Biologia (2023) 78:1701–1712
https://doi.org/10.1007/s11756-022-01265-7

ORIGINAL ARTICLE

Alienopterix santonicus sp. n., a metallic cockroach from the Late Cretaceous ajkaite amber (Bakony Mts, western Hungary) documents Alienopteridae within the Mesozoic Laurasia

Márton Szabó[1,2] · Péter Szabó[3] · Péter Kóbor[4] · Attila Ősi[1,2]

Received: 29 July 2022 / Accepted: 4 November 2022 / Published online: 8 December 2022

Abstract

Cockroaches (Blattaria s. str.) were documented from numerous amber localities around the world, representing both extinct and extant families. Alienopteridae is an extinct cockroach family known only from the Cretaceous of Gondwana (Brazil, Botswana, Myanmar amber) and the Cenozoic of North America. *Alienopterix santonicus* sp. n. from the Late Cretaceous amber of the Ajka Coal Formation (Bakony Mts, western Hungary) extends the rich geographical distribution of the family into Laurasia during the Mesozoic. As a member of the presumably pollinator cohort Alienopteridae, this species could have played an important role in the Ajka Coal ecosystem during the Santonian. The microrectangular structures of the forewing suggest that the new species likely possessed a metallic colouration already known from the group. Combined with the disruptive body pattern this could have served as an advanced camouflage. The microrectangular structures of the forewing were compared to integument microstructures of extant insects with metallic colouration. Various arthropod taxa are already known from ajkaite, and the new discovery further emphasizes the importance of this amber.

Keywords Fossil insect · Santonian · Blattaria · Umenocoleoidea

Introduction

Dictyoptera is a medium-sized group of insects with more than 10.000 described extant and fossil species, traditionally comprising cockroaches and termites (order Blattaria s. l.), mantises (order Mantodea) and the extinct family of water-walking insects (order Chresmoda) (Luo et al. 2022). Cockroaches (Blattaria s. str.) are one of the most dominant insect orders in Paleozoic and Mesozoic ecosystems (Vršanský 2008; Chen et al. 2019; Wappler and Vršanský 2021). Appearing in the Late Carboniferous (Tan 1980; Vršanský et al. 2002; Schneider and Werneburg 2006; Zhang et al. 2012), they are considered as ancestors of Isoptera, Mantodea and Chresmoda (Vršanský 2002, 2010, 2020). In the course of their 320 Ma-long evolution, cockroaches adapted to a wide range of ecosystems and developed a high degree of ecological, behavioural and morphological diversity. During the course of their evolution, there are now aquatic, pollinating, decomposing, jumping, mimicking, camouflaging, translucent, aposematic, parasitic, predatory, poisonous, eusocial, virus infection-symptomatic, holoptic, pectinate and bipectinate antennate, cavernicolous, injecting-ovipositor, brachypterous, cranefly-like and beetle-like forms (Chen

✉ Márton Szabó
szaboomaarton@ttk.elte.hu; szabo.marton.pisces@gmail.com

Péter Szabó
sz.piiit01@gmail.com

Péter Kóbor
kobor.peter@atk.hu

Attila Ősi
hungaros@gmail.com

1 Department of Paleontology and Geology, Hungarian Natural History Museum, Ludovika Tér 2, Budapest 1083, Hungary

2 Institute of Geography and Earth Sciences, Department of Palaeontology, ELTE Eötvös Loránd University, Pázmány Péter Sétány 1/C, Budapest 1117, Hungary

3 Environmental Analytical and Geoanalytical Research Group, Szentágothai Research Centre, University of Pécs, Ifjúság Útja 20, Pécs 7624, Hungary

4 Plant Protection Institute, Centre for Agricultural Research, Eötvös Loránd Research Network, Herman Ottó Út 15, Budapest 1022, Hungary

and Tian 1973; Wei and Ren 2013; Šmídová and Lei 2017; Vršanský et al. 2018; Hinkelman 2020, 2021; Hinkelman and Vršanská 2020; Mlynský et al. 2019; Li et al. 2020; Sendi et al. 2020; Chen et al. 2021; Sendi 2021; Oyama et al. 2021; Kováčová 2022). Blattaria comprises about 5,000 extant and 1,500 fossil species (Liang et al. 2019; Sendi 2021; Wappler and Vršanský 2021). Extinct taxa with externally protruding ovipositors are sometimes referred to as „roaches" or „roachoids", distinguishing them from the crown group of living true cockroaches (Li 2019; Koubová and Mlynský 2020). Fossil cockroaches are abundant, documented across numerous amber localities of various age. Most notable include North Myanmar (Vršanský et al. 2018), Baltic (Weitschat and Wichard 2002), Dominican (Gutiérrez and Pérez-Gelabert 2000; Poinar 2022) and Mexican amber (Solórzano-Kraemer 2007; Vršanský et al. 2011; Barna et al. 2019).

