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ORIGINAL ARTICLE

Batesian insect-insect mimicry-related explosive radiation of ancient alienopterid cockroaches

Peter Vršanský[1,2,3,4] • Günter Bechly[5] • Qingqing Zhang[6,7] • Edmund A. Jarzembowski[6,8] • Tomáš Mlynský[2,9] • Lucia Šmídová[10,11] • Peter Barna[2] • Matúš Kúdela[11] • Danil Aristov[3,12] • Sonia Bigalk[13] • Lars Krogmann[13] • Liqin Li[6] • Qi Zhang[6,7] • Haichun Zhang[6] • Sieghard Ellenberger[14] • Patrick Müller[15] • Carsten Gröhn[16] • Fangyuan Xia[17] • Kyoichiro Ueda[18] • Peter Vďačný[10] • Daniel Valaška[19] • Lucia Vršanská[19] • Bo Wang[6,20]

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Abstract
Batesian mimicry is a relationship in which a harmful organism (the model) is mimicked by a harmless organism (the mimic), which gains protection because predators mistake it for the model. It is the most widely studied of mimicry complexes and has undoubtedly played an important role in the speciation of various animals especially insects. However, little is known about the early evolution of this important behavior and its evolutionary significance owing to a dearth of paleontological records. Here we report several specialized representatives of the family Alienopteridae from the Early Cretaceous of Brazil, mid-Cretaceous Burmite, and the Eocene of the USA. They exhibit unique morphological adaptations for wasp and ant mimicry and represent one of the oldest evidence of Batesian mimicry in the insect fossil record. Our findings reveal at least 65-million-year coevolution between extinct alienopterids and aculeates. Phylogenetic Bayesian network analysis houses Alienopteridae within Umenocoleidae explosively radiating ~127 Ma. Alienopteridae is the only Mesozoic-type cockroach family which passed K/Pg.

Keywords Fossil insect · Mesozoic amber · Cretaceous cockroach · Mimicry · Hymenoptera · Blattaria

Introduction

Mimicry – one of the Darwinian proofs for the evolution is extensively studied in relation to insect phylogeny (Zrzavý and Nedvěd 1999; Brower 1996; Bocáková et al. 2016; Nadeau et al. 2016; Chouteau et al. 2016). Its long-term effect on phylogenetical patterns resulting from the evolutionary strategy shift from camouflage to aposematism remained obscure. Though, this shift-impact was predicted as a major cause of speciation (Mallet and Joron 1999) and continuous evolutionary movements of the model and the mimic (even after reaching identity) resulting in the elevated speed of evolution (Holmgren and Enquist 1999). Forgotten idea of "a strong selection against nonmimetic hybrids or intermediates contributing to speciation and species maintenance, by acting as a form of ecologically mediated post-mating isolation" also dates back to Wallace and Darwin (Mallet and Joron 1999). Mimicry-related speciation explains adaptive radiation: (Müllerian) co-mimics are usually unrelated, while closely related species almost always belong to different mimicry groups called rings (Turner 1984). Decay of mimicry rings ("after a few hundred miles") was postulated by Bates himself. Although the Batesian mimicry might occur in Cambrian (Topper et al. 2015) indications for its evolutionary impact are missing. Mimicks are rare in number (while mimicking groups approach 10% - Moland et al. 2005). However, the record is insufficient in quality or amount (sediments or amber) and it is difficult to link the extinct mimic with model. The mimicry could not reveal observable changes in diverse organisms. Significance of our fossils is in rapid change of diversification rate and in disparity explosion and evolutionary acceleration in standardly uniform cockroaches caused by the shift to pollen-related metabolism and with the mimicking of stinging hymenopterans. It provides unique insight into the

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Peter Vršanský, Günter Bechly, Qingqing Zhang and Edmund A. Jarzembowski contributed equally to this work.

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✉ Peter Vršanský
geolvrsa@savba.sk

Extended author information available on the last page of the article

impact of mimicry over the evolutionary trajectories. The result was intriguing: diversity index 1 (100%), and velvet ant, ant, diverse wasp as well as bumble-bee and bee mimics are observable within this single extinct group and never again in >320 Ma history (Zhang et al. 2012). Ironically, it was only this and none of the classical group of primitive cockroaches which passed the dinosaur-terminating K/Pg event (see Gao et al. 2018). Although it is impossible to indicate the mimicry as a triggering agent of these vast changes, the explosive radiation apparently correlate with them.

Methods

The nine Burmese amber specimens (prefix NIGP, five alienopterids, two wasps, and two ants) are deposited in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences; three Burmese amber specimens (BA17011–13) are temporarily housed at the NIGP and will eventually be deposited in the Lingpoge Amber Museum in Shanghai (specimens available for study by contacting B.W. or F.X.); one specimen from the Crato Formation (SNMS 66645) are at the Staatliches Museum für Naturkunde Stuttgart; three specimens from the Crato Formation (SC 187, SC Z11, and F103 coll. MSF) are at Michael Schwickert's private collection in Germany; two specimens from the Crato Formation (KMNH263–1 and MURJ) are at the Kitakyushu Museum of Natural History and Human History in Fukuoka; and the two specimens from the Green River Formation (USNM496006; USNM570034) are at the National Museum of Natural History in Washington, D.C.

Crato formation

The Crato Formation represents one of the richest Cretaceous Lagerstätten, yielding an exceptionally well-preserved and diverse palaeobiota. It extends from the northern flanks of the Chapada do Araripe located in northeastern Brazil. The fossil-bearing Nova Olinda Member is mainly composed of finely laminated limestone that was formed during the Early Cretaceous (approximately 125–113 million years ago, Aptian) (Martill et al. 2007). During the late Aptian to early Albian, the Araripe Basin was situated in a vast tropical belt (Martill et al. 2007).

Myanmar amber

Insects were obtained from a mine located near Noije Bum Village, Tanaing Town (Kania et al. 2015; Ross et al. 2010). The U-Pb dating of zircons from the volcanoclastic matrix of the amber gave a maximum age of 98.8 ± 0.6 million years (Shi et al. 2012). The bivalve borings in Burmese amber have been discussed recently and there is evidence that they are contemporaneous with the age of the bed (early Cenomanian - Smith and Ross 2018). Cockroaches from Burmite include predatory, bipectinate antennate, bark camouflaged, aposematic, possibly aquatic species and also true mantodeans and termites (and their parasites), representing a residuum of the major diversification point at 127 Ma (Poinar 1999, 2009a, b; Grimaldi and Ross 2004; Engel et al. 2009, 2016; Vršanský and Bechly 2015; Delclòs et al. 2016; Vršanský and Wang 2017; Vršanský et al. 2017, 2018; Šmídová and Lei 2017; Sendi and Azar 2017; Zhang et al. 2017; Podstrelená and Sendi 2018; Li and Huang 2018a, b).

Green river formation

The Green River Formation is exposed in a variety of sedimentary basins in northeastern Utah, southern Wyoming, and northwestern Colorado. The fossil-bearing Parachute Creek Member formed mainly during the middle Eocene (approximately 47 million years ago)(Hail and Smith 1994). The outcrops contain many insect compressions in oil shale. The flora suggests a tropical to subtropical climate with a distinct dry season (MacGinitie 1969).

Optical microscopy

To reduce the deformation caused by differential refractivity, we sandwiched the amber specimens between two coverslips and filled the space with glycerol. Photographs were taken using a Zeiss AXIO Zoom. V16 microscope system at the State Key Laboratory of Palaeobiology and Stratigraphy, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, or using a Nikon SMZ 18/NDS DS-Fi2 at the Slovak National Museum in Bratislava. In most instances, incident and transmitted light were used simultaneously. All images are digitally stacked photomicrographic composites of approximately 50 individual focal planes that were obtained using the free software Combine ZP for better illustration of the 3D structures. All images and Figures were prepared with the aid of CorelDraw X4 and Adobe Photoshop CS3.

Network analysis

Most parsimonious trees were computed in PAUP* 4.0b8 (Swofford 2003) using a heuristic search, 10 random addition taxon replicates, the accelerated transformation optimalisation algorithm (ACCTRAN) as well as the three bisection-reconnection branch-swapping (TBR) algorithm. ACCTRAN pushes evolutionary transformation of a character down the tree as far as possible, favoring reversals over parallelisms when the choice is equally parsimonious (Wiley and Lieberman 2011). TBR generates more neighbour trees during heuristic search than other traditionally used swapping algorithms (Yang 2014). Characters were treated as unordered and were 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 1000 replicates. A phylogenetic network was constructed in SplitsTree 4 (neighbour-net algorithm - Bryant and Moulton 2004) with bootstrap analysis (1000 replicates) in effect. This approach can infer and simultaneously depict all possible evolutionary trajectories present in the dataset (Huson et al. 2010). Consistent phylogenetic information is documented by treeness of the network, and noisy and conflicting information by star- and mesh-like patterns. The length of edges (branches) is a measure for the support of a split, i.e., bipartition of the taxa into two groups. The longer the edges the better the split is supported.

Recovery of the third dimension (Online Resource 5)

Recovery of a compressed sedimentary fossil was performed using photogrammetric scanning (Canon 5DSR (sensor 8688/5792 pixels), Canon MP-E 65 mm macro lens). Camera and a cloud of pixel-point position recognized, points transformed to third dimension triangular network, which form the final 3D model (9 M triangles, Fig. 4; reduced 0.5 M triangles are available for user-friendly application usage), covered with final color hi-res texture (32,768*32,768 pixels; Fig. 4e). Sharpness due to focal depth 0.42 mm was reached by using a combination of 40 snapshots with regular focus distance 0.4 mm (totaling over 2000) using ad hoc-developed automatized table with two external 400 W flashes, with diffusors (position avoiding reflections). AUGMENT application for mobiles and tablets is freely accessible (http://www.augmentedev.com/augmented-realityapps/) with free manual at http://www.augmentedev.com/help/adding-local-3d-models/ files (up to 35Gb) are available upon request.

Results

Systematic paleontology

Order Blattaria Latreille, 1810 **(s. str., i.e. disregarding Mantodea and Isoptera)**

Remark. Orders are not truly formalized units, so there is no need of synonymization of order Alienoptera with Blattaria, although it is self-apparent due to position of Alienopteridae within a cockroach superfamily Umenocoleoidea. These were proven to possess standard cockroach morphology.

Superfamily Umenocoleoidea Chen et Tian, 1973

Diagnosis of the superfamily (see Vršanský 2003; Kaddumi 2005) do not have to be extended with inclusion of Alienopteridae as they differ from Umenocoleidae only in reduction traits (reduction of forewings to a scale) and in genus-specific autapomorphies. General Bauplan of Umenocoleidae is retained.

