



FACULTY OF SCIENCE **Charles University**

DOCTORAL THESIS

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Cockroaches from Cenomanian Myanmar amber and their phylogenetical relevance

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I declare that I carried out this doctoral thesis independently under the supervision of Mgr. Peter Vršanský, Ph.D. and only with the cited literature. It has not been used to obtain another or the same degree.

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Dedication

First, I would like to thank my supervisor, Mgr. Peter Vršanský, Ph.D. (Earth Science Institute, Slovak Academy of Sciences), that gave me guidance and opportunity to work on Burmese amber. He also introduced me to the world of fossil cockroaches, which I will always appreciate.

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Last but definitely not least, I express my deepest gratitude to my family and friends, that cheered me up during the worst times and they were helpful every time I needed it.

Abstract

The dissertation presents an analysis of the cockroach fauna preserved in mid-Cretaceous Myanmar amber (98.9 Ma) also known as Burmese or Kachin amber. This study is key to understanding the evolutionary history of this insect order and brings new details in resolving the phylogeny of cockroaches. The work also reveals that most genera are known exclusively from Burmese amber. Certain genera are found to a lesser extent at other world sites, within Laurasia and Gondwana. 76 species described from Burmese amber demonstrate a remarkable spectrum of ecological and physical specializations, indicating the evolutionary adaptability of cockroaches. The families Alienopteridae and Umenocoleidae exhibit transitional characteristics, suggesting close relationship. The family Liberiblattinidae is known from 7 species in 3 genera. The family Blattulidae includes 4 species, with the genus *Oceloblattula* also found in Lebanese amber. The families Corydiidae and Blattidae exhibit morphological similarities, exemplified by species such as *Bubosa poinari*. Endemic families such as Manipulatoridae and Fractaliidae have specific ecological roles that were replaced by other insect groups in the course of evolution. The family Mesoblattinidae is recorded with six species, including some with preserved oothecae. The families Ectobiidae and Blaberidae are less common in Burmese amber, with a total of 4 species documented. Cockroaches in the Cretaceous period evolved to fulfill a wide range of ecological roles, including mimicking hymenopterans, pollination, predation, and troglobites. Some species have developed unique adaptations to defend and fight against predators, such as camouflage to blend in with the surroundings and, oppositely, aposematic coloration to deter them. This work fills a gap in the research of the details of phylogeny and taxonomy of cockroaches based on fossil material. The work highlights the importance of detailed fossil analysis for understanding evolutionary history and phylogenetic relationships of stem and crown groups of cockroaches.

Key words: Burmese amber, Cretaceous, cockroaches, phylogeny, taxonomy

Abstrakt

Dizertačná práca predstavuje analýzu fauny švábov zachovanej v mjanmarskom jantáre zo strednej kriedy (98,9 Ma), tiež označovanom ako barmský alebo kačinský jantár. Táto štúdia je kľúčová pre pochopenie evolučnej histórie tohto hmyzu a prináša nové detaily pri riešení fylogeniezy švábov. Práca tiež odhaľuje, že väčšinu rodov poznáme výlučne z mjanmarského jantáru. Naopak, v menšej miere určité rody nachádzame v aj na iných svetových lokalitách, v rámci Laurázie a Gondwany. Celkom 76 druhov opísaných z barmského jantáru demonštruje pozoruhodné spektrum ekologických a fyzikálnych špecializácií, čo svedčí o evolučnej prispôsobivosti švábov. Čelade Alienopteridae a Umenocoleidae vykazujú prechodné charakteristiky, čo naznačuje blízku príbuznosť. Čelaď Liberiblattinidae je známa zo 7 druhov v 3 rodoch. Čelaď Blattulidae zahŕňa 4 druhy, pričom rod *Oceloblattula* nájdeme aj v libanonskom jantári. Čelade Corydiidae a Blattidae vykazujú morfológické podobnosti, ktorých príkladom sú druhy ako *Bubosa poinari*. Endemické rodiny ako Manipulatoridae a Fractaliidae majú špecifické ekologické úlohy a rodové spojenia. Čelaď Mesoblattinidae je zaznamenaná so šiestimi druhmi, vrátane niektorých so zachovanými ootékami. Čelade Ectobiidae a Blaberidae sú v barmskom jantáre menej bežné, sú zdokumentované dokopy 4 druhy. Šváby sa v období kriedy vyvinuli tak, aby zastávali širokú škálu ekologických úloh, vrátane mimikovania blanokrídlovcov, opelovania, predácie a výskytu v jaskyniach. Niektoré druhy si vyvinuli jedinečné adaptácie na boj s predátormi, ako je kamufláž pri ktorom splynuli s okolím a naopak aposematické sfarbenie na ich odradenie. Táto práca vyplňa medzeru vo výskume detailov fylogeniezy a taxonómie švábov na základe fosílného materiálu. Práca vyzdvihuje dôležitosť podrobnej analýzy fosílií pre pochopenie evolučnej histórie a fylogenetických vzťahov kmeňových a korunových skupín švábov.

Kľúčové slová: burmský jantar, krieda, šváby, fylogenieza, taxonómia

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1. Introduction

1.1 Aim of the thesis

Cockroaches preserved in Mesozoic amber, are crucial in paleontological studies as they offer insights into the evolutionary processes and biodiversity of the past. Their study contributes significantly to the field of phylogeny and taxonomy, especially in the context of Cretaceous insect biodiversity. Despite the abundance of fossilized specimens, there is a persistent challenge in accurately resolving the phylogenetic tree of cockroaches. This research addresses the need for detailed and accurate descriptions of these fossilized cockroaches to enhance our understanding of their evolutionary history. The primary aim of this Dissertation is to gather data on the cockroach fauna preserved within mid-Cretaceous Myanmar amber. This objective emerges from the need to address the persistent challenges in resolving the phylogenetic tree of cockroaches. This work seeks to enhance our understanding of the evolutionary history of these insects. Accurate fossil descriptions are vital for the correct calibration of these phylogenetic trees. Additionally, the concept for this research was significantly influenced by the extensive accessibility of specimens provided by collectors engaged in scholarly research, who have made this material available.

1.2 Material and Methods

The amber pieces were covered with glycerine and cover slip to minimize optical distortions. The specimens were examined with a Motic SMZ171 stereo microscope. The photographs were made on Keyence VHX-7000 digital microscope. Image enhancement was done using Adobe Photoshop 2022-2024. Digital illustrations were made using iPad 11inch and Apple pen and Vectornator (now Curve) software. The text of the thesis was written in L^AT_EX. The script is available at my Github repository (<https://github.com/Luci-netizen>).

1.2.1 Geological setting

The cockroaches from this Dissertation thesis are exclusively from Kachin amber. It is important to note that the usage of the name "Myanmar amber" in this thesis implies to Kachin amber, commonly known as Burmese amber (Zheng et al., 2018). The age of the Kachin amber (the name comes from the state in northern Myanmar, where the amber localities are situated) is generally accepted at 98.9 Ma as calculated on U/Pb absolute dating of Zircons, which were found in the same layer of volcanic siltstones as the amber (Shi et al., 2012). This has been confirmed by the relative dating of the inclusions from

the amber (Zherikhin & Ross, 2000). Additionally to Kachin Myanmar amber, there is younger Talin amber from central Myanmar. The amber used in the research comes from the Hukawng Valley in Kachin, Myanmar (26°20'N, 96°36'E), as documented by Kania et al. (2015). These ambers range in hue from a pale yellow to a deep orange. Several pieces were more deeply embedded and required thorough cleaning and polishing using a variety of sandpapers from coarse to fine grit.

1.2.2 Abbreviations

The nomenclature for the wing venation in this thesis follows the Comstock & Needham (1898) system. C- costa, Sc- subcosta, M- media, R- radius, A- anal vein, CuA- cubitus anterior, CuP- cubitus posterior. HW- hind wing, FW- fore wing.

2. Cockroach systematics

The superorder Dictyoptera is believed to be monophyletic and it houses mantises, cockroaches, and termites, with termites being in-group of Blattodea (=cockroaches) (Vršanský, 2002; Inward et al., 2007; Klass & Meier, 2006; Legendre et al., 2015). The enigmatic family Chresmodidae is also sometimes considered Dictyoptera, interpreted as water-skimming cockroaches belonging in the superfamily Corydioidea (Vršanský, 2020; Vršanský et al., 2019a). The interfamilial relationships of cockroaches are not resolved and general consensus is still yet to be agreed on. However, the majority of the latest molecular analyses show an agreement on the superfamilial level discussed in the text below.

2.1 The ancient origin of the order

The classification of the Dictyoptera order's origin remains a subject of ongoing debate. The sister group to Dictyoptera is probably a late Palaeozoic order Paoliida. Their synapomorphy is a concave anterior CuA vein on the forewing (Prokop et al., 2014). The "dictyopterid-paoliid" wing pattern is further recognized by Schubnel et al. (2020). The molecular estimates of the origin depend on if we count the oldest roachoids as dictyopterans. Those are fossils of *Qilianiblatta namurensis* from Namurian (Carboniferous) (Zhang et al., 2013). According to some interpretations it is stem-Blattodea (Guo et al., 2013). The estimated origination time based on molecular analyses for stem Dictyoptera is Middle-Late Devonian, with the crown group dating back to Late Carboniferous-Early Permian (Legendre et al., 2015), which would be consistent with considering the Namurian fossils. The diversification of Dictyoptera according Misof et al. (2014), however, happened much later, after Permian extinction, which was criticized in Tong et al. (2015-07-31). Li (2022) claims the crown Dictyoptera originated in Early Jurassic with crown Blattodea originating in middle Jurassic. From the most conservative point of view, the oldest undoubted fossil of crown Dictyoptera is a mantid-like ootheca ichnofossil from Carnian (Triassic), Argentina (Cariglino et al., 2020). The oldest crown Blattodea is *Archimesoblatta* from early Jurassic of Connecticut, USA (Huber et al. (2003)). The interpretation of the authors suggests that termite fossil record extends to Jurassic/Cretaceous based on the presence in Chernovskiy Kopi, Russia (Vršanský & Aristov, 2014). The age of these strata are claimed to be much younger (around 70 Ma) in Zhao et al. (2021), however, the citation for this claim is missing. Jouault et al. (2021) completely disregard the fossils from Chernovskiy Kopi. The second oldest termite fossils are from Lebanese amber (Zhao

et al., 2021).

2.2 The hypotheses on the superfamiliar relationships

In recent times, the opinion where Blaberoidea being sister to a clade comprising Corydioidea and Blattoidea seems to prevail (fig. 2.1a). This hypothesis is based on the molecular analyses such as Djernaes et al. (2012), Djernæs et al. (2015), Legendre et al. (2015) and Evangelista et al. (2019). The synapomorphy of these two superfamilies is the bivalve ovipositor which is related to the ancestral mode of oviposition.

The alternative hypotheses are the topologies where either Corydioidea (Inward et al., 2007), fig. 2.1b) or Blattoidea (Bourguignon et al., 2018), (fig. 2.1c) is sister group to the rest. The type c.) was suggested as well on the morphological traits such as proventriculus, sclerites of male genitalia, musculature of female genitalia and type of oviposition (McKittrick et al., 1964; Roth, 1970). In this point of view, the oviposition of Ectobiidae+Blaberidae and Corydiidae is similar because they rotate the ootheca- however, Corydiidae rotates it in a rather different way- the ootheca has a special structure serving as a holder that the female cockroach can grab on and carry it around (Bell et al., 2007). In the terms of types of Blastokinesis, we can see grouping by the reversion (R) vs. non-reversion (N) type blastokinesis (Fujita & Machida, 2017). This hypothesis follows the topology from fig. 2.1c), where there is a branching of living Dictyoptera to Mantodea (N) and Blattodea (N) which branches to Blaberoidea (N) (containing Ectobiidae, Blaberidae, Corydiidae and Nocticolidae) and Blattoidea (R).

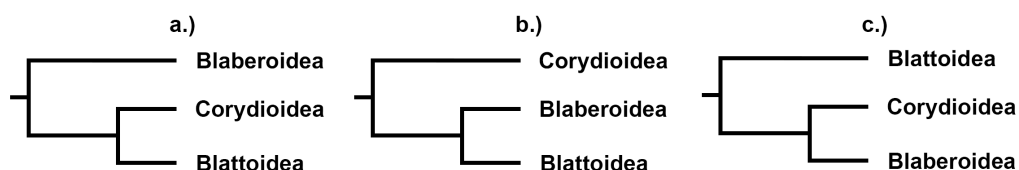


Figure 2.1: The tree topologies of major lineages in Blattodea according to various hypotheses. a.) Blaberoidea + (Corydioidea + Blattoidea) (based on Legendre et al. (2015)), b.) Corydioidea + (Blaberoidea + Blattoidea) (based on Inward et al. (2007)), c.) Blattoidea + (Corydioidea + Blaberoidea) (based on Bourguignon et al. (2018))

The systematics based on Vršanský et al. (2019b) hypothesizes about Blaberidae originating from the early diverging Cretaceous Blattidae. Termites are in the same lineage together with Corydioidea.

Opposed to Legendre et al. (2015), where the branches of Ectobiidae and Corydiidae + Nocticolidae are very long, in Evangelista et al. (2019) they are shorter, caused probably

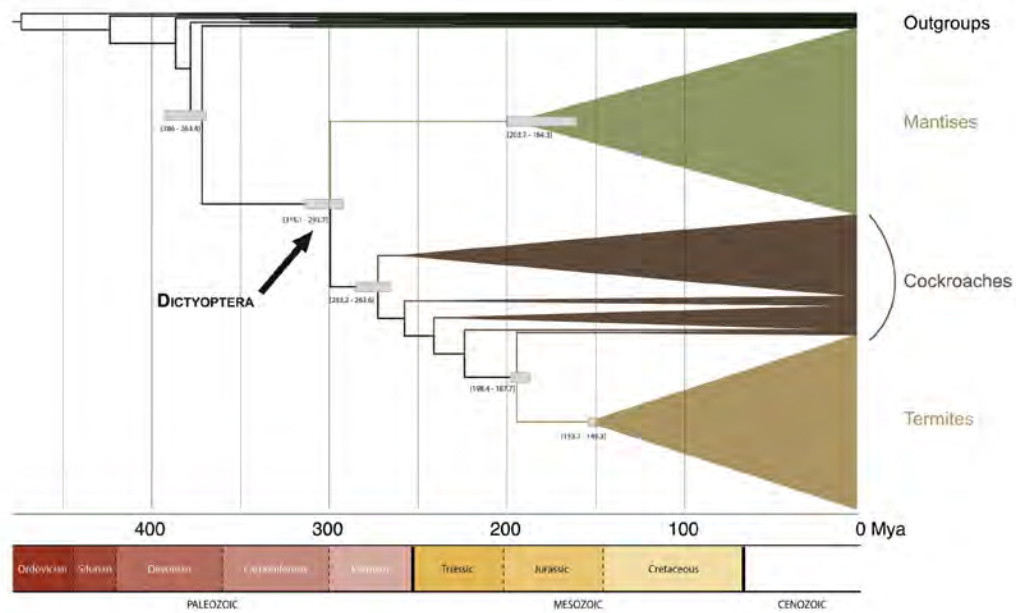


Figure 2.2: The chronogram from Legendre et al. (2015)

by the selecting the taxa representing higher diversity. The long branch of Nocticolidae is observed in Sendi et al. (2020b). The chronogram fig. 2.2 from Legendre et al. (2015) is inconsistent with the fossil record. Interpretations based on the fossil record show the origin on mantises from the family *Liberiblattinidae* (based on the wing venation, Vrřanský (2002)).

3. Review of Blattodea s.s. from Myanmar amber

Following chapter reviews and discussed the described species.

3.1 Phyloblattidae

The family Phyloblattidae is a stem family of "roachoids", existing before split of mantises. The richest fossil records comes from Carboniferous and Permian, when they were most diversified. They lived in the wet and every green ecosystems.

Pozabudnutie antiquorum Hinkelman et Vršanský, 2023 (fig. 3.1)

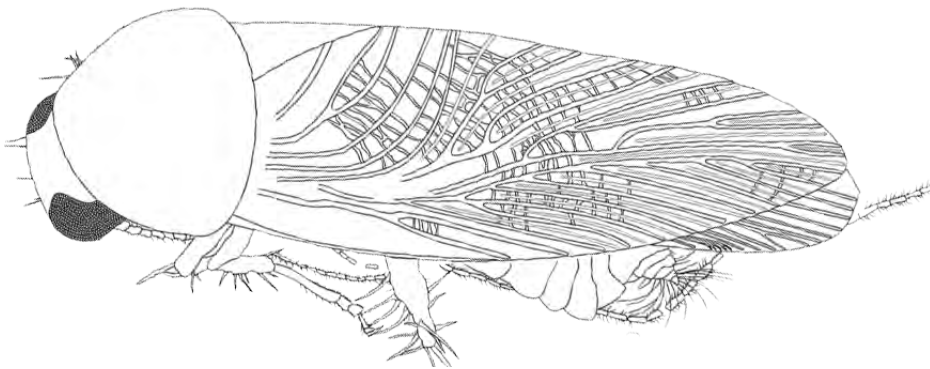


Figure 3.1: *Pozabudnutie antiquorum* modified from Vršanský et al. (2022)

This species was placed to Phyloblattidae based on symplesiomorphies such as short and wide body with short segments, terminal dichotomizations in hind wing, fore wing with directly descending M and CuA, dense reticulations, fore wing with non-parallel margins, three small ocelli and wide tarsi with thin claw. On the other hand, it differs by shorter Sc and different morphology of the ovipositor than other representatives of Phyloblattidae. If the placement in the family Phyloblattidae is correct, then it would be the longest cockroach lineage extending from Carboniferous to mid-Cretaceous. Nel et al. (2023) challenge the placement of the species in the family by the fact the new species is placed in the family Phyloblattidae based on symplesiomorphies, rather than apomorphies. Additionally, they claim the wing venation is non-phyloblattid (this is a problem of the the type species of the family- Vršanský, pers. com.).