Alienopteridae is a unique extinct cockroach family within the superfamily Umenocoleoidea (Vršanský et al. 2018; Sendi et al. 2020). This family was described from the Late Cretaceous (Cenomanian) North Myanmar amber (Bai et al. 2016), which is one of the most species- and specimen-rich amber deposits in the world (Grimaldi et al. 2002). Alienopteridae is the only Mesozoic-type cockroach family that successfully survived the K/Pg extinction event (Vršanský et al. 2018). The fossil record of Alienopteridae ranges from Early Cretaceous (Barremian) to Middle Eocene (Ypresian/ Lutetian) with at least 21 species across 16 genera. An undescribed member of this family was also documented from the Cretaceous of Botswana by McKay (2007) (Luo et al. 2022). For a summary of the fossil records of Alienopteridae see Table 1.

The Cretaceous is one of the most extensively studied periods in terms of cockroach evolution, with more than 200 formally described species (Vršanský 2019; EDNA fossil insect database 2022–07-28). However, European Cretaceous ambers still remain largely unexplored. The only evaluated significant European locality is Archingeay (France) with 17 cockroach specimens in amber (Vršanský 2009).

Regarding its geochemistry, age and its preserved inclusions, the so-called ajkaite is a unique Late Cretaceous type of amber, found in western Hungary. It is known to be rich in arthropod inclusions since the middle of the twentieth century (Tasnádi Kubacska 1957). Arthropod species, formally described from ajkaite are the ceratopogonid dipterans *Adelohelea magyarica* Borkent, 1997 and *Leptoconops clava* Borkent, 1997, the hersiliid spider *Hungarosilia verdesi* Szabó et al., 2022, the click beetle *Ajkaelater merkli* Szabó et al., 2022, and the wasps *Ajkanesia harmincipsziloni* Szabó et Brazidec, 2022, *Amissidigitus belae* Szabó et Brazidec, 2022 and *Spathiopteryx soosi* Szabó, Brazidec et Perrichot, 2022 (Borkent 1997; Szabó et al. 2022a, b,

Table 1 Summary of the fossil records of Alienopteridae Bai et al. (2016)

Genus	Species	Locality	Age	Literature
Aethiocarenus	*burmanicus*	Myanmar	Upper Cretaceous (Cenomanian)	Poinar and Brown (2017)
Alienopterix	*santonicus* sp.n.	Hungary	Upper Cretaceous (Santonian)	present paper
	mlynskyi	Myanmar	Upper Cretaceous (Cenomanian)	Vršanský et al. (2021b)
	ocularis	Myanmar	Upper Cretaceous (Cenomanian)	Vršanský et al. (2018)
	smidovae	Myanmar	Upper Cretaceous (Cenomanian)	Vršanský et al. (2021b)
Alienopterella	*stigmatica*	Myanmar	Upper Cretaceous (Cenomanian)	Kočárek (2019)
Alienopterus	*brachyelytrus*	Myanmar	Upper Cretaceous (Cenomanian)	Bai et al. (2016)
Apiblatta	*muratai*	Brazil	Lower Cretaceous (Albian)	Vršanský et al. (2018)
Caputoraptor	*elegans*	Myanmar	Upper Cretaceous (Cenomanian)	Bai et al. (2018)
	vidit	Myanmar	Upper Cretaceous (Cenomanian)	Vršanský et al. (2018)
Chimaeroblattina	*brevipes*	USA, Colorado	Middle Eocene (Ypresian/ Lutetian)	Vršanský et al. (2018)
Eminespina	*burma*	Myanmar	Upper Cretaceous (Cenomanian)	Chen et al. (2021)
Formicamendax	*vrsanskyi*	Myanmar	Upper Cretaceous (Cenomanian)	Hinkelman (2020)
Grant	*viridifluvius*	USA, Colorado	Middle Eocene (Ypresian/ Lutetian)	Vršanský et al. (2018)
Meilia	*jinghanae*	Myanmar	Upper Cretaceous (Cenomanian)	Vršanský et al. (2018)
Teyia	*branislav*	Myanmar	Upper Cretaceous (Cenomanian)	Vršanský et al. (2018)
	huangi	Myanmar	Upper Cretaceous (Cenomanian)	Vršanský et al. (2018)
Nadveruzenie	*postava*	Myanmar	Upper Cretaceous (Cenomanian)	Vršanský et al. (2021b)
Vcelesvab	*cratocretokrat*	Brazil	Lower Cretaceous (Albian)	Vršanský et al. (2018)
Vzrkadlenie	*miso*	Myanmar	Upper Cretaceous (Cenomanian)	Sendi et al. (2020)
new genus	two new species	Botswana, Orapa	Cretaceous	McKay (2007)