Family Alienopteridae Bai et al., 2016 (Bai et al. 2016, 2018)

= Aethiocarenidae Poinar et Brown, 2017**, syn. n. (Poinar and Brown 2017)**

Revised diagnosis. Adult. Head with chewing mouthparts, filiform antennae, interantennal ridge, three sublinearly located ocelli, large and strongly convex compound eyes; pronotum saddle-shaped, with supracoxal furrow, lateral parts bent downwards to cover pleural elements; mesoscutellum present; forewings short and strongly sclerotised, covering anterior part of hindwings; hindwings well-developed, extending beyond tip of abdomen, folded longitudinally but not transversely, resting on abdominal dorsum in repose, usually with pterostigma; profemoral brush present; meso- and metafemora lacking setal rows and patches; apicotibial notch on mid legs; all tibiae with two ventral terminal spines, of similar size and shape on all legs; tarsi five-segmented; large pretarsal arolium present between claws; cerci well-developed, multi-segmented.

Nymph. Head hypognathous with filiform antennae; three sublinearly located ocelli; large and strongly convex compound eyes; pronotum with supracoxal furrow; mesonotum and metanotum bearing long beaded setae; tarsi pentamerous, with pretarsal arolia; abdomen usually swollen; cerci very short, multi-segmented.

Included genera. Nine genera, the type genus *Alienopterus* Bai et al., 2016, *Caputoraptor* Bai et al., 2018, *Alienopterella* Kočárek, 2018, *Teyia* Vršanský, Mlynský et Wang, gen. n., *Meilia* Vršanský et Wang, gen. n., *Vcelesvab* Vršanský, Barna et Bigalk, gen. n., *Apiblatta* Barna et Bigalk, gen. n., *Grant* Aristov, gen. n., and *Chimaeroblattina* Barna, gen. n. For relations among genera and species see Fig. 2 (Character analysis in Online Resource 1 and Data matrix in Online Resource 2).

Remarks. Poinar and Brown (2017) described a new order, Aethiocarenodea**,** based on a specimen from Burmese amber, which is a nymph due to the absence of wings and undeveloped genitalia. This specimen and other numerous nymphs discovered share with the adults the head shape, filiform antennae, three ocelli, large and strongly convex compound eyes, elongated pronotum with a supracoxal furrow, pretarsal arolia, and short, multi-segmented cerci. Therefore, Aethiocarenidae is considered a synonym of Alienopteridae. It is apparent that *Aethiocarenus* is a nymph of taxa from the spectrum of *Teyia-Alienopterella*, however does not represent any of these genera and deserves a separate genus rank.

Occurrence. Early Cretaceous of Brazil, Late Cretaceous Myanmar amber, and Eocene of USA.

Teyia **Vršanský, Mlynský et Wang, gen. n.**

Type species. *Teyia branislav* Vršanský et Wang, sp. n.

Description. Head orthognathous, triangular-shaped (widest portion at apex), with constricted neck; antennae slightly longer than half of body length; maxillary palps longer than head; pronotum elongated, twice as long as head; constriction present between metathorax and first two abdominal segments; cerci well-developed, with 7–9 segments.

Derivation of name. The generic name is derived from the Chinese *teyi* meaning bizarre. Gender masculine.

Differential diagnosis. *Teyia* distinctly differs from the type genus *Alienopterus* in having the triangular-shaped head (widest portion at apex), constricted neck, longer maxillary palps, antennae slightly longer than half of body length, elongated pronotum, constriction between metathorax and first two abdominal segments, and cerci with more than five segments. Closely related *Alienopterella* Kočárek 2018 differs in having more robust habitus with short legs and without abdominal constriction. It also differs from the *Caputoraptor* in lacking the saw-like pronotal extension.

Teyia branislav **Vršanský et Wang, gen. et sp. n.** (Figs. 1a, 4a, b)

Diagnosis. Body length less than 9 mm; pronotum protruded laterally in the centre; cerci with 8 segments.

Description. Dark body with somewhat pale dorsal elevations. Body length 8.8 mm (anterior part of head to tip of tergite X). Head triangular, 0.8 mm long, 1.4 mm wide, with long (about 0.25 mm) and extremely thin setae. Eyes very large (diameter 0.56 mm), with extremely small ommatidia. Three large ocelli, arranged in an almost straight transverse line between compound eyes, with median ocellus placed slightly more anterad. Maxillary palps four-segmented, 1.14 mm long, covered with long sensilla chaetica; first palpomere very short and barely visible, with strong terminal spur; second palpomere reaching palp mid-length with about 29 sensilla chaetica in 4 rows and 4 longitudinal ridges present; third palpomere a third of palp length with 11 sensillae in two rows; setation reducing in size and density towards apex; terminal palpomere with very small and short fine sensillae in 15 rows. Labial palps short, 0.52 mm long, with three subequal segments and central ridge and densely setose. Antennae inserted below lateral ocelli, long and slender, 5 mm long, filiform, with 19 segments; scape comparatively short, 0.36 mm long; pedicel 0.2 mm long, constricted in the middle; other segments 0.20/ 0.12/ 0.21 / 0.15/ 0.17/ 0.22/ 0.24/ 0.37/ 0.18/ 0.24/ 0.24/ 0.25/ 0.24/ 0.23/ 0.23 mm long. Pronotum 1.6 mm long, 1.12 mm wide, with numerous long and thin setae, with pale stripe near paranotalia. Mesonotum very narrow, forming a ring around pronotum. Metathorax posteriorly narrowed. Hindwing fully developed, 5 mm long, about 2 mm wide, transparent with thick veins ending before wing margin and numerous cross-veins forming a fenestrate structure. Numerous sensillary holes present. Vein Sc nearly straight, curved near wing margin in the basal third. R1 reduced to two veins at margin. Distinct dark pterostigma, densely covered with long setae. RS long, straight forked subterminally and slightly curved posteriorly. M slightly sigmoidal and forked subterminally. CuA with three branches; CuP simple. Vannus greatly reduced, with veins A2 and A3 simple. Metanotum 1.52 mm wide. Abdomen with the first and second segments narrow, with numerous long and thin setae, segments dorsally with pale patches. Cerci 1.22 mm long with long setae. Forelegs moderately long; procoxae 0.6 mm long, 0.42 mm wide, conical, slightly narrowing from base to apex; femur 1.38 mm long, 0.12 mm wide with distinct anterior and posterior longitudinal rows of setae on ventral surface; tibia 0.68 mm long, 0.08 mm wide; tarsus 0.67 mm long (tarsomeres 0.23/ 0.13/ 0.10/ 0.09/ 0.12 mm long) with large arolium (0.06–0.07 mm in diameter). Mid legs longer than foreleg; femur 1.88 mm long; tibia 0.74 mm long; tarsus 0.75 mm long (tarsomeres 0.23/ 0.12/ 0.12/ 0.10/ 0.18 mm long). Hind legs longest, femur 2.2 mm long, tibia 1.3 mm long; tarsus 1.5 mm long (tarsomeres 0.72/ 0.26/ 0.20/ 0.12/ 0.22 mm long) with large arolium (0.12 mm in diameter).

Holotype. BA17011, a complete adult female, deposited in the Lingpoge Amber Museum in Shanghai.

Paratype. NIGP154577, a complete adult, deposited in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences.

Locality and horizon. Noije Bum Village, Tanaing Town, northern Myanmar; lowermost Cenomanian, mid-Cretaceous.

Character of preservation. Two complete adults, probably both females.

Derivation of name. The specific name is a stochastical combination of letters. Gender masculine.

Teyia huangi **Vršanský, Mlynský et Wang, gen. et sp. n.** (Figs. 1b, 4e-i;, Online Resource 3: Fig. 1S)

Description. Body length 9.9 mm. Head 0.9 mm long, 2.1 mm wide; eyes wide, 0.4 mm in diameter. Pronotum widest at base, 1.6 mm long, 1.1 mm wide. Antennae filiform, 4.5 mm long; first 15 antennomeres (total 29) length 3.0/ 1.0/ 1.0/ 1.5/ 2.0/ 2.0/ 4.0/ 2.5/ 2.5/ 4/ 2.5/ 2.5/ 2.5/ 2.5/ 2.0 mm. Metanotum width 2.4 mm. Hindwing 7 mm long. Abdomen at widest point 2.2 mm. Cerci short, 0.7 mm long, with 7 segments. Forelegs: femur 1.75 mm long, 0.2 mm wide; tibia 1.4 mm long; tarsus 1.1 mm long. Mid legs: femur 2.0 mm long; tibia 2.0 mm long; tarsus 1.5 mm long (tarsomeres 0.6/ 0.2/ 0.2/ 0.1/ 0.4 mm long). Hind legs: femur 2.7 mm long, 0.2 mm wide; tibia 2.5 mm long, 0.1 mm wide; tarsus 2.2 mm long (tarsomeres 1.00/ 0.25/ 0.30/ 0.30/ 0.30 mm long).

Holotype. NIGP154578, a complete adult, deposited in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences.

