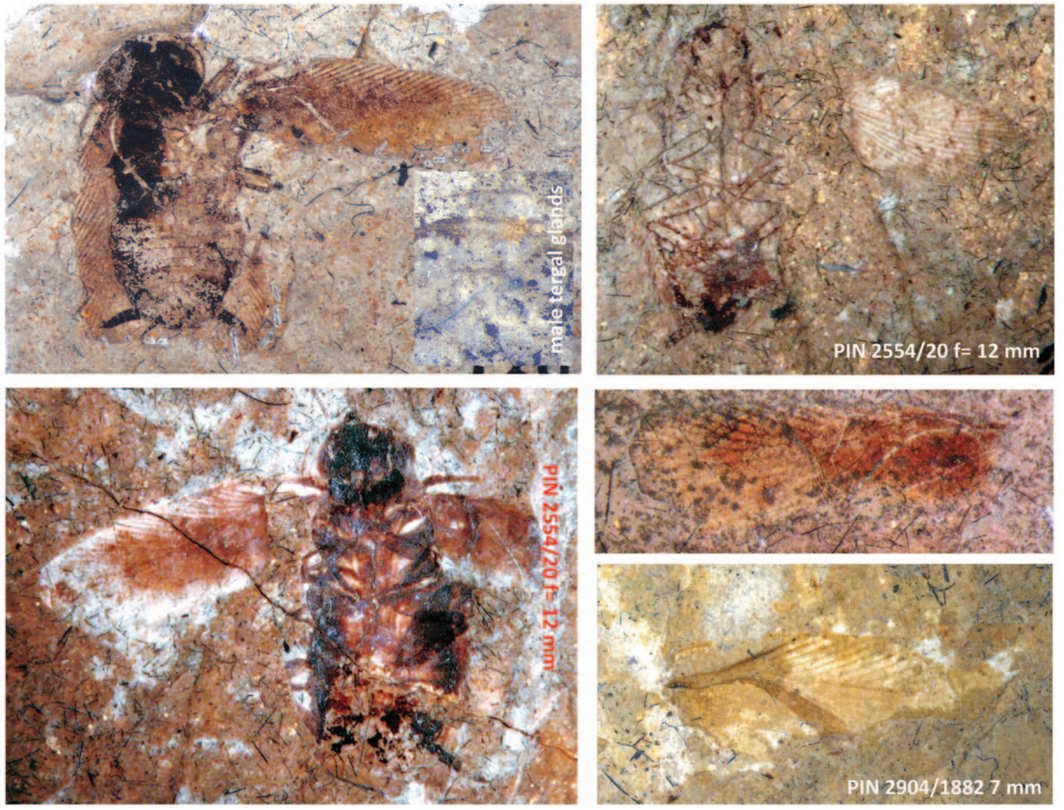
Diagnosis (after Vršanský 2009): The present taxon may be categorized within the Mesoblattinidae based on modern morphology of head with globular eyes and clypeus, with strong antenna bearing a row of short sensilla chaetica, by the derived form of pronotum and long marginal chaeta on head, nota and abdomen. Th e present genus may be diff erentiated from *Praeblattella* Vršanský, 2003 based on the characteristic pronotum coloration, which is sophisticated in *Praeblattella*. *Mesoblattina*, *Archimesoblatta* Vršanský, 2003 and *Hispanoblatta* Martínez-Delclós, 1993 differ by having a simpler form of pronotum (plesiomorphy). The derived form of pronotum is synapomorphic with the *Praeblattella,* autapomorphic in sophisticated pronotal coloration. The pronotum of *Hispanoblatta*, *Mesoblattina* and *Archimesoblatta* is plesiomorphic. *Brachymesoblatta* Vršanský, 2003 belongs to the Liberiblattinae. Thus, *Sivis* n. gen. may be the sister genus of *Praeblattella*.

Sivis lukashevichiae sp.n.
(figps. 97-98)

Holotype: PIN 2554/20. A complete female.
Type locality: Mikhailovka, Karatau, Kazakhstan.
Type horizon: Kimmeridgian Upper Jurassic, Karabastau Formation.

Additional material: PIN 2239/221, 183; 2554/29 (male); 2784/55, 80 (male), 911; 2904/317± (complete specimens); 2784/62; 2904/1882; 2997/1373 (isolated forewings). The same locality as the type.

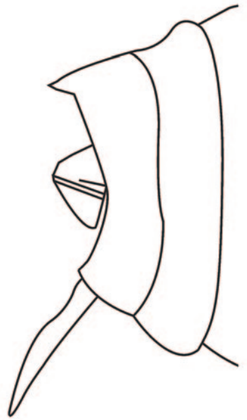
Differential diagnosis: Differs from *S. odpo* and *S. tykadlo* in being much larger.
Autapomorphy: Entirely pale costal area.
Description: Antenna very fine. Pronotum comparatively large, nearly round, but slightly transversal (~5/~4,5 mm), dark, with pale margin. Forewing only slightly overlapping the body outline, 10-12 mm long and 4-5 mm wide; mostly monochromatically dark colored, but with pale posterior margin and with pale intercalary space of radial veins. Pale is also s stripe in the costal field, which apparently was covered with pale color. Sc 4, R 17-24 (RS differentiated but with few 3-5 branches). Other branches greatly reduced, M with only 4-6 branches, CuA with 3-5 branches meeting margin. Legs short with sclerites having dark margins. Body very short, female rudimentary external ovipositor present, cerci long with at least 12 segments, multisegmented styli present in males. Male sexual tergal glands very small, both together wide only 1 mm.
Remarks: The holotype was preserved in a very special way – this sedimentary fossil after an application of alcohol reveals a significant degree of transparency so it resembles amber (but only one half, the positive; the negative was preserved in entirely different form). Unfortunately, no microstructures are visible. Small tergal glands cannot be considered as a primitive character similar as some earlier, more primitive, Middle Jurassic cockroaches of the family Fuziidae (Vršanský et al. 2009) have extensive glands.
The species can be categorised within the *Perlucipecta/Sivis/Nymphoblatta* complex on the basis of coloration shape. It can be further subordinate within Sivis due to dark coloration with pale margins. Nymphoblatta is substantially more setated.
Derivation of name: After Dr. Lena Lukashevich – superb person, a colleague and sometimes a friend.
Character of preservation: 9 complete specimens, 3 isolated forewings.
Taphonomy: Complete specimens and fully articulated complete forewings suggest no or short pre-depositional transport.







PIN 2554/20



Superfamily Blaberoidea Saussure, 1864

Type genus: *Blaberus* Serville, 1831; priority for family-group names based on *Blaberus* (Blaberiens Saussure, 1864; Blaberidae Brunner von Wattenwyl, 1865)

Statigraphic range: Upper Jurassic (FOD)-still living

Geographic range: Laurasian during the Mesozoic, cosmopolitan during Cenozoic and now

Composition: Ectobiidae Brunner von Wattenwyl, 1865; Blaberidae Saussure, 1864**;** Diplopteridae Walker, 1868;

Remarks: In the present concept, the superfamily comprices groups that possess advanced modern ootheca and which rotate it.

Family Blaberidae Saussure, 1864

Type species: *Blaberus* Serville, 1831; priority for family-group names based on *Blaberus* (Blaberiens Saussure, 1864; Blaberidae Brunner von Wattenwyl, 1865)

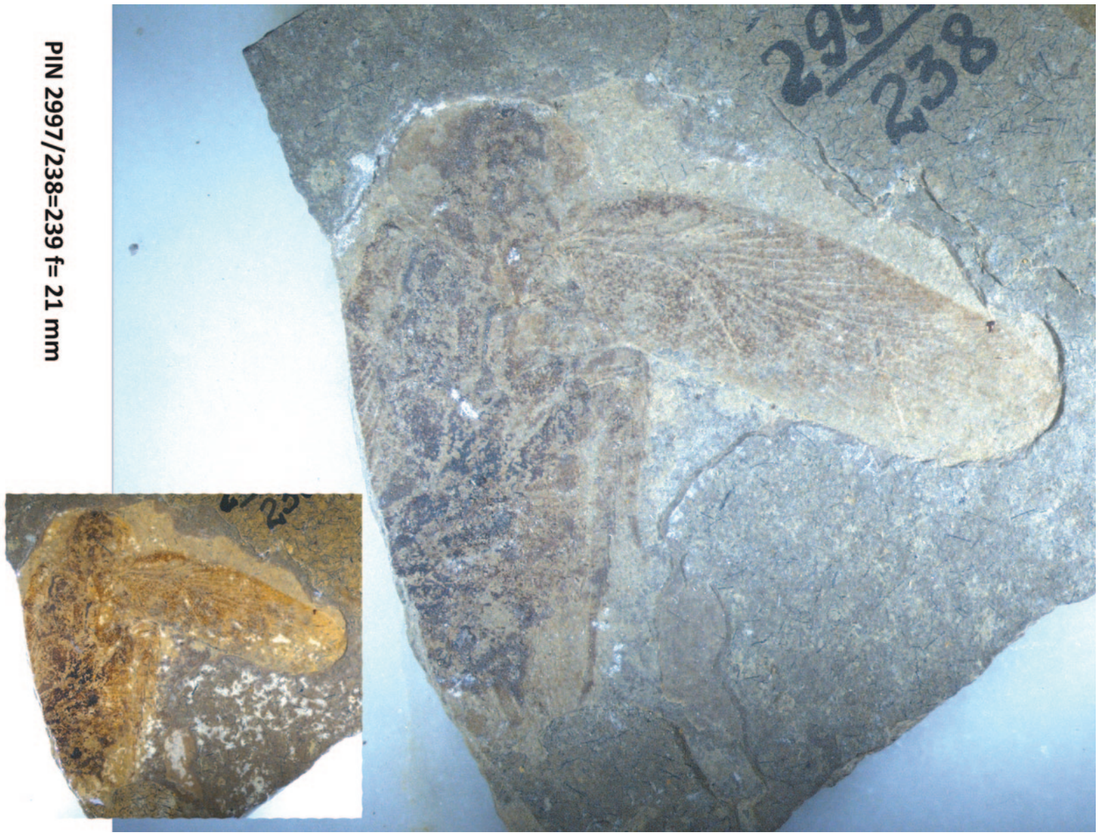
Statigraphic range: Upper Jurassic (FOD)-still living

Geographic range: Laurasian during the Mesozoic, cosmopolitan during Cenozoic and now

Genus *Morphna* Shelford, 1910

Type species: *Epilampra maculata* Brunner von Wattenwyl, 1865; by subsequent designation.

Composition: *Morphna amplipenni* (Walker, 1868); *M. auriculata* (Brunner von Wattenwyl, 1865); *M. badia* (Brunner von Wattenwyl, 1865)= *ramifera* (Walker, 1869); *M. clypeata* Anisyutkin & Gorochov, 2001; *M. decolyi* (Bolívar, 1897); M. *dotata* (Walker, 1869); *M. humeralis* Bruijning, 1948; *M. imperatoria* (Stål, 1877); *M. lucida* Anisyutkin, 2014; *M. maculata* (Brunner von Wattenwyl, 1865)= *polyspila* (Walker, 1868)= *shelfordi* (Kirby, 1903); *M. plana* (Brunner von Wattenwyl, 1865)= *biplagiata* (Bolívar, 1897)= *punctifera* (Walker, 1868)= (Kirby, 1903); *M. pustulata* Hanitsch, 1930; **EX** (**EXTINCT)** *M. cenozoica* Šmídová et Wedmann, 2021 (Eocenne, Messel, Germany); *M. palaeo* Vršanský et al. 2012 (Palaeocene, Amur, Russian Federation); *M. patricioi* (Eocene, Fonseca Formation, Brazil); *M. cretacica* Šmídová et al, 2021 (Cenomanian North Myanmar amber); Unformalised by Oyama et al. 2021 (Aptian Fukui Formation, Japan).



Statigraphic range: Upper Jurassic (FOD)-still living
Geographic range: Laurasian during Mesozoic, cosmopolitan during Cenozoic, now India and part of SE Asia

Diagnosis (after Shelford 1910): Body form rather dorsoventrally flattened. Vertex of head covered or almost covered by pronotum, which is trapezoidal, sub-cucullate and posteriorly produced obtusely. Tegmina and wings fully developed, exceeding the apex of the abdomen. Supra-anal lamina of typical Epilamprine shape. Cerci moderately long. Femora moderately armed with spines beneath. Posterior metatarsus equal in length to succeeding joints; all the joints entirely unarmed beneath, their pulvilli large, pulvillus of metatarsus apical but produced towards the base of the joint.

Morphna una sp.n.

(figps. 100, 103-105)

Holotype: PIN 2997/1417 (f= 19.5 mm). A complete adult winged male.
Type locality: Mikhailovka, Karatau, Kazakhstan.
Type horizon: Kimmeridgian Upper Jurassic, Karabastau Formation.

Additional material: PIN 2239/235; 2997/97, 238= 239 (f= 21 mm) (complete winged adult males); 2239/252 (f= 17.5 mm)(a forewing). The same locality as the type.

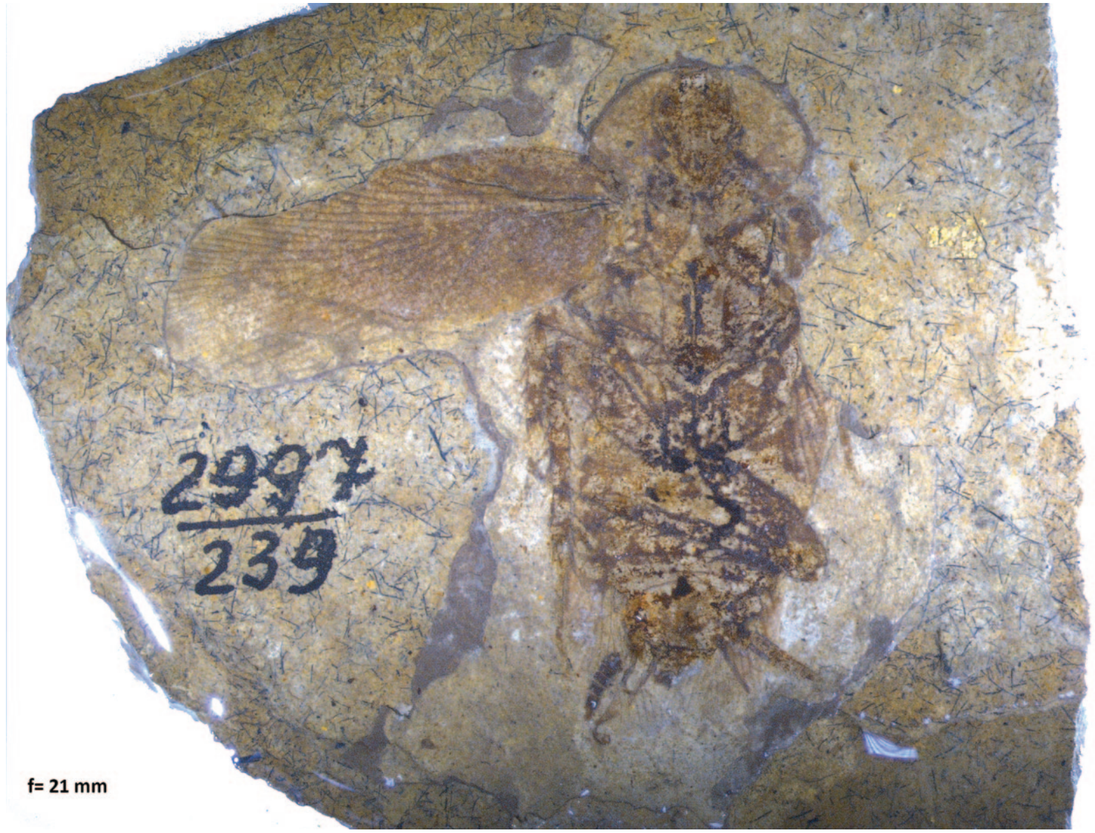
Differential diagnosis: From the Cretaceous representatives it differs in significanly larges size (*M. cretacica* f= 15 mm; unformalised species from Fukui f= ca. 15 mm). Known Cenozoic representatives are much larger or much smaller (*M. cenozoica* f= 34 mm; *M. palaeo* f= ca. 23 mm; *M. patricioi* f= ca. 12 mm). Living species also differ in size: *M. lucida* (f= 40 mm); *M. plana* (f= 27 mm); *M. clypeata* (f= 40-48 mm); *M. dotata* (f= 45-50 mm); M. (f= 25-26 mm); *M. maculata* (f= 40 mm); *M.* (f= 36-41 mm); *M. badia* (f= 38-41 mm); *M.* (f= 50 mm); *M.* (f= 46 mm); *M. decolyi* and *M.* are brachypterous.
Autapomorphies: sharp forewing apex.
Description: Head small, elongate (4.9/3.8 mm). Pronotum wide (6.2/9.5 mm), as wide as folded bases of both forewings, with slightly indicated central posterior extension. Body standardly wide (8.2 mm) with wide (3/0.5 mm) multisegmented cerci with wide cercomeres. Long narrow (2.9/0.2 mm) unsegmented styli; genital hook (*Hla* sensu Klass 1997) very large, 5.4 mm long.
Both wings appear monochromatically colored, possibly with exception of darker posterior part of the forewing. Forewing elongate, overlapping widely body in repose (19.5/ 7.8 mm), widest point is basally. Apex posed anteriorly, sharp, otherwise wing margins nearly parallel, posterior margin fluently and longly ascending to the apex. Vein distance is nearly regular, but distance among vein significantly smaller near apex. Costal vein if present then narrow and short, surely not overpassing Sc, costal area very wide, with subcosta widely branched and with basalmost long anterior branch (4+1). Except for the terminalmost branched vein, radial braches on straigth R stem simple or only terminally dichotomised (8+4), ascenting sharply; RS differentiated (4). Media and CuA expanded (10+12), but not reaching apex. CuP fluent but with the terminal cut. A straigth, branched. Legs moderately robust, with distinct posterior spurs on mid- and hindfemora. Mid femora and tibia (4/ 0.6 mm) unspecialised, latter with ca. 12 spurs. Mid tarsi 3.8 mm (long) and moderately robust, arolium present, claws symmetrical. Hind femora (7.3/1.9 mm) and tibiae (9/0.8 mm) robust, carinated with ca. 17 spurs, subequal to mid ones hindtarsi very long (5.7 mm).
Remarks: The taxon can be categorized within the family Blaberidae on the basis of anteriorly ascending long basalmost branch of Sc, sharply ascending R branches, terminal shortening of distance among veins, strong posterior femoral spurs and cercal structure with wide sensilar openings. It can further be placed in the tribe Morphnini based on primitive (original) state of the undreduced complete scheme of venation. At the present state of knowledge the taxon cannot be discriminated from the genus *Morphna* due to the (original) wide forewing.
Within the genus *Morphna*, it is not poss-

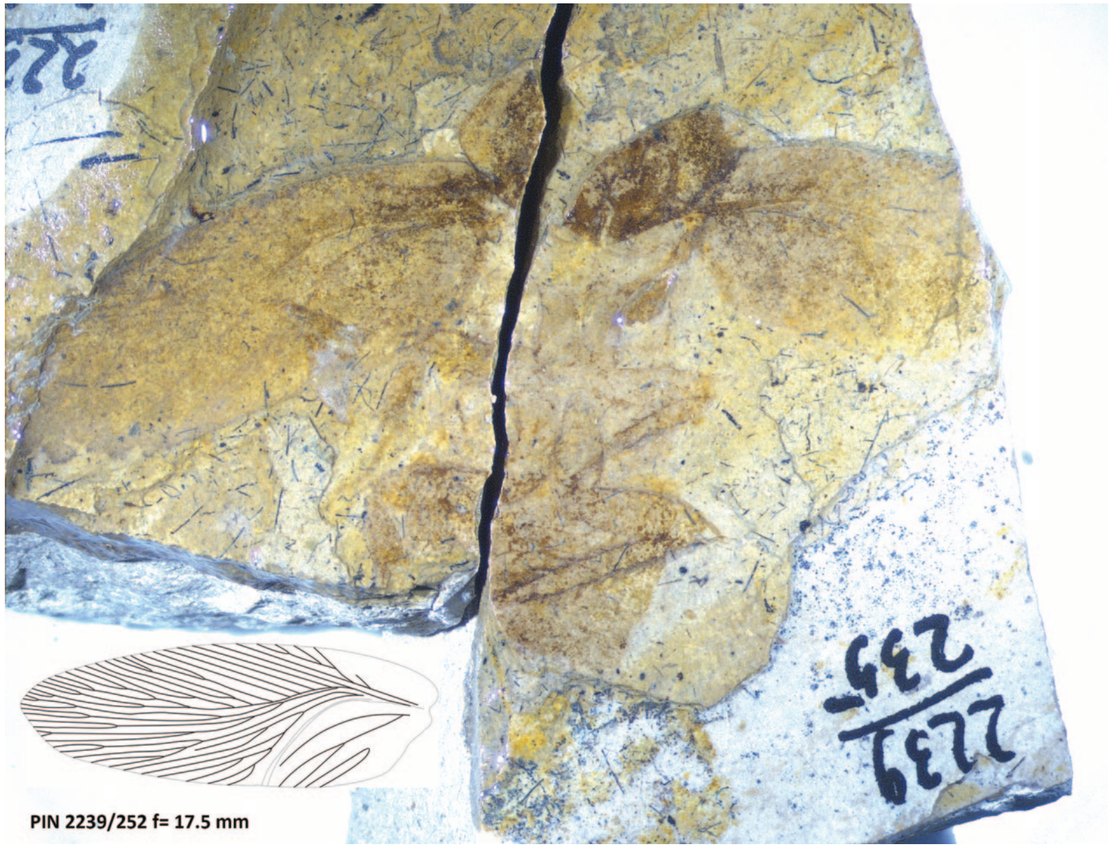
ible to establish relationships in a more detail, but living species are mostly much larger, while Cenozoic and Mesozoic species are standarly large.

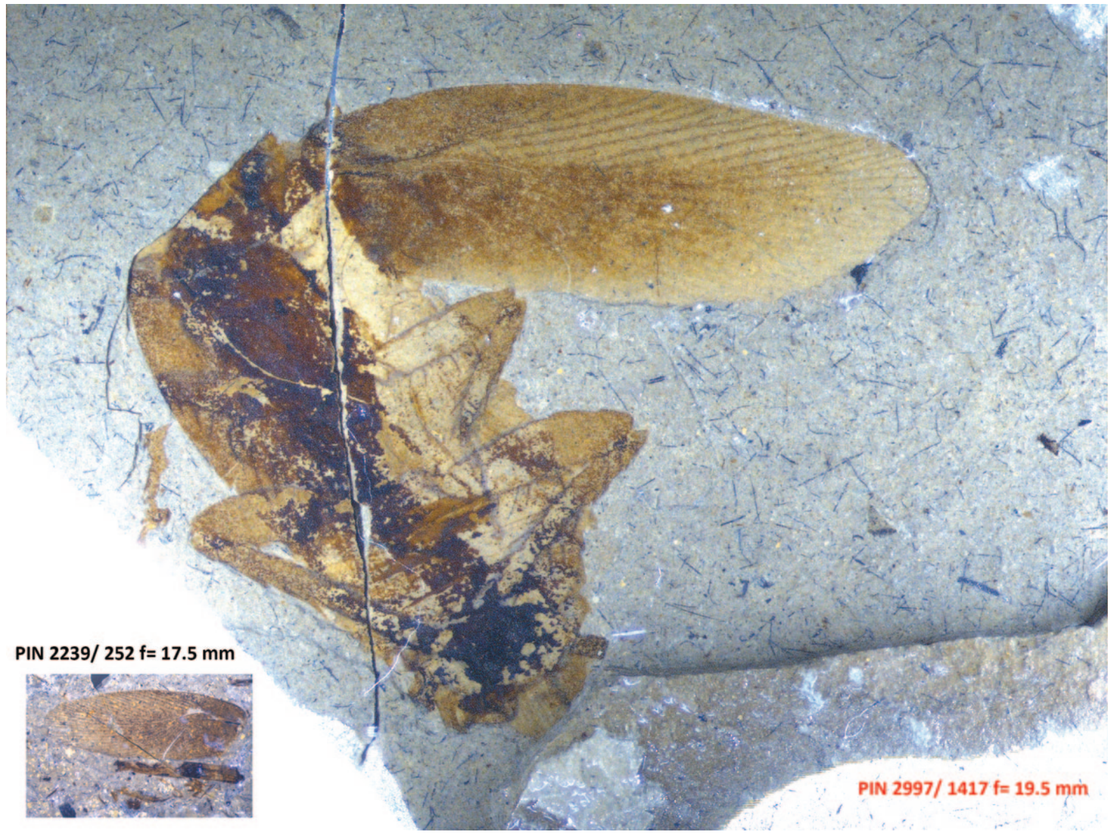
Derivation of name: *una* is Latin for one. Alluding to a single preserved significant specimen and also its first ocurrence as number one.

Character of preservation: four completely articulated adult winged males with missing head and cracked parts of pronotum; one forewing

Taphonomy: complete specimens along with a single possible isolated forewing suggest short or no pre-depositional transport and the rarity of this taxon. Missing head and part of pronotum seems post-depositional. The line of cracking is straigth and does not seem to be a predational trace.




PIN 2239/252 f= 17.5 mm


PIN 2239/ 252 f= 17.5 mm
PIN 2997/ 1417 f= 19.5 mm

Superfamily Corydioidea Saussure, 1864

= Polyphagoidea Saussure, 1864 - a junior subjective synonym of Corydioidea based on the First Reviser Principle of the ICZN Code (see below).

Type genus: *Corydia* Serville, 1831

Composition: Corydiidae.

Geographic range: cosmopolitan
Stratigraphic range: Upper Jurassic – extant

Diagnosis (after Princis 1963) : Flattened (body) shapes, most often short and wide. Prothorax and often the elytra covered with velvety hairs. This group is formed by the old genus *Corydia* of Burmeister. The antennae are a little shorter than the body or of equal length, moniliform. The head is small; the ocelli are sometimes distinct; eyes apart; the last section of the labial palps is thickened, of the length of the previous one. The prothorax is elliptical, but with the anterior edge more arched than the posterior; or in a semicircle with the middle of the front edge a little truncated; the posterior edge is always truncated or slightly arched, leaving the shield bare; but this is sometimes covered by the elytra. The surface of the prothorax is generally hairy; the edges are always ciliate; the elytra are flattened, sometimes entirely opaque and velvety, sometimes membranous in whole or in part, especially in their internal portion; when they are opaque, the anal furrow disappears; when this exists, it is generally bent almost at a right angle, which makes the anal field short and square (the genus *Melestora* excepted). The wings are very variable, offering only few veins; their posterior field, very small, folds under the anterior without folding. The legs are quite slender; very spiny shins; the thighs are unarmed or offer only spiniform hairs; the tarsal pads are very small. The abdomen is very broad and very flat, ending in a transverse superanal plate; the anal filaments are slender and quite long; the styles of males are hairy.

Family Corydiidae Saussure, 1864

= Polyphagidae Saussure, 1864- a junior subjective synonym of Corydiidae. Brunner von Wattenwyl (1865) as First Reviser (ICZN rule) chose to use Corydiidae (based on Corydiens Saussure, 1864) as the name for the group rather than Polyphagidae (this name was first used in this form by Walker, 1868). Corydiidae was in common usage until Princis incorrectly synonymised it in 1950 (for details see Kevan (1977)).

Type genus: *Corydia* Serville, 1831

Composition: Corydiinae Saussure, 1864; Euthyrrhaphinae Handlirsch, 1925; Holocompsinae Rehn, 1951; Latindiinae Handlirsch, 1925; "Tivinae"; Oulopterygiinae Rehn, 1951 and genera IS.

Geographic range: Cosmopolitan
Stratigraphic range: Upper Jurassic – extant

Diagnosis (in Burr, 1910, Brunner von Wattenwyl 1893; after Princis 1963): I bring together the Corydidae with the Helerogamides. It is true that the Corydides have the essential character of the angular suranal plate less pronounced, however the slight incision in the middle indicates the same conformation. On the other hand, I observed a very clear difference, in that the males of the Corydid group do not show any trace of a style at the edge of the subgenital plate and even the slight sinuosity which indicates the presence of this organ is missing, while the male Heterogamides all have the style or at least the emargination on the left side of the cited plate.

Subfamily Latindiinae Handlirsch, 1925

Type genus: *Latindias:* Stål, 1860

Composition: *Buboblatta* Hebard, 1920; *Bucolion* Rehn, 1932; *Compsodes* Hebard, 1917; *Gapudipentax* Lucañas, 2018; genus *Latindia* Stål, 1860; *Melestora* Stål, 1860; *Myrmecoblatta* Mann, 1914; *Paralatindia* Saussure, 1868; *Sinolatindia* Qiu, Che et Wang, 2016; *Stenoblatta* Walker, 1868.

Geographic range: SE Asia, Americas, Laurasia (and North Myanmar amber)

Stratigraphic range: Upper Jurassic – extant
Diagnosis: Terminal plate divided.

Genus *Okruhliak* gen.n.

Type species: *Okruhliak samoodpovedaniesi* sp.n. described below.

Composition: An undescribed species from the North Myanmar amber besides the type.

Geographic range: Laurasian (and North Myanmar amber)
Stratigraphic range: Upper Jurassic – Upper Cretaceous- ?

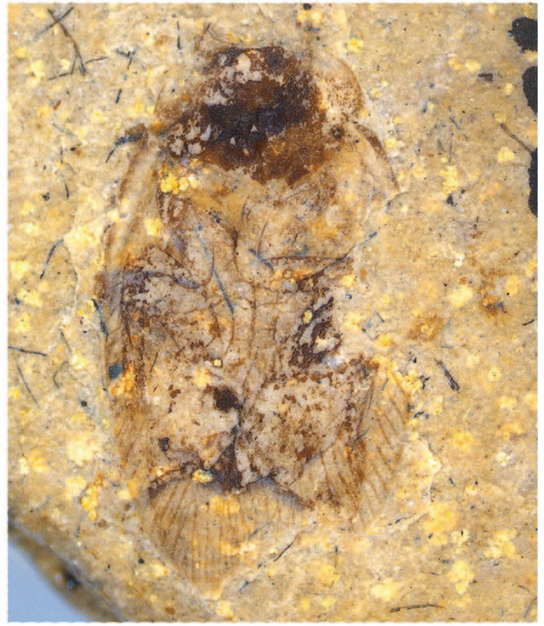
Differential diagnosis: Differs from *Spinka* Vršanský, Šmídová et Barna in Vršanský et al. (2019) and *Bimodala* Šmídová in Vršanský et al. (2019) in being more round and in lacking maculated coloration. From all living corydiids it differns in external ovipositor (Latindiinae have differently structured valvae). Blattidae differ in shape of abdomen and head. Most similar *Methana* Stål, 1877 and *Pelmatosiplha* Dohrn, 1887 have bigger clavus and standart shape of pronotum.
Autapomorphy: General round shape, triangular pronotum
Description: As for species
Remarks: According to characteristic blattid ovipositor structure, the classification of the present species is not unequivocal and revives possibility of categorization within Blattidae. Nevertheless, *Spinka* and *Bimodala* were transferred into Corydiidae (Šmídová 2021). On the basis of high similarity with these two genera (typical illusory 3-intercalary pattern) I am classifying this taxon within Corydiidae. Latindiinae are somewhat similar in modified (carved) shape of the wing and presence of externally protruding ovipositor valves, and as they have various shape of valves (e.g., *Brachylatindia* – see Qiu et al. 2019), I retain it preliminary within this subfamily. Thus within the family the genus retain original state of ovipositor, but due to incertainty it must be also discriminated from Blattidae. Only *Methana* and *Pelmatosiplha* have a similar head and body morphology but differ in having a bigger clavus and standard shape of pronotum.

***Okruhliak samoodpovedaniesi* sp.n.**
(figp. 109)

Holotype: PIN 2997/1439. A completely articulated winged adult female.
Type locality: Mikhailovka, Karatau, Kazakhstan.
Type horizon: Kimmeridgian Upper Jurassic, Karabastau Formation.

Diagnosis: Small round cockroach with total length about 7 mm, weakly melanised head and partially colored pronotum and wings. Head small, round, triangular (ca. 1.24/1.32 mm), incompletely covered by the pronotum, with large round unmelanised eyes 18-35 mm in diameter, widely (0.68 mm) separated. Antennal sockets moderately large (0.14 mm in diameter), ocelli and antenna unpreserved. Mandible wide, short.
Pronotum oval, nearly triangular (1.89/2.47 mm) with central posterior extension, dark colored with two small pale at anterior corners.
Forewing wide (5.25/1.94 mm), with round apex located centrally, and with subparallel margins, straight posterior margin and sharply cut short clavus. Costa wide, melanised, costal area rather long and narrow, with simple or weakly branched Sc. R with regular simple branches (ca. 15 veins at margin), nearly straight, apical branches sharphly curved towards anterior margin. M and CuA standardly developed (together possibly with only ca. 6 veins at margin). Anal veins (6) seems simple.
Hindwing slightly sharpened at centally posed apex, also very wide, seems round.
Body wide, sternal margins sharply curved, ovipositor outer valves widely protruding. Cerci rather wide (0.16 mm), moderately long-long (only partially preserved).
Legs massive, possibly burrowing. Forecoxae shifted anteriorly up to head. Midcoxae massive (R1.75/ 0.68 mm; L1.75/1.07 mm), midfemur also massive (1.26+/0.45 mm), with row(s) of short (0.1 mm) row(s) of ca. 11 posterior spurs; midtibia massive (/0.27 mm) with extremely massive (0.33/0.04 mm) spurs (a single one was preserved, but probably were common as suggested by indtibiae). Hindcoxa massive (R 1.46/0.86 mm); hindfemora massive (1.65/0.54 mm), carved with posterior row(s) of few short (0.08 mm) spines; hindtibia massive (1.67/0.31 mm) with at least 12 massive (0.33/0.06) spurs.
Derivation of name: *samoodpovedaniesi* is Slavic for “self-responding to your own”.
Character of preservation: One completely articulated winged adult female.





PIN 2997/ 1439 l= 7 mm



Taphonomy: A single specimen suggest a rarity or an incidental flight from more remote area – full articulation suggest burial near the source waterbody and no or short pre-depositional transport.

Genus *Cretaholocompsa* Martínez-Delclòs, 1993

Type species: *Cretaholocompsa montsecana* Martínez-Delclòs, 1993
Type locality: Montsec, Spain.
Type horizon: Early Barremian la Pedrera de Rubies Formation

Stratigraphic range: Kimmeridgian- Early Barremian
Geographic range: Laurasia (Europe and Asia)

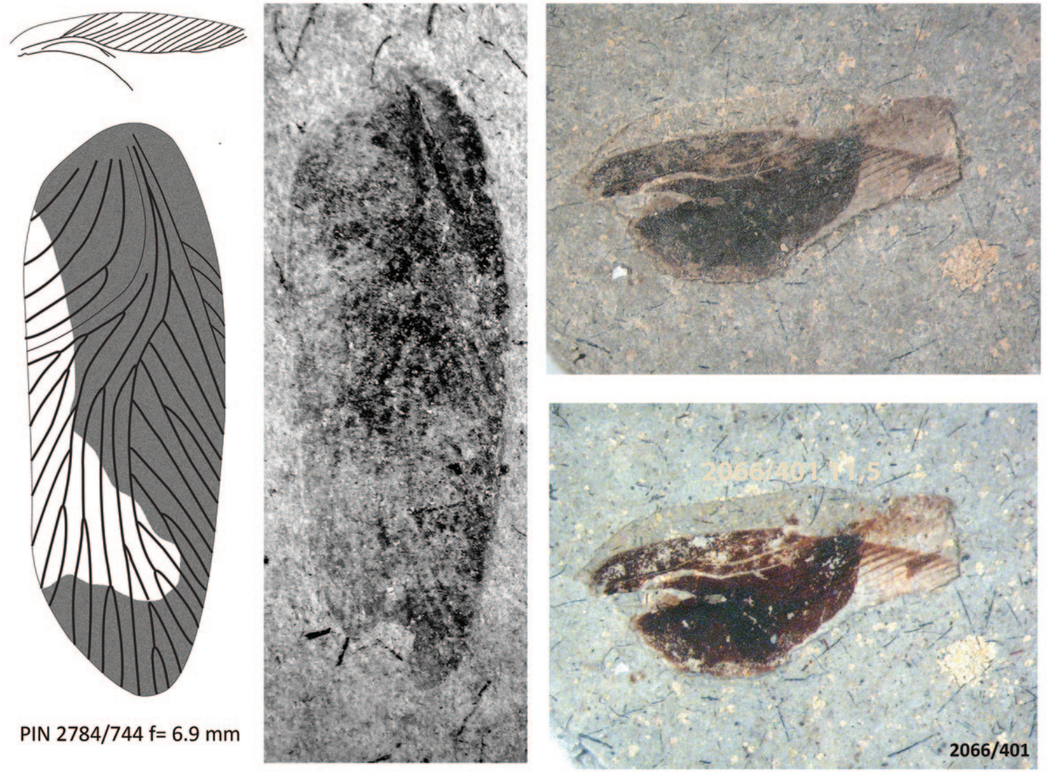
Diagnosis (improved Martínez-Delclòs (1993)): Small species (under 7mm) with partially or totally rigid forewings. Costal field is distinct, narrow, Sc sigmoidal and terminally branched.
R sigmoidal, comparatively narrow (about a third of the wing), RS undifferentiated. M expanded, overlapping apex from both sides. CuA elongated sigmoidal or extremely shortened and nearly straight. CuP sharply cut anteriorly, clavus very short. A reduced, but branched. Coloration varying from monochromatically dark through black with pale central macula up to partial coloration with dot.
Systematical remarks: The genus is transferred from Holocompsidae Rehn, 1951 into Liberiblattinidae on the basis of synapomorphies with *Liberiblattina* (without homplasies – see below). Holocompsidae are not anyway recognized as a separate family (e.g., Princis 1963, Vršanský et al. 2017) and *Holocompsa* Burmeister, 1838 is placed withing Corydiidae Saussure, 1864. Nevertheless, *Holocompsa* posses entirely reduced costal field and membraneous wing parts and does not represent a taxon related by any trait with *Cretaholocompsa*. According to a close relation with *Liberiblattina*, direct corydiid relation is also excluded.
In the example of the genus *Cretaholocompsa* we directly evidence how numerous beetle like cockroaches independently shot-off from Liberiblattinidae. In this case, the derivation is possible directly from the genus *Liberiblattina* (somewhat quadrate forewing, strongly sigmoidal Sc in narrow costal field, reduced veins, pale posterior area of clavus as unique synapomorphies) and even more specifically with identical coloration from *L. ihringovae*. These characters are absent in Umenocoleoidea, which were apparently derived from a very similar taxon (most probably also from *Liberiblattina*), leading to diverse explosively radiating Umenocoleoidea through more basal *Vitisma* Vršanský, 1999 and *Perspicuus* Koubová, 2020 (Vršanský 1999b, Koubová and Mlynský, 2022). *Fractalia* is another beetle-like group other than Umenocoleoidae.

Cretaholocompsa karatauensis sp.n. (figp. 111)

Holotype: PIN 2784/744. A nearly complete forewing.
Type locality: Mikhailovka, Karatau, Kazakhstan.
Type horizon: Kimmeridgian Upper Jurassic, Karabastau Formation.

Additional material: 2066/401; 2997/109 (forewings). The same locality as the type.

Differential diagnosis: The new species can be categorized with genus on the basis of unusual Sc, which is extremely strongly sigmoidal and elongated and branched terminally, and with very short clavuys and posterior ridge. It differs in coloration (macula is posed more terminally), much larger size (montsecana is only about 5 mm long forewing) and somewhat more membraneous character of wing compared to more rigid of *C. montsecana*.
Description: Forewing length 6.9 mm, margins not parallel. Costal field narrow, Sc slightly sigmoidal, with 6 veins at margins, inlcuding a terminal secondary dichotomisation. R sigmoidal, reaching nearly a half of the wings width, with 11 veins at margin, RS not differrentiated. M overlapping apex from both sides, sigmoidal, with 8 veins at margin, some branches are secondarily dichotomised. CuA normally developed, sigmoidal, long, with



two main stems and 8 veins at margin. CuP sharply curved anteriorly, without apical curvature. A simplified, dichotomised, with 5 veins at marin. A long longitutinal ridge is present anong the wing revealing a wide overlapping pale area. Membrane dark, sclerotised, with big pale macula termianed at posterior ridge.

Remarks: missing terminal part represent a mark of predation, either on land, or in waterbody. Wide R is a pleasiomorphy within genus, tracing its origin among LIberiblattina.
Derivation of name: after Karatau.
Character of preservation: three isolated damaged forewings.

Taphonomy: Two isolated damaged forewings with traces of predation indicate a longer predepositional transport.

Superfamily Raphidiomimoidea Vishniakova, 1973

= Latiblattoidea Vishniakova, 1968 derived from Latiblattidae "Vishniakova, 1968" (Labandeira as cited also in Gorochov 2005): noumen nudum

Composition: Raphidiomimidae Vishniakova, 1973; Phyloblattidae Schneider, 1983; Caloblattinidae Vršanský et Ansorge in Vršanský (2000); Liberiblattinidae Vršanský, 2002; Skokidae Vršanský, 2007; Manipulatoridae Vršanský et Bechly, 2015; Latiblattidae fam.n.; possibly *Voltziablatta*-group

Remarks: The family Raphidiomimidae Vishniakova, 1973 has a time priority over a different families Phyloblattidae Schneider, 1983 and Caloblattinidae Vršanský et Ansorge in Vršanský (2000), which, according to the compensation rule (ICZN) would become active in application of the family-group name in the case of the superfamilial rank. In spite of high similarity of these families at the superfamily level, Phyloblattidae are insufficiently well known to conclude whether these two families belong to the same superfamily. Missing are documentations for tergal glands (a major trait in the nitrogen fixation), unclear are the principal forewing reticulations and also hindwing structures, which might link Phyloblattidae directly with the *Voltziablatta*-group (including Argentinoblattidae etc.) and Corydioidea, without Caloblattinidae among others. Thus I keep superfamily status of the Raphidiomimoidea over Caloblattinoidea Vršanský et Ansorge in Vršanský (2000), with the reservation that the superfamily rank is not definitely excluded for this group to be represented by mainly Palaeozoic Phyloblattoidea Schneider, 1983 and that Raphidiomimoidea as specialized predators will be given a separate superfamilial status (in spite of identical both pairs of wings).

Family Raphidiomimidae Vishniakova, 1971

Type genus: *Raphidiomima* Vishniakova, 1971

Diagnosis: Predatory (mostly pursuit) elongated cockroaches with prognathous head, usually with eye divided by apodema, rarely globular, rarely with raptorial forelegs, usually legs were unspecialized.

Composition: *Cameloblatta* Vishniakova, 1971; *Divocina* Liang et al., 2012; *Falcatusiblatta* Liang et al., 2018; *Fortiblatta* Liang et al., 2008; *Graciliblatta* Liang et al., 2012; *Liadoblattina* Handlirsch, 1906; *Raphidiomimula* Grimaldi et Ross, 2004; *Rhipidoblattina* Handlirsch, 1906, *Chuanblatta* Liang et al. 2022 and genera designated here.

Stratigraphic range: Lowermost Jurassic (Dobbertin) – uppermost Cretaceous (probably Maastrichtian, LOD is Cenomanian burmite)
Geographic range: Cosmopolitan

Genus *Raphidiomima* Vishniakova, 1971

Type species: *R. chimaera* Vishniakova, 1971. Karatau.
Diagnosis (after Vishniakova, 1971): Head narrowed at base, head restricted to the dorsal side. Ocelli globular; palp longer than head, forewing more than 3.5 times longer than wide. Anteriormost M dichotomized more proximally than others. CuA1,2 subequal, rich. Foretfemora narrow, supination of the disto-ventral side rare.
Remarks: Since the description of these species, numerous raphidiomimids were described, but the type genus remains the one with the longest and narrowest forewings and with the most modified head (eyes in all other known taxa have eyes long, divided by apodema into two parts).

Composition: *R. cognata* Vishniakova, 1971 (Karatau); *R. krajka* Vršanský, 2020; *R. chimnata* Vršanský, 2020 (both Bakhar); *R. predlzena* Kováčová et al. 2023 (Phrae-Wihan)

Stratigraphic range: Middle Jurassic (Bakhar) – Late Jurassic (Karatau)
Geographic range: Laurasia/ restricted to Asia

Raphidiomima chimaera Vishniakova, 1971

Holotype: PIN 2066/480. A complete winged adult female. Karatau. Designated by Vishniakova (1971)
Additional material: PIN 2066/416±, 653±, 1055; 2239/273, 276±, 285; 2384/132±, 145, 194±; 2554/17±, 28, 140; 2994/ 186± (complete winged adults). Karatau. Designated by Vishniakova (1971). The same locality as the type.

Taphonomical remarks: The preservation of a complete specimens without isolated forewings seems suspicious, nevertheless, according to the very specific forewing it is clear that this species (and genus) is not represented further with isolated forewings. This rich material, nevertheless, contains also problematic specimens, which unlikely belong to this genus and species (such as figured 2554/17, which is most probably *Olzmasg*). Due to uncertainty I retain these specimens in the original placement, but discrepancy in taphonomy must be considered. Anyway this is a rare species and due to complete specimens surely originate near the deposition area.

Raphidiomima cognata Vishniakova, 1971

Holotype: PIN 2784/792. A complete winged adult female. Karatau. Designated by Vishniakova (1971)
Additional material: PIN 2904/60. A complete winged adult male. Karatau. Designated by Vishniakova (1971). The same locality as the type.

Taphonomical remarks: The preservation of a complete male and a female only seems suspicious, nevertheless, according to the very specific forewing it is clear that this species (and genus) is not represented further with isolated forewings.
Mutations: Holotype PIN 2784/792 contain a fusion of CuP with A1 (so that CuP is unusually branched). Nevertheless, this deformity is not counted as it occurs within the protective part- clavus. Anyways this is an extremely rare species and complete specimens surely originate near the deposition area.

Genus *Chuanblatta* Liang, Wang, Shih et Ren, 2021

Type species: *Chuanblatta huntianlingensis* Liang, Wang, Shih et Ren, 2021 (Daohugou).

Composition: *Chuanblatta lata* Liang, Wang, Shih et Ren, 2021 (Daohugou).

Stratigraphic range: Middle Jurassic – Lower Cretaceous
Geographic range: Laurasia

Diagnosis (after Liang et al. 2021): Differs from all other genera of Rahpidiomimidae in the patterns and coloration on forewing, hind wing and pronotum. In the forewing, dark coloration located on the part of R, M, and anal area, while light coloration, on the part of M, CuA, and anal area. Dark coloration on the tip of hind wing, and light coloration on the middle of hind wing and R area. Light and dark coloration pattern on the pronotum resembling the Chinese character of "川 , *chuan*", the edge of stripes uneven. Raptorial fore leg autapomorphic within Caloblattinoidea. Presence of male tergal glands unique (symplesiomorphy with Caloblattindae).

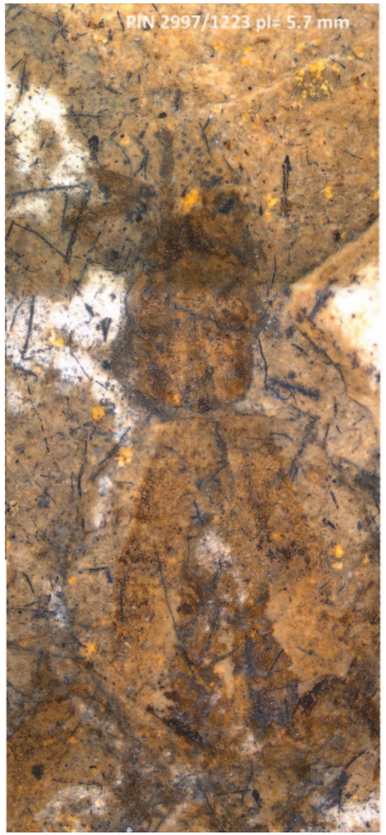
Chuanblatta stalosa sp.n.
(figps. 115-116, 118-121)

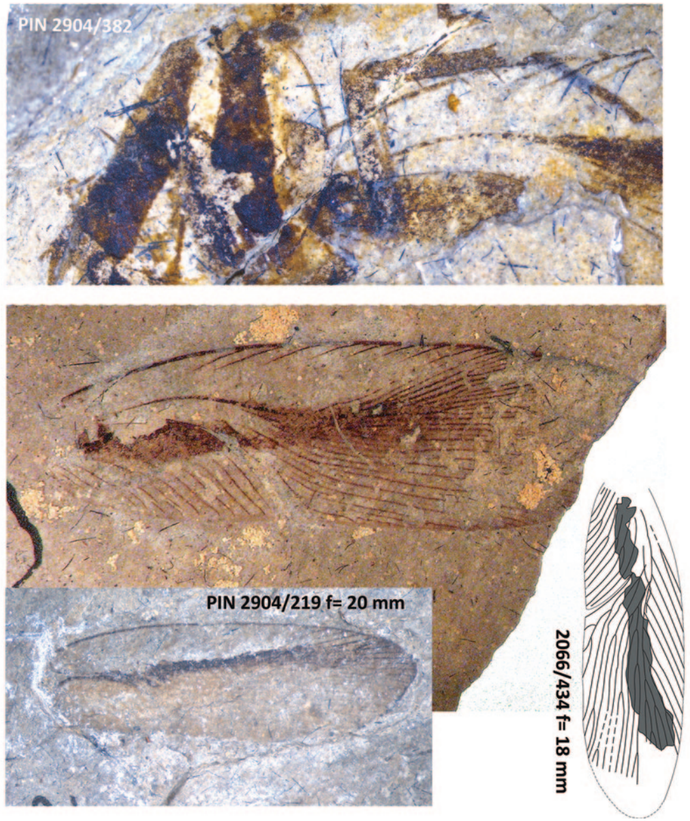
Holotype: PIN 2997/1384. A completely articulated winged adult male without legs and with antenna.
Type locality: Mikhailovka, Karatau, Kazakhstan.
Type horizon: Kimmeridgian Upper Jurassic, Karabastau Formation.

Additional material: PIN 2066/140 (fL); 2904/381, 1872; 2384/68± (w= 5.8 mm; male body with T glands), 123±, 130±, 133, 140 (female), 154 (FPleg), 162 (female); 2239/218 (w= 5.8 mm), 236±, 263 (w= 6.5 mm; male body with T glands); 2465/973; 2997/145, 216, 272, 283, 323, 1158, 1223, 1620, 4249± (complete specimens); 2066/430, 434, 436, 454; 2239/188, 200±, 213; 2384/128, 138, 141±*, 146, 157, unlabelled; 2465/909; 2511/102; 2784/740; 2904/25, 219, 248=237, 343, 349, 350, 351, 367, 1761,1895c; 2997/1191, 1199, 1220, 1225, 1263, 1300, 1414, 1595, 1617, 1668, 1689R (R= regurgite), 4250, 4418 (isolated forewings); 2904/ 382 (isolated pronotum); 2997/1674 (l= 16 mm; immature individual). The same locality as the type.

Differential diagnosis: Differs from its congeners from Daohugou in having shorter (not reaching apex) central pronotal stripe. C. *huntianlingensis* is generally smaller (11-19.7 mm) and differs in not having strong and colored C (costa). Sister species is thus *C. lata* (forewing length 14.03-21.5 mm), which, besides statistically, differs only in for of forewing with sharp apex and in having striped coloration of forelegs (completely dark in *C. stalosa*).
Description: Head prognathous, slightly elongate (2.5/1.7 mm), dorsally with two parallel thin dark stripes on pale background leading to antennal socket (0.46-0.6 mm in diameter). Antenna wide, filiform, multisegmented (27 antennomeres preserved, according to still wide segments, expected is long to very long







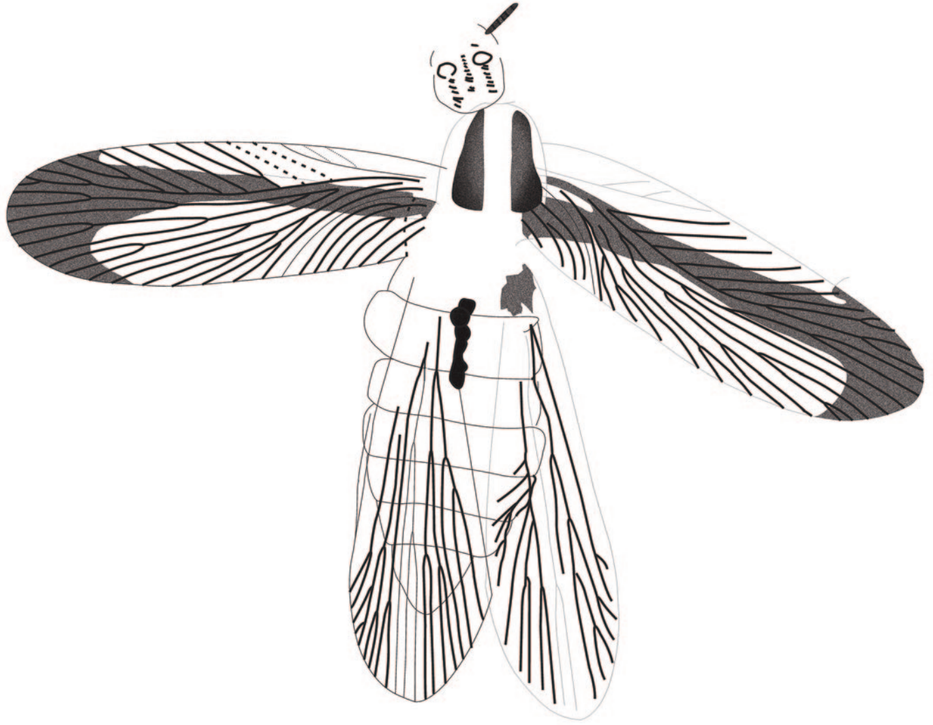
antenna), segments short (scape 0.5/0.12; pedicel 0.12/0.12 mm; then 0.12/0.1 mm at base). Palp very long (1.56/0.84/1.56/ 1.68/0.7 mm).
Pronotum slightly elongated (5/ 4.8 mm), basally slightly elongate at center, pale, with two wide converging dark stripes and the central short posterior one.
Forewing 11-22 mm long and 3.7-6.25 mm wide, with characteristic transverse stripe ending arrow like to both sides of the membrane (total number of veins meeting margin 37-56). Costal area very narrow, with Sc elongate but reaching only the length of the clavus, and with only 3-5 branches. R slightly sigmoidal, with branches only primarily dichotomized, 12-16 meeting margin. M expanded, overlapping apex, slightly sigmoidal, with 6-10 veins at margin. CuA simple, nearly straight, with 5-13 veins at margin. CuP simple, fluent, clavus long and narrow, with 7-11 veins at margin, branches are dichotomized mostly primarily, sometimes secondarily.
Hindwing elongate, transparent, with extremely narrow remigium (11-18/ 3.8mm) and simple pale Sc. Terminally, R1+RS (2-3+5-6 in holotype; up to 6+7 generally in other specimens) is dark (dark is also a CW) forming a kind of analogue of pterostigma, although membrane is not colored in this area. M might be ocassionally unusually greatly simplified with 3-8 straigth veins meeting margin. CuA with 7-9 (holotype)- 10 straigth veins and a simple straight CuP.
Male body comparatively narrow (ca. 4.8 mm wide), with small reniform pair of tergal T5 glands. Female ovipositor rather short.
Legs long, pale, with longitudinal dark rim, heavily carinated with up to 1.5 mm long strong tibial spurs.
Forelegs raptorial, with carnivore spurs organized on femur in two rows (up to 10 spurs in A row). Short terminal femoral spur present. Tibia long, with at least 8 (probably significantly more) strong and long spurs. Tarsus with long first taromere and half as long second tarsomere, shorter third tarsomere (together ca. 2.7 mm).
Mid femur robust (4.2/0.84 mm), tibia and tarsus short and robust (5.6/ 0.7 mm; 0.84, 0.84, 0.7, 0.42, 0.98 and 0.28 mm wide). Hind femur very robust 4.9/ 1.82 mm; tibia 9.8/ 0.7 mm extremely long and heavily carinated. Tarsus also short and robust (4.62/0.28), tarsomeres undistinguishable.
Remarks: This is the most common cockroach genus in Daohugou. Here it represents only a minor fraction of not only cockroaches but also a tiny proportion within “Caloblattinoidea”. The identical pronotum, including identical structure of coloration (converging stripes and a short central posterior one) and high degree of venation similarity suggest *Chuanblatta* is closely related to *Decomposita*. Preserved aesophagus content directly documents predatory way of life with tiny chitin stripes preserved (figp. 120) – thus diet were most probably minute insects, like *Cameloblatta* and unlike in some other genera of Raphidiomimidae from the site where big prey is expected.
It is necessary to consider that in Daohugou at least two closely related species of this genus occur, and their discrimination was possible only based on a comparative material counting more than 500 specimens (Liang et al. 2021). Thus it cannot be excluded that this material actually regards two closely related, indistinguishable species.
Surprisingly, these well-preserved species in both sites are hardly recogniseable not only on the basis of forewings but all characters. Different is basically only coloration- namely length of the central longitudinal pronotal stripe and color of forelegs. Such similarity was not expected among species from different sites (Daohuhou and Karatau) and in this particular case it suggests not only a close relation but also a short time-difference.
Mutations: Specimen (2384/141) posses an unspecifiable forewing vein-vein fusion; 2452/ 213 contain interminated anal vein in clavus.
Variability: Variability was performed in spite of statically insufficient material (n= 14) and possibility of presence two species within the bulk. Nevertheless, result is consistent with the context and the total number of veins meeting margin for these 14 specimens reaches only 13.2 (CV in %) which is a value adequate to other species within this family at the site. At the


PIN 2997/145 l= 21 mm
PIN 2997/1615 f= 15 mm


PIN 2465/973 l= 25 mm
PIN 2997/1158 l= 26 mm



PIN 2997/ 1384 fR= 11 mm



same time low is also variability in the anterior margin (CV_R= 13.69 %) of the wing suggesting a good flight. Compared with statistically significant sample size of the sister species *Chuanblatta huntianlingensis* from Daohugou (n= 43; CV= 7 %), this value is nevertheless, high. Moreover such low value seems to indicate a single population, but this presumption in this species alone must be taken with caution as the the number of specimens is statistically insignificant. One can see that in significant samples size, the CV for the species from Daohugou as nearly half as low. Again, this might reflect the generally lower variability at the site – i.e. see CV= 7.7 % for *Fortiblatta* from Daohugou. Another possible source of bias is exclusion of sister species *C. lata* from the Daohugou collection and recognizing it as a separate species. But intuitively this was not the case, as the total number of this species falls within the variability of C. *huntianlingensis.* Also sizes are comparable among *C. lata* and C. *huntianlingensis*.

Derivation of name: *stalo sa* is Slavic for "once happened".

Character of preservation: 24 complete specimens (at least one male and at least two females), 39 isolated forewings, 1 isolated clavus, 1 isolated pronotum, 3 isolated bodies (two males), 1 immature individual (categorized within this species on the basis of distinct stripes on body known from the North Myanmar species), 1 ocurrence within a vertebrate comprolite.

Taphonomy: Completely articulated specimen in this large species indicate a short pre-deposition time, but a high partition of isolated forewings combined with ocurrences of isolated bodies also suggest a long transportation. Thus it is probable this species inhabited a wide range within the waterbody structure and its inflow gradients. Ocurrence in the vertebrate coprolite or a regurgite also suggest its digestibility and participation in the food-webchain. Isolated hindwings probably occur in unidentifiable material.

Specimen	de-formity	length	width	Sc	R	M	CuA	CuP	A	RM	RCuA	MCuA	total	total without A
2997/1384L	11	3.7	3	11	9	6	1	6	20	17	15	36	30	
2997/1384R	11	3.7	3	12	8	6	1	7	20	18	14	37	30	
2384/162		15		3	15	8	10	1	11	23	25	18	46	35
2384/141	*	18.5		3	17	7	13	1	15	24	30	20	56	41
2465/909		18.5		3	15	6	9	1	13	21	24	15	47	34
2904/351		18		4	16	10	9	1	10	26	25	19	50	40
2904/343		18		4	14	10	7	1	11	24	21	17	47	36
2997/1199			4	16	8	8	1	9	24	24	16	46	37	
2997/4418	15	4.4	5	15	9	12	1	13	24	27	21	55	43	
2066/434		20	6.25	2	15	8	9	1	12	23	24	27	47	35
2997/145		16.3	5.3	3	15	10	8	1	12	25	23	18	49	37
2997/1615	15	5	3	19	9	8	1	14	28	27	17	54	40	
2904/211		20		6	18	9	15	1	9	27	33	24	58	49
2904/ 219		20		4	15	9	10	1	11	24	25	19	50	39
n		13	6	14	14	14	14	14	14	14	14	14	14	14
min		11	3.7	2	11	6	6	1	6	20	17	14	36	30
max		20	6.25	6	19	10	15	1	15	28	33	27	58	49
dev		3.113021	0.993856	1.01635	2.082106	1.157868	2.584825	0	2.555967	2.359223	4.201648	3.588749	6.393678	5.033951
ave		16.64	4.73	3.57	15.21	8.57	9.29	1	10.93	23.79	24.5	18.57	48.43	37.57
CV		18.7	21.01	28.47	13.69	13.51	27.82	0	23.38	9.92	17.15	19.33	13.2	13.4

Genus *Decomposita* Vršanský, 2008

Diagnosis (after Vršanský 2008) Head more or less globular, with tree distinct concave ocelli, and slender antennae. Pronotum small, nearly globular, slightly longitudinal. Forewing thin, soft and fragile, with narrow costal field, simple or branched Sc, simple R branches; M branches long and straight, CuA expanded, with the anteriormost branch straight and simple. Hindwing with simple Sc, R and RS differentiated; M expanded. Legs long and thin, with free coxae.

Autapomorphies: Pale leg spurs on dark legs

Remarks: In original work (Vršanský 2008), this taxon was categorised within Caloblattinidae with being explicitely named as ancestor of Raphidiomimidae, with numerous traits of this family, which included partially raptorial legs and pronotum smalôler than any known representative of the Caloblattinidae.

Related taxon was found to be represented by *Falcatussiblatta* Liang et al. 2019 (originally *Rhipidoblattina karatavica* Vishniakova, 1968) which turned to represent Raphidiomimidae (Liang et al. 2019). Caloblattinidae are additionallty large, thus this character is a strong apomorphy and has narrow radial area (Raphidiomimidae synapomorphy, although not as deeply expressed). Synapomorphies include forewing elongation with almost parallel wing margins. Thus this genus is treated here as belonging to Raphidiomimidae.

Decomposita triocella Vršanský, 2008 (figps. 125-130)

Holotype: PIN 2554/36 (l= 19 mm; 1, 15, 5, 5, 1, 11) (designated by Vršanský 2008). A complete winged adult. Sex unknown.

Additional material: PIN 2066/367 and 2554/30 (f= 15 mm) (designated by Vršanský 2008)

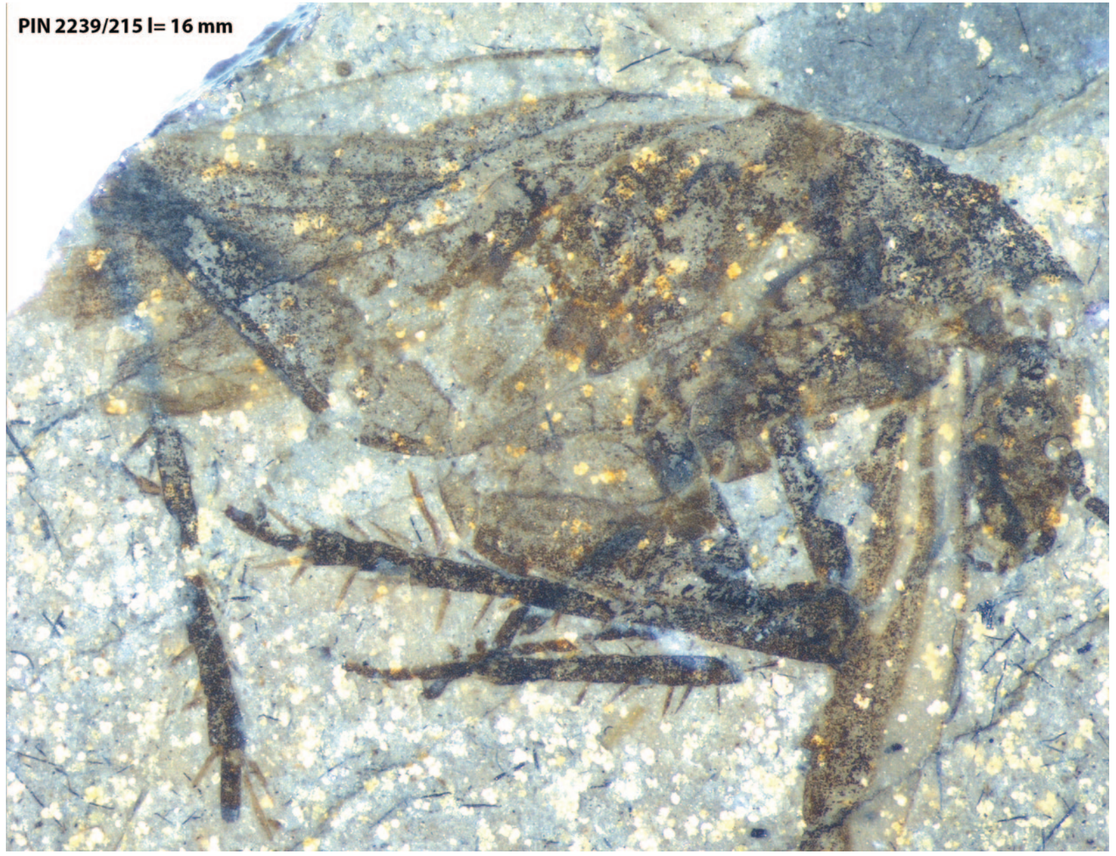
Additional material designated here: 2239/215; 2384/22±, 23, 28, 31± (l= 21 mm), 33 (w= 28 mm); 2784/752 (p= 3.8/4.0 mm), 758 (f= 15 mm), 792, 906; 2997/232 (complete specimens, sex unknown); 2066/365; 2384/74, 126±; 2452/385 (f= 15.5 mm); 2554/191 (f= 14 mm); 2784/ 888; 2904/83±, 281, 345 (f= 16 mm), 1865, 1884, 1897; 2997/788 (f= 13 mm), 1170, 1177, 1147±, 1192, 1237=1224, 1246, 1288, 1289, 1334 (16 mm), 1351, 1412, 1695, 4391 (forewings); 2239/274 (h= 14.5 mm; 1,7+10, 2, 8+1); 2384/106 (h= 12 mm); 2554/23 (h= 14 mm); 2997/17 (h= 13 mm), 28 (h= 18 mm), 31 (1.5+9.11+blind+1.), 1588 (h= 10.5 mm); 2867 (h= 16 mm) (hindwings). The same locality as type.

Redescription: Head globular, eyes large, three ocelli large. Lateral ocelli are closely approximated while the central ocellus is placed nearly among antennal foramens. Narrow mandibles possess very sharp and large teeth. Head with coloration, with 3 longitudina short stripes on occiput, and pale fenestrum around central ocelus. Pronotum nearly globular, colored (Figp. 126). Legs long and robust, the fore femora free, with very long coxa; tibia heavily carinated with spurs more pale (likely pale brown) compared with leg itself (likely black or dark brown). Forewings large; length/width ca. 12.5-19/ 5 mm. Costal space narrow, pale; Sc simple or with up to 6 branches. 9–23 R branches simple. Five-11 M branches long. CuA expanded, with 5-16 branches, anterior branches long and straight. A branched, with 9-12 veins at margin. Coloration as in Figp. 129. Hindwing with simple Sc, R 4-7, Rs 5-10; M 2-11. CuA with 8-11 veins, CuP simple.

Variability: Evaluated are 14 samples. This number is insignificant, but results are in concordance with other species at this locality and this family. CV for total number of veins at margin (38-53) is 12.67 % and 9.29 % disregarding A show over 3 % discrepancy and thus 3 % difference from these results are likely in the significant sample size. Additional percents are surely also possible. R with M is less variable than other combination of veins.

Mutations: 2384/126 posses a mutual fusion of two anal veins.

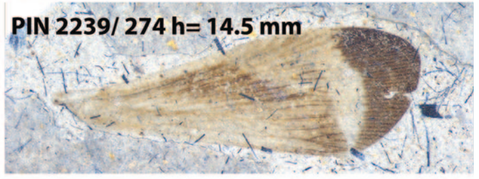
Character of preservation: 13 complete specimens; 27 isolated forewings; 8 isolated hindwings.



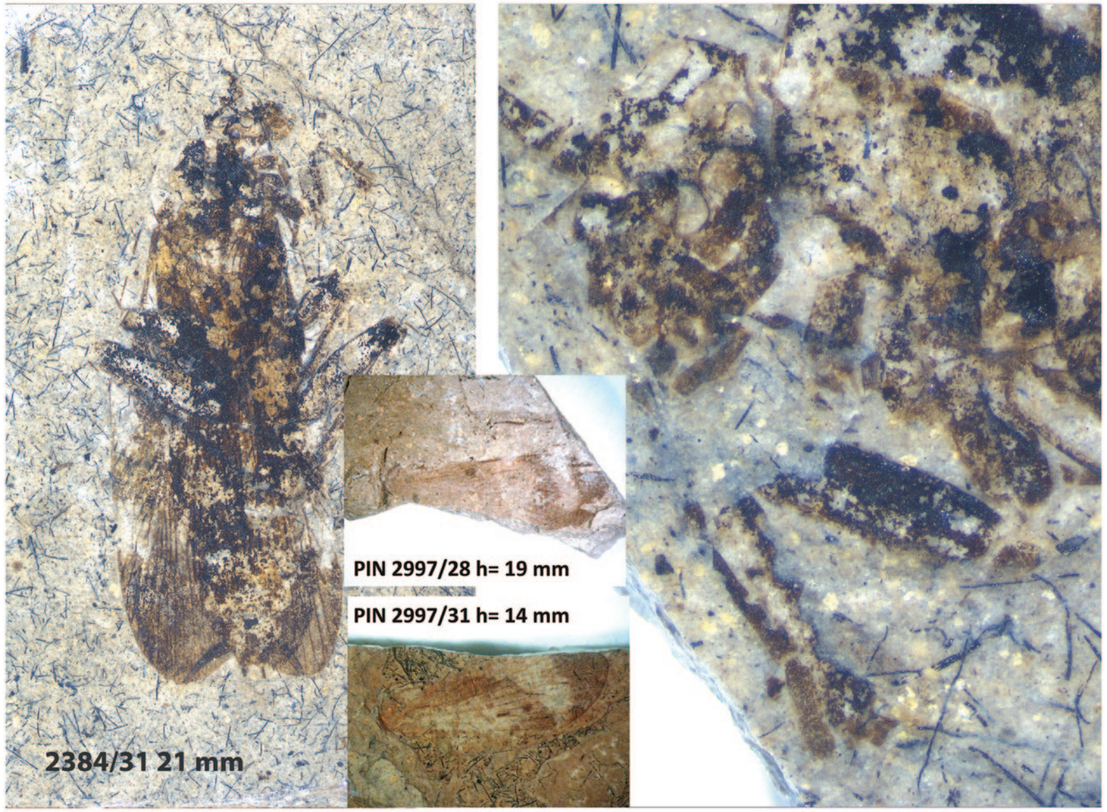
Decomposita triocella

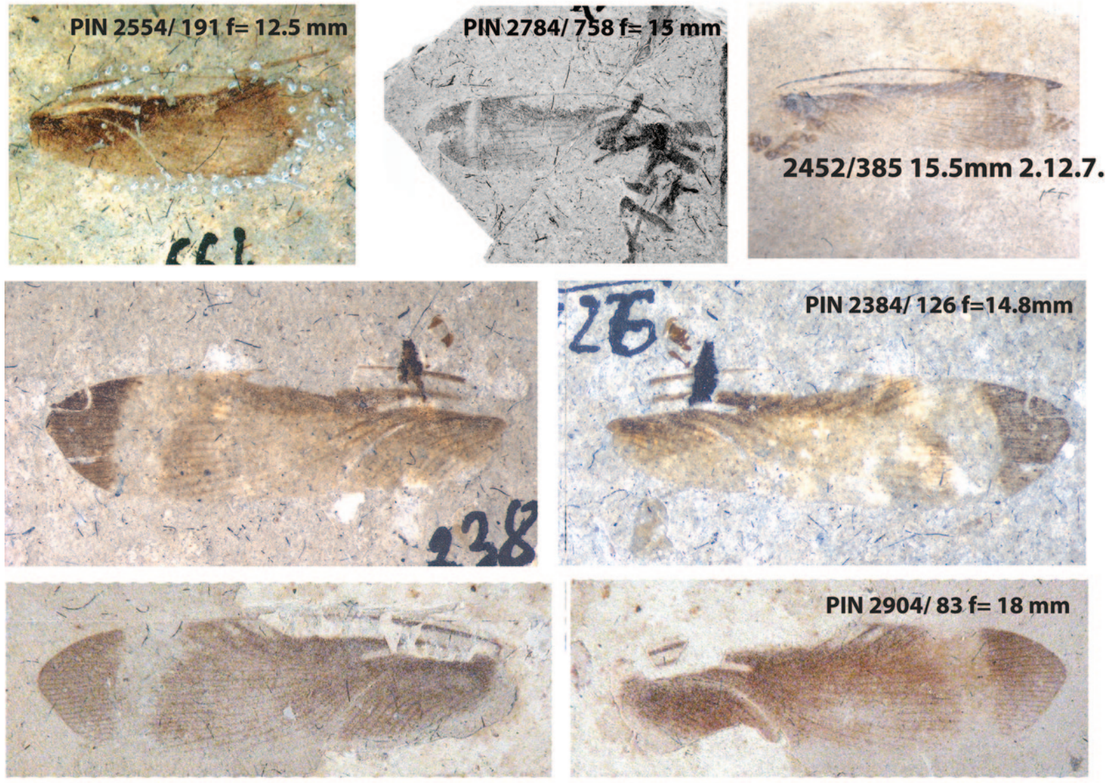


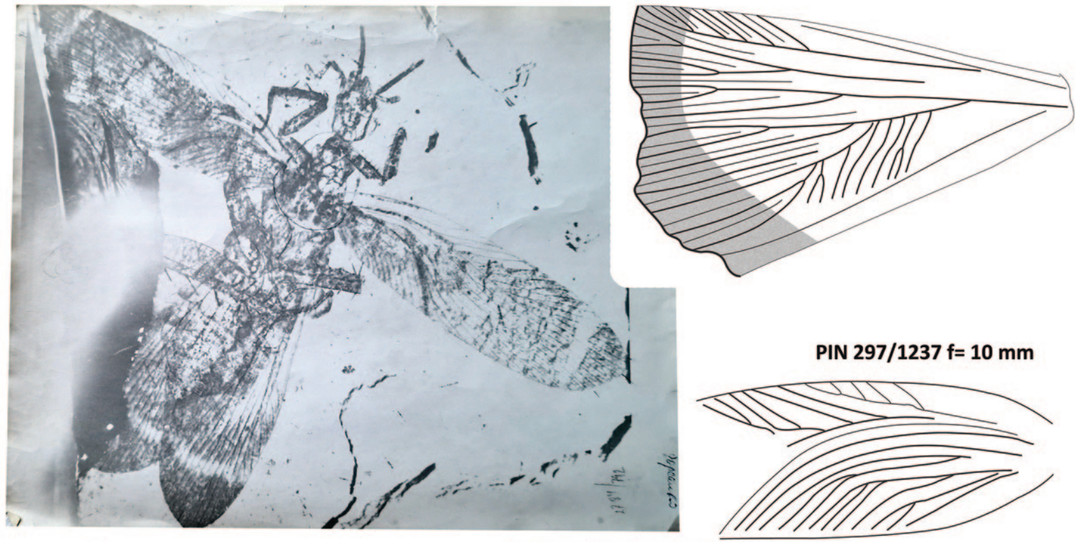



PIN 2239/ 274 h= 14.5 mm


PIN 2554/36 l= 19 mm
PIN 2384/33 w= 28 mm
PIN 2997/2867 h= 16 mm


2384/31 21 mm
PIN 2997/28 h= 19 mm
PIN 2997/31 h= 14 mm

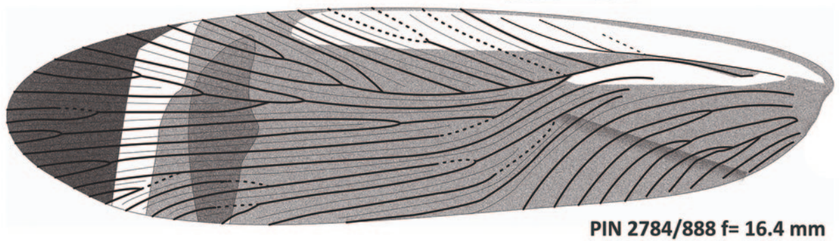

PIN 2554/ 191 f= 12.5 mm
PIN 2784/ 758 f= 15 mm
2452/385 15.5mm 2.12.7.
PIN 2384/ 126 f=14.8mm
PIN 2904/ 83 f= 18 mm



PIN 297/1237 f= 10 mm



2384/33 l= 28 mm



PIN 2784/888 f= 16.4 mm

Taphonomy: Presence of numerous specimens, numerous complete specimens, combined with numerous hidwing and and presence of exclusively forewings that are completely articulated, habitat was apparently near the deposition area and pre-depositional transport and/or duration in water was short.

Remarks: Wings were thin and fragile - they are cracked and folded, unlike any of the thousands of preserved Mesozoic cockroaches (Vršanský 2008).This pattern is here observed on numerous specimens. This suggest sporadic flight, similar to living praying mantis.

Specimen	length	Sc	R	M	CuA	CuP	A	RM	RCuA	MCuA	total	total without A
PIN 2554/ 36	19	1	15	5	5	1	11	20	20	10	38	27
2784/758fP	15	3	13	10	16	1	9	23	29	26	52	43
928	12.5	3	23	6	10	1	10	29	33	16	53	43
2904/83	18	5	9	11	14	1	12	20	23	25	52	40
2784/888	16.4	3	10	11	9	1	10	21	19	20	44	34
2997/1177	14	4	16	10	9	1		26	25	19		40
2997/1147±	17.6	3	13	9	7	1	12	22	20	16	45	33
2997/1412	16	3	13	8	9	1	9	21	22	17	43	34
2997/1695	15.3	6	13	9	7	1	9	22	20	16	45	36
2384/126±	14.8	5	12	7	12	1	10	19	24	19	47	37
2452/385	15.5	2	12	7	11	1	11	19	23	18	44	33
2904/345	16	4	10	10	9	1	9	20	19	19	43	34
2784/792R		2	15	6	8	1	12	21	23	14	44	32
2784/792L		3	16	6	7	1	13	22	23	13	46	33
n	12	14	14	14	14	14	13	14	14	14	13	14
min	12.5	1	9	5	5	1	9	19	19	10	38	27
max	19	6	23	11	16	1	13	29	33	26	53	43
ave	15.84	3.58	13.57	8.21	9.5	1	10.54	21.79	23.07	17.71	45.85	35.64
dev	1.7799174	1.3363062	3.4799267	2.0448273	2.9547875	0	1.3913653	2.7506243	3.9314176	4.2684634	4.2592283	4.5167576
CV	11.24	37.33	25.64	24.9	31.1	0	13.2	12.62	17.04	24.1	9.29	12.67

Decomposita pentavisia sp.n.
(figp. 133)

Holotype: PIN 2997/241 (f= 20 mm).
A complete winged adult.
Type locality: Mikhailovka, Karatau, Kazakhstan.
Type horizon: Kimmeridgian Upper Jurassic, Karabastau Formation.

Additional material: PIN 2997/1209. A forewing with a hindwing. The same locality as type.

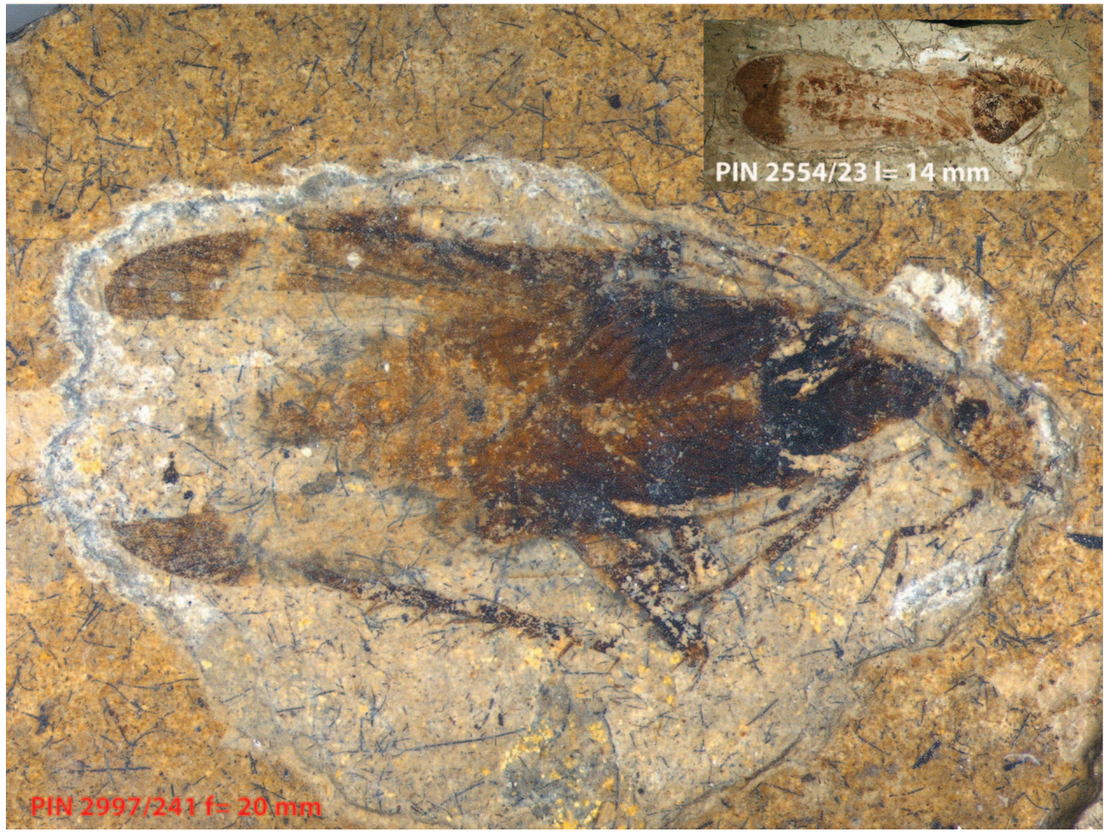
Differential diagnosis: Differs from the type species, its sister species *D. triocella* only in coloration: pronotum is without 2 stripes and both wing apexes are dark, and in longer clavus and hindtibia. Possibly this species is slightly larger (20 mm compared with 12.5-19 mm of *D. triocella*).
Autapomorphy: extremely long hindtibia
Description: Head preserved in upright position and was at least partially prognathous, and possibly fully prognathous. Occiput dark, rest of the head seems pale, probably very pale brown. Palps comparatively long (right palp 0.4/ 1.2/ 1.4/ 1 mm), stronglky melanised, dark. Labial palp short, possibly 2-segmented (0.4/ 0.5 mm), also strongly melanised, dark.
Pronotum slightly elongate (5.5/ 4.8 mm), pale, with dark margin and central area (lateral sides are pale).
Forewing elongate (20/ 5 mm), with narrow costal area. Costal vein wide, melanised; Sc nearly straight with 4-6 short offshoots. R sigmoidal, overlapping apex with 15 veins at margin. CuA with about 10 veins. CuP simple, rather sharply curved. Clavus long (8.2 mm), with 11 anal veins at margin. Diagonal kink present. Right wing overlapped. Coloration dark, with pale costal area, short pale M base and subabical transversal pale stripe.
Hindwing pale with dark apex.
Hindlegs extremely long, hindfemur (6.5/ 1.8 mm) with terminal femoral spur. Hindtibia (11.2/ 0.5 mm) with at least 15 up to 1.1 mm long spurs which are more pale compared with legs (and palps).
Derivation of name: after penta and visió (Latn for five and vision) – alluding to the 5 optical receptors (two eyes and lateral ocelli and central ocellus)
Character of preservation: one complete specimens, one fragment of a forewing with a hindwing.
Taphonomy: Completely articulated specimen along with completely articulated forewing (with clavus) and combined with hindwing in this large species indicate a short pre-deposition time sepent in waterbody.
Remarks: Pale tibial spurs are present also in other species within this genus.

Decomposita apicata sp.n.
(figp. 134)

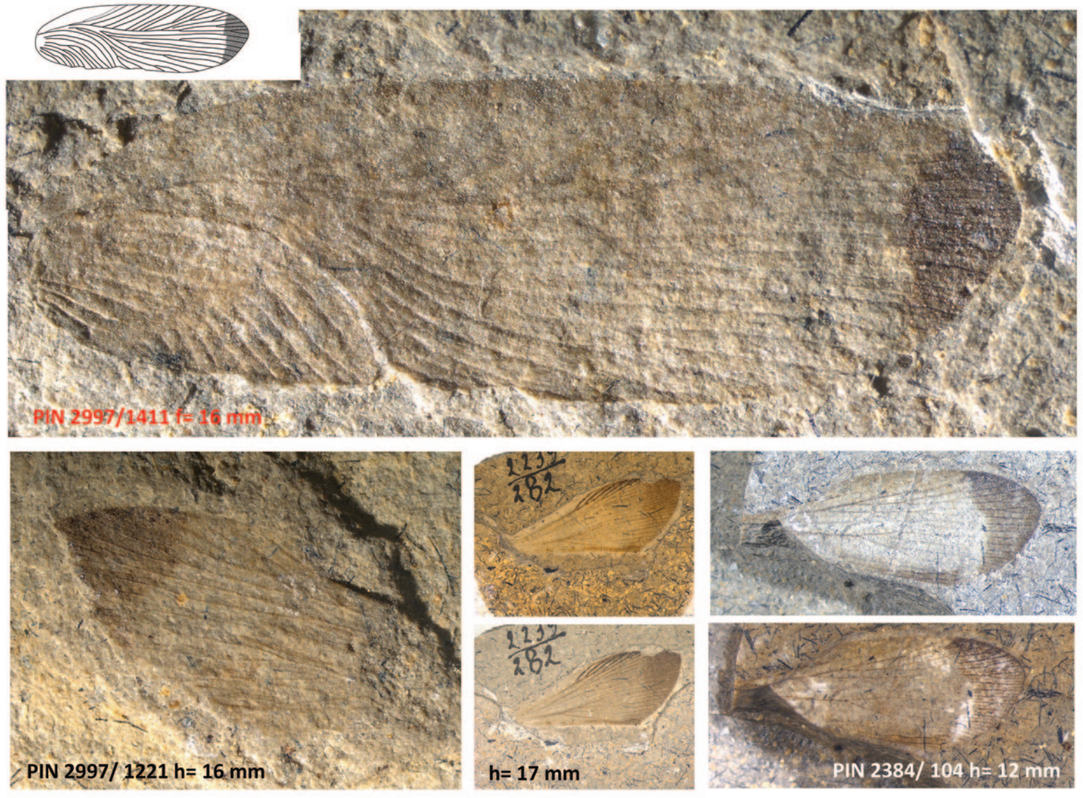
Holotype: PIN 2997/1411 (f= 16 mm). A completely articulated (with clavus) isolated forewing.
Type locality: Mikhailovka, Karatau, Kazakhstan.
Type horizon: Kimmeridgian Upper Jurassic, Karabastau Formation.

Additional material: PIN 2452/399; 2997/1336 (f= 14 mm) (forewings); 2239/282; 2997/282, 1221, 1310, 1139± (h= 18mm) (hindwings). The same locality as the type.

Differential diagnosis: Differs from congeners in size and in coloration restricted to the apical part of the wings.
Autapomorphy: colored apex only
Description: Forewing unmodified (ca. 14-16/ 5 mm), oval, with apex posed suncentrally anterior, with rather wide base and moderate (not narrow or wide) costal area. SC with 2 branches at margin; R nearly straight, with 16 veins at margin (12+4). M with 9 nearly straight veins curved posteriorly; CuA simplified with 5 veins at margin. CuP fluent, clavus moderately long with secondarily branched A (11 at margin) amd with diagonal kink indicated.
Hindwing 16-18 mm long, with moderately narrow remigium and colored apex. SC simple thin and straight, uncolored. R1 wide, colored dark, with narrow



Decomposita pentavisia



Decomposita apicata

branchings (3), RS rich and sophisticated. With both anterior and posterior offshoots (3 basalmost are colore dark), totally with 11 veins at margin. M strongly sigmoidal, with 5 veins at margin. CuA with secondarily branched veins (10) and with blingd branches, CuP Simple.

Derivation of name: *apicata* is after apex – referring to colored wing apexes.

Character of preservation: 3 isolated and completely articulated forewings, 5 isolated hindwings.

Taphonomy: Absence of a complete specimen suggest a pre-depostiional transport of this moderately rare-rare species.

Remarks: Hindwings are categorized within this species on the basis of identical size and coloration. This taxon is categorized in the present genus on the basis of high congruence in the shape, also somewhat transitional among more short *Rhipidoblattina* and more narrow *Liadoblattina;* but also in similarly structured but more simple coloration than within the genus. Other genera are not known to posses terminal stripe.

Decomposita basquatirgis sp.n.

(figps. 136-137)

Holotype: PIN 2784/726±. A complete winged adult female.

Type locality: Mikhailovka, Karatau, Kazakhstan.

Type horizon: Kimmeridgian Upper Jurassic, Karabastau Formation.

Additional material: PIN 2784/58=1720 (complete adult winged female); 2554/200; 2239/71, 153 (16 mm); 2384/137, 147± (14.5 mm); 2997/1230, 4348 (isolated forewings). All the same locality as the type.

Differential diagnosis: Differs from all species within the genus (and from all other genera of Raphidiomimidae except highly derived *Cameloblatta* as well as from related Rhipidoblatta) in having sophisticated coloration with 3 size levels of pale coloration patterns above the dark membrane.

Autapomorphy: sophisticated coloration with small pale fields and minor pale dots among veins and intercalaries

Description: Head hypognathous, small. Antenna filiform, wide. Pronotum slightly elongate, with wide, Y-shaped dark stripe anteriorly covering half of the pronotal width.

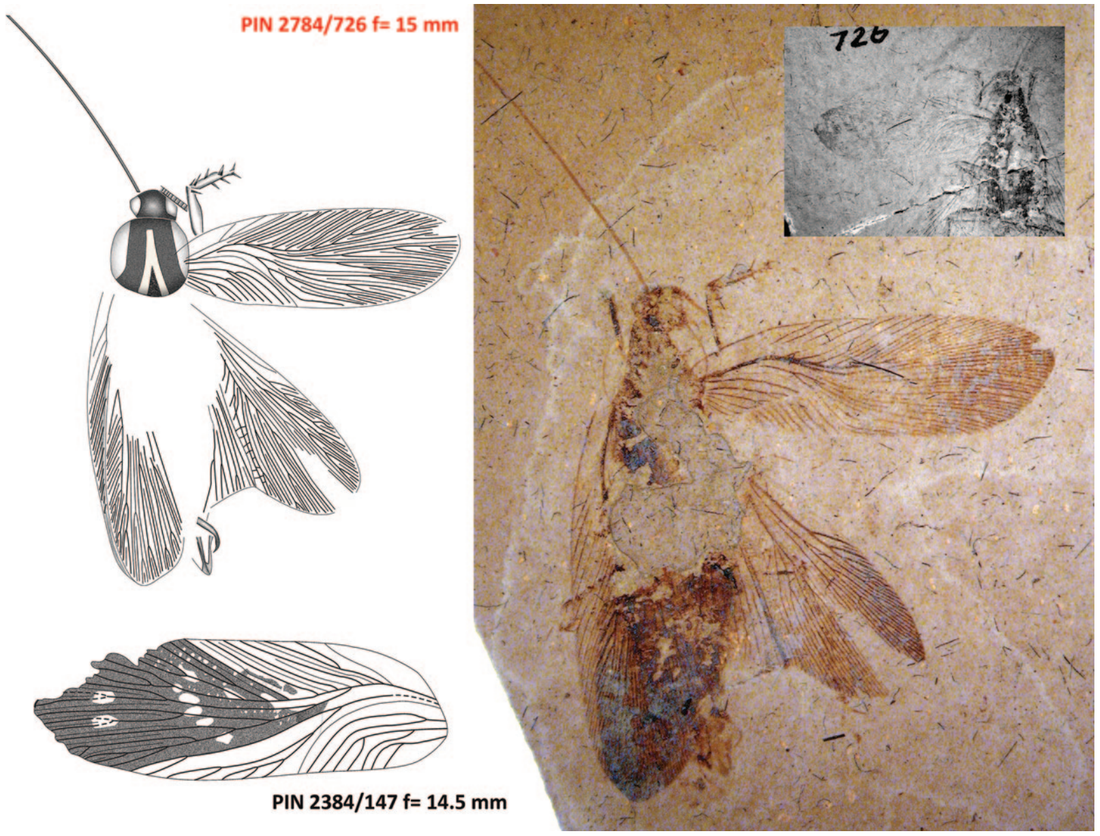
Forewing conservative, wide (15-16/ 4.1 mm), with veins and intercalaries mainly dark, but in pale areas veins and intercalaries are also pale. Cross-veins usually pale, sporadically dark. Costa distinct in anterior margin and colored, costal area wide, SC with 3-4 branches. R slightly sigmoidal, not reaching apex, R with 11-14 veins at margin, most veins are simple, only few are simply dichotomized, none is secondarily branched. M slightly sigmoidal, with 6-10 veins at margin. CuA long, sigmoidal, with up to 4 main stems and 7-13 veins at margin. CuP fluent, short, clavus simplified, with only 7-11 anal veins at margin. Coloration of the membrane dark in CuA, M and apical R, with ca. 12 pale oval dots in high equal to distance among veins. In radial area, also smaller dots are present among veins and intercalaries.

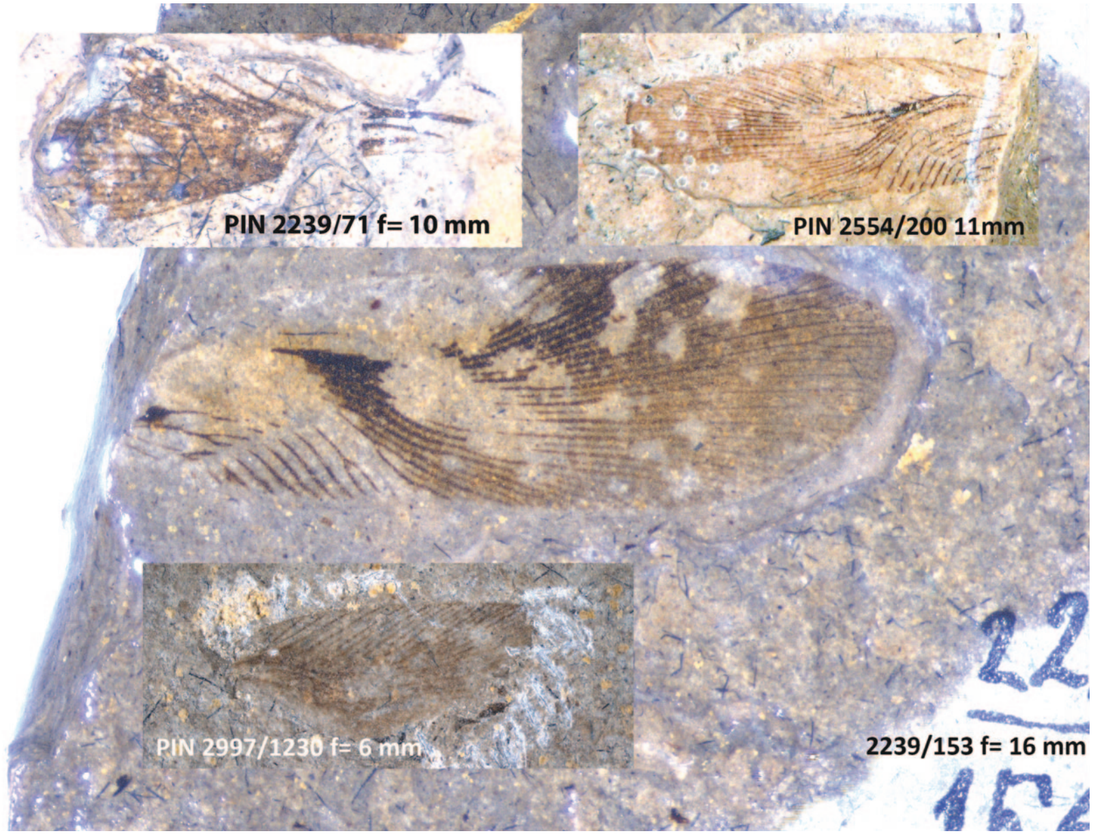
Hindwing similarly colored as the forewing, slightly shorter, with moderately wide remigium. Intercalaties and cross-veins present. Costal area very narrow, Sc nearly straight, softly colored, curved anteriorly near its apical part (termination at margin). R1 with 4-6 wide terminally ascending and forming sharp angle, veins reaching margin; RS differentiated near base and consisting of 4-9 veins at margin (some result from tertiary dichotomisations). M long and straight with about 5-7 veins at margin. CuA with secondarily branched veins (9 at margin) and additional dichotimised blind branches; CuP simple long running along A1 near margin of vannus. A2 in vannus dichotomized, at least A totally with at least 10 veins at margin.

Body black or very dark, cerci very short and curved, segments indistinct. Ovipositor very wide and moderately long. Two short styli present (segmentation indistinct).

Foreleg with free long coxae, short and robust femora (carination indistinct or unpreserved), tibia short, covered with strong spurs.

Derivation of name: *basquatirgis* басқатырғыш is Kazakh for aenigma (puzzle).


PIN 2784/726 f= 15 mm
726
PIN 2384/147 f= 14.5 mm

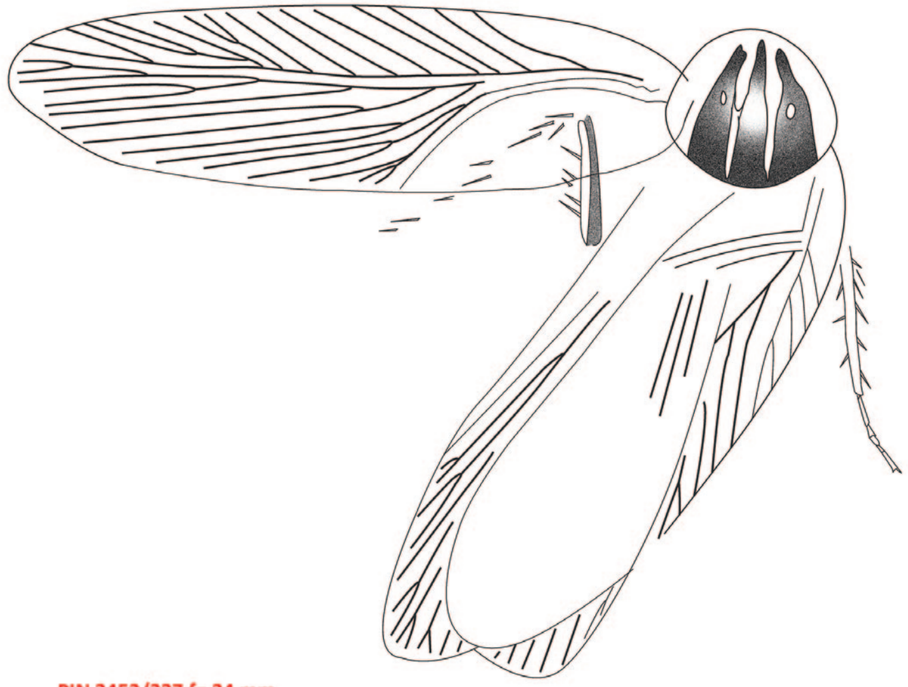

PIN 2239/71 f= 10 mm
PIN 2554/200 11mm
PIN 2997/1230 f= 6 mm
2239/153 f= 16 mm



Decomposita basquatirgis



Decomposita tristriata = original specimen commenting



PIN 2452/337 f= 24 mm

Deformities: 2384/147 posseses a number of deformities (M-M, M-CuA and A1-A2 fusion, the latter associated with blind A1 branch)
Character of preservation: two complete winged adult female; seven (three fully articulated) forewings.
Taphonomy: Presence of isolated, some disarticulated forewings suggest a transport prior to deposition and also a rarity of this easily determined species. This is supported with partially articulated (with antenna and one leg) specimen, damaged by predation (figp. 136).
Remarks: The (sophisticated) coloration is unusual within the genus and is rather characteristic for derived Raphidiomimidae (e.g., *Cameloblatta*). Nevertheless, the shape of the forewing is entirely conservative indiscernible from standard *Rhipidoblatta* and *Decomposita*. Thus the taxon is categorized within this family. There are no further phylogenetical links traceable with other genera except for simplified A similar (possibly due to size) in *Rhipidoblatta. brevivalvata* and *R. trimestre*. The coloration apparently derived by defragmentation of the coloration present in *Decomposita triocella*.

Decomposita tristriata sp.n.

(figps. 138-140)

Holotype: PIN 2452/337. A complete winged adult.
Type locality: Mikhailovka, Karatau, Kazakhstan.
Type horizon: Kimmeridgian Upper Jurassic, Karabastau Formation.

Differential diagnosis: Differs from its congeners in having larger size and in possessing three incomplete diverging dark stripes on the pronotum.
Autapomorphy: None except coloration and large size.
Description: Very large species. Pronotum unmodified, nearly round (5.7/ 5.7 mm), with fore margin slightly shorter compared with the posterior one, without posterior extension. Forewing elongate (24/ 6.8 mm), with colored apex and posterior part. Costa is strongly sclerotized and melanised, probably black. Costal area narrow, SC, rather short, simple or with up to 6 dichotomisation. R nearly straight, with 18 veins nearly reaching apex, RS not distinctly differentiated. M expanded, with straight branches of which 11 reach margin. CuA simplified, with 5 veins at margin. CuP very long, fluent. Hindwing very long (ca. 24 mm), not fully covered with the forewing. Femora with strongly sclerotized longitudinal stripes, tibia heavily carinated with short sharp spines.
Derivation of name: *tristriata* is after *tri* and *striatus* (Latin for three and stripes) – alluding to a coloration of the pronotum.
Character of preservation: One completely articulated winged adult without head.
Taphonomy: This specimen comes from slightly different sediment, which might indicate another bed. Specimen is lacking the head, otherwise is complete which suggest a short pre-depositional transport and short stay in water prior to deposition at the bottom.
Remarks: The present species is highly similar with *D. triocella*, but it is significantly larger and less melanised. Stripes on pronotum are converging and are fully separated, thin. This kind of coloration is present also in *Olzmasg* (which is standardly wide). Also this species seems most similar to stem *Liadoblattina*. In this context it is probable that this species is the most plesiomorphic within the genus. Also the coloration of wings seems simplest.

Genus *Liadoblattina* Handlirsch, 1906

Type species: Scudder, 1885

Diagnosis (after Vršanský and Ansorge, 2007): Medium sized, with both wings coloured. Forewings elongated, as much as 3 times as long as wide (length ca. 20 mm). Clavus more than twice as long as wide. Description: Wings membranous, with distinct coloration. Forewing with simple or weakly branched Sc and narrow costal space; gently curved R with about 15 branches, with M and Cu system developed to same degree (together with some 15 veins); rich A (at or above 10). Numerous cross-veins joined in intercalaries. Diagonal kink present in anal field. Hindwing with simple Sc, R divided into R1 and RS (10–20 veins); M with up to 5 or more branches; Cu rich with at least 8 veins. A1 reduced compared to other related species, with 2 branches and several blind branches.

Composition: *Falcatusiblatta karatavica* (Vishniakova, 1968) comb.n. (Karatau), *Liadoblattina euryptera* Vishniakova, 1983 (Iya); *Liadoblattina laternoforma* Lin, 1978 (Chaomidian); *Liadoblattina mongolica* Vršanský, 2003 (Bon Tsagaan); ?*Mesoblattopsis franconica* (Wurzburg); *Mesoblattopsis pruvosti* (Bartin, Turkey); *Liadoblattina dilatata* (Bode, 1953) (Lehre); *Liadoblattina simplicior* (Bode, 1953) (Gifhorn)

Stratigraphic range: Early Jurassic-Late Cretaceous
Geographic range: Laurasian

Remarks: *Liadoblattina* and *Falcatusiblatta* are very similar and the former differs only in simpler (plesiomorphically) coloration.

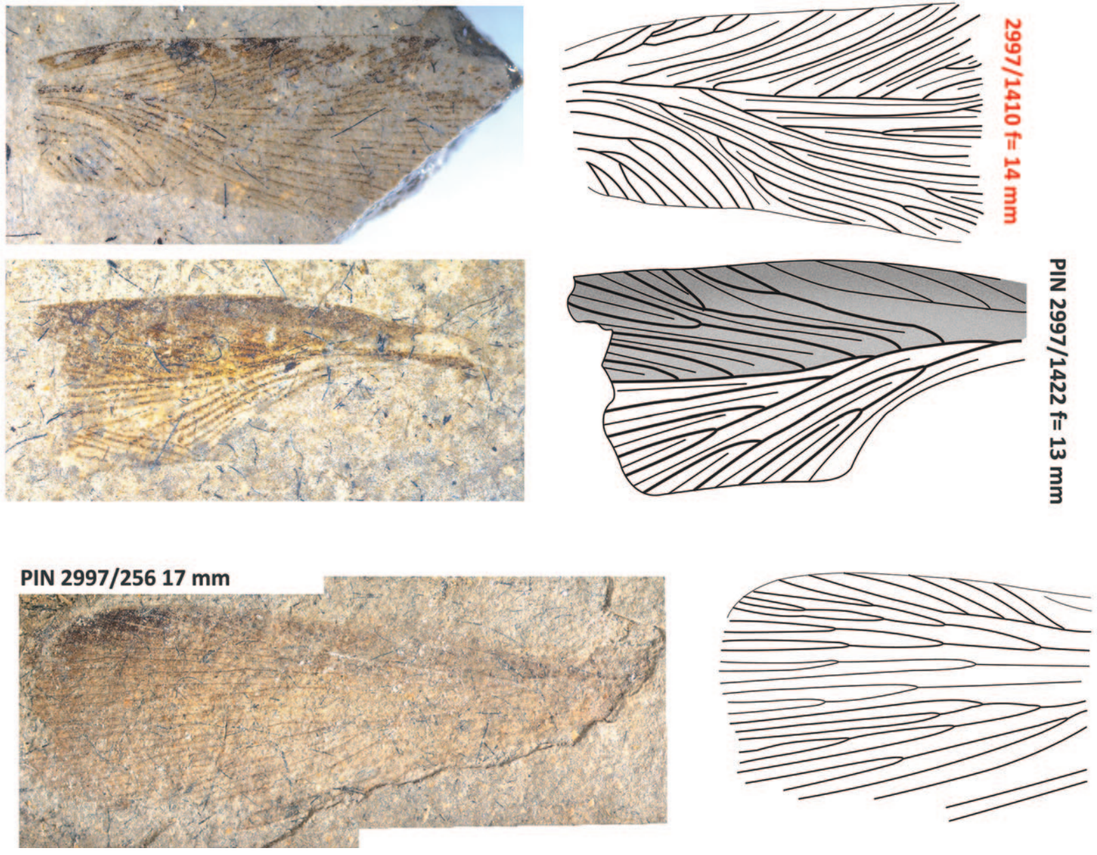
Liadoblattina crassivenata sp.n.

(figp. 143)

Holotype: PIN 2997/1422. A 13 mm long forewing fragment.
Type locality. Mikhailovka, Karatau, Kazakhstan.
Type horizon. Kimmeridgian Upper Jurassic, Karabastau Formation.

Additional material: PIN 2997/251 (complete specimen); 2239/278; 2384/103; 2997/1333 (f= 18 mm), 1342, 1410, 4383, 4280 (forewings); 2384/136, 256 (hindwings). The same locality as the type.

Differential diagnosis: Differs from congeners in size, in colored anterior half of the forewing and in having wide veins.
Autapomorphy: Dark colored anterior half of the wing, wide veins.
Description: Forewing narrow, 16-20 mm long and ca. 7 mm wide, veins and intercalaries distinct, wide and colored, intercalaries more pale comparing with main veins. Membrane transparent, anterior half (whole radial area) dark. Wing base narrow, costal field narrow, SC very long (as long as long clavus), sigmoidal, with 4-6 sharply ascending terminal branches. R nearly straight, radial area very wide, occupying whole anteriror half of the wing, with about 17 veins at margin. M nearly straight. CuA sigmoidal, with about 5 straightened veins ending well before apex. CuP fluent, clavus very long. A secondarily branched, with ca. 10 veins at margin.
Derivation of name: *crassivenata* is after *crassus* (Latin for fat, wide) and *vena* (vein).
Character of preservation: One compelte specimen, 8 isolated mostly disarticulated forewings, two hindwings.
Taphonomy: Isolated and disarticulated fragments suggest pre-depostitional transport.
Remarks: The species can be categorsied withing the genus ofn the basis of general appearance as well as proportions. Wide veins are rather characteristic for more advanced raphidiomimids and might suggest the transitional character state (to more advanced genera of predatory cockroaches of this family).



Genus *Falcatusiblatta* Liang, Shih et Ren, 2018

Type species: *Falcatusiblatta gracilis* Liang, Shih et Ren, 2018. Daohugou.

Composition: *F. qiandaohua* Liang, Shih et Ren, 2018 (Daohugou); *Rhipidoblattina karatavica* Vihniakova, 1968 (Karatau); *Falcatusiblatta* sp. (Mintaja – see Martin 2010: fig. 5C); species described below.

Stratigraphic range: Early Jurassic (Mintaja) – Late Jurassic (LOD)
Geographic range: Cosmopolitan

Diagnosis (after Liang et al. 2017): Differs from all other genera of Raphidiomimidae (Vishniakova 1973, Liang et al. 2009, 2012a, 2012b) by the presence of a very long ovipositor (plesiomorphy) with associated heteronomous cerci (autapomorphy) and forewing with an irregular pattern of light and dark patches (autapomorphy).

Falcatusiblatta karatavica (Vishniakova, 1968)

sensu Liang et al. 2018
(figp. 145)
***=Rhipidoblattina karatavica* Vishniakova, 1968**

Holotype: PIN 2066/441. A complete winged adult female. Designated by Vishniakova (1968)

Type locality: Karatau, Kazakhstan.
Type horizon: Kimmeridgian Upper Jurassic, Karabastau Formation.

Paratype: PIN 2239/353. A complete winged adult female. Designated by Vishniakova (1968). The same locality as the type. Additional material designated here: 2066/386; 2239/164, 222; 2384/151; 2904/191=197, 201 (complete specimens); 2066/365; 2239/222; 2465/907; 2784/858; 2997/276, 231±, 1430 (forewings). The same locality as the type.

Diagnosis (after Vishniakova, 1968): similar in form and anal area of forewing, dichotomisations of CuA and A2 to *R. angustata* Martynov, 1937 from Lower Jurassic sediments of Shurab, and differs in bigegr size and more numerous simple M and by character of its dichtomisations.

Remarks: Additional material allowed to recognize bigger size-variability with forewing length 12-16 mm and a complete specimen with venational scheme 5.14.9.12.1.11.
Systematical remarks: Detailed morphology gained with study of *Liadoblattina blakei* (Scudder, 1886) does not reveal any genus-level differences from *Rhipidoblattina karatavica* and thus the later is transformed: closely related *Falcatusi- blatta* possessed more sophisiticated coloration and thus this taxon is also retained (for all other designated species as well as *F. casovec* designated below).

Charater of preservation: 7 complete specimens, 7 isolated forewings.
Taphonomy: Presevation of the type species as well as 2384/151 with head in upright position support prognathous head in this group and predatory habits. Standard partition with the occurrence of completely articulated specimens with antenna and cerci in the collection suggest no pre-depositional transport of this spoecies rare near the deposition area.

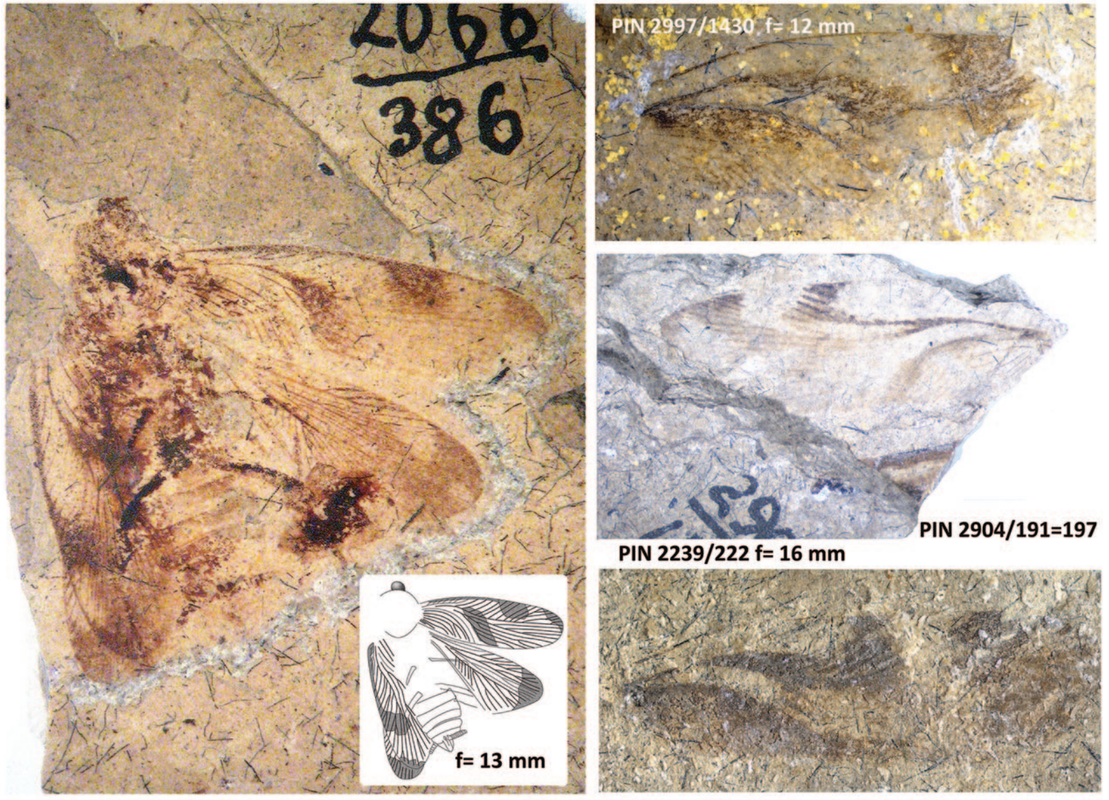
Falcatusiblatta casovec sp.n.

(figp. 146-147)

Holotype: 2784/606. A complete winged adult.
Type locality: Mikhailovka, Karatau, Kazakhstan.
Type horizon: Kimmeridgian Upper Jurassic, Karabastau Formation.

Additional material: PIN 2231/21; 2239/155, 157, 219; 2554/205; 2784/377, 793, 927, 938± (complete specimens); PIN 2039/44, 50±; 2239/202, 205, 259±, 274±; 2384/143; 2784/821; 2997/280, 1383, 4262±, 4370 (forewings); 2066/ 82; 2452/238; 2784/987; 2904/74 (hindwings). The same locality as the type.

Differential diagnosis: It differs from the type species *F. gracilis* Liang, Shih et Ren, 2018 from Daohugou only in coloration of the pronotum (type is without central stripe) and in larger size (F. gracilis fore-



Falcatusiblatta karatavica


PIN 2231/21 f= 14 mm

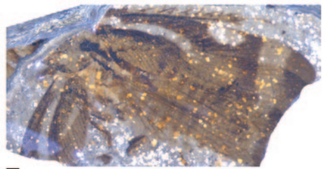

PIN 2239/205 f= 17 mm

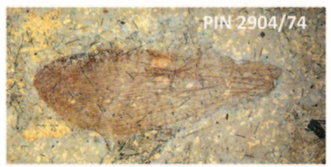

PIN 2784/927

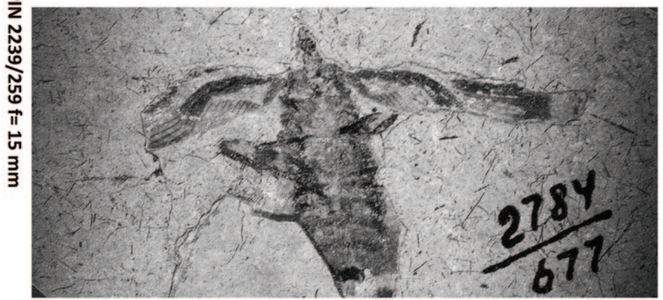

PIN 2239/202 f= 14 mm


PIN 2784/606


PIN 2784/606
PIN 2784/793 f= 16 mm




PIN 2904/74


PIN 2239/259 f= 15 mm
2784
677





wing length is 11-13 mm). Its sister species appears to be *F. qiandaohua* Liang, Shih et Ren, 2018, which seems that it might also have the central pronotal stripe, and is also smaller (forewing length under 13 mm) and more pronounced coloration (transversal pale subapical stripe incomplete). Also, the new species has significantly shorter ovipositor.

Other species in this genus differ in structure of coloration (without posterior fenestrum and without colored costal area). The same holds true for other species of the genus from Karabastau.

Description: Head only slightly elongate (2.4/ 1.8 mm), partially prognathous (preserved in upright position in three of six cases). Antenna rather short (ca. 14 mm), filiform, multisegmented (32 antennomeres in dark parts and additional ones in the white part – impossible to count, but totally about 60 segment), with narrow and short segments, in two areas pale after 10th segment and before the 19th from apex, while rest is dark. Palps very short (only roughly 0.15/ 0.9/ 1.2/ 0.9 mm). It is unclear whether there is any coloration of the head, and eyes seems to be slightly darker than the rest of the head. Thus head was probably largely pale. In contrast, palps and antenna were preserved very dark, which does not seem to be caused solely with the sclerotisation. They were likely very dark.

Pronotum slightly elongated (4.7/ 4 mm), with characteristic coloration presented with complete dark wide lateral and a central stripe (two intermedial stripes of PIN 2784/ 793 half-length are probably an artefact of preservation of legs).

Forewing length 11.7-17 mm, width 4.2-5 mm. Sc short, with 2-6 branches meeting margin. R with indistinctly differentiated RS with few branches (2-6), with 7-17 veins meeting margin. Media mostly with long straight branches (2-10 meet margin); CuA largely expanded (6-13). CuP simple, clavus rather wide covering 2/3 of wing width. Anal veins branched (6-13). Coloration basically dark, most probably pale brown or (less likely) dark yellow, with pale areas forming 1) apical trnaversal stripe, 2) sigmoidal long stripe running from base to center of the wing, 3) longitudinal stripe in clavus and 4) anterior subapical (before the stripe) longitudinal ovoid. Hindwing 14-16 mm with narrow remigium (as in all narrow species), a little (of roughly 1-2 mm – because of more terminal articulation – ending subequally with the forewings in repose) shorter than the forewing. Sc simple, R and RS differentiated (4-8+7-8) , M 2-5, CuA with 8 and up to 11 complete veins (meeting wing margin). Hindwing coloration dak in apical half with even more dark wide area of “pterostigma”, and with transversal pale subapical stripe.

Metanotum developed as extremely wide segment.

Body only slightly widened with 8 or 9 segments 4.3 – 5.7 mm wide. Cerci thin (ca. 0.3 mm) and possibly short (terminal segments unpreserved). Female ovipositor preserved short (only 2 mm), but it perhaps (due to long ovipositor present in sister species) represents only a rudiment of the original size.

Legs very long and thin. Forefemora long (4.3 mm as preserved), narrow, dark, possibly with a pale longitudinal rim, and with short (0.4 mm) terminal spur. Foretibia short and narrow (3.3/ 0.7 mm), sporadically carinated with about 6 short spines (0.4 mm). Foretarsus extremely long and strong (up to 2 times longer than tibia and nearly as wide – 4.2/ 0.5 mm), without arolium (while the type species *F. gracilis* possessed arolium on foreleg of TNP42411). Midfemora thin and short (3.74/ 0.7-1 mm), with longitudinal dark stripe, midtibia subequal to midfemora, with sprase (7) carination. Hindfemora somewhat more robust and longer 4.8/ 1 mm, hindtibia extremely long (ca. 6.7/ 0.5 mm), narrow and carinated, with at 13-23 spurs up to 1 mm long, hidntarsus preserved extremely short.

Remarks: The taxon can be categorized within *Falcatusiblatta* on the basis of forewing shape and characteristic coloration and venational scheme, and also elongated pronotum and partially raptorial legs.

It is remarkable that its sister species occur in Daohugou and not in Karabastau, nevertheless, at the same time it is important to mention that there are other species within the genus mutually more related within Karabastau as well as across other localities.

If we presume origin within the type species complex (*F. gracilis, F. qiandaohua and F. casovec*) from the earlier Daohugou species, then the coloration within this complex tend to descrease. Nevertheless, more probably this effect is caused with the ecosystem stage, or, even more probably, coloration simply tended to be more sophisticated.

More specifically, *F. karatavica* differs in larger forewing length (16-21.5 mm contrasting with-17 mm of *F. casovec*), different forewing and pronotum coloration (two versus five stripes of the present species) and in having significantly longer ovipositor. Other species were introduced below.

Notable is the sound difference in length of extremely long foretarsus (PIN 2784/ 606) and extremely short hindtarus (PIN 2784/927). This is unique, and barely it is a taxonomical character, much more likely it is an ontogenetical error. It needs commenting, because in fossil cockroach which I have studied, developmental errors in tarsi are extremely frequent (ca. 10 % of all specimens), with especially frequent a complete lack of a tarsomere (4-segmented tarsi). 4-segments are evidenced to grow under damaged tarsus in early developmental stages, nevertheless, this discrepancy is so frequent that it might represent a semi-standard morphotype.

Mutations: No deformity was detected on 44 preserved wings (25 specimens).

Variability: The coefficients of variation (tabp. 150) are based on insignifant number of samples (n= 11 instead of 30 required), just for orientation, and with other data can reveal significant results in the future. CV= 14.17 % is a comparative, slightly higher value to other raphidiomimids at the site. This difference might be real, but most probably it (2-3 % difference) might be caused with the small sample size.

Derivation of name: *casovec* is after *čas* (Slavic for time) and *vec* (Slavic for thing).

Character of preservation: 10 complete specimens (1 forewing with a hindwing), 12 isolated forewings, 4 hindwings (1 both hindwings).

Taphonomy: Stardard partition along with the completely articulated specimens with complete antenna suggest no or short pre-depositional transport and abundance in some of the ecosystems.

Specimen	length	width	Sc	R	M	CuA	CuP	A	RM	RCuA	MCuA	total	total without A
2239/259	15		4	7	8	11	1	10	15	18	19	41	31
2239/205	17		4	10	8	12	1	12	18	22	20	47	35
2231/21r	15.8	4.5	4	13	6	7	1	10	19	20	13	41	31
2231/21	16	4.6	4	13	5	7	1	10	18	20	12	40	30
793	16		3	13	5	7	1	11	18	20	12	40	29
793r	16		3	17	2	6	1	10	19	23	8	39	29
59			3	16	5	7	1	7	21	23	12	39	32
927			5	14	9	9	1	11	23	23	18	49	38
927R			5	16	9	10	1	11	25	26	19	52	41
unlabelled	14		6	15	10	13	1	10	25	28	23	55	45
2784/606	11.7		2	16	5	7	1	6	21	23	12	36	30
min	11.7	4.5	2	7	2	6	1	6	15	18	8	36	26
max	17	4.6	6	17	10	13	1	13	25	28	23	55	45
ave	15.19	4.55	3.9	13.64	6.55	8.73	1	9.81	20.18	22.36	15.27	43.55	33.73
dev	1.658259	0.070711	1.136182	2.975659	2.423371	2.412091	0	1.778661	3.156523	2.873072	4.670994	6.17031	5.386853
CV	10.92	1.55	29.13	21.82	37	27.63	0	18.13	15.64	12.85	30.59	14.17	15.97
n	8	2	11	11	11	11	11	11	11	11	11	11	11

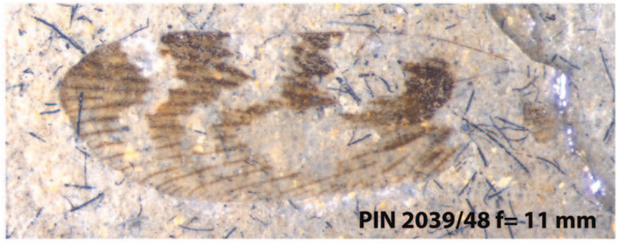
***Falcatusiblatta disrupta* sp.n.**

(figps. 152-154)

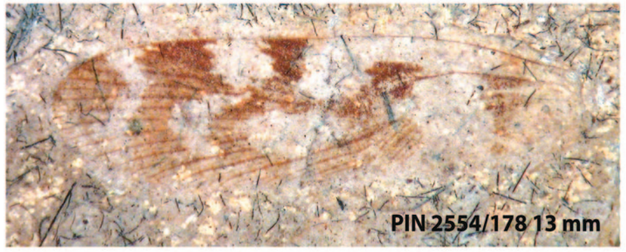
Holotype: PIN 2039/48. A completely articulated forewing.
Type locality: Mikhailovka, Karatau, Kazakhstan.
Type horizon: Kimmeridgian Upper Jurassic, Karabastau Formation.

Additional material: PIN 2239/264; 2335/66; 2554/45; 2997/1143 (complete specimens); 2066/109, 195, 463; 2384/66; 2904/195, 203, 373, 374; 2554/178; 2994/184, 192; 2997/1149±, 1267=1276, 1323, 1385, 1505, 4305 (isolated forewings). The same locality as the type.

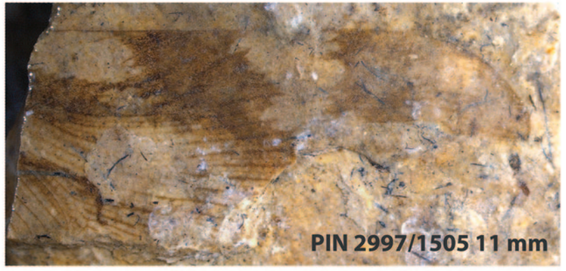
Differential diagnosis: Differs from *F. karatavica* from the same site in having much more sophisticated coloration, with zig-zag pattern. From other species. Species formerly categorized within *Liadoblattina* and *Mesoblattopsis* differ in having much more simple coloration within simple stripes. Species categorized within *Falcatusiblatta* differ in having apical macula instead of two stripes.
Autapomorhies: Robust head, zig-zag coloration.
Description: Moderately large cockroach 14-21 mm long. Head robust (3/ 2.7 mm).Forewing rather wide (11-17.5/ 3.8-5.3 mm), with sharphly cut plain ansd straight anterior margin. Apex is posed anteriorly, margins are parallel up to the final fourth of the length. Coloration sophisticated dark, with partially pale clavus, R base, anterior margin in a first hapf, central posterior pale macula and two anterior zig-zag “waves”. Intercalaries distinct, colored, cross veins in form of dense reticulations present. Costa distinct, SC indistinct, nearly merged with costa, short and probably ocassionaly simple and with up to 4 veins. R slightly sigmoidal, short, comparatively reduced, with 10-16 veins at margin, some of the braches are secondarily dichotomized. Expanded M widely overlapping apex with 7-8 veins at margin. CuA expanded, with 2 main strong stems (8+6 veins at margin). CuP fluent, clavus long, with few dichotomized A.
Mutations: One deformity (PIN 2904/184: M-CuA fusion) observed among 14 comparative wings. PIN 2997/1505 (figp. 152) additionally contains very unusual posteriormost forewing CuA turning backwards, but its interspaces contains standard intercalary and thus this unusuallity is not considered for a deformity (since not disrupting regularity of venation)
Remarks: Very reduced forewing anal system sugest *Liadoblattina* and other raphidiomimids diverged early in the evolution of the family, as advanced *Raphidiomima* has again secondarily branched, reticulated A similar to true mantodeans, while primitive raphidiomimids like all those occurring in Daohugou (*Divocina, Gracilblatta, Fortiblatta*) retained original state represented in Caloblattinidae and Phyloblattidae. Very wide size variability might suggest sexual dimorphism, hidden species or unusual size variability.
Derivation of name: *disrupta* is after disrupt – referring to the sophisticated camouflage
Character of preservation: Four nearly completely articulated specimen (with parts of legs; one just forewing with a hindwing), 18 completely articulated forewings (one broken into two parts; one both forewings).
Taphonomy: Completely articulated forewings along with one nearly complete specimen suggest short or no pre-depositional transport and indicate low to moderate abundance of this species. Broken specimen suggest predator damage at the bottom of the paleolake. Partition of fragments standard.

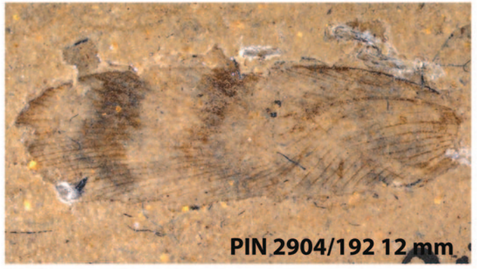

PIN 2039/48 f= 11 mm

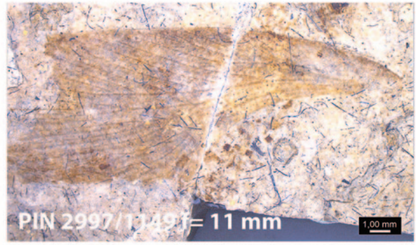

PIN 2904/195 f= 9.5 mm

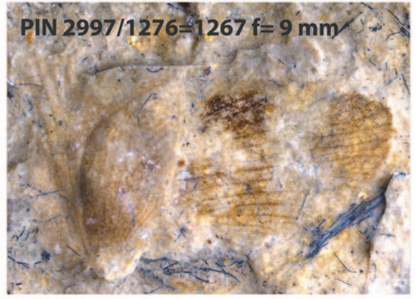

PIN 2554/178 13 mm

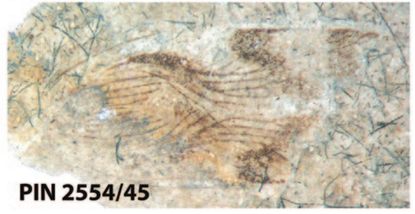

PIN 2904/184 f= 12.3 mm

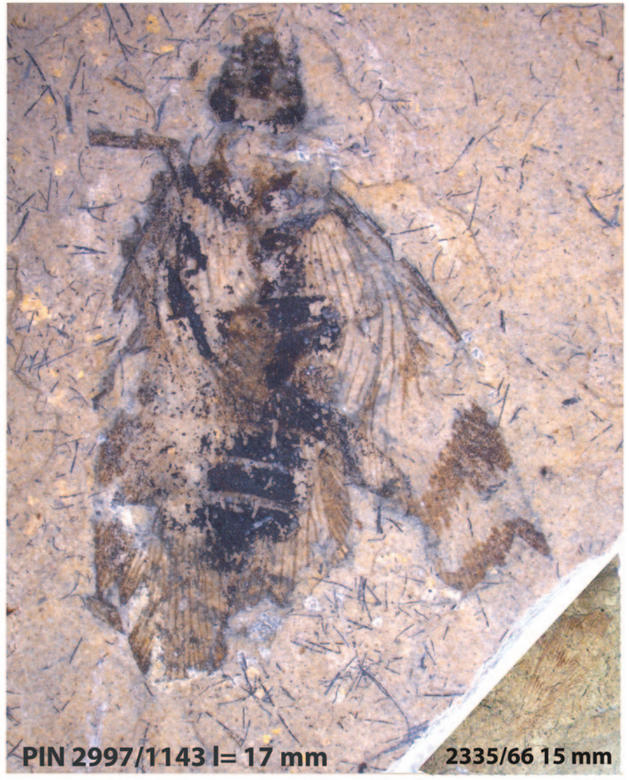

PIN 2997/1505 11 mm

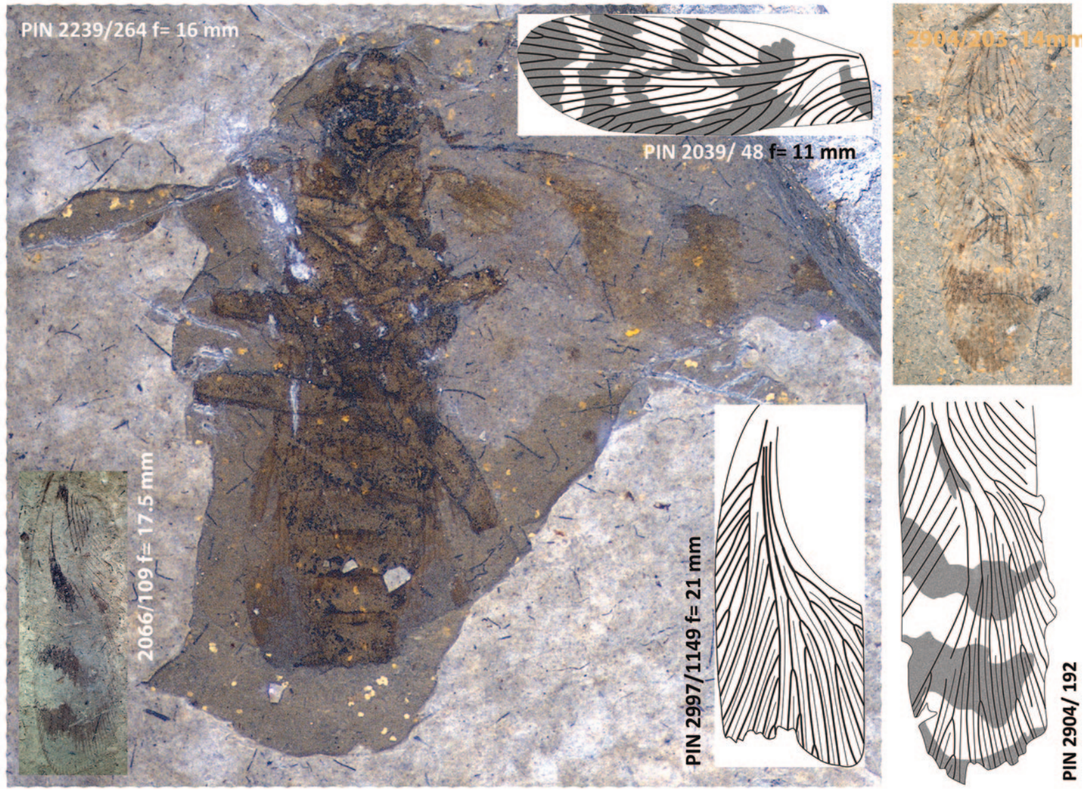

PIN 2904/192 12 mm


PIN 2997/1149 f= 11 mm
1,00 mm


PIN 2997/1276=1267 f= 9 mm


PIN 2554/45


PIN 2997/1143 l= 17 mm
2335/66 15 mm



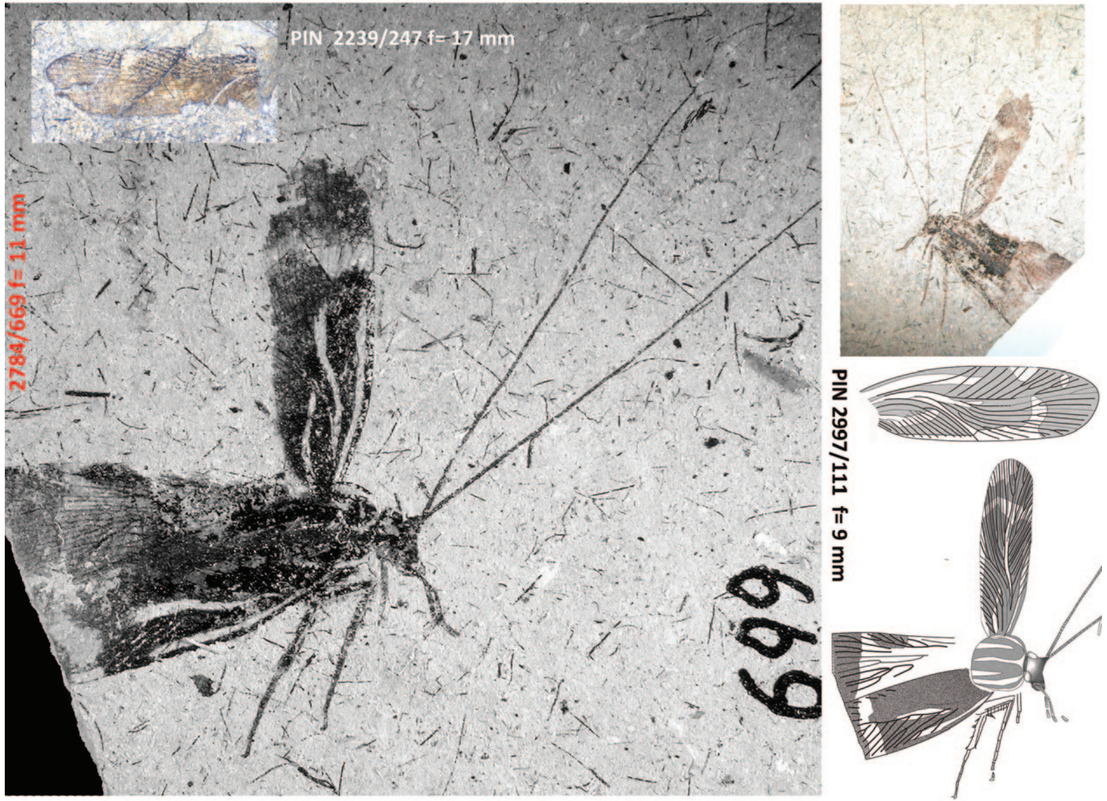
Falcatusiblatta disrupta

***Falcatusiblatta storozhenkoi* sp.n.**
(figps. 156-159)

Holotype: PIN 2784/669. A complete winged adult.
Type locality: Mikhailovka, Karatau, Kazakhstan.
Type horizon: Kimmeridgian Upper Jurassic, Karabastau Formation.

Additional material: PIN 2066/49; 2239/ 349; 2784/802; 2904/32; 2997/1619 (complete specimens); 2039/25±; 2066/ 278, 418; 2239/ 241, 247±; 256, 287, 2554/121, 131; 2784/ 706, 707, 757, 818; 2904/188, 207, 371; 2997/35, 38, 111, 1376, 1377, 4929=4928 (isolated forewings). The same locality as the type.

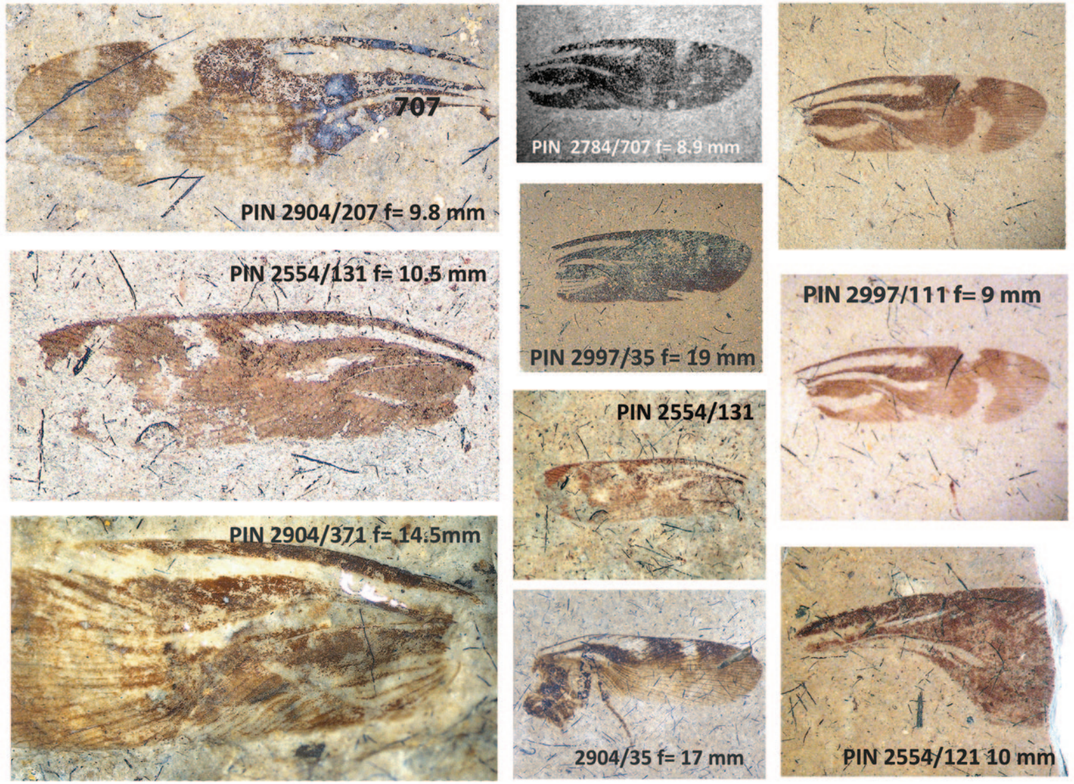
Differential diagnosis: Differs from *F. casovec* from the same site in having much more expressed dark coloration, white longitudinal sigmoidal pale stripes and this also regards the type species and its sister species *F: lata* from Daohugou. Other species at the site, *F. disrupta*, has zig-zag coloration pattern with more transversal stripes. *F. karatavica*, its sister species differ in being significantly paler, i.e., have more pale areas.
Autapomorhies: Possible small size, darker coloration, presence of 3 longitudinal stripes on forewing.
Description: Moderately large cockroach with forewing length 9-19 mm long. Head subprognathous, moderately robust, slightly elongate (2.4/ 1.4 mm), dark, possibly with pale patterns. Antenna extremely long (l= 30 mm), nearly twice as long as the body, multisegmented, with over 150 (NB!) Antennomeres, filiform. Eyes modified due to partial shift to prognathy, large (ca. 0.8/ 0.4 mm), globular, lateral, protruding beyond the head outline, pale.
Pronotum nearly globular (5/ 4.3 mm), with slightly indicated posterior central extension.
Forewing narrow (9-19/ 2.6-6.9 mm), with sharphly cut plain ansd straight anterior margin. Apex is posed anteriorly, margins are usually parallel up to the final fourth of the length. Coloration sophisticated dark, with dark clavus containing a short liongitudinal pale stripe, R base with costal area represented with another longitudinal pale stripe, third, longest stripe runs along the dichotomization of M and CuA from R. Additional two, anterior and bigger, posterior stripes runs transversely, ocassionally fuse together; terminal small macula is also pale. Intercalaries distinct, colored, cross veins also present. Costa distinct, costal area narrow, SC distinct, rather long, sigmoidal, with 2-7 short offshort leading to the margin. R slightly sigmoidal, short, comparatively reduced, with 8-20 veins at margin, some of the braches are secondarily dichotomized. Expanded M widely overlapping apex with 5-16 veins at margin. CuA expanded, with 2 main strong stems (3-16 veins at margin). CuP fluent, clavus long, with 6-14 dichotomized A.
Hindwing (on the basis of PIN 2904/ 32) 9 mm long, with simpleSC, R1 and RS differentiated (5+5), Media moderate, nearly straight, with 5 veins meeting margin. CuA expanded, with 7 veins at margin, CuP simple.
Body narrow, nearly equally wide at the whole length, 5.8 mm wide. Cerci multisegmented, very long (longer than body width).
Legs slender, cursorial, only moderately or weakly carinated with short sporadic spurs, and terminated with symmetrical claw without arolium. Forelegs possibly raptorial, black, posterior area pale; forefemur short (2/0.3 mm) and with short (0.15 mm) and strong curved posterior spines along the ridge (spurs are preserved only in anterior margin); foretibia very short (1.7/0.3 mm), possibly without carination; foretarsus extremely long (27 mm). Mid legs fully developed, with long tibia terminated with a bulk of terminal spurs; midtarsus extremely long (29 mm). Hindfemur (3/0.68 mm) with terminal femoral spur 0.7mm long; hindtibia 6.15 mm long, moderately carinated.
Mutations: Among 36 preserved wings (28 specimens), a single deformity was recognized in PIN 2904/35 – namely a very unusual lentiform widening of the forewing R vein (see figp. 525; known only in a Cenozoic caddis-fly from Slovakia – see Sukatcheva et al. (2006)).

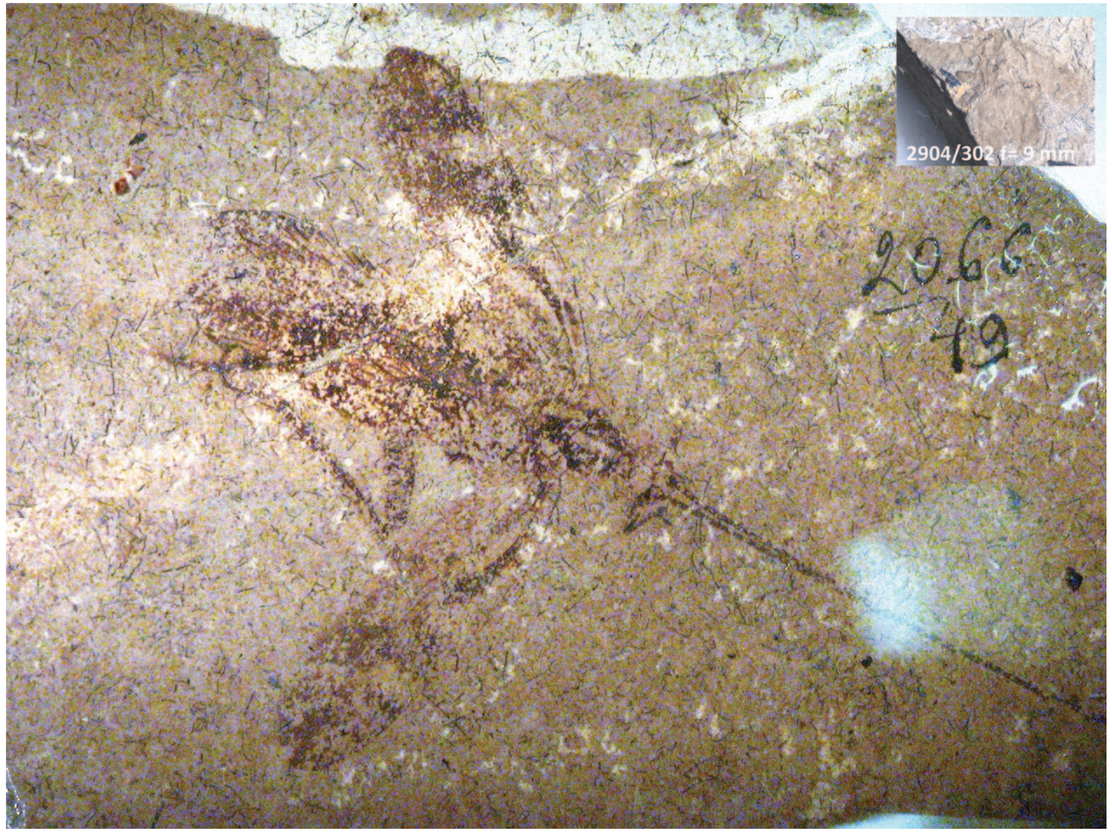

PIN 2239/247 f= 17 mm
2784/669 f= 11 mm
669

PIN 2997/111 f= 9 mm




PIN 2784/802


707
PIN 2904/207 f= 9.8 mm
PIN 2784/707 f= 8.9 mm
PIN 2554/131 f= 10.5 mm
PIN 2997/35 f= 19 mm
PIN 2997/111 f= 9 mm
PIN 2554/131
PIN 2904/371 f= 14.5mm
2904/35 f= 17 mm
PIN 2554/121 10 mm


2904/302 f= 9 mm
2966
19

Remarks: Specimens are categorized within this species on the basis of identical coloration.

Variability: was performed on insignificant sample size (n= 17, while 30 is required), so the data are not mathematically robust. Nevertheless, the result displayed a very high congruence with *F. casovec* (see above CV= 14.17 % for total number of veins compared with 14.98 of the present species), which suggest data close to actual value. Also data in respective veinal systems are comparative, so perhaps a difference not bigger than 1-2 % should be expected.

Derivation of name: after my early teacher and friend Sergej Storoženko. No comment.

Character of preservation: Six completely articulated specimens, 20 completely articulated forewings, 2 without clavus.

Taphonomy: Completely articulated specimens and except 2 specimens, all completely articulated forewings suggest short or no pre-depositional transport and indicate moderate abundance of this species. Two disarticulated clavi suggest transport. All things being the same, the species perhaps occupied habitats close to the deposition waterbody as well as more remote areas up streams. Partition of fragments standard, but the absence of hindwings seams real as hindwings are colored (see complte specimens) and should be recogniseable (absent in *incertae sedis* material).

Specimen	length	width	Sc	R	M	CuA	CuP	A	RM	RCuA	MCuA	total	total without A
2904/32	9		2	14	6	9	1	7	20	23	15	39	32
2997/ 4929=4928	8,5		4	8	7	7	1	11	15	15	14	27	38
2239/247	17		4	17	5	13	1	12	22	30	18	40	52
2784/707	9.8		3	10	6	9	1	9	16	19	15	29	38
2904/371	14.5		5	15	7	11	1	12	22	26	18	39	41
2066/49 L	DOPLNIT		5	15	8	11	1	9	23	26	19	40	49
2066/49 R			4	12	8	11	1	6	20	23	19	36	42
2784/757	10	5+8+	4	12	6	9	1	7	18	21	15	32	39
2554/131A	10.5		3	17	6	9	1	10	23	26	15	36	46
2554/131B			7	12	8	11	1	8	20	23	19	39	47
2784/ 669L			5	11	12	3	1	11	23	14	15	32	43
2997/111	9		5	15	7	13	1	14	22	28	20	41	55
2904/207	9.8		4	11	16	16	1		27	27	32	48	
2784/802 R			6	15	10	11	1	10	25	26	21	43	54
2784/ 802L			5	10	12	13	1	8	22	23	25	41	49
2997/35	19		5	16	9	10	1	10	25	26	19	41	51
2904/35	17	*fusion R-R lens	3	20	5	8	1	9	25	28	13	47	56
min	11.7	4.5	2	7	2	6	1	6	15	18	8	36	26
max	17	4.6	6	17	10	13	1	13	25	28	23	55	45
ave	15.19	4.55	3.9	13.64	6.55	8.73	1	9.81	20.18	22.36	15.27	43.55	33.73
dev	1.658259	0.070711	1.136182	2.975659	2.423371	2.412091	0	1.778661	3.156523	2.873072	4.670994	6.17031	5.386853
CV	10.92	1.55	29.13	21.82	37	27.63	0	18.13	15.64	12.85	30.59	14.17	15.97
n	8	2	11	11	11	11	11	11	11	11	11	11	11
CV	30.96		28.1	23.1	36.14	28.16	0	22.26	14.87	18.68	25.34	14.98	15.42

***Falcatussiblatta zaloha* sp.n.**
(figp. 163)

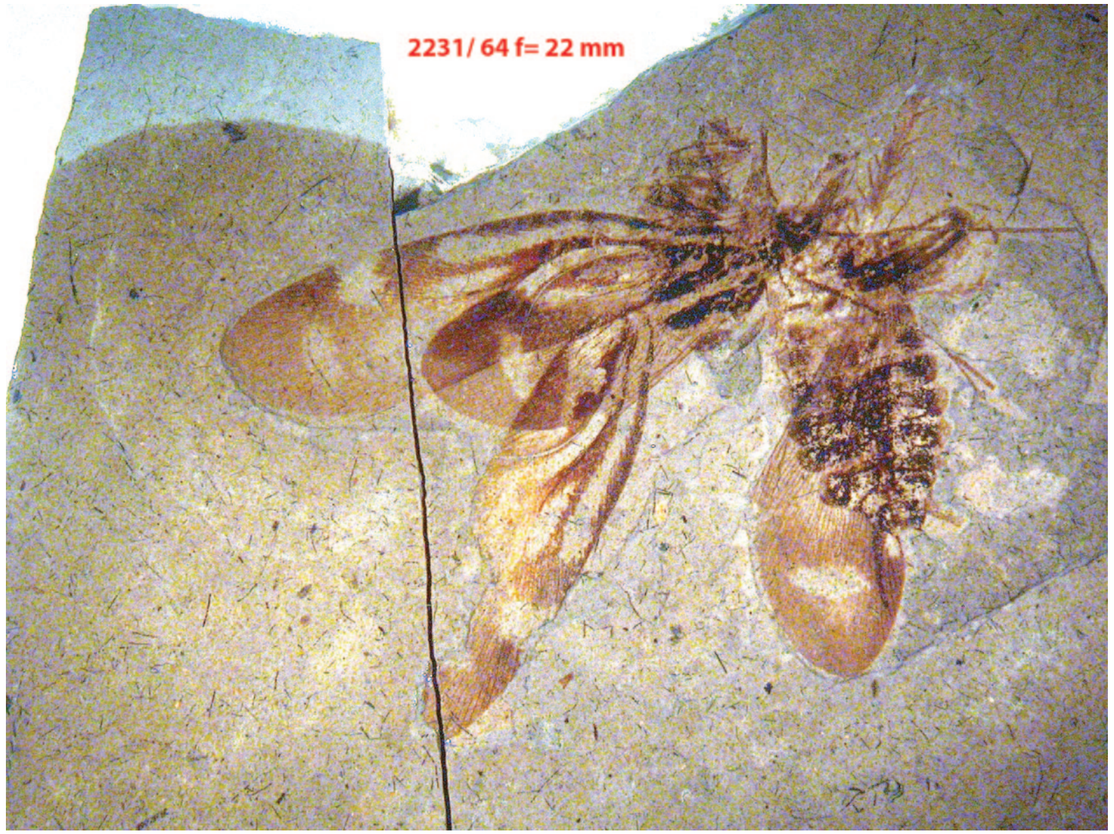
Holotype: PIN 2231/64. A complete winged adult male.
Type locality: Mikhailovka, Karatau, Kazakhstan.
Type horizon: Kimmeridgian Upper Jurassic, Karabastau Formation.

Differential diagnosis: Differs from other species in very large size and coloration details.
Autapomorhies: possible large size, sophisticated coloration of pronotum with symmetrical "eyes", presence of 4 longitudinal and 3 vertical stripes on forewing.
Description: Large cockroach with forewing length 22 mm. Head subprognathous, moderately robust, dark, possibly with pale patterns. Antenna probably extremely long (l= 11.7 mm preserved fragment), multisegmented, filiform.
Pronotum nearly globular (5.4/ 7.3 mm), with slightly indicated posterior central extension. Coloration sophisticated, with dark anterolateral stripes, central sophistically shaped stripes and small posterolateral maculae.
Forewing differently narrow (L-R 22-22/ 6-7 mm), with sharphly cut plain ansd straight anterior margin. Apex is posed anteriorly, margins are usually parallel up to the final fourth of the length. Coloration sophisticated dark, with dark clavus containing a short longitudinal pale stripe, R base with costal area represented with another longitudinal pale stripe. Additional two, anterior and bigger, central stripes runs transversely. Intercalaries distinct, colored, cross veins also present. Costa indistinct, costal area narrow, SC distinct, very short, sigmoidal, with 2 short offshorts leading to the margin. R slightly sigmoidal, long, with 17 veins at margin, most of branches were simple. Expanded M widely overlapping apex with 12-14 veins at margin. CuA expanded, with 2 main strong stems (3-6 veins at margin). CuP fluent, clavus long, with 8 dichotomized A.
Hindwing 20.8 mm long, with simple long straight SC, R1 and RS differentiated (8+8), Media moderate, nearly straight, with 5 veins meeting margin. CuA expanded, with 9 veins at margin. Coloration dark, with central transverse large pale macula and central anterior small macula
Body narrow, nearly equally wide at the whole length, 7.8 mm wide. Cerci multisegmented, very long, stylo long and narrow.
Remarks: This taxon is extremely similar to *Rhipidoblatta triky* and might represent the transitional taxon among these two genera.
Mutations: The specimen possessed numerous deformities. Possible (M-M) deformity occurred in the forewing. Another forewing possessed two blind branches of A in clavus and also a A-A lentiform fusion. Deformed was also the hindwing (CuA-CuA lentiform fusion).
Derivation of name: *záloha* is Slavic for backing.
Character of preservation: One completely articulated specimen with body and a hindwing shifted in sediment.
Taphonomy: Completely articulated specimen suggest short or no pre-depositional transport. Shifted parts of the specimen might suggest a bottom currents.

***Falcatussiblatta tooold* sp.n.** (figp. 165)

Holotype: PIN 2904/306. A complete specimen.
Type locality: Mikhailovka, Karatau, Kazakhstan.
Type horizon: Kimmeridgian Upper Jurassic, Karabastau Formation.

Differential diagnosis: Differs from other species in extremely large size and coloration details.
Autapomorhies: Very large size (over 25 mm).
Description: Large cockroach with forewing length 25 mm. Pronotum dark, with three longitudinal pale stripes, the central one does not reach the posterior margin. Forewing narrow (24.5/ 6.3 mm). Coloration sophisticated dark, with dark veins distinct on the pale area delimited by A1 and diagonal kink. Another pale stripe follows the clavus margin. Third stripe sis a narrow sigmoidal following the R stem and turning up near wing halve. Central



Falcatussiblatta zaloha





PIN 2231/ 64 f= 22 mm

Falcatussiblatta zaloha



L= 25 mm

Falcatussiblatta tooold

small pale area is present in the central area neat the anterior margin.
Derivation of name: *too old* is from English.
Character of preservation: One completely articulated specimen.
Taphonomy: Completely articulated specimen suggest short or no pre-depositional transport.

Genus *Cameloblatta* Vishniakova, 1973

Type species, formalized by monotypy**:** *Cameloblatta variegata* Vishniakova, 1973

Stratigraphic range: Upper Jurassic – Upper Cretaceous
Geographic range: Laurasian (and burmite)

Diagnosis (after Vishniakova 1973): Head basally widely rounded, eyes lateral, palp shorter that head. Anterior branch of forewing M dichotomized at the same level as M2. CuA1 more weakly branched than CuA2. Length/width ratio largetr than 3.5. Forefemora basally widened with frequent posterior short spurs.

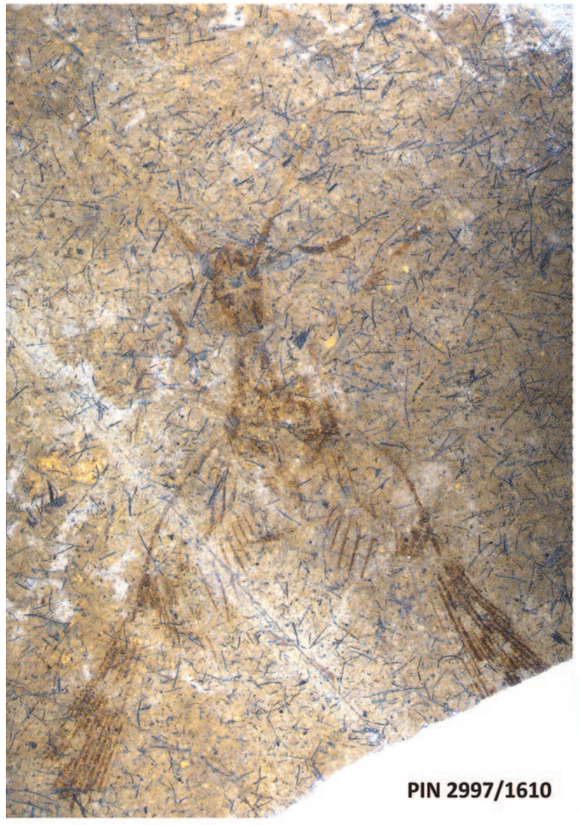
Cameloblatta variegata Vishniakova, 1973

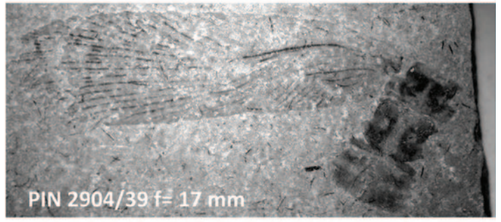
(figps. 167-168)

Holotype: PIN 2554/34 designated by Vishniakova (1973). A complete winged adult.

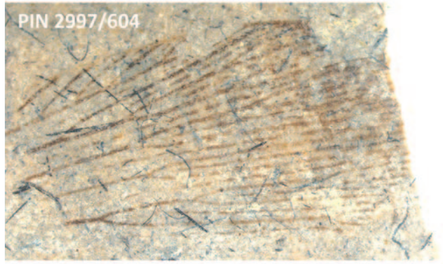
Additional material designated here on the basis of identical coloration**:** PIN 2066/307=308; 2554/34, 639; 2784/625, 634, 635, 639, 663; 2997/173, 1610, 1616 (complete specimens); 167/312; 2066/271±, 173, 181, 390±, 2066/391=387, 142; 2554/39, 40; 2784/ 644; 2904/39±, 224; 342, 2997/29± (forewings); 167/222; 2066/61, 68, 191, 484, 502, 503; 2384/63; 2554/165, 184, 198, 682; 2997/1604, 1561 (hindwings). The same locality as the type.

Remarks: The size variability revealed by a comparative material is significant, which is very unusual for the Mesozoic cockroaches, while common in directly unrelated predatory mantodeans.
Forewing can vary 12-18/ 3.5 mm (similarly variable is also *Aktassoblatta pullata* from the family Liberiblattinidae, also predatory). All 3 hindwings are on the bottom size variability (12-13 mm), which seems to resulted from taphonomical preference of preservation of smaller hindwings, which are comparatively more rigid. It might also explain rarity of preserved hindwings of this (and other large) species. SC might have 2-5 branches; R is extremely variable with 11-21 veins at margin; M is surprisingly conservative with 3 specimens bearing 11 veins at margin and one specimen 9, one 10, one 5, one 6; CuA 5-11; CuP simple; A is also very stabilized with dichotomized branches and 10-12 veins at margin.
Hindwing SC simple, but can have up to 7 short branches; R1 field narrow, with 3-7 veins meeting margin; RS 5-8; M 4.
Coloration of both wings seems to show little variability confined to details, which is surprising taking into consideration diffuse character of this kind of camouflage.
Important new trait preserved is a raptorial preadaptation of the forewing femur with double row, although without strong spurs, but with small spines. The completely raptorial foreleg was already recently documented in a raphidiomimid from Daohugou (Liang et al. 2021). The same genus *Chuanblatta* from Karatau is also with fully predatory foreleg.
Deformities: specimen 2784/634 posses a deformity, fusion of two respective CuA-CuA veins.
Character of preservation: 12 complete specimens, 14 isolated forewings, 14 isolated hindwings (of them 2 with articulated parts of body).
Taphonomy: Partition of complete specimens is unusually high, suggesting deposition close to the source area, without pre-depositional transport.

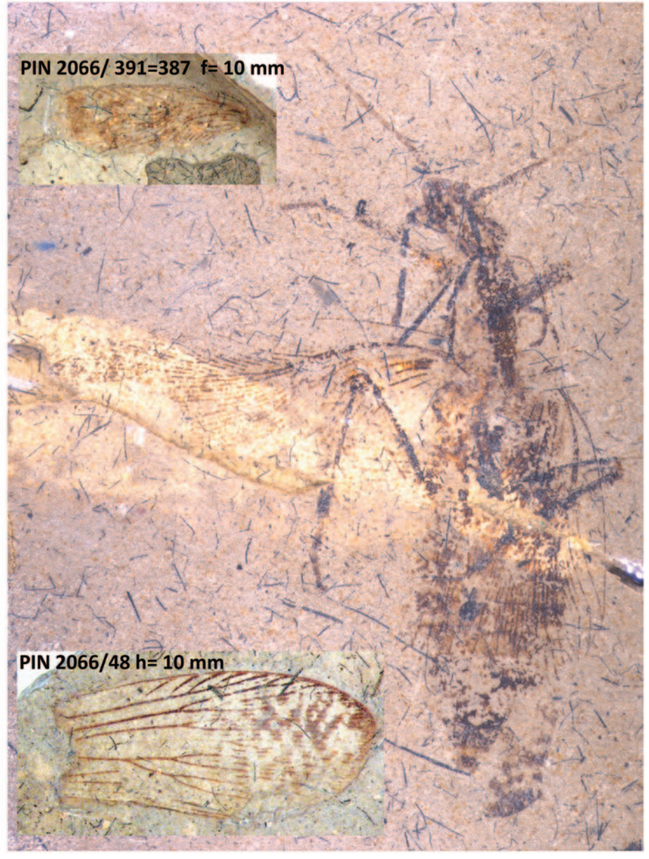


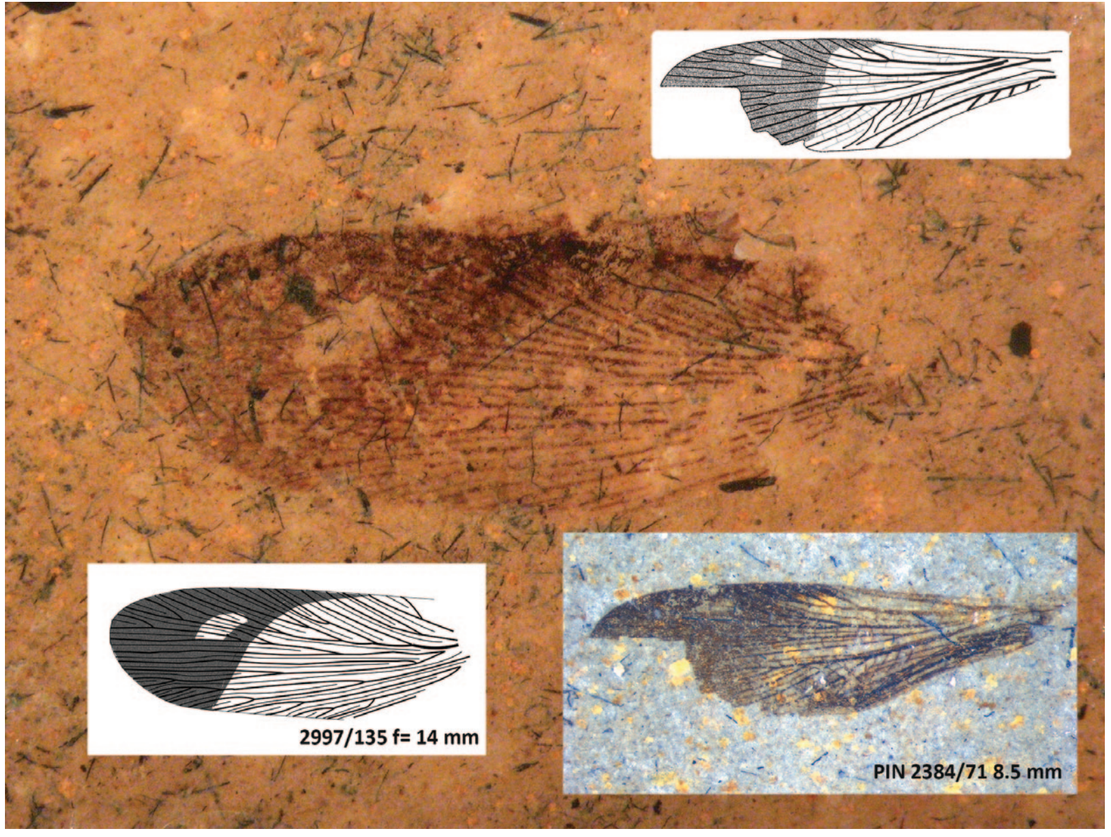





PIN 2997/604


PIN 2239/173 b= 18 mm


PIN 2066/ 391=387 f= 10 mm
PIN 2066/48 h= 10 mm


2997/135 f= 14 mm
PIN 2384/71 8.5 mm

Cameloblatta stress sp.n.
(figp. 169)

Holotype: PIN 2997/135. A damaged forewing.
Type locality: Mikhailovka, Karatau, Kazakhstan.
Type horizon: Kimmeridgian Upper Jurassic, Karabastau Formation.