c). Among others, undescribed specimens of Arachnida, Diptera, Hymenoptera and Coleoptera are known from museum collections. During the revision of several ajkaite amber pieces housed in museum collections across Hungary, an inclusion representing a new species of Alienopteridae, *Alienopterix santonicus* sp. n. is described together with its paleoecological and paleogeographical implications. This species now extends the Mesozoic record of Alienopteridae to Laurasia (previously only known from Gondwana and burmite during the Mesozoic).

Geological settings

Ajkaite is found in the Ajka Coal Formation, whose outcrops were discovered in the 1860's within the Ajka-Csinger Valley (Ajka-Csingervölgy in Hungarian) (Szabó 1871; Hantken 1878). Ajka-Csinger Valley is situated approximately four km southeast from the city of Ajka (Bakony Mountains, western Hungary) (see Fig. 1a, b).

The Ajka Coal Formation occurs in the Bakony Mountains (Transdanubian Range), sometimes reaching a thickness of 120 m (Fig. 1b). Seven main coal-beds have been documented with thickness ranging between 80–360 cm (Kozma 1991). The formation is concentrated in three carbonate terrain sub-basins: Ajka, Magyarpolány-Devecser, and Gyepükaján (see Császár and Góczán 1988; Siegl-Farkas 1988). It is built up as an alternation of coal or clayey coal beds, marls, sands and sandstone beds, as well as light grey to brownish carbonaceous to argillaceous pelitic rocks with interbedded molluscan lumachelles (Haas 1983). Based on palynological and nannoplankton remains, the Ajka Coal Formation was determined to be Santonian in age (Siegl-Farkas and Wagreich 1996; Bodrogi et al. 1998; Bodor and Baranyi 2012). Apart from the inclusions discovered in ajkaite (see above), the flora and