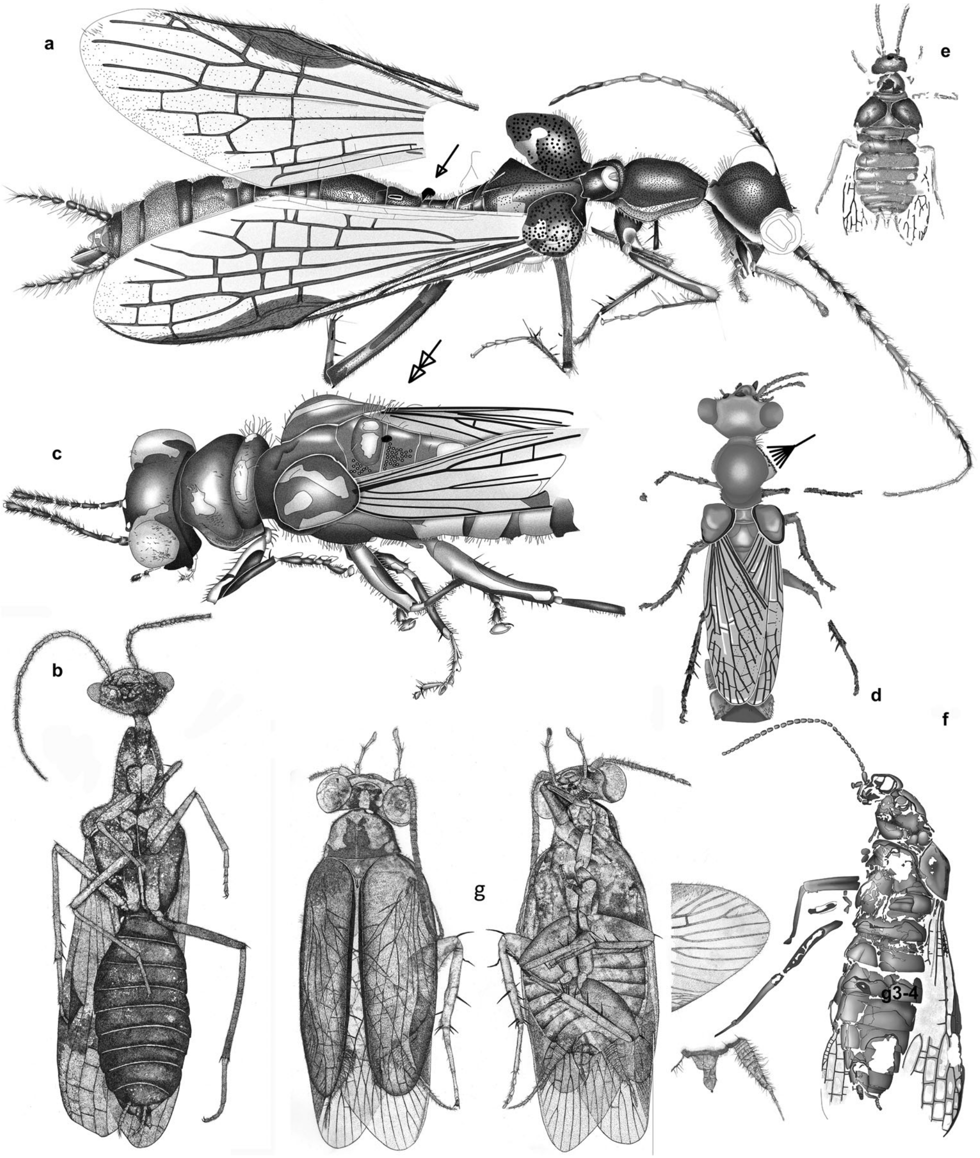


Fig. 1 Dinosaur age hymenopteran-mimicking cockroaches of the family Alienopteridae. (**a**) Ant-mimicking *Teyia branislav* sp. n. **holotype** BA17011 and (**b**) *Teyia huangi* sp. n. **holotype** NIGP154578 (both Myanmar amber); (**c**) solitary wasp or bee-mimicking *Meilia jinghanae* sp. n. **holotype** NIGP154579 (Myanmar amber); (**d**) toothed saw-possessing *Caputoraptor vidit* sp. n. **holotype** NIGP154580 (Myanmar amber); (**e**) *Apiblatta muratai* sp. n. **holotype** KMNH263–1 (Crato Formation); (**f**) *Vcelesvab cratocretokrat* sp. n. holotype SMNS 66645 (Crato Formation); (**g**) *Alienopterix ocularis* sp. n. **holotype** NIGP154581 (Myanmar amber)

Locality and horizon. Noije Bum Village, Tanaing Town, northern Myanmar; lowermost Cenomanian, mid-Cretaceous.

Character of preservation. One complete adult, probably a female.

Derivation of name. The specific name is after Mr. Huang Yijen, the collector of the type specimen. Gender masculine.

Differential diagnosis. Differs from the type species *T. branislav* in having the larger body (nearly 10 mm), the pronotum widest at base, and shorter antennae and cerci with 7 segments.

Remarks. The last several abdominal segments of amber insects are usually retracted and deformed during the taphonomic process. The cerci are clearly multi-segmented and adorned some hairs.

***Meilia* Vršanský et Wang, gen. n.**

Type species. *Meilia jinghanae* Vršanský et Wang, sp. n., here designated and by monotypy. hindwing with extremely simplified venation. *Caputoraptor* differs in lacking the saw-like pronotal extension.

Description. As for species.

Differential diagnosis. It differs from other genera in having larger eyes and hindwing without pterostigma. Furthermore, it distinctly differs from *Teyia* and *Alienopterella* in having the shorter head and pronotum. It is similar to *Alienopterus* in having the short pronotum and hindwing without pterostigma, but differs from the latter in having the head with very short neck and hindwing with extremely simplified venation. Caputoraptor differs in lacking the saw-like pronotal extension.

Derivation of name. The generic name is derived from the

Chinese *meili* meaning beautiful. Gender feminine.

Meilia jinghanae **Vršanský et Wang, gen. et sp. n.** (Figs. 1c, 5; Online Resource 4: Fig. 2S)

Description. Body small, covered with fine setae. Head hypognathous, strongly transversal and narrow, 1.0 mm long, 1.38 mm wide. Compound eyes strongly convex (hemispherical), 0.55 mm wide, 0.75 mm high, covered with barely visible small setae. Three large ocelli (0.15 mm in diameter) present anterodorsally, lentiform, protruding above surface, sublinear, 1 mm apart. Antennae (except first four antennomeres) covered with numerous short, thick setae (each segment bearing up to 70 setae); scape thick (0.13 mm wide) and long; pedicel very long, slightly sigmoidally curved; segments length 0.28/ 0.25/ 0.18/ 0.1/ 0.13/ 0.18/ 0.25/ 0.33/ 0.43/ 0.43/ 0.35 mm. Mouthpart appendages reduced; maxillary palps 1.1 mm long (palpomeres 0.18/ 0.28/ 0.25/ 0.35 mm long); labial palps 0.53 mm long (palpomeres 0.10/ 0.23/ 0.20 mm long). Pronotum 1.38 mm long, 1.25 mm wide, with 4 distinct pale bands. Paranotalia distinct as nearly reduced lateromedial, partially invaginated, rims. Mesonotum comparatively large. Forewings about 1.6 mm long. Metanotum with pale bands. Hindwing length as preserved 4 mm (estimated length 5 mm). Venation extremely simplified with simple, slightly sigmoidal Sc; R1 reduced to few veins at margin; RS simplified; M simple; CuA strong, dichotomized, with strong cross-veins; CuA and CuP separate with wide, simple intercalary vein. Body robust, with first two abdominal segments slightly narrowed (2.25 mm wide). Legs short with almost reduced carination; tarsi extremely well developed and wide, with large arolia (0.3 mm in diameter). Forelegs: femur thin, 1.5 mm long, 0.3 mm wide; tibia 1.1 mm long; tarsus 1.1 mm long (tarsomeres 0.40/ 0.25/ 0.20/ 0.25/ 0.40 mm long). Mid legs: femur 1.5 mm long; tibia 1.2 mm long; tarsus 1.5 mm long (tarsomeres 0.38/ 0.20/ 0.18/ 0.25/ 0.50 mm long). Hind legs: femur 1.7 mm long, 0.2 mm wide; tibia 2.1 mm long.

Holotype. NIGP154579, an adult with abdominal apex missing, deposited in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences.

Locality and horizon. Noije Bum Village, Tanaing Town, northern Myanmar; lowermost Cenomanian, mid-Cretaceous.

Character of preservation. One complete adult.

Derivation of name. The generic name is derived from the Chinese *meili* meaning beautiful. The specific name is after Xia Jinghan, daughter of the collector. Gender feminine.

Caputoraptor Bai et al., 2018

Type species. *C. elegans* Bai et al., 2018. Myanmar amber.

Differential diagnosis (after Bai et al. 2018). Differs from all known genera in possessing pronotum with saw-like edge with shapr teeth. Head is larger than in other species, ocelli were larger than in other known species. Otherwise the general habitus is similar to *Meilia*, but without coloration.*Teyia* and *Alienopterella* are significantly elongated. The type *Alienopterus* is also more elongated.

Caputoraptor vidit **Šmídová, Vršanský et Wang, sp. n.** (Figs. 1d, 8a)

Description. Dark black body overall length (head-end of the hind wing) 11.9 mm, densely covered with very short sensillae. Orthognathous head (length/width 1.64/ 3.16 mm) with all three dark large distinct lentiform ocelli (lateral ones directed to sides). Compound eye diameter 0.68 mm. Ommatidia unrecongiseable. Chewing mouthparts standard; maxillary palp length 1.8 mm. Antennae with flagellum segment lengths from the second to ninth (0.45/ 0.18/ 0.18/ 0.13/ 0.18/ 0.23/ 0.32/ 0.41/ 0.45 mm). Pronotum not covering head, elongate (length/width 2.3 mm/ 1.8 mm) with half spherical elevation in the center and platforms on anterior and posterior parts. Anteriormost part bearing extremely long hairs. Saw-toothed structure is present on the pronotal anterior margins, teeth sharply pointed and heavily sclerotised, some of them overlapping and with dark tips. Ca. 16 teeth present on each side. Forewings triangular (length/width 1.32/ 1.12 mm) heavily sclerotized and shortened with bulge and absent venation. Hind wings well developed (length/width 7.4/ 2.4 mm), transparent with regular venation folded longitudinally. Veins black, the thickest one with diameter ca. 0.44 mm. Intercalaries indistinct. Cross-veins present between CuA, M, R and Sc. Sc simple, sigmoidal, not reaching the half of the wing. R1 strongly sigmoidal with symmetrically unreduced 4 branches; RS very straight, simplified, branched terminally (R3, L4). Media simplified, branched in the terminal part (3). CuA with anteriormost branch ascending in wide angle, without secondary branches (symmetrically with 4 veins at margin). CuP simple; A1 simple, other anal veins strongly reduced (if, then few and all simple). Legs subequal, foreleg fifth tarsomere 0.67 mm long, with 0.36 mm long arolium. Tibia length/width 1.28/ 0.1 mm, femur width 0.16 mm, without spurs. Left middle leg tibia length/width 1.56/ 0.18 mm with 5 strong short straight spines, femur width 0.29 mm with ventral subapical spur, arolium 0.22 mm long. Tarsal segments (1–5) 0.59/ 0.2/ 0.2/ 2.88/ 0.4 mm long. Left posterior leg tibia length/ width 2.08/ 0.16 with 3 straight long spines on the proximal part and 1 spine on the distal part, arolium 0.18 mm long. Tarsal segments (1–5) 0.88/ 0.38/ 0.22/ 0.2/ 0.34 mm long. Right foreleg tibia width 0.11 mm, femur width 0.17 mm; arolium 0.14 mm long. Tarsal segments (1–5) 0.41/ 0.25/ 0.2/ 0.22/ 0.38 mm long. Right middle leg femur width 0.34 mm, tibia length/width 1.49/ 0.23 mm with 1 very strong short spine on the proximal part. Arolium 0.23 mm long. Right posterior femur width 0.44 mm, tibia width 0.15 mm bearing 3 spines on the proximal part. Arolium 0.11 mm long. Tarsal preserved segments (1–4)

0.88/ 0.31/ 0.23/ 0.2 mm long. Spines contain ca. 20 shortened setae. Numerous setae present on all segments of the leg (ca. 40/ 0.1 mm^2). First tarsomere on both hind legs is extremely elongated.

Holotype. NIGP154580. A complete cockroach body of uncertain sex.

Type locality. Hukawng valley, Myanmar.

Type horizon. Cenomanian Upper Cretaceous.

Character of preservation. One complete adult, probably a male.

Derivation of name. Stochastical combination of letters. Gender feminine.

Differential dagnosis. Differs from *C. elegans* in absence of coloration, presence of central elevation bearing ocelli and posteriormost head elevation ridge.

Remarks. Body is heavily and regularly covered with extremely fine sensilla, so that not all of them are possible to visualize. Therefore the drawing look like presenting only partially setated surface (especially on legs) while the real state is a regular cover.

Alienopterix Mlynský, Vršanský et Wang, gen. n.

Type species. *Alienopterix ocularis* sp. n. here designated and by monotypy. Myanmar amber.

Description: as for species.