3.2 Corydioidea

3.2.1 Manipulatoridae

This conspicuous family is so far known only from Myanmar amber. It represents early side branch of the stem group of Mantodea (Vršanský & Bechly, 2015), with the sister group Eadiidae. Other Mesozoic cockroach family is Raphidiomimidae, but this one has rather caloblattoid venation than corydioid (Vršanský & Bechly, 2015). Very contrasting is the ecological interpretation by the authors of the second species *Manipulatoides obscura* from this family (Li & Huang, 2022). They associate the morphology with florivorous diet rather than predatory life-style. Alternatively, they consider an option of kleptoparasitism on the cobwebs of spiders. The nymphs of this family have strongly convex frons. The autapomorphies of this family are saddle-like pronotum, elongated maxillary palps, and ocular sheaths that cover ocelli.

***Manipulator modificaputis* Vršanský et Bechly, 2015 (fig. 3.2a)** This is the type species for the family- the diagnosis is as for the family.

***Manipulatoides obscura* Li et Huang, 2022 (fig. 3.2b)** It is distinct from *Manipulator* due to its less pronounced leg spination, featuring type-C forefemoral spination rather than the type-A found in *Manipulator*. Moreover, the pronotum of *Manipulatoides* is flatter and has different pattern of colouration.

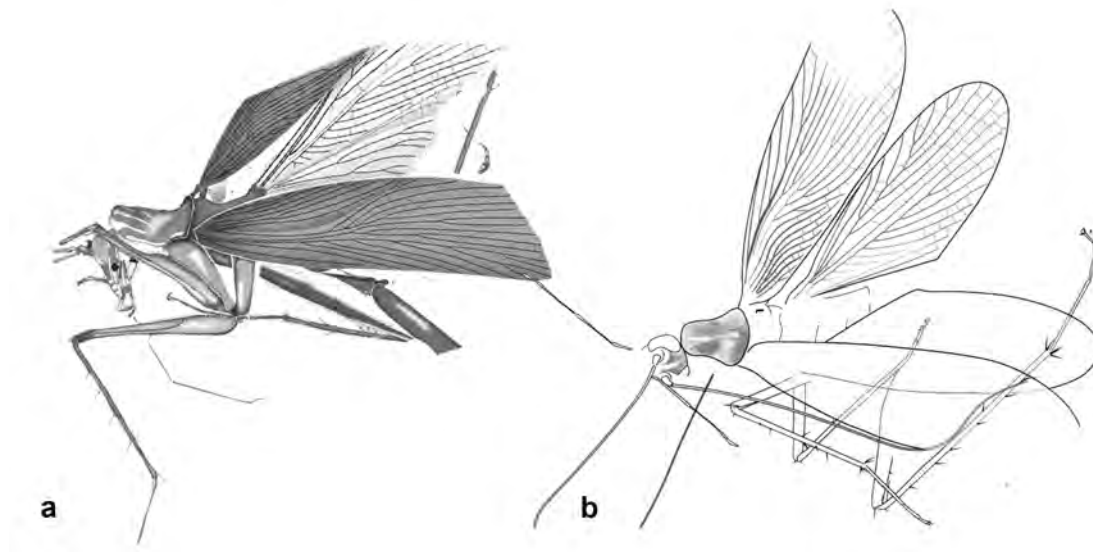


Figure 3.2: Representatives of the family Manipulatoridae from Myanmar amber a. *Manipulator modificaputis* modified from Vršanský & Bechly (2015), b. *Manipulatoides obscura* modified from Li & Huang (2022)

3.2.2 Fractaliidae

***Fractalia articulata* Hinkelman et Vršanský, 2021 (fig. 3.3)** The unique apomorphy of the family Fractaliidae is the breaking suture. The legs seem to have a raptorial function (although they seem cursorial).

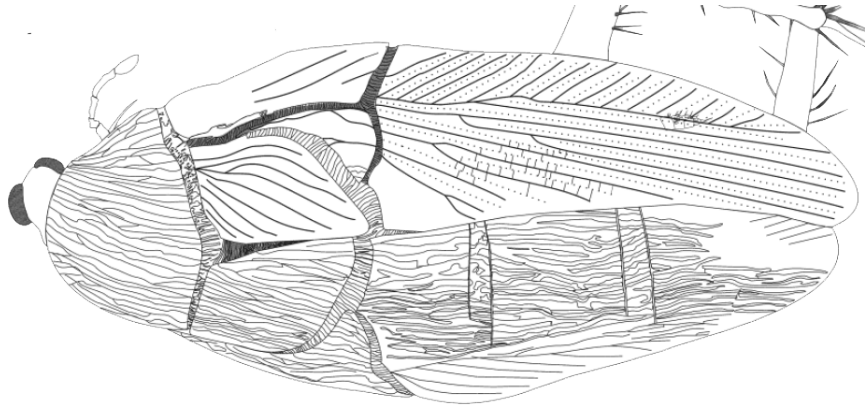


Figure 3.3: *Fractalia articulata* modified from Vršanský et al. (2021)

3.2.3 Corydiidae

The oldest representative of the family Corydiidae comes from Lower Cretaceous (Purbeck Formation, England). Alternatively, there is one unstudied impression of the wing from Upper Jurassic Gorevok in Altay, Russia, and one from Upper Jurassic, Karabastau which could hypothetically be a corydiid (Vršanský et al., 2022).

***Bimodala ohmkuhnlei* Šmídová, 2019 (fig. 3.4a)** Originally placed in the family Blattidae based on the resemblance with the genus *Spinka*, a close relative. They differ in the shape of pronotum and the colouration on the fore wings.

***Fragosublatta pectinata* Chen, Shih et Ren, 2021 (fig. 3.4b)** This species is related to the family Olidae (the replacement should be considered). Unlike the *Olenablatta vrsanskyi*, it lacks intercalaries and possesses larger pronotum.

***Magniocula apiculata* Qiu, Wang, et Che, 2019 (fig. 3.4c)** This species was placed to the subfamily Euthyrrhaphinae based on the presence of a minute body, an oversized clypeus extending beyond the antennal sockets, and two spines at the tip of the front femur. According to Sendi et al. (2020b), it belongs to Liberiblattinidae as the female possess externally protruding ovipositor (however representatives of Corydiidae, in fact, have bivalvate slightly protruding ovipositors).

***Magniocula paradoxona* Vršanská et Vršanský, 2022 (fig. 3.4d)** It differs from *M. apiculata* by having smaller eyes and by being more melanized.

***Nodosigalea burmanica* Li et Huang, 2018 (fig. 3.4e)** This cockroach has heterogeneous tarsi, having the tarsi on the first two pairs of legs with well-developed plantulae, while tarsi on hind legs carry spines, which authors interpret as adaptation for a rapid movement. According to Sendi et al. (2020b) it belongs to Olidae.

***Nodosigalea simplivena* Šmídová, 2022 (fig. 3.4f)** It differs from the *N. burmanica* by having four CuA veins, instead of 7.

***Pokemon oculiapertion* Vršanská, Hinkelman et Vršanský 2022 (fig. 3.4g)** Authors explain the placement in the family Corydiidae based on the similarities with certain characters of the genera *Magniocula*, *Spinka* and *Bimodala*. It has spotted fore wing.

***Piloscutumus discretus* Sendi, 2022 (fig. 3.4h)** Similar to *Magniocula*, but with richer setation on the fore wing and pronotum.

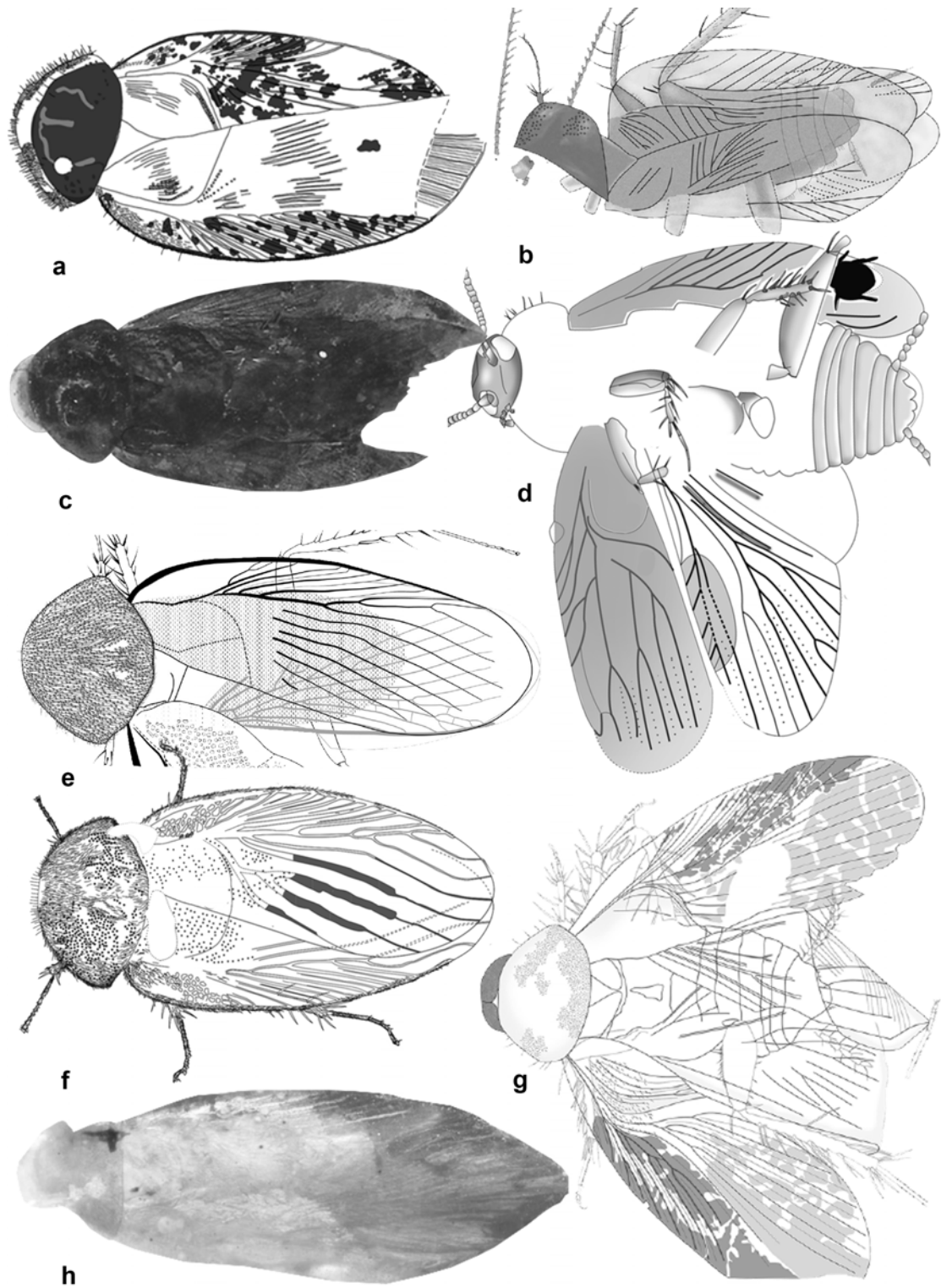


Figure 3.4: Representatives of the family Corydiidae from Kachin amber. a. *Bimodala ohmkuhnlei* modified from Vršanský et al. (2019b), b. *Fragosublatta pectinata* modified from Chen et al. (2021a), c. *Magniocula apiculata* modified from Qiu et al. (2019b), d. *Magniocula paradoxona* modified from Vršanský et al. (2022), e. *Nodosigalea burmanica* modified from Li & Huang (2018), f. *Nodosigalea simplivena* modified from Šmídová (2022), g. *Pokemon oculiapertion* modified from Vršanský et al. (2022), h. *Piloscutum discretus* modified from Vršanský et al. (2022)

Spinka fussa Vršanský, Šmídová *et* Barna, 2019 (fig. 3.5a) This species carries multiple body adaptations for the myrmecophily (more onto this in the chapter Vršanský *et al.* (2019b)).

Squamicaputa tubulosa Hinkelman *et* Koubová, 2022 (fig. 3.5b) It has four-segmented tarsi and sable-like shape of the fore wing.

Okruhliak vedec Vršanský *et* Hinkelman, 2022 (fig. 3.5c) *Okruhliak vedec* has almost completely round shape, which is the main character, distinguishing it from the other representatives. It has sable-like fore wings, like *Squamicaputa tubulosa*.

Corydoblatta subrotunda Hinkelman *et* Vršanský, 2022 (fig. 3.5d) *C. subrotunda* has fore wing of oval shape and "semimiliform" antennae.

Obscuroblatta rigida Hinkelman *et* Vršanský, 2022 (fig. 3.5e) The fore wings of this cockroach have thick a dark veins.

Table 3.1: A list of described species of the family Corydiidae from Myanmar amber

Genus	Species	Literature
<i>Bimodala</i>	<i>ohmkuhnlei</i>	Vršanský <i>et al.</i> (2019b)
<i>Fragosublatia</i>	<i>pectinata</i>	Chen <i>et al.</i> (2021a)
<i>Magniocula</i>	<i>apiculata</i>	Qiu <i>et al.</i> (2019b)
<i>Magniocula</i>	<i>paradoxona</i>	Vršanský <i>et al.</i> (2022)
<i>Nodosigalea</i>	<i>burmanica</i>	Li & Huang (2018)
<i>Nodosigalea</i>	<i>simplivena</i>	Šmídová (2022)
<i>Pokemon</i>	<i>oculiapertion</i>	Vršanský <i>et al.</i> (2022)
<i>Piloscutum</i>	<i>discretus</i>	Vršanský <i>et al.</i> (2022)
<i>Spinka</i>	<i>fussa</i>	Vršanský <i>et al.</i> (2019b)
<i>Squamicaputa</i>	<i>tubulosa</i>	Vršanský <i>et al.</i> (2022)
<i>Okruhliak</i>	<i>vedec</i>	Vršanský <i>et al.</i> (2022)
<i>Corydoblatta</i>	<i>subrotunda</i>	Vršanský <i>et al.</i> (2022)
<i>Obscuroblatta</i>	<i>rigida</i>	Vršanský <i>et al.</i> (2022)