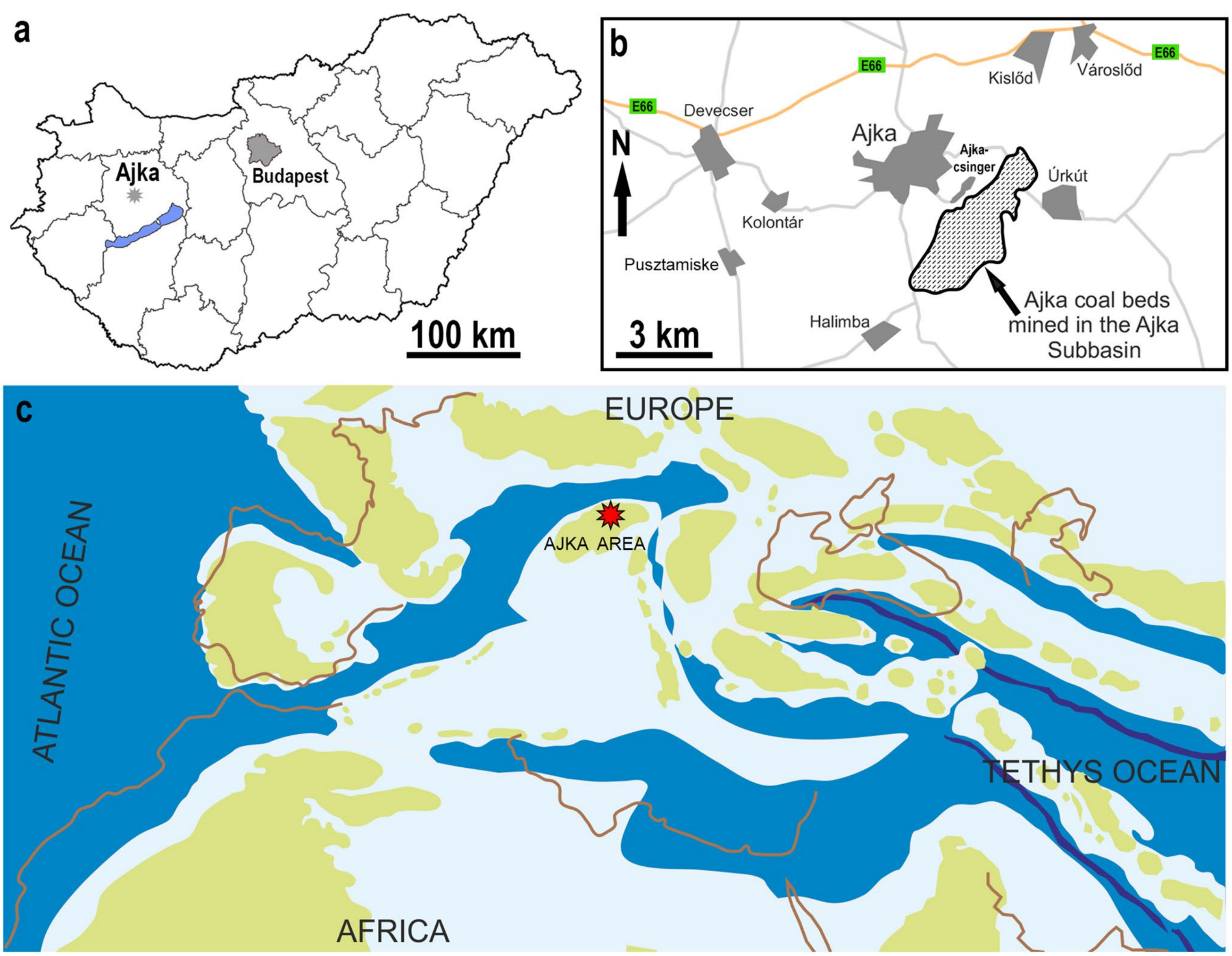

Fig. 1 **a** Locality map of Ajka and **b** the Ajka Coal Beds. **c** Map showing the position of the Ajka area within the European paleobioprovince during the Late Cretaceous (modified after Ősi et al. 2010)

fauna were documented by numerous authors (Ősi et al. 2016; Szabó et al. 2022a and references therein). During the Late Cretaceous, the depositional area of the Ajka coal was part of the western Tethyan archipelago (Fig. 1c).

Pieces of ajkaite available today are from the coal layers and are housed in private and museum collections. Coal bed 0 was by far the richest, being the uppermost of the coal deposits, with an average thickness of 70 cm. Unfortunately, 139 years of continuous deep mining of the coal was discontinued in 2004, with little opportunity to collect further specimens. Coal bed 6, the lowest one, is the only one which is still accessible in the area of the Bocskor-trench near Ajka. However, here the coal is loose and earthy, whereas the amber is small and brittle, mostly present in the form of drops or tiny splinters.

Material and methods

The here described specimen is housed in the paleontological collection of the Supervisory Authority of Regulatory Affairs (SARA; former Mining and Geological Survey of Hungary; Budapest).

Habitus photographs were taken by Kern Optics OZL 466 stereoscopic microscope mounted with Kern Optics OCD 832 (5 MPix) microscope camera (operating software: Kern&Sohn MicroscopeVIS 2.0 Pro). Close-up photographs of the head, antennae, pronotum and the forewings were taken with a QImaging MP5.0 digital microscope camera under a Nikon LV 100 polarized light microscope, and processed with Image Pro Insight 8.0 software. For scanning electron microscopic photography modern insect specimens were gold coated. Subsequently, a Jeol, JSM-IT500HR apparatus was used for the investigations (University of Pécs, Szentágothai Research Center; Pécs). We used Adobe Photoshop Image.20 software to compose the figures. Body dimensions of the inclusion have been measured by the free version of ImageJ 1.48v.

Systematics and terminology mainly follow that of Vršanský et al. (2018, 2021a, b), following the Comstock-Needham (1896) vein systems.