Derivation of name. Modified partially alluding to genus *Alienopterus*. Gender feminine.

Differential diagnosis. Differs from all representatives of the family in having fully developed forewings (hardened tegmina) and in lacking the separated posterior area of the pronotum. It is also more robust than all genera except *Meilia,* but have fully fat body. *Teyia* and *Alienopterella* are significantly more elongated. The type *Alienopterus* is also more elongated and also has distinct posteror are of pronotum.

Remarks. The taxon is categorized within Alienopteridae (supported with the phylogenetical analyses at Fig. 2) and not Umenocoleidae due to modified antenna, huge transversal eyes, hindwing with extremely long pterostigma, and tarsus structure (big arolium, fourth tarsomere with procesus, asymmetrical claw).

Alienopterix ocularis Mlynský, Vršanský et Wang, sp. n.

(Figs. 1g, 6a–c)

Description. Small beetle-like cockroach of an umenocoleoid appearance (overall length 8.8 mm). Head very large (width/ length/ height: 2.5/ 0.9/ 1.2 mm). Antennal pit large (0.2 mm diameter); Right antenna very wide (up to 0.2 mm) and short, with 44 antennomeres. Scape (R 0.4/ 0.2 mm; L 0.4/ 0.18 mm) and pedicel (R 0.16/ 0.12 mm; L 0.14/0.06 mm) differentiated. Antennomeres 2–44 subequal (L (44): 0.11/ 0.06/ 0.07/ 0.1/ 0.11/ 0.1/ 0.1/ 0.1/ 0.1/ 0.1/ 0.1/ 0.1/ 0.11/ 0.12/ 0.12/ 0.15/ 0.15/ 0.18/ 0.19/ 0.2/ 0.19/ 0.18/ 0.17/ 0.2/ 0.2/ 0.17/ 0.17/ 0.2/ 0.2/ 0.17/ 0.1/ 0.1/ 0.11/ 0.11/ 0.1/ 0.14/ 0.14/ 0.14/ 0.12/ 0.12/ 0.13/ 0.12/ 0.14 mm; R (44): 0.07/ 0.07/ 0.07/ 0.07/ 0.1/ 0.07/0.08/ 0.1/ 0.11/ 0.12/ 0.11/ 0.11/ 0.12/ 0.14/ 0.14/ 0.14/ **0**.14/ 0.14/ 0.14/ 0.15/ 0.14/ 0.15/ 0.15/ 0.15/ 0.15/ 0.15/ 0.15/ 0.15/ 0.15/ 0.15/ 0.1/ 0.1/ 0.1/ 0.1/ 0.11/ 0.11/ 0.1/ 0.1/ 0.09/ 0.09/ 0.09/ 0.11 mm)). Eyes extremely large (L 0.9/0 .9 mm; R 1/0.9 mm), ocelli invisible in holotype. Palps short (1.3 mm) and extremely symmetrical (R 0.3/ 0.15, 0.1/ 0.1, 0.4/ 0.15, 0.3/ 0.17, 0.2/0.2 mm; L R 0.3/ 0.15, 0.1/ 0 .1, 0.4/ 0.15, 0.3/ 0.17, 0.2/0.2 mm). Cervix slightly elongated (0.3/ 0.25 mm). Pronotum campaniform, 1.8 mm wide and 1.1 mm long, with distinct M-shaped coloration. Scutellum triangular; length/ width 0.9/ 1.1 mm. Forewings fully developed, 5.7 mm long and 2 mm wide, fully elytrized, cup-like *bunky* traceable; posterior margin distinct, up to 0.1 mm wide; microtrichial cover dense (up to ca. 15 per 0.1 mm^2); veins indistinct. Hind wing very large (6.8 mm long) overlapping forewing (1.3 mm) and body (1.9 mm). Pterostigma distinct and very long and wide (2.2/ 0.54 mm), R1 numerous, RS dense and rich. M simplified to 3 (L) – 4 (R) veins at margin, sigmoidally curved. CuA with 6 simple branches, CuP simple. A1 with long and wide branches. Abdomen without modifications, wide nearly 3 mm. Subgenital plate undivided, elongated, but transversal (0.3/ 0.6 mm) densely covered with sensilla, those at margin are very large (up to 0.05 mm; compared with much longer 0.09 mm at prior segment). Fore femur without spurs, 0.6 mm long and 0.17 mm wide; fore tibia 0.5 mm long and ca. 0.08 mm wide; tarsus 0.33 long. Mid femur 1.6 mm long and 0.6 mm wide; mid tibia 1.7 mm long and 0.2 mm wide; mid tarsi 1.7 mm long. Hind femoral spur extremely strong, 0.5 mm long; tibia 2.2 mm long (0.4 mm wide) also with two long and strong spurs (0.5 mm long) and 5 shorter spurs; tarsomeres very long (0.7/ 0.4/ 0.2/ 0.1/ 0.1 mm). Arolium indistinct, claws symmetrical or asymmetrical. Cercus with 16 segments, four terminal ones very narrow thin and long; extremely long and narrow (2 mm when curved – as measured/ 0.25 mm at widest point), without long sensilla (numerous short sensilla were preserved, longest about 0.35 mm). Ovipositor specialized, rigid, protruding 0.65 mm out of the body outline (0.43 mm from subgenital plate) 0.26 mm at widest point (0.23 mm in shaft),with numerous short chaeta and 6 very long (0.13 mm) spines; terminated with short paired (0.04 / 0.02 mm each) very rigid and heavily incrustated structure ended with two rows with 3short sensilla each.

Holotype. NIGP154581. A complete cockroach female.

Type locality. Hukawng valley, Myanmar.

Type horizon. Cenomanian Upper Cretaceous.

Character of preservation. One complete adult, a female.

Derivation of name. *ocularis* is pertaining to eyes. Gender feminine.

Remarks. The left antenna is significantly thinner (less than 0.1 mm) which is unlikely only due to taphonomy.

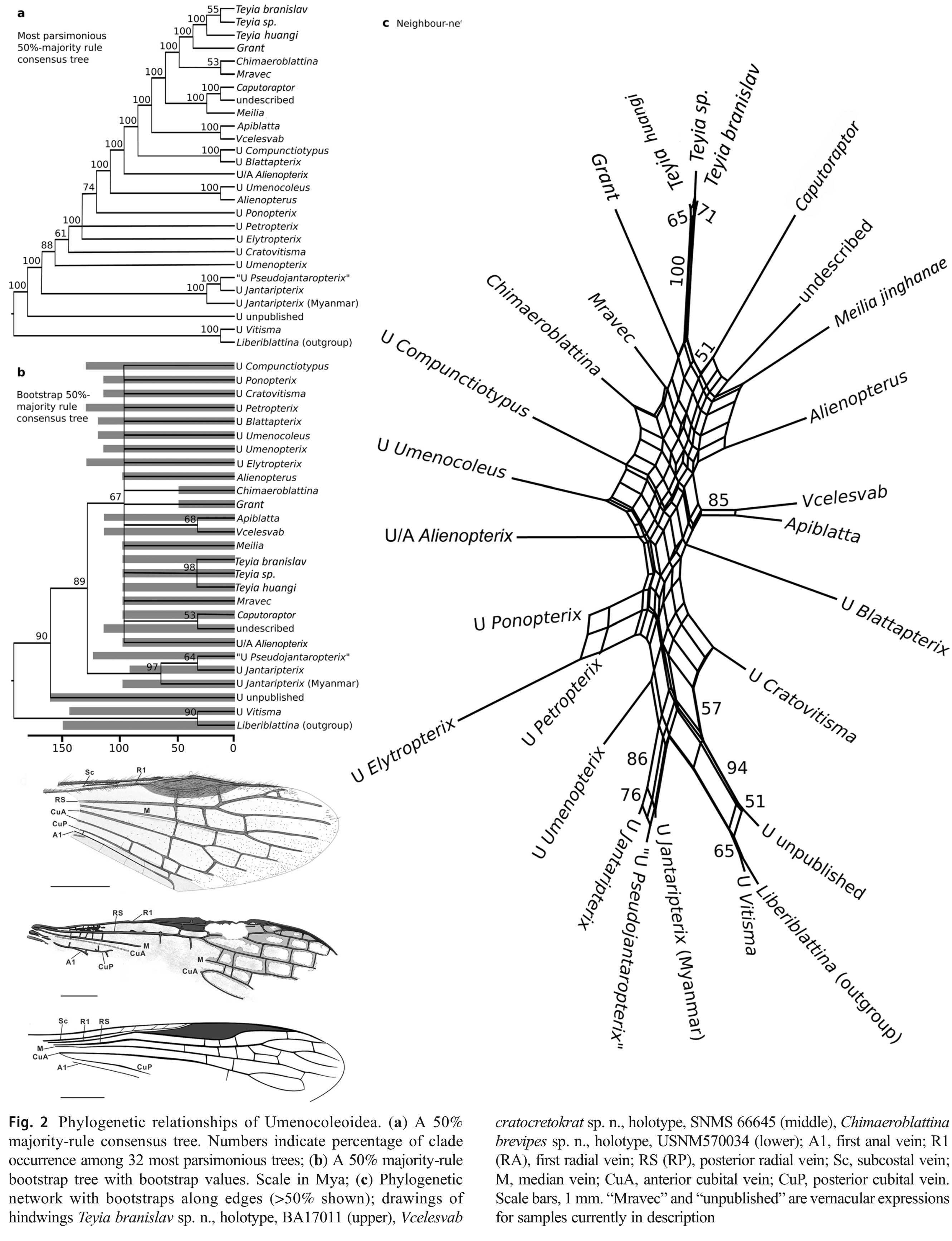


Fig. 2 Phylogenetic relationships of Umenocoleoidea. (**a**) A 50% majority-rule consensus tree. Numbers indicate percentage of clade occurrence among 32 most parsimonious trees; (**b**) A 50% majority-rule bootstrap tree with bootstrap values. Scale in Mya; (**c**) Phylogenetic network with bootstraps along edges (>50% shown); drawings of hindwings *Teyia branislav* sp. n., holotype, BA17011 (upper), *Vcelesvab cratocretokrat* sp. n., holotype, SNMS 66645 (middle), *Chimaeroblattina brevipes* sp. n., holotype, USNM570034 (lower); A1, first anal vein; R1 (RA), first radial vein; RS (RP), posterior radial vein; Sc, subcostal vein; M, median vein; CuA, anterior cubital vein; CuP, posterior cubital vein. Scale bars, 1 mm. "Mravec" and "unpublished" are vernacular expressions for samples currently in description

Instead it seems that, similarly as in other species, antenna morphology was destabilized.

***Vcelesvab* Vršanský, Barna et Bigalk, gen. n.**

Type species. *Vcelesvab cratocretokrat* Vršanský, Barna et Bigalk, sp. n., here designated and by monotypy.

Description. As for species.

Derivation of name. The generic name is derived from *včele* (Slavic for "to a bee") and *šváb* (Slavic for cockroach). Gender masculinum.