Additional material: PIN 2384/71=70 (l= 8.5 mm). A damaged hindwing. The same locality as the type.

Differential diagnosis: Differs from the type species in more extensive and fluent coloration with subapical aposematic dot.
Description: Forewing elongated, preserved fragment 14 mm long and ca. 4.7 mm wide. Veins, intercalaries and cross-veins (both also in HW) are very thick. SC branched, straight, with terminal dichotomization (basal part unpreserved). R shortened, with only 9 mostly simple branches, not reaching apex. M normally developed and overlapping aper, with 9 veins at margin. CuA with 10-11 sigmoidal (secondarily sigmoidal) veins at margin.
Hindwing with simple SC, R1 (4) and RS (10) differentiated, M expanded with 5 or more branches. CuA with 6 or more branches (apila part unpreserved) and 4 blind offshoots, CuP simple. A1 with 5 blind ofshots.
Coloration of the membrane is locally in small spots (impossible to specify due to preservation, but distinctly they are present similarly as in the type species) entirely missing, coloration of the rest of the membrane probably pale brown or pale yellow, possibly pale grey. Apically the membrane is very dark, possibly entirely black, but more probably (as locally veins are darker) dark brown. In this area, transparent or white spot is present.
Remarks: Elongated forewing with extremely long and nearly totally straight CuA, and wide soft dark colored intercalaries allow categorization within the genus *Cameloblatta*. There are few characters preserved disallowing the phylogenetic signal in them, but the conspicuous dot is not present in any representative of the family and is rather characteristic for Liberiblattinidae (which lack straight veins). Additionally, veins are specifically modified (some are locally sigmoidal) – a character known only in Raphidiomimidae and also homoplasically in modern (not in Cretaceous) Mantodea.
Derivation of name: *stress* alludes to stress this predator caused with its eye-like spot on the forewing.
Character of preservation: A single damaged forewing and a single preserved hindwing.
Taphonomy: It is difficult to conclude whether the forewing was completely articulated with clavus or not as it is damaged. The cause of damage could be taphonomical but also predation cannot be excluded. Also the hindwing was damaged.

Genus *Rhipidoblattina* Handlirsch, 1906

Type species: *Mesoblattina geikiei* Scudder, 1886, p. 454.

Compostion: *R. bakharensis* Vršanský, 2020, Bakhar, Mongolia, Middle-Late Jurassic; *R. beipiaoensis* (Hong, 1983), Haifanggou, Liaoning Province, China, the middle Jurassic; *R. boya* Martin, 2010, Mintaja, Australia, lower Jurassic; *R. bucklandi* Handlirsh, 1906–1908, England, UK, J/K; *R. chichengensis* Hong, New Assemblages of the Bakhar Locality 45 1997, Chicheng Country, China; *R. decoris* Lin, 1978; *R. emacerata* Zhang, 1986, Hebei Province, China, Jurassic; *R. forticrusa* Lin, 1986, South China; *R. fuxinensis* Lin, 1978, Liaoning Province, China, Lower Cretaceous; *R. geikiei* Handlirsch, 1906–1908, Browns Wood, England, UK, the Lower Jurassic; *R. gurvaniensis* Vishniakova, 1986, Mongolia, Lower Cretaceous; *R. hebeiensis* Hong, 1980, Hebei Province, China, the Middle Jurassic; *R. jilinensis* Lin, 1994, Jiutai, Jilin Province, China, Lower Cretaceous; *R. kisylkiensis* Martynova, 1951, Kyzyl-Kiya, Russia, Lower Jurassic; *R. konserva* Vršanský, 2020, Bakhar, Mongolia, Middle-Late Jurassic; *R. lanceolata* Hong, 1980, Chengde, China, Middle Jurassic; *R. laternoforma* Lin, 1978, Chaomidianzi, Liaoning Province, China, Lower Cretaceous; *R. liaoningensis* Hong, 1980, Chaoyang, Liaoning Province, China, Lower Jurassic; *R. liugouensis* Hong, 1983, Xiaofanzhangzi, Hebei Province, China, Middle Jurassic; *?Rhipidoblattina lonchopteris* Hong, 1980; R. longa Hong, 1980, Chengde Basin, China, Middle Jurassic; R. *maculata* Vishniakova, 1968, Karatau Mikhailovka, Kazachstan, Upper Jurassic; *R. radipinguis* Lin, 1986; Jiuquan Basin, Gansu Province, China, Mesozoic; *R. sisnerahkab* Vršanský, 2020, Bakhar, Mongolia, Middle-Late Jurassic; *R. tenuis* Hong, 1983, the Middle Jurassic; *R. tulunensis* (Vishniakova, 1983), Vladimirovka village, Irkutsk Region, Russia, Lower Jurassic; *R. yanqingensis* Hong, 1997, China, Upper Jurassic; *R. lacunata* Barna, 2014. Chernovskie Kopi, Transbaikalian Russia, J/K (Characters of *R. spathulata* Hong, 1982, suggest it belongs to Raphidiomimidae.)

Stratigraphic range: Lower Jurassic—Upper Cretaceous.
Geographic range: Cosmopolitan.

Original diagnosis (after Handlirsch 1906–1908): Well-developed intercalaries and distinct cross-veins; M and Cu branches oriented to the apical outer margin of wing is also characteristic feature for Lithoblattina, *Malmoblattina* and *Elisama.* Body of moderate size; forewings weakly sclerotised, exceeding the length of abdomen. Forewing anterior margin straight or weakly convex, posterior margin straight, apex weakly narrowed, placed approximately symmetrical along the longitudinal axis of forewing; length to width ratio of forewing 3.3–3.9: 1; SC ending at the level of A area, weakly dichotoming; R weakly curved, almost reaching forewing apex, occupying nearly 1/2 of its width; M richly dichotoming distally from CuA, with comb-like distributed branches directed to the outer margin; CuA reaching apex of posterior margin, branched into two stems; CuP evenly arcuate; A area high, elongated, with its length to width ratio 2.5: 1, A1 simple, A2 richly branched, majority of its branches distally dichotomising (modified after Vishniakova 1968).

Rhipidoblattina maculata Vishniakova, 1968
(figp. 172)

Type material: Holotype PIN 2239/355. A complete specimen. Designated by Vishniakova (1968).

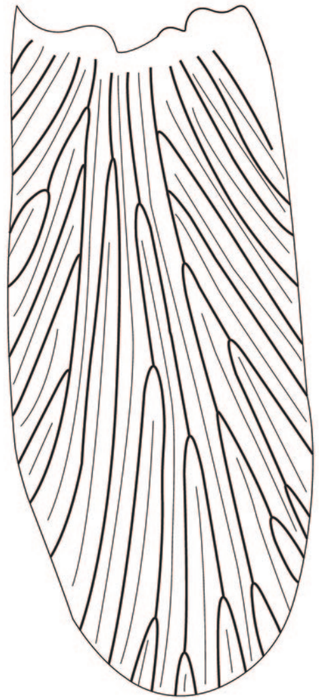
Additional material designated here: PIN2997/1585=1583 (f= 10 mm). A partially preserved forewing. 2997/269. A forewing. The same locality as the type.

Additional description (based on new forewings): Forewing 10-12 mm long, with complete maculate coloration. Venation regular, intercalaries and cross-veins present, radial area wide, M overlapping apex, with ca. 7 postariorly curved veins at margin, branches secondarily dichotomized. CuA posteriorly curved with at least 11 veins at margin.
Remarks: It seems the species reflects a bark niche (common in ambers rare in sedimentary record).
Character of preservation: 1 complete adult winged female, 2 complete isolated forewings.
Taphonomy: Two isolated forewings might reflect stochastic preservation or a slightly longer transport, but not especially long due to articulation of clavus. This is supported by a complete adult winged female.

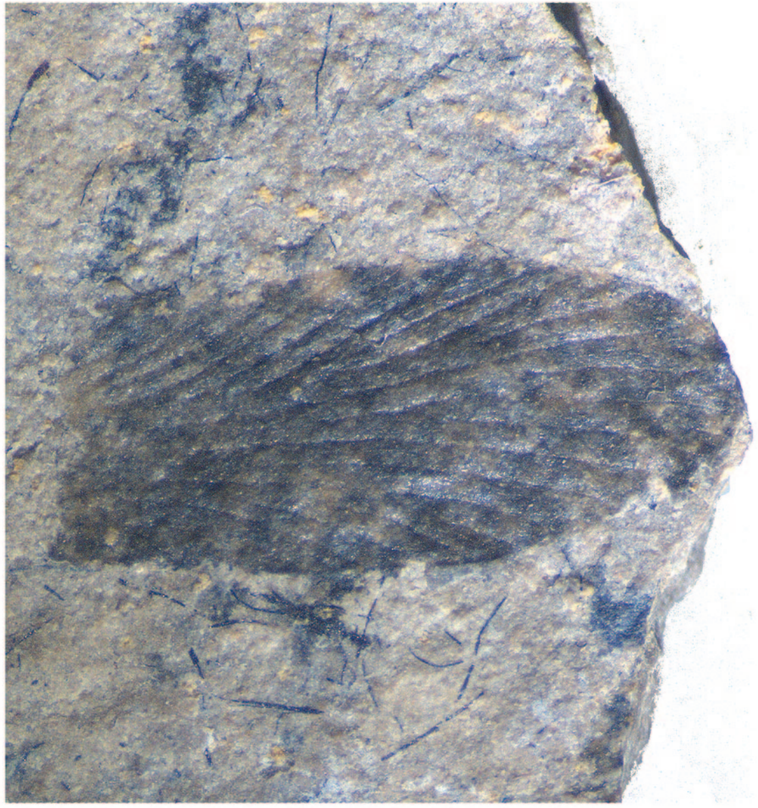
Rhipidoblattina dmitrievi sp.n.
(figps. 173-174)

Holotype: PIN 965/73± **G (GALKINO)**(f= 35 mm). A complete winged adult male.
Type locality: Galkino, Karatau, Kazakhstan.
Type horizon: Kimmeridgian Upper Jurassic, Karabastau Formation.

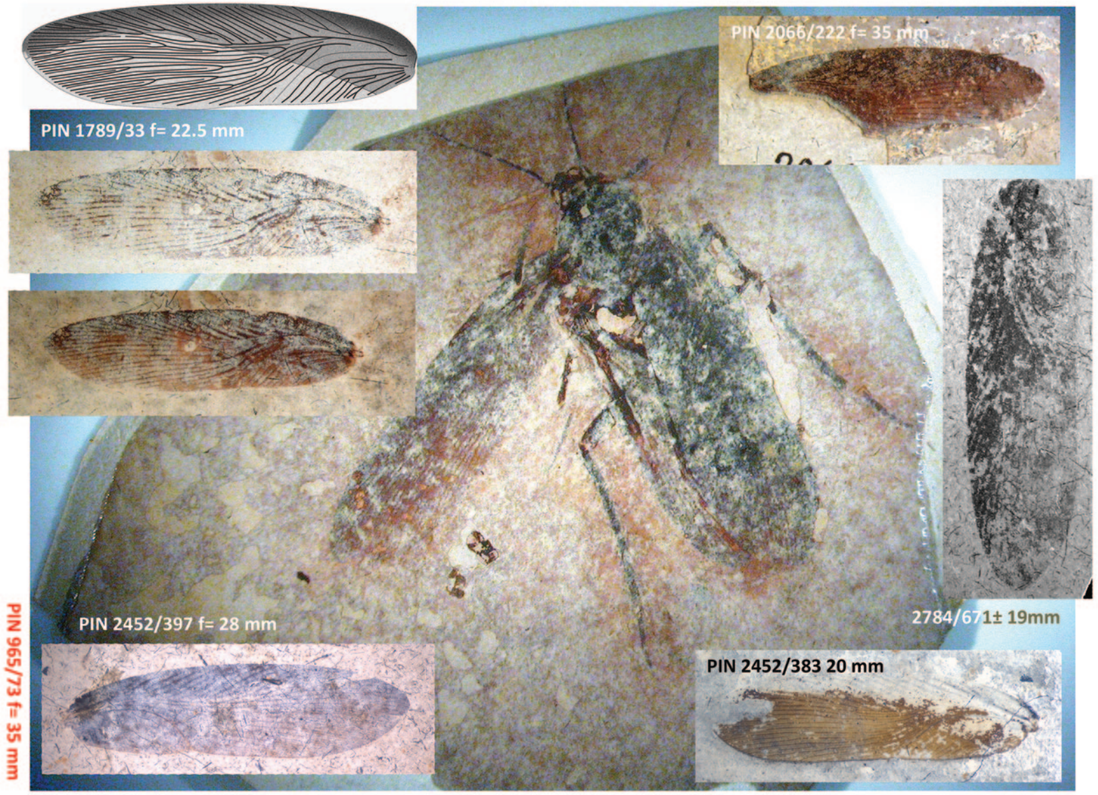
Additional material: PIN 1789/19 (complete male) **G**; 33 (f= 22.5/ 5.8mm; 3.19.6.8.1.13) **G**, 81c **G**; 2066/54, 222 (f= 25 mm), 289±, 334, 336; 2384/89 (f= 28.5 mm; 3.18.13.14.1.12); 2335/41; 2452/381±, 383 (f= 20 mm; 4.13.7.13.1.13), 387, 397 **G**; 2465/972 (labelled as 972/2465); 2784/626, 671± (f= 19 mm; 4.17.7.12.1.10), 755; 2904/17, 42; 2997/4302 (forewings). All except G= Galkino from Mikhailovka.



PIN 2997/1585=1583 f= 10.5 mm



Rhipidoblattina maculata



Rhipidoblattina dmitrievi





Differential diagnosis: Differs from its sister species *R. konserva* from Bakhar only in degree of membrane coloration (the present species has darker membrane, *R. konserva* possibly entirely pale), otherwise these taxa are indiscernible. Other species in this complex are either diversely colored or that much elongate. All other species are significantly smaller.
Autapomorphy: Extremely large species, one of the largest Mesozoic cockroaches.
Description: Extremely large species with overall length ocassionally overlapping 40 mm. Head hypognathous, but elongate (ca. 3.8-6/ 2.3-3.1 mm), monochromatically dark, with pale eyes 1.3/ 0.7 mm and possibly with a short narrow central pale occipital stripe. Antenna thin (2 mm at base), multisegmented, filiform, probably long (50 antennomeres preserved amounting to 5 mm length – a tiny fraction of the overal length). Scape and pedicel robust (6/ 4; 2/ 2 mm), other basal antennomeres only 0.6 mm long.
Pronotum slightly elongate, 6.3 mm long, probably homogenous dark. Body narrow, cerci strong.
Forewing seriously elongate 22-36/ 5.2-10 mm, margins parallel, apex posed anteriorly, in the first third of the width, ascending of posterior wing margin toward apex starts in apical fourth. Sc straight, with 3-4 veins at margin. R is sigmoidal, looks nearly straight due to whole forewing elongation, short, with 13-19 veins meeting margin and not overlapping apex. M weakly expanded, with 6-13 veins; CuA with 8- 14 nearly straight veins, CuP simple. Clavus 9.5/ 3.6 mm with 12-20 anal veins at margin.
Hindwing shorter (f= 35 mm = h= 30 mm) than forewing, completely covered by forewings during repose, monochromatically dark, with darker area of diffuse pterostigma. Sc short, simple, R1 and RS differentiated, other veins greatly reduced due to narrow (9.3 mm) vannus.
Legs extremely elongate. Forelegs preserved in “raptorial” position. Forefemur narrow (3.6/0.7 mm), with terminal apical spur. Forebia 3.4/ 0.4 mm, with at least 11 strong 0.7 mm long (short) spurs, foretarsus very long, up to 4.5 mm (as long as foretibia). Midfemur very strong (10.4/ 3.5 mm), midtibia subequal to the hindtibia (ca. 16.7/ 0.8 mm). Hindfemur narrow (11.7/ 2 mm), hindtibia extremely long (16.7/ 0.8 mm).
Remarks: General unspecialisaed venational scheme with extremely elongate forewings suggest placement within *Rhipidoblattina*. From most species within the genus it differs in being monochromatically dark-colored. At the same time, round pronotum reveal some congruence with Aktassoblata of the Liberiblattinidae, making derivation of this family also possible via *Rhipidoblattina* (although derivation from *Voltziablatta*-group and Phyloblattidae appears more probable).
Extremely long legs of the basal Raphidiomimidae suggest pursuit predation.
Character of preservation: 2 complete adult winged males, 18 complete isolated forewings, 1 with disarticulated clavus, 1 isolated disarticulated clavus.
Derivation of name: After Vladimir Jurievič Dmitriev, analytician in the PIN, for his kind interactions.
Taphonomy: Two complete specimens suggest short or no pre-depositional transport, supported with completely articulated forewings. In this case it is of special consideration, since wings are very large nd fragile, thus the disarticulation (would) last shorter period of time. One isolated clavus and one disarticulated clavus might support this.
Taphonomical remark: This species mostly occur in a completely diffent, more homogenous sediment of more pale (nearly white) color. This is also reflected by different collection numbers (965/ and 2452/ and 2465/) suggesting this collection represent another assemblage. At the same time, standard collection numbers are also represented (see “Additional material”).

Genus *Divocina* Liang, Vršanský et Ren, 2012

Type species *D. noci* Liang, Vršanský et Ren, 2012 from Daohugou, China, and by monotypy.

Diagnosis (after Liang et al. 2012): Differing from *Liadoblattina*, *Rhipidoblattina* Vishniakova, 1973 and *Cameloblatta* Vishniakova, 1973 in having semiglobular head, facets large, terga sharply cut, and all wings monochromatically colored to a great extent.

Stratigraphic range: Middle-Late Jurassic (LOD)
Geographic range: Laurasia s.s. (i.e., without burmite and southern plate blocks)

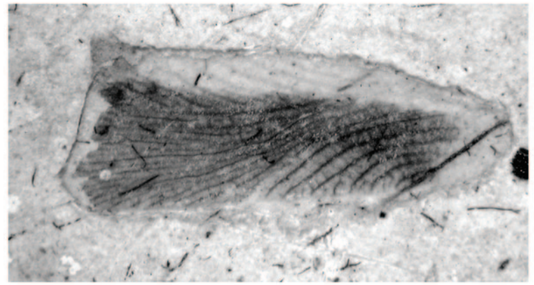
Divocina polnoci sp.n.

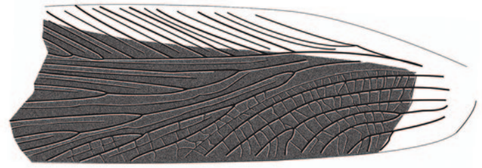
(figp. 177)

Holotype: PIN 2784/957=723. A winged adult with disarticulated body.
Type locality. Mikhailovka, Karatau, Kazakhstan.
Type horizon. Kimmeridgian Upper Jurassic, Karabastau Formation.

Additional material**:** PIN 2997/4240 14 mm (complete specimen); 2904/240; 2997/52; 2384/73 (f= 14 mm; 7.13.9.12.1.11), 139± (f= 15 mm; 3.10.13.9.1.8). The same locality as the type.

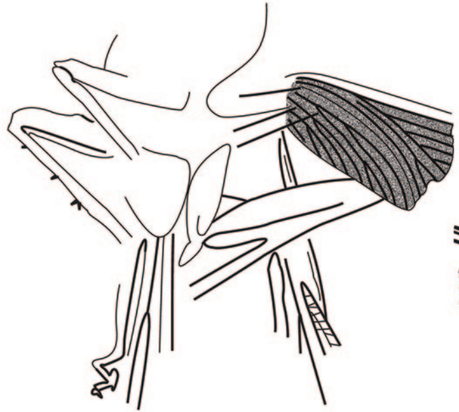
Differential diagnosis: From its only congener differs in having richer venation (plesiomorphy) and generally slighly larger size and more narrow and straight R, and by (forewing) coloration
Autapomorphy: Extremely narrow and straigth R, Y-shaped pale stripe.
Description: Forewing extremely elongate, 10-15 mm long and 2.8 mm wide, with regular venation, intercalaries present and cross-veins dense in posterior margin and clavus. Total number of veins recorded 44-53. Coloration of membrane and veins dark in most of the wing, but anterior margin is pale (inlcuding veins). Costal area narrow and short, shorter than clavus, SC with 2-7 veins at margin. R nearly straight, narrow, with R branches simple (10-13); M simplified, also straight (5-13); CuA expanded, slightly sigmoidal, tertiary branched, with 7-12 veins at margin. CuA fluent, simple, clavus very long and narrow, without diagopnal kink (while coloration seems to diffusely follow this virtual line), A rich (8-11), tertiary branched, strongly sigmoidal, with dense CW forming reticulations.
Legs Hindfemora and hindtibia subequal, thin and short, with sparse short spurs, but with posteror femoral folding ridge with 2 rows of spurs. Hindfemora robust, also with posterior carinated ridge. Hindtibia strong and long, heavily carinated (n> 17).
Remarks: The species can be categorised with genus on the basis of elongated forewing with a characteristic coloration (pale margin, dark membrane). Recogniseable differences are cosmetical. Dense net of cross-veins suggest an active, frequent and long-lasting flight.
Ridged mid- and hindfemora likely suggest raptorial forelegs.
Derivation of name: *polnoc* is Slavic for midnight – alluding to nocturnal habits of this genus.
Character of preservation: One complete specimen**,** 5 isolated forewings.
Taphonomy: A complete specimen under coeval presence of completely articulated forewings suggest short or none pre-depositional transport and rarity in the assemblage (as weaker flight abilities of such specialized forewing are unlikely).



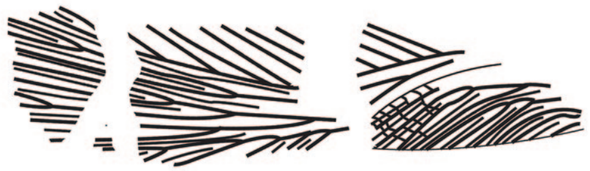


PIN 2784/723 f= 7 mm

PIN 2997/4240 l= 14 mm



PIN 3364/4240= 2997/4240 f= 14 mm



Genus *Olzmasg* gen.n.

Type species: *Olzmasg zi* sp.n. from Karabastau Formation described below, and by monotypy.

Differential diagnosis. The new genus differs from all other genera of Raphidiomimidae (Vishniakova 1973, Liang et al. 2009, 2012a, 2012b, 2018, 2021, Vršanský and Ansorge 2007, Grimaldi and Ross, 2004; Vršanský 2020) in the soft dark coloration on forewing, limited to a double short logitudinal stripe along R stem. Hindwing is entirely pale (symplesiomorphy with *Raphidiomima*). Except *Chuanblatta* it differs in unmodified pronotum (and similarly colored) and in possessing raptorial forelegs (this taxon is similar also in coloration to some extent and supported costa in both wings). Forewing with reduced and shortened SC along narrow costal area is synapomorphic with *Fortiblatta* and *Chuanblatta*. Unique are unmodified, although prognathous head, wide remigium, unstraight hindwing R1 and unmodified fore tibia (unique plesiomorphies).

Autapomorphies: greatly reduced M field in both wings and significantly shorter hindwing, with hugely expanded dense A1 in vannus.

Description: As for species.

Systematical remarks: The genus can be categorised within Raphidiomimidae on the basis of general venational scheme of both pair of wings and on prognathous head. On the basis of symplesiomorphic (with stem Caloblattinidae) venation, male tergal glands and unmodified morphology, the genus was apparently early derived within the family and do not relate with advanced genera *Raphidiomima, Graciliblatta, Divocina* and *Liadoblattina*. *Fortiblatta* with more expanded dark coloration (also on the apex of hind wing), was on the other hand more basal, without raptorial foreleg and with simpler venation. *Chuanblatta* Liang, Wang, Shih et Ren, 2021 from Daohugou and *Rhipidoblattina*, namely *R. sisnerakhab* Vršanský, 2020 and *R.* sp. from Bakhar Formation in Mongolia (see Vršanský 2020) possesed a high degree of similarity of venation (synapomorphic in SC simplified and narrowed shortened costal area) and seem most related sister taxon (synapomorphic also with raptorial forelegs). At the same time *Olzmasg* possess the symplesiomorphic (with *Chuanblatta* - see Liang et al. 2021) unmodified pronotum, unlike all other representatives of the family, and the most plesiomorphic, nearly unmodified, although prognathous head. Autapomorphic is strong support of the anterior margin of both wings, provided by highly sclerotized costa (in hindwing recorded for the very first time amongst cockraoches). For more details see phylogenetical scheme of Raphidiomimidae provided in a separate chapter and figure (figp. 622).

Derivation of name: OLZMASG is a letter representation of numbers 0-6.

***Olzmasg zi* sp.n.**
(figps. 179-183)

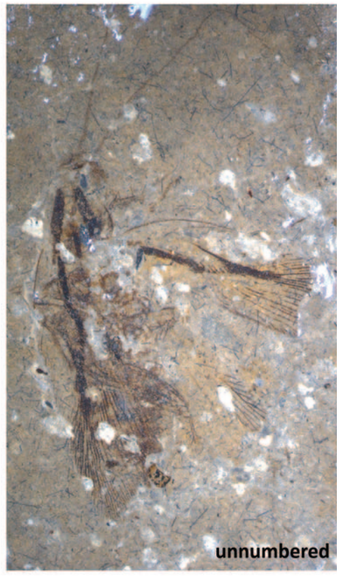
Holotype: PIN 2904/58 a completely articulated winged adult female (f= 16 mm: 2, 16, 8, 9, 1, 11; f= 15.2 mm: 2, 15, 8, 5,1, 14; 1, 5+7,0 2, 13+1; 1, 6+7, 3, 8+1).

Type locality: Mikhailovka, Karatau, Kazakhstan.

Type horizon: Kimmeridgian Upper Jurassic, Karabastau Formation.

Additional material: 2066/67, 46, 224; 2384/207+, 210±; 2784/670± (2, 15, 14, 17, 1, 12), 704, 804 (f= 20 mm: 2, 21, 6, 16, 1, 12; 3, 17, 8, 15 ,1, 14), 843; 2904/58; 2997/1598, 1599, 1607, 1601, 1602, 1611, 1612, 4284, 4269± (complete specimens); Unknown collection number/148, 132, 111; 1789/86 (f= 18 mm: ?, 15, 6, 8, 1, 10) **G**; 2452/535; 2066/296; 2554/90, 39 (2, 13, 10, 7, 1, 11); 2784/644, 809 (f= 22 mm: 2.14.5.11.1.14*blind branch), 919; 2384/142±; 2904/1868, 353, 352, 338, 346, 377, 368, 380, 378, 383+, 57±, 56±; 2997/1609, 1613, 4264±, 4421, 1163±; 4366, 1227, 1234, 227 (isolated forewings); 2239/395; 2384/105, 93, 209; 2784/750 (h= 16 mm: 1.5+11.6.10+), 781, 813, 815; 2039/39; 2904/43; 2997/1144± (h= 21 mm: 1.7+9.4+.5++1), 1317, 1266 (h= 19 mm: 1.5+15.6.8++1), 1293; 2997/4295, 4378; 2452/382 (h= 26 mm: 1.7+6.8.12+1*fusion), 100 (isolated hindwings); 2997/1600 (isolated head); 2784/730 (isolated leg). All except G= Gal-

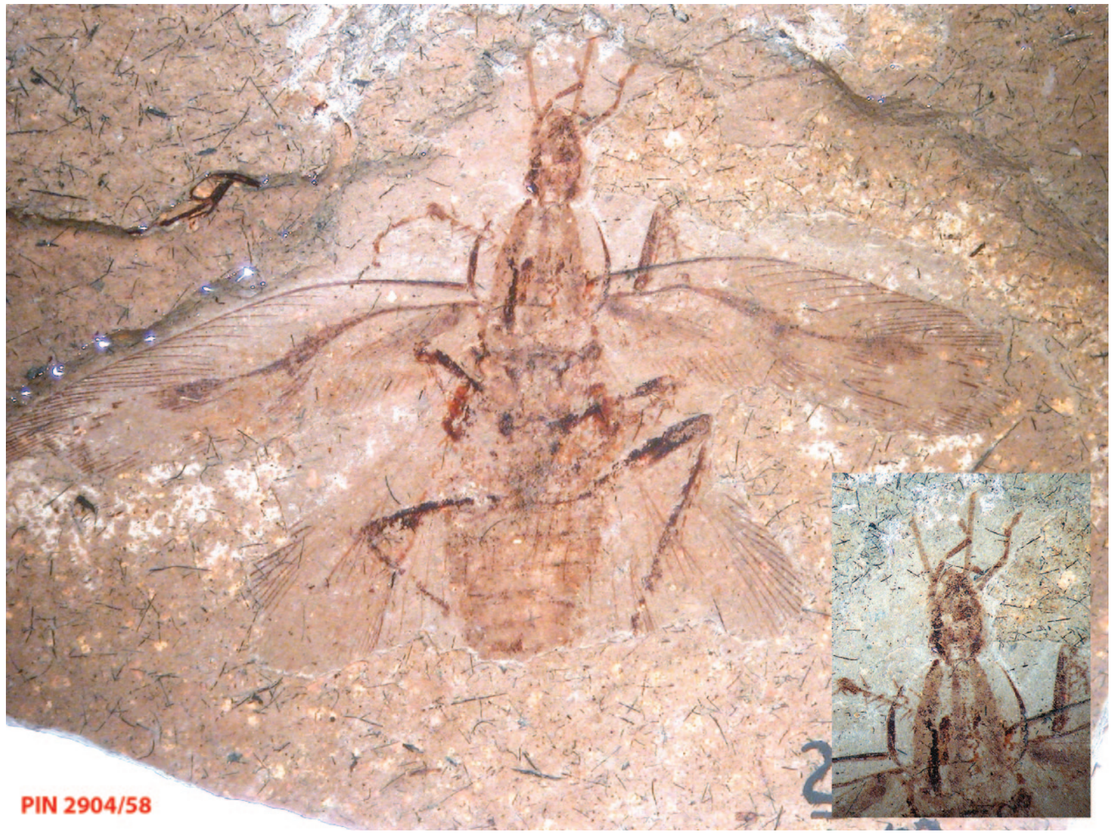


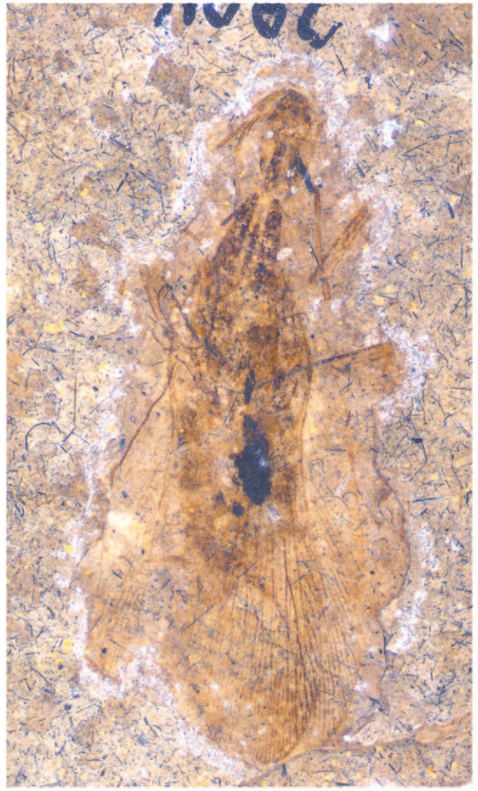






PIN 2904/ 58 w= 40 mm

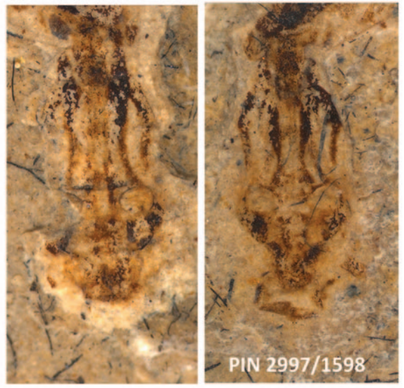






PIN 2904/353 l= 27 mm





PIN 2997/1598



PIN 2452/382



PIN 2784/809



PIN 2066/67 h= 15 mm



PIN 2554/39



kino from Mikhailovka.

Description (based on holotype with additions from other material marked): Very large species with wingspan of about 40 mm. Not as robuts as Fortiblatta, but within family can be considered for very robust, although the body is not as wide as in Sericoblatta (which male provides nuptial provisions). Head is not covered by a pronotum and was fully prognathous, elongate (3.91/ 2.49 mm), but standard, unmodified, without long neck (without stalk or a stem like in other Raphidiomimidae) otherwise characteristic for the family, pale, with two dark longitudinal stripes wide 0.36mm. Antenna thin, insufficiently preserved for revaling details about length or size of segments. Eye long and narrow, probably without apodeme. Central and lateral ocelli present. Palp rather long, 4-segmented (0.36/ 1.42/ 1.42/ 1.6 mm), thin 0.32 mm, unspecialised, terminal segment only slightly more oval. Labial palp very short, 2- segmented (first palpomere 0.9/ 0.18 mm), right terminal palpomere significantly widened (0. 72/ 0.36 mmm) and sclerotised, probably black, left one less expressed (0.72/ 0.28 mm). Other segments seems uncolored. Mandibles each with a double teeth and extremely elongate (like only recorded in Phyloblattidae and Caloblattinidae - this character was apparently present in all Raphidiomimidae), colored in margins.

Pronotum unmodified, slightly transversal (5.33/ 5.69 mm), but longitudinal stripes makes it illusory elongate, with short paranotalia, colored with 5 dark thin longitudinal stripes running all over the pronotal length. Body comparatively narrow, narrower than in other Raphidiomimidae species.

Forewings unmodified, long 17-24 mm, wide (L 20.4/ 5.51 mm, R 18.49/ 5.69 mm), with margins subparallel, venation regular, IC distinct, costal area slightly narrowed, costa distinct and colored; colored is also a narrow stripe along stem of R or M. SC simplified to 2 veins at margin dichotomised basally. R only slightly sigmoidal, nearly straight, with R1 (11-12) and RS differentiated (3), most R branches simple, some branched (sometimes terminally dichotomised). Medial field narrow, with M extremely simplified and nearly straight (4). CuA expanded, with two main strong stems and 8-9 veins at margin. CuP fluent. A dichotomised, especially posteriormost branches (homoplasy with mantodeans), with 11-14 veins at margin.

Hindwing is significantly shorter (both 14.04 mm and also other specimens 14 mm) and was apparently fully covered by the forewing in the repose. Remigium is plesiomorphically wide (up to 5.51 mm). Hindwing costa is the widest vein (up to 0.28 mm) and has no equivalent among Mesozoic and probably also among Palaeozoic cockroaches and nearly reaches apex. Costal area surprisingly wide, simple SC overlapping half of the wings length. R1 is not entirely straight and is more or less normally branched with dichotomisation charatecter, although the basalmost vein might ascend as from the straight stem (fluently curved), with 5-6 veins at margin; RS is also fully differentiated, standard, unmodified, tertiary branched, with 5-7 veins at margin. Medial field extremely narrowed and reduced, straight M with only 2-5 veins at margin. CuA with normally dichotomising branches (not descending from straight stem like in advanced groups) conservatively with 6 veins in the margin. Holotype left wing possesses simple CuA branches while the right one has one branch dichotomised. CuP simple. A1 extremely developed (in vannus), with 8 (NB!) densely distributed veins (autapomorphy), and other A veins also branched. Distance among A1 veins is smaller than among the rest of the veins, which are regular.

Legs very slender but not elongate, hardly sclerotized and colored, probably directly black. Foreleg raptorial, forefemur very long (4.09/ 0.71 mm), with posterior double row bearing 6 long (0.89 mm) strong spurs on one side, and without femoral terminal spine. Foretibia unmodified, very long (3.73/ 0.53 mm), with numerous, at least 11 long (up to 1.07 mm) strong spines on all sides. Fore tarsi unmodified, 5-segmented (1.96/ 0.89/ 0.53/ 0.35/ 0.53 mm), long, normally wide (0.18 mm), ended with symmetrical claw 0.5 mm long and a big round arolium (0.36 mm in diameter).

Midlegs longer than forelegs, but proportionaly short (in contrast to hidlegs also), hardly sclerotised and colored, probably directly black. Coxae (3.02/ 1.6 mm) and trochantera (0.89/ 0.89 mm) small, femora short and not esspecially robust (4.98/ 1.42 mm), with spines unpreserved; midtibia with numerous spines. Hind coxae (1.42/ 2.44 mm) and trochantera (1.78/ 0.89 mm) small, femora long and not robust (6.4/ 0.85 mm), with spines unpreserved; hindtibia very long (8/ 0.53 mm), with few (5) spines preserved (it is unlcear if it is a preservation state or a common character as in other Raphidiomimidae - because foretibial spurs are present in contrast to all other Raphidiomimidae).

Variability: This was performed on an insignificant sample size (n= 8) and revealed CVtotal= 14.88 %, which is a comparable value to raphidiomimids at the site.

Derivation of name: *zi* is a letter representation of number 21 (numerical count of numbers 0-6).

Character of preservation: 20 complete specimens; 33 isolated forewings, 18 isolated hindwings, 1 isolated head, 1 isolated leg.

Taphonomy: Numerous completely articulated specimens of this large species and at the same time high number of preserved isolated fore- and hindwings suggest that the species was very common in the deposition area as well as in higher parts of streams flowing into the paleolake. The species was the most common predatory dictyopteran at the site.

Remarks: The pale coloration suggest this predator was diurnal. Well developed wings with strongly supported anterior margin suggest this was an excellent flyier. Supported costa in hindwing might compensate the shorter hindwing. In this respect is notable the absence of pterostigma, which seems more functional in smaller species. Extremely remarkable is the autapomorphic reduction of medial area of both wings, as this barely represents an adaptive trait and rather is a stochastical reduction, directly indicating that the vein considered for M in fore- and hindwing is really the same corresponding veinal system and that these systems are correlated among fore and a hindwing. Slender legs are surprising in a massive cockroaches and these morphotypes are found exclusively in predatory groups, namely in pursuit predators, mantodeans, mutoviids and manipulatorids. Asymmetrical raptorial apparatus is homoplasic with primitive predatory Liberiblattinidae (*Stavba*) and mantodeans (*Burmantis hexispinea* Li et Huang, 2018). Important trait is the coloration stripe which in holotype occupies the same position on the wing. Nevertheless, it overlaps totally different veins (exclusively M in right wing and exclusively R in left forewing), which directly evidence that the control of coloration is venation-independent.

Mutations: One fusion (2784/809 – a blind unterminated vein); 2452/382 possessed CuA-CuA fusion.

Syncompressions: Specimen 2997/4284 was preserved with a titanopteran.

Specimen	Forewing	Length	Sc	R	M	CuA	CuP	A	RM	RCuA	MCuA	Without A	Total
2904/58	16	2	16	8	9	1	11	24	25	17	36	47	32
2904/58R	15.2	2	15	8	5	1	14	23	20	13	31	45	38
2784/670±		2	15	14	17	1	12	29	32	31	49	61	52
2784/804	20	2	21	6	16	1	12	27	37	22	46	58	38
2784/804R		3	17	8	15	1	14	25	32	23	44	58	41
1789/86	18	2	15	6	8	1	10	21	23	14	32	42	49
2554/39		2	13	10	7	1	11	23	20	17	33	44	42
2784/809	22	2	14	5	11	1	14	19	25	16	33	47	39
n	5	8	8	8	8	8	8	8	8	8	8	8	47
min	15.22	2	13	5	5	1	10	8	20	13	31	42	43
max	22	3	21	14	17	1	14	19	37	31	49	61	55
ave	18.24	2.125	15.75	8.125	11	1	12.25	23.875	26.75	19.125	38	50.25	
dev	2.808558	0.353553	2.434866	2.850439	4.503967	0	1.581139	3.181981	6.227818	5.938675	7.171372	7.478541	54
CV	15.4	16.64	15.5	35.08	40.9	0	12.9	13.33	23.28	31.05	18.87	14.88	49

Family Caloblattinidae Vršanský et Ansorge in Vršanský (2000)

Type species: *Blattina mathildae* Geinitz, 1883: 29, pl. 6, fig. 1
Stratigraphic range: lowermost Triassic-Campanian
Geographic range: Laurasia

Composition: *Asioblatta* Vishniakova, 1968; *Caloblattina* Handlirsch, 1906; *Decomposita* Vršanský,2008; *Etapia* Vishniakova, 1983; *Fusiblatta* Hong, 1980; *Ijablatta* Vishniakova, 1983; *Itchetuja* Vishniakova, 1983; *Kemerowia* Vishniakova, 1983; *Nuurcala* Vršanský, 2003; *Rhipidoblatta* Vishniakova, 1968;, *Rhipidoblattina* Handlirsch, 1906, *Samaroblatta* Tillyard, 1919; *Shartegoblattina* Vršanský, 2004; *Sogdoblatta* Martynov, 1937; *Soliblatta* Lin, 1986; *Taublatta* Martynov, 1937; *Taublattopsis* Vishniakova, 1985; *Thuringoblatta* Kuhn, 1938

Diagnosis (after Vršanský and Ansorge in Vršanský 2000)*:* Typical cockroaches in habitus, with more or less long ovipositor. Large cockroaches with forewing usually 15-30 (rarely up to 60 mm, exceptionally under 13 mm). Both wings membraneous or leathery. Forewing with Sc branched, RS expanded, M and Cu both richly branched. Cu obiguely S-shaped with most branches ending near ing apex. Clavus usually not surpassing wing midlength. Intercalary veins thick, distinct all over wing surface (visible even in poorly preserved specimens), dark color pattern rather typical. Hindwing with fan-like pleating on anal lobe. Sc branched or even reticulated, long. R with R1 and RS abundantly branched. M obliquely branched. Cu with many secondarily branched veins and possibly with several blind ranches that may also be secondarily branched. Wing usually with many reticulations.

Genus *Caloblattina* Handlirsch, 1906

Type species: *Blattina mathildae* Geinitz, 1883: 29, pl. 6, fig. 1
Stratigraphic range: Toarcian-Campanian
Geographic range: Laurasia

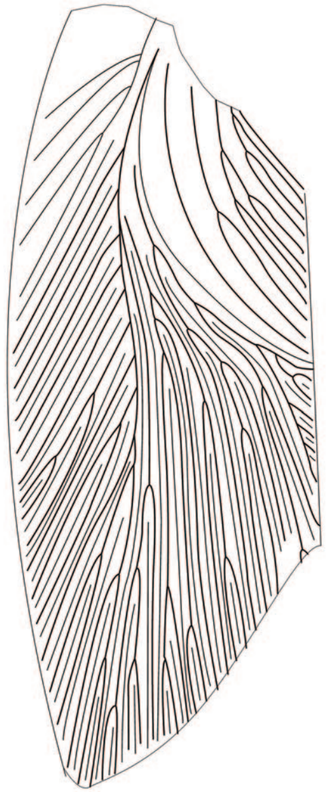
Composition: *C. liassina* Handlirsch, 1906 (Wainlode cliff, UK); *C. rubens* Vršanský, 2003 (Bon Tsagaan Nuur, Mongolia); *C. vremeni* Vršanský, 2020 (Bakhar, Mongolia); *C. hrachova* Majtaník in Majtaník and Kotulová (2023)(Tasgorosay, Kazakhstan)
Diagnosis (after Vršanský and Ansorge, 2007): Large species with rich venation and intercalaries that are visible even in poorly preserved material. Total number of veins about 65–75; forewing length about 25 mm; membrane heavily sclerotised.

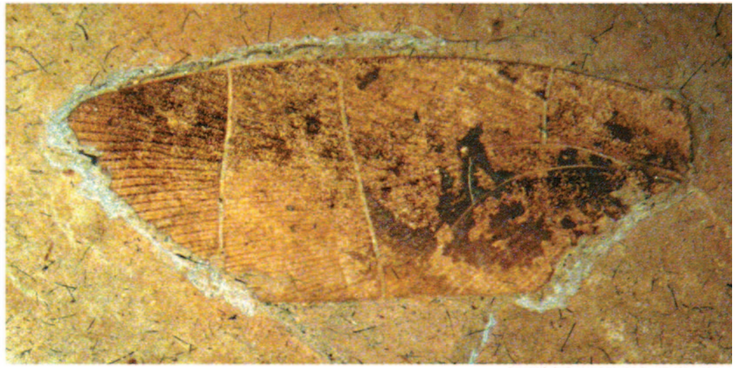
Caloblattina laesis sp.n.

(figp. 188)

Holotype: PIN 2554/156 (f= 30 mm).
Type locality: Mikhailovka, Karatau, Kazakhstan.
Type horizon: Kimmeridgian Upper Jurassic, Karabastau Formation.

Differential diagnosis: Differs from the formalised congeners in being significantly larger (largest specimen of *C. rubens* is under 30 mm)
Autapomorphy: Bigger size is very probably an autapomorpy.
Description: Big species with forewing robust (ca. 34/11.5 mm), leatherous, melanised, probably brown, with characteristic reticulation and “> > > >”- shaped profile among main veins. Costa distinct wide,





PIN 2554/156 f= 30 mm



running all along the fore margin, costal area very wide, subcostal with 5 strong branches. R slightly sigmoidal, with 17 veins at margin, most veins are simple and only one is secondarily branched, not reaching apex. M branches nearly straight, dense, with at least 14 veins at margin. CuA sigmoidal, expanded, with 13 veins at margin, posteriormost are shortly branched. CuP fluent, cclavus robust, with at least 10 secondarily branched A.

Deformities: Absence of deformities in this large species with forewings apparently basically protective is highly surprising.

Remarks: The species can be categorised within the genus on the basis of large and robust size, leatherous wing with numerous reticulations and track-like pattern among veins and intercalaries, and short CuA posterioormost branches. Within the genus there are no relation possible to trace since the high conservativity of this generally widespread Jurassic-Cretaceous genus (for unformalised distribution see Vršanský 2020).

Derivation of name: *laesis* is Latin for damaged.

Character of preservation: One damaged fully articulated forewing.

Taphonomy: The complete articulation might suggest a short pre-depositional transport, this wing, nevertheless, seems very rigid, limiting the former interpretation. Also it cannot be excluded that the anterior margin was predated. It seems more probable attempt of predation (or other mechanical damage) occurred during life, because the margin seems to have a more melanised healing tissue. Nevertheless, a developmental error also cannot be excluded with confidence.

Genus *Karatavoblatta* Vishniakova, 1968

Type species: *Karatavoblatta longicaudata* Vishniakova, 1968, and by monotypy.

Stratigraphic range: indigenous to Karabastau Formation.

Geographic range: indigenous to Karatau

Diagnosis (after Vishniakova 1968): Form, scheme and respective allignement of R, M and CuA, form and presence of archedyction and anal are similar to *Sogdoblatta* Martynov from Early Jurassic of Central Asia. Differs in poor SC, rich anterior branches and bigger size.

Karatavoblatta longicaudata Vishniakova, 1968

Holotype: PIN 2066/774. A complete winged adult female. Karatau. Designated by Vishniakova (1968).

Mutations: A single deformity was preserved as interminated blind A1 branch in the left 2066/774 forewing clavus- in clavus deformation ratio are not counted due to protective charcter of this structure (among 4 partially preserved wings).

Character of preservation: one complete female with long ovipositor.

Taphonomy: A completely preserved large adult suggest no pre-depositional transport and either rarity of the species in the ecosystem but also possibly weak flight abilities.

Genus Rhipidoblattinopsis Vishniakova, 1968

Type species: *Rhipidoblattinopsis latitergata* Vishniakova, 1968, and by monotypy.

Stratigraphic range: Indigenous to Karabastau Formation.

Geographic range: Indigenous to Karatau

Diagnosis (after Vishniakova 1968): Similar with *Rhipidoblattina* in form of R, M CuA and A and also in ovipositor structure. Differs in the form of pronotum and abdomen, and with development of lateral lobes of Tergites 3-7 and somewhat reduced T8-9 and by form of anal plates and cerci.

Rhipidoblattinopsis latitergata Vishniakova, 1968

Holotype: PIN 2239/352. A complete winged adult female. Karatau. Designated by Vishniakova (1968).

Mutations: None detected.
Character of preservation: 11 complete specimens, of them 2 females with long ovipositor and 1 male identified; 27 isolated forewings, 2 hindwings
Taphonomy: Completely preserved large adults suggest no pre-depositional transport. At the same time disarticulated wing might refer to distribution further up to the stream.

Additional material designated here: 2384/27± (female); 2554/19 (f= 13 mm), 35 (male, f= 13mm), 169 (f= 13 mm); 2997/100 (f= ca. 13 mm), 4251±, 4256±, 4263±, 4384, 4387 (complete specimens); 1789/25 (f= 12/3.8 mm) **G**, 74 **G**; 2066/61, 64, 66, 83, 116±, 135, 170, 175, 259, 314, 442, 448; 2239/237± (f= 13 mm); 2384/54±, 84 (5.20.7.12.1.11), 90 (10a); 2784/815±, 946; 2997/33, 44, 84, 203, 4293, 4344 (f= 13 mm), 4414 (isolated forewings); 2997/103 (h= ca. 13 mm), 1401 (hindwings). All except G= Galkino from Mikhailovka.

Aposema gen.n.

Type species: *Aposema gigantenna* gen. et sp. n. from Karabastau Formation, by monotypy.

Differential diagnosis: Differs from all representatives of the family by hardened forewings, elytrised also in its form and by coloration forming a distinct dot; and by a huge long ovipositor wide in base but also very wide, triangular shape.
Description: As for species.
Derivation of name: After *aposematism*.
Remarks: The genus can be categorized within Caloblattinoidea on the basis of extremely wide antenna with short segments (synapomorphy excluding Phyloblattidae and Palaeozoic families), multisegmented cercus and rich R venation (plesiomorphies). Raphidiomimidae are excluded on the basis of extremely wide antenna and globular head (plesiomorphies).
Within Caloblattinidae, the relation is nearly impossible to trace due to hard modification of all the body resulting from aposematic appearance. Head is standard, antenna, ovipositor and forewings modified. Thus, from standard unmodified caloblattinids, any degree of relation is revealed only by widely distributed J1-K2 genus *Nuurcala*, synapomorphic is triangular base of ovipositor and coloration (although much simpler, variable, but not aposematic). Colored are certain highly modified and thus excluded as belonging to direct relatives *Rhipidoblatta* and *Solemnia*. Possibly aposematic *Okras sarko* Vršanský, 2020 from Upper or Middle Jurassic Bakhar Formation in Mongolia with similar (probable synapomorphy) but much less expressed (plesiomorphy) coloration and similarly developed forewing R (symplesiomorphy) also might represent undirectly related taxon, but is is highly modified in being very small and having extremely short clavus (autapomorphies).

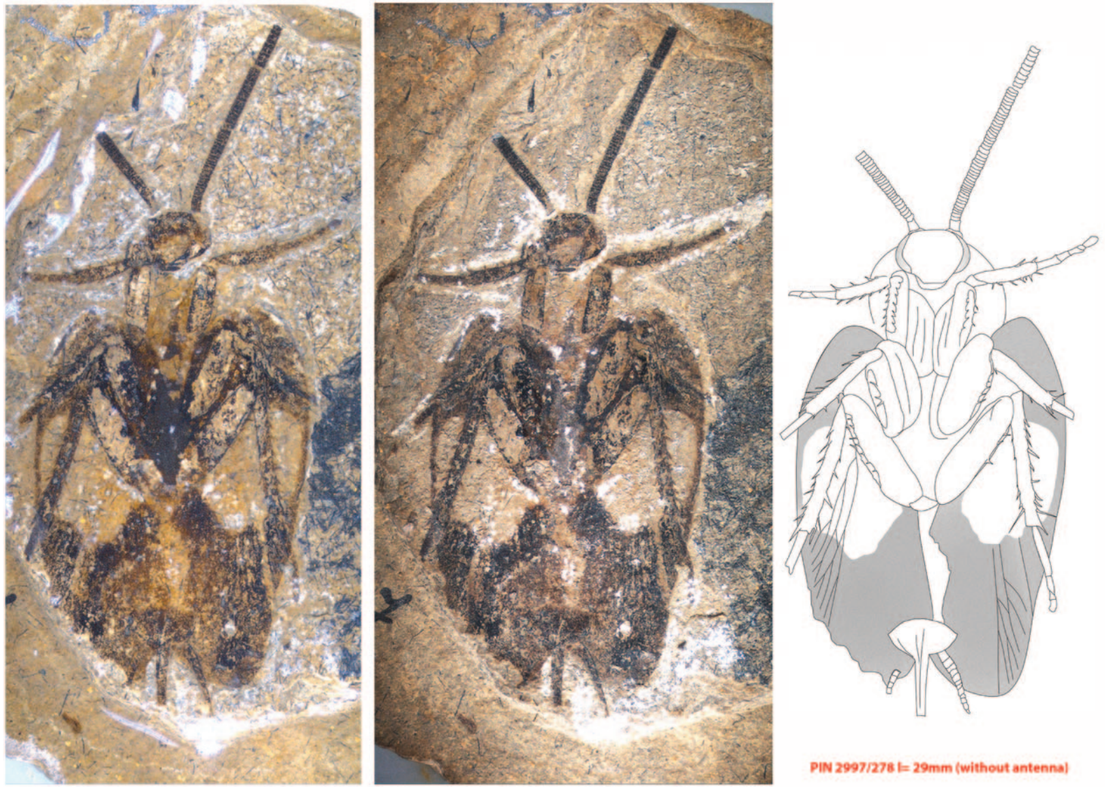
Aposema gigantenna gen. et sp. n.

(figps. 181-182)

Holotype: PIN 2997/278. A complete adult winged female.
Type locality: Mikhailovka, Karatau, Kazakhstan.
Type horizon: Kimmeridgian Upper Jurassic, Karabastau Formation.

Additional material**:** PIN 2554/4 (complete specimen); 2239/186=180 (isolated forewing). The same locality as the type.

Description (based on holotype with additional measurements from paratype PIN 2554/4**):** Huge robust species, with total size about 30 mm excluding extremities and ovipositor. Head standard, nearly globular, slightly elongated (4.117/3,58 mm; 5.92/ 4.31 mm in paratype) fully hypognathous and entirely covered by a pronotum. Eyes very long and narrow (2.96/ 0.79 mm in paratye, not connected, interocular space wide. Ocelli large (ca. 0.3 mm in diameter), of similar size, pale including the central ocellus. Antenna extremely wide (0.716) and sclerotized, apparently very dark and probably directly black, multisegmented, with segments extremely short (0.17-0,36 mm). Scape very long (1.253 mm), pedicle shorter than other



Aposema gigantenna







PIN 2554/4 f= 24mm



segments (0.79mm), short preserved fragment of antenna (13.067 mm) contain 39 antennomeres (46 in paratype in a preserved broken fragment). Total number of segments estimated on the basis of an average comparative antennal length, about 100. Palp 3-segmented (in paratype: 1.57/ 1.38/ 1.38 mm), with terminal segment slightly widened. Mandible extremely long and narrow like only recorded in Phyloblattidae.

Pronotum fully developed, transverse, 8.54 mm wide (9.26/ 10.84 mm in paratype), with fully developed paranotalia. Judging from good preservation of coloration at other parts of body, pronotum was probably uncolored. Body standardly, not heavily sclerotised, probably brown. Terminal sclerit straight on base and regulary simply curved at the end (5.907/ 2,327 mm. Cercus of moderate length (5.549 mm), normally wide on base, then thinner up to very thin at apex. It is heavily sclerotized, probably directly black. Segments seem very long, and only 8 segments are distinctly recognized (this number cannot be taken seriously as the preservation disallow the definitive conclusion, but paratype cercus also seems oligomerised). Ovipositor is triangular, very long (partially preserved long 4.475mm) and rather wide (completely preserved 6.30/ 1.77 mm in paratype), triangular, entirely heavily sclerotized, with both valves distinct. The middle part of the ovipositor bears a full-length deep longitudinal ridge.

Forewing long 24 mm (identically 24 mm in paratype), elongate, elytrised, more or less of standard (within the family) shape, very dark and with distinct huge pale macula in the central part. Costal area narrow, Costa distinct, dark and traceable through the entire anterior margin. Sc uncolored, short, branched, with at least 4 branches including a very basal vein. R expanded, extremely wide, reaching nearly the half of wings width, and with tertiary branched veins. Clavus normally developed, long, reaching ca a third of the lentgth of the wing. Hindwing shorter (21.48 mm in paratype), ending at the same position as forewing, also colored similarly as forewing, also forming a pale dot on a dark membrane. Sc simple, R partially reduced, with R1 (3) and RS (4) differentiated (both specimens with identical number of these veins), M with at least 6 veins at margin.

Legs extremely robust and short, heavily sclerotized, seems to be entirely hidden under forewings. Forelegs with short femur (R 4.3/ 1.43; L 4.48/ 1.62 mm) bearing 7 short strong spurs in each of the two rows (apparently some of the spurs in the holotype specimen were broken), without apical femoral spine. Foretibia of nearly identical length (R 3.94/ 1.25; L 3.22/ 1.25 mm), more narrow, with 2-5 short (0,36) thin spurs on each side and with a terminal spur (0.71 mm). Tarsomeres massive (R 1.43/ 0.9/ 0.72/?/? mm; L 1.79/ 1.07/ 0.9/ 1.07/ ? mm).

Midfemora extremely massive (R 7.16/ 2.69; L 6,623/2.15 mm), with posterior row bearing two rows with 7 strong spurs each, terminal apical femoral spine absent or unpreserved; midtibia also extremely massive (R 4.65/ 0.9; L 5.55/ 1.25 mm), with 5-7 strong spurs on each side, only probasitarsus fragment preserved.

Hindlegs with trochanter having no size analogue among fossil cockroaches (R 3.22/ 1.97 mm; L 3.58/ 2.14); femora also massive (R 8.59/ 2.5 mm; L 5,73/ 2.15 mm), ventrally with 5-7 strong spurs on each posterior side, without apical femoral spine. Hindtibia also extremely massive (R 11/ 1.07 mm; L 7.88/ 0.9 mm), with 5-11 strong and long (NB! only in hindleg up to 1.253 mm long) spurs on each side, also only 4 wide left tarsomeres (3.04/ 1.07/ 0.54/ 0.72 mm) preserved.

Remarks: The species apparently posses distinct uncolored dot on fully colored forewing, which is in its size apparently aposematic. Coloration of antenna, part of head and ovipositor is so distinct that it was apparently not only very dark and probably directly black but also very heavily sclerotized, which is surprising on antenna. There is no other fossil cockroach known to possess such huge antenna. Such antenna was probably counterproductive in a burrowing lifestyle indicated with massive legs, and might be effective as a passive protection against smaller predators.

Notable is size of spurs, which is extremely conservatively in cockroaches in terms of

distribution in one specimen: one specimen always have near-identical spurs in all legs. The present species is exceptional in that in hindtibia, spurs are longest, while in foretibia shortest. Differences are remarkable. Very unusual is also asymmetry in tibiae – right tibia are significantly longer and more narrow. This distinct on first sight as difference in hindtibia is nearly 30 % (11 mm vs. 7.9 mm).
Derivation of name: After *gigantic* and *antenna* – alluding to huge unparalleled antenna.
Character of preservation: 2 completele articulated specimens, one isolated forewing.
Taphonomy: Two complete and very large specimens under a near lack of isolated forewings suggest short transport and a rapid burial.

Genus *Asioblatta* Vishniakova, 1968

Type species: *Asioblatta punctata* Vishniakova, 1968, by monotypy.

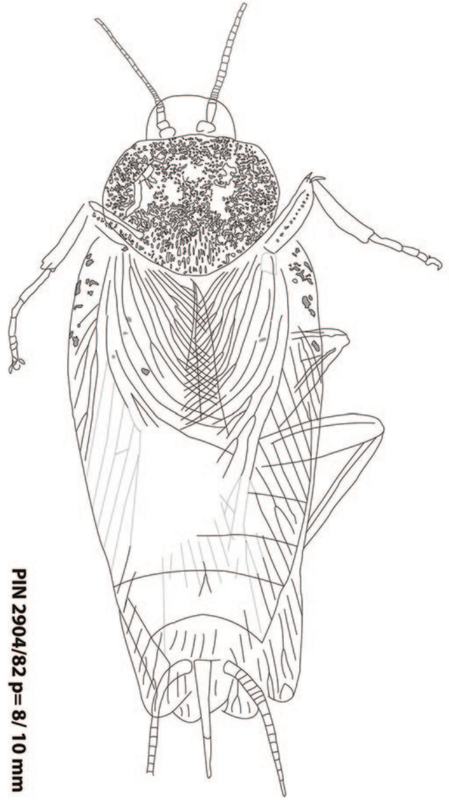
Differential diagnosis: differs from all known representatives of the family in having (small) dotted habitus and this coloration regards head, pronotum and also wings. It also has autapomorphically acascending anterior SC branches.
Description: as for species.
Systematical remarks: Long externally protruding ovipositor, multisegmented cerci, branched A and SC and mostly regular venation unequivocally categorise this taxon within Caloblattinidae. Anteriorly ascending SC branches are equivalent (homoplasy) to Blaberidae. Long first cercomere is equivalent to present in Olidae. The coloration in unique in the nearly 200 million years lasting history of the family, and moreover the ascending SC branches are autapomorphies allowing to erect a new genus. Modified cordiform pronotum is synapomorphic only with advanced *Srdiecko* known only from the same locality, and no other relations are being traced.
Derivation of name: after compost and regarding its presumed decomposition.

Asioblatta punctata Vishniakova, 1968 (figs. 195-197)

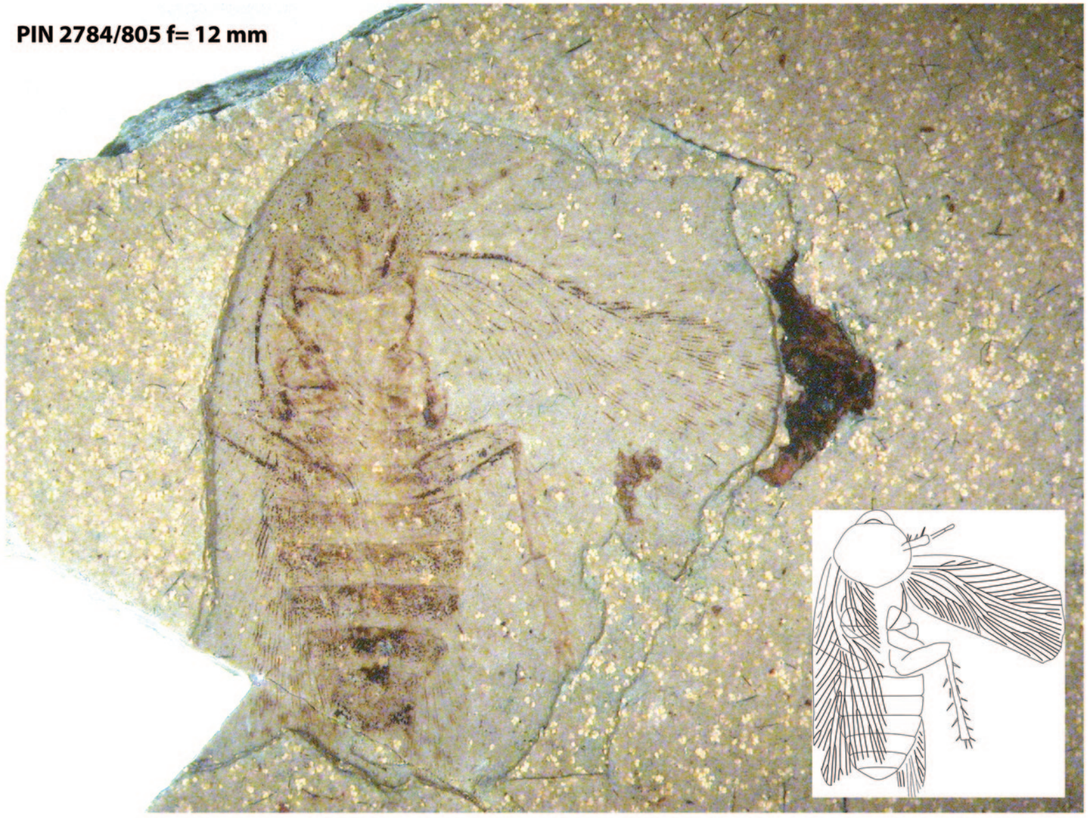
Holotype: PIN 2239/356. Completely articulated winged adult female. Designated by V.N. Vishniakova (1968).
Type locality. Mikhailovka, Karatau, Kazakhstan.
Type horizon. Kimmeridgian Upper Jurassic, Karabastau Formation.

Additional material designated by V.N. Vishniakova (1968): PIN 2384/35, 37.
Additional material designated here: PIN 2066/48, 101, 264; 2384/34, 229; 2452/511; 2904/18±, 79; 2784/629, 805; PIN 2904/82; 2997/1390 (complete specimens); 2066/460; 2784/824, 696; 2511/98 (m16+, 10CuA, 1A8+), 111; 2997/749±; 2384/36± (forewings); 2066 /408±; 2384/56±; 2554/84; 2997/4347 h= 25 mm (hindwings). The same locality as the type.

Redescription: Very large cockroach with total body length about 30 mm. Head globular, large (3.7 mm wide), with extensive but very narrow eyes, presence and/or position of ocelli obscure, but due to presence of interocullar ridge most likely present (at least the lateral ones). Deep colored puncturation of head apparent. Antennal sockets very large, scape very wide but short (0.3-0.9/ 0.4-0.5 mm), pedicel long not as wide, but wider than other at least 140 basally dark colored pale antennomeres long 30 mm or more. Palp very short, 5-segmented (0.3/ 0.4/ 1.9/ 1.3/ 0.9 mm). Labial palp extremely short, 2 segments preserved. Mandible robust, short.
Pronotum cordiform, transverse (6-8/ 9-10 mm) with distinct colored small puncturation, punctures transform into short stripes posteriorly.
Body 5.3 mm wide, fat, but rather narrow compared to other representatives of the family, with 5 very long segments with nearly straight margins preserved. Ovipositor long, narrow (6/ 0.6 mm), without distinct structure, simple, with a single pair of valvomeres preserved. Cerci multisegmented (16: 0.6/ 0.3/ 0.3/ 0.4/ 0.3/ 0.3/ 0.3/ 0.6/ 0.5/ 0.4/0.4/ 0.4/ 0.3/ 0.4/ 0.4/ 0.7 mm), first cercomere very long and






PIN 2784/805 f= 12 mm




PIN 2904/82 p= 8/10 mm

narrow, cercus narrow basally, then widened, curved posteriorly, with uneven cercomeres.,
Legs robust, pale, with longitudinal dark stripes. Forefemur 3.5/ 1.2 mm pale, with wide dark stripe along anterior margin and with a row of 12 very short strong spurs and with terminal apical spur. Tibia (3.5/ 0.8 mm) pale, with wide dark stripe along posterior margin at base. Three very long (0.9 mm) spurs visible at PIN 2784/ 805. Midleg very small, similarly colored as hindlegs, coxa small (1.8/ 0.7 mm). Hindlegs moderately robust, hindcoxa small (0.7/ 0.5 mm); hindfemora (2.9-6/ 1.1-1.7 mm), pale, with dark stripes along anterior and posterior margins and with 13 central very short rudimental spurs. Apical spur indistinct. Hindtibia (3.2/0.2 mm) pale, with with dark stripes along anterior and posterior margins and with 16 spurs 0.5 mm long.Forewings maculated, very wide and comparateively short (18-28/ 4.5-6.3 mm), venation regular except for clavus. Costa narrow, but distinct at least in standardly wide (as long as clavus) costal area. SC basally very wide and colored, with anterior and posteriorly ascending secondarily and tertiary branched veins, of which 4-7 meet margin.R basally sigmoidal, posteriorly nearly straight, with veins simple or simply branched, with 15-17 veins meeting margin. M standard, straight, with about 7 veins.
CuA extremely short and simplified, with 2-4 veins meeting margin. CuP fluent, clavus rather flat, with richly and secondarily branched A (17 in both wings).
Hindwings are shorter than the forewings, projected at the same level as forewing outlines, apex is sharp, but not as sharp as forewings, venation regular, maculate coloration present to some extent. SC simple, R with 9+14 branches, M 5, CuA with 7 and additional bling branches.
Deformations: A blind A1 branch occurs in a forewing clavus of 2784/805B, which is also a significantly smaller individual than others (ca. 18 mm vs. 26-28 mm forewing length).
Character of preservation: 15 complete specimens, 7 isolated forewings, 4 isolated hindwings.
Taphonomy: Completely articulated specimens in this large species indicate a short pre-deposition time. Apically broken hindwing might suggest this was an older specimen or a predation during or after life during deposition and transport.
Remarks: No mutation was recorded among 23 specimens and 34 partially visible wings (except for a blind A1 branch in forewing clavus of 2784/805B).

Genus *Rhipidoblatta* Vishniakova, 1968
= *Srdiecko* Vršanský, 2008 syn.n.

Type species. *Srdiecko tri* Vršanský, 2008

Remarks: A new extensive comparative material allowed to discriminate several new species and also to synonimise and categorise *Srdiecko* Vršanský, 2008 within this common and diverse genus.

Geographic range (Vršanský 2020): Laurasia s.s., Xiaofanzhangzi, Meitian, Mintaja, Daohugou, Kuntouyingzi, Zhouyingzi, Dongchangtai, Daokuntouyingzi, Chernovskie Kopi
Stratigraphic range: Early Jurassic-Early Cretaceous

Type species: *R. fusca* Vishniakova, 1968. Karabastau Formation.

Composition (formalised species only): *R. brevivalvata* Vishniakova, 1968 (Karabastau Formation); *R. grandis* Barna, 2014 (Chernovskie Kopi, Transbaikalian Russia)

Autapomorphies: Robust head, cord-like pronotum, narrow hindwing remigium, dark forewing CuP.

Diagnosis (after Vishniakova 1968): Large insects. Wings overlapping abdomen. Intercalary veins present. Anterior margin of the forewing fluently arcuate, posterior margin straigth, apex weakly narrowed and ascend towards anterior margin; length/width ratio 3: 1. SC shorter than clavus, straigth, weakly branched. R does not reach apex, sigmoidal, reahing less than a helf of the width; M sigmoidal, with comb-like bracnhes, dichotomised distally compared with CuA. CuA with two stems, reaching apex of the posterior part of the wing, arcuate. Anal area wideand elongate, with length width ratio 2: 1. A1 simple, A2 branched secondarily. Hindwing R1 comb-like. RS with two stems. M weak. Body of female elongate. Pronotum rounded, pentagona, slightly transverse. Legs cursorial, size rasing towards hindlegs; femora and tibiae carinated. Abdomen twice as long as wide, narrowing towards terminlia, formed with 10 segments. Anal terga weakly transverse, strongly arcuate posteriorly, 2-segmented. Cerci long, multisegmented, narrowed distally. Ovipositor straigth, overlaping apex of forewings, formed with three pairs of valves, outer valves shortened.

Remarks: Numerous completely preserved specimens enabled detailed classification and confident identification of numebrous distinct species within the genus complex, which would be in several cases impossible on the basis of isolated forewing only. Thus, any future studies must consider eventuiality of the presence of more sibling species within this genus once no comparative material was available.

Rhipidoblatta fusca Vishniakova, 1968 (figps. 200-205)

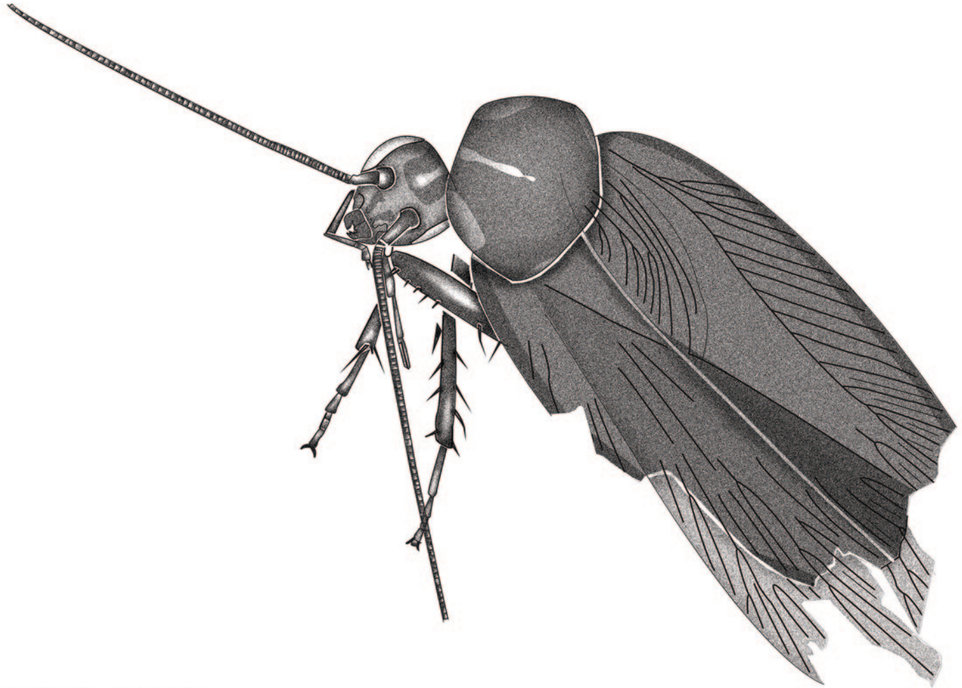
Holotype: PIN 2239/350. A complete adult winged female. Designated by V.N. Vishniakova (1968).

= *Rhipidoblatta tri* (Vršanský, 2008) comb.n.
= *Srdiecko tri* Vršanský, 2008

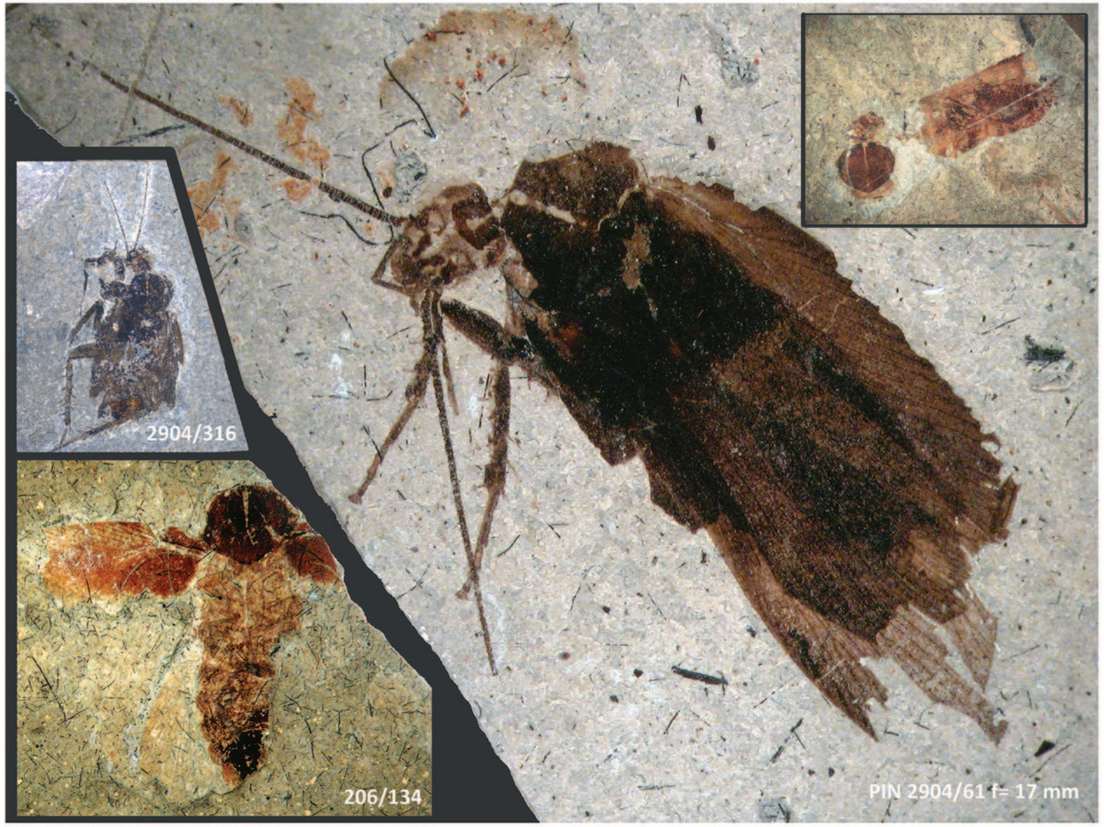
Holotype: designated by Vršanský (2008): PIN 1789/19= 39 (SAGU 39 in original description) **G**. A complete winged adult. Sex unknown.

Additional original material designated here: 124/6; 204/5 (f= 26 mm) (**KACHKARATA or G)**; 2066/261 (pf); 2384/47; 2231/28; 2335/94; 2904/61 (f= 17 mm), 62±, 134, 266 (fh), 316, 357, 358; 2997/89±, 115, 116 (fh), 190, 192, 205 (completely articulated winged adults); 2239/233±; 2335/8, 10 (f= /8mm), 21 (f= /10.8 mm), 23 (f= 30 mm), 24, 29 (f= /8 mm), 30 (f= 30/ 10.6 mm; 4, 24, 13, 17, 1), 63; 2554/104, 114± (f= 29 mm; 3, 21, 16, 17, 1, 20), 135, 157, 163, 181; 2784/650, 796± (f= 25/6 mm; 3, 20, 8, 11, 1, 10), 976; 2904/35 (f= 30 mm), 78 (f= 31/ 9 mm; 3.20.5.17.1.13), 151, 202, 253 (f= 28/ 8.7 mm), 262, 283, 286, 287 (f= 24 mm), 288, 1861; 2997/74± (f= 30/ 8.5 mm; 4, 7, 11, 10, 1, 11), 118±, 120, 123, 150, 222 (f= 25 mm), 223, 282, 1142±, 1146 (f= 20 mm), 1207, 1238, 1258, 1296 (f= 24 mm), 1315, 1328, 1380 (f= 29 mm), 1393, 1405, 1407, 1426, 1427, 1568, 1669, 1700, 4208, 4271±, 4291, 4405 (isolated forewings); 2554/115± (2, 5+13, 8, 11+blind); 2784/980 (h= 24 mm; 1, 6+21, 6, 14); 2997/15, 148, 209, 1211, 1213, 1988, 2810 (isolated hindwings). All except type (G= Galkino) and (204/5) from Mikhailovka.

Description (improved after Vishniakova (1968) and Vršanský (2008)). Large species reaching up to 25 mm and more. Head robust, almost globular almost as long as wide (5.8 mm), coloured, with pale triangle in the base of head. Antennal foramens are very large (diameter 1.0mm), antennal basalmost segments very wide and long (scape 0.99/ 0.43 mm). Other antennomeres (clearly more than 73 preserved on both sides – terminal segments apparently unpreserved or damaged during life) strongly sclerotized and melanised, verz wide and short (baslamost 0.14/ 0.28 mm), slightly more elongated anteriorly (terminal preserved one 0.3/ 0.14 mm). Three ocelli, probably not extending over the head surface, large (0.45mm), placed nearly linearly, the central ocellus slightly apically (in PIN 2904/61 ocelli are indistinct). Clypeus very large, mandibles robust, with two (R) or three (L) fine teeth respectively. Palpae fine, 4-



PIN 2904/61 f= 17 mm





PIN 2904/61 f= 17 mm



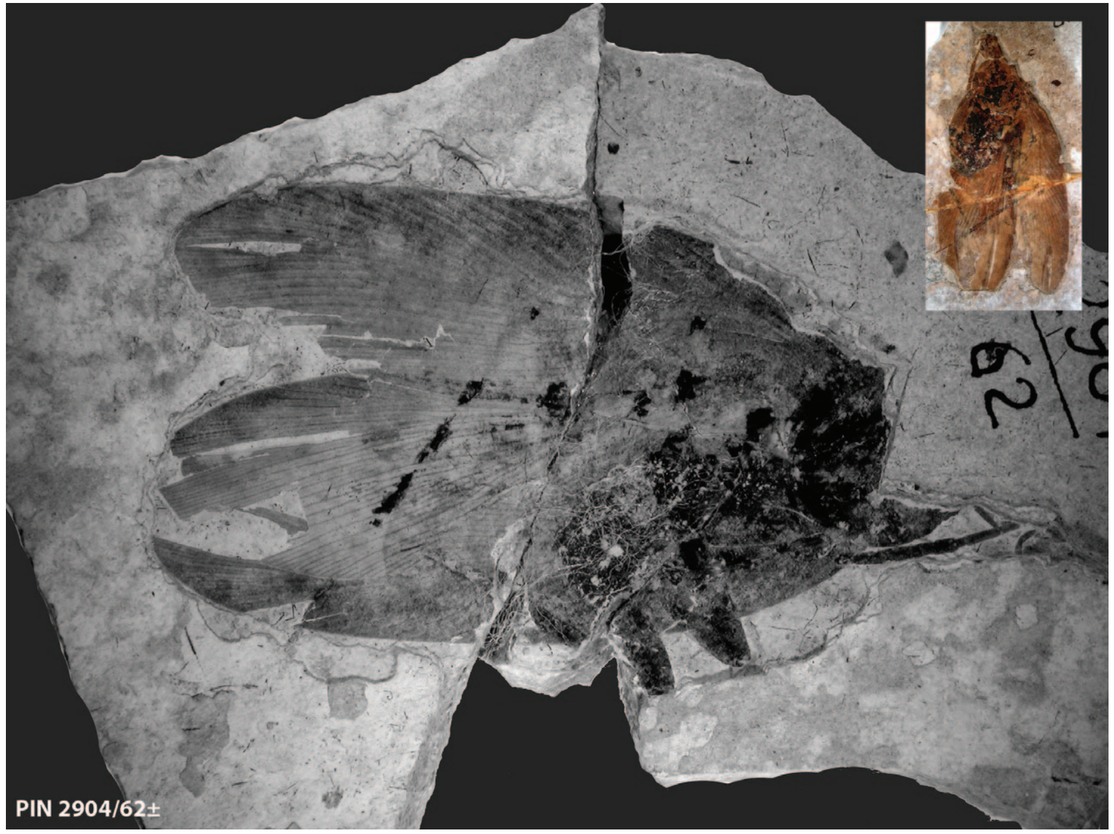



204/5
PIN 2784/796


PIN 2904/78 f= 31 mm


PIN 2784/980


PIN 2554/115


PIN 2904/62±

segmented (?; 0.56 /0.4; 0.84/ 0.3; 0.98/ 0.28 mm) and significantly shorter than head. Eyes are narrow and very long (2.1/ 0.56 mm). Pronotum cordiform (length/ width 5-7.4/ 7-8.3 mm), wlth distal coloration margins and a central longitutinal half-stripe. Body comparatively narrow, with long, multisegmented cerci.
Forewing moderately elongate (17-31/ 6.5-10.6 mm), completely finely colored (probably light brown) and with darker anterior hem. Costal area rather wide Sc standardly dichotomised (also basally), not straight, with 4 veins meeting margin. R only slightly sigmoidal, nearly straight, with all (NB!!) ca. 13 veins meeting margin simple, non dichotomised. CuP simple, fluent, clavus with anterirormost A simple, other 9 veins at margin dichotomised.
Hindwing with regular venation, narrow remigium. Sc simple, differentiated RS, and expanded media, coloured anteriorly and possibly very finely in the radial area. Legs robust, femora and tibiae colored and hardly sclerotized. Forefemur (3.5/ 1.12 mm) and foretibia (3.34/ 1.1 mm) longer compared to other legs in proportions. Foretarsus very long, unmelanised, 4-segmented (1.82/ 0.25; 0.7/ 0.25; 0.56/ 0.25; 0.77/ 0.2 mm), arolium large (0.55 mm in diameter), claws symmetrical. Mid femora with terminal spine, midtibia narrow; hindfemur robust, with terminal spine, hindtibia very long with at least 23 spurs of which 2 are terminal.

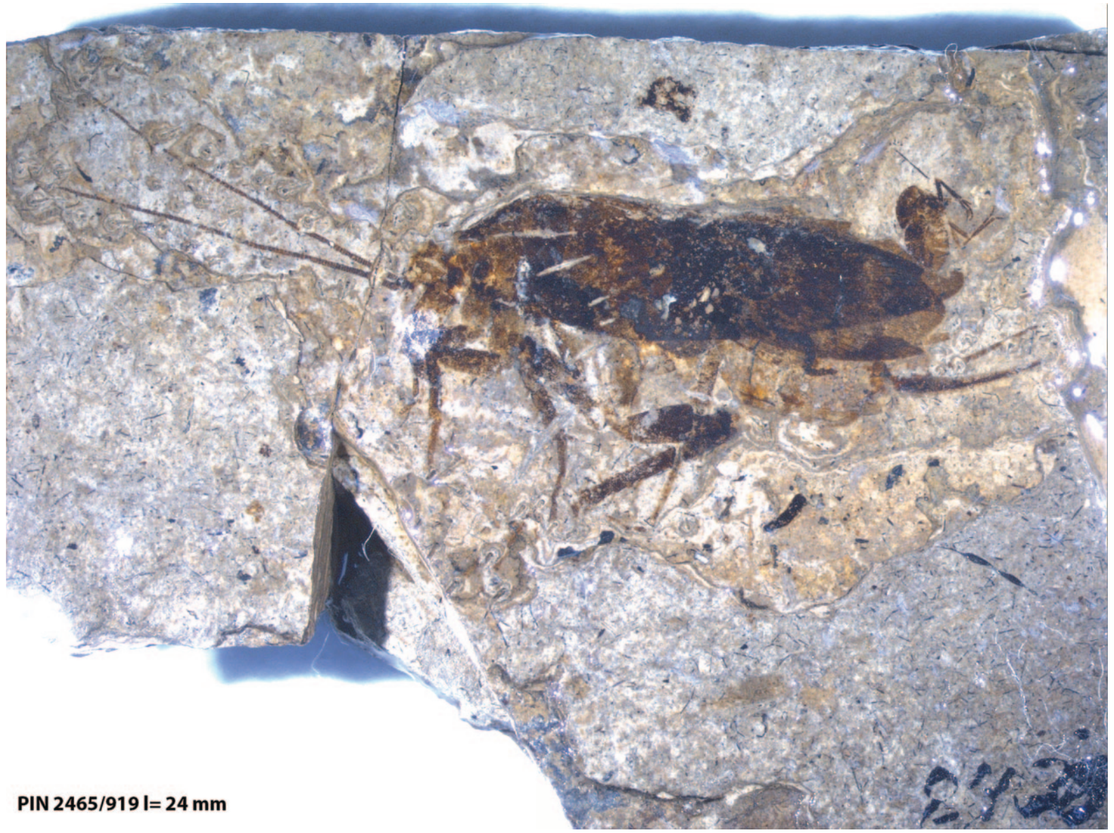
Remarks: Standardly brached SC is a strong plesiomorphy within family.
Mutations. Hindwing PIN 2784/980* contains a mutual CuA-CuA vein fusion.
Character of preservation: 21 completely articulated complete specimens (of them 2 isolated fore and hindwings), 58 isolated forewings, 9 isolated hindwings.
Taphonomy: Numerous complete specimens and presence of numerous hindwings combined with forewings articlulated with clavi suggest common presence in the original coenosis and short pre-deposition time. PIN 2997/89± contains preserved extremely fragile styli and palp supporting very short deposition time. As in the case of related *Decomposita*, this species often has wings (fore and also hindwings) that were apparently cracked during the life, suggesting sporadic flight similar to living mantodeans.

Rhipidoblatta brevivalvata Vishniakova, 1968 (figps. 207-209)

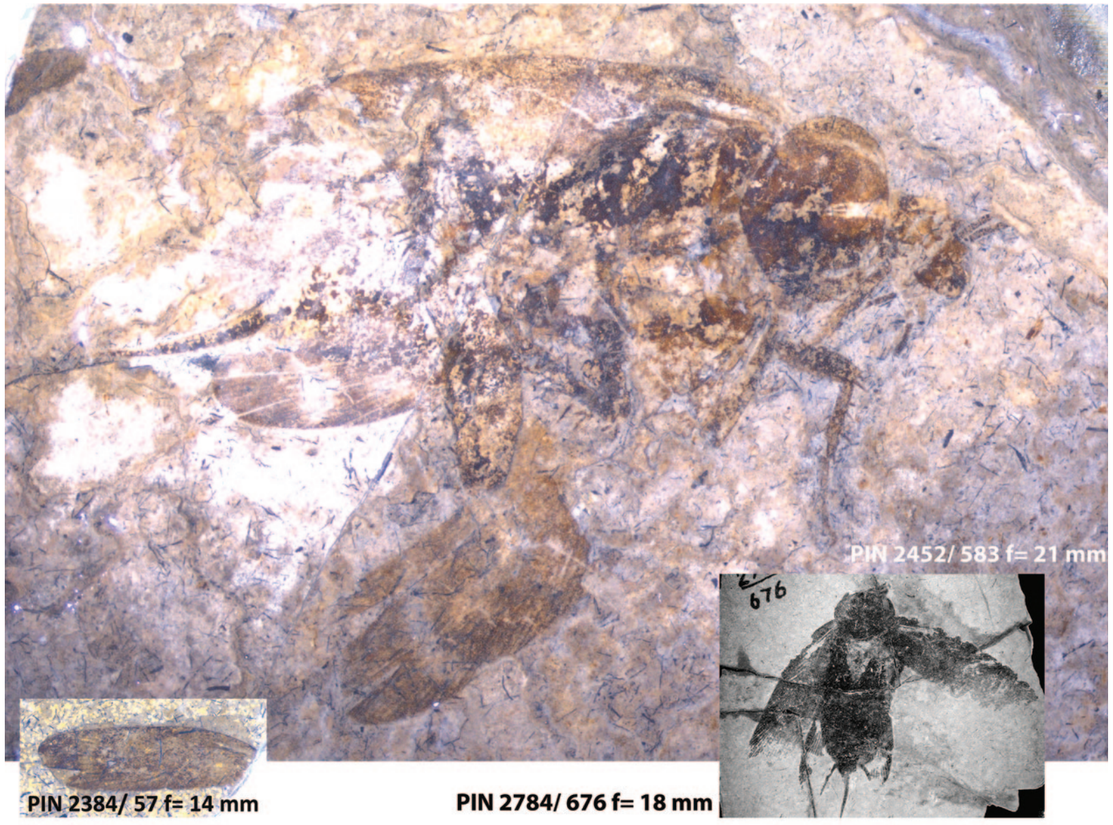
Holotype: PIN 2239/359. A complete adult winged female. (designated by Vishniakova 1968)
Type locality: Karatau, Kazakhstan.
Type horizon: Kimmeridgian Upper Jurassic, Karabastau Formation.

Additional material desigated here: PIN 2452/212, 583 (f= 21 mm; female); 2465/919 (l= 24 mm); 2554/34 (p= 7/ 5 mm); 2784/839 (p= 6/ 9.2 mm); 2997/ 1597 (f= 16-17 mm), 4429 (f= 25 mm) (complete specimens); 2384/57 (f= 14 mm), 67± (f= 20 mm); 2554/106 (forewings); 2784/676 (f= 17 mm); 2997/ 1553± (hindwings). All the same locality as the type.

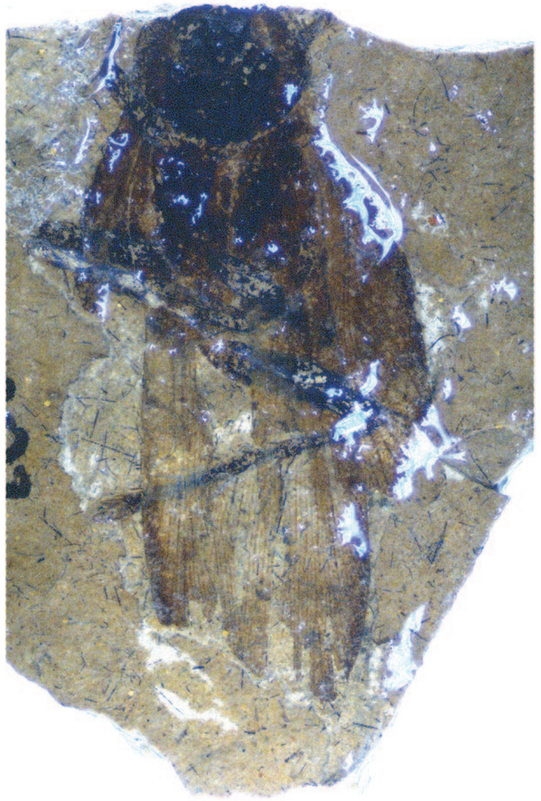
Diagnosis: Differs from *S. tri* in having partially colored hindwing, pale transversal stripe on a forewing and in having three longitudinal stripes on pronotum.
Redescription: Large species 20-30 mm long. Head short (4.5/ 3.2 mm), robust, nearly globular, dark, with pale wide long eyes. Antennal sockets large, 0.94 mm in diameter. Scape very large and wide (1.25/ 0.62 mm), antennomeres less sclerotized that in other species in genus, short and wide (0.15/ 0.31 mm at base), antenna long at least 27 mm. Palp short, 3 or 4-segmented, labial palp short. Mandible robust, comparatively small.
Pronotum cordiform, transverse (4.6-7/ 5-9.2 mm). dark, with 3 wide long longitudinal pale stripes (one central and 2 sublateral).
Forewing moderately elongate, 14-25 mm long and 5-9.2 mm wide, regular in shape and venation with intercalaries, widest in the middle, dark, with dark anterior margin and apical pale transverse elongate macula. Pale is also the Sc base. Costal area wide, with 6 Sc veins at margin. R is



PIN 2465/919 l= 24 mm







PIN 2997/1597 f= 16 mm

slightly sigmoidal, with 12 radial veins at the margin (R1 are mostly simple), 12 M and 16 CuA are slightly sigmoidal, CuP simple, fluent, clavus with 14 or more veins at the margin.
Hindwing with narrow remigium, shorter than forewing, terminating at the same level, colored, with terminal transverse elongate macula similar as forewing.
Legs short, femora and tibiae dark, tarsi pale, non-sclerotised hardly. Arolium present.
Forefemur (R: 3.1/ 1 mm) with apical spine, foretibia with at least 8 spurs (3.6/0.46 mm), foretarsus long (3.5/ 0.23 mm).
Midfemur moderately robust (9.8/2 mm), midtibia heavily carinated, midtarsus long.
Hindfemur robust (11.2/ 3 mm), hindtibia long and narrow (11.5/ 1.8 mm), tarsus very long 0.6 mm.
Female posseseed a long narrow and sharp externally protruding ovipositor (9 mm) and sharp long muiltisegmented non-oligomerised cerci .
Character of preservation: 8 complete articulated adults; three isolated forewings, two isolated hindwings; 3 females, 4 unknown sex, 3 or more of them perhaps males.
Taphonomy: A single isolated wings suggest autochtonous habitat on land near the deposition water body.

***Rhipidoblatta trimestre* sp.n.**
(figp. 211)

Holotype: PIN 2066/637 (f= 18 mm). A completely winged adult male.
Type locality: Mikhailovka, Karatau, Kazakhstan.
Type horizon: Kimmeridgian Upper Jurassic, Karabastau Formation.

Differential diagnosis: Differs from sister species *S. triky* (synapomorhic in pronotum coloration) in smaller size, in monochromatically colored hindwing, lack of the pale transversal stripe on a forewing, monochromatic legs.
Description: Head comparatively small, nearly globular, with dark and pale fields. Antenna hardly sclerotized and melanised, with wide and short antennomeres (basalmost 0.2 mm wide).
Pronotum visually slightly transverse, cordiform (5/ 5 mm), dark, with three longitudinal pale wide stripes. Body comparatively narrow, but fat. Legs seems monochromatically colored and melanised, including tarsus.
Forewing moderately elongate, 18 mm long and 5.5 mm wide, regular in shape and venation with intercalaries, widest in the middle, dark R slightly sigmoidal, nearly straight, with 17 veins at margin, radia field wide. M (6) and CuA (13) slightly sigmoidal. CuP simple, fluent, sclerotized, dark. A with at least 12 veins at margin.
Hindwing 17.3 mm long, with narrow remigium, shorter than forewing, terminating at the same level, monochromatically colored. Sc simple, short, R1 (4) and rich RS (10) differentiated, radial area very wide; M expanded, with 7 veins at the margin; CuA with secondarily dichotopmised anteriormost branch, totally with 10 veins at margin and additional blind branches present. CuP simple, A1 with 3 veins.
Derivation of name: *trimestre* is after trimester.
Character of preservation: 1 complete completely articulated adult male.
Taphonomy: Lack of isolated wings suggest autochtonous habitat on land near the deposition water body.

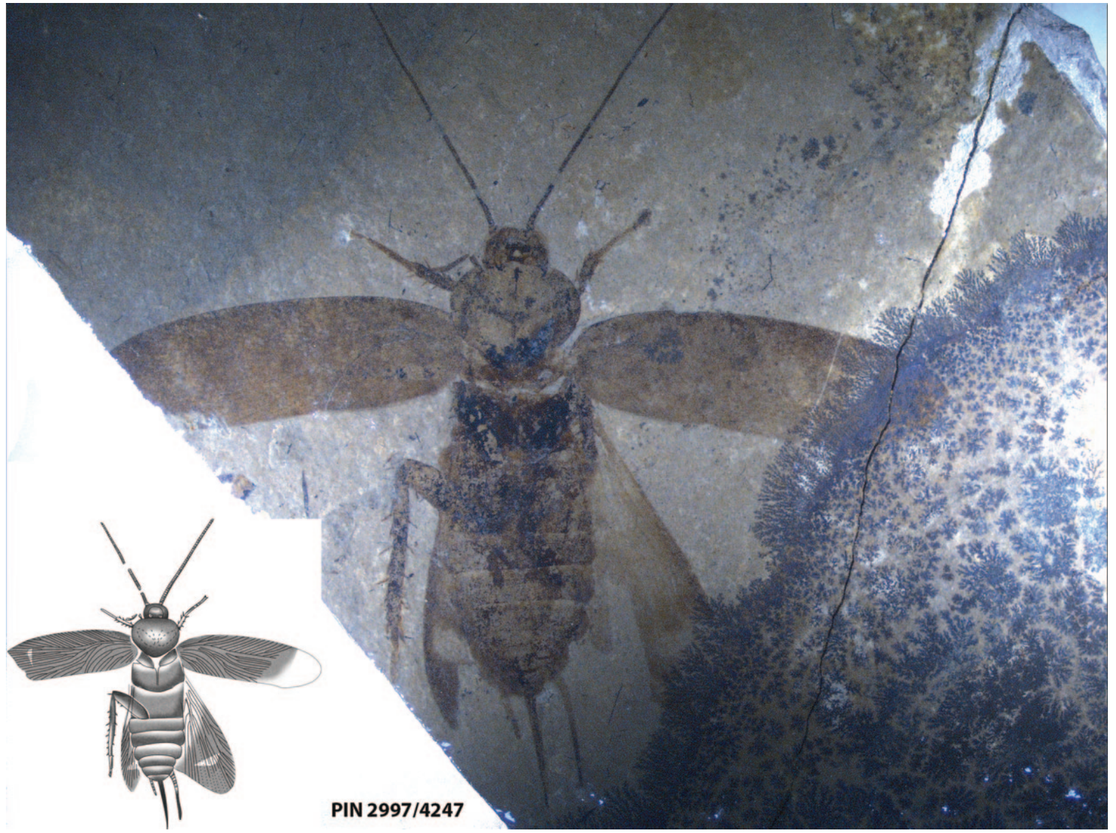


***Rhipidoblatta matriky* sp.n.**
(figps. 213-217)

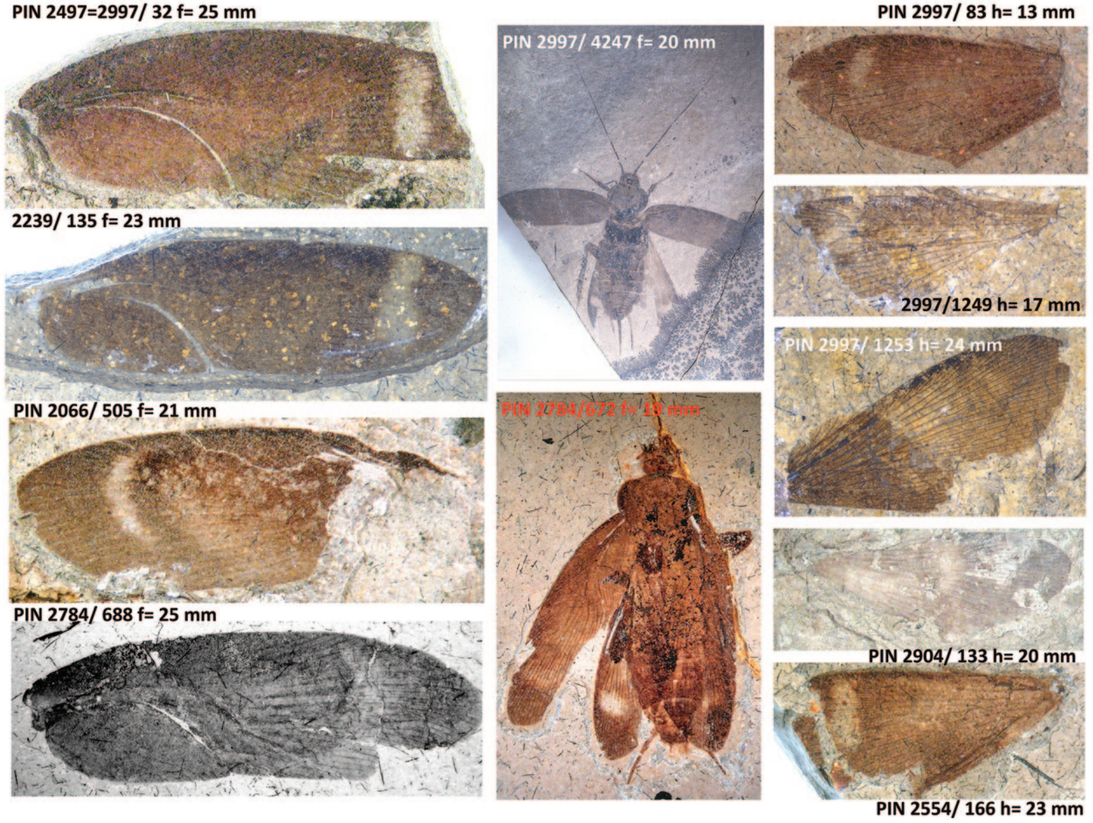
Holotype: PIN 2784/672. A completely articulated complete adult winged male (f= 19 mm).
Type locality. Mikhailovka, Karatau, Kazakhstan.
Type horizon. Kimmeridgian Upper Jurassic, Karabastau Formation.

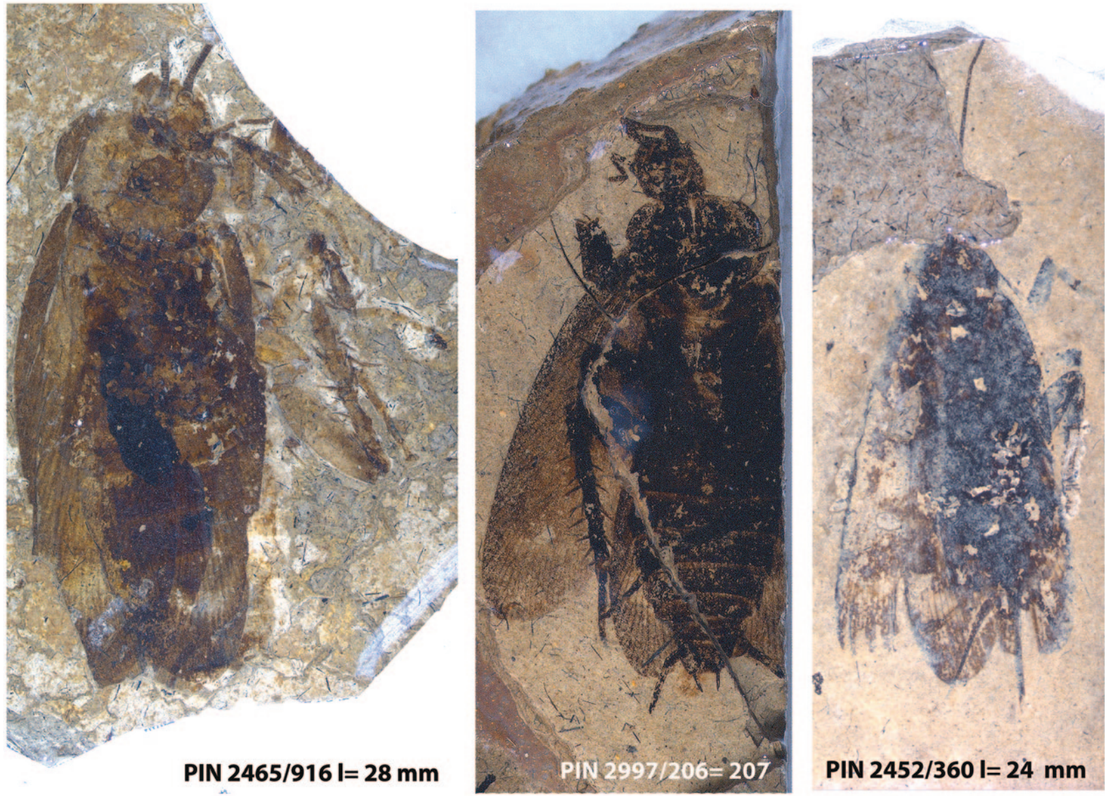
Additional material: 2231/2; 2239/135 (f= 22 mm; 5, 21, 9, 17, 1, 13), 360; 2452/360 (female; l= 24 mm); 2465/ 916 (l= 28 mm); 2511/103; 2554/113; 2784/636 (h= 17 mm), 672; 2997/206=207 (male), 750± (h= 20mm), 1265, 1270, 1273, 1517 (f= 24 mm), 4247 (female; f= 20 mm), 4376 (f= 16 mm; 4, 17, 10, 14, 1, 12), 4404 (complete specimens); 2066/505 (f= 21 mm); 2239/135 (f= 23 mm), 243 (f= 25 mm); 2384/135 (f= 20 mm; 1, 8+12, 5, 16, 1), 916*± (f= 28 mm); 2465/895, 921; 2497/32 (f= 25 mm); 2784/688 (f= 25 mm; 5, 15, 11, 12, 1, 12); 2904/133 (f= 20 mm), 231, 252; 2997/32 (f= 25 mm), 167, 178 (f= 16 mm), 180, 1138± (f= 23 mm; 4, 24, 9, 12, 1, 13), 1250 (f= 19 mm; 4, 20, 8, 12, 1, 10), 1346, 1577 (f= 20 mm), 4361 (f= 28 mm), 4362, 4377 (f= 28 mm); 4409 (f= 27 mm; 4, 29, 15, 7, 1, 13) (isolated forewings); 2064/141 (h= 18-19 mm; 1, 6+14, 5, 13+b+1), 167; 2384/101 (h= 20 mm; 1, 8+10, 6, 21+1); 2452/403; 2465/958 (h= 18 mm); 2554/166 (h= 23 mm; 1, 5+9, 5, 10+1); 2784/729± (h= 18 mm), 816; 2904/133 (h= 20 mm); 2997/83 (h= 17-19 mm), 155, 156, 213 (h= 17 mm; 1, 7+7, 6, 15++1), 233, 750 (h= 20 mm; 1, 5+13, 4, 15+1), 1253 (h= 24 mm), 1249 (h= 17 mm), 1253* (h= 23 mm; 1, 7+13, 7, 13+1), 1402 (h= 19 mm), 4255± (h= 17 mm; 3, 9+7, 7, 12+1), 4266± (h= 25 mm) (isolated hindwings). The same locality as the type.

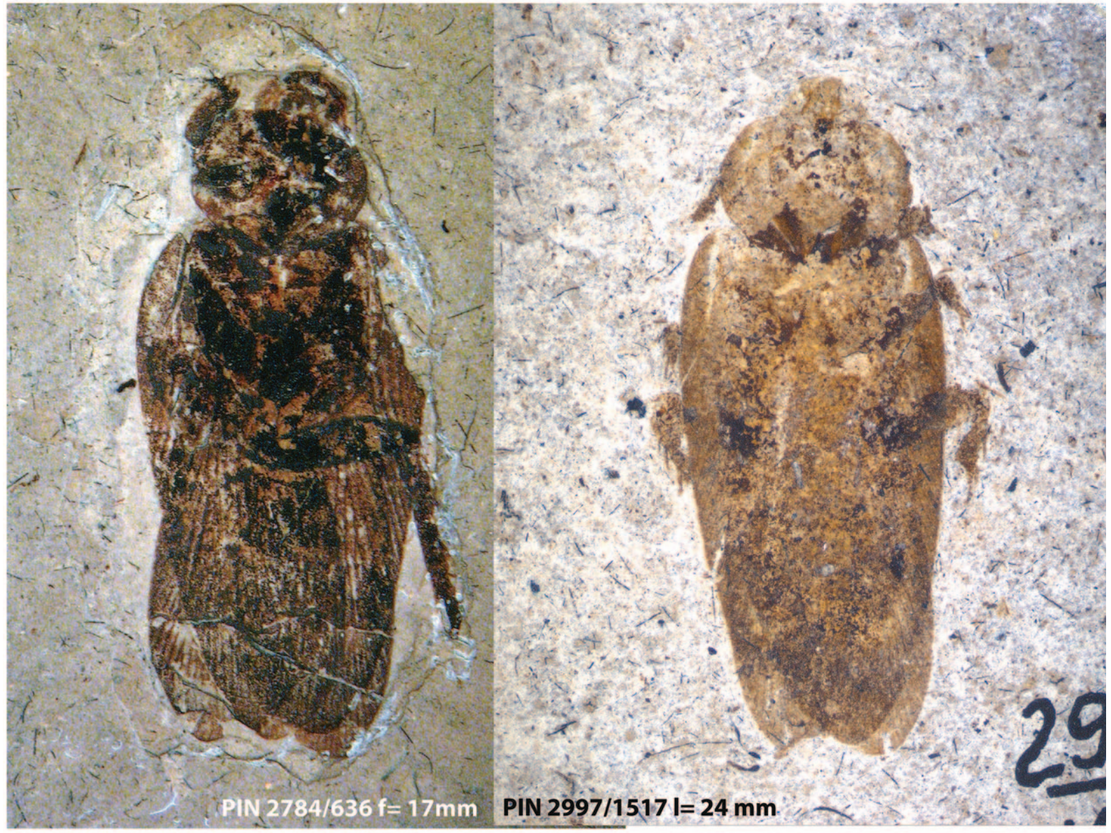
Differential diagnosis: The most common species in this genus can be differentiated on the basis of dark pronotum with pale areas restricted to narrow short rudiments at anterior margin (if any). It can be differentiated from *S. triky* based on smaller size and more extensive transverse apical elongate and curved pale macula.
Description: Moderately large cockroach. Head quadrate and only slightly elongate (3.1/ 3.04 mm) with strong mandibles. Eyes small and globular, wide (0.16/ 0.05 mm), dark. Three large pale ocelli present (0.05 mm in diameter). Palp very short and strong (?; ?; 0.06-0.16/ 0.03; 0.14-0.16/ 0.03 mm). Antenna filiform, 13.7 mm (as preserved) or longer, with at least 47 short and narrow (0.22-0.48/ 0.26-0.48) antennomeres.
Pronotum transverse (4.8-5.4/ 6.45-6.56 mm), cordiform, posteriorly slightly extended, monochromatic dark with narrow anterior pale margin. Forewing fully developed, 16-28 mm long, with apex posed anteriorly, with distinct shape ascending at posterior margin. Coloration monochromatic dark, with one variating transverse narrow pale stripe. Ocassionally also a paler area occur in the posterior margin to center. Sc simply branched (1-5). R richly branched, sigmoidal, short, not reaching apex (15-24); RS distinct within this system as simplified branch with about 3 veins. M rich expanded, sigmoidal (5-11). CuA expanded, with more straight anterior branches and sigmoidal posterior stem (12-17). CuP simple, fluent. A tertiary branched (7-13), diagonal kink weakly present (not distinct in all specimens).
Hindwing wide, 16-23 mm long, with pale base and dark apical half, in which a single transverse narrow pale stripe occurs. Sc simple, R1 and RS differentiated (4-9+7-14), R1 forms nearly a comb. M is very straight, rich (4-8). CuA rich and secondarily branched (10-21) and with additional blind branches. CuP simple.
Legs are robust, extremely strongly sclerotized and melanised - among femora only hind ones protrude beyong the forewings outlines at repose. Forefemora are so short and robust that they do not protrude beyond pronotum and are distinct only in specimen PIN 2465/916 preserved laterally (3.23/ 1.07 mm). Fore tibia also robust (4.15/ 0.77 mm), surprisingly not so heavily carinated, but with heavily carinated end. Foretarsus 4.15/ 0.11 mm long but fine and with fine arolium (0.11 mm in diameter) and symmetrical claws, and less sclerotized and also less melanised.

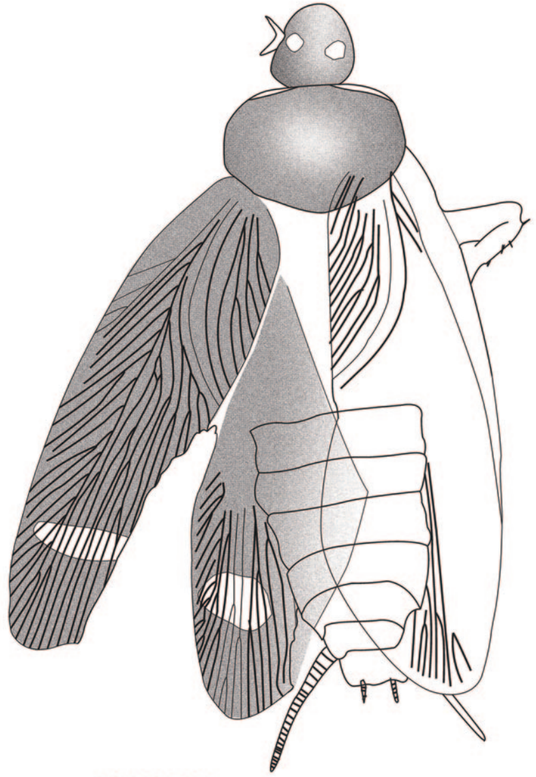


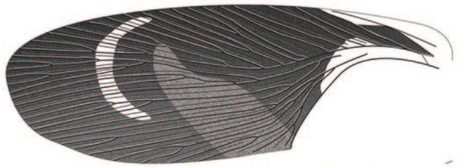
Rhipidoblatta matriky

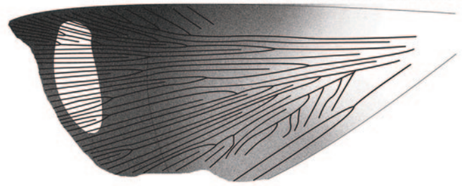

PIN 2497=2997/ 32 f= 25 mm
PIN 2997/ 4247 f= 20 mm
PIN 2997/ 83 h= 13 mm
2239/ 135 f= 23 mm
2997/1249 h= 17 mm
PIN 2997/ 1253 h= 24 mm
PIN 2066/ 505 f= 21 mm
PIN 2784/ 688 f= 25 mm
PIN 2904/ 133 h= 20 mm
PIN 2554/ 166 h= 23 mm


PIN 2465/916 l= 28 mm
PIN 2997/206= 207
PIN 2452/360 l= 24 mm

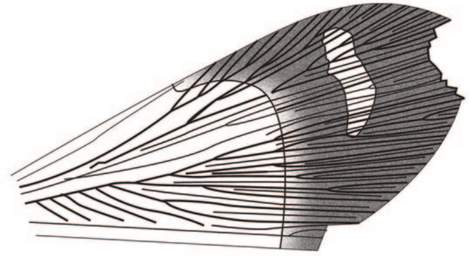



PIN 2784/672


PIN 2066/505 f= 21 mm


PIN 2554/166 h= 23 mm

PREDATION MARK


PIN 2997/750 h= 20 mm

Midlegs robust, hindfemur extremely robust (also visible only in laterally preserved specimen) 6.96/ 2.01 mm. Mid tiabia long and robust (8.97/ 0.93 mm) and also not heavily carinated (only six 0.9 mm long spurs are discerned). Hindlegs are longest, although also very short. Hindtrochanter robust, Hindfemora robust (5.28-5.77/ 1.54-1.77), with termional femoral spur, tibia very long 12.9/ 1.05 mm, moderately carinated (12+) with 1.04 mm long spurs.

Body surprisingly not very wide (6.8-7.6 mm), with 7-9 segment distinguished. Male 2 long (1.1 mm) symmetrical 7- segmented (1st stylomere elongate) styli present. Cerci long 5.4-7.1 mm, multisegmented, with 24 cercomeres. Ovipositor 5.25-6 mm long with clearly distinguished two lateral valves and the empty corridor among them.

Mutations: Hindwing 2997/1253 has an interminated vein; 2997/83 posses a mutual fusion of M veins. 2384/916 posses a forewing vein fusion.

Derivation of name: *matriky* is Slavic for “having tricks” and also “of a matricary”.

Remarks: The strong extremities combined with short palps and hard sclerotisation combined with head fully covered by pronotum and dark coloration suggests not only hidden lifestyle but also possibly a burrowing habits. Surprising in this mode of life is a low degree of carination and also comparatively narrow body.

Specimen 2497/32 (f= 25 mm) might possibly be erroneously marked as this number corresponds to Kenderlyk, Kazakhstan, a different locality. Nevertheless, this dominant genus and strikingly similar species might also possibly occur unless the Kenderlyk is Triassic and the number is thus only wronly labelled and/or poorly visible.

Character of preservation: 19 complete specimens (2 males, 2 females), 24 isolated forewings, 21 isolated hindwings.

Taphonomy: Presence of numerous complete specimens with preserved fine details such as styli and antenna suggest short stay in water prior to burial and abundance in the assemblage close to waterbody. High partition of hindwing suggest extremely short pre-depostiional transport. It is notable that also this species is charactrerised by preservation of stirred wings (fore- and hidnwings). Among all specimens, only single one is compact, without damages (PIN 2239/135).

***Rhipidoblatta matrikarky* sp.n.**

(figps. 219-220)

Holotype: PIN 2339/257±. A complete winged adult. Sex unknown.

Type locality: Mikhailovka, Karatau, Kazakhstan.

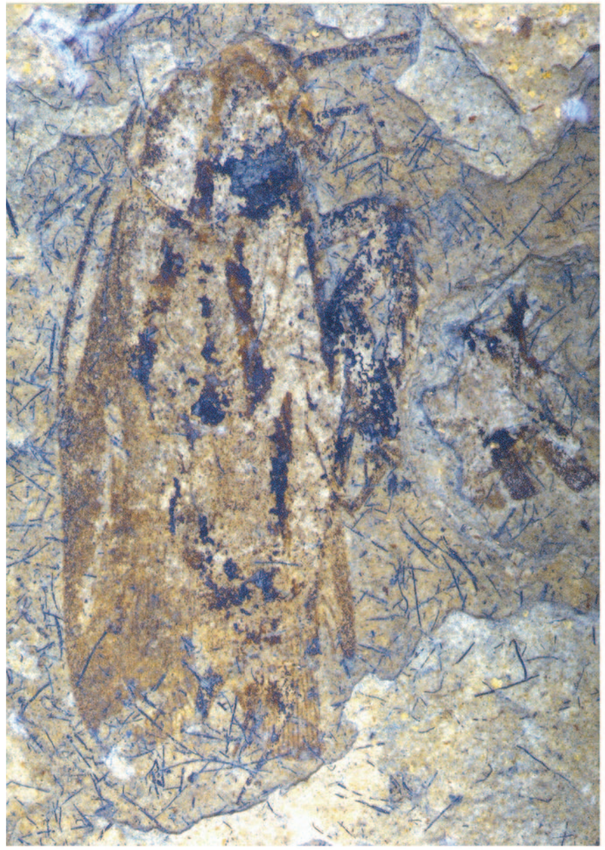
Type horizon: Kimmeridgian Upper Jurassic, Karabastau Formation.

Additional material: PIN 2997/151. A completely articulated winged adult female (f= 16 mm); 2066/281, 318, 405 (f= 22 mm), 458; 2904/290; 2997/1395 (isolated forewings). The same locality as the type.

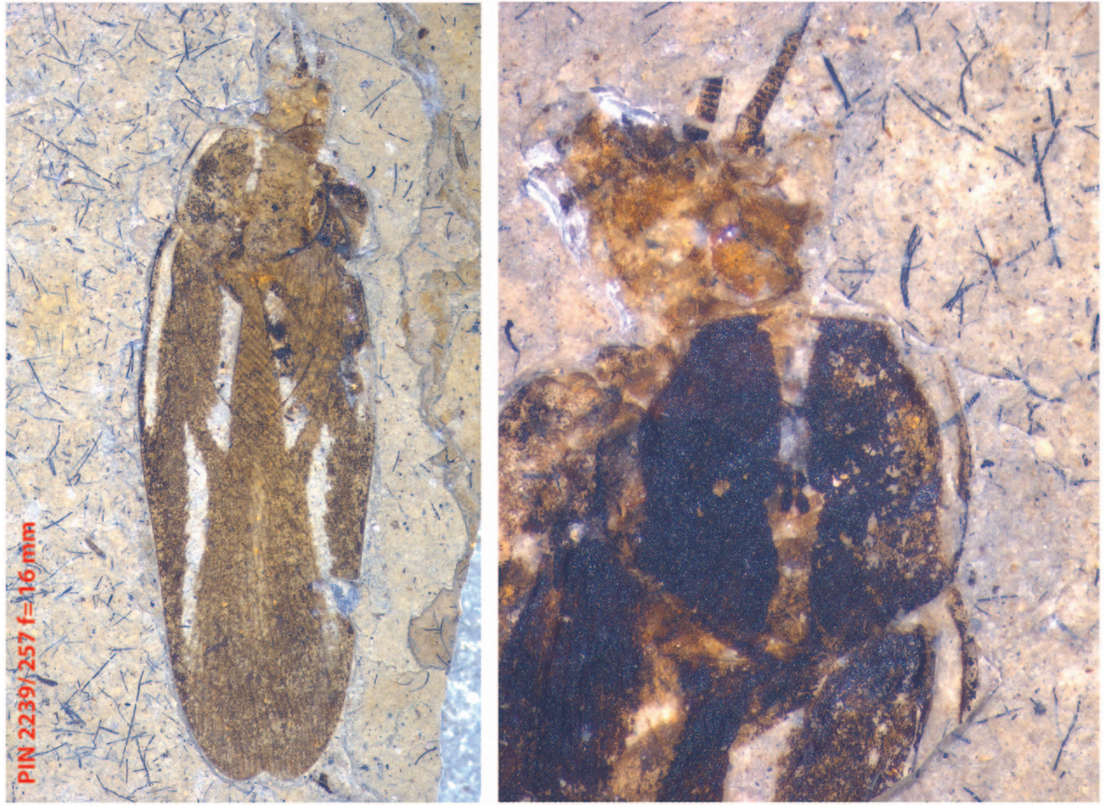
Differential diagnosis: Differs from all species within genus in smaller size, comparatively small pronotum and in coloration of pronotum and very specific coloration of sophistically-shaped forewings with 3 longitudinal stripes.

Autapomorphies: Small pronotum (generally unusual within family); longitudinal forewing striation, forewing shape sophisticate with depressed anterior margin (no homoplasies).

Description: The smallest species withing the genus, with complete body length under 20 mm. Elongate habitus is exemplified with longitudinal pale stripes on pronotum and forewings. Head robust, as long as wide (2.5/2.3 mm) with large antennal sockets 0.85 mm in diameter. Scape extremely wide and short (0.85/







0.59 mm), pedicel very wide and also comparatively short (0.51/ 0.34 mm), only as long as 5 consequent short and wide (0.28 mm) hardly sclerotized and melanised antennomeres. Palp standard, 4-segmented (?, 4/ 2, 11/ 2, 12/ 2, 1/ 1 mm) and also melanised as well as labial palp (ca. 2.8 mm long, likely 4-segmented). Mandible very short and robust, with 2 (R) and 3 (L) teeth respectively, uncolored.
Pronotum cordiform, small (3.7/ 4.7 mm), dark, with one central and 2 lateral longitudinal pale stripes. Within the central pale stripe, two small dark double dots occur.
Forewings elongate (14.5-16/ 3.8-4.1 mm), with sophisticated shape, base is wide, than the margin is shortly straight, then anterior margin is depressed, apex is round, posed slightly anterirorly, posterior margin simply straight. Clavus is simply fluent with ca. 9 anal veins at margin (mostly dichotomized and secondarily dichotomized).
Sc with 4 branches at margin, R strongly sigmoidal (14), M slightly sigmoidal, with 7 veins at margin, CuA expanded, sigmoidal (14), CuP simple, very dark.
Forewing with regular intercalaries and cross-veins, dark, with 3 pale longitudinal stripes (the first, anterior follows the dark forewing hem and terminates in the level of clavus; the middle one follows the sigmoid of R main stem; the last, shortest follows the diagonal kink and follows in rest of the wing).
Hindwing shorter, terminated at the same level as forwings, without coloration except for the dark anterior hem.
Legs very robust, short. Fore-, mid- and hindfemur colored, melanised (R: 3.4/ 1; ?; ? mm), with terminal spur; as well as all three tibiae (R: 3.5/ 0.7; 4/ 0.9; ? mm). Tarsi uncolored, first tarsomere rather short (?; 18/ 4; 18/ 3mm), arolium absent, claws symmetrical.
Body wide and fat, female ovipositor very long, sharp and narrow, distinctly composed of two longitudinal valves.
Derivation of name: *matrikarky* is Slavic for "of the matricary" and also "matricaries".
Remarks: This species can be categorized within the genus on the basis of autapomorphic cordiform pronotum and long externally protruding ovipositor. Forewing and hindwing is with dark anterior hem as in *S.tri*, hindwing is otherwise oncolored, like only in *S. tri*. Pronotum coloration is similar only to *S.triky*. Elongate forewing ressemble that of the Raphidiomimidae. But fat and wide, but narrow compared to other representatives of the family except *Asioblatta*.
Character of preservation: 2 complete adults (an unknown sex and a female), one completely articulated, one without legs, 6 isolated completely articulated (with clavus) forewings.
Taphonomy: Just two isolated wings suggest autochtonous habitat on land near the deposition water body.

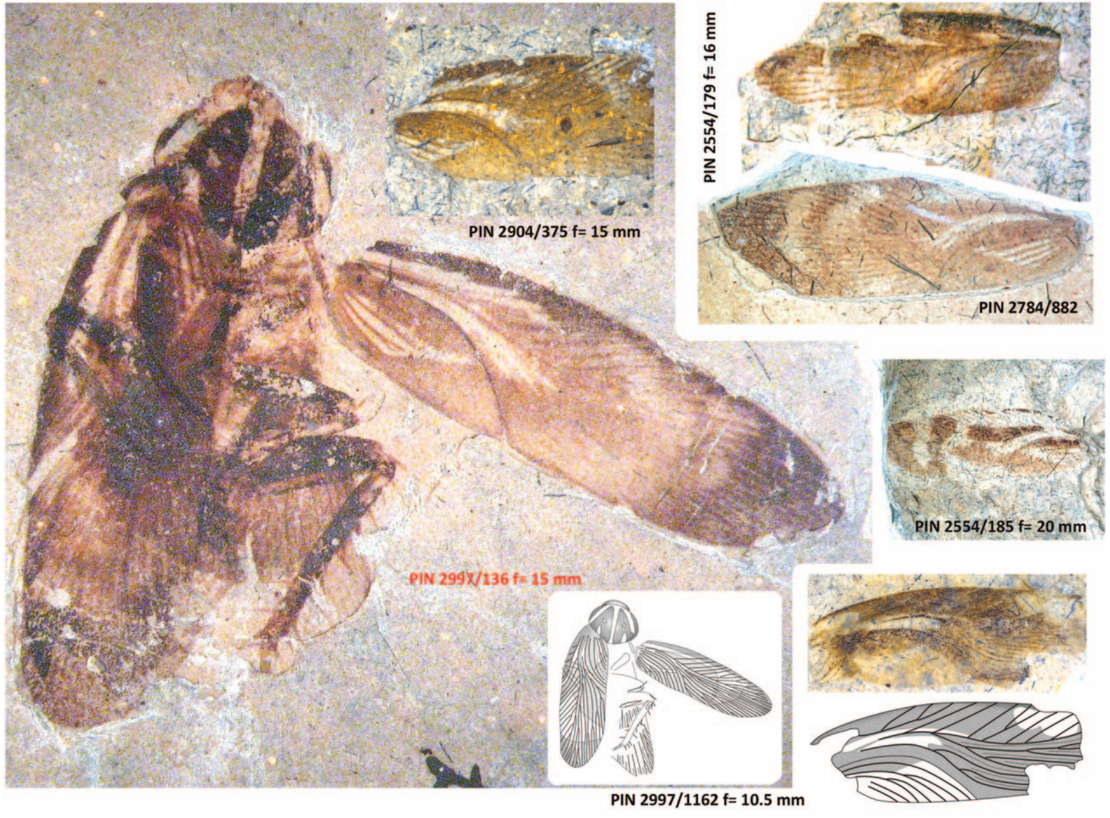
***Rhipidoblatta triky* sp.n.**

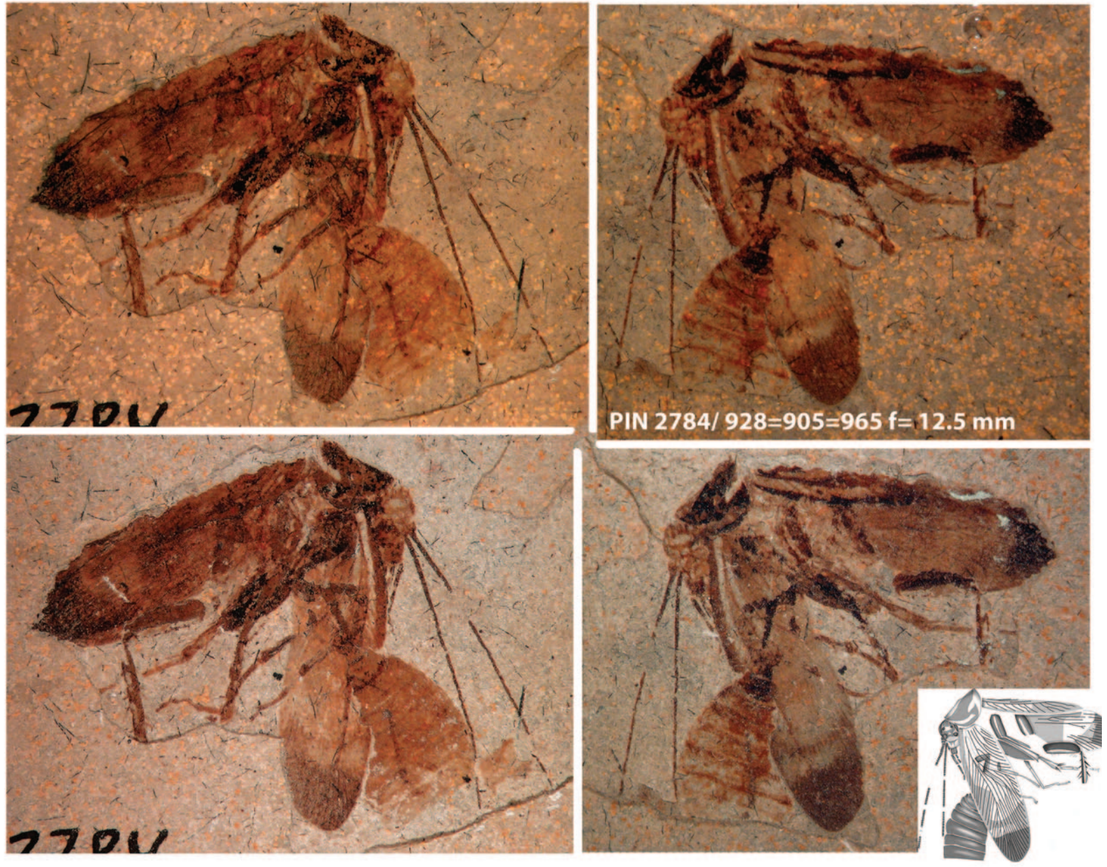
(figps. 222-223)

Holotype: PIN 2997/136 (f= 15 mm). A completely articulated complete winged adult without body (sex unknown).
Type locality: Mikhailovka, Karatau, Kazakhstan.
Type horizon: Kimmeridgian Upper Jurassic, Karabastau Formation.

Additional material: PIN 2784/928=965 (905 in photolabels) (f= 12.5 mm; 3, 23, 7, 11,1, 10); 2997/277; 2904/1860 (f= 15 mm) (complete specimens; sex unknown); 2554/99, 179, 185 (f= 20 mm; 15, 7, 9, 1, 13); 2784/882 (?. 18, 8, 5, 1, 10); 2904/35, 125 (f= 15 mm; ?, 14, 8, 7, 1, 8), 158 (f= 17.5 mm; 3, 17, 7, 10, 1, 12), 375 (f= 15 mm); 2997/221, 1162± (f= 10.5 mm); 4346 (f= 16 mm; 6.11+4.6.17.1.9+) (forewings). The same locality as the type.

Differential diagnosis: Differs from congeners in having sophisticated forewing coloration combined of dark and light dark stripes and areas.
Autapomorphies: Sophisticated coloration of forewing including a pale "mirror" with conspicuous dark veins on it. Possibly also more straight ovipositor.
Description: Head elongate (2.5/1.7 mm), pale, with sophisticated dark pattern formed with two lateral occipital short stripes and a central divided dark stripe, apical two dark "triangles" posed close to


PIN 2904/375 f= 15 mm
PIN 2554/179 f= 16 mm
PIN 2784/882
PIN 2554/185 f= 20 mm
PIN 2997/136 f= 15 mm
PIN 2997/1162 f= 10.5 mm


PIN 2784/ 928=905=965 f= 12.5 mm

another, and and dark central semicircular area of head with a pale aperture. Antenna very long (10 mm as preserved), dark, with subapical segment sequence pale, and with at least 58 antennomeres including scape and pedicel (without pale parts where antennomeres are indistinct and also without missing apical part). Antennal socket very large, dark, 0.42 mm in diameter. Scape extremely robust up to 0.42 mm wide, but very short; pedicel also very robust (2.5/ 0.33 mm). Antennomeres rater short and wide (0.08-0.32/ 0.16-2.1 mm). Two distinct, lens-like lateral oceli present (0.16 in diameter).

Pronotum transverse with small central posterior extension (3.9/5 mm), dark, with sophisticated coloration pattern formed with pale central stripe, lateral and anterior wide pale margins and posterior short lateral symmetrical stripes. Forewing elongate (12.5-20/4.14-6.3 mm) with sophisticated coloration pattern composed of two different hues of dark membrane coloration, pale horizontal and pale longitudinal stripes and also pale coloration of intercalaries within the clavus, forming "mirror" with dark veins. Sc simply branched, fine (3-6). R very rich, expanded, long, overlapping aperx and with clearly differentiated RS as the posteriormost rather isolated dichotomized branch containing up to 4 veins (15-23). M rather simplified, sigmoidal (6-8). Cua expanded, sigmoidal and with richly branched short posteriormost veins forming a comb with up to 5 veins (5-17). CuP fluent, simple. Anal veins not numerous, but tertiary dichotomized (8-13). Diagonal kink distinct (sometimes expressed as a more area pale).

Hindwing shorter, covered by forewing in repose, with dark membrane and very dark apex, and with two pale fenestra (anterior subapical and posterior subapical).

Legs slender, very long and with extremely long 4-segmented tarsi. Forecoxa robust (1.25/ 0.5 mm), dark, without coloration pattern; forefemur very short (2.25/ 0.17 mm), dark, with posterior pale halve; foretibia long (1.66/0.5 mm), with very long (3 mm), 4-segmented tarsus (1.67/ 0.15; 0.58/ 0.17; 0.25/ 0.13; 0.42/ 0.18 mm), terminated with symmetrical claw and small arolium (0.12 mm in diameter). Midlegs patterned (see hindlegs), with very long (3.3 mm), 4-segmented tarsus (0.92/ 2.3; ?; ?; 0.34/0.13; 4.17/ 0.17 mm), symmetrical claw and small arolium (0.17 mm in diameter). Hindfemora robust (4.6/ 1.3 mm), with 9 posterior fine spines (or strong sensilla) and with terminal femoral spur 1.02 mm long. They are also likely dark, sclerotized and with pale posterior side. Hindtibia also patterned(elongate coloration), very long, strong, slightly curved (6.3/0.74 mm) and with at least 15 spurs long up to 1.21 mm.

Body fat and wide (4.8 mm) with 8 segments preserved (likely incomplete), long ovipositor seems more straight compared other species in the genus.

Remarks: This species is remarkably similar to *Decomposita* (*triocella*), which has more simplified venation, coloration, and is more advanced and predatory. It cannot be excluded that the lineage of predatory cockroaches represented by *Decomposita* originated from *Rhipidoblatta* aff. *triky*. The coloration belongs to the most sophisticated one.

Deformations: 2784/928=905=965 posses mutual fusion of the hindwing M veins; 2554/185 posses mutual fusion of two radial veins.

Derivation of name: *triky* is Slavic for tricks.

Character of preservation: 4 complete adults (unknown sex),11 isolated forewings.

Taphonomy: Complete specimens and isolated wings might suggest combined origin or short depostional transport.

Rhipidoblatta trika sp.n.

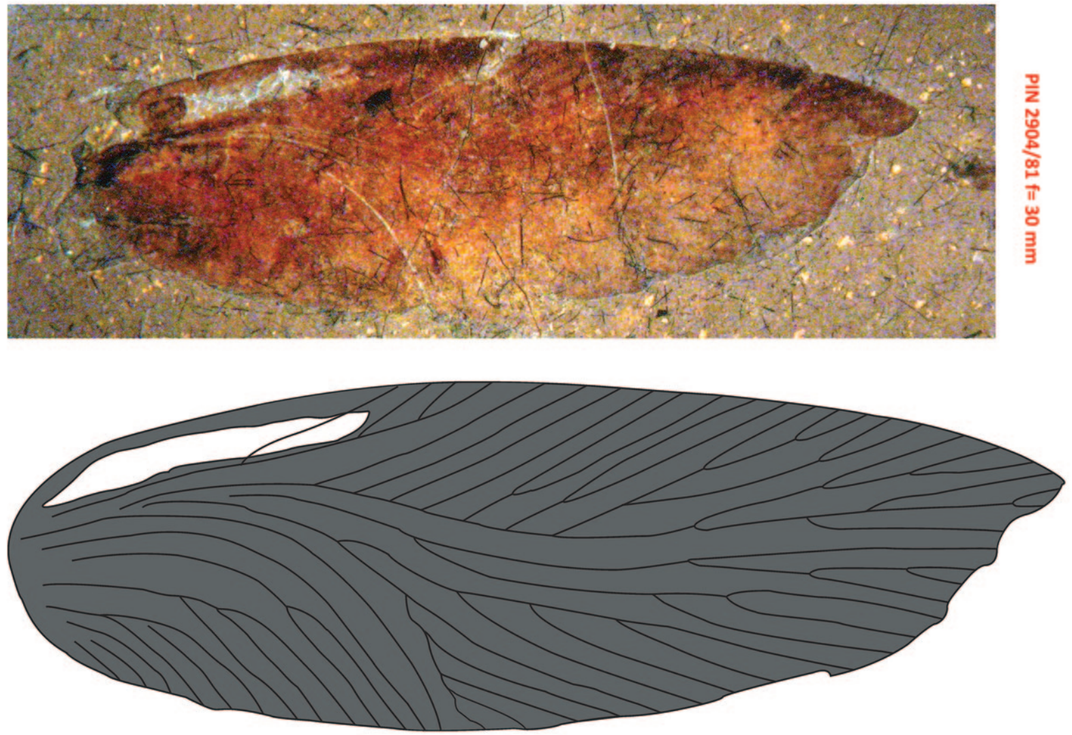
(figp. 225)

Holotype: PIN 2904/81 (f= 30 mm). Completely articulated forewing.

Type locality. Mikhailovka, Karatau, Kazakhstan.

Type horizon. Kimmeridgian Upper Jurassic, Karabastau Formation.

Additional material: PIN 2997/163± (f= 26 mm). Complete specimen. The same locality as the type.



Differential diagnosis: Differs from congeners in having pale costal fenestrum.
Autapomorphies: None possibly except for coloration and size
Description: Forewing large (26-30/ 9 mm), arcuate in thše center, dark with pale fenestruim in costal area. Costal area narrowed, Sc with 4 short branches. R area wide, radial vein strongly sigmoidal with 20 veins at margin, RS differentiated (7). M strongly sigmoidal, with more than 7 veins meeting margin. CuA comb-like, with 9 veins at margin, posteriormost short branch sigmoidal. CuP simple, fluent; anal veins branched (12). Diagonal kink indistinct or absent.
Derivation of name: *trika* is a stochastical combination of letter alluding to *trik* (Slovak for trick).
Character of preservation: 1 complete adults (unknown sex),1 isolated forewing.
Taphonomy: Complete specimens and isolated but completely articulated forewing might suggest origin near source waterbody or short depostional transport.

Genus *Memento* gen.n.

Type species: *Memento mori* sp. described below, and by monotypy.

Differential diagnosis: Differs from all representatives of the family in unmodified wings and wide unmodified pronotum (plesiomorphies). From all the known Caloblattinidae it differs in raptorial forelegs and insectivory. *Olzmasg* differs in modified forewing anterior margin.
Autapomorphies: Colored intercalaries along with transparent membrane are autapomorphic within family (homoplasic in numerous living groups and also in Cretaceous *Praeblattella* (Mesoblattinidae) and Permian *Mutovia* (Mutoviidae).
Description: As for species.
Systematical remarks: Simplified Sc suggest a Mesozoic-living group, while the secondarily branched A and short and wide antennomeres indicate categorization within Caloblattinoidea. Caloblattinidae are indicated with wide pronotum. The genus is advanced within the family as it is indicated by short Sc and modified sophisticated raptorial legs. Strong modification of generally widespread characted disallows the systematic position within the family, but slightly indicated posterior central extension of pronotum (synapomorphy) migh suggest origin or common ancestry with *Rhipidoblatta*. Prognathous head might suggest early derivation in respect to advanced Raphidiomimidae. Closely related to *Olzmasg*.
Remarks: It is a paradox, but this taxon, originally considered for true Caloblattinidae due to totally unmodified body (wide, with male tergal glands), forewing and also hindwing, and with unmodified short legs revealed the best documentation for the predatory way of life. This includes fully raptorial forelegs legs, which might suggest that raptorial legs were later reduced in advanced Raphidiomimidae. And the total evidence at least for cadaverevory includes gut content with chitin particles.
Another remarkable feature is the oligomerization of cercus, with only 8-9 segments, likely caused with its overall reduction in size. This is interesting as all families within the superfamily are characterized with long and multisegmented cerci.
Derivation of name: After *memento* (latin for to remember; such as *memento mori*).

Memento mori gen. et sp.n.

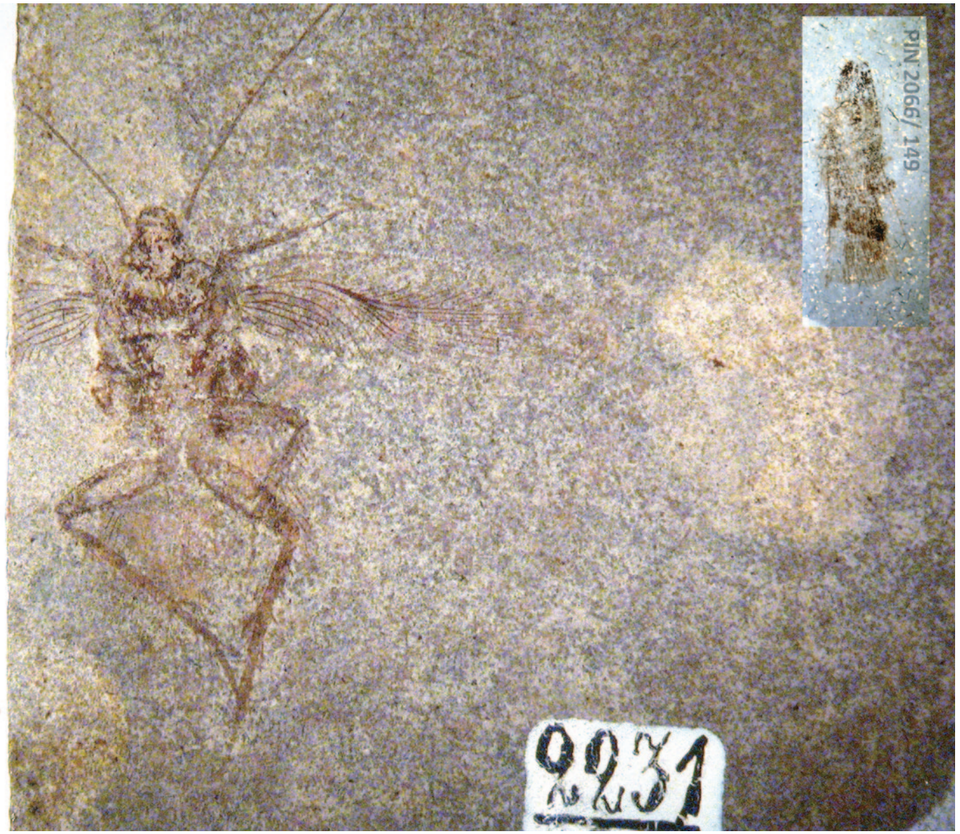
(figps. 228-240)

Holotype: PIN 2066/384±. A complete winged adult. Sex unknown.
Type locality. Mikhailovka, Karatau, Kazakhstan.
Type horizon. Kimmeridgian Upper Jurassic, Karabastau Formation.

Additional material: PIN 2066/475 (f= 15

Specimen	l	w	SC	R	M	CuA	CuP	A	RM	RCuA	MCuA	Total	Total without A
2997/95±	13.5		5	16			1	13					
2066/384±L	15		3				1	11					
2066/384±R	15		1			8	1	13					
2231/61	13		5	13	9	5	1	10	22	18	14	43	33
2784/825			5	15	13	11	1	10	28	26	24	55	45
2784/922	16		4	18	10	12	1	13	28	30	22	58	45
2997/47 (female)	14		5	17	14	12	1	14	31	29	26	63	49
2997/, 62	16		5	17	17	19	1	16	34	36	36	75	59
2066/506	16	4,9	5		13	16	1	15			29		
2066*/522	13		7	13	13	16	1	12	26	29	29	62	50
2554/204	18		5	19	13	10	1		32	29	23		48
2784/ 647±	13		3	21	11	14	1	11	32	25	35	61	50
2904/), 348L)	12		3	12	8	9	1	9	20	21	17	42	33
2904/), 348R	14		3	13	11	8	1	8	24	21	19	44	36
2904/354	18		6	18	14	11	1	18	32	29	25	68	50
2904/370	16		5	14	7	12	1	13	21	26	19	52	39
2997/ 1268	17		5	22	9	9	1	12	31	31	18	58	46
2997/ 254	13			15	6	16	1		21	31	22		
n	17		17	15	15	16	18	16	14	14	15	12	13
min	12		1	12	6	5	1	8	20	18	14	42	33
max	18		7	22	17	19	1	18	34	36	36	75	59
ave	14.85		4.41	16.2	11.2	11.75	1	12.38	27.29	27.21	23.87	56.75	44.85
dev	1.852066		1.416811	3.028437	3.028437	3.696846	0	2.604483	4.905704	4.774589	6.563301	10.19024	7.646853
CV	12.47		32.13	18.69	27.04	31.46	0	21.04	17.98	17.55	27.5	17.96	17.05

PIN 2231/ 61 f= 13 mm

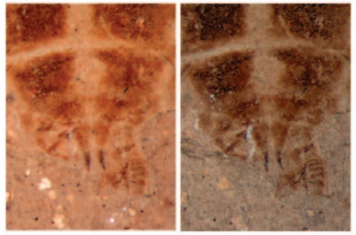






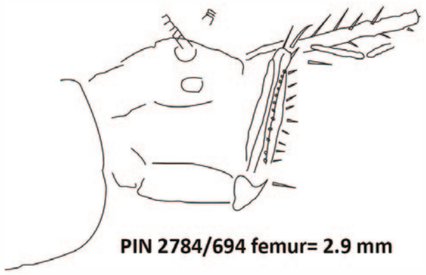
PIN 2784/837





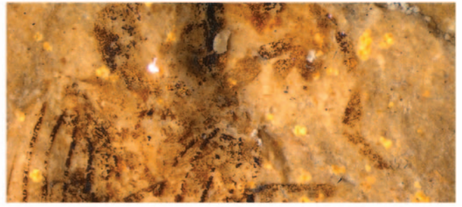


PIN 2554/27



PIN 2784/694 femur= 2.9 mm

PIN 2904/524 pw= 6 mm

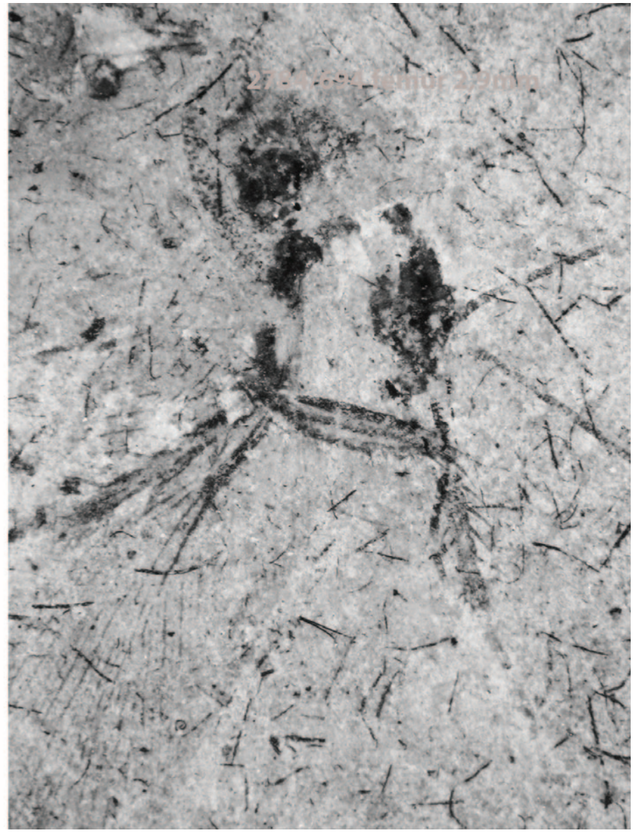


2997/62=49 f= 16 mm

PIN 2904/75



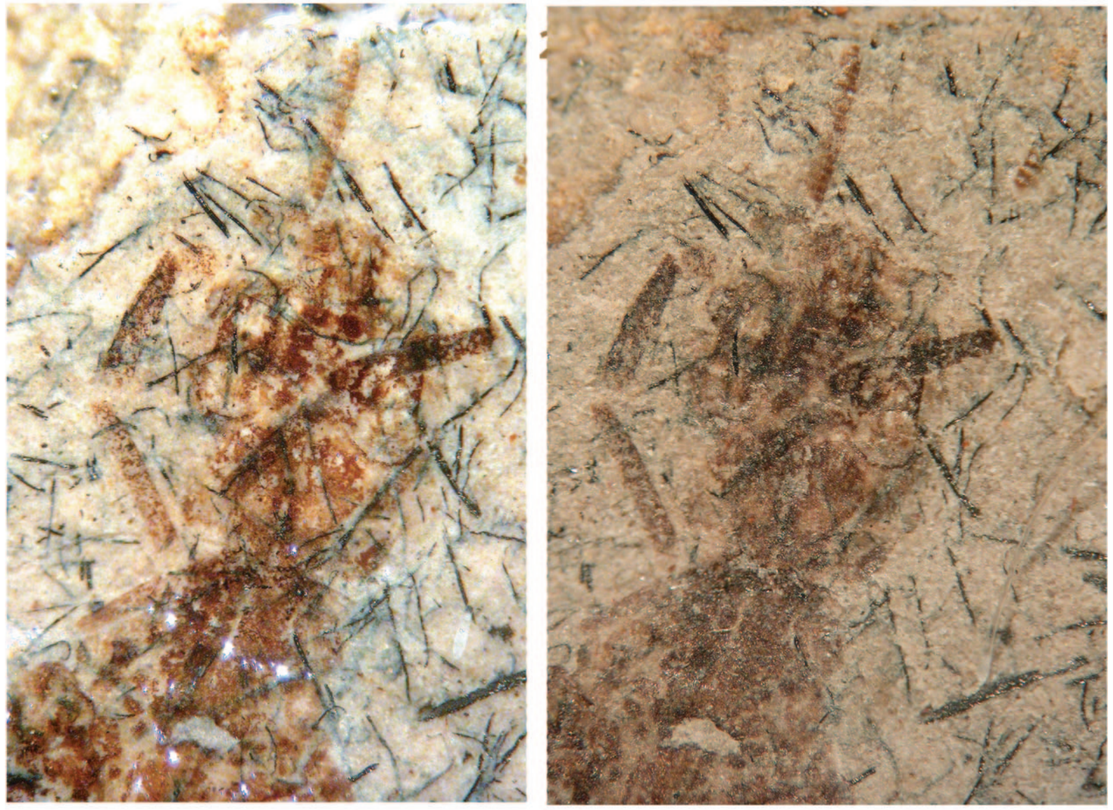




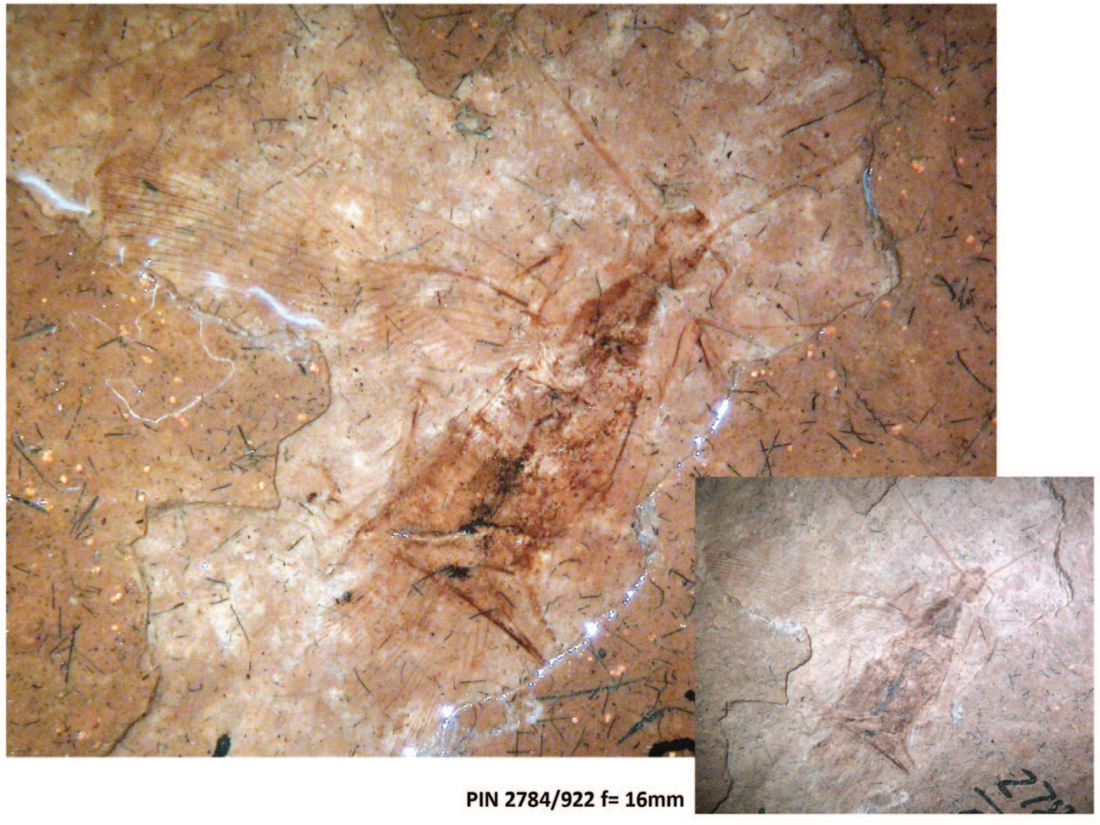


PIN 2904/ 75







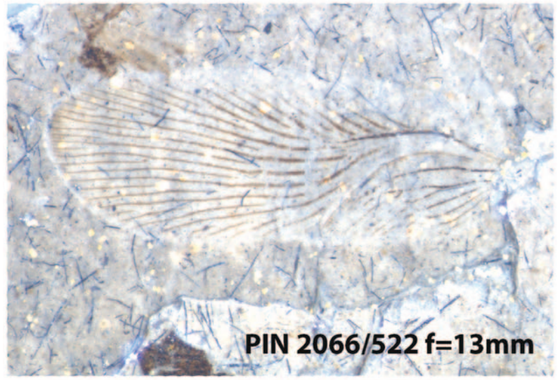


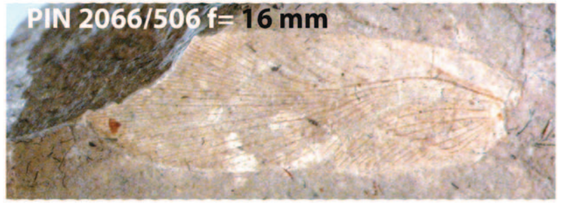
PIN 2784/922 f= 16mm

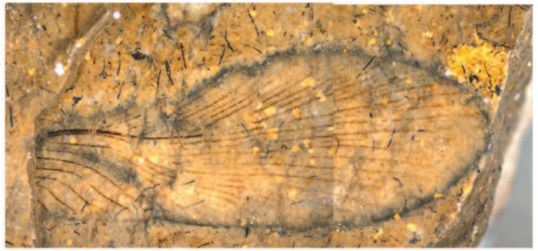


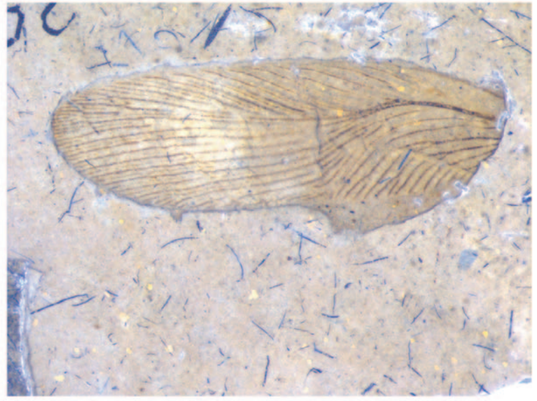
PIN 2997/95 f= 13.5 mm


PIN 2452/213 f= 11 mm


PIN 2066/522 f=13mm


PIN 2066/506 f= 16 mm


PIN 2997/254 f= 13 mm

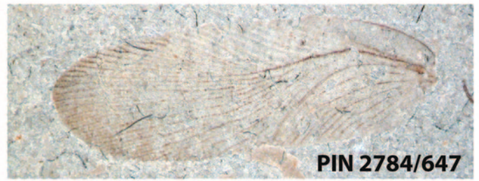

PIN 2904/370 f= 16 mm

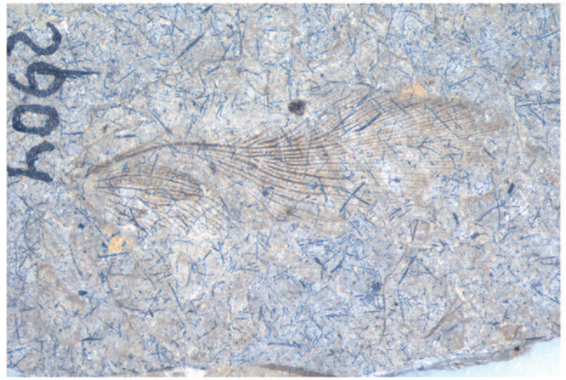

PIN 2997/49 l= 16 mm

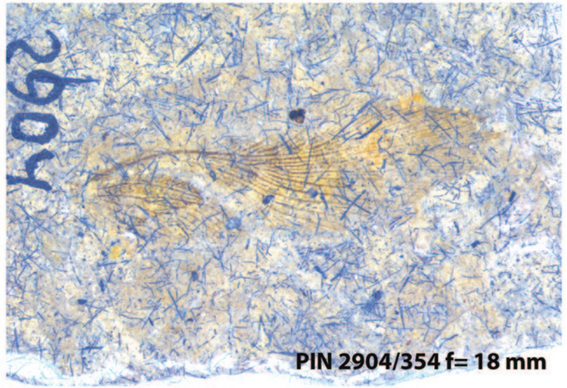


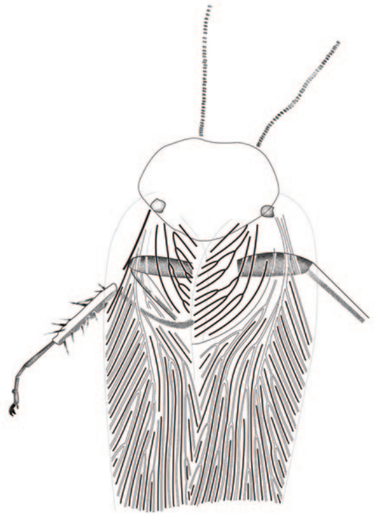

PIN 2554/204 f= 18 mm

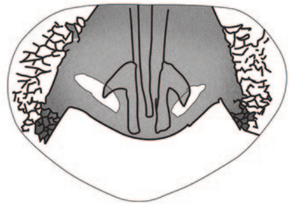


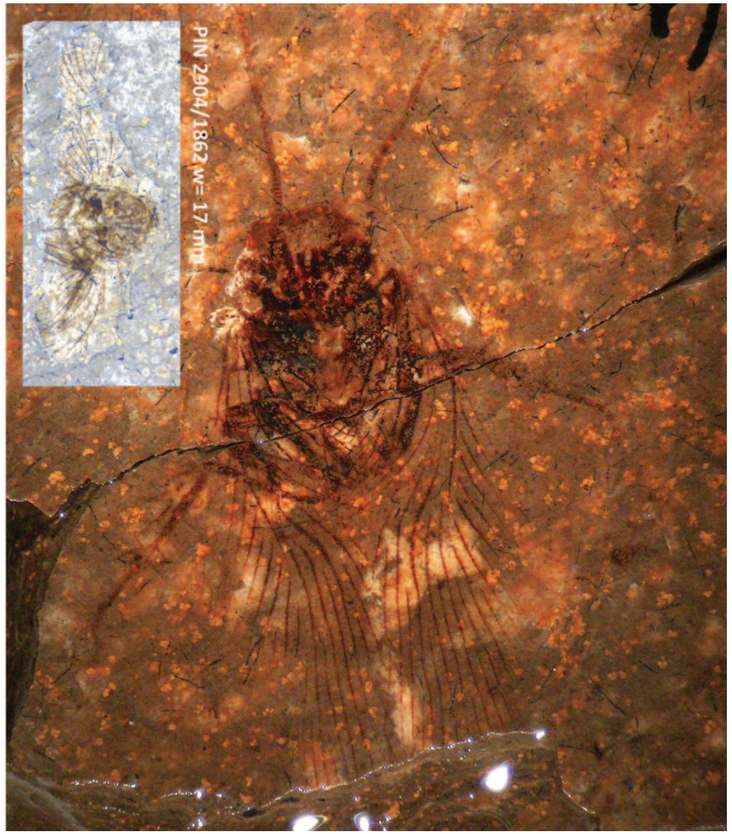

PIN 2784/647

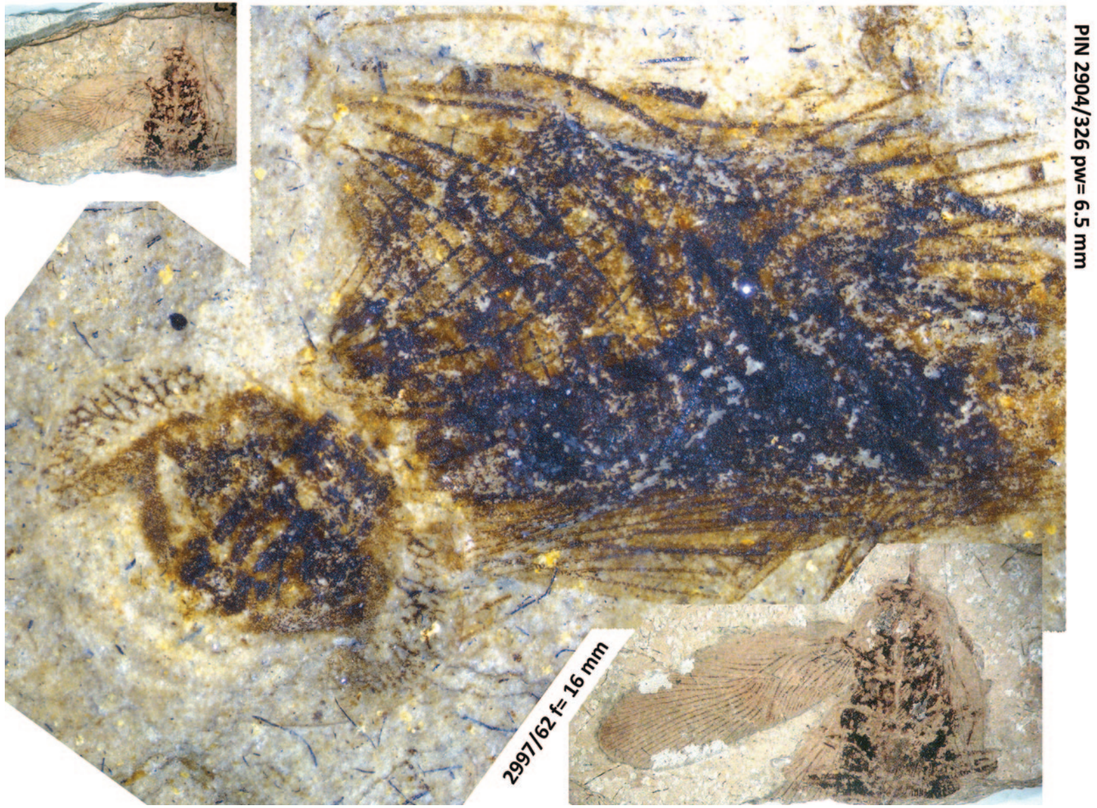

2904


2904
PIN 2904/354 f= 18 mm


PIN 2066/384 l= 17 mm


PIN 2904/326 pw= 6.5 mm


PIN 2904/1862 w= 17 mm



mm); 2231/61; 2239/163 (f= 13 mm), 203, 234 (f= 15 mm), 240 (f= 15 mm); 2384/25 (l= 17 mm; male with tergal glands), 134 (f= 15.5 mm); 2554/133; 2784/694± (raptorial leg), 825 (1, 4+9, 4, 7+1), 922; 2904/71 (p= 4/4 mm, f= 16/4.6 mm), 221, 304±, 324, 326 (pw= 6.5 mm), 1682 (w= 17 mm), 1871; 2997/47 (female), 62, 95± (female), 767 (f= 14 mm), 1228 (f= 13 mm), 1618, 1603, 1614 (complete specimens); 1789/218 **G**; 2066/65, 444, 506, 522; 2239/140 (f= 13 mm), 175 (f= 17 mm), 176 (f= 15 mm), 228 (f= 13 mm), 253 (f= 14 mm), 262 (f= 13 mm); 2452/213 (f= 11 mm); 2384/155, 156 (f= 15 mm); 2554/117, 118, 122, 149, 175, 202, 204; 2784/647± (one terminal dichotomisation CuA), 963, 967, 978, 954; 2904/157, 193, 226 (f= 14 mm), 227 (f= 15 mm), 348, 354, 366, 370, 1888; 2997/112, 188, 194, 244, 254, 1138±, 1218, 1592, 1885, 1476, 2823 (f= 14 mm), 2827, 1216, 1268, 1355, 1319, 1269, 1278, 4358 (f= 15 mm), 4411 (f= 13 mm) (isolated forewings); 2784/837; 2904/355, 341, 187, 198, 148, 208; 2997/266, 692, 1155, 1303, 1307, 1308, 1322, 1423, 2824, 1415, 1404, 1392, 1203 (h= 13 mm), 1200, 1240 (h= 25 mm), 1387 (h= 25 mm, 1, 8+9, 10, 16+blind), 1198 (isolated hindwings); 2066/283, 449 (isolated leg); 2904/337 (immature with preserved gut with chitin). All except G= Galkino from Mikhailovka.