Systematic Paleontology

Order Blattaria, Latreille 1810 = Blattodea Brunner von Wattenwyl, 1882 (cockroaches without termites, mantodeans and chresmodids)

Superfamily Umenocoleoidea Chen et Tian, 1973

Family Alienopteridae Bai et al., 2016

= Aethiocarenidae Poinar et Brown, 2017

Type genus: *Alienopterus* Bai, Beutel, Klass, Wipfler et Zhang in Bai et al. (2016). For composition see Table 1

Stratigraphic range: Barremian—Eocene

Geographic range: Gondwana and Laurasia (by the present study)

Remarks (after Bai et al. 2006). Based on the following characters, the specimen belongs to the family Alienopteridae: filiform antennae elongated from the first antennomeres, large and strongly convex compound eyes, saddleshaped pronotum and elytrized forewings with microrectangular structures (Vršanský et al. 2021b).

Subfamily Alienopterixinae Vršanský in Vršanský et al. (2021b)

Genus *Alienopterix* Mlynský, Vršanský et Wang, in Vršanský et al. (2018)

Type species: *Alienopterix ocularis* Mlynský, Vršanský et Wang, 2018

Stratigraphic range: Cenomanian—Santonian

Geographic range: North Myanmar amber and Hungarian ajkaite amber (present study)

Remarks (after Vršanský et al. 2018). Following the fully developed forewings and the lack of separated posterior area of the pronotum, the ajkaite specimen represents the genus *Alienopterix* (after Vršanský et al. 2018). This genus is also more robust compared to other genera of the family, with a unique rectangular microstructure on the forewings. The present study follows Vršanský et al. (2018) on the basis of asymmetrical claws known within this genus (and all Alienopteridae but not Umenocoleidae) and lack of clavus (like in Alienopteridae, unlike Umenocoleidae), and also saddleshaped pronotum without paranotalia and without basal delimiting ridge, however, the genus is included in Umenocoleidae by Luo et al. (2022). To further discuss the correct systematic position of *Alienopterix* is beyond the scope of the present paper.

***Alienopterix santonicus* sp. n.**

urn:lsid:zoobank.org:act:58D42E91-3DA5-47C1-ADE7-282CFCA0FC99

Figures 2, 3, and 4

Description. Small, beetle-like cockroach. Head large and wide (0.4 mm long and 1.2 mm wide) with densely spaced and short microtrichiae (Fig. 2c). Epicranium 0.7 mm wide. Epicranial sutures not visible. Compound eyes very large and globular. Left eye complete (~ 0.5 × 0.3 mm in dorsal view). Ocular facets obscure, very small in diameter. Area between the eyes wide (0.6 mm). Antennomeres of the right antenna are filiform, 22 preserved. Antennomeres are almost 2.5 × as long as wide. Antennal segments are covered with short sensillae up to 0.03 mm in length (Fig. 2d).

Pronotum very slightly vaulted and trapezoidal/ saddle-shaped with arched anterior and posterior margins, without paranotalia, wider than long (length/ width ~ 0.8/ 1 mm). Entire surface of pronotum is densely covered by short, small sensillae (Fig. 3a). Head not covered by pronotum,