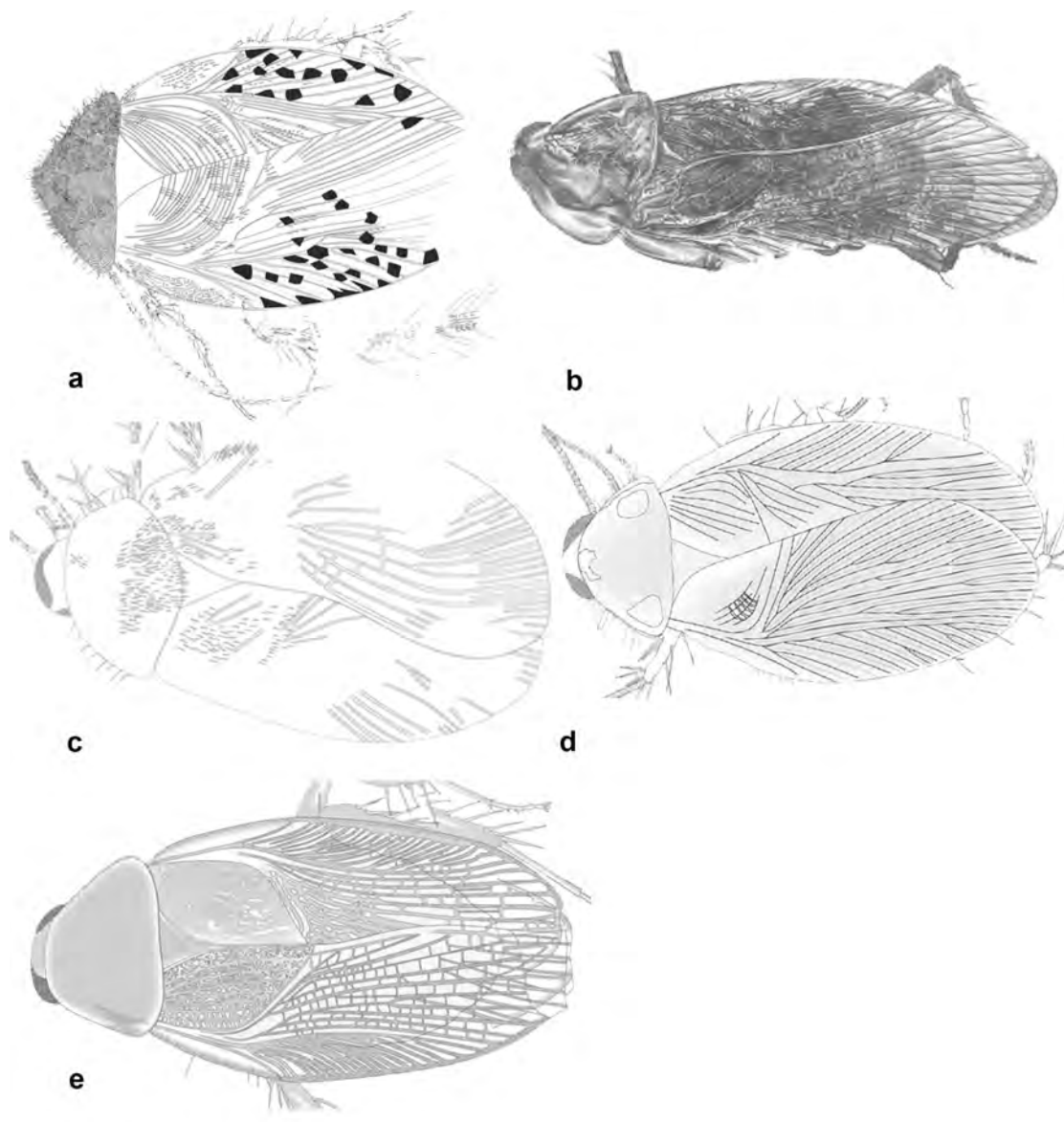


Figure 3.5: Representatives of the family Corydiidae from Kachin amber. a. *Spinka fussa* modified from Vršanský et al. (2019b), b. *Squamicaputa tubulosa* modified from Vršanský et al. (2022), c. *Okruhliak vedec* modified from Vršanský et al. (2022), d. *Corydoblatta subrotunda* modified from Vršanský et al. (2022), e. *Obscuroblatta rigida* modified from Vršanský et al. (2022)

3.2.4 Nocticolidae

The family of cave cockroaches Nocticolidae has number of cavernicolous adaptations such as loss the pigmentation, elongated limbs and small eyes. Based on the newest analyses, Latindiinae and Nocticolidae (Nocticolinae) are indeed closely related, as observed from fossil record (Han et al. (2023)).

***Crenocticola burmanica* Li et Huang, 2019 (fig. 3.6a)** The placement in the family is justified by the presence of small clavus and vannus, both pairs of wings membranous

and straight veins.

***Crenotricula svadba* Podstrelená, 2020 (fig. 3.6b)** *C. svadba* differs from *C. burmanica* in having comparatively elongated genital *hla* sclerite and slight variations in body proportions. It is worth noting that the position of this sclerite may have differed due to preservation factors.

***Mulleriblattina bowangi* Sendi et Vidlička, 2020 (fig. 3.6c)** The placement in the family is based on the small size, pale colouration, elongated extrimities, reduced wings, and tarsal arolium.

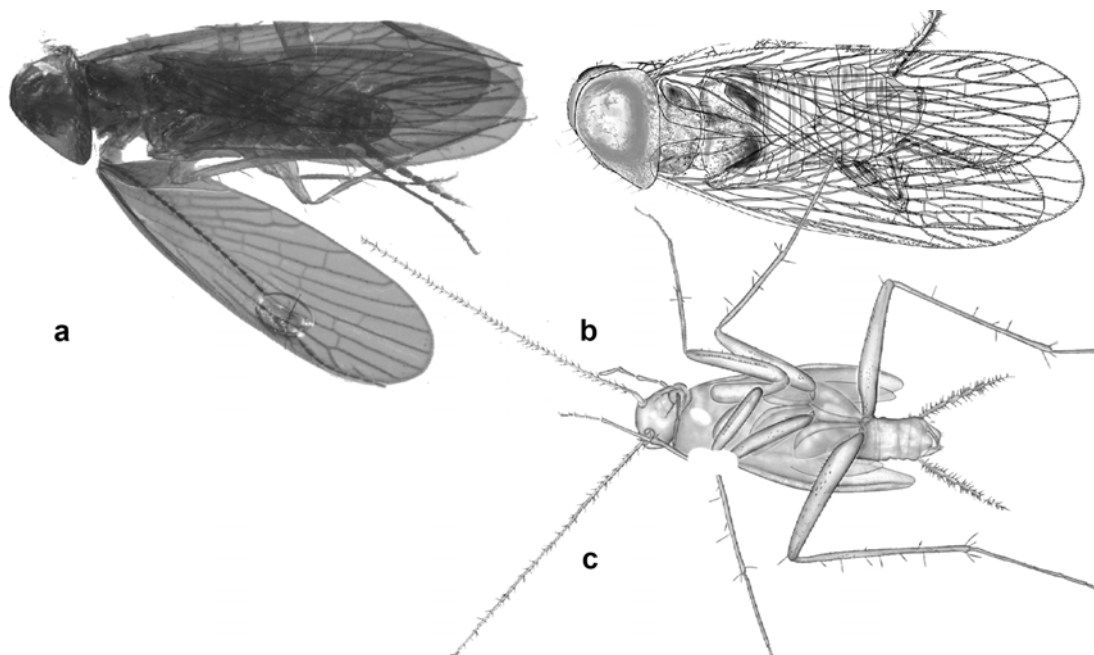


Figure 3.6: Representatives of the family Nocticolidae from Kachin amber. a. *Crenotricula burmanica* modified from Li & Huang (2020a), b. *Crenotricula svadba* modified from Sendi et al. (2020b), c. *Mulleriblattina bowangi* modified from Sendi et al. (2020b)

Olidae

The representatives of this group have pectinate antennae. They are closely related to Corydiidae (although their common ancestor was previously believed to be shared with Blattidae).

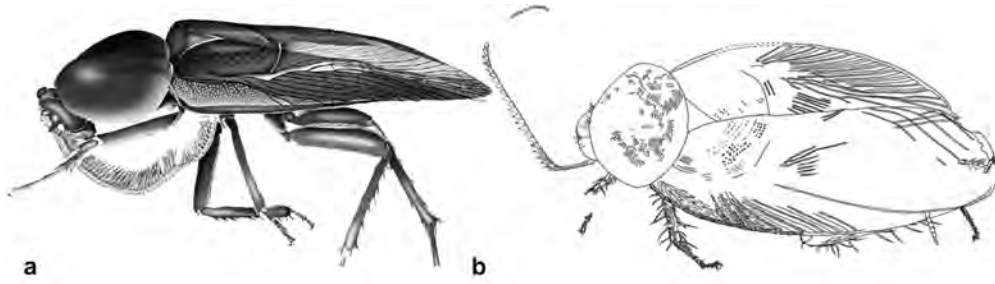


Figure 3.7: Representatives of the family Olidae from Kachin amber. a. *Ol xiai* modified from Vršanský & Wang (2017), b. *Olenablatta vrsanskyi* modified from Šmídová (2022)

***Ol xiai* Vršanský et Wang, 2017 (fig. 3.7a)** The only known cockroach species with fully developed bipectinnate antennae. The most notable autopomorphies are: rich setation, ocelli covered by roof-like covering sheaths and reduced femoral spine.

***Olenablatta vrsanskyi* Šmídová, 2022 (fig. 3.7b)** Similarly as *Fragosublatta pectinata* (fig. 3.4b), it has antennal protrusions, somewhat pectinate. The morphology is similar to *Bimodalia ohmkuhnlei* (fig. 3.4a).

3.2.5 Alienoptera

Originally described as a suborder sister to Mantodea The phylogenetic analysis with this result was made based on 58 characters. The characters indicating the sister relationship are mainly femoral brush, male genitalia (strong asymmetry) Bai et al. (2016). Shortly after, an alternative view was published by Vršanský et al. (2018a), that used 130 characters. In this view, the level of the Alienoptera was changed from order to family, and transferred to Blattodea, based on the similarities with the representatives of the family Umenocoleidae. This discovery was further developed in the work by Vršanský et al. (2021), where the authors describe winged alienopterids, that ultimately proves the common origin of Umenocoleidae and Alienopteridae. The consensus was presented in the paper Luo et al. (2021), where it was agreed that the Umenocoleidae and Alienopteridae form monophyly (named "Alienoptera"), which is sister group to Mantodea. It's worth mentioning that if Alienopteridae were to be synonymized with Umenocoleidae, the name 'alienopterids' would be replaced by 'umenocoleids,' a term that was coined much earlier in scientific literature. The representatives show highly diverse morphologies (disparity), ranging ants, wasps to even transformational mimicry.

Alienopteridae

Table 3.2: A list of described species of the family Alienopteridae from Myanmar amber

Genus	Species	Literature
<i>Aethiocarenum</i>	<i>burmanicus</i>	Poinar Jr & Brown (2017)
<i>Alienopterella</i>	<i>stigmatica</i>	Kočárek (2019)
<i>Alienopterus</i>	<i>brachyelytrus</i>	Bai et al. (2016)
<i>Alienopterix</i>	<i>mlynskyi</i>	Vršanský et al. (2021)
<i>Alienopterix</i>	<i>ocularis</i>	Vršanský et al. (2018a)
<i>Alienopterix</i>	<i>smidovae</i>	Vršanský et al. (2021)
<i>Caputoraptor</i>	<i>elegans</i>	Bai et al. (2018)
<i>Caputoraptor</i>	<i>vidit</i>	Vršanský et al. (2018a)
<i>Eminespina</i>	<i>burma</i>	Chen et al. (2021b)
<i>Formicamendax</i>	<i>vrsansky</i>	Vršanský et al. (2021)
<i>Meilia</i>	<i>jinghanae</i>	Vršanský et al. (2018a)
<i>Nadveruzenie</i>	<i>postava</i>	Vršanský et al. (2021)
<i>Teyia</i>	<i>branislav</i>	Vršanský et al. (2018a)
<i>Teyia</i>	<i>huangi</i>	Vršanský et al. (2018a)

***Aethiocarenum burmanicus* Poinar et Brown, 2017 (fig. 3.8a)** This species was originally assigned to its new order Aethiocarenodea, as an apterous adult. Later it was recognized that it is in matter of fact a nymph of an alienopterid (Vršanský et al. (2018a)). In Luo et al. (2021) it was assigned to the group of Morphotype I of alienopterid nymphs. These nymphs are gymnosperm pollinators and resemble ants.

***Alienopterus brachyelytrus* Bai, Beutel, Klass, Wipfler et Zhang, 2016 (fig. 3.8b)**
Alienopterus brachyelytrus is a type species for the family Alienopteridae.

***Alienopterella stigmatica* Kočárek, 2018 (fig. 3.8c)** The author of this taxon was first to observe unequal length of claws on tarsi. He compared the morphology and function of euplantulae with rock crawlers and hypothesizes about the predatory mode of life, that filled the niche of predators of freshly evolved angiosperm pollinators.

***Alienopterix mlynskyi*, Sendi 2021 (fig. 3.8d)** One of the fully fore winged representatives of Alienopteridae. It was differentiated from the other representatives of the genus by smaller amount of cercomeres, red compound eyes and slender antennomeres with scarce sensillae.

***Alienopterix ocularis*, Mlynský, Vršanský et Wang, 2018 (fig. 3.8e)** Type species of the genus. It was differentiated from the Umenocoleidae by having modified antennae, huge transversal eyes, hindwing with extremely long pterostigma and asymmetrical claw, and big arolium.

***Alienopterix smidovae*, Hinkelman, 2021 (fig. 3.8f)** Unlike the type species, it lacks pronotum colouration and has structured rectangular surface on the fore wings.

***Caputoraptor elegans*, Bai, Beutel et Wipfler, 2018 (fig. 3.8g)** The species has modified edge of the pronotum with indentations. The authors of the taxon interpreted this character as a structure to cling on the male during the copulation, as all known individuals of this species were females. In contrast, Kočárek (2018) interpreted this indented structure to squeeze the prey, since the studied individual was an immature male.

***Caputoraptor vidit*, Šmídová, 2018 (fig. 3.8h)** This species is discussed in detail in the section 5.2.

***Eminespina burma*, Chen, Zhang et Shi, 2021 (fig. 3.8i)** The species has "bunky" on the forewings. It has cylindrical pronotum, which authors compare to zorapteran *Zorotypus cenomanianus* (they list more characters, but those, however, do not seem to be similar only to zorapterans).

***Formicamendax vrsansky*, Hinkelman, 2020 (fig. 3.8j)** This species shows advanced staged of ant mimicry, including the elbowed antennae. The holotype of this species is preserved with attached angiosperm pollen on the leg.

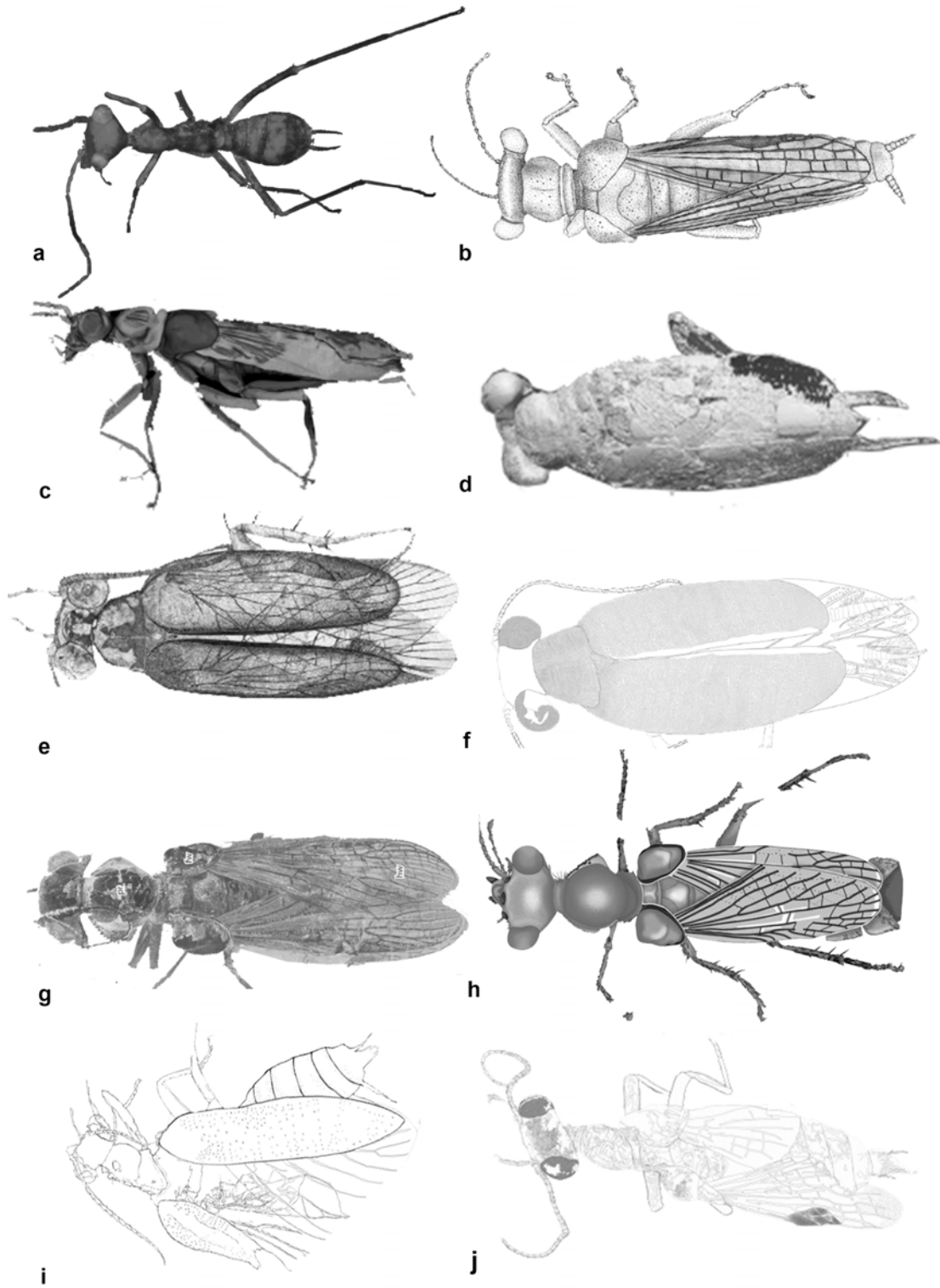


Figure 3.8: Representatives of the family Alienopteridae from Kachin amber. a. *Aethiocarenum burmanicus* modified from Poinar Jr & Brown (2017), b. *Alienopterus brachyleytrus* modified from Bai et al. (2016), c. *Alienopterella stigmatica* modified from Kočárek (2019), d. *Alienopterix mlynskyi* modified from Vršanský et al. (2021), e. *Alienopterix ocularis* modified from Vršanský et al. (2018a), f. *Alienopterix smidovae* modified from Vršanský et al. (2021), g. *Caputoraptor elegans* modified from Bai et al. (2018), h. *Caputoraptor vidit* modified from Vršanský et al. (2018a), i. *Eminespina burma* modified from Chen et al. (2021b), j. *Formicamendax vrsansky* modified from Hinkelman (2020)

***Meilia jinghanae*, Vršanský et Wang, 2018 (fig. 3.9a)** The species resemble the *Alienopterus brachyelytrus*. Unlike the type species for the family, it has aposematic colouration similar to living solitary bee *Epeleoidea coecutiens*.