Description: Head elongated, prognathous (3.2/ 1.9-3.6 mm) in repose completely covered with pronotum, dark, with pale part of the eye above apodema. Head base rectangular, rest of the head partially oval. Antennal sockets extremely large (0.6-0.7 mm in diameted), antenna standard (long 12 mm as incompletely preserved), antennomeres very short and wide (0.1-0.2/ 0.3 mm), mandibles large. Palp looks 3-segmented with segments 2 and 3 toghether 3.2 mm long.

Pronotum standard, unmodified, wide, transverse cordiform (4.5-5.7/ 5.4-7.6 mm), with fine sophisticated coloration reticulation dark pattern on pale paranotalia.

Body very wide (5.4-6 mm), unmodified, males with well developed tergal glands (on last four terga).

Cerci short and wide (1.8/ 0.3 mm) with only 9 segments preserved (n= 4), with striation of dark and pale areas and each segment with 6 large wide sensilla on dorsal side (preserved only as large round holes). Styli present in both sexes, short (0.5 mm), 2-segmented.

Female supraanal sternum very wide and short, with supporting structures of unknown origin (possibly modified inner valvae 0.9 mm long with dark base) and moderately long (protruding 1.8 mm beyond supraanal plate) ovipositor.

Legs short, femora pale, with wide dark antrerior and posterior margins and central stripe, tibiae longitudinally colored half pale half dark, tarsi dark. Foreleg raptorial, not especially long, but comparatively longer relative to other (very short) legs. Forecoxa free, standard (2.2/ 1.8 mm), forefemur (2.9-3.7/ 0.7-1.1 mm) with two rows of 9 and 12 strong long (up to 0.5 mm) posterior spines and with long terminal femoral spur. Foretibia of comparable length, fine (3.7/ 0.3 mm), carinated, with eight 0.6 mm long spurs. Foretarsus 3 mm long. Midfemur short and narrow (3.6-4.5/ 0.9-1.4 mm), dark, with terminal femoral spine, midtibia short (3.6/ 1.2 mm), with 12 spurs, s. Hindcoxa nearly 2 mm long, sophisticatedly-shaped, hindfemora also narrow, not robust (3.8-4.8/ 0.95-1.5 mm), posteriorly with two rows of 6 spurs each, with central row of spurs preserved as pitts and with terminal femoral spur as long as tibial spurs. Hindtibia (4.7-7.3/ 0.95-1.1 mm) with up to 18 up to 1 mm long spines. Hindtarsi very long and narrow (4.7/ 0.4 mm), first tarsomere very long, second-third tarsomeres subequal, terminal tersomere with claw slightly shorter, without arolium (2.35/ 0.77/ 0.77/ 0.77/ 0.5 mm).

Forewings 12-18 mm long, 4.9-6 mm wide, fore margin slightly arcuate. Intercalaries present and colored, main veins pale except for a basal dot and apex. Sc very short, shorter than clavus, simple or with up to 7 long and short branched. R slightly sigmoidal, with ocassionally tertiary dichotomized branches, at least 12 and up to 22 veins terminated in margin. M strongly sigmoidal, often simplified,



possibly with only 6 (and up to 17 veins) at margin; CuA with 5-19 long branches terminated at margin, CuP simple and fluent, clavus short, with tertiary dichotomized and usually richly branched A (8-18). Diagonal kink distinct.

Hindwing with transparent membrane, and with colored main veins and also intercalaries, especially expressed in the apical half. Usually about 13 mm long but two specimens with up to 25 mm long, with wide remigium. Sc simple, long, R1 (4-5) and RS (up to 9 branches) differentiated. Media with long straight branches, sometimes simplified with only 4 veins at margin. CuA well expressed, ocassionally with main anterior offshoot, with up to 8 veins at margin and with blind branches, some of them might dichotomise. CuP simple.

Variability: it likely suffers from the insignificant sample size (12-13), reflected in nearly 10 % difference among total number of veins compared to veins without A (17.96 vs 17.05 %). Addditionally this number is extremely high. High is also the size variability and intuitively two sets are present within the material possibly representing different sexes (f= 18 mm vs 13 mm). Additionally two very large (h= 25 mm) hindwings were preserved suggesting further expression of the variability. It also cannot be excluded that the variability within this species was actually very high – possibly a result of its numerous plesiomorphic traits. But intuitively, due to very high variability of CuA, general variability was lower that obtained from restricted data.

Mutations: There is an interesting link among structures observed in the specimen 2066/384. Two unusual characters, carvings regards two structures, pronutum and forewing, so these structures are apparently linked. Also the unusual (reversed) coloration comprise also coloration of legs generally in this species, suggesting also some linkage among genes responsible for these unusualities among different parts of the body. Other specimens are without depressions.

Vein deformations 2452/213 posses an unfinished blind A. Out of clavus, no deformity was recorded among studied material.

Derivation of name: after *mori* (Latin for a death: memento mori means *remember death – keep in mind death*).

Character of preservation: 28 complete specimens; 55 isolated forewings; 24 isolated hindwings, 2 isolated legs, 1 immature individual with preserved gut content (with chitin).

Taphonomy: This taxon is easily recognise-able due to unique (in this locality) coloration pattern. Also according to the preserved complete specimen and adequate ratio of hindwings it is very probable that this species was actually common in the actuocenosis near the burial waterbody. PIN 2997/348 evidences partial floating of the sediment, a rare occasion in Karabastau material, common in other sites such as polar Russia (in preparation). Specimen 2904/326 contained detailed preservation of pronotal coloration structure.

Family Skokidae Vršanský, 2007

Genus *Skok* Vršanský, 2007

***Skok svaba* Vršanský, 2007**
(figs. 245-247)
(see Vršanský 2007 for detailed description and discussion)

Holotype: PIN 2554/44. Complete winged adult female.
Type locality: indigenous for Karatau.
Type horizon: Karabastau Formation.

Additional material designated by P. V. Vršanský (2007): PIN 2554/77 (complete winged adult with unknown sex); 2066/322 (left forewing); 2784/684 (immature individual). The same locality as the type.
Additional material designated here: 2997/1279, 4416 (forewings). The same locality as the type.

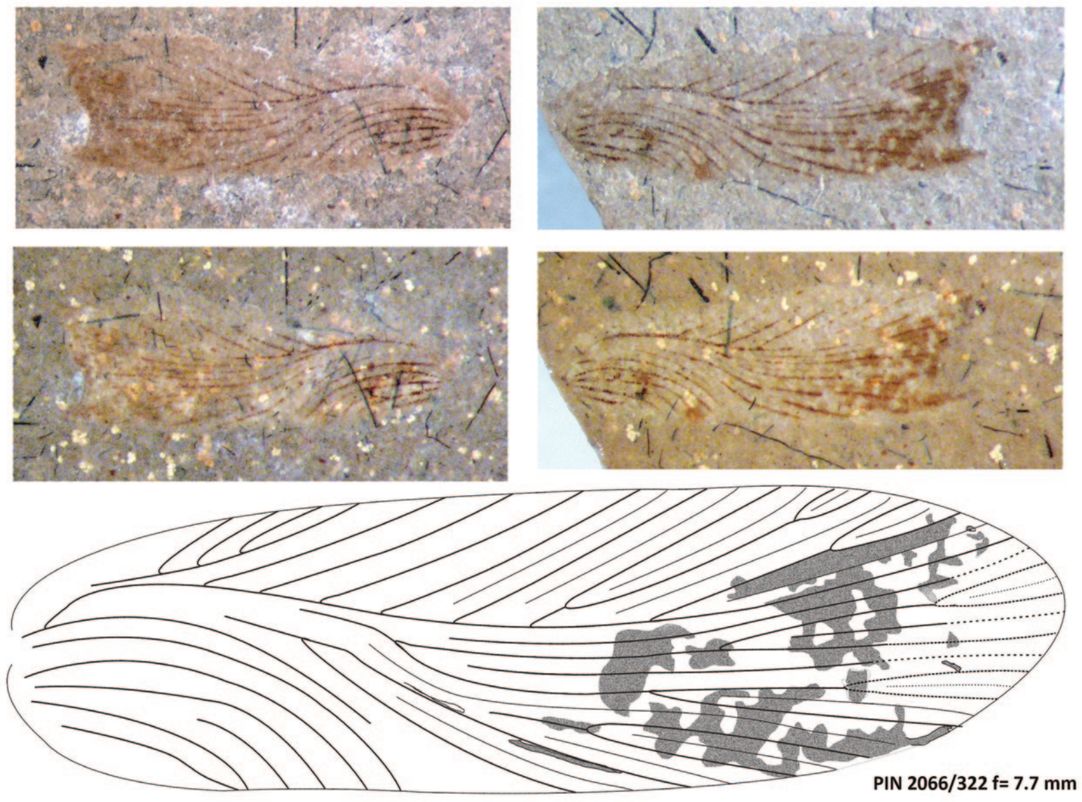
Systematical remarks: Variability within this species is (expected) higher as revealed with forewing specimen 2997/1279 (8.5 mm long, 7.7- 8.1 mm observed previously), Sc can reach only 3 veins (4-5 observed previously); R 12 (9-11 observed previously); M 9 (6-10 observed previously); CuA 7 (4 observed previously); A 8 (7 observed previously).
Character of preservation: 2 complete adults, 3 isolated forewings, one immature.
Taphonomy: Complete adults combined with the immature document habitats near the source waterbody sediments. It evidence this species was extremely rare and autochtonous (pollinator – Vršanský 2007).

Latiblattidae fam.n.

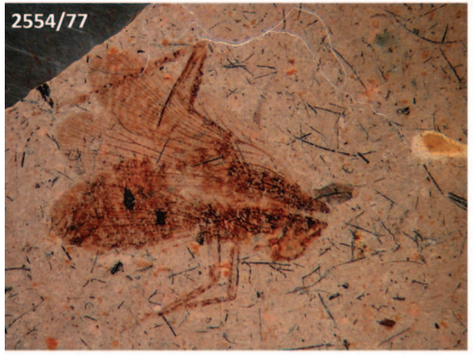
Type genus: *Latiblatta* Vishniakova, 1968.
Compostion: *Fosilia* gen.n. is categorized within this family on the basis of identical ovipositor, although did not posses permanenly joined forewings.

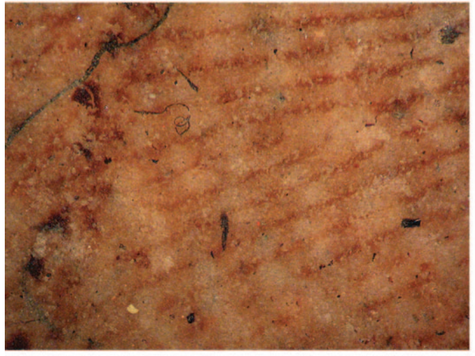
Type locality: Indigenous for Karatau.
Type horizon: Karabastau Formation.

Differential diagnosis: differs from Caloblattinidae and Phyloblattidae in having very wide pronotum and usually a forewing fixation mechanism, very long clavus (resp. short rest of the forewing) usually keeping forewings connected also during flight. Ovipositor is extremely wide basally forming nearly an isosceles triangle. From it, a long straight narrow tube protrudes. Oviposition likely involved injection of oocytes within hardened egg case, primitive precursor of ootheca.
Desription: As for emended species descriptions (for original designation see Vishniakova 1968).



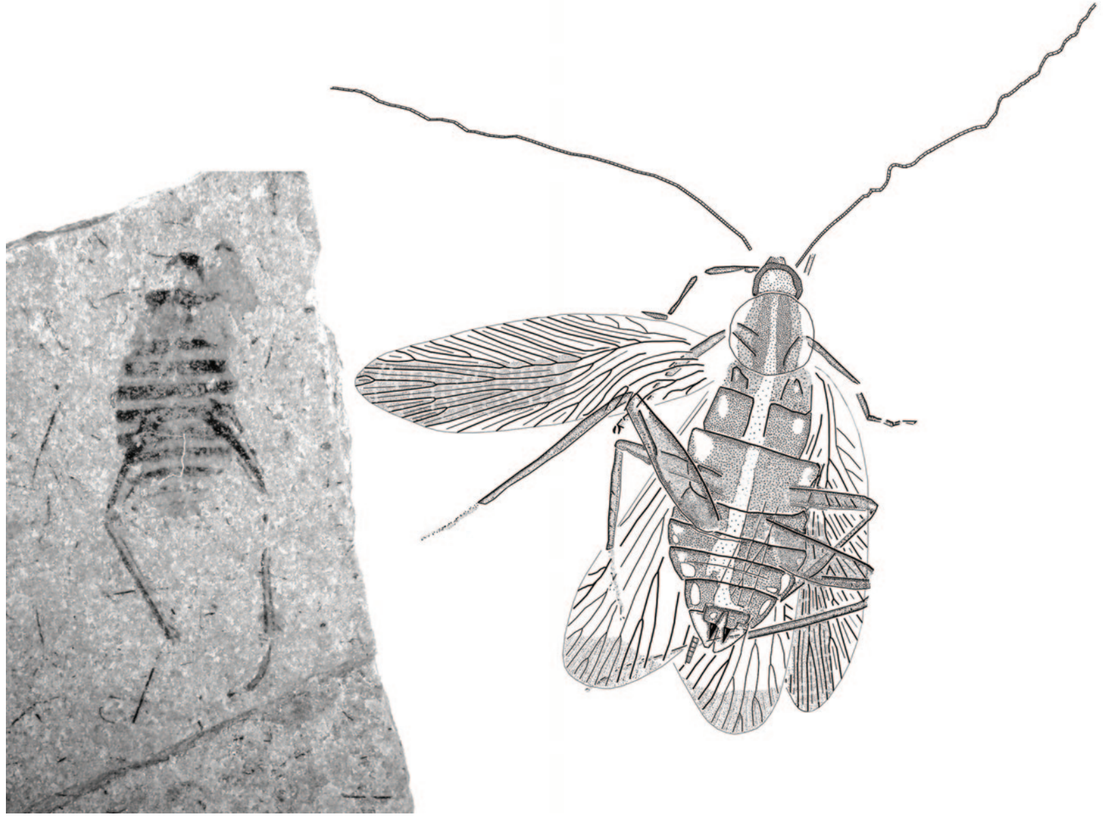
Skok svaba







2554/44



Systematical remarks: This taxon is apparently derived directly from advanced Caloblattinidae and is considered a separate family due to specific habitus and flight style. Plesiomorphicaly forewings might overlap.
Remarks: As this family was indigenous, potential candidates for the source genus might be eventually find at the site. Unusual Sc is extremely strongly sigmoidal and elongated and branched terminally, and with very short clavus. Modified body makes its relationships difficult to acess, but on the other side it traces the origin of the family Latiblattidae being synapomorphic in construction of the body and hardened elytra. Latiblattidae originated from this particular group of the Caloblattinidae, suggesting small individuals were phylogenetically primitive. This inference is supported with further specialization and further widening of larger species. Derivation from the genus *Rhipidoblatta* is substained with the pronotum, which retained original shape of the genus and also partially the pronotal coloration (of *R. tri*). The venation basically represents the simplified (somewhat brachypterised) forewing or *Rhipidoblatta*.The tubular ovipositor is unique within cockroaches, but occurs also in specialized miniaturized Liberiblattinidae, where it was evidenced to transfer separated oocytes and thus injecting the hardening ootheca (see also Sendi 2021) as presumed by Vishniakova (1968).

Genus *Latiblatta* Vishniakova, 1968

Type species: *Latiblatta lativalvata* Vishniakova, 1968, and by monotypy.
Type horizon: indigenous to Upper Jurassic Karabastau Formation (FOD, LOD)
Type locality: indigenous to Karatau

Remarks: *HHongoblatta orientalis* (Hong, 2002) (*Blattidae)* from Ypresian Eocene Fushun amber belonged to *Latiblatta* along with *Hongoblatta spinosa* (Hong, 2002) according to Hong (2002), but see Özdikmen (2008).

Latiblatta lativalvata Vishniakova, 1968

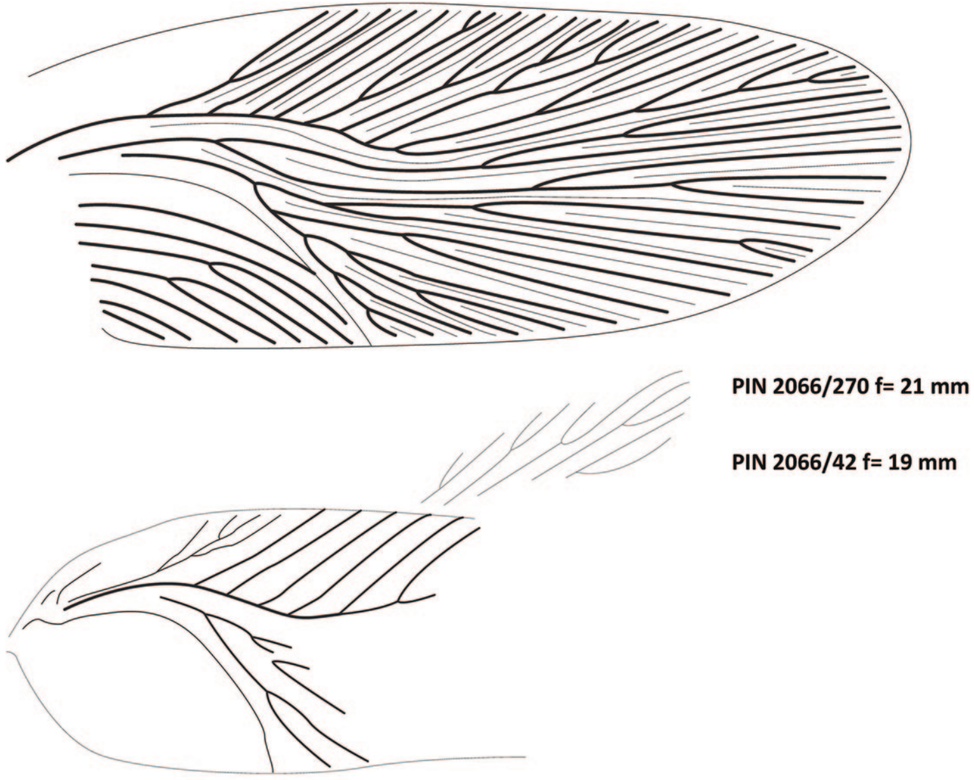
(figps. 249, 252-256)

Holotype: PIN 2066/477. A completely winged adult female. Designated by Vishniakova (1968)
Type horizon: indigenous to Upper Jurassic Karabastau Formation
Type locality: indigenous to Karatau

Additional material designated by Vishniakova (1968): PIN 2066/470, 770; 2384/192 (all complete females).
Specimen PIN 2239/351 was extracted from this species (see species below).

Additional material designated here: PIN 1784/960± **G**; 2066/144 (f= 19 mm), 437 (l= 20 mm, female); 2239/178± (pw= 10 mm); 2384/45 (l= 25 mm), 66 (female); 2554/11 (f= 17 mm), 18 (f= 17.3 mm), 35; 2784/637, 668± (f= 18 mm; female), 738 (closed), 812 (f= 17 mm), 900; 2904/40, 48± (f= 15 mm), 80 (female), 85 (female), 321 (f= 17 mm), 330 (f= 18 mm), 358; 2465/984 (f= 18 mm); 2997/53± (f= 18 mm), 134, 1347, 1551± (f= 16-17 mm), 1572 (f= 15 mm), 1571± (f= 15 mm), 1581 (f= 15 mm), 4239± (pw= 9 mm, l= 22 mm; female) (complete individuals); PIN 2044/144; 2066/151, 247, 270, (f= 21 mm), 509 (f= 21 mm, 4.18.8.10.1.12); 2239/167± (f= 18 mm), 242 (f= 16 mm, 6.13.9.7.1.9*); 2465/928 (f= 18 mm); 2904/215 (f= 15 mm); 2997/1566 (f= 15 mm) (isolated forewings); 2997/1348 (isolated hindwings). The same locality as the type.

Autapomorphies: none detected, possibly size, strongly arcuate clavus and also possibly luminescence, golden beetle-like flight (with connected forewings).
Remarks: Specimen PIN 2066/42 seems to have preserved basalmost branches of Sc, so called ScA or CP. These veins are preserved in primitive cockroaches but also through the taxonomic spectrum and perhaps are only rare preserved, but standardly occurred. This species is preservd with wings outstretched and apparently was not so well adapted to “golden-bettle”-like flight. Short cercomeres are as in Caloblattinidae, but only a feew segments were preserved in all specimens suggesting a brittle character.



Mutations: Deformation of forewing veins is detected at specimen PIN 2239/242.

Variability: Performed on insignificant number of specimens, nevertheless reveal result consistent with other representatives of the related caloblattinids at site (CV= 17.33 % for total number of veins (15.54 % with A)) and can be useful evaluating larger data. Adding the last two samples nevertheless change the figure for over 2 % (bias of low sample size).

Redescription: Habitus robust. Head comparatively small, hypognathous, globular, monochromatic dark, with huge nearly holoptic eyes. Antenna filiform only about 7 mm long, antennomeres narrow. Pronotum very large, transverse, monochromatically dark, fore and hind margins semicircular (5-6/ 5.6-8.5 mm). Body wide (fat), with 10 segment. Cerci wide, multisegmented, cercomeres very short.

Ovipositor with triangular lam2 (sensu Vishniakova 1968) and long tubular v1 protruding 2.1 mm beyond v2 and v3 end. Legs very short with nearly entirely or entirely reduced carination, but terminal femoral spur present. Forefemur 3.2/ 0.7 mm, foretibia 2.8/ 0.18 mm, foretarsi 1.6 mm long; midfemur 4.8/ 0.9 mm, midtibia 3.5/ 0.7 mm; hind femur 4.8/ 0.9 mm, hindtibia 4.3/0.4 mm.

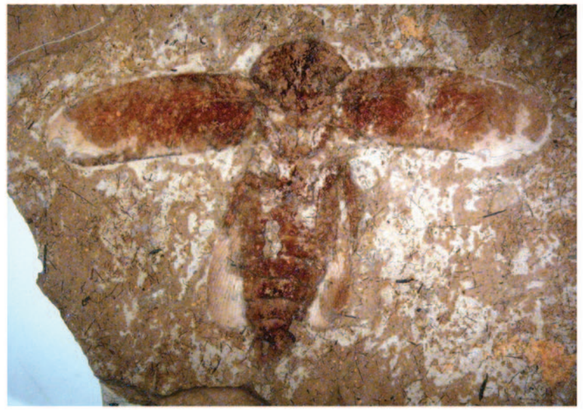
Forewing monochromatical, not extremely dark, most probably dark brown (14.3-21/ 5-10.6 mm), with distinct narrow intercalaries. Margins not parallel, Costal field narrow, subsosta sigmoidal, with up to 6 veins at margin. R narrow, only reaching a third of the wings width, with 10-23 veins at margin, RS undifferentiated. M with 6-13 veins at margin. CuA seem nearly straight and with 7-14 veins. CuP sharphy curved anteriorly, without posterior curvature. A tertiary branched, with 9-14 veins. Diagonal kink indistinct.

Hindwing transparent or pale brown. Costal field narrow, SC simple, R differentiated into R1 and RS (3+8), M expanded (6), Cu rich (11+1). Pterostigma absent.

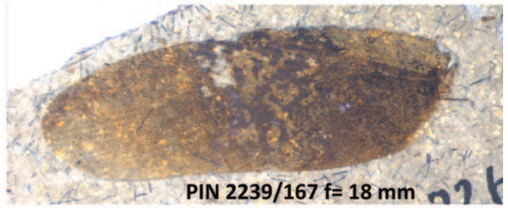
Character of preservation: 34 complete specimens, 10 isolated completely articulated forewings, 1 isolated hindwing.

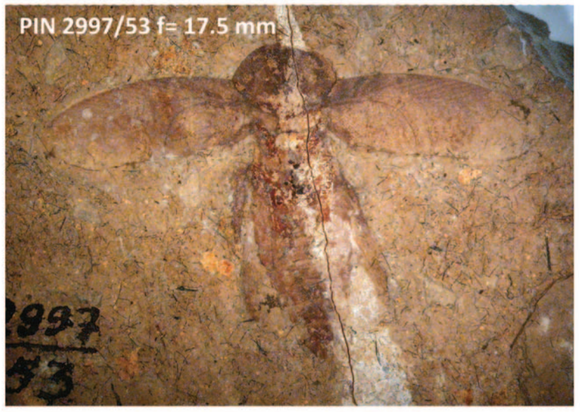
Taphonomy: Complete specimens suggest short or no pre-depositional transport. Only females are confinedly identified (n= 5), which does not necessarily mean bias or shift in sex ratio.

specimen	length	width	Sc	RRS	M	CuA	CuP	A	RM	RCuA	MCuA	total without a	total
2066/509	21		4	18	8	10	1	12	26	28	18	41	53
2239/242	16		6	13	9	7	1	9	22	20	16	36	45
2066/270	21		6	20	9	9	1	10	29	29	18	45	55
2239/167	18		5	23	12	14	1	14	35	37	26	55	69
2997/53R	17.5		5	12	11	13	1	11	23	25	24	42	53
2997/53L	17.5		4	16	9	9	1	14	25	25	18	39	53
2066/437R	15		4	14	9	9	1	14	23	23	18	37	51
2066/437L	15		4	19	13	14	1	14	32	33	27	51	65
2997/144	16		5	13	13	9	1	13	26	22	22	41	54
2066/477L	16		3	15	6	9	1	11	21	24	15	34	45
2066/477R	16		3	13	6	8	1	10	19	21	14	31	41
N	11		11	11	11	11	11	11	11	11	11	11	11
Min	15		3	12	6	7	1	9	19	20	14	31	41
Max	21		6	23	13	14	1	14	35	37	27	55	69
dev	2.124532		1.035725	3.549648	2.46429	2.42712	0	1.897367	4.824182	5.243177	4.433345	7.119755	8.251722
AVE	17.18		4.45	16	9.55	10.09	1	12	25.55	26.09	19.64	41.09	53.09
CV	12.37		23.27	22.19	25.8	24.05	0	15.81	18.81	20.1	22.57	17.33	15.54




PIN 2239/242 f= 16 mm


PIN 2239/167 f= 18 mm

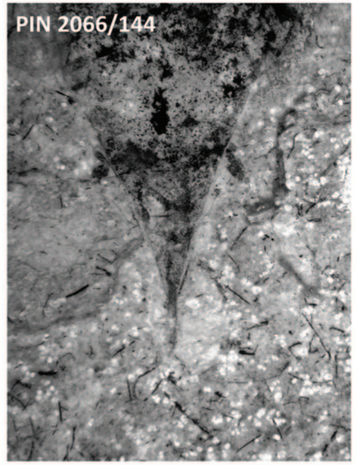

PIN 2997/53 f= 17.5 mm

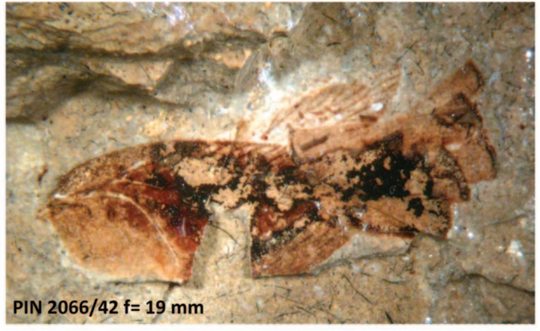

PIN 2066/509 f= 21 mm


PIN 2066/270


PIN 2465/925 b= 18 mm

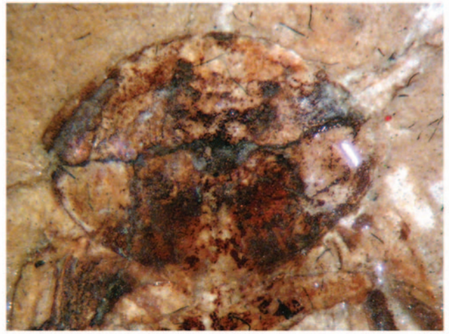



PIN 2066/144

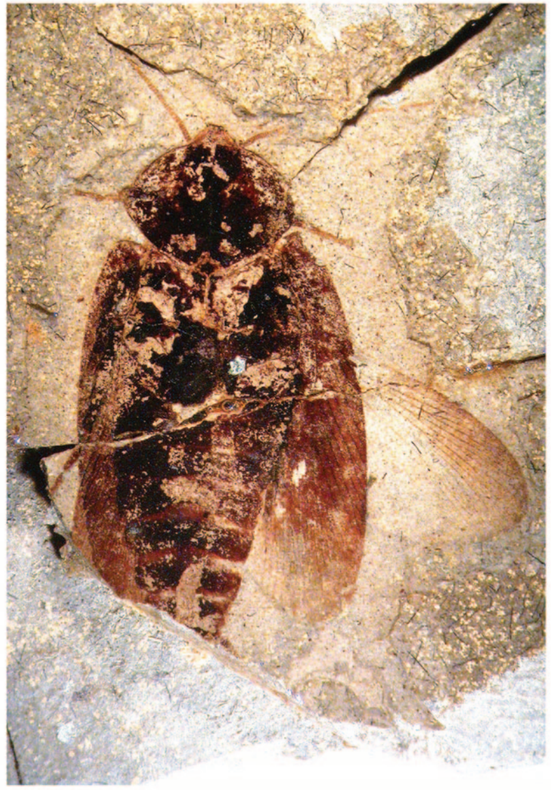

PIN 2066/42 f= 19 mm







PIN 2904/40 w=8 mm





PIN 2784/900 ca. 4 mm

PIN 2066/437 l=20 mm



PIN 2904/363 l= 28 mm (with ovipositor)

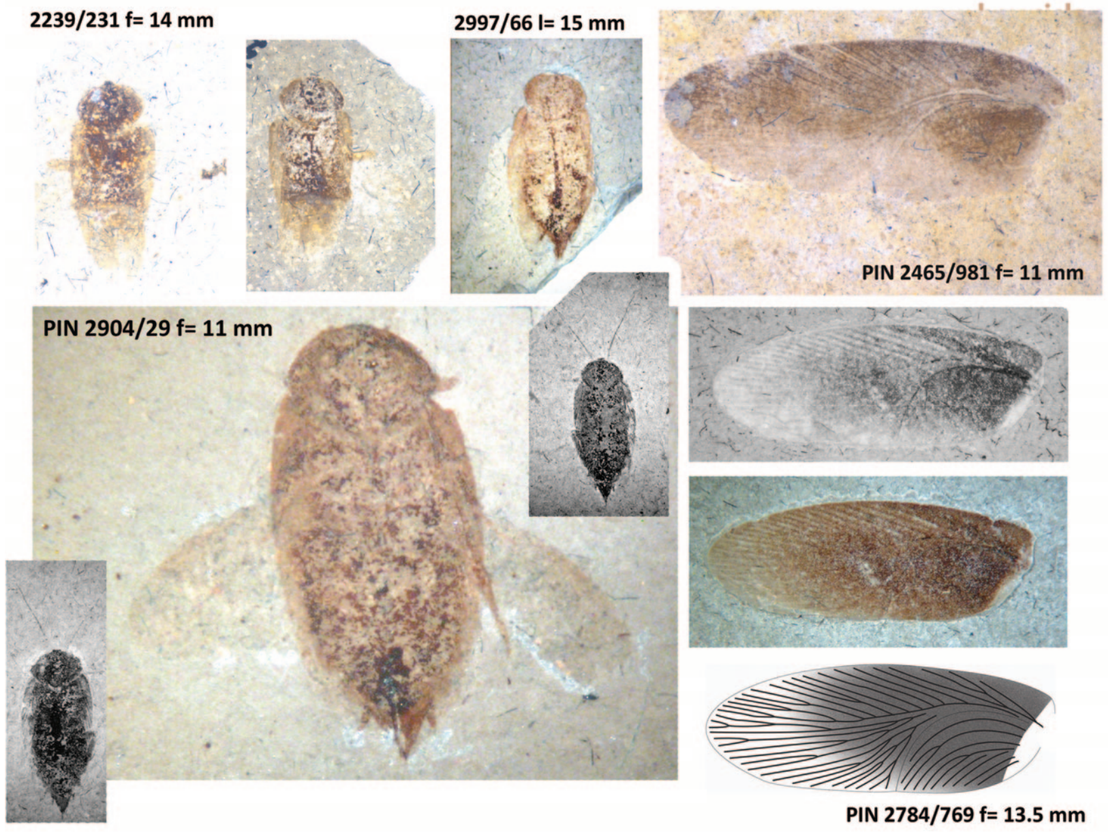
***Latiblatta osud* sp.n.**
(figps. 258-262)

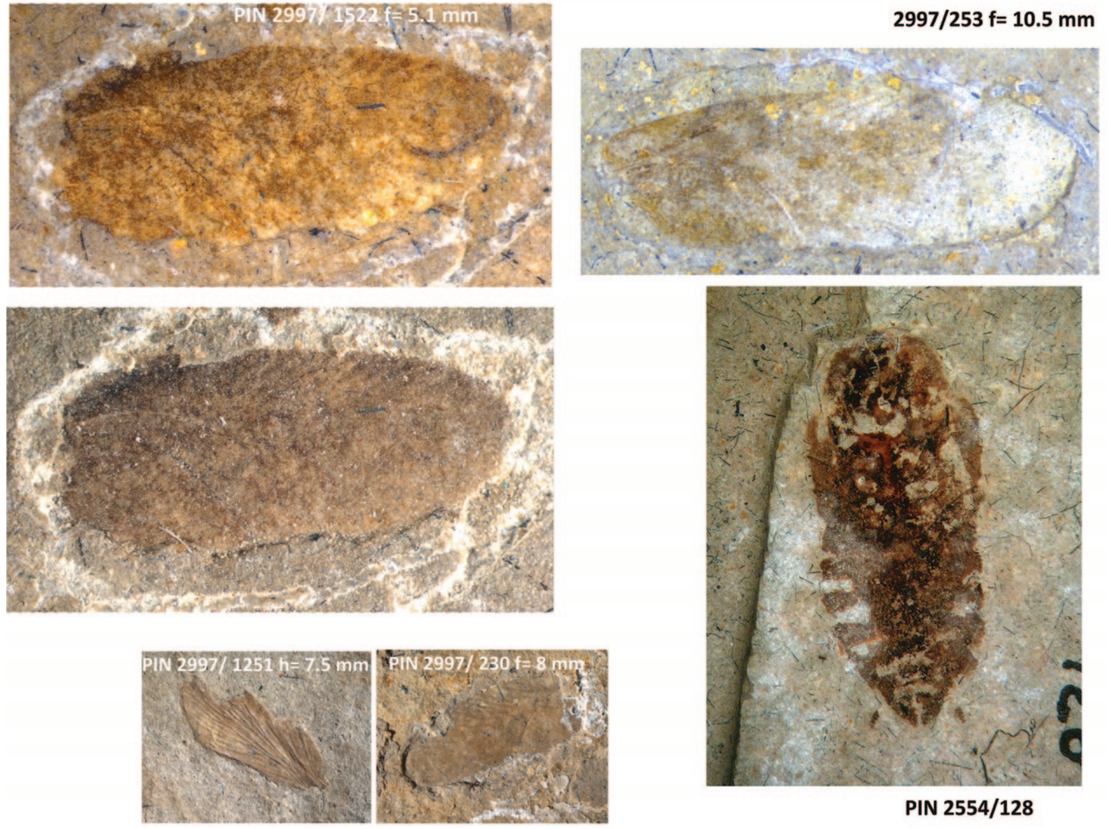
Holotype: PIN 2784/997. A complete winged adult female.
Type locality: Mikhailovka, Karatau, Kazakhstan.
Type horizon: Kimmeridgian Upper Jurassic, Karabastau Formation.

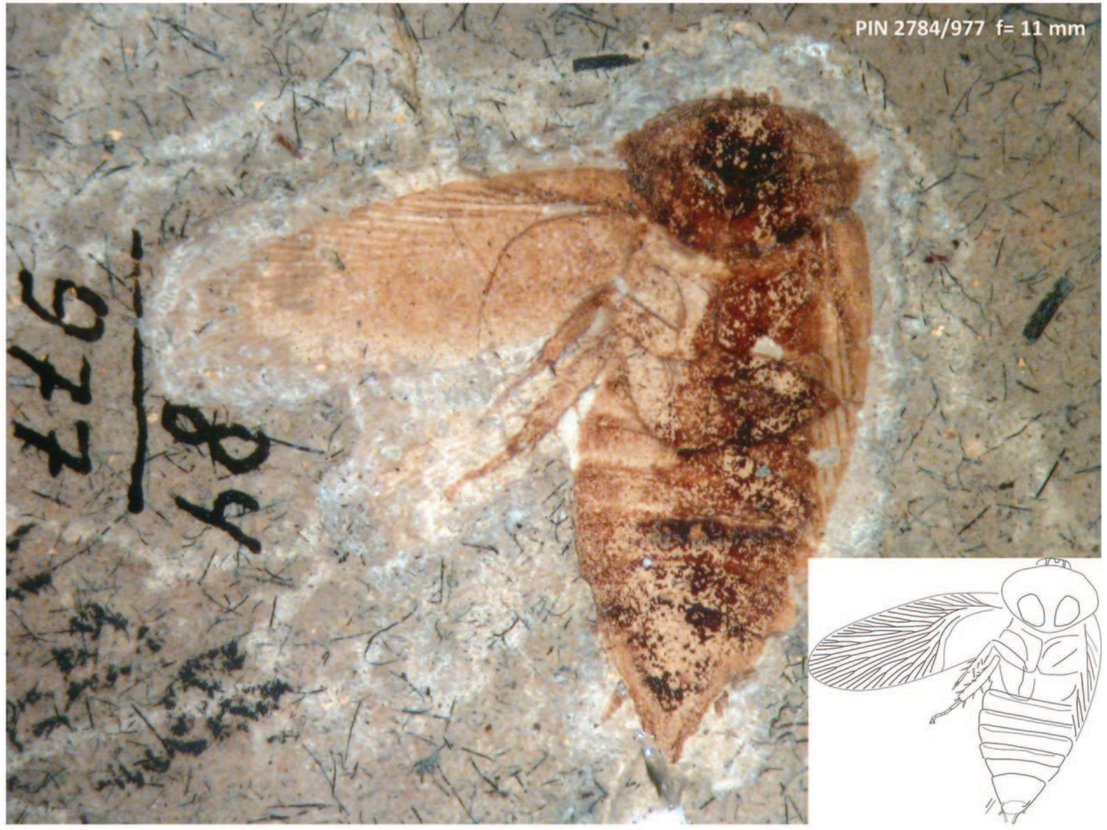
Additional material: 2239/164±, 231 (f= 12.5 mm), 255± (f= 10 mm); 2554/21; 2784/771, 977, 835, 836 (f= 11.7 mm), 739 (l= 17 mm), 795 (l= 17 mm); 2904/29± (f= 11 mm); 2997/66 (female, f= 11 mm), 114 (female), 159= 2554/128 (f= 8.5 mm) (complete specimens); 2064/401 (f= 11 mm); 2384/1116, 1119; 2465/981 (f= 11 mm, 3.16.7.12.1.11); 2784/667 (f= 11 mm), 769=724 (f= 13 mm), 787, 881 (5.14.5.7.1.10), 834, 847; 2904/158 (f= 9 mm); 2994/1522; 2997/78 (f= 12 mm), 169 (f= 12 mm, 6.11.13.8.1.12), 230 (f= 8 mm), 253 (f= 10.5 mm), 255, 1294 (isolated forewings); 2465/962 (h= 11 mm, 1.4+9.7; "MA+MP"); 2997/1251 (h= 7.5 mm), 4298=4304 (h= 5 mm) (isolated hindwings). The same locality as the type.

Autapomorphies: Small size
Differential diagnosis: Differs from its only congener in being significantly smaller, with forewing length under 13 mm, in proportionally smaller pronotum and narrower body, and in cerci more wide basally.

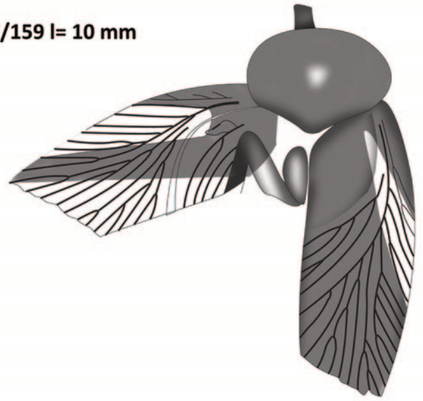
Description: Head very small, completely hidden by pronotum except part of eyes and narrow interocular space. Pronotum large, transverse, monochromatically dark, form of two semicircular shapes (3.2-5.1/5-6.4 mm).
Forewing resemble brachypterous form of *Rhipidoblattina* (8-14/4.7-5.5 mm), with narrow costal area, costa indistinct, Sc branched basally (2-6, usually 3). R and RS differentiated (10-13+4), not reaching apex, bracnches secondarily dichotomized. M expanded, only slightly sigmoidal (10). CuA expanded, only slightly sigmoidal and with short posteriormost branch (9-11). CuP simple, fluent, A tertiary dichotomized (11-14). Diagonal kink indistinct, but slightly indicated in 2465/981 (with some reticulations also present).
Hindwing with narrow costal area, Sc simple. R1 and RS diffrerentiated (3+8+). Straight M (3) fused with RS rather posteriorly, in the basal third (nevertheless, this character might be specimen-specific 2997/1251 due to fusion of M with CuA and consequent deformity). CuA (7) secondarily dichotomized, CuP simple. A1 simple and straight, A in vannnus numerous.
Body wide (5.3 mm), female subgenital plate elongated, triangular. Cerci multisegmented, 0.2 mm wide basally, cercomeres short, preserved fragments not longer than 1 mm.
Ovipositor lam2 triangular forming nearly isosceles triangle, tube unpreserved, likely very delicate.
Legs even shorter than in the congener, apparently adhjacent to body during (frequent) flight. Midfemur 2.4/ 0.7 mm with terminal femoral spur, other spurs indistinct, mid tibia 2/0.4 mm very short, with only 3 terminal spurs 0.3 mm long, midtarsi 1.8 mm long. Hindfemur possibly robust 3 mm long, hindtibia 33/0.4 mm, with very sporadic (8) spurs up to 0.5 mm long, hindtarusus more robust (1.4/0.2 mm), terminated with massive claw 0.2 mm wide.
Mutations: Hindwing PIN 2997/1251 posses M-CuA fusion.
Derivation of name: After *osud* (Slovak for fate).
Character of preservation: 15 complete specimens, 18 isolated forewings, 3 isolated hindwing.
Taphonomy: Complete specimens suggest short or no pre-depositional transport. Only females (n= 6) are confinedly identified due to presence of ovipositor. This does not necessarily mean there is any shift in sex ratio. Anyway it is important in stressing the presence of sibling species excluding possibility of these two representing different sexes.


2239/231 f= 14 mm
2997/66 l= 15 mm
PIN 2465/981 f= 11 mm
PIN 2904/29 f= 11 mm
PIN 2784/769 f= 13.5 mm

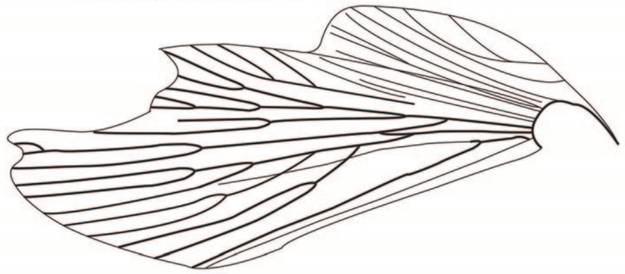

PIN 2997/ 1522 f= 5.1 mm
2997/253 f= 10.5 mm
PIN 2997/ 1251 h= 7.5 mm
PIN 2997/ 230 f= 8 mm
PIN 2554/128

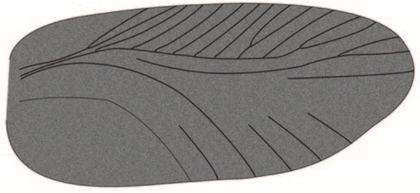


PIN 2997/159 l= 10 mm



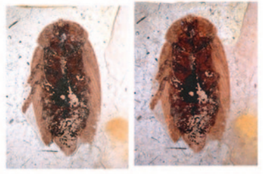
PIN 2997/1251 h= 7.5 mm

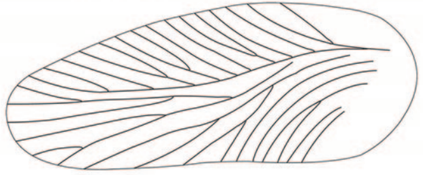




PIN 2997/159 l= 10 mm

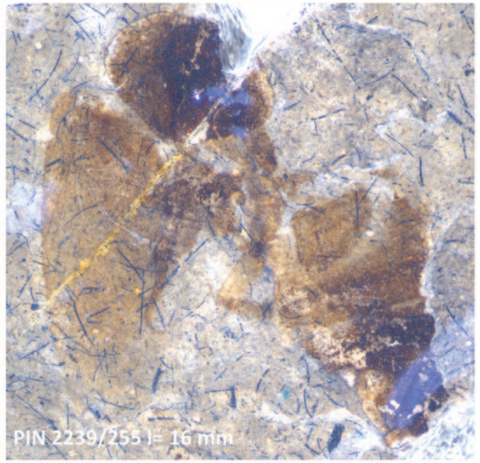
PIN 2784/739 l= 17 mm

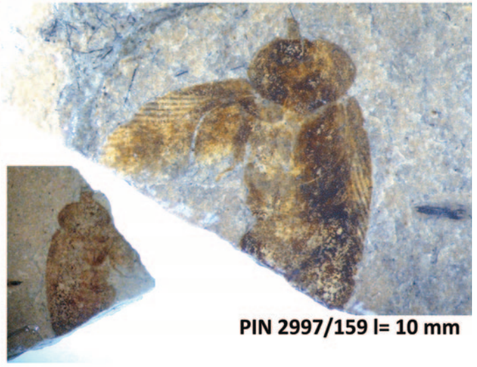




PIN 2997/230 f= 8 mm







Genus Fosilia **gen.n.**

Type species: *Fosilia tubuliovipositorica* sp.n., and by monotypy.

Stratigraphic range: Upper Jurassic – Upper Cretaceous.
Geographic range: Laurasia (including/ with North Myanmar amber).

Differential diagnosis: Differs from all representatives of the family Caloblattinidae in having tubular ovipositor, while retained original morphology of wings, and with narrowed costal area. From *Latiblatta* it differs in standard unmodified forewing morphology.
Autapomorphy: Extremely long tubular ovipositor (homoplasic in *Microblattina* and *Alienopterix*)
Description: As for species.
Derivation of name: fosilia is Slavic for a fossil. Gender feminine.
Remarks: The new genus can be categorized within Latiblattidae on the basis of wide forewing with branched Sc and A, common intercalaries, unwidened, unspecialized regular veins and tubular ovipositor.
Within the family Caloblattinidae, the new genus can be discriminated from uniformly colored *Aktassoblatta*, *Asioblatta*, *Caloblattina*, *Etapia* (with short clavus), *Fusiblatta*, *Ijablatta*, *Kemerowia*, *Paleovia*, *Rhipidoblattina*, *Samaroblatta*, *Samaroblattula*, *Shartegoblattina, Sogdoblatta, Taublatta*, *Taublattopsis. Nuurcala* possesed a more sophisticated pattern (and thus cannot represent the stem genus) and standard non-tubular ovipositor. *Decomposita* differs in more primitive ovipositor and in more advanced shape (elongated wings and pronotum) and also cannot be considered for the stem. *Dazhublattella* has more primitive costal area with reticulations and reticulate structure of forewing similar to *Caloblattina. Itchetuja* differs in possessing shorter spurs and shorter posterior femoral spines. Thus the most probable stem is represented by the genus *Rhipidoblatta*, which is very diverse in morphological structures while retaining the original state of the wings. Nevertheless, lack of the distinct posterior central extension as in Rhipidoblatta suggest that also the know representatives of this genus cannot be considered for the stem of the present genus and its reproduction strategy.

Fosilia tubuliovipositorica **sp.n.**

(figps. 264-267)

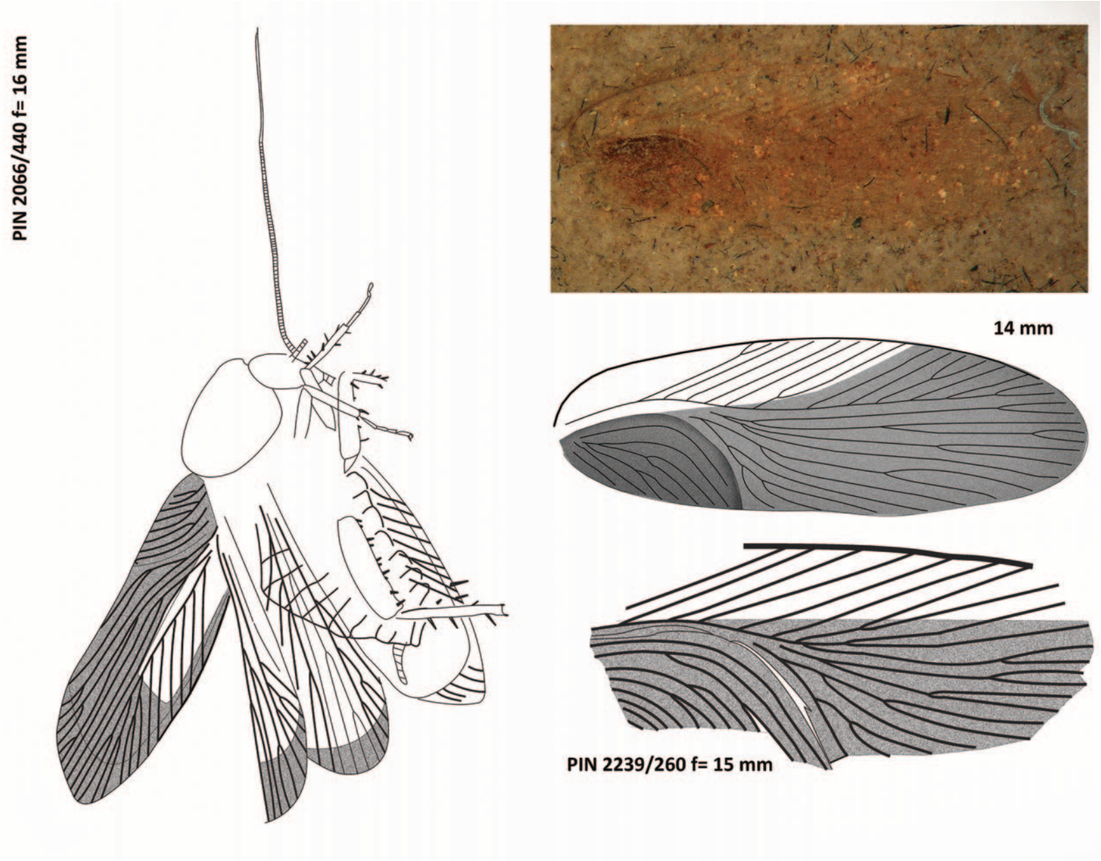
Holotype: PIN 2997/1591. A completely articulated female with preserved ovipositor.
Type locality: Mikhailovka, Karatau, Kazakhstan.
Type horizon: Kimmeridgian Upper Jurassic, Karabastau Formation.
Additional material: PIN 2066/440 (f= 16 mm); 2239/351; 2904/363; 2997/ 235, 257, 275 (complete specimens); 2554/152 (f= 14 mm); 2904/276 (f= 12 mm); 2239/260 (isolated articulated forewings). The same locality as the type.

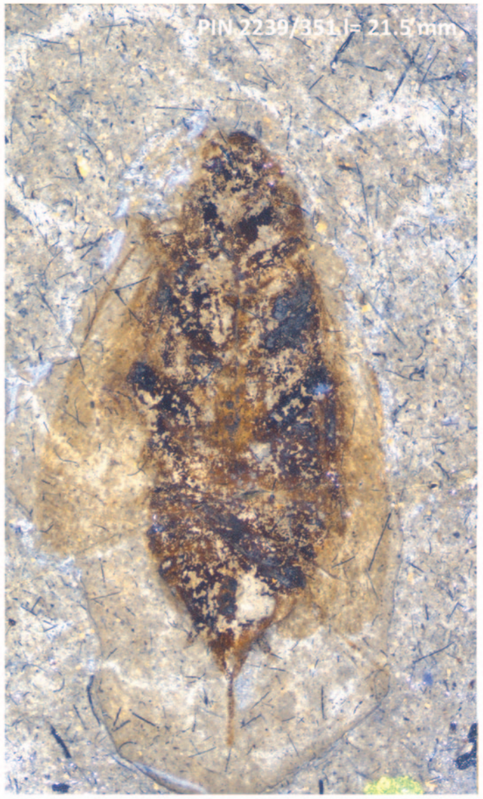
Diagnosis: Head dark (but not black), hypognathous, triangular, 3.3 long and 2.9 mm wide. Eyes widely divided (1.5 mm), pale, round (length/ width 1.1/ 0.6 mm) with small facets. Ocelli present, central ocellus white, round, small, only about 0.1 mm in diameter. Antennal socket very large, up to 0.5-0.6 mm in diameter, with robust scape (0.5/ 0.5 mm), antenna long at least 16 mm, filiform, with wide basal and narrow apical antennomeres. Mandible long, robust (1.7/ 0.6 mm), clypeus present.
Pronotum nearly round, slightly transverse (ca 5.5/ 6.5 mm), with weakly developed paranotalia and with slightly indicated medial posterior extension, with colored central area (disc) and pale margins.
Body moderate, up to 6.6 mm wide, with margins nearly parallel basally, with proximal segments deeply carved. Ovipositor outer valves wide (2-2.5 mm) and up to 3 mm long. Inner valves form an extremely narrow and long tube (5/ 0.2 mm). Only very short narrow (under 0.4 mm) 11-12 fragments of basal cercomeres were preserved, cercus apparently multisegmented probably with up to about 20 segments (but it cannot be excluded 12 is the final number). Styli very short (ca. 0.5 mm),

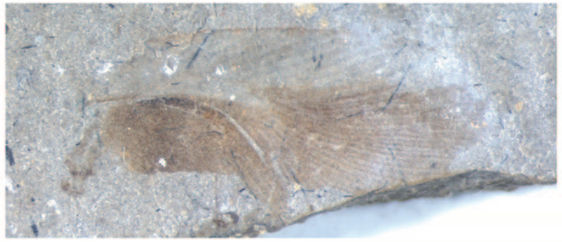

PIN 2997/1591 l= 24 mm (5 mm ovipositor)




PIN 2997/257 l= 19 mm

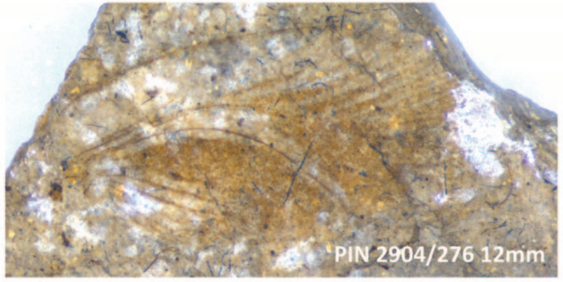

PIN 2066/440 f= 16 mm
14 mm
PIN 2239/260 f= 15 mm







PIN 2239/ 260 f= 13 mm











3- segmented; male styli long with few segments (1.5 mm).
Legs short, dark, melanised, probably black. Forecoxa massive (2.0/ 0.9 mm), trochanter present but indistinct, forefemur rather robust (2.3/ 0.7 mm), with posterior spines in ridges; foretibia short (2.3/ 0.5 mm) with numerous spurs (ca. 8); foretarsi ca 2.5 mm long, unspecialised (1/ 0.5/ 0.4/ 0.1/ 0.5 mm), claw symmetrical, arolium present. Mid coxa massive (2.5/ 1.7 mm), trochanter small (0.4/ 0.2 mm); midfemora large (4/ 0.9 mm) with posterior row(s) of spines, and terminal femoral spur; midtibia (/0.5 mm) heavily carinated, with 14 or more spurs. Hind coxa massive (3/ 1.5 mm); trochanter large (1.2/ 0.5 mm); hindfemora large (5.4 /1.1 mm), with posterior row(s) of 7 large and some smaller spines, and terminal femoral spur; hindtibia with at least 20 spurs.
Forewing wide, unspecialized, 14-17 mm long and 4.5- 6 mm wide, light dark colored (probably pale brown), with pale (transparent, white or pale yellow) basal anterior half. Costa very strong and colored, long, costal area rather narrow, with nearly straight Sc weakly branched, with 1-5 veins at the margin. R nearly straight, with mostly simple branches, 9-12 veins at margin, apicalmost vein branched, followed with 4 differentiated RS branches. M nearly straight with 3-8 veins at margin. CuA expanded, sigmoidal, with 7- 9 veins at margin, posteriormost short offshoot followed by long branches which nearly reach apex. CuP rather sharphy curved, with 8-9 branched anal veins.
Hindwing as long as forewing, transparent with darker apex, with long Sc and R1 reduced to 4 short veins and RS with 5 veins.
Derivation of name: *tubuliovipositorica* is after *tubulus* (tube) and *ovipositor* – alluding to tubular ovipositor.
Character of preservation: 7 completely articulated individuals (at least 3 of them females, 1 likely a male), 3 isolated forewings.
Taphonomy: Completely articulated specimens (with partially preserved cerci) suggest no or short pre-depositional transport. Species was apparently not abundant. Absence of isolated hindwings might suggest also their difficult identification among isolated hindwings (which might be present among IS materials)
Remarks: This type of (tubular) ovipositor disables laying or transferring eggs through it and serves exclusively of transmission of oocytes into a precursor of ootheca (without keel), possibly actually hardened at surface. This process is elaborated in detail in discussion.
Small round ezes with small facets suggest diurnal way of life.

Family Liberiblattinidae Vršanský, 2002

Type genus and species: *Liberiblattina ihringovae* Vršanský, 2002. Karatau.

Stratigraphic range: Early Jurassic - terminal Cretaceous
Geographic range: cosmopolitan

Composition: *Aktassoblatta* Vishniakova, 1971*; Brachyblatta* Vršanský, 2002*; Cryptoblatta* Sendi et Azar in Vršanský et al. (2019); *Elisamoides* Vršanský, 2004; *Entropia* Vršanský, Liang et Ren, 2012*; Gurvanoblatta* Vishniakova, 1986*; Hydrokhoohydra* Vršanský in Vršanský et al. (2019); *Kazachiblattina* Vršanský, 2002, *Kurablattina* Martin, 2010; *Leptolythica Vršanský, 2008; Liberiblattina* Vršanský, 2002*; Spongistoma* Hinkelman in Sendi et al. (2020), *Miniblattina* Sendi, 2021; *Stavba* Vršanská et Vršanský in Vršanský et al. (2019).

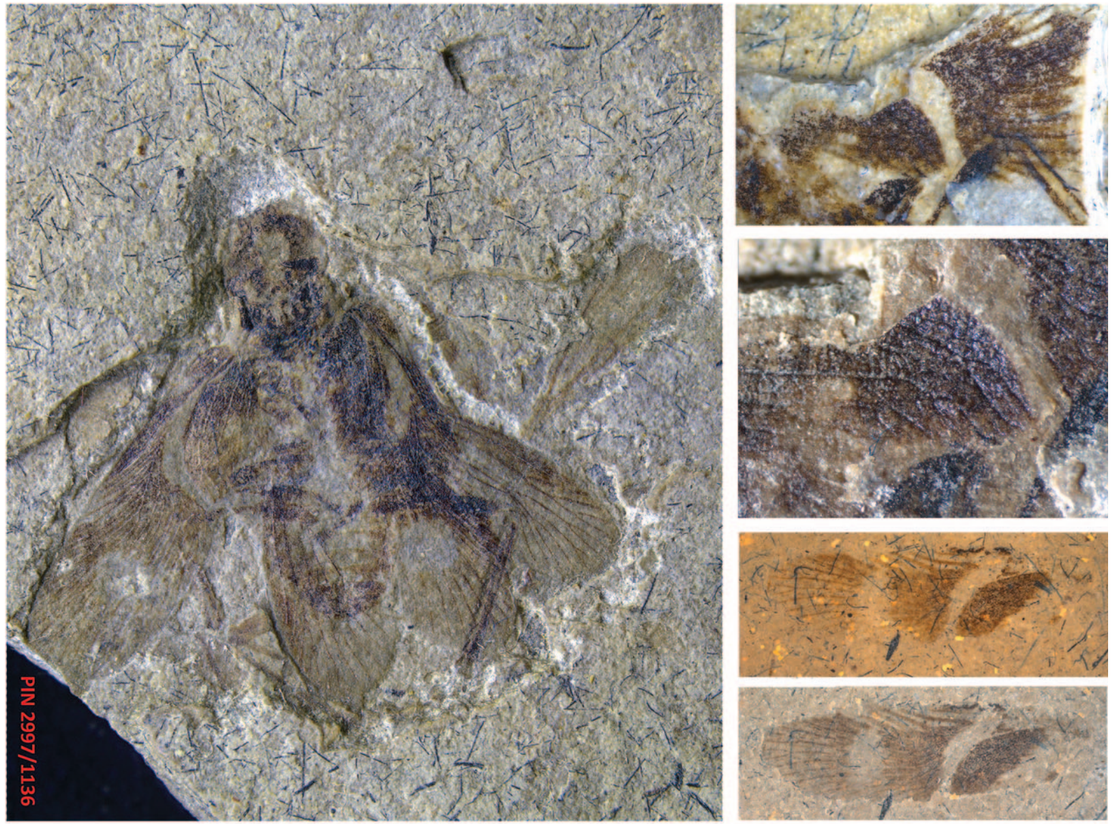
Diagnosis (after Vršanský 2002): Forewing with regular venation with terminal dichotomisation limited to the clavus. Costal field narrow with Sc long and branched. R field narrow with R ending prior to wing apex. M and Cu sigmoidal, M reaching wing apex. CuP strongly curved. Anal veins branched mostlv in apical third. Hindwing with fan-like pleating with possible reduction of number of pleating veins, with R differentiated into R1 and RS, possibly with precursors of pterostigma; M richly branched; CuA with 5 or more branches. Female with short external ovipositor.

Genus *Liberiblattina* Vršanský, 2002

Type species: *Liberiblattina ihringovae* Vršanský, 2002;. Karatau.

Stratigraphic range: Late Jurassic (FOD)
Geographic range: indigenous to Karatau

Systematical remarks: The type species apparently comprises both males and females (with distinct externally protruding ovipositor) and coloration and venation did not differ significantly. Nevertheless, other 3 species described below (except *L. kontrapunktata* - a single specimen with parallel margins) might eventually represent only two species with two sexes in two of them. Due to differences in venation, different forms within a same species were excluded.
Species within this genus having non-parallel margins reveal traces of derivation from the genus *Ano*.
The characterstic coloration and several diagnostic characters (Sc, ascending posterior margin) allowed to identify this genus and access its extremely variable shape of the wing. This is common in Palaeozoic and living (post KPg) cockroaches, but such evidence was missing among the Mesozoic, where cockroach genera very very uniform in shape of the wing (see also other groups within present locality) .
Obscure is the presence of unique, intelligent (counterindicative) coloration within this Mesozoic genus, white veins are present in dark membrane but also dark veins on transparent membrane.
Also this genus evidences a general pattern of so called “diversification ring” (Vršanský et al. 2019; figp. 619) and is indigenous, but present here with 8 distinct species.



***Liberiblattina ihringovae* Vršanský, 2002** (figps. 270, 272)

Holotype: PIN 2997/1136. A complete adult winged male. Designated by P.V. Vršanský (2002)
Type locality: Karatau, Kazakhstan.
Type horizon: Kimmeridgian Upper Jurassic, Karabastau Formation.

Additional material designated here: PIN 2066/565 (f 7, 7, 8, 8, 1, 8; h 1, 2+5, 3, 8+blind, 1); 2997/42 (complete specimens); PIN 2904/242; 2784/717; 2997/34, 4330, 4265 (forewings); PIN 2554/"Drawing186". The same locality as the type.

Redescription: Head very large, wider than 0.75 % of the pronotum, pale, with two dark wide longitudinal stripes. Eyes very large, globular, pale, widely separated. Three small pale round ocelli present. Antenna long and wide, with very short segments (0.1/ 0.5 mm). Pronotum comparatively small, transverse (2.1/ 3.5 mm).
Body comparatively narrow (3 mm), dark, strongly melanised, cerci multisegemnted (13), narrow and comparatively short (1.5/ 0.2 mm). Male terminal tergite very short (0.7/ 1.5 mm). Female with short externally protruding ovipositor.
Forewing elongate (10.6-11/ 4 mm). Costa indistinct, costal area very narrow, but anterior base sharphly arcuate. Sc long and abundantly branched (2-9). R strongly sigmoidal, short, not reaching apex, frequently dichotomized, RS indistinct (7-10+2-4). M sigmoidal, expanded, overlapping apex (3-10). CuA sigmoidal, expanded, with posteriormost branch with three terminal branchelets (6-10); CuP simple, sharply cut, A rich and secondarily dichotomized (8-10). Membrane dark, with sophisticated pale coloration pattern composed of subapical posterior big dot; wide pale stripe along clavus, pale small dot in costal area, small pale area in clavus and pale interveinal area in basal part of radial area.
Hindwing with distinct pterostigma. Sc long, straight, simple. R1 and RS differentiated (3-5+4). M with anterior and posterior branches (4-6). CuA posteriorly curved (5-7).
Legs short and robust, cursorial, strongly carinated, dark, strongly melanised. Fore femur very short and robust (1.6/ 0.6 mm), terminal spur unpreserved, three large and robust (0.5 mm) posterior spurs present; foretibia also robust and short (1.5/ 0.4 mm), carination absent; foretarsi very robust, 5-segmented (0.3; 0.3; 0.3; 0.2; 0.4/ 0.3 mm), claws massive, arolium huge (0.4 mm in diameter). Midfemur robust (3/ 0.8 mm), with terminal spur and 8 massive posterior spurs (0.6 mm); midtibia short and robust (2.6/0.5 mm), without carination except for long 2-3 terminal spurs midtarsi short and robust (0.3; 0.5; 0.4; 0.3; ? / 0.35 mm). Hindfemur long and comparatively thin (/0.7 mm), with anterior and posterior spurs (5+5); hindtibia long (4.8/ 0.5 mm) and strongly carinated with 9 short spurs preserved (on a short fragment).
Systematical remarks: Also specimen PIN 2997/34 (l= 11 mm 4.7.6.7.1.10) has the diagnostic blind branches leading from the anteriormost A to the CuP and the characteristic white dot on the black clavus.
Character of preservation: 4 complete specimens, 6 isolated forewings, one hindwing.
Taphonomy: Due to high partition of complete individuals preserved it seems reasonable to assume that the species lived in close approximity with the deposition waterbody.

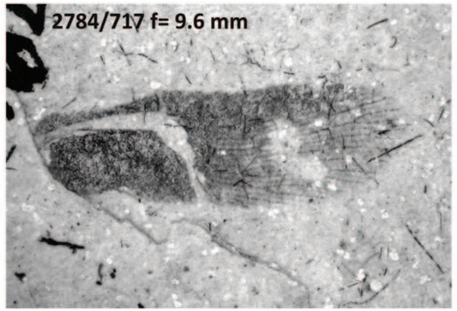
***Liberiblattina cunicula* sp.n.**
(figp. 274)

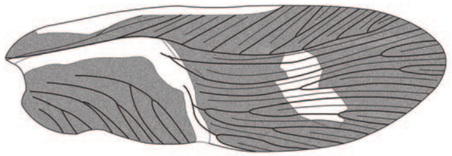
Holotype: PIN 2997/369. A completely articulated winged adult.
Type locality: Mikhailovka, Karatau, Kazakhstan.
Type horizon: Kimmeridgian Upper Jurassic, Karabastau Formation.

Additional material: PIN 2997/1197 (disarticulated forewing); PIN 2231/31 (complete winged adult). The same locality as the type.

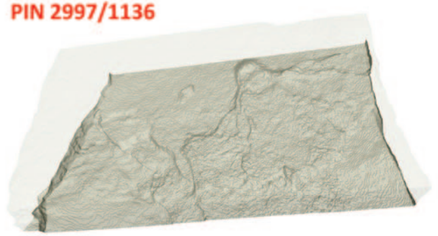
Differential diagnosis: Differs from its sister type species in degree of coloration







PIN 2997/1136



Virtual reverse ultranarrow parallel cast (microtomographic scan) from inside the sediment

(smaller but more distinct anterior pale macula, smaller central dot and more extensive rim of clavus) and in considerably different, robust habitus.
Description: Very robust, moderately small cockroach with overall length over 20 mm. Head robust, globular, very large and wide at least 3.9 mm. Eyes very large, dark, not protruding beyong head outline. Obscure central field resembling elevated area with 6 central ocelli present. Pronotum very large, transverse (4.97/6.81 mm), monochromatically dark, paranotalia indistinct.
Forewing ca. 20 mm long, dark, with small and very distinct anterior pale macula, smaller central dot and extensive rim of clavus. Legs likely burrowing, forefemur extremely robust (4.87/1.73 mm).
Remarks: The robust habitus very probably suggest a burrowing habitus (type species *L. ihringovae* was apparently free-living) and is highly congruent with mastotermitids.
Derivation of name: *cunicula* is Latin for burrowing – alluding to preseumed lifestyle.
Character of preservation: Two complete adults, one disarticulated isolated forewing without clavus.
Taphonomy: Complete specimens indicate short or no pre-depostiional transport, while disarticulated forewing susggest a long time spent in water (predation excluded on the basis of clavus disarticulation). This species might be rather common, its raritz might be caused with the hidden, presumably burrowing lifestyle with rare flight.

Liberiblattina cipka sp.n.

(figp. 275)

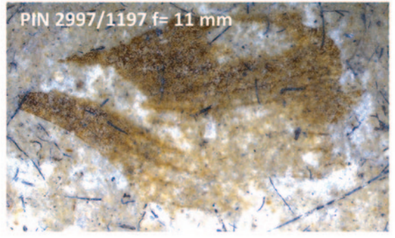
Holotype: PIN 2997/1489. An incompletely preserved complete forewing (10 mm) with clavus.
Type locality: Mikhailovka, Karatau, Kazakhstan.
Type horizon: Kimmeridgian Upper Jurassic, Karabastau Formation.

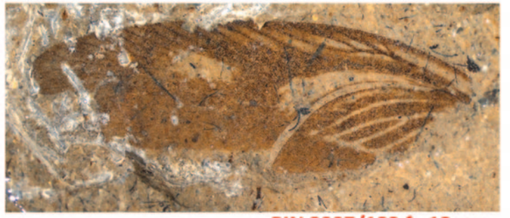
Additional material: PIN 2997/1260; 2066/87 (f= ca. 8 mm). The same locality as the type.

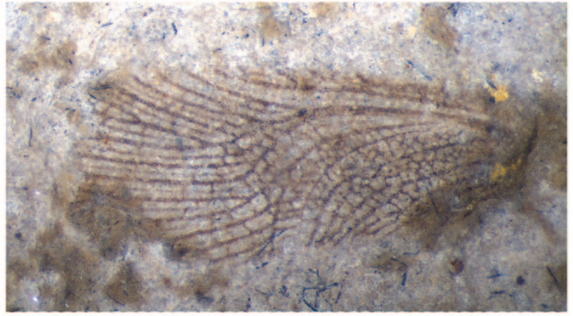
Differential diagnosis: Differs from all species except *contravenata* in being significantly larger (forewing length up to 15mm) and from all species in entirely lacking membrane coloration.
Description: Forewing length 8-15 mm long, margins parallel. Veins dark, wide, intercalaries colored but more pale compared to main veins, probably brown. Sc branched, elongated, slightly sigmoidal with 8 veins at margin, costal field very narrow. R strongly sigmoidal, with 8 or more veins at margin. M strongly sigmoidal, sharply descending, possibly only with 3 veins at margin. CuA probably reaching apex, with at least 8 veins at margin. CuP sharply curved anteriorly, without terminal curvature. 9 anal veins at margin, most of them are dichotomized. Coloration of membrane absent, clavus and adjacent nearest CuA vein area with numebrous reticulations.
Systematical remarks: Due to completely preserved coloration of veins and intercalaries it is excluded that the membrane coloration was simply unpreserved. The membrane is uncolored. Due to completely parallel wing margins and the overall shape of the wing, this species is closely related to the type species and to *L. kontrapunktata* and due to reduction of coloration, even more related to the latter. Due to coloration of *Ano* and more basal species, reduction of coloration is most probably autapomorphic. This type of coloration (dark probably black veins and more pale probably brown intercalaries) is rather typical for most Blattulidae including *Blattula* and also basal liberiblattinid *Eublattula* Handlirsch, 1939. The sharply descending M resembles *Elisamoides* Vršanský, 2004.
Derivation of name: after čipka (Slovak for lace).
Character of preservation: two incompletely preserved forewings with clavus, one without clavus.
Taphonomy: One complete forewing might indicate a longer predepositional transport, but it might be also a stochastical indicator. Most of the species with articulated individuals are also represented by isolated forewings.


PIN 2904/369 h= 20 mm

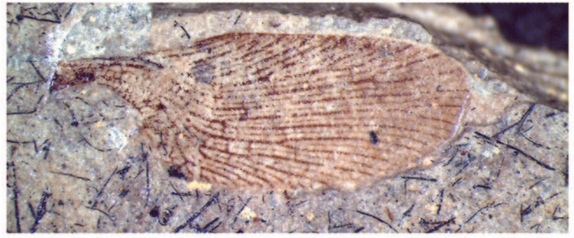

PIN 2231/31 b= 19 mm


PIN 2997/1197 f= 11 mm

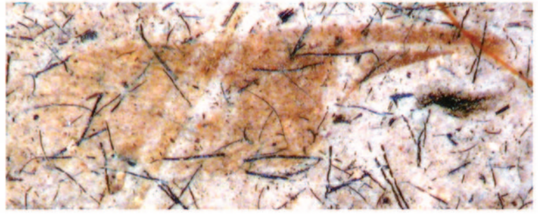

PIN 2997/183 f= 12 mm






PIN 2066/87 f= 7.7 mm

2554/85




PIN 2997/1489 f= 10 mm

Liberiblattina kontrapunktata sp.n.
(figp. 319)

Holotype: PIN 2997/130. An incomplete forewing with disarticulated unpreserved clavus.
Type locality: Mikhailovka, Karatau, Kazakhstan.
Type horizon: Kimmeridgian Upper Jurassic, Karabastau Formation.

Differential diagnosis: Differs from the type species in being smaller and in having less developed coloration restricted to two maculas. From *Liberiblattina* spp. described below it differs in shape of the wing and in bearing no reductions and also in coloration.
Description: Forewing length 9 mm, margins parallel, hind margin ascent towards apex apically. Sc branched, elongated, slightly sigmoidal, costal field very narrow, R slightly sigmoidal, with ca. 14 veins at margin. RS is barely differentiated. M strongly sigmoidal, with 6 veins at margin. CuA nearly reaching apex, with 6 veins at margin. CuP sharply curved anteriorly, without terminal curvature. Coloration is restricted to a small dark stripe around anterior CuA and colored apex with darker area anteriorly.
Systematical remarks: This species is closely related to the type species and differs mostly by size and coloration. The polarization of these characters in the phylogenetical analysis would remain probably impossible as coloration of both species is apomorphic and highly specialized (reduced or sophisticated).
Derivation of name: After *counter* and *point* alluding to two maculas, one pale one dark.
Character of preservation: one incomplete forewing with disarticulated clavus.
Taphonomy: One isolated forewing with detach of clavus indicate a longer predepositional transport.

Liberiblattina kontravenata sp.n.
(figp. 275)

Holotype: PIN 2997/183 f= 12 mm. An incomplete forewing with marks of predation.
Type locality: Mikhailovka, Karatau, Kazakhstan.
Type horizon: Kimmeridgian Upper Jurassic, Karabastau Formation.

Additional material: PIN 2997/375, 4345, 4286, 4382; PIN 2384/43; PIN 2554/85 (isolated forewings). The same locality as the type.

Differential diagnosis: Differs from the type species in having forewing margins not parallel and in very different, more extensive dark coloration. From other specie it differs in bearing no reductions and also in coloration.
Description: Forewing length 12-15 mm, margins not parallel, fore margin descends towards apex. Sc branched, elongated, sigmoidal, with 3-4 bracnhes at margin, costal field narrow, R slightly sigmoidal, with 14-23 veins at margin. RS is barely differentiated. M sigmoidal, with 4-9 veins at margin. CuA nearly reaching apex, with 7-15 at margin. CuP sharply curved anteriorly, without terminal curvature. Anal veins simplified, with 9-15 veins at margin – more veins are (one secondarily) dichotomized. Coloration is dark with white dot in center of the membrane, white costal field (SC veins are dark) and white basal A veins.
Systematical remarks: The species closely related to type species on one side (similar coloration) and complex of all the rest following species lacking parallel wing margins.
Derivation of name: after coutner and vein – alluding to contrast between coloration of veins and membrane.
Character of preservation: Seven incomplete forewings, two with partially disarticulated clavus.
Taphonomy: Two isolated forewing with marks of predation and partial, total detach of clavus respectively indicate a longer predepositional transport.

Liberiblattina luminanala sp.n.
(figp. 278)

Holotype: PIN 2904/27. A complete forewing f= 9.5 mm.
Type locality: Mikhailovka, Karatau, Kazakhstan.
Type horizon: Kimmeridgian Upper Jurassic, Karabastau Formation.

Additional material: PIN 2039/32; 2597/122 (complete forewings). The same locality as the type.

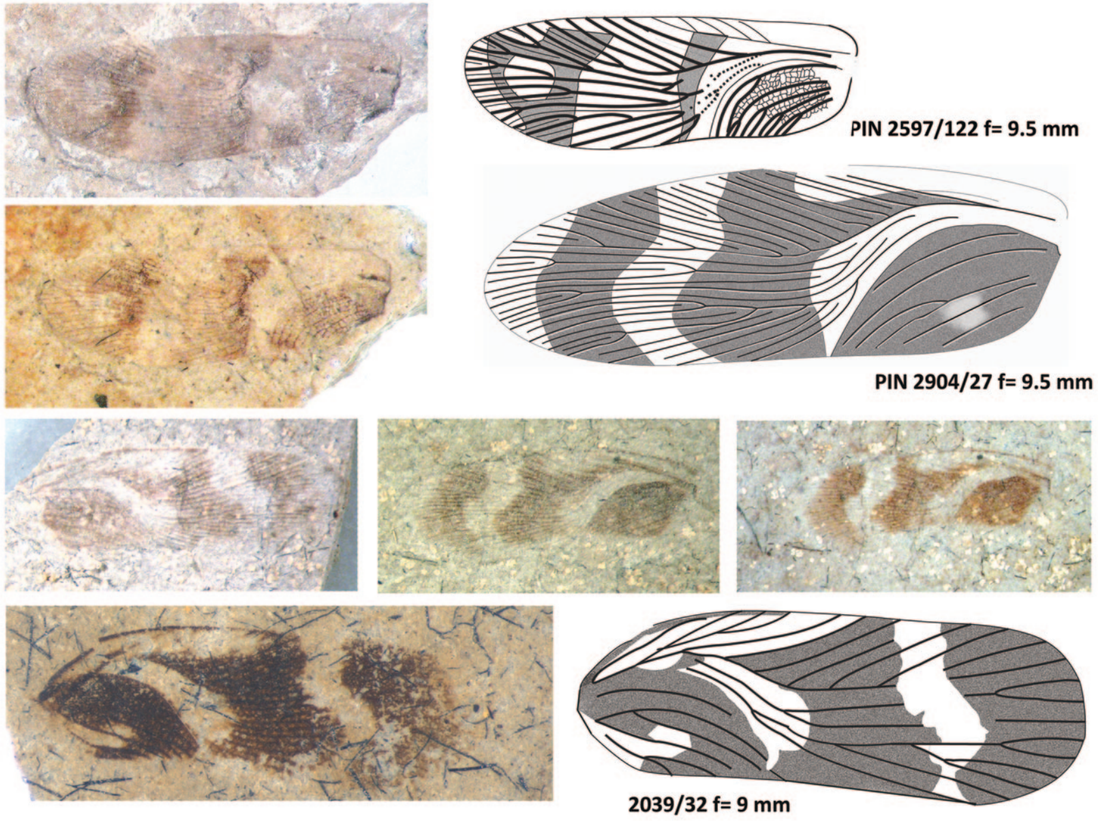
Differential diagnosis. From its sister type species differs in being more robust, forewing is less elongated. Coloration is highly similar, but it lacks apical macula, instead a stripe is present, apex is without coloration and basal anterior macula lacks the darkly colored veins present in *L. ihringovae*.
Description: Forewing length 9**-**9.5 mm, margins not parallel, fore margin descends towards apex. Sc nearly straight, slightly sigmoidal, simple, with terminal dichotomization (indistinct) or with up to 6 veins, R strongly sigmoidal, with 10-11 veins at margin. RS is not differentiated. M simplified, sigmoidal, with 5-11 veins at margin. CuA nearly reaching apex, with 6 veins at margin. CuP sharply curved anteriorly, without terminal curvature. Anal veins simplified, with 7-9 veins at margin – a single to three veins are dichotomized. Coloration include a completely colored clavus and two dark stripes.
Systematical remarks: Differences from *L. ihringovae* are slight and mostly related with simplification, which includes simplification of Sc, A and simpler coloration. At the same time, new species is only slightly smaller than *L. ihringovae* and reveal high similarity (including the general habitus) with genus *Ano* Vršanský, 2020 from earlier sediments of Bakhar in Mongolia. In this respect all these characters might be considered plesiomorphical. Spacimen 2597/122 has nearly parallel wing margins.
Derivation of name: After *lumen* and *anal* (both Latin) – alluding to pale coloration of a field within clavus.
Character of preservation: three complete forewings.
Taphonomy: Three isolated forewings might indicate a longer predepositional transport, but due to completeness of them it probably is a stochastical indicator, most of specimens even in species containing completely preserved individuals, are preserved as isolated forewings.

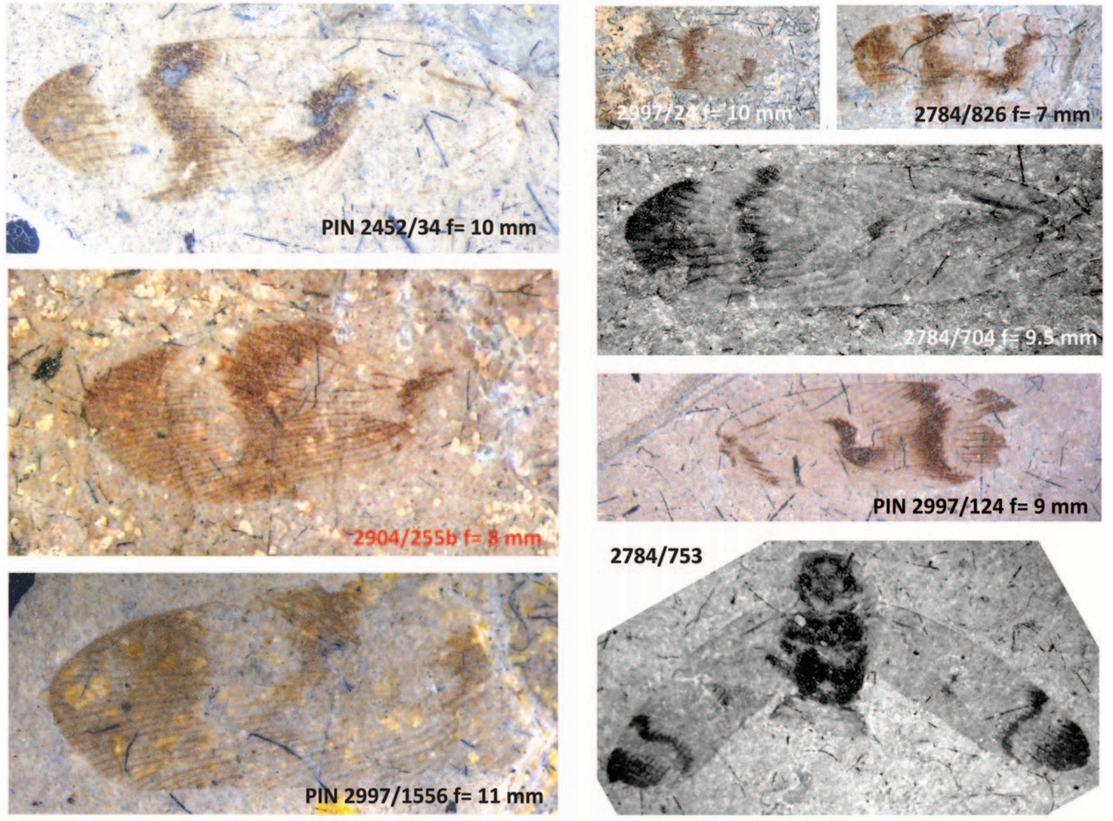
Liberiblattina liberiblattina sp.n.
(figps. 279-281)

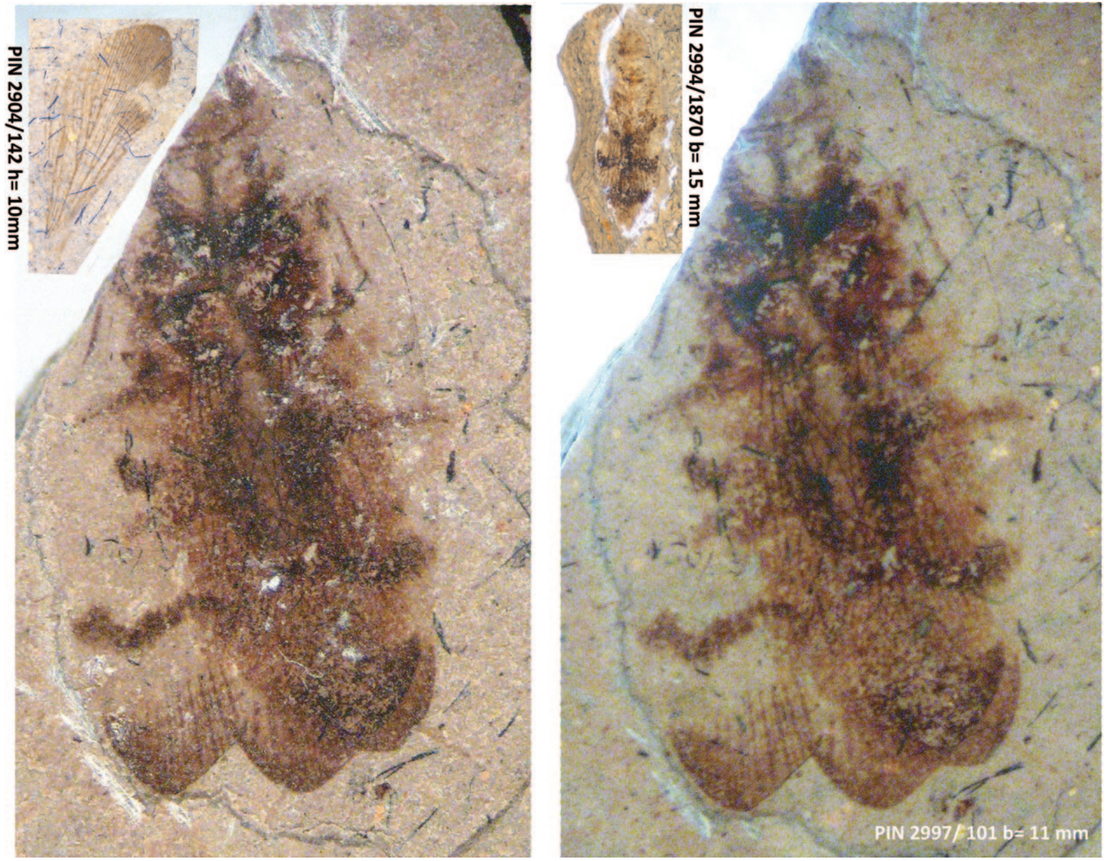
Holotype:. PIN 2904/255. A complete forewing incompletely recovered from the sediment.
Type locality: Mikhailovka, Karatau, Kazakhstan.
Type horizon: Kimmeridgian Upper Jurassic, Karabastau Formation.

Additional material: PIN 2784/753 (forewings with pronotum); 2066/99, 158 (f= 10.8 mm); 2239/116 (f= 10.5 mm); 2994/1870 (l= 15 mm); 2997/101 (l= 11 mm)(complete specimens); 2452/34 (f= 10 mm); 2784/704, 826 (f= 7-8mm); 2997/24, 124, 129 (f= 9 mm), 1556 (isolated forewings); 2904/142=145 (h 10 mm; 1.4+12.2.6+b+1) (isolated hindwing). The same locality as the type.

Differential diagnosis: Differs from the type species and *L. kontrapunktata* in being smaller and in having unparallel wing margins. From other species it differs in extent of colorations and in bearing no reductions .
Description: Forewing length 8 mm, margins non parallel, fore and hind margin tending towards apex centrally. R strongly sigmoidal, RS is barely differentiated. M sigmoidal, expanded with about 11 veins at margin. CuA nearly reaching apex, with 6 or moreveins at margin. Coloration is dark with white terminal macula terminated at margin, white macula in center of the membrane and white posterior CuA field.
Systematical remarks: Closely related to two above species (no specification possible).
Derivation of name: repetition of the genus name.
Character of preservation: Two complete specimens, one articulated forewings with pronotum; 11 isolated forewings, one isolated hindwing.

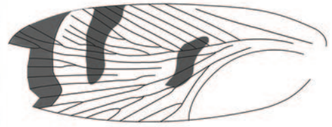

PIN 2597/122 f= 9.5 mm
PIN 2904/27 f= 9.5 mm
2039/32 f= 9 mm


PIN 2452/34 f= 10 mm
2997/241 f= 10 mm
2784/826 f= 7 mm
2784/704 f= 9.5 mm
2904/255b f= 8 mm
PIN 2997/124 f= 9 mm
2784/753
PIN 2997/1556 f= 11 mm

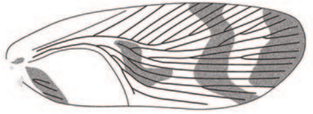




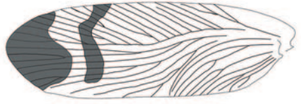




2997/129 f= 9 mm
2997/124=129 f= 9 mm

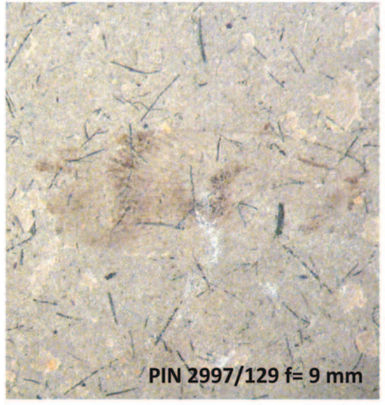


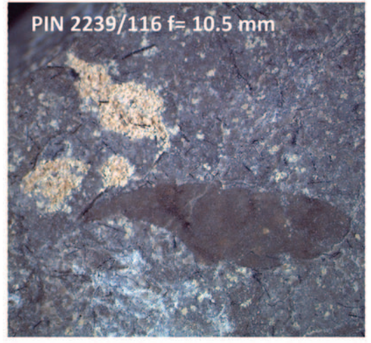
2784/704 f= 9.5 mm



2784/753 f= 9.9 mm

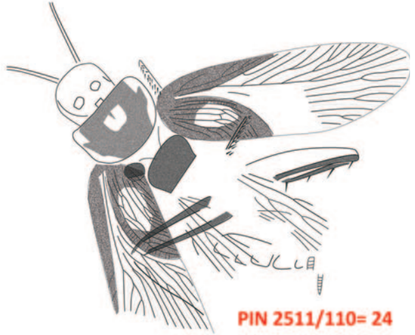












Taphonomy: Three nearly completely articulated winged adults, and numerous isolated forewings might indicate a longer predepositional transport, but it might also be a stochastical indicator, most of specimens even in species containing completely preserved individuals, are preserved as isolated forewings. Nevertheless, only partial articulation as in the present specimen 753 is rare in Karabastau and perhaps also might suggest transportation of some of the individuals.

Liberiblattina paleontologica sp.n.

(figp. 282)

Holotype: PIN 2511/24=110. A complete adult winged female.
Type locality: Mikhailovka, Karatau, Kazakhstan.
Type horizon: Kimmeridgian Upper Jurassic, Karabastau Formation.

Differential diagnosis: Differs from all species except its sister species, *L. cunicula* in pronotum shape with straight anterior margi, from *L. cunicula* in a more sophisticated coloration of the pronotum and a simple coloration of the forewing.
Autapomorphies: Sophisticated coloration of pronotum.
Description. Head nearly as wide as pronotum, eyes long and narrow, ocelli very small, closely approximated. Antenna very thin and fine, segments indistuinguished. Pronotum very small, colored mostly dark, with pale inner area, anterior margin straigth. Forewing with strong branches and fine intercalaries. Sc branched terminally, and basally, with 4 veins (both wings). R branches secondarily and tertiary branched, with 13 veins at margin; M reduced to 2-3 veins; Cu expanded with 8 veins (both wings). A richly branched with numerous fusions, 11-12 vein at margin. Hindwing possibly without coloration. Hindfemora very long and wide, with posterior dark rims and pale interspace. Fore and midtibiae with number of short nad strong spines. Ovipositor rudiment present.
Remarks. The species can be categorized within *Liberiblattina* on the basis of forewing shape and venation but also very specific pronotal shape, which place this species in relation with its siter species *L. cunicula*.
Deformities: Remarkable features of the specimen are indistinct antennomeres (they are recogniseable in each other sample) and also numerous deformities of both wings.Numerous deformities were preserved in the clavus, namely triple connection of the anteriormost A with the CuP and mutual connection to the same branch (A1), in the left wing and also in the right forewing connection of A2 with A1 and mutual connection of A3.
Derivation of name: *paleontologica* is after paleontology.
Character of preservation: One completely articulated adult winged female.
Taphonomy: Completely articulated specimen suggest short or no pre-depositional transport.

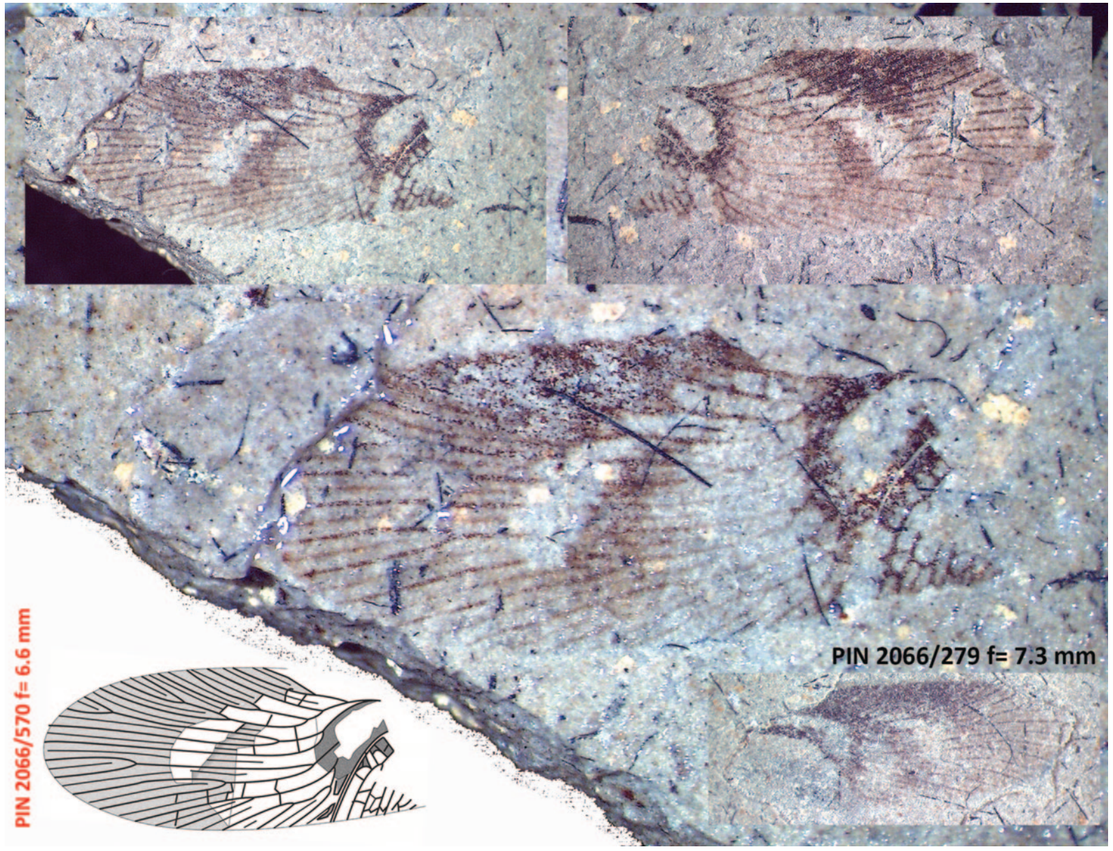
Liberiblattina zokamuvypadli sp.n.

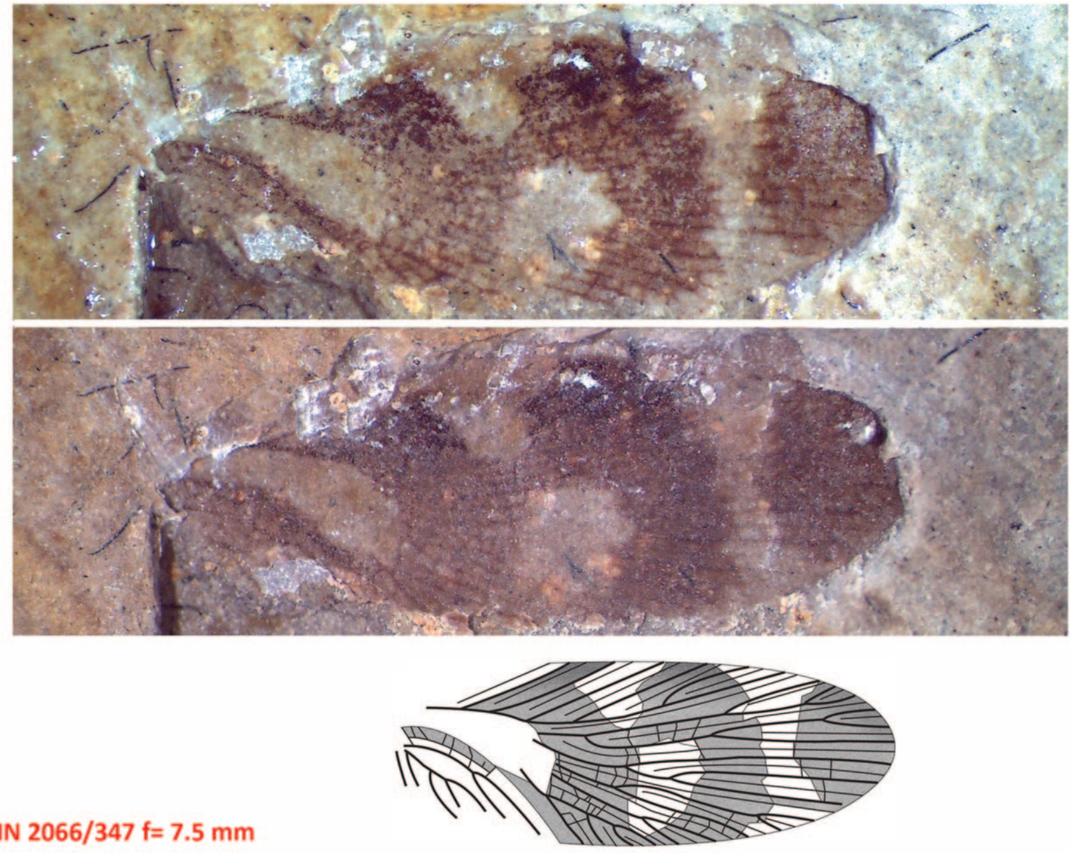
(figp. 284)

Holotype PIN 2066/570±. Articulated forewing (with clavus)
Type locality. Mikhailovka, Karatau, Kazakhstan.
Type horizon. Kimmeridgian Upper Jurassic, Karabastau Formation.

Additional material: PIN 2066/279 (f= 7.3 mm). Disarticulated forewing. The same locality as the type.

Differential diagnosis: Differs from all species in possessing two reverse eye pattern.
Autapomorphies: Sophisticated coloration with two reversed eyes.
Description: Forewing with strong branches and strong intercalaries. R short, branches secondarily and tertiary branched, with 8 or more veins at margin; M reduced to 4-5 veins; Cu expanded with up to 10 veins. A richly branched with numerous reticulations, 6 veins at margin (as preserved the total number is expected at 10-12). Dark coloration present in apical half (except central transversely elongate pale eye pattern, and very dark coloration also surrounds basal cubital transversely elongate pale second eye pattern – also in anteriormost part of clavus.


PIN 2066/279 f= 7.3 mm
PIN 2066/570 f= 6.6 mm


PIN 2066/347 f= 7.5 mm

Remarks: The species can be categorized within *Liberiblattina* on the basis of forewing shape and venation with reticulations
Deformities: No deformity recorded on the holotype.
Derivation of name: *zokamuvypadli* (Slavic for "he jumped off his eye") alluding to eye pattern. This is also a methaphore for resemblance of a father and a son.
Character of preservation: Two adult forewings, one completely articulated.
Taphonomy: Completely articulated forewing combined with the disarticulated one suggest short pre-depositional transport.

Liberiblattina neniocom sp.n.

Holotype: PIN 2066/347. Articulated forewing (with clavus)
Type locality: Mikhailovka, Karatau, Kazakhstan.
Type horizon: Kimmeridgian Upper Jurassic, Karabastau Formation.

Differential diagnosis: Differs from all species except its sister species, *L. zokamuvypadli* in having reverse basal *Eye* pattern. *L. zokamuvypadli* differs in having two reverse *Eye*-like coloration on each forewing.
Autapomorphies: sophisticated coloration with a reverse eye and two additional dots.
Description: Forewing with strong branches and intercalaries. R short, branches mostly simple, one of them is secondarily branched, with 7 or more veins at margin; M with 11 veins; Cu with 6 veins, posteriormost branch strong, with 4 veins at margin. A richly branched with numerous reticulations, 7 veins at margin (as preserved the total number is expected at 10-12). Dark coloration fundamental, pale areas present in clavus (except anteriormost area among A1 aintercalary and CuP), subapical transverse narrow stripe, and two pale central dots (anterior and separated posterion one).
Remarks: The species can be categorized within *Liberiblattina* on the basis of forewing shape and venation with reticulations, close relation with *L. zokamuvypadli* and fundamental pattern similar to that of the type species.
Deformities: No deformity recorded on the holotype.
Derivation of name: *neniocom* (Slavic for "it is not about anything") alluding to sophisticated modern coloration pattern. This is also a methaphore for not being a (fore)father.
Character of preservation: one adult forewings, completely articulated.
Taphonomy: Completely articulated forewing suggests short pre-depositional transport.

Liberiblattina oddajsami sp.n.

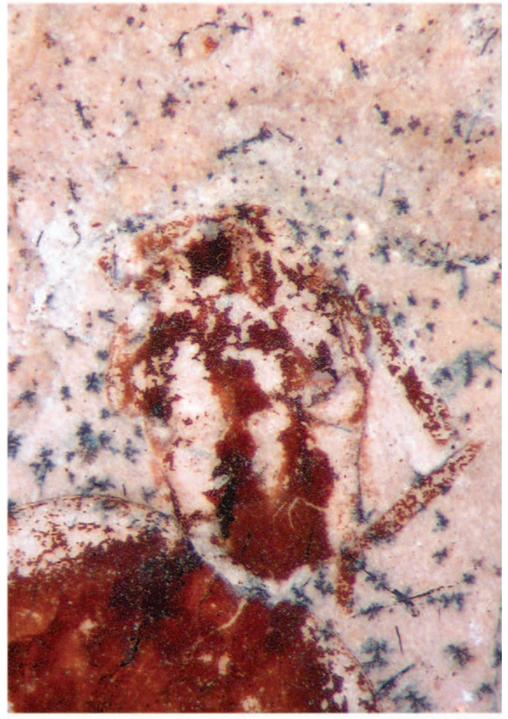
(figg. 287)

Holotype: PIN 2784/783. A complexly articulated adult female.
Type locality: Mikhailovka, Karatau, Kazakhstan.
Type horizon: Kimmeridgian Upper Jurassic, Karabastau Formation.

Additional material: 2554/31, 32± (complete specimens). The same locality as the type.

Differential diagnosis: Differs from all species except its sister species, type species and *L. kontravenata* in having "missing" anterior coloration area. Type species has more extensive clavus-copying pale areas and *L. kontravenata* differs in not having this coloration at all.
Autapomorphies: none because of sophisticated coloration synapomorphic with other species and plesiomorphic character of the original pronotum.
Description. Head elongate, more thatn twice as long as wide, dark, with pale eyes and pale central elongate field. Palp very long and thin, 4-segmented. Pronotum very robust, oval, elongate, about 1.5 times longer than wide. Forewing dark with narrow and short pale area near clavus and missing coloration in the small anterior field. Body narrow, legs cursorial, with standard but shortened carination.
Remarks. The species can be categorized





PIN 2554/32

PIN 2784/783

within *Liberiblattina* on the basis of forewing shape and venation with characteristic coloration pattern, close relation with type species and L. kontravenata (all three "missing" coloration in the anterior area). This species was very likely predatory as suggested with reduced size of spines – apparent adaptation towards active moving, and combined with narrowed body and elongate extremities (including palps).
Deformities: No deformity recorded.
Derivation of name: *oddajsami* (*oddaj sa mi is* Slavic for "give yourself to me") alluding to this species was the last one determined, avoiding classification.
Character of preservation: Three complete specimens.
Taphonomy: Completely articulated specimens and lack of isolated forewings suggests no pre-depositional transport and rare occurrence near the source area.

Genus *Ano* Vršanský, 2020

Type species: *Ano da* Vršanský, 2020. Middle Jurassic Bakhar, Mongolia.

Composition: *A. net* Vršanský, 2020*; A. nym* Vršanský, 2020; and species designated here. Middle Jurassic Bakhar, Mongolia.

Stratigraphic range: Middle-Late Jurassic
Geographic range: Laurasia

Differential diagnosis (after Vršanský 2020). *Ano* is a highly variable taxon, differing from other representatives of the family in distinct rather simple coloration forming a simple single-dot pattern (other representatives of the family are either without coloration like *Stavba*, with simple macula like *Elisamoides* or with more sophisticated patterns like *Liberiblattina*). Differences occur in the unparallel margins of rather short and wide forewings with distinct pseudovein (see labelled fig. 13i; characteristic for mantodeans). Venation is usually characterised with a basally branched rather short Sc, but sometimes terminal branchelets are present or Sc can be rarely even simple; R slightly sigmoidal with R rarely secondarily branched, RS might be differentiated; M curved, not sigmoidal; CuA with basally differentiated 2 main stems, A branched, sometimes terminally; CuP fluent.

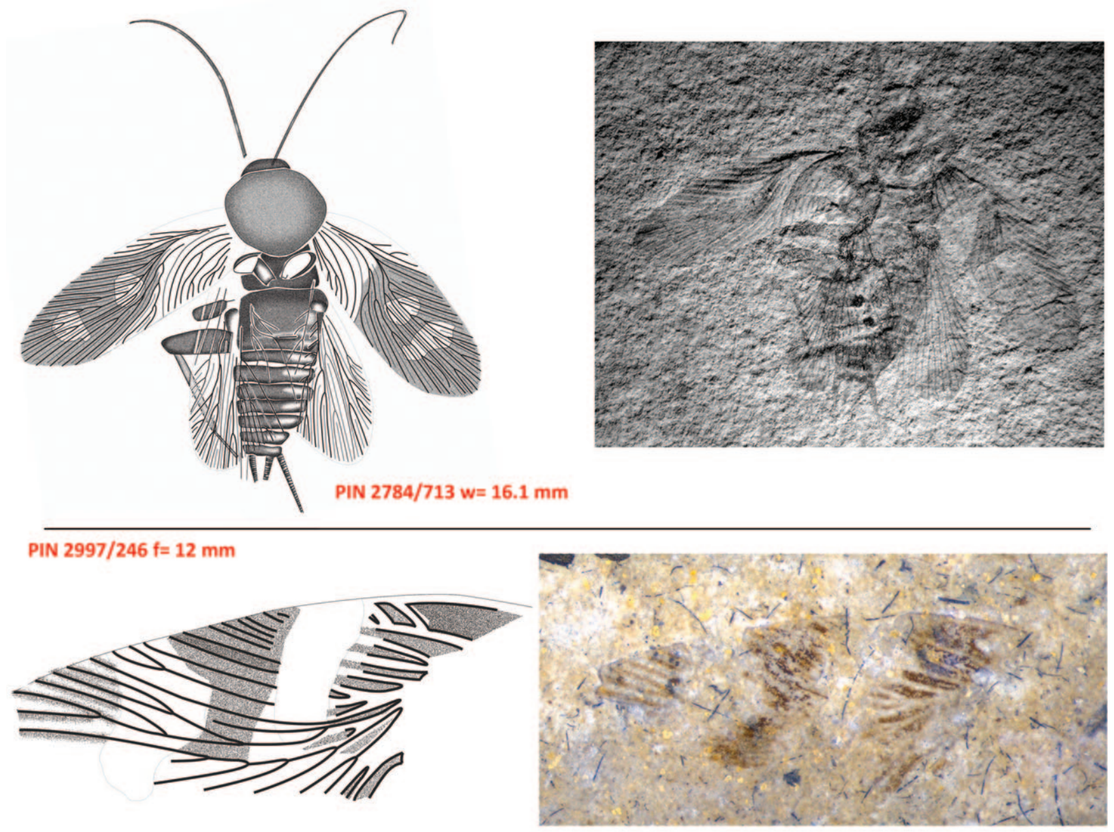
Remarks. Numerous species new species in these two species complexes (*Liberiblattina*/*Ano*) reveal transitions and are a direct evidence for the diversification reduction ring cascade (see Vršanský et al. 2019)(figp. 620). There is a fluent transition among these wo genera and they are both retained just because there is a significant difference for instance among burrowing *L. cunicula* and fragile *Akinisia chorevei* (and *Ano naslosa*).

Ano tak sp.n. (figp. 289)

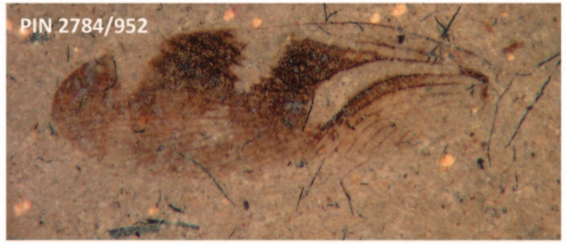
Holotype: PIN 2784/713. A complete adult winged male.
Type locality: Mikhailovka, Karatau, Kazakhstan.
Type horizon: Kimmeridgian Upper Jurassic, Karabastau Formation.

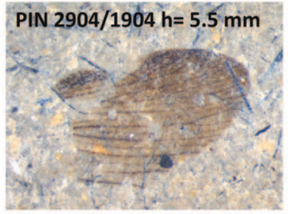
Additional material: PIN 2784/691± (complete specimen; LH 1.4+7.5.5+RH 1.4+7.4.4+); 2997/4410 (isolated forewing). The same locality as the type.

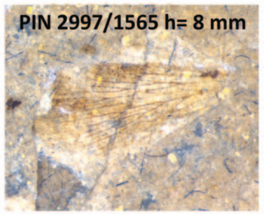
Differential diagnosis: Differs from the species from Bakhar in having more sophistated coloration of forewings and in plesiomorphic state of the larger round pronotum (compared with cordiform of *A. da*). *A. net* is additionally larger (10.5 mm) and more extensively and more simply colored, predominantly dark. *A. nym* is













even larger (14 mm) with similarly sophisticated coloration with two pale areas, but the second macula is rather a pale stripe on generally dark membrane.
Autapomorphies: Two pale dots on dark areas – apparently an aposematic signal more sophisticated than in congeners.
Description: Head large, globular, monochromatically dark. Antenna very thin and moderatelyt long, plastic (8.3/ 0.1 mm) Pronotum very large, round (3/ 3.5 mm), extending centrally at posterior margin, monochromatically dark. Body wide (i.e., fat), but comparatively narrow. Cerci very long (2.2/ 0.2 mm), multisegmented, filamentous, without structures or widenings (widest at base and fluently narrowing), approximately with 30 cercomeres (25 preserved); styli similarly long (preserved 1.1 mm with 11 preserved stylomeres – but this seems to be a bare half of the original size) and wide and also multisegmented with stylomeres of similar structure and size as cercomeres.
Forewings wide (8.1-9/ 2.9-3 mm), with apex posed anteriroly, ascend of the posterior margin starts in apical quarter. Costa indistinct, costal are rather wide, Sc very long, nearly reaching the apical half, with 3-4 veins at margin, which inlcude the terminal as well as the basal dichotomisations. R strongly sigmoidal, nearly reaching apex, with indicated R1 and RS (5-7+5-6). M descending late, with 3-5 sigmoidal branches meeting margin. CuA strongly sigmoidal with 5-6 veins at margin. CuP rather fluent, long, but shorter than SC, with 7-10 (branched) anal veins. Clavus with diagonal kink. Intercalaries present, cross-veins indistinct. Membrane basically dark except clavus, costal area and two distinct round pale spots.
Hindwing long, apparenly not overlaid completely during repose. Sc simple, R1 sigmoidal (conservatively 3 or 4 in two specimens) without pterostigma, and RS (5-7); M straigth (2-5); CuA with tertiary branches veins (8 at margin) and additional blind branches; CuP simple. Remigium A1 widely branched.
Legs moderately robust, hindfemora monochromatically dark (2.5/ 0.8 mm), hindtibia monochromatic dark (3.2/ 0.3 mm). Hindbasitarsus long and thin, monochromatic dark (1.2/ 0.1 mm).
Remarks: *A. da* has variable size, with forewing lengths 5.8-10 mm, with variable coloration and sum of forewing veins at margin 17-21 (compared with 26 of the new species – excluding A).
Mutations: There is no distinct deformity apparent among 9 preserved wings, although one of the forewing M branches of the holotype might be possibly incomplete (terminated before margin).
Derivation of name: after *tak* (Slavic for "so").
Character of preservation: two complete specimens, one possibly isolated forewing.
Taphonomy: Complete specimens with articulated cerci and fine styli suggest no pre-depositional transport. Antenna is sharply curved although not broken, suggesting its plasticity.

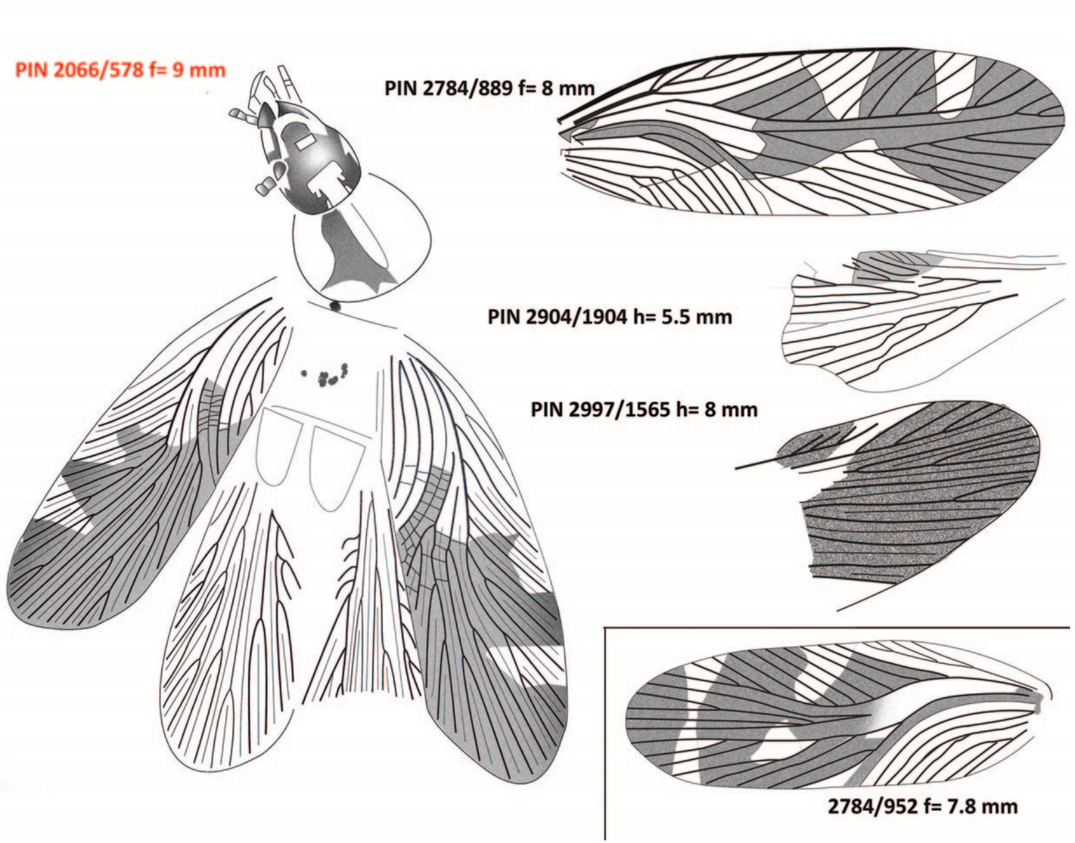
Ano mal sp.n.

(figp. 290, 292)

Holotype: PIN 2066/578 (l= 9 mm). A complete winged adult; sex unknown.
Type locality: Mikhailovka, Karatau, Kazakhstan.
Type horizon: Kimmeridgian Upper Jurassic, Karabastau Formation.

Additional material: PIN 2784/889 (f= 8 mm), 952 "karatavica" (isolated forewings); 2904/161, 1904 (h= 7 mm); 2997/260, 284, 1440± (h= 8 mm; 1.5+4.5.6+1), 1565 (isolated hindwing(s)). The same locality as the type.

Differential diagnosis: Differs from the species from Bakhar in having more sophisticated coloration of forewings (but of basic type – i.e., without strictly delimited aposematic dots). Somewhat similar coloration was present in much larger *A. palindrom*, which had pale veins.
Autapomorphies: Robust, sophisticately colored head and coloration of forewings.
Description: Head large, elongate (2.4/ 1.6 mm), dark with pale clypeus and occiput. Antenna not very thin. Forewings wide (7.8-9/ 2.5-2.9 mm), with apex posed centraly, ascend of the posterior margin starts in apical fifth. Costa distinct,



costal are narrow, Sc long, with 3-5 veins at margin, which inlcude the terminal as well as the basal dichotomisations and also the one anterior offshot. R strongly sigmoidal, not reaching apex, with indicated R1 and RS (5-7+3-6). M descending early, near base, with 4-10 sigmoidal branches or straigth (and even terminaly dichotomised) veins meeting margin. CuA strongly sigmoidal with 5-9 veins at margin. CuP rather fluent, long, but shorter than Sc, with 7-10 (branched) anal veins. Clavus with diagonal kink. Intercalaries present, cross-veins indistinct. Membrane basically dark except clavus (except A1 area which is usually dark), costal area pale stripe following clavus, and two transverse pale stripes: one central one apical, frewuently decayed into 4 areas.
Hindwing long, apparenly not overlaid completely during repose. Sc simple, R1 sigmoidal (variable 3-5) with pterostigma, and RS (5-7); M straigth (1-5); CuA with tertiary branches veins (6-7 at margin) and additional blind branches; CuP simple. Vannus A2 widely branched. Except pterostigma, dark is also terminal half of the hidwing (short pale area between this colored part and pterostigma).
Remarks: This species is a standart regarding the size within the genus. Due to similarities in coloration, it might appear ancestral for *A. palindrom*.
Simplification of M in PIN 2904/1904 is unusual (if occur than in conservate such as in Ectobiidae).

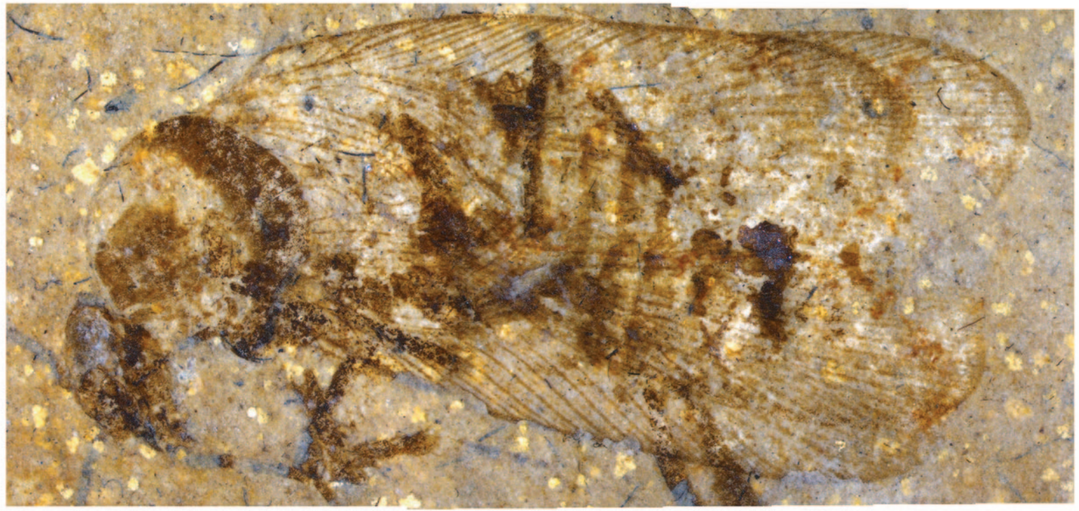
Mutations: There is no distinct deformity apparent among 12 preserved wings, although 2784/ 889 and 952 and also the holotype on both sides, have both very unusually anterior offshot of Sc, which is apparenly a mutation. Nevetleless, it is not counted among detrimental deformities as it is fixed and regularity of veins was not obstructed.
Derivation of name: *mal* is Latin for bad. Regarding for preservation state.
Character of preservation: one complete specimen, two isolated forewings, 6 isolated hindwings.
Taphonomy: Complete specimen with disarticulated body and broken antennae and palps, and isolated wings suggest predepositional transport.

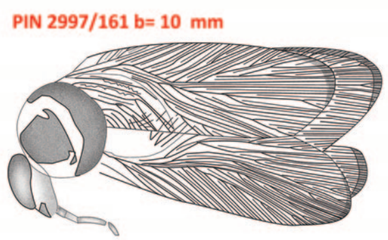
***Ano si* sp.n.** (figp. 294)

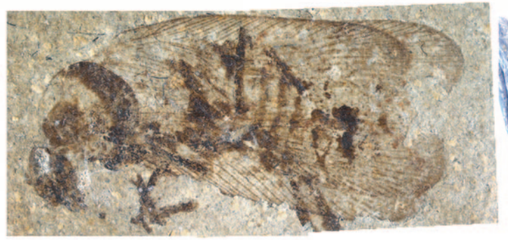
Holotype: PIN 2997/161 (b= 10 mm). A complete adult winged male.
Type locality: Mikhailovka, Karatau, Kazakhstan.
Type horizon: Kimmeridgian Upper Jurassic, Karabastau Formation.

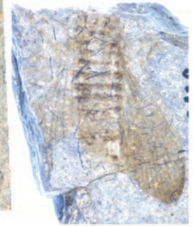
Additional material: PIN 2066/411 (b= 16 mm); 2239/277 (body with male tergal glands); 2997/170, 1589 (complete specimens); 2997/1285, 1369, 1285 (isolated forewings). The same locality as the type.

Differential diagnosis: Differs from its congeners in less developed coloration of wings restricted to apex and in coloration of pronotum with wide ral posterior margin and dark central dot, and in striated body.
Autapomorphies: Distinct colored costa, pronotum with central anterior aposematic dot, striated body, posteriorly curved tibial spurs (ancestral or homoplasic only to Eadiidae).
Description: Small cockroach with overall length ca. 10 mm. Head large, globular, monochromatically dark, with huge globular eye. Palp comparatively long. Pronotum comapraticely large, round (3/2.6 mm), softly extending centrally at posterior margin, pale, with large dark anterocentral dot (1.1 mm in diameter). Body wide (i.e., fat), but comparatively narrow. Forewings wide (8.5/ 2.8 mm), with apex posed anteriroly, ascend of the posterior margin starts in apical fifth. Membrane transparent, with narrow apical dark area. Intercalaries present all over the wing including clavus and costal area. Cross-veins indistinct except for clavus and adjacent CuP. Costa distinct, strong ansd strongly melanised, costal area rather standard, Sc standard, branched (5), which inlcude the terminal as well as the basal dichotomisations. R strongly sigmoidal, nearly reaching apex, with indicated R1 and RS (13-18+2-5). M descending early, with 6-9 sigmoidal branches meeting margin. CuA strongly sigmoidal with 5-7 veins at margin. CuP rather fluent, long, but









shorter than Sc, with 11 (branched) anal veins. Clavus with diagonal kink indistinct. Hindwing long, significantly protruding during repose. Veins wide, membrane transparent, apex narrowly dark.
Legs moderately robust.
Remarks: General habitus well enables categorisation within the genus, while the coloration of the forewing is greatly reduced. Here the aposematic signal is rached with the dominant pronotal dot and thus the dot on the forewing is not necessary anymore. Costa become colored instead.
Extremely important are preserved male tergal glands, unknown in the whole family. Within the genus, relations are imposisble to establish in spite of good preservation, but the taxon reveal tendency towards strengthtening of carination, which might suggest need of passsive protection associated with more open lifestyle or exactly the reverse- burrowing adaptations.
Posteriorly curved tibial spurs are known only in Eadiidae and this character might appear transitional to them..
Mutations: There is no distinct deformity apparent among 13 preserved wings, although the **holotype** contains two unusual irregular areas among veins (M-M; M-CuA).
Derivation of name: *si* is Slovak for “you are being” or “you exists”.
Character of preservation: 5 complete specimens, 3 isolated forewings.
Taphonomy: Preservation of complete specimens only might suggest short on no pre-depositional transport (isolated hindwings would be difficult to discriminate from other species which is not the case for forewings).

Ano palindrom sp.n. (figp. 289)

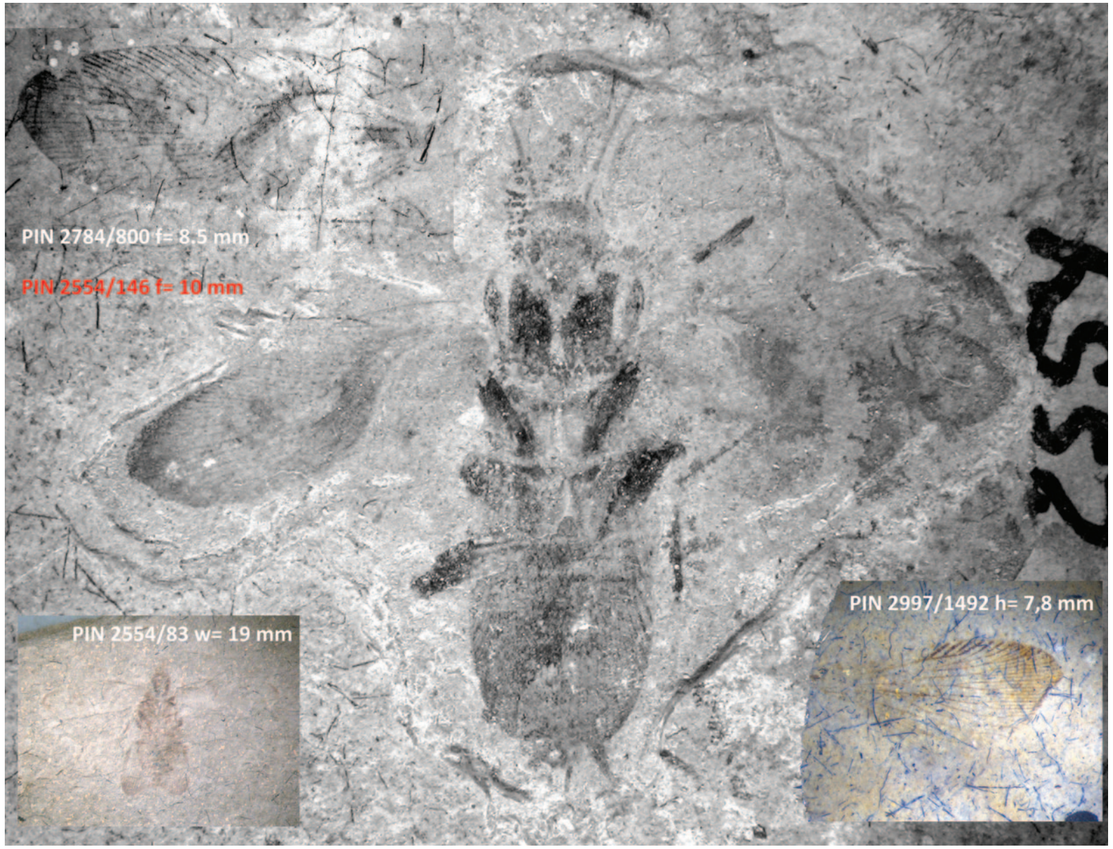
Holotype: PIN 2997/246. A forewing fragment.
Type locality: Mikhailovka, Karatau, Kazakhstan.
Type horizon: Kimmeridgian Upper Jurassic, Karabastau Formation.

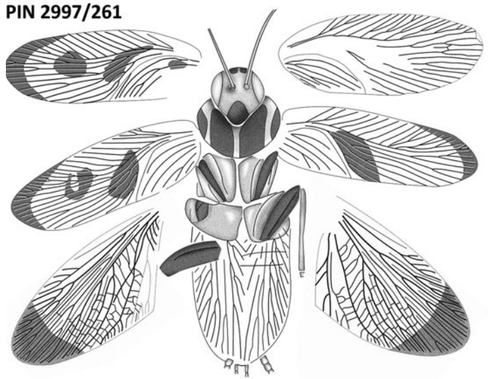
Differential diagnosis: Differs from the known species by larger size (up to 18 mm) and in having reversed coloration with pale veins.
Autapomorphies: Reversed colors, with pale veins.
Description: Forewings wide, ca. 18 mm long (14 mm as preserved). Costa distinct but pale, costal area rather wide, SC long, with maximum 2 veins at margin, which inlcude the terminal dichotomisations. R strongly sigmoidal, nearly reaching apex. Membrane basically dark except clavus, costal area and two distinct large transversal stripes. Intercalaries present, crossveins seems absent.
Remarks: The taxon evidences capability of the genus to reach bigger size and might be transitional towards *Liberiblattina***.**
Derivation of name: *palindrom* is Slavic and Latin for palindrome.
Character of preservation: one damaged forewing.
Taphonomy: Damaged and disarticulated forewing suggest a longer pre-depositional transport (or longer stay in water prior to burial) possibly suggesting presence further from the depostion waterbody. There species could be more common.

Ano ona sp.n.
(figps. 296-309)

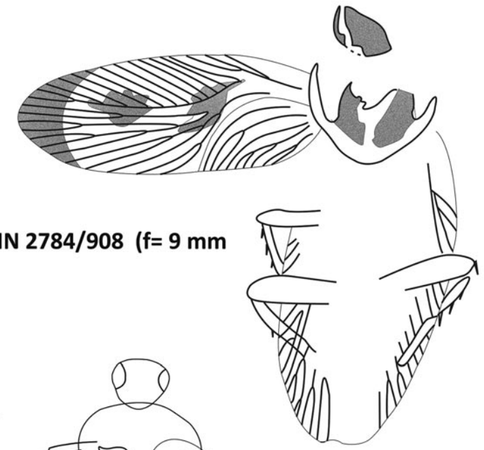
Holotype: PIN 2554/146. A nearly complete adult winged female (without hindwings).
Type locality: Mikhailovka, Karatau, Kazakhstan.
Type horizon: Kimmeridgian Upper Jurassic, Karabastau Formation.

Additional material: PIN 2039/35; 2066/147, 303, 512=517; 2239/176; 2384/131, 167, 168; 2452/409; 2554/74, 59, 83; 2784/unknown number (drawing), 724, 830, 838, 844, 892, 908=902, 912, 903; 2904/36, 44±, 112, 347 (f= 8.5 mm), 365, 1719, 1876, 1887; 2997/264, 1210, 4257, 4349 (h= 10 mm) (complete specimens); 2039/28, 38, 49, 54; 2239/198, 286 (f= 11.5 mm); 2452/55, 374, 497, 653; 2784/649, 800, 879; 2997/148, 261, 1193 (f= 8 mm), 2851 (f= 9 mm) (forewings); 2239/275; 2452/395 (h= 11 mm); 2554/187; 2784/956; 2904/91, 176=177*,

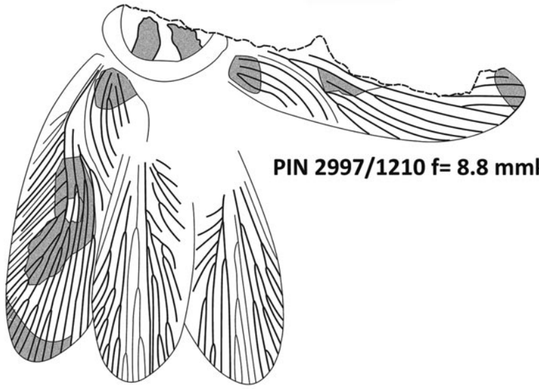




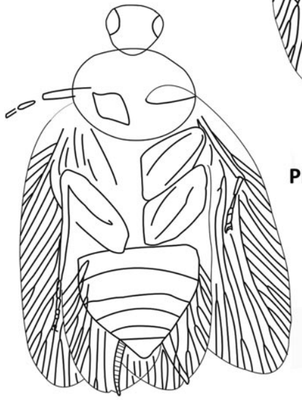
PIN 2784/879 8.8 mm



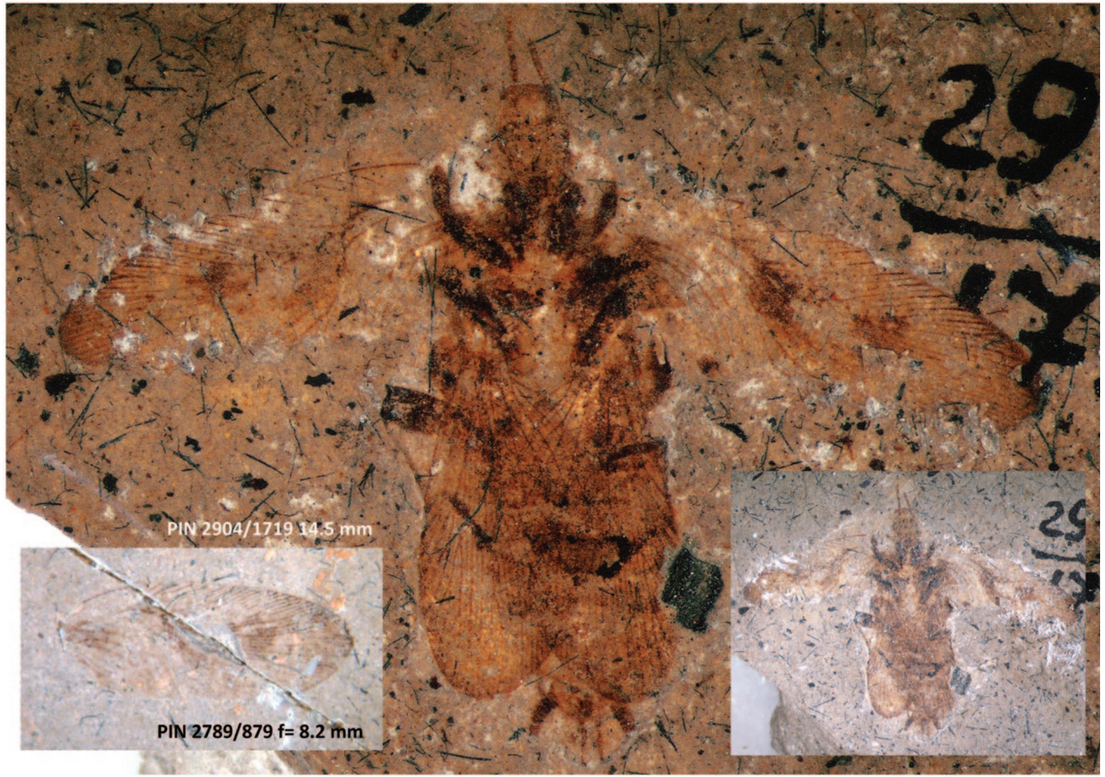
PIN 2784/2266 PIN 2554/146

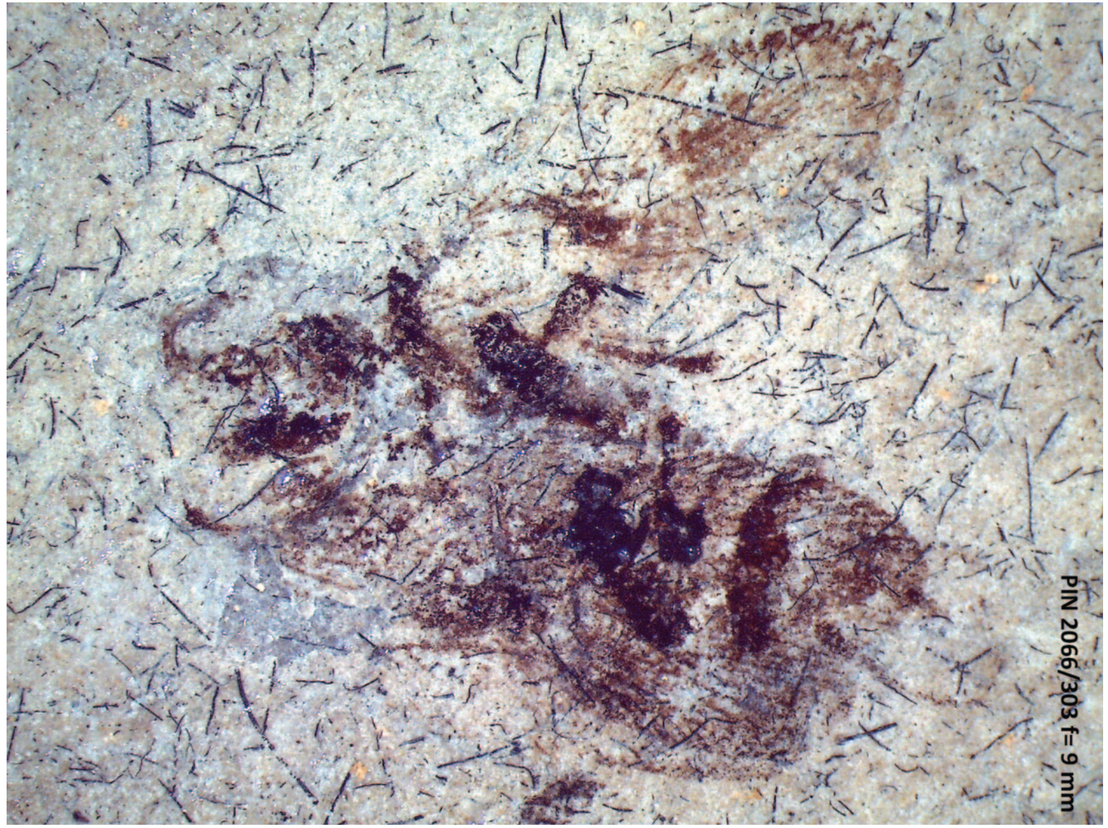


PIN 2997/1210 f= 8.8 mmk



PIN 2784/649 f= 9 mm


PIN 2904/1719 14.5 mm
PIN 2789/879 f= 8.2 mm

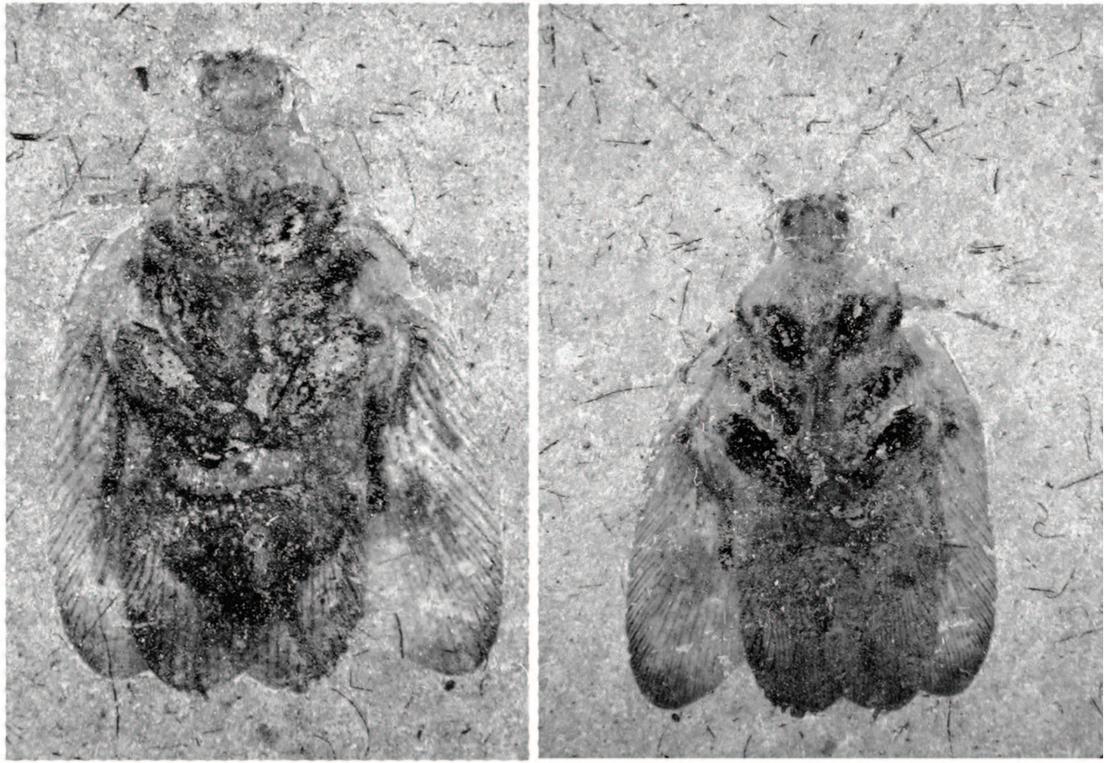

PIN 2066/303 f= 9 mm


PIN 2039/35 fR= 9 mm

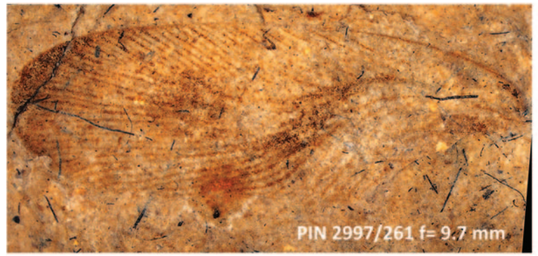

2784/912 f= 9 mm

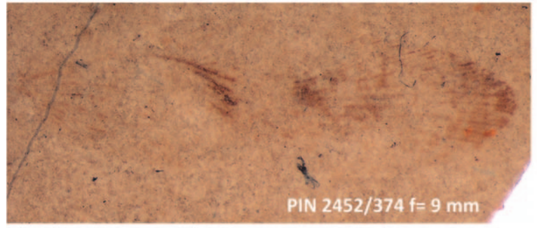


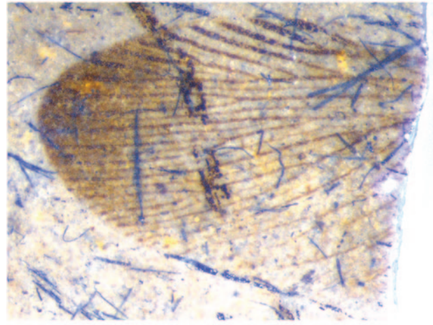

PIN 2904/44



PIN 2784/649 f= 8 mm





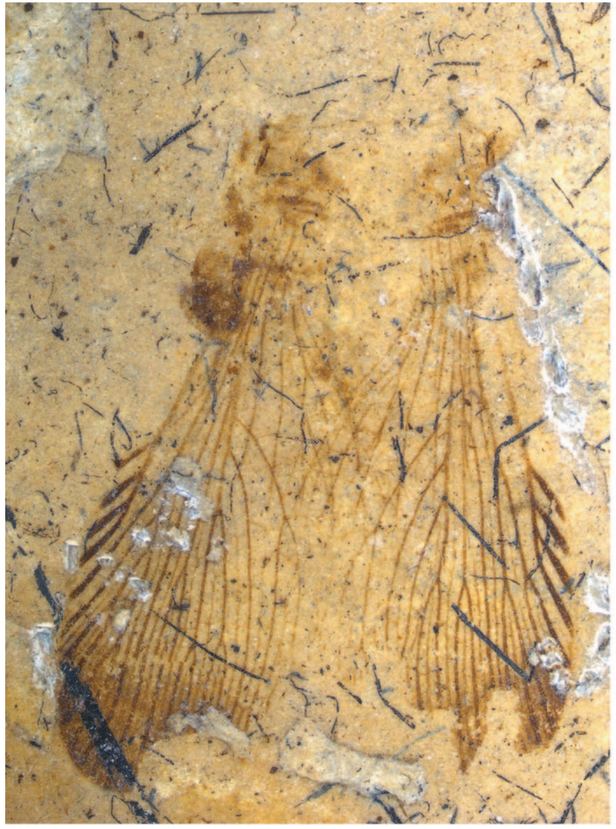


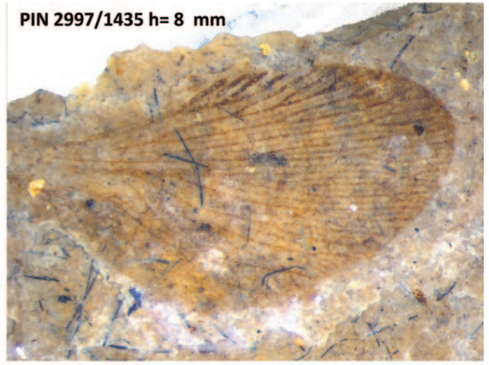
PIN 2997/148 h- 6 7 mm (expected)

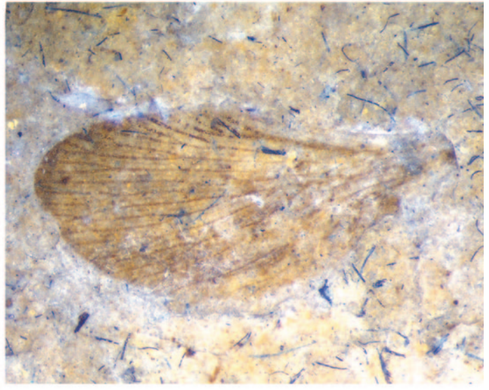




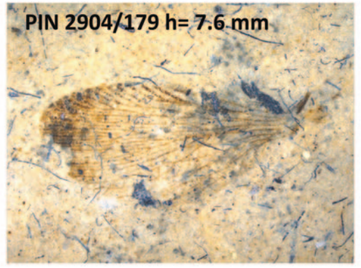


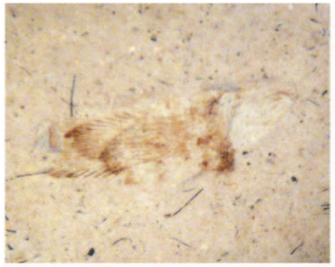



PIN 2997/1435 h= 8 mm



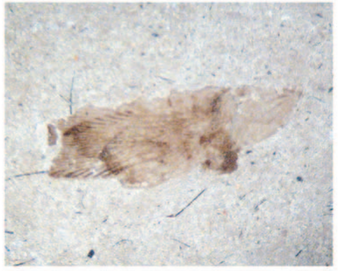

PIN 2904/112 h= 9 mm

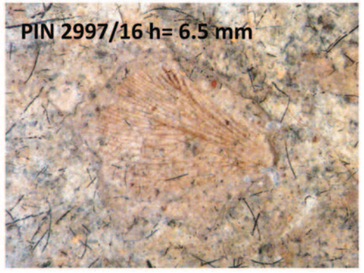

PIN 2904/179 h= 7.6 mm

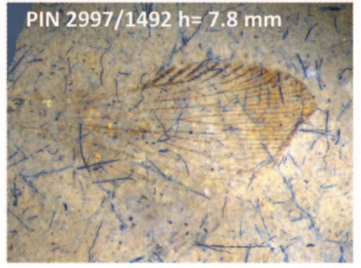


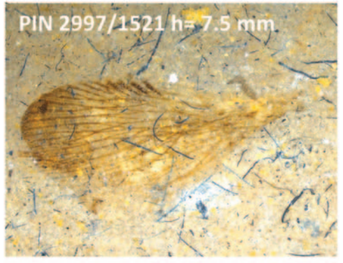

PIN 2784/956 h= 6 mm

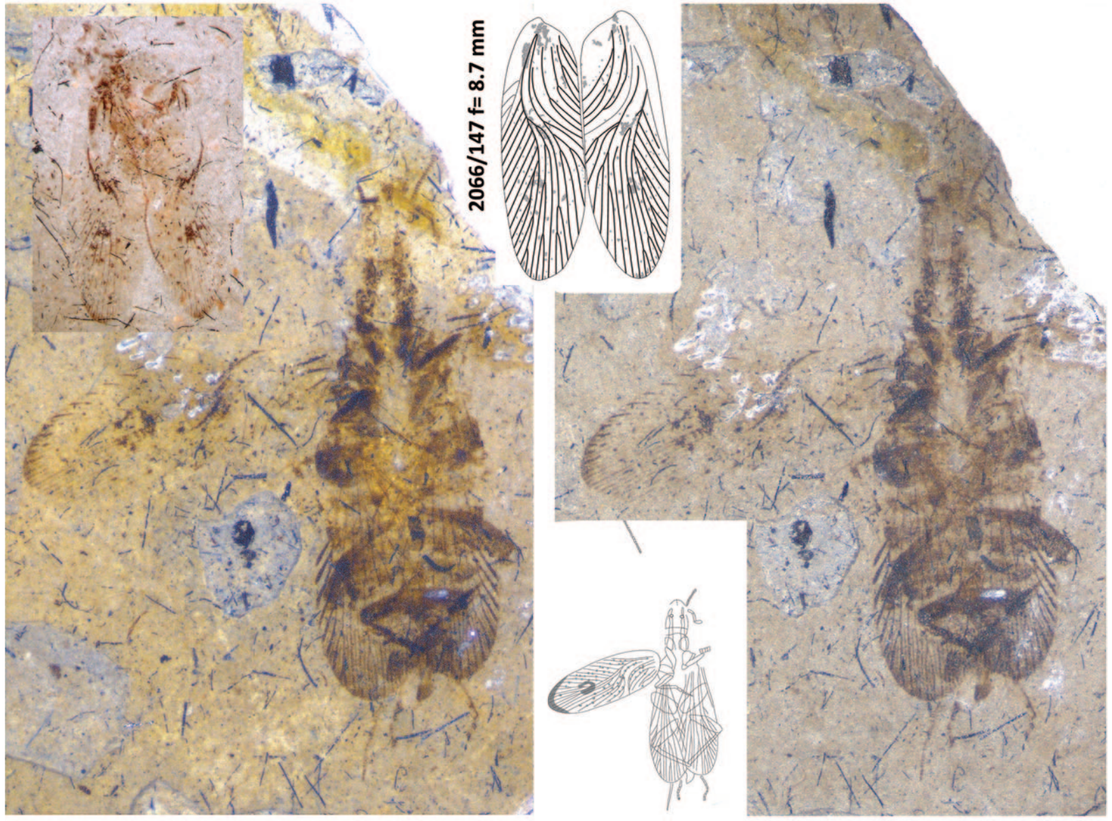

PIN 2554/187 h= 11 mm



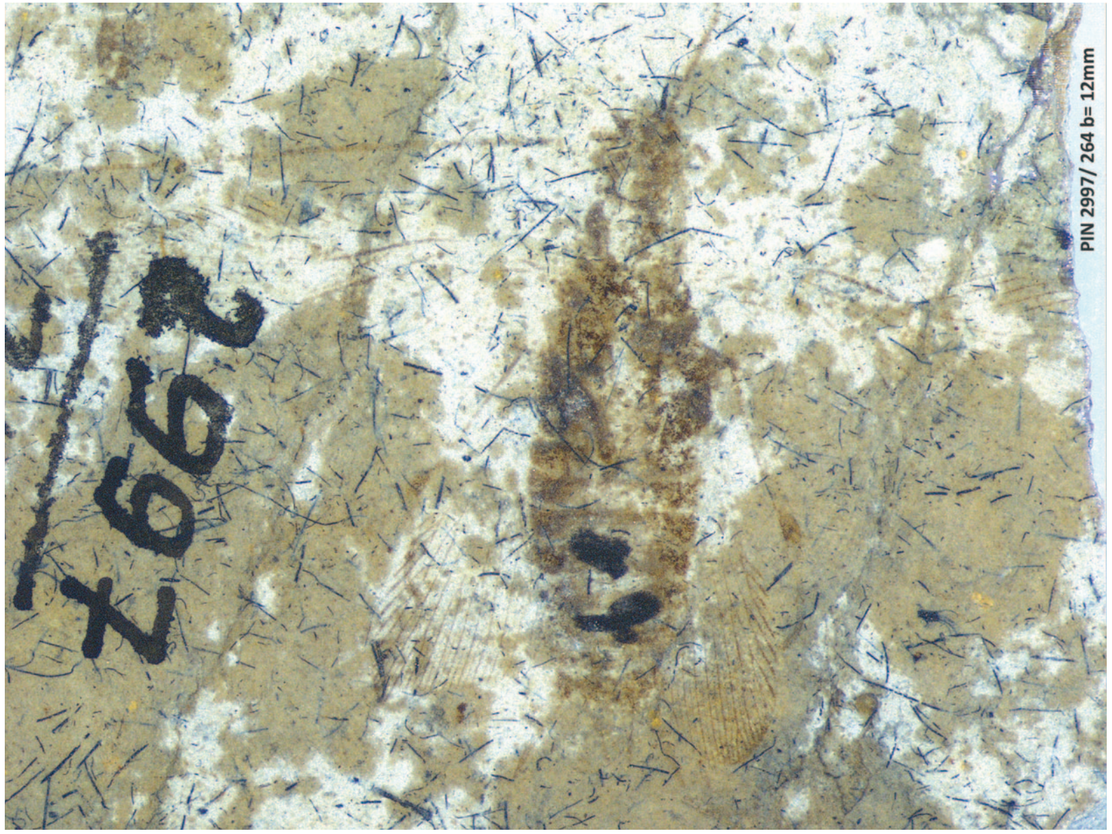

PIN 2997/16 h= 6.5 mm


PIN 2997/1492 h= 7.8 mm


PIN 2997/1521 h= 7.5 mm


2066/147 f= 8.7 mm


2066
f= 16 mm


PIN 2997/ 264 b= 12mm


1,00 mm
PIN 2997/1210 f= 8.8 mm

179, 236, 1873; 2997/16, 24±, 28, 45 (h= 11 mm), 119 (11 mm), 126, 132, 143, 148, 214, 776, 1180=1184, 1327, 1409, 1435±, 1486 (h= 7 mm), 1507 (h= 10 mm), 1519 (h= 8 mm), 1521, 1605 (h= 9 mm), 1666, 2824 (h= 9 mm), 4259±, 4325, 4400 (h= 10 mm) (single hindwings); 2784/1492, 2266; 2904/112, 1890; 2997/54, 264, 1547 (hL= 7.9 mm, hR= 7.9 mm), 4338± (both hindwings). The same locality as the type.

Differential diagnosis: Differs from other species in possessing more advanced coloration combined from sophisticated terminal transverse stripe and basal longitudinal stripe, but most imporantly from eye-like central spot and numerous distinct small dotts located on intercalaries. Pronotum is also uniquely (not especially advancely) colored.

Autapomorphies: Eye-like colored forewing spot, minor colored dark dots forming intercalaries

Description: Head globular, comparatively large, longitudinal (4/ 3 mm), with two short longitudinal dark stripes on base; antenna only slighhtly longer than body and shorter than wings (under 9 mm); palps comparatively short (overal length under 1.5 mm); mandible black, very large, unconcealed. Pronotumonly slightly transversal (roughly 4/ 5 mm in holotype), with four wide longitudinal stripes (medial stripes are twice as wide as lateral). Forewing most robust basally, only three times as long (8.5-14.5 mm) as wide. Coloration with distinct dark „eye“, apex , stem of M and CuA dichotomisation and basal A2, but with aberrations. Subcosta simple to 5-branched, anteriormost veins meeting margin of wing nearly as in the same relative position as clavus. Vast majority of R1 branches simple, RS differetiated, but indistinct or with up to (11-)16 branches. Radial field covers between ½- ⅓ of witng width. M 4-8 branches at margin, overlapping or meeting apex; CuA with 5-13 veins, anteriormost branches reaching the apical 1/5 of wing´s length. Clavus reaching one third of the wing overal length, with 6-9 anal veins at margin (some branches are basally or terminally dichotomised).

Hindwing (6-13.5 mm long) with coloured apex, with Sc simple; R1 (3-7, with pterostigma indicated or absent) and RS (4-13) differentiated; M with 2-7 veins at margin, normally plesiomorphically expanded, but with one specimens (2384/131) having reduced to 2 veins in both wings; CuA (3-10), CuP simple, but the specimen (2039/28) with CuP dichotomised.

Legs very short (hind femora ca. 4 mm long, tibiae 6 mm), cursorial, not specially massive, all femora dark (preserved, likely black in vivo), other parts pale.

Body not very wide, cerci multisegmented very long (4 mm) and narrow, styli also long (1 mm), with at least 4 segments.

Remarks. The species is closely related to type species from the Middle Jurassic Bakchar of Mongolia. Long cerci ressemble lineage leading to mantodeans (inlcuding Eadiidae and Manipulatoridae) and also that of the basal Umenocoleidae (*Jantaropterix*). The present species has more advanced forewing coloration which might reflect slightly younger age.

Deformities: Hindwings 2997/1435 contains 1A2-CuA fusion and 1436 contain a single CuA-CuA fusion of veins. Hindwing 2904/176=177 posses CuA-M fusion.

Variability: Forewing vatiability of total number of veins reveal significantly low number (CV= 5.71 %, n= 15) even without A (CV= 8. 1 %, n= 17). It is necessary to stress that both these numbers are statistically insignificant, and some problems appear also from the discrepancy of these two numbers resulting from insufficient sample size, but real variability will not differ of more than 2 %. Very low is also variability of anterior margin (RM) and R with CuA (10.14 %; 10.98 %). It is interesting that these two numbers are very similar, which is very unusual and this might be the reason for the generally low variability. It is possible that this species controlled the variability globally and strictly and not only at the anterior margin – very likely an evidence for active, precise and long flight.

Hindwing variability is statistically significant and is characterised with higher values (CV for total number of remigium veins 15.19 %). Notably, in all statistically significant (other species), variability of hindwing is higher that that of the forewing, which is counterintuitive due to higher expected aerodynamical impact of much larger hindwing in the flight stroke.

Derivation of name: *ona* is Slavic for *she*. A pallindrome.

Character of preservation: 33 complete specimens, 15 isolated forewings, 43 complete hindwings (8 both).

Taphonomy: Preservation mostly of the complete specimens, combíned with more preserved hindiwngs compared with isolated forewings (which are more pale and thus more difficult to observe during collection) suggest autochtonous origin of the source forest near waterbody, abundance in the ecosystem and minimal predepostiional transport and short duration in waterbody prior to burial.

Ano naslosa sp.n.

(figp. 312)

Holotype: PIN 2066/420 f= 1.7 mm. Partially damged forewing with a part of thorax.

Type locality: Mikhailovka, Karatau, Kazakhstan

Type horizon: Upper Jurassic Karabastau Formation

Differential diagnosis: Differing from all fossil cockroaches in miniature size

Autapomorphies: Extremely small cockroach at the same time with exception of supported costa lacking any distinct miniaturisation adaptations. Venation is standard with alternating veins and intercalary veins of standard width.

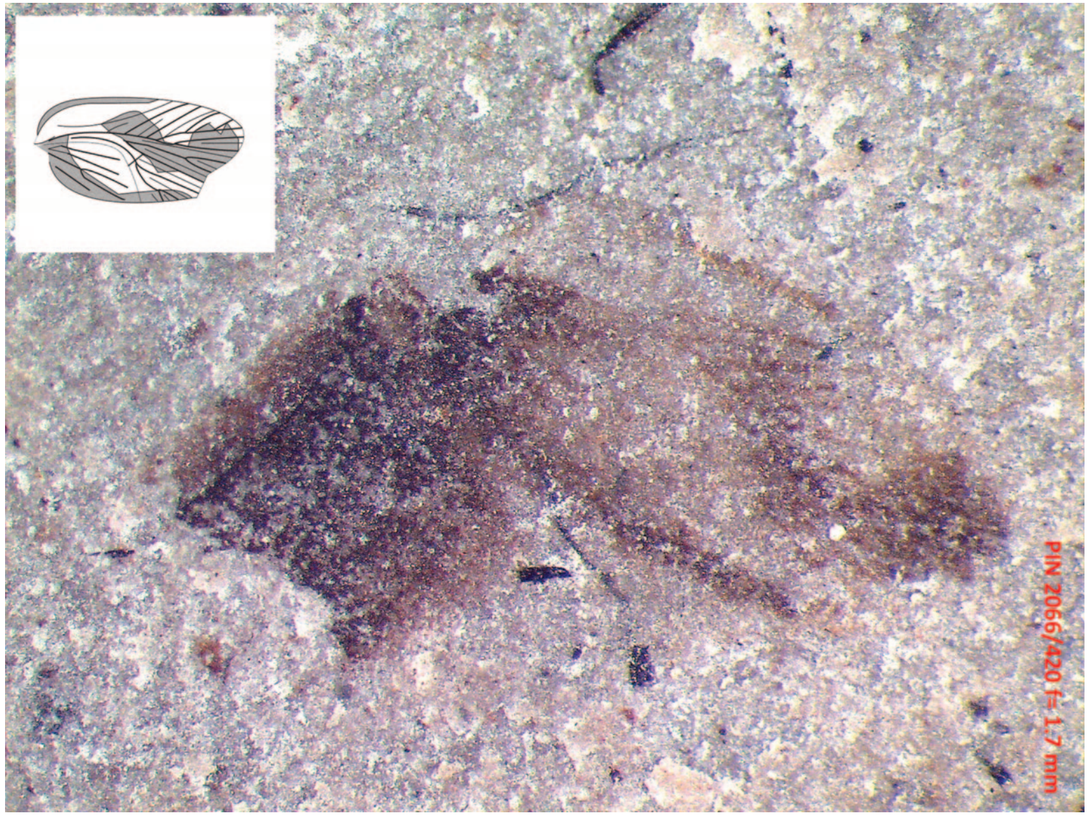
Description: Only ca. 2.0 mm long cockroach forewing with arcuate fore margin with quadrate basis. Veins and intercalary veins of standard length regularly alternate. Costa distinct and strongly melanised. Sc simple surved. R strongly sigmoidal, wide, likely not reaching apex, with 5 or 6 veins at margin. M sigmoidal, with 3 or 4 veins CuA also standard, sigmoidal, with 3 veins at margin. CuA sharp, fluent, simple. A branched (5). Pseudovein present, diagonal kink possibly present.

Remarks: It does not seem safe to erect a new genus on the basis of a forewing fragment, although it is probable that this species would deserve its generic status. It is categorised within the genus *Ano* on the basis of pseudovein, coloration and sharply curved CuP. At the same time it has coloration highly congruent with dominant *A. ona*. Miniaturised specimen is excluded on the basis of colored costa and coloration of the posterior margin.

Derivation of name: After *naslo sa* (Slovak for found) – alluding to the rediscovery of the lost specimen.