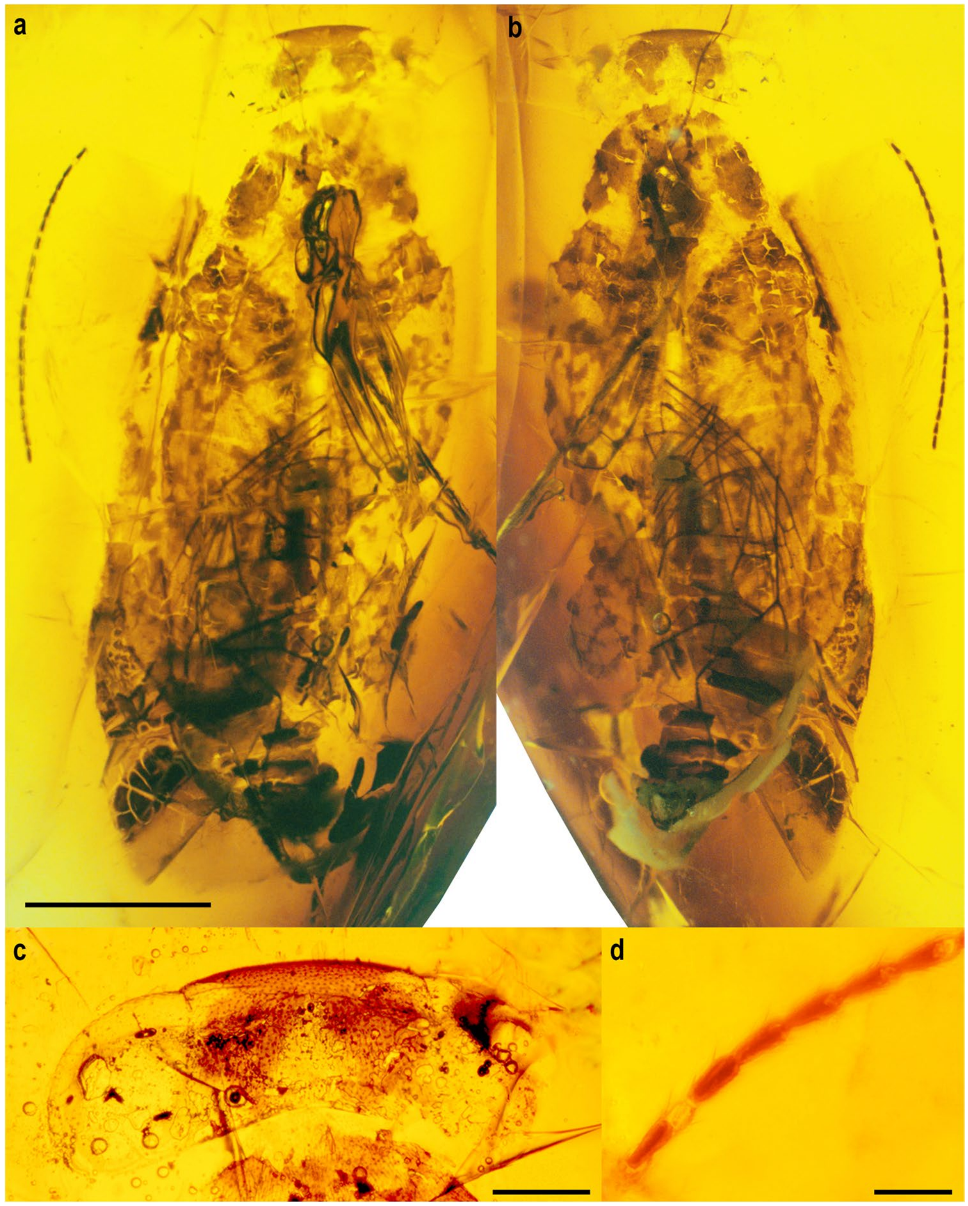

Fig. 2 *Alienopterix santonicus* sp. n. (SARA AT.10.24.1), holotype. **a** Habitus in dorsal view. **b** Habitus in ventral view. **c** Head in dorsal view. **d** Details of antennules. Scale bars: 0.5 mm (**a**, **b**), 0.2 mm (**c**), 0.1 mm (**d**)

indicating mobility of head with a possible neck. Scutellum triangular, ~0.12 mm long and ~0.16 mm wide (Fig. 3a).

Forewings fully developed, with ellipsoidal/ lentoid outline, clavus apparently not delimited. Left forewing is 3.7 mm long and 1.3 mm wide. Forewing venation is obscure. Dorsal surface of the forewings covered by microrectangular structures, arranged in medio-laterally running rows (Fig. 3c–e). Dense and short microtrichiae on the dorsal surface of the forewings up to 0.02 mm long, following the arrangements of the microrectangular structures (Fig. 3d, e).

Left hindwing venation is partly visible through the left forewing, and well-visible from ventral view. SC slightly visible and simple, CuP simple, R1 and RS traceable, RS with at least four branches posteriorly. Pterostigma dark. Vannus (A2 veins) clear and veer-like pleated. The left hindwing also shows several mutations or deformities (sensu Vršanský 2003, 2005; Vršanský et al. 2017), at least one (and possibly up to 3) R1-RS fusions and a serious CuA-CuA fusion (Fig. 4a). Due to weak visibility, additional deformities cannot be excluded.

Cercus short and straight, number of cercomeres is obscure (10 or 11). Cercomeres with sensilla.

Symmetrical colouration on head and pronotum, asymmetrical pigmentation on forewings. Head with bow-like pattern between the eyes. The pronotum bears a complex and almost symmetrical ornamentation consisting of dark and relatively large spots, low in number (number of visible spots is 5). The forewings are ornamented by an asymmetrical pattern of irregularly shaped and arranged small maculae, sometimes fused into short stripes and rosettes (Fig. 4a).