Differential diagnosis. Differs from other genera in having the small head, shorter pronotum widening posteriorly, robust body with the first two abdominal segments wide, five-segmented cerci and sophisticated vein coloration. The taxon appears robust, like standard cockroaches, unlike *Teyia* and *Alienopterella* or *Caputoraptor. Meilia* is similar in general habitus, but has siginificantly longer head and pronotum. *Alienopterix* is very similar, but has complete forewings and even shorter pronotum without basal ridge.

***Vcelesvab cratocretokrat* Vršanský, Barna et Bigalk, gen. et sp. n.** (Figs. 1f, 7f, Online Resource 5)

Description. Body length 12.1 mm. Head small, subhypognathous, 1.0 mm long. Antennae 6.5 mm long; scape 0.5 mm long; pedicel 0.4 mm long; flagellomeres 0.2–0.3 mm long, 0.1–0.2 mm wide. Pronotum 2.5 mm long; mesonotum 1.9 mm long; metanotum 3.2 mm long. Forewing 2.5 mm long, 1.3 mm wide, with sharp apex, few veins visible near anterior margin. Hindwing 9.9 mm long, extending beyond end of abdomen. Pterostigma 3.8 mm long with maximal width of 0.5 mm. Abdomen 7.5 mm long. Cerci short, 0.7 mm long, slightly thinned distally, five-segmented, 1st cercomere longest. Mesofemur length as preserved, 2.3 mm, 0.5 mm wide; mesotibia 2.2 mm long. Metafemur 3.2 mm long, 0.4 mm wide; metatibia 2.8 mm long.

Holotype. SNMS 66645, a complete adult, deposited in the Staatliche Museum für Naturkunde Stuttgart.

Locality and horizon. Chapada do Araripe, Brazil; Nova Olinda Member, Crato Formation, Lower Cretaceous (Albian).

Character of preservation. One complete adult, probably a female.

Derivation of name. The specific name is a stochastical combination of letters partially alluding to Crato (type locality), Cretaceous (type age) and suffix –krat (suffix for "a critter"). Gender masculinum.

***Apiblatta* Barna et Bigalk, gen. n.**

Type species. *Apiblatta muratai* Barna and Bigalk, sp. n., here designated and by monotypy.

Description. As for species.

Differential diagnosis. *Apiblatta* is the most standardly (like standard umenocoleid cockroach) looking alienopterid. It differs from closely related of a similar habitus *Vcelesvab* in having the larger head (longer than half pronotum length), shorter antennae (twice as long as pronotum), the hindwings with R veins developed, and longer cerci with 10 segments. It is robust like *Alienopterix*, without abdominal constriction, but with scale-like forewings. *Teyia*, *Meilia, Alienopterella* and *Caputoraptor* are all significantly elongated.

Derivation of name. The generic name is derived from apis (Latin for bee) and Blatta (Latin for cockroach). Gender feminine.

***Apiblatta muratai* Barna et Bigalk, gen. et sp. n.** (Figs. 1e, 7c–e)

Description. Body length 10.7 mm, maximum width of abdomen 4.5 mm. Head 1.3 mm long, 2.6 mm wide, with laterally and posteriorly positioned eyes. Maxillary palps with very short palpomeres. Antennae short, approximately 4 mm long; scape 0.5 mm long, cylindrical widening distally, slightly constricted at centre; pedicel short, cylindrical, 0.3 mm long; 30 or more flagellomeres extremely short, slightly wider than long (0.2–0.3 mm long), widest distally. Pronotum narrow, 2 mm long, constricted near the posterior end, widened caudally reaching its maximum width (2.3 mm). Mesonotum, 2 mm long, 4.5 mm wide, trapezoid with rounded lateral sides. Metanotum wide, short, 3.9 mm long, 0.8 mm wide. Forewing sclerotized, 2.4 mm long, 1.7 mm wide. Hindwings slender and long, approximately 7.0 mm long and 2.3 mm wide, clearly longer than abdomen and cerci; apex positioned medially, with darker pigmentation; veins distinct; crossveins present. R1 straight with 3–5 branches; long pterostigma present anteriorly near the apex; RS with 5–7 branches; M simplified to maximum 2 veins at margin, straight, CuA with up to 5 simple branches. Abdomen wide but not exceeding the maximum width of thorax, subovoidal, 5.1 mm long, 4.1 mm wide, lateral sides smoothly rounded. Second segment of abdomen widest. Darker maculae visible on dorsal side of first four abdominal segments, one on each side of central line. Cerci comparatively slender, 1.2 mm long, tapering towards their distal end, 10-segmented; first cercomere longest and widest (both length and width about 0.2 mm); other cercomeres about 0.1 mm long. Forelegs: femur 0.5 mm wide; tibia 1.2 mm long, 0.3 mm wide; first tarsomere 0.5 mm, long; second tarsomere 0.2–0.3 mm long; third tarsomere 0.2 mm, long. Mid legs: tibia 1.7 mm long; first tarsomere 0.7 mm long; second tarsomere 0.3 mm long; third tarsomere 0.2 mm long; fourth tarsomere 0.1 mm long; claws 0.5 mm long. Hind legs: femur 0.5 mm wide; tibia 2.9 mm long; first tarsomere 1.2 mm long, 0.2 mm wide.

Holotype. KMNH263, a complete adult, deposited in the Kitakyushu Museum of Natural History.

Locality and horizon. Chapada do Araripe, Brazil; Nova Olinda Member, Crato Formation, Lower Cretaceous (Albian).

Character of preservation. Three complete adults, two females.

Derivation of name. The specific name is after Dr. Murata, the collector of the type specimen. Gender feminine.

***Grant* Aristov, gen. n.**

Type species. *Grant viridifluvius* Aristov, sp. n., here designated and by monotypy.

Description. As for species.

Derivation of name. The generic name is derived from a grant (financial support). Gender masculinum.

Differential diagnosis. It distinctly differs from other genera in having the large, narrow body, head longer than pronotum, and wide antennae**.** Body large (> 20 mm long), extremely narrow; head large and subprognathous, with eyes not protruding from the head outline; antennae wide; pronotum shorter than head. This taxon is highly specialized, so no similarities with other genera (except for scale-like forewing share with all taxa except *Alienopterix*) can be traced. Similarly as myrmecomorph *Teyia*, unlike *Alienopterella*, this taxon has elongated legs.

***Grant viridifluvius* Aristov, gen. et sp. n**. (Fig. 7a)

Description. Body thin, 23.2 mm long. Head large, 5.1 mm long, subprognathous, with small laterally positioned eyes and distinct maxillary palps. Three ocelli present. Antennae with very wide segments, scape and pedicel obscured, basal-most flagellomeres of subequal length and width, subsequent flagellomeres somewhat elongated. Pronotum 3.2 mm long, shorter than head. Mesonotum 5.0 mm long. Forewings small, 2.1 mm long, ovoid with sharp apices. Hindwings straight, fragmentary veins reaching to half of abdominal length. Abdomen 12.8 mm long, its anterior third slender, cylindrical, posterior two-thirds wider with prolonged, ovoid shape. Legs with small coxae and small trochanters, slender femora, and tibiae bearing a few short spines. Forelegs shortest, hind legs longest; tarsomeres not preserved. Forelegs: coxae 1.1 mm long; trochanter 0.8 mm long; tibia about 4.3 mm long; femur about 3.8 mm long, with two spines on ventral side. Mid legs: femur 4.7 mm long, with two terminal spines. Mid legs: femur 5.6 mm long, with three spines (0.3 mm, 0.4 mm, 0.4 mm long) present on ventral side of femur and three terminal spines (0.4 mm, 0.4 mm, 0.4 mm long). Hind legs: trochanter 0.8 mm long; femur 7.5 mm long; tibia 9.2 mm long, with two small spines (0.3 mm, 0.4 mm long) present on ventral side of tibia near mid length and three small spines (0.3 mm, 0.3 mm, 0.4 mm long) close together on ventral side near tibia's distal end and three terminal spines (0.3 mm, 0.5 mm, 0.5 mm long).

Holotype. USNM496006, a complete adult with detached cerci, deposited in the National Museum of Natural History, Washington, D. C.

Locality and horizon. Anvil Points Area, Labandeira Site, Colorado, USA; Parachute Creek Member, Green River Formation, middle Eocene.

Character of preservation. One complete adult.

Derivation of name. The specific name is derived from *viridis* (Latin for green) and *fluvius* (Latin for river), in reference to the Green River Formation. Gender masculinum.

***Chimaeroblattina* Barna, gen. n.**

Type species. *Chimaeroblattina brevipes* Barna, sp. n., here designated and by monotypy.

Description. As for species.

Derivation of name. The generic name is derived from *chimaera* (Latin for a monster composed of the parts of more than one animal) and *Blatta* (Latin for cockroach). *Blattina* refers to a fossil representative. Gender feminine.

Differential diagnosis. It distinctly differs from other genera in having the trapezoidal head, pronotum slightly narrow in the centre, and shorter fore legs. Habitually it resemble *Alienopterella* with similarly constricted waist, while constriction of *Teyia* is more significant. *Alienopterella* and *Teyia* were more elongated, Teyia additionally had more elongated legs. Grant differs in being entirely myrmecospecialised. *Meilia* do not have the waist constriction and had large head. *Vcelesvab* and *Apiblatta* differed in having very fat bodies and more or less standard cockroach morphology. *Alienopterix* possessed fully developed forewings. Head of *Chimaeroblattina* was unique, trapezoidal, widest basally; pronotum elongated, slightly narrow in the centre; constriction present between metathorax and first two abdominal segments; fore legs much shorter than thorax.

***Chimaeroblattina brevipes* Barna, gen. et sp. n.** (Fig. 7b)

Description. (Fig. 2l). Body robust, 10.7 mm long. Head large, 1.1 mm long, trapezoidal, widest basally. Thorax 3.3 mm long. Pronotum 1.8 mm long, slightly narrow in the centre, distinctly narrower than mesonotum. Mesonotum 1.1 mm long, widest thoracic segment (about 2.5 mm wide). Metanotum 0.5 mm long, almost as wide as mesonotum anteriorly, narrowing posteriorly, where its width is similar to that of the first abdominal segment; transition from mesonotum to metanotum is contiguous, both forming a subcircular shape. Forewing strongly reduced. Hindwings well developed, 6.3 mm long, slightly extending over the end of the abdomen. Sc in its distal half sinusoidal, membrane of cells between its branches with distinctly darker colouration. R1 with two branches delimiting a distinct pterostigma. RS branched in apical fifth with 3 branches. M simple. CuA branched in apical fourth with two branches. CuP and anal veins poorly preserved. Abdomen elongate, 4.9 mm long, 2.6 mm wide, subovoidal, broadest posteriorly. Fore leg about 2.4 mm, protibia 0.9 mm long; protarsus 0.9 mm long, with two claws. Mesotibia 1.1 mm long, 0.2 mm wide.

Holotype. USNM570034AB, a complete adult, deposited in the National Museum of Natural History, Washington, D. C.

Locality and horizon. Anvil Points Area, Labandeira Site, Colorado, USA; Parachute Creek Member, Green River Formation, middle Eocene.