Character of preservation: One articulated forewing with prothorax

Taphonomy: Completely articulated forewing adhjacent to prothorax suggest short or no pre-depositional transport and rarity within ecosystem



specimen hindwings	length	fusion	Sc	R1	RS	M	CuA	CuP	R1+RS	total remigium
2997/1666	9		1	3	4	4	5	1	7	18
2452/409			1	6						
2039/38	8.5		1	5	7	5	7	2	12	27
2039/35	9		1	3	8	7			15	
2039/35R			1	3	9	7			16	
2784/724	9		1	5	8	5	5	1	13	25
2784/724R	9		1	3	7	5	6	1	12	23
2384/131	11.5		1	4	8	2	8	1	10	24
2384/131	11.5		1	5	8	2	7	1	10	24
2997/4338	10		1	5	6	3	8	1	9	24
2997/433R	10		1	5	6	3	8	1	9	24
2784/2266L	8		1	4	7	6	9	1	13	28
2784/2266R	8		1	5	8	4	9	1	12	28
2997/1547L	7.9		1	4	8	3	7	1	11	24
2997/1547R	7.9		1	4	6	4	8	1	10	24
2997/1435	8		1	4	7	5	10	1	12	28
2997/1492	7.8		1	3	5	7	7	1	12	24
2997/1327	9		1	6	7	5	6	1	12	26
2904/176=177	???	CuA+M	1	3	9	6	9	1	15	29
2997/4259+			1	7	13	7	9	1	20	38
2997/143	7		1	4	6	4	7	1	10	23
2784/956	6		1	3	6	5	5	2	11	22
2904/179	7.6		1	3	9	5	7	1	14	26
2554/187	11		1	7	9	6	9	1	15	33
2997/1521	7.5		1	3	9	4	9	1	13	27
2997/776	9		1	4	7	5	7	1	12	25

specimen hindwings	length	fusion	Sc	R1	RS	M	CuA	CuP	R1+RS	total remigium
2997/4257L	8		1	3	8	3	7	1	11	23
2997/4257R	8		1	3	9	3	7	1	12	24
2997/1180=1184	10		1	5	6	6	4	1	12	23
2997/1409	11.5		1	4	5	5	5	1	10	21
2997/264R	12		1	5	5	4	6	1	9	22
2997/264L	12		1	4	7	4	4	1	11	21
2904/1719	13.5		1	6	5	4	5	1	9	22
2384/168L	9.8		1	3	7	6	3	1	13	21
2384/168R	9.8		1	3	8	3	3	1	11	19
2997/148	7		1	3	5	5	9	1	10	24
Unlabelled R			1	4	5	6	7	1	11	24
Unlabelled L			1	4	5	3	7	1	8	21
2997/1210L	8		1	3	8	5	9	1	13	27
2997/1210R	8		1	3	7	4	5	1	11	21
n	34		40	40	39	39	37	37	39	37
min	6		1	3	4	2	3	1	7	18
max	13.54		1	7	13	7	10	2	20	38
ave	9.11		1	4.1	7.1	4.62	6.84	1.05	11.69	24.51
dev	1.716015		0	1.172331	1.713643	1.369122	1.833538	0.229243	2.407815	3.723959
cv	18.84		0	28.59	24.14	29.63	26.81	21.83	20.6	15.19

specimen forewings	l	w	Sc	R	M	CuA	CuP	A	RM	RCuA	MCuA	total	total without A
2554/146 R	10		5	15	5	9	1	6	20	24	14	41	35
2554/146L	10		3	15	4	8	1	7	19	23	12	38	31
2452/374A	9		3	14	6	10	1	7	20	24	16	41	34
2997/261	9.7		3	11	8	6	1		19	17	14		29
2784/800	8.5	3.2	1	16	4	7	1		20	23	11		29
2239/176	11		3	14	4	9	1	7	18	23	13	38	31
2039/35	9		3	16	8	7	1	7	24	23	15	42	35
2039/35R	9.6		4	14	7	8	1	7	21	22	15	41	34
2066/892	9		5	14	7	7	1	7	21	21	14	41	34
2784/879	8.6		3	14	6	6	1	7	20	20	12	37	30
2066/147L	10		1	14	4	8	1	9	18	22	12	37	28
2066/147R	10		5	13	4	8	1	9	17	21	12	40	31
2997/4257	8.5			11	6	8	1	9	17	19	14		
2904/1719L	14.5		5	12	4	13	2	9	16	25	17	45	36
2997/1210	8.8		3	13	6	6	1	8	19	19	12	39	31
2784/649	9		4	12	5	7	1	8	17	19	12	37	29
2066/303	9		5	13	6	8	1	6	19	21	14	39	33
			3	13	7	5	1	9	20	18	12	38	29
n	17		17	18	18	18	18	16	18	18	18	15	17
min	8.5		1	11	4	5	1	6	16	17	11	37	28
max	14.5		5	16	8	15	2	9	24	25	17	45	36
ave	9.66		3.47	13.56	5.61	7.78	1.06	7.63	19.17	21.34	13.39	39.6	31.7
dev	1.42349		1.28051	1.464169	1.419979	1.800508	0.235702	1.087811	1.886484	2.275186	1.649916	2.261479	2.568188
CV	14.74		36.9	10.8	25.31	23.14	22.24	14.26	9.84	10.66	12.32	5.71	8.1

Genus *Hra* Vršanský, 2020

Type species: *Hra disko* Vršanský, 2020. ?Upper Jurasic Bakhar Formation (Bed 275/1), Mongolia.

Composition: *Hra bavi* Vršanský, 2020 (275/1), *Hra nie* Vršanský, 2020 (268/14), both Bakhar; *Hra* sp., undescribed from Arkagala, Russian Federation.

Stratigraphic range: (Middle) or Late Jurassic- Albian
Geographic range: Laurasian

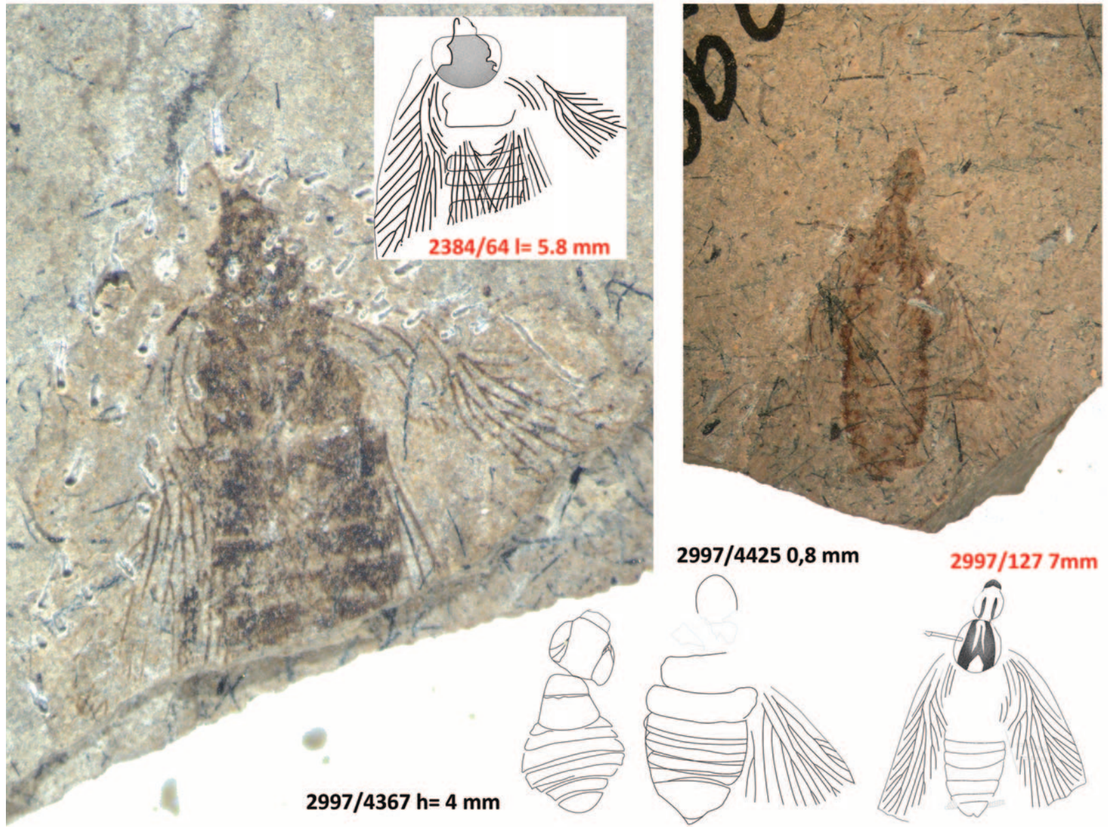
Diagnosis (after Vršanský 2020): It differs from all Liberiblattinidae except *Elisamoides* in all main branches (R, M, CuA) strong, sigmoidally curved (R slightly, almost reaching apex); strong intercalaries joined with cross-veins, not fully straight. *Elisamoides* differs in having narrow radial field at base, and simplified sharply descending M; original state of CuA (expanded); and having hindwing pterostigma. Wing main venation and intercalaries wide, CW present. Forewing base wide, costal area short and wide; SC branched; R field short, RS indistinct due to reduction; M not reduced, standard, covering apex; CuA reduced to few branches within narrow cubital field; clavus normally long (1/3–1/4 of the wing length), A simple. Hindwing long, SC long and simple, R1 and RS differentiated, M straight, reduced to some three veins at margin, CuA secondarily branched. Female external ovipositor short.

Hra nice sp.n.
(figp. 317)

Holotype: PIN 2997/127. A completely articulated winged adult.
Type locality: Mikhailovka, Karatau, Kazakhstan.
Type horizon: Kimmeridgian Upper Jurassic, Karabastau Formation.

Additional material: PIN 2384/64 (l= 5.8 mm, female); 2997/4367 (h= 4 mm, drawing) (complete specimens); 2997/440, 738 (forewings); 2784/153; 2997/5143 (hindwings); 2997/4425 (w= 0.8 mm) (immature individual). The same locality as the type.

Differential diagnosis: Differs from all species except *H. nie* (forewing length 5 mm) in small size and from *H. nie* in more apically ascending posterior margin.
Autapomorphies: none, defined by plesiomorphy within the genus and family.
Description: Small cockroach with overall length under 8 mm. Head elongate (0.7/0.48 mm), with a coloration pattern including two thin lateral longitudinal stripes and its basal trasverse junction. Eyes apparently large (although specific margin are impossible to identify on the specimens).
Pronotum small, nearly round (0.88/ 0.79 mm), posteriorly extended, pale, with two dark wide stripes and central Y-shaped thin stripe.
Forewing standardly-shaped (4.5-5.5/ 1 mm), with posterior part ascending apically, membrane transparent, without coloration, veins colored, intercalaries either missing or uncolored (unpreserved). Sc simple, long, slightly sigmoidal, nearly straight. R narrow, also nearly straight, with most branches simple (9-11); M with 4-6 long straight branches; CuA unspecialized, appearing as conservative branches, with 5 veins at margin. Clavus elongate, fluent, A reduced to four branches of which posteriormost was branched.
Hindwing usually ca. 5 mm long, with a very wide remigium, membrane transparent. Sc simple, R nearly straight, with terminal branches (4-5) ascending in a regular, unsharp way, RS (4) wide. M is reduced to 2-3 (rarely 7) veins at margin. CuA with 4-7 veins at margin, posteriormost branch dichotomized, CuP simple, sigmoidal.
Body narrow; terminal tergite very long; ovipositor extremely short, wide. Cerci extremely short and wide (0.38/ 0.16 mm).
Derivation of name: *hranice* is Slavic for boundaries.
Character of preservation: three complete specimens (one female), two isolated forewings (1 ff), two isolated hindwings, one immature individual.
Taphonomy: exclusive presence of complete specimens combined with a putative



immature individual suggest rarity of the species and habits near the terminal-depositing waterbody.

Remarks: The species can be categorised within basal Liberiblattinidae on the basis of branched hindwing CuA branches (excluding Blattulidae) and simpliefied forewing Sc. From also small *Stavba* it differs in having modified (small) pronotum, forewards directing head and wide hindwing remigium. Within *Hra* it differs in minute size but more pleasiomorphic shape of regular forewing. Similarly as Stavba, also *Hra* was apparently characterised with high interspecific variability of a forewing shape.

Genus *Elisamoides* Vršanský, 2004

Type species: *Elisamoides mantiformis* Vršanský 2004. Shar-Teg, Mongolia. Upper Jurassic or Early Cretaceous.

Composition: *Elisamoides cantanbillingensis* Martin, 2010 (Mintaja), *Elisamoides cudak* Kováčová et al. 2023 (Phrae-Nan, Thailand); undescribed (Bakhar and Chernovskie Kopi).

Geographic range: Laurasia and Gondwana, circumtropical

Stratigraphic range: Early Jurassic – Early Cretaceous

Differential diagnosis (improved after Vršanský 2004): R, M simplified, and Cu (rich) all sharphly curved, intercalaries not straight but joined with cross-veins; M sharply descending from R stem.

Elisamoides sediomasle sp.n.

(figg. 319)

Holotype*:* PIN 2904/152 (f= 5.3 mm as preserved). An isolated forewing fragment.

Type locality. Mikhailovka, Karatau, Kazakhstan.

Type horizon. Kimmeridgian Upper Jurassic, Karabastau Formation.

Additional material: PIN 2904/119 (h= 4.5 mm; 1,1+4,2,4+1). An isolated hindwing. The same locality as the type.

Differential diagnosis: Differs from *E. mantiformis* (f= 8 mm) and *E. cantanbillingensis* (f= 9-10 mm) in being significantly smaller and in being monochromatically colored.

Description: Wings monochromatically dark. Forewing ca. 6.5 mm long, with indistinct costa, costal area extremely narrow, Sc probably long, but indicstinct . R simplified, strongly curved, with only ca. 9 veins at margin (most branches are dichotomised, simple posteriormost branch is extremely shor), M sharphly descending from R stem, strongly sigmoidal, expanded, with two main stems (anterior is branched anteriorly, posterior one posteriorly) and with 9 veins at margin. CuA with posteriorly curved branches and short posteriormost vein. CuP sharphy curved, clavus short.

Hindwing very short, just about 5 mm. Costa indistinct, costal area very narrow, Sc indistinct, straight R1 (3) and RS (4) differentiated. M simplified (2). CuA also simplified into 4 straigth branches, CuP simple. A1 area wide, A1 sigmoidal, with 6 veins at margin (one branch is dichotomised).

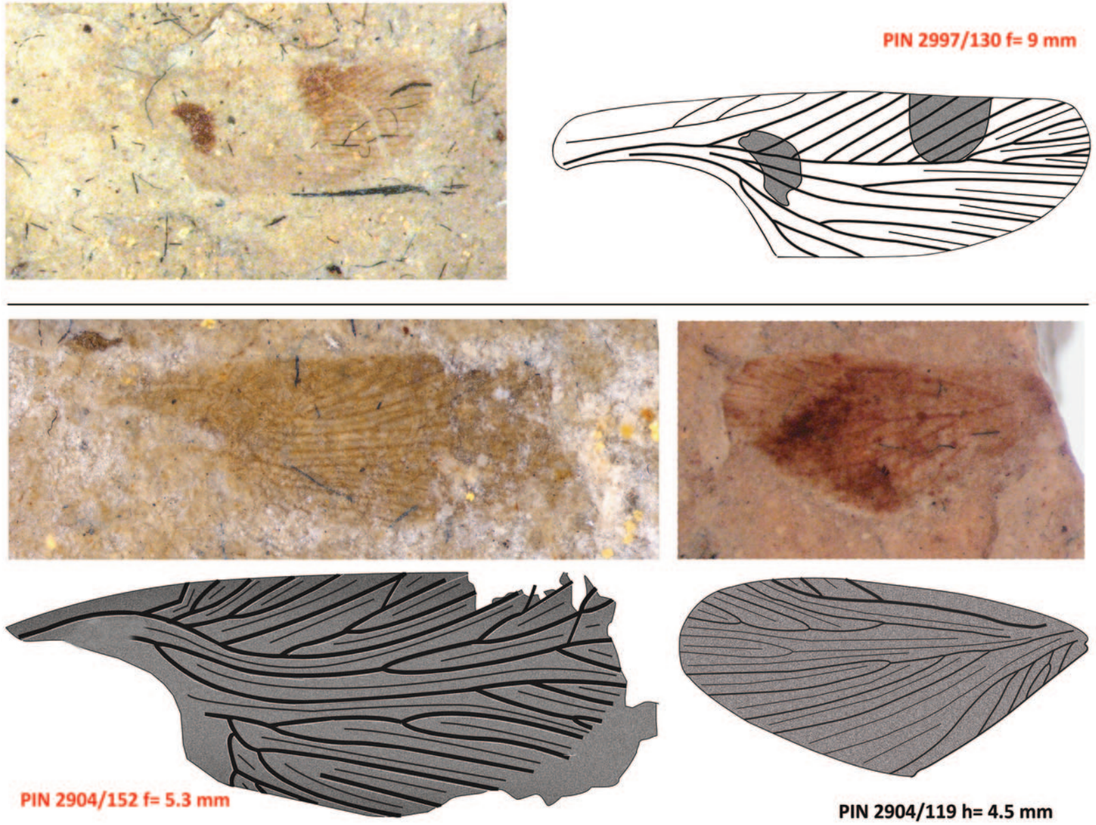
Mutations. PIN 2904/152 is, in addition to bear traces of predation, highly deformed specimen, with numerous vein deformities, including R-R fusion, strangely broken SC so than IC is broken, a M-M fusion and also a R-M fusion.

Remarks: Hindwing is regular, i.e., without a deformity, but contains highly unusual branching of remigium A1 blind branch.

Derivation of name: sediomasle is a deformed palindrome with meaning “is sitting on the butter” (lacking food).

Character of preservation: One damaged forewing, one complete hindwing.

Taphonomy: Preservation of isolated wings is perhaps stochastical due to the rarity of the species, but at the same time, the predation damage on the forewing holotype suggest a longer pre-depositional transport.



Liberiblattina kontrapunctata and *Elisamoides sediomasle*

Genus *Hydrokhoohydra* Vršanský in Vršanský et al. (2019)

Type species: *Hydrokhoohydra aquabella* Vršanský in Vršanský et al. (2019), and by monotypy; Galkino, Karatau.

Composition: Undescribed species (immatures preserved) from Crato, Bakhar, Burmite, Lebanese amber.

Geographic range: Laurasia and Gondwana, circumtropical
Stratigraphic range: Late Jurassic (Kimmeridgian)- Late Cretaceous (Cenomanian)

Differential diagnosis (after Vršanský et al. 2019): differs from all representatives of the family in having a triangular pronotum in the adult stage, extremely wide FW costal field and extremely expanded FW M (while R is greatly reduced with 8–12 veins at margin). The extremely elongated clavus with reduced number of veins and the colored body of immatures are also unique. Notably, only the adult stage has the head covered by the pronotum.

Hydrokhoohydra aquabella Vršanský in Vršanský et al. (2019)

(figps. 321-322)

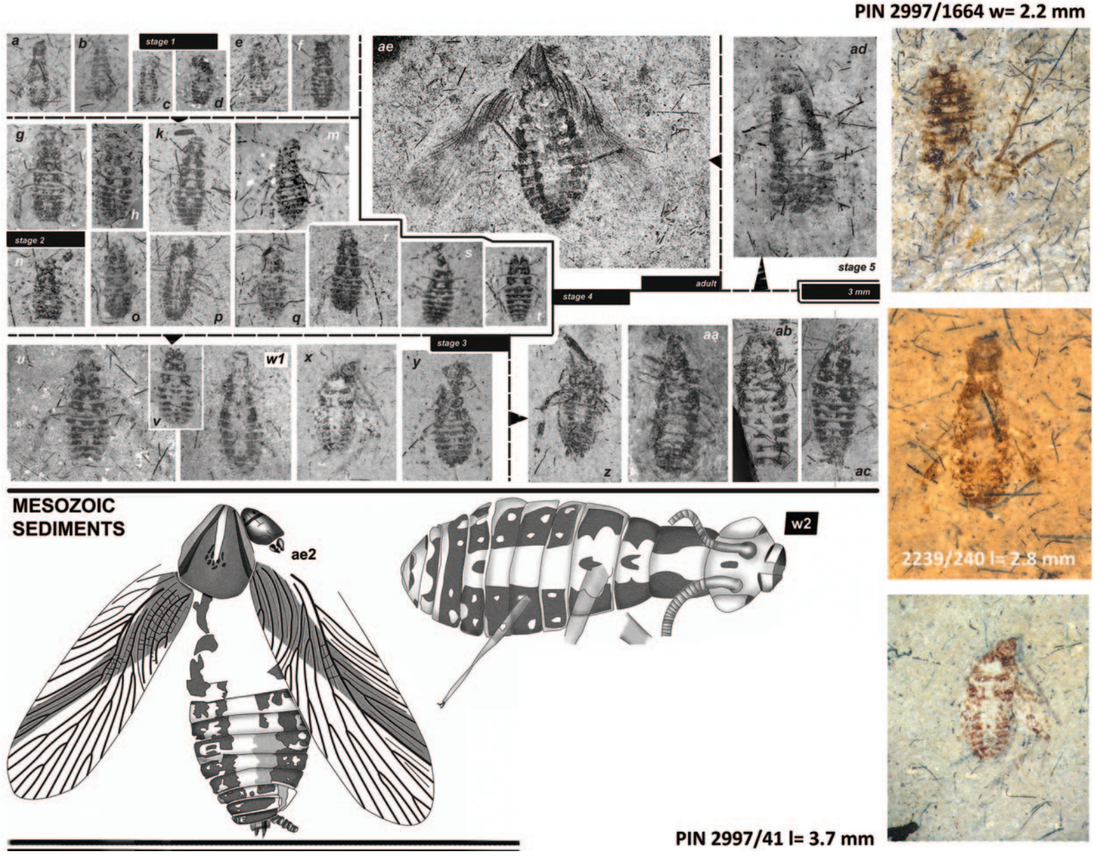
Holotype: PIN 2452/945. Designated by Vršanský et al. (2019)
Type locality. Karatau, Kazakhstan.
Type horizon. Kimmeridgian Upper Jurassic, Karabastau Formation.

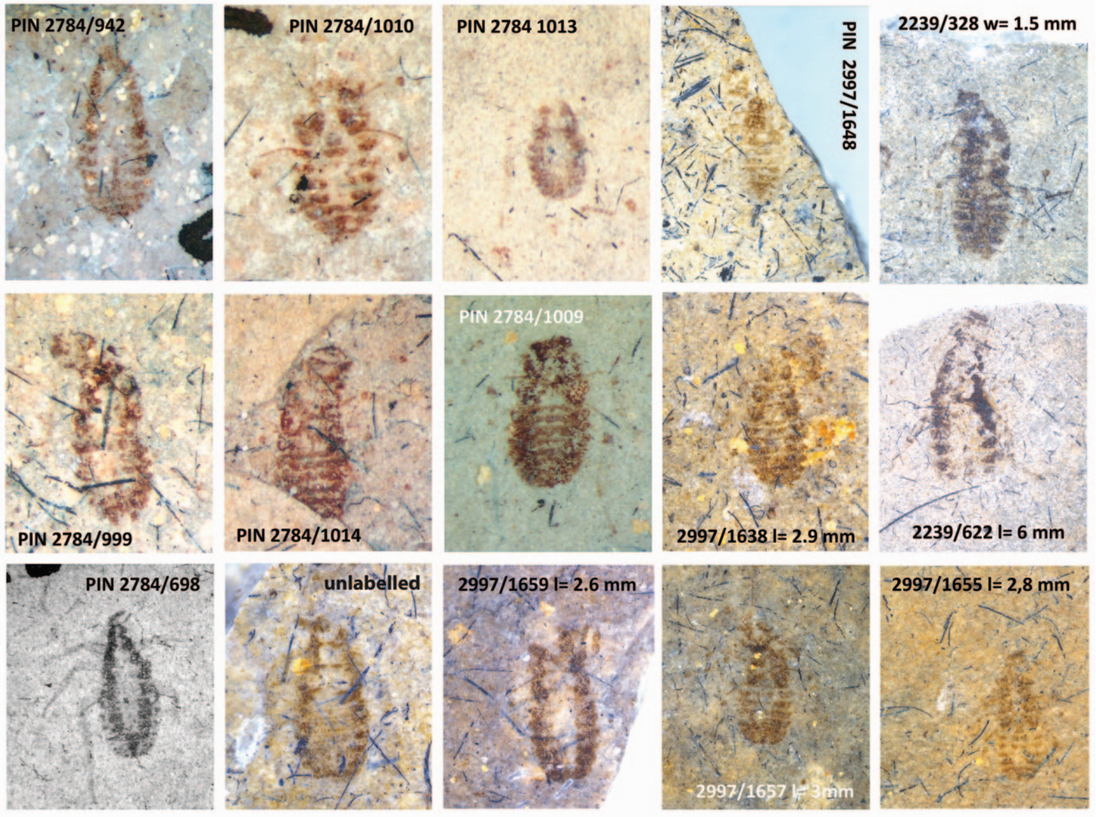
Additional material (in addition to 27 specimens in label of Vršanský et al. (2019): Fig. 2): STAGE 1: 2452/355 (w= 0.8 mm) 2452/575 (w= 1 mm); 2239/340 (l= 2.8 mm); 2239/341 (w= 0.9 mm); STAGE 4: 2465/947 (l= 5 mm); 2239/339 (l= 5.5 mm); unlabeled (l= 5.4 mm); 2239/320 (l= 5.2 mm); 2997/4385 (l= 5.4 mm); 2339/922 (l= 6 mm); ADULT: 2384/186 (forewing f= 186, 3, 12, 4, 10, 1, 7); 2997/4368 (body fragment). Designated by Vršanský et al. (2019). The same locality as the type.

Additional material (legend of the Vršanský et al. (2019): Fig. 2): (PIN; Stage 1: 2239/540; 2384/1274 (l= 2.8 mm); 2239/327 (w= 0.8 mm), 344; 2997/1635; 2452/239; Stage 2: 2239/692 (l= 4.2 mm); 2997/1632; 2239/333 (l= 3.5 mm); 2784/789; 1739/136; 2239/318 (l= 3.3 mm), 338 (l= 1.5 mm), 384 (l= 3.3 mm), 366 (l= 3.4 mm); 2452/234; 2066/541; Stage 3: 2239/316 (l= 4.4 mm), 331 (w= 1.5 mm); 2997/ 1625, 41; 2239/364; Stage 4: 2384/194 (w= 2 mm); 2066/515; 2997/154; 2239/323 (l= 6 mm); Stage 5: 2784/982; Adult female: 2452/945 w= 2.6 mm). Designated by Vršanský et al. (2019). The same locality as the type.

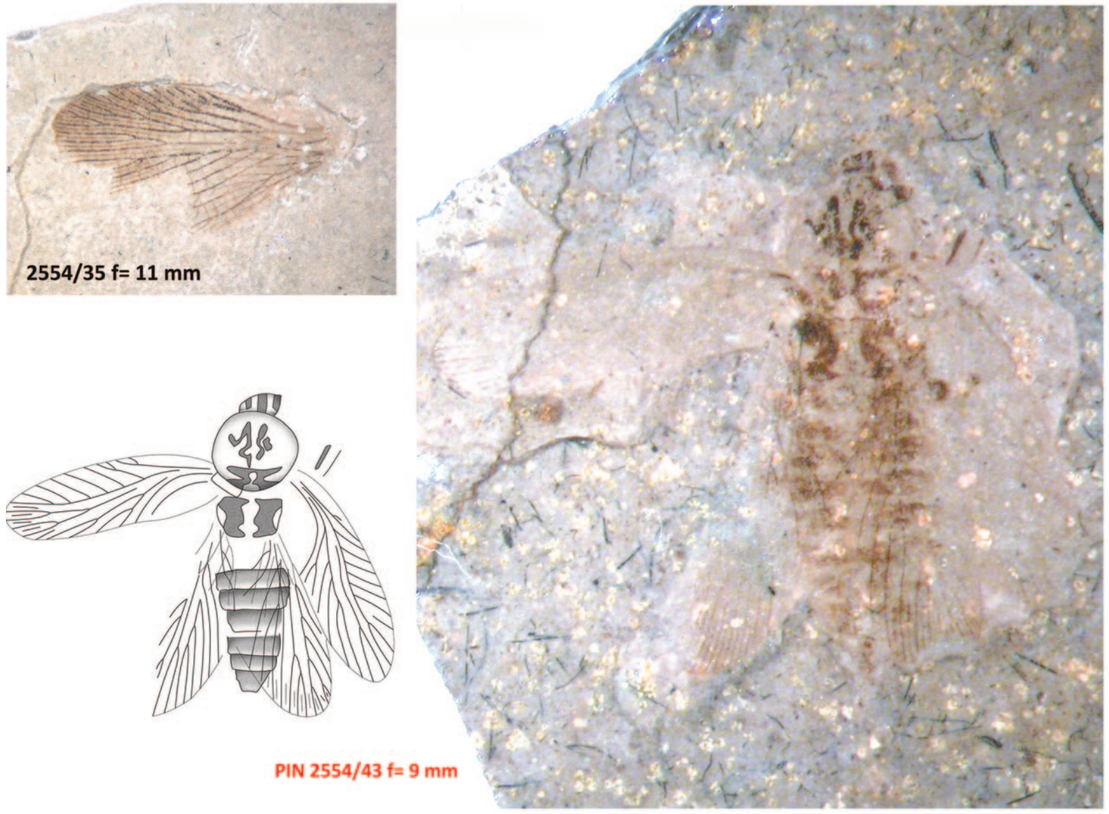
Additional material designated here: STAGE 2: 1789/136 (l= 2.7 mm) **G**; 2452/234 (w= 1.1 mm), 2784/1014 (w= 1 mm), 1010 (w= 1.2 mm); 2997/1655 (l= 2.8 mm), 1657 (l= 3 mm), 1638 (l= 2.9 mm); STAGE 3: 2066/495 (w= 1.7 mm); 2997/41 (w= 1.4 mm); STAGE 5: 2997/1664 (tergal glands; w= 2.2 mm). All except G= Galkino from Mikhailovka.

Remarks: Additional material is designated here on the basis of characteristic coloration. Majority belong to stage 2, 2 specimens to stage 3, which is concordant with statistical distributions of immature instars.
Character of preservation: 1 completely winged adult, 1 isolated forewing; 47 immature individuals.
Taphonomy: (Semi)aquatic immature individuals are ocassionally complete with fine antenna which suggest autochtonous habit in the deposition body lake. On the other hand, one isolated forewing might suggest the pre-depostional transport. Moreover, most of the immatures are represented only by the body.





Hydrokhoohydra aquabella



Miniblattina inflatica

Genus *Miniblattina* Sendi, 2021

Type species: *Miniblattina libera*, and by monotypy. Lebanese amber.

Stratigraphic range: Upper Jurassic (FOD) – Lower Cretaceous
Geographic range: circum(sub)tropical

Diagnosis (after Sendi 2021): Differs from other species within the family in having small size, long tubular external ovipositor, sharply triangular subgenital plate

Miniblattina inflatica sp.n.
(figp. 323)

Holotype: PIN 2554/43. A complete adult winged (probably a male).
Type locality: Mikhailovka, Karatau, Kazakhstan.
Type horizon: Kimmeridgian Upper Jurassic, Karabastau Formation.

Additional material: PIN 2384/124± (f= 11.4 mm; forewing); 2554/35 (h= 11 mm; hindwing). The same locality as the type.

Differential diagnosis: Differs from the type species in larger size, and consequently more rich and straigth venation.
Autapomorphy: Large size.
Description: Head comparatively small and narrow (1.5 mm), with characteristical (for numerous Liberiblattinidae) three equally wide (0.45 mm) longitudinal dark stripes, otherwise pale.
Pronotum rather large, ovoid, (3.2/ 3.6 mm), with distinct paranotalia and sophisticated color pattern with posterior Ω-shaped and central reversed W-shaped with dot inside dark areas.
Mesonotum narrow (1.5/ 2.4 mm) also with sophisticated dark "S2" pattern.
Forewings short and wide 9-11.4/ mm, with sharp apex posed centrally. Intercalaries present apically. Sc with 2 branches at margin, dichotomized terminally; R stem slightly sigmoidal, with 8-9 simple or simply dichotomized branches. M sigmoidal, greatly reduced to 2-4 branches at margin; CuA sophistically sigmoidal (due to reduction) with 4-6 veins at margin. CuP sharply curved, clavus large, 4.3 mm long, with few anal branches (only 1 is visible as preserved).
Hindwing longer than forewing, up to 11 mm and was not overlapped with the forewings during the repose. Apex is more round than the forewing. SC was simple, R1 and RS (7) differentiated; M greatly simplified, with only 2-3 straigth branches at margin. CuA with 6 branches, CuP simple. A1 present in remigium and with blind ranches.
Body apparently narrow, only 3.5 mm wide, dark and possibly with coloration pattern.
Forelegs massive, pale, with longitudinal dark stripe.
Remarks: The species can be categorized within the family on the basis of complex hindwing characteristics with branched CuP. Within the genus it is categorized on the basis of greatly simplified forewing venation, which is only possible during miniaturization. So it is clear that the large size is autapomorphic character. Similar is also unusual ratio of forewing/ hindwing with much larger hindwing.
Derivation of name: *inflatica* is after inflatable, referring to enlarged size.
Character of preservation: One complete specimen, one forewing, one hindwing.
Taphonomy: Standard distribution appear present in this species with a complete specimen, suggesting no or short pre-depositional transport. As small species are presumed to be active flyiers, species is expected to be extremely rare in the assemblage.

Genus *Makacka* gen.n.

Type species: *Makacka akcakam* sp.n., and by monotypy
Type locality: Karatau, Kazakhstan
Type horizon: Karabastau Formation

Stratigraphic range and geographic range: indigenous

Differential diagnosis: From other genera within the family it differs in small pronotum and rather large quadrate head (similar to possibly related *Entropia* Vršanský, Liang et Ren, 2012).
Autapomorphies: Extremely strong costa basally
Description: as for species
Remarks: This genus is categorsised within Liberiblattinidae on the basis of strong main veins combined with strong intercalaries and the venation.
Derivation of name: *makačka* is Slavic for hard work – alluding to difficult classification procedure.

Makacka akcakam sp.n.
(figp. 326)

Holotype: PIN 2784/801. A complete adult male.
Type locality: Mikhailovka, Karatau, Kazakhstan
Type horizon: Karabastau Formation

Additional material: PIN 2066/777=977 (l= 6.2 mm); 2904/308; (complete specimens); 2997/58=68 (f= 6.7 mm) (isolated forewings); 2904/308 (h= 7.5 mm; 1.3+5.3.4+1)**;** 2997/1703 (isolated hindwings). All the same locality as the type.

Autapomorphies: Colored terminal halve of the body
Description: Small to morderately long (18 mm) cockroach, with coloration restricted to dark head, patterned pronotum and terminal halve of the body and wings. Head elongate, possibly prognathous, nearly twice as long as wide. Eyes very large. Palps moderately long, with short basal segment and three equally long palpomeres. Antenna with wide antennomeres, nearly as long as body (as preserved).
Pronotum nearly round (3.36/ 4 mm) dark, with pale central and wide anterolateral stripes.
Forewing short (6.2-7.5/ 2.2 mm). Intercalaries and cross-veins distinct, coloration restricted to apex. Costa distinct, hardly melanised and overlapping apex. Costal area narrow and shortened, SC short, but branched basally and also apically (5). R nearly straight, long, overlapping apex, with RS differentiated (7+4). M nearly straight (5). CuA also nearly straight (6), CuP sharply curved, simple.
Body very wide, cerci long and strong (3.6/0.42 mm), with 10 cercomeres. Genital plate bearing cerci modified in a sophisticated asymmetrical shape and 3-segmented stylus 1.1 mm long.
Legs short, hindtibia with at least 3 large spurs.
Derivation of name: *Makačka ak čakám* is a palindrome (Slavic) meaning "hard work of (if) waiting". Alluding to the ghard classification procedure.
Character of preservation: 3 complete specimens (males); 1 isolated forewing, 2 isolated hindwings.
Taphonomy: Complete specimens combined with isolated (but articulated, i.e., with clavus) suggest short pre-depostiional transport and rarity in the source ecosystem.

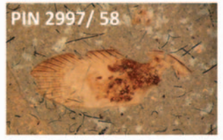
Makacka akmacaka sp.n.
(figp. 327)

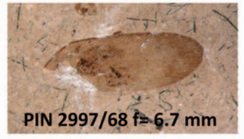
Holotype: PIN 2997/1673 (l= 20 mm). A complete adult female.
Type locality: Mikhailovka, Karatau, Kazakhstan
Type horizon: Karabastau Formation

Differential diagnosis: Differs from the type species in being significantly larger and also in lacking the colored termianl part of the body.
Autapomorphy: Large size is likely an autapomorphy – judging from extremely small disproportional pronotum.
Description: Head large, globular at occiput, generally quadrate, 2 mm wide, dark, with central longitudinal pale stripe and two short lateral subtransversal pale stripes. Pronotum small, nearly globular (3.33/ 3.8 mm), dark, with two wide lateral (and possibly also central) pale stripes. Body rather narrow (4.44 mm), with 8 distinct sclerites. Ovipositor rather wide (0.55 mm), possibly short (as preserved). Cerci preserved short (1. 77 mm), but it is not clear if totally. Forewings long (15 mm), well-developped, membraneous,















PIN 2066/ 977 l= 6.2 mm



PIN 2997/1673 (l= 20 mm)

transparent. Main veins, interacalaries and cross-veins thick. Costal area narrow, base cut, costa strong, melanised, dark, overlapping apex. Sc branched basally (2). R only slighlty sigmoidal, not reaching apex (12). CuP simple, clavus short, sharply cut, with 10 dichotomised A. Diagonal kink and pseudovein indistinct (if any). Hindwing slightly protruding beyong the forewing outline in repose. Legs thin, dark, hindfemur also thin (1.01 mm).

Mutations: Holotype possessed a mutual R-R fusion.

Derivation of name: *Makačka ak mačká* is a wordplay (Slavic) meaning "hard work if he/she/it waits for me". Also alluding to the extremely hard classification process of these two taxa.

Remarks: This species is unstandardly categorized within the same genus on the basis of similar pronotum (including coloration) and hard costa. While 3 complete adults of the *M. akcakam* are males, the present specimen is an adult female. In spite of that, we do not know any such distinct sexual dimorphism (f= ca. 7 vs. ca. nearly 20) and thus erection of a new species appears safe.

Character of preservation: 1 complete adult female.

Taphonomy: Complete specimen and the lack of isolated forewings suggest short pre-depositional transport and rarity in the source ecosystem.

Genus *Aktassoblatta* Vishniakova, 1971

Type species: *Aktassoblatta fusca* Vishniakova, 1971
Type locality: Karatau, Kazakhstan
Type horizon: Karabastau Formation

Stratigraphic range and geographic range: indigenous

Composition: *Aktassoblatta pullata* Vishniakova, 1971. Karatau collection 2066/.

Diagnosis (after Vishniakova 1971): Differs from *Rhipidoblatta* in more expressed branchings of anterior M, different A2 and coeval branching of M and CuA, more rich hindwing M and form of pronotum.

Aktassoblatta fusca Vishniakova, 1971 (figps. 332-356) = ***Paleovia praecarnia*** Vršanský, 2008 syn.n; holotype PIN 2554/33.

Discussion: Reason for synonimisation of *P. praecarnia* is a complex knowledge gained on the basis of study of *A. fusca*. It was thought that *P. praecarnia* is a carnivore with partially prognathous head (Vršanský 2008), which, nevertheless, is found to be also the case of the *A. fusca*. Thus these taxa were synonymised here.

Holotype. PIN 2239/347. A complete adult winged male. Designated by V.N. Vishniakova (1971).

Additional material designated by V.N. Vishniakova (1971) and here: PIN 1/192 **G**; 965/72 **G**; 1789/29 **G**, 78 **G**; 2066/120, 260, 324 (female), 433, 515; 2231/27, 60; 2239/147±, 148, 158, 150 ±, 151, 161, 178, 181, 185, 182, 190, 217, 254±, 265, 348; 2335/32, 87, 92; 2384/32± (female), 39, 49, 51 (b), 76, 77, 95, 96, 113, 125, 127, 152; 2452/214, 339, 367, 371; 2465/534, 902, 926, 935, 959; 2511/ 90, 96, 113, 114, 115; 2554/8±, 33 (*P. praecarnia* holotype), 171; 2784/632, 654, 686±, 788, 811, 819±, 896, 898, 929; 2904/64, 72 (female), 77 (male), 88± (male), 240, 262, 272, 295, 310, 313, 318, 320, 332±, 335, 359, 385 (female), 1716, 1867; 2997/37, 43, 107, 153±, 172, 175±, 205±, 210, 240±, 242, 268, 281, 799, 1145± (female), 1165, 1167, 1168, 1178, 1206, 1208, 1226, 1243, 1349± (female), 1350, 1378, 1380, 1421, 1550, 1554, 4290, 4340, 4353, 4381, 4389, 4392, 4394, 4397, 4399, 4422, 4428, 4430 (complete specimens); SAGU 44 (formerly "167/222") (c), 20; 167/297; 1789/8 **G (GALKINO)**, 65 **G**, 67 **G**, 77± **G**, 218 **G**, 219 **G**, 220 **G**, 221 **G**, 224 **G**, 226; 2066/81, 90, 96, 115, 129, 136, 137, 160c, 167, 190±, 183, 198, 206, 209, 238, 266, 270, 312, 323, 328, 332c, 357, 407±, 449=443, 455, 464, 493, 513, 696, 4923; 2239/170, 171, 189, 206±, 211±, 212, 214, 216, 218±, 225, 227, 238=239, 248, 250, 553; 2335/ 37, 51, 55, 78, 88; 2352/343±; 2384/40, 42, 45, 59, 70, 72, 78, 79, 81±, 87, 88±, 89, 91±, 92c, 94, 98, 102, 108±, 109, 111, 112, 150, 159, 160, 161, 163±; 2452/215, 369, 344 (c), 372, 390, 391, 397, 667; 2465/625, 901, 936, 957, 959; 2511/93, 112; 2554/13, 24, 87, 97, 105, 118, 120±, 130, 134, 148, 155, 161, 162, 163, 171, 180, 195; 2783/761; 2784/656, 687±, 690, 695*, 699, 700, 702, 732, 747=741, 761, 807, 814±, 832c, 846, 849, 873, 904, 913=907, 914, 966, 969, 971; 2904/19, 23±, 31, 33, 50, 52±, 54±, 73, 84±, 185, 189, 196, 205, 209, 210, 211, 212, 214=218, 217, 222, 225, 228, 229, 232, 234, 235, 239, 241, 243, 245, 246, 251, 254, 258, 259, 261, 267, 268, 269, 271, 273, 274, 275, 277, 279, 280, 284, 289, 291, 293, 307, 340, 344, 1419, 1420, 1853±, 1854±c, 1863, 1867, 1877, 1879; 2997/36, 39, 46±, 48, 50, 59, 63, 87, 104, 142, 147, 149, 158, 166, 171, 173, 174, 176, 177, 182, 187, 195, 212, 228, 237, 265, 1152±, 1154±, 1157, 1159, 1160±, 1166, 1169, 1174, 1194, 1196, 1240, 1242, 1247, 1248, 1252, 1256, 1257, 1259, 1298, 1295, 1311, 1332, 1337, 1340, 1345, 1353, 1356, 1357, 1358, 1362, 1367, 1382, 1388, 1389, 1391c, 1393, 1398±, 1564, 1580, 1584, 1594, 1668k (k= coprolite), 1673c, 1693, 1698, 1701c, 1941, 4237, 4275, 4279, 4287, 4296, 4300, 4303c, 4308, 4309, 4351, 4352, 4361, 4369, 4368c, 4371, 4379, 4380, 4384, 4388, 4396, 4398, 4401, 4403, 4408±c, 4412, 4415, 4417 (isolated forewings); 220/167; 965/68 **G**; 2066/56=59, 103, 106, 154, 155, 177, 202, 218±, 228, 246, 255, 282±, 289, 325, 366, 446; 2239/266±, 269, 272, 280, 281, 283, 284, 289, 290; 2335/ 43, 52, 73; 2384/53*, 75; 2452/380; 2465/918, 924; 2456/376; 2511/ 99; 2554/84, 98, 100, 160±, 192; 2784/664*, 665±, 735, 749, 776, 923±; 2904/76, 137, 144, 155±, 138, 139±, 140, 143, 146= 164, 149, 150, 156, 163, 164, 169, 170, 172±, 409, 925, 1864, 1866; 2997/22, 51, 56, 85, 102, 138, 208, 217, 247, 1141±, 1150, 1161, 1176, 1182, 1187, 1204, 1235, 1357, 1361, 1555, 1558, 1576, 1675, 1691, 1694, 1698, 2822±, 4237, 4242, 4282, 4283, 4294, 4354 (isolated hindwings). All except G= Galkino from Mikhailovka.

Differential diagnosis (updated): Monochromatic forewing and lacking sophisticated coloration pattern. Ovipositor short, tubular. Head near-prognathous with eye divided with apodema into two parts. Forewing unspecialized but with advanced liberiblattinid shape. Legs unspecialized.

Autapomorphy: Near-complete dense dark forewing melanisation

Redescription: Moderately large species. Head monochromatically dark, possibly with occipital darker horshoe-shaped macula. Prognathous (2-3.7 /1.15-2.8 mm), eyes very large and narrow (1.23/0.23-0.3 mm), divided by apodema into two parts (figp. 352). Three small lentiform ocelli present. Mandible massive, not especially long. Palps long (4 mm), but with short terminal palpomere (?; 0.23/1.3; 0.65/ 1.3; 0.65/ 1.2; 0.5/ 0.09 mm). Antennal socket very large, round, antenna multisegmented, segments short and not especially wide (0.27 mm). The longest preserved fragment 16 mm (usually only very small fragments suggesting fragililty).

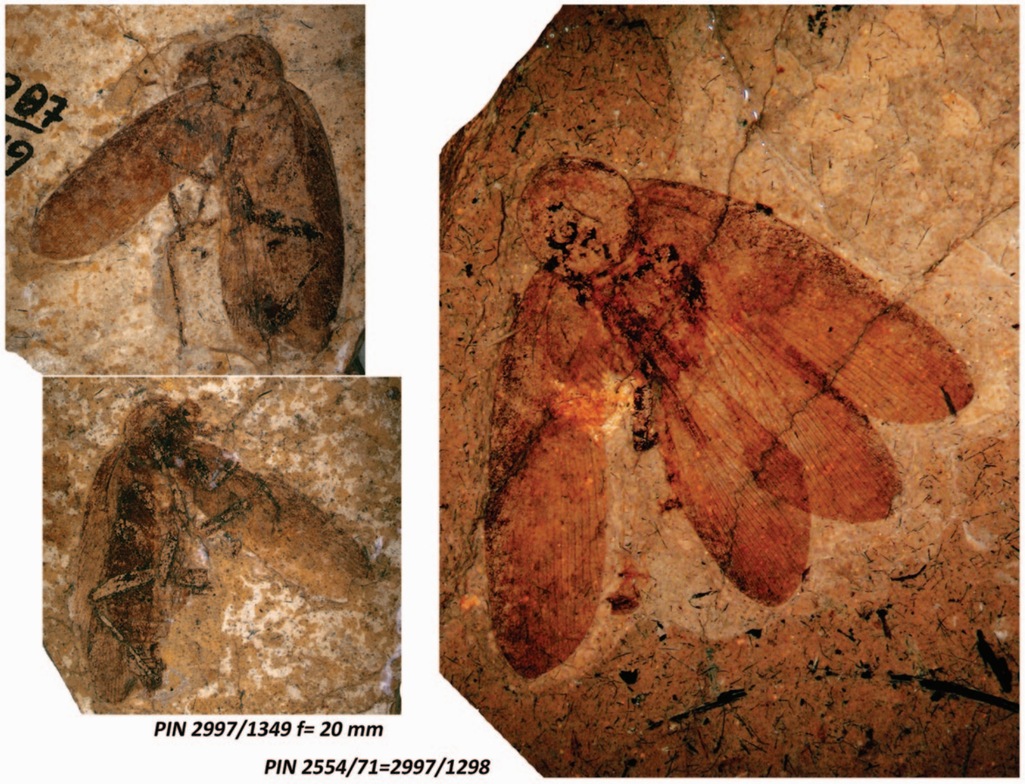
Pronotum unspecialized, nearly oval, without extensive paranotalia (5.4-5.9/ 5.4-5.8 mm), monochromatically dark. Forewing usually monochromatic dark, sometimes with lighter central part (which is taphonomic, but might reflect lighter coloration or lesser melanisation), moderately long ((9)13-26/ 5-7.7 mm). Shape is advanced, with parallel margins, anteriorly posed apex with sharply descending posterior part (longer descent than ascend). Intercalaries present, halve cross-veins observed only in 3 specimens (2452/397, 254/180, 2784/969) of which in later two specimens observed as interrupted decays of coloration – suggesting fine character of halve cross-veins (not true cross-veins, rather partial reticulations). Costal area standard (not narrowed), costa rarely distinct as a more melanised fine branch not reaching a helf of the wing. Sc branched basally, usually with 3 branches (2-8). R slightly sigmoidal (11-27), usually not reaching apex (asymmetrically reaching in holotype), RS differentiated (usually 3-5). M standard, sigmoidal basally, then nearly straight (2-14). CuA sigmoidal, 6-16 veins at margin, posteriormost vein sigmoi-

dal, sometimes 2-3- branched. CuP simple, rather sharply curved. A secondarily branches (8-20). Diagonal kink present, but usually barely visible (tending to reduce).
Hindwing 10-21 mm long, membrane transparent, but with dark apex and whole anterior margin likely prolonging kind of pterostigma (darker whole margin only). Remigium rather narrow (5.6-7.7 mm). Intercalaries present, halve cross-veins detected only in two specimens and thus vere likely rather fine (2784/664 and 2511/99). Costal area narrow, Sc simple nearly straight, slightly curved apically or slightly arcuate. R1 simply branched (3-12), RS expanded, ascending in sharp angle, with 3-23 veins at margin, reaching about apex (R1+RS: 6-29). M nearly entirely straight or very slightly sigmoidal (2-13). CuA with anterior and posterior (secondary) branches, rather straight, slightly sigmoidal (7-15) and with bling branches forming reticulations. CuP simple or simply dichotomized. A1 probably simple in remigium. Total number of remigial veins without A1: 21-53.
Body rather narrow, with 9-10 visible unspecialized segments. Cerci short and robust basally (2.7/0.27 mm), multisegmented (10-14). Female ovipositor short robust, tubular, with parallel margins and central aperture (1.4/0.7 mm). Male styli 3.6 mm long and composed of basal more robust (1.1/0.5 mm) and strongly melanised stylomere and terminal narrow and thin stylomere (this might in the matter of fact be composed with up to 4 separate stylomeres, nevertheless, this character is not well visible).
Remarks: It must be taken seriously that, on the basis of isolated forewings, this taxon was during surveying of the collection categorized within 7 different species (and two different families Liberiblattinidae and Caloblattinidae) and only the complete survey reveals that it is most probably a single highly variable species with carnivorous traits (and *A. pullata* Vishniakova, 1971 is another possible synonym), which is also supported with size distribution and distribution of total number of veins, both revealing the normal distribution.
Soft indistinct color patter visible after post-profcessing under alcohol suggest the monochromatic and very dark coloration is.apomorphic state, originating from sophistically colored species like the type species. Normally sclerorisation was advanced, so only in few specimens, tracing of veins was possible.
Ecological remarks: The most common liberiblattinid at the site and eudominant species. Surprisingly, no one immature is with confidence attributed to this species, while numerous immature individuals are categorized within other dominant groups within Blattulidae.
Pollination: Specimen 2066/324 (figp. 505) is entirely covered in pollen, but the pollen is also distributed near the specimen, so the pollinating function is highly probable, but not confirmed (which is generally impossible on sedimentary fossil except more high probability when preserved in gut).
Dimorphism: In spite of this inference, the variability seems fluent and it is impossible to even recognise both sexes only based only on wings. Thus the sexual dimorphism was not distinctly expressed in this taxon. Moreover, besides Terminalia, there are no morphological differences detected.
Variability: Restricted variability of hindwings (n= 22) reveal high remigium CV= 21.79 %. Such high value might mean insufficient sample size (30 required – see Ross 2012), even when usually much smaller sample size reveals comparative results. It might also mean that more species are contained in the analysis, this, nevertheless, was not supported on the basis of analysed forewings (n= 61). Its CV= 12.07 % for total number of veins is standard, concordant with the phylogenetical stage of the taxon. The normal distribution of number of veins and sizes support a single taxon represented in this dataset (see figp. 505). Also distribution and ranges of CV for veins in respective venational systems is standard supporting the former presumption (CV_R= 17.07; $_M$= 34.68; $_{CuA}$= 23.47) and reflects the weight the anterior margin bears during the flight.
Mutations: Eight deformities (sensu Vršanský 2005) were recorded among the comparative material (n= 518), namely in

PIN 2384/53 (R-M fusion); 2554/180 (R-R fusion); 2784/664 (R-R fusion in hindwing), 2784/695 (A-A fusion), 2554/171 (R-R fusion); 2997/149 (A-A fusion); 2997/158 (unspecified); 2997/1298 (CuA-CuA fusion). Fusions within clavus (A-A) are not considered as it is in protective part of the wing without arodynamical disruption, but surprisingly there are three R-R fusions which are generally very rare due to directly affecting the flight ability forming turbulences in the anterior margin. This might well be stochastic parameter as partition in general in the site as well as in this particular species, deformity ratio is extremely low.
Syncompressions: Specimen PIN 2997/1208 was preserved with a forewing of *Blattula brevicaudata*. Specimen 2904/239 was preserved with excellent thrip (and withheld for Thysanoptera collection). Specimen 2997/ 1141+ was preserved along with a liberiblattinid most probably representing *Ano ona***.**
Predation: 2997/1174 contain a detached stripe of the dark forewing membrane and might represent a trace of predation.
Systematic remarks: Carnivory a plesiomorphic state inherited from the Raphidiomimidae. Prognathous head with apodema-divided eyes and long palps is a plesiomorphic state of Raphidiomimidae. Short terminal palpomere is a derived state. Short pronotum is either a plesiomorphic (pre-raphidiomimid) state or a derived state later elaborated in LIberiblattinidae. Unspecialised legs are plesiomorphis. Ovipositor is derived, extremely shortened, while long cerci a styli are plesiomorphic at level of Caloblattinidae/Raphidiomimidae. Forewing with original state of venation (Claoblattinidae/Raphidiomimidae) without narrowed costa (Caloblattinidae), but of advanced shape characteristic for Liberiblattinidae. This classical species generally closely resemble type genus *Liberiblattina*, but retained prognathous head and lacks coloration (autapomorphy also within Raphidiomimidae).
Character of preservation: 127 complete specimens (with 6 identified males (including 2997/196 absent in the list) and 6 females); 306 isolated forewings, 102 isolated hindwings.
Taphonomy: Specimens PIN 2997/1298 (forewings only – the same number exist for a complete specimen), 2997/147 and 142 were preserved in retained 3D aspect in morerought grained sediment..All compression specimens have (very limited) preserved third dimension, but this one seems in original 3D vaulting. Specimen 2997/1145± retained preserved palpomere chaetotaxy (see figp. 352). Specimen 2997/4275 was apparently present on a very different sediment, suggesting different sedimentatrion within Bed. Certainly a majority of preserved isolated legs probably belong to this taxon (see incertace sedis material).
Standard partition suggest common occurrence of this species in actuocenosis, possibly both close to the deposition as well as more remote up the inflows as some damages disarticulated specimens and several isolated clavi (n= 12) might suggest.

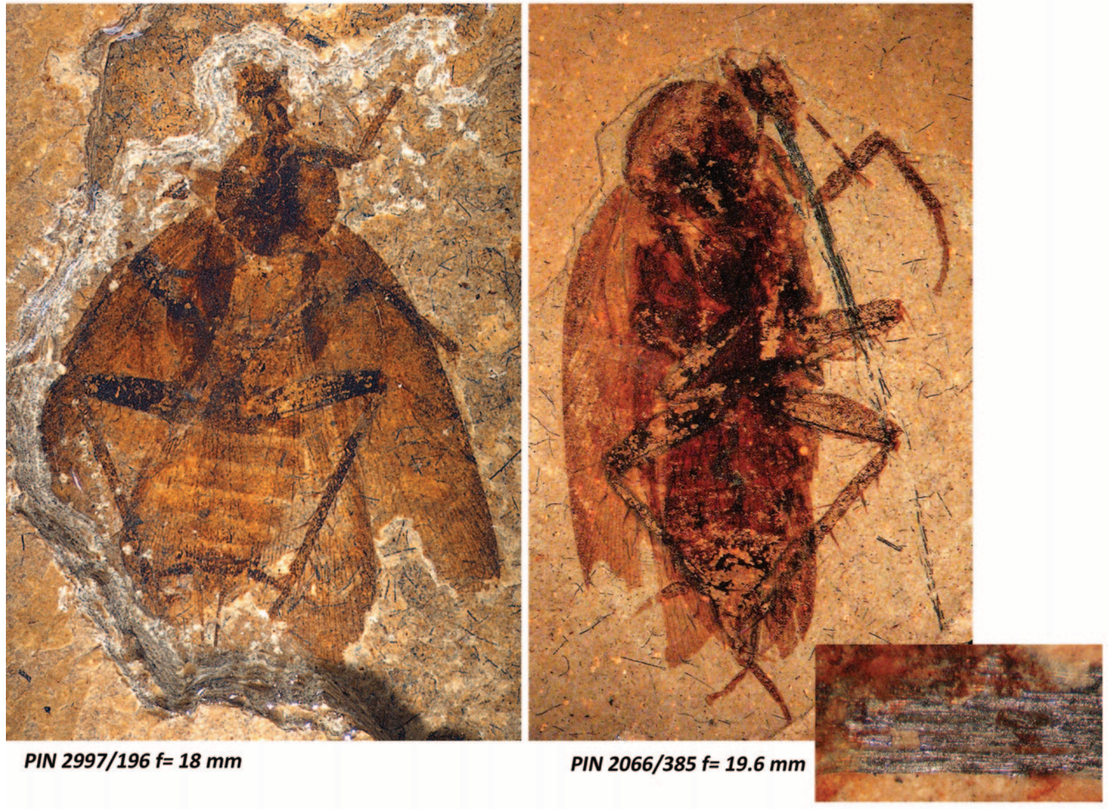

2554
f= 25 mm


PIN 2784/898



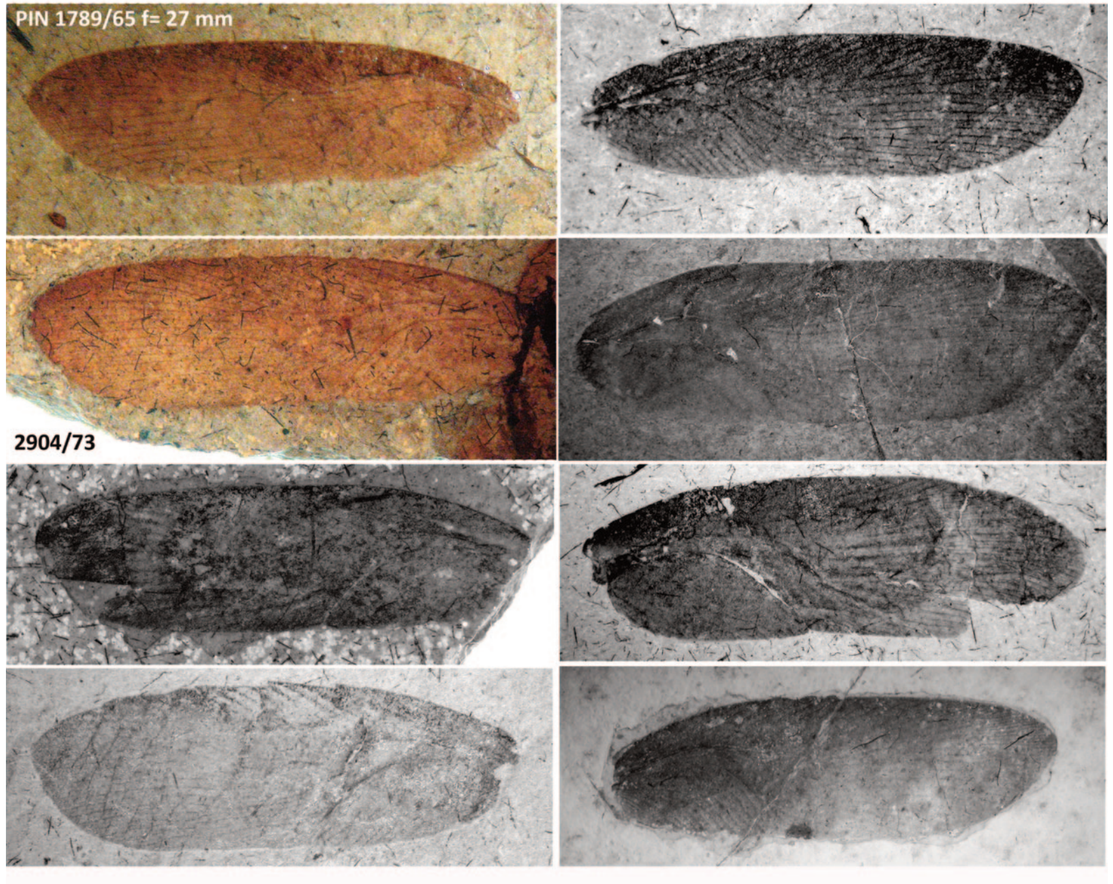
PIN 2997/1349 f= 20 mm

PIN 2554/71=2997/1298



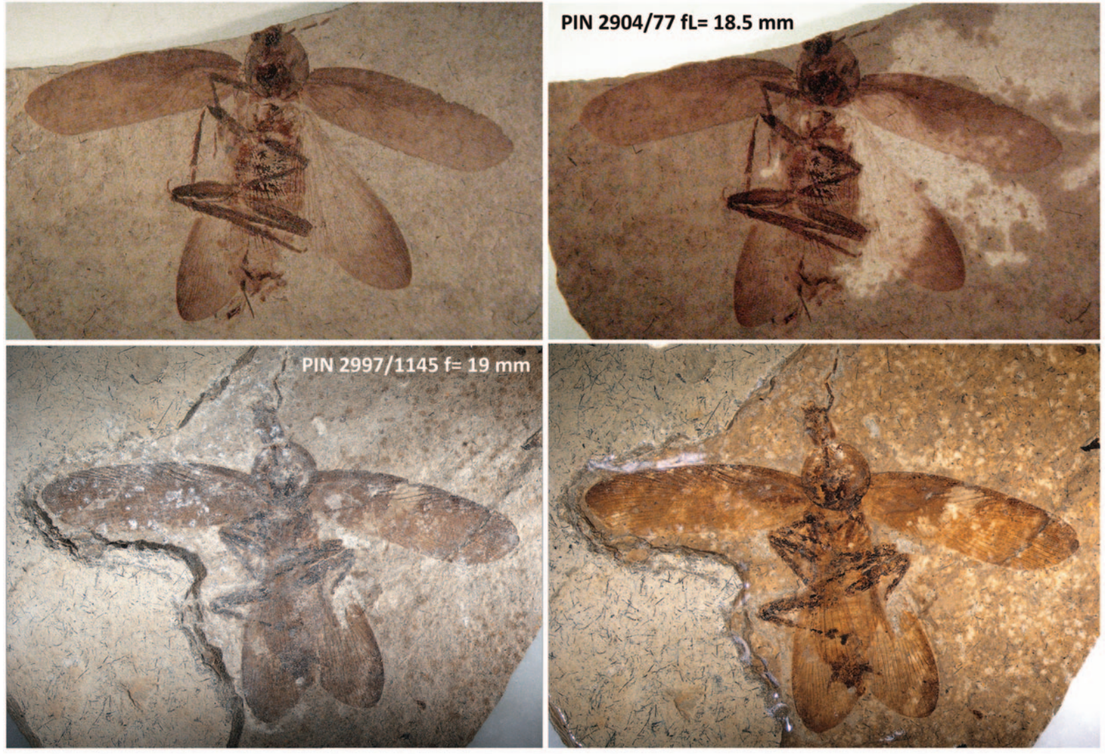
PIN 2997/196 f= 18 mm

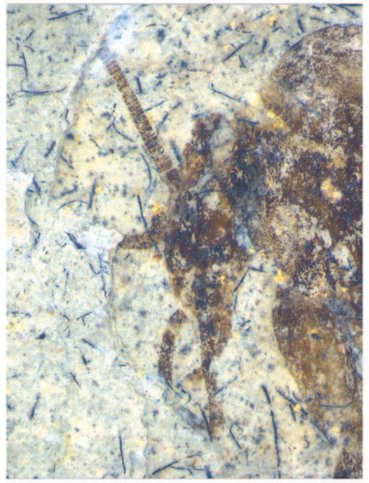
PIN 2066/385 f= 19.6 mm

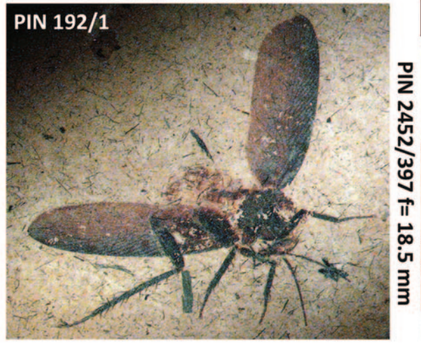


Aktassoblatta fusca


PIN 2452/ 380 h= 15 mm
PIN 2452/ 372
h= 17 mm
PIN 2997/ 87 18 mm
2997
/1298
PIN 2554/71=2997/1298 f= 20 mm


PIN 2904/77 fL= 18.5 mm
PIN 2997/1145 f= 19 mm

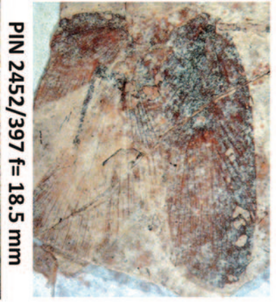




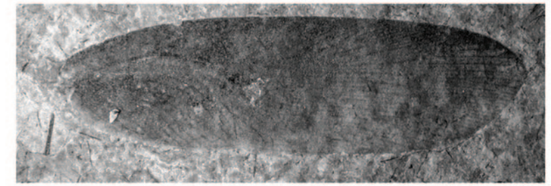
PIN 2904/64 f= 18 mm

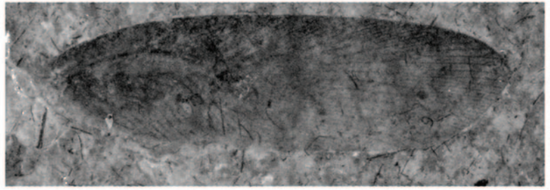


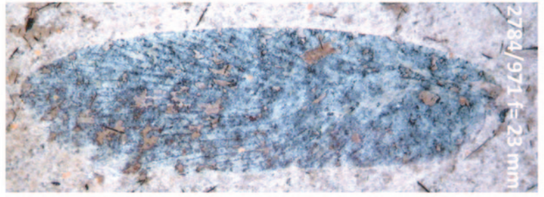
PIN 2452/397 f= 18.5 mm

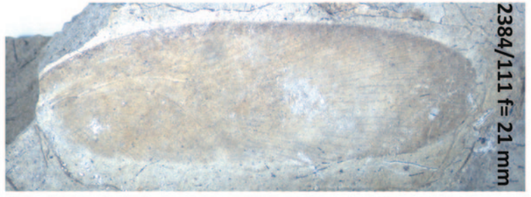


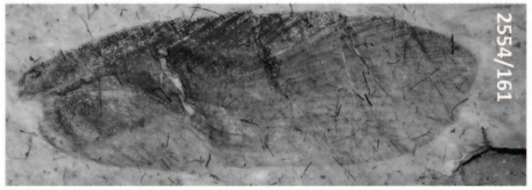


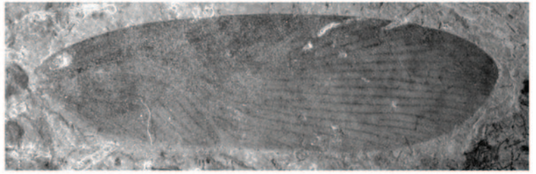








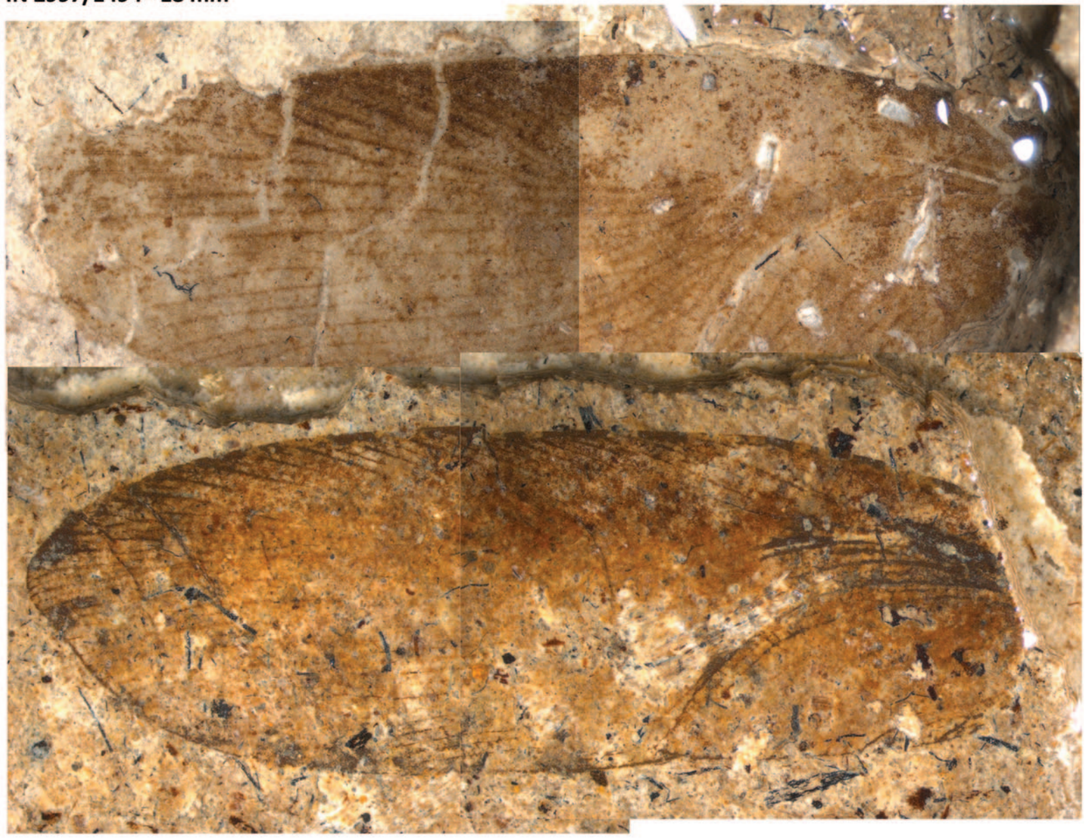


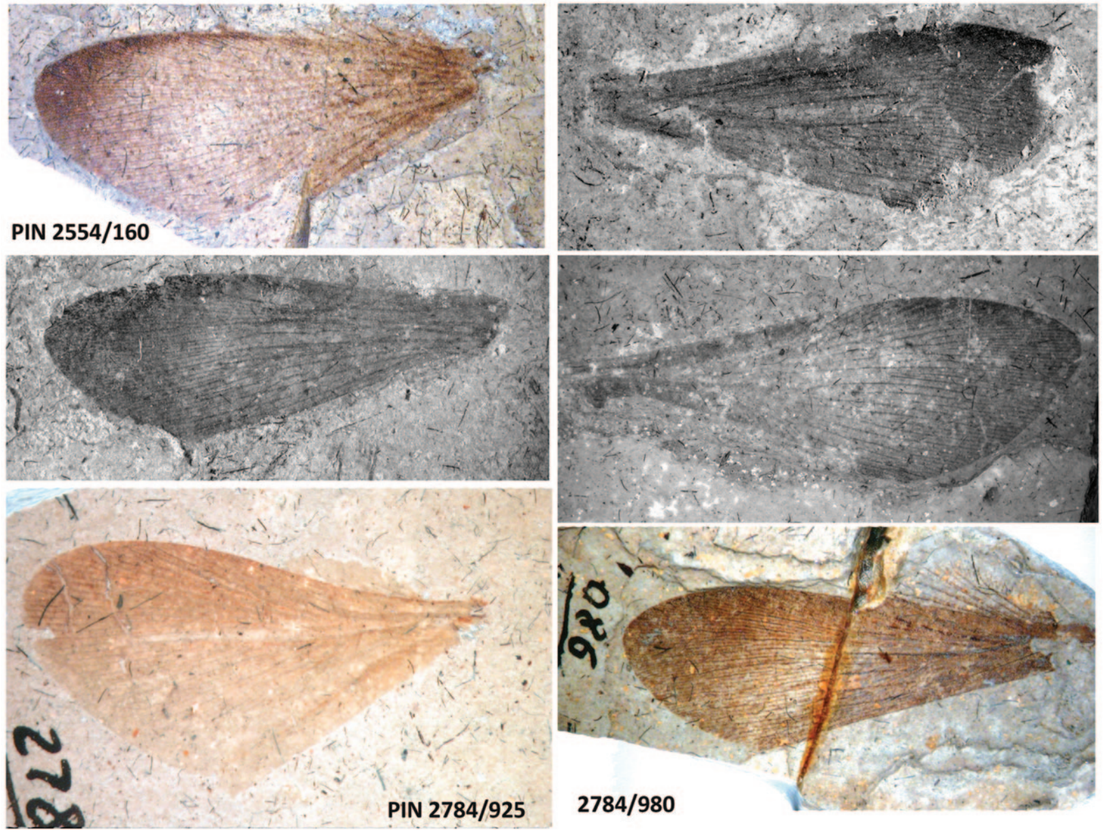




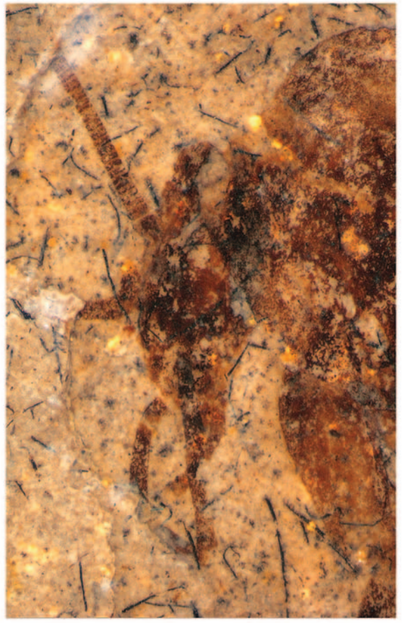


PIN 2997/149 f= 18 mm



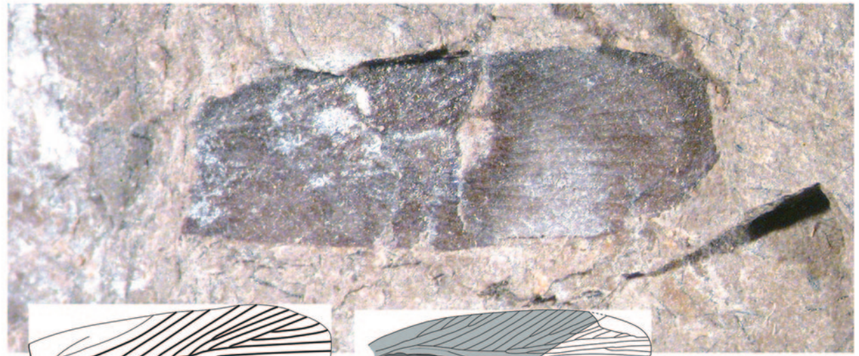






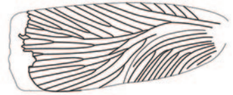


2904/64 f= 18 mm



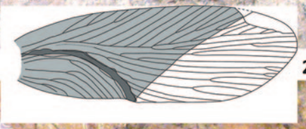


2066/ 270 21 mm



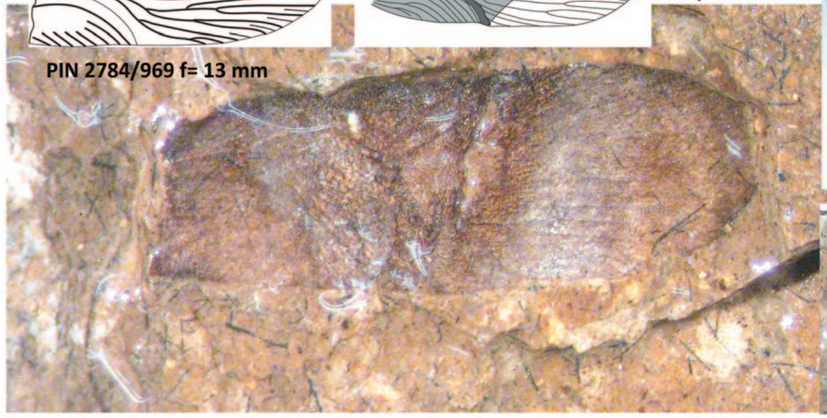
2904/52 f= 15 mm





2465/901 f= 19 mm

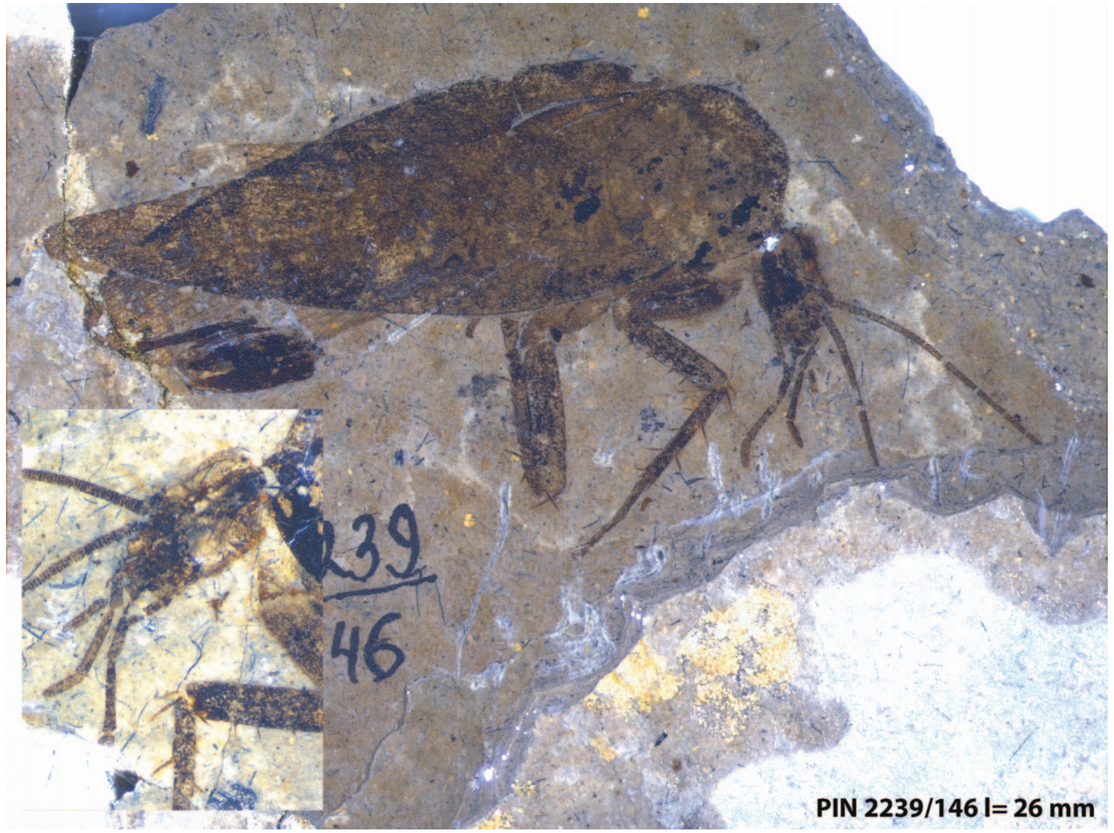
PIN 2784/969 f= 13 mm



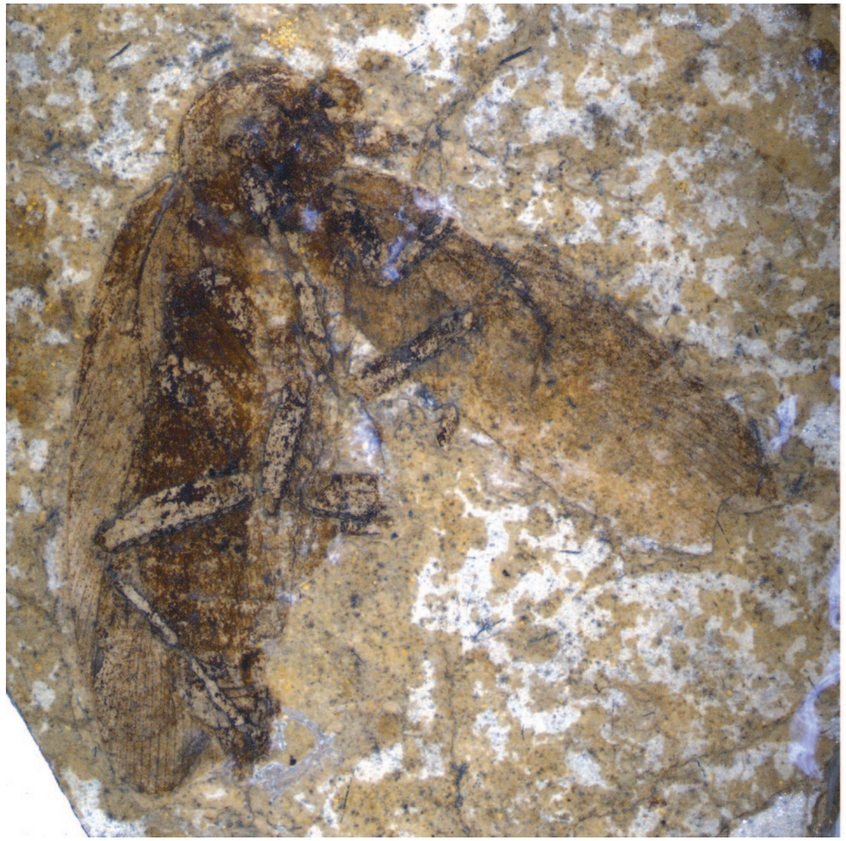





PIN 2239/ 182 b= 5 mm
PIN 2554/ 161 17.8 mm
PIN 2904/ 52


PIN 2239/146 l= 26 mm

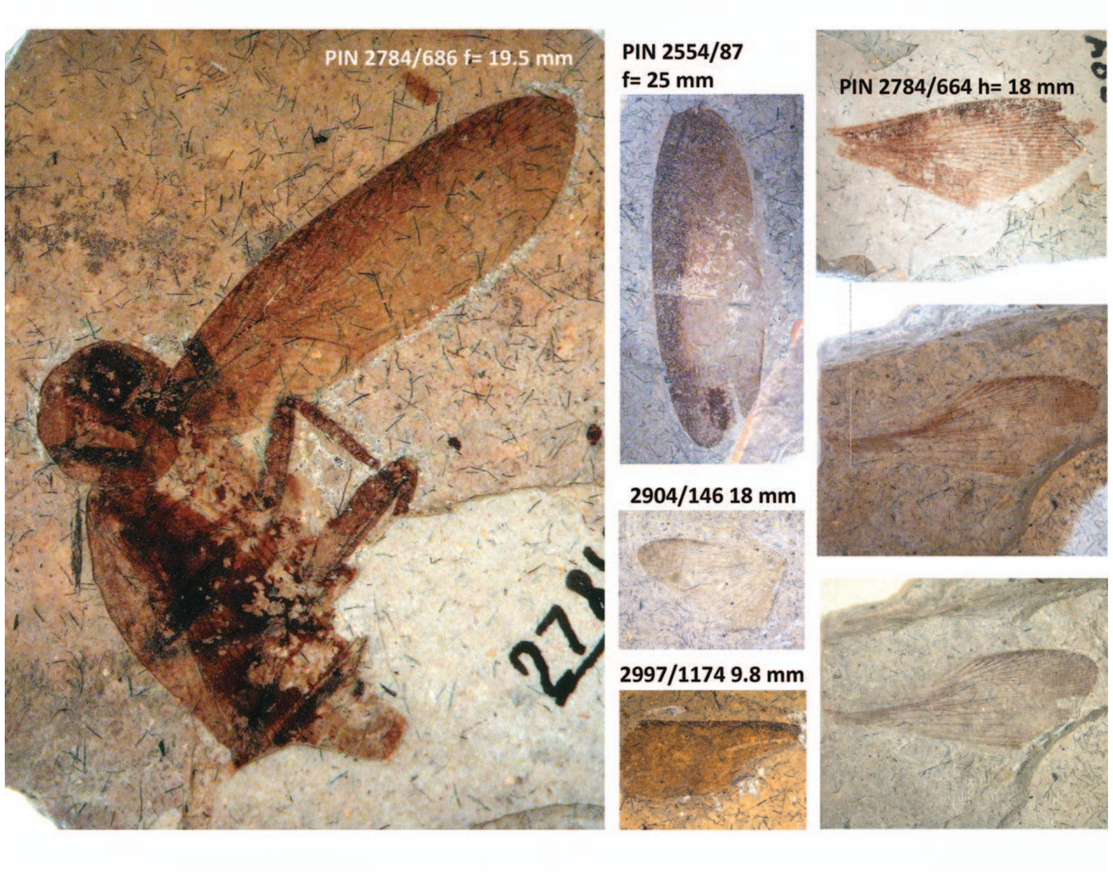






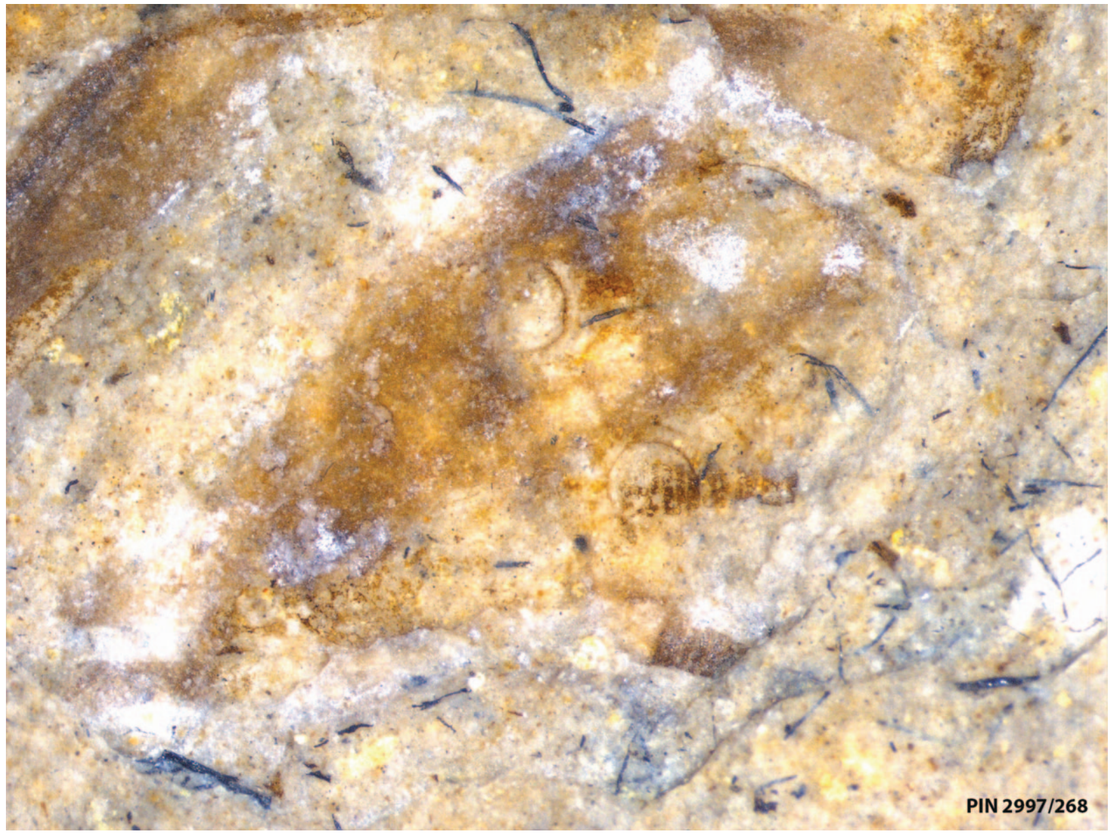


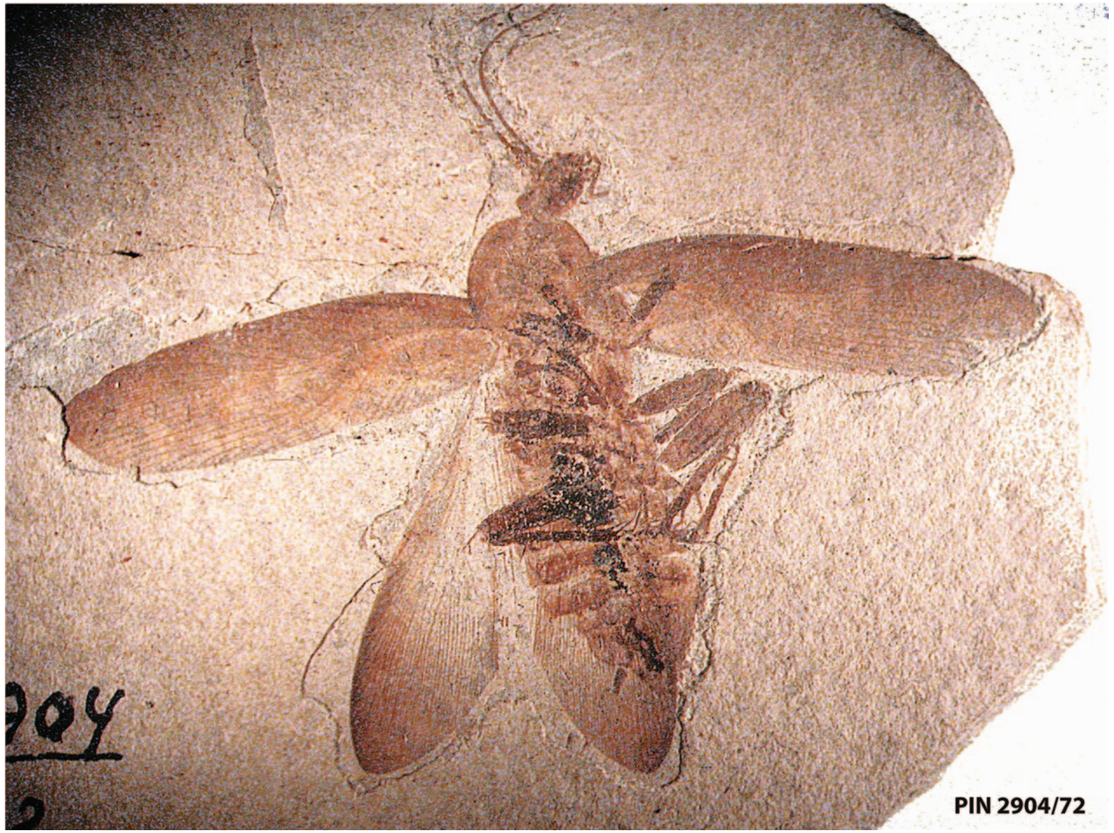
PIN 2997/ 1349 f= 20 mm

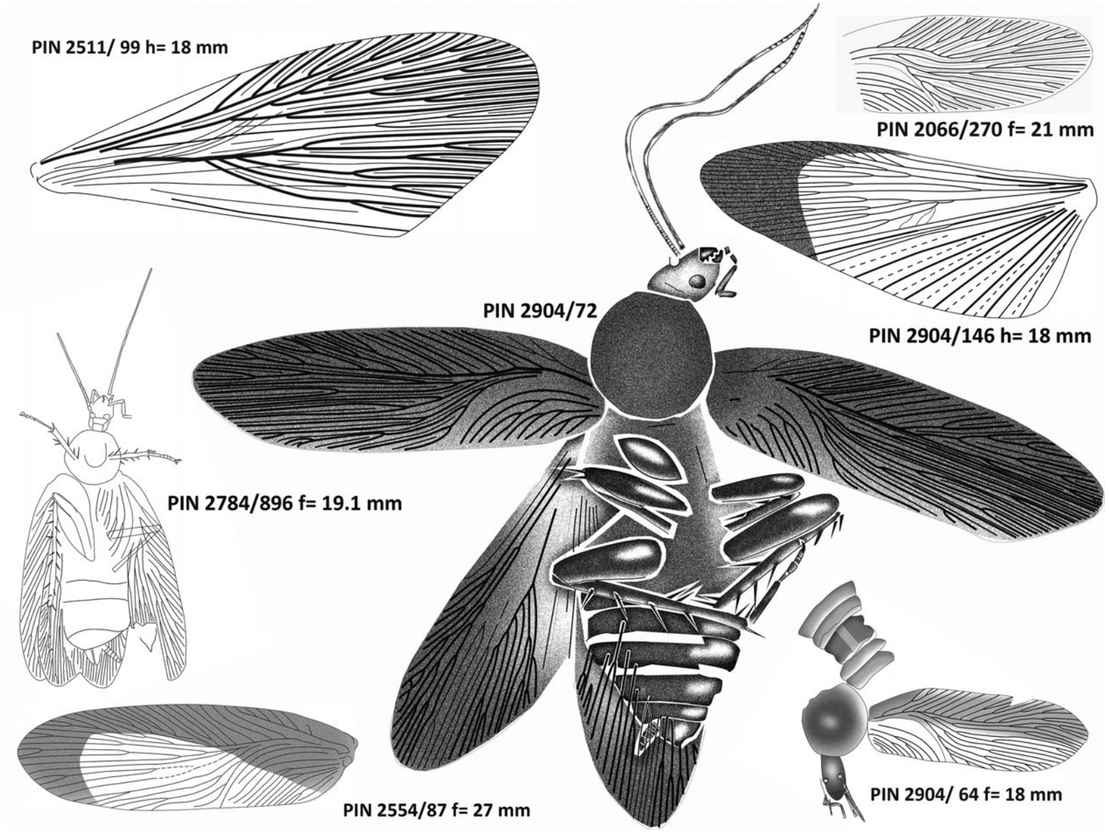

PIN 2784/686 f= 19.5 mm
PIN 2554/87
f= 25 mm
PIN 2784/664 h= 18 mm
2904/146 18 mm
2997/1174 9.8 mm

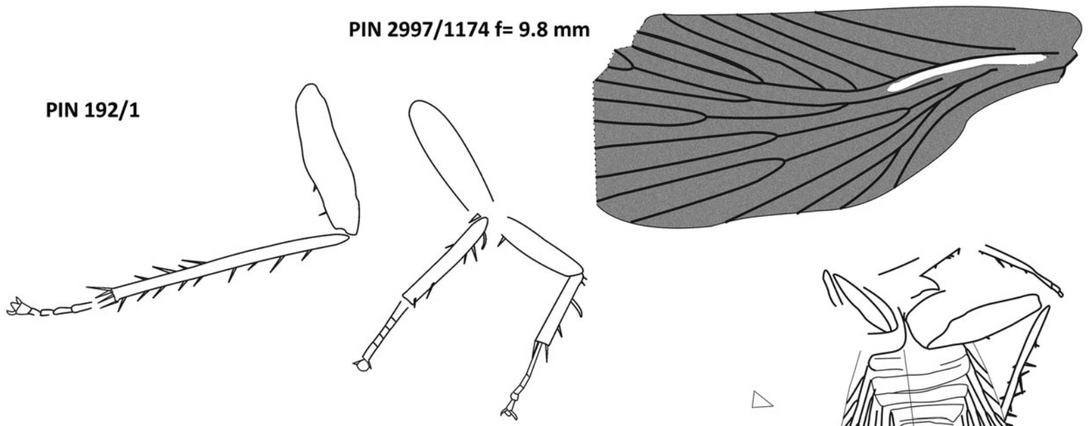

PIN 2554/33 f= 20.5 mm


PIN 2997/1145

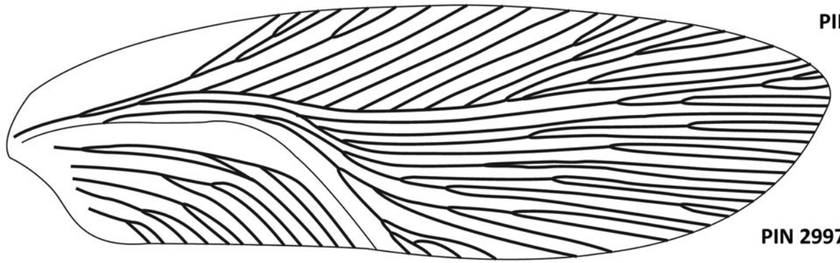

PIN 2997/268


PIN 2904/72


PIN 2511/ 99 h= 18 mm
PIN 2066/270 f= 21 mm
PIN 2904/72
PIN 2904/146 h= 18 mm
PIN 2784/896 f= 19.1 mm
PIN 2554/87 f= 27 mm
PIN 2904/ 64 f= 18 mm



PIN 2066/ 324 b= 10 mm



PIN 2997/4381 f= 24.9 mm

specimen forewings	length	width	Sc	RRS	M	CuA	CuP	A	RRSM	RCuA	MCuA	suma without a	total
2384/45+	19		4	17	10	12	1	10	27	29	22	45	55
2384/42	20		6	16	10	12	1	12	26	28	22	45	57
2239/ 206+	19		6	21	9	11	1	13	30	32	20	48	61
2452/369	21		4	17	6	9	1	10	23	26	15	37	47
2352/343±	20		4	15	8	13	1		23	28	21	41	
2554/ 134	19		3	17	7	9	1	12	24	26	16	37	49
2554/180	21.5	7	6	20	11	14	1	20	31	34	25	52	72
2554/192	20		4	15	2	15	1		17	30	17	37	
2066/433 L	24		3	21	7	7	1	11	28	28	14	39	50
2784/656	20		8	12	13	12	1	15	25	24	25	46	61
1789/65	21		4	20	8	10	1	14	28	30	18	43	57
1789/8	20.5		4	17	9	12	1	13	26	29	21	43	56
2784/971	23		6	20	3	12	1	14	23	32	15	42	56
2784/ 695	19		4	17	8	11	1	12	25	28	19	41	53
2784/686±	19.5		3	19	6	8	1	12	25	27	14	37	49
2784/846	18.2		4	16	5	9	1	10	21	25	14	35	45
2784/807	20		3	15	11	12	1	10	26	27	23	42	52
2554/105	18		3	15	9	9	1	12	24	24	18	37	49
2554/13 L	21		3	18	13	7	1	10	21	25	20	42	52
1/192 R	20		3	18	6	8	1	10	24	26	14	36	46
1/192 L	17		4	20	5	12	1	10	25	32	17	42	52
2554/171 R	21.5		7	17	6	12	1	11	23	29	18	43	54
2554/171 L			5	17	8	9	1	10	25	26	17	40	50
2904/251		5	5	17	7	10	1	12	24	27	17	40	52
2904/239	17	5.5	4	19	9	11	1	13	28	30	20	44	57

specimen forewings	length	width	Sc	RRS	M	CuA	CuP	A	RRSM	RCuA	MCuA	suma without a	total
2904/73	17.5	5	3	17	6	9	1	9	23	26	15	36	45
1789/226	18.5	5.5	3	19	5	10	1	10	24	29	15	38	48
2997/1398			3	20	9	10	1	8	29	30	15	43	51
2452/397	19	6.3	3	17	5	9	1	12	22	26	14	35	47
1789/220	20.5	6	3	20	7	7	1	9	27	27	14	38	47
2997/1145± L			4	14	8	7	1	13	22	21	15	34	47
2997/1145± R			3	19	9	7	1	13	28	26	16	39	52
2997/87	19		3	14	7	8	1	12	21	22	15	33	45
2384/98	19.8		4	11	9	16	1	11	20	27	25	41	52
2384/11	21		5	16	9	14	1	14	25	30	23	45	59
2904/1716 R	21	6	5	15	7	8	1	11	22	23	15	36	47
2904/1716 L	21	5.5	4	19	5	10	1		24	29	15	39	
2335/32 R	19.8	6	5	15	5	8	1	10	20	23	13	34	44
2335/32L	20	5.8	5	15	6	9	1	10	21	24	15	36	46
2997/1564	18.3		3	16	14	9	1	10	30	25	23	43	53
2997/ 1340	20.5		4	18	11	13	1	15	29	31	24	47	62
2904/77 R	18.5	5.7	6	16	3	6	1	10	19	22	9	32	42
2904/77 L	19.5	5.7	5	15	5	9	1	10	20	24	14	35	45
2997/1152± L	20.8		4	16	7	9	1	10	23	25	16	37	47
2997/1152± R			4	16	8	9	1	10	24	25	17	38	48
2384/150	2384/150		3	22	7	12	1	12	29	34	19	45	57
2997/1256	17.8		3	13	8	10	1	11	21	28	23	40	51
2997/1257	18.5		5	11	13	9	1	12	24	20	22	39	51
2904/72	20	5.6	3	14	7	6	1	10	21	20	13	31	41
2904/72	20	5.8	3	14	9	8	1	10	23	22	17	35	45

specimen forewings	length	width	Sc	RRS	M	CuA	CuP	A	RRSM	RCuA	MCuA	suma without a	total
2554/87	26	7.8	6	21	12	7	1	12	33	28	19	47	59
2465/ 901	19.7		3	21	5	9	1	9	26	30	24	39	48
2784/969	19		2	13	3	8	1	9	16	21	11	27	36
2554/161	17.8		3	13	8	12	1	12	21	25	20	37	49
2554/155	17	5	3	16	6	8	1	10	22	24	14	34	44
2784/849	22		4	16	9	7	1	11	25	23	16	37	48
2997/1332	21.5		5	20	8	7	1	11	28	27	15	41	52
2997/1298	20		6	20	11	8	1	10	31	28	19	46	56
2904/277	20		4	18	9	8	1	14	27	26	17	40	54
2554/33	20.5		3	16	6	9	1	10	22	25	15	35	45
2997/149	18		6	15	7	8	1	11	22	23	15	37	48
2997/1252	16		5	22	14	9	1	11	36	31	23	51	62
2066/270	21		4	27	6	12	1	9	33	39	18	50	59
2997/4381	24.9		4	17	12	13	1	12	29	30	25	38	50
N	57	17	64	64	64	64	64	61	64	64	64	64	61
Min	16	5	2	11	2	6	1	8	16	20	9	27	36
Max	26	7.7	8	27	14	16	1	20	36	39	25	52	72
Mode													
AVE	19.9	2.8	4.1	17.1	7.8	9.7	1	11.3	24.8	26.9	17.7	39.8	51
DEV	1.847592	0.70882	1.214986	2.918494	2.705401	2.276465	0	1.943744	3.883216	3.625821	3.826566	4.939214	6.154744
CV	9.28	25.32	29.63	17.07	34.68	23.47	0	17.2	15.66	13.48	21.62	12.41	12.07

specimen HW	length	Sc	R1	RS	M	CuA	CuP	R	remigium total
2239/281	18	1	12	6	13	1	1	18	34
2784/735	18.5	1	10	10	7	13	1	20	42
2904/ 925	21	1	6	23	8	14	1	29	53
2554-160		1	6	9	8	13	1	15	38
965/68	19	1	4	7	7	15	1	11	35
2554/171		1	5	1	5	12	1	6	25
2554/171R		1	6	10	7	13	1	16	38
2904/138	18.5	1	4	12	7	9	1	16	34
2904/137	17.5	1	4	3	5	7	1	7	21
2997/4242 R		1	7	6	13	9	1	13	37
2452/372±	17	1	4	12	8	11	1	16	37
2452/380		1	6	9	3	12	1	15	32
2335/43	17	1	3	9	2	7	1	12	23
2997/102	19	1	5	10	4	14	1	15	35
2904/77RH	17.5	1	5	10	5	10	2	15	33
2904/72	20	1	4	11	5	12	1	15	34
2511/99	18	2	5	14	3	11	1	19	36
2997/1298		1	7	11	6	13	1	18	39
2066/324 R	10	1	4	7	4	7	1	11	24
2066/324 L	10	1	5	4	6	7	1	9	24
2784/980		1	5	5	9	12	2	10	34
2904/164=146	18	1	4	14	4	9	2	18	34
ave	17.27	1	5.5	9.23	6.32	10.9	1.14	14.73	34.14
n	15	22	22	22	22	22	22	22	22
min	10	1	3	3	2	7	1	6	21
max	21	1	12	23	13	15	2	29	53
dev	3.13885	0	2.087377	4.587061	2.851672	2.505405	0.35125	4.958704	7.440529
cv	18.18	0	37.95	49.7	45.12	22.99	30.81	33.66	21.79

Aktassoblatta pullata Vishniakova, 1971

Holotype: PIN 2066/773. A complete winged adult male. Designated by V.N. Vishniakova (1971).

Discussion: Vishniakova (1971) recognized two species within the present genus on the basis of different size partition and difference in male terminalia. With the extensive material, size is highly vatiable within this taxon, making the synonimisation possible. I am not qualified to recognize the differences in genital appendages, but I feel this differences might be taphonomical or falling within individual variability. Taking all these into consideration I decide to retain the original taxon by Vishniakova. For additional argument of this retention is also the distribution of size and total number of veins of *A. fusca* (see variability paragraph). *A. pullata* is by far the largest specimen (l= 28 mm contrasting to 16-26 mm in A. fusca), nevertheless, it was apparently selected as the largest one, and it has the forewing variability charcteristics of *A. fusca* (total number of veins nearly exacly in the middle of the range of *A. fusca*). Total evidence for synonimising these taxa is, to conclude, missing, thus these species were retained both (disregarding additional difference in terminalia). Morphologically, disregarding terminalia, it is just the biggest specimen of the *Aktassoblatta*-complex.

Character of preservation: one complete adult.

Taphonomy: Sole adult winged male would suggest no pre-depositional transport, nevertheless, due to incertain taxonomy, such conclusion would be preliminary.

Katatychi gen.n.

Type species: *Katatychi symptosi*sp.n. designated below; by monotypy.

Differential diagnosis: Differs from representatives of the superfamily in having near-prognathous head with minor mandibles. Dot-like pattern is also not recorded in Caloblattinidae, neither in Raphidiomimidae. Moreover this pattern is reversed (pale dot on dark coloration).
Autapomorphies: Elongate, possibly prognathous head with extremely small mandibles; coloration forming clear dots; termite-like appearance
Description: As for species.
Derivation of name: kata tychi κατά τύχη is Greek for *by chance*.
Systematical remarks: Head is entirely unique, and the antenna is narrow, unlike in other representatives of the superfamily. Elongated pronotum is also rather characteristic for Raphidiomimidae, but in this case this perhaps relates to generally elongate habits (like in termites with a similar head and reduced mandibles). Forewing is also highly modified, and while it retained the superfamily characteristics (4-segmented palp; richly branched SC and A; terminal dichotomization of posteriormost CuA; diagonal kink), the elongate, fluently narrowing shape is unique along with its coloration. Partial coloration of the clavus is also very unusual. For the superfamily very unusual is nearly straight R with mostly simple branches. Forewing is most similar to *Solemnia* Vršanský, 2008, which nevertheless has standard head (plesiomorphy). Coloration and head with supporting posterior ridge and possibly also wing shape are rather characteristic for primitive Liberiblattinidae (*Entropia* Vršanský et al. 2008), with the diagonal kink is distinct.

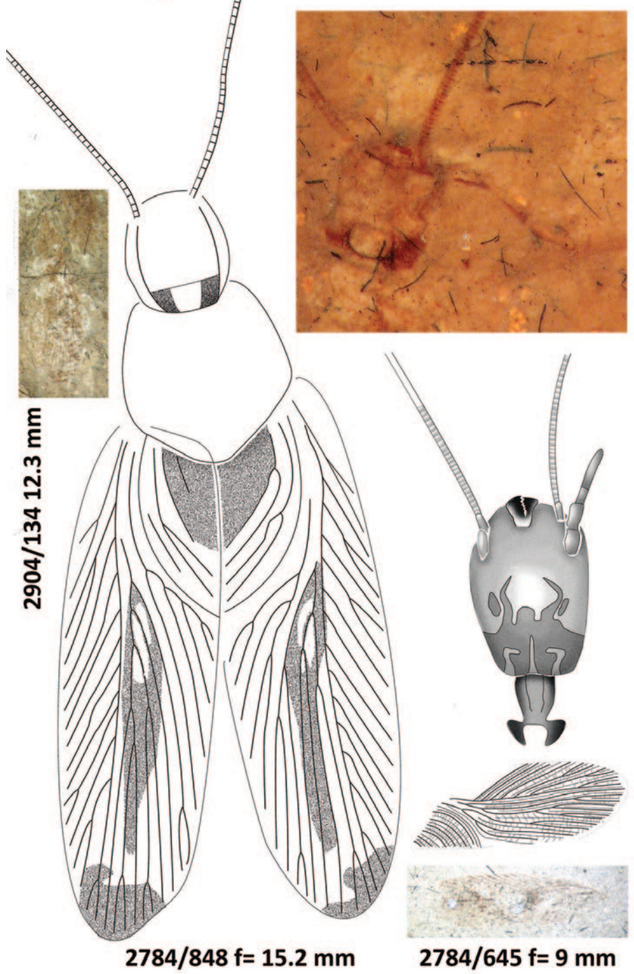
Katatychi symptosi sp.n.

(figp. 363)

Holotype: PIN 2784/848 (f= 11 mm). A complete winged adult with antenna, and disarticulated extremities.
Type locality: Mikhailovka, Karatau, Kazakhstan.
Type horizon: Kimmeridgian Upper Jurassic, Karabastau Formation.

Additional material: PIN 2066/256; 2784/951 (f= ca. 10 mm); 2554/96 head (complete specimens); 2784/645 (f= 9 mm; ?.15.8.7.1.7); 2904/134 (f= 12.3 mm) (completely articulated forewings with clavus). The same locality as the type.

Description: Moderately large cockroach with overall size over 15 mm. Head highly modified, with basal supporting ridge, at least partially prognathous, with long and very thin antenna with moderately long antennomeres (2.3/ 2.1 mm; unlike Caloblattinidae or Liberiblattinidae), sophisticaltely colored at basis. Palp 4- segmented, 4 mm long, first palpomere short (1.08/ 0.5; 2.16/ 0.5; 5.4/1; 5.7/ 1.08 mm); labial palp very long, massive, 4- segmented (1.3 mm: 0.24/0.18; 0.28/0.18; 0.18/0.09; 0.44/ 0.09 mm). Mandible extremely small (ca. 0.4/ 0.4 mm). Neck distinct, robust and long.
Pronotum slightly (visually strongly elongate due to converging lateral margins) elongate (3.5/ 3.3 mm), anterior margin straight, posterior margin slightly extended centrally.Forewing with indistinct intercalaries and CW, reticulated, indstinct coloration forming a posteriormost anal dark field and a longitudinal widened dark stripe on a transparent membrane, and forming a symmetrical central pale dot on each of the forewings (figp. 363, (digitally enhanced contrast and under alcohol) and with parallel margins (length/width 10-12.3 mm/ ca. 3.5- 3.8 mm). Sc with one simply dichotomed branch, significantly shorter than clavus. R straight, RS not differentiated, R rarely with secondarily branches (15-16 veins meeting margin). Posterior branches of M slightly sigmoidaly curved (3-10 veins at margin). CuA short, with 5-9 veins at margin. Clavus short, strongly arcuate, with only 4-6 visible sparse branches. Hindwing preservation obscured, but apparently caloblattinoid and with the same or similar coloration pattern as the forewing.
Body narrow (3.6 mm).
Deformities: Blind branch descending from left forewing CuP inslde clavus is highly unusual character (2784/848). Spe-







Katatychi symptosi

cimen PIN 2784/645 possessed standard (out-of-clavus), CuA-CuA deformity.
Remarks: Sophistated coloration of highly specialized head with specialized, strong labial palp and also strong palps combined with extremely reduced mandibles and narrow body suggest a different, non-standard diet, possibly fungivory.
Derivation of name: symptosi σύμπτωση is Greek for *chance*.
Character of preservation: four complete adults, two completely articulated isolated forewings.
Taphonomy: Unique shape and coloration makes this taxon easily recognized, thus it can be concluded that the species was rare and according the predominantly complete specimens preserved, living near the deposition waterbody.

Genus *Kazachiblattina* Vršanský, 2002

Type species: *Artitocoblatta asiatica* Vishniakova, 1968 and by monotypy.
Type locality: Karatau, Kazakhstan
Type horizon: Karabastau Formation

Differential diagnosis (after Vršanský 2002): Head with distinct lateral ocelli; pronotum oval. Forewing with parallel margins, with branched Sc; curved R (without differentiated RS) and richly branched M reaching apex of the wing; Cu branches almost straight; anal veins may be tertiary branched. Hindwing with simple Sc, RS differentiated; M richly branched (up to 7 and possibly more); CuA with blind branches; CuP straight.
Systematical remarks: In spite of a single preserved specimen, the coloration of the forewing is similar to *Perlucipecta*. Nevertheless, this coloration occurs also in other taxa, in *Kazachiblattina*, hindwings are also colored, and the hidwing venation is liberiblattinid-like.

Kazachiblattina asiatica (Vishniakova, 1968)
= *Artitocoblatta asiatica* Vishniakova, 1968

Holotype PIN 2239/168. A complete specimen. Designated by V.N. Vishniakova (1968).
Character of preservation: one completely articulated specimen (with complete antenna)
Taphonomy: Rarely complete antenna suggest basically absence of pre-depositional transport and rarity in the ecosystem close to sedimentary area.
Mutations: none recorded.

Genus *Akinisia* gen.n.

Type species: *Akinisia chorevei* sp.n. described below, and by monotypy.

Differential diagnosis: It differ from all corydioids including *Volziablatta*-group (strongest plesiomorphy, symplesiomoprhy with Phyloblattidae, Raphidiomimidae and Caloblattinidae) in possessing extremely long ovipositor. On the other hand it possess extremely modified (simplified) round, small pronotum. It is the most fragile known representative of the family. Closely related *Ano* (synapomorphic structure of coloration) differs in having wide wings and modified pronotum. Even more similar appears *Kazachiblattina* with similarly round (but bigger) pronotum, shorter ovipositor and non-elongated wings. *Gurvanoblatta* differs in being not as elongated and in modified shape of forewing with ascending posterior margin.
Autapomorphies: Tiny habitus, small round pronotum, elongated wings with narrowed wing base (numerous homoplasies in other families and in the whole Raphidiomimidae).
Description: As for species.
Systematical remarks: This genus can be categorized within Corydioidea on the basis of lacking the weer-like pleating of the hindwing (syanpomorphy of Corydioidea excluding advanced Caloblattinidae or Phyloblattidae). This is remarkable, because otherwise the forewing reveal high

congruence with the advanced Phyloblattidae (like *Pozabudnutie*) and also primitive Raphidiomimidae (similar to *Divocina* or *Liadoblattina* and *Falcatussiblatta*).
This place *Akinisia* at the base of the modern lineage (the basalmost *Volziablatta*-group is insufficinently known).
Based on high similarity with *Ano* (and *Entropia* with even more sophisticated coloration and even wider wings), it is preliminary placed within Liberiblattinidae, although the long ovipositor was not observed in this family and it cannot be excluded that shift to Liberiblattinidae occurred after its reduction. Generally the most traits are symplesiomorphic with Phyloblattoidea or Caloblattinoidea, including the simply-structured venation without any modification (like *Ano* except for narrowed wing and its base).
Within Liberiblattinidae, *Stavba* (simplified) and *Liberiblattina, Brachymesoblatta* (expanded) differ in structure of Subcosta. Very primitive, and non-elongated forewing also have aquatic *Hydrokhoohydra*, with modified pronotum *Elisamoides* and *Kurablattina* differs mainly in structure of shorter clavus and sharply descending M. Wings of highly modified and are unknown.
Derivation of name: *akinisía* is Greek for immobility.

Akinisia chorevei sp.n.
(figps. 366, 668-371)

Holotype: PIN 2784/803± (=805)*. A completely articulated winged adult male.
Type locality: Mikhailovka, Karatau, Kazakhstan.
Type horizon: Kimmeridgian Upper Jurassic, Karabastau Formation.

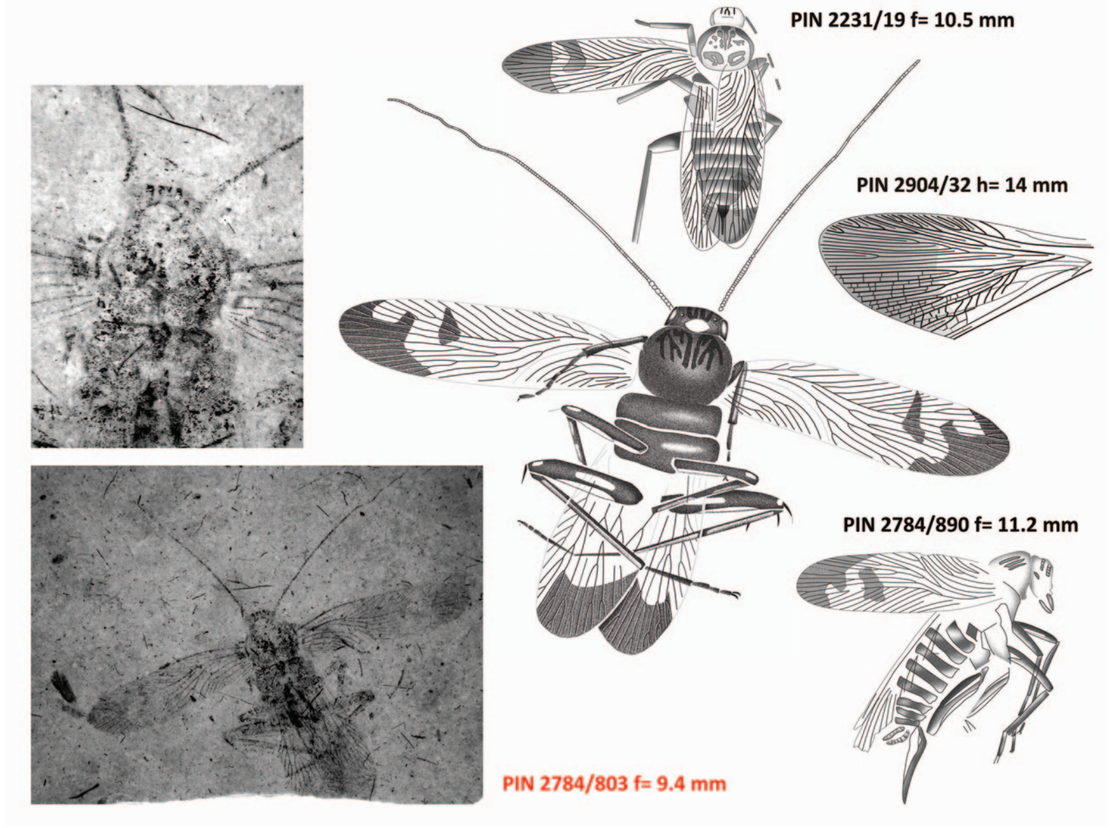
Additional material: PIN 2066/84; 2231/19; 2452/394, 433; 2784/746, 762, 790, 946; 995; 2997/1453 (complete specimens); 2066/158; 2452/540; 2465/377, 970; 2784/697, 748, 756, 766, 770, 890, 947, 983, 985, 986, 989, 992, 996, 2269; 2997/110, 781, 1171, 1189 (isolated forewings); 167/305; 1789/62 (h= 9.7 mm) **G**; 2035/38; 2039/43; 2066/412; 2384/85 (h= 13 mm), 92 (h= 11.5 mm); 2554/67, 129; 2784/641, 720, 727, 773, 822, 918, 990, 944, 997, 2272; 2904/32; 2997/30, 40, 210, 771, 785, 1201 (h= 8 mm), 1413 (h= 13 mm), 1555, 1562, 1569; unnumbered (isolated hindwings). All except G= Galkino from Mikhailovka.

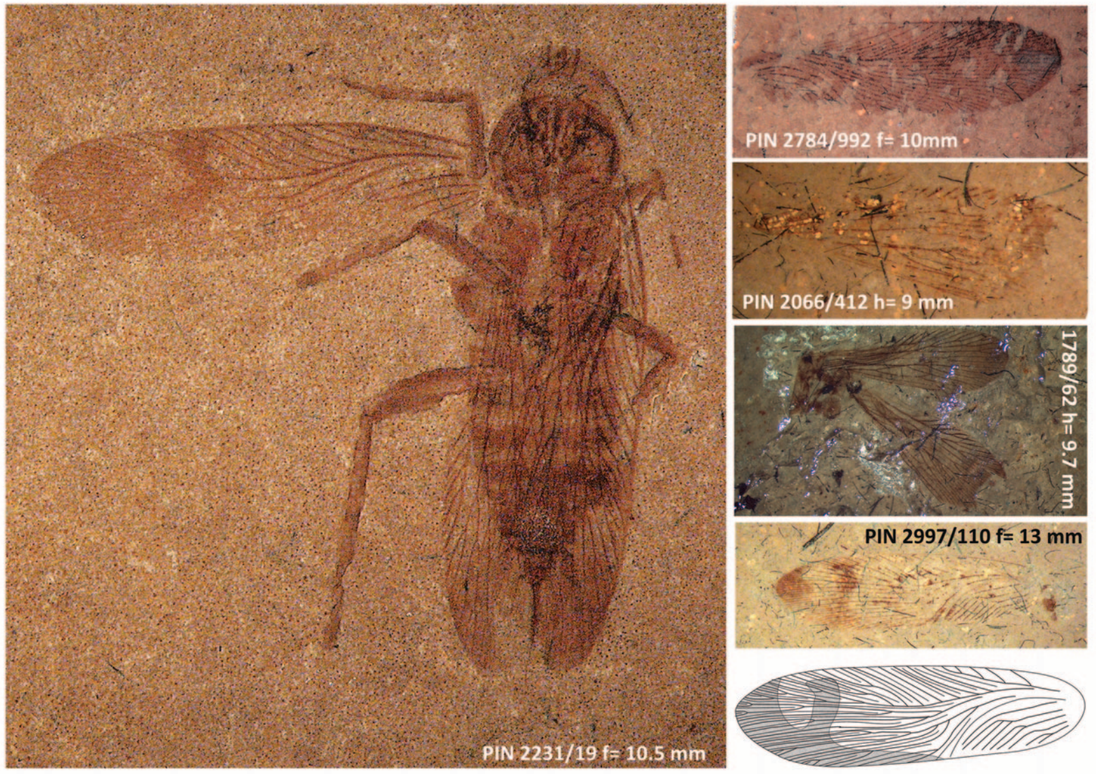
Description: Tiny medium-sized cockroach with fragile body and length ca. 12-17 mm. Head small, globular, only slightly elongate, pale, with 4 dark longitudinal narrow stripes, not entirely covered. Eyes very long and narrow (0.93/ 1.17 mm), small round (0.13 mm in diameter) lateral ocelli present (head was never preserved in position allowing to see whether the central ocellus was preserved). Antennal sockets round and very small (0.13 mm in diameter), antenna very long (11.5 mm as preserved – possibly up to 1 mm more actually), longer than body or wings, with alternating pale and dark areas. Antennomeres not especially long (basally 0.15/ 0.13 mm, terminally 0.19/ 0.13 mm), total 128 or more in number.
Pronotum very small, round (1.74-2.38/ 2.44-2.65 mm), not covering the whole head, pale, with sophisticated network of dark stripes in anterior margin.
Body narrow (3.2 mm wide), terga and sterna straight (7 recognised in female PIN 2231/19, but possibly additional two are a part of the ovipositor; nine isolated by preservation in 2784/ 890: 0.47/ 0.7/ 0.65/ 0.72/ 0.7/ 0.46/ 0.46/ 0.35/ 0.3 mm). Styli preserved in a female (2784/890), cerci thin, 1.3 mm long (long) with at least 6 stylomeres. Female thin ovipositor very long and thin (1.3/0.2 mm) but with massive 0.7/0.6 mm base (possibly composed of tergites) and then fluent narrowing.
Forewing very fragile and elongate (8.4-15/ ca. 3.5 mm), with transparent membrane with dark subapical dot and colored apex with a lobe. Costal vein present, costal area narrow, with 3-6 subcostal veins at margin, its dichotomisations simple. R strongly sigmoidal, with simple branches, secondary dichotomization was recorded only in the terminal offshoot (RS), total number of radial veins 11-20. Media simplified and straight, with 3-89 veins at margin. CuA might be expanded, slightly sigmoidal

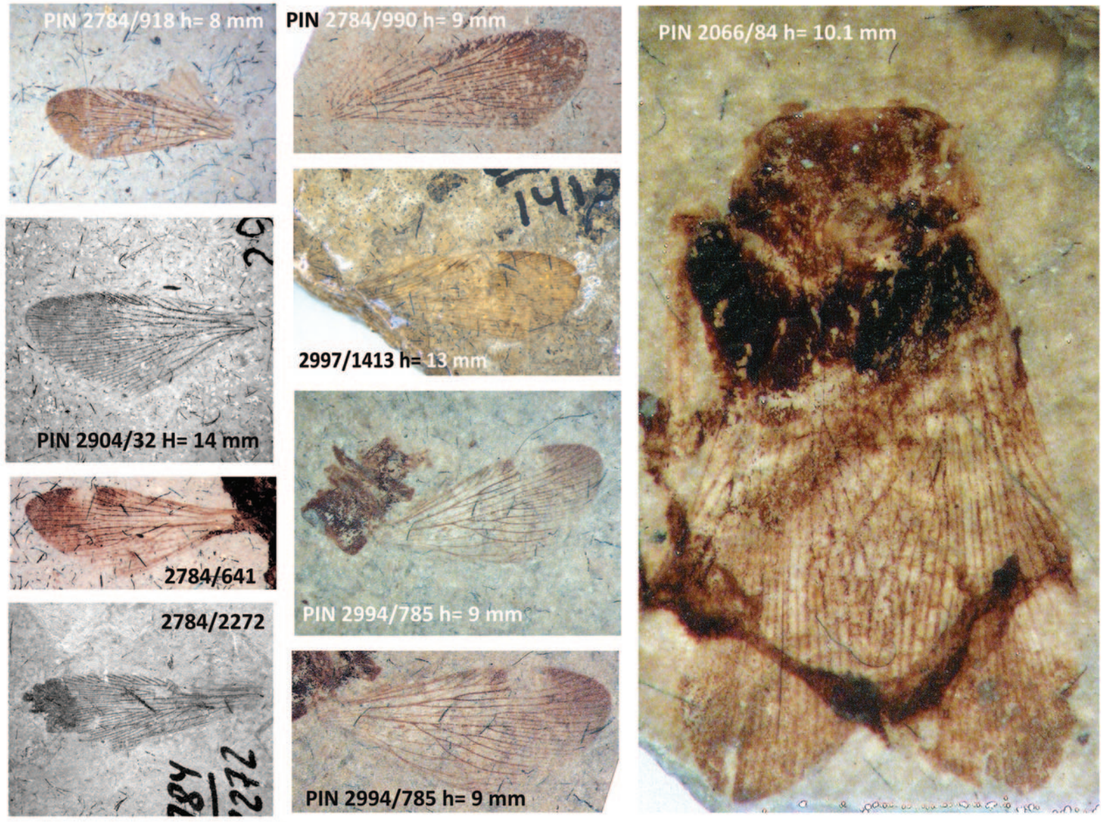


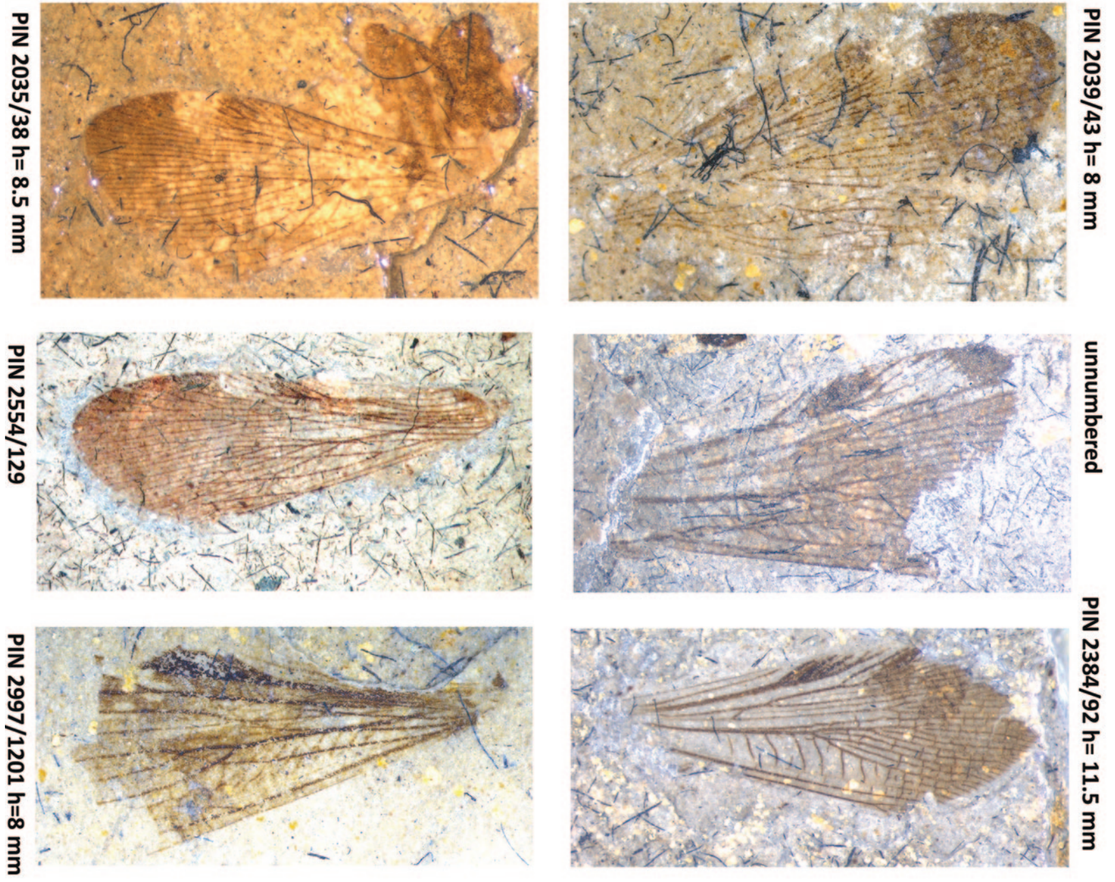
(5-10). CuP simple, comparatively fluent. Anal veins (6-11) simply and secondarily branched. Total number of veins 30-40,
Hindwing narrowed, with remigium width only about as wide as forewing 7.7-14 mm long. Sc simple, 8-19 R branches long, R1 rather wide (2-9 veins), RS also expanded (4-10). Media nearly straight, sometimes greatly simplified (2-10). CuA with 3-9 branches at margin (some secondarily dichotomized); CuP simple, in one case apparently dichotomised terminally. Vannus pleated as a whole, non-veer-like. Total number of remigial veins 20-33.
Legs cursorial, thin and long, with high degree of spur and spine reduction (forelegs with terminal tibial spurs only; midlegs with terminal femoral spurs and terminals tibial spurs only; hindlwgs with terminal femoral spur and 2-3 tibial spurs). Forelegs unusually long, femur thin, only 0.41 mm wide; foretibiae elongate (1.99/ 0.26 mm), slightly widened terminally and with short terminal spur or two; tarsus very long and thin (0.93; 0.4; 0.4; 0.4; 0.53/ 0.13 mm). Midlegs very tiny and short; midfemur (2.91/ 0.53) with 0.51 mm long terminal spur; midtibia without carination (2.9/ 0.26 mm). Hindlegs more robust, hindfemur (3.7/ 0.68 mm) with 0.73 mm long femoral spur but otherwise without carination; hindtibia (4.63/ 0.36 mm) with 2 or 3 short (under 0.36 mm) spurs; hindtarsus long and thin (1.3;0.39; 0.16; 0.32/ 0.17 mm) and with symmetrical long claws without arolium.

Mutations: Similarly as in most of other small species, also *M. tripudium* do not bear a deformity of the membrane, but two specimens (2997/110; 2784/803±*) contain an unfinished blind A vein in the clavus – an extremely rare occurrence.
Remarks: Tiny individuals with elongated wings suggest an active way of life with an active flight. The (statistically insignificant) low values for wing variability might support this. At the same time, the standard hypogranthous and small head does not seem to evidence a predatory lifestyle. PIN 2784/890 evidence rare lateral preservation. Interesting is also specimen 2997/785 with extremely rare, dichotomised CuP. Long antennomeres support placement within Corydioidea as Phyloblattids and caloblattinids have very short antennomeres, especially the basal ones. Antenna is unusually long and this length was observed only in cave species (Sendi et al. 2020), in which antennomeres are doubled in length. In the present case, the length is reached with polymerisation, 128 or more short segments is extremely high number. Very interesting is also the reduction of spurs, known only in Umenocoleoidea: Alienopteridae and Umenocoleidae.
Variability: Study on forewingsd was performed on statistically insignificant sample size (n= 12-14). Total number of veins revealed CV 8.63 %, which was in the range of revealed CV for statistically significant samples at the locality. Also ranges are consistent among venial systems. Veins without A reveal a very similar number (8.99 %) providing more support for roughly correct data.
Unlike, hindwing data on less limited sample size (n= 22-23) consistently reveal CVs jump from 24.02 % ® to 50.05 % (M) possibly only evidencing insufficient data, in spite of the fact that the general number looks very promising (remigium 13.86 %) and consistent with statistically significant samples (little higher variability than forewings). By adding larger specimens which in original determination belonged to another species (but otherwise lacking diagnostic traits and with identical coloration, i.e., 2465/970 for a forewing; larger 2904/ 32, 2784/ 2272, 2997/785, 944 and standard-size 2066/84, 2784/641, 990 for a hindwing) variability was influenced significantly: improved on 4 specimens (larger and possibly representing another taxon in spite of lacking any such forewings) and other 3 specimens slightly stabilized results of the variability in respective systems, but total CV for remigium changed from 8.82 % into 13.86 % suggesting in this case far more data are required for a stable result and these results must be regared only in the bulk with data for other species (significant and insignificant), and alone are only informative. Nevertheless, experience reveal only cosmetical differences in 22 specimens (compared with 30 required).
Derivation of name: *chorévei* is Greek for


PIN 2231/19 f= 10.5 mm
PIN 2904/32 h= 14 mm
PIN 2784/890 f= 11.2 mm
PIN 2784/803 f= 9.4 mm


PIN 2231/19 f= 10.5 mm
PIN 2784/992 f= 10mm
PIN 2066/412 h= 9 mm
1789/62 h= 9.7 mm
PIN 2997/110 f= 13 mm


PIN 2784/918 h= 8 mm
PIN 2784/990 h= 9 mm
PIN 2066/84 h= 10.1 mm
2997/1413 h= 13 mm
PIN 2904/32 H= 14 mm
2784/641
PIN 2994/785 h= 9 mm
2784/2272
PIN 2994/785 h= 9 mm


PIN 2035/38 h= 8.5 mm
PIN 2039/43 h= 8 mm
PIN 2554/129
unnumbered
PIN 2997/1201 h=8 mm
PIN 2384/92 h= 11.5 mm

specimen forewings	length	width	Sc	R	M	CuA	CuP	A	RM	RCuA	MCuA	total	total without A
2784/803±L*	9.4		5	14	7	6	1	9	21	20	13	42	33
2784/803±R*	9.3		3	15	5	9	1	9	20	24	14	42	33
2784/890	11.2		3	14	5	10	1	8	19	24	15	41	33
2231/19L	10.5		4	13	7	8	1	7	20	21	15	43	36
2231/19R	10.5		4	15	3	9	1	10	18	24	12	42	32
2784/766	9		3	16	6	5	1	7	22	21	11	38	31
2784/992	10		5	15	6	10	1	10	21	25	16	47	37
2784/983±	8.5		5	11	6	9	1	8	17	20	15	41	33
2784/989	9		6	12	6	8	1	8	18	20	14	41	33
2784/986	9.5		5	13	7	6	1	10	20	19	13	42	32
2784/ 770	8.4		3	15	6	5	1	6	21	20	11	36	30
2997/110 *	13	3.5	5	15	8	10	1	11	23	25	18	50	40
2465/970	15		3	20	7	8	1		27	28	16		39
n	13		13	13	13	13	13	12	13	13	13	12	13
min			3	11	3	5	1	6	17	19	11	36	30
max			6	20	8	10	1	11	27	28	18	50	40
ave	10.25		4.15	14.46	6.08	7.92	1	8.58	20.54	22.38	14.08	42.08	34
dev	1.8932403		1.068188	2.1838569	1.255756	1.846688	0	1.505042	2.5695455	2.7549489	2.0599975	3.6296339	3.0550505
cv	18.47		25.74	15.11	20.65	23.32	0	17.54	12.51	12.31	14.63	8.63	8.99

specimen HW	length	Sc	R1	RS	M	CuA	CuP	R	RM	RCu	MCu	Total remigium
2784/803±L*	1	5	9	2	5	1	14	16	20	8	23	
2784/803±R*	1	5	7	3	5	1	12	15	18	9	22	
2231/19L		1	4	8	2	5	1	12	14	18	8	21
2784/ 997		1	3	7	5	3	1	10	15	14	9	20
2784/ 773	9	1	6	9	8			15	23			
2554/67.	9	1	2	6	6	4	1	8	14	13	11	20
2784/822	9	1	7	9	3	6	1	16	19	23	10	25
2066/412	9	1	6	6	2	4	1	12	14	17	7	20
2904/32	14	1	4	7	8	7	1	11	19	18	15	28
2784/2272	14	1	9	10	7	5	1	19	26	21	12	33
2997/785	9	1	6	8	3	7	2	14	17	21	10	27
/944	13	1	6	7	4	6	1	13	17	19	10	25
2066/84	10.1	1	4	4	5	8	1	8	13	17	13	23
2784/990	9	1	6	7	4	6	1	13	17	20	17	25
2784/641	9.5	1	6	10	3	7	1	16	19	24	19	28
2784/918	7.7	1	5	6	4	5	1	11	15	17	10	22
2035/38	8.5	1	5	9	5	7	1	14	19	22	13	28
2554/129		1	6	10	2	6	1	16	18	23	9	26
2039/43	8	1	3	8	7	8	1	11	18	20	16	28
2997/1413	13	1	4	4	10	9	1	8	18	18	20	29
2066/84R	10.1	1	5	4	8	4	1	9	17	14	13	23
2066/84L	10.1	1	4	6	9	5	1	10	19	16	15	26
1789/62	9.7	1	7	2	9	8	1	9	18	17	17	28
n	18	23	23	23	23	22	22	23	23	22	22	22
min	7.7	1	2	2	2	3	1	8	13	13	7	20
max	14	1	9	10	10	9	2	19	26	24	20	33
ave	10.1	1	5.13	7.1	5.17	5.9	1.05	12.22	17.39	18.64	12.32	25
dev	1.996312	0	1.5463843	2.1513853	2.5875958	1.5708381	0.2132007	2.9841478	2.9655466	3.0007214	3.7719057	3.4641016
cv	19.77	0	30.14	30.3	50.05	26.62	20.3	24.42	17.05	16.09	30.62	13.86

a dance. The name alluding to the dance of the immobility (in fossil): ακινησία χορεύει.

Character of preservation: 11 complete adult winged specimens (one identifiable male and one identifiable female with ovipositor); 22 isolated forewings; 31 isolated hindwings.

Taphonomy: Presence of numerous completely articulated individuals of both sexes as well as isolated forewigns and hidwings of this tiny species suggest an abundance in the actuocenosis. The transport is obscure as this tiny species might decayed very quickly.

FAMILY MANIPULATORIDAE VRŠANSKÝ ET BECHLY, 2015

Type genus: *Manipulator* Vršanský et Bechly, 2015. North Myanmar amber.

Composition: *Manipulatoides* Li et Huang, 2022. North Myanmar amber.

Geographic range: cosmopolitan
Stratigraphic range: Upper Jurassic-Upper Cretaceous.

Diagnosis (after Li and Huang, 2022): Medium to small-sized cockroach, with elongate pronotum and appendages. Head nimble, hypognathous in repose, wider than anterior half of pronotum and narrower than the posterior half of pronotum. Eyes bulging, reniform or subglobose, moderate size among cockroaches. Along the higher margin of antennal socket is a crescent fenestra (transparent area), above which is a brim-shaped protrusion. It is uncertain whether the fenestra and the ocellus are identical. The fenestra may be the ocellus itself or contains the ocellus as a part. Maxillary palpi longer than double head length. Pronotum longer than width, widest at posterior one-fifth. In macropterous species, tegmen length-width ratio approximately 10:3; vannus of hindwing small, folding over flatly, not fanwise. Basally between RP and M of hindwing is a short vein, seemingly a vestigial M branch rather than a cross-vein. Legs long, foreleg longer than body, hindleg almost double the length of foreleg. Males with hook-like phallomere on the left side. Female seventh sternum (subgenital plate) bivalvate, valvulae concealed.

Genus *Manipulator* Vršanský et Bechly, 2015

Composition: Type species, *M. modificaputis* Vršanský et Bechly, 2015; possibly a specimen from Crato Formation in Brazil; Spanish amber (L. Šmídová in prep.) and the present species.

Stratigraphic range: Upper Jurassic-Upper Cretaceous.
Geographic range: Cosmopolitan.

Diagnosis (after Vršanský and Bechly 2015): Extremely elongated extremities, including semi-raptorial forelegs and extremely long leg-like maxillary palps, modified three basal antennal segments, extremely elongated neck, ocelli with roof-like covering sheaths; elongated saddle-like pronotum; and numerous minute trichoid sensilla (minute hairs). Elongated forewing is unique in having short simply dichotomized at base SC and in dense venation with long A branches within clavus.

Manipulator olim sp.n.

(figps. 376, 378-381)

Holotype: PIN 2239/201±. A completely articulated winged adult female.
Type locality: Mikhailovka, Karatau, Kazakhstan.
Type horizon: Kimmeridgian Upper Jurassic, Karabastau Formation.

Additional material**:** PIN 2239/174 (f= 22 mm); 2904/339; 2997/1671 (complete adult winged male specimens); 2904/136 (h= 20 mm)(isolated hindwing). The same locality as the type.

Differential diagnosis: differs from *M.*



modificaputis in being much larger (over 16 mm), in having shorter and generally smaller pronotum and slightly shorter extremities and in coloration (pronotum without stripes, but stripped legs and forewing). Different are shapes of the laterall ocelli-covering sheath and huge antennal sockets.

Autapomorphies: Larger size (homoplasic in true mantodeans), narrow longitudinal pale stripe on forewing, huge antennal sockets.

Description: Moderately large predatory cockroach with total body length ca. 16 mm. Head triangular (2.9/ 3.1 mm). Compound eyes very large (1.7/ 0.85 mm), globular, extending beyond the head outline. Lateral ocelli extremely developed, with triangular covering sheath. Central ocellus absent or indistinct. Antennal sockets extremely large, 0.8 mm in diameter, antenna wide, with moderately long segments (0.22/ 0.23 mm). Mandible small, only about 0.85 mm wide when both combined. Clypeus well-developed, 0.85/ 0.45 mm long/wide. General head coloration pale (including eyes), dark are mandibles, occiput with ocelli-covering sheaths and a two thin lateral longiutudinal face stripes. Maxillary palp long, palpomeres narrow, 4 or 5-segmented (?, ?, 1.7, 1.47, 0.85 mm long), terminal segment short and cup-like. Labial palp short, 2-segmented (0.23/ 0.17; 0.57/ 0.17 mm).

Pronotum saddle-shaped, campaniform, small (4/ 1.4 mm), dark, with two large posterior pale fenestra.

Forewing significantly elongate, ca. 13 mm long and less than 2.5 mm wide, dark, with longitudinal narrow pale stripe, long clavus and without pseudovein and posteriorly dichotomized A.

Hindwing long, with simplified CuA and distinctly colored intercalaries.

Body comparatively narrow, 4 mm wide, terga structured or with dense hard sensillar cover, very dark laterally, pale dark in center, margins more or less straight.

Cursorial legs very long and narrow, each segment including coxa, trochanter, femor and tibia dark, with pale longitudinal stripe. Forelegs with extremely free articulations including long coxa (2/ 0.58 mm), elongate trochanter (0.4/ 0.17 mm) and very long forefemur (3.4/ 0.58 mm), carved basally, foretibia very long (4/ 0.69 mm). Mid coxa long, femora short, tarsi long, likely 5-segmented. Hind legs with very long femur, extremely long and narrow tibia (6.9/ 0.46 mm) with only sporadic and short (0.52 mm long) spurs (2 preserved) and 4-segmented tarsi (2/ 0.28; 0.97 /0.17; 0.57/ 0.14; 0.57/ 0.14 mm) with wide large claws (5 wide), possibly with arolia.

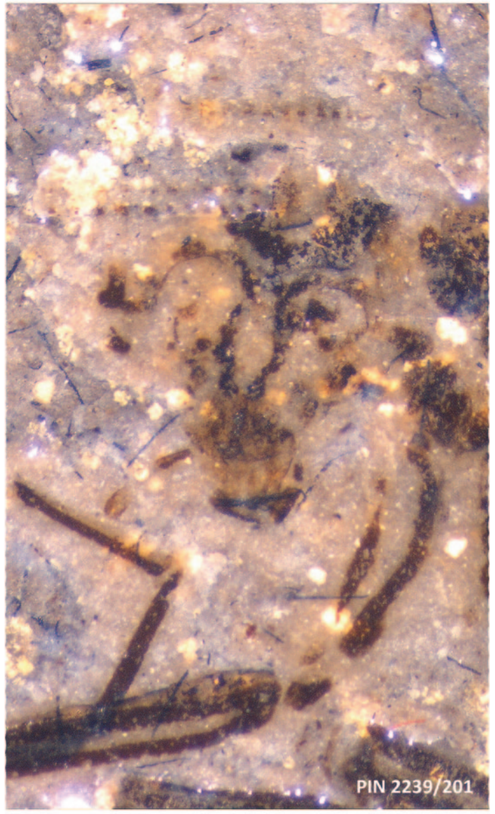
Systematical remarks: Saddle-like pronotum, mantid-like head and long extremities allow categorization within the family. At the same time lack of pseudovein confirm excluded direct relations with Mantodea. The categorization within the genus is lacking conflict, although the preservation state disallows the definitive confirmation of the generic placement. Erection of a new genus lacks any support at the present state of the knowledge. Generally the taxon is highly similar with *M. modificaputis*, including the characteristic coloration of head in this species conform with stripped forewing (unlike monochromatic in *M. modificaputis* and taxa from burmite). Palps are not as long as in *M. modificaputis* indicating a plesiomorphic state. Also the ovipositor is significantly longer than in undescribed *M. modificaputis* females and generally the new species is significantly larger and thus erection of a new species, also taking into conisderation a significant time-gap appears safe. Coloration of pronotum is similarly as in *M. modificaputis* and other undescribed species from burmite sophisticated, but lacks serious stripes (plesiomorphy). Undescribed species from Crato and Solnhofen are also similarly large owing to preferential preservation of larger specimens in sediments when compared with amber record.

Derivation of name: *olim* is Latin for *once* or *of the past*.

Characer of preservation: Four completely articulated winged adults (1 female, 2 males), one isolated hindwing.

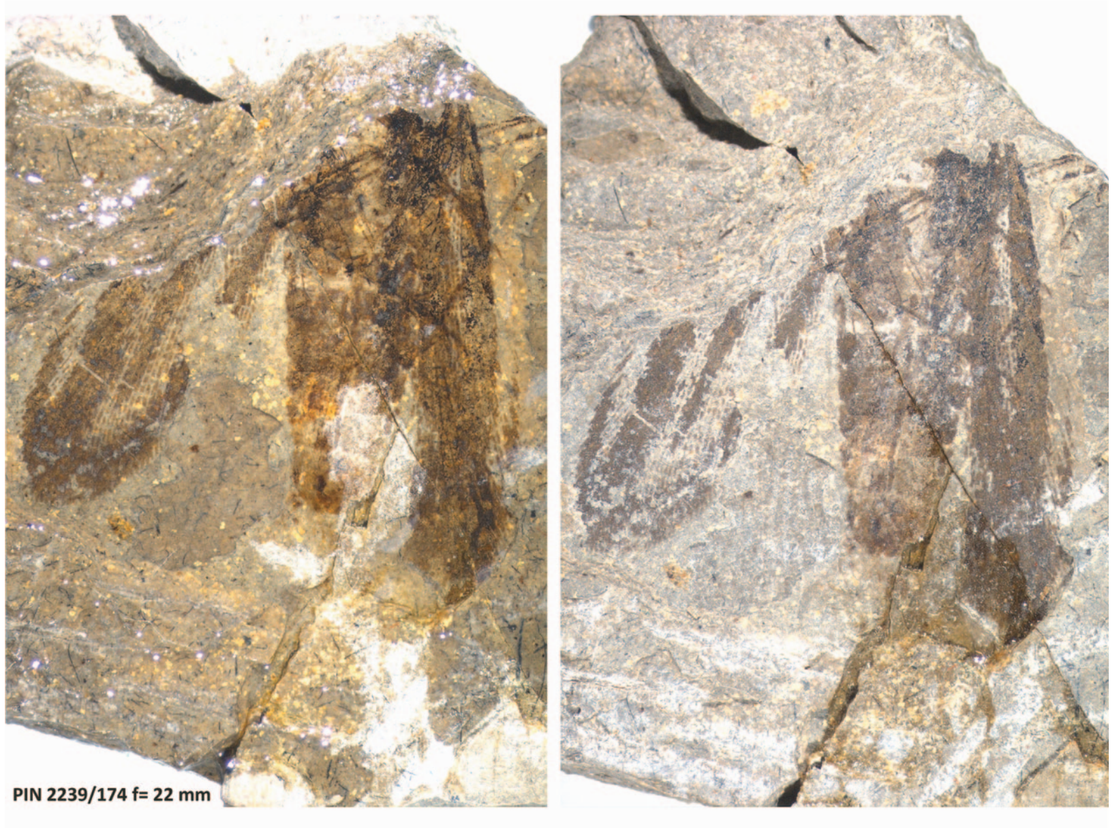
Taphonomy: Due to full articulation of mouthparts, these specimen were not transported for a serious distance. It is also impossible to estimate the rarity of this species, as *M. modificaputis* was a specialized resin, near-tree predator, so its

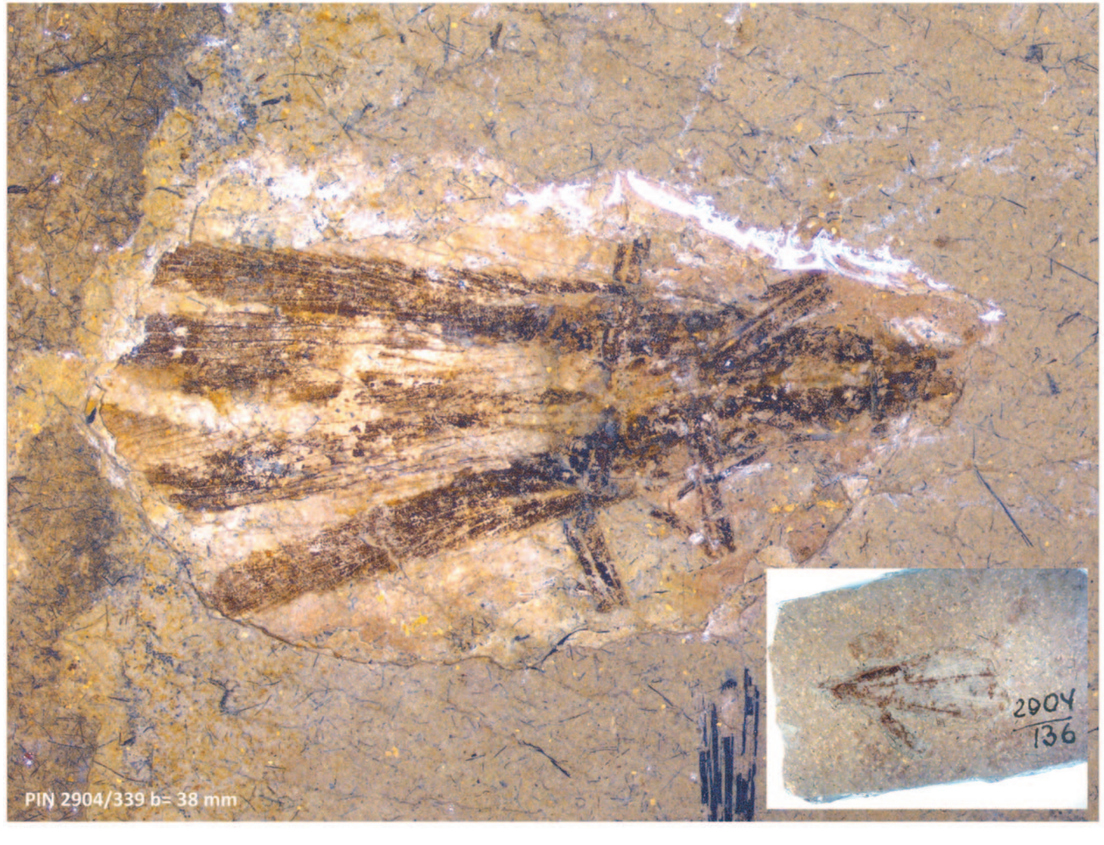






PIN 2997/ 1671 l= 21 mm


PIN 2239/174 f= 22 mm


PIN 2904/339 b= 38 mm
2004
136

rarity in sediments is not surprising. Also the flying abilities does not seems to be preferential and were most probably equivalent to sporadic flight of praying mantis, while narrowed wings suggest improved quality of flight. Isolated hindwing was apparently more seriously transported.

Superfamily Umenocoleoidea Chen et Tan, 1973

(holophyletic within Liberiblattinidae)

Type genus and species: *Umenocoleus sinuatus* Chen et Tan, 1973. Yumen, China, Early Cretaceous.

Stratigraphic range: Early Jurassic- Eocene
Geographic range: cosmopolitan

Composition: Alienopteridae Bai et al., 2016= Aethiocarenidae Poinar et Brown, 2017.

Diagnosis: Originally beetle-like cockroaches with forewings modified into elytra with cup-like bunky. Elytra are often reduced to diverse extent up to near complete reduction. During the redesupression of shortened forewings into normally developed ones often without clavus. Hindwing corydioid (as in Blattulidae but with unreduced CuA), often secondarily fenestrate. Head large, globular or triangular, pronotum mostly with reduced paranotalia and posterior ridge. Female with short ecternally protruding ovipositor. Cerci originally long and with numerous long filaments. It is expected that most of the species are actively living, well-flying pollinators, often mimicking diverse hymenopterans.

Family Umenocoleidae Chen et Tan, 1973

Type genus and species: *Umenocoleus sinuatus* Chen et Tan, 1973. Yumen, China, Early Cretaceous.

Stratigraphic range: Early Jurassic - terminal Cretaceous
Geographic range: Cosmopolitan

Composition (after Kováčová 2022, Sendi et al. 2022): *Antophiloblatta* Sendi in Sendi et al. (2020a); *Blattapterix* Vršanský (2003b); *Compunctiotypus* Kaddumi (2005); *Cratovitisma* Bechly (2007), Podstrelená and Sendi (2018); *Elytropterix* Vršanský (2003b); *Jantaropterix* Vršanský et Grimaldi in Vršanský (2003b), Mlynský et al. (2019); *Laticephalana* Luo et al. (2021); *Lepidopterix* Sendi in Sendi et al. (2020a); *Perspicuus* Koubová in Koubová and Mlynský (2020); *Petropterix* Vršanský (2003b), Oyama et al. (2021); *Ponopterix* Vršanský et Grimaldi in Vršanský (1999a), Lee (2016); *Umenocoleus* Chen and Tan (1973); *Umenopterix* Lee, 2016; *Vitisma* Vršanský (1999b, 2003b, 2005a), Vršanský and Ansorge (2001), Oyama et al. (2021), Kováčová, 2022 (Myanmar; China; Jordan; Brazil, Lebanon, Myanmar; Mongolia; Lebanon, Myanmar, USA; Myanmar; Lebanon; Myanmar; China, Japan, Mongolia, Russia; Brazil, China; China; Brazil; Japan, Mongolia, Russia, Spain); *Nigropterix* Sendi et al. 2023 (Kazakhstan, Myanmar).

Diagnosis (revised by Luo et al. 2021; and see superfamily diagnosis): Head transverse–cylindrical, orthognathous; compound eyes large, oval; antennae with numerous wide segments and very long setae in transverse rows; pronotum subdivided by transverse supracoxal furrow; forewings sclerotized, covered by cup-shaped punctures (*"bunky"*); venation simplified or sometimes indistinct, adsutural line present; distal part of hindwings distinctly projected beyond forewing apex; stem R reduced, with few branches, possibly with pterostigma; stem M branched; stem CuA with many branches; stem CuP simple; cerci with long setae and few segments; females with short external ovipositor.

Genus *Maloval* gen.n.

Type species: *Maloval hlavolam* sp.n. described below, and by monotypy.

Differential diagnosis: Differs from all groups of beetle-like cockroaches in original unmodified hindwing Bauplan, forewing lacking anterior supporting ridge and in autapomorhies (see species description).
Description: As for species.
Derivation of name: *Maloval hlavolam* is a Slovak palindrome meaning "He painted a puzzle" - referring to sophisticated taxonomic procedure and also sophisticated coloration.
Systematical remarks: The (original) structure of the hindwing with secondarily branched CuA allow categosisation within basal Corydioidea exclusive Blattulidae, Mantodea, Isoptera, Skokidae, Eadiidae, Umenocoleidae, Alienopteridae and Manipulatoridae., i.e., in Liberiblattinidae..It is nevertheless difficult to categorise it unequivocally within Liberiblattinidae because the structure of the forewing is alread**y u**menocoleid/alienopterid and the taxon might be simply most primitive umenocoleid with plesiomorphic hindwing. Nevertheless, diagnostic umenocoleid bunky are not rpeserved consistently over the forewing, and venation is original at least in the apical part (again plesiomorphies). Strong synapomorphy of umeno-

coleids, anterior supporting rim was also absent and pronotum is typical for liberiblattinids like in all *Ano* and in *Liberiblattina robusta* and *L. cunicula*. As if presenting a true umenocoleid this specimen will cause serious changes to all current system of cockroach evolution, specifically divergence of Umenocoleidea along with Mantodeans, termites and nocticolids, and specifically dating of all these diversifications, it seems more reasonable to categorise this taxon within Liberiblattinidae. Although the fact that this taxon might belong to Umenocoleidae must also be considered in the future..

Within Liberoblattinidae, head is unique, while the identical pronotum is present in *Ano* and some *Liberiblattina*. Body with few segments is present in *Liberiblattina* and also in some Umenocoleidae. The elytra is unique within the family, although numerous representatives have partially elytrised tegmina. Hindwing is identical with some Liberiblattina species and also the *L. ihringovae* (type species of the genus and family).

Disregarding the classification within Liberiblattinidae or Umenocoleidae, it is clear that the species shares numerous synapomorphies namely with the type species *L. ihringovae* and originated from one of the species in the genus *Liberiblattina* or from some unknown closely related taxon.

***Maloval hlavolam* sp.n.**

(figg. 385)

Holotype: PIN 2465/937. A completely articulated adult male.

Type locality: Mikhailovka, Karatau, Kazakhstan.

Type horizon: Kimmeridgian Upper Jurassic, Karabastau Formation.

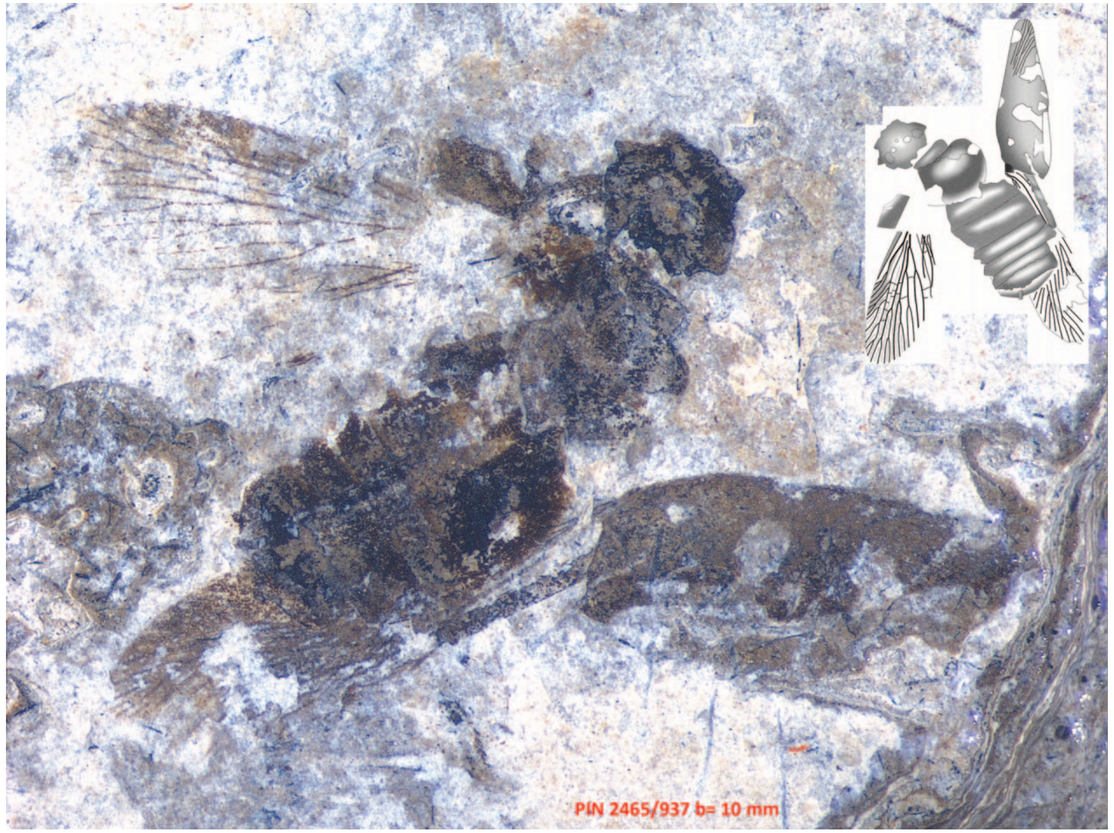
Autapomorphies: Colored posterior forewing rim, small eyes on protrusion, colored hindwing costa, “waved” posterior margins of terga

Description: Head dark, very large (2/ 2.7 mm), modified, round, with rather small but protruding eyes and two large lateral ocelli. Central ocellus (1.4 mm in diameter) is very laarge and distinct but not as large as lateral ones (2 mm in diameter). Antennal sockets extremely developed (up to 5 mm in diameter).

Pronotum massive (2.5/ 3 mm), with straigth anterior margin, paranotalia and posterior central extension. Coloration of pronotum
dark with lateral subanterior pale spots.

Forewing 7.3 (/2.5) mm long strongly modified and entirely elytrised including the apex, although veins and also intercalaries are distinct in the apical part. R stem is traceable shortly in the anterior third (narrow R). Shape is also modified, with strongly arcuate anterior margin and nearly straigth posterior margin with distinct posterior rim (mostly without coloration, but colored in central part). *Bunky* probably present in the basal part, but unequivocal diagnostics in this respect was not possible. Coloration dark, with pale round and sophisticated areas as following: a transverse short basal stripe, basal anterior small macula, two pale appendages of the rim, central and terminal half-dots in the anterior margin, apical posterior macula and small stripe in the area of colored rim.

Hindwing unmodified, 8 mm long and with very wide (2.4 mm) remigium. Veins distinct, diversified in respect to width, intercalaries distinct in all anterior part and partially in anteriormost branches of CuA. Cross-veins sporadic. Costal area narrow, dark colored, very long, simple straigth SC reaching half of the wings length. R with distincctly differentiated R1 and RS. Stem of R1 strongly sigmoidal, R1 branch secondarily branched (3). RS stem nearly straigth, with 3 sigmoidal separate branches, in 2 cases secondarily branched. RS together with 8 veins meeting margin. R1 and part of RS foring distinct pterostigma ovelapping bracnhes and reaching intercalry. M in original state, with two parallel branches in terminal fourth, each dichotimising, together wirth 4 veins at margin. CuA with secondarily branched veins, branching comprises also the posteriormost branch, CuA together with 7 veins meeting margin. CuP simple. A1 in remigium branched, with at least one branch incomplete. Vannus pleating simple.



Hindtibia robust, long (3.4/ 0.3 mm), distincly with basic striated coloration pattern, although sophisticated pattern composed of small colorations cannot be excluded.
Body narrow with 6 segments distinct, posterior margins of at least terminal and subterminal terga with “wave” margin.
Cercus thin, with 4 segments preserved, apparently more were present.

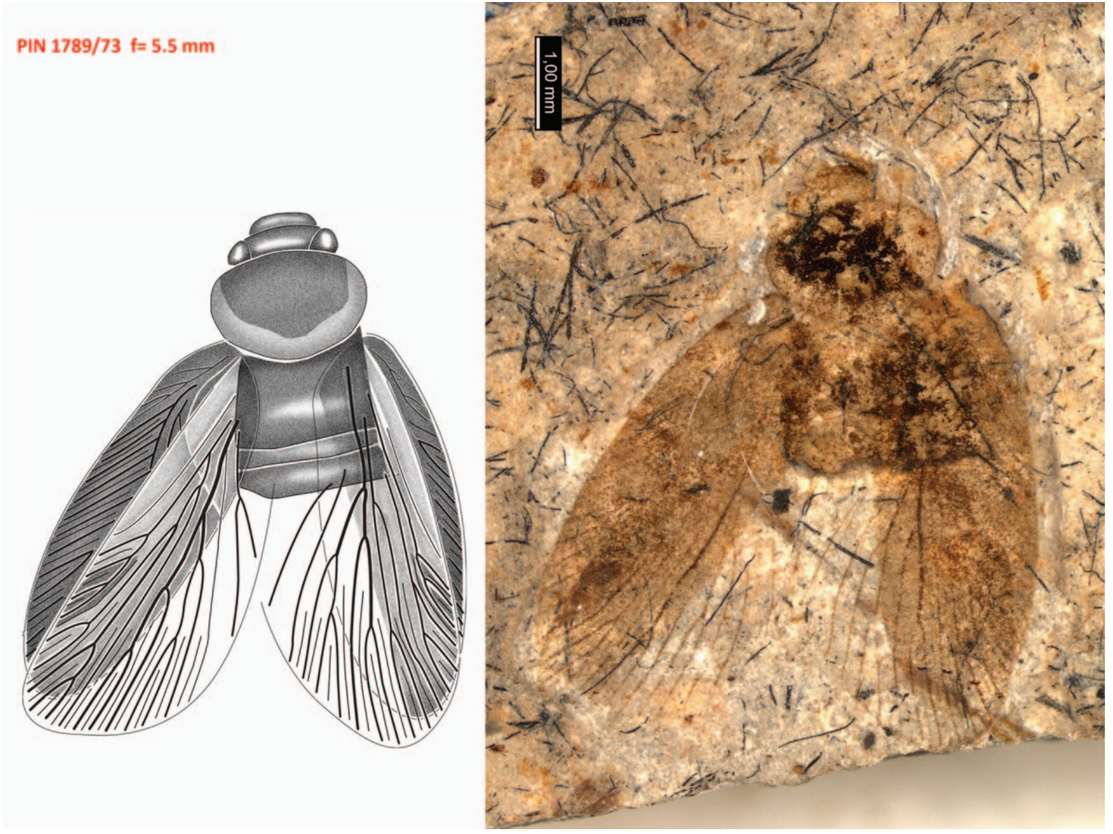
Derivation of name: *hlavolam* is Slovak for aenigma.
Character of preservation: One completely articulated but damaged specimen (without antenna).
Taphonomy: Complete specimen suggest short or no pre-depositional transport, supported with articulation of fine cerci. On the other hand the right forewing is shifted and was apparently stirred from the specimen. Left hidnwing is remote from body which also suggest manipulation after deposition. Most probably we see here predation, because the left forewing is stirred, fragmented and rotated. As such specimen would be unable to fly, most probably this manipulation/ predation took place post-mortem.

Fractaliidae
Vršanský et Hinkelman in Vršanský et al. (2021)

Type genus and species: *Fractalia articulata* Hinkelman et Vršanský in Vršanský et al. (2021)
Stratigraphic range: Kimmeridgian–Cenomanian
Geographic range: Laurasia and burmite

Composition: *Fractalia articulata* Hinkelman in Vršanský et al. (2021); *Fractalia aristovi* Vršanský in Vršanský et al. (2021); undescribed *Fractalia* sp. from lithographic limestone of Eichstätt in Germany (specimens 4310 and 4817 “*Lithoblatta lithophila* Germar, 1839” trifoss.com).