***Nadveruzenie postava*, Vršanský, Hinkelman et Sendi, 2021 (fig. 3.9b)** Together with the genus *Alienopterix* it belongs to the subfamily Alienopterixinae, that is characterized by pronotum without posterior portion that is present in other alienopterids and fully developed fore wings. It differs from the genus *Alienopterix* by fenestrate structure of the fore wings.

***Teyia branislav*, Vršanský et Wang, 2018 (fig. 3.9c)** The genus *Teyia* was created to accomodate alienopterids with narrow pronotum, and triangular head.

***Teyia huangi*, Vršanský, Mlynský et Wang, 2018 (fig. 3.9d)** It differs from the type species by minor details, such as shorter antennae, slightly longer body and number of cercomeres.

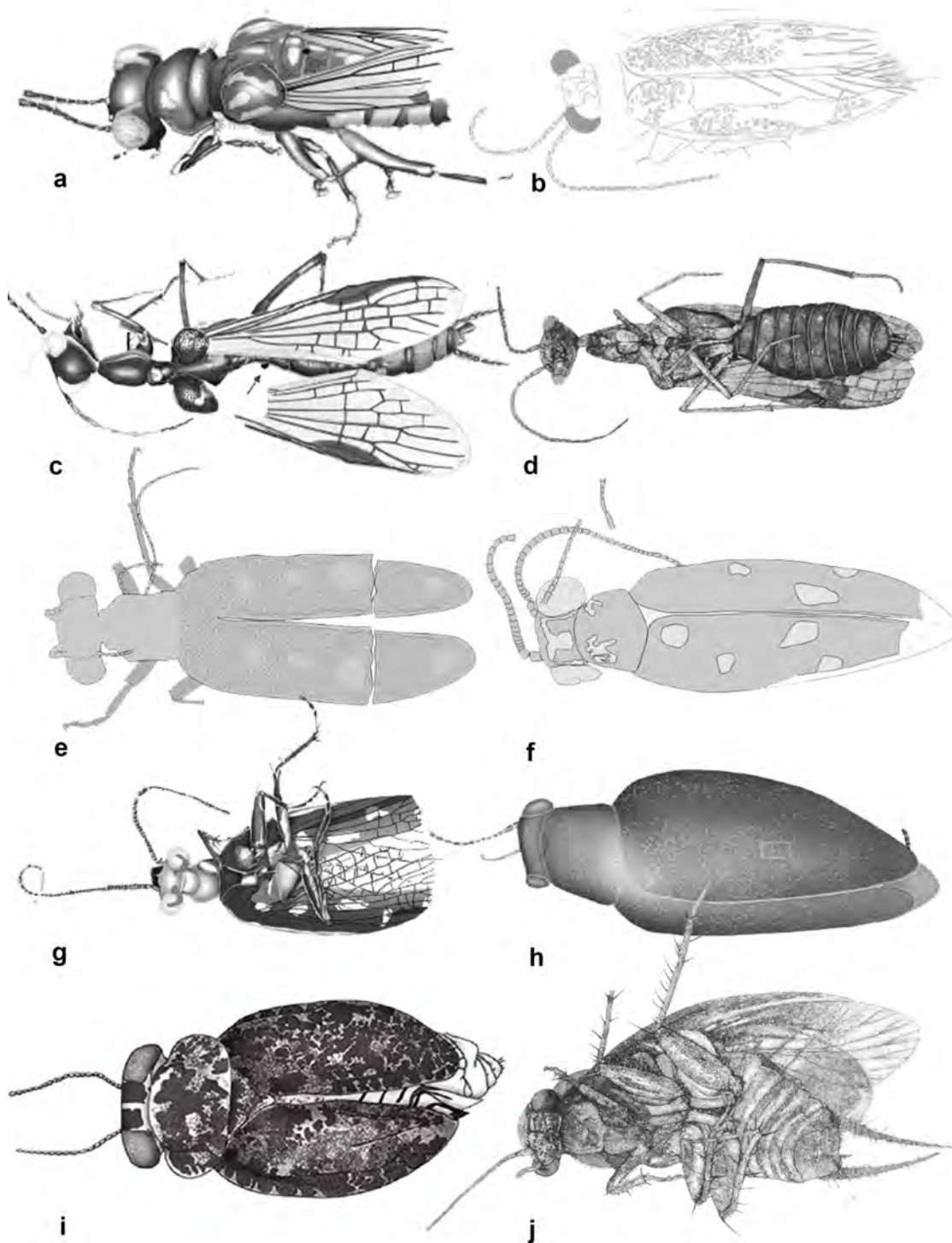


Figure 3.9: Representatives of the family Alienopteridae and Umenocoleidae from Kachin amber. a. *Meilia jinghanae* modified from Vršanský et al. (2018a), b. *Nadveruzenie postava* modified from Vršanský et al. (2021), c. *Teyia branislav* modified from Vršanský et al. (2018a), d. *Teyia huangi* modified from Vršanský et al. (2018a), e. *Vzrkadlenie karneri* modified from Sendi et al. (2023a), f. *Vzrkadlenie saintgermaini* modified from Sendi et al. (2023a), g. *Vzrkadlenie miso* modified from Sendi et al. (2020a), h. *Antophiloblatta hispida* modified from Sendi et al. (2020a), i. *Cratovitisma bechlyi* modified from Podstrelená & Sendi (2018), j. *Jantaropterix ellenbergeri* modified from Mlynský et al. (2019)

Umenocoleidae

Table 3.3: A list of described species of the family Umenocoleidae from Myanmar amber

Genus	Species	Literature
<i>Vzrkadlenie</i>	<i>karneri</i>	Sendi et al. (2023a)
<i>Vzrkadlenie</i>	<i>saintgermaini</i>	Sendi et al. (2023a)
<i>Vzrkadlenie</i>	<i>miso</i>	Sendi et al. (2020a)
<i>Antophiloblatta</i>	<i>hispida</i>	Sendi et al. (2020a)
<i>Cratovitisma</i>	<i>bechlyi</i>	Vršanský et al. (2018a)
<i>Jantaropterix</i>	<i>ellenbergeri</i>	Mlynský et al. (2019)
<i>Perspicius</i>	<i>pilosus</i>	Koubová & Mlynský (2020)
<i>Perspicius</i>	<i>vranskyi</i>	Koubová & Mlynský (2020)
<i>Archaeospinapteryx</i>	<i>tartarensis</i>	Sendi et al. (2023a)
<i>Trapezionotum</i>	<i>vranskyi</i>	Sendi et al. (2023a)
<i>Poikiloprosopon</i>	<i>celiae</i>	Sendi et al. (2023a)

***Vzrkadlenie karneri*, Sendi et Cumming, 2023 (fig. 3.9e)** The splotches on the fore wing are aligned along the fore wing.

***Vzrkadlenie saintgermaini*, Sendi et Cumming, 2023 (fig. 3.9f)** This species unlike the others in the genus, has coloured intraocular space. The distribution of the splotches without colouration and the colouration on the antennae are different as well.

***Vzrkadlenie miso*, Sendi et Cumming, 2023 (fig. 3.9g)** This species is a type for the genus. It was created to accommodate alienopterids that have compound eyes with sophisticated colouration, elongated bodies, fully developed fore wings with splotches that appear to be missing the elytrization. The nymphs are preserved with attached pollen grains.

***Antophiloblatta hispida*, Sendi, 2020 (fig. 3.9h)** The dorsal portion of the body of this species is fully covered by sensillae. It has reduced mouthparts and long needle-like ovipositor. The shape of the fore wing is strongly vaulted (that authors compare to the genus *Elytropterix*). It was preserved with pollen grains, the mouthparts indicate nectarivory.

Cratovitisma bechlyi, Podstrelená, 2018 (fig. 3.9i) Unlike the other umenocoleids, *C. bechlyi* has short ovipositor. It has bark colouration on the pronotum and fore wings.

Jantaropterix ellenbergeri, Mlynský, Wu et Koubová, 2019 (fig. 3.9j) The authors see the differences with the Lebanese species *J. lebanesis* in the lacking posterior part of pronotum and weak sclerotization of the fore wings. In the light of new observations we can see both characters are seen in other representatives of Umenocoleidae (and Alienopteridae) from Myanmar amber (see fig. 3.8f, fig. 3.9b, f, h, etc.). The nymphs of the species *Jantaropterix ellenbergeri* were preserved in a single piece of amber as eusynclussions (sensu Solórzano-Kraemer et al. (2023)), indicating these cockroaches laid eggs in mass together.

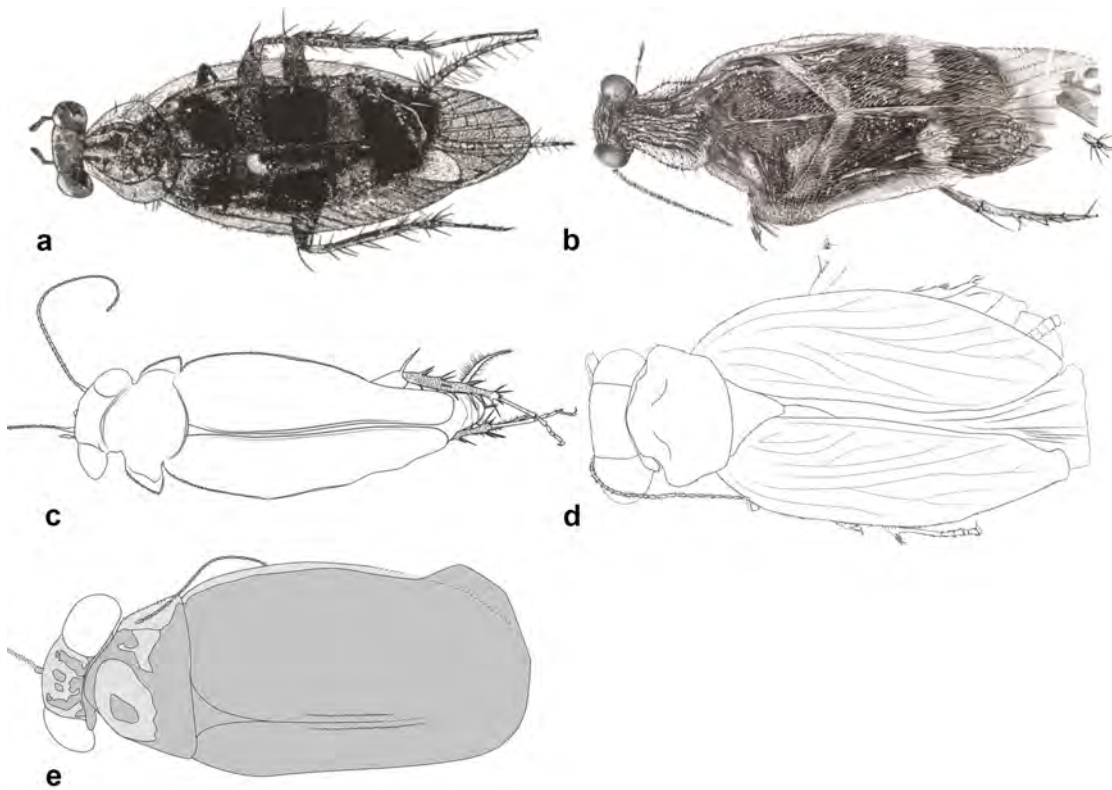


Figure 3.10: Representatives of the family Umenocoleidae from Kachin amber. a. *Perspicuus pilosus* modified from Koubová & Mlynský (2020), b. *Perspicuus vrsanskyi* modified from Koubová & Mlynský (2020), c. *Archaeospinapteryx tartarensis* modified from Sendi et al. (2023a), d. *Trapezionotum vrsanskyi* modified from Sendi et al. (2023a), e. *Poikiloprosopon celiae* modified from Sendi et al. (2023a)

Perspicuus vrsanskyi, Mlynský, 2020 (fig. 3.10b) The genus *Perspicuus* is closely related to the genus *Vitisma*. It differs by: having long hairs, the colouration on the fore wings, and more elongated body.

***Perspicuus pilosus*, Koubová, 2020 (fig. 3.10a)** *Perspicuus pilosus* differs from the type species *P. vrsanskyi* by minor differences such as smaller size and different distribution of pale areas on the fore wings. It is dominant species from burmite.

***Archaeospinapteryx tartarensis* Sendi et Cumming, 2023 (fig. 3.10c)** This species was designated for the umenocoleid cockroaches with distinctive shape of the pronotum with lateral protrusions.

***Trapezionotum vrsanskyi* Sendi et Cumming, 2023 (fig. 3.10d)** Umenocoleid with irridiscent colouration, superficially looking like *Cratovitisma*, but with different shape of pronotum and without bark colouration. The holotype is preserved with *Clas-sopolis* pollen on the head.

***Poikiloprosopon celiae* Sendi et Cumming, 2023 (fig. 3.10e)** *Poikiloprosopon celiae* has sophisticated coluration of the head, with eye-looking pattern on the pronotum. The overal shape of the body is similar to a beetle.

3.2.6 Liberiblattinidae

Table 3.4: A list of cockroaches from Myanmar amber belonging to the family Liberiblat-tinidae

Genus	Species	Literature
<i>Spongistoma</i>	<i>angusta</i>	Sendi et al. (2020a)
<i>Stavba</i>	<i>babkaeva</i>	Vršanský et al. (2018b)
<i>Stavba</i>	<i>vrsanskyi</i>	Chen (2020)
<i>Stavba</i>	<i>jarzembowski</i>	Li et al. (2020)
<i>Stavba</i>	<i>magnoculara</i>	Sendi (2022a)
<i>Stavba</i>	<i>delicata</i>	Sendi (2022a)
<i>Facioblatta</i>	<i>perfidia</i>	Hinkelman (2022c)

***Spongistoma angusta* Hinkelman, 2020 (fig. 3.11a)** The species *Spongistoma an-gusta* has mouthparts with unique adaption with ability for "sponging", i. e. sucking up liquid food. The catergorization in the family is based on plesiomorphic characters (same venation as the genus *Stavba*).

***Stavba babkaeva* Vršanská et Vršanský, 2019 (fig. 3.11b)** The species was placed in Libriblattinidae due to thick Sc and composition of HW. The paratype of this species is preserved with malformed wing.

***Stavba vrsanskyi* Chen, Chun et Chen, 2020 (fig. 3.11c)** It was placed in the genus based on similarities to *S. babkaeva*.