Character of preservation. One complete adult.

Derivation of name. The specific name is derived from *brevipes*, Latin for short legs. Gender feminine.

Discussion

Taxonomic interpretation

We conducted phylogenetic analyses using a dataset of 27 species with 130 morphological characters. Both maximum parsimony (MP) and Bayesian inference (BI) analyses resolve new fossils within Umenocoleoidea and Alienopteridae (Fig. 2). Our new fossils can be attributed to Alienopteridae based on the combination of characters: multi-segmented cerci, presence of profemoral brush, and apicotibial notch on mid legs (usually invisible in compression fossils), forewings fully sclerotised and strongly reduced, non-folded hindwing with complex venation, and ultimate tarsomere distinctly bent upwards (invisible in some compression fossils).

Maximum parsimony (based on Online Resources 1 and 2)

Analysis reveals 32 equally parsimonious trees (203 steps). A 50% majority-rule consensus cladogram of them has a clear hierarchical structure (Fig. 2a). Bootstrap analysis left most relations statistically unsupported and most nodes collapsed into polytomies (Fig. 2b). All taxa, except for *Liberiblattina* and *Vitisma*, are classified together in a large clade with 87% bootstrap support, significantly supporting monophyly of Umenocoleoidea (including both families Umenocoleidae and Alienopteridae. The ordinal status for Alienoptera was rejected and incorporation of *Alienopterus* within Umenocoleidae (marked as "U" in the schemes) was supported. *Jantaropterix* and "*Pseudojantaropterix*", as a single formal genus, form a statistically significant clade (96% bootstrap) in a sister position to rest analyzed taxa. These are, however, placed in a polytomy along with two distinct groups: *Teyia* sp., *T. branislav*, *T. huangi* (99% bootstrap) and *Apiblatta*, *Vcelesvab* (70% bootstrap for these two sole taxa from the Crato Formation). Network analyses corroborated this phylogeny. Star-like pattern of the network might indicate a rapid radiation of major clades (genera) and the mesh-like structure of the network reflects either lack of phylogenetic signal (rapid radiation) or conflicting morphological signal in the dataset (Rajter and Vďačný 2016). Most of the taxa reveal a long independent evolution supported by numerous autapomorphies (long edges in the network), with three distinct well supported groups: *Jantaropterix*, "*Pseudojantaropterix*" (86% bootstrap); *Teyia* sp., *T. branislav*., *T. huangi* (100% bootstrap); and *Apiblatta, Vcelesvab* (83% bootstrap) (Fig. 2c). *Alienopterella* (Kočárek 2018) and undescribed alienopterid reported from Orapa (McKay 2007) are not included in analyses.

Possible similarities with hymenopterans

The alienopterid *Teyia* from Burmese amber is 8.4–10 mm long, and it displays unique body characteristics including a triangular-shaped head with a constricted neck, filiform antennae, an elongated pronotum, and a distinct constriction between the metathorax and first two abdominal segments (Fig. 1a-e). In addition, the hindwing of *Teyia* has a distinct pterostigma, reduced venation and vannus, and is remarkably similar to a typical hymenopteran wing when the hymenopteran forewing is coupled with the hindwing (Online Resource 3: Fig. 1S). These characteristics make *Teyia* distinct from other extinct and extant cockroaches, which commonly have a flat body with wide pronotum and abdomen and well-developed hindwings (Bell et al. 2007). The body plan, size and wing morphology show that *Teyia* closely resembles some large aculeate Hymenoptera, especially ampulicid wasps and winged sphecomyrmine ants from Burmese amber (Figs. 1a, b, 8). Extant ampulicid wasps are cockroach hunters, and they are among the most common hymenopteran families in Burmese amber (Ohl and Spahn 2010). Sphecomyrmine ants are the most frequent stem-group ants in Burmese amber and other Late Cretaceous ambers (Barden and Grimaldi 2016, see also Perrichot et al. 2016), although most are apterous workers. Therefore, the high abundance of both ampulicids and sphecomyrmines supports the suggestion that they are potential models for *Teyia*.

The pterostigma is a region composed of highly pigmented and slightly sclerotized cuticle in an anterior cell of the wing (Chapman 2012). It is present in many Odonata, extinct Orthoptera (e.g., Elcanidae), Psocoptera, Mecoptera, Megaloptera, and Hymenoptera; it provides weight and strength to the leading edge of the wing and thus prevents the wing from fluttering during changes in the stroke by adding weight to the leading edge (Norberg 1972). The darkened patch of wing membrane seen in the fossil is interpreted as a pterostigma as it appears to be lightly sclerotized and thickened and so was probably used for flight. It bears a resemblance to that of the wasp model being similar in location and shape and so may have been used to mimic wasps, but it differs from the wasp model in having dense hairs and as the darkened patch appears to be sclerotized and thickened its primary function was probably for flight rather than mimicry. The borders of the pterostigma are not coincident with the course of veins.

The alienopterid *Meilia* from Burmese amber probably displays a resemblance to some aculeate Hymenoptera (for example, Crabronidae and Sphecidae from Burmese amber) in having a wide head, large eyes and a robust body. Remarkably, *Meilia* displays well-preserved colour patterns, which rarely occurs in amber insects and provides valuable ecological information (Figs. 1c Online Resource **4**: Fig. **2**S). The alternating dark and light transverse bands on the abdomen of *Meilia* are similar to those of aculeate Hymenoptera and are a classic warning signal to predators (Ruxton et al. 2004).

The alienopterids *Vcelesvab* and *Apiblatta* from the Crato Formation are the earliest known alienopterids, and they differ from Burmese amber specimens in their short head and pronotum and wide, non-constricted abdomen (Fig. 8e-f). They probably resemble other aculeate wasps (Scoliidae, Angarosphecidae) from the same locality and deposit in general appearance (Fig. 8f, h), including size, head shape, long antennae, robust body, and hindwings with reduced venation and pterostigma (Peters et al. 2017). The alienopterids *Chimaeroblattina* and *Grant* from the Green River Formation represent the most recent occurrence of alienopterids, showing that this family persisted for more than 65 million years. *Grant* differs from other alienopterids and cockroaches in having a large, prognathous head and an elongate body (Fig. 7a); this aspect looks like some ants from the same locality. However, its poor preservation prevents a more precise association with a potential model. The second genus, *Chimaeroblattina*, has a habitus that is similar to that of alienopterids from the Crato Formation, but differs from the latter in having a slightly constricted abdomen and shorter legs (Fig. 7b). *Chimaeroblattina* probably imitated

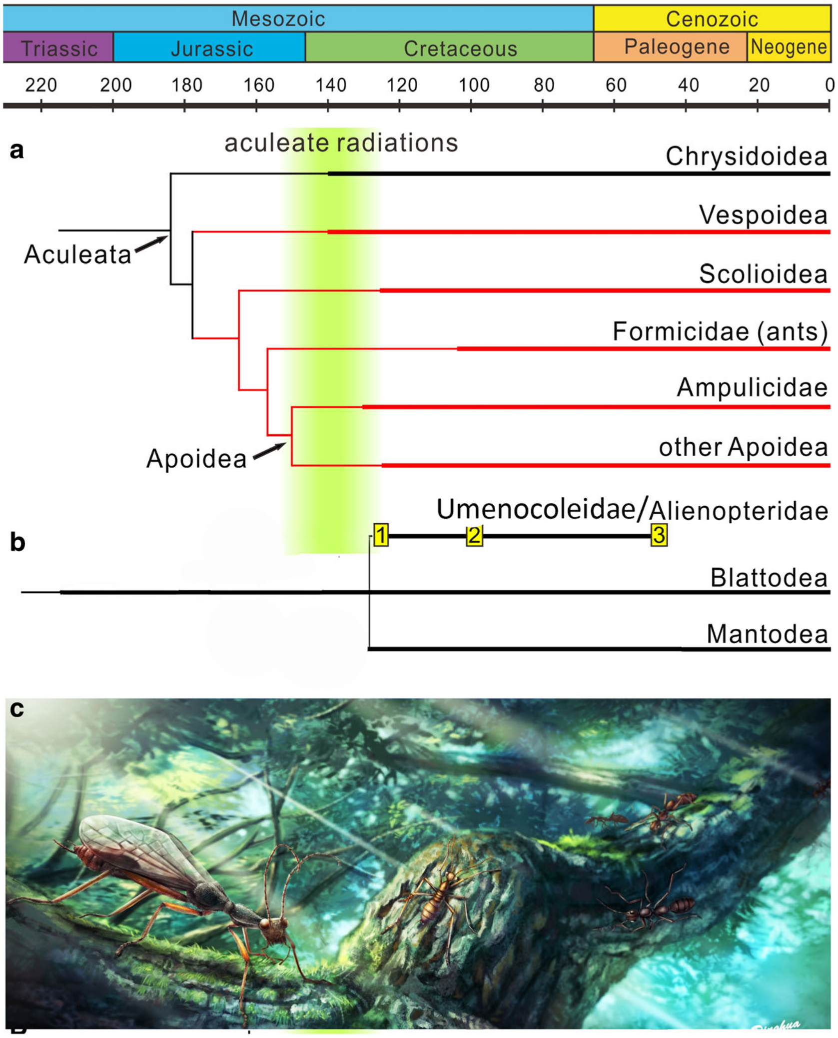


Fig. 3 **a** Simplified evolutionary history of Aculeate Hymenoptera (Branstetter et al. 2017; Peters et al. 2017) and (**b**) Dictyoptera (Grimaldi and Engel 2005; Vršanský et al. 2017). Thick lines indicate the known extent of the fossil record. Branches representing potential wasp models are red. The light green area represents the time when aculeate lineages experienced radiations (Barden and Grimaldi 2016). Alienopterid fossils are indicated with yellow vertical bars: 1, Early Cretaceous Crato Formation of Brazil (125–113 million years); 2, mid-Cretaceous Burmese amber (99 million years); 3, Eocene Green River Formation of USA (47 million years). (**c**) Ecological restoration of Cretaceous alienopterids and ants in amber forest. The insect with wings (left) is an alienopterid adult; the insect (centre) is an alienopterid nymph; and the three insects (right) are sphecomyrmine ant workers

some derived aculeate Hymenoptera, particularly bees. Bees underwent evolutionary radiation during the Late Cretaceous and early Cenozoic and displayed high diversity during the Eocene (Engel 2001; Barden and Grimaldi 2014). They have powerful defense mechanisms such as painful stings and group defense, and most predators avoid them (Ruxton et al. 2004). Consequently, bees are a likely model for *Chimaeroblattina*. In conclusion, these new alienopterid adults display a resemblance to some coeval aculeate Hymenoptera in outer appearance