Differential diagnosis: Differs from other cockroach families, except termites, in having a forewing breaking suture, from termites in having the body and hindwings completely covered by elytrised forewings, pronotum with partially concave anterior margin, large number of tibial spurs and all 6 legs “raptorial”, mantodean–like. Hind wing standard primitive umenocoleoid (long Sc, slightly curved R1 with few branches, pterostigma overlapping up to nearest intercalary; Rs simplified (3–5), branched M; CuA with numerous branches; CuP simple or with two veins at margin; A1 branched, its field wide).



Fractalia aristovi

Genus *Fractalia* Hinkelman et Vršanský in Vršanský et al. (2021)

Type species: *Fractalia articulata* Hinkelman in Vršanský et al. (2021)
Type locality: Hukawng, North Myanmar
Type horizon: Cenomanian burmite

Composition: *F. aristovi*
Stratigraphic range: Kimmeridgian (FOD)-Cenomanian
Geographic range: Laurasia and burmite

Diagnosis: as for family

Fractalia aristovi Vršanský in Vršanský et al. (2021)

(figp. 387)

Holotype: PIN 1789/73 **GALKINO**; head, pronotum, and all wings with a fragment of the abdomen.

Type locality: Karatau, Kazakhstan
Type horizon: Upper Jurassic Karabastau Formation

Character of preservation: One complete winged adult with disarticulated body.
Taphonomy: As an active flight is presumed for beetle-like species with regulated hindwing veins, suggested is high rarity of this species in the assemblage. It was most probably a very rare taxon with specialised, possibly pollinating habits, as it occurs only in 4 specimens in all (long) history.

Family Operamidae fam.n.

Type genus: *Operam* gen.n. described below, and by monotypy.

Type locality. Indigenous to Karatau, Kazakhstan.
Type horizon. Kimmeridgian Upper Jurassic, Karabastau Formation.

Differential diagnosis: Differs from its stem – and all representatives of the family Liberiblattinidae (and from all other known Mesozoic cockroaches) in having extremely elongated forewing (longer than in Raphidiomimdae), but margins are parallel. Also it differs in extremely shortened cerci and in galleric coloration of the abdomen and zig-zag coloration of the forewing (present also homoplasically in one raphidiomimid described below).
Autapomorphies: Extremely elongate parallel forewing, zigzag coloration pattern, patterned abdomen, extremely short cerci.
Derivation name: After the type genus
Remarks: The posteriorly branched SC and A, and short R allow categorization of this highly modified taxon within Corydiopidea close to Liberiblattinidae. Nevertheless, the most of the characters are unique, disallowing the trace the origin properly. While the coloration with a distinct subapical dot is similar only to the family type species *Liberiblattina ihringovae*, the only other zig-zag patterned species *Falcatusiblatta disrupta* (Raphidiomimidae by homoplasy*)*.
Coloration and structure of the pronotum is similar to certain Umenocoleidae and it seems this taxon originated from the same stem as this (super)family. *Bunky* were absent. Venation fully traceable, unmodified, including branched A.
Short cerci is character counterindicative for Umenocoleidae, and might be related to comparatively large size.

Genus *Operam* gen.n.

Type species: *Operam testudina* sp.n. described below.
Compostion: *Operam monita* and *Operam simpla* spp.n. described below. The same locality as the type.

Description: As for the new species.

Derivation of name: *operam* is Latin for attention. Gender feminine.

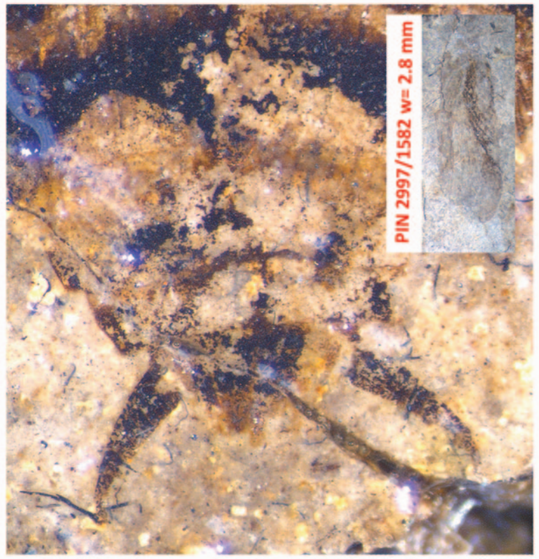
Operam testudina sp.n.

(figps. 390-391)

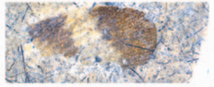
Holotype: PIN 2239/226± (l= 30 mm). The completely articulated winged adult male.
Type locality. Mikhailovka, Karatau, Kazakhstan.
Type horizon. Kimmeridgian Upper Jurassic, Karabastau Formation.

Differential diagnosis: Large species, with forewing longer than 25 mm. Coloration different from *monita* in having uncolored costal area.
Description: Very large cockroach with overall length over 30 mm. Head pale, with longitudinal dark central stripe, very large and wide (8.3 mm), with large round dark eyes (3/ 1 mm). Palps very short. Pronotum 3D, vaulted, dark, with lateral anterior pale areas, possibly without paranotalia (6.3/ 10 mm).
Forewing not reaging body end, with more or less parallel margins, elongate



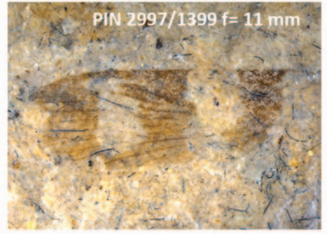


2997/1692 f= 6.5 mm



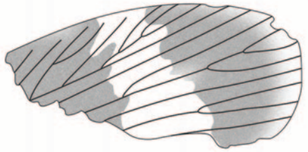


2239/499 f= 10 mm

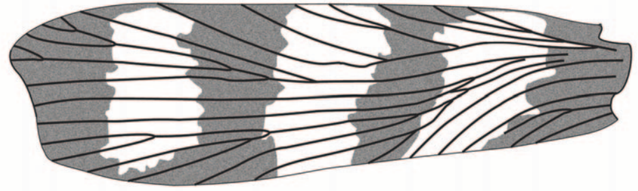




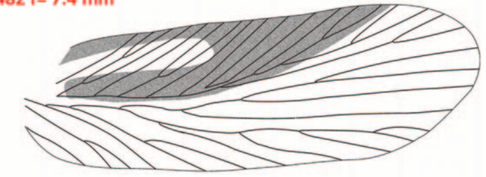
PIN 2997/1692 h= 6.5 mm



PIN 2239/499 f= 10 mm



PIN 2997/1482 f= 7.4 mm



(26/ 3 mm), dark, with pale anterior areas (basal, subbasal and central), hardly sclerotized, veins and intercalaries distinct.
Hindwing overlapping body and much longer than forewings.
Body wide, with unique patterned abdomen. Cerci extremely short (2/ 0.4 mm), oligomerised, with only ca 10 cercomeres.
Derivation of name: *testudine* is a vault in Latin – alluding to the tower-appearing coloration of abdomen.
Character of preservation: 1 completely articulated adult winged male.
Taphonomy: Complete articulation suggest short or even none predepositional transport of otherwise the most commonly preserved forewings. Apparently either a rare species, or normally remotely allochtonous.
Remarks: Aposematism is strongly supported with the abdominal striation, which is distinct. In this respect, obscure are the shortest cerci ever observed on a Mesozoic cockroach, but in the ant-parasitising groups such as *Spinka* Vršanský, Šmídová et Barna in Vršanský et al. (2018).

Operam monita sp.n.
(figps. 390-391)

Holotype: PIN 2239/499 (f= 10 mm; 4.10.6.7.1.7). A completely articulated forewing.
Type locality: Mikhailovka, Karatau, Kazakhstan.
Type horizon: Kimmeridgian Upper Jurassic, Karabastau Formation.

Additional material: PIN 192/2 **G**; 2997/1399, 1692, 4390 (f= 14 mm) (f= ca. 8 mm) (completely articulated forewings). All except G= Galkino from Mikhailovka.

Differential diagnosis: Small species (forewing length= 10-11 mm).
Autapomorphies: Extremely narrowed forewing.
Description: Forewing small and extremely elongated (10-11/ 3.08 mm), with margins parallel nearly for the whole width, costal area is reduced to a short (much shorter than clavus) narrow stripe. Costa distinctly running nearly to apex, colored, rather strong, as strong as other veins. SC as long as clavus, straight, with 3 branches at margin. R sigmoidal, but very short and reduced, with only 4 simple and one dichotiomised (6 in total) veins at margin. M standard, with 9 mosly straight veins at margin widely overlapping apex. CuA also standard, only slightly sigmoidal, with 8 veins at margin, basalmost short branch sharphly descending. CuP fluent, long, A simplified, with 5 veins at margin, one branch is diáchotomised.
Derivation of name: *monita* is Latin for warning.
Character of preservation: 5 completely articulated forewings.
Taphonomy: complete articulation suggest short pre-depositional transport of otherwise the most commonly preserved forewings.
Remarks: The zigzag coloration with direction changing on both veins and intercalaries is extremely rare in Mesozoic cockroaches, and basically is known only in Caloblattinidae PIN 2039/48 from the same site. Thus it is very difficult to estimate meaning of such aberrant coloration pattern. On the one hand it clearly makes an impression of aposematism, one another, the zigzag patten rather indicate a sophisticated crypsis. Nevertheless, strongly modified shape of the wing again suggests aposematism.

Operam simpla sp.n.
(figps. 390-391)

Holotype: PIN 2997/1582 (f= ca. 12 mm; 7.8 mm as preserved). A completely articulated forewing.
Type locality: Mikhailovka, Karatau, Kazakhstan.
Type horizon: Kimmeridgian Upper Jurassic, Karabastau Formation.

Differential diagnosis: Differs in having simpler coloration, but with longitudinal dot in the anterior part.
Autapomorphies: Dot-like coloration.
Description: Forewing small and extremely elongated (ca. 9/ 2.8 mm), with margins parallel nearly for the whole width, costal area is reduced to a short (much shorter than clavus) narrow stripe. Costa distinctly running nearly to apex, colored, rather strong, as strong as other veins. Scshorter than clavus, straight. R slightly sigmoidal, but very short and reduced, with only 12+2 (RS indicated as differentiated) veins at margin. M reduced to 4 mosly straight veins at margin overlapping apex. CuA expanded, slightly sigmoidal, with 7 veins at margin, basalmost short branch dichotomised. CuP fluent, long, A simplified, with 5 veins at margin, anteriormost branch is dichotomised. Coloration possibly forms a stripe and possibly a dot.
Derivation of name: *simpla* is after simple.
Character of preservation: One completely articulated forewing.
Taphonomy: Complete articulation suggest short predepositional transport of otherwise the most commonly preserved forewings. Apparently a rare species.

Superfamily Blattuloidea Vishniakova, 1982 stat.n.

Type genus: *Blattula* Handlirsch, 1906

Stratigraphic range: Hettangian–Maastrichtian
Geographic range: Cosmopolitan

Composition*:* Blattulidae Vishniakova, 1982.

Differential diagnosis: Differs from other cockroach superfamilies, in having simple SC, hindwing CuA without secondary branches, usually simple CuP, female with short externally protruding ovipositor.
Remarks: After it becomes clear that Blattulidae does not belong to Corydioidea, their superfamiliar status becomes necessary. The hindwing is highly congruent within Raphidiomimoidea and specially Liberiblattinidae and differs only in having simple CuA branches. Head is hypognathous, likely a plesiomorphy within order (it is thus pleasiomorphic also within Raphidiomimoidea).

Family Blattulidae Vishniakova, 1982

Type genus: *Blattula* Handlirsch, 1906

Stratigraphic range: Hettangian–Maastrichtian
Geographic range: Cosmopolitan

Composition*:* Vršanský, 2009; Handlirsch, 1906; Vishniakova, 1982; Giebel, 1856; Vršanský, 2009; Wang et al., 2007; Qiu et al., 2019; Vršanský, 2005; Wang et al., 2007; Vršanský, 2008; Anisyutkin et Gorochov, 2008; *Pravdupovediac* Sendi et al., 2023; Vršanský, 2005; Vršanský, 2008; Cifuentes-Ruiz et Vršanský, 2006.

Differential diagnosis: Differs from other corydioid cockroach families, in having simple SC, hindwing CuA without secondary branches, usually simple CuP, female with short externally protruding ovipositor.

Genus *Elisama* Giebel, 1856

Type species: *Blattidium molossus* Westwood, 1854

Composition: *Araripeblatta bolzoni* Mendes et Coelho, 2007*; A. dornellesi* Mendes et Coelho, 2007*; A. oliveirai* Mendes et Coelho, 2007*; A. simplex* Mendes et Coelho, 2007*; A. toledoi* Mendes et Coelho, 2007 (all Crato)*; Cteblattina arcta* Scudder, 1886 (Durlston Bay)*; C. dignata* Wang, 1987 (Yixian)*; Elisama algeriaensis* Vršanský in Vršanský et al. (2021) (Brezina)*; E. brevis* Mendes, 2000 (Crato)*; E. cuboides* Wang et al., 2007*; E. exetenuata* Ren, 1995 (all Yixian)*; E. fragmentaria* Vršanský, 2005 (Sharin-Gol)*; E. globosa* Vršanský in Sendi et al. (2023)(lebanite)*; E. grandis* Vršanský, 2003 (Bon Tsagaan)*; E. hindwingnii* Lee, 2016 (Crato)*; E .incerta* Vršanský, 2003 (Bon Tsagaan)*; E. kneri* Giebel, 1856 (Dinton)*; E. minor* Giebel, 1856 (Purbeck)*; E. parallela* Vršanský, 2003 (Bon Tsagaan)*; E. pterostigmata* Vršanský, 2004 (Shar-Teg)*; E. scudderi* Handlirsch, 1906 (Durlston Bay)*; E. tsaganica* Vršanský, 1999 (Bon Tsagaan)

Stratigraphic range: Late Jurassic (Kimmeridgian) – Upper Cretaceous (Campanian)
Geographic range: Laurasia and Gondwana, cosmpolitan

Diagnosis (after Sendi et al. 2023b): Small sized cockroaches with wide head, three ocelli residing in the forehead between the compound eyes; short palps; pronotum transverse, oval, simple-shaped; forewings with small posterior macula near clavus; females with short convex ovipositor; male terminalia with styli.

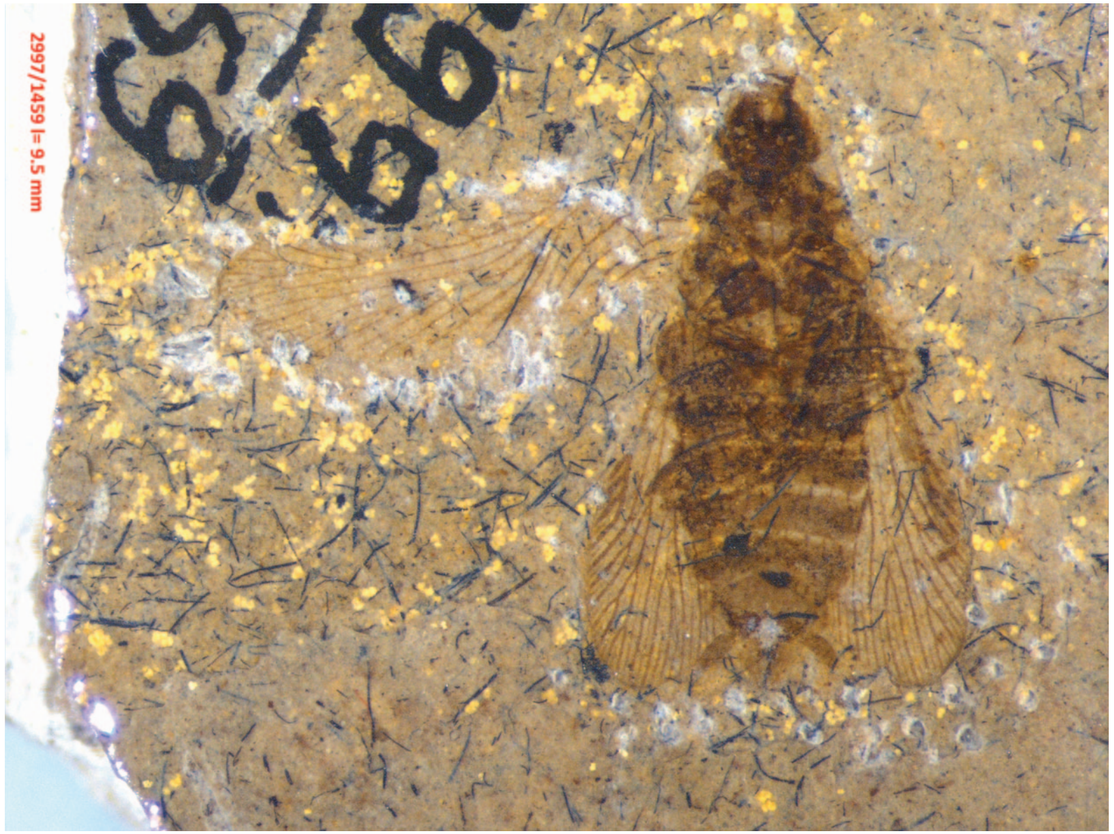
Elisama prelistama sp.n.

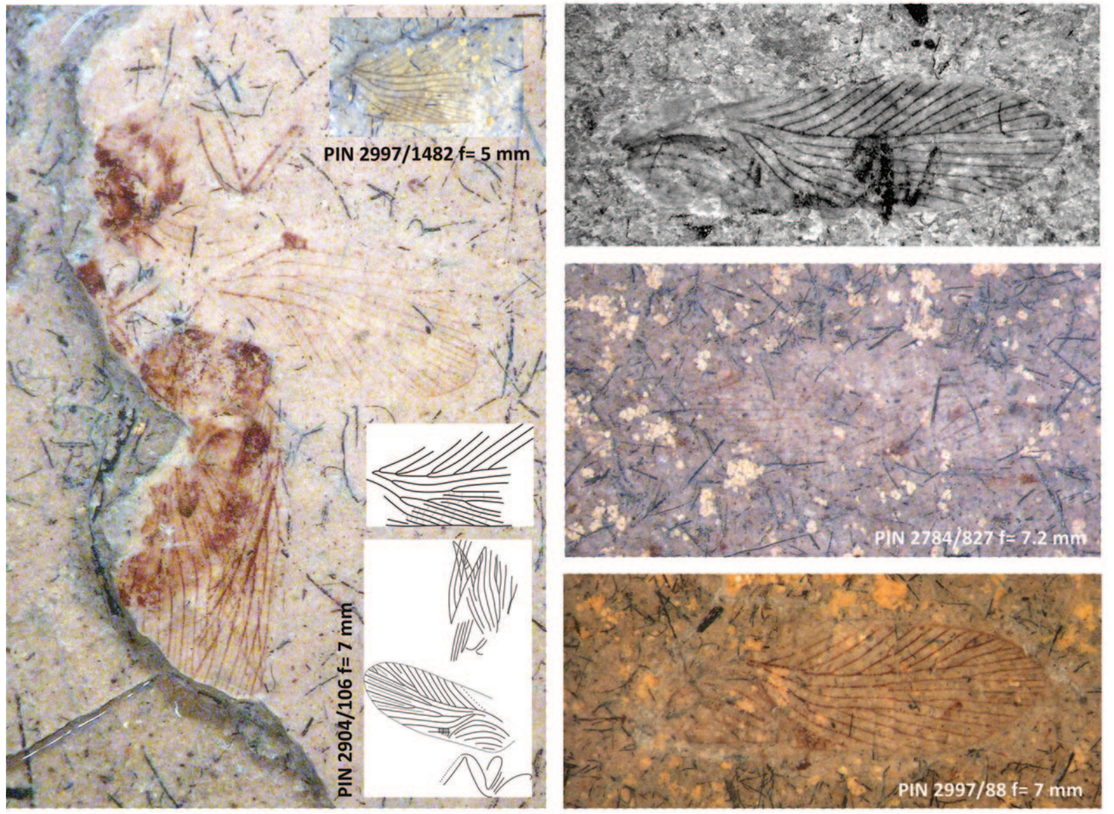
(figps. 396-397)

Holotype: PIN 2997/1459. A completely articulated winged adult male individual (9.5 mm total length).
Type locality: Mikhailovka, Karatau, Kazakhstan.
Type horizon: Kimmeridgian Upper Jurassic, Karabastau Formation.

Additional material: PIN 2904/106 (f= 6.2/1.8 mm; 1.13.2.5.1.5) (completely articulated winged adult); 2784/827 (f= 7.2 mm; 1, 13, 3, 7, 1, 5); 2904/131 (f= 7.3/2.4 mm; 1.11.4.5.1.6); 2997/88 (f= 7.8/2.4 mm; 1.14.5.6.1.6); 1482 (forewings). The same locality as the type.

Differential diagnosis: Differs from all representatives of the genus in having less developed forewing dark macula and in straight hindwing veins with dichotomised CuA.
Autapomorphy: Macula might be regarded for autapomorphy, later retained in more or less direct descendants.
Description: Head hypogranthous, rather small (1.8/ 1.7 mm), dark, possibly with short wide central pale stripe and possibly also with pale eyes. Pronotum with two wide longitudinal stripes.
Forewing 6.2-7.8 (but possibly up to 10 mm) long and 1.8-2.4 mm wide, with parallel margins, apex slightly sharpened, posed slightly anteriorly. Main veins dark, brobably brown, intercalaries pale (present but indistinct). Sc simple, long, reaching a third of the length of the wing, slightly sigmoidal, costal area narrow. R regular, with 11-14 vein at margin, RS not differentiated. M simplified to 2-5 veins at margin, straight; CuA with 5-7 veins at margin. CuP simple, standard. A simple (5-6). Dark macula is present in basal CuA area near margin.
Hindwing with dark probably brown veins and pale, indistinct intercalaries. Sc simple long, R1 and RS differentiated (3-4+7); M with 3 veins; CuA rich (5-6), with branches long, nearly straight and ocassionally (asymmetrically) secondarily dichotomised, CuP simple.
Body 3.2 mm wide and rather short. Cercus short, multisegmented, ca. 0.21 mm wide.
Legs with all three femora robuist (ca. 1.1/0.5; 1.8/0.6; 2.5/0.9), without striated coloration, pale only with longitudinal dark stripes.
Character of preservation: two complete specimens, 4 complete forewings.
Taphonomy: Two completely articulated specimens (one with whole cerci) suggest no or short pre-depositional transport. This genus and species was apparenly rare in the assemblage and probably also in the sopurce ecosystems (and generally in the Jurassic – this is characteristic and nearly exclusively Cretaceous taxon).
Systematical remarks: The new species shows a close relation to most common


2997/1459 l= 9.5 mm


PIN 2997/1482 f= 5 mm
PIN 2904/106 f= 7 mm
PIN 2784/827 f= 7.2 mm
PIN 2997/88 f= 7 mm

Blattula, which nevertheless, also have distinct intercalaries. Closely related is also specialised *Vrtula* Vršanský, 2008. Kridla Vršanský, 2005, *Habroblattula* Wang et al. 2007, *Huablattula* Qiu et al. 2019, *Macaroblattula* Wang et al. 2007, *Ocelloblattula* Anisyutkin et Gorochov 2008, *Svabula* Vršanský, 2005= *Huablattula* Qiu et al. 2019 and *Batola* Vršanský, 2009 differ in more extensive coloration. *Xonpepetla* Cifuentes-Ruiz et Vršanský in Cifuentes-Ruiz et al. (2006), *Orbablattula* Martínez-Delclòs 1993 and *Nannoblattula* Handlirsch, 1906 lacks coloration (except apex) and was more wide wings. *Globula* Vršanský, 2009, *Blattulites* Vishniakova, 1982, and *Nula* Vršanský, 2008 cannot be compared due to presence of immatures only.

Derivation of name: Stochastical combination of letters, partially alluding to прелест (Russian for charm) and also „pre"-relation.

Genus *Blattula* Handlirsch, 1906

Type species: *Blattina langfeldti* Geinitz, 1880, p. 521; subsequent designation by Handlirsch (1906). *Blattina dobbertinensis* Geinitz, 1884 (designated by Becker-Migdisova 1962: 103) is now considered a junior synonym of *Blattula langfeldti* (Geinitz, 1880). Dobbertin, Germany, Lower Jurassic

Stratigraphic range: Hettangian–Maastrichtian

Geographic range: Cosmopolitan

Composition*: Blattula aberrans* Vishniakova, 1982, Kubekovo, Russia, Middle Jurassic; *B. anuniversala* Vršanský, 2020, Bakhar, Mongolia, Middle Jurassic; *B. bacharensis* Vršanský, 2020, Bakhar, Mongolia, Middle Jurassic; *B. brevicaudata* Vishniakova, 1968, Karatau-Mikhailovka, Kazachstan, Jurassic; *B. ctinoida* Lin, 1986, Quiyang, Hunan, Lower Jurassic; *B. choutinensis* Vršanský, 2008, Houtiyn-Hotgor, Mongolia, Upper Jurassic; *B. delicatula* Ren, Lu et Guo, 1995, Gaositai railway station, Hebei Province, China, Upper Jurassic; *B. disjuncta* Handlirsch, 1906-1908, Wiltshire, England, UK, Jurassic/Cretaceous; *B. dubia* Handlirsch, 1939, Mecklenburg, Germany, Lower Jurassic; *B. exetenuata* Ren, 1995, Gaositai railway station, Hebei Province, China, Upper Jurassic; *B. extensa* Vishniakova, 1982, Iya River, Russia, Lower Jurassic; *B. flamma* Vršanský, 2020, Bakhar, Mongolia, Middle Jurassic; *B. hymena* Lin, 1986, South China *B. iensis* Vishniakova, 1982, Iya River, Russia, Lower Jurassic; *B. incompleta* Handlirsch, 1906–1908, Stensham, England, UK, Upper Triassic; *B. kellos* Zhang, 1986, N. Hebei, China, Jurassic; *B. lanceolata* Vishniakova, 1982, Novospasskoye village, Middle Jurassic; *B. liaoningensis* Hong, 1986, Beipiao, Liaoning, Middle Jurassic; *B. micro* Vršanský, 2020, Bakhar, Mongolia, Middle Jurassic; *B. mini* Vršanský, 2020, Bakhar, Mongolia, Middle Jurassic; *B. mongolica* Vršanský, 2004, Shar-Teg, Mongolia, Upper Jurassic; *B. pachohymena* Lin, 1985, South China, Zhongshan, Guangxi, Lower Jurassic; *B. platypa* Ren, Lu et Guo, 1995, Gaositai railway station, Hebei Province, China, Upper Jurassic; *B. prestwichii* Handlirsch, 1906-1908, England, UK, Jurassic/Cretaceous; *B. rudis* Ren, Lu et Guo, 1995, Qinglongtou village, China, Lower Jurassic; *B. similis* Vishniakova, 1982, Iya River, Siberia, Russia, Lower Jurassic; *B. universala* Vršanský, 2020, Bakhar, Mongolia, Middle Jurassic; *B. vidlickai* Vršanský, 2004, Shar-Teg, Mongolia, Upper Jurassic; *B. wilmotti* Martin, 2010, Mintaja, Western Australia, Lower Jurassic; *B. zaoshangensis* Lin, 1986, South China.

Differential diagnosis (after Vršanský and Ansorge 2007): *Blattula* is very similar in wing venation to the mainly Lower Cretaceous *Elisama* Giebel, 1856. The most striking difference is a dark macula in *Elisama* forewings.

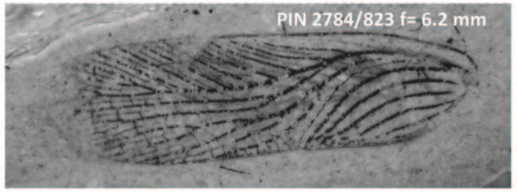
Blattula gracilicosta sp.n.

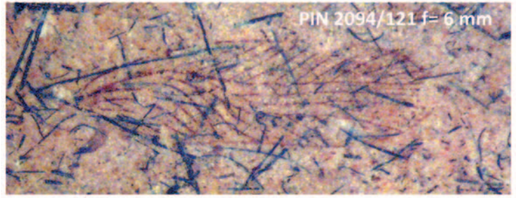
(figp. 399)

Holotype: PIN 2784/823 f= 6.2 mm; 1, 12, 3, 5, 1, 6. A completely articulated (with clavus) forewing.

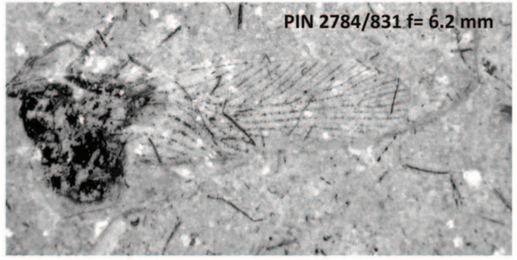
Type locality: Mikhailovka, Karatau, Kazakhstan

Type horizon: Upper Jurassic Karabastau Formation





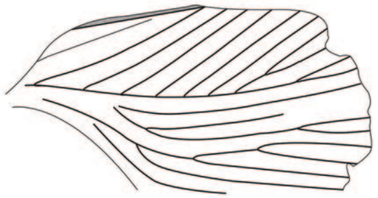






Blattula gracilicosta







Additional material: PIN 2066/491 (complete specimen); PIN 2384/174 f= 6 mm; 1, 11, 2, 5, 1, 6; 2452/544 f= 5.8 mm; 1, 10, 4, 4, 1; 2784/828 f= 7 mm; 1, 12+, 4, 5, 1, 5; 831 f= 6.2 mm; 1, 12, 3, 5, 1, 6; 2904/121 f= 6/1.5mm; 1, 12, 4, 7, 1, 4; 2997/757 f= 6 mm; 1, 16, 3, 6, 1 (isolated forewing, one with articulation); 2384/170 h= 6 mm; 1, 4+5, 3, 6+1; 1, 4+6, 3, 6+1; 182 h= 6 mm; 2997/759 h= 6 mm; 1, 5+6, 3, 5+1, 6A2; 4331 h= 5.5 mm (isolated hindwings). The same locality as the type.

Differential diagnosis: Differs from all representatives of the genus in having extremely narrow forewing costal field, totally prallel margins up to the base of the wing (specific costal area).
Autapomorphy: Narrow forewing costal area
Description: Veins wide. Forewing with parallel margins, and slightly sharpened apex posed centrally, 6-7 mm long. Sc simple, costal field extremely narrow. R after basal sigmoidal curving nearly straight, with 11-13 at the margin. M restricted to nearly straight 2-4 veins at margin. CuA more or less standard, with 5-7 veins at margin, CuP curved sharply anteriorly, with slight indication of posterior curving at the wing margin. 5-6 simple anal veins present.
Hindwing with extremely wide radial veins and distinct pterostigma. Hindwing length 5.5-6 mm. Sc simple, R with 4-5+6 veins at margin. M conservatively with 3 veins. CuA with 5-6 veins at margin, CuP simple. A2 unusually (PIN 2997/859) with 2 secondarily dichotomised branches.
Systematical remarks: It is impossible to establish relation of this species, as it has a standart general morphology (except for narrow costal area) combined with very wide veins. It cannot be excluded that this taxon derived from the most comon species originating directly at the site.
Derivation of name: After costal area and *gracilis* (Latin for narrow).
Preservation state: One nearly completely articulated specimen (unpreserved parts of the body resulted from the collecting; 1 forewing with parts of the attached body, 6 complete forewings, 4 hindwings.
Taphonomy: Standard ratio of forewings to hindwings combined with articulated specimen indicate short if any pre-depositional transport.

Blattula fragilia sp.n.

(figp. 400)

Holotype: PIN 2904/130 f= 13/4 mm; 1, 10, 5, 5, 1.
Type locality: Mikhailovka, Karatau, Kazakhstan
Type horizon: Upper Jurassic Karabastau Formation

Additional material: PIN 2066/292 f= 13 mm; 2904/95 (ffhh), 1875 (ffhh) (complete specimens); 2066/159 f= 11-13mm; 191 f= 13 mm; 1, 7+4+, 2+; 389=410; 2784/646 f= 12 mm; 1, 13, 6, 7, 1, 5; 964 f= 12.5 mm (isolated forewings, one with pronotum); PIN 2554/53 (isolated hindwing). The same locality as the type.

Differential diagnosis. Differs from most representatives of the genus and family in being large, from *Blattula mongolica* Vršanský, 2004 and *Blattula zaoshangensis* Lin, 1986 of a comparable size differs in expanded CuA reaching apex. *Blattula velika* Vršanský, 2020,
Blattula kiensis Martynov, 1937 and *Blattula liaoningensis* Hong, 1986 are larger and except *B. velika* also with comparatively reduced CuA (14-15 mm).
Autapomorphy: strongly sclerotised costa
Description. Very large (within family) representative with forewing length ca. 13 mm. Head with two dark stripes. Forewing margins are not entirely parallel. Sc simple, comparatively short, approximately reaching the level of clavus, which is ca. One third of the length of the wing. R with 10-13 branches at margin, RS is not differentiated. M is not sigmoidal, with 4-6 veins at the margin; CuA reaches or nearly reaches apex with 5-7 veins at margin. CuP sharphly curved, 5 simple A present. Hindwing transparent, long, with distinct intercalaries.
Systematical remarks. The species belong to the genus *Blattula* due to absence of coloration and characteristic simplified ve-

nation. Fragmentary material disallows tracing of phylogenetical relations within the genus. It is simply (possibly phenetically only) similar to large representatives of the genus. It is nearly indiscernible from the Eearly Cretaceous *B. mongolica* from Shar-Teg in Mongolia. Differing CuA can be an individually-variating character. This is apparently a separate lineage within the genus.

Derivation of name. After *fragilii* (Latin for fragile).

Preservation state. 1 partially disarticulated specimen with head and pronotum, 6 fragmentary forewings, 1 fragmentary hindwing, 2 both forewings with hindwings.

Taphonomy. Presence of fragmentary and disarticulated specimens might indicate some transport prior to deposition. Due to presence of 3 partially articulated specimens this transport was probably not significant and fragmetary nature of preservation might be caused with the fragility of the species. Fragility is indicated with transparent membrane, thin sporadic veins and weak intercalaries.

Blattula summa sp.n.

(figp. 403)

Holotype: PIN 2904/107 8.5/ 2 mm; 1, 14 (4 RS), 3, 5, 1. Disarticulated forewing without clavus.

Type locality: Mikhailovka, Karatau, Kazakhstan

Type horizon: Upper Jurassic Karabastau Formation

Additional material: PIN 2452/107 (complete specimen hhb); 2066/400± f= 8 mm; 2904/175 f= 8.6 mm; 2452/57 (f= 7.8 mm; 1, 13, 3, 6, 1), 603, 629 (isolated forewings); 2452/338 (isolated hindwings). The same locality as the type.

Differential diagnosis. Differs from all representatives of the genus in being extremely elongate with narrow forewing. *B. brevicaudata* is additionally smaller.

Autapomorphy: extreme elongation

Desription: Extremely elongate forewing (7.8-8.5/2 mm), with high degree of parallelity among wing margins. Costal field narrow, SC as long as clavus (also very long), nearly straight, simple. R strongly sigmoidal, wtih 13-14 veins at margin. M greatly simplified, curved, with only 3 veins meeting margin. CuA standard, long, with 5-6 veins at margin. CuP is elongate, sharphly curved anteriorly, without terminal curvature at the margin meeting point. Coloration present on SC/R base and in apex, where IC are traceable.

Remarks: Well visible coloration on wing basis suggest really low degree of coloration of the membrane except apex (where cross-veins are distinct).

Systematical remarks: Little diagnostic characters are preseerved except for the elongation. It cannot be excluded the taxon derived directly from *B. brevicaudata* or its earlier predecessor/ equivalent. Sigmoidal R is surprising in such a narorow wing.

Derivation of name: After *summa* (Latin for extreme) – alluding to extreme elongation.

Character of preservation: One complete articulated specimen, 6 isolated forewings, 1 two hindwings.

Taphonomy: complete specimen and articulated hiondwings suggest short transport, although forewing without clavus (type) suggest rather moderate to long transportration prior to deposition.

Blattula ahanaha sp.n.

(figp. 404-405)

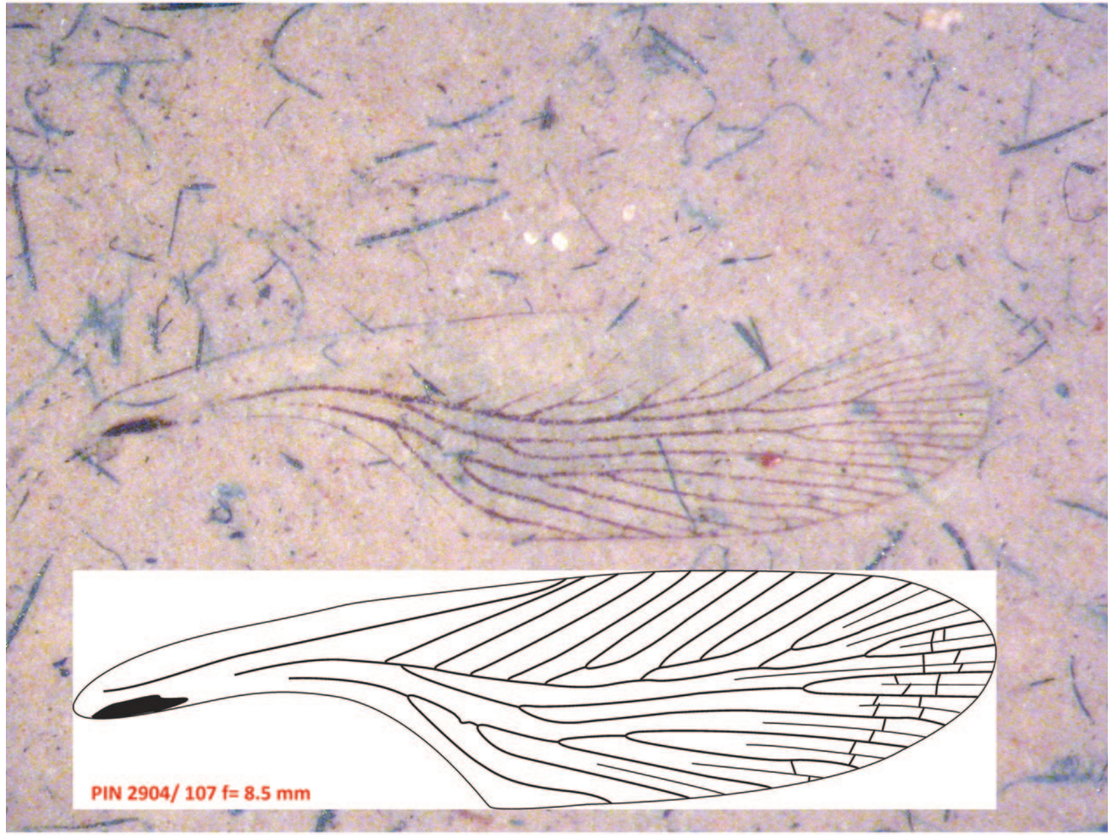
Holotype: PIN 2554/13. A complete adult female.

Type locality: Mikhailovka, Karatau, Kazakhstan

Type horizon: Upper Jurassic Karabastau Formation

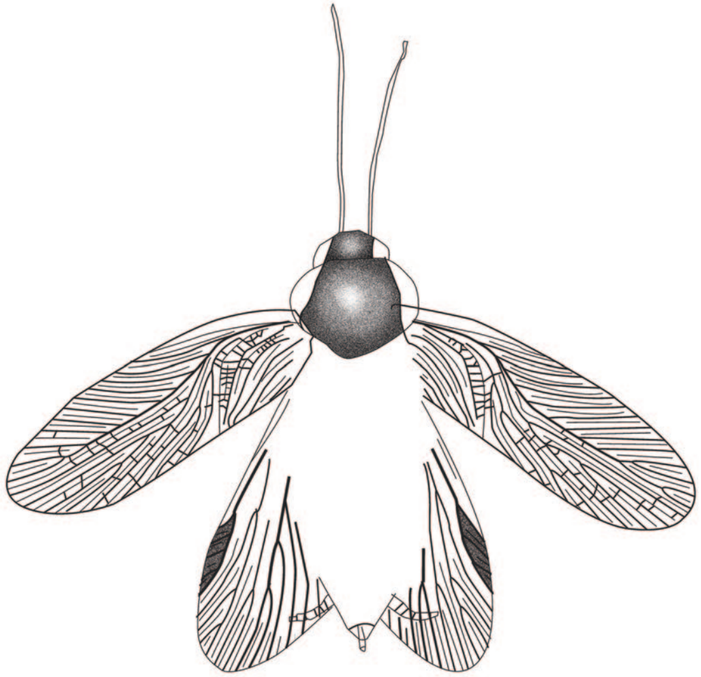
Additional material: PIN 2784/751 (hh); 2904/47; 2997/93 (complete hindwings). All the same locality as the type.

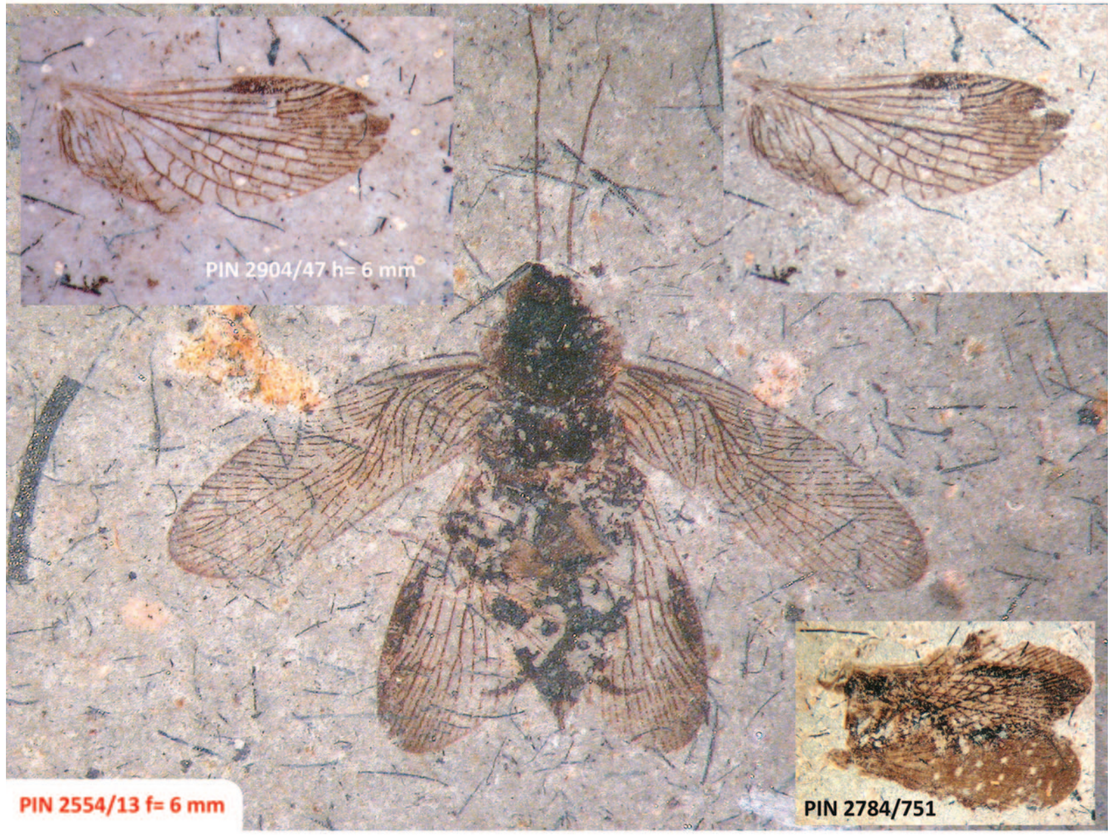
Differential diagnosis: Differs from *B. extensa* (Toarcian of Iya; forewing length 4.0 mm) and from *B. microscopica, B. extensa, B. disjuncta, B. dubia, B. vidlickai* and *B. willmotti* in being larger and from all other representatives of the genus in being



Blattula summa

PIN 2554/13 f= 6 mm





much smaller. Similar size group are only *Blattula prestwichii* (Scudder, 1886) (Berriasian of Purbeck, FW length 6.5 mm; differs in longer basal wing area) and *Blattula turanica* Martynov, 1937 (Pliensbachian of Kyzyl-Kiya, 6.7 mm; differs in having longer basal area - clavus). *B. rectinervosa* differs in not having developed HW pterostigma and in not having completely dark pronotum.

Autapomorphy: Very dark species (including head) with distinct veins and pterostigma

Description: Moderately small blattulid cockroach. Head globular, ca. 1.2 mm wide, dark (probably black) with large globular more pale eyes (probably pale brown).Antenna filiform, short, about 5 mm long and 0.1 mm wide.

Pronotum nearly round, slightly transverse (1.8/ 2.2 mm) and with posterior central extension, dark (probably black) with slightly more pale (probably dark brown) margins.

Body wide (3.1 mm), strongly sclerotized, with triangular subanal plate with narrow short externally protruding ovipositor. Cerci long, oligomerised, strongly sclerotized, with ca. 8 cercomeres.

Forewings elongate (6/ 1.8 mm) with narrow costal area, veins (black) and intercalaries (dark brown) heavily sclerotized and colored, membrane transparent but due to heavy coloration of wide veins, habitus is dark. Sc short, wide and simple; R strongly sigmoidal, with strong stem and 12-13 mostly simple veins at the margin (only the posteriormost 1 or 2 veins are dichotomised into 4 veins – RS indication). M simplified with 4-5 veins but strong stem; CuA with 3 veins at margin. CuP sharply curved, simple. A simple (5), with reticulations supporting the dark habiutus. Hindwing shorter (5.7 mm) than forewing (both terminate at the same level beyond the abdomen) and with distinct pterostigma covering R1. Cross-veins strong, present in apical part and whole cubital area. Veins strong, dark, black, M and intercalaries dark brown. Sc long, straight, simple. R1 and RS differentiated (3-4+4); M simplified with 2 veins at margin. CuA with 5 branches, CuP simple.A1 simple, with 4 blind branches; A2 richly branched (4), with 2 stems); A3 and A4 also dichotomised. Pleating not weer-like.

Remarks: Hindwings are attributed to this species on the basis of identical size and presence of pterostigma.

Systematical remarks: As this size cohort is undocumented in Middle-Upper Jurassic, it is improbable that this cohort parallelly coexisted. Most probably these species (also *B. rectinervosa*) originated from some of the larger representatives, as no traces of miniaturisation were observed. Similar larger species with pterostigma occurs also in the site (*B. gracilicosta, B. druha*), which differs in more sophisticated pronotum coloration. As in the case of the former, *B. ahanaha* seems derived directly fromn *B. rectinervosa* as it is more colored inlcuding completely dark head and pronotum, characters unusual in *Blattula*.

Ecological remarks. It is notable that this size cohort is absent in most of the described Jurassic and Cretaceous sites, because it is very common in the Karatau (153 specimens of *B. rectinervosa*) and also in Bakhar in Mongolia (*B. flamma* Vršanský, 2020 and *B. bacharensis* Vršanský, 2020, 16/ 1,182 specimens). Due to hard sclerotisation and dark coloration with pale eyes it can be hypotethised that this species was nocturnal.

Derivation of name: *ahanaha* is a palyndrome with (Slovak) meaning *ecce nuda*.

Character of preservation: 1 complete specimen with disarticulated legs and palps but articulated antenna; 4 isolated hindwings on 3 specimens.

Taphonomy: Completely articulated specimen might suggest a short transport prior to deposition. This is supported with only 2 preserved hindwings. Very probably, additional also few (2-4) forewings are hidden unrecognised among forewings or *B. rectinervosa*.

Blattula rectinervosa Vishniakova, 1971

(figps. 408-413)

Holotype: PIN 2239/106. A completely articulated winged adult male. Designated by V.N. Vishniakova (1971).

Type locality: Karatau, Kazakhstan

Type horizon: Upper Jurassic Karabastau Formation

Additional material designated by V.N. Vishniakova (1971): PIN 2066/557, 2239/113 (complete specimens).

Addditional material designated here: PIN 2066/73± (F= 5.2 mm), 172 (l= 6.5 mm), 174 (l= 6.3 mm), 316, 394, 432, 474, 511±; 2384/192; 2554/56, 61, 66, 69, 70, 79-2; 2784/799, 817, 897, 909, 916, 1006; 2904/92, 97, 115, 116 (with palps), 1905; 2997/26, 146, 248±, 414, 651, 1460, 1498, 4297 (completely articulated specimens); 1789/79 **G**; 2066/19 (f= 6 mm), 49, 72 (f= 6 mm), 166 (f= 5 mm), 276± (f= 6 mm), 277±, 356, 358; 2239/56, 89; 2384/174; 2554/48, 62; 2784/680 (f= 6.8 mm), 716-2, 719, 840, 866, 876, 955, 961, 973, 2273; 2904/567; 2997/19, 183, 252, 1461, 1510, 1517-2, 1525, 1526, 1528, 1529, 1530, 1533 (isolated forewings); 167/105 **G OBNAZHENIE 1**, 294 **G**, 310 **G**; 1789/53 **G**, 68 **G**; 2066/53 (h= 6 mm), 176, 194 (h= 6 mm), 208 (h= 5.7 mm), 339, 341, 466, 468, 490; 2239/268; 2384/170, 182, 184 (*fusion), 950; 2554/72 (*fusion), 76, 92; 2784/734, 2271; 2784/660; 2904/26, 47, 98 (h= 6.3 mm), 123, 124 (h= 6.5 mm), 125; 2997/23 (h= 5. 8 mm), 80, 200, 211, 410, 413, 415, 1306, 1365, 1442±, 1478, 1480 (hh),1494, 1496, 1499, 1504, 1531, 1542 (isolated hindwings); 2066/69, 112 (l= 5.5; w= 1.4 mm), 372 (w= 1.3 mm), 452± (w= 1.4 mm), 482± (w= 1 mm), 499 (l= 4 mm); 2784/132 (l= 2 mm), 681 (l= 4.2 mm), 683 (l= 3 mm), 685 (w= 2 mm), 698 (l= 4.2 mm; w= 1.7 mm), 765 (l= 2.8 mm; w= 1.3 mm), 829 (l= 3.7 mm; w= 1.3 mm), 853 (w= 1.4 mm) , 861 (l= 4.1 mm; w= 1.5 mm), 862 (l= 2.7 mm; w= 1.3 mm); 863 (w= 0.7 mm), 865 (w= 1 mm), 867 (w= 1.7 mm), 869 (w= 1.4 mm), 875 (w= 1.5 mm), 887 (l= 2.3 mm), 894 (w= 1.5 mm), 942 (l= 3.1 mm; w= 1.4 mm), 949 (l= 3 mm), 1009 (w= 2.3 mm) , 1012 (w= 2.8 mm) , 1013 (w= 1.4 mm), 8583 (l= 2.6 mm) (larvae). All except G= Galkino from Mikhailovka.

Differential diagnosis (after Vishniakova, 1971): Differs from *B. brevicaudata* by more straight R, M and CuA, form of terminalia and by shorted forewings, from *B. langfeldti* venation of R and M and from all others in shorter RS.

Redescription (emended diagnosis from Vishniakova, 1971): Head wide, globular, without typical stripes, partially protruding beyond the comparatively small pronotum. Antenna thin and very long, with segments not wide, as long as body (longest preserved fragment 5 mm long). Palp very short, 4-segmented, only as long as width of head.

Pronotum transverse (2.3/ 2.6 mm), with short posterior central extension, coloration with two dark stripes.

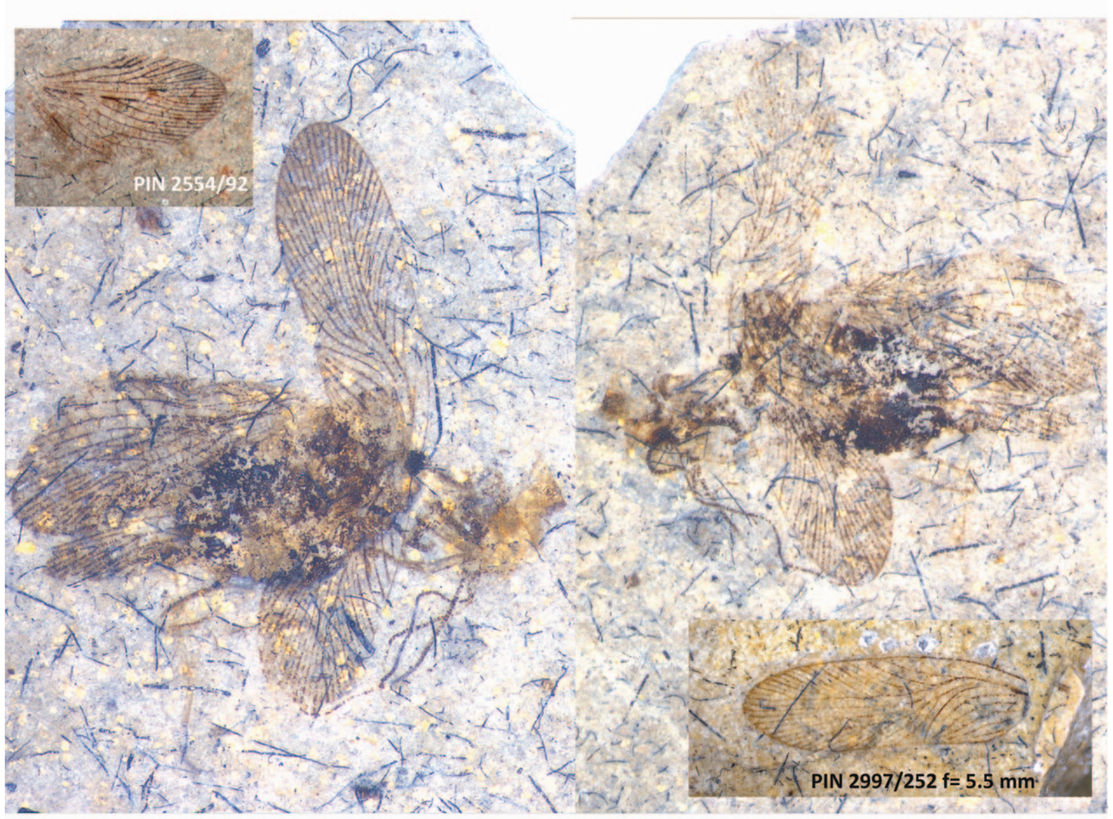
Forewing elongate 5.3-6.3/ 1.76-2 mm, membrane transparent, veins dark, intercalaries more pale, cross-veins distinct. Costa narrow but distinct and sclerotised, overlappin whole wing, costal area narrow. Sc simple, reaching third of the wing length. R stem very wide and strongly sigmoidal, RS is usually distinctly differentiated (R+RS= 9-15), M comparatively strongly sigmoidal, with 2-5 veins at margin. CuA short, with 4-7 veins at margin. CuP simple, clavus sharply curved anteriorly, without apical curvature. 4-6 simple A present.

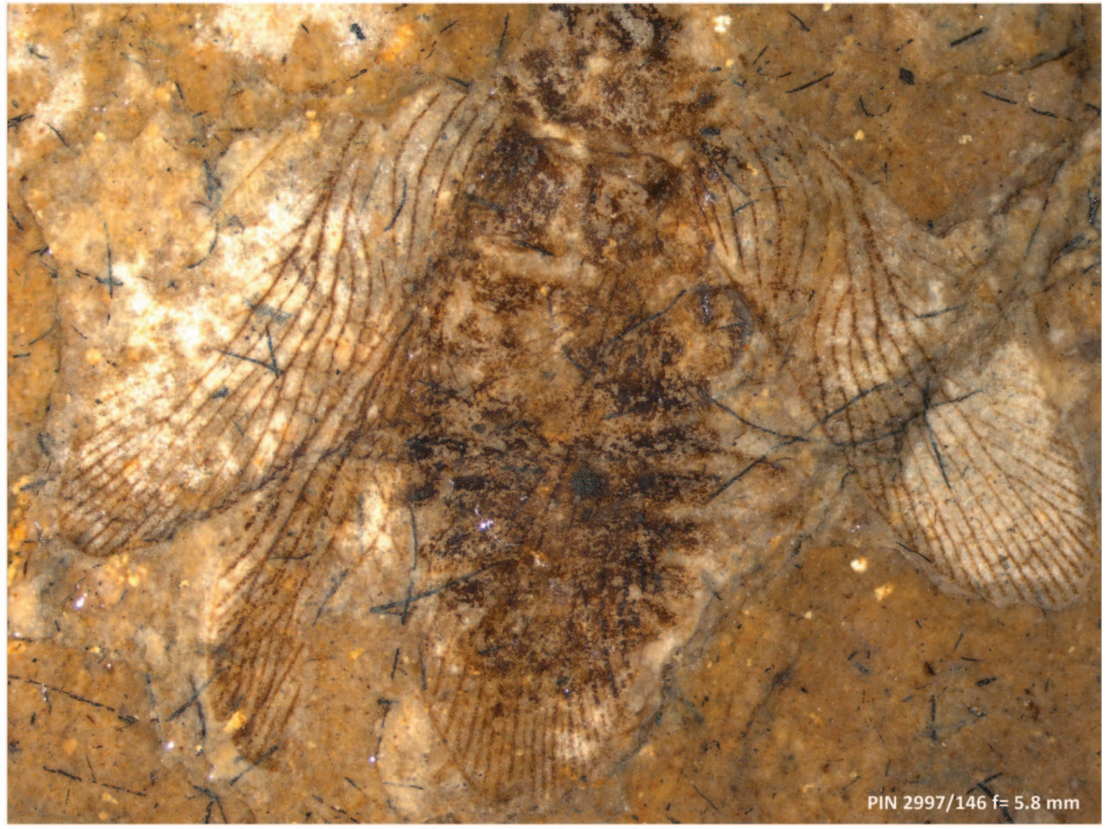
Hindwing 5.5-6.5 mm long, apex slightly sharpened, pterostigma absent. Sc simple, R1 (3-6) and RS (3-8) differentiated. M simplified into 2-4 veins at margin. CuA with 4-7 simple branches, CuP simple, rarely simply dichotomised. Apex sometimes colored.

Body fat, wide, cerci preserved short-type, multisegmented, with up to 13 cercomeres, dark, possibly with pale „stripes“. Female Ovipositor short-type, protruding as a moderately long narrow tube.

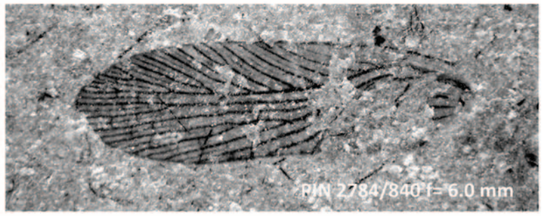
Character of preservation: 37 articulated specimens, 37 isolated forewings, 49 isolated hindwings, 30 larvae.

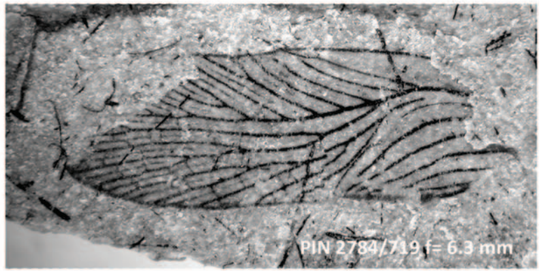
Taphonomy: In this particular case, when the (extremely high) number of spe-

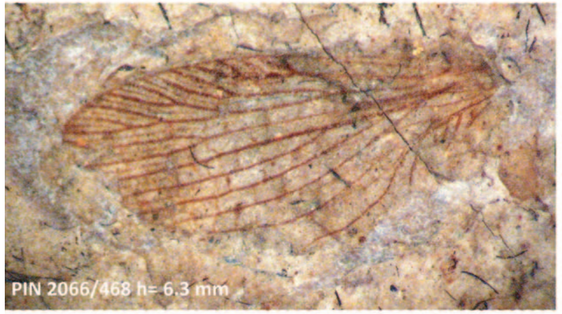

PIN 2554/92
PIN 2997/252 f= 5.5 mm


PIN 2997/146 f= 5.8 mm

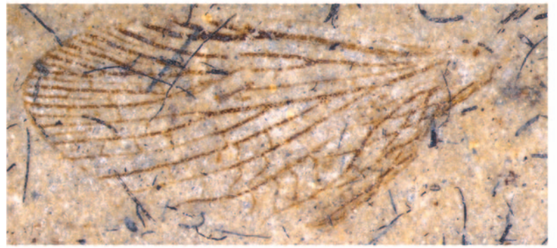

PIN 2239 f= 6 mm

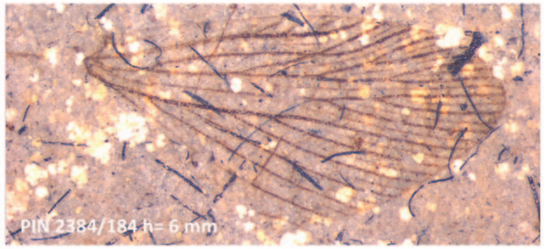

PIN 2784/840 f= 6.0 mm

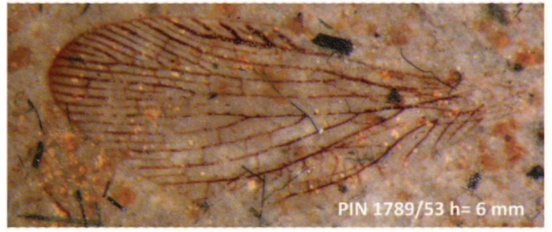

PIN 2784/719 f= 6.3 mm

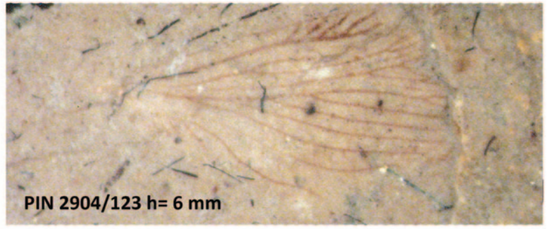

PIN 2066/468 h= 6.3 mm

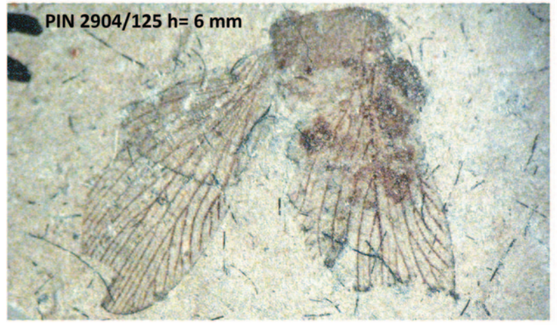

2904/51

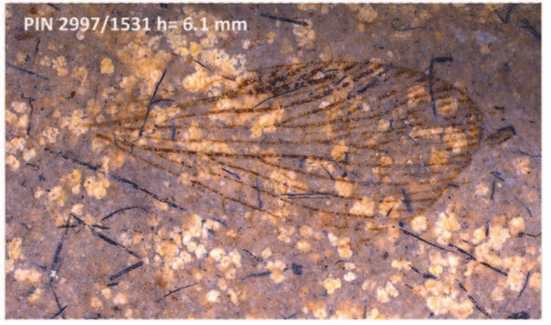



PIN 2384/184 h= 6 mm

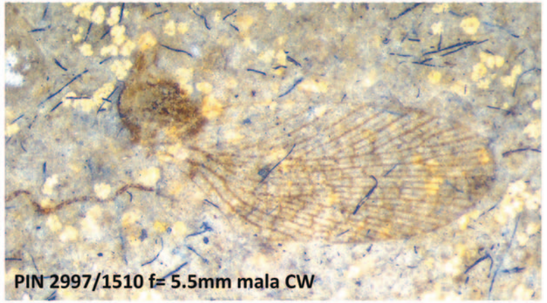

PIN 1789/53 h= 6 mm


PIN 2904/123 h= 6 mm


PIN 2904/125 h= 6 mm

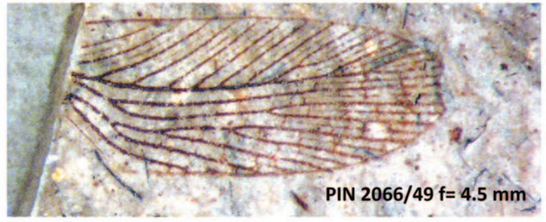

PIN 2997/1531 h= 6.1 mm

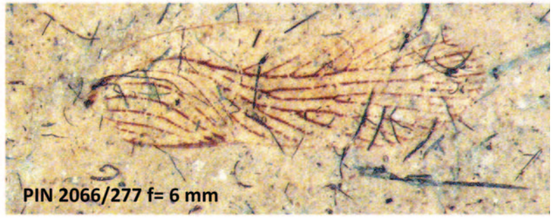


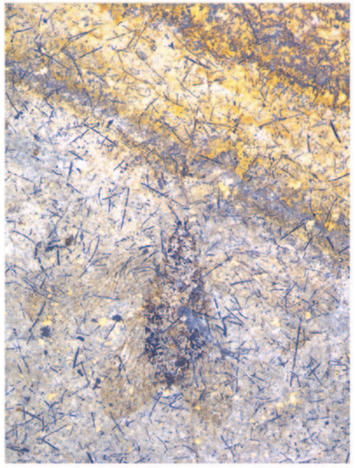






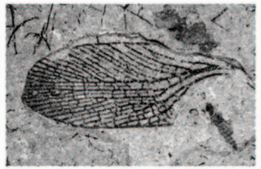






PIN 2984/651 f= 5.8 mm







cimens is balanced with number of isolated fore- and hindwings, it might be speculated that this species is performing mass flights as in the case of living *Ectobius sylvestris* in moderate zone forests. This inference has a support with a very similar situation in numerous Jurassic and Cretaceous localities evidencing source area near the source waterbody. It must be additionally stressed that this cosmopolitan and pan-Mesozoic eudominant genus is basically absent in amber record. Furthermore such periodical ocurrence might provide some support for frequent parallel ocurrence of numerous species within this genus. Additionally this hypothesis might be explanatory to extremely low variability of this species (see below). Interesting is also higher content of hindwings, which must be evaluated in the context of taphonomy of other cockroaches at the site. Collection bias might not be definitely excluded in this representative collection as hindwings of this genus are specially conspicuous and thus easily noticeable during collection. Numerous putative immature individuals suggest also habits near water. Looking at their size distributions it intuitively seems there are three individuals of the first instar stage, 6+8 of the following two stages and rare stages 4-7, which is a standard distribution of dominant cockrapoch species in the sedimentary record wtih rare ocurrence of the first fragile stage.

Variability: Standard (see Vršanský 2000), but values from total number of veins meeting margin are extremely low for forewings (7.8 % and only 5.5 % including A which is disrupting taking into consideration significant difference among these two numbers, which are usually near-identical) and standard for a hindwing without A (9.62 %). This is apparenly related to very small (and strictly conservative) size and strict aerodynamical control. It is important that this sample size (n= 35 for hindwings) is statistically significant and also that usually variability is counter-intuitively higher for the hindwing, which bears a more aerodynamical load, but perhaps can control strength of veins.

Deformities: Three deformities are present among 114 winged specimens (containing more wings), which is 2.63 %. Deformed is one forewing (PIN 1789/79 **G**) and two hindwings (PIN 2384/184; 2554/72). Deformities influenced forewing Anal and hindwing RS1-RS2 systems. Low deformity ratio supports strict vein control.

specimen forewings	l	w	Sc	R	M	CuA	CuP	A	RM	RCuA	MCuA	Total	with A
2784/ 973	6		1	11	3	5	1		14	16	8	21	
2066/277±	6		1	11	4	6	1	5	15	18	10	23	28
1789/79	5.6		1	10	4	4	1	5	14	17	8	20	25
2784/840	6		1	15	3	5	1	5	18	20	8	25	30
2784/719	6.3		1	12	5	5	1	5	17	17	10	24	29
(*)2784/866f			1	14	5	6	1		19	20	9	27	
(*)2239/56	5.8		1	9	4	5	1	6	13	14	9	20	26
(*)2384/192	6		1	13	2	6	1	6	15	19	8	23	29
6*2997/146 R	5.8		1	9	3	6	1	5	12	15	9	20	25
6*2997/146 L:	5.8		1	13	3	5	1	5	16	18	8	23	28
(*)2904/92	6		1	13	2	5	1	6	15	18	7	22	28
6* 2904/116	6	2	1	13	3	6	1	6	16	19	9	24	30
6* 2997/26 L	5.9		1	13	3	5	1	6	16	18	8	23	29
(*)2784/897			1	11	4	5	1	5	15	16	9	22	27
2784/716-2 f			1	13	3	5	1	5	16	18	8	23	28
2997/252	5.5		1	10	3	6	1	5	13	16	9	21	26
2997/1510	5.5		1	9	4	6	1		13	15	10	21	
2239/106	6		1	13	4	6	1	5	17	19	10	25	30
2239/ unnumbered	6		1	13	3	7	1		16	20	10	25	
5-6*2066/356	5.9		1	15	3	4	1		18	19	7	24	
2066/49	5.5		1	13	3	5	1		16	18	8	23	
2384/174	6		1	11	2	5	1	6	13	16	7	20	26
2784/955	5.3		1	12	4	5	1	5	16	17	9	23	28
2239/55L			1	13	3	6	1	4	16	19	9	24	28
2239/55R			1	11	3	7	1	5	14	18	10	23	28
2997/651L	5.8		1	11	4	5	1	5	15	16	9	22	27
2997/651R	5.8		1	11	4	5	1	5	15	16	9	22	27

specimen forewings	l	Sc	R	M	CuA	CuP	A	RM	RCuA	MCuA	Total	with A
min	5.3	1	9	2	4	1	4	12	14	7	20	25
max	6.3	1	15	5	7	1	6	19	20	10	27	30
N	22	27	27	27	27	27	21	27	27	27	27	21
ave	5.84	1	11.93	3.37	5.41	1	5.25	15.3	17.48	8.7	22.7	27.71
Dev	0.234336126	0	1.685365195	0.791694781	0.747264718	0	0.538958431	1.705529803	1.649484077	0.953326759	1.771891966	1.521277659
CV	4.01	0	14.13	23.49	13.81	0	10.27	11.15	9.44	10.96	7.8	5.5

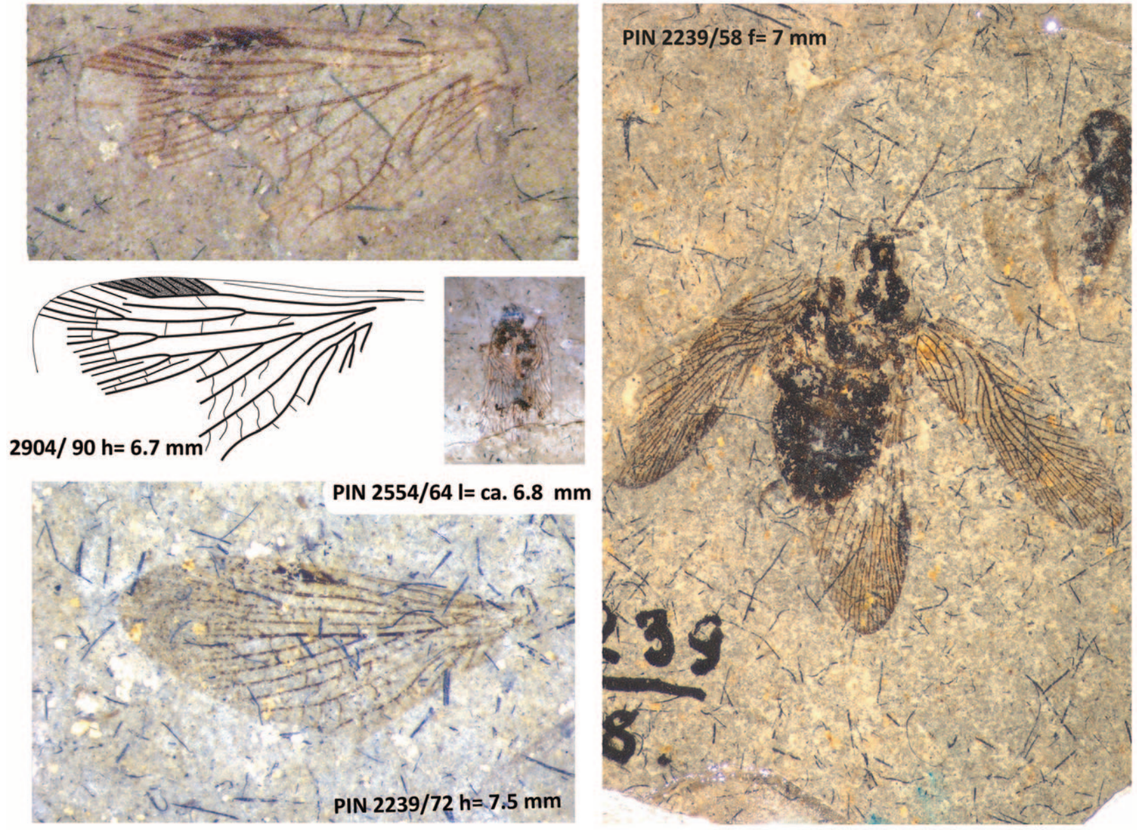
specimen hindwings	l	Sc	R1	RS	M	CuA	CuP	A1	R	R+M	R+Cu	MCu	Without A
2066/490	5.5	1	5	5	3	7	1		10	13	18	11	22
2066/466	6	1	3	7	2	4	1		10	12	15	7	18
2066/468	6.5	1	4	7	2	4	1	6	11	13	16	7	19
2554/92	5.6	1	3	6	4	5	1		9	13	15	10	20
2784/716	6.2	1	3	4	3	4	1	8	7	10	12	8	16
6* 2904/123	6	1	5	4	4	6	1	7	9	13	16	11	21
6* 2904/125 1.4+8.2.5+2!	6	1	4	8	2	5	2		12	14	19	9	22
(*)2997/200	5.8	1	3	5	3	5	1		8	11	14	9	18
(*)2997/1306	5.8	1	5	8	3	5	1	4	13	16	19	9	23
(*)2997/1494	6.5	1	4	4	3	4	1		8	11	13	8	17
(*)2784/734		1	4	6	2	7	1	6	10	12	18	10	21
(*)2997/80	6	1	4	6	2	7	1	6	10	12	18	10	21
(*)2784/897		1	3	6	3	6	1		9	12	16	10	20
(*)2997/211	6	1	3	6	3	5	1		9	12	15	9	19
6* 2997/ 1542		1	3	6	2	5	1		9	11	15	8	18

specimen hindwings	l	Sc	R1	RS	M	CuA	CuP	A1	R	R+M	R+Cu	MCu	Without A
(*)2997/415		1	4	4	2	5	1		8	10	14	8	17
(*)2997/413		1	5	5	2	6	1		10	12	17	9	20
6*2997/1531	6.1	1	5	5	3	5	1		10	13	16	9	20
(*)2997/1478L	6	1	4	5	2	4	1		9	11	14	7	17
(*)2997/1478R	6	1	4	5	2	4	1		9	11	14	7	17
2384/184 fuzia	6	1	5	6	3	6	1		11	14	18	10	22
5-6*2384/950	5.7	1	6	3	2	5	1	4	9	11	16	8	18
(*)294/167	6	1	3	6	3	6	1		9	12	16	10	20
(*)2554/72 *FUYIA		1	5	5	2	6	1		10	11	17	9	20
6*1789/53	6.3	1	5	5	2	5	1	6	10	12	16	8	19
(*)2784/660	5.8	1	5	5	2	5	1		10	12	16	8	19
(*)2904/26		1	5	6	2	6	1		11	13	18	9	21
2239/ no number	6	1	4	6	2	6	1		10	12	16	9	20
2239/106L	5.5	1	4	5	3	4	1		9	12	13	7	18
2239/106R	5.5	1	5	7	2	5	1		12	14	17	7	21
2997/651L	5,5	1	3	5	2	6	1		8	10	14	8	18
2997/651R	5.5	1	4	4	2	6	1		8	10	14	8	18
2239/55L		1	5	5	2	6	1		10	12	16	8	20
2239/55R		1	5	5	2	6	1		10	12	16	8	20
n	26	35	35	35	35	35	35	9	35	35	35	35	35
Min	5.5	1	3	3	2	4	1	4	7	9	12	7	15
Max	6.5	1	6	8	4	7	1	8	13	16	16	11	23
Ave	5.93	1	4.14	5.4	2.43	5.29	1	5.89	9.54	11.94	15.69	8.57	19.29
Dev	0.280950767	0	0.87926631	1.142752096	0.608068992	0.9258201	0	1.269295518	1.335991748	1.392054283	1.843453099	1.170362294	1.856172985
CV	4.74	0	21.24	21.16	25.02	17.5	0	21.55	14	11.66	11.75	13.66	9.62

***Blattula druha* sp.n.**
(figp. 419)

Holotype: PIN 2239/58. A complete winged adult male (f= 7 mm 1, 11, 3, 6, 1, 6; R: 1, 4+4, 2, 5+1; L: 1, 3+6, 3, 6+1).
Type locality: Mikhailovka, Karatau, Kazakhstan
Type horizon: Upper Jurassic Karabastau Formation
Additional material: PIN 2554/64 (f= 6.7-6.9 mm) (complete specimen); 2239/57, 67, 72 (h= 7.2 mm; 1, 5+7, 2, 6+1); 2904/90 (h= 6.7 mm; 1, 5+3, 3, 5+1, 5; 2997/1490 (h= 6.5 mm), 1646, 4323 (h= 6.8 mm; 1, 4+6, 2, 6+1, 8A1) (isolated hindwings). The same locality as the type.

Differential diagnosis: Forewing are indiscernible from *B. brevicaudata* (see comparison of this species), these sister species differ only in presence of pterostigma in hindwing and different coloration of the pronotum (round sophisticated pattern).
Autapomorphy: Sophisticated coloration of the pronotum with round pale macula within dark spot formed of 3 round dark maculas.
Description: Moderately small cockroach. Head globular, elongate (1.4/1.1 mm), all except pale eyes and pale central round area (possibly around the central ocellus) very dark, most probably black. Antenna long, filiform, unpecialised, constantly 0.1 mm wide, 2.5 mm as preserved, but apparently longer. Palp very short, robust, terminal segments 0.5 and 0.8 mm long and up to 0.2 mm wide.
Pronotum slightly transverse (1.8/ 2.2 mm), nearly oval, with short central posterior extension; pale, with three large (one central posterior and two lateral anterior) oval dark maculas (probably black). Metanotum extremely wide (up to 3.2 mm). Body 2.8 mm wide, also very strongly melanised and probably black. Cerci short, curved (preserved) and very wide (1.1/ 0.25 mm), with about 8 segments, very strongly melanised, probably black.
Forewing elongate (7/ 2 mm), membrane pale, with veins distinctly colored dark (probably black) and intercalaries (probably dark brown) ocurring throughout the membrane except for the central part. Cross-veins distinct mainly in cubital area. Sc simple, R slightly sigmoidal, with 11 simple veins. Simply dichotomised are only 2 apical branches (RS indication). M with 3 veins. CuA sigmoidal, with 6 veins; CuP simple, sharphly curved, with posteriormost curvature. A (6) simple.
Hindwing longer that forewing (6.7-7.5 mm), with pale membrane, but with dark appearance due to black main veins and very dark and wide intercalaries and cross-veins combined with possibly dark apex. Sc simple; R1 (4-5) covered with dense dark pterostigma, RS differentiated (3-7). M slightly anteriorly curved, with 2-3 veins at margin. CuA with 5-6 simple veins, CuP simple. A1 with 3 branches, in the specimen (PIN 2904/90) the central blind branch (unusually) dichotomised.
Systematical remarks: It is notable, that *B. brevicaudata* (and the present species) are easity recogniseable from other species within genus on the basis of hindwings, while forewings of these two species are visually and statistically (two specimens of the present species fall within the variability of *B. brevicaudata* near average) identical. So etiher both species originated from the same, unknown, ancestor, and/or more probably, they represent coexistinct coeval chronospecies. Pterostigma is a highly fluctuating character without distinct phylogenetical signal, and there are no other wing plesiomorhies, so it is impossible to claim which species is more basal based on the wings only. It might seems that the new species is slighly more colored and has also more sophisticated coloration pattern of the pronotum, thus it is more likely derived. The same pattern was observed in *B. ahanaha* suggesting there is a tendencey withing *Blattula* towards more extensive melanine content and regulation. This is supported with presence of *Blattula*-derived coloured Blattulidae ocurring at the site as well (as elsewhere). Also it can be excluded *B. ahanaha* and *B. druha* represent the same species, different sexes, because *B. ahanaha* (female) is smaller, and both have different melanine control and coloration pattern.
Deformities absent.



Blattula druha - holotype at right

Derivation of name: After *druhá* (Slavic for the second one, *druh* is also a species).
Character of preservation: Two completely articulated specimens, 7 isolated hindwings.
Taphomony: According to a complete specimens, the species was probably rare but lived close to deposition area. More hindwings are apparently only partially caused with the lack of determination confidence of the forewings as these are unrecogniseable from *B. brevicaudata* – in all other Blattula species at the site hindwings predominate, and due to rarity of the species, only roughly 2-5 forewing are likely concealed in the *B. brevicaudata* material (where they only insignificantly influence variability numbers).

Blattula brevicaudata Vishniakova, 1968

(figp. 421-422, 425-452)

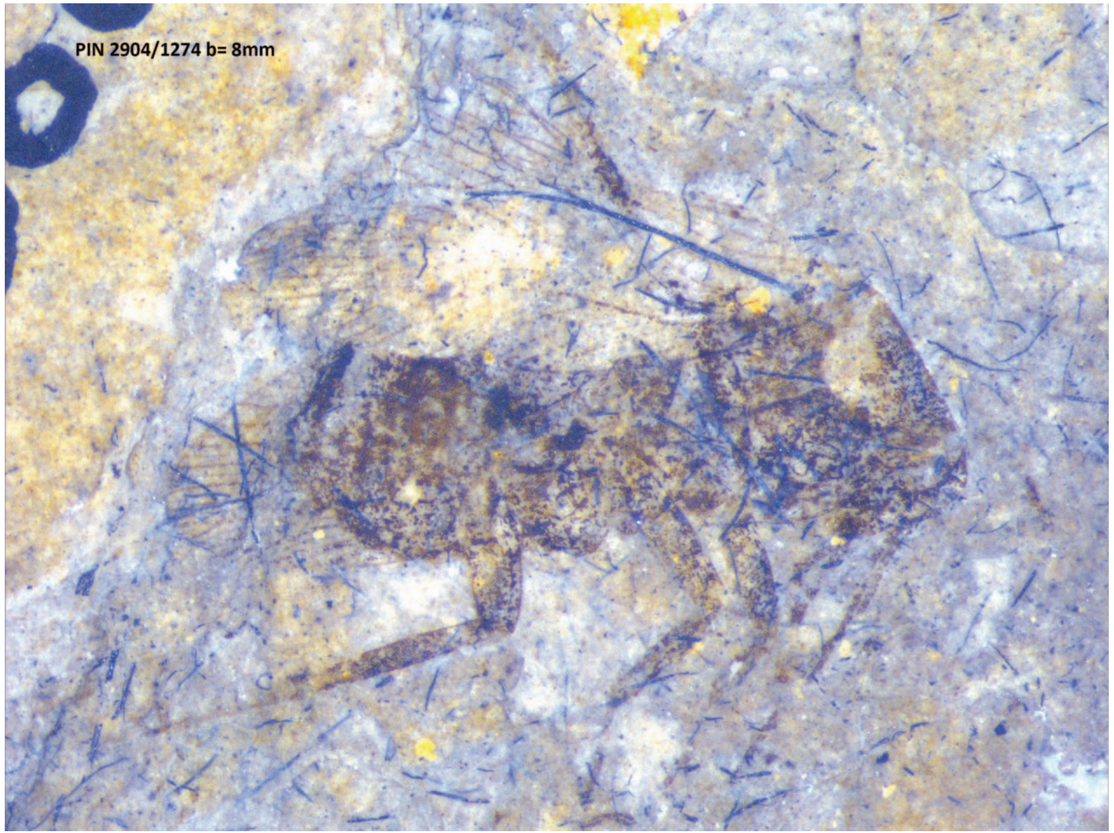
Holotype: PIN 2239/114±. A completely preserved winged adult female. Designated by V.N. Vishniakova (1968).
Type locality: Karatau, Kazakhstan
Type horizon: Upper Jurassic Karabastau Formation

Additional material designated here: PIN 167/289, 299, 309 (f= 7.8 mm); 1789/64 **G**, 83 **G**; 2066/ unnumbered±, 30, 44, 72, 82, 89, 93, 110, 118±, 164, 189 (carbonized), 192 (carbonized), 201±, 241=242, 255, 268, 290, 311, 329, 363±, 402, 462±, 641 (l= 7.7 mm); 2239/56; 2335/34; 2384/26 (b), 164, 176, 190; 2452/147, 350, 385 (fh), 388, 626; 2554/55, 93, 94, 102, 142; 2784/640, 661, 689, 703, 708, 712, 745, 764, 782, 874 (l= 7-8 mm), 893, 910 (f= 7 mm), 937±, 950, 960, 970, 972, 975, 998, 1000 (three stripes on head), 1003, 1005±, 1007; 1011, 2904/20±, 24±, 41, 46, 99 (ffhh), 103 (h= 7.5 mm), 100, 113 (ffhh), 171, 200, 1274, 1855±, 1858, 1892, 1896; 2997/73, 75, 102, 121, 139, 156 (l= 7.6 mm), 234, 245, 274, 1135±, 1190, 1233, 1370, 1438±, 1444±, 1447, 1448 (f= 6.9 mm), 1450, 1451, 1452, 1454, 1455, 1457, 1462 (f= 8 mm), 1472 (l= 7.5 mm), 1474, 1495, 1509, 1527, 1534, 1536, 1544, 3924; unnumbered specimen (complete specimens); GEOLCOM/7, 8; PIN 167/292, 296, 298, 301, 302, 304, 307, 308; 965/70 **G**, 71; 1789/30 (ff) **G**, 72 **G**, 82 **G**; 2066/86, 95=91* (deformity), 114, 119=122 (f= 6.5 mm), 123, 126, 128, 152, 162, 169 (ff), 182, 207 (ff), 219±, 232, 234=235, 253, 262, 264, 285±, 315±, 317±, 320±, 330±, 360± (f= 8 mm), 388, 414±, 451±, 481A, 481B, 643 (f= 7.8 mm), unnumbered; 2239/56A, 56B±, 62, 63, 66, 68, 69, 78, 89, 90, 95, 101, 342; 2384/177, 188, 193=195; 2452/34 (f= 7 mm), 72, 77, 174, 340, 349, 373 (f= 5.5 mm), 429, 529; 2554/46, 54, 55, 57, 58 (different sediment), 60, 65, 68, 88, 147 (f= 7.4 mm); 2784/662, 693, 714, 718, 721, 731, 732, 740±, 758, 763, 767, 786, 791, 784, 832, 842, 854 (f= 7.5 mm), 864, 871, 886 (ff), 915, 932, 933±, 935±, 943, 959, 991 (f= 7.3 mm), unnumbered; 2904/80 (f= 7.5/2.2 mm), 93, 104 (f= 4.5 mm), 111, 118, 122, 132, 160, 176, 178, 181; 2997/21, 54±, 57, 70, 76, 86, 168, 201* (deformity), 215, 220, 225, 267±, 1231, 1281, 1432±, 1433±, 1434±, 1436±, 1441±, 1449 (ff), 1456, 1458, 1463, 1465, 1481, 1483, 1487, 1489, 1501, 1502, 1506 (f= 7. 9 mm), 1508, 1511, 1512, 1518 (ff), 1524, 1535, 1545, 1648 (different, yellow sediment, numerous veins 1, 15, 3+, 5+, 1, 6), 4310, 4315* (f= 6.8 mm; deformity), 4318, 4319, 4322, 4324, 4327, 4328, 4332 (f= 7 mm), 4336, 4338 (isolated forewings); 167/105, 146, 300, 306 (hh); 1789/9 **G**, 15 **G**; 53 **G**; 2039/46; 2066/9, 15 (h= 7 mm), 68, 70, 71±, 92, 125, 130±, 150, 176, 184, 185, 196 (hh), 197, 213, 214, 227, 240 (unusually twice secondarily branched CuA, non-weer-like pleating with branched A; h= 7.1 mm), 244, 245, 258±, 274=275, 293, 319±, 337 (h= 6.5 mm), 346, 352=350, 353±, 357, 362, 374± (h= 8 mm), 382, 398, 410 (with *A. fusca* clavus and a rostrum), 415±, 419, 421, 447, 487±, 489, 496±, 500, 782* (*= deformity); 2239/75, 373± (hh); 2384/175, 179, 180±, 186, 189; 2452/374, 624; 2554/51, 52, 75, 78, 80, 89; 2784/692, 711, 920, 968; 2904/57, 90 (h= 6.5 mm), 101, 108, 109 (hh), 117, 120 (h= 7 mm), 124, 126, 127, 128, 129, 1889; 2997/23, 226, 259, 730, 1467, 1469, 1470, 1471, 1475, 1477, 1491, 1493, 1497, 1500,









1513, 1514, 1515, 1516, 1520 (hh), 1523, 1532, 1537, 1541, 1543, 1546, 1549, 4314, 4316, 4321, 4326, 4329 (isolated hindwings); 2066/413±L, 507; 2554/136 (l= 3 mm), 151 (l= 2.8 mm); 2784/851 (w= 1.2 mm); 1001 (w= 1.3 mm); 2997/203, 1623± (l/w= 4/1.7 mm), 1628 (l= 3.3 mm), 1630 (l= 4.1 mm), 1635 (l= 3.5 mm), 1643 (l= 1.3-1.4 mm), 1645 (l/w= 4/1.8 mm), 1646 (l/w= 2.4/0.8 mm), 1647 (w= 1 mm), 1649 (w= 1.8 mm) (immature individuals). All except G= Galkino from Mikhailovka.

Diagnosis (after Vishniakova 1968): With size and character of R, M, CuA identical with *B. prestwichii*, differing with narrower costal area, more numerous R and more sigmoidal CuA. CuA and A resemble *Blattula* sp. (Martynov 1937) but differs character of R and M.

Redescription (contribution to data by Vishniakova 1968): Head wide, globular, with typical two-three stripes, partially protruding beyond the comparatively small pronotum. Antenna thin and long, with segments not wide, as long as body (longest preserved fragment 5 mm long. Palp very short, 4-segmented, only as long as width of head.

Pronotum transverse (2.3/2.6 mm), with short posterior central extension, coloration with dark uniform, partially divided disc.

Body fat, wide, cerci preserved short (0.95/0.19 mm), multisegmented, with 13-14 cercomeres, dark, witrh pale „stripes“. Two male asymmetrical styli up to 0.6 mm long and possibly 3-segmented present. Female Ovipositor short-type, protruding as a moderately long narrow tube.

Forewing elongate 6-8.2/1.9-2.5 mm, membrane transparent, veins dark, intercalaries more pale, cross-veins distinct. Costa narrow but distinct and sclerotised, overlappin whole wing, costal area narrow. Sc simple, rarely with up to 3 short branches, reaching third of the wing length. R stem very wide and strongly sigmoidal, RS is usually distinctly differentiated (R+RS= 8-17), M comparatively strongly sigmoidal, with 3-5 veins at margin. CuA short, with 2-7 veins at margin. CuP simple, clavus sharply curved anteriorly, without apical curvature. 4-7 simple A present.

Hindwing 6-8.3 mm long, apex slightly sharpened, pterostigma absent. Sc simple, R1 (3-6) and RS (3-8) differentiated. M simplified into 2-5 veins at margin. CuA with 4-86 simple branches, CuP simple, rarely simply dichotomised. Apex sometimes colored.

Legs short.

Character of preservation: 118 complete specimens (two carbonised); 170 isolated forewing specimens (some specimens representing both forewings); 114 hindwing specimens (5 specimens representing both hindwings), 16 immature individuals.

Taphonomy: PIN 2554/58 and 2997/1648 are preserved within a clearly different, yellow-colored more coarse sediment suggesting different sedimentation cycles within 2554 and 2997 collections.

Completely articulated specimens with fine extremities, palps and antenna (combined with the presence of immature indiviiduals) suggest no pre-depositional transport and habitats close to deposition waterbody, supported with balanced number of isolated fore- and hindwings. In contrary to other dominant species at the site, forewings sligtly predominate. This does not seems to be caused with the determination incertainty as number of complete specimens and forewings is balanced similarly as in *B. rectinervosa*. Nevertheless, surprisingly most legs were unpreserved in adults, in contrast to immature individuals, where legs are frewuently complete.

Preservation of immature individuals of diverse instars indicate flushing of young individuals into the waterbody, most probably during rains. Most of them are completely preserved excluding possibility of being dead when trapped on the waterbody. The presence of 16 immatures is extremely high number taking into consideration extreme rarity of cockroach larvae in the sedimentary record (while they dominate amber records – see Sendi et al. 2023).

Additionally it must be stressed that also within the rest imaature material (see discussion) usrely there are hidden numerous additional immature individuals of this species (see also figps. 45-47)..

Preservation in regurgites/coprolites con-

firms these presumptions and abundance of possibly still living cockroaches on the water surface where they were consumed by the fish (see Discussion for general information of coprolites with cockroaches within Karatau).

Syncompressions: Due to small pieces of rock usually collected, syninclusions are limited to regurgites/coprolites. Besides *B. brevicaudata* they contain (PIN 2997/1425) *Rhipidoblatta triky* forewing (the species is contained in another coprolite 2997/1686 as well, along with *B. rectinervosa*, linking these two species together). PIN 2904/190 contains *B. brevicaudata* and an indetermined odonatan.

Variability: Highly significant sample number needs detailed analysis and allows generalisations in respect to congeners, confamiliars and all cockroaches (see **Discussion/ Variability**). It needs to be mentioned that it cannot be excluded that within this set, separate species analogical to *B. nebude* erected below, are hidden. That species holotype specimen (PIN 2997/273) can be statistically discriminated only on the basis of unusually simplified CuA, and sincerely, was recognised initially only on the basis of different pronotum coloration. There are some indications that further species might be hidden in the dataset as there is no clear preservation of the pronotal coloration patterns some of which clearly consist on pale coloration details (PIN 2384/176, 179), while others might me monochromatic (PIN 2904/20). Nevertheless, these cannot be confirmed confinely due to taphonomical reasons. Furthermore, such hidden species and/or hidden variabilities are potentially present in any dataset, so such eventuality does not skew data in any unusual way. Influence of such individuals to this dataset is cosmetical. Adding *B. nebude* defined below as a separate species would change variability from 8 to 7.92 % and from 9.14 to 9.09 % for dataset including and excluding A respectively – namely it illusory even decreases variabilty coefficients of the more common species. Such influence of course might differ due to real difference of the potentially sibbling species unrecognised at one single site.

What is important, study of this statistically significant dataset confirms very low variability of the genus *Blattula*. What is even more important that it confirms statistically rather different variability of sets including and excluding A and namely much lower variability of set with A. Thus the higher variability without A is not an artefact, but a confirmed value.

Additionally this sets confirms previous (insignificant) results on the lower variability of forewing anterior margin (CV_R= 12.4 compared with CV_M= 29.6 and CV_{CuA}= 19.1 % %).

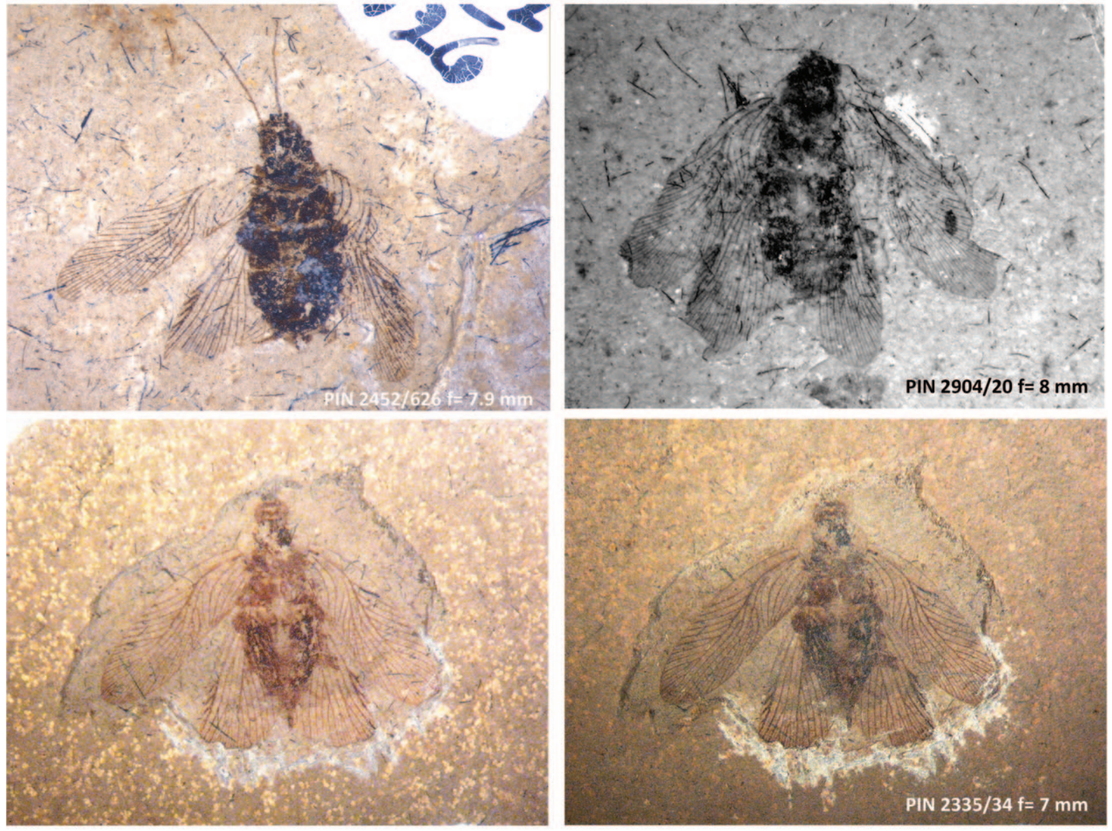
Interesting is also the particular variability of SC. Subcosta is extremely conservative and usually family-diagnostic character. In Blattulidae it is nearly exclusively simple, in few known cased simply dichotomised, but rarely with up to 5 short branches. Here it can be shown how a small deviation might cause significant change in value of variability. While branched SC does not significantly influence the total number of veins at the margin, variability within the SC system is greatly influence with a single deviant specimen with SC possessing 3 branches (PIN 2904/100). SC always having CV= 0 is with this single specimens (among 114) changes CV to 18 %.

Remarkable is significantly lower variability of the forewing length (CV= 6.81), which needs validation on the forewing area, which is more strictly binded to the vein distributions (Oružinský and Vršanský 2017).

Extremely important is comparison of the forewing variability with the variability of the hindwing remigium, analogical to forewing without clavus (see Vršanský and Kazimírová 2023).

Hindwing reveals nearly identical variability (9.38 compared with 9.14 %) and also in this case, hindwing length is less variable and again the value is basically identical with the forewing legth (CV= 6.91 compared with 6.81 %). Also this needs validation on the remigium areas.

Remarkable case is PIN 2904/20 difference of 16/19 veins.



Blattula brevicaudata

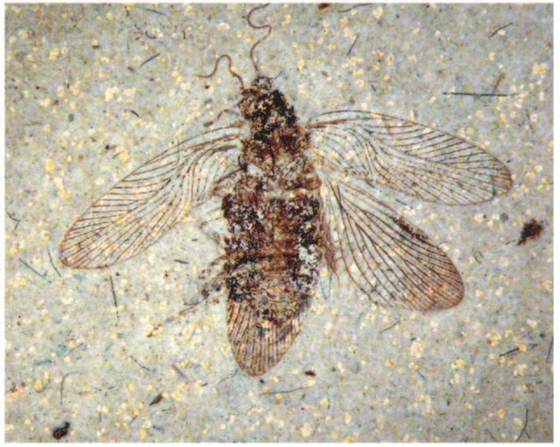


PIN 2384/176 f= 7.8 mm



PIN 2384/179 h= 8 mm



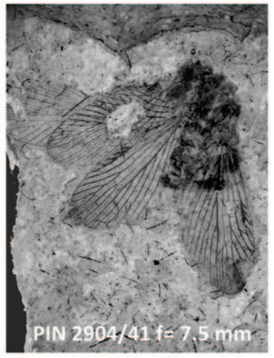


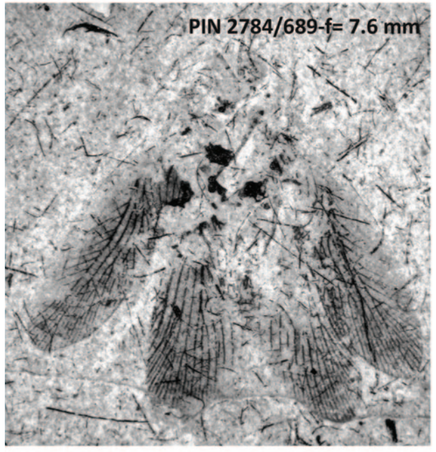


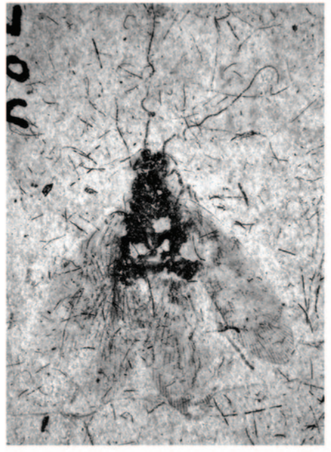


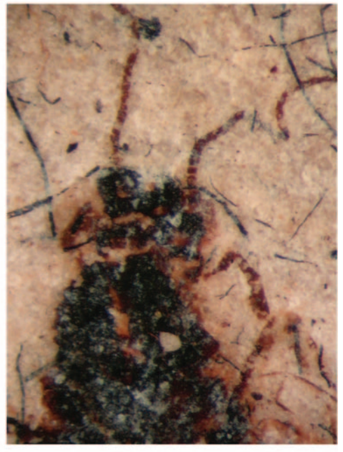

2784

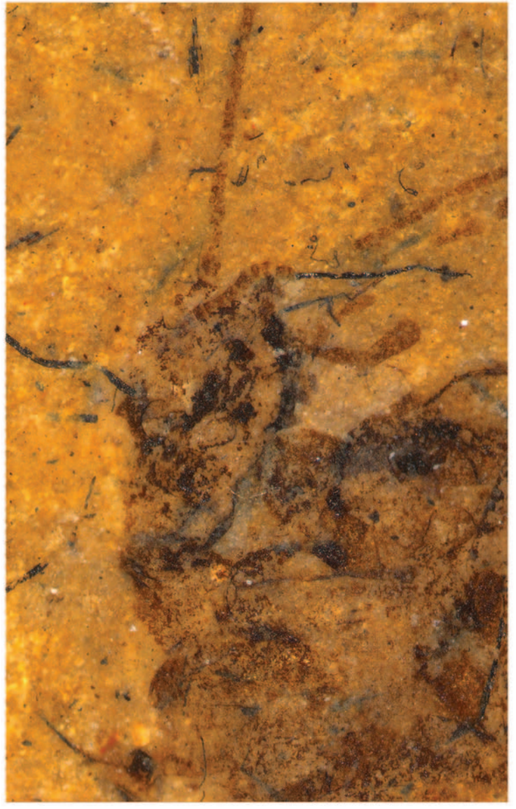

PIN 2784/782

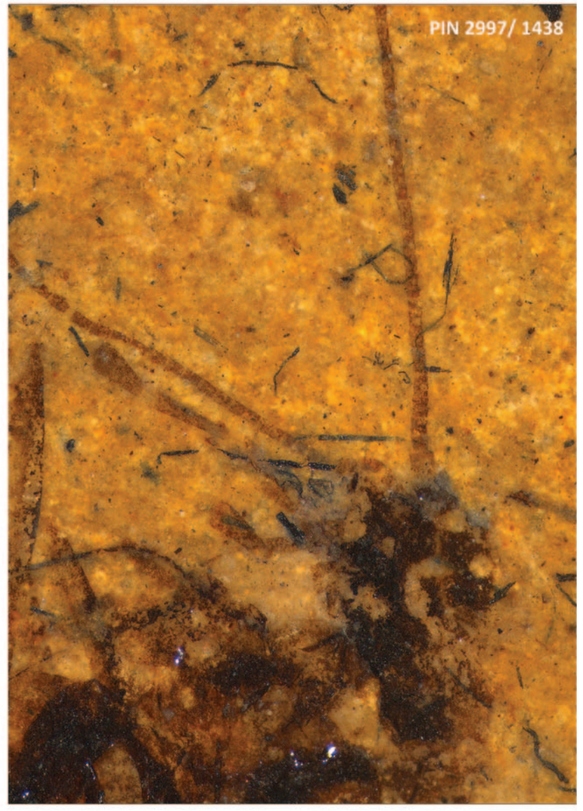

PIN 2904/41 f= 7.5 mm


PIN 2784/689-f= 7.6 mm








PIN 2997/ 1438


PIN 2997/245 f= 7.5 mm

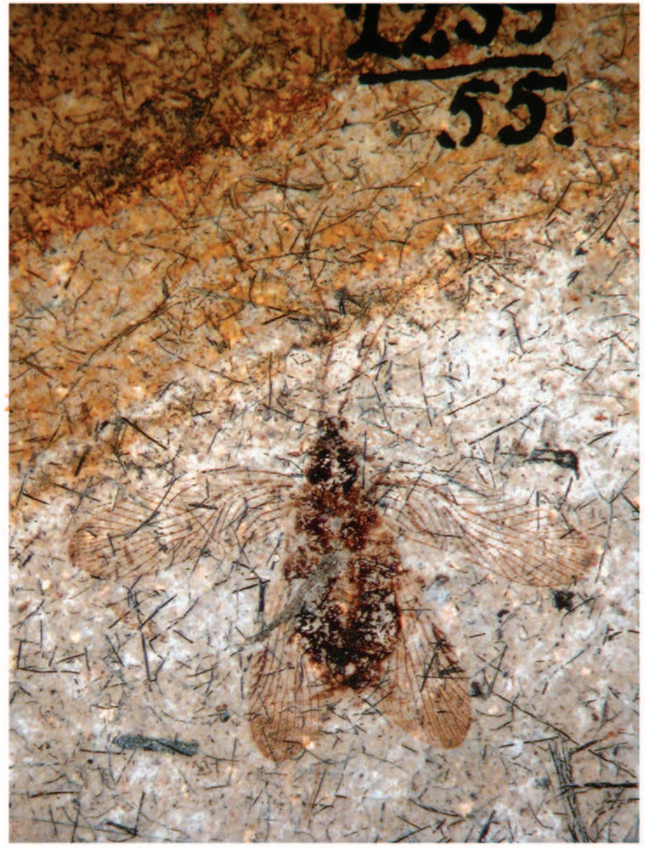

1,00 mm
PIN 2997/1454 f= 7.6 mm

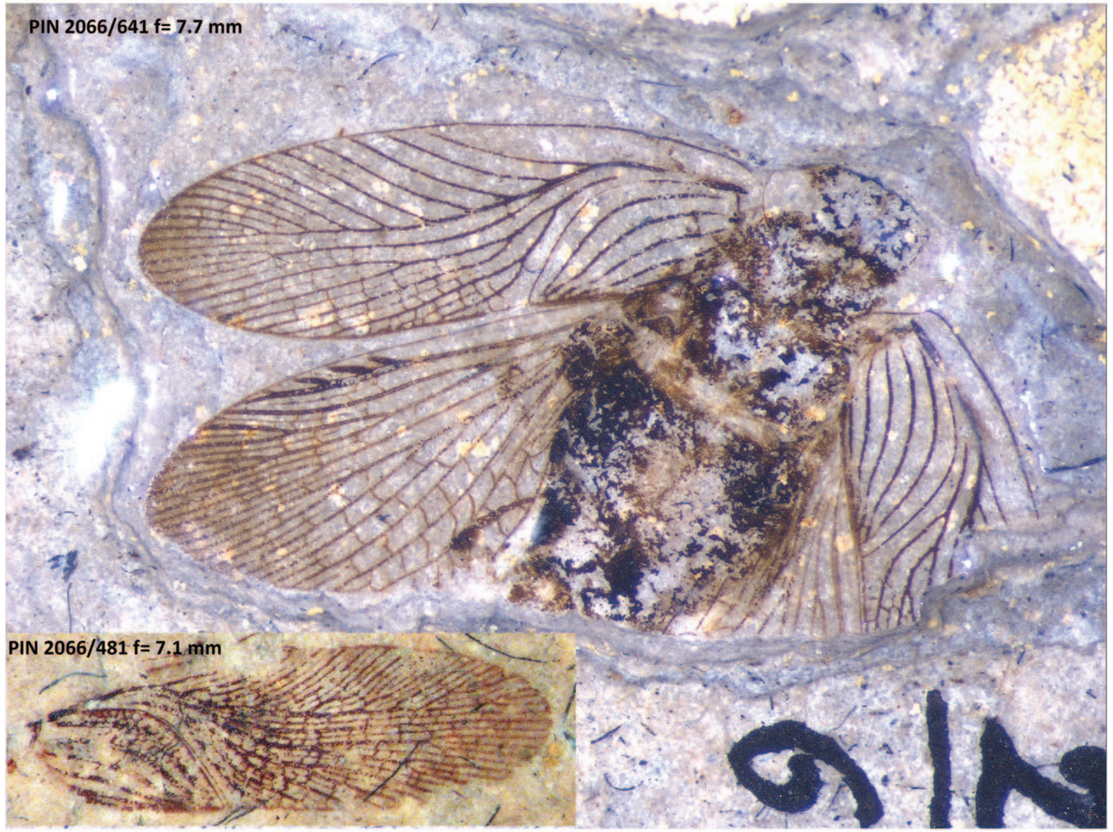

PIN 2239/ 69 f= 8 mm
PIN 2784/ 745 f= 6.7 mm

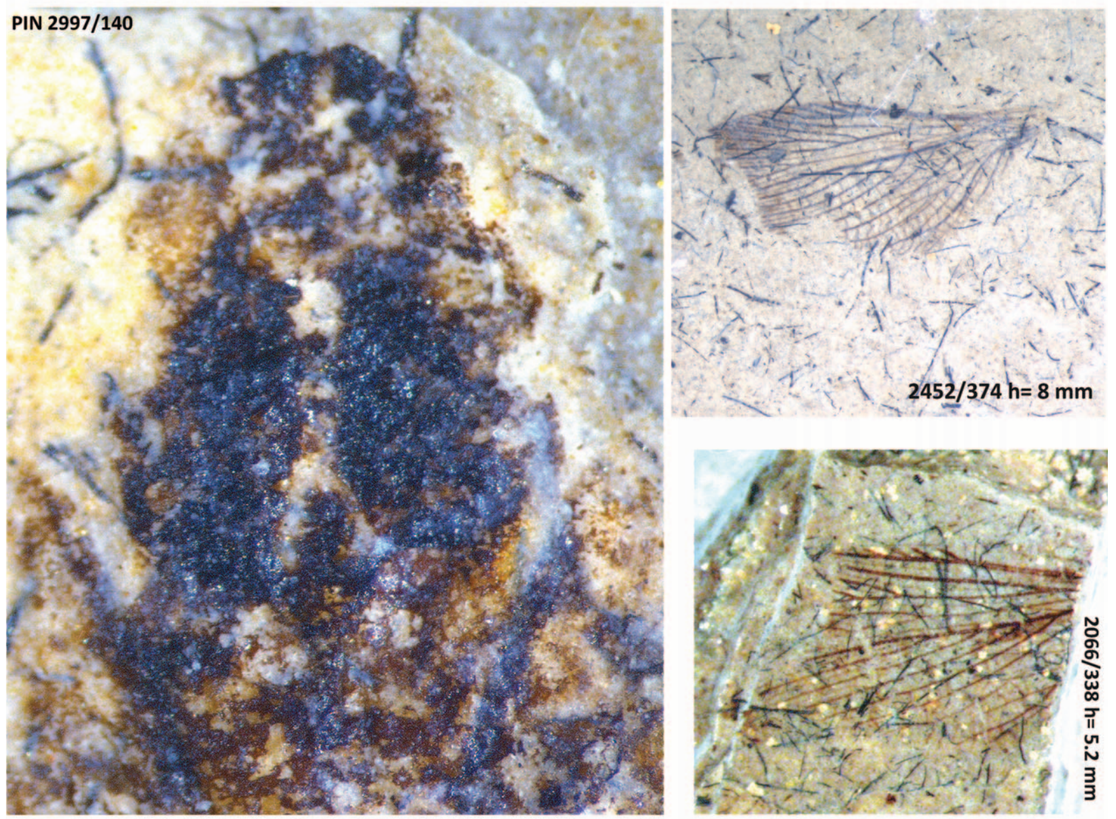

PIN 2784/ 640

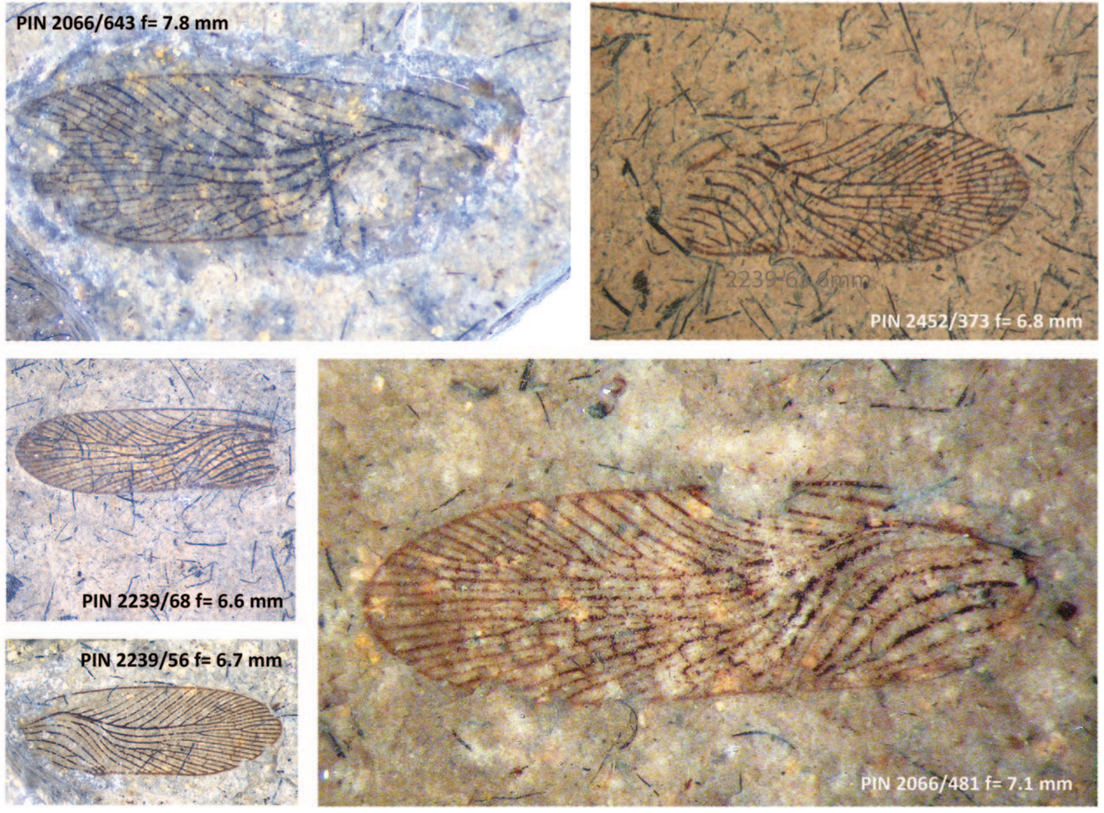

PIN 2904/ 100 h= 6.45 mm

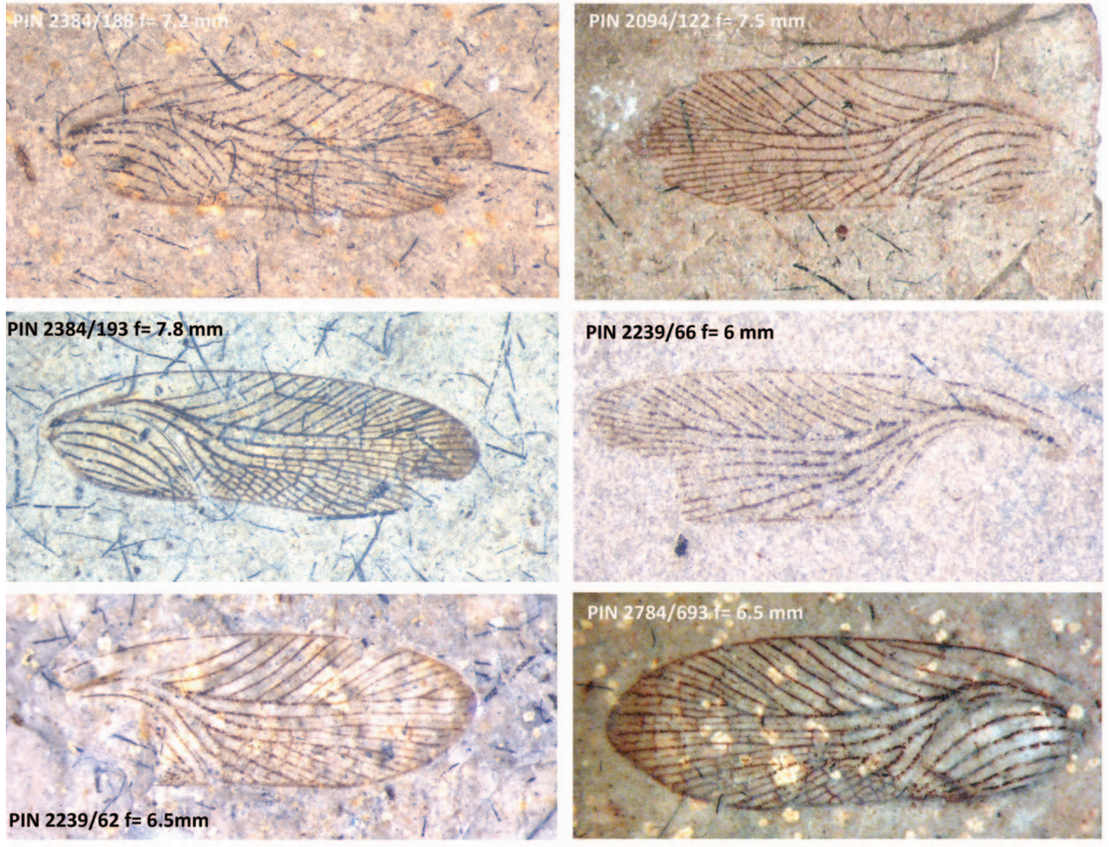


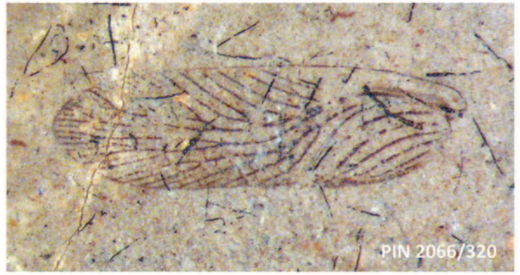



PIN 2066/641 f= 7.7 mm
PIN 2066/481 f= 7.1 mm

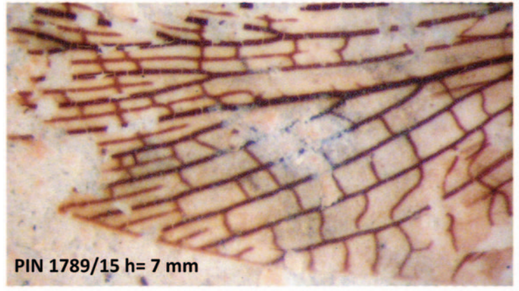

PIN 2997/140
2452/374 h= 8 mm
2066/338 h= 5.2 mm


PIN 2066/643 f= 7.8 mm
PIN 2452/373 f= 6.8 mm
PIN 2239/68 f= 6.6 mm
PIN 2239/56 f= 6.7 mm
PIN 2066/481 f= 7.1 mm

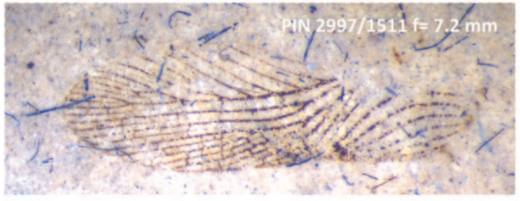

PIN 2384/188 f= 7.2 mm
PIN 2094/122 f= 7.5 mm
PIN 2384/193 f= 7.8 mm
PIN 2239/66 f= 6 mm
PIN 2239/62 f= 6.5mm
PIN 2784/693 f= 6.5 mm

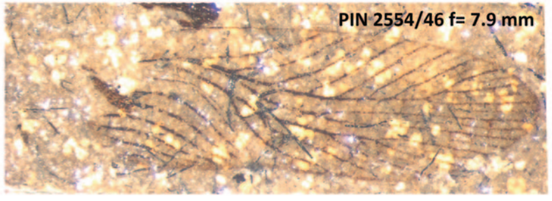

PIN 2066/320


PIN 2904/132 f= 7.8 mm

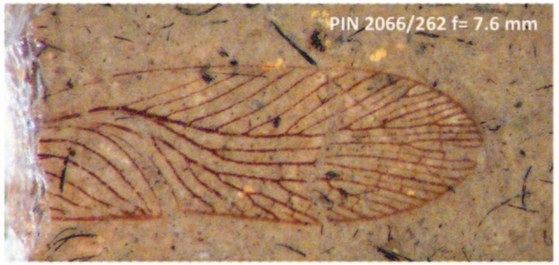

PIN 1789/15 h= 7 mm

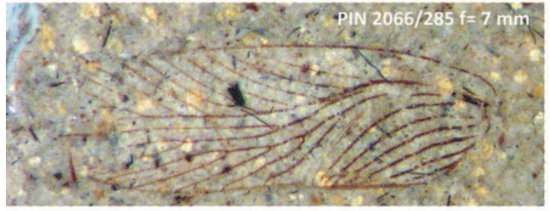

PIN 2239/75

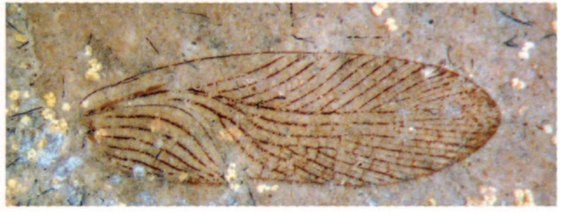

PIN 2997/1511 f= 7.2 mm

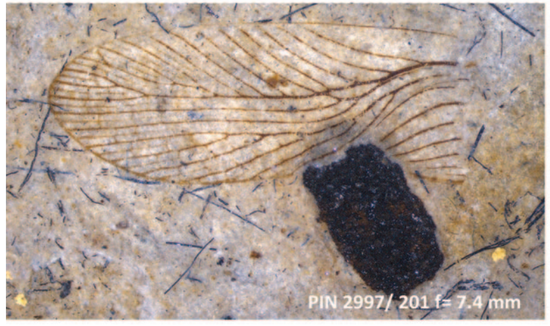

PIN 2554/46 f= 7.9 mm


PIN 2066/264 f= 7 mm


PIN 2066/262 f= 7.6 mm

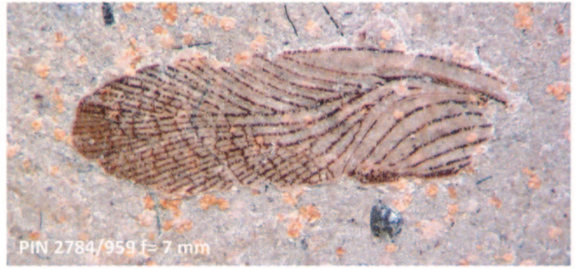

PIN 2066/285 f= 7 mm



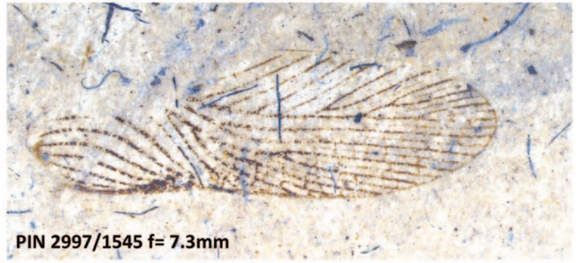

PIN 2997/ 201 f= 7.4 mm

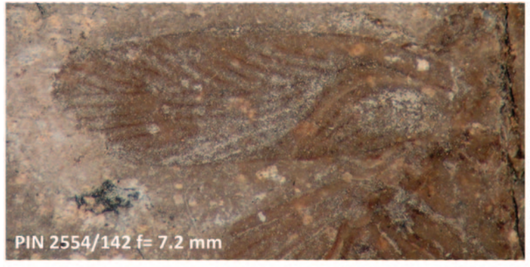

PIN 2066/219 f= 7.2 mm

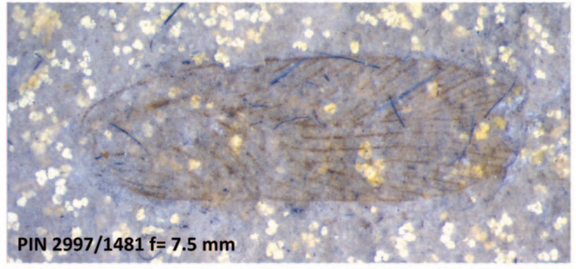

PIN 2239/95 f= 7mm

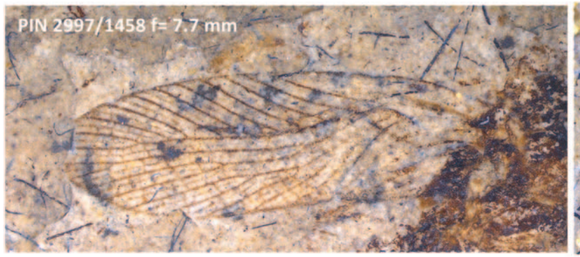

PIN 2784/959 f= 7 mm

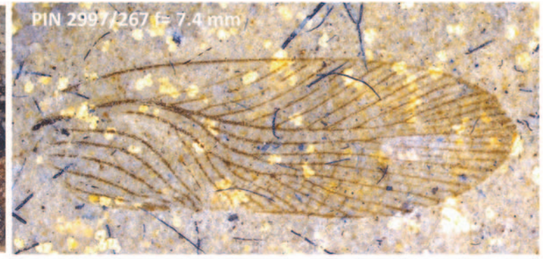

PIN 1789/72 f= 6 mm

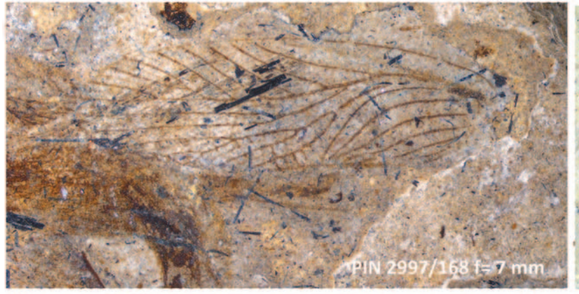

PIN 2997/1545 f= 7.3mm


PIN 2554/142 f= 7.2 mm

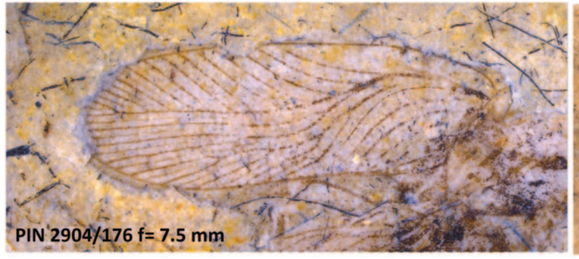

PIN 2997/1481 f= 7.5 mm

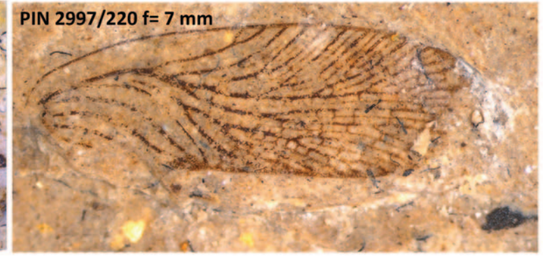

PIN 2997/1458 f= 7.7 mm

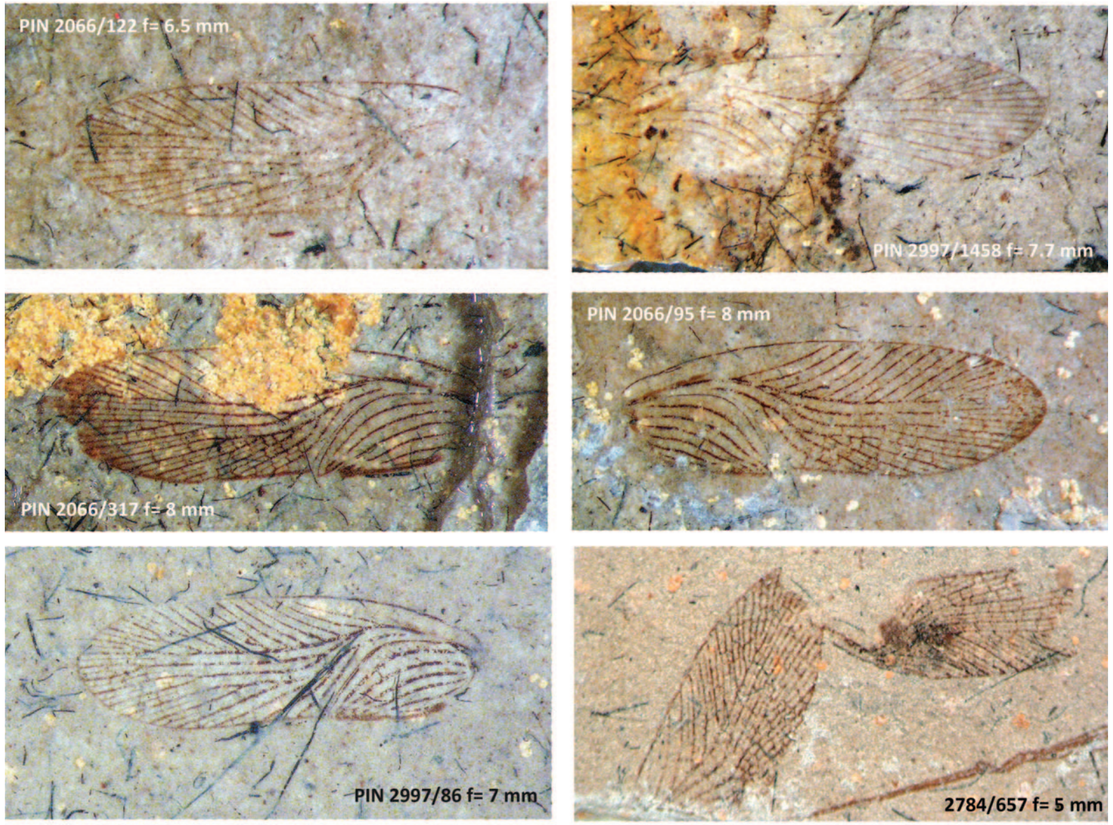

PIN 2997/267 f= 7.4 mm

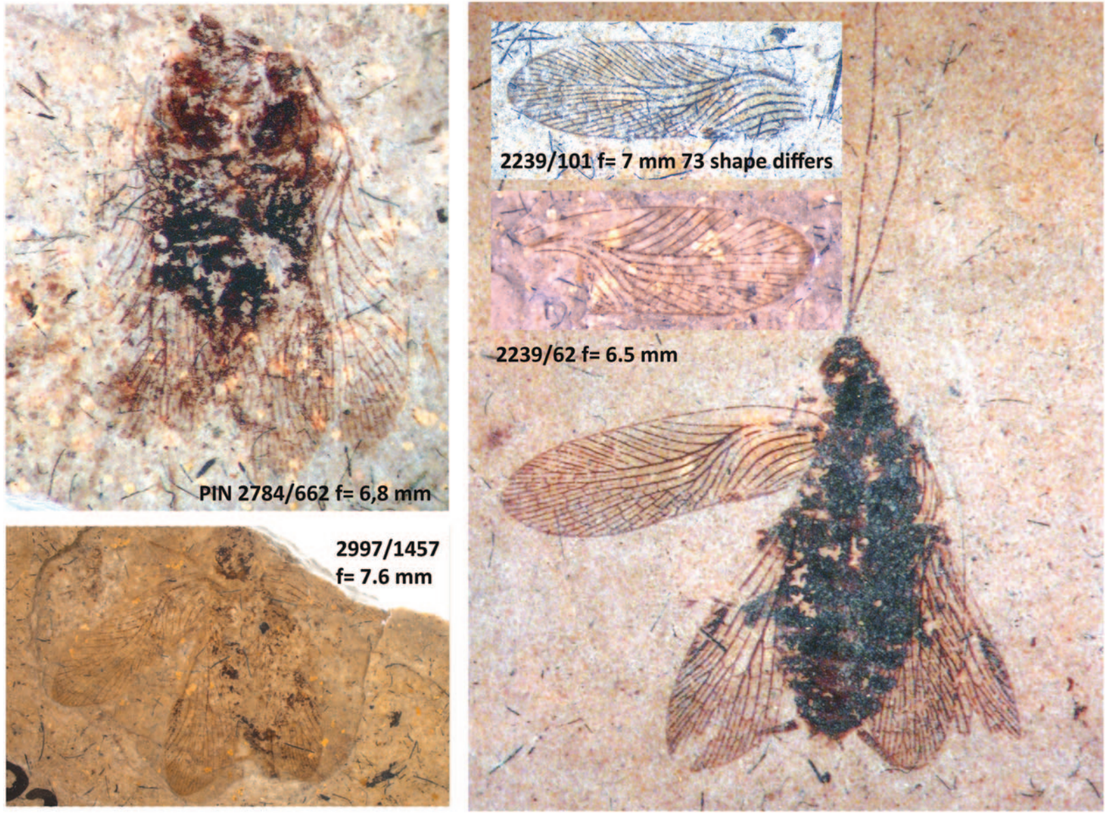

PIN 2997/168 f= 7 mm

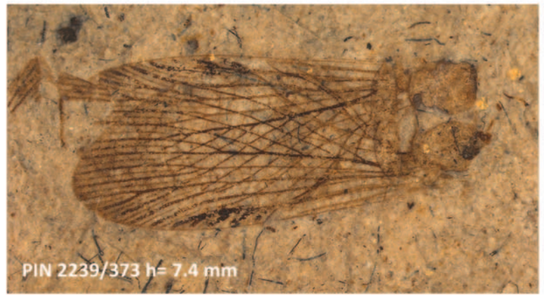

PIN 2997/215 f= 7.6 mm


PIN 2904/176 f= 7.5 mm

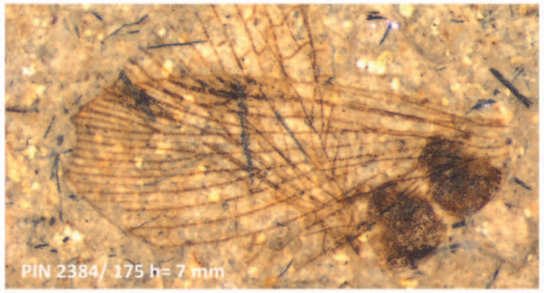

PIN 2997/220 f= 7 mm

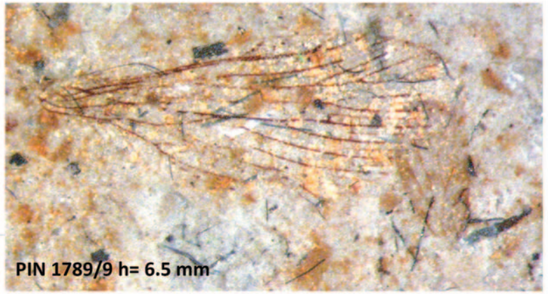

PIN 2066/122 f= 6.5 mm
PIN 2997/1458 f= 7.7 mm
PIN 2066/317 f= 8 mm
PIN 2066/95 f= 8 mm
PIN 2997/86 f= 7 mm
2784/657 f= 5 mm

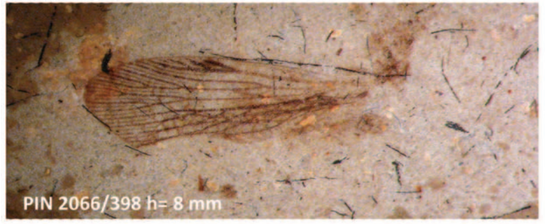

PIN 2784/662 f= 6,8 mm
2997/1457
f= 7.6 mm
2239/101 f= 7 mm 73 shape differs
2239/62 f= 6.5 mm

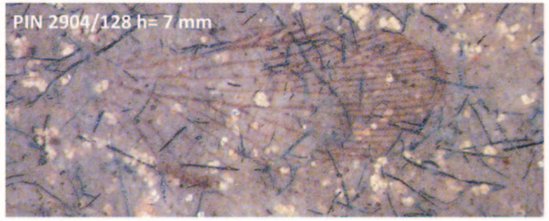

PIN 2239/373 h= 7.4 mm

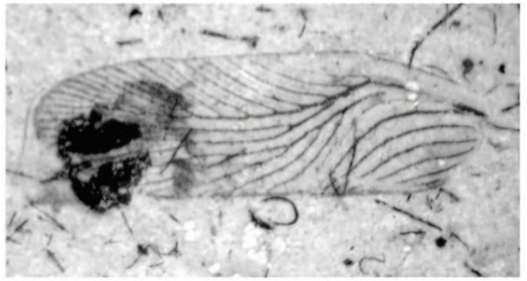

PIN 2554/78 h= 7 mm

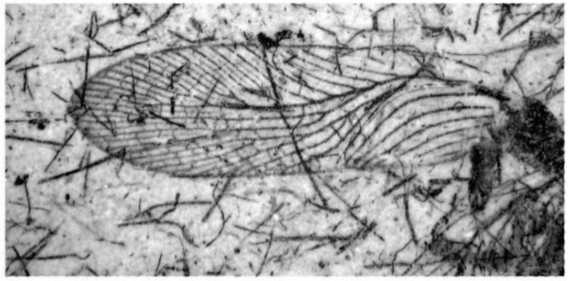

PIN 2384/ 175 h= 7 mm

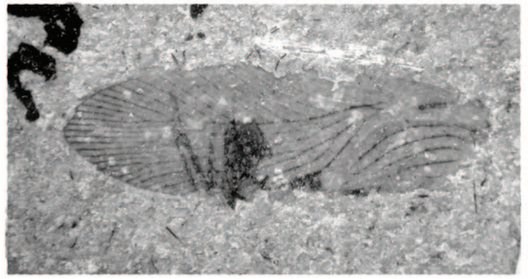

PIN 1789/9 h= 6.5 mm

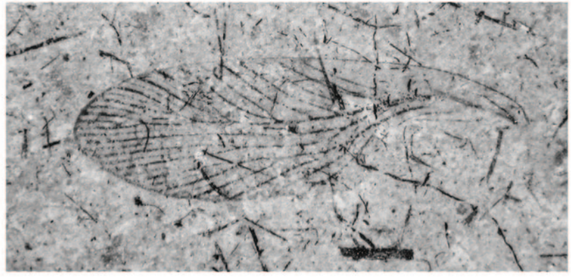

PIN 2066/398 h= 8 mm

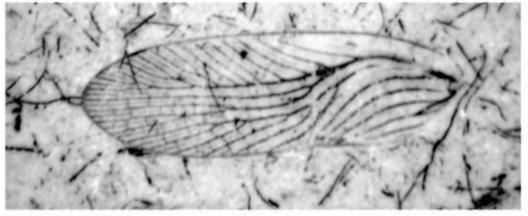

PIN 2904/128 h= 7 mm

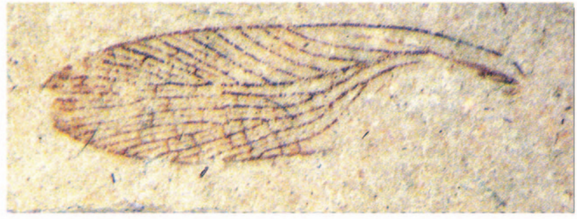


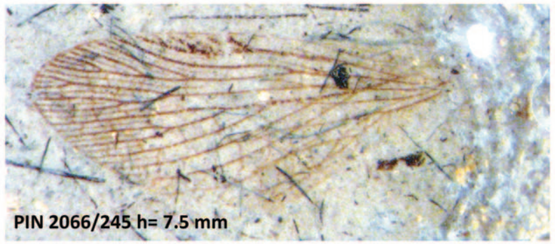


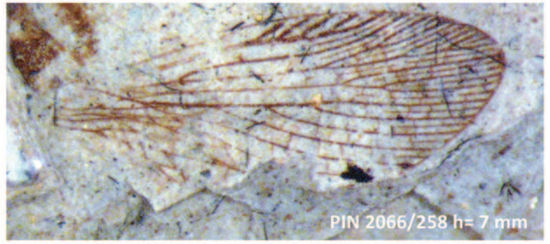


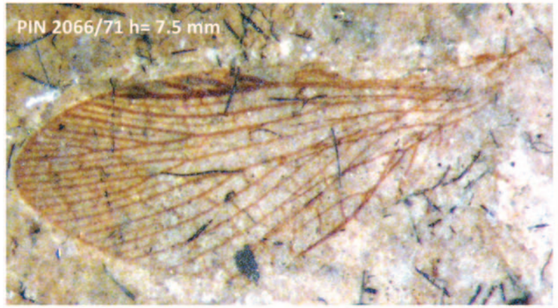







PIN 2066/245 h= 7.5 mm

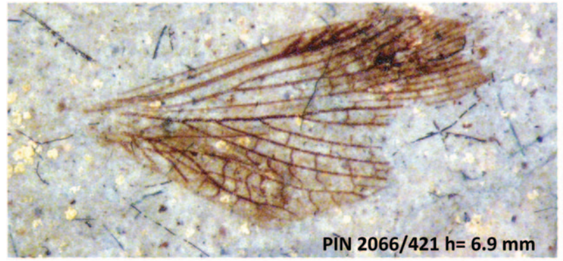

PIN 2066/258 h= 7 mm


PIN 2066/71 h= 7.5 mm

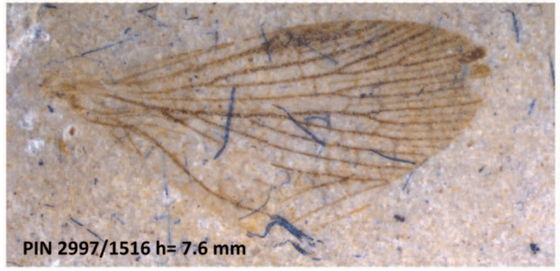

PIN 2066/782 h= 6.3 mm

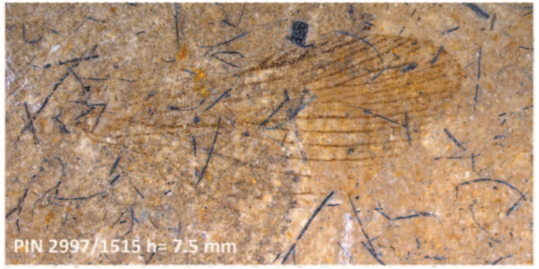
PIN 2997/131 h= 6.5 mm

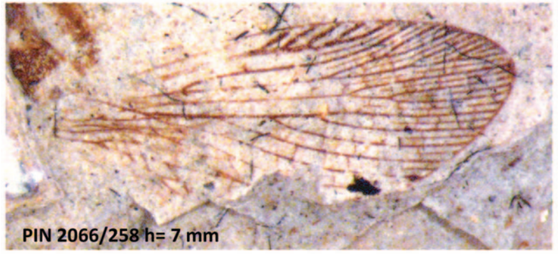

PIN 2066/337 h= 6.5 mm

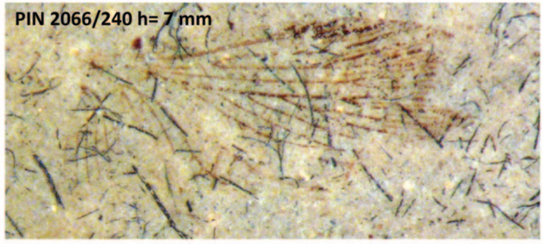

PIN 2066/421 h= 6.9 mm

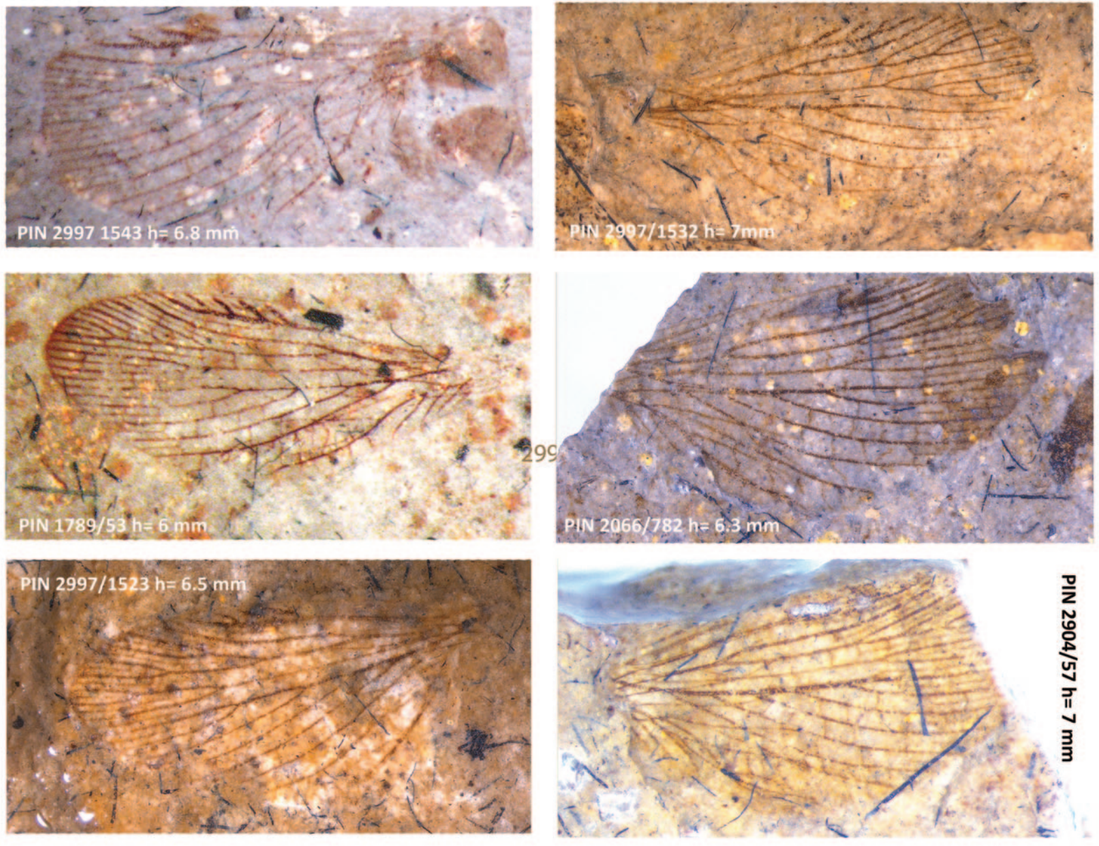

PIN 2554/89 h= 7 mm

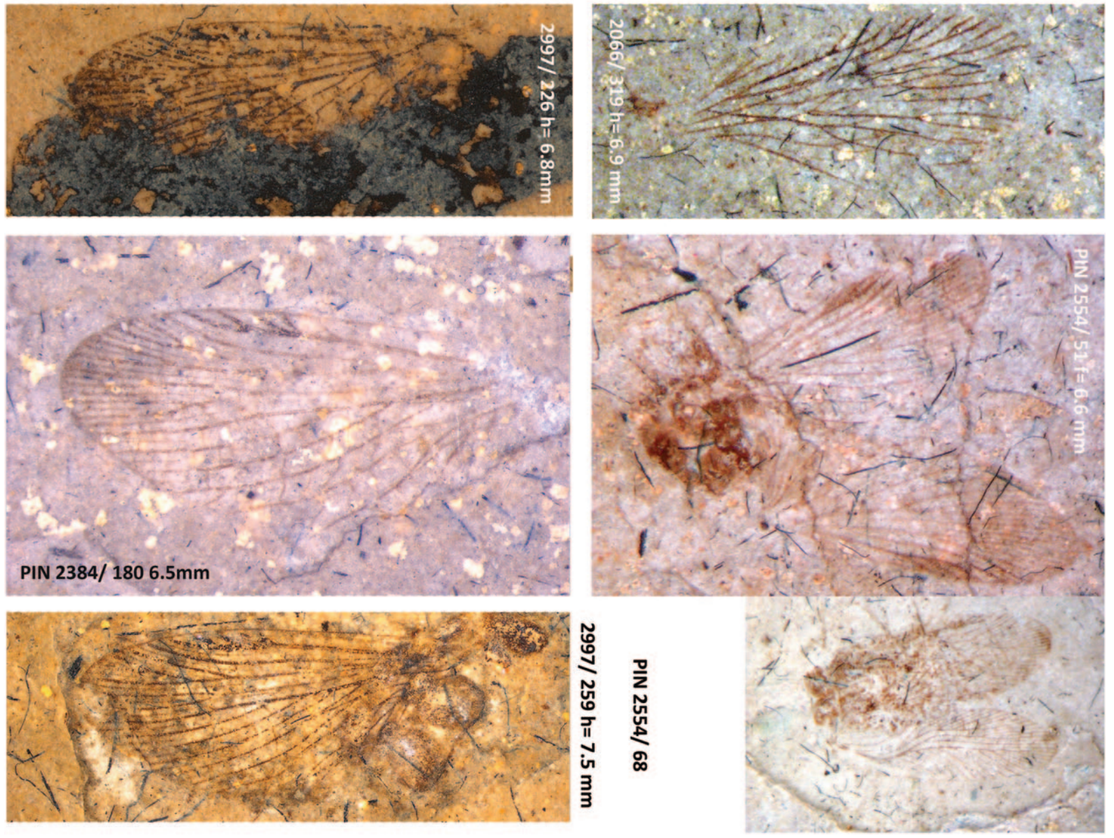

PIN 2997/1516 h= 7.6 mm

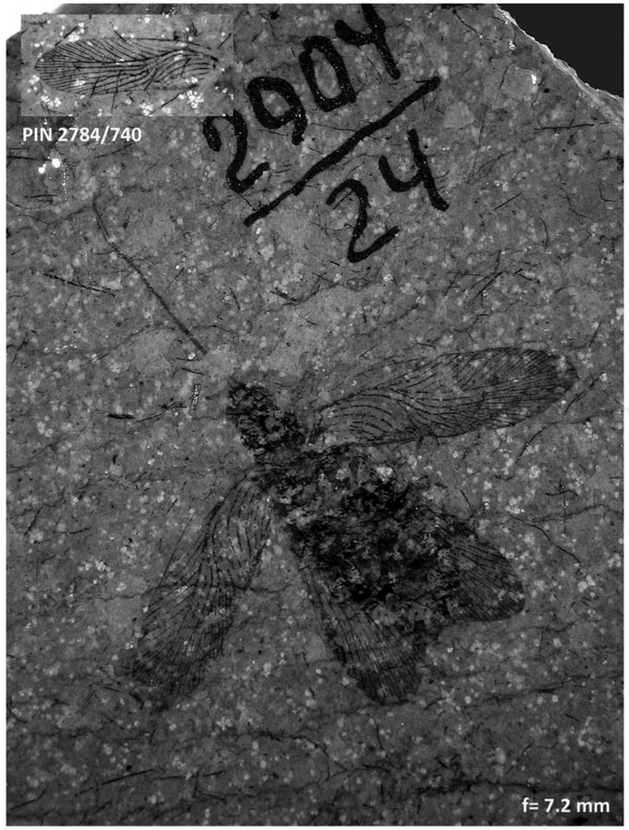

PIN 2997/1515 h= 7.5 mm

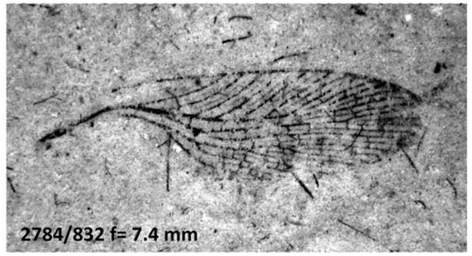

PIN 2066/258 h= 7 mm

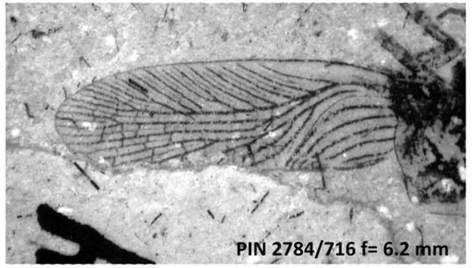

PIN 2066/240 h= 7 mm

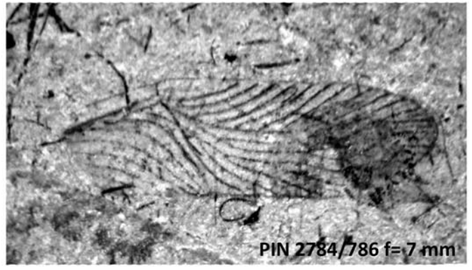

PIN 2997 1543 h= 6.8 mm
PIN 2997/1532 h= 7mm
PIN 1789/53 h= 6 mm
PIN 2066/782 h= 6.3 mm
PIN 2997/1523 h= 6.5 mm
PIN 2904/57 h= 7 mm

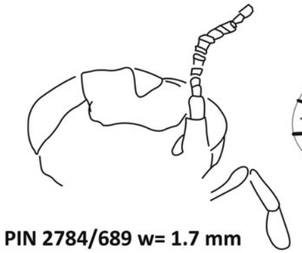

2997/ 326 h= 6.8mm
2066/ 319 h= 6.9 mm
PIN 2384/ 180 6.5mm
PIN 2554/ 511 h= 6.6 mm
2997/ 259 h= 7.5 mm
PIN 2554/ 68


PIN 2784/740
2904
24
f= 7.2 mm

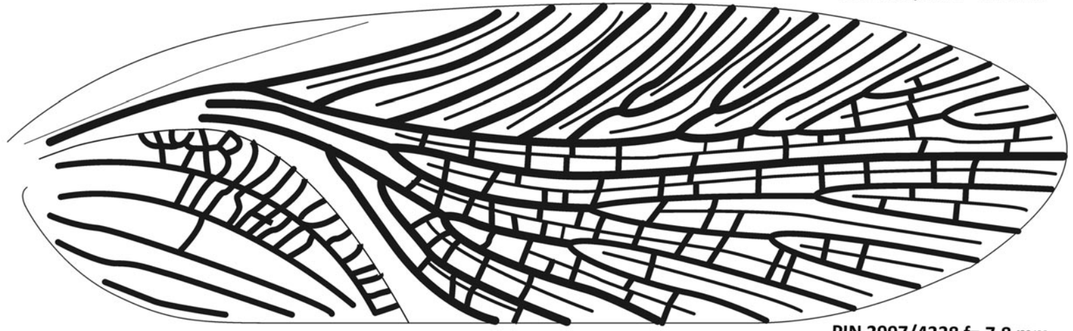

2784/832 f= 7.4 mm

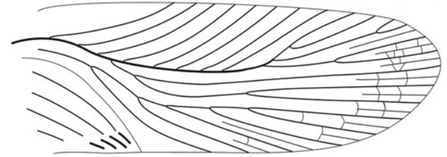

PIN 2784/716 f= 6.2 mm

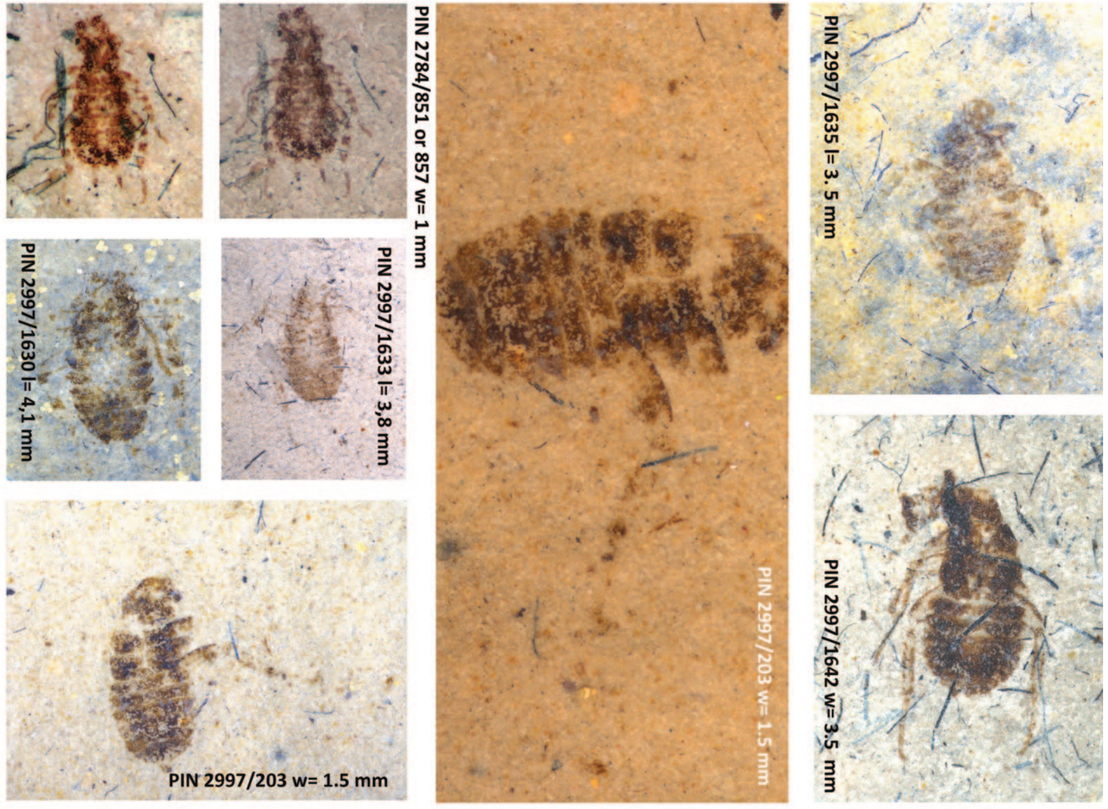

PIN 2784/786 f=7 mm


PIN 2784/689 w= 1.7 mm


PIN 2784/693 f= 6.5 mm


PIN 2066/481 f= 7.1 mm


PIN 2997/4338 f= 7.8 mm



Comparing respective veinal systems might reveal importance in the flight aerodynamics, but possibly also morphological relation of the veins. Thus Radial systems are highly comparable, 12.4 – 12.56 %. Hindwing "RS" (19.34 %) reveals low variability, which might mean this vein simply really corresponds to R1 (RA). Reverted polarity is characterised for hindwing M with variability comparable to forewing M (CV= 26.96/27.76 %). Cubital systems reveal very different values for fore- and hindwings (19.1/13.73 %).

Remarkably, all preserved pronota are of identical size.