***Stavba jarzembowskii* Li, Zhao, Gao, Wang et Xiao, 2020 (fig. 3.11d)** It was placed in the genus based on: "*very small size, pale colouration (except for legs with dark longitudinal stripes), form of the forewing with sharp apex and rather short and wide costal field with simplified Sc, and having primitively raptorial legs with asymmetrically distributed spines on the front femur.*"¹

***Stavba magnioculara* Sendi, 2021 (fig. 3.11e)** The fore wing apex is round, unlike *S. jarzembowskii* and *S. babkaeva*. The R veins are similar to *S. vrsanskyi* and *S. delicata*. It has elongated head and very long antennae (around 140 antennomeres)

***Stavba delicata* Sendi, 2021 (fig. 3.11f)** It differs from other species of this genus by triangular pronotum.

***Facioblatta perfidia* Hinkelman, 2022 (fig. 3.11g)** Placement to the family Libriblattinidae is based on the presence of narrow Sc field, strongly curved CuP, strong sclerotisation in the anal area with fusion of veins, numerous cross-veins and reticulations. The special adaptation of this species is a spot interpreted as aposematic coloration

¹Li et al. (2020)

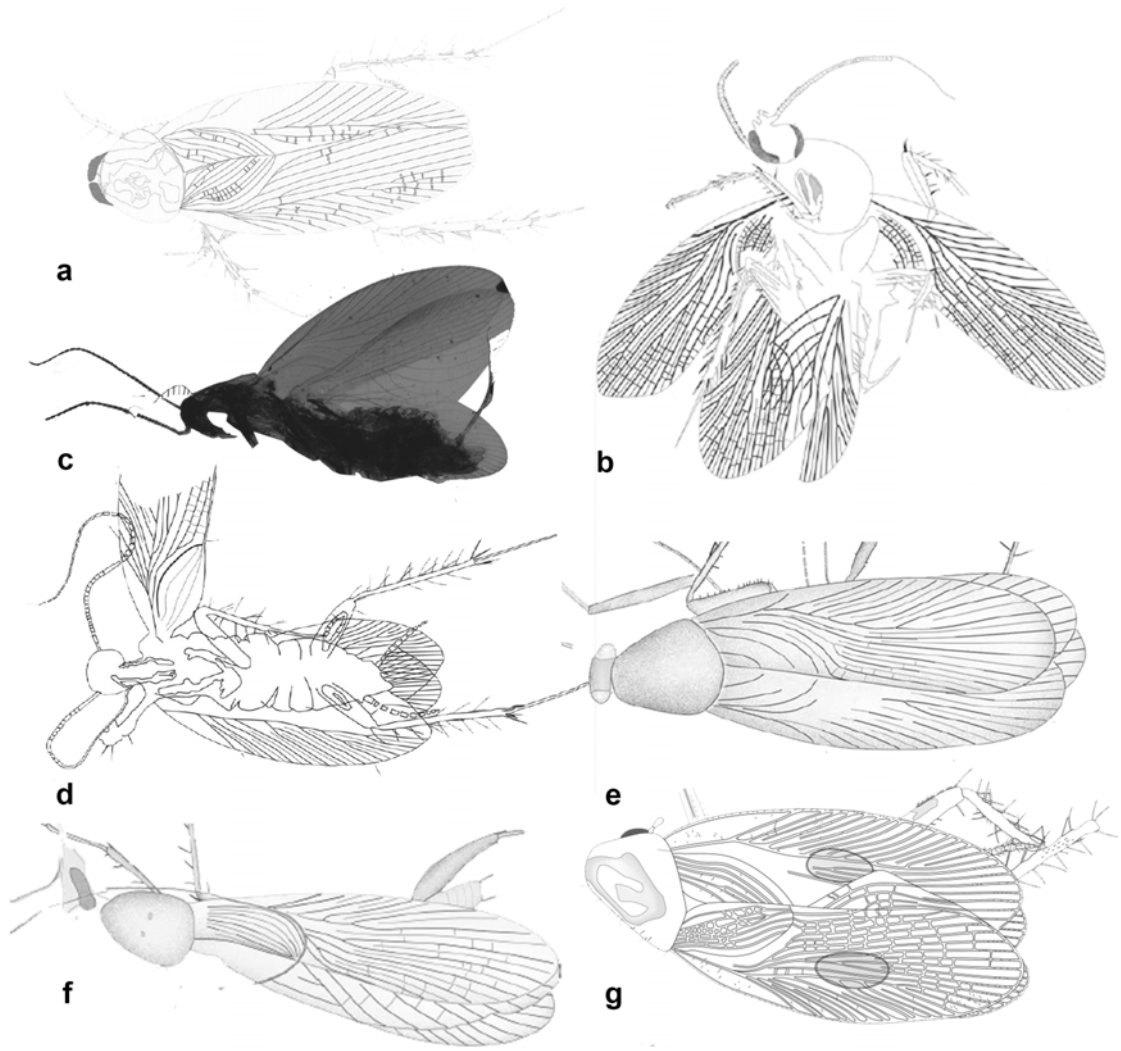


Figure 3.11: Representatives of the family Liberiblattinidae from Kachin amber. a. *Spongistoma angusta* modified from Sendi et al. (2020a), b. *Stavba babkaeva* modified from Vršanský et al. (2018b), c. *Stavba vrsanskyi* modified from Chen (2020), d. *Stavba jarzembowskii* modified from Li et al. (2020), e. *Stavba magnoculara* modified from Sendi (2022a), f. *Stavba delicata* modified from Sendi (2022a), g. *Facioblatta perfidia* modified from Hinkelman (2022c)

3.2.7 Blattulidae

Table 3.5: A list of cockroaches from Myanmar amber belonging to the family Blattulidae

Genus	Species	Literature
<i>Huablattula</i>	<i>vrsanskyi</i>	Zhang et al. (2023)
<i>Huablattula</i>	<i>hui</i>	Qiu et al. (2019a)
<i>Huablattula</i>	<i>jiewenae</i>	Qiu et al. (2019a)
<i>Ocelloblattula</i>	<i>margarita</i>	Vršanský et al. (2021)

***Huablattula vrsanskyi* Zhang, Li et Luo 2023 (fig. 3.12a)** Unlike the other species, it lacks pterostigma. The holotype of the species is female, possessing an ovipositor with sheaths. It has unique colouration on the pronotum and branched A vein on the fore wing.

***Huablattula hui* Qiu, Wan et Che 2019 (fig. 3.12b)** The placement in the family Blattulidae is established based on similar appearance with *Ocelloblattula*. It differs from the other *Huablattula* representatives by different shape and the pattern of the stripes of the pronotum.

***Huablattula jiewenae* Qiu, Wan et Che 2019 (fig. 3.12c)** This species has well-defined dark spot on the interior portion of the fore wing. It has four dark stripes on the pronotum.

***Ocelloblattula margarita* Koubová et Vršanský, 2021 (fig. 3.12d)** This species differs from *Ocelloblattula ponomarenkoi* by narrower pronotum and absence of distinct coloration.

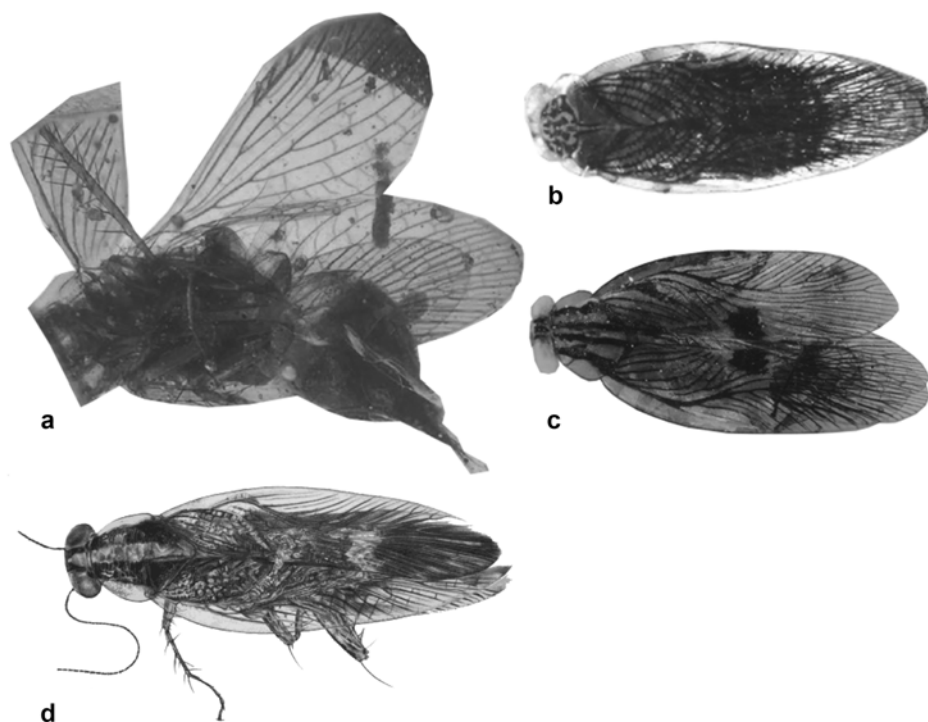


Figure 3.12: Representatives of the family Blattulidae from Kachin amber. a. *Huablattula vrsanskyi* modified from Zhang et al. (2023), b. *Huablattula hui* modified from Qiu et al. (2019a), c. *Huablattula jiewenae* modified from Qiu et al. (2019a), d. *Ocelloblattula margarita* modified from Vršanský et al. (2021)

3.3 Caloblattinidoidea

3.3.1 Raphidiomimidae

Raphidiomimula burmitica Grimaldi *et* Ross 2010 (fig. 3.13a) This is the only described representative of this family up to date. It is based on immature individual with elongated extremities, palps and mouthparts.

3.3.2 Ensiferoblattidae

Ensiferoblatta oecanthoides Li *et* Huang, 2023 (fig. 3.13b) *E. oecanthoides* and whole family Ensiferoblattidae as it is defined now, is closely related (if it does not belong completely) to the family Raphidiomimidae. These cockroaches are not dorso-ventrally flattened and are significantly elongated. Most of the members of the family Raphidiomimidae have externally protruding, but significantly shorter ovipositor as *E. oecanthoide*, however, *Falcatusiblatta gracilis* from Daohugou Formation, China has stout and strong ovipositor, too, probably adapted for laying the eggs within the soil or crevices (Liang *et al.*, 2018).

3.3.3 Family *incertae sedis*

Proceroblatta colossea Li *et* Huang, 2023 (fig. 3.13c) *P. colossea* probably belongs to the family Raphidiomimidae as well. It differs from the *E. oecanthoide* by having longer maxillary palps, richer spination on the legs, and longer cerci.

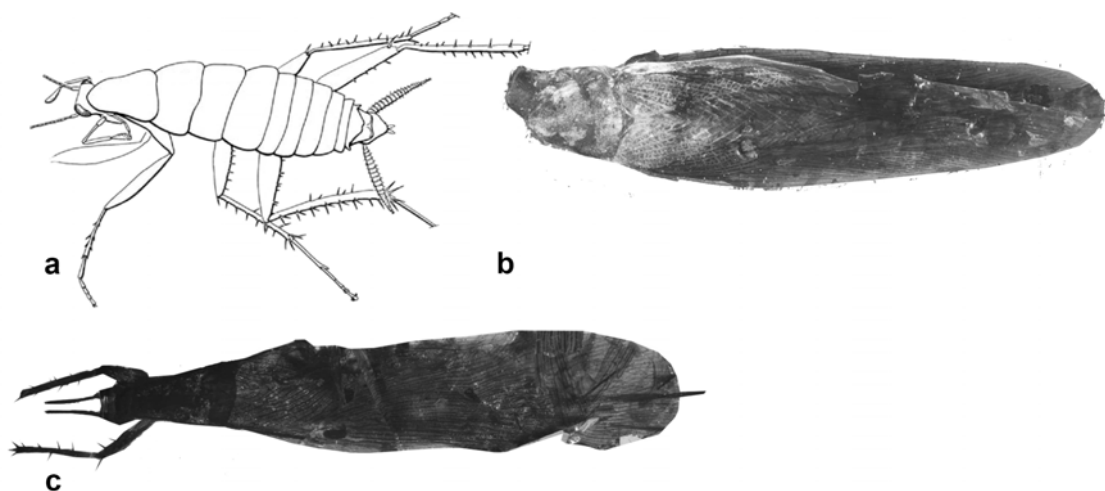


Figure 3.13: a. *Raphidiomimula burmitica* modified from Grimaldi & Ross (2004), b. *Ensiferoblatta oecanthoide* modified from Li & Huang (2023), c. *Proceroblatta colossea* modified from Li & Huang (2023).

3.4 Blattoidea

3.4.1 Mesoblattinidae

Table 3.6: A list of cockroaches from Myanmar amber belonging to the family Mesoblattinidae

Genus	Species	Literature
<i>Mesoblatta</i>	<i>maxi</i>	Hinkelman & Vršanská (2020)
<i>Sivis</i>	<i>tykadlo</i>	Kováčová (2023)
<i>Spinaeblattina</i>	<i>myanmarensis</i>	Hinkelman (2019)
<i>Mongolblatta</i>	<i>sendii</i>	Hinkelman (2022b)
<i>Cuniculoblatta</i>	<i>brevialata</i>	Hinkelman (2022a)
<i>Perlucipecta</i>	<i>lacrima</i>	Vršanský & Sendi (2023)

***Mesoblatta maxi* Hinkelman, 2020 (fig. 3.14a)** It has pronotum with sophisticated colouration, common in the family Mesoblattinidae. The authors add multisegmented styli together with irregular area between M and R veins as characters defining Mesoblattinidae. Long basal segment of terminalia in their opinion connect Mesoblattinidae with Olidae—that proves the relationship with Blattidae. The holotype was recorded with coprolites, that contain cycas pollen, diverse protists and bacteria. The work contains description of flagellate chlorophyte *Chlamydomonas hanublikanus* preserved from Burmese amber.

***Sivis tykadlo* Kováčová, 2023 (fig. 3.14b)** It is the first adult representative of the genus. All the other *Sivis* representatives are nymphs. This genus is characteristic with its dark continuous colouration on the pronotum.

***Spinaeblattina myanmarensis* Hinkelman, 2019 (fig. 3.14c)** The genus *Spinaeblattina* was created to house Cretaceous cockroaches with mesoblattinid habitus that have straight long simple branches. The author moreover, moves the *Piniblattella yixianensis* to this genus. The species from Myanmar amber, *S. myanmarensis* differs from the Yixian species by the shape and colouration of the pronotum, smaller body and slender tarsi.

***Mongolblatta sendii* Hinkelman, 2020 (fig. 3.14d)** The species differs from other representatives of the genus by minor differences (number and shape of fore wing veins).

Cuniculoblatta brevialeta Hinkelman, 2022 (fig. 3.14e) The only brachypterous member of Mesoblattinidae. The author hypothesizes the species was burrowing, based on the presence of strong pigmented legs and big pronotum.

Perlucipecta lacrima Vršanský et Sendi, 2023 (fig. 3.14f) The holotype of the species carries fascinating malformed cercus. The placement in this genus was based on slender antennae, rounded pronotum with pattern, colored fore wing except the costal area, short Sc, expanded M and narrow CuA.

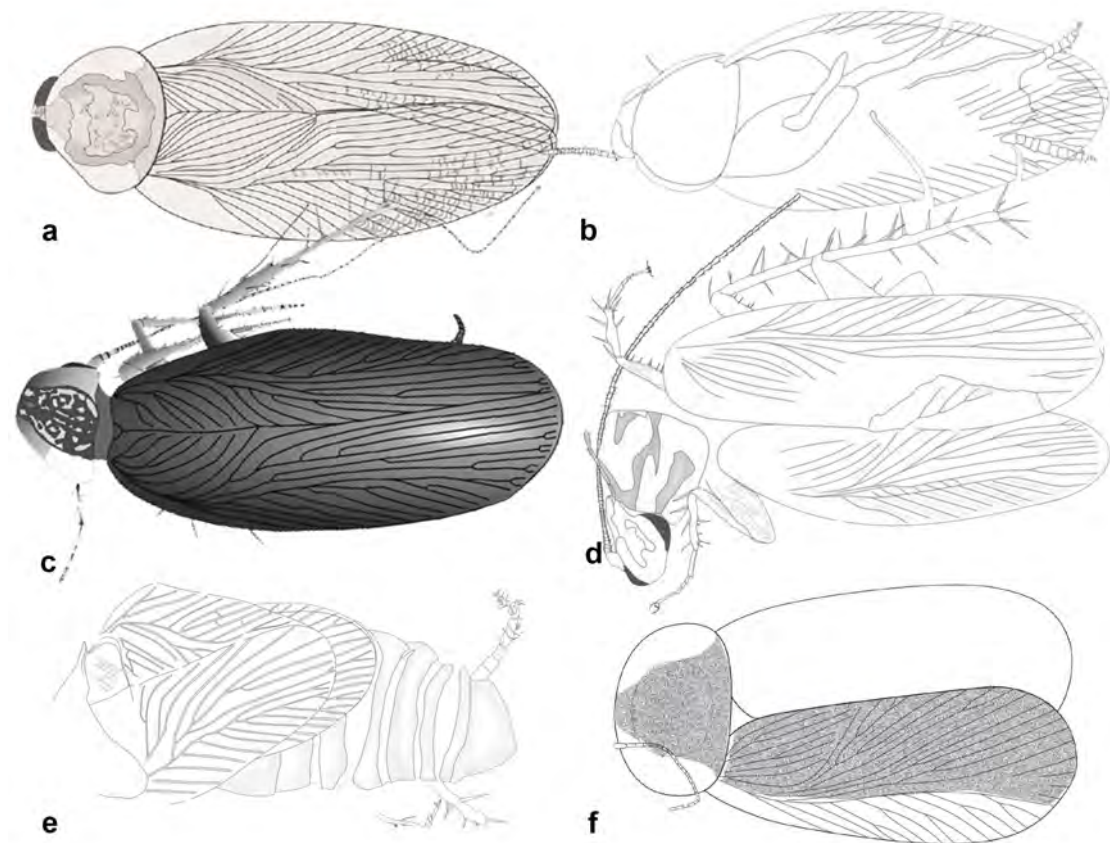


Figure 3.14: Representatives of the family Mesoblattinidae from Kachin amber. a. *Mesoblatta maxi* modified from Hinkelman & Vršanská (2020), b. *Sivis tykadlo* modified from Kováčová (2023), c. *Spinaeblattina myanmarensis* modified from Hinkelman (2019), d. *Mongolblatta sendii* modified from Hinkelman (2022b), e. *Cuniculoblatta brevialeta* modified from Hinkelman (2022a), f. *Perlucipecta lacrima* modified from Vršanský & Sendi (2023)

3.4.2 Blattidae

Balatronis cretacea Šmídová et Lei, 2017 (fig. 3.15a) *Balatronis cretacea* was the first described representatives of the family Blattidae from Burmese amber. It has aposematic colouration on the pronotum in the form of intricate pattern. The fore wings

have discontinuous colouration.