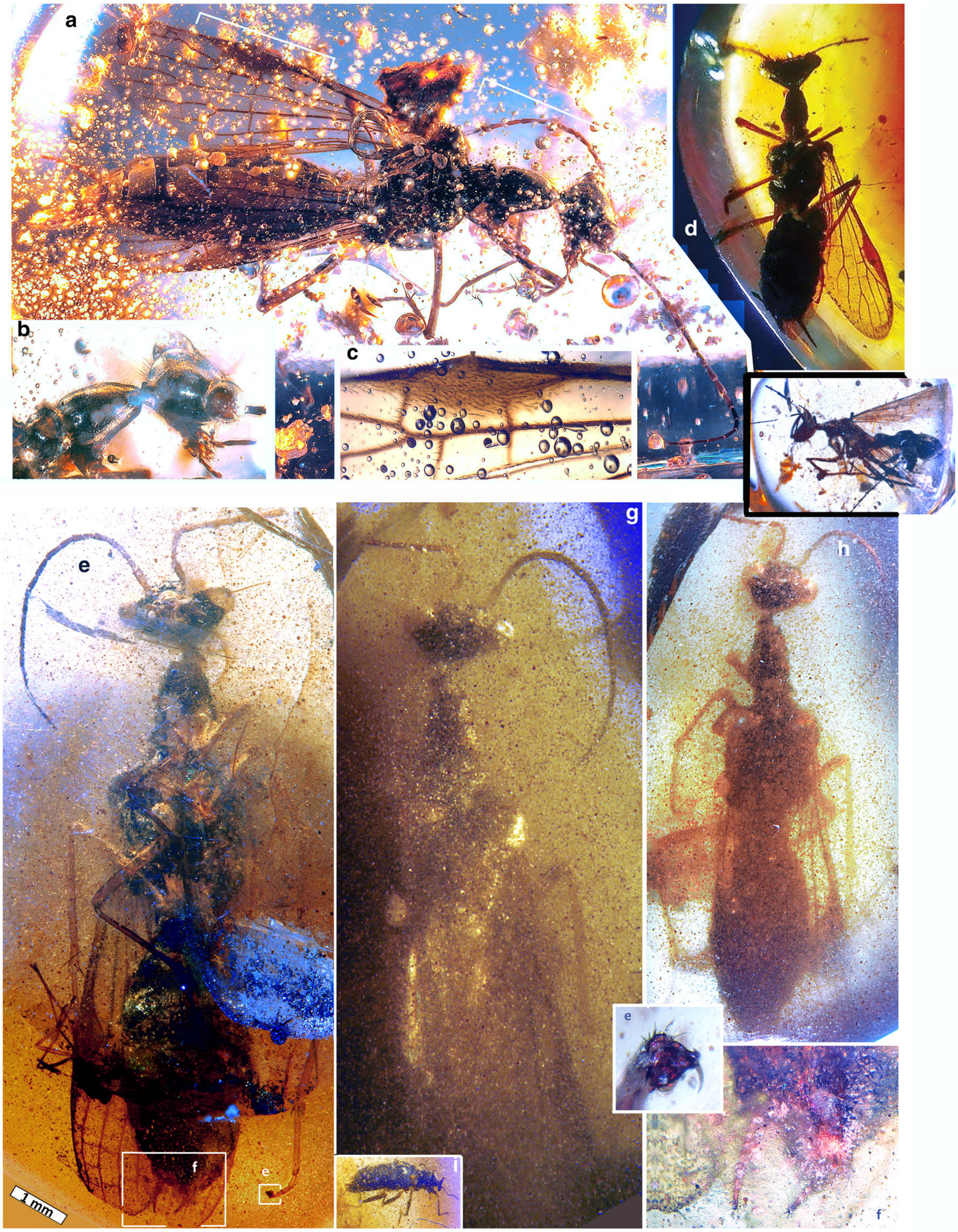


Fig. 4 **a-c** Dinosaur age ant-mimicking myrmecomorphs *Teyia branislav* sp. n. holotype BA17011, (**d**) undescribed specimen and (**e-g**) *Teyia huangi* sp. n. holotype NIGP154578 ((**h**) with syninclusion) and its presumed ant model (all Myanmar amber)

including body size, head and pronotum shape, long antennae, and robust body. In particular, some alienopterids have a waist-like constriction (distinct in *Teyia*; less distinct in *Chimaeroblattina* and *Grant*) and hindwings with reduced venation and a distinct pterostigma, providing robust morphological evidence of wasp mimicry.

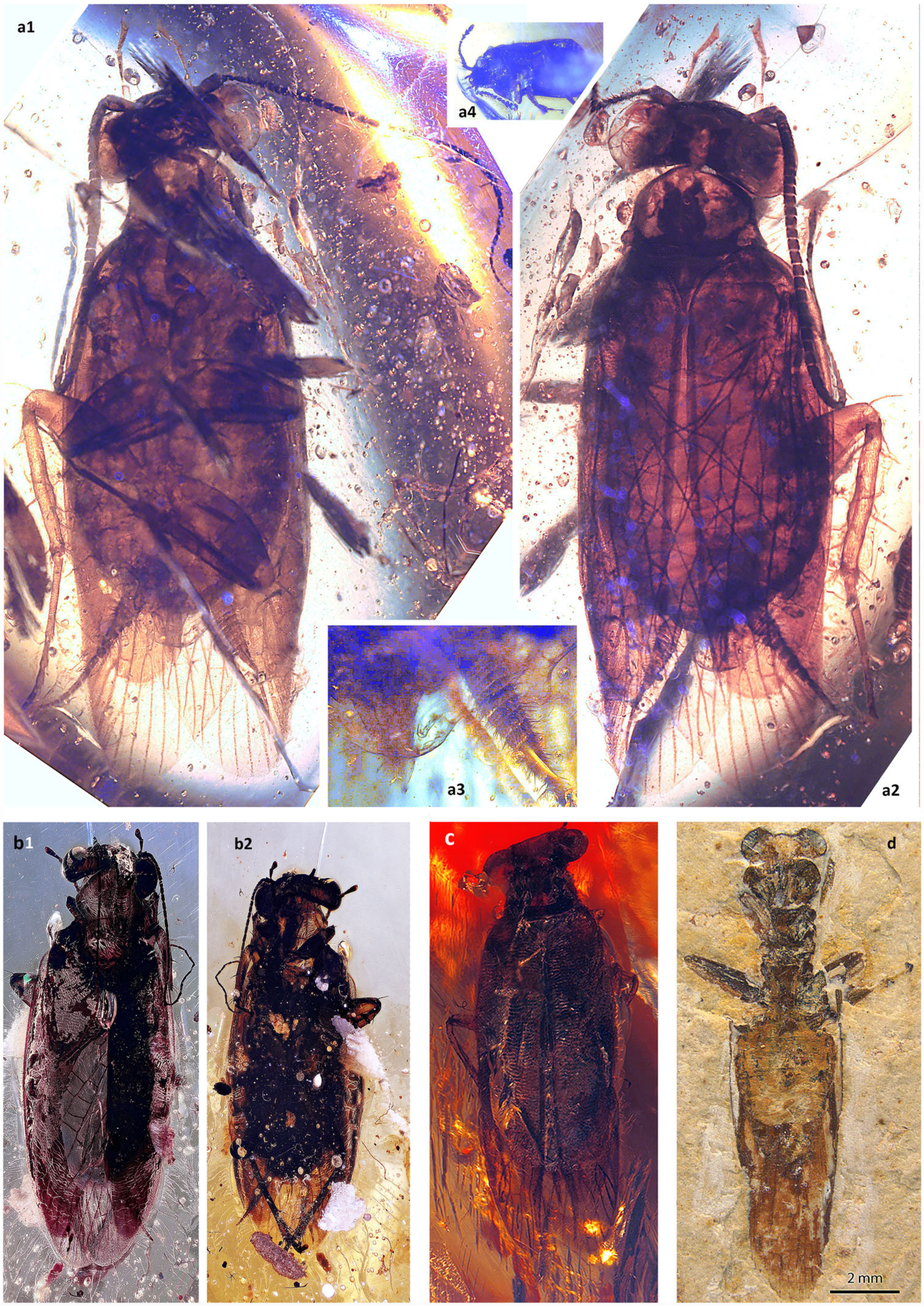
To access the ecological requests of the model or mimic is impossible at the present state of the knowledge. Alienopterids were not predatory, but instead pollinators and pollivores. The ecological relation to ants and role of ants in gymnosperm/ early angiosperm pollination and protection is obscure (Fig. 3).

Fig. 5 Dinosaur age wasp or solitary bee-mimicking pollinator *Meilia jinghanae* sp. n. holotype NIGP154579 (Myanmar amber) and its model-type living *Epeleoides coecutiens*. (**a**) Details of head, (**b**)ventral view, (**c-d**) tarsi, (**e**) detail of arolium with asymmetrical claw, (**f-g**) fore- and hind wing, (**h**) dorsal view, (**i**) antenna

Evolutionary implications

Batesian mimicry is widespread in modern insects (Quicke 2017; but not in cockroaches – Vidlička 2001). Aculeates, including bees and ants, are the most frequently mimicked models for Batesian mimicry (Ruxton et al. 2004). A wasp mimic *Cratomyia mimetica* (Zhangsolvidae) is already known (Grimaldi 2016). A case of mimicry in Burmese amber is cerambyid *Ornatomalthinus* interpreted as a putative Batesian mimic of a venomous lycid beetle model proposed by Poinar and Fanti (2016). The new alienopterid adults mimic ancient aculeate wasps, bees and ants respectively.

Fig. 6 Dinosaur age beetle-like *Alienopterix ocularis* sp. n. (Myanmar amber). (**a**) Holotype NIGP154581 (a1-4: dorsal, ventral view, ovipositor with cerci and syninclusion, respectively); (**b-c**) specimens in private collections (b1, 2: dorsal and ventral view, respectively); (**d**) undescribed specimen from Crato SMNS 66528



Like other stem-group cockroaches, these new alienopterids had small mandibles, lacked raptorial forelegs and were phytophagous or omnivorous. They would have gained protection by mimicking aculeates. The fossil record of Batesian mimicry in insects is very sparse, and the additional record was from the Paleocene, involving mimicry by a heteropteran based on an aculeate model (Wappler et al. 2013). Our discovery provides the earliest record of Batesian mimicry in insects, extending its occurrence back to the Early Cretaceous.