Mutations: Four vein deformities are recorded on 402 specimens (most of 118 of complete of them have preserved more thank one complete wing). PIN 2066/95=91 posses terminal R dichotomy (without intercalary); 2997/201 (R-M fusion) and 2066/782 unique hidnwing CuA-CuA irregularity – veins are not entirely fused but are greatly approximated (CuA-CuA fusion is otherwise the most common fusion). Such strict controll basically without deformities suggest extremely keen competition within balanced ecosystem and also extremely active flight disallowing bearing deformities influencing aerodynamics during the flight.

specimen Forewing (*fusion)	l (in mm)	w (in mm)	SC	R	M	CuA	CuP	A	RM	RCuA	MCuA	SUM	SUM (without A)
167/292	7.7	2.2	1	11	3	5	1		14	16	8		21
167/307	6.8		1	11	3	5	1		14	16	8		21
1789/72	6.8		1	10	4	6	1	6	14	16	10	28	22
2066/91*	8		1	13	4	5	1		17	18	9		24
2066/95=91	7.9		1	13	4	5	1	6	17	18	9	30	24
2066/114			1	12	4	8	1		16	20	12		26
2066/122	6.2		1	13	3	5	1		16	18	8		23
2066/123	7		1	12	4	7	1	5	16	19	11	30	25
2066/152			1	12	4	5	1	5	16	17	9	28	23
2066/219±	7.2		1	14	6	5	1		20	19	11		27
2066/262	7.4		1	13	4	7	1	6	17	20	11	32	26
2066/264	7		1	14	4	5	1		18	19	9		25
2066/285	7		1	13	4	5	1	6	17	18	9	30	24
2066/317±	8		1	11	4	6	1	6	15	17	10	29	23
2066/320	7.1		1	13	4	5	1	5	17	18	9	29	24
2066/481	8.1		1	10	3	6	1	5	13	16	9	26	21
2066/481B	7.1		1	14	5	5	1	5	19	19	10	31	26
2066/641	7.7		1	10	2	5	1	5	12	15	7	24	19
2066/643			1	12	3	6	1		15	18	9		23
2239/56	6.7		1	12	4	5	1	5	16	17	9	28	23
2239/56C±	7.5		1	8	3	9	1	5	11	17	12	27	22
2239/56B1	6		1	13	3	6	1	6	16	19	9	30	24
2239/56B2	6.7		1	12	4	9	1	5	16	21	10	32	27
2239/62	6.8		1	11	3	5	1	6	14	16	8	27	21
2239/63	6		1	10	5	5	1	6	15	15	10	28	22
2239/68	6.6		1	14	5	6	1	5	19	20	11	32	27
2239/69	8		1	12	4	5	1	5	16	17	9	28	23
2239/75			1	14	4	5	1	6	18	19	9	31	25

specimen Forewing (*fusion)	l (in mm)	w (in mm)	SC	R	M	CuA	CuP	A	RM	RCuA	MCuA	SUM	SUM (without A)
2239/95	7		1	12	4	5	1	6	16	17	9	29	23
2239/101	7		1	13	3	4	1	5	16	17	7	27	22
2239/114R	7.5	2.3	1	12	4	5	1	6	16	17	9	29	23
2239/114L	7.5	2.3	1	13	5	6	1	6	18	19	11	32	26
2239/342			1	13	3	6	1		16	19	9		24
2335/34 L	7.5	2.4	1	11	3	6	1	5	14	17	9	27	22
2335/34 R	7.5	2.4	1	12	2	5	1	5	14	17	7	26	21
2384/176	7.8		1	11	5	6	1	6	16	17	11	30	24
2384/188	7.2		1	11	4	6	1	5	15	17	10	29	24
2384/193=195	7.8		1	12	4	6	1	6	16	18	10	30	24
2452/174	7		1	12	4	6	1		16	18	10		24
2452/349			1	13	5	7	1		18	20	12		27
2452/373	6.8		1	10	4	5	1	6	14	15	9	27	21
2452/626	7.9		1	12	3	7	1	5	15	19	10	29	24
2554/46	7.9		1	13	4	5	1	5	17	18	9	29	24
2554/55(?)L	7.9		1	12	3	6	1	5	15	18	9	28	23
2554/55(?)R	7.9		1	12	3	7	1	5	15	19	10	29	24
2554/55B	7.7		1	10	5	3	1	6	15	13	8	26	20
2554/57	7		1	13	4	6	1		17	19	10		25
2554/60			1	13	4	6	1		17	19	10		25
2554/65A			1	12	4	6	1		16	18	10		24
2554/68fh	7.9		1	14	3	6	1	4	17	20	9	29	25
2554/142	7.2		1	12	3	4	1	5	15	16	7	26	21
2784/640L	8		1	11	4	5	1	4	15	16	9	26	22
2784/640R	8		1	13	3	4	1	5	16	17	7	27	22
2784/689L	7.6		1	17	6	6	1	6	23	23	12	37	31
2784/689R	7.6		1	15	5	5	1	6	20	20	10	33	27
2784/693	6.5		1	12	3	6	1	5	15	18	9	28	23

specimen Forewing (*fusion)	l (in mm)	w (in mm)	SC	R	M	CuA	CuP	A	RM	RCuA	MCuA	SUM	SUM (without A)
2784/716	6.2		1	13	3	5	1	6	16	18	8	29	23
2784/721	7.6		1	14	3	6	1		17	20	10		25
2784/791	6.9		1	14	4	6	1	5	18	20	10	31	26
2784/718	7.3		1	13	3	7	1	6	16	20	10	31	25
2784/740			1	15	3	5	1	6	18	20	8	31	25
2784/745	6.7		1	12	5	8	1	5	17	20	13	33	27
2784/763	6.9		1	12	4	5	1	6	16	17	9	29	23
2784/786 f	7		1	12	5	5	1	5	17	17	10	29	24
2784/832	7.4		1	9	3	6	1		12	15	9		20
2784/842	6.8		1	13	4	5	1	6	17	18	9	30	24
2784/915	7		1	13	4	7	1	5	17	20	11	31	26
2784/ 943	8		1	9	3	6	1		12	15	9		20
2784/ 959	7		1	13	4	7	1	6	17	20	11	32	26
2784/970			1	12	4	3	1	5	16	15	7	26	21
2904/20L±	8		1	12	4	7	1	5	16	19	11	30	25
2904/20±R	8		1	12	4	7	1	5	16	19	11	30	25
2904/46	7.8		1	11	5	6	1	6	16	17	11	30	24
2094/122 (2094)	7.5	2.4	1	13	3	7	1	6	16	20	10	31	25
2904/93	7.3	1.9	1	10	3	4	1	6	13	14	7	25	19
2904/100	6.5		3	12	3	6	1	5	15	18	9	30	25
2904/132	7.8	2.2	1	13	3	7	1	6	16	20	10	31	25
2904/176	7.5		1	13	3	5	1	6	16	18	8	29	23
2904/181			1	12	6	5	1	7	18	17	11	32	25
2904/200	7		1	10	3	7	1	5	13	17	10	27	22
2904/24R	7.6		1	13	2	7	1	5	15	20	9	29	24
2904/24L	7.6		1	15	2	7	1	5	17	22	9	33	27
2997/57	8		1	10	5	5	1		15	15	10		22
2997/70	7.9		1	10	5	5	1		15	15	10		22

specimen Forewing (*fusion)	l (in mm)	w (in mm)	SC	R	M	CuA	CuP	A	RM	RCuA	MCuA	SUM	SUM (without A)
2997/75L	7.2	1.9	1	11	3	5	1	6	14	16	8	26	21
2997/75R	7.2	1.9	1	11	2	6	1		13	17	8		21
2997/76	7.8		1	12	3	5	1	7	15	17	8	29	22
2997/86	6.3	2.5	1	15	4	6	1	6	19	21	10	33	27
2997/215	7.6		1	12	3	6	1		15	18	9		23
2997/732	7		1	14	3	7	1		17	21	10		26
2997/1434	7.9		1	12	4	7	1	6	16	19	11	31	25
2997/1481	7.5		1	13	3	5	1	6	16	18	8	29	23
2997/1501	7.5		1	14	3	5	1		17	19	8		24
2997/1511	7.2		1	11	2	5	1	6	13	16	7	27	21
2997/168	7		1	9	2	5	1	5	11	14	7	23	18
2997/201*	7.4		1	14	2	6	1*	6	16	20	8	30	24
2997/220	7		1	14	4	5	1	5	18	19	9	30	25
2997/245 R			1	12	3	4	1	5	15	16	7	26	21
2997/245L			1	11	4	5	1	5	15	16	9	27	22
2997/267±	7.4		1	11	5	6	1	5	16	17	11	29	24
2997/274			1	12	3	4	1	5	15	16	7	26	21
2997/1454	7.5		1	11	4	5	1	6	15	16	9	28	22
2997/1456	7.8		1	12	3	5	1		15	17	8		22
2997/1457	7.5		1	13	3	7	1	5	16	20	10	30	25
2997/1458	7.7		1	11	4	7	1	6	15	18	11	30	24
2997/1509	7.5		1	11	3	5	1		14	16	8		21
2997/ 1535			1	10	7	3	1		17	13	10		22
2997/ 1545	7.3		1	12	2	5	1	6	14	17	7	27	21
2997/4310	6.7		1	10	3	7	1		13	17	10		22
2997/4318	7.3		1	11	3	6	1	6	14	17	9	28	22
2997/4322	7.5		1	12	3	6	1	6	15	18	9	29	23
2997/4328	6.8		1	10	3	5	1	5	13	15	8	26	21
2997/4336	7.3		1	10	2	7	1	6	12	17	9	27	21
2997/ 1534	7.3		1	11	2	5	1	6	13	16	7	26	20

speci-men Forewing (*fusion)	l (in mm)	w (in mm)	SC	R	M	CuA	CuP	A	RM	RCuA	MCuA	SUM	SUM (without A)
N	99	11	114	114	114	114	114	87	114	114	114	87	114
Ave	7.32	2.22	1.02	12.06	3.61	5.68	1	5.51	15.68	17.74	9.27	28.95	23.4
Min	6	1.9	1	8	2	3	1	4	11	13	7	23	18
max	8.2	2.5	3	17	7	9	1	7	23	23	13	37	31
dev	0.4986438	0.222792	0.1873172	1.495036553	0.973169	1.0848565	0	0.5881299	1.8837715	1.8769804	1.3322752	2.3173162	2.1398838
CV	6.81	10.04	18.36	12.4	26.96	19.1	0	10.67	12.01	10.58	14.37	8	9.14

specimen hindwings	length	sc	R1	RS	M	CuA	CuP	A1	R	RM	RCu	MCu	Total (without a)
1789/9	6.5	1	5	5	2	4	1	7	10	12	15	7	19
2554/78	7	1	5	4	2	5	1	5	9	11	15	8	19
2066/382	7.5	1	4	5	2	5	1	4	9	11	15	8	19
2066/487±	7.3	1	3	6	3	5	1		9	12	15	9	20
2066/293		1	3	8	3	6	1		11	14	18	10	23
2066/258	7	1	5	5	3	6	1	6	10	13	17	10	22
2066/258B	7	1	5	6	3	5	1		11	14	16	8	21
2066/245	8	1	6	5	4	6	1		11	15	18	11	24
2066/240	7	1	5	5	2	7	1	7	10	12	18	10	22
2066/150	7.1	1	5	6	3	6	1		11	14	18	10	23
2066/92	7.5	1	5	6	3	6	1		11	14	18	10	23
2066/125	7.5	1	4	8		5	1		12		18		
2066/71	7.8	1	5	5	3	6	1	7	10	13	17	10	22
2066/782	6.3	1	4	5	2	5	1	5	9	11	15	8	19
1789/53	6	1	5	5	2	5	1	6	10	12	16	8	20
2554/89	7	1	5	6	3	6	1		11	14	18	10	23
2904/57	7	1	4	4	2	6	1		8	10	15	9	19

specimen hindwings	length	sc	R1	RS	M	CuA	CuP	A1	R	RM	RCu	MCu	Total (without a)
2904/41L	7.5	1	5	6	2	6	1		11	13	18	9	22
2904/41R	7.5	1	5	6	2	7	1		11	13	19	9	22
2904/46	7.8	1	5	4	3	5	1		9	12	15	9	20
2066/319±	8.3	1	4	7		7	1		11		19		
2066/421±	6.9	1	4	6	2	5	1	5	10	12	16	8	20
2066/398±	8	1	4	4	4	5	1	5	8	12	14	10	20
2997/4316	6.7	1	5	6	2	6	1		11	13	17	8	21
2997/4314	7.2	1	6	5	2	6	1	6	11	13	17	8	21
2554/51L	6.6	1	3	5	2	5	1		8	10	13	7	17
2554/51R	6.6	1	3	5	2	5	1		8	10	13	7	17
2384/180±	6.5	1	5	5	4	5	1	5	10	14	15	9	21
2997/730	6.7	1	5	6	2	6	1		11	13	17	8	21
2997/23	6.8	1	4	5	2	5	1		9	11	14	7	18
2904/101		1	4	4	4	6	1		8	12	14	10	20
2904/108	7	1	4	5	2	6	1	5	9	11	15	8	19
2904/127	6.5	1	5	5	2	6	1		10	12	16	8	20
2904/128	7	1	4	5	2	7	2	5	9	11	16	9	20
2239/373l±	7.4	1	5	5	2	6	1		10	12	16	8	20
2239/373r±	7.4	1	4	5	2	7	1		9	11	16	9	20
2384/179	8	1	5	4	3	6	1		9	12	15	9	20
2384/189	7	1	4	6	2	8	1		10	12	18	10	22
2384/175	7	1	4	5	2	5	1		9	11	14	7	18
2039/46	7	1	3	4	3	7	1		7	10	14	10	19
2997/4321	7	1	5	5	3	5	1	5	10	13	15	8	20
2997/4329	7	1	4	6	2	6	1	8	10	12	16	8	20
2452/374	8	1	4	6	3	7	1	3	10	13	17	10	22
2997/4326	7.3	1	5	5	2	6	1	7	10	12	17	8	20
2997/1471	7	1	3	6	3	5	1		9	12	14	8	19
2997/1491	7.5	1	3	4	3	4	1		7	10	11	7	16
2997/1514	7.8	1	3	4	2	5	1		7	9	12	7	16

specimen hindwings	length	sc	R1	RS	M	CuA	CuP	A1	R	RM	RCu	MCu	Total (without a)
2997/1500	7.5	1	4	5	2	5	1	3	9	11	14	7	18
2997/1543		1	4	4	2	5	1		8	10	13	7	17
2997/1467		1	5	5	4	6	1		10	14	16	10	22
2997/259	7.5	1	5	5	3	6	1		10	13	16	9	21
2997/1523	7	1	4	5	3	6	1		9	12	15	9	20
2997/1515h	7.5	1	4	5	2	5	1		9	11	14	7	18
2997/1532	7	1	4	4	3	4	1		8	11	12	7	17
2997/226	6.8	1	5	4	3	5	1		9	12	14	8	19
2554/80	7	1	4	6	3	6	1		10	13	16	9	21
2384/176	7.8	1	5	5	2	7	1		10	12	17	9	21
2452/626	7.9	1	5	4	2	6	1		9	11	15	8	19
2997/75	7	1	4	5	2	5	1	4	9	11	14	7	18
2335/34R		1	5	4	2	6	1		9	11	15	8	19
2335/34L		1	3	5	2	5	1		8	10	13	7	17
2997/1516	7.5	1	5	4	2	6	1		9	11	15	8	19
unnumbered	7.5	1	5	5	3	6	1	7	10	13	16	9	21
2997/1457		1	4	6	2	6	1		10	12	16	8	20
29977/274		1	4	5	3	5	1		9	12	14	8	19
2997/245		1	4	5	3	5	1		9	12	14	8	19
2239/114R	7	1	4	5	2	5	1	4	9	11	14	7	18
2239/114L	7	1	3	5	2	6	1	4	8	10	14	8	18
2066/9		1	5	5	2	4	1		10	12	14	6	18
2554/78*DEF	7	1	5	4	2	5	1	5	9	11	14	7	18
2239/56r	6.8	1	3	4	2	5	1		7	9	12	7	16
2239/56r	6.8	1	3	4	2	6	1		7	9	13	8	17
2066/481	8	1	5	4	2	6	1		9	11	15	8	19
unnumbered		1	5	4	2	5	1		9	11	14	7	18
2904/24R	6.7	1	4	5	2	6	1		9	11	15	8	19
2904/24L	6.7	1	3	5	2	6	1		8	10	14	8	18

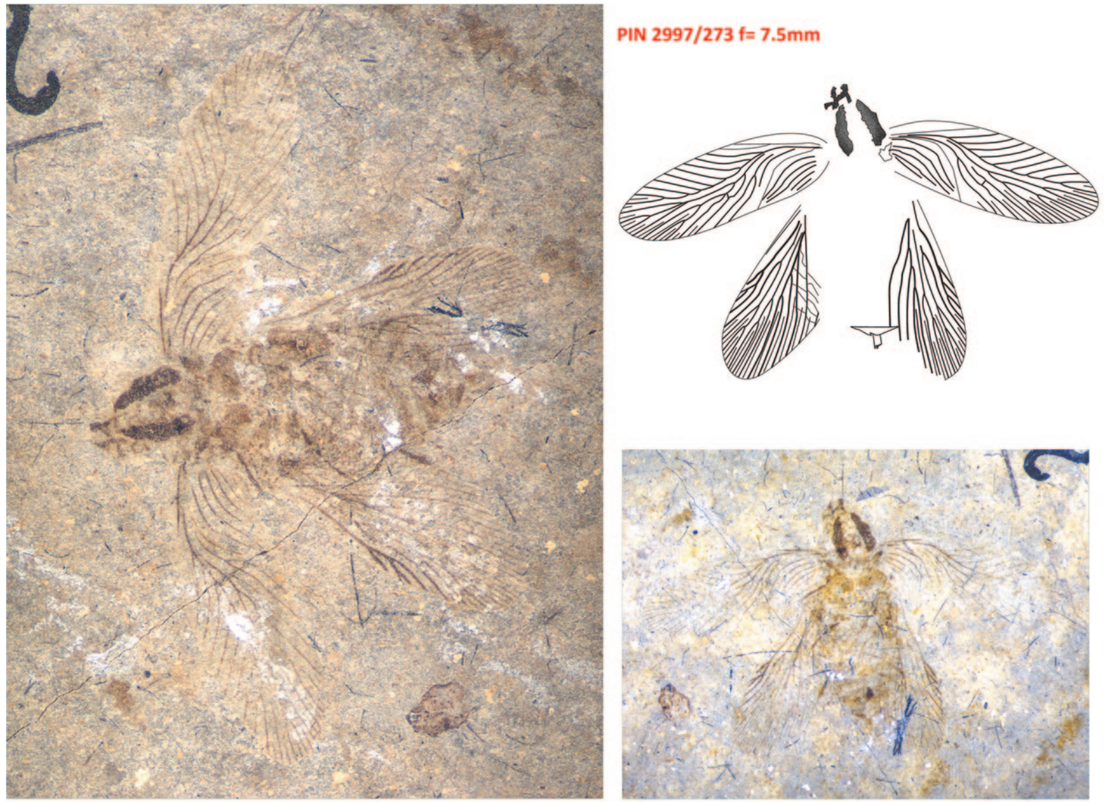
specimen hindwings	length	sc	R1	RS	M	CuA	CuP	A1	R	RM	RCu	MCu	Total (without a)
2904/20L	8.2	1	4	5	3	5	1		9	12	14	8	19
2904/20R	8.2	1	4	3	2	5	1		7	9	12	7	16
2997/76	7.5	1	6	4	2	5	1		10	12	15	7	19
2784/970L		1	5	5	2	5	1		10	12	15	7	19
2784/970R		1	5	4	2	5	1		9	11	14	7	18
2784/689L	7.8	1	4	5	2	5	1		9	11	14	7	18
2784/689R	7.8	1	4	6	2	6	1		10	12	16	8	20
2997/1454	7.8	1	3	4	2	5	1		7	9	12	7	16
2784/745	7	1	5	3	4	5	1		8	12	13	9	19
2784/640		1	5	4	2	6	1		9	11	15	8	19
2066/641	7	1	5	4	2	6	1		9	11	15	8	19
2997/131	6.5	1	4	8	5	6	1		12	17	18	11	25
N	74	88	88	88	86	88	88	24	88	86	88	86	86
Min	6	1	3	3	2	4	1	3	7	9	11	6	16
Max	8.3	1	6	8	5	8	2	8	12	17	19	11	25
Ave	7.22	1	4.34	4.99	2.45	5.59	1.01	5.33	9.33	11.73	15.18	8.26	19.53
Dev	0.49876	0	0.78617894	0.964834	0.680086	0.767686	0.1066	1.34056	1.171712	1.426014	1.765216	1.118676	1.901688
CV (%)	6.91	0	18.11	19.34	27.76	13.73	10.55	25.15	12.56	12.16	11.63	13.54	9.38

***Blattula nebude* sp.n.**
(figp. 463)

Holotype: PIN 2997/273 (f= 7.5 mm; 1 ,11, 8, 2!!!, 1, 6; L 1, 11, 7, 2, 1, 6; Lh=Rh= 7.5 mm; 1, 4+4, 3, 5+1). Part and counterpart of a complete articulated adult female.
Type locality: Mikhailovka, Karatau, Kazakhstan
Type horizon: Upper Jurassic Karabastau Formation

Additional material: PIN 2997/1431± (complete specimen); 2904/1898; 2997/140 (isolated pronota). All the same locality as the type.

Differential diagnosis: Differs from *B. brevicaudata*, its sister taxon only in different pronotum coloration with two long longitudinal stripes and in simplified forewing CuA (2). Total number of veins 28-29 is consistent with that of *B. brevicaudata* (25-33); 18 total remigium veins is consistent with that of *B. brevicaudata* (16-24).
Autapomorphy: CuA simplification (2)
Description: Head hypognathous, concealed under pronotum, in natural active position likely protruding beyong the pronotum outline by eyes. Shape oval, wide 0.78 mm, with large eyes. Pale, with typical two interconnected dark stripes.
Pronotum slightly transverse, oval, without posterior central extension and well developed pale paranotalia. Centre of the pronotum is with two dark longitudinal stripes.
Forewing elongate (7.3/ 2.48 mm), margins paralel, apex posed nearly centrally, intercalaries and cross-veins distinct, membrane transparent. Costa melanised, narrow and short, reaching only contact with SC, costal area narrow, SC nearly straight, simple or simply dichotomised. R stem sigmoidal, RS undifferentitated, with 9-10 veins at margin. M expanded to all apex, with 7-9 veins at margin. CuA with 2 veins at margin (and a blind branch). CuP simple, sharply curved, without terminal curvature towards margin. A (5 or 6) simple.
Hindwing 6.7 mm long, with pleating of vannus not veer-like. Remigium narrrow, triangular. SC simple, straight, short. R1 very distinct, heavily scleroitised, colored and wide, without pterostigma, with 4 veins meeting margin (in holotype R1 is asymmetricallly (4-4) secondarily branched). RS differentiated, with 4 veins at margin. M with 3 veins. CuA with 5 simple branches, CuP simple. A1 present in remigium, with 6 blind branches.
Body wide. Ovipositor tubular, short.
Remarks: The bad message for taxonomists is that this species was recognised only on the basis of different pronotum coloration. Good message is that it was supported by one forewing trait, namely the simplified CuA with 2 veins contrasting with 4-8 of *B. brevicaudata* (n= 114; 3 in one case). The bad message is that this might be, although with small probability, stochastical. Otherwise the wing fits the variability of *B. brevicaudata* (see *B. brevicaudata* variability discussion above).
Mutations (this specimens is not inlcuded in the total count): Multiply deformations present in forewings (M trichotomy, CuA blind branch; and unusually secondarily branched R1 in a hindwing). Remarkable is symmetrical M-CuA (M-M) deformity respectively on both forewings. It distinctly reveal that a mutation is restricted to area (position in wing) and not to a specific vein system.
Derivation of name: *nebude* is Slavic for "will not be anymore"
Character of preservation: 2 complete specimens; 2 isolated pronota.
Taphonomy: Completely articulated specimens suggest a short trasport prior to deposition, while two isolated pronota reveal contrary. In this respect, dominant *Blattula* species rarely have preserved isolated pronota, which support longer transport in the present species. Taphonomy with isolated pronota lacking in *B. brevicaudata* supports discrimination of these two species based on morphology.

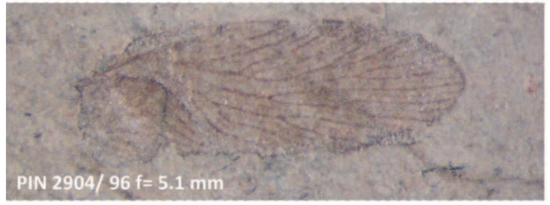


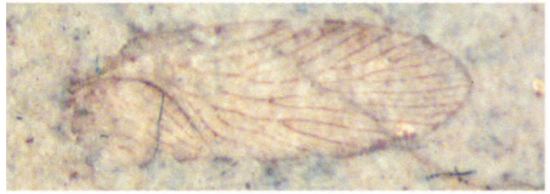
***Blattula microscopica* sp.n.**
(figs. 465-471)

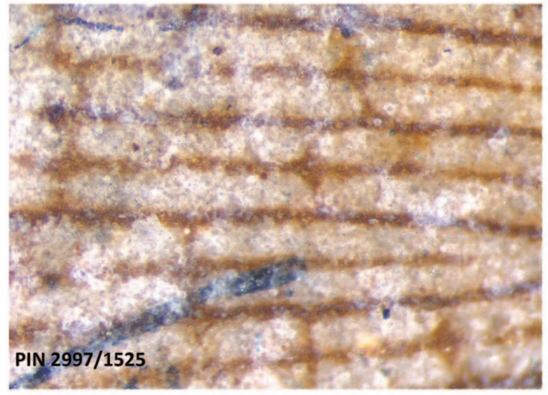
Holotype: PIN 2066/471=432. Part and counterpart of a complete articulated adult male.
Type locality: Mikhailovka, Karatau, Kazakhstan
Type horizon: Upper Jurassic Karabastau Formation

Additional material: PIN 1789/73 (l= 5.5 mm) **G**; 2239/79, 84, 378 (l= 7 mm up to ovipositor tip), 1766; 2384/183, 198 (f= 5 mm); 2452/392 (f= 5 mm); 2904/1903 (f= 5.3 mm), 1878; 2997/1445; (complete specimens); (*)167/295 (f= 4.8 mm); 2066/79 (f= 5.5 mm), 165 (f= 5 mm), 339 (f= 5 mm) 2784/657; 2904/96; (isolated forewings); 1789/225 **G**; 2066/143, 338 (h= 5.2 mm), 355, 379, 716 (h= 4.9 mm), 746; 2239/61, 374; 2384/158, 169, 948, 955; 2554/54; 2784/895, 931; 2904/51±; 2997/1504, 1548; 4333 (h= 5 mm) (isolated hindwings). All except G= Galkino from Mikhailovka.

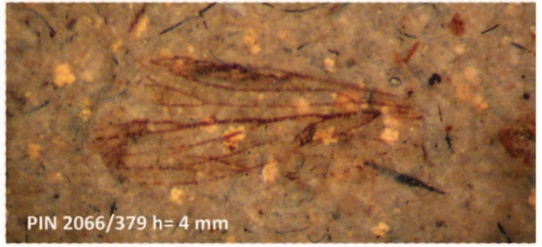
Differential diagnosis: Differs from *B. extensa* (Toarcian of Iya; forewing length 4.0 mm) in being slightly larger and from all other representatives of the genus in being much smaller. Similar size group (4.5-5.5 mm) are only *B. disjuncta* (Berriasian Wiltshire; differs in wider R); *B. dubia* (Toarcian of Dobbertin; significantly more reduced forewing venation); *B. vidlickai* (Barremian of Shar-Teg; more anteriorly shiofted FW apex) and *B. willmotti* (Toarcian of Mintaja; significanlty more developed FW CuA, M nearly reduced to few apical area).
Description: Head hypognathous, concealed under pronotum, in natural actiove position likely protruding beyong the pronotum outline. Shape oval, wide (1.0 mm), with large eyes. Dark, probably without typical two dark stripes. Ocelli unpreserved.
Pronotum slightly transverse (ca. 2/ 1.7 mm), oval, with posterior centra extension and well developed pale paranotalia. Centre of the pronotum is dark, with pale V-shaped area.
Forewing elongate (4.8-5.8/ ca. 1.7 mm), margins non paralel due to miniaturisation – posterior margin is straight, anterior one is arcuate. Costal are is very narrow, SC is nearly straight, simple, rarely branched (2-3). R stem is sigmoidal, RS undifferentitated, with 9-13 veins at margin. M expanded to all apex, with up to (2-) 6 veins at margin. CuA with 2-7 veins at margin. CuP simple, sharphly curved, without termional curvature towards margin. A (4-6) simple.
Hindwing 4-5.7 mm long, with pleating of vannus not veer-like. Remigium narrrow (in smallest individuals) to very high, triangular. SC simple, straight, short. R1 very distinct, heavily scleroitised, colored and wide, without pterostigma, with 1-5 veins meeding margin. It might be strongly sigmoidally curved in smallest individuals up to nearly straight in largest. RS differentiated, with 1-7 veins at margin. M with up to 5 veins, sometimes reduced to as ingle vein as in Ectobiidae. CuA with 4-7 simple branches, CuP simple. A1 present in remigium, with up to 7 blind branches.
Legs short and robust, tibiae BW-striated. Body comparatively narrow, but fat body seems preserved; terminalia reveal surprisingly short ovipositor.
Remarks: All specimens are categorized within this species on the basis of identical (very small) size.
Systematical remarks: Species in the genus *Blattula* belonging to the small cohort differ in composition of veins related to reduced size. No miniaturisation is yet present in size over 4 mm, but veins are reduced in different way across this small species. Differently is modified also shape, so distinguishing of the present species is safe. Tracing the origin of the present small species is impossible, although origin from most common *B. brevicaudata* is excluded on the basis of wing shape and more extensive coloration of *B. brevicaudata*. More likely this cohort of miniature species parallely occurs across time and space in the Jurassic and Cretaceous.
Ecological remarks: On the basis of fat body, these cockraoches are presumed detritivores, and some related taxa were proved as dung decomposers (Vršanský et al. 2012). Nevertheless, judging from the

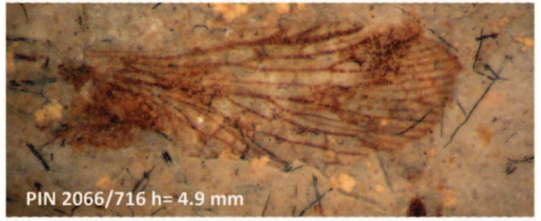


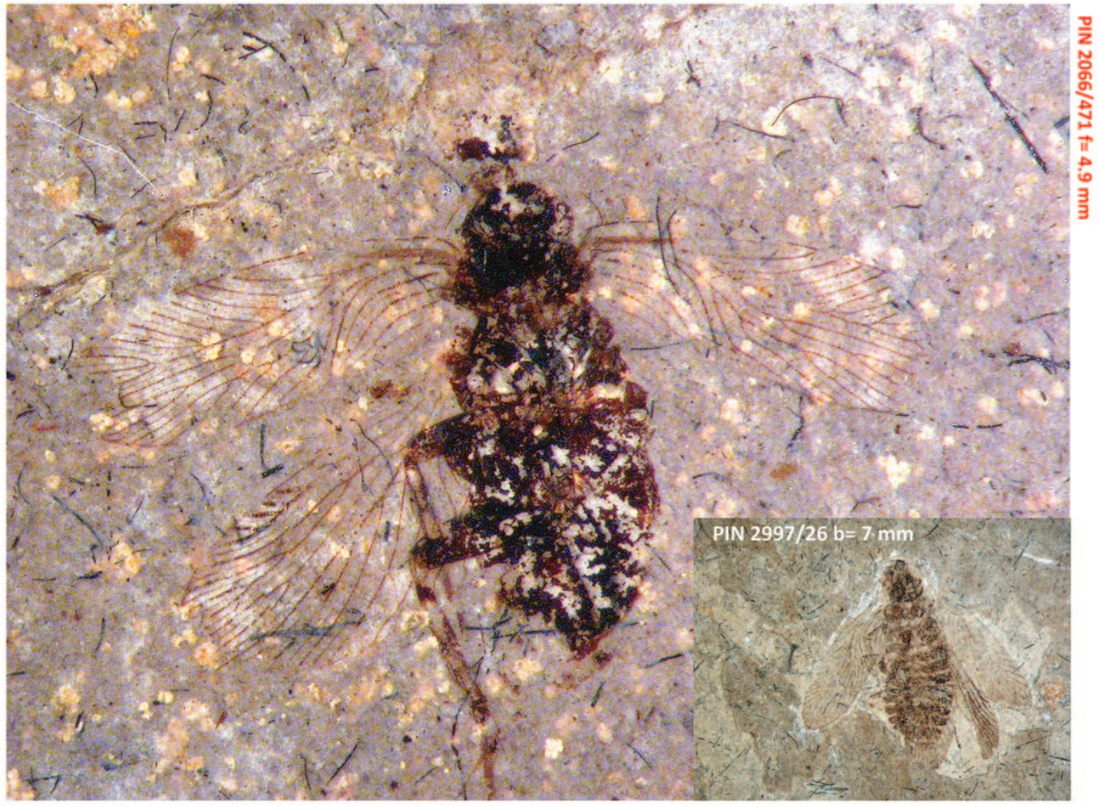




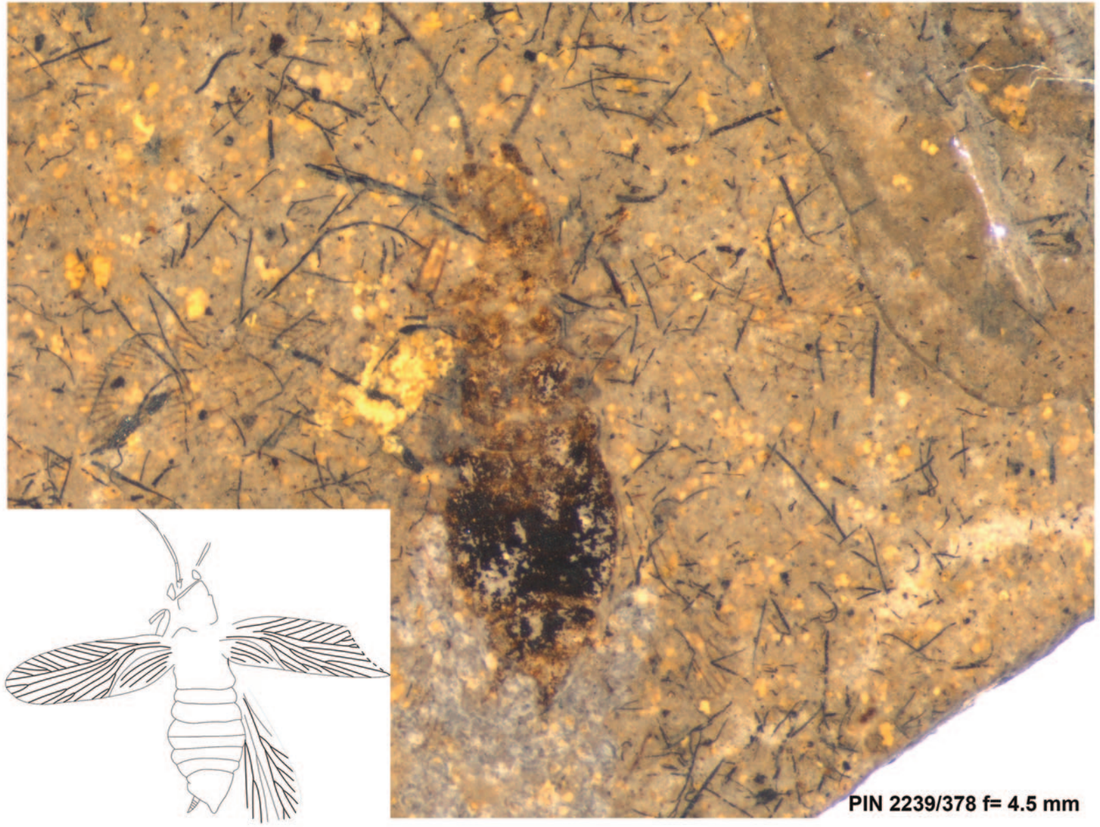


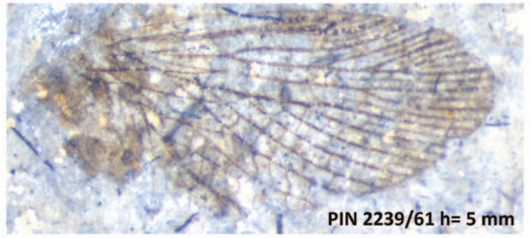




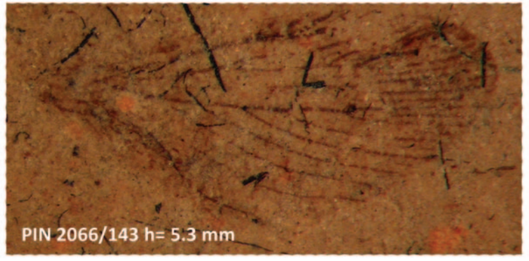

PIN 2066/471 f= 4.9 mm
PIN 2997/26 b= 7 mm

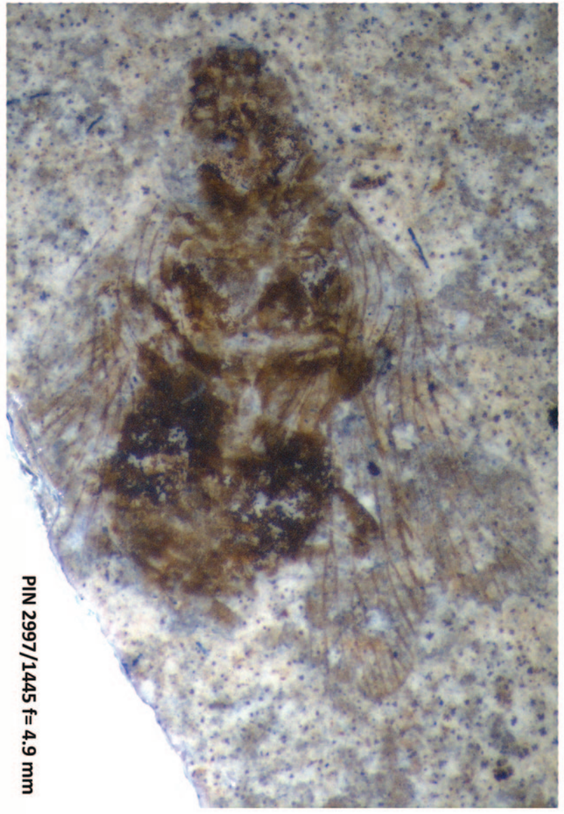

PIN 2066/432 f= 4.8 mm
PIN 2239/76 f= 5.8 mm

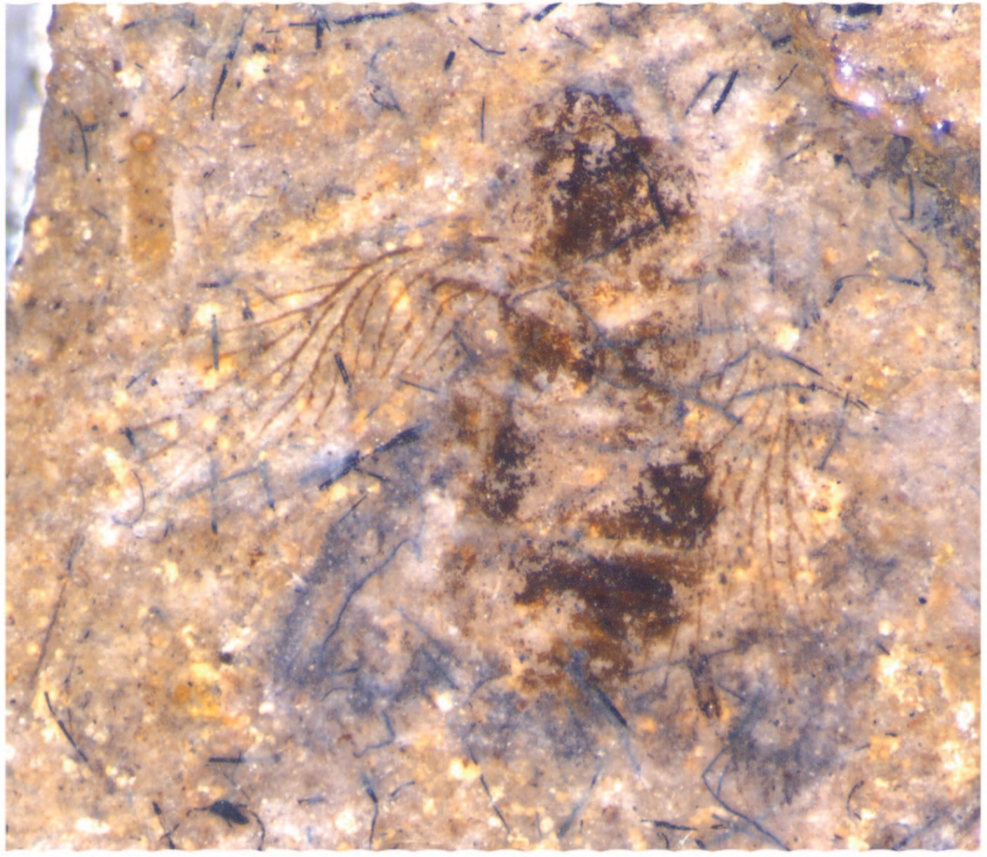

PIN 2239/378 f= 4.5 mm


PIN 2239/61 h= 5 mm

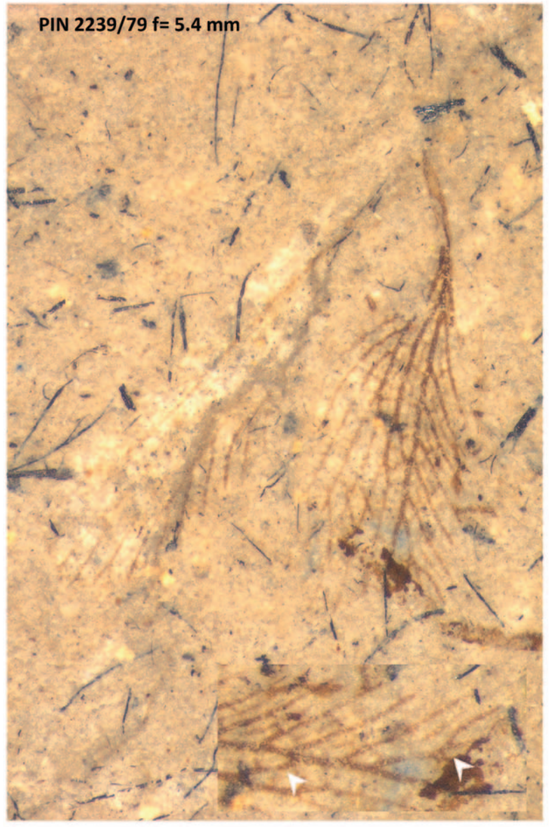

PIN 2904/47

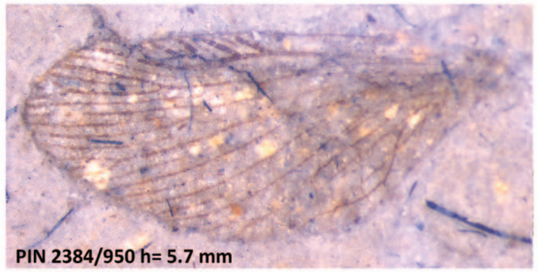

PIN 2066/143 h= 5.3 mm

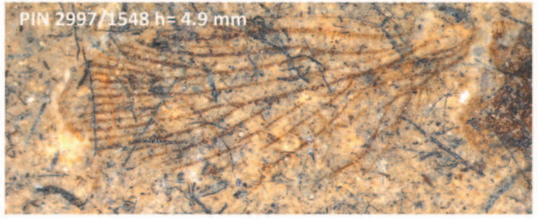

PIN 2997/1445 f= 4.9 mm



PIN 2239/84 f= 4,7 mm









specimen forewings	l	w	Sc	R	M	CuA	CuP	A	RM	RCu	MCu	Without A	Total
2066/471L	4.8		1	10	3	5	1	5	13	15	8	20	25
2066/471R	4.9		1	10	3	4	1	4	13	14	7	19	23
2066/356	5		2	13	3	5	1		16	18	8	24	
2784/657	5		1	11	2	5	1		13	16	7	20	
2784/ 955	5.3		1	12	4	5	1	5	16	17	9	23	28
2066/49	5.1		1	13	3	5	1		16	18	8	23	
2066/356	5		3	13	3	4	1		16	17	7	24	
2066/432L	4.8		1	12	3	4	1	5	15	16	7	21	26
2066/432R	4.8		1	10	3	5	1	5	13	15	8	20	25
2384/ 948	5		1	10	3	7	1		13	17	10	22	
2997/1445	4.9		1	12	3	5	1	5	15	17	8	22	27
2904/96	5.1	1.7	2	10	4	4	1	6	14	14	8	21	27
2239/378L	5		1	12	5	3	1	5	16	15	8	22	27
2239/378R	5		1	12	5	3	1	5	16	15	8	22	27
2239/76	5.8		1	9	6	2	1	5	15	11	8	19	24
2239/79	5.4		1	10	3	6	1		13	16	9	21	
min	4.8		1	9	2	2	1	4	13	11	7	19	23
max	5.8		1	13	6	7	1	6	16	18	10	24	28
N	16		16	16	16	16	16	10	16	16	16	16	10
Dev	0.25811819		0	1.327591805	1.032795559	1.211060142	0	0.471404521	1.364734406	1.778341924	0.816496581	1.590335394	1.595131482
ave	5.06		1	11.19	3.5	4.5	1	5	14.56	15.69	8	21.44	25.9
CV	5.1		0	11.86	29.5	26.91	0	9.43	9.37	11.33	10.2	7.42	6.16

specimen hindwings	l	Sc	R1	RS	M	CuA	CuP	A1	R	R+M	R+Cu	MCu	Total (without a)
2066/471	4.9	1	5	4	2	5	1		9	11	15	8	18
2066/746	5	1	3	4	3	4	1		7	10	12	8	16
2066/ 143	5.4	1	5	5	2	6	1		10	12	17	9	20
2066/355	5	1	4	4	2	7	1		8	10	16	10	19
2784/931	5.1	1	3	7	3	7	1		10	13	18	11	22
2066/143	5.3	1	4	5	2	6	1	6	9	11	16	9	19
2066/338	5.2	1	5	5	2	6	1	6	10	13	17	9	20
2066/337	5.2	1	5	5	3	6	1	5	10	13	17	10	21
2066/379	4	1	3	4	2	5	1		7	9	13	8	16
2784/895	5	1	5	5	2	5	1		10	12	15	7	19
2997/1504	5	1	4	4	3	5	1		8	11	13	8	18
2239/374	5	1	3	7	3	5	1		10	13	15	8	20
2384/158	5	1	4	4	4	6	1		8	12	14	10	20
2239/ 61	5	1	4	5	2	6	1		9	11	15	8	19
2997/1548	4.9	1	3	4	2	6	1		7	9	13	8	17
2554/54	5.5	1	4	5	1	5	1		9	10	14	6	17
2904/51	5	1	3	4	2	5	1	7	7	9	12	7	16
2066/716	4.9	1	3	4	3	4	1		7	10	11	7	16
2904/47C		1	4	4	2	5	1		8	10	13	7	17
2384/950	5.7	1	3	7	3	6	1		10	13	16	9	21
N	19 4	20	20	20	20	20	20	4	20	20	20	20	20
min	4	1	3	4	1	4	1	5	7	9	11	6	16
Max	5.7	1	5	7	4	7	1	7	10	13	18	11	22
Ave	5.06	1	3.85	4.8	2.4	5.5	1	6	8.65	11.1	14.6	8.35	18.55
Dev	0.337170892	0	0.812727701	1.056309365	0.680557047	0.827170192	0	0.816496581	1.225818738	1.447320573	1.95744194	1.268027893	1.877147893
CV	6.66	0	21.1	22	28.36	15.04	0	13.6	14.17	13..04	13.4	15.19	10.12

identical pronotum with *Ocelloblattula* Anisyutkin et Gorokhov, 2008 and *Huablattula* Qiu, Wang et Che, 2019, it cannot be excluded that these species were predatory.

This species occur in both bird/ pterosaur coprolites/ regurgites. In 2997/1686 it is preserved as a broken isolated forewing. In 2452/578 it occurs as a both complete juncioned hindwings. This evidences important role of these cockroaches in active food chain. Co-presence of other species in these coprolites is discussed separatedly in a discussion chapter "coprolites/regurgites".

Mutations: PIN 2066/356 is an individual which poses a single defromity. Specimen 2239/79 is a completely deformed individual with multiply deformation of a forewing (R, R-M).

Variability: as expected on the basis of small regular and regulated venation, CV of forewing veins meeting margin is very low (7.42 %) as well as variation within respective venation systems variating around ca 10 % on both sides of the wing. This is due to size (posterior and anterior margins are similarly important during flight, which contrast with bigger species, where stress is on anterior margin) and also taxonomy, this group generally possessed very low variabilkity of forewing venation. Hindwing variability is also very low, in remigium 10.12 %, which is a comparable value (due to compensation in vannus, which is impossible to measure on fossils). In spite of insignificant sample size (16 and 20 respectively), these values notably support the very low values obtained for *Blattula* species analysed with statistically significant number of samples.

Derivation of name: *microscopica* is after microscope – alluding to its small size.

Character of preservation: 12 complete specimens; 6 isolated forewings; 20 isolated hindwings.

Taphonomy: Completely articulated specimens and numerous preserved hindwings suggest a short transport prior to deposition. This is supported with high number of preserved individuals. Notably, this cohort of small representatives of the family is not that common in sediments as should be predicted. This cohort of non-colored small Blattulidae is absent also from ambers. Higher partition of hindwings might be caused with better preservation potential of a bit larger hindwings, but also some of the hindwings might represent HW of a slighlty larger species described above. Neverteheless, underrepresentation of forewings is further exemplified with number of complete specimens which is higher that number of forewings. Only number of forewings is unadequate. This pattern is observed also in more numerous *B. rectinervosa*.

Genus *Macaroblattula* Wang, Liang et Ren, 2007

Diagnosis (after Wang et al. 2007): Forewing Sc area with a dark macula and Sc terminally branched, CuP strongly curved, all branches strong and dark. Hind wing with pterostigma, R1 and RS differentiated, CuA strong, with several veins reaching the margin.

Type species: *Macaroblattula ellipsoides* Wang, Liang et Ren, 2007, Early Cretaceous, China.

Type locality: Huangbanjigou, Chaomidian Village, China

Type horizon: Lower Cretaceous Yixian Formation

Macaroblattula velipsespilev sp.n.

(figp. 475)

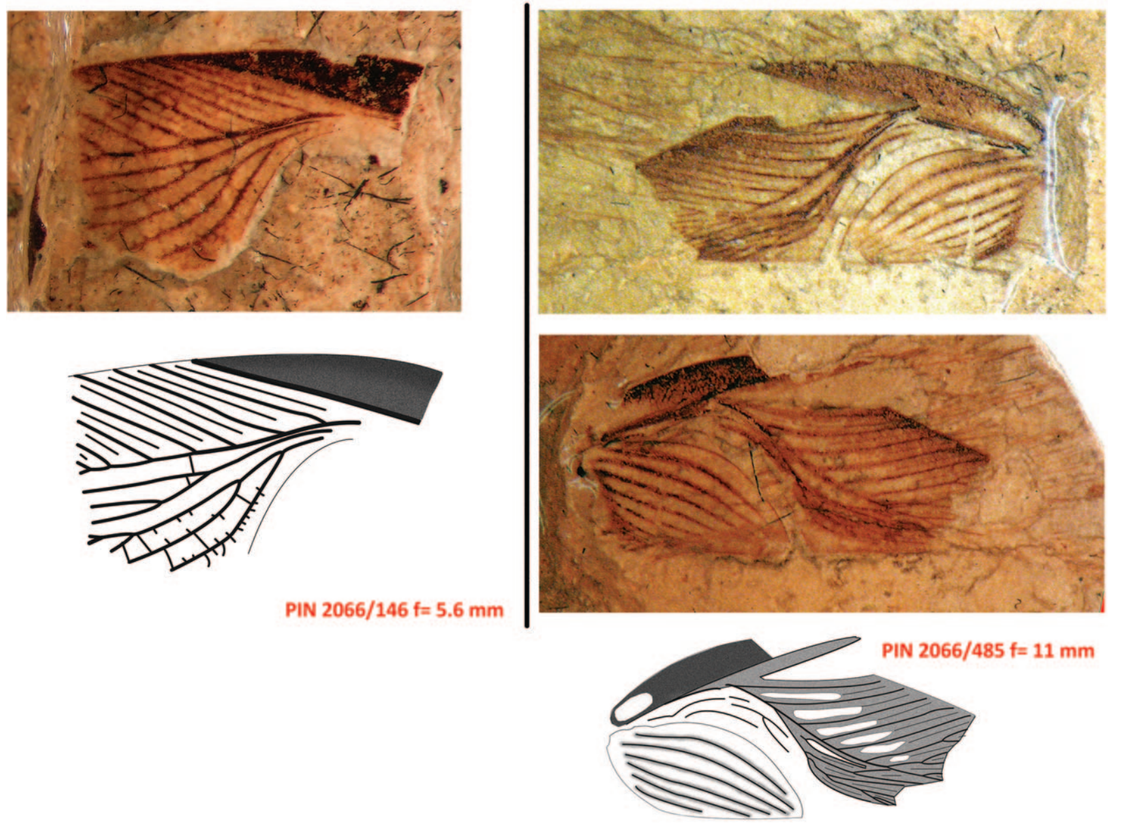
Holotype: PIN 2066/146. Forewing fragmented during collection and/or preparation.

Type locality: Mikhailovka, Karatau, Kazakhstan

Type horizon: Upper Jurassic Karabastau Formation

Additional material: PIN 2997/761 (9 mm). The same locality as the type.

Differential diagnosis: Differing from its



only congener in being somewhat smaller (about 8-9/ 3 mm contrasting with 11/ 3.5 mm of *M. ellipsoides*) and in lacking distinct terminal branchelets of Sc.
Autapomorphies: none, and lacking autapomorhy of the type species
Description: Subcosta terminates in the same length as clavus, is very dark (black), rest of the membrane is pale (likely transparent). First 6 branches of R apparently simple; M with at least three long branches; CuaA with numerous crossveins preserved as CW bases.
Remarks: Forewing Sc terminal branches are indistinct if any (plesiomorphy), otherwise the both taxa are extremely similar in general morphology as well as in running of visible veins (simple basal R branches are characters of individual variation commonly known in other species including the family) in spite of a significant difference in size and time of existence.
Derivation of name. After *v elipse spi lev* (Slovak palindrome with meaning "in elipsis a lion is sleeping") – partially alluding to type species name.
Character of preservation: Two damaged (one disarticulated) forewings.
Taphonomy: Two isolated and damaged forewings suggest pre-depositional transport.

Genus *Pseudomantina* Sendi et Vršanský in Vršanský et al. (2021)

Type species: *Pseudomantina occisor* Sendi in Vršanský et al. (2021). Lebanon amber.
Composition: Type species, *P. nigroalba* Vršanský, in Vršanský et al. (2021) (Karabastau). *P.* sp. (Yixian)

Stratigraphic range: Late Jurassic (Kimmeridgian) – Lower Cretaceous (Barremian)
Geographic range: Laurasia and Gondwana, circumtropical

Differential diagnosis (after Vršanský et al. 2021): Differs from most Liberiblattinidae in having 'SC' simplified, and from possibly related *Ocelloblattula, Kridla, Habroblattula* and *Svabula* in possessing simplified coloration restricted to anterior forewing margin, having more elongate forewing (and not round at apex at least in *P. nigroalba*) and in more pronounced raptorial leg carination. Most similar taxon, *Svabula* Vršanský, 2005 known from sediments of Semen and Sharin-Gol (Russia and Mongolia) and from Myanmar amber, differs in having more wide wings with wide radial area, shorter 'SC' and more limited coloration.

Pseudomantina nigroalba Vršanský in Vršanský et al. (2021)

(figp. 477)

Holotype: PIN 2554/49. Imprint of a completely articulated forewing 5.3 mm long. Designated by Vršanský et al. (2021).
Type locality: Karatau, Kazakhstan.
Type horizon: Kimmeridgian Upper Jurassic, Karabastau Formation.

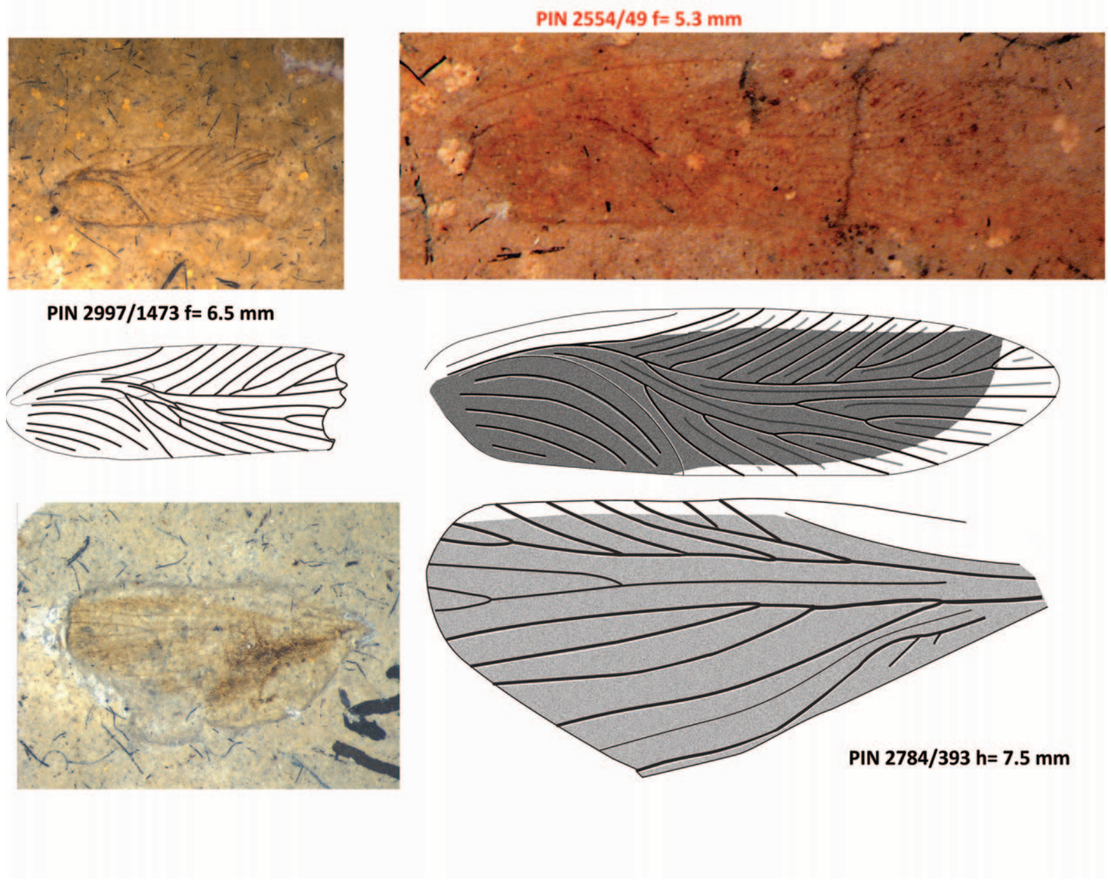
Paratypes: PIN 2997/1473, 515 (forewings); 2784/393 (hindwing). Designated by P.V. Vršanský et al. (2021). The same locality as the type.

Character of preservation: 3 isolated forewings, one isolated hindwing.
Taphonomy: isolated forewings and also a hindwing might indicate short pre-depositional transport.

Genus *Asvab* gen.n.

Type species: *Asvab bavsa* sp.n., and by monotypy.

Differential diagnosis. Differs from all representatives of the family except *Okienkula* gen.n. in having main veins surrounded by pigment, and from *Okienkula* in having not coloured costal field, but all veins, not just A. *Habroblattula* has, in addition to vein coloration, sophisticated membrane coloration.



Pseudomantina nigroalba

Autapomorphy: none due to coloration of veins being possibly synapomorphic with *Okienkula* and *Habroblattulla*.
Description: as for species.
Remarks: Similar unique autapomorhy of coloration around the main veins again occur in two cockroaches in one locality (and a single one more in Yixian), namely in the present species and in *Okienkula*, which, nevertheless, in this case might eventually be a synapomorphy.
Derivation of name: after *A šváb* (Slovak for "and a cockroach").

Asvab bavsa sp.n.

(figg. 479-485)

Holotype: PIN 2904/105± (IC indistinct). Completely articulated winged adult female.
Type locality: Mikhailovka, Karatau, Kazakhstan
Type horizon: Upper Jurassic Karabastau Formation

Additional material: PIN 2039/27, 37, 42± (l= 13 mm); 2066/118 (w= 19 mm), 269 (f= 10 mm), 304 (f= 9 mm), 424 (f= 10 mm, pronotum two stripes), 3900 (f= 10 mm); 2239/65; 2384/178 (f= 10 mm), 181; 2784/723; 2904/37; 2997/143, 1443, 4243 (f= 8 mm) (complete specimens); 167/291, 311; 2035/37, 40, 53; 2039/30, 41, 53; 2066/163 (f= 10.7 mm), 166 (f= 10.7 mm), 168 (f= 9 mm), 231 (f= 10 mm), 254 (f= 9 mm), 450-545 (indistinct number), 478 (f= 11 mm), 479; 2384/172, 173; 2452/145, 146, 490; 2554/50; 2784/388, 638, 646, 648, 802 (f= 10.4 mm), 936, 528(628) (f= 10 mm); 2904/94, 110 (f= 8.5-9/2.1 mm), 244 (f= 11 mm), 265 (f= 11.5 mm), 1886 (f= 10 mm); 2997/60, 229, 1254 (c= 5.3 mm), 1314, 1321, 1366 (c), 4335 (f= 10 mm), 4343, 4263=4253 (c= 4 mm); unlabelled (isolated forewings); 2066/287, 288 (h= 9 mm), 294, 397±, 473, 484± (h= 10 mm), 517 (colored tip); 2554/53; 2904/153; 2997/505, 1466, 1479, 1540 (isolated hindwings). The same locality as the type.

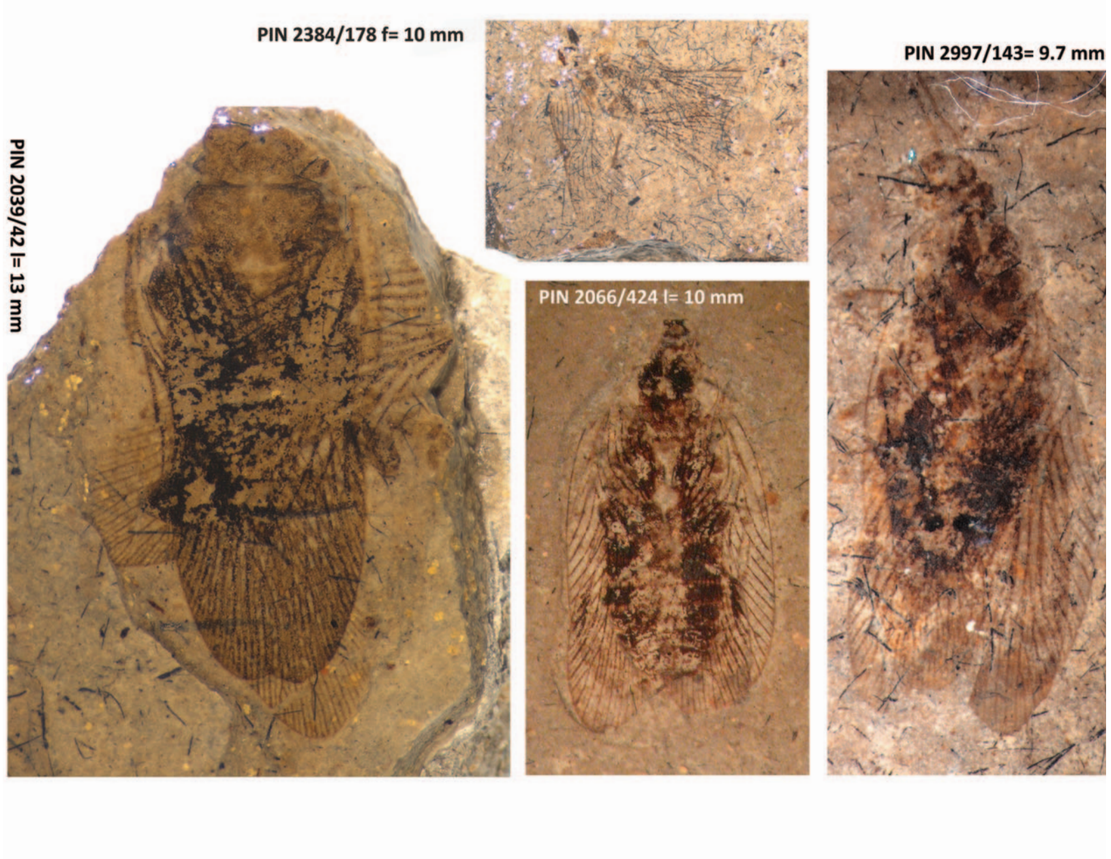
Description: Moderately large species (considering mostly small representatives of this family), with total length reaching 10-13 mm or slightly more. Colored species.
Head with eyes and clypeus dark.
Pronotum pale, with one central posterior and two lateral anterior dark maculas (forming pale central fenestrum).
Body black, 3.2-4.7 mm wide. Female ovipositor, external, short, very wide (1 mm) at base, tubular (0.2 mm in diameter). Cerci multisegmented, thin (0.1 mm).
Forewing elongate (8-11.5/ 2.1-2.6 mm) with unusually parallel margins, slightly sharpened apex posed strictly anteriorly. Membrane mostly transparent, but colored around main veins and also with dark coloration near posteriormost CuA and adjacent anal area. Main veins dark (most probably dark brown, not black, because body is colored more darkly), intercalaries dark only in apical part – this area variate from totally absent (most specimens) to apical distinct narrow area (PIN 2035/40), up to covering nearly all wing (PIN 2035/37; 2452/49). Costa wide, colored very dark, coloration reaches apex; SC simple, but rarely terminally dichotomised. R comparatively straight, with 9-17 veins at margin. In specimens with more extended R, RS is indicated and pre-RS branch can be tertiary dichotomised, otherwise in most specimens R branches are mostly simple. M with 2-8 branches, softly descending and comparatively straigth. CuA comparatively straight (3-10). CuP simple, usually fluent, A simple (5-8).
Hindwing shorter than forewing (9-10 mm), main veins wide and dark (probably dark brown), intercalaries also wide and dark (probably pale brown), distinct in the apical half of the wing. SC simple. R1 and RS differentiated (3-5+6-13). M straight (2-4), colored as all other veins except stem of M (not terminal veins at margin!), which is pale and of reverse polarity. CuA conservative with 6-7 veins at margin; CuP simple. A1 extremely arcuate, with 2-4 blind branches.
Mutations: A single (holotype) mutual CuA-CuA hindwing fusion is recorded among 108 preserved more or less complete wings and 3 isolated clavi.
Variability: Forewing venation variability reveal comparative values 10.3 % (all veins) and 12.57 % (all veins except A) for

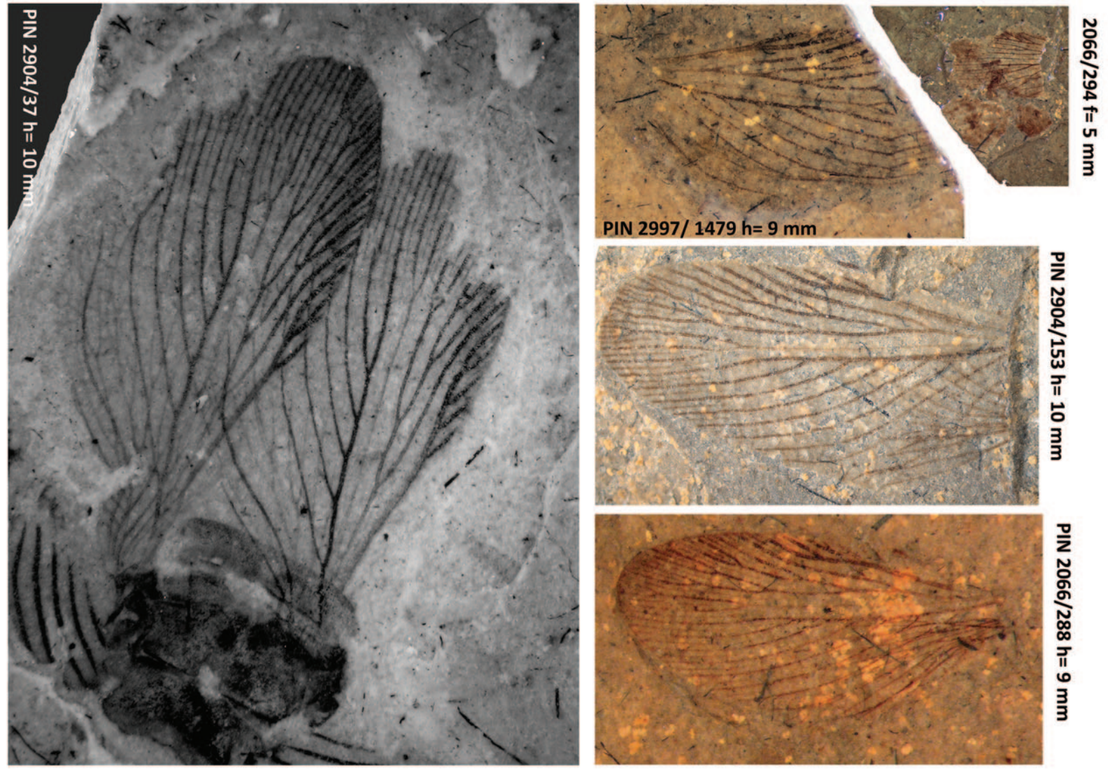


PIN 2384/181 f= 11.5 mm



PIN 2904/105 f= 10 mm


PIN 2384/178 f= 10 mm
PIN 2997/143= 9.7 mm
PIN 2039/42 l= 13 mm
PIN 2066/424 l= 10 mm


PIN 2904/37 h= 10 mm
PIN 2997/ 1479 h= 9 mm
2066/294 f= 5 mm
PIN 2904/153 h= 10 mm
PIN 2066/288 h= 9 mm



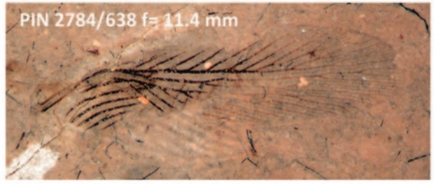
PIN 2452/490 f= 11 mm



PIN 2997/1254 c= 5.3 mm



PIN 2904/94



PIN 2784/638 f= 11.4 mm



PIN 2066/478 f= 10 mm



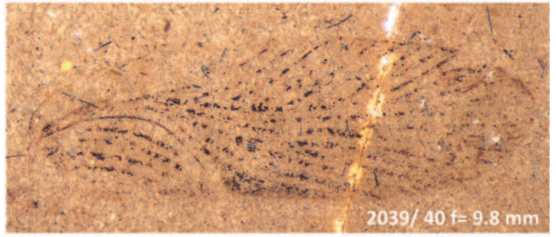
2784/ 648 f= 9.9 mm



PIN 2035/ 37 f= 10 mm



PIN 2035/ 40 9.8 mm



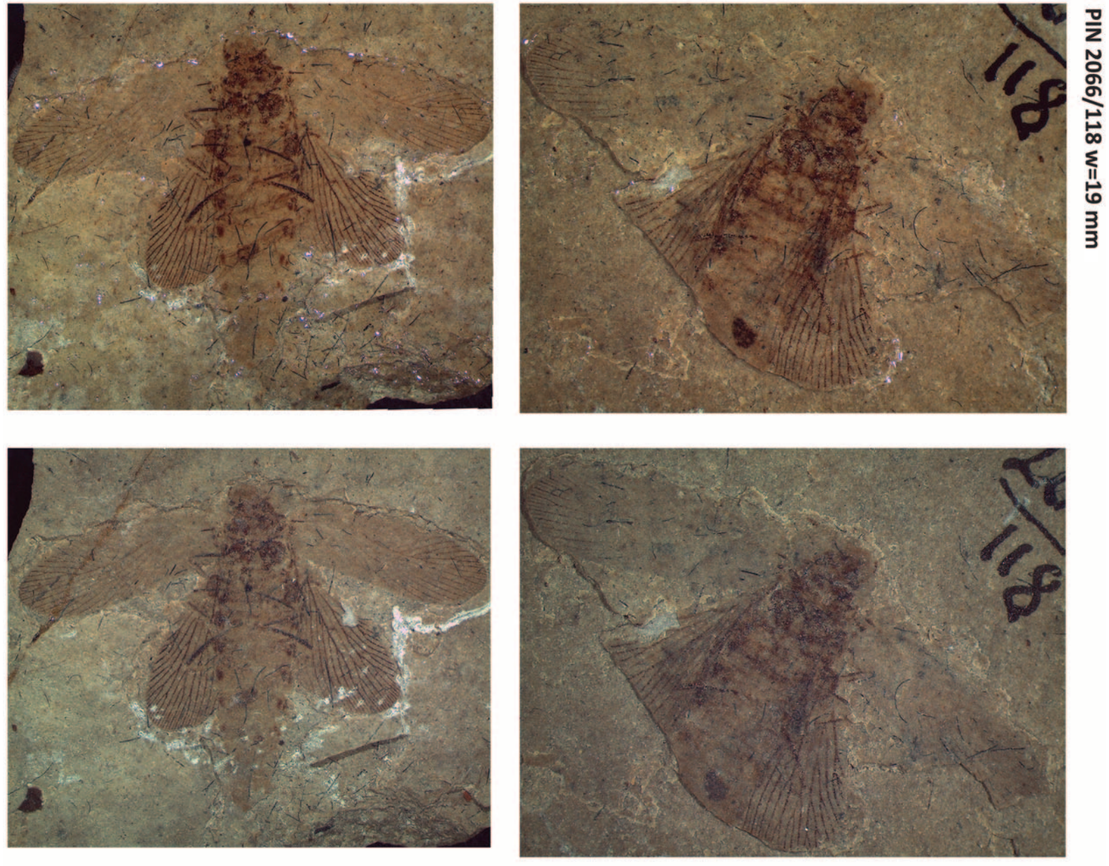
2039/ 40 f= 9.8 mm



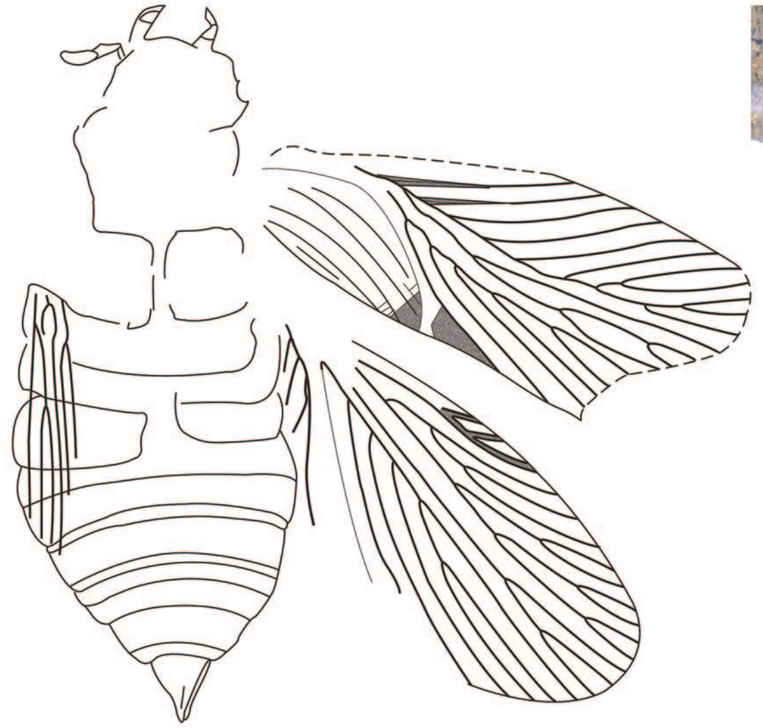
2384/ 173 f= 7.5 mm



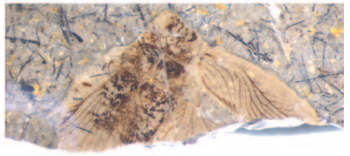
PIN 2035/ 53 f= 9.7 mm



PIN 2904/105 f= 10 mm



PIN 2239/65 w= 5mm



21 (18 complete) specimens. It must be notified that the sample size required for significant values is 30, but changes more than 2 % cannot be expected analysing more specimens.This values are standard, surprisingly low taking into consideration progressive character of the species and its expected contemporaneous origin. On the other side the species is rather small (as all representatives of the family) and presumed well-flying, so its low variability is adequate. In this respect, the variability of hindwings (mostly different specimens) 11.33 % is supportive.

Interesting is also different length of forewings (2066/118: 9.2/ 8.6 mm), while hindwing are identical (8.0 mm).

Remarks: Remarkable is the identical coloration along the costal area and identical pattern around CuP. This woul support the speculation about that the clavus originally represented the separate wing and that the cockroach wing might be composed of two separate wings (Vršanský and Kazimírová 2023).

Remarkable si also that CuA was comparatively straight and standard, but in both specimens with more extensive coloration they run parallelly with the margin. Notable is also that this colored species allowed recognition of the stem of hindwing "M" had a different polarity and coloration. This is a direct confirmation stem hindwing "M" representing "-" polarity vein, possibly M(-) (MP).

Body was preserved well sclerotised and very dark in all specimens, but all specimens have preserved pale central area over the body. This might be caused either by real color, preservation state and/or disruption of coloration caused with the gut content.

Especially remarkable is preservation of numerous specimens (PIN 2239/65; 2039/42; 2997/143; 2904/153; 2066/288; 2997/1479; 2066/294; 2784/638; 2066/478; 2384/181; 2384/173) in the sediment full of pollen and with cones. This barely can be an indirect evidence for pollination, but it might reflect living in environment of pollen-full gymnosperms.

Derivation of name: After *A šváb bav sa* (palindrome, in Slovak with meaning "and have a fun cockroach").

Character of preservation: 17 complete specimens, 45 isolated forewings (of them 3 isolated clavi),13 isolated hindwings.

Taphonomy: Abundance of completely articulated specimens with antenna would suggest short or no pre-depositional transport. Nevertheless, most specimens are isolated fore and hindwings suggesting common presence in some of the Karabastau ecosystems. This combined with the fact that most of the complete specimens are highly damaged and usually without heads indicate either pre-burial predation in water (of this colorful species) or rather a moderate pre-depositional transport.

specimen hindwings	length	width	Sc	R	M	CuA	CuP	a	RM	RCuA	MCuA	Total	Sum with a
2997/143	9.7		1	11	7	7	1	7	18	18	14	27	34
2904/105	10	2.6	1	14	6	7	1	6	20	21	12	28	34
2035/37	10		1	14	3	3	1	8	17	17	17	22	30
2035/,40	9.8		1	14	8	7	1	6	22	21	15	31	36
2035/,53	9.7		1	14	6	7	1	6	20	21	13	29	35
2904/94			1	16	5	6	1		21	22	11	29	
2784/648	9.9		1	17	4	7	1	6	21	24	11	30	36
2784/638	11.4		1	17	6	10	1	7	23	27	16	35	42
???:			1	15	5	9	1	7	20	24	14	31	38
2784/723	10.5		1	14	3	6	1		17	20	9	25	
2997/1443	9		1	11	7	7	1	7	18	18	14	27	34
2452/490	11		1	11	3	6	1	6	14	17	9	22	28
2384/173			1	14	5	7	1		19	21	12	28	
2039/40;	9.8		1	14	7	7	1	6	21	21	14	30	36
2039/53	9.7		1	14	5	7	1	6	19	21	12	28	34
2784/646	11		2	15	5	8	1	5	20	23	13	31	36
2066/424L	10		1	10	7	7	1	6	17	17	14	26	32
2066/424R	10		1	9	2	10	1	6	11	19	12	23	29
2384 181	11.5		1	10	7	6	1	7	17	16	13	25	32
2039/27	10		1	14	3	3	1	7	17	17	6	22	29
2066/118L	9.2		3	15	3	9	1	6	18	24	12	30	36
2066/118R	8.6		3	14	4	7	1	5	18	21	11	29	34
N	19		21	22	21	22	22	22	22	22	22	22	19
min	8.6		1	9	2	3	1	5	11	16	6	22	28
Max	11.5		3	17	8	10	1	8	23	27	17	35	42
Ave	10.09		1.14	13.4	5.14	6.95	1	6.32	18.57	20.29	12.48	27.52	33.83
Dev	0.752946283		0.478091444	2.248809209	1.711306936	1.731425857	0	0.749268649	2.730776969	2.83095138	2.50237982	3.45859867	3.485263092
CV	7.46		41.94	16.78	33.29	24.91		11.86	14.7	13.95	20.05	12.57	10.3

specimen hindwings	lewngth	sc	R1	rs	m	cua	cup		Total rem
2904/105±	10	1	3	9	3	7	1		24
2904/153	10	1	3	11	4	7	1		27
2997-1479	9	1	3	6	2	6	1		19
2554/53	11	1	3	13	3	7	1		28
2904/37HH	10	1	4	9	2	6	1		23
2904/37HH	10	1	5	7+	2	6	1	4+	25
2066/287 =288	9,5	1	5	8	3	7	1	5	25
2066/473±	9	1	4	7	2	6	1		21
2066/288	9	1	5	8	3	7	1	5	25
2066/118L	8	1	4	7	3	6	1		21
2066/118R	8	1	4	8	3	6	1	2	23
n	11	11	11	11	11	11	11		11
min	8	1	3	6	2	6	1	2	19
max	11	1	5	13	4	7	1	5	28
ave	9.4	1	3.9	8.6	2.72	6.45	1	4	23.7
dev	0.966091783	0	0.831209415	2.065591118	0.646669791	0.522232968	0	1.732050808	2.686667419
cv	10.28		21.31	24.02	23.77	8.1			11.33

Genus *Spono* gen.n.

Type species: *Spono spono* sp.n. described below, and by monotypy.

Differential diagnosis: Differs from the predatory colored *Ocelloblattula* and *Pravdupovediac* in coloration restricted to apex and basal macula and from all except *Pravdupovediac* in wide costa reaching all the wing. *Pravdupovediac* posses a modified wing shape.
Autapomorphy: Wide costa possibly running all over the forewings (wide black margin around the whole forewings)
Description: as for species.
Derivation of name: after *spona* (Slovak for buckle). Gender feminine.
Remarks: Wide forewing veins combined with small size and somewhat extensive coloration allow categorization of the present taxon within the predatory representatives of the family Blattulidae. *Svabula* (= *Huablattula*) and *Habroblattula* posses a very similar coloration and shape of the wing, but lacks the distinct wing margin appearing from Costa (except for the basis). Other abovementioned genera have more pronounced coloration. It is impossible to sketch the scenario of morphological transformation within this group, but likely the wide margin was derived also within this group (as standard blattulids do not have this trait at all)..

Spono spono sp.n.

((figp. 490)

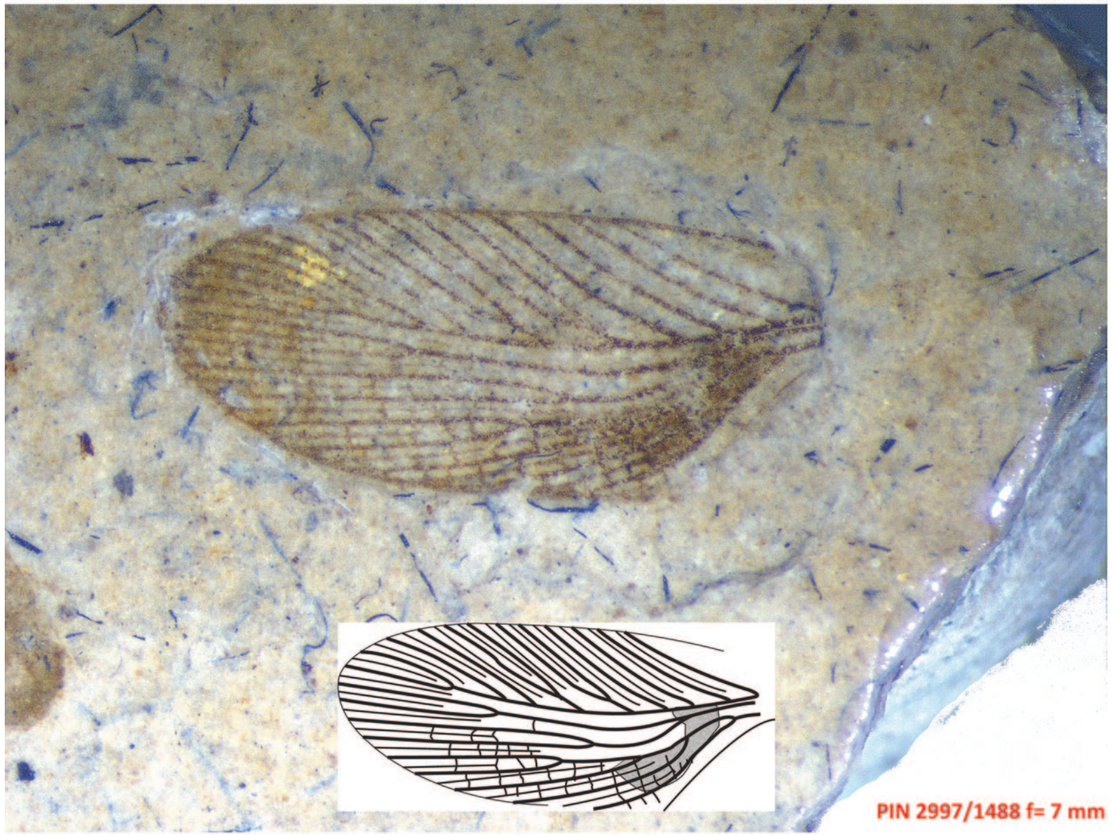
Holotype: PIN 2997/1488. Isolated forewing with disarticulated clavus.
Type locality: Mikhailovka, Karatau, Kazakhstan.
Type horizon: Kimmeridgian Upper Jurassic, Karabastau Formation.

Description: Forewing moderately small, ca. 7 mm as preserved. Margins are more or less parallel, veins and intercalaries thick, cross-veins visiblke in the cubital area. Membrane transparent except for more dark apex and very dark large, ovoid basal macula. Costa very wide, running all along the wing margin – i.e., whole margin is widely colored. SC simple; R with 12 simple veins, RS undifferentiated. M slightly sigmoidal, with 4 veins at margin. CuA sigmoidal, with 5 veins, CuP simple, not specially sharply curved.
Derivation of name: same as for genus.
Character of preservation: one incomplete forewing.
Taphonomy: Partially disarticulated forewing combined with a single ocurrence might suggest longer pre-depositional transport and/or rarity in the source and/or deposition area. Alternatively this taxon might evidence a different deposition basin as suggested by a different (yellow) sediment (1283).

Genus *Okienkula* gen.n.

Type species: *Okienkula ojedinela* described below, by monotypy.

Diagnosis: Differs from all genera except *Macaroblattula* Wang, Ren et Liang,2007 in havning colored costal field. The new genus is unique in having colored nwhole forewing except clavus, and with pale fenestrate pattern.
Description: As for species.
Derivation of name. Modified after *okno* (Slavic for window), referring to the fenestrate coloration pattern.
Remarks. Taking into consideratio lack of coloration of vast majority representatives of the family, coloration of membrane outside costal area should be considered for a trait, derived from otherwise very similar *Macaroblattula* from Cretaceous Yixian Formation slightly younger in age. Coloration should not be refferent as a diagnostic character at genus level, but due to uniqueness of coloration within Blattulidae (only *Ocelloblattula ponomarenkoi* Anisyutkin, 2008; *Habroblattula drepanoides* Wang, Liang et Ren, 2007; *Huablattula* Qui et al. 2019 and *Pravdupovediac* Sendi et al., 2023 are described coloured among more than 200 species), estsablishment of a new genus seems safe. Moreover, also *Macaroblattula velipsespilev* sp.n. from this same locality Karatau is small (about 6 mm).



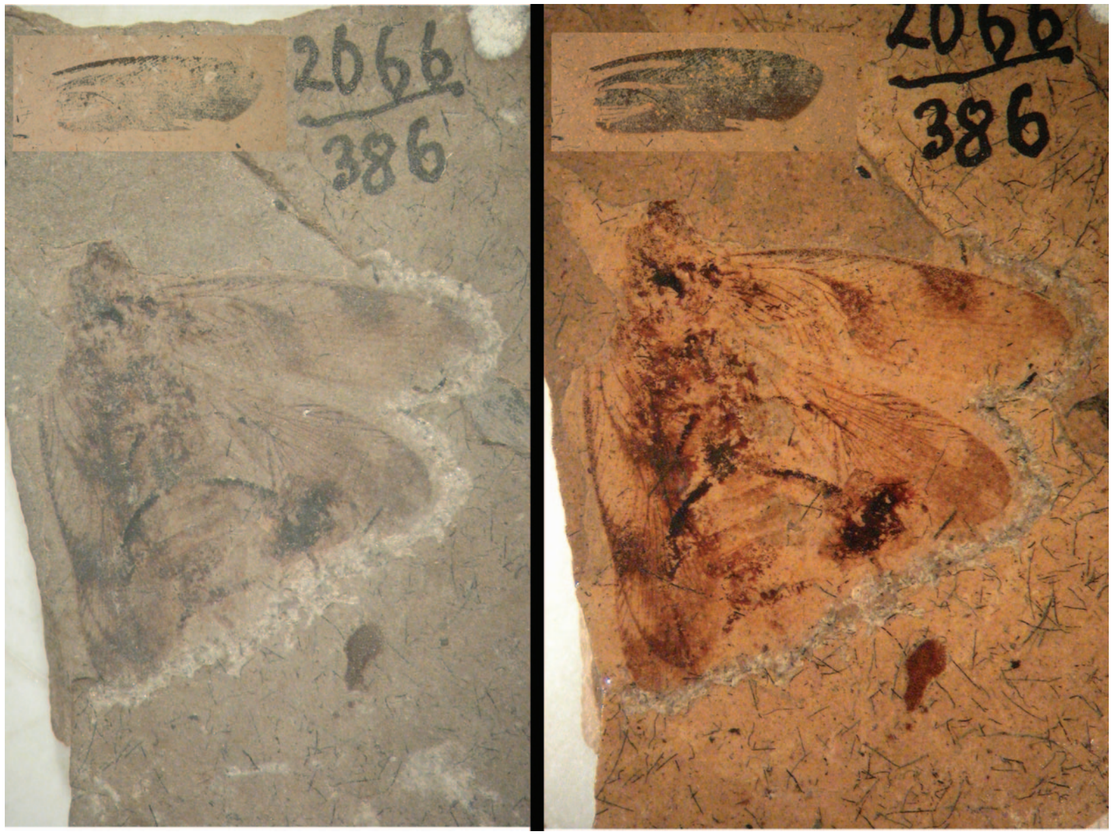
***Okienkula ojedinela* sp.n.**
(figp. 475)

Holotype: PIN 2066/485. Largely decomposed forewing fragment.

Type locality: Mikhailovka, Karatau, Kazakhstan
Type horizon: Upper Jurassic Karabastau Formation

Description. Forewing length estimated at 13 mm, costal area with simple Sc as long as clavus, black. Rest ot the membrane except clavus dark, with pale fenestra. Clavus pale, but 7 anal veins veins with dark surrounding. R with at about 15 veins meeting margin, basal 5 without dichotomisations.
Remarks. The wing has an unusual decomposed forewing (cracked), appointing to the advanced stage of decay (see Duncan et al. 2003).
Deformities: The fusion of veins is illusory, caused with the crossing of cracking fragment of wing.

Derivation of name: After ojedinela (Slavic for that which become alone, and also unique (fem.)).
Character of preservation: One disarticulated and damaged forewing
Taphonomy. Inference of damaged forewing taken together with the uniqueness of sample (n= 1), it is very probable that the sample underwent a significant transport prior to deposition and was living outside of the main sample size source area.



Without and/or with alcohol

DISCUSSION

TAXONOMIC PROCEDURE

Most of the complete specimens, either partially articulated whole cockroaches or their complete wings were photographed, so their trans- and cross-check is also possible. There was a near-infinitive number of checking provided by myself during the study and there was more than 400 versions of the manuscript. Some (known) taxa such as *Blattula* were easily recogniseable to the genus level, but their final species-determination lasted up to the last stages. Here, mainly complete specimens were determined and consequently fore and hindwings could be attributed, and finally immature individuals. Here I must sincerely say that coloration was of a great help, due to high degree of similarity in this group. Also I must sincerely express that even after 30 years of experience, without complete specimens, I would not be able to recognize sister species within some species complexes. Other end of the spectrum was represented with entirely new families erected, which needed complex phylogenetical analysis and all what it takes. There is continuum among these extremes, but generally taxonomy is based mostly on forewings (as usually) and to lesser degree on the complete specimens and isolated hidwings. Genitalia were usually of a little help. Anyway, in the final form, reader has the material on hand determined to high degree of confidence and I determined only material, where I was sure – evidence for this statement is a huge of indetermined specimens. I have some additional doubts about *Asvab bavsa*, where two distinct groups are present, and I am afraid of splitting them – so far there is not enough evidence for erecting two separate species.

BIOLOGICAL SPECIES-LEVEL RECOGNITION

On the basis of a comparative and completely preserved sedimentary record as in Karatau, one will expect a significant advance in recognizing the level of biological species. Just to remind the problematics, due to incertain sedimentology and taphonomy, which are still in pampers in the freshwater lacustrine records, it is sometimes still not clear among fossils in sedimentary palaeontology if we deal with populations, chronospecies or whole genera. This is not clear even in the most common species. Not solving this further, we can try to make this problem more sophisticated. If we look in the amber record, we see a clear pattern of occurrence of the numerous closely related species within both Lebanon (Sendi et al. 2023b) and North Myanmar amber (Vršanský et al. 2021b). Not diving too deep we recognize numerous (over 10) closely related species of *Alienopterix* Mlynský in Vršanský et al. (2018) and none of them would be possible to recognize in the sedi-

mentary record. They all have different microstructure of elytra and also different structural colors. We additionally have genitalia-based differences on many others (*Nodosigalea, Crenocticola, Svabula/Huablattula*, *Teyia*, *Caputoraptor, Ocelloblattula*). The same pattern we observe in *Pravdupovediac* from Lebanon amber. To sum up, these differences are interpreted caused due to the huge time interval in which amber has sedimented and all of them are of little help solving this problem in sedimentary record (often such resolution is missing even for extant species). An unpublished investigations of one-surface records of species from Green River, revealed something between species and genera (transitional variability). This problem can be partially accessed here on the basis of well-sampled dominant species. Unfortunately size-distribution of eudominant *Aktassoblatta fusca* also did NOT solve this problem (see ffigp. 505).

Size distribution of *A. fusca*-complex alone shows normal distribution (figp. 505), but sister species do not necessarily have to differ by size. Vishniakova (1971) nevertheless, recognized a sister species *A. pullata*, again not helping much to our analysis since the holotype is at the same time the largest specimen and might really represent another species. In my own observations in Karabastau, I was unable to recognize any "super" closely related species. There are well-recognised closely related species (in species complexes within *Rhipidoblatta, Blattula, Liberiblattina, Ano* and others to lower degree), but these are well-separated taxa, recogniseable from each other after some effort on the basis of forewings only. I did not separate any of the species presented here on the basis of body or genitalia characters (as it is common in Myanmar and Lebanon ambers). Either the sedimentary material presented here disallows such procedures, either my cognitive capabilities are not strong enough to record differences with plained third dimension, or simply sedimentary record of Karatau (and possibly most of others too) sedimented so shortly that populations did not diverged into separate species. Nevertheless, I am recognizing in this work nine closely related species of *Blattula*.

In this context one observation is particularly interesting and counterindicative. In Karabastau (and in most other *Lagerstätten* such as in Bon Tsagaan, Baissa, Bakhar, Daohugou) we usually recognize more assemblages in collections, frequently displayed with the presence of sister species, which should not live coevally, together. This is also the case is for Karabastau. There are highly probably two assemblages mixed together as numerous Blattulidae (specifically *Blattula*-complex) species reveal. This is standard. Nevertheless, in the huge sedimentary record, never a microstructure-based or micromorphology-based (or genitalia-based) hidden species was recognized. So it is clear, that either capabilities of palaeoentomologists are insufficient, or, more likely, that the diverse ecosystems (expressed as different assemblages) merging in one locality are somewhat "punctuated". My intuition greatly based and supported by the lifeform distribution (Paragraphs below) feels that ecosystems, similarly as species, also occur in some "quantum" modes, meaning that they are discrete.

As always, there is an exception – within the genus *Blattula*. Within 9 well-recognised species there are at least three (*B. brevicaudata, B. druha, B. ahanaha),* which cannot be discriminated visually and statistically on the basis of venation of the forewings, while other characters are very specific (different hindwings and pronota). This uniequivocally means that definitely in the fossil record of cockroaches we, fortunately with very small degree, cannot deal with species but with species-complexes. The degree of this "generosity" can be quantified as number of complete determinable specimens divided by the number of recognized species (with identical forewings). Thus, specimens in these taxa (418+9+4= 431) divided by 3 identified species is 144 – each specimen with number can represent unidentified species. We see that the degree of this "contamination" is not banal (possibly up to 9 unrecogised species with the present material). Even worse is situation with complete specimens, which are so well preserved that were also documented. Here the number is significantly higher: 121 documented complete specimens (1, 2, 118)= 39. It means within each 100 specimens there are 2.5 (totally up to 32) hidden species within the studied (forewing) material.

POLYMORPHISMS

To summarise the abovementioned information, one might expect at least to some degree polymorphic cockroach species. These are nevertheless, nearly impossible to identify. Polymorphic groups (tending to brachyptery) were already recorded in *Nuurcala coloris* Kováčová, 2022 from Aptian Shar-Tologoy in Mongolia (Kováčová 2023a), and that is basically surprisingly all.
One (and I) can intuitively predict polymorphic species within groups with sophisticated coloration such is often the case in modern fauna. But in spite of the rather wide effort I could not with certainty identify any polymorphisms, even within Liberiblattinidae*, Ano. Liberiblattina* and/or within *Falcatussiblatta*. Basically among the huge bulk of species within these complexes, there are always characters other than coloration preventing from identifying these groups as polymorphic. The only possible exception is *Liberiblattina cipka* sp.n., which lacks any coloration at all and possibly represents polymorphic form of some of the other colored species. Even in this case, I decide to erect a new species rather than categorizing it within an existing one, because the holotype specimen is extremely large and the only species with comparable size is excluded for representing its morphotype because of numerous autapomorphic characters.

PROBLEMATIC SPECIMENS

As it is usual in any massive and/or extensive study, some very problematic specimens appeared. At the very beginning, the most problematic appeared within Liberiblattinidae (*Akinisia*) which possesses a long externally protruding ovipositor. According to all indications, they should represent the stem for living groups and should laid ootheca-precursors. This conflict was solved recognizing that ootheca can be laid also with a long ovipositor - to penetrate hardened case and insert oocytes inside (Vishniakova 1968, 1971; see also Sendi 2021b and Vršanský et al. 2021 for oocytes inside ovipositor), and also by a fact that not all Liberiblattinidae are a stem (and recognizing a high diversity of reproduction strategies among them).

The problematic specimens evaluated at the very end unequivocally reveal "untrustily" specimens of Blaberidae (unknown from the Jurassic and from the Cretaceous only since Šmídová et al. (2021) and Oyama et al. (2021)). This not only caused a huge ghost-range, but also required reevaluation of the whole Blaberoidea and Blattoidea and their relations. The *Morphna* species originally thought to be simply put in incertae sedis, finally fits into a totally modified scheme, which is now more consistent with molecular data (Djernaes et al. 2020, Evangelista et al. 2019, 2021).

The specimen which still bring wrinkles is the putative umenocoleid (PIN 2465/937), first because it is a single one, second it belongs to the rare collection PIN 2465/ (nevertheless this collection contains taxa restricted to the Jurassic as well as Karatau indigenous typical Jurassic taxa). Having this specimen separatedly I would without big hesitation place is among Umenocoleidae. Nevertheless, this record is 34 Ma earlier than expected for any umenocoleid or a related group. If it really represent the crown Umenocoleoidea, origins of all major groups (Umenocoleidae, Alienopteridae, Nocticolidae, Mantodea, Isoptera) must be shifted, which is a brutal change to the general scheme. I must say that this is not entirely impossible, as *incertae sedis* taxa resembling these groups are present in Karabastau (*Sociala, Manipulator, Lovec*). Unfortunately there is not a single counterindication and thus

this specimen was categorized within Umenocoleidae and this modified scheme also fits with molecular data (see above).

The same caution I underwent was in *Sociala*, but the evidence convinced myself that it represents a true termite, needing reevaluation of the general phylogenetical scheme and fossil calibrations (or move whole Karatau into the 127Ma Barremian Cretaceous). One more termite is also present in coeval Kota, India. In this light it also cannot be excluded that Chernovskie Kopi with termites is, in concordance with original stratigraphy, Jurassic (see Vršanský and Aristov 2014, Barna 2014).

I am unable to classify within Caloblattinidae several more or less completely preserved specimens (see 2997/1586± (h= 25 mm; figp. 36)).

There is definitely one addional species of very small Raphidiomimidae with a huge head and a central ocellus (PIN 2384/281; figp. 37), which I left as incertae sedis due to a lack of preserved characters.

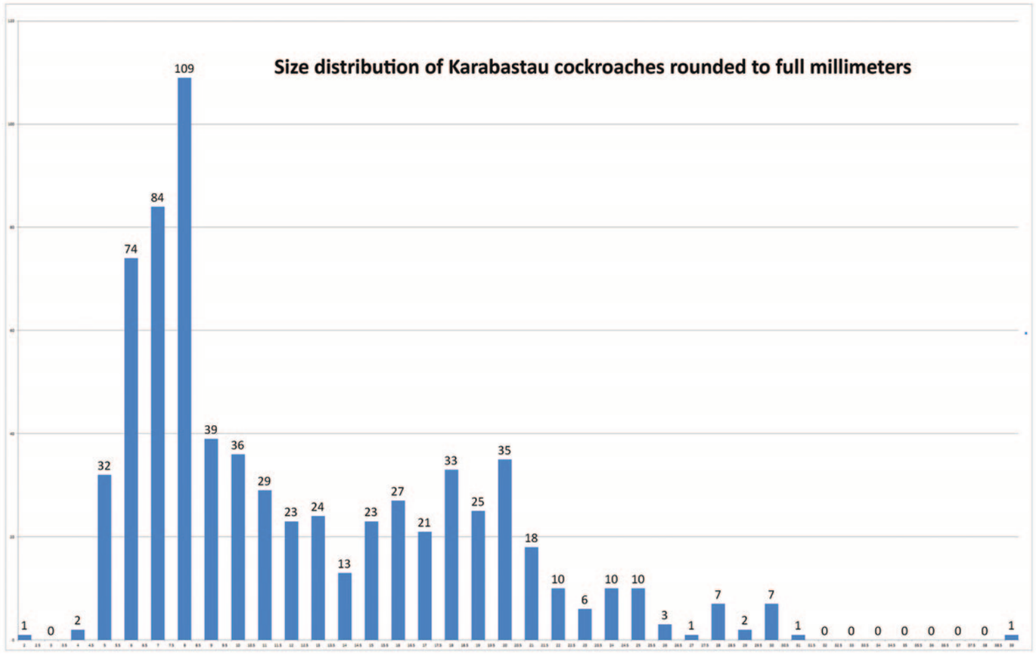
SYSTEMATICS BASED ON COMPLETE COMPARATIVE MATERIAL

The complex procedure neverthess allowed to approach this problematics that were lasting for more than a century (the systematical rank observed in fossils). Informative in this respect are numerous species that were recognized based on complete specimens in the genera *Decomposita, Rhipidoblattina, Latiblatta, Ano* and *Liberiblattina.* 671 specimens revealed taxonomic richness in the genus *Blattula* and its 9 species otherwise unrecogniseable among isolated forewings.
The most suitable information is provided by the notoriously (J1-K2) abundant cosmopolitan genus *Rhipidoblatta*. Preservation of solely forewings reveals a single variable species in the Karatau, while complete specimens reveal 6 clearly differing species and one additional species (see figps. 200,-205, 207-209, 211, 213, 214-217, 219-220, 222-223, 225.). It has a unique pronotum, that could never be categorized within its genus based on forewings only. In spite of the suspiction that we observe here 2 very different assemblages, this has serious consequence on the evaluation of localities with solely forewings preserved. It cannot be completely excluded that each specimen represents a separate species. To repeat, this serious problem (of facultative observation of genera and not uniform biological species) was currently well-documented also in Myanmar amber, where specimens of the genus *Alienopterix* Mlynský, Vršanský et Wang in Vršanský et al. (2018) with sophistically structured forewings reveal each specimen as a separate species (n= 10), while it is impossible to reach the same conclusion on the basis of the simply-structured genus *Jantaropterix* Vršanský et Grimaldi in Vršanský (2003) – Mlynský et al. (2019), Vršanský et al. (2021)) – in analogy possibly also representing 10 different species. This inference (about presence of multiple species wihin locality) is further supported by species revealing male genitalia namely the presence of at least 2 species of the genus *Crenocticola* Li et Huang, 2019 (Li and Huang 2020, Sendi et al. 2020) in burmite. To simplify, the situation in amber is different as it was proposed that responsibility for this “hidden diversity” lie in the long deposition time

of the amber. In the case of burmite it was estimated at up to 30-50Ma (Vršanský et al. 2019, 2023). Nevertheless, on the basis of cockroaches, the long deposition time was presumed also for main sedimentary Lagerstatten such as Baissa or Bakhar among others (Zherikhin et al. 1999, Vršanský 2020). This regards mainly localities with multiple different (cyclic) layers, but apparently there could be also a significant time period in a deposition within a single bed.

SIZE

Measurements taken were rounded to 0.1 mm only and sometimes to 0.5 mm - therefore a carefull size/area analysis has a qualitative character only. Nevertheless, due to a complete lack of interest in these data reveals a significant advance to the field even on the basis of such rough measuring (figps. 498-506). Distributions are rounded to .5. Completely measured wings (n= 706) were subjected to this analysis revealing spectacular results. First of all it is necessary to stress the statistically significant analysis of the two dominant species, of which *Blattula brevicaudata* is too small in size to reveal any deviations from the normal distribution, although data being not counterindicative in this respect. Thus of a primeval interest are data obtained on *Aktassoblatta fusca*, supporting character-analysis-based expertise that all specimen in this complex represent a single species. Data (figps. 498-506) do not have sample size large enough to reveal significant data, but normal distribution cannot be falsified (normality test: W= 0.85; p= 0.06; Potentially Symmetrical pval=0.408) and also support *A. pullata* as a separate species (28 mm in contrast to 25 mm of largest specimen of *A. fusca*). Disregarding the two largest specimens (23, 25 mm), which might also potentially represent *A. pullata* or another species, the dataset results in full normality. While there are some indications (assymetries) in size distribution on the low-resolution patterns of *Blattula brevicaudata*, possibly enabling interpretation related to sex ratio and polymorphism, 64 specimens of *Aktassoblatta fusca* are distributed ideally normally, making sexual dimorphism highly unlikely. This is extremely interesting as these species possessed highly (sexualy) bimorphic morphology including an external ovipositor. The data, provided for the first time in an ovipositor-bearing cockroach that suggests low parental investment in females and possibility of laying more or less sporadic and not numerous, low quality eggs. On the other side, ootheca-producing modern cockroaches are known for the dimorphism since the Cretaeous period (see Vršanský 2003a). Going more widely to the family size-analyses, one can see normal distribution of Caloblattinidae-Raphidiomimidae (decomposers+predators) and rather normal distribution (4-13 mm) of the Blattulidae cohort, with a strange hiatus around 9 mm. This hiatus is extremely peculiar as it is even more pronounced in Liberiblattinidae (2-27.5 mm), where the distribution clearly forms two normal peaks (9; 19 mm), with hiatus near 16 mm. Looking at the general picture of the size distributions of all cockroaches, data reveal a spectacular discrete distribution, a four-wave pattern with peaks (7; 19; 24.5; 29 mm) with significant hiati at 14, 23 and 27 mm. It is necessary to claim that although taphonomy greatly contributes to the skew and bias in data (acting against smaller and non-flying species


Size distribution of Karabastau cockroaches rounded to full millimeters
1
0
2
32
74
84
109
39
36
29
23
24
13
23
27
21
33
25
35
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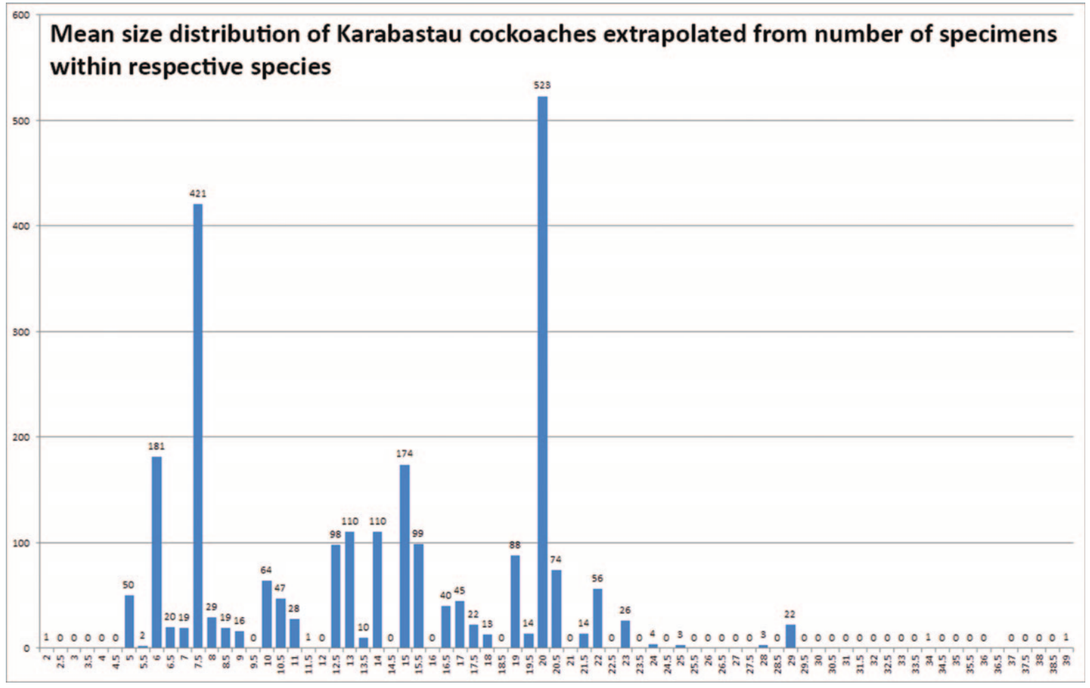
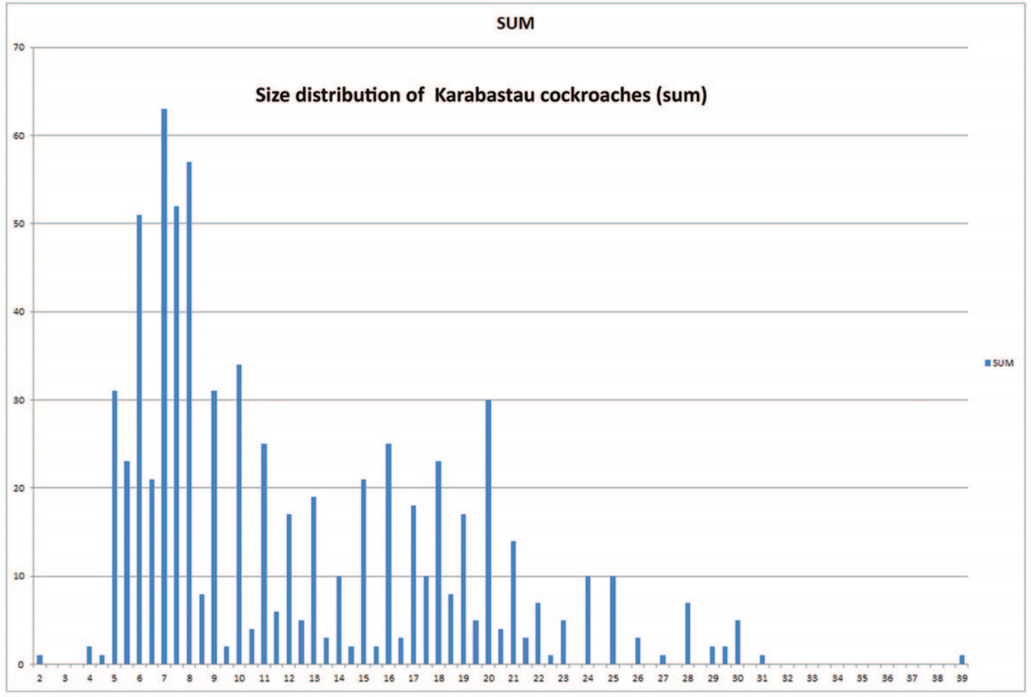
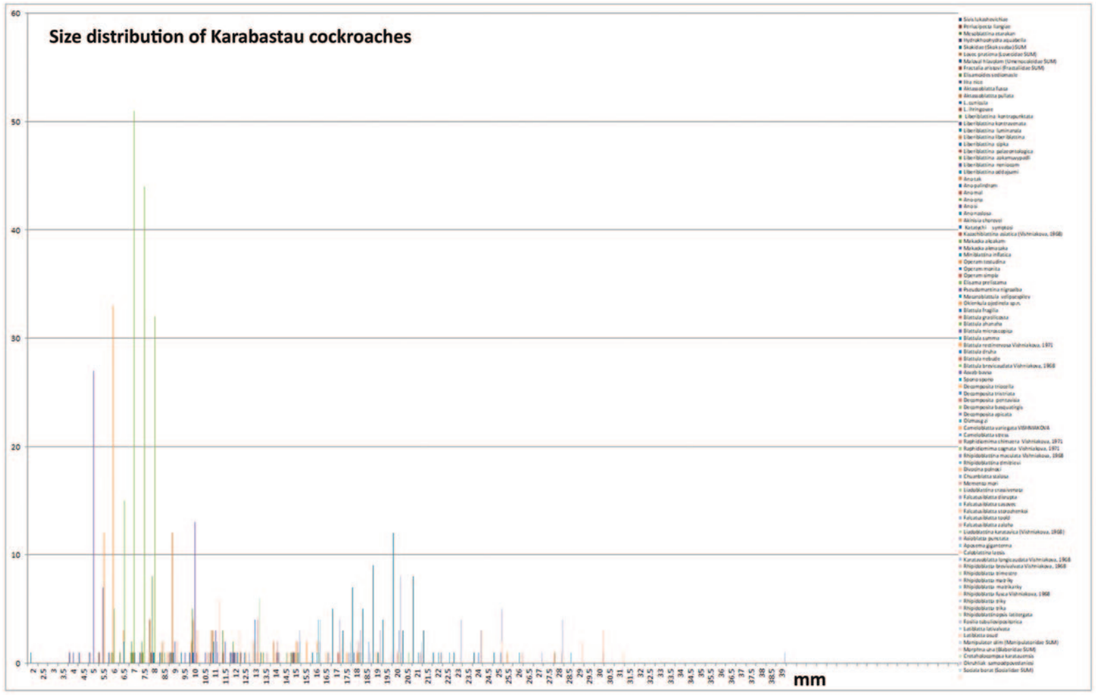
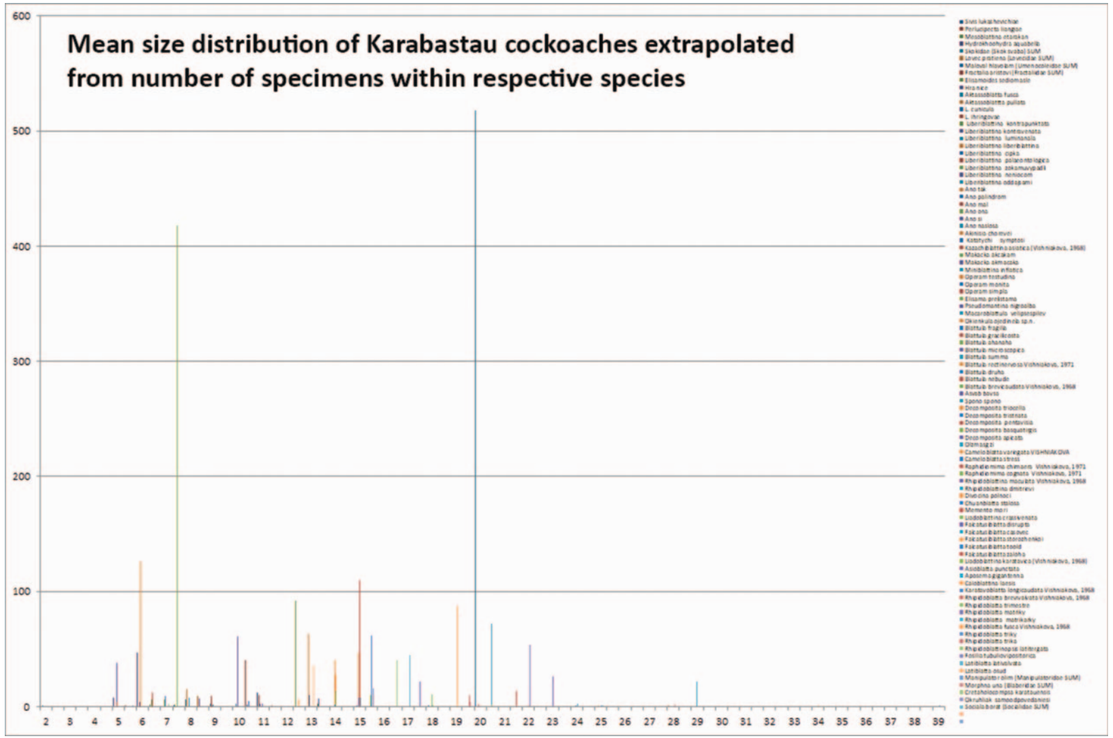
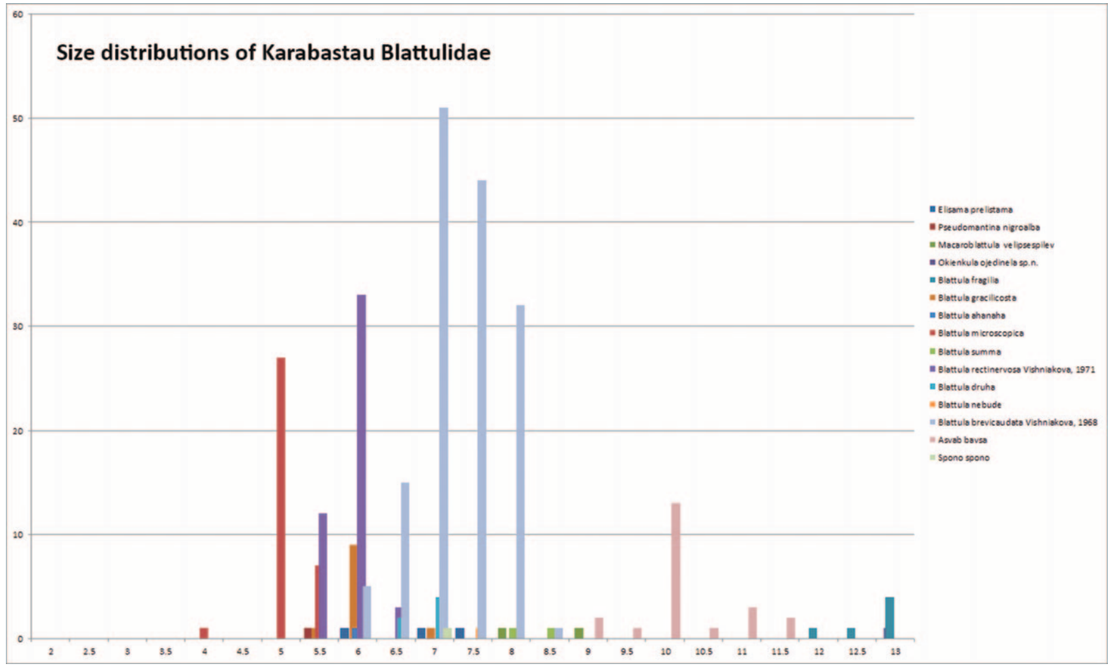
0
0
0
0
0
1

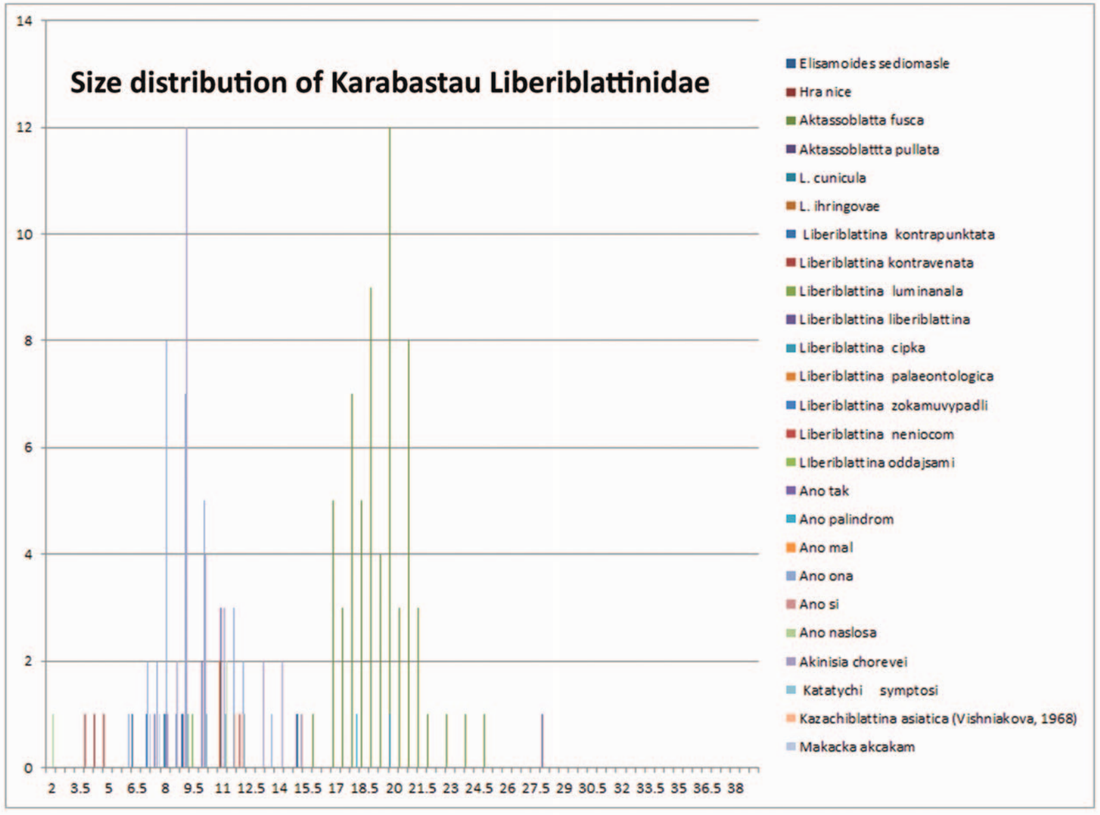

Mean size distribution of Karabastau cockoaches extrapolated from number of specimens within respective species
600
500
400
300
200
100
0
1
0
0
0
0
0
50
2
181
20
19
421
29
19
16
0
64
47
28
1
0
98
110
10
110
0
174
99
0
40
45
22
13
0
88
14
523
74
0
14
56
26
4
3
22

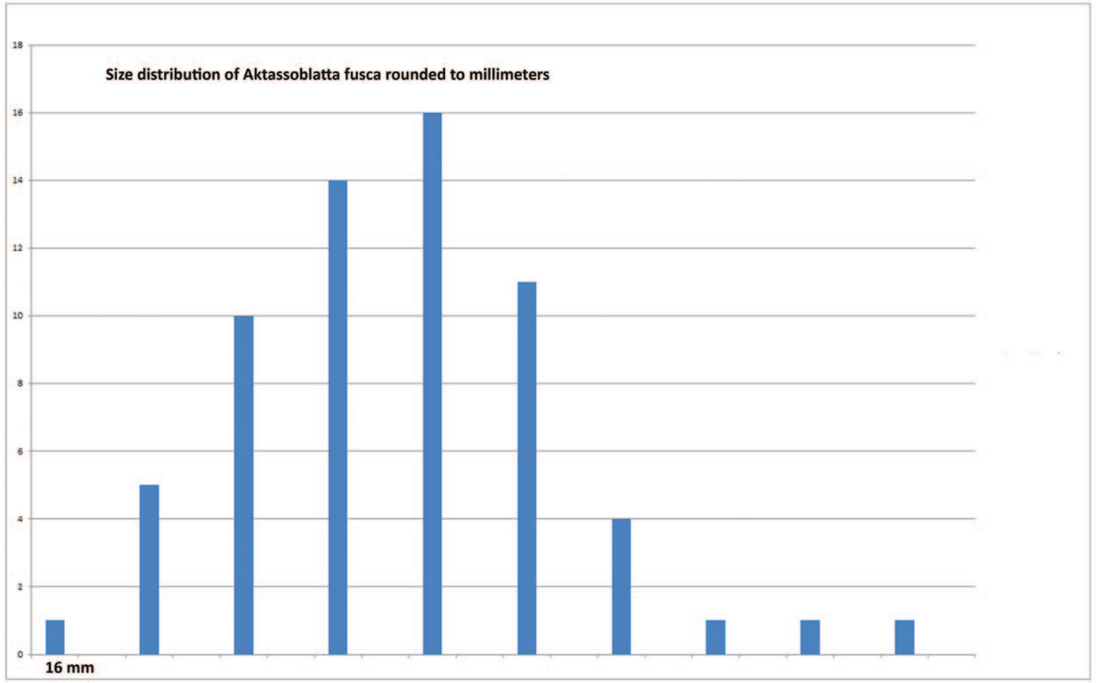

SUM
Size distribution of Karabastau cockroaches (sum)
SUM

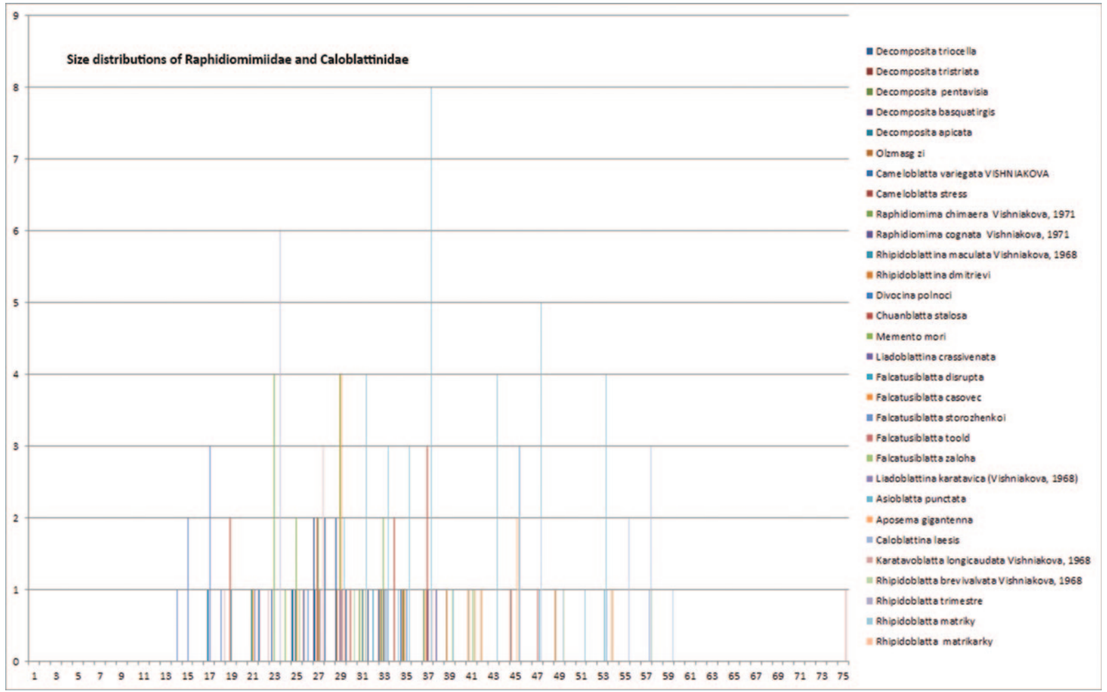

Size distribution of Karabastau cockroaches
mm


Mean size distribution of Karabastau cockoaches extrapolated
from number of specimens within respective species


Size distributions of Karabastau Blattulidae
Elisama pre listama
Pseudomantina nigroalba
Macroblattula velipsepilev
Okienkula ojedinela sp.n.
Blattula fragilis
Blattula gracilicosta
Blattula ahanaha
Blattula microscopica
Blattula summa
Blattula rectinervosa Vishniakova, 1971
Blattula druha
Blattula nebude
Blattula brevicaudata Vishniakova, 1968
Asvab bavsa
Spono spono


Size distribution of Karabastau Liberiblattinidae
Elisamoides sediomasle
Hra nice
Aktassoblatta fusca
Aktassoblattta pullata
L. cunicula
L. ihringovae
Liberiblattina kontrapunktata
Liberiblattina kontravenata
Liberiblattina luminanala
Liberiblattina liberiblattina
Liberiblattina cipka
Liberiblattina palaeontologica
Liberiblattina zokamuvypadli
Liberiblattina neniocom
Liberiblattina oddajsami
Ano tak
Ano palindrom
Ano mal
Ano ona
Ano si
Ano naslosa
Akinisia chorevei
Katatychi symptosi
Kazachiblattina asiatica (Vishniakova, 1968)
Makacka akcakam
0
2
4
6
8
10
12
14
2 3.5 5 6.5 8 9.5 11 12.5 14 15.5 17 18.5 20 21.5 23 24.5 26 27.5 29 30.5 32 33.5 35 36.5 38


Size distribution of Aktassoblatta fusca rounded to millimeters
0
2
4
6
8
10
12
14
16
18
16 mm



present in ambers), this general pattern with hiati is not taphonomical and is reflected also in real living ecosystems (which will be discussed elsewhere). Size-biases in other insect might be ruled by different processes, but cockroaches are greatly uniform in life forms and being strictly dominated by decomposers (other cohorts are generally rare, and predatory Raphidiomimidae are responsible only for one of the peaks). Thus the discrete distribution of such a rich assemblage is more than remarkable (some other sites did not reveal such strict hiati- to be analysed elsewhere). Nevertheless, the discrete character of the environment in respect to size jumped out also in another context – in the phylogenetical network analysis of the respective localities, where phylogenetical signal in one locality is strong and clades can be discriminated even after bootstrapping. This clear pattern totally diminishes after including all species and there are no hiati, neither supported clades, suggesting only a discrete character of each respective actuocenosis and ecosystem itself, but not species in general (see also Vršanský et al. 2021). Reason of the hiatus-based size distributions is obscure and likely related with predation. Nevertheless, the result is clear – such assemblage will tend to specialization among predators. Furthermore, it cannot be excluded that this pattern is dynamical and the hiati "migrate" due to replacements of dominant species. *Blattula brevicaudata* is an indigenous species and species in this genus can vary in size, so the rather immediate replacent of the species for another species in the same genus can also change the size pattern dynamically. The same hold true for another codominant, *B. rectinervosa*, or eventuially these two species could also be mutually replaced. Codominant *Ano ona* with numerous species mean the same pattern can repeat in all codominant species. Eudominant normally distributed *Aktrassoblatta fusca* is an indigenous genus, which does not require further explanation and the same applies for codominant *Memento mori*.

Average-species size (14.5 mm calculated as average size per species) distributions (n= 2,448) calculated as extrapolation of a mean forewing size to number of specimens within species reveal slightly different pattern (figp. 502 extrapolated) which might relate to genetical predisposition of the species functionally expressed and realized in real phenotypes (see the paragraph above). Average species (disregarding gaps at the level of 0.5 mm and rounded only to full mm) reveal more or less continuous distribution of average sizes in the interval 5-23 mm and thus revealing an evidence for the potential of the assemblage to cover all sizes within this interval. Surprising is the hiatus in the interval 11.5-12 mm, which is nevertheless, covered in actual sizes (and even numerous) of cockroaches which have a different average size. Surprising is the 22-29 mm "empty" interval, which is in actuocenosis covered with plurivalent individuals of the species having a lower average size – coevally this might explain a dominance of this (indigenous; *A. fusca*) species, which covered "empty" space. It is necessary to stress, that, however improbable this statement seems (due to huge sample size), that these patterns might appear local. This inference is based on more or less continuous size-distribution in coeval Kota, India and also other studied intervals at Bon Tsagaan and Bakhar, both Mongolia. Amber size-distribution is strictly normal due to sticky character of the resin, but the amber size-normality is not real, but caused with the container/carrier character and usually contains very small specimens only.

AREAS

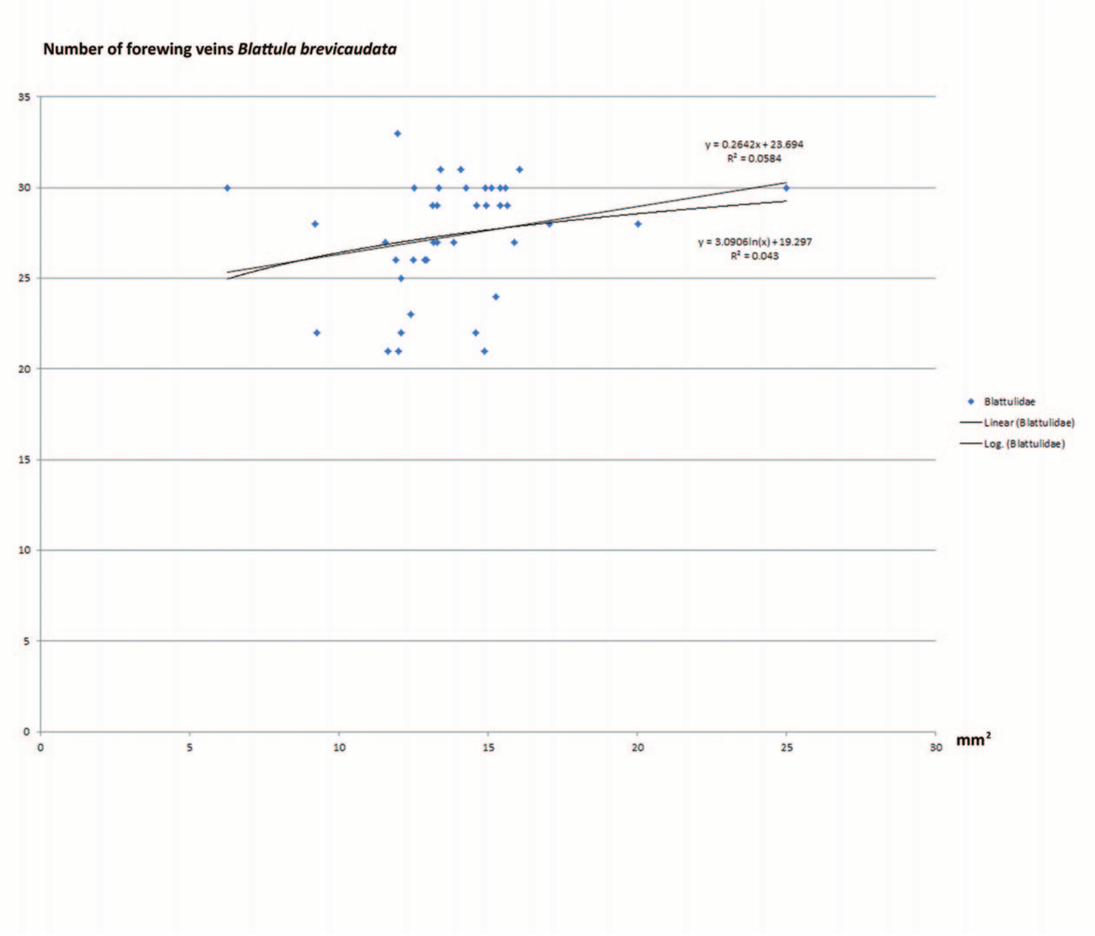
Area is a characteristic somewhat independent on morphological traits of the wing. Furthermore it was discovered that within (some) studied species, areas are independent on the number of veins on them. The same study (Oružinský and Vršanský 2017), nevertheless, reveals also a striking interspecific dependence of areas on number of veins when average per species was considered.

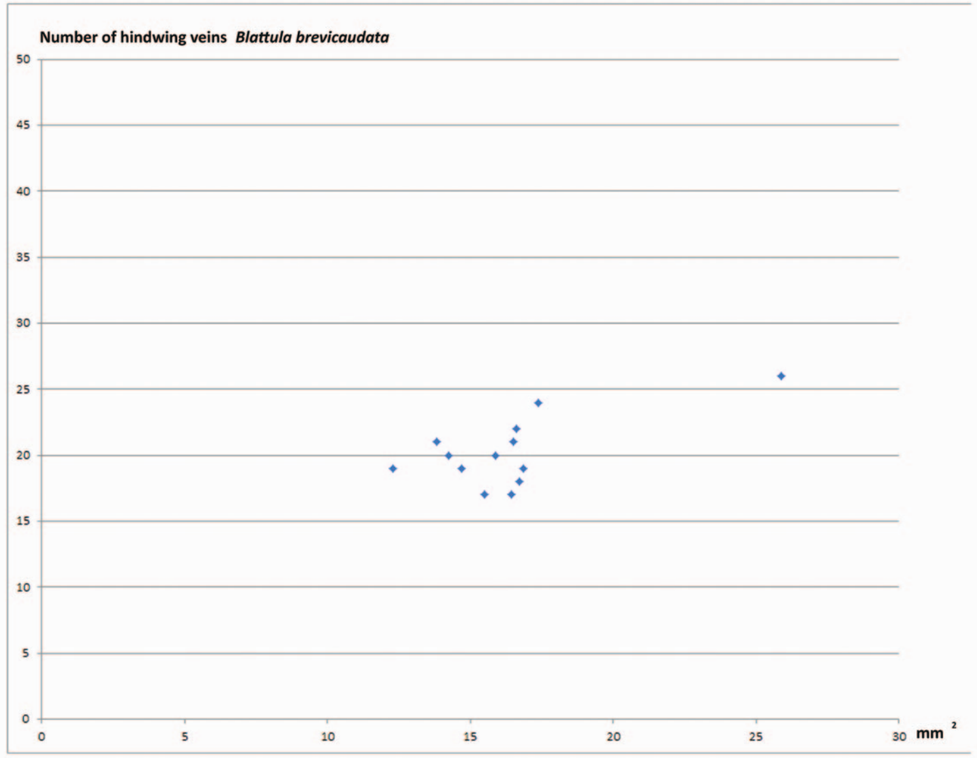
The present study enabled to further support these data and two dominat species with a significant sample size (*Blattula brevicaudata* – figps. 509-510; *Aktassoblatta fusca* – figp. 512) reveal intraspecific independence of number of veins on areas. Consider that data are slightly differing from general variability data as other datasets were taken into consideration (only complete wings). Thus, *Blattula brevicaudata* reveals average number of forewing veins 27.35, average area 13.85 mm^2 and 1.97 vein per 1 mm^2 (while all Blattulidae reveal 27.85 average veins; 14.08 mm2 and 1.98 vein per 1 mm^2). This is inconsistent with 16.24 mm^2 and 25.04, which is 1.54 vein per 1 mm^2 in the hindwing in the same species *Blattula brevicaudata*.

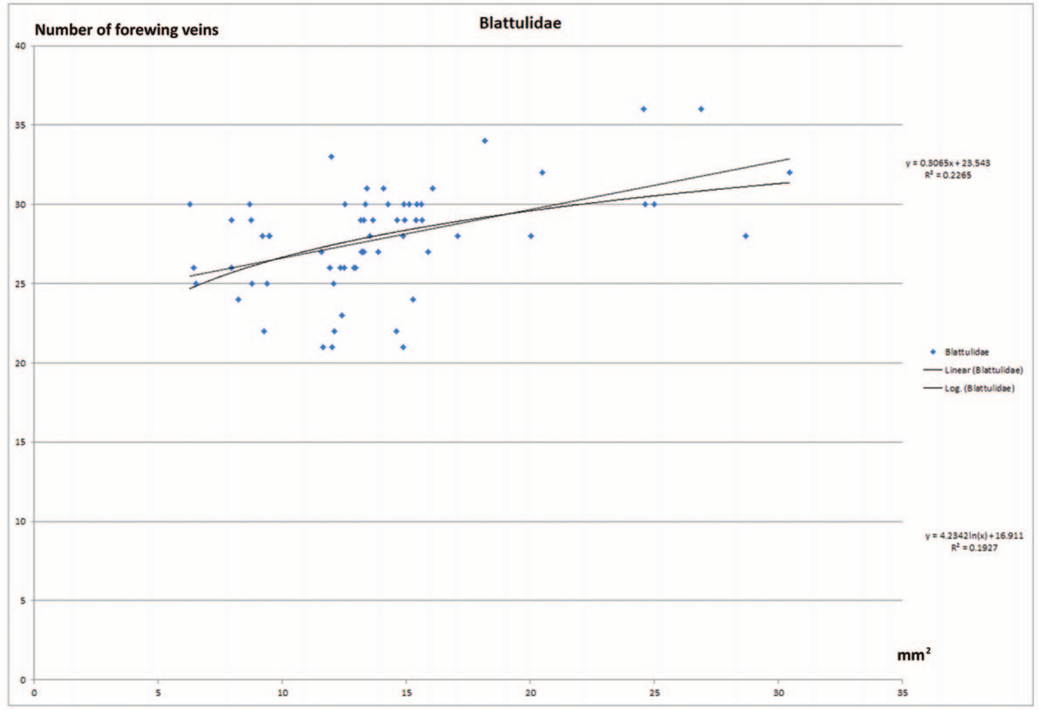
Aktassoblatta fusca reveals average area 100.07 mm^2 and 48.73 average veins and 0.49 vein per 1 mm^2 (while all Liberiblattinidae have average area 68.77 mm^2 and average veins 43.45 and 0.63 vein per 1 mm^2). These two dataset of *B. brevicaudata* and *A. fusca* are complanatory to those used in Oružinský and Vršanský (2017) and also useful in accessing the trends in the future. Other families reveal also diverse data: Raphidiomimidae (45.35 average veins; 66.3 mm^2 average area; and 0.68 vein per 1 mm^2), Caloblattinidae (54.1; 95.84; 0.56), Mesoblattinidae (43; 34.77; 1.24), Umenocoleidae (?34; 13.37; ?2.5), Fractalidae (32; 6.99; 4.6), Skokidae (32; 14.52; 2.2) Operamidae (35; 28.37; 1.23), Latiblattidae (49.78; 80.07; 0.62), Blaberidae (58; 113.11; 0.51). These data might invoke some optimism regarding differences at family level, nevertheless, data are too diffuse to be diagnostic. Moreover they largely depend on size also within respective families and thus a density of veins cannot be considered reliable at the present, within these data.

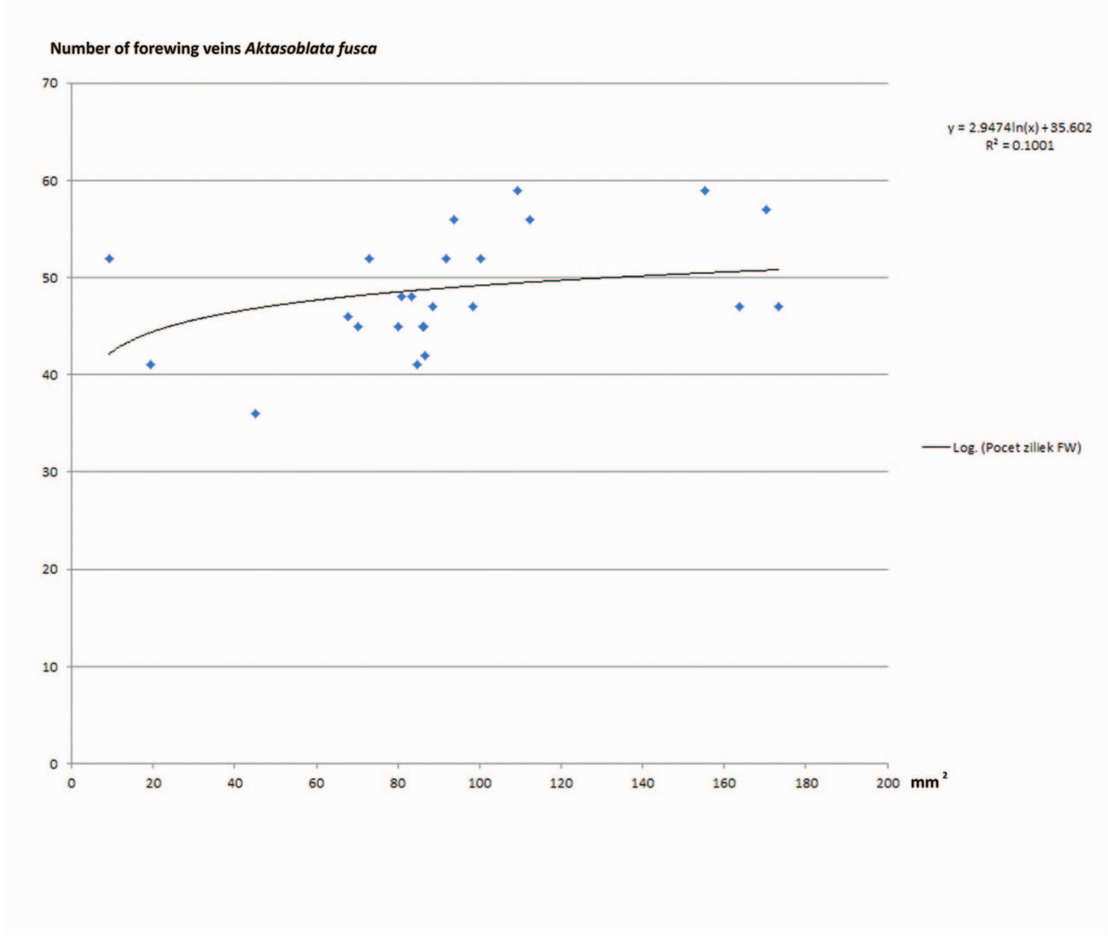
Interesting due to high similarity are also general figures for all forewings (38.63 veins; 56.3 mm^2; 0.69 veins per 1 mm^2; R2= 0.62 power) and hindwings (25.46; 34.65; 0.74; R2= 0.62 power) taken together.

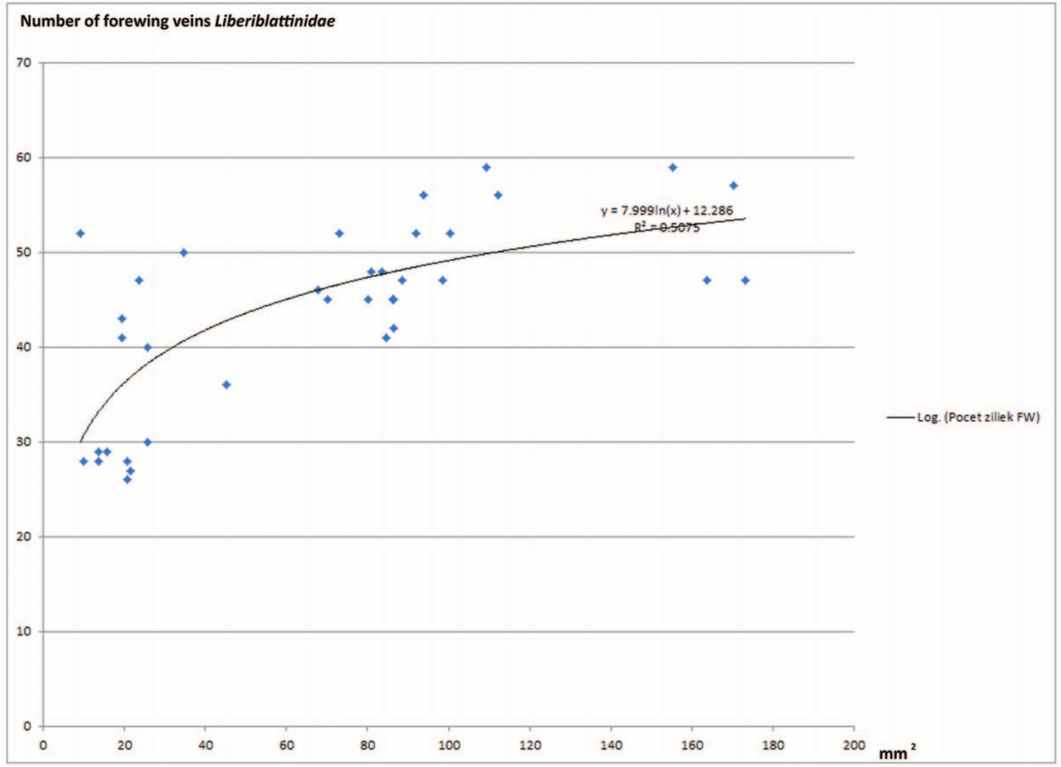
Thus we see a clear dependence and pattern of the genetical coding of the growth of veins, which is nevertheless greatly influenced by ontogeny. This should be supported and confirmed by study of the average distance among veins at margin. It is additionally an intellectual challenge to discriminate the discrete number of veins and continual quadrate area – a study accessible in the future on the basis of more comparative material from multiple sites.

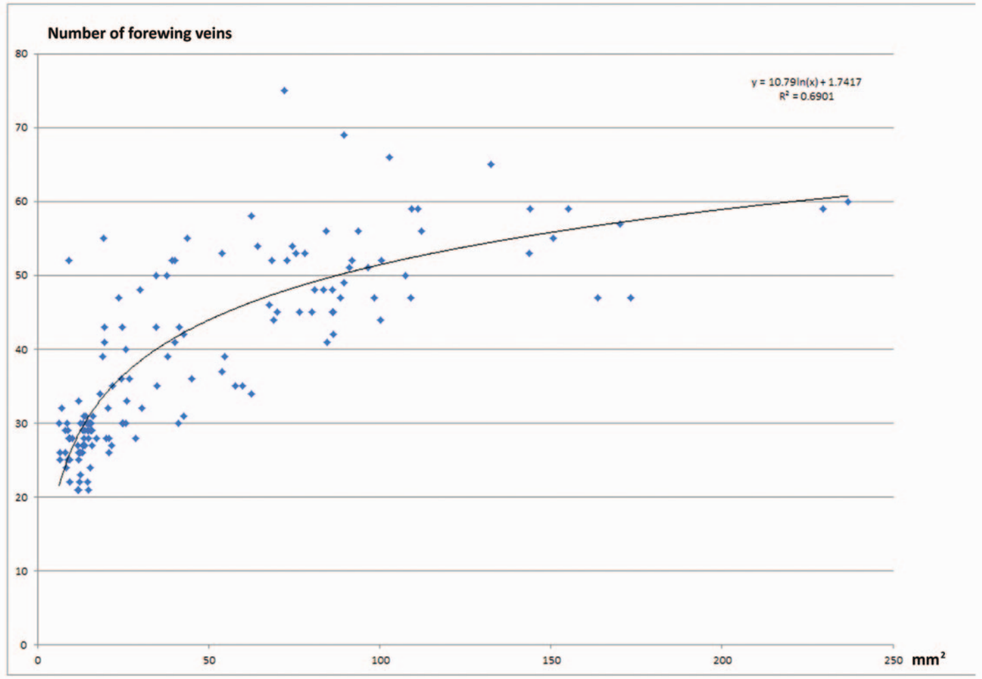



Number of hindwing veins *Blattula brevicaudata*
50
45
40
35
30
25
20
15
10
5
0
0
5
10
15
20
25
30
mm ²


Number of forewing veins
Blattulidae
40
35
30
25
20
15
10
5
0
0
5
10
15
20
25
30
35
y = 0.3065x + 23.543
R² = 0.2265
Blattulidae
Linear (Blattulidae)
Log. (Blattulidae)
y = 4.2342ln(x) + 16.911
R² = 0.1927
mm²


Number of forewing veins *Aktasoblata fusca*
y = 2.9474ln(x) + 35.602
R² = 0.1001
Log. (Pocet ziliek FW)
mm²
0
10
20
30
40
50
60
70
0
20
40
60
80
100
120
140
160
180
200


Number of forewing veins *Liberiblattinidae*
y = 7.999ln(x) + 12.286
R² = 0.5075
Log. (Pocet ziliek FW)
mm²
0
10
20
30
40
50
60
70
0
20
40
60
80
100
120
140
160
180
200

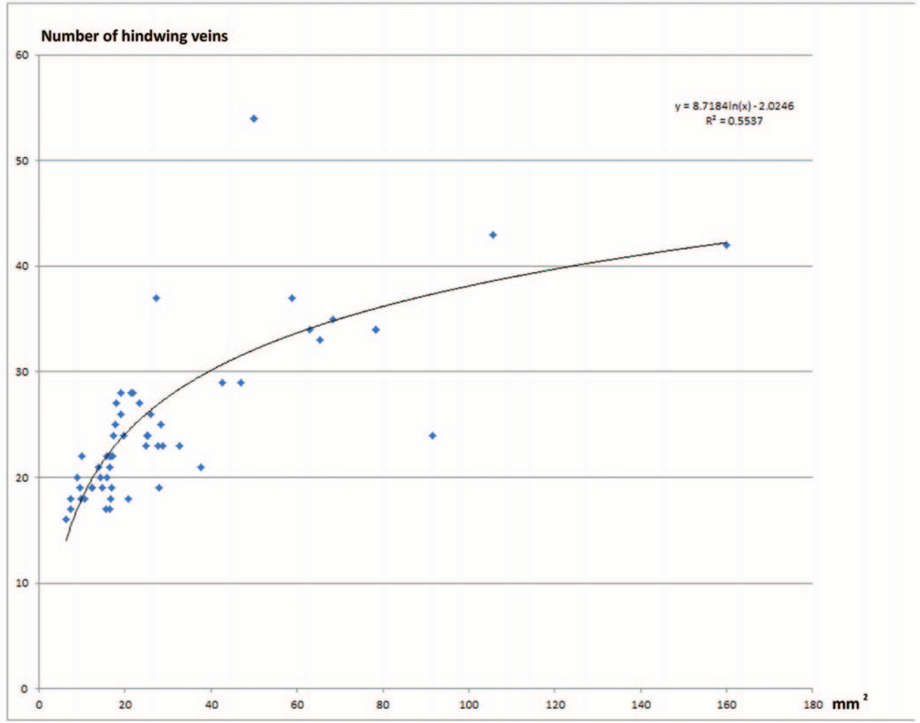




INPUT EXAMPLE

2066-322

Total forewing areas



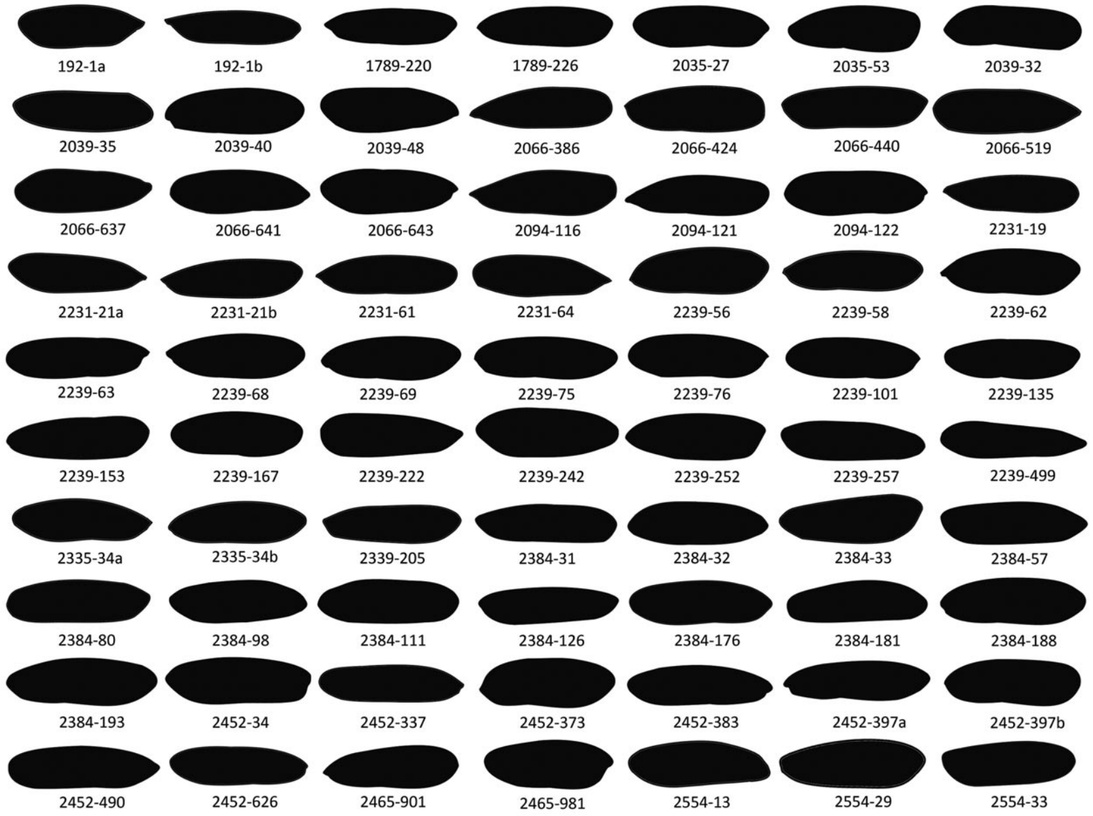


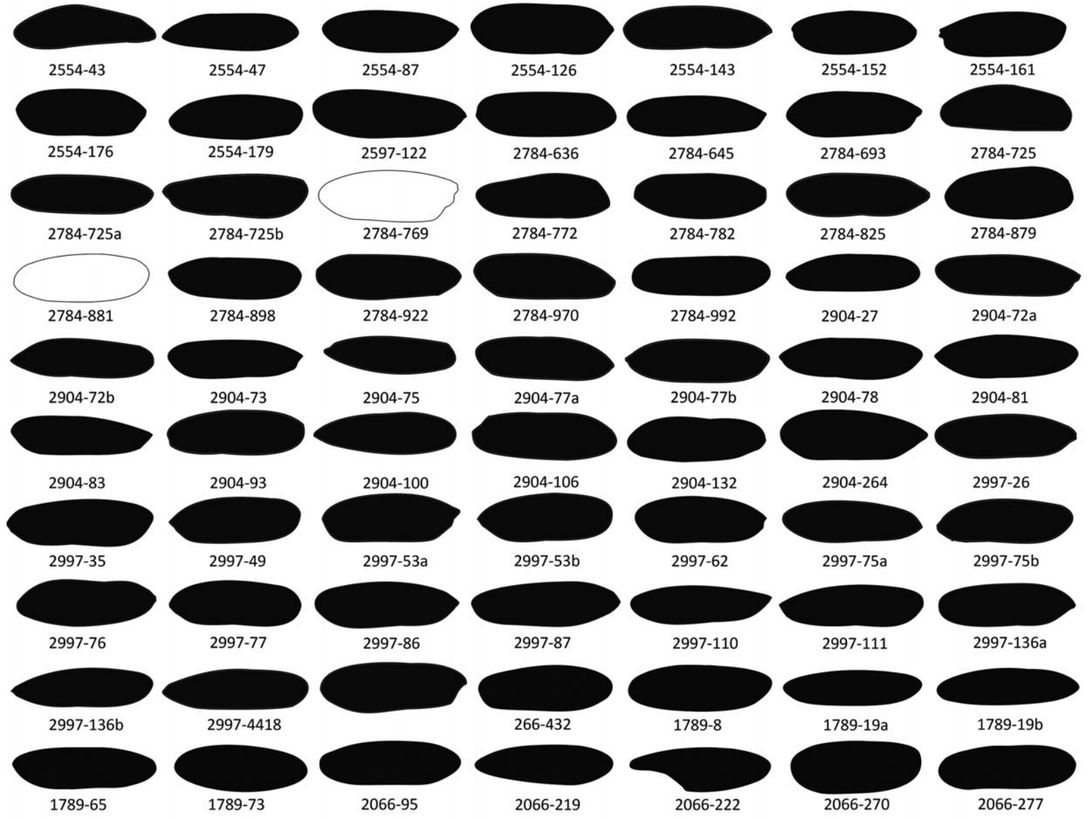
INPUT EXAMPLES

2465-937

2997-1615

Total hindwing areas


192-1a
192-1b
1789-220
1789-226
2035-27
2035-53
2039-32
2039-35
2039-40
2039-48
2066-386
2066-424
2066-440
2066-519
2066-637
2066-641
2066-643
2094-116
2094-121
2094-122
2231-19
2231-21a
2231-21b
2231-61
2231-64
2239-56
2239-58
2239-62
2239-63
2239-68
2239-69
2239-75
2239-76
2239-101
2239-135
2239-153
2239-167
2239-222
2239-242
2239-252
2239-257
2239-499
2335-34a
2335-34b
2339-205
2384-31
2384-32
2384-33
2384-57
2384-80
2384-98
2384-111
2384-126
2384-176
2384-181
2384-188
2384-193
2452-34
2452-337
2452-373
2452-383
2452-397a
2452-397b
2452-490
2452-626
2465-901
2465-981
2554-13
2554-29
2554-33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2554-176
2554-179
2597-122
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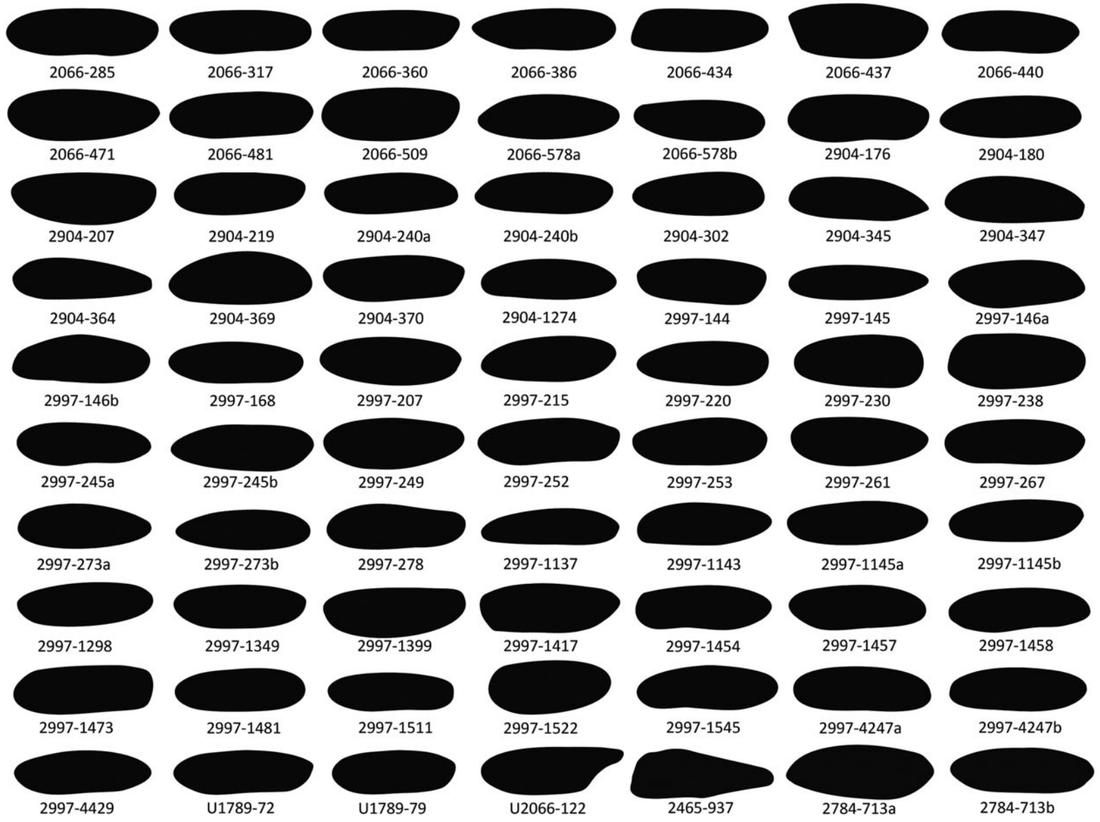
2784-645
2784-693
2784-725
2784-725a
2784-725b
2784-769
2784-772
2784-782
2784-825
2784-879
2784-881
2784-898
2784-922
2784-970
2784-992
2904-27
2904-72a
2904-72b
2904-73
2904-75
2904-77a
2904-77b
2904-78
2904-81
2904-83
2904-93
2904-100
2904-106
2904-132
2904-264
2997-26
2997-35
2997-49
2997-53a
2997-53b
2997-62
2997-75a
2997-75b
2997-76
2997-77
2997-86
2997-87
2997-110
2997-111
2997-136a
2997-136b
2997-4418
266-432
1789-8
1789-19a
1789-19b
1789-65
1789-73
2066-95
2066-219
2066-222
2066-270
2066-277


2066-285
2066-317
2066-360
2066-386
2066-434
2066-437
2066-440
2066-471
2066-481
2066-509
2066-578a
2066-578b
2904-176
2904-180
2904-207
2904-219
2904-240a
2904-240b
2904-302
2904-345
2904-347
2904-364
2904-369
2904-370
2904-1274
2997-144
2997-145
2997-146a
2997-146b
2997-168
2997-207
2997-215
2997-220
2997-230
2997-238
2997-245a
2997-245b
2997-249
2997-252
2997-253
2997-261
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2997-273b
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2997-1298
2997-1349
2997-1399
2997-1417
2997-1454
2997-1457
2997-1458
2997-1473
2997-1481
2997-1511
2997-1522
2997-1545
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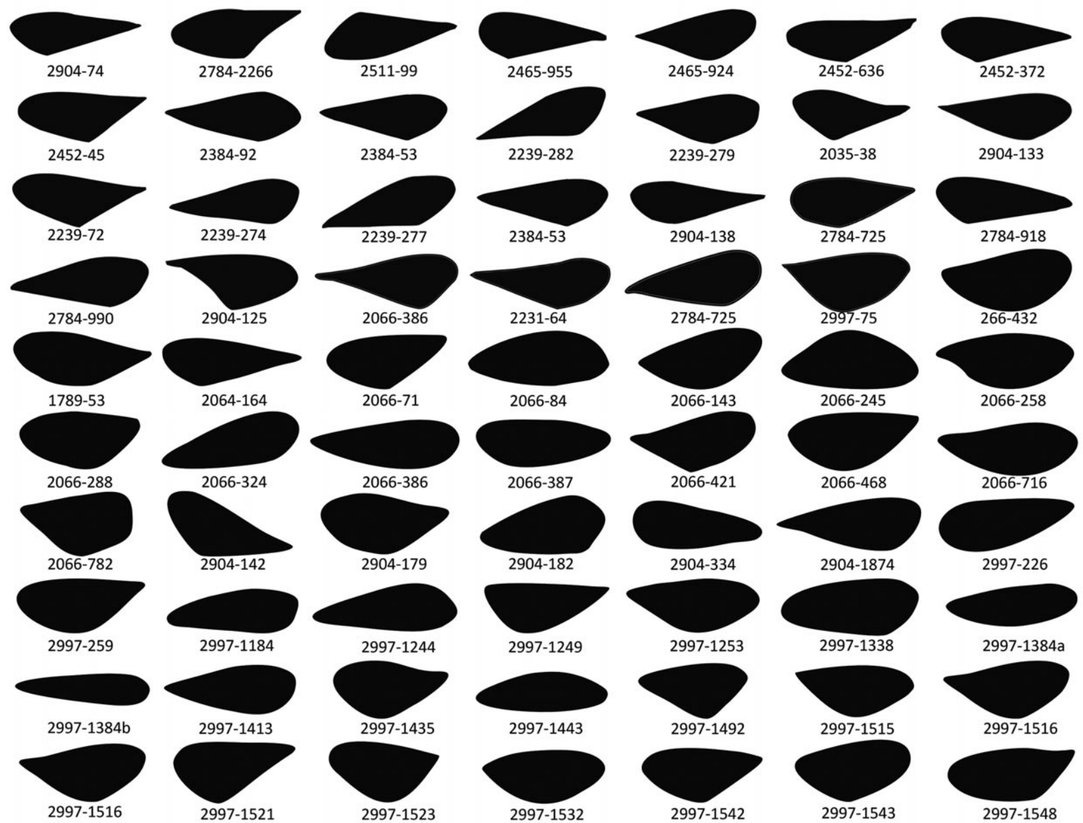
2784-713a
2784-713b


2904-74
2784-2266
2511-99
2465-955
2465-924
2452-636
2452-372
2452-45
2384-92
2384-53
2239-282
2239-279
2035-38
2904-133
2239-72
2239-274
2239-277
2384-53
2904-138
2784-725
2784-918
2784-990
2904-125
2066-386
2231-64
2784-725
2997-75
266-432
1789-53
2064-164
2066-71
2066-84
2066-143
2066-245
2066-258
2066-288
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2997-1542
2997-1543
2997-1548

SEXUAL DIMORPHISM

Sexual dimorphism reveals the most surprising pattern observed in the size. More precisely to say, its absence. While there is a wide dimorphism in carefuly studied advanced Mesozoic cockroaches (see *Piniblattella vitimica; Praeblattella* spp. in Baissa and Bon Tsagaan), basically all living cockroaches (Hu et al. 2010) and also most of the carefully studied Palaeozoic cockroaches (see Hornig et al. 2018), it was impossible to unequivocally identify and classify sexual dimorphism in the present cockroaches. It is necessary to say that modern cockroaches are underrepresented in Karatau, disallowing to identify their dimorphism and the same is true for Palaeozoic groups. Nevertheless, all Mesozoic cockroaches that were present in sufficient amound did not reveal the sexual dimorphism either. There is probable dimorphism hidden in insufficient data of large, especially predatory species preserved in low number (see Liang et al. 2021). Also the genus *Makacka* might reveal this dimorphism, nevertheless, it is very improbable. Nevertheless, there are two species (*Blattula brevicaudata*, Blattulidae and *Aktassoblatta fusca*, Liberiblattinidae) preserved in high number and with well-identified sexes. Surprisingly nor in the small dominant blattulid, neither in large dominant liberiblattinid, dimorphism (of size) was expressed at all. Also there is no morphological difference besides the terminalia. This only suggest comparatively low female investment in egg production and parental care, as these traits result in bigger size of females.

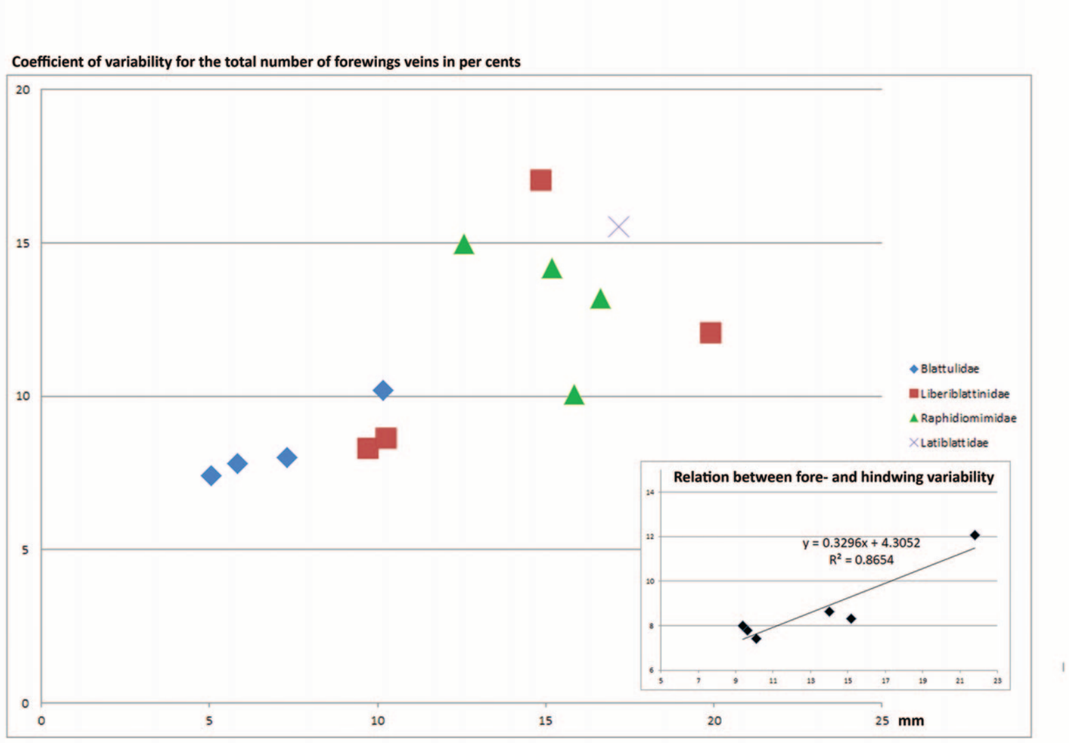
VARIABILITY

Variability data are among the most important results of the present study.

The first preliminary results studying the variability in wing venation patterns in cockroaches showed a trend of decreasing variability (Vršanský 2000). They caused a wide scientific communication, while it became clear that it refers to the proof of the old law of Rosa (1899) (Henning 1965). It is also called Rosa's rule, which was forgotten because no one could either confirm or refute this hypothesis.

For a long time, no one made progress regarding this research, due to the hard-to-access data. Again, as with mutations, obtaining variability data requires a morphologically regular pattern preserved in the desired quality and especially in the desired quantity.
The wing venation of cockroaches meets both parameters. Ross (2012) analyzed these patterns and concluded that 30 or more complete wings of the same species are required to obtain a statistically significant result

In the original work, in addition to living cockroaches, I analyzed 11 different fossil species, and subsequently data were obtained for another 21 species from the Triassic to the Cenozoic and another 13 species from the Karatau locality in Kazakhstan (Vršanský 2003b, 2020; Oružinský and Vršanský 2017; Liang et al. 2009ab , 2012, 2018, 2021; Vršanský et al. 2009; Vršanský and Ansorge 2007, Wei and Ren 2013; Wang et al. 2007ab; Hinkelman 2022b).



Thus currently 52 species of cockroaches with a distinct phylogeny reveal variability trends.

As mentioned above, this trend was originally established as Rosa's law, but supporting experimental data was lacking. Cockroaches reveal this (independently acquired) evolutionary trend, but whether it is only specific to cockroaches remains unclear. It will be challenging to obtain another model sufficiently numerous and with stable development-independent data for a similar study, although trilobites have supported this trend (Wagner 2000), and are proving to be a priority for biological theory (Flegr 2010).