***Bubosa poinari* Šmídová 2020 (fig. 3.15b)** The species *Bubosa poinari* has striking bark colouration. More about the species in the chapter 5.4

***Cercoula brachyptera* Li et Huang, 2020 (fig. 3.15c)** Brachypterous species *Cercoula brachyptera* was assigned to the family Blattidae based on leg spination and bivalvate ovipositor.

***Cretaperiplaneta kaonashi* Qiu, Liu, Wang et Che, 2020 (fig. 3.15d)** The assignment near genus *Periplaneta* was made based on "head roundly triangular, vertex unconcealed by pronotum; 2) eyes large, wide apart, interocular space narrower than the distance between antennal sockets; 3) pronotum smooth, distal half narrower than basal half, anterior margin and posterior lateral corners rounded, hind margin slightly protruded; 4) male with tegmina and wings fully developed, exceeding the end of abdomen, venation complex; 5) legs with long spines, hind margins of femora with two rows of long but sparse spines, front femur type A2; 6) tarsomere 1 longer than the rest combined, arolia present; 7) subgenital plate symmetrical (or weakly asymmetrical); 8) styli slender; 9) cerci large, segmented and tapered toward apex."²

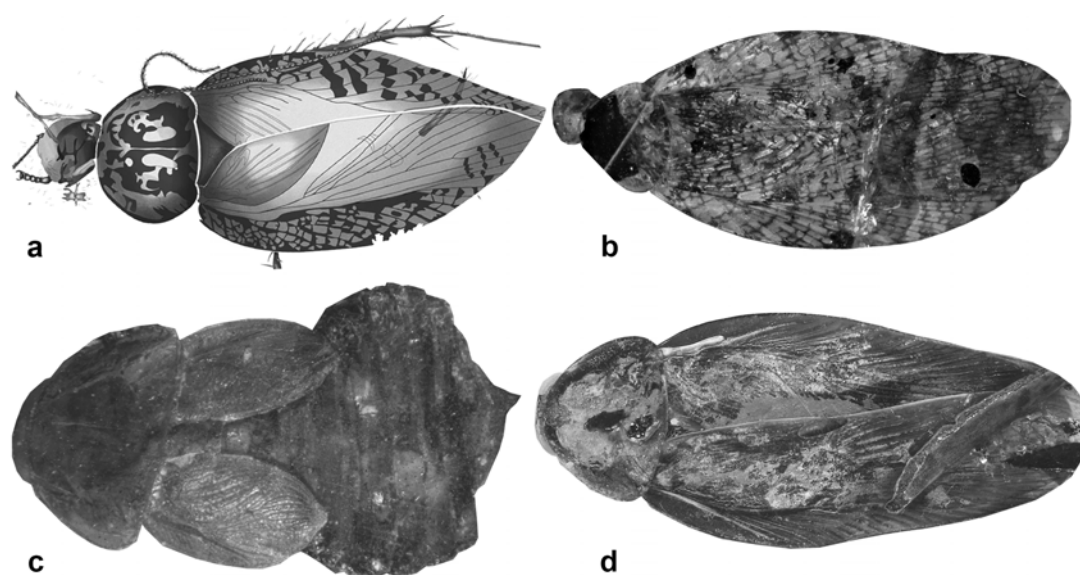


Figure 3.15: Representatives of the family Blattidae from Kachin amber. a. *Balatronis cretacea* modified from Šmídová & Lei (2017), b. *Bubosa poinari* modified from Šmídová (2020), c. *Cercoula brachyptera* modified from Li & Huang (2020b), d. *Cretaperiplaneta kaonashi* modified from Qiu et al. (2020)

²Qiu et al. (2020)

3.4.3 Family *incertae sedis*

***Hypercercoula jiewenae* Qiu, 2022** This cockroach was assigned to superfamily Blattoidea by the author Qiu (2022) based on the presence of spine-like process near the apex of the genital hook. They further compare the relationship with *Cercoula brachyptera* since they share slender, soft, slightly moniliform and acuminate cerci.

3.5 Blaberoidea

3.5.1 Blaberidae

Vršanský et al. (2013) considers this family not to emerge from the family Ectobiidae, as it is evident from molecular analysis, but from the family Mesoblattinidae, based on branched Sc and A.

***Morphna cretacica* Šmídová, 2022 (fig. 3.16)** This species was assigned to the family Blaberidae based on the venation characters- richly bifurcated Sc, wide R field, and presence intercalary veins and cross veins. More about this species in the chapter section 5.5.

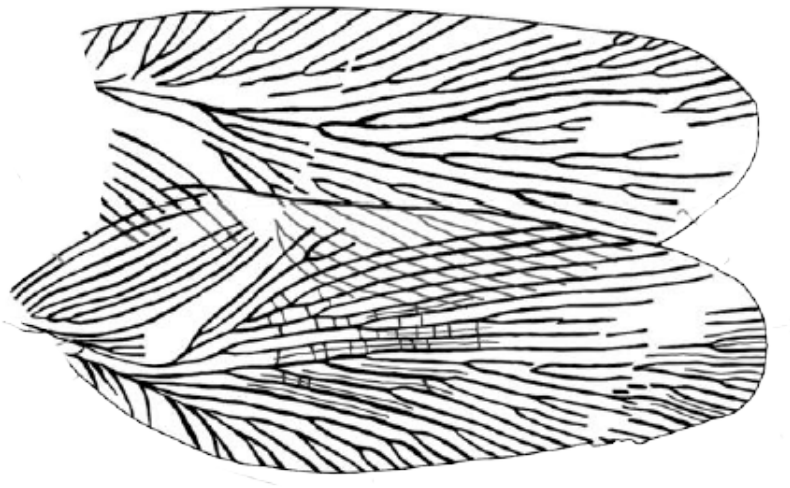


Figure 3.16: *Morphna cretacica* (Blaberidae) from Kachin amber modified from Šmídová et al. (2022).

3.5.2 Ectobiidae

This family is represented in Myanmar amber by three subfamilies: Ectoviinae (extinct) and living Pseudophylodromiinae and Blattelinae Sendi (2022b). The origin probably lays in the Mesoblattinidae.

***Ectoovia protecta* Sendi, 2022 (fig. 3.17a)** Sendi (2022b) made for this species its own subfamily which is characteristic of having bivalvate subgenital plate and very narrow FW R veins. It has strongly chitinized fore wings.

***Caligoptera hinkelmani* Sendi, 2022 (fig. 3.17b)** Assigned to the family Ectobiidae based on the presence of simplified HW M and tentavily assigned to the subfamily Blattelinae.

***Latiblattella karlgruberi* Sendi, 2022 (fig. 3.17c)** This cockroach was assigned to still living genus *Latiblattella* based on the big size and wing characters such as shape of the forewing margins straight, curved R, straight M and CuA and mdoerately stout spines.

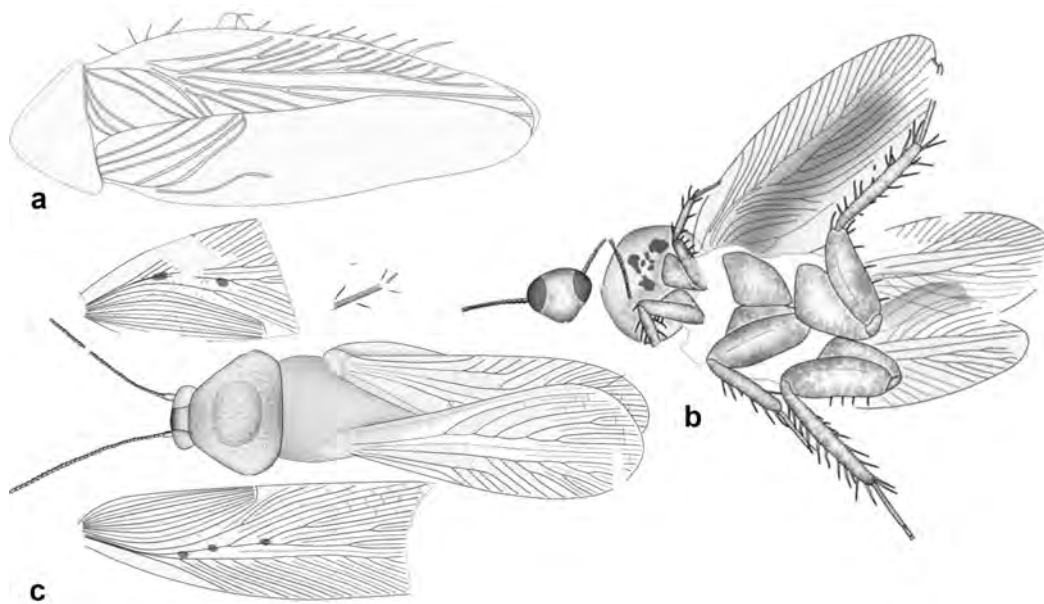


Figure 3.17: Representatives of the family Ectobiidae from Kachin amber. a. *Ectoovia protecta* modified from Sendi (2022b), b. *Caligoptera hinkelmani* modified from Sendi (2022b), c. *Latiblattella karlgruberi* modified from Sendi (2022b)

4. Cockroaches in other Cretaceous ambers

One of the striking features of Cretaceous ambers is the incredible diversity of faunas they contain. Different amber deposits from this period have yielded a wide range of organisms, including insects, arachnids, plants, feathers, and even small vertebrates. These amber inclusions provide valuable insights into the composition and structure of ancient ecosystems.

4.1 Canadian ambers

There is no work done on the relative diversity of the inclusions in Canadian ambers. However, the most represented orders seem to be Diptera, Hymenoptera and Hemiptera in the respective order (McKellar et al., 2010). As per today, there are no cockroaches recorded from the amber.

4.2 Taimyr amber

Cockroaches represent 0.3% of the collected material, which is extraordinarily low. This amber is very small in size, only the nymphs are recorded. The small size of amber pieces and the fact that this amber is the northernmost from all Cretaceous ambers might explain the low number of cockroach inclusions (Vršanský, 2019).

Table 4.1: A list of cockroaches from Yantardakh and Kheta ambers

Name of the species	Family	No. specimens	Literature
<i>Perlucipecta</i> sp.	Mesoblattinidae	1	Vršanský (2019)
Species indet.	Blattulidae	2	Vršanský (2019)
Species indet.	Liberiblattinidae	6	Vršanský (2019)
Species indet.	family incertae sedis	2	Vršanský (2019)

4.3 New Jersey (Raritan) amber

As anticipated, the most numerous animal group are arthropods. There is approximately 104 described species in 59 families including a mushroom basidiocarp and a tartigrade. 30% of all inclusions are nematoceran flies. A mantis *Ambermatniss wozniaki* and a termite *Carinatermes nascimbenei* are described from this amber, important for our understanding

of dictyopteran phylogeny.

Table 4.2: A list of cockroaches from Raritan amber

Name of the species	Family	No. specimens	Literature
<i>Jantaropterix new-jersey</i>	Umenocoleidae	adult and nymph	Vršanský (2003)

4.4 French amber

The Archingeay amber dates back to Late Albian (Early Cretaceous). Cockroaches constitute 4% of all inclusions (fig. 4.1). The most numerous family is Blattulidae. This amber represents a litter fauna.

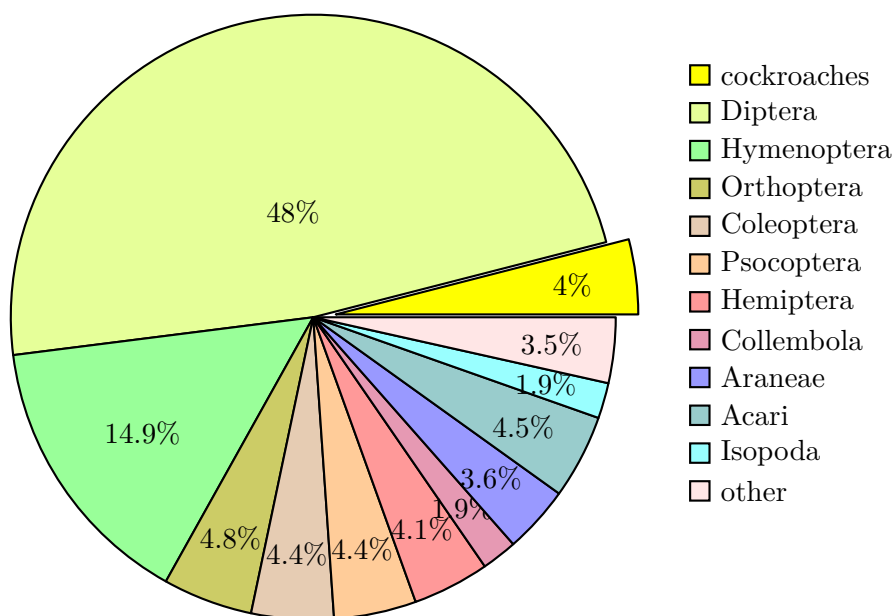


Figure 4.1: The pie chart showing the distribution of inclusions in Archingeay amber (modified from Perrichot (2004))

Table 4.3: A list of cockroaches from Archingeay, Buizine, and Sisteron ambers

Name of the species	Family	No. specimens	Literature
<i>?Blattella lengleti</i> (Buizine)	Ectobiidae	1	Vršanský (2008)
<i>Sociala perlucida</i>	Socialidae	1	Vršanský (2010)
gen. et sp. indet.	Caloblattinidae	1	Vršanský (2009)
<i>Batola nikolai</i>	Blattulidae	7	Vršanský (2009)
Continued on next page			

Table 4.3 – continued from previous page

Name of the species	Family	No. specimens	Literature
<i>Globula lake</i>	Blattulidae	3	Vršanský (2009)
<i>Leptolythica vin-centi</i>	Liberiblattinidae	1	Vršanský (2009)
-	Family indet.	2	Vršanský (2009)
<i>Eadia aidae</i>	Eadiidae	1	Vršanský (2009)
<i>Sivis odpo</i> (Sisteron)	Mesoblattinidae	2	Vršanský (2009)

4.5 Spanish amber

The cockroach fauna in Spanish amber is currently under investigation.

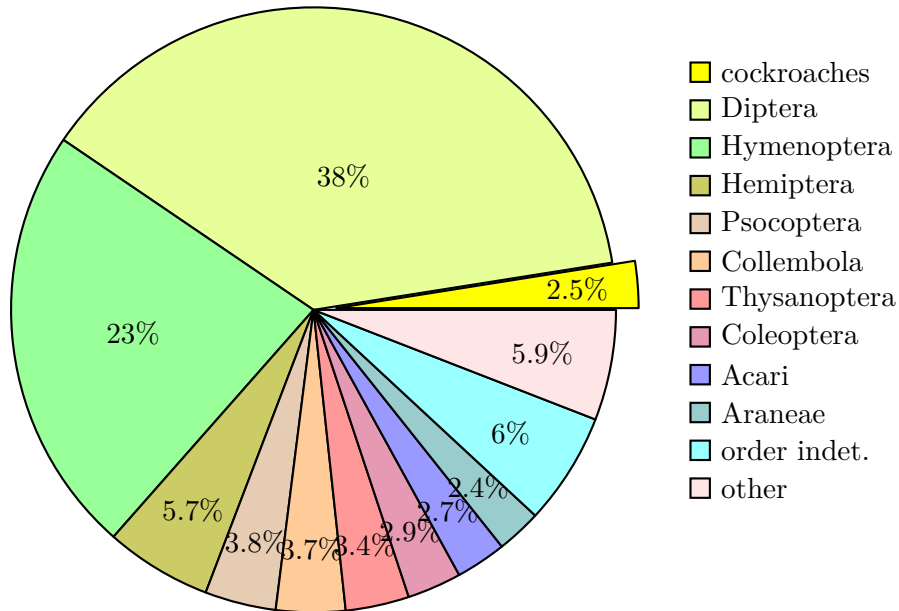


Figure 4.2: The pie chart showing the distribution of inclusions in Spanish amber (modified from Delclòs et al. (2007))

4.6 Lebanese amber

There are rich deposits of Lower Cretaceous Levant amber (Choufani et al., 2015), cockroaches are documented from ambers from Lebanon, Jordan and Syria. Additionally to these three countries, Levant amber is also known from Israel (without cockroach inclusions). The biggest quantities are, however, in Lebanon. The age ranges from the Lower Jurassic to Cenomanian (Azar et al., 2010). The resin that gave origin to Lebanese amber was produced in the gymnosperm forest, near the sea shore (Sendi et al., 2023b). This

amber contains the most ancient representatives of the families Blattidae and Ectobiidae.