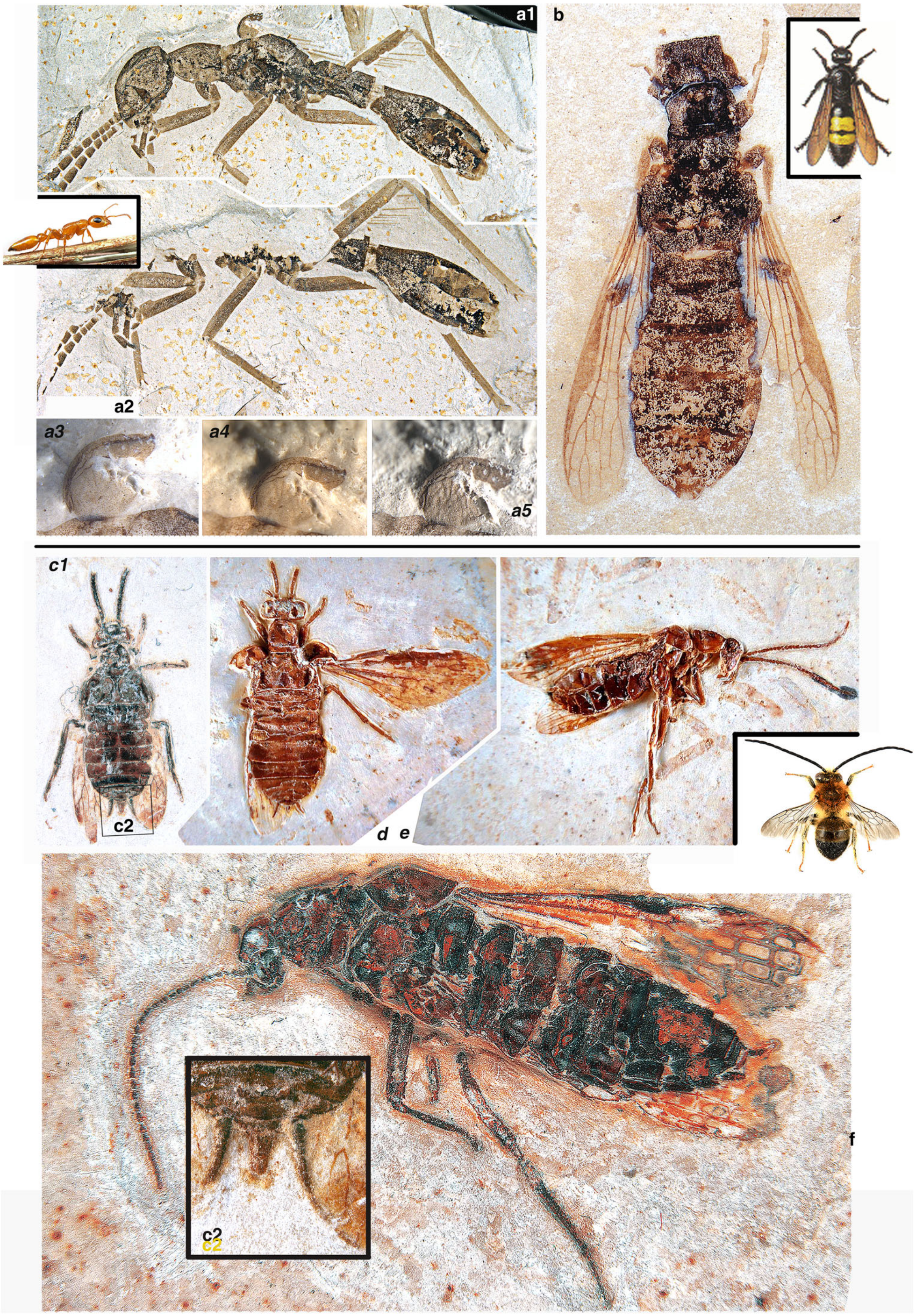


Fig. 7 Hymenopteran-mimicking cockroaches (Alienopteridae) preserved in sediments. (**a**) Ant-mimicking *Grant viridifluvius* holotype USNM 496006 AB (a1, a2: positive and negative (reversed), respectively; a3-5: details on forewing under diverse illumination); (**b**) wasp-mimicking *Chimaeroblattina brevipes* holotype USNM 570034 AB**.** (both Green River, Colorado; Eocene); (**c-e**) Wasp or solitary bee-mimicking *Apiblatta muratai* sp. n. KMNH263–1; (**f**) *Vcelesvab cratocretokrat* sp. n. holotype SMNS 66645 (all Crato, Brazil; Aptian Cretaceous). *Tetraponera*, *Scolia* and *Eucera* as putative model types

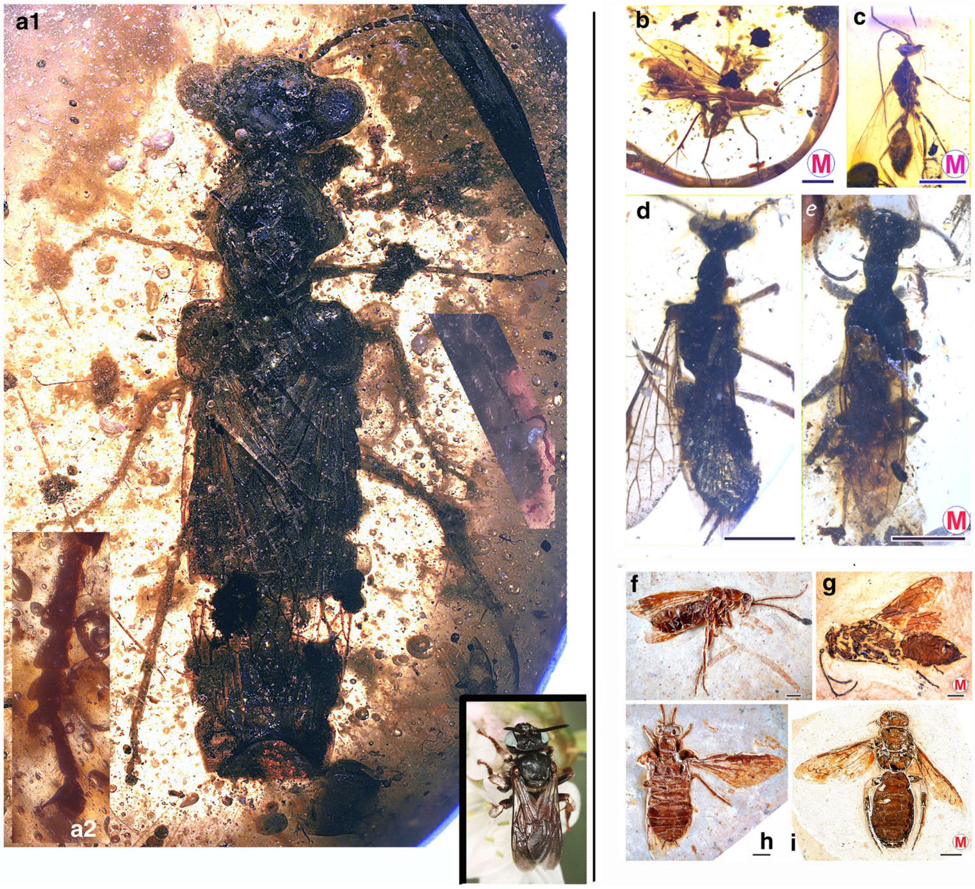


Fig. 8 Alienopteridae and their potential models from mid-Cretaceous Burmese amber. (**a**) Dinosaur age wasp mimicking and tooth-armed saw-like pronotum bearing *Caputoraptor vidit* sp. n. holotype NIGP154580 and its living model-type *Epeleoides* female (alternative model types are Black Cockroach Hunters; e.g., *Tachysphex nigerrimus*); (**b**) Vespoid wasp model, BA17013; (**c**) Winged sphecomyrmine ant model; (**d**) *Teyia branislav* sp. n., paratype, NIGP154577, dorsal aspect; (**e**) Ampulicid wasp, NIGP154582, dorsal aspect; (**f**) *Apiblatta* sp., SC Z11, from Crato Formation; (**g**) Scoliidae, *Cretoscolia brasiliensis model type*, MURJ, from Crato Formation; (**h**) *Apiblatta* sp., SC 187, from Crato Formation, ventral aspect; (**i**) Angarosphecidae, *Cretosphex magnus*, F103 coll. MSF, from Crato Formation, dorsal aspect. The red capital letter M indicates the potential model. Scale bars, 2 mm

Batesian mimicry is extremely rare in extant cockroaches, with only a few species mimicking beetles (Schmied et al. 2013; Vršanský et al. 2016). Our discovery provides evidence that Batesian mimicry was not only present in the ancient lineages but also involved different models. By the Early Cretaceous, many new predaceous arthropods (including some spiders, lacewing larvae, and ants) and vertebrates (including lizards, birds, and mammals) had evolved (Wang et al. 2016; Luo 2007; Xu et al. 2014). In addition, aculeate lineages experienced radiations during the latest Jurassic–early Cretaceous (Barden and Grimaldi 2016), and they had already displayed high abundance and diversity by the mid Early Cretaceous (Figs. 4, 5, 6, 7 and 8). Model-mimic coevolution probably favored the evolution of body shapes of alienopterids corresponding to the more frequent models (Quicke 2017; Ceccarelli and Crozier 2007; Kikuchi and Pfennig 2010).

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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Affiliations

Peter Vršanský[1,2,3,4] • **Günter Bechly**[5] • **Qingqing Zhang**[6,7] • **Edmund A. Jarzembowski**[6,8] • **Tomáš Mlynský**[2,9] • **Lucia Šmídová**[10,11] • **Peter Barna**[2] • **Matúš Kúdela**[11] • **Danil Aristov**[3,12] • **Sonia Bigalk**[13] • **Lars Krogmann**[13] • **Liqin Li**[6] • **Qi Zhang**[6,7] • **Haichun Zhang**[6] • **Sieghard Ellenberger**[14] • **Patrick Müller**[15] • **Carsten Gröhn**[16] • **Fangyuan Xia**[17] • **Kyoichiro Ueda**[18] • **Peter Vďačný**[10] • **Daniel Valaška**[19] • **Lucia Vršanská**[19] • **Bo Wang**[6,20]

[1] Institute of Zoology, Slovak Academy of Sciences, 845 06 Bratislava, Slovakia

[2] Earth Science Institute, Slovak Academy of Sciences, 840 05 Bratislava, Slovakia

[3] Paleontological Institute, Russian Academy of Sciences, 117868 Moscow, Russia

[4] Research Center of Quantum Informatics, Institute of Physics, Slovak Academy of Sciences, 84511 Bratislava, Slovakia

[5] Böblingen, Germany

[6] State Key Laboratory of Palaeobiology and Stratigraphy, Center for Excellence in Life and Paleoenvironment, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing 210008, China

[7] University of Sciences and Technology of China, Hefei 230026, China

[8] Department of Earth Sciences, Natural History Museum, London SW7 5BD, UK

[9] Balneological Museum Piešťany, SK-921 01 Piešťany, Slovakia

[10] Faculty of Natural Sciences, Comenius University, 84215 Bratislava, Slovakia

[11] Faculty of Natural Sciences, Charles University, 2, 12843 Praha, Czech Republic

[12] Cherepovets State University, 162600 Cherepovets, Russia

[13] Staatliches Museum für Naturkunde Stuttgart, D-70191 Stuttgart, Germany

[14] Kassel, Germany

[15] Käshofen, Germany

[16] Amber Council at Geological-Palaeontological Institute, University of Hamburg, 20146 Hamburg, Germany

[17] Shanghai, China

[18] Kitakyushu Museum of Natural History & Human History, Fukuoka 805-0071, Japan

[19] Bratislava, Slovakia

[20] Key Laboratory of Zoological Systematics and Evolution, Institute of Zoology, Chinese Academy of Science, Beijing 100101, China