So lets take a look on the detailed analysis of the Karatau variability (figp. 521; Tab. 522).

Variability directly relates to the number of veins (as the calculation formula deviation/average directly includes this parameter). One would predict that according to the direct relation among (average) number of veins and wing area (Oružinský and Vršanský 2017), variability will relate to size. Nevertheless, relation with size is entirely missing. There is neither relation of variability with size nor with size variability (R2= 0.1-0.17), which is not only surprising but also due to extremely low support also entirely unexpected. At the same time it reveals direct evidence for the hidden variation.

In this context, the statistically significant relation (r^2=0.87) between variability of the forewing with the variability of hindwing is neither banal, nor trivial (see figp. 521).

	FW variability	ave size	Blattulidae	Liberiblattinidae	Raphidiomimidae	Latiblattidae	HW variability	FW variability	Size variability
B. microscopica	7.42	5.06	7.42				10.12	7.42	5.1
B. rectinervosa	7.8	5.84	7.8				9.62	7.8	4.01
B. brevicaudata	8	7.32	8				9.38	8	6.81
A. ona	8.31/8.1	9.7		8.31/8.1			15.19	8.31	18.84
A. chorevei	8.63	10.25		8.63			13.86/14	8.63	18.47
A. bavsa	10.2/10.3	10.18/10.09	10.2/10.3				11.33	10.2/10.3	6.63
D. triocella	9.29	15.84			10.06			9.29	11.24
A. fusca	12.07	19.9		12.07			21.79	12.07	9.28
C. stalosa	13.2	16.64			13.2			13.2	18.7
F. casovec	14.17	15.19			14.17			14.17	10.92
F. storozhenkoi	14.98	12.56			14.98			14.98	30.96
O. si	14.88	18.24			14.88			14.88	15.4
L. lativalvata	15.54	17.18				15.54		15.54	12.37
M. mori	17.05	14.85		17.05				17.05	12.47

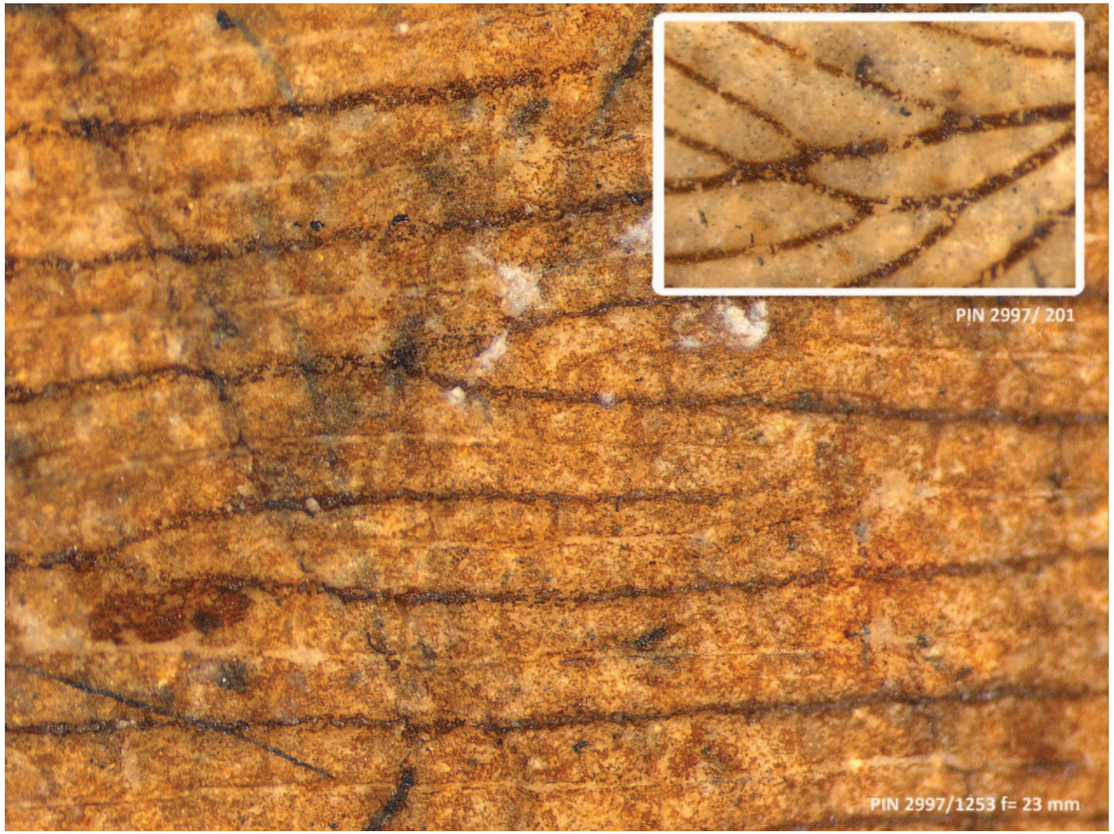
The more, counterintuitively hindwing, more seriously involved in aerodynamics and weight uplift, variability is seriously higher (see figure for exact equation). This was observed in the original study (Vršanský 2000) and referred to control of the strength of veins in the cockroach hindwing.

Importantly data reveal similar CV percentual values within the genus (*Blattula*, 7.42, 7.8, 8; *Falcatussiblatta* 14.17, 14.98 – and related *Olzmasg* 14.88) at the same locality. Also notable is lower variability of the conservative *Blattula* compared with advanced *Asvab* (10.2). Similar data in this one particular locality do not related to stratigraphy and taphonomy, but to a similar time to last diversification.

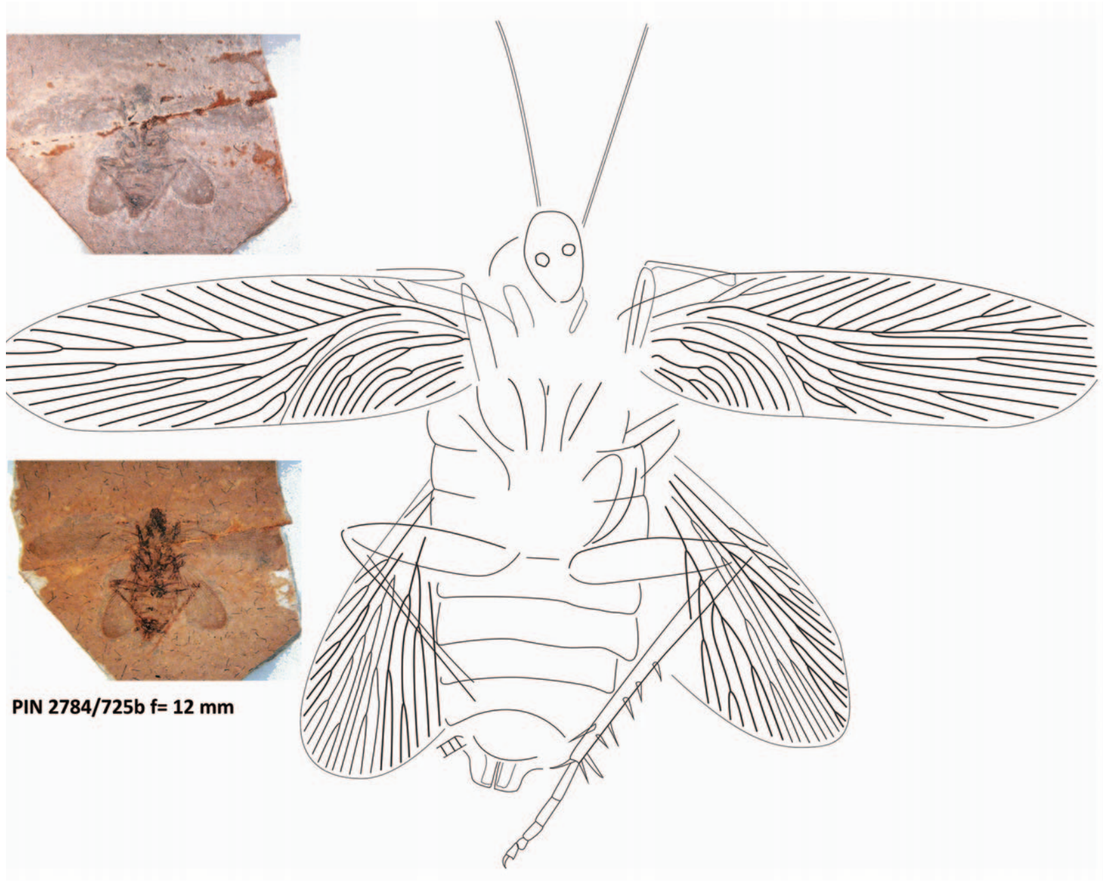
Logically correlated are veins including and excluding forewing A, nevertheless a significant difference and lower variability of all veins including A suggest that these two systems, forewing and its clavus are coordinated, which is again not trivial as these systems are highly independent (including frequent occurrence of deformities within clavus).

MUTATIONS

Disregarding fixed deformities and extremely rare deformities in the protective non-aerodynamic clavus (n= 17; such as fixed-as-stable-morphotype blind anterior branches of A1 in *Lovec pratiena* indicating a single population of this species within Karatau), deformities were recorded in the following taxa. *Sociala borat* (1/1, numerous); *Chuanblatta stalosa* (1/63); *Decomposita basquatirgis* (1/10, numerous); *Falcatussiblatta storozhenkoi* (1/36 wings); *Cameloblatta variegata* (1/40); *Rhipidoblatta fusca* (1/88); *Rhipidoblatta matriky* (3/64); *Rhipidoblatta triky* (2/15); *Latiblatta lativalvata* (1/45); *Latiblatta osud* (1/36); *Olzmasg zi* (2/72); *Liberiblattina paleontologica* (1/1, numerous); *Ano tak* (1/3); *Ano ona* (3/92); *Elisamoides sediomasle* (1/2, numerous); *Makacka akmacaka* (1/1); *Aktassoblatta fusca* (8/518); *Katatychi symptosi* (1/5); *Blattula rectinervosa* (3/114); *Blattula brevicaudata* (4/402); *Blattula microscopica* (2/38, numerous); *Asvab bavsa* (1/108). In total wing mutations affected only 57 specimens and possibly in 40 specimens the wing deformities affected aerodynamics, amounting only to 1.6 %, which is the lowest known recorded partition of deformed individuals in history compared to 6.4 % of the coeval Kota, India (which is also extremely low value). Analysing distribution one can see extremely low value in small individuals, which is logical as a single deformity more likely influences flight, which can be lethaly. Nevertheless, in large individuals partition is also very adequately low (see *Aktassoblatta fusca* (8/518)) and proportional to small individuals (*Blattula brevicaudata* (4/402). In very large species deformities were not recorded at all, or extremely rare (*Olzmasg zi* (2/72); *Rhipidoblatta fusca* (1/88)) – see 27 % in Yixian, China and over 40 % at the P/T boundary. So there is truly an extremely low value, comparable to the climatic optimum in Bakhar (5 % including clavi). Interesting is that among these 40 cases, 5 represent numerous deformities, suggesting a more general environmental and/or developmental stress. (Additionally remarkable is specimen not included in the count, holotype of *Blattula nebude*, with multiply



Mutation details



Defromed specimen

deformations and symmetrical M-CuA (M-M) deformity respectively on both forewings, which distinctly reveal that a mutation is restricted to area (wing position) and not to a specific veinal system.) Also notable is the absence or near-absence in explosively radiating indigenous groups, which were considered as rapidly evolving in Karatau. Nevertheless, *Liberiblattina* was proved to occur also in remote Kota, India suggesting this genus was not indigenous, but cosmopolitan and extremely short-living due to rapid diversification/extinction rates and phylogeny. In contrast, only 1 of 50 specimens is affected with numerous deformities and none with a single one. An interesting deformity is in specimen PIN 2904/110* (A-A fusion) because this specimen is at the same time significantly larger (13 mm compared to 8.5-11.2 mm of others) than the second largest representative of the species. Statistically significant correlation between the mutations and cockroach phylogeny (r^2= 0.9 including insignificant samples) is put in another light with the present research. On the one hand, mutations are nearly absent in Karatau. On the contrary, there are several new lineages either meaning their necessary shift to the previous Diversification Point (188-190Ma instead of 127Ma), or, more likely that these diversification points also do not reveal data for originations of the lineages, but only their (explosive) radiations. In such a case it would likely mean that in the Diversification (Radiation Points in the new sense) Points characterized with high mutation rates, whole ecosystem elements become to radiate in a response to the mutation load throughout the whole biota (we surely presume that the mutation load ratio (relative ratio over time, not mutation rate itself NB!) is the same for all organisms). And new (but already existing lineages) become to massively radiate. This whole theory must be reconsidered, because, unless Karatau is whole Lower Cretaceous and not pre-127MaDP, numerous lineages must be shifted back to the 188-190MaDP. This seems easy in the case of mantodeans (considering Rahpidiomimidae at the 188-190MaDP) and in the origin of crown cockroaches (as Mesoblattindae in the 188-190MaDP are evidenced to posses ootheca) and also in the case of Ectobiidae (not recorded prior 127MaDP). Nevertheless, this logic does not work in the case of Umenocoleidae, before 127MaDP recorded only in Karatau (and Koty). The same case is for termites. It seems rather difficult to shift their origin from 151Ma Karatau into 188-190MaDP, but molecular data are consistent with these terms (see also Djernaes and Murienne 2022; Ewart et al. 2024).

PRINCIPALLY NEW MORPHOSTRUCTURES

The cockroaches from Karabastau were the basis for understanding of the morphology of the ancient cockroaches and in numerous respects also for understanding of the morphology of cockroaches in general, regarding the living forms. It was Vishniakova (1964, 1968, 1971) who correctly interpreted sophisticated and numerous structures of terminalia and wings, and Vršanský (2008) added the head including the presence of central ocellus. New structures observed on this material follow in this paragraph. Unfortunately, from the macromorphological perspective, the wing articulation still remain an unexplained enigma. **Pterostigma.** *Chuanblatta stalosa* specimen PIN 2997/1384 shows that flight stabilization using the fore margin can be reached not only by pterostigma and coloration of R1 veins but also (in this predatory active species) by widening of the apical RS branches and their sclerotisation. **Bunky** were present in the earliest umenocoleid. **Vannus folding** in a liberiblattinid specimens 2784/990 reveal a simple fold, non-weer-like, which suggest this corydioid homoplasy blattuloid synapomorphy developed as early as in the earliest liberiblattinids. **Certain Latiblattidae did not outstretch forewing during flight. Forewing costa** is truly a variable character and must be taken more seriously in future studies. **The ovipositor** in Liberiblattinidae differs from the long one up to tubular in *Aktassoblatta* (see 2066/324). Tubular ovipositor in Latiblattidae support injections of isolated oocytes into hardening oothecal (see also Vishniakova 1968, Sendi 2021a). **The head of Raphidiomimidae** was not necessarily prognathous in all species as shown by *Ensiferoblattta* Li et Huang (Li and Huang 2023). On the other hand, modern movable mantis-like head was present in *Manipulator*.

BRACHYPTERY

Brachyptery must be considered with highest caution in sedimentary record. Forewings of Latiblattidae possessed all attributes of a brachypterous wing and cockroach. Nevertheless, we clearly see on a completely preserved specimens that this species is at least in most cases fully winged and capable of flight. Moreover the forewing overlaps body in all cases. Possible exception is PIN 2554/128, where the preservation is unclear. So while brachyptery cannot be finally excluded for some Latiblattidae, it also remain unconfirmed for the Jurassic and Karatau. In Upper Cretaceous brachyptery was recently confirmed in several burmite species (Li and Huang 2021, Hinkelman 2021b) and it was rather common during the Cenozoic – as documented in Baltic amber (Shelford 1910, P. Vršanský et al. in preparation). In Lower Cretaceous, possibly brachypterous forewings were preserved in Bon Tsagaan (Vršanský 2003).

APOSEMATISM

Aposematism relates to the presence of advanced visually-hunting predators, with poisonous content of the bodies within cockroaches and/or more advancely with a Batesian mimicry. These characteristic in cockroaches were broadly discussed (Šmídová and Lei 2016; Sendi and Azar 2016, Vršanský et al. 2018, 2019; Hinkleman 2023). The first unequivocally aposematic cockroach with *Eye* pattern form comes from an undescribed *Subioblatta* present in the Triassic of Madygen (see Hinkelman 2021: figs. 6bd, 7bd), but it is the only Triassic record documented so far. While Cretaceous records of aposematism are common, Jurassic records are extremely sporadic and basically restricted to Karabastau. Among Jurassic taxa, 6 different coloration patterns were recognized among 11 species, ranging from irregular and connected stripes/ spots, small isolated singular/ dual dots, single large irregular dot, inverted white felds on black surface, a colored CuP with singular dot and even a completely structured "eye-spot" (present species; see Hinkelman 2023). Aposematism is present in the large *Aposema* (Caloblattinidae) and besides Karabastau also found in Cretaceous Polar regions. In Karabastau, there is a wide range of coloration patterns discussed above, many of which have something close to aposematic coloration unless they directly represent it. Nevertheless, the clear *Eye* is distinctly formed in *Ano ona, Liberiblattina zokamuvypadli (Liberiblattinidae)* and *Olzmasg si* (Raphidiomimidae). Moreover the distinct dot(s) (reversed) are also present in *Cameloblatta stress* (Raphidiomimidae), *Operam testudina* (Operamidae), *Maloval hlavolam* (Umenocoleidae) and possibly also in most if not all *Ano* and *Liberiblattina* species.

EGG CASE

This is a major reproductive novelty of living cockroaches compared to isolated eggs or egg-conglomerates that were laid by extinct groups. Possibly the main driver in this respect is the parasitic Evanoidea. These are hymenopterans that are specialized in attacking these egg-case, or ootheca and it was presumed that their specialization is only a result of an extremely high load to isolated eggs and their predation or parasitism respectively. Cockroaches belonging to modern lineages (i.e., Blattoidea and derived groups), namely Mesoblattinidae with archaic ootheca – see Hinkelman (2019) appeared well before Karbastau, namely in the basalmost Jurassic of U.S.A. (Huber 1973). In Karabastau, the genera *Mesoblattina* and *Perlucipecta* are present (n= 52; documented to possess ootheca in Yixian and Sinuiju – see Wei and Ren (2013), So et al. (2021)). Due to rarity of these taxa in Karabastau it is not surprising that the direct evidence of ootheca is missing. Additional putative taxa with ootheca are *Morphna* una (n= 5) and *Okruhliak samoodpovedaniesi* (n=1).

Primitive precursor ootheca (prootheca) was nevertheless, apparently present also in earlier groups. As mentioned earlier, the short tubular ovipositor with extremely narrow diameter was recently proved to not transmit eggs, instead isolated oocytes (preserved in amber) in some Cretaceous beetle-like Umenocoleidae (*Alienopterix* Mlynský et al. in Vršanský et al. 2018) and also in a miniaturized liliberiblattinid *Miniblattina* Sendi, 2021 (Vršanský et al. 2021, Sendi 2021). The same process is evidenced here in *Fosilia* of the Caloblattinidae/Latiblattidae. It is very probable that the species represent the same genus preserved also in a Myanmar amber sample sold to a private collection. Fortunately, this kind of ootheca was documented (Li and Huang 2019) and it is logical that it is the kind of ootheca resembles those in mantodeans. But this oothecae were also commonly preserved in the Triassic of Argentina, where they can be associated only with Caloblattinidae, Phyloblattidae and/or the *Voliziablatta*-group (see Cariglino et al. 2020), as mantodeans and umenocoleoids evolved much later. Thus a protection of hatch was developed well before the true ootheca with keel and calcium oxalate crystals – a keen protection which triggered sophisticated co-evolution of modern cockroaches and evaniid parasites. Now the task is to identify parasites of primitive oothecas as it might happen, isolated egg hatching was restricted to very first cockroaches, and starting with Permian in the caloblattinid lineage, eggs were already protected in hard proothecae (where oocytes were delivered separately from the forming of the case).

PARASITES OF OOTHECA AND PRE-OOTHECA

Normally it is impossible to trace taxa in a keen interaction with cockroaches with rare direct (Hinkelman and Vršanská 2020) and indirect (Vršanský et al. 2013) exceptions on their commensals. On the other hand, direct parasites on their egg-cases, ootheca, provide rare long-lasting interactions. Evaniidae are now rather well-studied due to their specialized morphology, and with 42 records prior to 2018 (EDNA fossil insect database active 2024-04-20). The origin and evolution of the whole superfamily Evanioidea was recently accessed by Joault et al. (2022). Nevertheless, it seems that only the family Evaniidae and not other families within the superfamily, parasitise cockroach ootheca, and these are unknown from Karatau. Nevertheless, due to the (rare) presence of cockroaches with ootheca within Karatau, it cannot be excluded, that some of the evanioid species were classified within Preaulacinae; Nevaniinae Zhang & Rasnitsyn, 2007 or Anomopterellinae Rasnitsyn 1975 (Rasnitsyn 1972, 1973, 1975, 1983; Zhang et Rasnitsyn 2008) already attacked on fully developed advanced oothecae of mesoblattinid Karabastau cockroaches. Abundant records from other localities (n= 138) relates to true ootheca parasites. Nevertheless, my suggestion to look at this problematic deeper, as now in my view it is sure that numerous other taxa also possessed ancient kind of otheca (Latiblattidae, Liberiblattinidae, Blattulidae – see above) which did not required specialized morphology of the parasite and will be more difficult to identify.

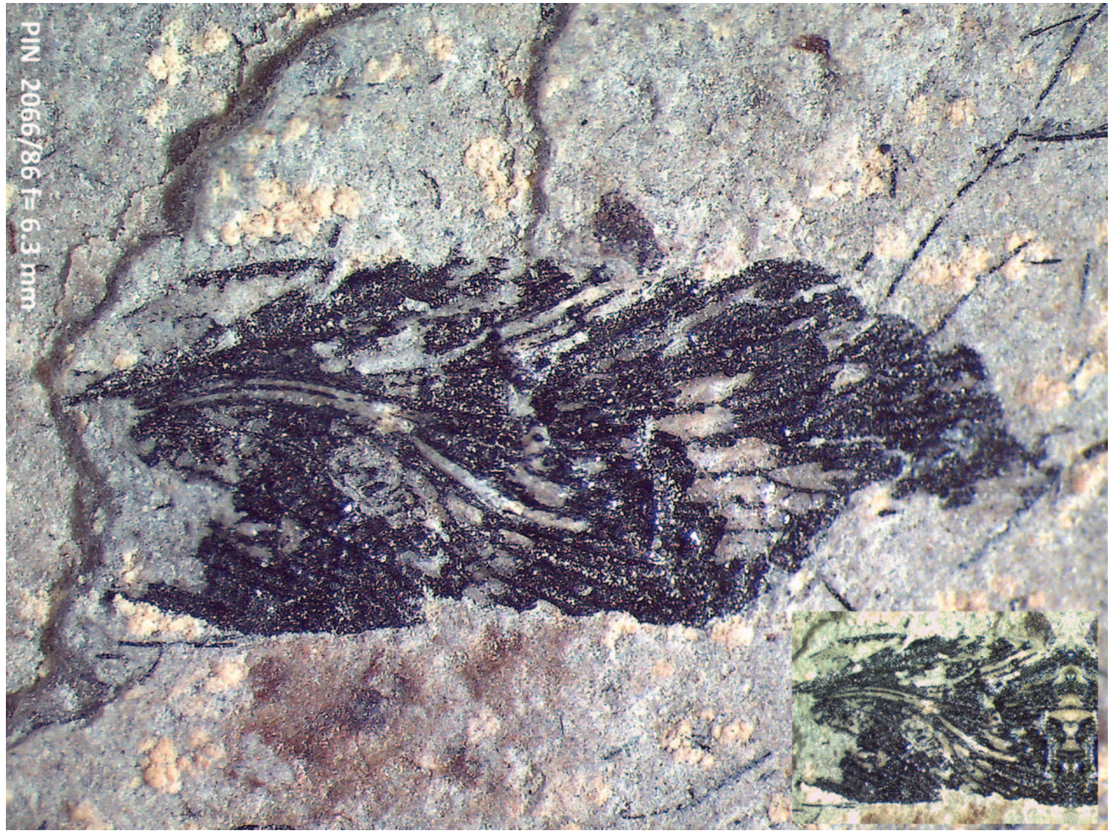
MICROSTRUCTURES

Carbonised specimens are extremely rare, because carbonisation was extremely rarely operating on dead cockroaches. Thus the preservation of sensillar structures is virually absent. It is strange, but microstructures are usually lacking even distributional preservation. With few exception, there is no standard description of sensillar cover. It is surprising as other insect from the site often bear sensilla (see Lukachevich 2012).

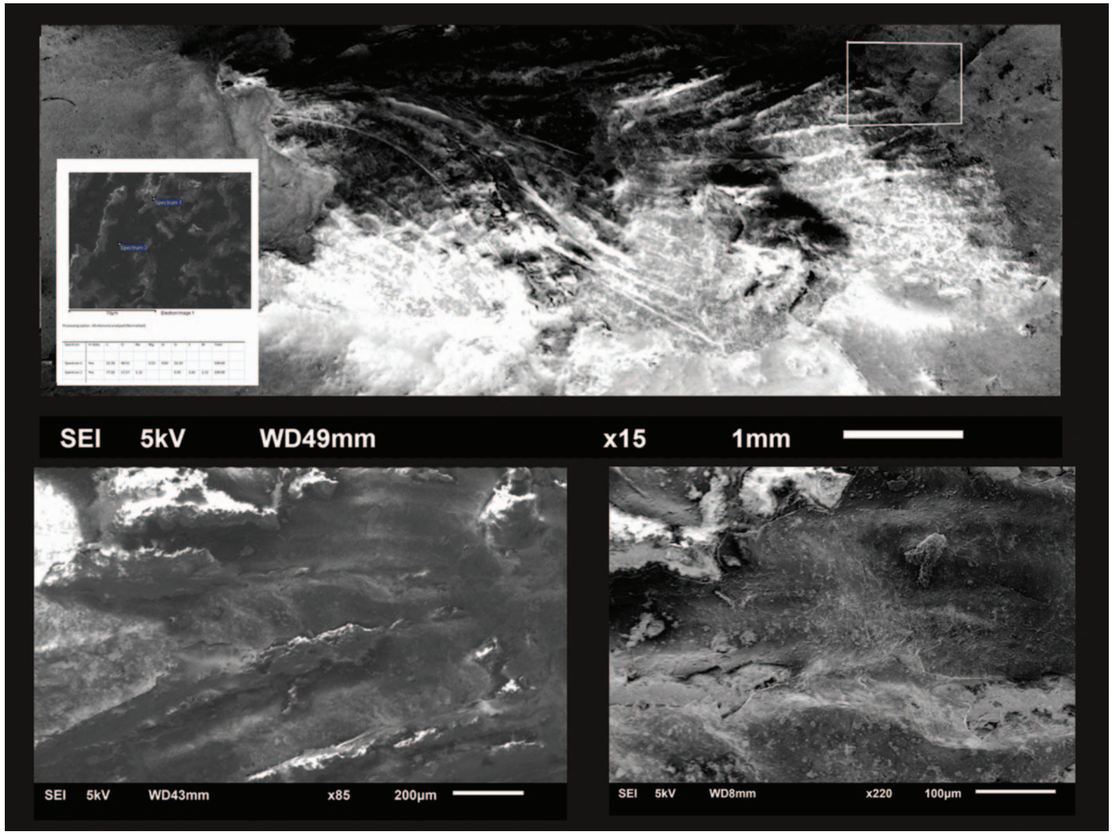
A preserved carbonised wing (PIN 2066/189) is uniqueness for Karabastau. Mechanism for the carbonization of the colored parts of the fine wing membrane is obscure. Comparing the surrounding matrix, carbonized part contains significantly more carbon (77.42 vs 22.56 % of the matrix) and less silicon (0.95 vs. 26.20 %) and traces of bromium and sulphur unrecognized in the matrix. The matrix contains more oxygen (46.11 vs 17.57 %) aluminium (9.6 %) and magnesium (5.56 %) unrecognized in the carbonized wing. The preservation is excellent (figp. 531-532) revealing veins, intercalary veins, cross-veins as well as sparse regularly distributed microseta.

Carbonised specimens were notably collected during the same expedition and apparently closely to each other ordinately as numbers are close (PIN 2066/189 and 2066/192 respectively).

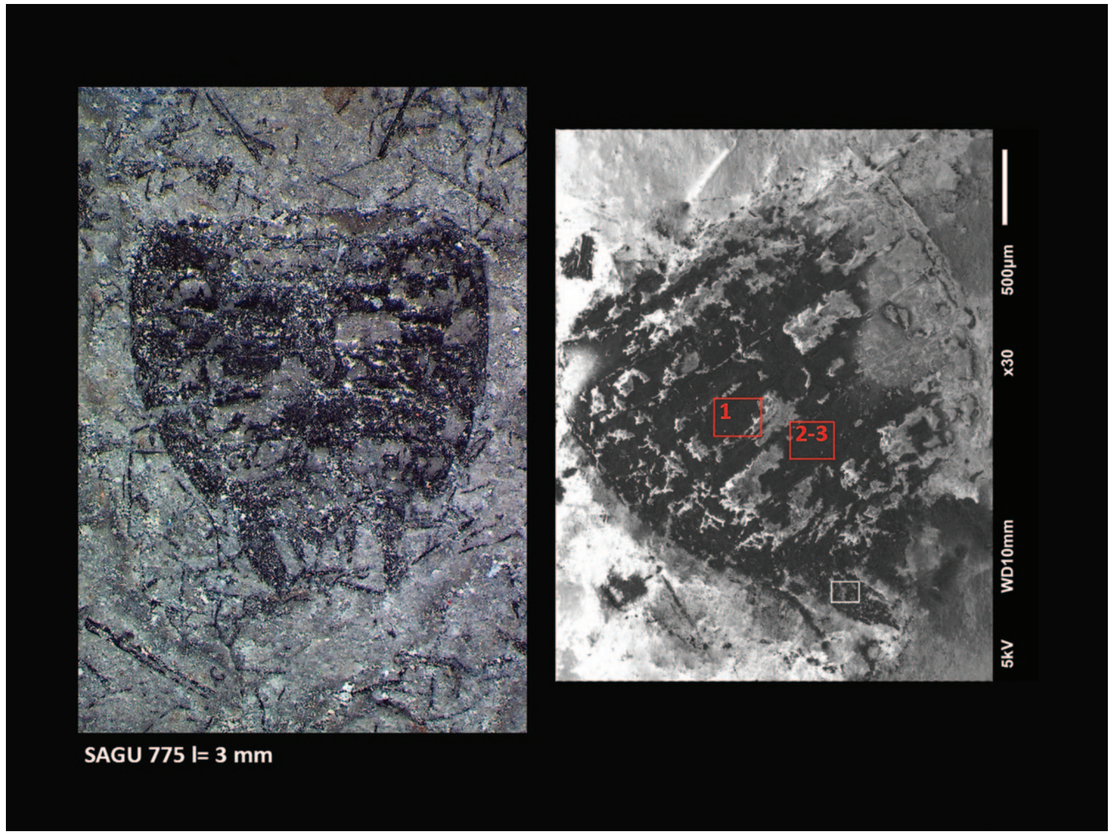
Similar elemental values are observed for the only carbonized caloblattinid body SAGU-775. Comparing the surrounding matrix, the carbonized part contains significantly more carbon (54.76-60.88 vs 31.43 of the matrix). Matrix contains natrium (0.93 %), more oxygen (53.10 vs 28.56-35.82 %), but less aluminium (4.02-2.74 v 2.71 %) and magnesium (0.63 vs. 5.18 %). Silicon is similar in matrix and carbonized wing (6.61 vs. 5.91-6.09 %). Rarely present are damaged sensillar holes as well as walls of sensilla chaetica. Sclerite junctions were well preserved. Heat and/or radiation cannot be ruled out as a responsible agent for carbonisation (see Majtaník and Kotulová 2023).



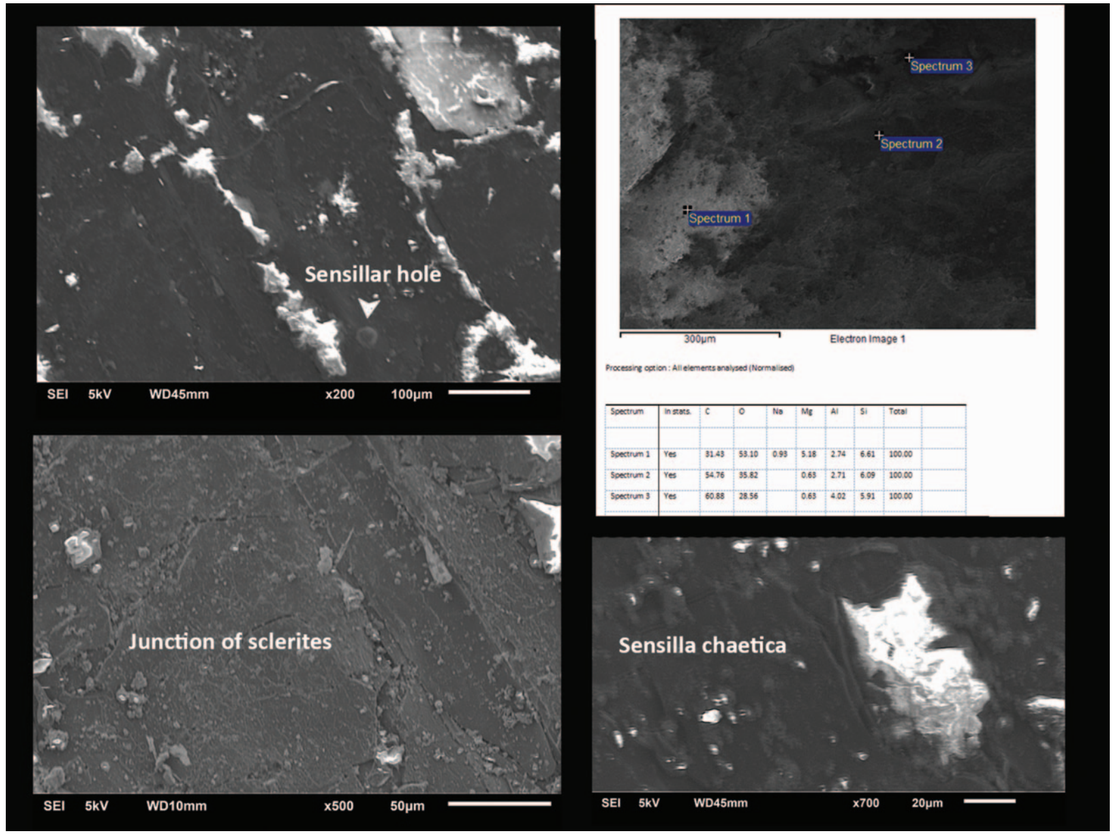
Carbonised forewing



Carbonised forewing



Carbonised body



COLORATION

Due to favourable taphonomy, coloration was preserved in most of the cockroaches. It is best visualized when applying alcohol and/or polarized light. As seen in the figures (figg. 48), alcohol makes the sediment surface microlayer transparent, enabling to look slightly deeper to the rock, where parts of the cockroaches were preserved. Characteristic coloration in many cases helped with identification of respective species and consequently to recognize their intraspecific variability. Type of coloration are accessed in a detail in the chapter **Forms**. Mean coloration for the species established previously was (25.44 %) and the total colored area was 36 %. It is a very low value comparable to Koty in India and Shar-Teg in Mongolia, much lower than in Daohugou in China and in previous time periods. This possibly suggests a change towards more active lifestyle. Coloration (along veins) is surprisingly detectable aslo on CT (see figg. 25).

TAPHONOMY

(tabps. 542-549)

The assemblage was claimed as attempted to be unbiased by professional collectors (specialist entomologists), who claimed not aiming at aestethical specimens. High partition of isolated forewings (n= 1,281; 40.13 %) and hindwings (n= 633; 19.8 %) seems to support this.

Nevertheless, some bias, which is usually common, which is accessible by the meta-study of collection numbers, where partition of forewings and hindwings differ (see Table). Differences are nevertheless, mosly indistinct.

Remarkable is the near absence of isolated clavi (n= 16 among 659 indetermined specimens), either associated with short pre-depositional transport or with selection of collector. It is possible that collectors did not collected these fragments, although the probability is low, as highly fragmentary (damaged) forewings occur in the collection as well. Anyway, from 244 analysed photographs of isolated forewing (complete specimens never have disarticulated clavus), 35 (14.3 %) were preserved with(out) (disarticulated) clavus, so isolated clavi must be somewhere. Partition of forewings and hindwings can be compared with other (also claimed non-bias-attempted) localities (Bakhar: 22.8; Shar-Teg: 28.8; Shurab: 29.4 %; Dobbertin 39.5; Kota 26.2 %). Apparently the collection is unbiased to a large degree compared to others and in case of Daohugou this study might be threated as a reference, although in Daohugou, also hindwings were collected well.

Complete specimen partition (28.2 %) and specifically combined with 186 immature individuals suggest short pre-depositional transport and also supports predicted splashing (by rains?) from the river/lake banks.

Carbonised specimens were rare (see above).

Rare amber-like preservation occurred (specimen 2554/20) – after applying alcohol, the specimen looked like embedded in amber – the reason was silicification.

While mostly forewings were collected, a high number of specimens is represented by completely articulated winged adult individuals (sex ratio Male/Female: 24/48), which is uniquity of Karatau (and Daohugou). The sex ratio is important in designating similar/different flight activity, resp. different burial ration (see Šmídová 2021, Šmídová et al. 2024). In this case, strong bias towards females is apparently caused with their easier identification. Degree of this bias is difficult to estimate, my intuition based on the low degree of dimorphism says females might be slightly more common.

In all other sites, completely articulated specimens are extremely rare. Some specimens were even preserved laterally. Damage by predators is frequent (n= 13; See paragraph **Cockroaches as food**). Furthermore, it can be suggested that the species originating from more remote (higher on the flow) areas will be more rare and more damaged. This should be reflected in numerous taxa counting few individuals and in damaged condition.
Nevertheless, it is hypothetically valid only possibly for few taxa, namely *Liadoblattina crassivenata, Cameloblatta stress, Caloblattina laesis, Liberiblattina cipka, L. kontrapunktata, L. kontravenata, L. zokamuvypadli, L. neniocom, Cratoholocompsa karatauensis* and *Ano palindrom* (n= 10/95). Thus it is very probable that none of the species or very few ones originate exclusively up in the stream.
Significant pre-depositional transport was



Bottom movement

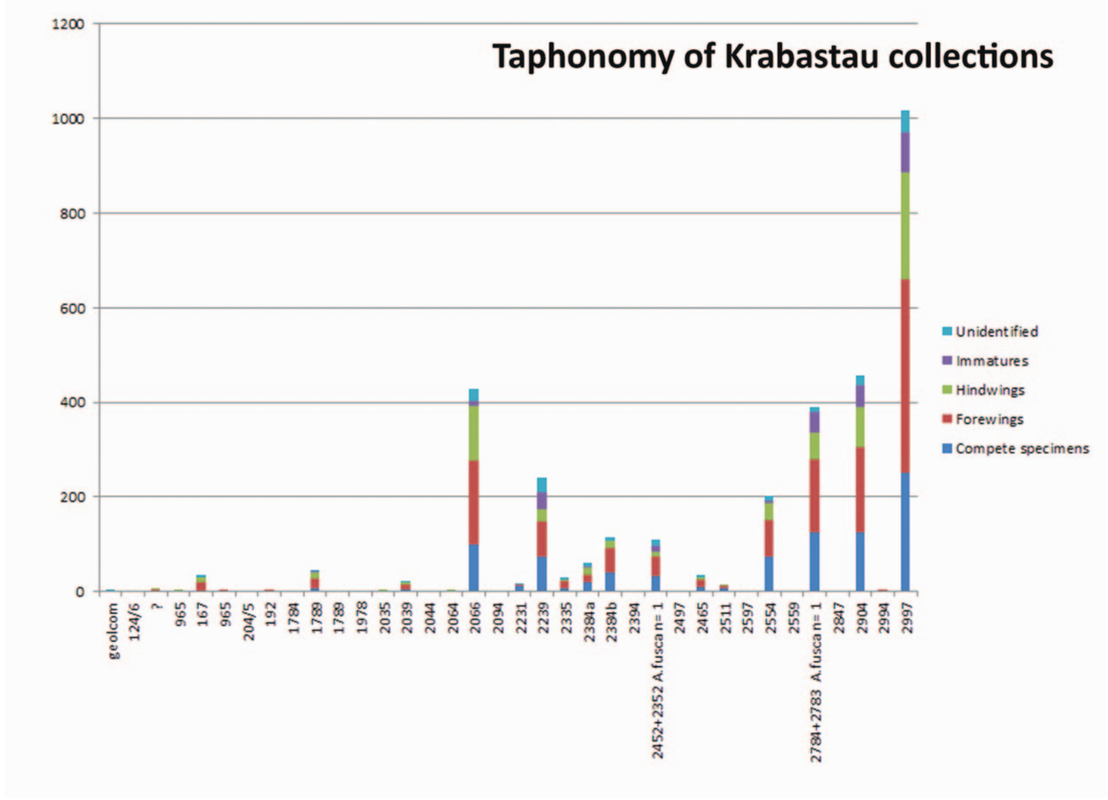
revealed additionally for specimens in other 5 taxa, while most are nearly undamaged and might be living close to the source lake.

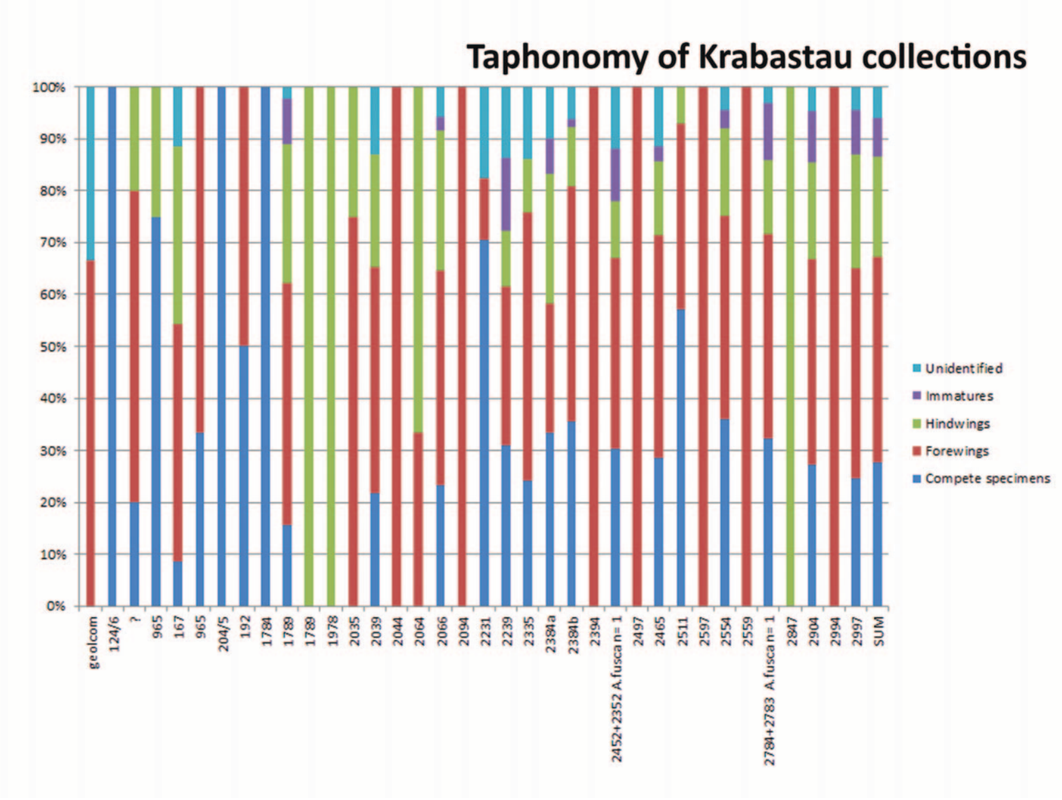
Unfortunately, we are still not in the stage of the knowledge knowing the ecological preferences of respective groups (see **Ecological preferences** paragraph), so it is difficult unless impossible to designate the source of the respective species. We can also reversely assume by degree of damage respective species.

There are assumptions for intense predation by fish and predatory dragonfly immature individuals (Panfilov 1961; but see Gekker 1948). Additionally, a considerable pre-burial transport on the basis of diverse odonatans, ephemeras, cockroaches (including a complete preservation of smaller species compared with larger species preserved mostly as wings (Panfilov 1968)) suggests more distant allochtonous cohort are also present in collections. Phasmids suggest habitats near the source lake.

Position of fossilized isolated wings follows the stratification. In some other localities such as in Kota in India, this is rarely not held, but in Karatau always. Position of the complete analysed cockroaches (n= 174; see photographs), greatly relates to their dorsoventral flattening, so the lateral position is rare (n=10). 44 are preserved with all 4 wings outstretched, 50 with forewing and hindwing on one side, 66 in nearly fully folded position. 4 are disarticulated. This seems to me a stochastical distribution biased towards horizontal preservation (in contrast to lateral) due to dorsoventral flattening. Positively biased is also the preservation of complete specimens without outstreched any wing and with only one side outstretched. The least are all 4 wings outstretched, which seems that either the insects fallen into the surface with outstretched wings and were rather quickly (more quickly than burial) compacted. Or more probably, that they begin outstretching on the bottom but most retained in a spasm.




Taphonomy of Krabastau collections
1200
1000
800
600
400
200
0
Unidentified
Immatures
Hindwings
Forewings
Compete specimens
geolcom
124/6
?
965
167
965
204/5
192
1784
1788
1789
1978
2035
2039
2044
2064
2066
2094
2231
2239
2335
2384a
2384b
2394
2452+2352 A.fusca n= 1
2497
2465
2511
2597
2554
2559
2784+2783 A.fusca n= 1
2847
2904
2994
2997


Taphonomy of Krabastau collections
100%
90%
80%
70%
60%
50%
40%
30%
20%
10%
0%
Unidentified
Immatures
Hindwings
Forewings
Compete specimens
geolcom
124/6
?
965
167
965
204/5
192
1784
1788
1788
1978
2035
2039
2044
2064
2066
2094
2231
2239
2335
2384a
2384b
2394
2452+2352 A.fusca n= 1
2497
2465
2511
2597
2554
2559
2784+2783 A.fusca n= 1
2847
2904
2994
2997
SUM

	geolcom	124/6	?	965	167	204/5	192	1784	1789	2035	2039	2044	2064	2066	2094	2231
Raphidiomimidae indet.									0/0/0/1					1/0/0/1		
Liberiblattinidae indet.					0/0/2/0				1/0/1/0					1/1/3/0		
Blattulidae indet.														7/1/0/0		
Caloblattinidae indet.									1/2/0/0		1/0/0 /0			7/15/16/0		1/2/0/0
Mesoblattinidae indet.																
Incertae family									0/1/4/1					3/9/7/2		
Isolated clavi					1									4		
Unidentificable pronota														1		
Unidentified fragments	1				3											1
Unidentified fragments											3					
Liberiblattinidae																
Unidentified fragments																
Raphidiomimidae																
Bodies Liberiblattinidae																
Bodies Caloblattinidae														4		2
Unidentificable bodies																
Unidentificable legs									1					16		
Unidentificable head																
Sivis lukashevichiae																
Perlucipecta liangiae			1/0/0		0/1/0									1/4/0		1/0/0
Mesoblattina etarakan																
Hydrokhoohydra aquabella									0/0/0/2					0/0/0/3		
Skokidae *(Skok svaba)* SUM														0/1/0		
Lovec pratiena (Lovecidae SUM)														1/0/0		
Malovol hlavolam (Umenocoleidae SUM)																
Fractalia aristovi (Fractalidae SUM)									1/0/0							
Elisamoides sediomasle																
Hra nice																
Aktassoblatta fusca				1/0/1	0/3/1		1/0/0		2/10/0					5/30/16		2/0/0
Aktassoblatta pullata														1/0/0		
L. cunicula																1/0/0
L. ihringovae														1/0/0		
Liberiblattina kontrapunktata																
Liberiblattina kontravenata																
Liberiblattina luminanala											0/1/0					

2239	2335	2384a	2384b	2452+2352 *A.fusca* n = 1	2497	2465	2511	2597	2554	2784+2783 *A.fusca* n = 1	2904	2994	2997	SUM	TOTAL
3/0/0/1		1/0/0 /1	1/0/0						1/3/0/1		3/0/0/2		0/3/2/3	10/6/2/10	28
0/3/0/0			0/2/0 /0			0/1/0/0			3/0/1/0	1/1/9/0	2/0/4/0		5/4/12/0	13/12/32/0	57
0/0/0/5				0/0/0/1					0/0/0/1	0/0/0/1	0/0/0/3		0/0/0/4	7/1/0/15	23
5/1/5/4	0/1/0/0		6/0/0 /0	12/1/3/0					10/8/4/0	8/10/4/2	18/12/10/3		38/22/12/6	107/74/54/15	250
											0/0/0/1			0/0/0/1	1
0/1/0/5	0/0/2/0	0/0/0 /3	1/1/0 /0	1/0/0/3			1/0/0/0		0/7/1/3	3/1/1/13	0/6/1/1		6/2/4/14	15/28/20/45	108
				1							2		8	16	16
1			1							2	1			6	6
9		4		4		3			3	1	4		15	48	48
2	2	2		4									2	15	15
				1										1	1
1			2											3	3
	1			1						6	1		10	25	25
1									4		1		3	9	9
18	1		4	2		1			2	3	12		8	68	68
1														1	1
2/0/0									2/0/0	4/1/0	1/1/0		0/1/0	9/3/0/0	12
1/2/0/1				0/0/0/1					3/2/0	1/1/0	4/4/0		4/7/0/1	16/21/0/3	40
									1/0/0		0/1/0		1/0/0	2/1/0/0	3
0/0/0/18			0/1/0 /2	1/0/0/5		0/0/0/1				0/0/0/4			0/0/0/12	1/1/0/47	49
									2/0/0	0/0/0/1			0/2/0	2/3/0/1	6
1/0/0											3/0/3		0/0/1	5/0/4/0	9
						1/0/0								1/0/0/0	1
														1/0/0/0	1
											0/1/1			0/1/1/0	2
			1/0/0							0/0/1			2/2/1/1	3/2/2/1	8
16/15/9	3/5/3		12/26 /2	4/9/1		5/5/3	5/2/1		3/17/5	9/23/6	18/61/21		41/100/33	127/306/102	535
														1/0/0/0	1
													1/1/0	2/1/0	3
									0/0/1	0/1/0	0/1/0		3/4/0	4/6/1/0	11
													0/1/0	0/1/0/0	1
			0/1/0						0/1/0				0/5/0	0/7/0/0	7
								0/1/0			0/1/0			0/3/0/0	3

	geolcom	124/6	?	965	167	204/5	192	1784	1789	2035	2039	2044	2064	2066	2094	2231
Liberiblattina liberiblattina														0/2/0		
Liberiblattina cipka														0/1/0		
Liberiblattina palaeontologica																
Liberiblattina zokamuvypadli														0/2/0		
Liberiblattina neniocom														0/1/0		
Liberiblattina oddajsami																
Ano tak																
Ano palindrom																
Ano mal														1/0/0		
Ano ona											1/2/2			3/0/0		
Ano si														1/0/0		
Ano naslosa														0/1/0		
Akinisia chorevei			0/0/1		0/0/1				0/0/1	0/0/1	0/0/1			1/1/1		1/0/0
Katatychi symptosi														1/0/0		
Kazachiblattina asiatica (Vishniakova, 1968)																
Makacka akcakam														1/0/0		
Makacka akmacaka																
Miniblattina inflatica																
Operam testudina																
Operam monita							0/1/0									
Operam simpla																
Elisama prelistama																
Pseudomantina nigroalba																
Macroblattula velipsespilev														0/1/0		
Okienkula ojedinela sp.n.														0/1/0		
Blattula fragilia														1/3/0		
Blattula gracilicosta														1/0/0		
Blattula ahanaha																
Blattula microscopica					0/1/0				1/0/1					1/3/6		
Blattula summa														0/1/0		
Blattula rectinervosa *Vishniakova, 1971*					0/0/3				0/1/2					9/8/9/6		

2239	2335	2384a	2384b	2452+2352 *A.fusca* n=1	2497	2465	2511	2597	2554	2784+2783 *A.fusca* n=1	2904	2994	2997	SUM	TOTAL
0/1/0				0/1/0						1/5/0	0/0/1	0/1/0	2/1/0	3/11/1	15
													0/2/0	0/3/0	3
							1/0/0							1/0/0/0	1
														0/2/0/0	2
														0/1/0/0	1
									2/0/0	1/0/0				3/0/0	3
										2/0/0			0/1/0	2/1/0/0	3
													0/1/0	0/1/0/0	1
										0/2/0	0/0/2		0/0/4	1/2/6/0	9
1/2/1		3/0/0		1/4/1					4/0/1	9/3/3	8/0/7		4/4/28	34/15/43	92
1/0/0													3/3/0	5/3/0/0	8
														0/1/0	1
		0/0/2		2/1/0		0/2/0			0/0/2	6/14/10	0/0/1		1/4/10	11/22/31	64
									1/0/0	2/1/0	0/1/0			4/2/0/0	6
1/0/0														1/0/0/0	1
										1/0/0	1/0/1		0/1/1	3/1/2	6
													1/0/0	1/0/0/0	1
		0/1/0							1/0/1					1/1/1	3
1/0/0														1/0/0/0	1
0/1/0													0/3/0	0/5/0/0	5
													0/1/0	0/1/0/0	1
										0/1/0	1/1/0		1/2/0	2/4/0/0	6
									0/1/0	0/0/1			0/2/0	0/3/1/0	4
													0/1/0	0/2/0/0	2
														0/1/0/0	1
									0/0/1	2/0/0	2/1/0			5/4/1/0	10
			0/1/2	0/1/0						0/3/0	0/1/0		0/1/2	1/7/4/0	12
									1/0/0	0/0/1	0/0/1		0/0/1	1/0/3/0	4
4/0/2		2/0/4		1/0/0					0/0/1	0/1/2	2/1/1		1/0/3	12/6/20/0	38
				1/3/1							0/2/0			1/6/1	8
2/2/1		1/0/4	0/1/0						6/2/3	6/10/3/24	5/1/6		8/12/18	37/37/49/30	153

	geolcom	124/6	?	965	167	204/5	192	1784	1789	2035	2039	2044	2064	2066	2094	2231
Blattula druha																
Blattula nebude																
Blattula brevicaudata Vishniakova, 1968	0/2/0			0/2/0	3/8/4				2/3/3		0/0/1			23/31/43/2	0/1/0	
Asvab bavsa					0/2/0					0/3/0	3/3/0			5/8/7		
Spono spono																
Decompositа triocella														1/1/0		
Decompositа tristriata																
Decompositа pentavisia																
Decompositа basquatirgis																
Decompositа apicata																
Olzmasg zi			0/3/0						0/1/0		0/0/1			3/1/0		
Cameloblatta variegata Vishniakova, 1971					0/1/1									1/6/6		
Cameloblatta stress																
Raphidiomima chimaera Vishniakova, 1971														4/0/0		
Raphidiomima cognata Vishniakova, 1971																
Rhipidoblattina maculata Vishniakova, 1968																
Rhipidoblattina dmitrievi				1/0/0					1/2/0					0/5/0		
Divocina polnoci																
Chuanblatta staloso														1/4/0		
Memento mori									0/1/0					2/4/0+2legs		1/0/0
Liadoblattina crassivenata																
Falcatusiblatta disrupta											0/1/0			0/3/0		
Falcatusiblatta casovec											0/2/0			0/0/1		1/0/0
Falcatusiblatta storozhenkoi											0/1/0			1/2/0		
Falcatusiblatta toold																
Falcatusiblatta zaloha																1/0/0
Liadoblattina karatavica (Vishniakova, 1968)														2/1/0		
Asioblatta punctata														3/1/1		
Aposema gigantenna																
Caloblattina laesis																
Karatavoblatta longicaudata Vishniakova, 1968														1/0/0		

2239	2335	2384a	2384b	2452+2352 *A.fusca* n = 1	2497	2465	2511	2597	2554	2784+2783 *A.fusca* n = 1	2904	2994	2997	SUM	TOTAL
1/0/3									1/0/0		0/0/1		0/0/3	2/0/7/0	9
											1/0/0 (p)		3/0/0 (1p)	4/0/0/0	4
2/13/2	1/0/0	4/3/5		5/9/2					5/10/6/2	24/28/4/2	15/10/13		34/50/31/10	118/170/114/16	418
1/0/0		2/2/0		0/3/0					0/1/1	1/7/0	2/5/1		3/11/4	17/45/13/0	75
													0/1/0	0/1/0/0	1
1/0/1			4/2/1	0/1/0					2/2/1	4/1/0	0/6/0		1/14/5	13/27/8	48
				1/0/0										1/0/0/0	1
													1/1/0	1/1/0/0	2
0/2/0			0/2/0						0/1/0	2/0/0			0/2/0	2/7/0/0	9
0/0/1				0/1/0									0/2/4	0/3/5/0	8
0/0/1			2/1/3	0/1/2					0/2/0	4/4/4 plus one leg	2/11/1		9/9/6/one head/one leg	20/33/18/0	73
			0/0/1						3/2/4	5/1/0	0/3/0		3/1/2	12/14/14	40
			0/0/1										0/1/0	0/1/1/0	2
3/0/0			3/0/0						3/0/0				1/0/0	14/0/0/0	14
										1/0/0	1/0/0			2/0/0	2
1/0/0													0/2/0	1/2/0/0	3
	0/1/0	0/1/0		0/4/0		0/1/0				0/3/0	0/2/0		0/1/0	2/20/0/0	22
			0/2/0							0/1/0	1/0/0		1/1/0	2/4/0/0	6
3/3/0		1/0/0	6/6/0			1/1/0	0/1/0			0/1/0	2/10/0+1P		10/13/0/1	24/39/0/1	65
4/6/0		2/2/0		0/1/0					1/7/0	3/5/1	7/9/6/1		8/20/17	28/55/24/1+2	110
0/1/0			0/1/1										1/6/1	1/8/2/0	11
1/0/0	1/0/0		0/1/0						1/1/0		0/4/0	0/2/0	1/6/0	4/18/0/0	22
3/4/0			0/1/0	0/0/1					1/0/0	5/1/1	0/0/1		0/4/0	10/12/4	26
1/4/0									0/2/0	2/4/0	1/3/0		1/6/0	6/22/0	28
											1/0/0			1/0/0/0	1
														1/0/0/0	1
2/1/0			1/0/0			0/1/0				0/1/0	2/0/0		0/3/0	7/7/0	14
1/0/0			4/1/1	1/0/0			0/2/0		0/0/1	2/2/0	3/0/0		1/1/1	15/7/4	26
0/1/0									1/0/0				1/0/0	2/1/0/0	3
									0/1/0					0/1/0/0	1
														1/0/0/0	1

	geolcom	124/6	?	965	167	204/5	192	1784	1789	2035	2039	2044	2064	2066	2094	2231
Rhipidoblatta brevivalvata Vishniakova, 1968																
Rhipidoblatta trimestre														1/0/0		
Rhipidoblatta matriky													0/0/2	0/1/0		1/0/0
Rhipidoblatta matrikarky														0/4/0		
Rhipidoblatta fusca Vishniakova, 1968		1/0/0				1/0/0			1/0/0					1/0/0		1/0/0
Rhipidoblatta triky																
Rhipidoblatta trika																
Rhipidoblattinopsis latitergata									0/2/0					0/12/0		
Fosilia tubuliovipositorica														1/0/0		
Latiblatta lativalvata								1/0/0				0/1/0		5/4/0		
Latiblatta osud													0/1/0			
Manipulator olim (Manipulatoridae SUM)																
Morphna una (Blaberidae SUM)																
Cretaholocompsa karatauensis														0/1/0		
Okruhliak samoodpovedaniesi																
Sociala borat (Socialidae SUM)																
SUM	0/2/0+1	1/0/0	1/3/1	2/2/1	3/16/12+4	1/0/0	1/1/0	1/0/0	10/23/12/4+1	0/3/1	5/10/5+3	0/1/0	0/1/2	103/175/116/14+25	0/1/0	11/2/0+3

2239	2335	2384a	2384b	2452+2352 *A.fusca* n=1	2497	2465	2511	2597	2554	2784+2783 *A.fusca* n=1	2904	2994	2997	SUM	TOTAL
1/0/0		0/2/0	0/1/0	2/0/0		1/0/0			1/0/0	1/0/1			2/0/1	8/3/2	13
														1/0/0/0	1
2/2/0		0/2/0	0/0/1	1/0/1	0/1/0	1/2/1	1/0/0		1/0/1	3/1/2	0/3/1		9/12/12	19/24/21	64
1/0/0											0/1/0		1/1/0	2/6/0/0	8
1/1/0	1/9/0	1/0/0							0/6/1	0/3/1	7/11/0		6/28/7	21/58/9	88
									0/3/0	1/1/0	1/4/0		2/3/0	4/11/0/0	15
											0/1/0		1/0/0	1/1/0/0	2
1/1/0		1/2/0							3/0/0	0/2/0			6/7/2	11/26/2	39
1/1/0									0/1/0		1/1/0		4/0/0	7/3/0/0	10
1/2/0	1/0/0	2/0/0				1/1/0			3/0/0	5/0/0	7/1/0		8/1/1	34/10/1	45
3/0/0			0/2/0			0/1/1			1/0/0	7/6/0	1/0/0	0/2/0	3/6/2	15/18/3	36
2/0/0											1/0/1		1/0/0	4/0/1/0	5
1/1/0													3/0/0	4/1/0/0	5
										0/1/0			0/1/0	0/3/0/0	3
													1/0/0	1/0/0/0	1
											1/0/0			1/0/0/0	1
76/71/26/34+33	7/16/5+4	20/15/15/4+6	41/53/13/2+7	33/40/12/10+13	0/1/0	10/15/5/1+4	8/5/1	0/1/0	67/80/36/7+9	126/152/55/47+12	125/181/85/11+21	0/5/0	248/406/230/52+46	900/1281/633/186+192=3192	2539+659=3198

ASSEMBLAGE ANALYSIS ON THE BASIS OF COLLECTION NUMBERS

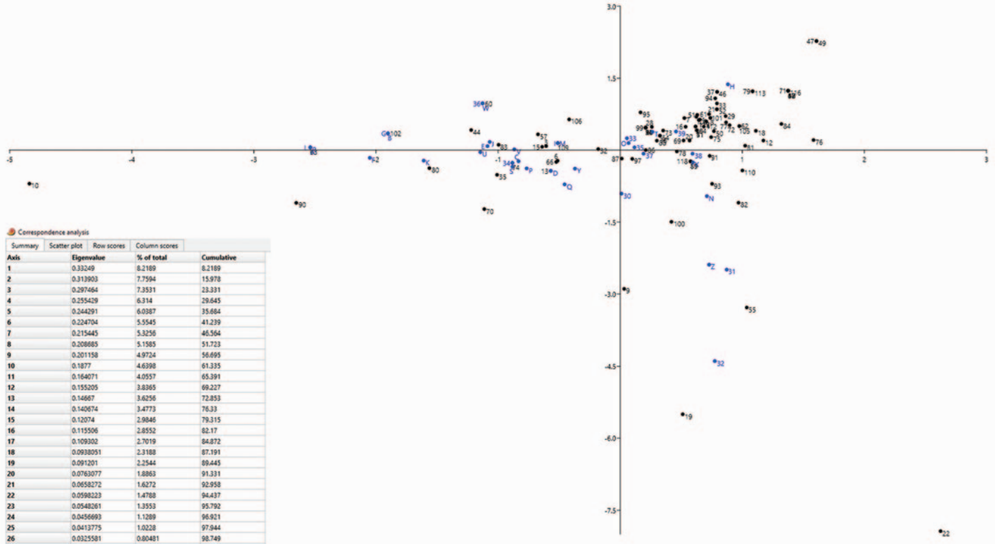
Assemblage analysis within Karabastau is poorly elaborated. Consensus is established (Rohdendorf 1968) that all the localities, mainly Galkino and Mikhailovka, belong to a single Karabastau Formation and respective Beds differ only due to taphonomical situation (different fish taphonomy). The Correspondence analysis performed based on the collection numbers only reveals differing (species-principal) of Collection numbers 204; 124; 2511; 2094; 2597; Geolcom; 1978; 2035, 2847 and 2497. All these differences are simply related to ocurrences of only few samples within these collections and surely do not represent any supported differences as all of them contain dominant or codominant species. There is no statistical difference among collection numbers. More informative (Collection-Number-principal) correspondence analysis WITH RESTRICTED DATA reveal strict difference of Operamidae (FOD) in the PIN Collection 192, but they also rarely occur in other collection numbers, a difference that disappeared with complete data. A minor difference is revealed by *Fractalia* and *Maloval* – both unique specimens of Umenocoleidae/Fractalidae (both FOD) in Collections 2465 and 2789, both collections with occurrence of dominant taxa as well. *Elisamoides* is separated due to a single occurrence, which nevertheless, also co-occur with dominant species.Separated *Liberiblattina zokamuvypadli* with a single occurrence also coincides with the dominant collection (PIN 2066). To summarise, collection-based analysis do not reveal any conclusive data, but might indicate a special collection conditions in some rare species. These indications seems too numerous (and in three cases they represent FODs of whole families – Umenocoleidae, Fractalidae and Operamidae) to represent only stochastical finds by separate collecting years and will be further evaluated due to respective Beds – especially within these 3 families.

ASSEMBLAGE ANALYSIS ON THE BASIS OF ACTUAL BEDS

There are two distinct main localities within the Karabastau Formation, namely Galkino and Mikhailovka. All but 55 of specimens originate from Mikhailovka. Thus any comparison lack significance. In Galkino, only *Aktassoblatta fusca (12/535), Operam monita, Latiblatta lativalvata, Rhipidoblattina dmitrievi* (5/22) *Olzmasg zi, Rhipidoblattinopsis latitergata* (2/40), *Rhipidoblatta tri, Memento mori, Hydrokhoohydra aquabella, Fractalia aristovi, Blattula rectinervosa (6/153), B. brevicaudata (9/418), B. microscopica (2/38)* ocurred. The taphonomical situation in Galkino is also similar for adults/FW/HW/immature individuals (11/19/11/1 compared with total 900/1281/633/186), so there is not any measurable taphonomical difference either. Moreover the diagnostic *Hydrokhoohydra aquabella* represents a (semi)aquatic taxon suggesting also similarity in water environment. The only difference is thus presence of *Fractalia aristovi*, which is a significant difference (the sole representative of the family), which can, nevertheless, be stochastical. Another important inference originates from the shared occurrence of *Blattula rectinervosa, B. brevicaudata* and *B. microscopica* strongly suggesting that these 3 species really lived together and/or that the both sites are stratigraphically identical. The number of indetermined specimens is slightly higher (n=13; 23.6 %, compared with 20.6 % in total), but not drastically. While there is a clear taphonomical diffence among more patient Galkino and more dynamic Mihailovka established on the basis of fish acummulations (Gekker 1948), these patterns are surely reflected also in insect asseblage (presence of larger species in Galkino) – nevertheless, these patterns are statistically insignificant. Additionally some taxa are present in clearly different more hard-grained sediments (such as *Decomposita tristriata* – see figp. 138), these difference, nevertheless, might be caused with the supply of sandy/dusty materials by rare winds (Gekker 1948).

ECOLOGICAL DOMINANCE

Dominant species were *Blattula brevicaudata* Vishniakova, 1968 (n= 418), *B. rectinervosa* Vishniakova, 1971 (n= 153; Blattulidae); *Aktassoblatta fusca* Vishniakova, 1971 (n= 535), *Memento mori* (n= 110) and *Ano ona* (n= 92; Liberiblattinidae). Cohorts recorded eudominant predators: manipulatorids, lovecids, diverse liberiblattinids, blattulids and raphidiomimids (1+1+27+15+22= 66 spp.; n= 3+9+791+745+508= 2,056); somewhat golden-beetle-like latiblattids (4 spp., n= 55); (semi)aquatic (1 sp.; n= 1 and 43 larvae); brachypterous (n=), presumed beetle-like pollinator (n= 1) and possible liberiblattinid pollinators (1 sp., n= 6 and 1 larva). Codominant decomposers represented Caloblattinidae (n= 261; 10.3 %). Modern Blaberidae (FOD, n= 5), Corydiidae (FOD; n= 1), eusocial Socialidae (FOD; n= 1), and Mesoblattinidae (n= 55) were rare. Rare were also Fractaliidae (FOD; n= 1), golden beetle-like Latiblattidae (FOD, LOD; n= 55), Operamidae fam.n. (FOD, LOD; n= 7), beetle-like Umenocoleidae (FOD; n= 1) and holoptic Skokidae (FOD, LOD; n= 6). Decomposing Fuziidae and water-skimming Chresmodidae were absent.



Correspondence analysis

Summary | Scatter plot | Row scores | Column scores

Axis	Eigenvalue	% of total	Cumulative
1	0.33249	8.2189	8.2189
2	0.313903	7.7594	15.978
3	0.297464	7.3531	23.331
4	0.255429	6.314	29.645
5	0.244291	6.0387	35.684
6	0.224704	5.5545	41.239
7	0.215445	5.3256	46.564
8	0.208685	5.1585	51.723
9	0.201158	4.9724	56.695
10	0.1877	4.6398	61.335
11	0.164071	4.0557	65.391
12	0.155205	3.8365	69.227
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20	0.0763077	1.8863	91.331
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25	0.0413775	1.0228	97.944
26	0.0325581	0.80481	98.749
27	0.0240658	0.59489	99.344
28	0.0172415	0.4262	99.77
29	0.0055527	0.13726	99.907
30	0.00375135	0.09273	100
31	2.26006E-31	5.5867E-30	100
32	4.04971E-32	1.0011E-30	100
33	1.90017E-32	4.6971E-31	100
34	1.81866E-32	4.4956E-31	100
35	5.50928E-33	1.3618E-31	100

Genus-based correspondence analysis of Collections (Collection-Principal)

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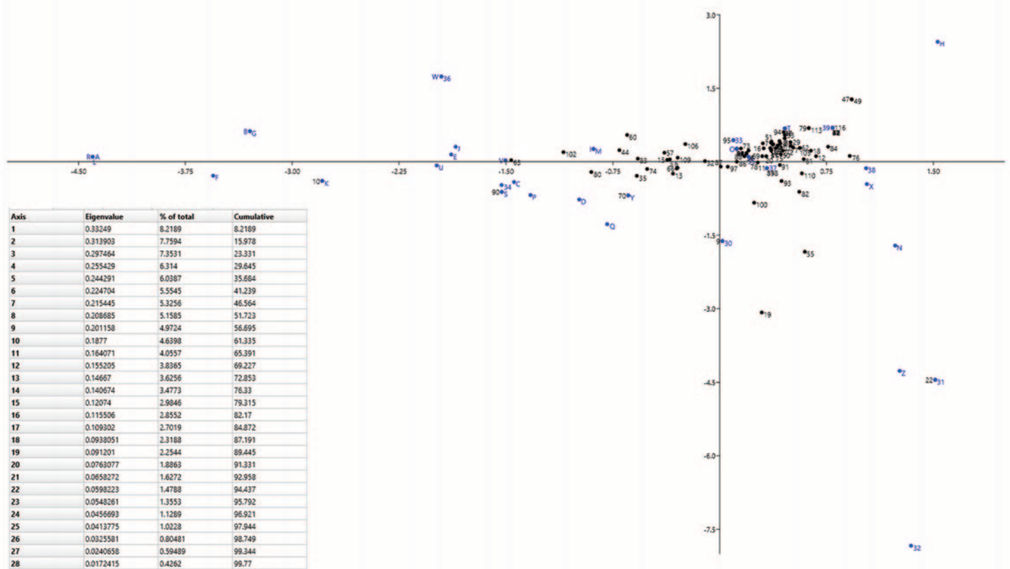

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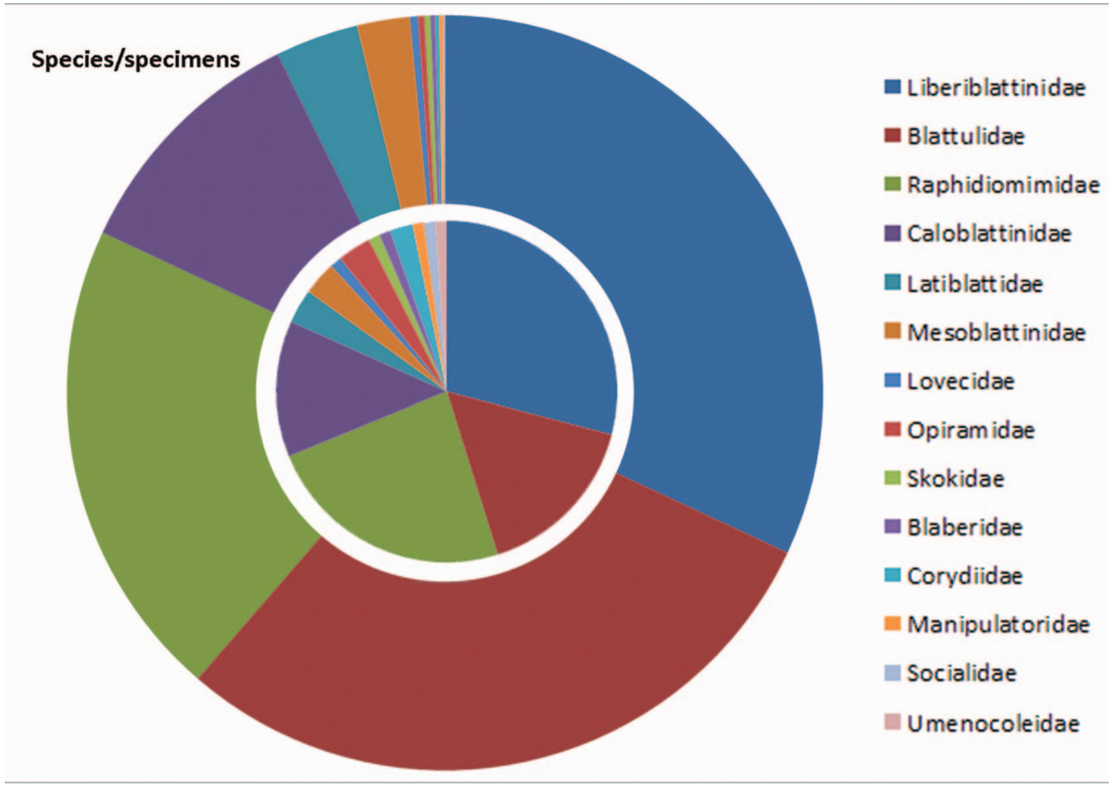
numbers represent genera (see matrix); letters represent colletions



ECOLOGICAL PREFERENCES

Knowledge on ecology is too weak to determine the exact locations of the present insects (i.e. cockroaches). We do not know even the rough niches of the dominant groups such as Ano, *Liberiblattina* and *Hra*. Exceptions are few. Besides the (semi)aquatic *Hydrokhoohydra,* beetle-like free living Latiblattidae, possible pollinators (see **Pollinator** paragraph), there can be presumed open lifestyle for the few probably diurnal (?*Blattula, Elisama*) and nocturnal (*Divocina*, *Lovec, Pseudomantina*) predators, while most of the predators (*Akinisia, Asvab, Cameloblatta, Decomposita, Falcatusiblatta, Macaroblattula, Memento, Olzmasg, Okienkula, Raphidiomima, Liadoblattina, Rhipidoblattina, Chuanblatta)* are obscure in their ecological preferences. An exception is *Caloblattina* though that occurs in marsches (see Majtaník and Kotulová 2023). Unknown are also preferences of modern *Mesoblattina,* while *Perlucipecta* and Sivis are frequent in amber record (Vršanský and Sendi 2022, Sendi et al. 2023b, Kováčová 2023) suggesting a dense forest and/or highly plurivalent habitats – and the same apply for *Okruhliak* (Vršanský et al. 2023b). The dominant genus *Rhipidoblatta* also frequently occurs in amber. Living *Morphna* can also be of help and suggests either ancient but modern or extremely conservative living habitats. *Manipulator* also seems to be a diurnal dense forest predator. None of this indicators help us to support taphonomical ocurrences (stream/vs lake: upland vs. lowland forests or more damaged parts).

DIVERSITY

Diversity indexes 3.241/7.407 (SW/Hulbert) makes Karabastau among the highest diversity assemblage in history, comparable only to roughly coeval Kota in India, Upper Cretaceous burmite (where is much higher disparity also compared with living ecosystems) and contemporaneous tropical rainforests.
These values, nevertheless, must be taken with caution, as correlation of these two indexes is statistically insignificant (r^2= 0.75) for cockroaches over time and both are restricted meaning that the first one underestimates the effect of small sample size – and therefore here it is extremely high also due to largest sample size. The second one is too sophisticated to reflect reality and possibly exaggerates smaller sample sizes. Nevertheless both are extremely high and the huge diversity is apparently not an artefact also due to similarly rich roughly coeval Kota – it is high even if we accept several independent time-splitted assemblages. Also the disparity of forms is high enough to conclude the high real diversity (higher than in the contemporaneous rainforests and higher only in burmite).

Dominance of species and specimens within families (figp. 554) are discussed separately. It is evident that the vast majority of diversity as well as ecological dominance was driven by the main Mesozoic families. What is disrupting is the huge number of species in indigenous groups (discussed in special paragraph). The special consideration need a huge diversity of the predatory cohort (over 20 %

and possibly up to 80 % of specimens and species), which were apparently dominant predators in several subcohorts, from huge top predators like *Manipulator* or *Olzmasg*, up to minute raptors within Blattulidae, Liberiblattinidae and among Blattulidae. Predators are very restricted in burmite due to size distribution of much smaller cockroaches in amber medium, and predatory cockroaches s.s. are a great exception today (see the only known case of gelous-matter producing predatory cockroach). Beetle-like cockroaches (dominant in burmite), jumping cockroaches (a single living species), eusocial groups (constituting up to 8 % of biomass of the advanced living ecosystem) as well as modern ootheca-producing cockroaches (exclusively present in living ecosystems – ovipositor-bearing cockroaches are extinct now) constituted insignificant proportion of the whole assemblage.

DISPARITY OF FORMS

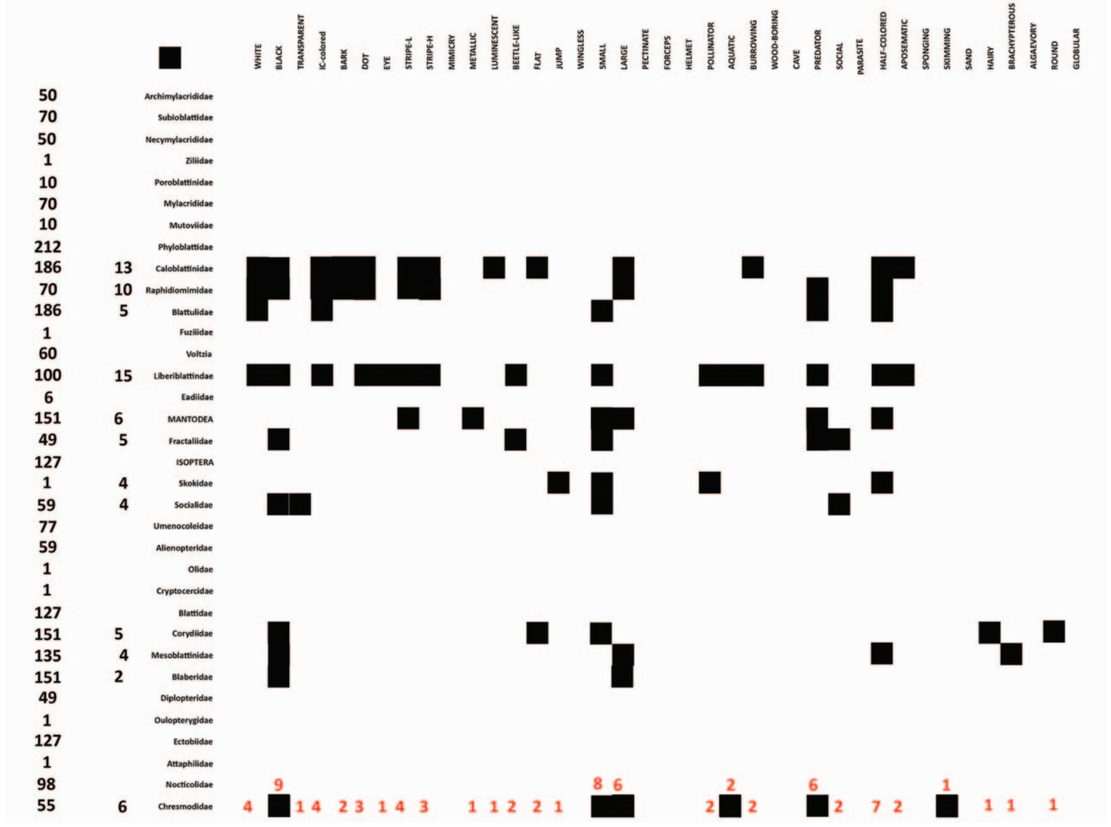
While it might appear slightly problematic to quantitatively evaluate diversity and recognise biological forms appropriately, disparity of forms reveal a bright picture. It is not clear and any evidence is lacking about Carboniferous, Permian, Triassic, Early and Middle Jurassic cohorts other than diverse predatory and decomposition cockroaches (including the bizzarre Fuziidae indigenous to Daohugou, China). On the other side, the Late Cretaceous (and the same estimations are for the Early Cretaceous after 127Ma Diversification Point) reveal evidence for all living cohorts of cockroaches including cave fungi-diggesting (Sendi et al. 2020), eusocial termites, metallic, pollinating, nocturnal, dinosaur-dung -processing, aposematic, semiaquatic, ant-parasitic, Batesian mimics and all others. Only fossil evidence for cyanobacteria-feeding of living *Melyroidea* is missing. So the Late Jurassic is a critical point, at least revealing golden-beetle-like Latiblattidae indigenous to Karabastau expected to be pollinators (it will be impossible to identify them elsewhere on the basis of forewing only at the present state of knowledge). Also brachyptery has possible first record here, but preservation is highly unlikely, that it also has no relavance in respect to FOD. It is clear that predatory cockroaches were already modern in Early Jurassic (in spite of missing of crown mantodeans) and that the coloration alreay comprise all forms possibly including metallic. Smallest as well as very large forms were already present in Karabastau and probably also earlier. Fungi-diggesting cockroaches are known starting from the Cretaceous (Vršanský et al. 2022), (semi)aquatic and aposematic ones are present in Karabastau (Vršanský et al. 2019), but are expected to radiate earlier. Eusocial forms are also present. Socialidae and *Fractalia* posses wing-breaking sutura and nuptial flight cannot be excluded to be fixed with other social traits. Nevertheless, this group was rare (n= 1; N= 2 in Myanmar amber), what makes this probability very low (although *Melyroidea* and *Aclavoidea* are rare in living collections as well - Hinkelman et al. (2020)) and near-zero is also probability of capturing this group in other sedimentary rock. As other eusocial organisms did not exist, excluded are also ant, but no termite parasites (Cretaceous *Spinka*; living Attaphilidae). Nevertheless, *Okruhliak* might be associated with first termite nests too. Missing are cave organisms, but such evidence even in the case of their existence is unlikely. Nevertheless, at least Nocticolidae radiated much later.

So while there is a extremely high disparity of forms at Karabastau, it is impossible to declare a significant rise in comparison with Daohugou(China) or Bakhar (Mongolia). Nevertheless, in the case of the strongly modified and aposematic *Operam* (aposematically alone are also other taxa such as *Aposema*) I have a strong feeling that it represent a mimic of an unknown organism as stingers are unknown at that time.

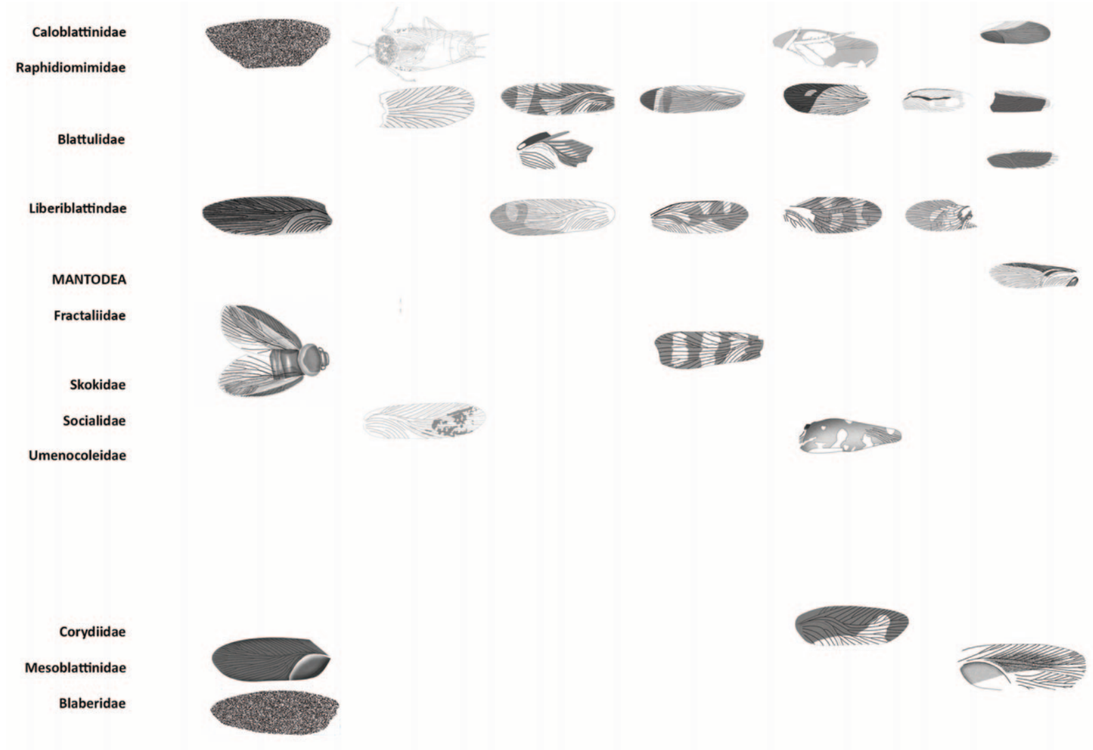
LIFE FORMS

The following life forms/ forms of coloration were recognised. Here and in all consequent publications they will be marked ***Bold italic underline***:

White - the most common uncolored form.
Black - the most common dark-colored forewing.
Small - miniaturised species.
Large – species significantly larger than normal.
Stripe L - forewing with longitudinal stripe.
IC colored - colored intercalaries.
Half-colored - half of forewing colored.
Stripe H - forewing with horizontal stripe.
Aposematic - distinct signal for predator.
Predator - predatory form.
Dot - presence of a dot(s) on a forewing.
Beetle-like - beetle like forms with elytrised forewing.
Wingless - wingless forms.
Pollinator - pollen transfer.
Bark - bark spotted coloration of forewings.
Burrowing - soil, rotting ground wood burrowing form.
Mimicry - resemblance of stinging insects.
Wood-boring - wood boring form.
Hairy - hairy body and/or pronotum and/or wings.
Brachypterous - short-winged forms.
Round - round shape of forewings.
Globular - globular habitus.
Metallic - metallic body or forewings.
Transparent - transparent appearance (mostly in caves).
Social - semisocial to social (limited to *Cryptocercus*, true termites, Socialidae and Oulopterygidae).
Flat - flat habitus.
Cave - troblobionts.
Aquatic - aquatic forms.
Parasite - parasitisation in ant and termite, and possibly in dinosaur and bird nests.
Eye - dot-like pattern of forewing forming an illusory eye.
Luminescent - luminescent (limited to *Lucihormetica* and possibly Karabastau *Latiblatta*).
Jump - jumping adaptations (limited to Karabastau Skokidae and *Saltiblattella*).
Pectinate - pectinate antennae (limited to (all) Olidae and some Corydiidae from North Myanmar amber).
Algaevory - algaevory (limited to *Melyroidea* from Ecuador, Peru, Brazil and Bolivia).
Skimming - skimming form (limited to Jurassic-Cretaceous Chresmodidae and possibly another group in North Myanmar amber)
Sponging - sponging mouthparts (limited to *Spongistoma* and certain *Stavba* from North Myanmar amber).
Sand - sand grain form (limited to *Leioperoblatta* from Iran).
Helmet - female-capturing helmet (limited to *Helmablatta* from Vietnam).
Forceps - cerci forming forceps (limited to (all) Daohugou Fuziidae).
Butterfly-like - forewing scales (limited to *Lepidopterix* from Lebanese amber (Sendi et al. 2020); this form is excluded due to near-impossible identification as a fossil).
Decomposition- nitrogen-fixating decomposition form. This form is also excluded



Lifeform matrix



Restricted lifeform matrix

as it is an original form omitted only possibly in some derived Nocticolidae and possibly in some *Melyroidea*.

It is remarkable that only a few common insect forms are missing among cockroaches. True herbivores, honey-producents, biting (mosquito-like) and plant suckers (bug-like) have probably never evolved. True silk/web- producers are present in several living tropical species which use webs for protection and/or predation. Extra-oral diggestion also was not proved, and it seems that one undescribed Eocene species from Green River, Colorado, USA might have produced sound sound. One undescribed species from Myanmar amber apparenly mimicked stinking bugs and possibly might have stinked.

WITHIN-FAMILY LIFEFORMS

Among families, data can be acessed to some significant degree only in dominant genera. Within Caloblattinidae, ***Black*** is reached 9 times in Karabastau. *Rhipidoblatta* reveals 9 different forms, while *Liberiblattina* 7. ***Dot*** is acessed 3 times (*Liberiblattina+Ano, Decomposita+Olzmasg, Rhipidoblatta*) in Karatau. The extremely conservative *Blattula* with 9 species reveal only 2 forms, but produced numerous different genera with their own forms. This is a direct evidence for the huge potential of most of the taxa explosively produce numerous lifeforms. Nevertheless, sometimes as in the Triassic it takes a while reaching at least the basal forms- likely a direct evidence for the systemic ecosystem restrictions.

PHENETICAL ANALYSIS

Restricted-data similarity analysis for forewings, hindwings and bodies combined (figps. 608-609) copies results refrained from the phylogenetical analyses. All families are well-clusterred besides *Camelloblatta+Raphidiomima*, which are nested closer to Liberiblattinidae etc. – the same pattern obtained from the phylogenetical analyses. This from inspection an excellent result in the matter of fact might mean that the topology of the phylogenetical networks is correct (also in statistically unsupported nodes) due to phenetical similarity. This fact is highly pessimistic due to considering the network topologies. Thus only statistically supported nodes and also topologies must be taken into consideration. This might sound tautologically, but from the phylogenetical analyses it seems that network topologies are correct also without support. They might be not – just being similar.

Total-forewing-data similarity analysis (figp. 609) reveals (homoplasic due to partial miniaturisation) similarity of the corydiid *Okruhliak* with Blattulidae, while another corydiid *Cretoholocompsa* is within Liberiblattinidae. The bulk *Camelloblatta+Raphidiomima* (but with *Katatychi*) is again near Liberiblattinidae. *Manipulator* is here (phylogenetically correctly) within Liberiblattinidae, close to *Akinisia*. *Fosilia* is far from *Latiblatta*. *Kazakhiblattina* is within Raphidiomimidae. Other data are consistent with phylogenetical analyses (also *Morphna* is placed near Mesoblattinidae).
Thus, in the future analyses, the phylogenetical "additive value" – value of phylogeny over a similarity, might be quantified was a quantified difference among similarity values and Bayesian supports. This, nevertheless, as it results form the phylogenetical analysis and its incompleteness, does not have much value in restricted data (from one locality only).

NIGHT LIFE

Diurnal preferences are surprisingly evidenced in low number. There is a presumption about diurnal habits in the richly and sophistically colored species such as *Maloval* (pollinator), most predatory Raphidiomimidae, Liberiblattinidae and in all aposematic species (*Aposema, Ano*). Nocturnal evidence is limited to the earliest mantodean *Lovec*. *Divocina* was also possibly nocturnal judging from its Dauhugou counterpart. Nevertheless, the cockroaches would benefit from nocturnal niches and numerous cockroaches could be possibly nocturnal due to their dark coloration. One example is the dominant *Aktassoblatta* with dark hindwings, which would be not advantageous during the day. Nevetheless, evidence for this is missing. 50 species, i.e., more than a halve of all species are colored and their diurnal habits seems to be supported. Possible nocturnality is also expanded to few species in *Rhipidoblatta*. Unfortunately this evidence is not conclusive as also some colored European mantodeans with *Eye* pattern are nocturnal (Vršanský 2010b).

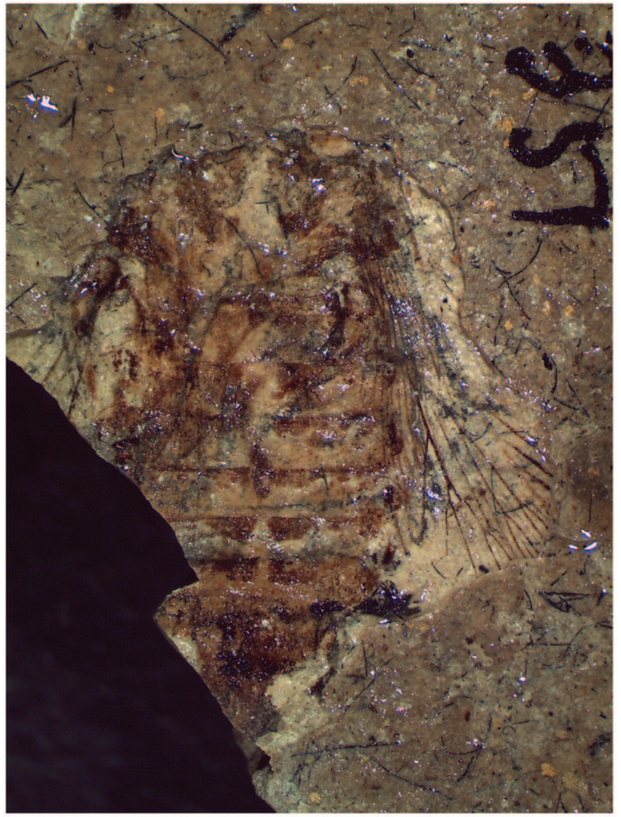
PARASITES

Parasites are among the leading factors in the evolution of life attending all levels of organization of biota from viruses up to social behavioural parasites, with their importance being principal. Cockroaches never can be considered for being completely parasitic even specialized Attaphilidae and other nest parasites always contribute to the cleansing functions of the host. Their partial parasitism thus did not influence their phylogeny principally. On the other hand, cockroaches host plethora of parasites starting from viruses (Vršanský et al. 2019a) and ending with termite nest parasites. Nevertheless, this influence was perhaps constant, as there is no unequivocal evidence for a significant variations in influence of parasites to evolution of cockroaches, termites, mantodeans or chresmodids. One significant exception are hymenopteran parasites of eggs and ootheca discussed in the other paragraphs. Karatau cockroaches apparently produced true ootheca (at least *Mesoblattina, Sivis* and *Perlucipecta* of the Mesoblattindae), but these genera originated well before Karatau time and even here their diversity did not rise significantly. Thus even so complex ecosystems did not modified the evolution and/or radiation of cockroach groups through parasites.

COMMENSALS

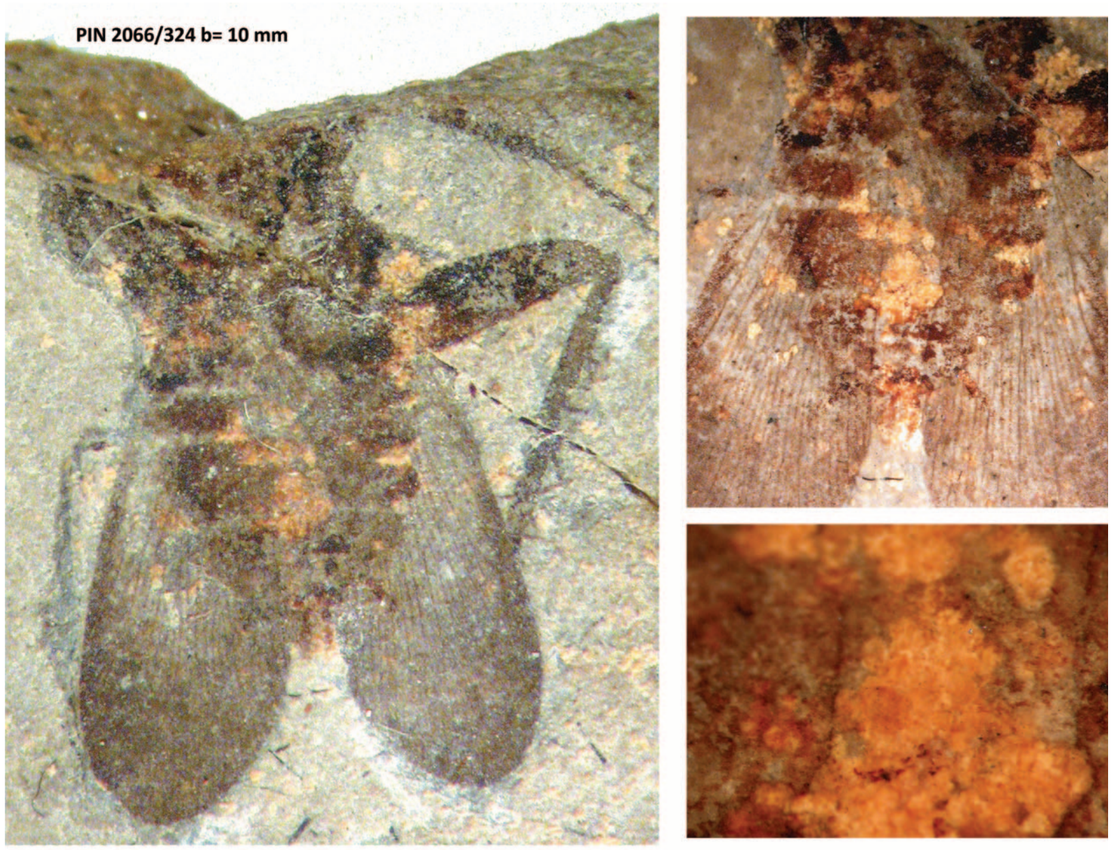
Commensals reveal another story. Nitrogen-fixing microorganisms are possibly responsible for the system success of cockroaches from their very beginning since the Palaeozoic (unless they were basally all predatory) and surely from the earliest Jurassic. Deviations from their main function (in decomposition) sometimes result in a separate level of factors operating on their evolution and environment. The (indirect) evidence revealed by Karatau material is the commensal-caused wood decomposition responsible for the origin of termites (Vršanský et al. 2019b). This cosmetical skill perhaps did not significantly influenced Karatau forest ecosystems, but with the first record it is clear that here (or somewhere) before, this huge modern capability trigerred complete reorganization of the decomposition chain. The importance of this process is can be seen today in Yakushima, where major Sugi trees (*Cryptomeria japonica*) with extremely high content of resin lay on the ground undecayed for centuries and ecosystems are extremely poor in favourable conditions.

Other commensals indirectly evidenced in fossil cockroaches are nitrogen-fixators. This evidence is older than Karatau, namely in Daohugou (Vršanský et al. 2009), but possibly it is much older. Evidence for nitrogen fixation are specialized male tergal glands providing nitrogen nuptial gifts to females seen in *Hydrokhoohydra* (figp. 321) and in *Perlucipecta* (figps. 94-95). And nitrogen can be only fixed by endosymbionts.



PIN 2066/357 l= 7.6 mm

Tergal gland



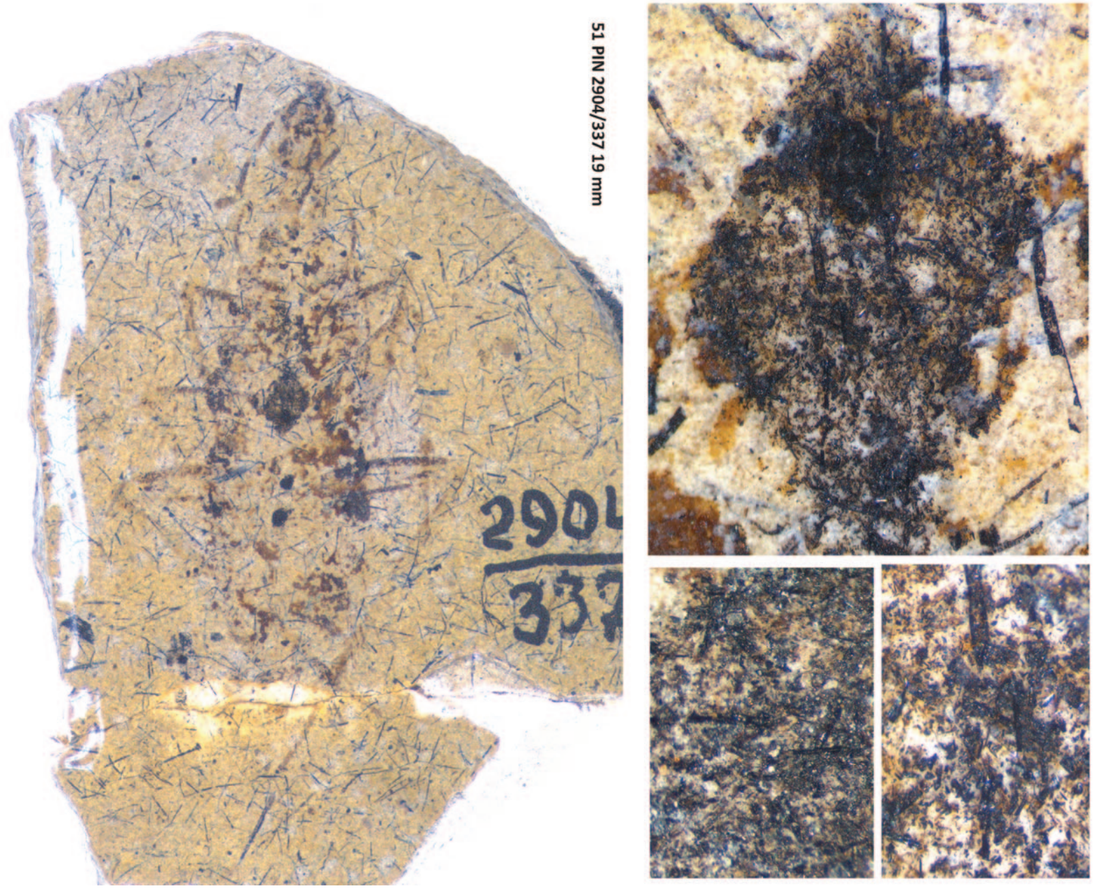
Aktassoblatta fusca covered with *Classopolis* pollen

POLLINATION

Pollination by cockroaches, specifically of a diverse spectrum of plants including ferns, cycasses, gymnosperms and angiosperms are an established fact (Nagamitsu 1997; Vršanský et al., 2018, 2020; Hinkelman 2019; Hinkelman and Vršanská 2020; Sendi et al. 2020b, 2023; Xiong et al. 2020). These vast evidences nevertheless reflect Cretaceous ecosystems and no one evidence comes from the Jurassic and/or a previous time periods. Here in Karabastau, the evidence is diffused, but in sum satisfactory. Unidentified pollen grains were present in digestive tract of holotypes of *Sociala borat* (Isoptera: Socialidae) and *Skok svaba* (Skokidae) suggesting at least sporadic specialized pollyvory and/or "anthophagy". *Aktassoblatta fusca* specimen 2066/324 (figp. 564) is entirely covered in pollen, but the pollen is also distributed near the specimen, so the pollinating function cannot be excluded, but also not soundly confirmed. Numerous specimens of *Asvab bavsa* (Blattulidae; PIN 2239/65; 2039/42; 2997/143; 2904/153; 2066/288; 2997/ 1479; 2066/294; 2784/638; 2066/478; 2384/181; 2384/173) in the sediment with abundant pollen grains and with cones, reflect at least life in environment of pollen-full gymnosperms, confirmed by flora (see **Flora** pragraph). *Classopolis* pollen consumed by Cretaceous cockroaches (Hinkelman and Vršanská 2020) and also by other insects in Karatau (see Insect Context) is not unequivocally preserved within guts of cockroaches in Karatau.

PREDATORY COCKROACHES

As claimed above, unless all basal cockroaches were predators (phyloblattid-raphidiomimid-liberiblattinid lineage definitely was), which cannot be excluded, validated predators were already diversified in Permian (Mutoviidae; with raptorial legs), but extremely likely also much earlier in the Carboniferous, where unequivocal evidence is missing. Origin of cockroaches as predators is still possible. In the Early Jurassic, common were also highly specialized Raphidiomimidae and in Middle Jurassic Daohugou, the predatory cockroaches represent the dominant cohort among cockroaches (Liang et al. 2009ab, 2012, 2019, 2021). Raphidiomimidae were dominant (20 % of cockroach specimens) and also diverse in Karabastau (up to 69.5 % of cockroach species). What is a qualitative shift from Daohugou (and also Bakhar) are cockroaches directly in the mantodean lineage. The corydioid lineage is represented with *Manipulator olim* sp.n. (Manipulatoridae), and the more or less direct lineage leading to true mantodeans is represented by *Lovec pratiena* gen. et sp. n. (Lovecidae). Both Raphidiomimidae and *Lovec pratiena* gen. et sp. n. are directly documented as predators based on their gut content with chitinous stripes (figp. 567). It still can be obscured claiming their scavengyvory (*Manipulator* surely ocassionally eats living insects captured by resin in burmite), but their habitus suggests an active lifestyle (which can secondarily be pollinating). A predatory way of life in basal Blattulidae is unknown. While predatory way of life was confirmed for *Ocelloblattula* and *Huablattula* (Taniguchi et al. 2021) and was very probable for *Habroblattula*, other blattulids apparently provided dung-decomposition (Vršanský et al. 2013). In spite of a huge comparative material it was impossible to determine the diet of *Elisama*. Nor dozens adults neither a dozen immature individuals distinctly preserved gut content. Taking this huge negative evidence and experience (in this particular site) of preservation of the gut content and its chitin particles in other predatory cockraoches into consideration, predatory Blattulidae (see also Anisyutkin and Gorokhov 2008) were very likely rare in Karabastau and absent within *Blattula* and *Elisama* lineages (likely present in others)



AQUATIC COCKROACHES

Aquatic lifestyle of cockroaches was recently revised with *Hydrokhoohydra* from Karatau as one of the most significant species (Vršanský et al. 2019). Predisposition to (semi)aquatic habits is well-documented in Karatau by presence of immature individuals in the record, which means they were splashed into the source rivers or even directly to the lake by rains etc. (see also **Insect context** paragraph). Present are immature representatives of the families Blattulidae, Raphidiomimidae, Caloblattinidae, Mesoblattinidae and Liberiblattinidae – i.e., virtually all. Blattulidae and Caloblattinidae were disqualified from producing any novelty in their 180Ma lasting existence, but why predatory Raphidiomimidae and decomposing Mesoblattindae did not enter water is one of the greatest enigmas. The disability of transferring endosymbionts is not true, as *Hydrokhoohydra* apparently had this capability (see male tergal glands – figp. 321). So while most of insects are (or were) capable of water invasion, aquatic cockroaches remain very rare also in living ecosystems. Why? The question was already raised in personal communication by Prof. P Prokop and I do not know the reason behind this.

EUSOCIALITY

Contact with wood is one of the key factors in cockroaches **level-up**. Eusociality is only one of the life forms, but later contributed to the revolution of the ecosystem. With exception of algaevorous *Melyroidea* (Hinkelman et al. 2020), Socialidae with true termites are possibly along with *Fractalia* the only true eusocial results of cockroach evolution. Eusociality was discussed in detail by Vršanský (2010) and Hinkelman et al. (2021). It must be additionally stressed that the rise to a higher level of complexity and organization is, besides the origin of first cell, the biggest mystery and enigma of life. All approaches were successfully declined as being responsible for the level-up. As Flegr and Toman correctly claimed, the level-up is the only possible solution in the compartmened systems (Toman 2020). Nevertheless, the only possible solution does not means it will be performed (but the probability is high in small numbers due to capillary effect (see **Way Up** paragraph)). And many other lineages remain in massive non-sociality. It is very likely that according to the hypothesis raised here, rising towards eusociality is also possibly only in small systems and later in massive agglomerations is impossible.

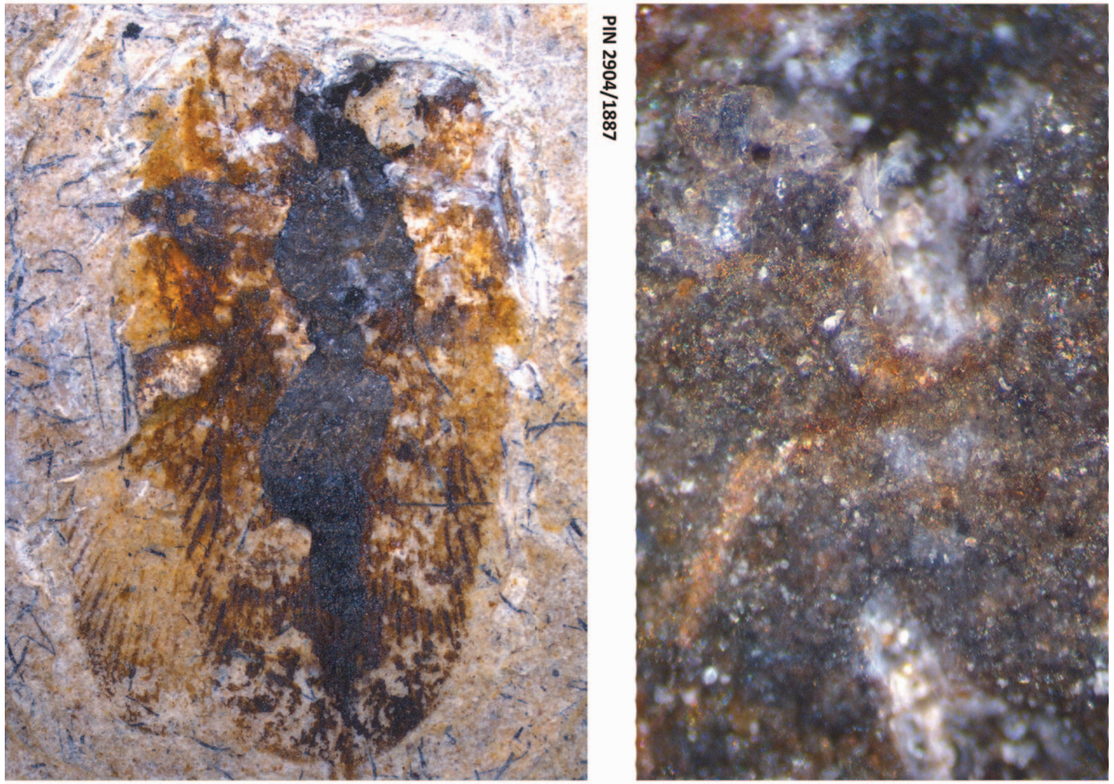
FOOD

Due to extremely conservative habits of cockroaches over time, it might be presumed that food preferences for cockroaches were always the same and we could apply an actualistic approach. This is not the case. Living cockroaches are active predators in a single case (unpublished), algaevorous in a single case (Hinkelman et al. 2020), fungivorous in a single lineage (Sendi et al. 2020), anthophilous in a single case (unpublished) – other extant cockroaches are more or less decompositors. **Decomposition** is evidenced with the Nitrogen-fixing vertically transferred endosymbionts and mostly well evidenced macromorphologically by the presence of male tergal glands used in nuptial feeding. Decomposition and tergal glands are well documented in the Permian and Jurassic (see Vršanský et al. 2009) and it visible also in several species within Karatau (see above). Surprisingly decomposition is poorly evidenced within Karatau material, namely as a homogenous debris in the gut of *Asioblatta maculata* (2066/101; which is furthermore preserved within a regurgite, evidencing nice example of a food chain. The same (totally homogenous) content is present in two other indetermined caloblattinids (2904/333, 1343; figp. 572 and 573 respectively). One of the dominant liberiblattinids *Ano ona* was also apparently detrivorous, and very likely rather strictly specialized as evidenced with totally homogenous (very small, unrecogniseable particles) gut content apparently constituted evidence for feeding from several fasting (2904/1887; figp. 570). A homogenous diet was preserved also in *Liberiblattina ihringovae* (2066/248; figp. 577) confirming other than predatory way of life in the family type (while some others were apparently predatory).

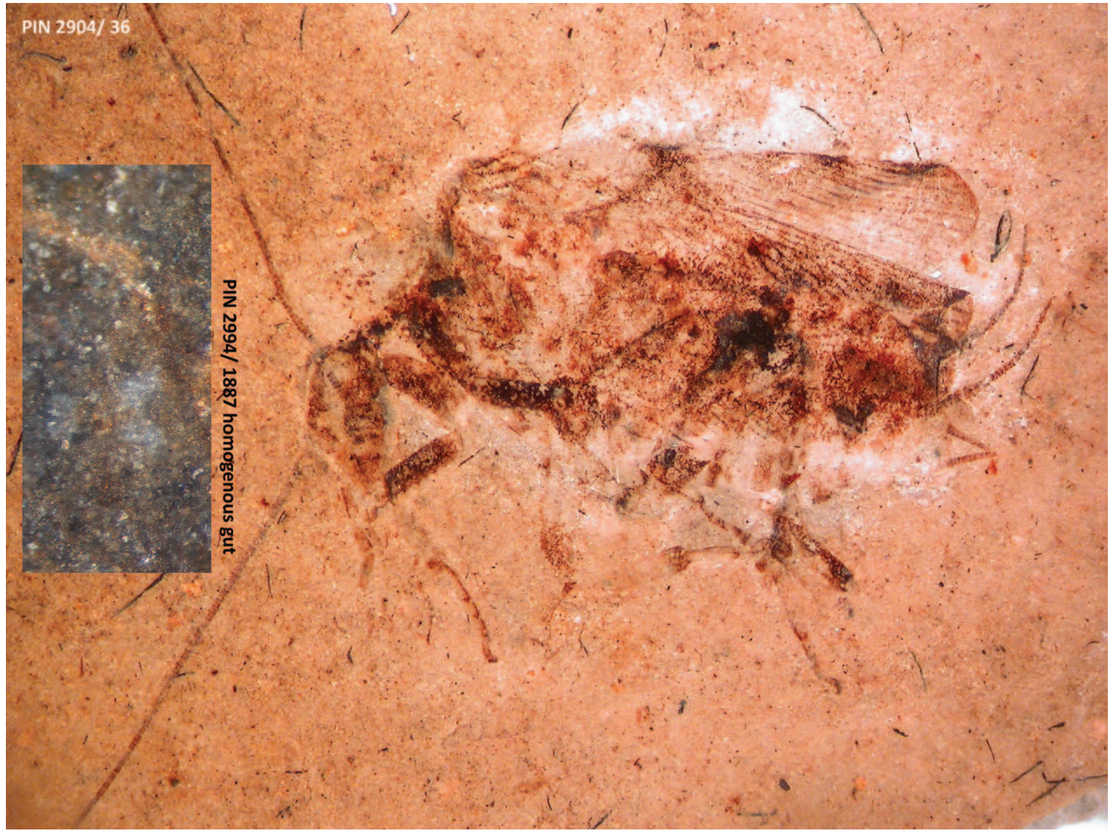
Interesting gut content with "mineral rocks"was preserved within an indetermined caloblattinid (2997/165; figp. 576). Besides very heterogenous grains, it contains also minute residuum of a rocks, possibly a dust or sand up to 0.29 mm long. Remarkably, these "rocks" were never preserved within the sediment containing these fossils and likely are fully allochtonous in respect to preservation sediment (surely autochtonous during life).

On the contrary, predation or at least cadaverivory is, on the basis of chitin stripes, well documented on the gut-content of several lineages, in mantodean *Lovec pratiena* (2904/334; figp. 81, a3). While in *Lovec*, the gut content is formed a more or less homogenous mass of chitin of consumed insects, in a raphidiomimid *Memento mori*, these stripes are massive up to 0.05 mm wide (2904/337; figp. 240) and 1 mm long. Similarly long, but about one half time thinner (and more deformed by digestion), chitin stripes were preserved within a gut of *Chuanblatta stalosa* (2997/1384; figp. 120). Nevertheless, small chitin stripes, oínly several times longer than wide were also preserved in an indetermined caloblattinid (2997/1578; figp. 574).

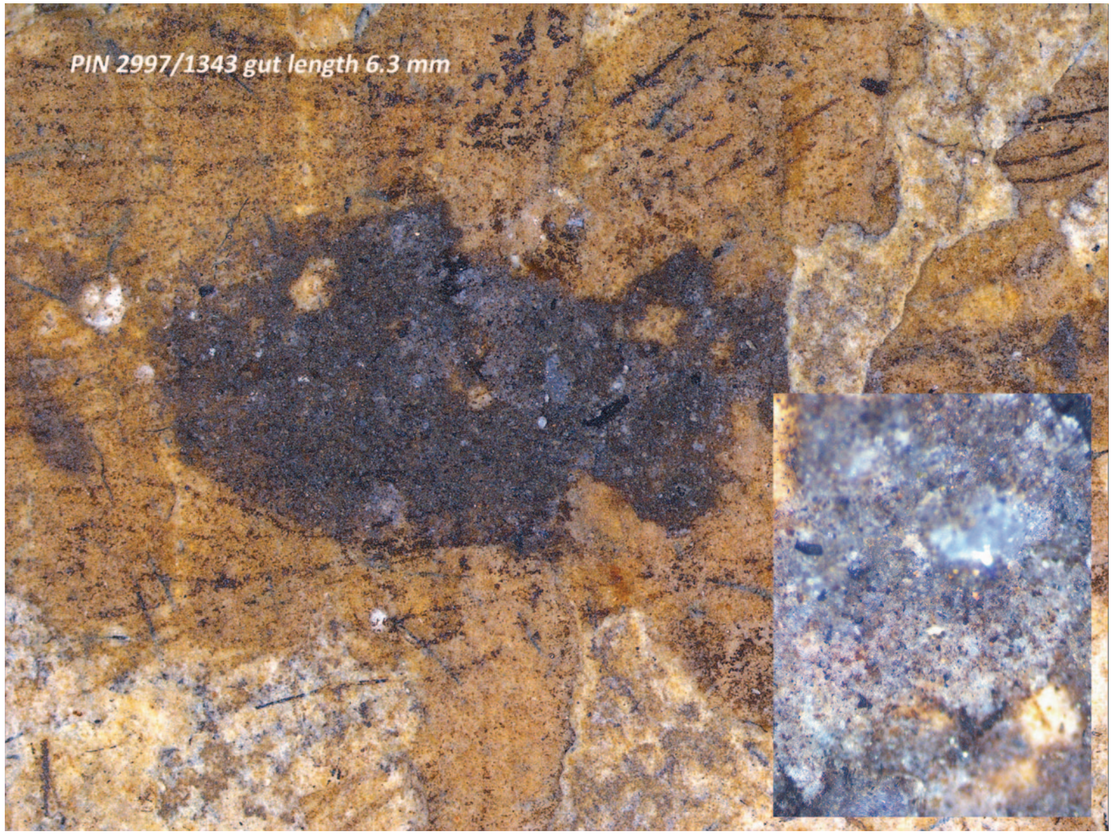
Pollivory and/or anthophyli is another cohort rarely present in living cockroaches and also in Karatau. Heterogenous material which also includes a pollen was preserved in an indetermined caloblattinid (2384/50±; figp. 575) and liberiblattinid *Aktassoblatta fusca* (2066/324; figp. 324). Unfortunately these pollen are not well preserved and are indeterminable. Nevertheless, due to their common occurrence they very likely represent the main pollen preserved also in sediments (but not *Classopolis*). Pollivory is presumed also from *Maloval* and *Fractalia* (due to mass evidence from beetle-like cockroaches from ambers), but without local evidence. Good evidence was present on aesophagus of *Skok svaba* (figp. 247) – a huge pollen (0.3 mm and more in diameter), likely representing *Classopolis* or



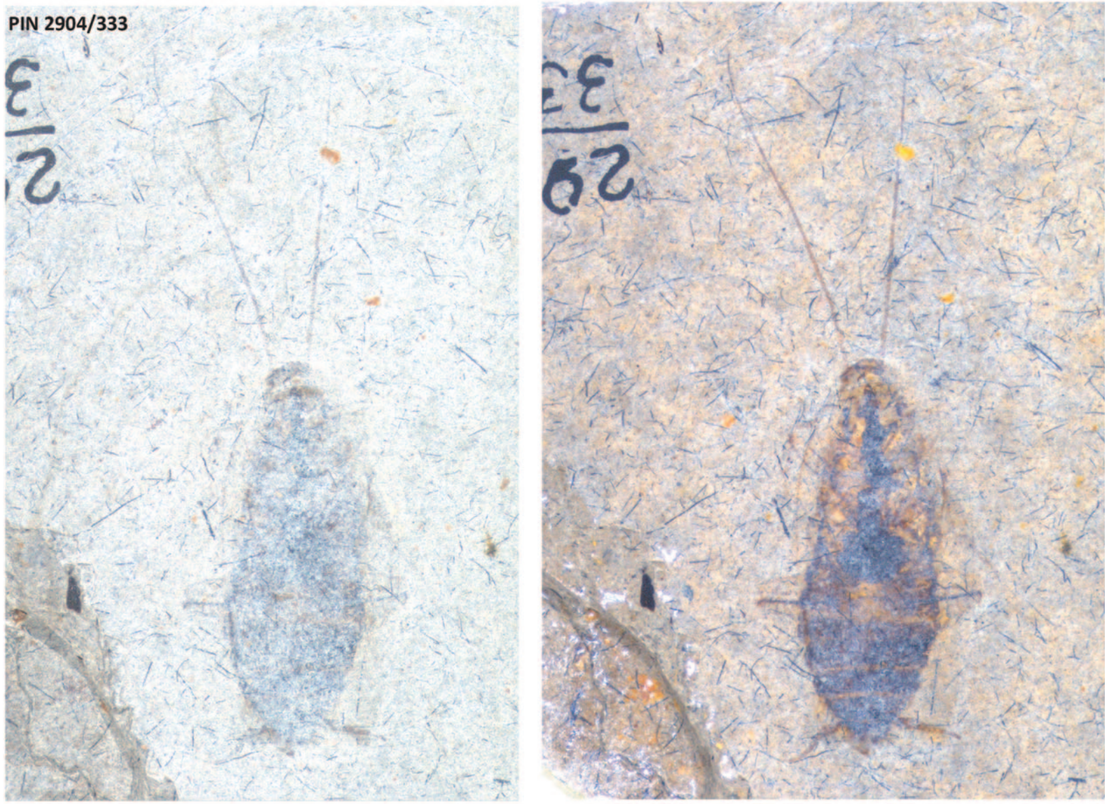
Homogenous gut content of a liberiblattinid



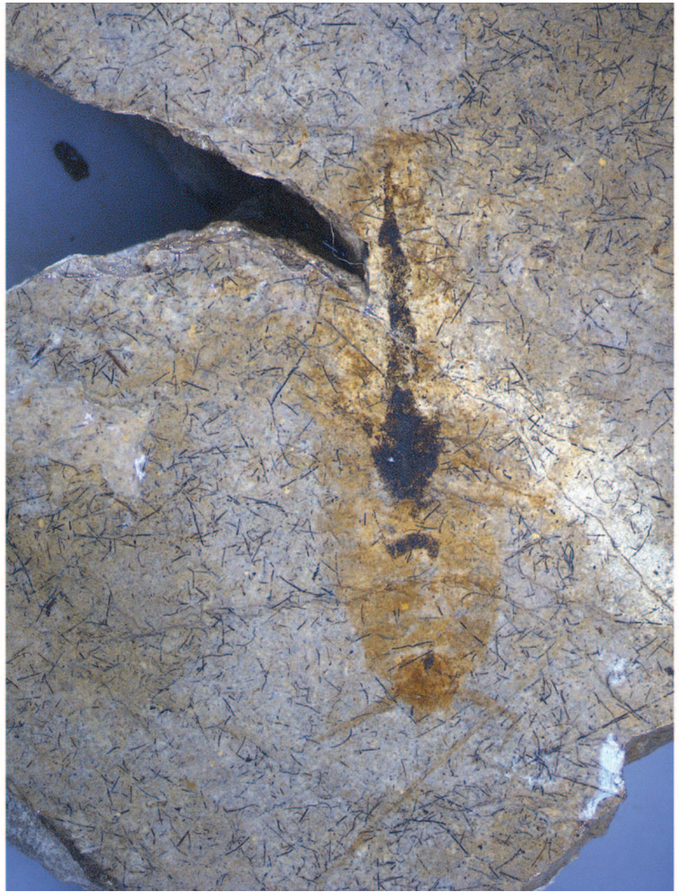
Homogenous diet of liberiblattinid *Ano ona*

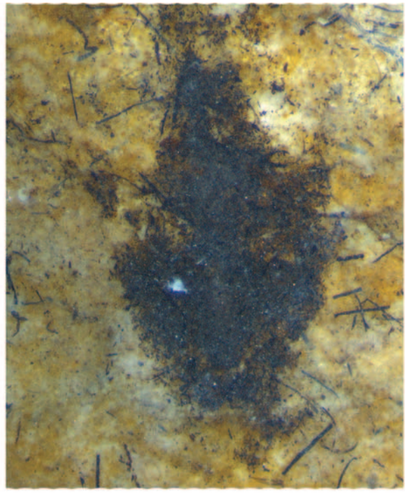


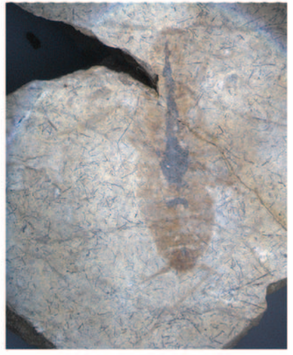
Homogenous gut content of a caloblattinid



Homogenous gut content of a caloblattinid

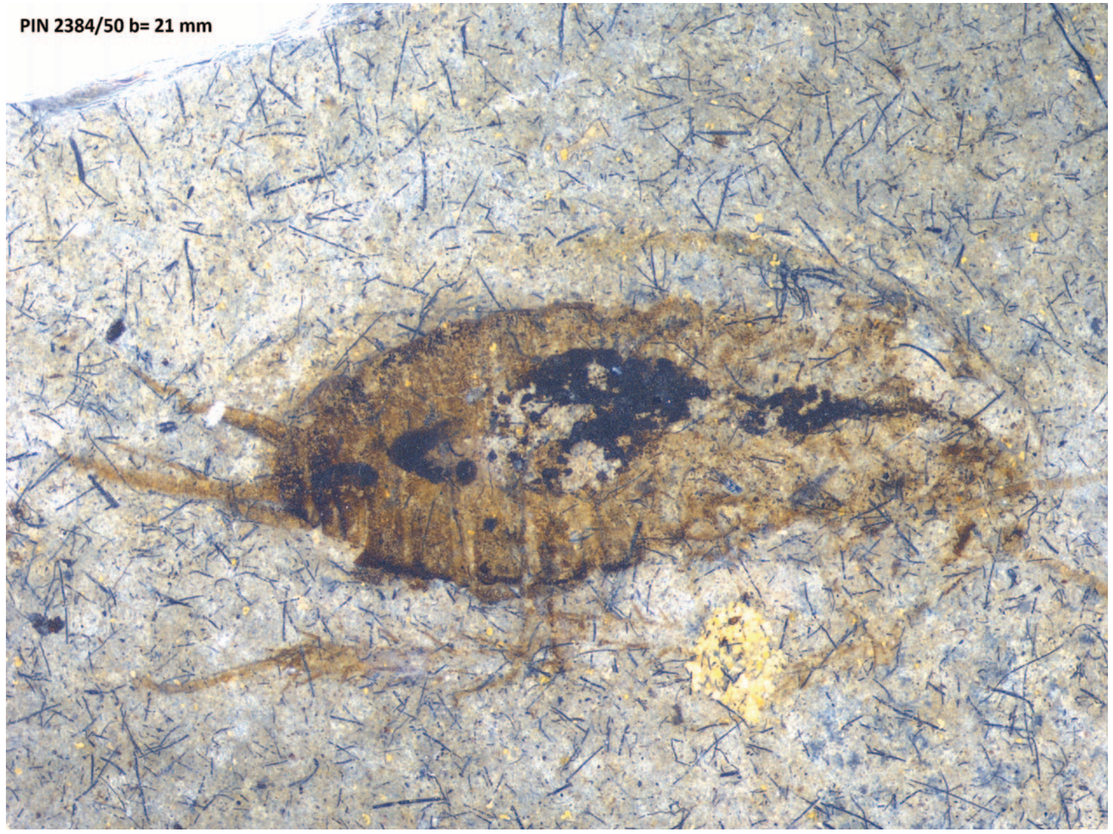


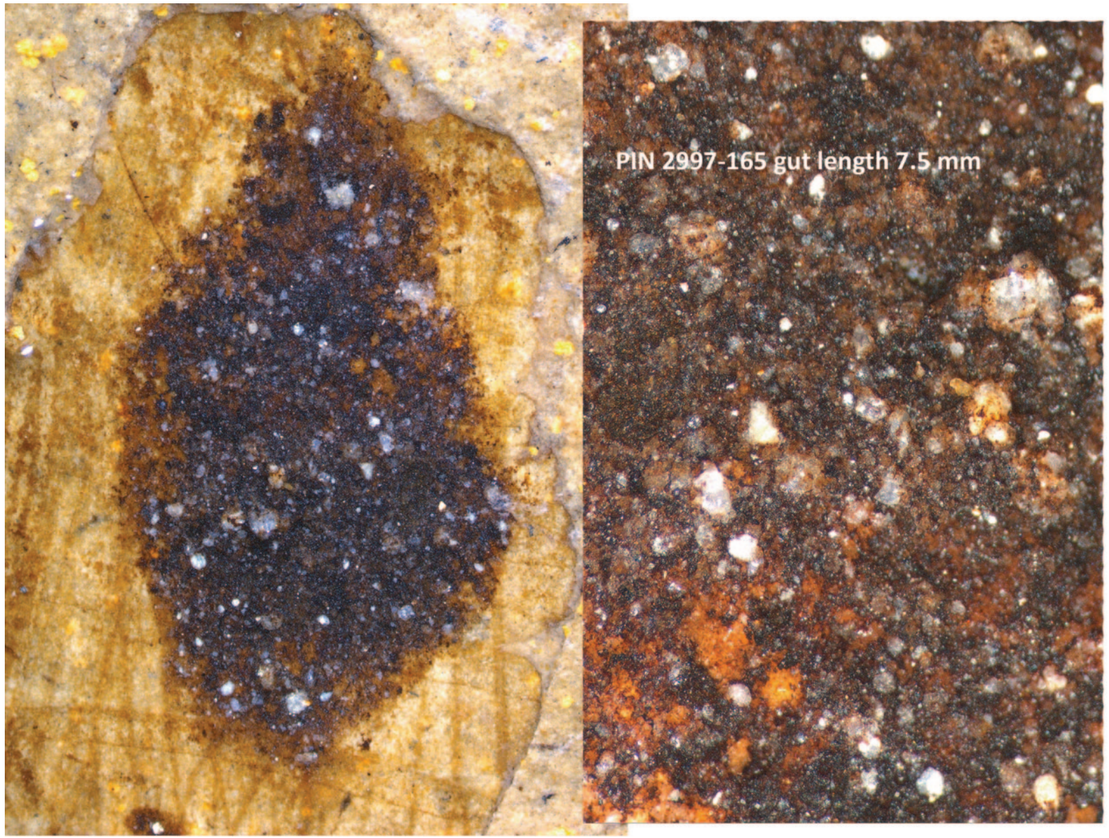




PIN 2997/1578

PIN 2384/50 b= 21 mm





Caloblattinid gut content with minerals



Heterogenous gut content of a liberiblattinid

similar (possibly cheirolepidiacean) pollen. Large and numerous pollen (0.59 mm in diameter possible *Classopolis*) was surprisingly preserved also in the gut of the first social animal on planet *Sociala borat* (figp. 86), which apparently represented a (non)specialized pollivore.

COCKROACHES AS FOOD

On the other side, evidence of cockroaches being food for predators represent the further vertical structure of ecosystem. It is highly probable that the predatory cockroaches were predating and cadaverivoring over their smaller relatives, although evidence from burmite suggest also a predation on much larger prey by *Manipulator modificaputis*.

There is a numerous direct evidence for predation on Karatau cockroaches represented with biting marks on (damaged) forewings (PIN 2452/213 *Memento mori,* 2997/1230 *Decomposita basquatirgis,* 2554/156 *Caloblattina laesis, Asioblatta punctata,* 2997/183 *Liberiblattina kontravenata,* 2904/152 *Elisamoides sediomasle,* 2997/1174 *Aktassoblatta fusca,* 2784/744 *Cretaholocompsa karatauensis,* 2465/937 *Maloval hlavolam*); hindwings (unnumbered *Lovec pratiena,* 2904/61 *Rhipidoblatta tri,* 2384/71 *Cameloblatta stress*, 2997/4247 *Rhipidoblatta matrikýý,* 2784/664 *Aktassoblatta fusca*); and (broken) legs (2452/517 and unnumbered – see figp. 582, possibly *Aktassoblatta fusca*). Problem of this evidence is that no one is unequivocally caused by terrestrial predators such as lizards or pterosaurs. Instead, all of them might be caused with the predation by aquatic organisms, predominantly fishes, after falling into the lake and/or streams leading to lakes. Some fragmentation might be also caused at the bottom (see figp. 537).

Direct evidence is represented by nine regurgites and coprolites. Although all these structures were identified as unequivocal pterosaur regurgites (Ansorge 1993, Stumpf et al. 2015), there are also indications that some Jurassic fish might also produce consistent coprolites like this (Zaton and Rakocinski 2014). As I do think they rather represent pterosaur regurgites, I do not see this evidence as unequivocal and I am threating both these possibilities together. As in the case of the indirect (biting) evidence, it is also rather unfortunate decision as pterosaur regurgites/coprolites would suggest share habitats of predominantly the sky; while fish coprolites suggest share habitats around lake and streams leading to the lake. Indiscriminating these two evidences lead to some more general, but safe evidence. So I am threating both groups together. **(1)** "Regurgite" PIN 2997/1686 contains dominant *Blattula rectinervosa* with *Asioblatta punctata* and *Rhipidoblatta triky* (Figp. 580). **(2)** "Three pieces of a coprolite" 2997/1668 contains dominant *Aktassoblatta fusca* with *Chuanblatta stalosa*. **(3)** "Regurgite" 2997/1425 contains dominant *Blattula brevicaudata* and *Rhipidoblatta triky* . **(4)** "Coprolite" 2904/190 contains *Blattula brevicaudata* and an odonate (Figp. 581). **(5)** "14 mm regurgite" uncatalogised contains *Divocina noci, Memento mori*, *Operam monita*. **(6)** "36 mm regurgite" uncatalogised contains dominant *Ano ona* and an odonatan (Figp. 583). **(7)** "Regurgite" 2997/1151± contains odonatan with *Memento mori* and *Chuanblatta stalosa*. **(8)** "Regurgite" 2452/578 contains *Blattula brevicaudata* and *B. microscopica.* **(9)** "Regurgite" 2239/271 contains *Aktassoblatta fusca*, *Blattula brevicaudata* and *Falcatussiblatta ?disrupta* (Figp. 581).

To summarise, regurgite/coprolite data revealed interesting patterns. Besides dominant and very common species (*Aktassoblatta fusca (4), Blattula brevicaudata (4), B. rectinervosa, B. microscopica, Memento mori (2), Ano ona, Chuanblatta stalosa (2)*), we have here rather rare *Asioblatta punctata* and *Rhipidoblatta triky*, which might be due to stochastical reasons. Also extremely rare *Operam monita* and also extremely rare *Divocina noci* are present in the same specimen.

It is thus possible to classify all coprolite/regurgite species, i.e., *Aktassoblatta fusca, Chuanblatta stalosa, Blattula brevicaudata, B. rectinervosa B. microscopica* and *Falcatussiblatta ?disrupta, Divocina noci, Memento mori*, *Operam monita, Rhipidoblatta triky,* and *Asioblatta punctata* in the same actuocenosis. Notable is presence of *Divocina noci*, which was considered for a nocturnal taxon, in the bulk, suggesting crepuscular activitity of the predator and/or habits of the regarded species (already suggested also for *Aktassoblatta fusca*). On the other hand sophistically colored species (*Falcatussiblatta ?disrupta, Operam monita*) and pale species (all *Blattula, Asioblatta punctata*) suggest more diurnal time periods.

Frequent co-occurrence with odonatans support near-water habitats (unless directly aquatic predation).

Double evidence:
***Asioblatta punctata* with gut content**
2066/101

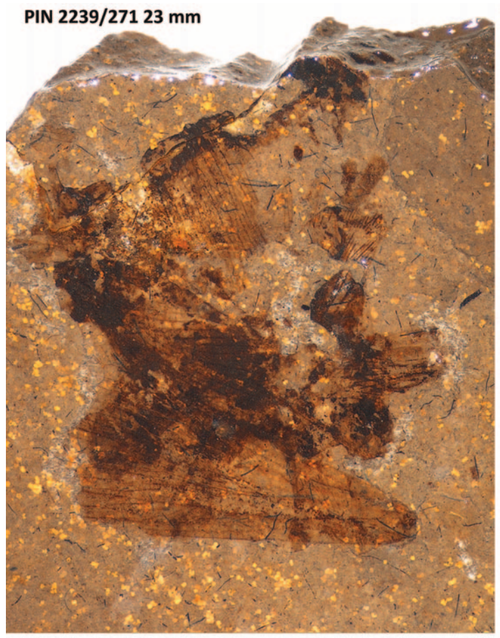


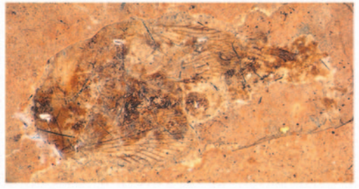




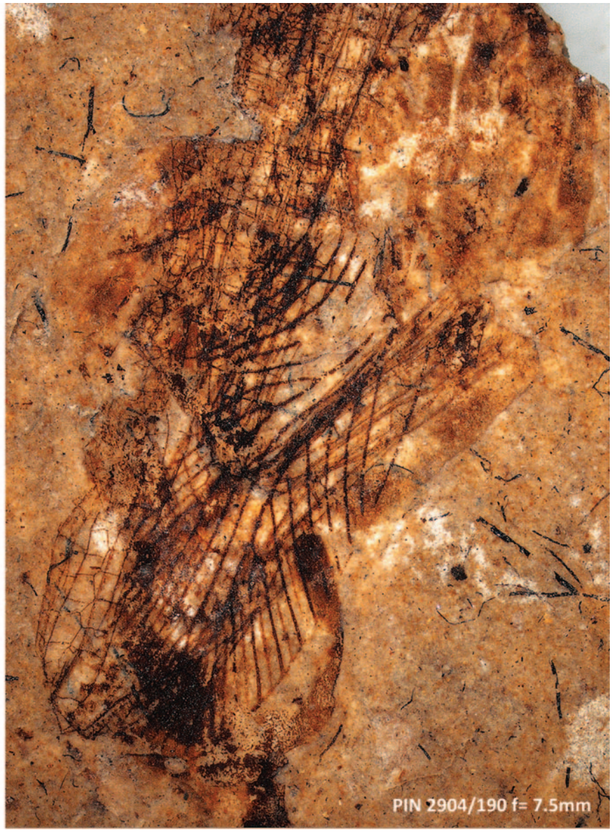


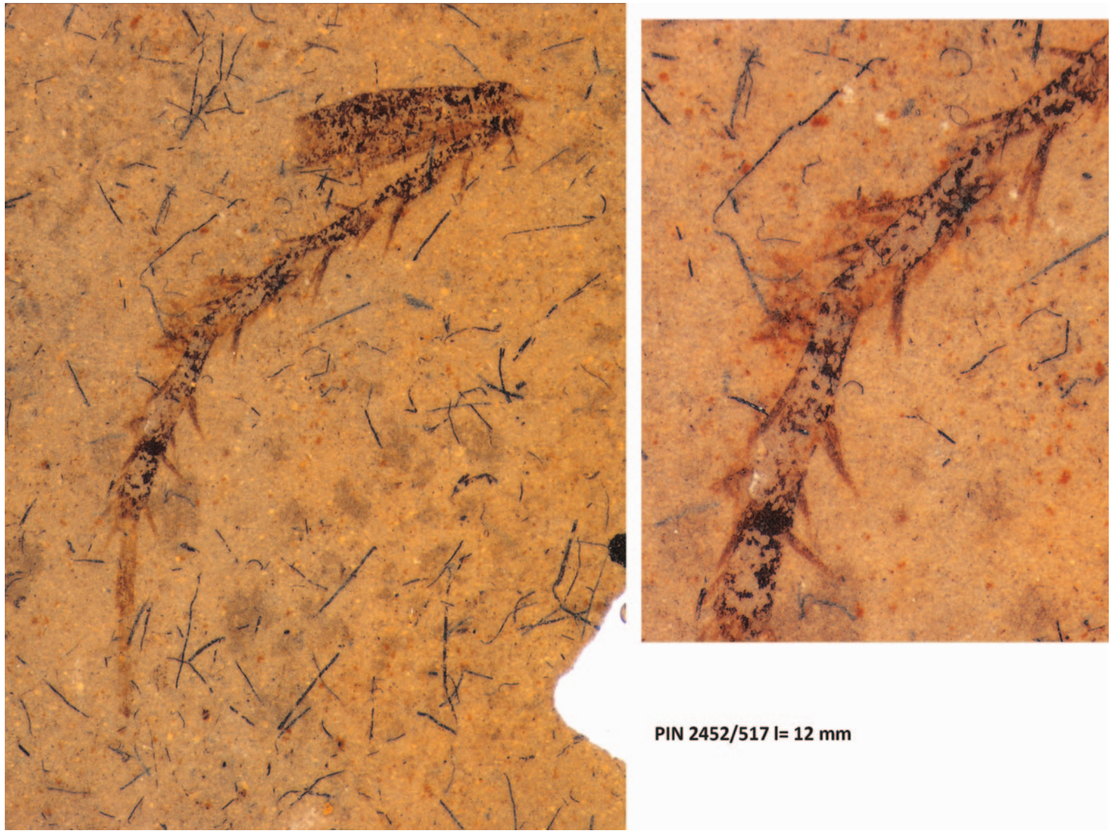
PIN 2997/1686 regurgite with *Asioblatta punctata*





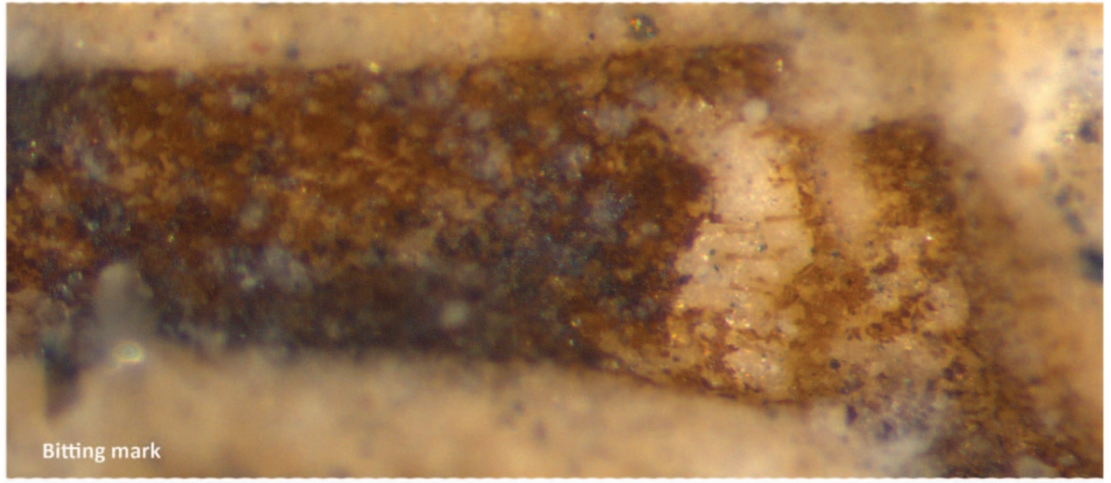
PIN 2452/578 13 mm

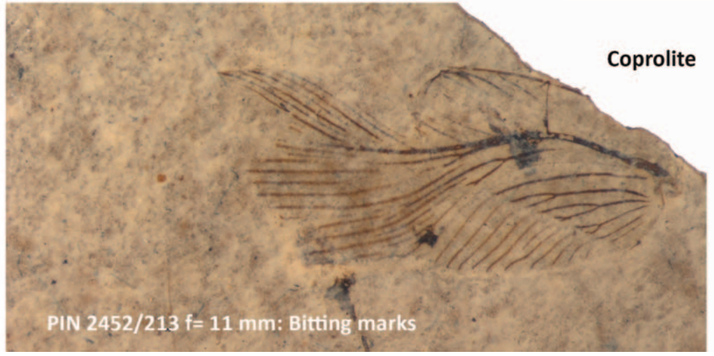


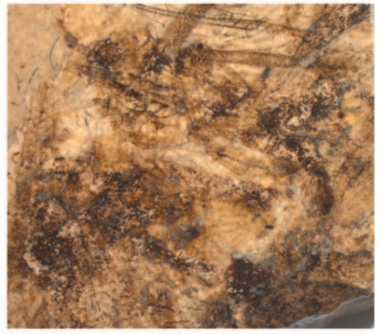


PIN 2452/517 l= 12 mm

Trace of predation



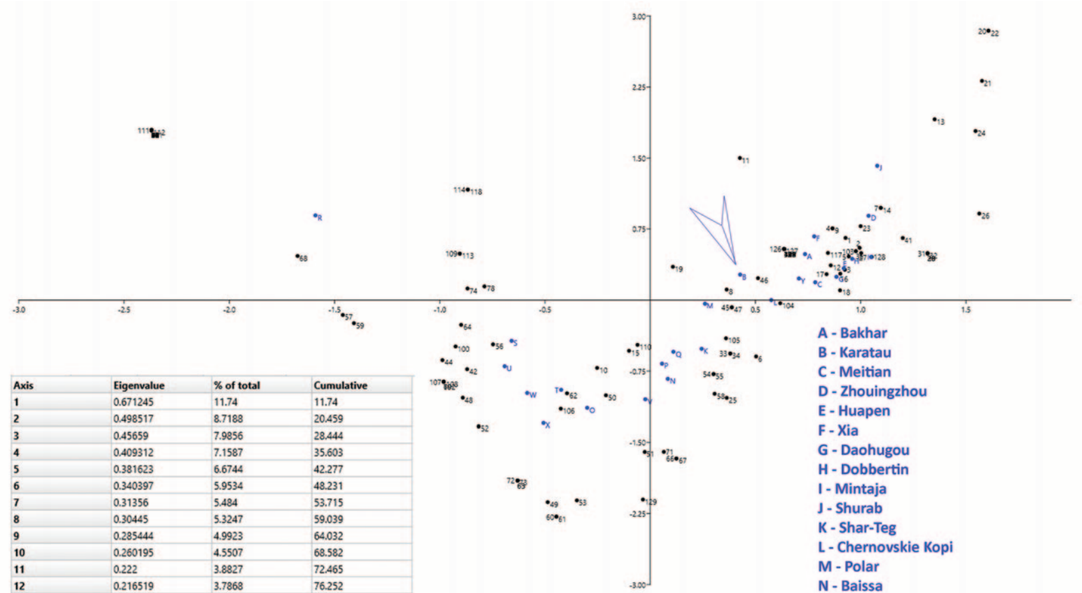




Bitting marks

CORRESPONDENCE ORDINATION ANALYSIS

Column (locality)-dependent analysis reveals smooth transition among statistically separated Jurassic and Cretaceous localities. A separate position is occupied by North Myanmar amber caused with overrepresentation of samples from this amber and its numerous indigenous genera. Karatau is among Jurassic sites the most closely related to the Cretaceous ones – due to occurrence of numerous younger lineages and sample overrepresentation. This purely statistical phenomenon is caused with asymmetry of distribution of older and younger taxa and the preference of latter in Upper Jurassic and Cretaceou sites (see also Rasnitsyn et al. 2016). Nevertheless, a clear relation with Koty is apparent (figp.585).



Axis	Eigenvalue	% of total	Cumulative
1	0.671245	11.74	11.74
2	0.498517	8.7188	20.459
3	0.45659	7.9856	28.444
4	0.409312	7.1587	35.603
5	0.381623	6.6744	42.277
6	0.340397	5.9534	48.231
7	0.31356	5.484	53.715
8	0.30445	5.3247	59.039
9	0.285444	4.9923	64.032
10	0.260195	4.5507	68.582
11	0.222	3.8827	72.465
12	0.216519	3.7868	76.252
13	0.199138	3.4828	79.735
14	0.187041	3.2713	83.006
15	0.164321	2.8739	85.88
16	0.146427	2.5609	88.441
17	0.142406	2.4906	90.931
18	0.119878	2.0966	93.028
19	0.108414	1.8961	94.924
20	0.100204	1.7525	96.677
21	0.0722096	1.2629	97.939
22	0.0519841	0.90918	98.849
23	0.0477571	0.83525	99.684
24	0.0180724	0.31608	100

Column-principal analysis of Jurassic faunas

PALAEOZOIC CONTEXT

The Mesozoic cockroach fauna can be categorized within more or less discrete impoverished (Palaeozoic) Triassic fauna, (Mesozoic-type) Jurassic fauna, (advanced Mesozoic terminal here established Jurassic and Cretaceous) Cretaceous fauna and modern fauna (starting to occurring in the Jurassic and common in some Early Cretaceous sites). Surprisingly, there is nor a single Palaeozoic relic, neither any Triassic group. It is surprising as in burmite, Houtyin-Hotgor and also Bon Tsagaan, such relics were identified (Vršanský 2003, 2008; Vršanský et al. 2023). Burmite specimen was disqualified from the Phyloblattidae due to non-consistence with the *Phyloblatta* type (Nel et al. 2023). This nevertheless, does not mean that this is not a Palaeozoic group – its closest relative is also from the Permian and Triassic as in original description.

JURASSIC CONTEXT

The closest site to Karatau is more or less coeval Bakhar in Mongolia, which led to possibility of Bakhar representing younger, Late Jurassic fauna (Vršanský 2020). Generally, characteristic Jurassic taxa are numerous and dominant (*Blattula, Falcatussiblatta, Raphidiomima, Rhipidoblatta, Ano, Chuanblatta, Hra, Liadoblattina, Caloblattina, Elisamoides, Mesoblattina*) and the Karatau is in this respect typical Jurassic fauna. As can be seen from the table below (Tab ****), this type of assemblage is typical for numerous localities in China, including the most important Daohugou. Nevertheless, all of them except Mongolian Bakhar (significantly) lack the following two aspects. In spite of the huge sample size in Daohugou and some other Jurassic sites in China and Australia (see Martin 2010), it cannot be definitely excluded that this lack is caused only by rarity of the following two cohorts (see immediately below). The overlap of taxa can be extracted from the table, but I specifically address three main localities Kota, Bakhar and Daohugou in separate paragraphs. In regarding related Lagerstätten and also smaller sites, especially important are taxa missing in Karatau. Besides those from Kota, Bakhar and Daohugou, these were unequivocally represented only by indigenous taxa such as *Kurablattina* Martin, 2010 from Mintaja and many others (indigenous taxa are often dominant). The significant non-indigenous taxon missing is only *Nuurcala* (dominant in all Upper Jurassic-Lower Cretaceous sites). Missing are also advanced *Praeblattella* and *Archimesoblatta*, taxa which (rarely) occur from the basalmost Jurassic.

OTHER JURASSIC GENERA

Disregarding Daohugou with its indigenous Fuziidae and highly diverse indigenous genera of Raphidiomimidae, special and/or indigenous Jurassic genera are nearly missing out of Karatau.
Entropia is extremely similar to *Ano* and weakly preserved *Lithoblatta* from Solnhofen likely represents already common taxon. Blattulid genera need revision, but surely not all are represented in Karatau. *Nuurcala* is likely also present in Karatau (among indetermined material). Basically only *Kurablattina* of Mintaja, and *Okras* with *Solemnia* and liberiblattinid *Dostavba* from Bakhar are remarkable. Remarkable is also already mentioned absence of *Praeblattella*. Due to wide occurrence and also presence in Shar-Teg, interesting is also absence of *Shartegoblattina*. More wide occurrence have also *Sogdoblatta* and *Taublatta* apparently absent in Karatau.

KOTA CONTEXT

There are numerous shared genera with the other Jurassic sites (see (see Tabp. 630). Nevertheless, the complex comparison is only possible with *Lagerstätten*. The relation with the Kota Formation in India, was postulated recently (Vršanský et al. 2024) and here only the main difference is provided. Kota, with less than 300 specimens basically represent the same assemblage with all taxa shared. The only difference is smaller size of Kota cockroaches and presence of (extremely small) *Influencer*, a putative pollinator of main gymnosperm tree (?*Frenelopsis*) which might be a Gondwanan element. This taxon is surprisingly dominant in Kota and although clearly different, and might represent a direct link to the *Vitisma* like *V. coriacea* Sendi, 2024 (Sendi 2024a). All other taxa are shared, supporting close palaeogeographical and temporal relations in spite of spatial distance.

BAKHAR CONTEXT

Bakhar is another locality to be designated as representing a very similar and spatiotemporary related site (Vršanský 2020). Among 13 genera from Bakhar, shared are seven (*Ano, Blattula, Caloblattina, Hra, Perlucipecta, Raphidiomima, Rhipidoblattina*) thus revealing a high similarity. Another four indigenous (*Dostavba, Okras, Truhla, Polliciblattula*) and one with restricted range (*Solemnia*) confirm relation to Karatau. Only global common and dominant *Praeblattella*, rare in Bakhar, was possibly missing in Karatau.

DAOHUGOU CONTEXT

Daohugou is potentially an even more important site compared with Karatau. Nevertheless, its general evaluation is basically lacking at the present. Evaluated are numerous indigenous genera of the indigenous Fuziidae (Vršanský et al. 2009; Guo and Ren 2011ab; Wei et al. 2012, 2013; Liang et al. 2012). Its indigenous character is a significant proof for the Theory of Reduction Ring (Vršanský et al. 2019). It lacks over 3,000 Karatau specimens, which is significant. Well-evaluated are several predatory lineages shared with Karatau (*Divocina, Chuanblatta, Rhipidoblattina, Falcatussiblatta*), while *Fortiblatta* Liang et al. 2009 and *Graciliblatta* Liang et al. 2012b are missing in Karatau (Vršanský et al. 2012; Liang et al. 2012b, 2017, 2019, 2021, unpublished). *Pseudomantina* (Liang et al. 2023) of the Blattulidae was also shared. *Entropia* Vršanský et al. 2012 (Liberiblattinidae) can also be considered for a shared taxon due to high congruence with new representatives of the genus *Ano*. To summarise Daohugou is closely related to Karatau, in a lesser degree than Bakhar. This relation might, nevertheless, approach closer after description of new taxa from Daohugou

ACTUAL CRETACEOUS CONTEXT

The reason for doubts about the completeness of the Jurassic fossil record (in spite of ca. 40,000 samples) is the occurrence of mesoblattinid *Archimesoblatta* in the basalmost Jurassic of U.S.A. (Huber et al. 2003) and thus Mesoblattinidae (with ootheca) must occurred that time. As seen from the table, mesoblattinids occurred rarely in Bakhar and also in other sites. Karatau is nevertheless, the earliest “mass” occurrence of the ootheca-bearer. Other Cretaceous elements are *Cameloblatta* (Cretaceous of Sinuiu), *Fractalia* (burmite), *Pseudomantina* (lebanite, Daohugou), *Aposema* (Russian polar Cretaceous), *Cretaholocompsa* (Montsec), *Elisama* (dominant Tithonian-Maastrichtian cosmopolitan taxon), *Manipulator* (burmite, Crato, Spanish amber ?Solnhofen), *Perlucipecta* (dominant Middle Jurassic-Maastrichtian cosmopolitan taxon), *Sivis* (burmite, lebanite, Archingeay), *Sociala* (Archingeay). It must be also stressed that indigenous umenocoleid *Maloval* represents an advanced (Cretaceous) taxon. In this respect, Karatau is a typical Cretaceous, advanced site. As we pointed difficulty of transferring age more terminally than Kimmeridgian, the conclusion is that the advanced Cretaceous fauna was greatly formed in the Kimmeridgian, although with very rare representatives.

LIVING BIOTA CONTEXT

On the other hand there is the first record of the modern (living) fauna represented by Blaberidae. It must be remembered that this group was effectively escaping fossil record until very recently only in Myanmar, China and Japan (Šmídová 2021, Oyama et al. 2021, unpublished observation) and that its actual origin cannot be excluded before terminal Triassic. The similar fate is for Corydiidae, with a single sample (see also Vršanský et al. 2023b).

EVOLUTION

Among about a dozen levels of general evolution-inducing factors, most are present in cockroach evolutionary principles and nearly all of them were addressed in the present study. They are described one by one:

STASIS EVIDENCE

One important conclusion can paradoxically be established from the span of genera. In contrast to umenocoleid, fractalid, *Elisama, Sociala, Cameloblatta, Okruhliak* and *Cretaholocompsa* suggests affinities to Cretaceous localities (and *Ano* suggesting relevance with Bakhar). The completely preserved *Chuanblatta stalosa* is a species which is barely recogniseable (basically only cosmetical coloration details) from it congener *C. lata* from Daohugou. We have here a strong direct evidence for binds and extremely low morphological variations between species from Karatau and Daohugou on one side and with Cretaceous (and Bakhar) on the other side. These localities at both sides are well dated: Daohugou Reference Point (161 Ma) and Yixian Reference point (127 Ma) respectively representing the minimum span of 34 Ma (*Sociala* can be bid at down to 98 Ma). Even in the case Karatau lies exactly between them, we have a direct evidence for 17 Ma morphological stasis. This might not sound disrupting, nevertheless, the conservativeness of cockroaches at this level was rejected from the previously known materials (Vršanský et al. 2022) and this is the first direct evidenced case of such long conservativeness. On the other side extremely rapid evolutionary tempo is discussed above and below.

STRATIGRAPHIC INDICATORS

Cockroaches were recently being proved as sensitive fine stratigraphic indicators (Vršanský, in preparation). Their use in stratigraphy was applied in several Palaeozoic (Schneider et al. 2020; see also Anisyutking 2007) and Cretaceous (Ross 2001; Vršanský 1998, 2008b) localities. Duration of genera (see below) proves an Upper Jurassic-earliest Cretaceous stage.

Due to the occurrence of the highly similar locality in Kota (dated Middle-Upper Jurassic), a Cretaceous age might be excluded with high confidence. As Kota indicators significantly suggest a Kimmeridgian-Tithonian age and due to occurrence of more primitive taxa in Karatau, and Kota binds (taphonomy, size and coloration) with Tithonian Shar-Teg, Kimmeridgian age or basalmost Tithonian age seems to be supported for Karabastau. Kimmeridgian age was also supported by the Kimmeridgian tectonics in situ (see Gekker 1948 for Balashov) and also by pollen and flora (although the terminal Callovian is not excluded on the basis of pallinological analysis – see **Flora** paragraph).

PHYLOGENY

According to the Theory of reduction-rings (Vršanský et al. 2019d), the genera and families tell little about the phylogenetical stage of evolution at spatiotemporary closely associated localities. Such locality is actually a single one, Kota, and a broader context is thus directly observable. Furthermore, phylogenetical stage of the species within the same genera provide (usually) direct clues. Other clues represent respective indicators as coloration, mutations or size, discussed paragraph-by-paragraph below.

PHYLOGENETIC SIGNAL – DURATION OF COCKROACH GENERA OCCURRING IN KARABASTAU

As we can see from the chart (figp. 592), Palaeozoic groups were nearly entirely missing during Karatau time. An exception are small representatives of this family, which were recorded in the North Myanmar amber (Phyloblattidae: *Pozabudnutie* – this species was excluded from the family due to incongruence with the type genus, which, nevertheless, do not discredit its Palaeozoic type) and thus must have existed also during the Jurassic period; also larger representatives might have ghostly survived as they were recorded in Cretaceous Bon Tsagaan (Vršanský 2008, Vršanský et al. 2022). These were, nevertheless, not recorded. Recorded were Caloblattinidae, which is a family appearing during the Lopingian Permian, but with occurrence of different genera. So basically there are no Palaeozoic groups in Karatau. From the other side of the time, there are two families still living today, namely Corydiidae and Blaberidae (and also Mantodeans and termites). All of these are extremely rare, so we can basically say, the cockroach fauna of the Karabastau is virtually Mesozoic like.

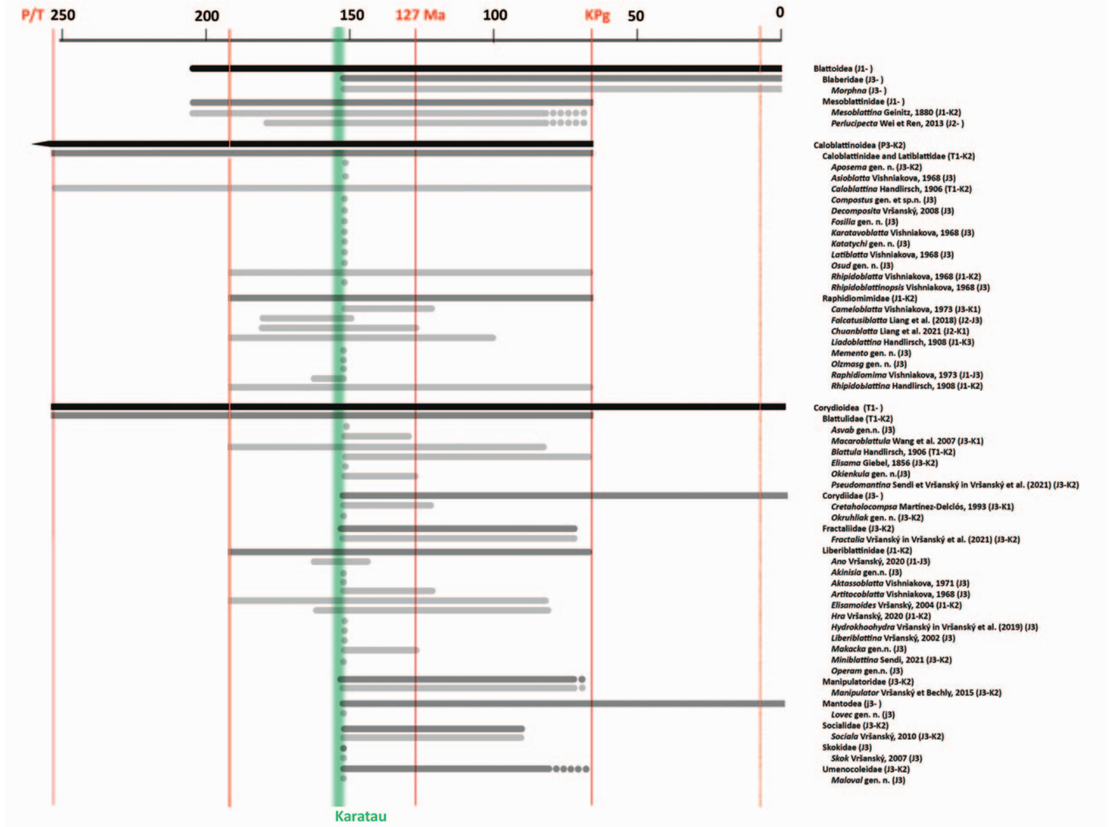
Diving more specifically into record of respective genera, and disregarding indigenous ones here (n= 14) (threated separately elsewhere), one can observe a bulk of other restricted genera (n= 11): *Aposema* is limited to a Cretaceous polar Khetana; *Raphidiomima* to Bakhar and Phrae-Nan; *Cameloblatta* to North Korea; *Chuanblatta* to Daohugou; *Macaroblattula* to Yixian; *Pseudomantina* to Yixian and Lebanon amber; *Cretaholocompsa* to Montsec; *Okruhliak* to North Myanmar amber; *Fractalia* to Solnhofen and N Myanmar amber; *Manipulator* to Crato and N Myanmar amber; *Sociala* to Archingeay.

Wide-time-range taxa are represented only by 7 taxa: *Caloblattina, Rhipidoblatta, Rhipidoblattina, Mesoblattina, Perlucipecta, Blattula* and *Morphna*. This might be surprising and counterintuitive as cockroaches are generally thought to be conservative, which is not the case.

All other taxa are restricted Jurassic-Cretaceous elements.

To sum up, not only indigenous groups are the most commonly represented here, additionally the indigenous genus bear the most dominant species (NB!): *A. fusca*.

Notably, most cockroach taxa, namely genera and families originate and terminate in 62 Ma periodicity cycles. This trend is also apparent here in the first P/T and second Diversification point, while this trend is not apparent in later two. This is caused that the chart cannot contain taxa originating later than Karatau.