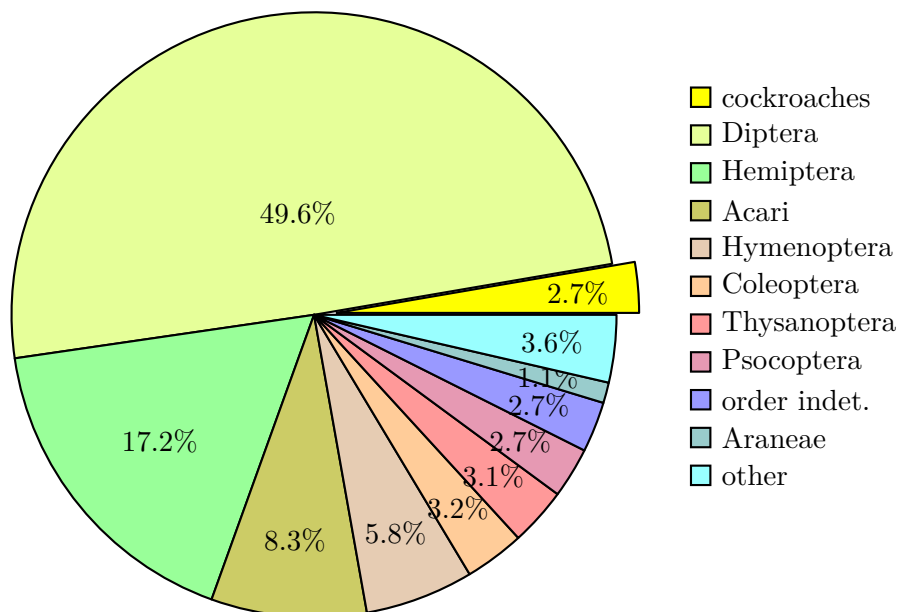


Figure 4.3: The pie chart showing the distribution of inclusions in Lebanese amber (modified from Azar et al. (2010)) but note only 0.4% of cockroaches is reported in Sendi et al. (2023b). It is hypothesised that low viscosity of resin resulted in lower occurrence of cockroaches.

Table 4.4: A list of cockroaches from Levant amber

Name of the species	Family	Amber	Literature
<i>Compunctiotypus hudai</i>	Umenocoleidae	Jordan	Kaddumi (2005)
<i>Cratovitisma cor-texi</i>	Umenocoleidae	Lebanon	Podstrelená & Sendi (2018)
<i>Cratovitisma spinosa</i>	Umenocoleidae	Lebanon	Sendi et al. (2023b)
<i>Grandocularis kur-nubinsi</i>	Umenocoleidae	Jordan	Kaddumi (2005)
<i>Lepidopterix veg-randis</i>	Umenocoleidae	Lebanon	Sendi et al. (2020a)
<i>Pseudojantaropterix lebani</i> (originally as <i>Jantaropterix</i> in Vrřanský (2003))	Umenocoleidae	Lebanon	Vrřanský (2003)

Continued on next page

Table 4.4 – continued from previous page

Name of the species	Family	Amber	Literature
<i>Cryptoblatta aquatica</i>	Liberiblattinidae	Lebanon	Vršanský et al. (2019a)
<i>Elisama globosa</i>	Blattulidae	Lebanon	Sendi et al. (2023b)
<i>Ocelloblattula ponomarenkoi</i>	Blattulidae	Lebanon	Anisyutkin & Gorochov (2008)
<i>Pravdupovediac neklam</i>	Blattulidae	Lebanon	Sendi et al. (2023b)
<i>Pravdupovediac maaloufi</i>	Blattulidae	Lebanon	Sendi et al. (2023b)
<i>Pseudomantina occisor</i>	Blattulidae	Lebanon	Vršanský et al. (2021)
<i>Miniblattina libera</i>	Liberiblattinidae	Lebanon	Sendi (2022a)
<i>Anenev asrev</i>	Blattidae	Syria	Vršanský et al. (2019b)
<i>Balatronis lebanensis</i>	Blattidae	Lebanon	Sendi & Azar (2017)
<i>Neoblattella nechapetomu</i>	Ectobiidae	Lebanon	Sendi et al. (2023b)
<i>Nymphoblatta azari</i>	Mesoblattinidae	Lebanon	Vršanský (2004)

4.7 Hungarian amber

The age of fossiliferous Hungarian amber is Santonian. It is found in Ajka Cocal Formation. It is one of the small Cretaceous amber localities. As per today, there is one formally described cockroach *Alienopterix santonicus* with striking metallic colour (Szabó et al., 2022).

4.8 Discussion

The Myanmar amber definitely contains a most numerous record of cockroaches from amber and sediment. When we compare the percentages of cockroaches from different ambers, we can observe the French amber has the highest abundance of cockroaches (4%), while in Spanish and Lebanese amber the numbers much lower (2.5% and 2.7%, respectively) and comparable. Myanmar amber exhibits a significant overlap in taxa with Lebanese amber, particularly in the presence of genera like *Cratovitisma*, *Perlucipecta*, *Jantaropterix*, *Ocelloblattula*, *Balatronis*, and an as-yet-undescribed representative of the

genus *Archimesoblatta*. Additionally, *Perlucipecta* can also be found in Taimyr amber. However, it's noteworthy that Taimyr amber primarily features liberiblattinids, along with its own indigenous genera.

5. Results

5.1 Vršanský et al. (2018b)

Vršanský P., Vršanská L., Beňo M., Bao T., Lei X.J., Ren X.J., Wu H., Šmídová L., Bechly G., Jun L., Yeo M. (2019). Pathogenic DWV infection symptoms in a Cretaceous cockroach. *Palaeontographica Abteilung A*, 314, 1-10.

Minute size of viruses usually disqualifies them from fossilization. Yet, there are some indirect evidences of pathogenic viruses from the fossil record. The paper evaluates such case and possible reasons for forewing deformations in *Stavba babkaeva*, with a significant discussion on the role of genetics and viruses, while also touching upon the complex history and evolution of viruses.

5.1.1 Systematic work

In this paper, the first cockroach belonging to the family *Liberiblattinidae* from Myanmar amber was described. *Stavba babkaeva* (fig. 3.11b) is a cockroach of small size, pale coloration and short Sc.

5.1.2 Pathogens leading to deformities in insects

Physical deformation related to polymerisation of the amber is ruled out because other parts of the body remain unaffected and there is no evidence of physical damage like shrinking or rupture. The undeveloped hindwings and specific patterns of melanization suggest that moulting is not the cause of the deformation. While genetic mutations in some species lead to wing morphology changes, the studied cockroach does not exhibit such genetic mutations. There are references to various genes and hormones that control wing development and expansion, with *bursicon* being a key player. Mutations in associated genes could lead to wing and body deformities. The deformities caused by environmental factors, as observed in recent insects from areas affected by nuclear accidents, tend to be asymmetrical unlike the studied specimen.

The wing deformations could be due to a virus infection, specifically the Deformed Wing Virus (DWV). The virus is known to affect bees, causing deformities.

5.2 Vršanský et al. (2018a)

Vršanský P., Bechly G., Zhang Q., Jarzembowski E.A., Mlynský T., Šmídová L., Barna P., Kúdela M., Aristov D., Bigalk S., Krogmann L. (2018). Batesian insect-insect mimicry-related explosive radiation of ancient alienopterid cockroaches. *Biologia*, 73, 987-1006.

The species I described in this paper is *Caputoraptor vidit* (fig. 3.8h), which I assigned to its genus based on very specific pronotal indentations. The difference however, from its type species is the shape of the head- which is copying the shape of the pronotum in *C. elegans*, while these head protrusions are missing in *C. vidit*.

The paper studies the mimicry in cockroaches and its impact on evolutionary strategies. The paper presents an insight into the intricate dynamics of mimicry among the extinct family Alienopteridae, coupling phylogenetic analyses with morphological studies. While the alienopterid adults mimic ancient aculeate wasps, bees, and ants, they, like other stem-group cockroaches, were phytophagous or palynovores, potentially deriving protection through the mimicry of aculeates.

5.2.1 Systematics work

The paper disputes the systematic position of the originally described alienopterids and places it to the order of cockroaches (Blattodea). There is in total 9 newly described species: *Teyia branislav* (Myanmar amber, fig. 3.8d), *Teyia huangi* (Myanmar amber, fig. 3.8d), *Meilia jinghanae* (Myanmar amber, fig. 3.9a), *Caputoraptor vidit* (Myanmar amber, fig. 3.8h), *Alienopterix ocularis* (Myanmar amber, fig. 3.8e), *Vcelesvab cratocretokrat* (Crato Formation), *Apiblatta muratai* (Crato Formation), *Grant viridifluvius* (Green River Formation), *Chimaeroblattina brevipes* (Green River Formation).

5.2.2 Insect mimicry

Cockroaches with mimicry show swift acceleration of diversification and a surge in disparity in conventionally uniform cockroaches. This is attributed to a transition towards a diversification driven by pollinators. The genus *Teyia* was mimicking the large aculeate Hymenoptera (ampulcid wasps and winged sphecomyrmine ants). The genus *Meilia* is preserved with colouration and was probably mimicking aculeate hymenopterans from the families Crabronidae or Sphecidae. Genera *Vcelesvab* and *Apiblatta* were mimicking wasps from the families Scoliidae, Angarosphecidae. The genus *Grant* probably mimicked the

unspecified ant, while *Chimaeroblattina* mimicked bees. The specialization of the morphology probably led to extinction of this mimicking family.



Figure 5.1: The interpretation of the living habitat of *Meilia jinghanae*. Gouache painting, author: L. Šmídová.

5.3 Vršanský et al. (2019b)

Title: Vršanský P., Šmídová L., Sendi H., Barna P., Mueller P., Ellenberger S., Wu H., Ren X., Lei X., Azar D., Šurka J. (2019). Parasitic cockroaches indicate complex states of earliest proved ants. *Biologia*, 74, 65-89.

The findings from this paper suggest that specialized myrmecophily developed soon after ants became eusocial. Similar cockroaches have also been found in Lebanese and Syrian amber. This concurrent evolution indicates that early ants had weak internal defenses, allowing infiltration by various organisms, while the presence of ant-mimicking species points to a need for strong external defenses against predators. These ancient cockroaches show unique adaptations for myrmecophily, such as shorter legs and antennae, and camouflaging behaviors. The same amber also contains ants, ant mimics, and other yet-to-be-described insects associated with ant nests. These discoveries suggest that parasitic cockroaches significantly impacted Mesozoic tropical forest ecosystems and influenced the development of complex nests in early social insects. Similar living species have been observed in the rainforests of South Yunnan.

5.3.1 Systematic work

Three new species were described in this paper, namely *Anenev asrev* from Syrian amber, *Bimodala ohmkuhnlei*, *Spinka fussa* both from Burmese amber. Holotype of *Anenev asrev* is a nymph with stucked debris on the dorsal portion of the body, serving as camouflage. The species *Spinka fussa* was interpreted as a relative of *Balatronis*. That was, later on, disproven (Šmídová, 2022).

5.3.2 Cockroach myrmecophily

Living myrmecophilous cockroaches are minute and they have rich sensillae. The relation with ants was based on the presence of these characters- indeed *Spinka fussa* is of small size, its body is covered with small hairs and it has shortened legs and antennae. Different insect species have evolved diverse ways to integrate into ant societies. Some mimic ant chemicals or behaviors to blend in, while others offer nourishment or services. For example, certain butterfly larvae secrete substances that attract and appease ants, who in turn protect them from predators. Another example is aphids, which produce a sugary substance called honeydew that is highly attractive to ants; in exchange, ants protect aphid colonies. This fascinating aspect of ecology highlights the complex and often intricate relationships

that can evolve in nature, showcasing the mutual benefits that can arise from interspecies interactions.



Figure 5.2: The interpretation of the living habitat of *Spinka fussa*. Gouache painting, author: L. Šmídová.

5.4 Šmídová (2020)

Šmídová, L. (2020). Cryptic bark cockroach (Blattinae: *Bubosa poinari* gen. et sp. nov.) from mid-Cretaceous amber of northern Myanmar. *Cretaceous Research*, 109, 104383.

The work focuses on the description on striking fossil cockroach, that was named *Bubosa poinari*, derived after the resemblance with living representatives *Buboblatta*. New species was assigned to the family Blattidae.

5.4.1 Systematic work

The species *Bubosa poinari* resembles the living genus *Buboblatta*. species share various features like slender legs with thin spikes and bark-colored tegminae. However, they have distinct pronotum shapes; *B. armata* has a wider pronotum compared to the triangular one of *Bubosa*. *B. armata*, classified under the family Corydiidae, has features similar to the Blattidae subfamily, as noted by Hebard (1920). The unique lateral spikes on the femur are present. This new species is categorized under Blattoidea and Blattidae mostly due to specific vein patterns.

5.4.2 Bark colouration

Th bark-like coloration suggests it lived in close approximation to trees, and its small pronotum hints at a life inside crevices or wood. However, its developed wings suggest an active lifestyle. Another species with bark coloration, *Cratovitisma bechly* and *Spinka fussa* have been discovered in Myanmar amber. The Myanmar amber (as other amber too) records the fauna that lived around the trees and reflects the similar group composition than the sticky traps attached on the tree trunk (Kraemer et al., 2018). The bark camouflage is present in other insects recorded from Myanmar amber- such as bark lice, planthopper and neuropterans (Kiesmüller et al., 2022; Jiang et al., 2019; Wang et al., 2016), respectively).



Figure 5.3: The interpretation of the living habitat of *Bubosa pinnari*. Gouache painting, author: L. Šmídová.

5.5 Šmídová et al. (2022)

Šmídová, L., Vidlička, Ľ., & Wedmann, S. (2022). Appearance of the family Blaberidae (Insecta: Blattaria) during the Cretaceous and a review of fossils of this family. *Palaeontographica Abteilung A*, 71-79.

Recent molecular analyses suggest the Blaberoidea superfamily, to which Blaberidae belongs, originated over 170 million years ago (Bourguignon et al., 2018; Evangelista et al., 2019) with significant evolutionary divergences occurring around 100 million years ago. Despite this, the earliest blaberid fossils, are much younger. The oldest blaberid comes from Barremian of Japan (Oyama et al., 2022). Other notable fossils include *Paratropes fossilis* from Eocene Israeli sediments, *Morphna paleo* from the Paleocene of Russia, and '*Gyna*' *obesa*, also Paleocene, from France, all exhibiting characteristics justifying their classification within Blaberidae. *Eolampra longicauda* from the Eocene of Germany and *Pycnoscelus garnderi* from the UK's Eocene strata share these traits. Records from the Eocene in the USA include three Diplopterinae species and one from Baltic amber (*Stegoblatta irmgardgroehni*). The recently described *Morphna cenozoica* from the Eocene of Messel adds to this list. However, the classification of *Zetobora brunneri* from the Eocene of the USA is uncertain. *Blaberites rhenana* from the Oligocene, Germany, showcases several Blaberidae characteristics, such as a well-developed humeral area and branching in the major wing veins, suggesting a rich, albeit incomplete fossil history for the family.

5.5.1 Systematic work

In this paper, there are two species described and one change in the systematic placement. Both new species belong to the genus *Morphna*, one from Kachin amber and the other from Eocene Messel lake, Germany. The Cretaceous representative *Morphna cretacica* was at the time the oldest representatives of Blaberidae, although nowadays, it is the second oldest Blaberidae after the lower Cretaceous *Morphna* from Japan (Oyama et al., 2022). The species *Fonsecoblatta patricioi* was assigned to Morphinini.

5.5.2 Paleogeography of the Morphinini

The subfamily Epilamprinae is in present day widely distributed across Neotropical, Afrotropical, Indomalayan, and Australasian regions. The earliest South American fossil, *Fonsecoblatta patricioi*, from Fonseca Formation (Oligocene, Brazil). Molecular studies, specifically of the genera *Epilampra* and *Galiblatte*, suggest a divergence of these groups from an Aus-

tralian and Indomalayan ancestor around 98 million years ago, coinciding with the continental shifts of South America and Africa. This pattern of divergence through vicariance is also considered for the genus *Morphna*, though it might have reached South America through transoceanic dispersal. The Eurasian *Morphna* species, such as *Morphna paleo* and *Morphna cenozoica*, may have migrated north during the Paleocene-Eocene Thermal Maximum, paralleling certain mammal and plant species migrations. Present-day *Morphna* species are predominantly found in Southeast Asia. Fossil records indicate a limited Mesozoic distribution for epilamprines, with known specimens including *Morphna cretacica* and ?*Morphna* sp. from Japan. It was only in the Cenozoic that blaberid species went through global dispersion. The ecological success of epilamprines during the Cenozoic may have been facilitated by the oviposition behavior of modern blaberids, which involves a rotation and retraction of their ootheca before hatching.

5.6 Šmídová (2022)

Šmídová, L. (2022). New genus and species of the families Olidae and Corydiidae (Corydioidea, Blattodea) from mid-Cretaceous Kachin amber. *Palaeontographica Abteilung A*, 61-70.

The paper studies cockroaches that were previously interpreted as relatives of the family Blattidae. In fact, they exhibit common characteristics with the Corydiidae family, such as a prominent clypeus and ocelli, nodulose pronotum, hairy extremities, and complex cerci. *Nodosigalea simplivena* is distinct from *Ol xiai* due to its filliform antennae, an ancestral trait. Dense setation might suggest a link to an ant-associated lifestyle or adaptation to arid environments, despite amber evidence pointing to tropical origins. All identified specimens are male, suggesting potential parallels in behavior with other male-dominated species like *Ergaula capensis*. Interestingly, unlike many cockroach families where males predominate, Umenocoleidae and Alienopteridae show female dominance. Coloration in these insects may not solely be due to fossilization but could represent their natural iridescence, as seen in *Alienopterix smidovae*. Lastly, the evolution of (bi)pectinate antennae in cockroaches is uncertain, but evidence suggests a single diversification event may have occurred.

5.6.1 Systematic work

A new cockroach species, *Nodosigalea simplivena*, belonging to the Corydiidae family is second representative of the genus, that was described by Li & Huang (2018). Additionally, a new genus and species, *Olenablatta vrsanskyi*, from the related family Olidae, represented by very well preserved adult male. The family Olidae has been reclassified from the Blattodea to the Corydioidea superfamily, along with the species *Spinka fussa* and *Bimodala ohmkuhnlei*, due to shared complex features such as a notably curved CuP vein, hardened clavus, posteriorly arching main veins, extended first cercomere on multi-segmented cerci, enlarged ocelli and clypeus, and a certain degree of body setation.

5.6.2 Pectinnate antennae

There are various evolved shapes of antennae among insects, such as pectinate, bipectinate, or plumose. The fossil record indicates that 26 insect species across six orders, predominantly males, exhibit branched antennae (Chen et al., 2021a). Pectinnate antennae in cockroaches, both living and extinct, is very rare, with the notable exceptions of

Ol xiai, *Olenablatta vrsanskyi* and *Fragosublatta pectinata*.

5.7 Šmídová et al., 2023

Šmídová L., Bruthansová, M., & Hain M. (2023). The ootheca-bearing cockroach *Praeblattella* indicates primitive external egg retention in the Cretaceous. (Palaeontographica Abteilung A- in review)

The idea for the paper "The ootheca-bearing cockroach *Praeblattella* indicates primitive external egg retention in the Cretaceous" arised from encountering striking amber inclusion that was preserved with exceptional detail and seemed to be very similar to living Ectobiidae species. The paper consists of descriptions of two new *Praeblattella* species from Cenomanian Kachin amber, one ootheca ichnospecies from Cenomanian Kachin amber and one ootheca ichnospecies of Turonian Kyzyl-Zhar, Kazakhstan.

5.7.1 Systematic work

Studied cockroach inclusions were placed in the genus *Praeblattella*, a cosmopolitan genus known from various Cretaceous localities. The characters that justify the placement in the genus were mainly the colouration following the veins on the fore wing. The pattern of the venation is seen in Ectobiidae (the comb-like R and simple Sc), which was the reason why I considered moving the genus *Praeblattella* in the family Ectobiidae. However, the described species *Praeblattella patrickmuelleri* and *P. continuosa* are for *status quo* placed in the family Mesoblattinidae. Additionally, the paper contains descriptions of two new ichnofossils, *Blattootecichnus brevis*, which is preserved attached to the holotype of *P. continuosa*, and *Blattootecichnus kyzylzharensis* preserved in the sediments of Kyzyl-Zhar in Kazakhstan (this fossil was previously studied by my supervisor).

5.7.2 Ootheca ichnofossils

A structure called ootheca is a name reffering to an egg case including the eggs produced by certain insect groups. It is assumed it evolved once in the order Dictyoptera. Similar structures (not homological), evolved in total of 16 orders (Vilímová et al., 2023). Cockroach ootheca is produced by colleterial glands, which form a substance that hardens exposed to the air. We can found oothecae in fossil record, too. In total, there is four described oothecae ichnofossils, but this number does not reflect their real scarcity.

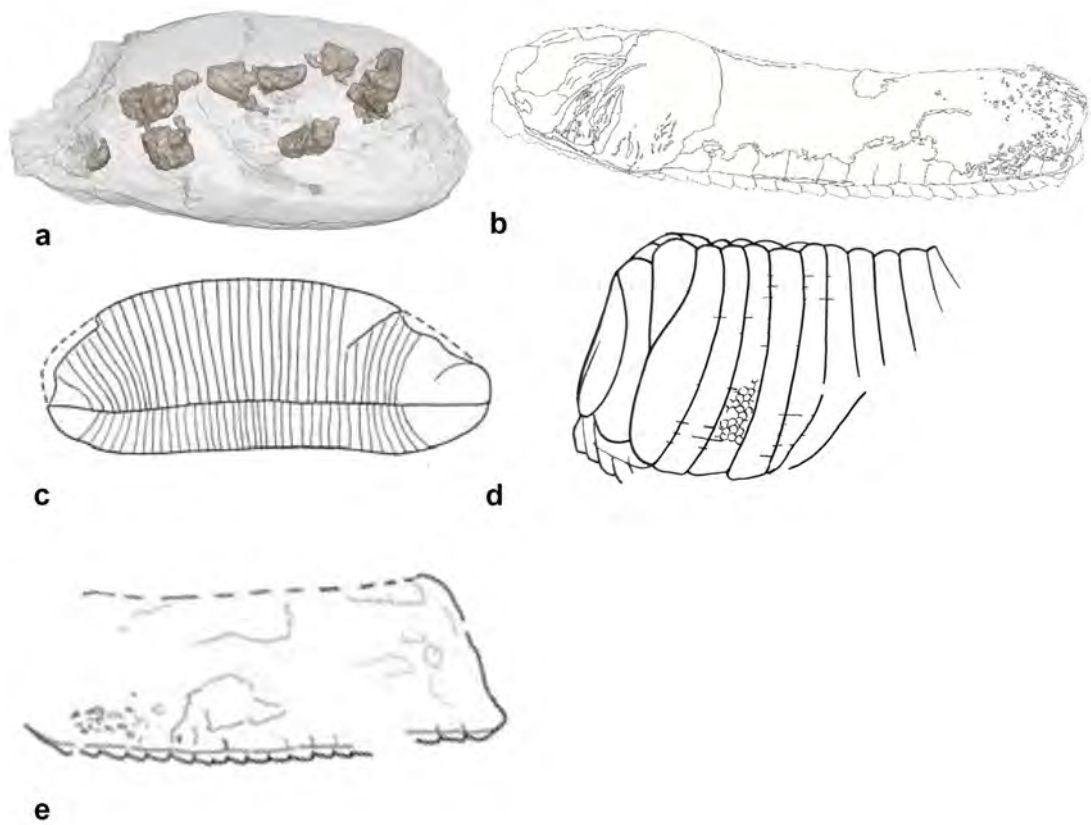


Figure 5.4: Formally described oothecae from the fossil record. a. *Blattootecichnus brevis* from Šmídová et al. (2024), b. *Blattoothecichnus argenteus* from Hinkelman (2019), c. *Oothecichnis negevianus* from Anisyutkin et al. (2008), d. *Blattootecichnus kyzhylzharensis* from Šmídová et al. (2024), e. *Blattoothecichnus ectobiidaeus* from Sendi (2022b)

6. Conclusions

The research of the fossil record of cockroaches, the ancient insect order is broadening our understanding of their evolutionary history, their roles in the past ecosystems, and patterns of their geographical distribution. Myanmar amber captures mid-Cretaceous tropical amber forest, where cockroaches adapted to a wide array of ecological niches. Various species evolved distinctive lifestyles, including various hymenopteran mimics, pollinators, predators, and cave dwellers. Some exhibited adaptations such as camouflaging with their surroundings or displaying warning aposematic coloration to deter predators.

Ancient Carboniferous-Permian roachoid family Phylloblattidae is represented by species *Pozabudnutie antiquorum*.

The family Alienopteridae is represented by 13 species, most of them are females. The only known Cretaceous occurrence is from Myanmar amber. The alienopterids are closely related to the umenocoleids (ought to be synonymized by Vršanský et al. (2018a)). This appears evident after studying the taxa such as *Alienopterix* (Alienopteridae) or *Vzrkadlenie* (Umenocoleidae), which have transitional characters of both families. Family Umenocoleidae is represented by 11 species in 8 genera. Based on the observation of syninclusions of the holotype of *Jantaropterix ellenbergi* that record numerous immatures we can conclude this species laid eggs together.

Family Liberiblattinidae is known with 7 species in 3 genera.

There is in total four species of the family Blattulidae recorded so far, in two genera. Genus *Oceloblattula* is known besides the Burmese amber, from Lebanese amber.

The representatives of Corydiidae and Blattidae recorded from Burmese amber share similar morphology indicating the close relationship. This is the case of *Bubosa poinari*, which has venation pattern of Blattidae, but it has almost identical morphology than the genus *Buboblatta*, which is placed in the family Corydiidae (subfamily Latindiinae). Moreover, we can observe this based on *Spinka* and *Bimodala* fossils that were originally described in the family Blattidae, but they were later moved to Corydiidae.

There is in total 13 described species in the family Corydiidae, all the genera are monospecific, except the *Nodosigalea* and *Magniocula*. Cave cockroaches (family Nocticolidae) are known with three species (in two genera).

Endemic family Manipulatoridae (however, observed in Spanish amber, too) is represented with two species, their lifestyle is interpreted either as a predator or herbivore.

Another endemic family- Fractaliidae- is interpreted as a common ancestor of major

dictyopterid lineages according to the authors of the taxon.

The family of cockroaches with pectinnate antennae Olidae is formally known with two species (potential third species *Fragosublatta pectinata* is placed in the family Corydiidae now). Similar as in *Spinka* and *Bimodala*, Olidae shows synapomorphies with the family Corydiidae.

Roachoid superfamily Caloblattinidoidea is known by the two families- Raphidiomimidae, Caloblattinidae and one species family *incertae sedis*.

Cosmopolitan family Mesoblattinidae is recorded with six species. Three of the species holotypes are recorded with their oothecae.

Living family Blattidae is known by four species. The first one to be described was *Balatronis cretacea*, which has aposematic colouration on the pronotum. Species *Bubosa poinari* is having camouflaging colouration- indicating the habitat in close proximity to the trees.

The family Ectobiidae is scarce in the Burmese amber, with only three species described, one of them belonging to extinct subfamily.

We documented the first occurrence of the family Blaberidae is from mid-Cretaceous Burmese amber. We described the species *Morphna cretacea*, belonging to family Blaberidae, (but it is important to note the fossil from Lower Cretaceous, Japan- placement in the genus *Morphna* is tentative (Oyama et al., 2022)) in mid-Cretaceous (Burmese amber, Šmídová et al. (2022)), in the Eocene (Messel, Germany Šmídová et al. (2022)) and later in Paleocene (Tsayagan Formation, Russia, Vršanský et al. (2013)).

The cockroach species found in Myanmar amber predominantly reflect local origins, although 11 genera, namely: *Jantaropteria*, *Cratovitima*, *Ocelloblattula*, *Spinaeblattina*, *Praeblattella*, *Mongolblatta*, *Sivis*, *Perlucipecta*, *Balatronis*, *Morphna* and *Latiblattella*—have their distribution not only in Burmese amber but in other deposits, reflecting a mix of global distributions from various ancient landmasses (Laurasia and Gondwana).

With 76 species described from Burmese amber, the Mesozoic era's cockroaches exhibited an extraordinary array of ecological and physical specializations. This remarkable assemblage underscores the need for ongoing research and a multidisciplinary method to glean valuable insights into the evolution and ecological history of cockroaches and their related groups.

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8. Attachments

A Published articles

A.1 Articles included in the thesis

Appendix no. 1

Vršanský P., Bechly G., Zhang Q., Jarzembowski E.A., Mlynský T., **Šmídová L.**, Barna P., Kúdela M., Aristov D., Bigalk S., Krogmann L. (2018). Batesian insect-insect mimicry-related explosive radiation of ancient alienopterid cockroaches. *Biologia*, 73, 987-1006.

Appendix no. 2

Vršanský P., **Šmídová L.**, Sendi H., Barna P., Mueller P., Ellenberger S., Wu H., Ren X., Lei X., Azar D., Šurka J. (2019). Parasitic cockroaches indicate complex states of earliest proved ants. *Biologia*, 74, 65-89.

Appendix no. 3

Vršanský P., Vršanská L., Beňo M., Bao T., Lei X.J., Ren X.J., Wu H., **Šmídová L.**, Bechly G., Jun L., Yeo M. (2019). Pathogenic DWV infection symptoms in a Cretaceous cockroach. *Palaeontographica Abteilung A*, 314, 1-10.

Appendix no. 4

Šmídová, L. (2020). Cryptic bark cockroach (Blattinae: *Bubosa poinari* gen. et sp. nov.) from mid-Cretaceous amber of northern Myanmar. *Cretaceous Research*, 109, 104383.

Appendix no. 5

Šmídová, L. (2022). New genus and species of the families Olidae and Corydiidae (Corydioidea, Blattodea) from mid-Cretaceous Kachin amber. *Palaeontographica Abteilung A*, 61-70.

Appendix no. 6

Šmídová, L., Vidlička, Ľ., & Wedmann, S. (2022). Appearance of the family Blaberidae (Insecta: Blattaria) during the Cretaceous and a review of fossils of this family. *Palaeontographica Abteilung A*, 71-79.

Appendix no. 7

Šmídová L., Bruthansová, M., & Hain M. (2023). The ootheca-bearing cockroach *Praeblattella* indicates primitive external egg retention in the Cretaceous. (Submitted to Palaeontographica Abteilung A).

A.2 Articles not included in the thesis

Barna, P., **Šmídová, L.**, & José, M. A. C. (2019). Living cockroach genus *Anaplecta* discovered in Chiapas amber (Blattaria: Ectobiidae: *Anaplecta vega* sp. n.). PeerJ, 7, e7922.

Barna, P., Zelagin, D., & **Šmídová, L.** (2023). A new Eocene cockroach species from the Green River Formation of Colorado, USA. Biologia, 1-7.

B Declaration of the supervisor

As the supervisor of Mgr. Lucia Šmídová, I declare that the student contributed to the works that were submitted as part of her dissertation thesis in the following proportion:

Appendix no. 1

Vršanský P., Bechly G., Zhang Q., Jarzembowski E.A., Mlynský T., Šmídová L., Barna P., Kúdela M., Aristov D., Bigalk S., Krogmann L. (2018). Batesian insect-insect mimicry- related explosive radiation of ancient alienopterid cockroaches. *Biologia*, 73, 987-1006.

2% processing of samples and taxonomic part

Appendix no. 2

Vršanský P., Šmídová L., Sendi H., Barna P., Mueller P., Ellenberger S., Wu H., Ren X., Lei X., Azar D., Šurka J. (2019). Parasitic cockroaches indicate complex states of earliest proved ants. *Biologia*, 74, 65-89.

25% processing of samples and taxonomic part

Appendix no. 3

Vršanský P., Vršanská L., Beňo M., Bao T., Lei X.J., Ren X.J., Wu H., Šmídová L., Bechly G., Jun L., Yeo M. (2019). Pathogenic DWV infection symptoms in a Cretaceous cockroach. *Palaeontographica Abteilung A*, 314, 1-10.

3% processing of samples

Appendix no. 4

Šmídová L. (2020). Cryptic bark cockroach (Blattinae: *Bubosa poinari* gen. et sp. nov.) from mid-Cretaceous amber of northern Myanmar. *Cretaceous Research*, 109, 104383.

100% conceptualization, processing of samples, processing of the taxonomic part, interpretation of results, preparation of the manuscript

Appendix no. 5

Šmídová L. (2022). New genus and species of the families Olidae and Corydiidae (Corydioidea, Blattodea) from mid-Cretaceous Kachin amber. *Palaeontographica Abteilung A*, 61-70.

100% conceptualization, processing of samples, processing of the taxonomic part, interpretation of results, preparation of the manuscript

Appendix no. 6

Šmídová L., Vidlička L., & Wedmann S. (2022). Appearance of the family Blaberidae (Insecta: Blattaria) during the Cretaceous and a review of fossils of this family. *Palaeontographica Abteilung A*, 71-79.

80% conceptualization, processing of samples, processing of the taxonomic part, interpretation of results, preparation of the manuscript

Appendix no. 7

Šmídová L., Bruthansová, M., & Hain M. (2023). The ootheca-bearing cockroach *Praeblattella* indicates primitive external egg retention in the Cretaceous. (Submitted to *Palaeontographica Abteilung A*).

80% conceptualization, processing of samples, processing of the taxonomic part, interpretation of results, preparation of the manuscript


Mgr. Peter Vršanský, Ph.D