Duration of cockroach genera in 62Ma cycles

Blattoidea **(J1-)**
- Mesoblattinidae **(J1-)**
  - *Mesoblattina* Geinitz, 1880 **(J1-K2)**
  - *Perlucipecta* Wei et Ren, 2013 **(J2-K2)**

Blaberoidea **(J1-)**
- Blaberidae **(J3-) FOD**
  - *Morphna* **(J3-) FOD**

Caloblattinoidea **(P3-K2)**
- Caloblattinidae **(T1-K2)**
  - *Aposema* gen. n. **(J3-K2) FOD**
  - *Asioblatta* Vishniakova, 1968 **(J3) I**
  - *Caloblattina* Handlirsch, 1906 **(T1-K2)**
  - *Decomposita* Vršanský, 2008 **(J3) I**
  - *Karatavoblatta* Vishniakova, 1968 **(J3) I**
  - *Katatychi* gen. n. **(J3) I**
  - *Osud* gen. n. **(J3) I**
  - *Rhipidoblatta* Vishniakova, 1968 **(J1-K2)**
  - *Rhipidoblattinopsis* Vishniakova, 1968 **(J3) I**
- Latiblattidae (J3)
  - *Latiblatta* Vishniakova, 1968 **(J3) I**
  - *Fosilia* gen. n. **(J3) I**

- Raphidiomimidae **(J1-K2)**
  - *Cameloblatta* Vishniakova, 1973 **(J3-K1)**
  - *Falcatusiblatta* Liang et al. (2018**) (J2-J3)**
  - *Chuanblatta* Liang et al. 2021 **(J2-K1)**
  - *Liadoblattina* Handlirsch, 1908 **(J1-J3)**
  - *Memento* gen. n. **(J3) I**
  - *Olzmasg* gen. n. **(J3) I**
  - *Raphidiomima* Vishniakova, 1973 **(J1-J3) FOD**
  - *Rhipidoblattina* Handlirsch, 1908 **(J1-K2)**

Corydioidea **(T1-)**
- Blattulidae (**T1-K2)**
  - *Asvab* gen.n. **(J3) I**
  - *Macaroblattula* Wang et al. 2007 **(J3-K1) FOD**
  - *Blattula* Handlirsch, 1906 **(T1-K2)**
  - *Elisama* Giebel, 1856 **(J3-K2) FOD**
  - *Okienkula* gen. n**. (J3) I**
  - *Psudomantina Sendi et* Vršanský in Vršanský et al. (2021**) (J3-K2) FOD**
  - *Spono* gen.n. **(J3) I**

Corydiidae **(J3-) FOD**
- *Cretaholocompsa* Martínez-Delclós, 1993 **(J3-K1) FOD**
- *Okruhliak* gen. n. **(J3-K2) FOD**

Fractaliidae **(J3-K2) FOD**
- *Fractalia* Vršanský in Vršanský et al. (2021) **(J3-K2) FOD**

*Liberiblattinida**e*** **(J1-K2)**
- *Ano* Vršanský, 2020 **(J1-J3)**
- *Akinisia* gen.n. **I**
- *Aktassoblatta* Vishniakova, 1971 **(J3) I**
- *Artitocoblatta* Vishniakova, 1968 **(J3) I**
- *Elisamoides* Vršanský, 2004 **(J1-K2) FOD**
- *Hra* Vršanský, 2020 **(J1-K2)**
- *Hydrokhoohydra aquabella* Vršanský in Vršanský et al. (2019) **(J3) I**
- *Liberiblattina* Vršanský, 2002 **(J3) LOD**
- *Makacka* gen.n. **(J3) I**
- *Miniblattina* Sendi, 2021 **(J3-K2) FOD**

Operamidae fam.n. **(J3) I**
- *Operam* gen.n. **(J3) I**

Manipulatoridae **(J3-K2)**
- *Manipulator* Vršanský et Bechly, 2015 **(J3-K2) FOD**

Mantodea **(J3-) FOD**
- *Lovec* gen. n. **(J3) I**

Socialidae (**J3-K2)**
- *Sociala* Vršanský, 2010 **(J3-K2) FOD**

Skokidae **(J3) I**
- *Skok* Vršanský, 2007 **(J3) I**

Umenocoleidae **(J3-K2) FOD**
- *Maloval* gen. n. **(J3) I**

PHYLOGENETICAL SIGNAL WITHIN TAXA

A phylogenetical signal is present in the codominant species *Ano ona* representing genus *Ano*, which was dominant in most Middle-Upper Jurassic sites. *Ano da* seems to be most advanced, while other species at Karatau (see tabp. for ocurrences of *Falcatussiblatta, Fractalia, Cameloblatta, Pseudomantina, Raphidiomima* (see also Kováčová et al. 2023), *Rhipidoblatta, Rhipidoblattina* (occurring also in Layiang, unpublished), *Aposema, Caloblattina, Chuanblatta, Cretaholocompsa, Divocina, Elisamoides, Liadoblattina, Macaroblattula, Mesoblattina, Miniblattina, Okruhliak, Perlucipecta, Sivis, Blattula, Morphna, Manipulator, Hra*), none of which reveals such a signal. On the other side, *Elisama* is common in Tithonian and in Cretaceous sites and seems most primitive in having smallest macula. *Sociala* occurs also in the Albian and is plesiomorphically large. Lack of intrageneric phylogenetical signal in such a abundant material suggest none or minor changes within genera. If we focus on the present genera, we see that some of them last a significant period of time and this stasis is significant. It reflect a well-based evidence for the frozen taxa (see Flegr 2010, Vršanský et al. 2017). Most of *Liberiblattina* species are more primitive than those occurring in Kota, but highly advanced species also occur, contributing to the lack of the signal.

PHYLOGENETICAL ANALYSIS

Phylogenetical analysis performed on the basis of the above matrices reveals advance in several prinical respects. (1) It reveals the structure of the most diverse assemblage in the history. This is non-trivial because it has been shown previously that the structure highly depends on the complexity (totality) of data (Vršanský 2020, Vršanský et al. 2021a). Thus the most complete data from a single locality should reveal supports most close to the reality – or at least provide limits for (restricted) data originating from a single site. These can be compared to the true values obtained from all localities combined. (2) Completely preserved individuals enabled for the very first time to compare tree and network supports for taxa measured on the basis of forewings only (n= 83; usual approach, missing in analyses are *H. nice, L. oddajsami, L. cipka, A. palindrom, B. fragilia, D. polnoci, L. crassivenata, S. borat, A. gigantenna, M. akcakam, M. akmacaka, M. velipsespilev, O. ojedinela*) and on the forewings (n= 52) with hindwings (n= 52) combined (n= 52). I added also all observable body (n= 52; missing in analyses are additionally *F. aristovi* and *D. apicata* without bodies) characteristics, which further modified supports, both in trees and in networks. Notably the wings characters are mostly neutral in respect to phylogeny, while recognised body characters mostly relate to lifestyle and represent rather life-forms. (3) Finally, as some taxa are restricted to Karatau, they are displayed excusively within this dataset. Their relation is briefly discussed and their true position within the global data environment is estimated.

Restricted network analysis for bodies only reveals basically support for terminal taxa only and Latiblattidae (86.8 %). Supported are Raphidiomimidae s.s. (*Raphidiomima* with *Cameloblatta*; 84.9 %). There is not a strict support for the respective families, supported are only Blattulidae (58.5 %) with *Miniblattina* (Liberiblattinidae), due to miniaturisation.

RESTRICTED NETWORK ANALYSIS FOR FOREWINGS (AND HINDWINGS ONLY; SUPPORTS UNDER 50 NOT SHOWN) ONLY [FOREWINGS WITH HINDWINGS] AND ALL DATA (FOREWINGS WITH HINDWINGS WITH BODIES) TOGETHER (in bold)

reveals support for the family Blattulidae 88.7 % (50.5 %) [95.5 %] **97.7 %**) and 96.2 % [86.1 %] **78 %** for Blattulidae without *Asvab;* 89.5 % [68.8 %]**78.4 %** without *Asvab* and *Elisama* (i.e., genus *Blattula*). 63.8 % [66.1 %] is supported *Blattula microscopica* with *B. brevicaudata*. Mesoblattinidae is also well-supported 99.6 % (93.3 %) [100 %] **99.9** %. Due to high diversity and disparity of forms, close derivation of the marginal taxa, and paraphyly, family Liberiblattinidae is not supported, but supported are genera *Liberiblattina* 92.5 % [93.8 %] **96.8 %**; *L. ihringovae* with *L. palaeontologica* 91.6 % [76.4 %] **79.9 %**; *Ano* 63.3 % [58.9 %] **73.8 %**; *A. tak* with *A.ona* with *A.si* 53.8 % [69.2 %] **81.6 %;** and *Aktassoblatta* 97 % (53.7 %) [99.7 %] **100 %**. Surprisingly also Raphidiomimidae are not supported due to relation of *Akinisia* (Liberiblattinidae) on one topological end and Caloblattinidae on another (and putative paraphyli in respect to *Manipulator*). Supported is the cluster of *Raphidiomima cognata* with *R. chimaera* 94.7 % (57.9 %) [94.5 %] **91.6 %** and *R. cognata* with *Cameloblatta* 87.9 % **78.2 %** and all three taxa 96.3 % (53.5 %) [93.7 %] **99.7 %**. Another raphidiomimid cluster with low support 58.6 % is *Falcatussiblatta* with *Liadoblattina* and *Decomposita* (but without *D. tristriata* and *D. basquatirgis*; while other *Decomposita* species also have low support 53.8 %. Strong support 96 % (73 %) [98.6 %] **96.8 %** is for *Liadoblattina= Falcatussiblatta* with *Falcatussiblatta*. Latiblattidae are well-supported 97.6 % [98.8 %] **100 %**. Supported 60.4 % [54.6 %] **61.8 %** are also Latiblattidae with *Rhipidoblattinopsis* and *Karatavoblatta.* Thus Caloblattinidae are also not supported and are paraphyletic in respect to Latiblattidae. Within Caloblattinidae, supported is genus *Rhipidoblatta* 70.9 % [75.5 %] **85.7 %;** 62.6 % [75.1 %] **76.6 %** *R.matriky* with *R. brevivalvata* and 98.1 % **84.1 %** [93.2 %] *R. fusca* with *R. trimeste*.

Decomposita [75 %], *Decomposita* with *Falcatussiblatta* [64.7 %] and *Decomnposita triocella* with *Falcatussiblatta* [64.7 %]reveals support in combined forewings with hindwings only.

(60.6 %) support additionally appears for the hindwings of *Blattulidae, Lovec* and *Miniblattina*.

All data combined also reveal new supports (*Rhipidoblattinopsis* with *Karatavoblatta* **83.2 %;** *Ano ona* with *A. si* **67.2 %**; Blattulidae without *B. nebude* **81.5 %**. Surprising is weak support for an illusory re-

lation of Mesoblattinidae with Skokidae (68.6 %) **67.4** % [66 %]. *Decomposita* become well-supported **88.6 %**. Weak support appears for *Decomposita* with *Falcatussiblatta* with *Liadoblattina* (but without *D. tristriata*) **62.5 %**.

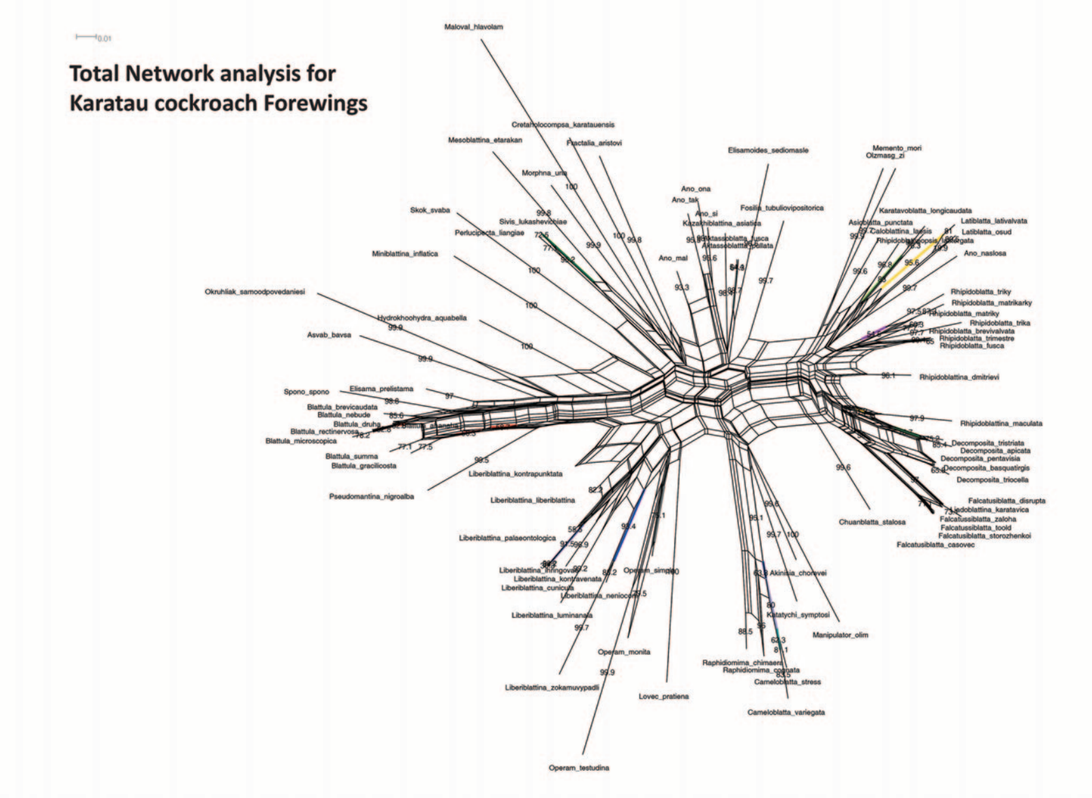
To summarise this analysis, the total data are delimiting all families well and support ancestral status of Liberiblattinidae (in respect to Skokidae, Umenocoleidae and Mantodeans). What is new is their unequivocal ancestry in respect to Blattulidae as well. Also they reveal ancestry in respect to Mesoblattinidae, which is discussed below. Caloblattinidae are ancestral in respect to Latiblattidae. Manipulatoridae are in this analysis raphidiomimid ingroup, which is also discussed below. Alternative approach enables to consider all presently studied cockroaches as raphidiomimid-ingoups.

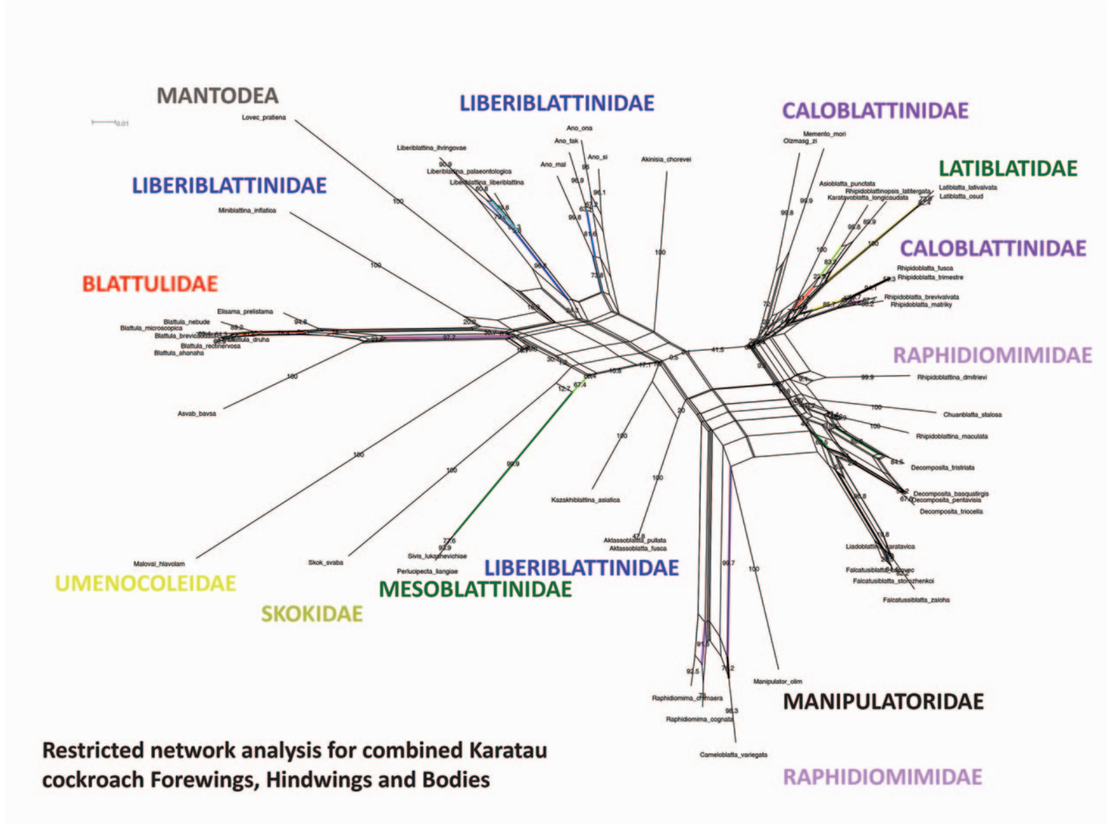
It must be stressed that in addition to the supported clades, this (combined) network analysis reveal a fully intuitive topology (except position of *Skok*), in spite of the fact that most of the family-rank nodes are statistically unsupported. This mostly results from paraphyli of Liberiblattinidae to most of taxa including Mantodea, and its here-revealed derivation from the Raphidiomimidae.

THE TOTAL NETWORK ANALYSIS PERFORMED ON THE BASIS OF ALL AVAILABLE KARATAU FOREWINGS

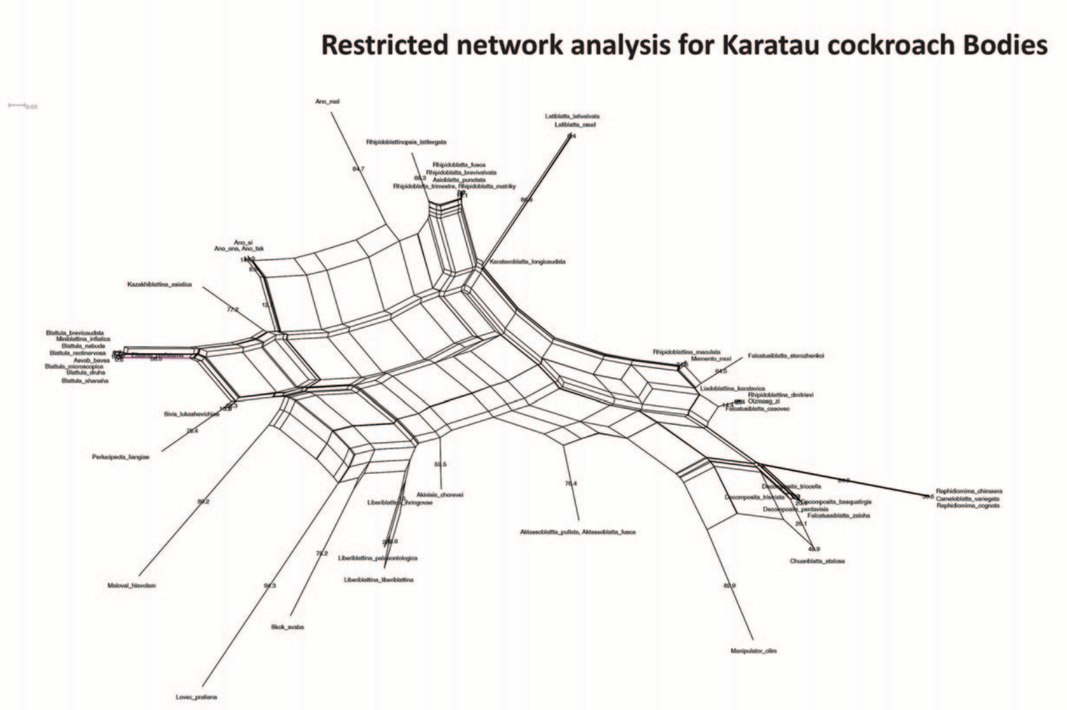
comprising all species reveal a different supports. Similar is support for Mesoblattinidae *Perlucipecta* and *Sivis* (95.2 % surprisingly *Mesoblattina* absent in the former dataset is not supported within Mesoblattinidae significantly). Similarly supported, but much weakly is *Aktassoblatta* (88.7 %) and Latiblattidae (95.6 %). *Decomposita* is also supported (70.7 %). Supported are additionally *Karatavoblatta* and *Caloblattina* absent in the former dataset (88 %); *Rhipidoblatta triky* with *R. matriky* and *R. matrikarky* (54.5 %). 51.2 % is support for *Decomposita* with *Falcatussiblatta* species (*F. disrupta, F. karatavica?*). 93.4 % is support for *Liberiblattina zokamuvypadli* a *L. neniocom*. 91.5 % is for *L. ihringovae and L. kontravenata*. Blattulidae are supported without *Pseudomantina* (58.7 %) also without *Elisama* (56.3 %) and a weak support is for 52.1 % *B. rectinervosa, B. microscopica, B. druha*. Operamidae have support 75.1 %. Significant support (95.1 %) is for *Cameloblatta* (80 %) with *Raphidiomima* (63.3). Clear message is that only terminal taxa are supported in this forewing-restricted but otherwise completedataset.

And again, although not statistically significant, topology of the network fully supports intuition and formal classification (single (of 82) exception is position *Fosilia* out of Latiblattidae).
Average support for supported (over 50 %), non-terminal clades is (1121.4/ 82) **13.68** %. This is a devastating decrease from Restricted dataset (1652/51) **32.4 %**.



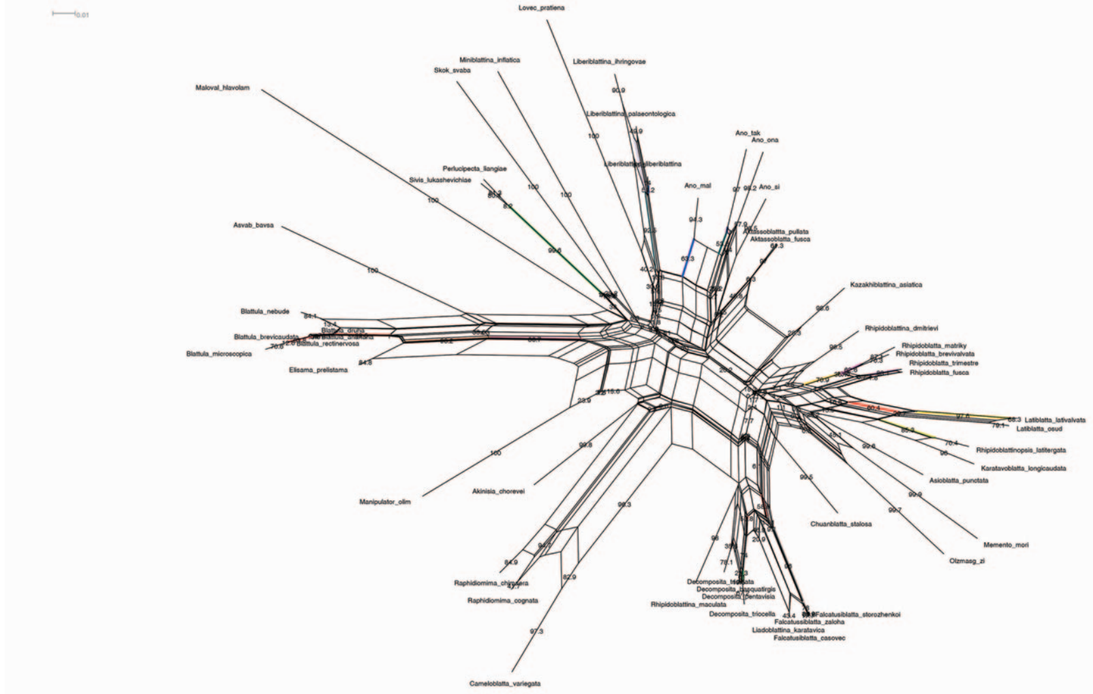


Restricted network analysis for combined Karatau cockroach Forewings, Hindwings and Bodies

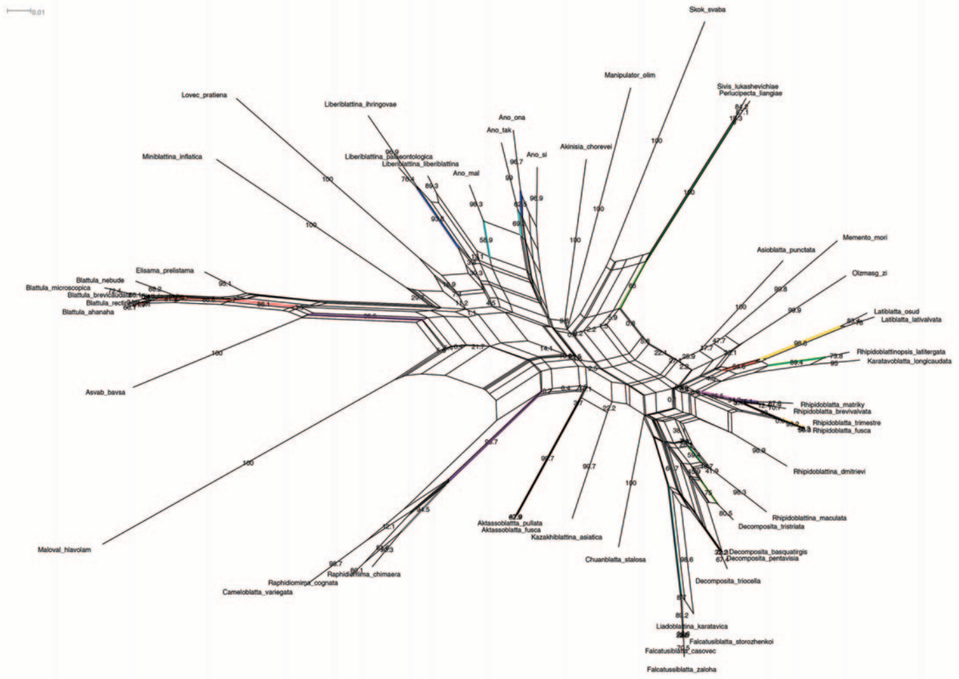


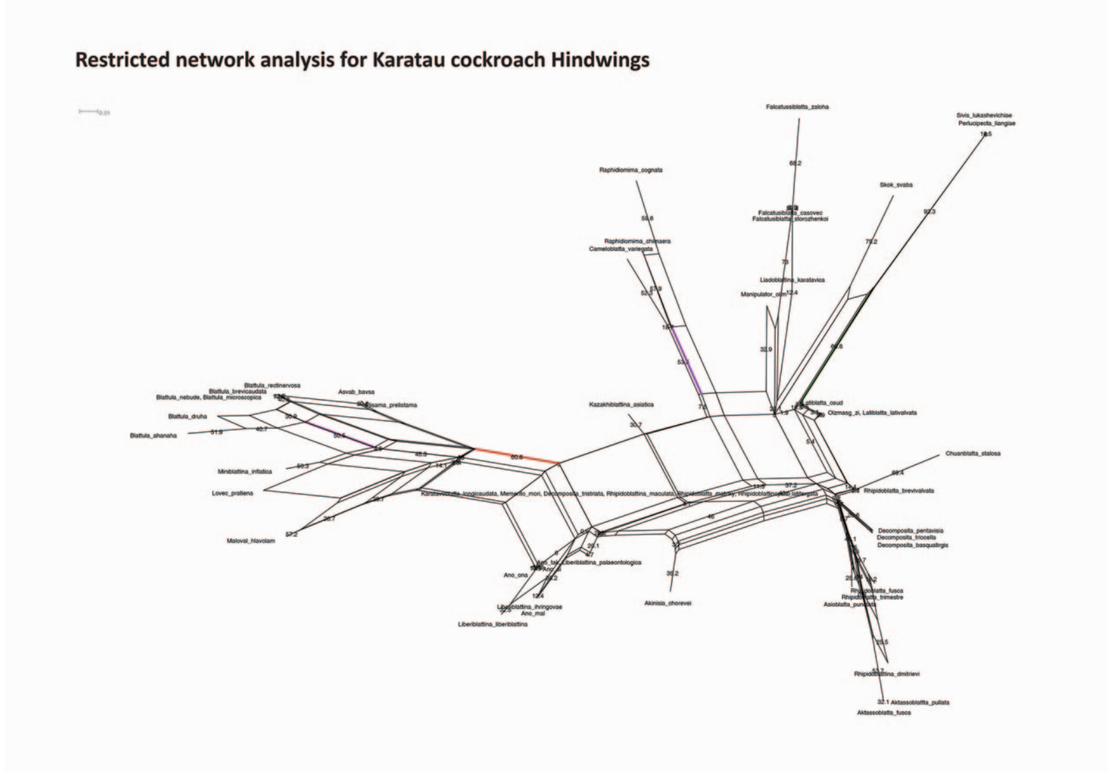
Restricted network analysis for Karatau cockroach Bodies

Restricted network analysis for Karatau cockroach Forewings



Restricted network analysis for combined Karatau cockroach Forewings with Hindwings





TO SUMMARISE RESTRICTED NETWORK ANALYSIS AND TOTAL NETWORK ANALYSIS - PERSPECTIVE

Interpretation (of the Total Network analysis) was especially difficult mainly due to great proportion of negative results. To repeat, as pointed out previously, supports decrease!!! with completeness of data – the more complete data, the less significant supports for clades (see Vršanský et al. 2019d, Hinkelman 2023). Here it is especially pronounced as the Karatau dataset of fossil cockroaches is the most complete one so far known. And except supported terminal taxa we do not see a single statistically significant support at the family level. Thus a result of this huge performed analysis is devastating and demotivating for cockroach students. Cockroach forewing morphology alone do not reveal and will not reveal any robust supports (because it will further decrease with rising of data). Forewings can be analysed and results can be obtained, but supports will be illusory obtained in limited sample sizes only. This is greatly unfortunate, as most of the preserved structures in other localities represent isolated forewings. So basically no one locality in the future can be accessed on the basis of forewings only. Possible future exceptions are Daohugou, Yixian and burmite where results can differ slightly. Nevertheless, as seen above, decrease from the same locality from 82 to 51 analysed speciens results in increase of average support from 13.68 to 32.4 %.

As seen (of Restricted Network), these results are even more pronounced in analyses of hindwings only and bodies only.

Positive message is that combining data (forewings with hindwings and bodies), results become robust again. This is remarkable as supports for hindwings only and bodies only are low. Apparently adding these datasets eliminates influence of numerous forewing homoplasies. Again, this suggest a huge perspective in complex analyses for major Lagerstätten Daohugou, Yixian and burmite, where resuts are expected to be statistically significant in clade supports for a single assemblage.

One can argue that again, in providing massive and robust analyses combining complex data from more (or all) localities, supports will again disappear, but this statement needs practical verification. Anyway this analysis works for one timecut, so in the future can complex data can be gained from 3D Networks. It also cannot be excluded that with more (complex) data, support will be moved to higher levels. Lets see.....

Also, results must be taken with caution due to anoter restriction – Karabastau contains basically all Jurassic taxa. Cretaceous taxa are irrelevant in the topology, but Triassic taxa can alter the results as "*Volziablatta*-group" might be the stem for all major lineages (Blattoidea/ Raphidiomimoidea/ Corydioidea). This is nevertheless, out of the scope of the present analysis.

What is motivating is, that even without high percentual supports, the topology of the network is valid (but see below).

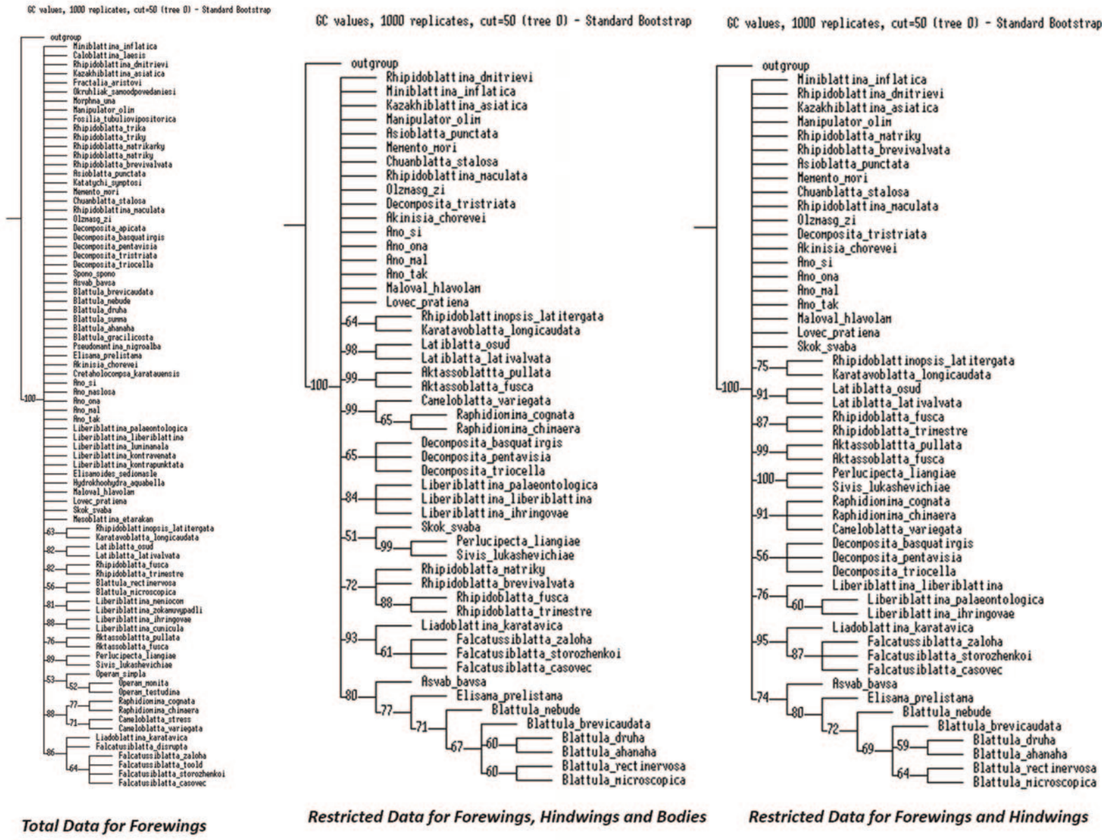
PARSIMONY ANALYSIS

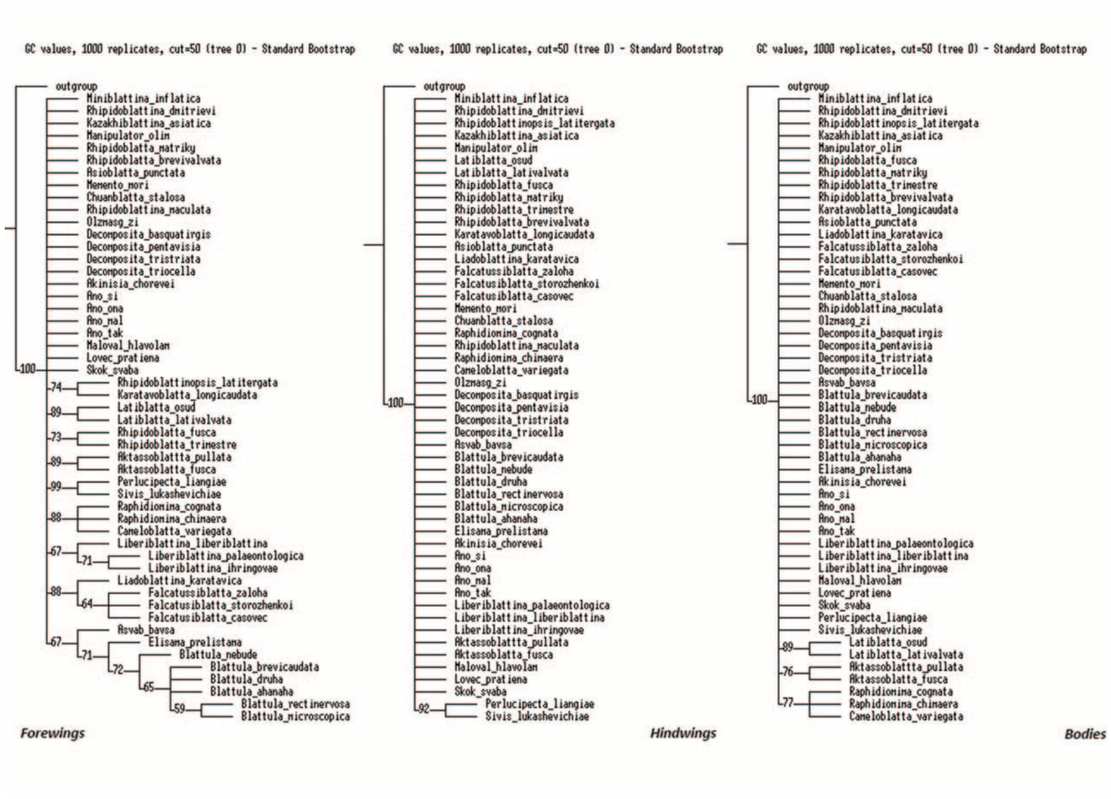
This method is used for a complementary comparison only. While it is impossible to designate a completely preserved outgroup ("*Voltziablatta*"-group complete specimen is unknown), to reveal rooted results, it was performed here adding superplesiomorphic taxon (all zeroes) as an outgroup. This method was applied in the past (see Vršanský et al. 2023) with satisfactory results. It must be noted, that this method is only possible when characters are polarized in the character matrix and thus their polarization follows previous results and experience. Thus the results reveal maximum possible supports and the real supports might be only lower. Supports are low already, so take a look on comparison with other performed analyses.

Total Data forewing parsimony analysis does not reveal any reliable supports (besides terminal taxa). Of these only 82 % would be reliable for Latiblattidae, nevertheless, this does not includes *Fosilia* of the same family. The same for *Perlucipecta* with *Sivis* (89 %) of Mesoblattinidae without *Mesoblattina*. So only reliable, but low, family-level support is for Operamidae (53). Supported (86 %) is also *Falcatussiblatta* with *Liadoblattina,* also an incomplete raphidiomimid clade. These results are highly consistent with Total Data Network.

Partial Data for combined Forewing, Hindwings and Bodies [Forewings and Hindwings only], similarly as in similarity and Network analyses are far more satisfactory. Besides terminal clades (namely *Rhipidoblattinopsis* with *Karatavoblatta* (64 %)**[75]**, *Latiblatta* (98 %) **[91]**, *Aktassoblatta* (99 %) **[99]**, *Decomposita* (without *tristriata* 65 %) **[56]**, *Liberiblattina* (84 %) **[76]**, *Rhipidoblatta* (72 %) **[]**, *Falcatussiblatta* (93 %) **[95]**, Mesoblattinidae **[100]** supported again (99 %) **[91]** is *Raphidiomima* with *Cameloblatta;* and (93 %) *Falcatussiblatta* with *Liadoblattina*, and also (80 %) **[74]** Blattulidae (and 77 % **[80]** Blattulidae without *Asvab* and 71 % **[72]** for *Blattula* only). Supported (51 %) is again *Skok* with Mesoblattinidae. *R. fusca* with *R. trimestre* is also supported **[87].**

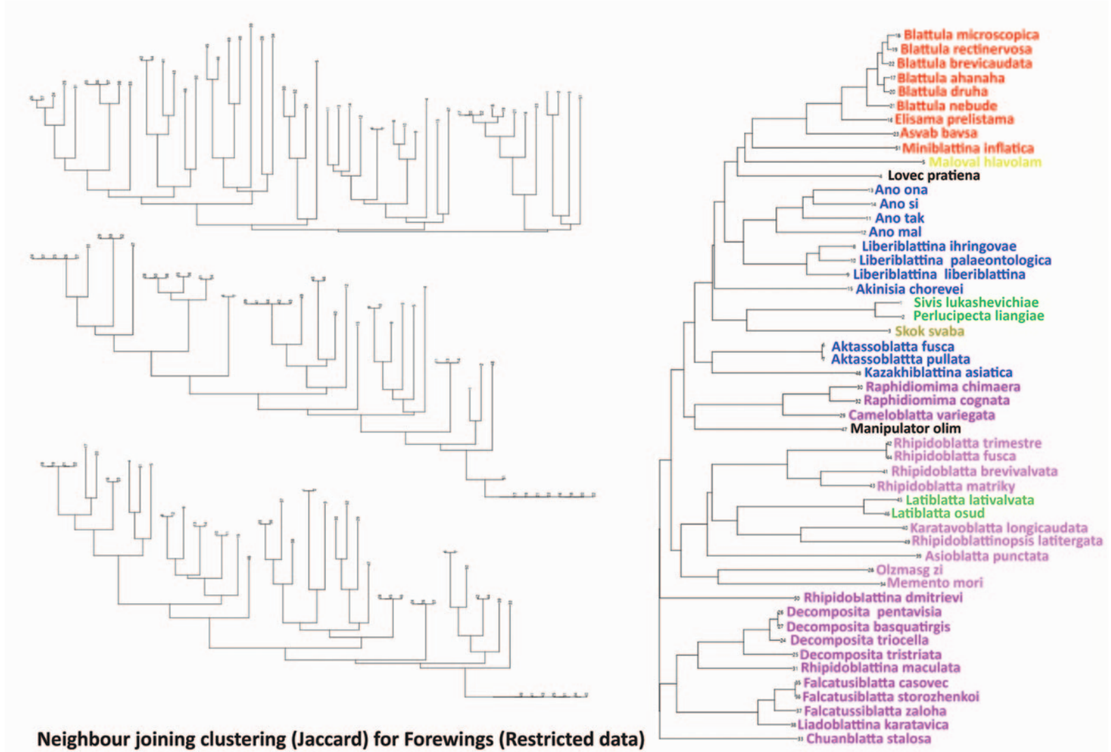
Partial Data for Bodies reval supports only for Latiblattidae (89 %), *Aktassoblatta* (76 %) and *Raphidiomima* with *Cameloblatta* – i.e., not even terminal taxa were supported.
Partial Data for Hindwings are even more diffuse with a single support for Mesoblattinidae (92 %).
Partial Data for Forewings supports some terminal taxa (*Rhipidoblattinopisis* with *Karatavoblatta* (74 %), *Latiblatta* (89 %), *R. fusca* with *R. trimestre* (73 %), *Aktassoblatta* (89 %), *Perlucipecta* with *Sivis* (99 %), *Liberiblattina* (67 %) and *Falcatussiblatta* (including *karatavica*) (88 %). It again supports *Raphidiomima* with *Cameloblatta* (88 %). Blattulidae (67 %), Blattulidae without *Asvab* (71 %), *Blattula* (72 %) are also supported.



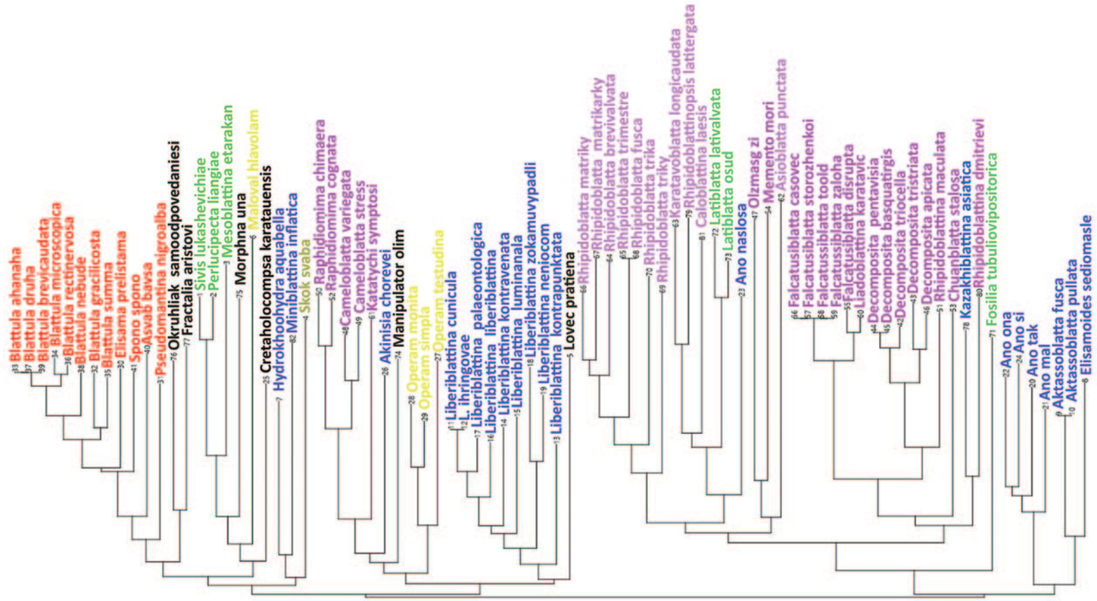


LINEAGES EVOLVING TAXONOMICALLY VS. IN LIFE FORMS (DIVERSIFICATION RATE ASYNCHRONITY)

It seems evident that potentially lifeforms evolve nearly immediately, while realised niches are postponed frequently on the scale of (dozens) millions of years. Different lineages behave differently when comparing phylogenetical and phenetical (form) evolution even within Karatau, while the pattern obtained has general validity (respective families behave similarly over time). Most striking paradox directly referring to obscured *species evolution* is evidenced in dominant families Blattulidae and Caloblattinidae, with 15/714 and 12/261 species/specimens respectively (7, 6 genera; 5, 13 forms) only in Karabastau. Neither in Karatau, nor in any other site, 190 million year dominance of these families did not lead to any offshot except for indigenous Fuziidae restricted to Dauhogou. The same holds true for predatory Raphidiomimidae which reached optimum at Karatau (also in Daohugou) with 10 life forms, 22/501 species/specimens and 7 genera. On the other hand, Liberiblattinidae with 15 life forms, 10 genera and 27/776 species/specimens permanently produced numerous offshots (Fractaliidae, Umenocoleoidea, Nocticolidae, Mantodea, Isoptera, Skokidae, Corydiidae and others out of Karabastau). Other families have restricted ocurrences within Karabastau. Thus taxon evolution and lifeform evolution is a two-layer process within respective taxa. It is of a priority interest that differences among these two layer are quantifiable. While the diversification rate extracted from Karatau (compared with Daohugou/Bakhar) record on the basis of percentage of indigenous (this excludes relation of homoplasic and/or original state of fundamental types) taxa reveals ratio 28/48 (58.3 %); form-diversification ratio extracted from Karatau record on the basis of percentage of indigenous forms reveals ratio 7/25 (28 %). (Taking into consideration time-difference among Daohugou and Bakhar for maximum 13 Ma, these data mean 0.04 and 0.02 per 1 Ma respectively.) This result in counterintuitive value of slower diversification rate of new (unique) lifeforms. Nevertheless, simpler life forms evolve nearly immediately and are responsible for most general homoplasies, unless present originally. The independent approach to access the same difference (among diversifications of genera and lifeforms) lies in direct comparisom of phylogenetical and phenetical similarities (see also paragraph **Similarity analysis**). Moreover, we can compare forms as characters within respective families, which reveals a relation of richer (with more genera) families (see Figps. 608-609). And again, it is hardly understandable, but these rich families did not produce any descendant.



Neighbour joining clustering (Jaccard) for Forewings (Restricted data)
Neighbour joining clustering (Jaccard) for Hindwings (Restricted data)
Neighbour joining clustering (Jaccard) for Bodies; and Forewings, Hindwings and Bodies combined (Restricted data)



Neighbour joining clustering (Jaccard) for All forewings

GHOST RANGES

Ghost ranges were identified as a relevant (numerical) source of information (Rasnitsyn 2000). This test performed on cockroaches reveal absence of data in 57 of exactly 300 relevant 10-million-year old pinns for whole evolution of cockroaches. This means 19 % of the family-rank cockroach fossil record (n= 110,000) is apparently missing. But, only in four cases (pinns), the ghost-range must be added according to the phylogenetical analysis and prediction, i.e., only this is (4) the ghost range s.str. and only in these two cases (1 plus 3= 4) evaluation of lengths of ghost-ranges would make sense, which is nevertheless, close to zero (0.013 %). That means that the family-rank cockroach and the general evolutionary pattern is virtually complete and uninfluenced by the ghost-ranges (in spite of exactly 19 % of 10 Ma pinns misssing). The present record (Karabastau) did not filled (inside) missing ghost-ranges of families Phyloblattidae and *Voltziablatta*-group. On the other hand it is the only record of the family Skokidae, Operamidae and Latiblattidae. In case of Fractaliidae and Socialidae it created long (4 pinns) ghost-ranges s.l. being supplemented by 98 Ma and 92 Ma Myanmar and Archingeay ambers respectively. In the case of Corydiidae it formed a 1-pinn ghost range. A real problem this vast record caused only in the case of Blaberidae (4-pinn ghost range) and an umenocoleid.

GHOST RANGES OF FORMS

Ghost ranges of forms were never approached before and represent independ and complementary information. To a complete surprise, the total missing pinns represent nearly identical number of 16.2 % (90 of 556 forms). In the case of lifeforms, these ghost ranges are true as forms are not heritable and in contrast to families can appear more times independently. Thus their occurrence is purely intuitive and in reality can be only lower (because they can not truly represent missing ghost-ranges but instead can be truly absent in reality). In a single case (3 pinns) the form can be predicted earlier on the basis of phylogenetical information (cave form in Nocticolidae 130 estimated - 100 recorded), which also mean that the record of forms is practically complete in respect to first origin. Very probably this logic also apply to inner ghost ranges, nevertheless, this logic (in contrast to phylogenetical ghost-ranges) cannot be apllied to the prove itself. That means cockroach record is, in relation to life forms, complete to 83.8 %. In this context, contribution of the Karabastau is much more significnant than the phylogenetical record. Karabastau alone filled 23 of the historically totally possible 34 pinns. In 11 cases it is the first occurence of a life form in the history, which is the highest number among any time pinns and locality. It barely represents a sampling bias as it is immediately predecessed by Daohugou pinn (with at least 10,000 collected cockraoches). Only in 5 cases it formed a ghost ocurrence, in all cases a short-one (1, 1, 1, 2, 4).

INDIGENOUSNESS

Nineteen (21) genera are **indigenous**. The whole families Latiblattidae (*Latiblatta, Fosilia*), Skokidae (*Skok*) and Operamidae (Operam) are indigenous to Karabastau. Near-indigenous *Liberiblattina* with 10 species and *Decomposita* with 5 species directly support a reduction ring. *Cameloblatta* (1) is also indigenous once not representing a senior synonym for *Paekhtoblatta* from North Korea.

So on one side the low degree of cosmopolitan genera, there is enormous endemism, which has no equivalent in history. Just for comparison, this matter was discussed previously (Vršanský 2020), but globally there are only 18 other indigenous genera known (no one in spatiotemporary adjacent Bakhar in Mongolia). The more obscure is this pattern, as these indigenous taxa are rather common to very common and dominant. Most of them are additionally represented with more that one species. Also indigenous genera predictably occur in Liberiblattinidae (nearly always indigenous), but also in totally conservative Caloblattinidae and Blattulidae.

PALAEOGEOGRAPHY REVEAL DIVERSE GEOGRAPHIC PATTERNS OF GENERA

Five genera are cosmopolitan: *Blattula* with 9 species directly support a reduction ring, *Elisama, Perlucipecta, Caloblattina* and *Liadoblattina*. Number of cosmopolitan genera is surprisingly extremely low, moreover taking into consideration wide distribution of most of Jurassic and Cretaceous cockroaches. Only *Blattula* and *Liadoblattina* occur also in Australia, widespread *Caloblattina* and *Elisama* are represented with a single species each (n= 1, 1). So the partition of cosmopolitan taxa is reduced to minimum. Reasons are entirely obscure, the more obscured with high number of specimens.

It seems, as there are hi-res rich fossil records at Daohugou and Bakhar, that there was a diversity culmination at the ecosystem level, which must be later diminished. It is a bit hardly to imagine as consequent Lagerstätten, Barremian Yixian and Lebanese ambers are rich again, and there is no indication of earlier decline, although rich sites were absent. Baissa nevertheless might be Aptian, with the fully expressed diversity in spite of colder (temperate warm) climate.

Three genera are **Laurasian:** *Rhipidoblatta* with 8 species directly support a reduction ring, *Mesoblattina* and *Hra*. Possibly, advanced Umenocoleidae is wholy Laurasian family. This partition is again very low.

Two genera *Ano, Morphna* is obscurely **restricted to narrow region within Laurasia** – in a long term. *Morphna* is problematic as the whole family nearly escaped Mesozoic fossil record (Fukui, Khetana, North Myanmar amber), but *Ano* is the eudominant genus nearly everywhere in the region including Bakhar. How is possible that such common and abundant and long-lasting genus has restricted occurrence is obscure and hardly explainable. A possible explanation would be a total long-lasting

isolation or even a small microcontinent joining Bakhar, Daohugou and Karatau, similarly as in the case of Greater Adria (Vršanský et al. 2021c). Nevertheless, *Ano* (*Hra* and *Liberiblattina*) occurs also in Gondwana Kota, which suggests rater *Ano* being an extremely short-living taxon and all these localities representing a short period of time.

Two genera have a sole analogue in the **North Myanmar amber**: *Okruhliak*, *Fractalia* (n= 1, 1). This number says little – it is small- the same congruence as with the remote Lebanese amber and also very rare species in Myanmar (n= 1, 1). They also evidence extremely limited ocurrence of genera found in Karatau.

Two genera are **Gondwanan** - *Pseudomantina* and *Miniblattina* are found only in Lebanese amber (n= 1, 1). This occurrence is likely only purely stochastical as it is a rare taxon (n= 1, 4). They also evidence extremely limited ocurrence of genera found in Karatau.

Six genera have **restricted occurrence**. *Aposema* is find only in Russian polar Khetana, *Pseudomantina* and *Miniblattina* are found only in Lebanese amber, *Chuanblatta* only in Daohugou. *Sociala* is found only in Archingeay amber. *Macaroblattula* occurs only in Yixian. Partition of these groups is standard.
There is no need to specify occurrence due to climate as tropical elements occurred beyond the polar circle during the Jurassic and Cretaceous (Vršanský et al. in preparation).

At the suborder level, surely mantodeans and termites are restricted to Laurasia during the Jurassic as these are the sole (FOD) records. The same holds true at the family level for Blaberidae, Corydiidae, Skokidae (i), Manipulatoridae, Latiblattidae (i) and Umenocoleidae and Operamidae (i). Cosmopolitan Mesoblattinidae comprise thee cosmopolitan genera *Mesoblattina, Sivis* and *Perlucipecta*. Fractaliidae is a shared taxon with North Myanmar amber containing both Gondwanan and Laurasian elements. Cosmopolitan Blattulidae comprise cosmopolitan *Blattula, Elisama, Macaroblattula, Pseudomantina* and thre indigenous genera (*Asvab*, *Okienkula* and *Spono*). Cosmopolitan Liberiblattinidae comprise cosmopolitan *Ano, Hra, Miniblattina*. *Liberiblattina* as the most diverse genus nearly restricted to Karabastau is find also in Gondwanan Kota like due to coeval sedimentation. Cosmopolitan Raphidiomimidae comprise cosmopolitan *Falcatussiblatta, Cameloblatta* and *Liadoblattina* and *Rhipidoblattina*. Laurasian are *Decomposita, Divocina, Chuanblatta*. Restricted occurrence is *Raphidiomima* (Bakhar). Cosmopolitan Caloblattinidae comprise comspolitan *Caloblattina, Rhipidoblatta. Aposema* is restricted (Khetana). *Asioblatta, Karatavoblatta* and *Rhipidoblattinopsis* are indigenous. To summarise, the record of Karatau is highly indigenous (see paragraph indigenosity) and further thee genera have very restricted Laurasian range and one of the with Gondwanan Kota. Only 15 genera are cosmopolitan- only three are widely Laurasian. This taken together suggest a part of the cockroach assemblages which is very conservative and shared among supercontinents, very few long-term restricted taxa (to Laurasia). On the other hand some time-restricted taxa such as *Liberiblattina* (shared with Kota of Gondwana) together with predominance oif indigenous genera suggest extremely rapid genus, and to less extent also family turnover.

Ano Bakhar, Kota
Aposema Khetana
Blattula Kubekovo, Bakhar, Quiyang, Houtiyn-Hotgor, Gaositai railway station, Wiltshire, Mecklenburg, Iya River, South China, Stensham, N. Hebei, Novospasskoye village, Beipiao, Shar-Teg, Zhongshan, England, Qinglongtou village, Mintaja, Kota
Caloblattina Wainlode cliff, Bon Tsagaan Nuur, Bakhar, Tasgorosay, Kota
Cameloblatta burmite, Sinuiu
Chuanblatta Daohugou
Cretaholocompsa Montsec
Divocina Daohugou, Kota
Elisama burmite, Crato, Yixian, Brezina, lebanite, Bon Tsagaan, Shar-Teg, Durlston Bay, Sharin-Gol, Dinton, Purbeck, Sinuiu

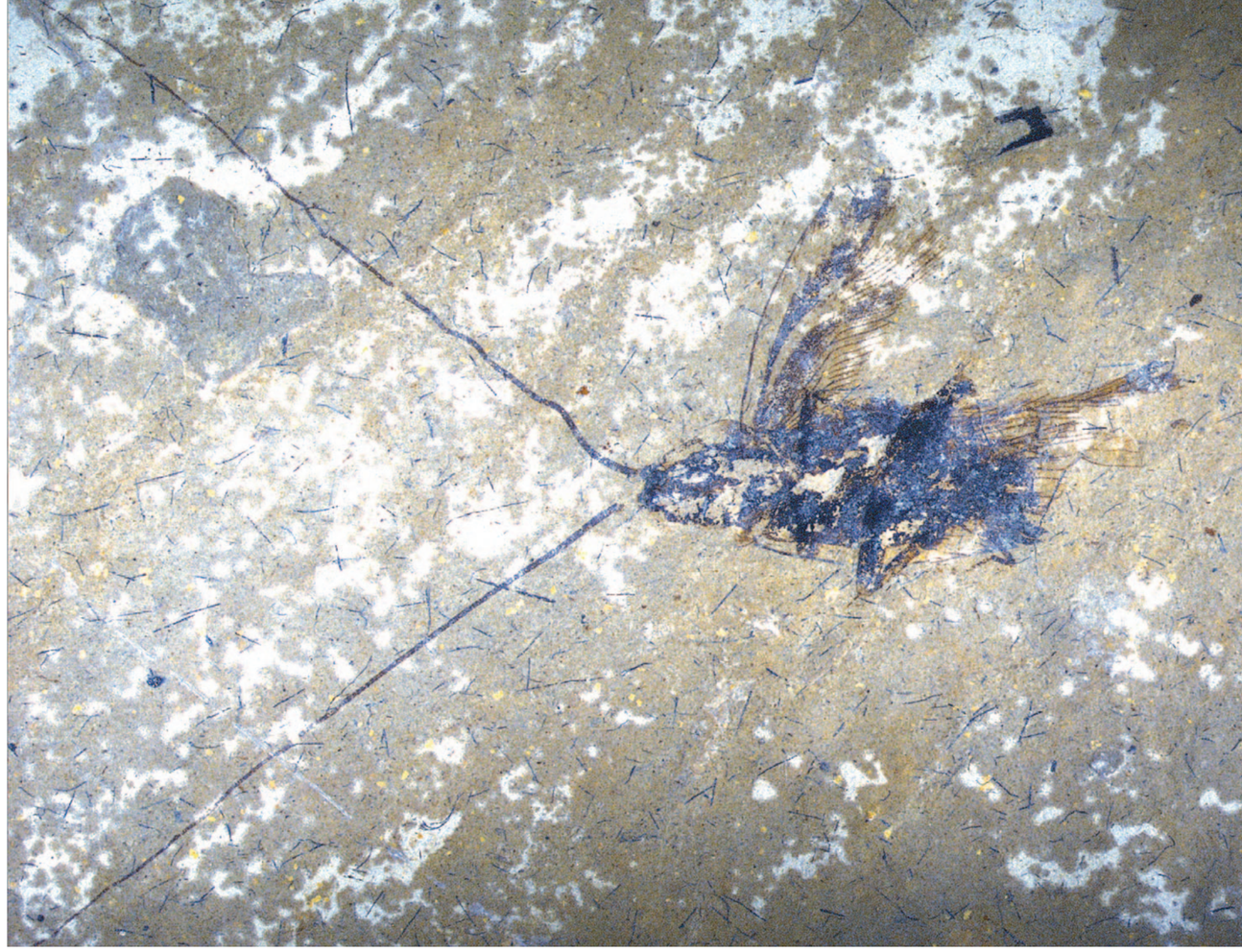
Elisamoides Shar-Teg , Phra-Wihan
Falcatusiblatta Daohugou, Mintaja, Phra-Wihan, Kota
Fractalia burmite
Hra Bakhar, Kota
Liberiblattina Kota
Liadoblattina Iya, Chaomidian, Bon Tsagaan, Lehre, Gifhorn, Bartin Turkey, Wurzburg
Manipulator Crato, burmite, Solnhofen
Macaroblattula Yixian, Kota
Mesoblattina Dobbertin, Zhouangzi, Kota, ?Schambelen, Kota
Miniblattina lebanite
Morphna burmite, Kitadani (living also in SE Asia and India)
Okruhliak burmite
Perlucipecta Yixian, burmite, lebanite, Crato, Kota, Sinuiu
Pseudomantina Daohugou, lebanite
Raphidiomima Phra-Wihan, Bakhar, Kota
Rhipidoblatta Xiaofanzhangzi, Meitian, Mintaja, Daohugou, Kuntouyingzi, Zhouyingzi, Dongchangtai, Daokuntouyingzi, Chernovskie Kopi
Rhipidoblattina Daohugou, Bakhar, Haifanggou, Mintaja, England, Chicheng Hebei, South China, Liaoning Province, Browns Wood, Gurva-Erenyi Nuur, Hebei Province, Jiutai, Kyzyl-Kiya, Chengde, Chaomidianzi, Chaoyang, Xiaofanzhangzi, Chengde Basin, Jiuquan Basin, Vladimirovka village, Chernovskie Kopi.
Sivis burmite, Archingeay
Sociala Archingeay

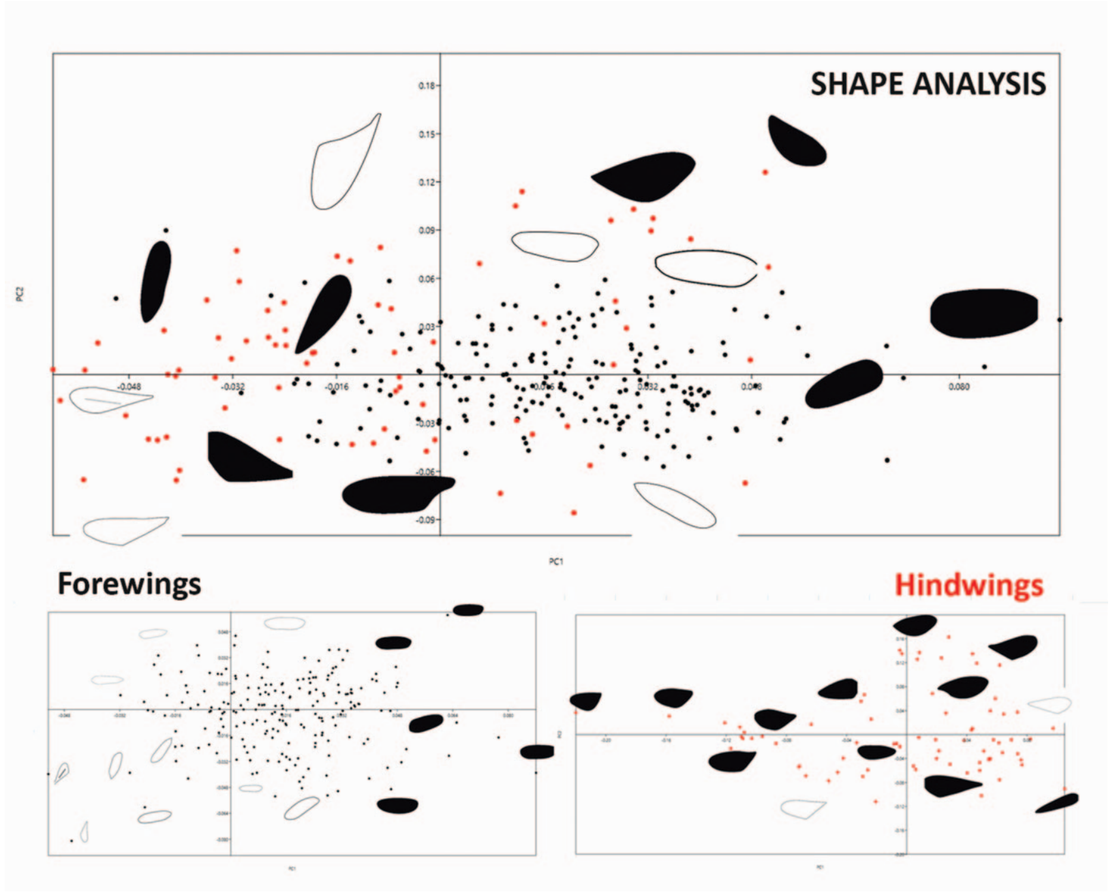
OTHER SYNCOMPRESSIONS

Besides coprolites, little material bears any syncompression due to effective cutting of samples. Examples are PIN 2066/777 (*Makacka akcakam*) preserved along with an unidentified trichopteran (2066/1225). 2066/433 (*Aktassoblatta fusca*) was preserved along with the dermapteran 2066/3583. 2066/389=410 (*Blattula fragilia*) was preserved along with a rostrum of a predatory insect. Because of high content of organics and high number of fossils, suprisingly none syncompression was extracted from the effective photodocumentation.

GENERALISATIONS

Cockroaches constitute 9.7 % of collected insects (Panfilov 1968), which is comparable with Dobbertin (4.3 %), Mintaja (28.3 %), Solnhofen (1.3 %), Kota (31.8 %), Shar-Teg (3.4 %), Bakhar (23.4 %), Daohugou (9.09 %), Shurab (11.5 %) (see Vršanský and Ansorge 2007; Vršanský 2004, 2020; Bechly 2007; Martynov 1937; Martin 2010).





Shape analysis for Combined data, Forewings and Hindwings

SHAPE ANALYSIS

Shape analysis (figp. 616) for performed on cockroach wings for the first time. Dataset which excluded *Maloval hlavolam* – an umenocoleid forewing which resembles a hindwing to a high extent, did not reveal any segregation of forewings, hindwings and/or combined data (separated were two damaged forewings – one of them *Latiblatta osud* - and possibly damaged *Skok,* which are not shown on the charts, and hindwing incorporated into forewing analyses for the check of data reliability – see figps. 616). Other taxa were not separated at all, which is a considerable result, as expected was separation of well-established taxa (at species level). Even data combining forewings and hindwings reveal certain overlap, which means that the cockroach shapes are even less promising paramer not only in phylogenetical studies but also in one-level plain taxonomy. These data will be presented in a more detailed way elsewhere (M. Stroka, in preparation).

Method of Analysis : Covariance; Number of Data : 283; Number of Harmonics : 20; Number of Analyzed Harmonics : 20; Number of Principal Components : 80(= Number of Analyzed Coefficients (NAC)); Number of Effective Principal Components : 5; Analyzed Coefficients : a1 b1 c1 d1 a2 b2 c2 d2 a3 b3 c3 d3 a4 b4 c4 d4 a5 b5 c5 d5 a6 b6 c6 d6 a7 b7 c7 d7 a8 b8 c8 d8 a9 b9 c9 d9 a10 b10 c10 d10 a11 b11 c11 d11 a12 b12 c12 d12 a13 b13 c13 d13 a14 b14 c14 d14 a15 b15 c15 d15 a16 b16 c16 d16 a17 b17 c17 d17 a18 b18 c18 d18 a19 b19 c19 d19 a20 b20 c20 d20

CONVERGENT MODES: FASHIONS

Concept of Fasnions within ecosystems – certain modes which are unique in respective ecosystems is, according to my opinion, one of the most interesting problems of the early biology. These “shared” uniquenesses cannot be easily explained nor with the selection (unless entering Müllerian Mimicry-rings), neither with the Reduction Ring Hypothesis (Vršanský et al. 2019), discussed below.

I am not aware on any reliable explanation to these trends, although a vertical/horizontal transmission by viruses etc. cannot be excluded.

One can test this pattern by providing uniquenesses of Karatau in respect to previous and/or following sites/*Lagerstätten*, eventually to all other biota of past and present.

In Karatau, there is an appearance of ***Maculata*** form (*Asioblatta, Ano, Cameloblatta, Rhipidoblattina*), this nevertheless can barely be tested as this form is a bark form and was only rarely preserved in sediments. Moreover this form is common in other (amber) sites.

Nevertheless, we have outburst of two subforms in the Karatau, which are extremely rare elsewhere. Thus, the subform with a dark longitudinal forewing stripe occurs in 8 genera and species (*Chuanblatta, Olzmasg, Lovec, Decomposita basquatirgis, Falcatussiblatta casovec, Cameloblatta variegate, Hydrokhoo- hydra, Manipulator olim*). The ***Eye*** form occurs in 18 species and at least 9 genera (*Cretaholocompsa,* possibly *Decomposita triocella, Falcatussiblatta disrupta, F. zaloha, Cameloblatta stress, Rhipidoblatta brevivalvata, R. matriky, Liberiblattina ihringovae, L. cunicula, L. kontravenata, L. paleontologica, L. zokamuvypadli, L. neniocom, Ano tak, Ano ona, Akinisia, Maloval, Operam testudina, O. monita*), while it was barely recorded elsewhere (*Vitisma, Cretaholocompsa*).

To my opinion this a good evidence for an ecosystem fashion.

"REDUCTION RING HYPOTHESIS" SPIRAL (ALL IS REDUCING WHETHER POSSIBLE)

Reduction Ring concept (Vršanský et al. 2019) explains adaptive radiations as explosions of diversity related to reduction of morphological (and other) traits, and in cockroaches were proved to be nearly exclusively (87 % and more) responsible for the evolution.

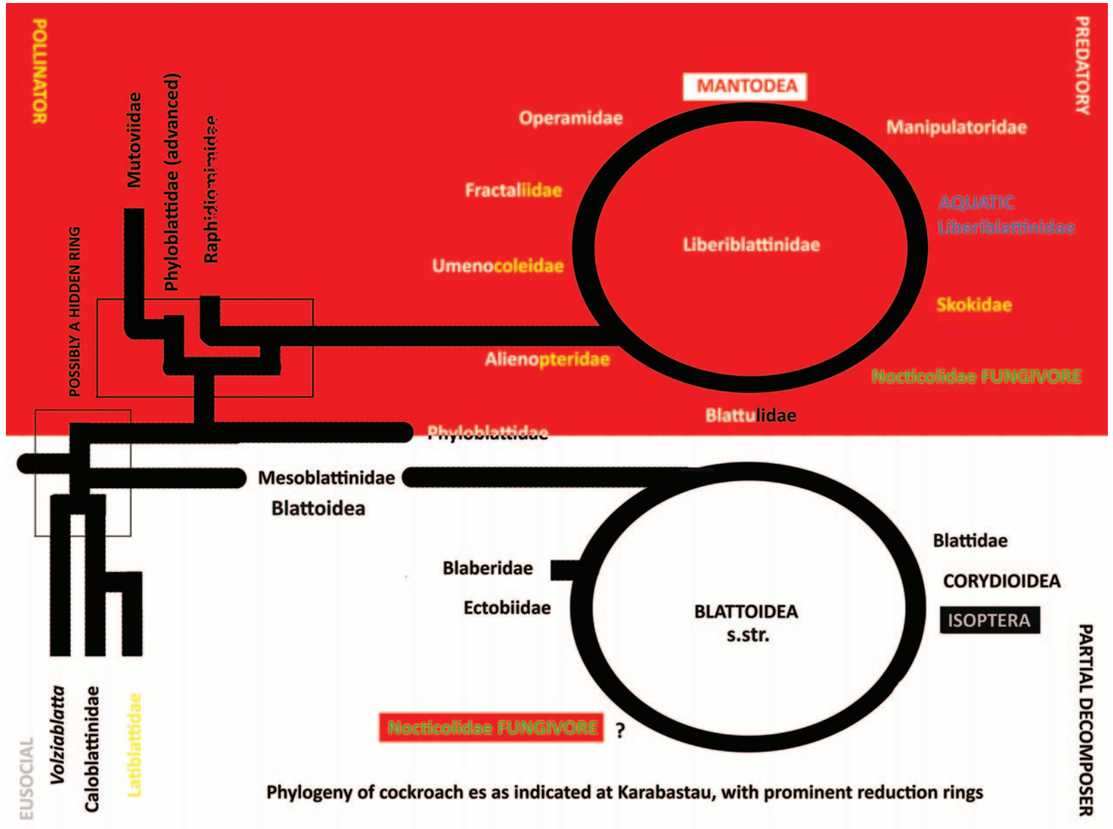
As Reduction ring is retained only in the beggining, after the creative compensation stages, it is mostly distinct at the species level. Again, there is huge bias in observation towards structured ecosystems (with high diversity) and due to this principle the diversity will be rising faster and reduction rings will be more complete (surviving more often) in more complex ecosystems.

Complexity is rising exponentially due to self-organisation resulting from decaying reduction rings. This was postulated also as a reason for higher diversity in tropics (higher insulation enabling higher loses caused by reduction – Vršanský et al. 2021b). Additionally, reduction means also reduction of size possibly enabling more smaller species to coexist. The most comparative material enabled to clearly see the diversification pattern, and for the first time also its complex distributions.

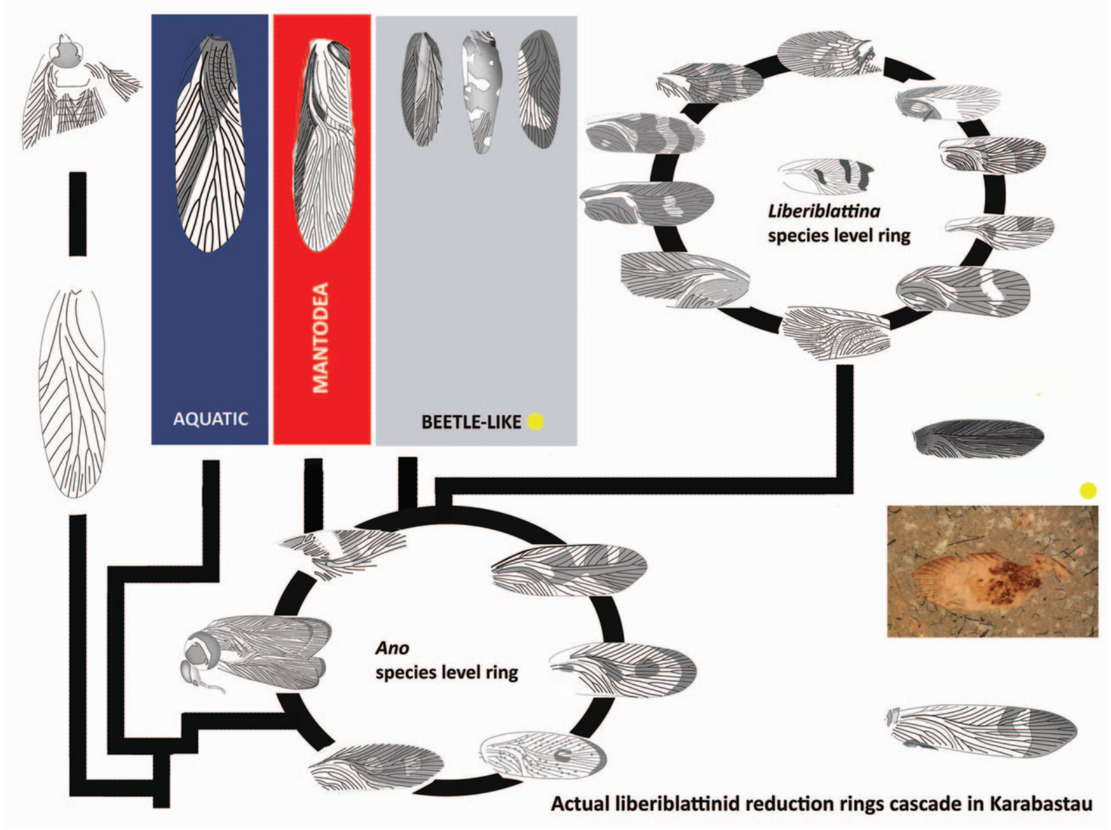
At family level, the pattern is possibly blurred by extinctions, but the prominent reduction ring (figp. 619) is still distinct, operated by a liberiblattinid-derived 10 families (Umenocoleidae, Skokidae, Fractaliidae, Operamidae, Corydiidae, Socialidae, Aquatic Liberiblattinidae, Lovecidae and Manipulatoridae). It must be stressed that only such comparative material enables to see this major ring. To specify, of these 10 ring (family) offshoots, 4 are indigenous (Lovecidae, Skokidae, Operamidae, aquatic liberiblattinids) and 3 represent the only sedimentary record (Fractaliidae, Socialidae, Manipulatoridae) and Umenocoleidae with Corydiidae are the only Jurassic sedimentary records. So it is basically impossible to repeat this pattern on the family level and only Daohugou has a potential proving the pattern (and its Fuziidae support this – see Vršanský et al. 2019d).

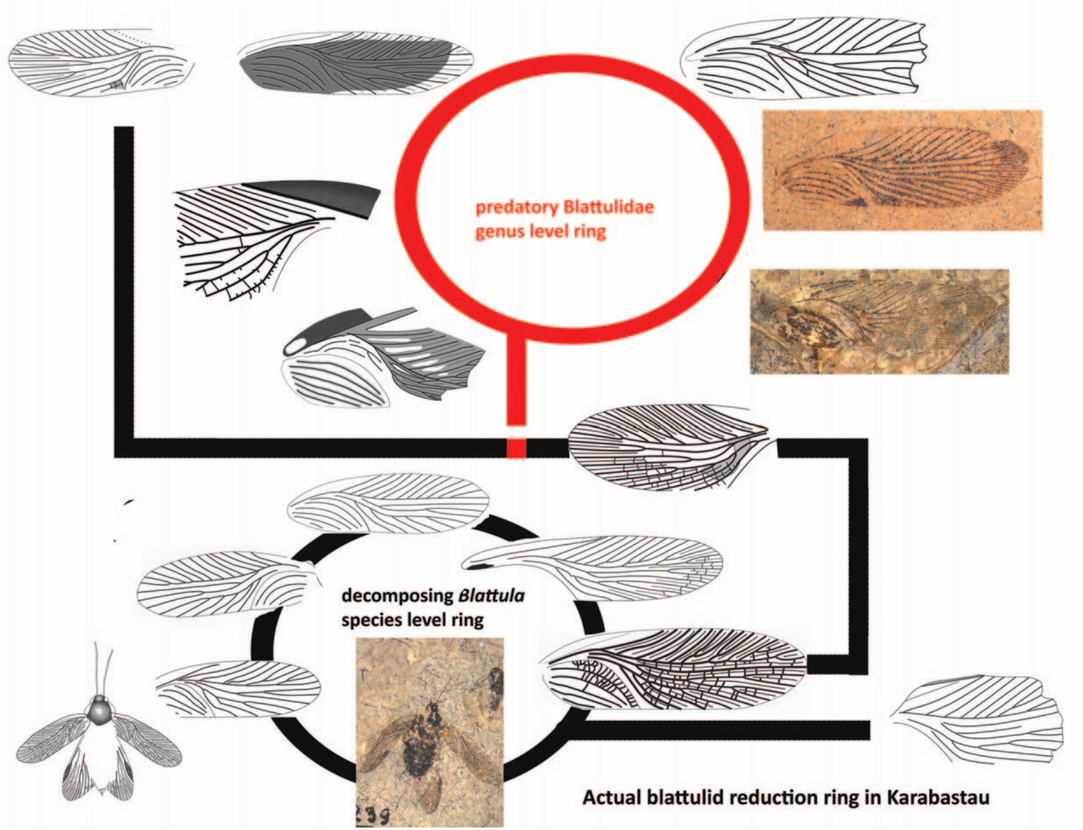
On the genus level, the pattern is still vastly influenced by extinctions and in Karatau it is documented (see figp. 620) by *Hra/Ano/Liberiblattina/Maloval/Akinisia* and *Falcatussiblatta/Decomposita/Rhipidoblatta* complexes. Again, these rings can be documented only on localities with huge number of samples of which considerable number was preserved as complete specimens, and under the condition of high diversity ecosystems. The genus rings can be after some effort observed in Fuziidae and Raphidiomimidae of Daohugou (see Vršanský et al. 2019). Also it can be observed in well-studied burmite nocticolids, umenocoleoids and corydiids (see Sendi et al. 2020ab, 2023; Vršanský et al. 2023).

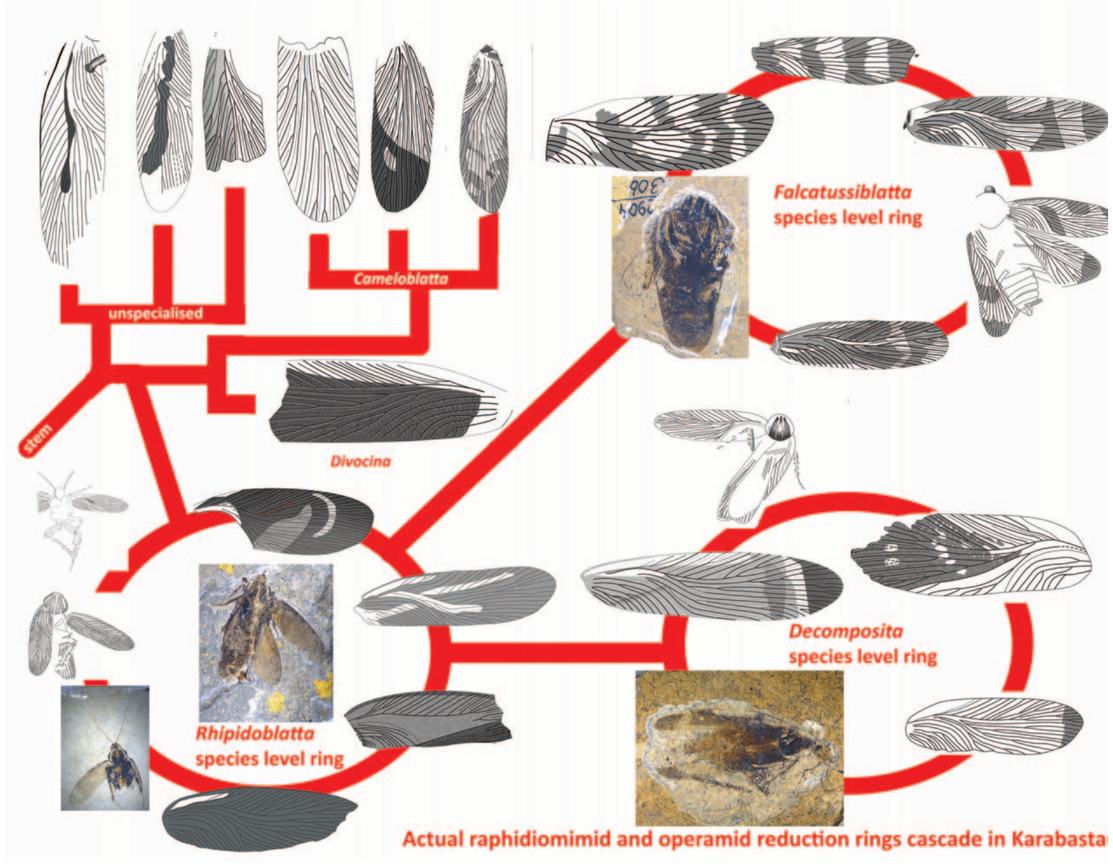
At species level the most diagnostic is Ring of *Liberiblattina* (10 distinct species; figp. 620). Point is that this genus is common (n= 50), nearly indigenous (occurring in coeval Kota; 2 species). The same holds true for the dominant *Decomposita* (5 spp.) (figp. 622). Other prominent ring is formed by a common Jurassic genus *Ano* (6 spp.). There are also "classical" (after this description) ring of genera *Blattula* (9 spp.), *Falcatussiblatta* (6 spp.) and *Rhipidoblatta* (7 spp.), nevertheless, in contrast to previously mentioned rings, it is difficult to conclude, whether these later rings formed in Karatau, or earlier and are only inherited in Karatau. Thus reduction rings are observed in indigenous, cospomopolitan and also in geographically restricted palaeospecies. Similar species rings are extremely common in living cockroaches, many of which have hundreds of species,

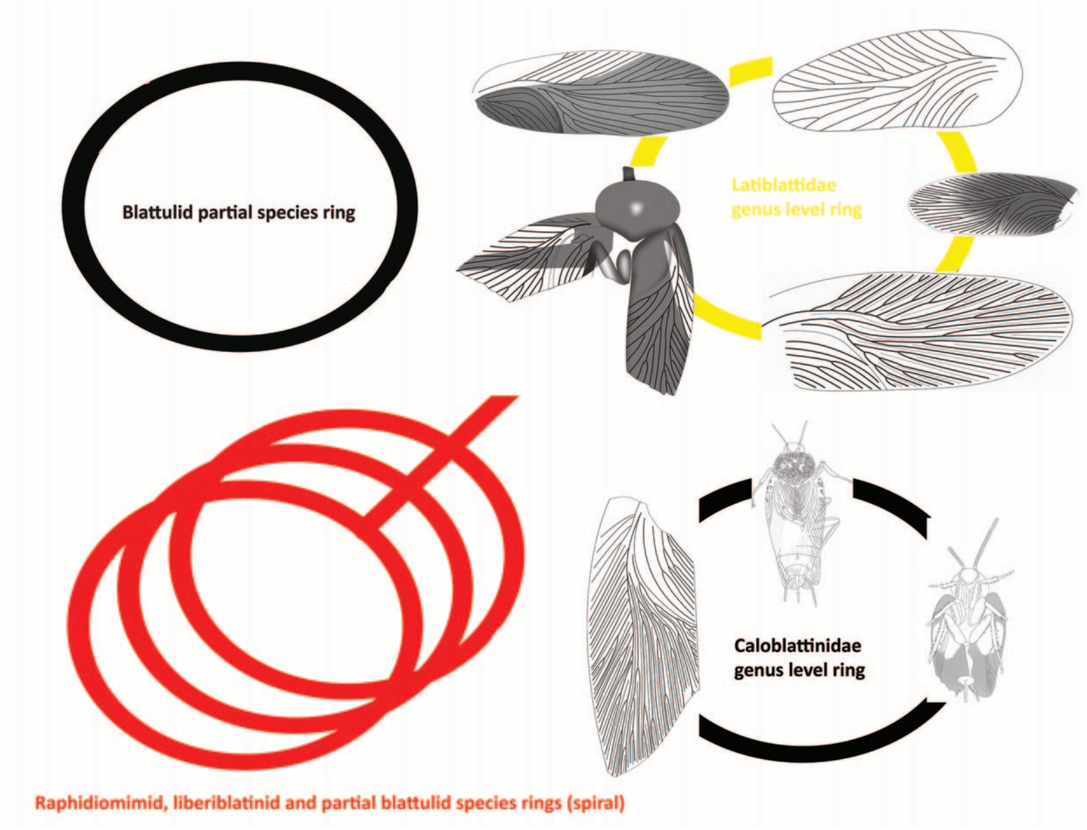


Phylogeny of cockroach es as indicated at Karabastau, with prominent reduction rings


AQUATIC
MANTODEA
BEETLE-LIKE
Liberiblattina
species level ring
Ano
species level ring
Actual liberiblattinid reduction rings cascade in Karabastau


predatory Blattulidae
genus level ring
decomposing *Blattula*
species level ring
Actual blattulid reduction ring in Karabastau


Falcatussiblatta
species level ring
Cameloblatta
unspecialised
stem
Divocina
Decomposita
species level ring
Rhipidoblatta
species level ring
Actual raphidiomimid and operamid reduction rings cascade in Karabasta


Blattulid partial species ring
Latiblattidae
genus level ring
Caloblattinidae
genus level ring
Raphidiomimid, liberiblatinid and partial blattulid species rings (spiral)

and frequently dozens species in one site. Among fossil material such species rings were well identified in burmite within diverse genera (*Stavba, Magniocula, Teiya, Alienopterix, Perspicuus, Vzrkadlenie*). Unfortunately, other *Lagerstatten* are either too primitive, with too fragmentary preservation (as Baissa or Bakhar) or insufficiently evaluated to reveal such data. Perspecive candidates are only Daohugou and Yixian with completely preserved specimens.

According to this concept, one of the most interesting evolutionary theories – of homological rows (Vavilov 1935), must be also reconsidered in this light.

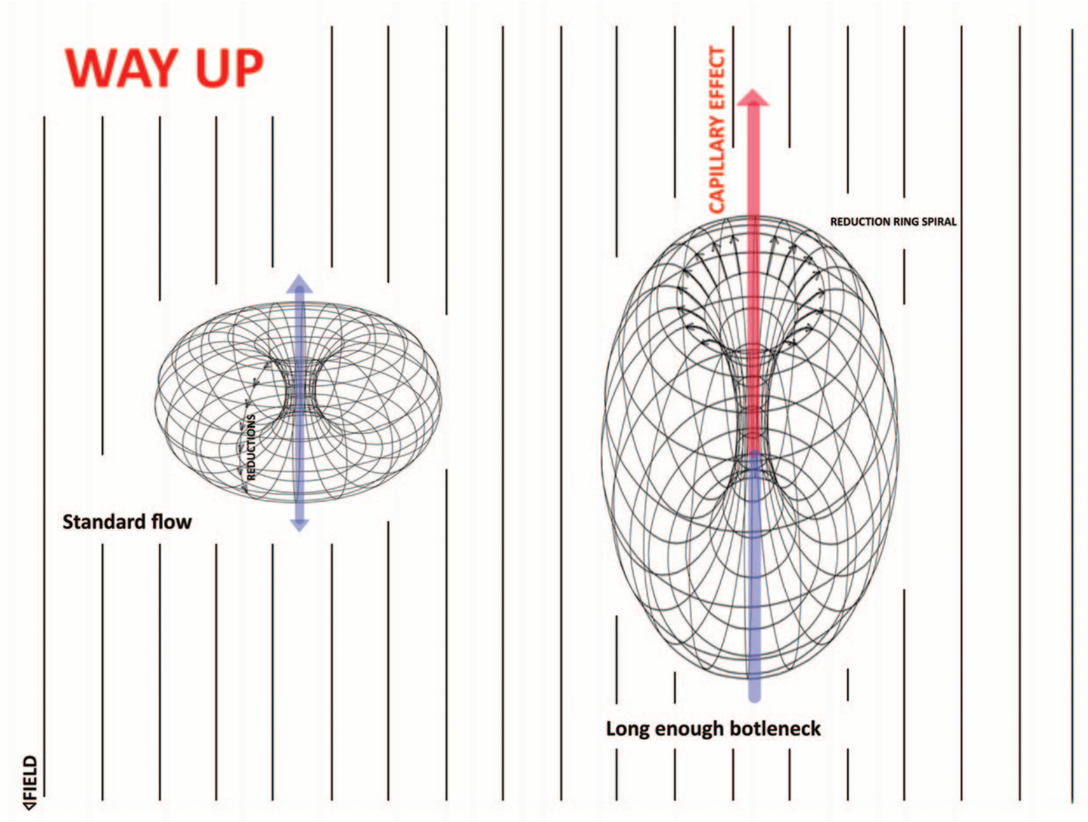
WAY UP

Thus, the wast majority of evolution is explained by reductions. To quantify this majority we can disregard Caloblattinidae as they did not provide any offshoot besides Fuziidae, which are absend in Karabastau. From all Raphidiomimidae, the Reduction ring explains all but the first raphidiomimid – presumably the first predator. I will also excude this group from the count as it is unclear whether ancient predecessor within "Phyloblattidae" also was not a predator. I will also exclude the first predatory blattulid as they occurred also in predecessing Daohugou. Thus in Karabastatu all was explained but first umenocoleid/fractalid/operamid (or its common ancestor), *Skok, Sociala*, *Manipulator* and a common ancestor of Latiblattidae – thus 5 taxa. This count can be distorted on one side with earliest ocurrences to be found in Daohugou, and "minor rings" represented by *Ano* and *Liberiblattina*. Thus the ratio of taxa unexplained by the Theory of Reduction rings is about 5.3-7.4 %. Again it must be explicitely declared that this is the richest and most critical site in history and the real value can be only (significantly) lower. It cannot be excluded that for the whole history, taxa subjected to the Capillary compensation were 20 or less numerous.

It has also been shown previously (Sendi et al. 2020) that other unexplained proportion, under 13 % is represented by true, but very rare simple dichotoimies.

To provide the general picture, basically there are only very unnumerous principal taxa, which are unexplained by the theory. It is the first cockroach ever (presumed to incorporate N-fixing endosymbionts), *Stavba* (as source for termites, nocticolids and true mantodeans), first eusocial true termite, first eusocial cockroach in another lineage-*Melyroidea*, first umenocoleid/fractalid/operamid (possibly *Vitisma* or its closest relative from Kota, India), the first fuziid, first blattoid (with true modern ootheca), first latiblattid, skokid, diplopterid (viviparous) and attaphilid (ectoparasitic). This is a tiny insignificant fraction of the total diversity – nevertheless, the most significant fraction at all.

Here I provide update of the Theory of Reduction rings, which explains only (totally dominant) radiations in reduction processes. Here I am establishing the CAE- concept, a hypothesis attempting to explain the three major processes of evodution: **(1) C** "constructive capillary compensation" (organising-to-complexity) – **(2) A** "adaptive" stabilisation — **(3) E** "explosive reduction". The explosive reductions are covered by the theory and adaptive stabil-



isation is greatly elaborated by former evolution students. Here I erect the least numerous, but most important part of the evolution, the innovations, the creative or better said constructive part of evolution.

I already declared this passively creative part is greatly due to compensations, which means that taxa forced by any reduction need to seek less complex, and more specialised (thus more effective) "way-out". Thus they are disqualified from the complex fate and role in ecosystem, but still can be usefull and will get chance to survive as strick specialists. This might be slightly discomfortable to imagine due counterintuitive progrees on this way, but just imagine research – study of the whole Karatau insect fauna will lead nowhere as this is impossible dring a single lifespan. Thus I, disqualified from the general knowledge, fully focused on less complex, but very specialised cockroaches, brought some general knowledge and this compensation paid well.

Structure of the compensation is simple, but it is extremely difficult to imagine and I consider this for my major discovery/understanding of any (including the quantum) principle. Math beyond this logic is coevally 2D and 3D, which is rather hard for intuition – a concept used for understanding black hope surfaces. Also, to greatly simplify, it is the same structure as an advanced quibit (toroid) changing its diameter and aperture – with aperture approaching the lower limit, the balance (in the directed field) is being shifted against the field. This is approaching intuition and also I select its name according to this principlne in the macroscopic workd – a capillary effect (responsible for tunnelling other levels).

Suprisingly it is not entirely impossible to quantify this effect on the evolutionary scale. Good case (for a phase transition) is a transition towards eusociality. While it is impossible to validate the lowest limit for this phase transition, we have an empiric evidence of eusocial insects reduced in population size. And this limit is 18-25 individuals (see Vršanský 2010). It can happen, that level up towards eusociality is possible only in slightly higher, but surely not lower level. The highest samples size in this "capillary" is unkown, but intuitively it would not be much higher. This also explains why there are numerous abundant and highly gregarious species without eusocial structure. That one is either formed at the very beginning or not at all. This might be added to the hypothesis of level-up on the basis of compartmentisation (Toman and Flegr 2020), postulating "no-other-escape" in the hierarchical rise. In the capillary case, when possibilities are few, this might statistically work (but not later). Thus we can imagine gene pool as donut (toroid) with reducing radiations contributing back to the main pool. This is a balanced state: stasis. When the capillary effect is formed, whole bulk can move against the direction of the elimination and local entropy. The direction is firm as in capillary-effect, the field repolarisation (polarisation swhitches) are impossible.

The reason is the topology of the doonut where predominantly interacting are "particles" within the neighboring parts of the toroid body. In the capillary effect caused by the narrow bottleneck, additional interaction responsible for "tunnelling" is added – interaction of the adjacent parts of the "hole", of the inner circuit. As, for example in the eusociality transition, this lowest limit is anyway extremly high (18 (human) – 25 (blesmols)), it can be expected that the upper limit is also close to 30-40 (eusocial insects lower limit). It also must be remembered that this is only an inner circuit diameter and that the bottleneck must be high enough – and thus the limit of circuit interactions must be stable-in-time till a phase transition occurred.

So the basical topology of the toroid is present from an advanced quibit model, through a spiral magnetic field of a black hole through the gene-flow model. Principle behind this topology is that during the formation of capillary effect, polarity switches are impossible.

ECOSYSTEM REVOLUTION

The Middle Cretaceous Biocenotical Crisis (sensu Zherikhin 1978) also threated as Cretaceous Terrestrial Revolution (Lloyd et al. 2008) was the major change of ecosystems towards the insect-pollinated angiosperms. Since their definitions, vast new data came across the research in various fields contesting trigger of this vast change in the Cretaceous. Cockroaches as pollinators (Sendi et al. 2020b) are also represented with *Fractalia* and *Maloval,* ocurring also in Karatau. To my personal opinion, it cannot be definitely excluded that *Maloval* already represents a pollinator of angiosperms as some advanced umenocoleoids (see Hinkelman 2020). Nevertheless, most of the umenocoleids represented gymnosperm-pollinators with the proved evidence for cheirolepidiaceans (Labandera et al. 2007). From this standpoint, there is not firm evidence for the earliest binds with angiosperms, although it cannot be definitely excluded. *Maloval* is a conspicuously colored umenocoleid, so if it pollinated cheirolepidiaceans, it might be presumed at least a specialized gymnosperm "flower".
Predatory revolution is expected much earlier, as this cohort was entirely specialized in more ancient Daohugou.
The same is expected for Parasite revolution, although this evidence is entirely missing; nevertheless, evidence might be possible due to discovery of Jurassic amber in Lebanon (Vršanský et al. 2019b, 2024).
Besides these aspects, the ecosystem revolution also comprised herbivory (of angiosperm leaves). Left without evidence. Nertheless, its second face, the wood decomposition seems already present in Karatau (*Sociala*). According to the rising evidence for Jurassic angiosperms (Li et al. 2019), we might conclude that the revolution seeds could appear in Kimmeridgian or even earlier.

GCNRPS

The GCNRPs concept is introduced here as **Global Contemporary Nature Reference Points.** These are designated here on the basis of collections comparable in amount of samples (it is impossible to access the similar *structure* of collections) to some of the contemporary sites. Basically this term is necessary to designate North Myanmar for the first of such sites as several tons of transparent amber makes virtual trespassing the world of dinosaurs possible. The same amount was collected for centuries in the Baltic, although of less difference from the living fauna. I also included the Lebanese amber, as, in spite of having significantly reduced number of specimens, still bears a remarkable information from the older, Early Cretaceous time periods. After some doubts, I decide to include the sedimentary *Lagerstätten* as well, as the amber material allows principial comparison and synthesis. Cenozoic Messel with preservation of colors is substituted with Lower Cretaceous Yixian and Baissa sediments and Middle-Late Jurassic Daohugou and Karabastau treated here. Thus the consequence is following: Messel Gruße (GCNRP1), Baltic amber (GCNRP2), North Myanmar amber (GCNRP3), Lebanon amber (GCNRP4), Crato (GCNRP5), Yixian (GCNRP6) and Baissa (GCNRP7) sediments, Karabastau (GCNRP8), Daohugou (GCNRP9) with occurrences of rather completely preserved ecosystems. Earlier *Lagerstätten* does not reveal data sufficient enough either in amount of collected terrestrial biota or in their preservation state (such as Green River or Carboniferous-Permian sites). Reference points serve to compare the state, structure and ecological factors of ancient ecosystems with those of the present.

GCNRP8= KARATAU

As claimed above, Karatau is characterised as the first ecosystem complex enough to be directly compared with the living rainforests. This is extremely surprising as the biome is composed mainly of gymnosperm plants and such ecosystem is unknown in the living biota due to presence of more advanced angiosperms – and limited extent of gymnosperms in rich (sub)tropical ecosystems;. Nevertheless, we directly observe a comparable diversity and disparity of forms in several cohorts. This situation is not unique, albeit the more interesting as in burmite (where the disparity is higher than in modern rainforests in many aspects), a small fraction of biota is addicted to early angiosperms and, moreover, many groups represent pollinators of gymnosperms (the cohort now extinct). In Karatau, these cohorts did not evolve yet, so the high diversity ands disparity of forms is more than surprising. Only *Maloval* and *Fractalia* potentially (no evidence exist) might contributed to the gymnosperm pollination and *Sociala* might be responsible for pollination of unknown plant groups. The rest evidence is for the complexly structure food chain of predators, which contribute to the most of the diversity and abundance of cockroaches (and a mantid). Thus, we directly evidence a fully structured (when compared with living rainforests) decomposition chain, suggesting also the same structure of primary producers, less influenced with the herbivores (see Zherikhin 1978). Also, in Karatau we directly evidence numerous parasitic and parasitoid groups, making the dynamics of the food chain with more than 2 directions and thus chaotic. Symbiosis is also (indirectly) evidenced by cockroaches as the provision of nuptial Nitrogen gifts is only possible to symbiotic Nitrogen-fixing endosymbiotic protists and bacterians. Thus, to conclude, we evidence here at Karatau fully structured ecosystem lacking only advanced angiosperms (grasses) and their pollinators as the only difference with the modern biota. After the consequent post-Karatau decline near J/K boundary, the ecosystems fully recovered again in Upper Cretaceous as evidenced in burmite. Judging from the full fungal spectrum, including entomopathiogenic fungi in burmite (Luo et al. 2023), but also in Early Cretaceous lebanite (Sendi et al. 2023), also the fungal stratum interconnecting trees and forest in one unison unite, was also already formed in Karatau.

DATA

Tab. Major Jurassic and Cretaceous assemblage analysis

	Bak	Kar	Mei	Zho	Hua	Xia	Dao	Dob	Min	Shu	Sha	Che	Po-lar	Bais-sa	Bon T	Mont-sec	Yix-ian	NM	Leba-nese	Cra-to	NJ	Sinuiu	Fukui	Sharin-Gol	Koty	Arch
Ano	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Blattula	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	1	0	0	0	0	1	0
Caloblattina	1	1	1	1	1	0	1	1	1	1	0	1	1	1	1	0	1	0	0	0	0	0	0	0	1	0
Dostavba	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hra	1	1	1	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0
Nuurcala	1	1	1	0	0	0	1	0	0	0	0	0	0	1	1	0	1	0	0	0	0	1	0	0	0	0
Okras	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Perlucipecta	1	1	1	1	0	0	1	0	0	1	0	0	1	1	0	0	1	1	1	1	0	1	0	0	1	0
Polliciblattula	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Praeblattella	1	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	1	1	0	1	1	0	1	0	1	0
Raphidiomima	1	1	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Rhipidoblattina	1	1	1	1	1	1	1	1	1	1	0	1	1	1	0	1	1	0	1	0	0	0	0	0	1	0
Solemnia	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Truhla	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Chresmoda	1	1	0	0	0	0	1	0	0	0	0	0	0	1	1	1	1	1	1	1	0	0	0	0	0	0
Elisamoides	1	1	0	0	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Euryblattula	0	1	0	0	0	1	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Rhipidoblatta	0	1	1	0	1	0	1	1	1	0	0	1	1	1	0	0	1	0	0	0	0	0	0	0	0	0
Mongolblatta	0	1	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	0	0	0	1	0
Taublatta	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Samaroblattula	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mesoblattula	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mesoblattina	0	1	0	1	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Sogdoblatta	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

	Bak	Kar	Mei	Zho	Hua	Xia	Dao	Dob	Min	Shu	Sha	Che	Po-lar	Bais-sa	Bon T	Mont-sec	Yix-ian	NM	Leba-nese	Cra-to	NJ	Sinuiu	Fukui	Sharin-Gol	Koty	Arch
Breviblattina	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Kurablattina	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Divocina	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Entropia	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Fuzia	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Parvifuzia	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Colorifuzia	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Fortiblatta	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Artitocoblatta	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Asioblatta	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Decomposita	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Karatavoblatta	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Latiblatta	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Paleovia	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rhipidoblattin-opsis	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Skok	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Falcatusiblatta	0	1	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Batola	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1	1	0	0	0	1	0	0
Facioblatta	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Svabula	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0	0
Aurora	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Aposema	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Stictolampra	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Petropterix	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0	0	0	1	0	0	0
Vitisma	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	1	1	0	0
Elisama	0	1	0	0	0	0	1	0	0	0	1	0	0	1	1	1	1	1	1	1	0	1	0	1	0	0
Shartegoblat-tina	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	0	0	0	0	0	1	0	0
Cretophotina	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	1	0	0	0	1	0	0

	Bak	Kar	Mei	Zho	Hua	Xia	Dao	Dob	Min	Shu	Sha	Che	Po-lar	Bais-sa	Bon T	Mont-sec	Yix-ian	NM	Leba-nese	Cra-to	NJ	Sinuiu	Fukui	Sharin-Gol	Koty	Arch
Piniblattella	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	1	0	1	0	0
Aktassoblatta	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Cameloblatta	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Spinaeblattina	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1	0	0	0	0
Jantaropterix	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0	0	0
Archimesob-latta	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	1	1	0	0	0	0	0	0	0	1	0
Brachymesob-latta	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0
Tarakanula	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Elytropterix	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
TERMITES	0	1	0	0	0	0	0	0	0	0	0	1	0	1	1	1	1	1	1	1	1	0	0	1	0	0
Ponopterix	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Cratovitisma	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1	1	0	0	0	0	0	0
Raptoblatta	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Gurvanoblatta	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Baissomantis	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Balatronis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0
Neoblattella	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Liberimala	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Habroblattula	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0
Apiblatta	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Vcelesvab	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Morphna	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0
Mesoblatta	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Bubosa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Ol	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Manipulator	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0
Cretaperipla-neta	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0

	Bak	Kar	Mei	Zho	Hua	Xia	Dao	Dob	Min	Shu	Sha	Che	Po-lar	Bais-sa	Bon T	Mont-sec	Yix-ian	NM	Leba-nese	Cra-to	NJ	Sinuiu	Fukui	Sharin-Gol	Koty	Arch
Alienopterus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Alienopterix	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Meilia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Teyia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Formicamendax	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Caputoraptor	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Alienopterella	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Spongistoma	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Vzrkadlenie	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Anthophillob-latta	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Aethiocarenus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Cercoula	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Mulleriblattina	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Crenocticola	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Eminespina	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Enervipraeala	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Laticephalana	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Nodosigalea	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Perspicuus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Stavba	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Burmantis	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1	1	1	0	0	0	0	0
Magniocula	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Lepidopterix	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Sericoblatta	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Macaroblattula	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0
Cretaholocom-psa	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
MANTODEA	0	1	0	0	0	0	0	0	0	1	0	1	1	1	1	1	0	1	1	1	1	1	1	1	0	0

	Bak	Kar	Mei	Zho	Hua	Xia	Dao	Dob	Min	Shu	Sha	Che	Po-lar	Bais-sa	Bon T	Mont-sec	Yix-ian	NM	Leba-nese	Cra-to	NJ	Sinuiu	Fukui	Sharin-Gol	Koty	Arch
Pravdupovediac	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Cryptoblatta	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Miniblattina	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0
Pseudomantina	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0
Nigropterix	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Trapezionotum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Sivis	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	1
Okruhliak	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Asvab	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Operam	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Liberiblattina	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Fractalia	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Akinisia	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Okienkula	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Spono	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Makacka	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Memento	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Makacka	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hydrokhoohydra	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Katatychi	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Kazachiblattina	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Influencer	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Gen.n.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Leptolythica	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Globula	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Batola	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Eadia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1

AD HOC PHYLOGENETICALLY ANNOTATED CHARACTER LIST FOR 89 NUMBERED FOREWING CHARACTERS (AFTER VRŠANSKÝ 2020), LETTERED FOREWING CHARACTERS (AFTER SENDI ET AL. 2022) AND NEW CHARACTER STATES (LETTERS BEFORE NUMBERS). NEW HINDWING CHARACTERS ARE ALSO PRESENT (H1-20).

Forewing characters:

1. Margins parallel—synapomorphy of advanced cockroaches
2. Wing base extended proximally—synapomorphy of *H. bavi* and homoplasically others

2B. Wing base quadrate—autapomorphy of *Compunctiotypus*

3. Shape significantly elongate—autapomorphy of advanced Raphidiomimidae, homoplasy of *Pseudomantina*

3B. Wing shape simplified—autapomorphy of *Lepidopterix*, homoplasy in *Miniblattina* (due to miniaturisation)

4. Shape not wide—synapomorphy of advanced Mesozoic cockroaches, this plesiomorphy at the level of order was retained in certain Caloblattinidae and others
5. Shape widened apically—synapomorphy of certain Blattulidae, homoplasic in modern cockroaches

5B. Shape widened in clavus—autapomorphy of *Ocelloblattula*

5C. Shape widened medially—autapomorphy of *Pseudojantaropterix*

A5. Shape with depressed anterior margin-convergent in independent groups

B5. Shape round-autapomorphy of *Vedec*

6. Apex posed centrally—synapomorphy of Corydioidea including Blattulidae; with homoplasies
7. Apex very sharp—this otherwise rare character is homoplasically widespread in present ambers
8. Apex round—synapomorphy of certain Blattulidae and Liberiblattinidae

8B. Apex posed posteriorly—autapomorphy of *Pravdupovediac*; homoplasic in *Neoblattella nechapetomu*

9. Size very small—autapomorphy of some Blattulidae; homoplasic in *Miniblattina* and *Lepidopterix*

9B. Venation not traceable—synapomorphy in elytrised forewings

9C. Forewing sclerotised—autapomorphy of Umenocoleidae; homoplasic in numerous living lineages

9D. Forewing with bunky—autapomorphy of Umenocoleidae; homoplasic in numerous living lineages

A9. Forewing significantly longer than body-autapomorphy of *Sociala,* homoplasic in advanced mantodeans and also predatory Raphidiomimidae

10. Venation regular at margin—synapomorphy of Phyloblattoidea and derived groups
11. Venation regular also in R-M area—synapomorphy of Corydioidea and modern groups
12. Venation regular in clavus—synapomorphy of advanced cockroaches including Corydioidea (also Blattulidae)
13. Venation extremely reduced—synapomorphy with *Polliciblattula*, homoplasic with *Miniblattina* and *Lepidopterix*
14. Venation moderately rich—synapomorphy of advanced Mesozoic cockroaches; plesiomorphically venation was very rich at the level of order
15. Main veins coloured white—autapomorphy
16. Main veins thick—synapomorphy of certain Liberiblattinidae
17. Intercalaries indistinct—synapomorphy of advanced Mesoblattinidae
18. Intercalaries thick—synapomorphy of certain Liberiblattinidae
19. Intercalaries coloured more pale compared to main veins—synapomorphy of certain Liberiblattinidae and Blattulidae

19B. Intercalaries overgrown with melanic coloration—autapomorphy of *Pravdupovediac*

20. Intercalaries absent in clavus—synapomorphy of advanced Mesozoic cockroaches, this plesiomorphy at the level of order retained in Caloblattinoidea and some other primitive groups
A20. Intercalaries interrupted-autapomorphy of *Manipulator*
21. Cross-veins absent—synapomorphy (symplesiomorphically present at the level of Neorthroblattinidae and derived groups)
22. Membrane coloured—homoplasic character along the taxonomic spectrum
A22. Wings not opening during flight-autapomorphy of certain *Latiblatta*
23. Coloration patterned (most simply as lines or stripes)—synapomorphy of certain Caloblattinidae
A23. Coloration patterned (most simply as lines or stripes, but combined at least with 2 different types)—synapomorphy of certain Caloblattinidae
B23. Coloration with pale stripes within dark membrane
C23. Coloration dark, with pale radial area
24. Coloration maculate or simply dotted—homoplasies of *Okras* and *Raphidiomima* and others
25. Coloration sophisticated (dots formed of stripes)—synapomorphy of certain advanced Liberiblattinidae
26. Coloration sporadical—autapomorphy; homoplasic in numerous lineages
26B. Coloration monochromatic dark—in the present localities restricted to beetle-like cockroaches (in Karatau also others)
A26. Coloration aposematic, with big dot-autapomortphy of *Aposema*
B26. Apex colored only-autapomorphy
C26. Coloration in zig-zag pattern—autapomorphy of Operamidae and homoplasically in rare species along tasxonomic spectrum
D26. Coloration forming *Eye*-autapomorphy
E26. Coloration forming reversed pale *Eye*—autapomorphy of *Cratoholocompsa* and some *Ano*
F26. Membrane colored around main veins-autapomorphy of *Asvab*
27. Costal area narrow—synapomorphy of advanced Liberiblattinidae
27B. Coloration following margin of clavus—autapomorphy of *Neoblattella nechapetomu*
28. Costal area shortened—synapomorphy of some Blattulidae
29. Costal area elongate—synapomorphy of Liberiblattinidae
29B. Costa overlapping apex—autapomorphy of *Pravdupovediac*
A29. Costa all over the wing—autapomorphy of *Spono*
B29. Costal area with pale fenestrum—autapomorphy of *Sivis*, homoplasically in others
30. SC simple—synapomorphy of some Blattulidae, SC is plesiomorphically branched at the level of order
31. SC sigmoidal—synapomorphy of certain Corydioidea
32. SC branched basally but not apically—synapomorphy of advanced Mesozoic cockroaches, original state of terminal branches retained in some Caloblattinoidea but also in primitive Corydioidea
A32. SC long, straigth and richly branched-synapomorphy with mantodeans
33. R sigmoidally curved—synapomorphy of Corydioidea
34. R narrow—apomorphy; R is plesiomorphically wide at the level of order
35. R veins simple—synapomorphy of advanced Mesozoic cockroaches; R is plesiomorphically tertiary (or at least secondarily) branched
35B. RS differentiated as a simple vein—residuum of the plesiomorphically well-developed RS
36. RS not differentiated—apomorphy, R is plesiomorphically differentiated at the level of order
37. Basalmost R not branched extensively—synapomorphy of advanced Mesozoic cockroaches, this plesiomorphy at the level of order retained in *Praeblattella*
38. R not reaching apex—synapomorphy of Liberiblattinidae
39. M sharply descending from R stem—synapomorphy of *Elisamoides* and some advanced Liberiblattinidae
40. M and CuA not sigmoidal—synapomorphy of Corydioidea
41. M and CuA posteriorly curved apically—autapomorphy of Raphidiomimidae
A41. CuA reduced-autapomorphy, CuA expanded is plesiomorphy of cockroaches
42. Posteriormost CuA sigmoidal—synapomorphy of certain Caloblattinidae and Raphidiomimidae; homoplasic in *Ocelloblattula*
43. Clavus small—autapomorphy of advanced Raphidiomimidae; homoplasically present in some Blattulidae and Caloblattinidae, and in *Pseudojantaropterix*
43B. Clavus reduced—autapomorphy of *Compunctiotypus*
44. Clavus without diagonal kink—synapomorphy of modern cockroaches (certain Phyloblattidae and derived groups retained this trait in plesiomorphic state)
45. Clavus with dense cross-veins—synapomorphy of certain Corydioidea and homoplasic in Raphidiomimidae
46. Clavus sharply curved—synapomorphy of certain Corydioidea
47. Clavus extremely narrow—autapomorphy of Raphidiomimidae; homoplasic with *Ocelloblattula*
48. Clavus anteriorly shortly cut—synapomorphy of certain Corydioidea (including Blattulidae) and advanced living-type cockroaches (extremely expressed in Ectobiidae)
48B. Clavus with fenestrate structure and coloration—autapomorphy of predatory Blattulidae with homoplasies
49. Pseudovein present—synapomorphy of certain Liberiblattinidae and Mantodeans
50. A simple—synapomorphy of most of Blattulidae and homoplasically in modern groups
51. A number reduced—synapomorphy of Blattulidae; ocessionally homoplasic in miniaturised groups
52. A veins coloured—autapomorphy of *R. krajka*; homoplasic in *Neoblattella nechapetomu*
53. A not sharply posteriorly curved—synapomorphy of advanced cockroaches; Caloblattinidae and Raphidiomimidae retained the original state
A53. A1 without proximal branches—synapomorphy of modern cockroaches
A54. A not secondarily branched—synapomorphy of modern cockroaches (plesiomorphy at the level of order is branched)
54. Distance between CuP and A1 insignificant—synapomorphy of advanced Mesozoic cockroaches, this plesiomorphy at the level of Phyloblattidae was retained in Caloblattinoidea.

Hindwing characters:

H1 Vannus not folding weer-like-synapomorphy of modern Corydioidea and Blattulidae
H2 R1 differentiated into a set of veins-synapomorphy of Blattoidea
H3 R1 greatly simplified-autapomorphy of *Chuanblatta*
H4 Pterostigma present-homoplasic across taxonomic spectrum
H5 Venation reduced-synapomorphy of modern corydioid cockroaches
H6 M simplified-synapomorphy of Blattoidea, homoplasically in Corydioidea
H7 M simple-autapomorphy of Ectobiidae
H8 CuA not secondarily branched—autapomorphy of Blattulidae
H9 CuA without blind branches-synapomorphy of modern cockroaches
H10 A1 present curved in remigium-synapomorphy of Corydoidea except basal Liberiblattinidae
H11 Apex colored-autapomorphy, homoplasic across the taxonomic spectrum
H12 Coloration sophisticated with stripes of diverse colors-autapomorphy, homoplasic across the taxonomic spectrum
H13 Dot
H14 Membrane monochromatically colored-synapomorphy
H15 Apex sharp
H16 Hindwing very long-autapomorphy of *Sociala*
H17 R strong-synapomorphy of Blattulidae
H18 CuA strong-synapomorphy of Umenocoleidae and *Fractalia*
H19 Intercalaries indistinct-autapomorphy
H20 Cross-veins indistinct-autapomorphy

Rest body characters:

B1. Head exteremely large: synapomorphy of mantodeans, termites, fractalids and umenocoleoids
B2 Head globular: synapomorphy of Corydioidea
B3 Head elongate: (in some cases possibly prognathous, but in Falcatussiblatta in hypognathous condition – see *Ensiferoblatta* (REF)
B4 Palps very short: synapomoprhy of Blattulidae, with homoplasies
B5 Central ocellus absent: synapomorphy of advanced cockroaches
B6 Antenna with not wide and short segments: synapomorphy (pleasiomorphic state was retained only in Caloblattinidae)
B7 Pronotum elongate: synapomorphy of advanced Raphidiomimidae, homoplasic in *Manipulator* and *Lovec*
B8 Pronotum cordiform: synapomorphy of advanced Caloblattinidae, homoplasic in *some* Liberiblattinidae
B9 Paranotalia absent: synapomorphy of derived cockroaches such as *Maloval*
B10 Body narrow: synapomorphy along taxonomic spectrum
B11 Ovipositor short or internalised: synapomorphy of advanced Liberiblattinidae, Blattulidea and modern cockroaches (ovipositor is plesiomorphically very long in Caloblattinidae, some Raphidiomimidae and some early-derived Liberiblattinidae)
B12 Ovipositor invisible: synapomorphy of modern cockroaches
B13 Ovipositor tubular: autapomorphy of Latiblattidae, homoplasic in some Liberiblattinidae
B14 Cerci oligomerised: synapomorphy of advanced cockroaches (pleasiomorphis state of multisegmented 15-20 cercomeres was retained in Caloblattinidea and Raphidiomimidae)
B15 Cerci very short: autapomorphy of Operamidae, homoplasic in termites
B16 Fore legs raptorial with retained cursorial function: synapomorphy with mantodeans, homplastically present in families Phyloblattidae, Caloblattinidae, Eadiidae, Blattellidae, Rahidiomimidae
B17 Fore tibia long: synapomoprhy of Raphidiomimidae, homoplasic in *Manipulator*
B18 Extremities burrowing: synapomorphy of some Liberiblattinidae, homoplasic in living lineages
B19 Golden beetle-like
B20 Jumping

	1	2	2B	3	3B	4	5	5B	5C	A5	B5	6	7	8	8B	9	9B	9C	9D	A9	10	11	12	13	14	15	16	17	18	19	19B	20	A20	21	22	A22	23	A23	B23	C23	24	25	26	26B	A26
Sivis lukashevichiae	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1	0	0	1	0	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0
Perlucipecta liangiae	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1	0	0	1	0	0	0	1	0	1	1	0	0	0	0	1	0	0	0	0	0
Mesoblattina etarakan	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1	0	0	1	0	0	0	1	0	1	1	0	0	0	0	0	0	0	1	0	0
Skok svaba	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	1	1	1	1	1	0	1	0	0	1	0	0	0	0	0	0	0	1	0	0	0
Lovec pratiena	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	1	0	1	0	1	1	0	1	0	0	1	0	1	0	1	0	0	0	0	0
Maloval hlavolam	0	1	1	0	0	0	0	0	0	1	0	1	1	0	0	0	0	1	1	0	0	0	0	0	1	0	1	0	0	0	0	1	0	0	1	0	1	1	1	0	0	1	0	0	0
Hydrokhoohydra aquabella	1	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0	0	0	0	0	1	1	1	0	1	1	1	0	1	1	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0
Elisamoides sedio-masle	1	0	0	0	0	1	0	0	0	0	0	?	0	?	0	0	0	0	0	0	1	1	?	0	1	0	1	0	1	0	0	?	0	1	1	0	0	0	0	0	0	0	0	1	0
Aktassoblatta fusca	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	1	0	1	1	0	1	0	1	1	0	0	0	0	0	0	0	0	1	0
Aktassoblattta pullata	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	1	0	1	1	0	1	0	1	1	0	0	0	0	0	0	0	0	1	0
L. cunicula	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	1	0	1	1	0	1	0	1	1	0	1	1	1	0	0	1	0	0	0
L. ihringovae	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	1	0	1	1	0	1	0	1	1	0	1	1	1	0	0	1	0	0	0
Liberiblattina kontra-punktata	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	?	0	1	0	1	0	1	1	0	?	0	1	1	0	1	0	0	0	0	0	0	0	0
Liberiblattina kontra-venata	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	1	0	1	0	1	1	0	1	0	1	1	0	1	1	1	0	0	1	0	0	0
Liberiblattina lumi-nanala	0	0	0	0	0	1	1	0	0	0	0	0	0	1	1	0	0	0	0	0	1	1	1	0	1	0	1	0	1	1	0	1	0	1	1	0	1	1	1	0	0	1	0	0	0
Liberiblattina liberi-blattina	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	1	0	1	1	0	1	0	1	1	0	1	1	0	0	0	1	0	0	0
Liberiblattina palaeon-tologica	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	1	0	1	1	0	1	0	1	1	0	1	1	0	0	0	1	0	0	0
Liberiblattina zokamu-vypadli	1	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0	0	0	0	0	1	1	0	0	1	0	1	0	1	1	0	0	0	0	1	0	1	1	1	0	0	1	0	0	0
Liberiblattina nenio-com	1	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	1	0	0	1	0	1	0	1	1	0	0	0	0	1	0	1	1	1	0	0	1	0	0	0
Ano tak	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	1	0	1	0	1	1	0	0	0	0	1	0	1	1	1	0	0	1	0	0	0
Ano mal	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	1	0	1	1	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0
Ano ona	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	1	0	1	1	0	0	0	0	1	0	1	1	0	0	0	0	1	0	0
Ano naslosa	0	1	0	0	0	0	0	1	0	0	0	0	0	?	0	1	0	0	0	0	1	0	0	0	0	0	0	0	1	1	0	0	0	1	1	0	1	0	0	0	0	0	0	0	0
Ano si	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	1	0	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Cretaholocompsa karatauensis	0	0	0	0	0	1	0	1	0	0	0	0	1	0	0	0	0	1	0	0	1	1	1	0	1	0	1	1	0	0	0	1	0	1	1	0	1	0	1	0	0	0	0	0	0
Akinisia chorevei	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1	0	1	1	0	1	0	1	1	0	1	0	0	0	0	0	0	0	0

B26	C26	D26	E26	F26	27	27B	28	29	29B	A29	B29	30	31	32	A32	33	34	35	35B	36	37	38	39	40	41	A41	42	43	43B	44	45	46	47	48	48B	49	50	51	52	53	A53	A54	54
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	1	2	2B	3	3B	4	5	5B	5C	A5	B5	6	7	8	8B	9	9B	9C	9D	A9	10	11	12	13	14	15	16	17	18	19	19B	20	A20	21	22	A22	23	A23	B23	C23	24	25	26	26B	A26
Operam testudina	1	0	0	1	0	1	1	0	0	0	0	1	0	1	1	0	0	1	0	0	1	?	1	0	1	0	1	0	1	1	0	1	0	0	1	0	1	1	1	0	0	1	0	0	0
Operam monita	1	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	1	0	1	0	1	1	0	1	0	0	1	0	1	0	1	0	0	1	0	0	0
Operam simpla	1	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	?	0	1	0	1	0	1	1	0	?	0	0	1	0	1	0	0	0	0	0	0	0	0
Elisama prelistama	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	1	0	0	0	0	1	0	1	0	0	1	0	0	0	0	0	1	0	0	0	0
Pseudomantina nigroalba	1	0	0	1	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	1	1	0	1	0	1	0	1	1	0	1	0	1	1	0	0	0	0	1	0	0	0	0	0
Blattula gracilicosta	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	1	0	1	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Blattula ahanaha	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	1	0	1	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Blattula microscopica	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1	1	0	1	0	1	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Blattula summa	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	1	0	1	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Blattula rectinervosa	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	1	0	1	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Blattula druha	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	1	0	1	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Blattula nebude	1	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0	0	0	0	0	1	1	1	0	1	0	1	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Blattula brevicaudata	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	1	0	1	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Asvab bavsa	0	0	0	0	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	1	1	1	0	1	0	1	0	1	1	1	1	0	0	1	0	1	0	0	0	0	0	0	0	0
Spono spono	1	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0	0	0	0	0	1	1	1	0	1	0	1	0	1	1	0	1	0	0	1	0	0	0	0	0	1	0	0	0	0
Decomposita triocella	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0
Decomposita tristriata	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Decomposita pentavisia	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0
Decomposita basquatirgis	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0
Decomposita apicata	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Olzmasg zi	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0	0	0	1	0	0	1
Cameloblatta variegata	1	1	0	1	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	1	0	1	0	1	0	0	1	0	0	1	0	1	1	1	0	1	1	0	0
Cameloblatta stress	1	1	0	1	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	1	0	1	0	1	0	0	1	0	0	1	0	1	0	1	0	0	1	0	0
Raphidiomima chimaera	1	1	0	1	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	1	1	0	0	1	0	1	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Rhipidoblattina maculata	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0
Raphidiomima cognata	1	1	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	1	0	1	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Chuanblatta stalosa	1	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0
Memento mori	0	0	0	0	0	0	0	1	0	1	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0

B26	C26	D26	E26	F26	27	27B	28	29	29B	A29	B29	30	31	32	A32	33	34	35	35B	36	37	38	39	40	41	A41	42	43	43B	44	45	46	47	48	48B	49	50	51	52	53	A53	A54	54
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	1	2	2B	3	3B	4	5	5B	5C	A5	B5	6	7	8	8B	9	9B	9C	9D	A9	10	11	12	13	14	15	16	17	18	19	19B	20	A20	21	22	A22	23	A23	B23	C23	24	25	26	26B	A26
Falcatusiblatta disrupta	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	1	0	0	1	0	0	0
Falcatusiblatta casovec	1	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	1	0	0	1	0	0	0
Falcatusiblatta storozhenkoi	1	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	1	0	0	1	0	0	0
Falcatussiblatta toold	1	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	1	0	0	1	0	0	0
Falcatussiblatta zaloha	1	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	1	0	0	1	0	0	0
Liadoblattina karatavica (Vishniakova, 1968)	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	1	0	0	1	0	0	0
Katatychi symptosi	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1	0	1	1	0	0	0	0	1	0	1	1	0	0	0	1	0	0	0
Asioblatta punctata	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Karatavoblatta longicaudata	0	1	0	0	0	0	0	0	1	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rhipidoblatta brevivalvata	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	1	0	1	0	0	0	0	0	0
Rhipidoblatta trimestre	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	1	0	
Rhipidoblatta matriky	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	1	0	1	0	0	0	0	0	0
Rhipidoblatta matrikarky	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	1	1	1	0	0	0	0	0	0
Rhipidoblatta fusca	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	1	0	
Rhipidoblatta triky	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	1	0	1	1	1	0	0	1	0	0	0
Rhipidoblatta trika	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	1	0	1	0	0	0	0	0	0
Fosilia tubuliovipositorica	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0	0	1	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0
Latiblatta lativalvata	0	1	1	0	0	0	0	1	0	0	0	1	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1	0	0	0	0	0	0	0	1	0
Latiblatta osud	0	1	1	0	0	0	0	1	0	0	0	1	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1	0	0	0	0	0	0	0	1	0
Manipulator olim	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0	0	1	0	1	1	0	1	1	1		0	0	0	0	0	0	0
Morphna una	0	1	0	0	0	0	0	0	1	0	0	0	1	1	0	0	0	0	0	0	1	1	1	0	0	0	0	1	0	0	0	1	0	1	1	0	0	0	0	0	0	0	0	1	0
Okruhliak samoodpovedaniesi	0	0	0	0	0	0	0	0	1	0	1	1	0	1	0	0	0	0	0	0	1	1	1	0	1	1	1	0	1	1	0	1	0	1	1	0	0	0	0	0	0	0	0	1	0
Fractalia aristovi	0	0	0	0	0	0	0	0	1	0	0	1	0	1	0	0	0	1	1	0	1	1	0	0	1	0	1	0	1	1	0	1	0	1	1	0	0	0	0	0	0	0	0	1	0
Kazakhiblattina asiatica	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1	0	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0
Rhipidoblattinopsis latitergata	0	1	0	0	0	0	0	1	0	0	0	?	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

	B26	C26	D26	E26	F26	27	27B	28	29	29B	A29	B29	30	31	32	A32	33	34	35	35B	36	37	38	39	40	41	A41	42	43	43B	44	45	46	47	48	48B	49	50	51	52	53	A53	A54	54
Falcatusiblatta disrupta	0	1	0	0	0	1	0	0	0	1	0	0	0	0	1	0	1	0	0	0	0	1	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
Falcatusiblatta casovec	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	1	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
Falcatusiblatta storozhenkoi	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	1	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
Falcatussiblatta toold	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	1	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
Falcatussiblatta zaloha	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	1	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
Liadoblattina karatavica (Vishniakova, 1968)	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1	0	1	0	0	0	0	1	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
Katatychi symptosi	0	0	1	0	0	1	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	1	1	0	1
Asioblatta punctata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Karatavoblatta longicaudata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
Rhipidoblatta brevivalvata	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Rhipidoblatta trimestre	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0
Rhipidoblatta matriky	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0
Rhipidoblatta matrikarky	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Rhipidoblatta fusca	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0
Rhipidoblatta triky	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1
Rhipidoblatta trika	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	1	0	0	0	0	1	1	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0
Fosilia tubuliovipositorica	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	1	1	1	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	1
Latiblatta lativalvata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Latiblatta osud	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Manipulator olim	0	0	0	0	0	1	0	0	0	0	0	0	0	1	1	1	1	1	0	0	1	1	0	1	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	1	0	0
Morphna una	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	1	0
Okruhliak samoodpovedaniesi	0	0	0	0	0	1	0	1	0	0	0	0	1	0	0	0	1	0	1	0	1	1	1	0	1	0	0	0	0	0	1	0	1	0	1	0	0	1	1	0	1	1	1	0
Fractalia aristovi	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	1	1	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0	0	0	0
Kazakhiblattina asiatica	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	1	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
Rhipidoblattinopsis latitergata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1

	1	2	2B	3	3B	4	5	5B	5C	A5	B5	6	7	8	8B	9	9B	9C	9D	A9	10	11	12	13	14	15	16	17	18	19	19B	20	A20	21	22	A22	23	A23	B23	C23	24	25	26	26B	A26
Rhipidoblattina dmitrievi	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	1	0
Caloblattina laesis	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0
Miniblattina inflatica	1	0	0	0	0	1	0	1	0	0	0	1	0	1	0	1	0	0	0	0	1	0	1	1	1	0	1	0	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0

	B26	C26	D26	E26	F26	27	27B	28	29	29B	A29	B29	30	31	32	A32	33	34	35	35B	36	37	38	39	40	41	A41	42	43	43B	44	45	46	47	48	48B	49	50	51	52	53	A53	A54	54
Rhipidoblattina dmitrievi	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	
Caloblattina laesis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Miniblattina inflatica	0	0	0	0	0	1	0	0	1	0	0	0	1	0	0	1	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0	0

	1	2	2B	3	3B	4	5	5B	5C	A5	B5	6	7	8	8B	9	9B	9C	9D	A9	10	11	12	13	14	15	16	17	18	19	19B	20	A20	21	22	A22	23	A23	B23	C23	24	25	26	26B	A26
Sivis lukashevichiae	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1	0	0	1	0	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0
Perlucipecta liangiae	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1	0	0	1	0	0	0	1	0	1	1	0	0	0	0	1	0	0	0	0
Skok svaba	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	1	1	1	1	0	1	0	0	1	0	0	0	0	0	0	0	1	0	0	0
Lovec pratiena	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	1	0	1	0	1	1	0	1	0	0	1	0	1	0	0	0	0	0	0	0
Maloval hlavolam	0	1	1	0	0	0	0	0	0	1	0	1	1	0	0	0	0	0	1	1	0	0	0	0	0	1	0	1	0	0	0	0	1	0	0	1	0	1	1	0	0	1	0	0	0
Aktassoblatta fusca	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	1	0	1	1	0	1	0	1	1	0	0	0	0	0	0	0	1	0
Aktassoblatta pullata	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	1	0	1	1	0	1	0	1	1	0	0	0	0	0	0	0	1	0
L. ihringovae	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	1	0	1	1	0	1	0	1	1	0	0	0	0	1	0	0	0	0
Liberiblattina liberi-blattina	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	1	0	1	1	0	1	0	1	1	0	1	1	0	0	0	1	0	0	0
Liberiblattina palaeon-tologica	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	1	0	1	1	0	1	0	1	1	0	1	1	0	0	0	1	0	0	0
Ano tak	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	1	0	1	0	1	1	0	0	0	0	1	0	1	1	1	0	0	1	0	0	0
Ano mal	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	1	0	1	1	0	1	0	0	1	0	1	0	1	0	0	0	0	0	0
Ano ona	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	1	0	1	1	0	1	0	0	1	0	1	1	0	0	0	0	1	0	0
Ano si	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	1	0	1	1	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0
Akinisia chorevei	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1	0	1	1	0	1	0	1	1	0	1	0	0	0	0	0	0	0	0
Elisama prelistama	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	1	0	0	0	1	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0
Blattula ahanaha	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	1	0	1	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Blattula microscopica	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1	1	0	1	0	1	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Blattula rectinervosa	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	1	0	1	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Blattula druha	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	1	0	1	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Blattula nebude	1	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	1	1	1	0	1	0	1	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Blattula brevicaudata	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	1	0	1	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Asvab bavsa	0	0	0	0	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	1	1	1	0	1	0	1	0	1	1	1	1	0	0	1	0	1	0	0	0	0	0	0	0	0

	B26	C26	D26	E26	F26	27	27B	28	29	29B	A29	B29	30	31	32	A32	33	34	35	35B	36	37	38	39	40	41	A41	42	43	43B	44	45	46	47	48	48B	49	50	51	52	53	A53	A54	54
Sivis lukashevichiae	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	1	1	0	0
Perlucipecta liangiae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	1	1	0	0
Skok svaba	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	1	0	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	1	0	1	
Lovec pratiena	0	0	0	0	0	1	1	0	1	0	0	0	0	0	0	0	1	1	0	1	0	1	1	1	1	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0
Maloval hlavolam	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	1	0	?	0	?	1	0	0	0	0	0	1	0	0	0	0	0	0	1	1	0	1	1	?	0
Aktassoblatta fusca	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1	0	0	1	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	1
Aktassoblatta pullata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1	0	0	1	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	1
L. ihringovae	0	0	0	1	0	1	0	0	1	0	0	0	0	0	0	0	1	0	1	1	1	1	1	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	1	0	1
Liberiblattina liberi-blattina	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	1	1	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	1	0	1
Liberiblattina palaeon-tologica	0	0	0	1	0	1	0	0	1	0	0	0	0	0	0	0	1	0	1	0	0	1	1	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	1	0	1
Ano tak	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0
Ano mal	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	1	0	0
Ano ona	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0
Ano si	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	1	1	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0
Akinisia chorevei	0	0	0	1	0	1	0	0	0	1	0	0	0	1	0	1	1	0	0	0	0	1	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0
Elisama prelistama	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0	1	0	1	0	0	1	0	0	1	0	0	0	0	0	1	1	1	0	0	1	0	1	0	0	1	1	1	1
Blattula ahanaha	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0	1	0	1	0	0	1	0	0	1	0	0	0	0	0	1	1	1	0	0	1	0	1	1	0	1	1	1	1
Blattula microscopica	0	0	0	0	0	0	0	0	0	1	1	0	1	1	0	0	1	0	1	0	0	1	0	0	1	0	0	0	0	0	1	1	1	0	0	1	0	1	1	0	1	1	1	1
Blattula rectinervosa	0	0	0	0	0	0	0	0	0	1	1	0	1	1	0	0	1	0	1	0	0	1	0	0	1	0	0	0	0	0	1	1	1	0	0	1	0	1	1	0	1	1	1	1
Blattula druha	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0	1	0	1	0	0	1	0	0	1	0	0	0	0	0	1	1	1	0	0	1	0	1	1	0	1	1	1	1
Blattula nebude	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	1	0	0	1	0	0	1	0	0	0	0	0	1	1	1	0	0	1	0	1	1	0	1	1	1	1
Blattula brevicaudata	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0	1	0	1	0	0	1	0	0	1	0	0	0	0	0	1	1	1	0	0	1	0	1	1	0	1	1	1	1
Asvab bavsa	0	0	0	0	1	1	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	1	0	0	1	0	0	1	0	0	1	0	1	0	0	1	0	1	0	1	1	1	1	0

	1	2	2B	3	3B	4	5	5B	5C	A5	B5	6	7	8	8B	9	9B	9C	9D	A9	10	11	12	13	14	15	16	17	18	19	19B	20	A20	21	22	A22	23	A23	B23	C23	24	25	26	26B	A26
Decomposita triocella	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0
Decomposita tristriata	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Decomposita pentavisia	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0
Decomposita basquatirgis	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0
Olzmasg zi	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0	0	0	1	0	0	1
Cameloblatta variegata	1	1	0	1	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	1	0	1	0	1	0	0	1	0	0	1	0	1	1	1	0	1	1	0	0	0
Raphidiomima chimaera	1	1	0	1	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	1	1	0	0	1	0	1	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Rhipidoblattina maculata	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0
Raphidiomima cognata	1	1	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	1	0	1	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Chuanblatta stalosa	1	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0
Memento mori	0	0	0	0	0	0	0	1	0	1	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Falcatusiblatta casovec	1	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	1	0	0	1	0	0	0
Falcatusiblatta storozhenkoi	1	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	1	0	0	1	0	0	0
Falcatussiblatta zaloha	1	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	1	0	0	1	0	0	0
Liadoblattina karatavica (Vishniakova, 1968)	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	1	0	0	1	0	0	0
Asioblatta punctata	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Karatavoblatta longicaudata	0	1	0	0	0	0	0	0	1	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rhipidoblatta brevivalvata	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	1	0	1	0	0	0	0	0	0
Rhipidoblatta trimestre	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0
Rhipidoblatta matriky	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	1	0	1	0	0	0	0	0	0
Rhipidoblatta fusca	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0
Latiblatta lativalvata	0	1	1	0	0	0	0	1	0	0	0	1	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1	0	0	0	0	0	0	0	1	0
Latiblatta osud	0	1	1	0	0	0	0	1	0	0	0	1	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1	0	0	0	0	0	0	0	1	0
Manipulator olim	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0	0	1	0	1	1	0	1	1	1		0	0	0	0	0	0	0
Kazakhiblattina asiatica	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1	0	1	1	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0

	B26	C26	D26	E26	F26	27	27B	28	29	29B	A29	B29	30	31	32	A32	33	34	35	35B	36	37	38	39	40	41	A41	42	43	43B	44	45	46	47	48	48B	49	50	51	52	53	A53	A54	54
Decomposita triocella	0	0	0	0	0	1	0	0	0	1	0	0	0	1	0	1	1	0	0	1	0	1	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
Decomposita tristriata	0	0	0	0	0	1	0	0	0	1	0	0	0	1	0	1	1	0	0	0	0	1	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
Decomposita pentavisia	0	0	0	0	0	1	0	0	0	1	0	0	0	1	0	1	1	0	0	0	0	1	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
Decomposita basquatirgis	0	0	0	0	0	1	0	0	0	1	0	0	0	1	0	1	1	0	0	0	0	1	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
Olzmasg zi	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Cameloblatta variegata	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	1	0	0	1	0	1	1	0	0	0	0	1	0	0	0	0	0	0	1	1	0	1
Raphidiomima chimaera	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	1	0	0	1	0	0	0	0	1	0	0	0	0	0	0	1	1	0	1
Rhipidoblattina maculata	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	1	1	0	0	1	1	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Raphidiomima cognata	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	1	0	1	1	0	0	0	0	1	0	0	0	0	0	0	1	1	0	1
Chuanblatta stalosa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0
Memento mori	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	1
Falcatusiblatta casovec	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	1	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
Falcatusiblatta storozhenkoi	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	1	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
Falcatussiblatta zaloha	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	1	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
Liadoblattina karatavica (Vishniakova, 1968)	0	0	0	0	0	1	0	0	0	1	0	0	0	1	0	1	0	0	0	0	0	1	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
Asioblatta punctata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Karatavoblatta longicaudata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
Rhipidoblatta brevivalvata	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Rhipidoblatta trimestre	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Rhipidoblatta matriky	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	1	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Rhipidoblatta fusca	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Latiblatta lativalvata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Latiblatta osud	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Manipulator olim	0	0	0	0	0	1	0	0	0	0	0	0	0	1	1	1	1	1	1	0	0	1	1	0	1	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0	0	1	0	0
Kazakhiblattina asiatica	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	1	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1

	1	2	2B	3	3B	4	5	5B	5C	A5	B5	6	7	8	8B	9	9B	9C	9D	A9	10	11	12	13	14	15	16	17	18	19	19B	20	A20	21	22	A22	23	A23	B23	C23	24	25	26	26B	A26
Rhipidoblattinopsis latitergata	0	1	0	0	0	0	0	1	0	0	0	?	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rhipidoblattina dmitrievi	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	1	0	
Miniblattina inflatica	1	0	0	0	0	1	0	1	0	0	0	1	0	1	0	1	0	0	0	0	1	0	1	1	1	0	1	0	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	

B26	C26	D26	E26	F26	27	27B	28	29	29B	A29	B29	30	31	32	A32	33	34	35	35B	36	37	38	39	40	41	A41	42	43	43B	44	45	46	47	48	48B	49	50	51	52	53	A53	A54	54
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
0	0	0	0	0	1	0	0	1	0	0	0	0	1	0	0	1	0	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	1	1	0	0

	H1	H2	H3	H4	H5	H6	H7	H8	H9	H10	H11	H12	H13	H14	H15	H16	H17	H18	H19	H20
Sivis lukashevichiae	0	1	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	1	1
Perlucipecta liangiae	0	1	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	1	1
Skok svaba	1	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	1	1
Lovec pratiena	?	0	0	1	1	1	0	0	1	1	0	0	0	0	0	0	1	1	0	0
Maloval hlavolam	1	0	0	1	1	0	0	0	1	1	1	0	0	0	0	0	1	1	0	0
Aktassoblatta fusca	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0	0	0	0
Aktassoblattta pullata	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0	0	0	0
L. ihringovae	1	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0
Liberiblattina liberi-blattina	1	0	0	1	0	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0
Liberiblattina palaeon-tologica	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0
Ano tak	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0
Ano mal	1	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0
Ano ona	1	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0
Ano si	1	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0
Akinisia chorevei	1	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0
Elisama prelistama	1	0	0	0	1	0	0	1	1	1	0	0	0	0	0	0	1	0	0	0
Blattula ahanaha	1	0	0	1	1	1	0	1	1	1	1	0	0	0	0	0	1	0	0	0
Blattula microscopica	1	0	0	0	1	1	0	1	1	1	0	0	0	0	0	0	1	0	0	0
Blattula rectinervosa	1	0	0	0	1	1	0	1	1	1	0	0	0	0	0	0	1	0	0	0
Blattula druha	1	0	0	1	1	1	0	1	1	1	0	0	0	0	0	0	1	0	0	0
Blattula nebude	1	0	0	0	1	1	0	1	1	1	0	0	0	0	0	0	1	0	0	0
Blattula brevicaudata	1	0	0	0	1	1	0	1	1	1	0	0	0	0	0	0	1	0	0	0
Asvab bavsa	1	0	0	0	1	0	0	1	1	1	0	0	0	0	0	0	1	0	0	0
Decomposita triocella	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Decomposita tristriata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Decomposita pen-tavisia	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Decomposita basquatirgis	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Olzmasg zi	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0

	H1	H2	H3	H4	H5	H6	H7	H8	H9	H10	H11	H12	H13	H14	H15	H16	H17	H18	H19	H20
Cameloblatta variegata	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	1	1	0	0
Raphidiomima chimaera	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	1	1	0	0
Rhipidoblattina maculata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Raphidiomima cognata	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1	0	1	1	0	0
Chuanblatta stalosa	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Memento mori	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Falcatusiblatta casovec	0	0	0	1	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0	0
Falcatusiblatta storozhenkoi	0	0	0	1	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0	0
Falcatussiblatta zaloha	0	0	0	1	0	0	0	0	1	0	1	1	1	0	0	0	0	0	0	0
Liadoblattina karatavi-ca (Vishniakova, 1968)	0	0	0	1	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0
Asioblatta punctata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Karatavoblatta longicaudata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rhipidoblatta brevivalvata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rhipidoblatta trimestre	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Rhipidoblatta matriky	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rhipidoblatta fusca	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Latiblatta lativalvata	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Latiblatta osud	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Manipulator olim	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0
Kazakhiblattina asiatica	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Rhipidoblattinopsis latitergata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rhipidoblattina dmitrievi	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0
Miniblattina inflatica	1	0	0	0	1	1	0	0	1	1	0	0	0	0	0	0	1	1	0	0

	B1	B2	B3	B4	B5	B6	B7	B8	B9	B10	B11	B12	B13	B14	B15	B16	B17	B18	B19	B20
Sivis lukashevichiae	0	1	0	0	0	1	0	0	0	1	1	0	0	1	0	0	0	0	0	0
Perlucipecta liangiae	0	1	0	0	0	1	0	0	0	1	1	1	0	1	0	0	0	0	0	0
Skok svaba	1	1	0	0	?	1	0	0	0	1	1	0	0	0	0	0	1	0	0	1
Lovec pratiena	1	1	0	?	0	1	1	0	0	1	1	0	0	1	1	1	1	0	0	0
Maloval hlavolam	1	1	0	?	0	1	0	1	1	1	1	0	?	0	0	0	0	0	0	0
Aktassoblatta fusca	0	0	1	0	0	1	0	0	0	0	1	0	0	0	0	1	1	0	0	0
Aktassoblattta pullata	0	0	1	0	0	1	0	0	0	0	1	0	0	0	0	1	1	0	0	0
L. ihringovae	1	1	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0
Liberiblattina liberiblattina	1	1	0	0	1	0	0	0	0	1	?	0	0	?	?	0	0	0	0	0
Liberiblattina palaeontologica	1	1	0	0	1	0	0	0	0	1	?	0	0	0	0	0	0	0	0	0
Ano tak	0	1	0	0	0	1	0	1	0	0	1	0	0	0	0	0	0	0	0	0
Ano mal	1	0	1	0	0	1	0	1	0	0	?	?	?	0	0	0	0	0	0	0
Ano ona	0	1	0	0	0	1	0	1	0	0	1	0	0	0	0	0	0	0	0	0
Ano si	0	1	0	0	0	1	0	1	0	0	1	0	0	0	0	0	0	0	0	0
Akinisia chorevei	0	1	0	0	0	1	0	0	0	1	0	0	0	0	0	0	1	0	0	0
Elisama prelistama	0	1	0	1	0	1	0	0	0	0	1	0	0	?	?	0	0	0	0	0
Blattula ahanaha	0	1	0	1	0	1	0	0	0	0	1	0	0	1	0	0	0	0	0	0
Blattula microscopica	0	1	0	1	0	1	0	0	0	0	1	0	0	1	0	0	0	0	0	0
Blattula rectinervosa	0	1	0	1	0	1	0	0	0	0	1	0	0	1	0	0	0	0	0	0
Blattula druha	0	1	0	1	0	1	0	0	0	0	1	0	0	1	0	0	0	0	0	0
Blattula nebude	0	1	0	1	0	1	0	0	0	0	1	0	0	1	0	0	0	0	0	0
Blattula brevicaudata	0	1	0	1	0	1	0	0	0	0	1	0	0	1	0	0	0	0	0	0
Asvab bavsa	0	1	0	1	0	1	0	0	0	0	1	0	0	1	0	0	0	0	0	0
Decomposita triocella	0	0	1	0	0	0	1	0	0	1	0	0	0	0	0	1	1	0	0	0
Decomposita tristriata	0	0	1	0	0	0	1	0	0	1	0	0	0	0	0	1	1	0	0	0
Decomposita pentavisia	0	0	1	0	0	0	1	0	0	1	0	0	0	0	0	1	1	0	0	0
Decomposita basquatirgis	0	0	1	0	0	0	1	0	0	1	0	0	0	0	0	1	1	0	0	0
Olzmasg zi	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	1	1	0	0	0

	H1	H2	H3	H4	H5	H6	H7	H8	H9	H10	H11	H12	H13	H14	H15	H16	H17	H18	H19	H20
Cameloblatta variegata	0	0	1	0	1	0	1	0	0	1	1	0	0	0	1	1	1	0	0	0
Raphidiomima chimaera	0	0	1	0	1	0	1	0	0	1	1	0	0	0	1	1	1	0	0	0
Rhipidoblattina maculata	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0
Raphidiomima cognata	0	0	1	0	1	0	1	0	0	1	1	0	0	0	1	1	1	0	0	0
Chuanblatta stalosa	1	0	1	0	0	0	1	0	0	1	0	0	0	0	0	1	1	0	0	0
Memento mori	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0
Falcatusiblatta casovec	0	0	1	0	?	0	0	0	0	1	0	0	0	0	0	?	?	0	0	0
Falcatusiblatta storozhenkoi	0	0	1	0	1	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0
Falcatussiblatta zaloha	0	0	1	0	?	0	1	0	0	1	0	0	0	0	0	1	1	0	0	0
Liadoblattina karatavica (Vishniakova, 1968)	0	0	1	0	?	0	0	0	0	1	0	0	0	0	0	?	?	0	0	0
Asioblatta punctata	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Karatavoblatta longicaudata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rhipidoblatta brevivalvata	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Rhipidoblatta trimestre	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Rhipidoblatta matriky	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Rhipidoblatta fusca	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Latiblatta lativalvata	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0
Latiblatta osud	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0
Manipulator olim	1	0	0	0	1	0	1	0	0	1	0	0	0	1	0	1	1	0	0	0
Kazakhiblattina asiatica	0	0	0	0	1	1	0	0	0	0	1	0	0	1	0	0	0	0	0	0
Rhipidoblattinopsis latitergata	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Rhipidoblattina dmitrievi	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	1	1	0	0	0
Miniblattina inflatica	0	1	0	?	?	1	0	0	0	0	?	?	?	1	0	0	0	0	0	0

Matrix for assemblage analysis ordered according to Tabp. 630 (species distribution) with columns representing Collections and rows representing its species.

0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	1	0	1	0	1
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0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1
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0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	1
0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
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0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	1	0
0	0	0	1	1	0	0	1	0	1	1	0	0	0	1	0	0	0	1	1	1	0	0	1	1	0	1	1	0	1	0	1	0	1	0	1
0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1	0	1	0	1	0	1
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

0	0	0	0	0	1	0	0	0	0	1	0	0	0	1	0	0	0	0	0	1	1	0	0	1	0	1	0	0	0	0	1	0	1	0	1
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	1	0	1
0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	1	0	0	1	1	0	0	0	1	0	1	0	1
0	0	0	0	0	0	0	0	0	1	1	0	0	0	1	0	0	0	1	1	0	1	0	0	1	0	0	0	0	1	0	1	0	1	0	1
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	1	1	0	0	1	0	0	0	0	0	1	0	0	0	1	1	1
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1	1	0	0	0	1	1	0	0	0	0	1	0	1	0	1	0	1
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	1	0	0	0	0	0	0	0	0	0	1	0	1	0	1	0	1
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	1	0	0	1	0	0	0	0	1	0	1	0	1
0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	1	1	0	0	1	0	1	0	1	0	1	0	1
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0	1	0	1	0	0	1	0	1	0	1	0	0	1
0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1	1	0	1	0	1	1	1	1	1	0	1	0	1	0	1	0	1
0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
0	1	0	0	0	1	0	0	1	1	0	0	0	1	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	1	0	1	0	1	0	1	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1	0	1	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1
0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	1	0	1	0	0	0	0	0	0	0	1	0	1	0	0	0	1
0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	1
0	0	0	0	0	0	0	0	1	0	0	0	1	0	1	0	0	0	0	1	1	1	0	0	0	0	1	0	0	1	0	1	0	1	0	1
0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	1	0	0	1	0	0	1	0	1	0	1	1	1
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
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Specimen	HW remigium area	HW vannus area	HW total area	FW area	FW veins	HW veins	Taxon
2784-918	15.79	13.22	29.01			22	*akinisia*
2784-725	23.37		23.37	37.87	39		*memento*
2784-769			0	29.83	48		*aatiblatta osud*
2784-693 f			0	11.69		28	*brevicaudata*
2784-772			0	34.49	43		*linagae*
2784-879			0	19.53	41		*ano ona*
2784-881			0	42.64	42		*latiblatta osud*
2784-922			0	62.34	58		*memento mori*
2784-970			0	12.49	26		*brevicaudata*
2784-990	17.7	6.68	24.38			25	*akinisia*
2784-992			0	23.76	47		*akinisia*
2784-2266	21.42		21.42			28	*ano ona*
2554-152			0	54.72	39		*fosilia*
2554-176			0	58.29			
179			0	69.39	?		*triky*
2554-204			0	86.04	48		*memento*
2784-636			0	76.31	?		*matriky*
2784-645			0	19.08	39		*katatychi*
2554-13	9.57		9.57	9.18	52		*aktassoblatta fusca= praecarnia*
2554-29			0	19.43	?		*sivis*
2554-33			0	82.58	?		*aktassoblatta fusca= praecarnia*
2554-43			0	22.99	?		*inflatica*
2554-47			0	40	41		*rhipidoblatta*
2554-87			0	155.25	59		*aktassoblatta fusca*
2784-969			0	45.09	36		*aktassoblatta fusca*
2904-27			0	25.7	30		*luminanala*
2239-222			0	62.58	34		*karatavica*
2339-205			0	57.77	35		*casovec*
2384-126			0	53.79	37		*triocella*
2384-31			0	76.92	?		*triocella*

Area analysis table

Specimen	HW remigium area	HW vannus area	HW total area	FW area	FW veins	HW veins	Taxon
2384-32			0	96.83	?		*aktassoblatta fusca*
2384-33			0	40.68	?		*triocella*
2384-53	52.18		52.18			?	*aktassoblatta fusca*
2384-57			0	47.63	?		*Rhipidoblatta brevivalvata*
2384-80			0	26	33		*sivis*
2384-92	32.91		32.91			?	*aktassoblatta fusca*
2384-98			0	100.39	52		*aktassoblatta fusca*
2384-111			0	109.23	59		*aktassoblatta fusca*
2997-4418			0	43.6	55		*chuanblatta*
2239-242			0	76.63	45		*lativalvata*
2239-252			0	84.27	56		*morphna*
2239-257			0	60.72	NEDASA		*matrikarky*
2239-274	47.05		47.05			29	*triocella*
2239-277	27.65		27.65			23	*ano si*
2239-279	56.73		56.73				*is*
2239-282	68.44		68.44			35	*apicata*
2239-499			0	21.94	35		*operam monita*
2452-490			0	28.69	28		*bavsa*
2384-176			0	15.41	30		*brevicaudata*
2384-181			0	30.46	32		*bavsa*
2384-188			0	13.16	29		*brevicaudata*
2384-193			0	14.92	30		*brevicaudata*
2452-383			0	91.06	51		*dmitrievi*
2452-626			0	13.28	29		*brevicaudata*
2465-924	91.67		91.67			24	*aktassoblatta fusca*
2465-981			0	37.62	50		*osud*
2035-27			0	24.99	30		*brevicaudata*
2035-38	19.01		19.01			28	*akinisia*
2384 - 126			0	53.79	37		*triocella*
2384-31			0	76.92	?		*triocella*

Specimen	HW remigium area	HW vannus area	HW total area	FW area	FW veins	HW veins	Taxon
2035-40			0	24.62	30		*bavsa*
2035-53			0	26.9	36		*bavsa*
2039-32			0	21.5	27		*luminanala*
2039-35			0	19.51	43		*ano ona*
2039-40			0	24.56	36		*bavsa*
2039-48			0	30.53	NEDASA		*disrupta*
2239-135			0	102.7	66		*matriky*
2239-153			0	64.39	54		*basquatirgis*
2239-167			0	89.63	69		*lativalvata*
2452-34			0	25.83	40		*liberiblattina liberiblattina*
2452-397			0	163.76	47		*Aktassoblatta fusca*
2465-955	35.53		35.53		?		
2066-637			0	79.03	?		*trimestre*
2066-641	14.38		14.38	15.27	24		*brevicaudata*
2066-643			0	16.19	?		*brevicaudata*
2239-	7.53		7.53	8.85	?		
2239-56			0	11.92	26		*rectinervosa*
2239-58			0	14.86	28		*druha*
2239-62			0	12.01	21		*brevicaudata*
2239-63			0	9.27	22		*brevicaudata*
2239-69			0	17.06	28		*brevicaudata*
2239-72	16.54		16.54			22	*druha*
2239-76			0	8.22	24		*microscopica*
2239-101			0	15.87	27		*brevicaudata*
192-1			0	67.79	46		*aktassoblatta fusca*
192-1			0	72.95	52		*aktassoblatta fusca*
2094-116			0	8.68	30		*rectinervosa*
2094-121			0	8.76	29		*gracilicosta*
2094-122			0	14.09	31		*brevicaudata*
2465-901			0	24.62	30		*bavsa*

Specimen	HW remigium area	HW vannus area	HW total area	FW area	FW veins	HW veins	Taxon
2904-93			0	12.08	25		*brevicaudata*
2904-100			0	6.27	30		*brevicaudata*
2904-106			0	13.23	27		*elisama*
2904-125	9.86		9.86			22	*rectinervosa*
2904-132			0	16.07	31		*brevicaudata*
2904-133	105.56		105.56			43	*matriky*
2904-138	63		63			34	*aktassoblatta fusca*
2994-785	23.45		23.45			27	*akinisia*
1789-220			0	98.48	47		*aktassoblatta fusca*
1789-226			0	81.04	48		*aktassoblatta fusca*
2904-73			0	70.13	45		*aktassoblatta fusca*
2904-74	65.43		65.43			33	*casovec*
2904-77	93.1		93.1	86.52	42		*aktassoblatta fusca*
2904-77	93.1		93.1	86.19	45		*aktassoblatta fusca*
2904-78			0	229.45	59		*rhipidoblatta fusca*
2904-81			0	236.97	60		*trika*
2904-83	11.34		11.34	12.18			*druha*
2066-424			0	20.47	32		*bavsa*
2066-519			0	10.05	28		*ano mal*
2554-126			0	53.89	53		*mesoblattina*
2904-72	78.28		78.28	84.67	41	34	*aktassoblatta fusca*
2904-72	78.28		78.28	86.44	45	34	*aktassoblatta fusca*
2066-440			0	65.25	?		*tubuliovipositorica*
2231-21			0	42.55	31		*casovec*
2231-21			0	41.2	30		*casovec*
2231-61			0	41.32	43		*memento*
2231-64			0	100.12	44		*zaloha*
2335-34			0	12..09	22		*brevicaudata*
2335-34			0	11.65	21		*brevicaudata*
2452-337			0	135.41	?		*tristriata*

Specimen	HW remigium area	HW vannus area	HW total area	FW area	FW veins	HW veins	Taxon
2452-372	58.87		58.87			37	*aktassoblatta fusca*
2452-373			0	13.86	27		*brevicaudata*
2452-397			0	173.22	47		*aktassoblatta fusca*
2452-636	104.94		104.94				
2997-75	15.45		15.45	12.89	26		*brevicaudata*
2997-75	15.45		15.45	12.95	26		*brevicaudata*
2997-76			0	14.93	29		*brevicaudata*
2997-77			0	24.7	43		*perlucipecta*
2997-110			0	34.72	50		*chorevei*
2997-111			0	19.27	55		*storozhenkoi*
2997-26			0	7.96	29		*rectinervosa*
2997-35			0	96.55	51		*storozhenkoi*
2997-49			0	69.71			*memento*
2997-53			0	78.01	53		*lativalvata*
2997-53			0	75.44	53		*lativalvata*
2997-62			0	72.03	75		*memento*
2997-86			0	11.97	33		*brevicaudata*
2997-87			0	80.17	45		*aktassoblatta fusca*
266-432				6.44	26		*microscopica*
266-432	7.28					18	*microscopica*
1789-8				112.21	56		*aktassoblatta fusca*
1789-19				184.67	?		*tri*
1789-19				179.47	?		*tri*
1789-53	9.41					19	*rectinervosa*
1789-65				170.34	57		*aktassoblatta fusca*
1789-73				6.99	32		*aristovi*
2064-164	77.02						
2066-71	16.6					22	*brevicaudata*
2066-84	28.85					23	*akinisia*
2066-95				16.45			
2066-143	8.79					20	*microscopica*

Specimen	HW remigium area	HW vannus area	HW total area	FW area	FW veins	HW veins	Taxon
2066-219				11.57	27		*brevicaudata*
2066-222				133.07	?		*dmitrievi*
2066-245	17.37					24	*brevicaudata*
2066-258	13.82					21, 22	*brevicaudata*
2066-270d				150.81	55		*lativalvata*
2066-277				9.48	28		*rectinervosa*
2066-285				12.54	30		*brevicaudata*
2066-288	28.31					25	*bavsa*
2066-317				15.64	29		*brevicaudata*
2066-324	25.31					24	*aktassoblatta fusca*
2066-324	25.1					24	*aktassoblatta fusca*
2066-386				39.23	52		*karatavica*
2066-386				40.1	52		*karatavica*
2066-387	27.19					37	*variegatta*
2066-421	14.23					20	*brevicaudata*
2066-434v				109.02	47		*stalosa*
2066-437				132.35	65		*lativalvata*
2066-440				59.89	35		*tubuliovipositorica*
2066-468	12.35					19	*rectinervosa*
2066-471				6.52	25		*microscopica*
2066-481				13.4	31		*brevicaudata*
2066-509				143.6	53		*lativalvata*
2066-578				20.81	28		*ano mal*
2066-578				20.87	26		*ano mal*
2066-716	6.3					16	*microscopica*
2066-782	14.69					19	*brevicaudata*
2904-142	25.89					26	*liberiblattina liberiblattina*
2904-176				15.81	29		*ano ona*
2904-179	19.02					26	*ano ona*
2904-180				20.04	28		*brevicaudata*
2904-182	32.76						

Specimen	HW remigium area	HW vannus area	HW total area	FW area	FW veins	HW veins	Taxon
2904-207				28.18	?		*storozhenkoi*
2904-219				107.52	50		*stalosa*
2904-240				475.86	?		*aktassoblatta fusca*
2904-240				459.75	?		*aktassoblatta fusca*
2904-302				21.82			
2904-334	37.59					21	*lovec pratiena*
2904-345				68.87	44		*triocella*
2904-347				19.82	?		*ano ona*
2904-364				18.42			*is*
2904-369				118.76	?		*cunicula*
2904-370				68.45	52		*memento*
2904-1274				15.6	30		*brevicaudata*
2904-1874	9.78					18	*lovec*
2997-144				74.37	54		*lativalvata*
2997-145				89.52	49		*stalosa*
2997-146				9.39	25		*rectinervosa*
2997-146				9.48	28		*rectinervosa*
2997-168				12.41	23		*brevicaudata*
2997-207				79.72	?		*matriky*
2997-215				15.31	?		*brevicaudata*
2997-220				13.35	30		*brevicaudata*
2997-226	12.28					19	*brevicaudata*
2997-230				21.86	?		*osud*
2997-238				144.03	59		*morphna*
2997-245				14.6	22		*brevicaudata*
2997-245				14.88	21		*brevicaudata*
2997-249				18.01			
2997-252				7.97	26		*rectinervosa*
2997-253				37.82	?		*osud*
2997-259	16.51					21	*brevicaudata*
2997-261				26.74	?		*ano ona*

Specimen	HW remigium area	HW vannus area	HW total area	FW area	FW veins	HW veins	Taxon
2997-267				14.63	29		*brevicaudata*
2997-273				13.67	29		*nebude*
2997-273				13.53	28		*nebude*
2997-278				222.69	?		*aposema*
2997-1137				133.13			*is*
2997-1143				73.26	?		*disrupta*
2997-1145				88.51	47		*aktassoblatta fusca*
2997-1145				91.96	52		*aktassoblatta fusca*
2997-1184	24.97					23	*ano ona*
2997-1244	32.75					23	*akinisia*
2997-1249	106.26					NEDASSA	*matriky*
2997-1253	160.04					42	*matriky*
2997-1298				93.79	56		*aktassoblatta fusca*
2997-1338	51.93						
2997-1349				109.04	?		*aktassohlatta fusca*
2997-1384	27.93					19	*stalosa*
2997-1384	20.84					18	*stalosa*
2997-1399				34.79	35		*operam monita*
2997-1413	42.68					29	*akinisia*
2997-1417				111.03	59		*morphna*
2997-1435	21.85					28	*ano ona*
2997-1440	17.18					22	*ano mal*
2997-1443				18.18	34		*bavsa*
2997-1454				15.31	?		*brevicaudata*
2997-1457				15.12	30		*brevicaudata*
2997-1458-				14.27	30		*brevicaudata*
2997-1473				12.33	26		*pseudomantina*
2997-1481				15.4	29		*brevicaudata*
2997-1492	19.68					24	*ano ona*
2997-1511				13.19	27		*brevicaudata*
2997-1515	16.71					18	*brevicaudata*

Specimen	HW remigium area	HW vannus area	HW total area	FW area	FW veins	HW veins	Taxon
2997-1516	16.84					19	*brevicaudata*
2997-1521	17.92					27	*ano ona*
2997-1522				9.25	28		*osud*
2997-1523	15.89					20	*brevicaudata*
2997-1532	15.5					17	*brevicaudata*
2997-1542	10.62					18	*rectinervosa*
2997-1543	16.44					17	*brevicaudata*
2997-1545				13.28	27		*brevicaudata*
2997-1548	7.25					17	*microscopica*
2997-1615	50.06					54	*stalosa*
2997-1615	50.06					54	*stalosa*
2997-4247				109.3	?		*matriky*
2997-4247				103.03	?		*matriky*
2997-4429				166.29	?		*Rhipidoblatta brevivalvata*
U1789-72				9.2	28		*brevicaudata*
u1789-79				8.78	25		*rectinervosa*
u2066-122				10.35	?		*brevicaudata*
2465/937	17.04			13.37	35		*maloval*
2784/713				61.06	36		*Ano tak*
2784/713				54.4	33		*Ano tak*
2066/322	14.52				32		*skok*

DECLARATION OF INTERESTS

I declare that I do not have any financial, political and/or religional interests which would bias the present work in any stages of the production as I am fully responsible for the whole content including graphical visualisation and layout (except for reference style selected by opponents). Personal and intellectual interests are optimalised.

Multiple affiliations are within the same academic body, non-govermental non-profit organisation and in Russian organisation operating within the framework of interacademic exchange, which except for the salary, provided all the necessary for performing the collection part of the study (pre-Ukraine war official exchanges).

Data and materials availability: All data performed are included in this publication. Data for shape analysis are extracted from figps. 516-519.

Protection: Since 1924 (B.P Trizna, Director Chimkent Museums) it is protected as Karatau Paleontological Reserve, the first "Geopark/Reserve" in the Soviet Union.

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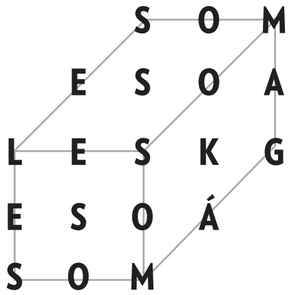
PS

The careful reader certainly discovered certain inconstancies and also pure errors. I was planning to dedicate one more full year to finalization and polishing of the manuscript. Nevertheless a local paleontologist, who was preparing a work of similar extent (more than 40 years) died without publishing his work. All his life-long effort was senseless. This forced me to promptly terminate this study. Hopefully my children, V.N. Vishniakova, and nations of Republic of Kazakhstan understand. Generally, it was 30 years. Adventure and pleasure of depth.

"Death is like a life. But totally different."
Former President at a funeral speach



Who never ever had
A fossil cockroach on the hand
Will misunderstand
A resident