Type material. SARA AT.10.24.1. (holotype, ?male).

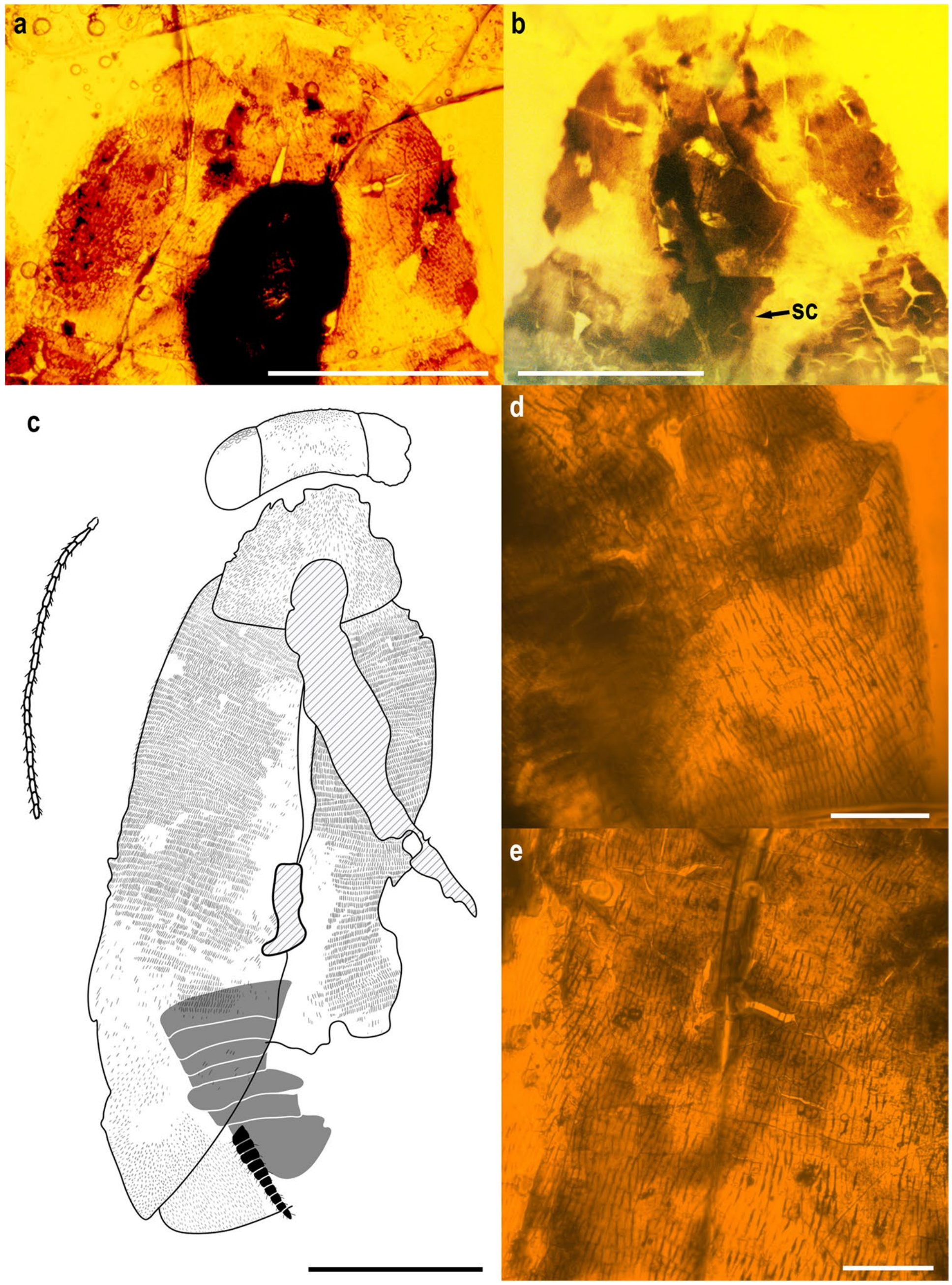

Fig. 3 *Alienopterix santonicus* sp. n., (SARA AT.10.24.1), holotype. **a** Pronotum in dorsal view. **b** Pronotum with scutellum (sc) in ventral view. **c** Line drawing of the habitus in dorsal aspect, showing the arrangement of the ornamentation of the forewings. **d**, **e** Dorsal surface of the forewings, possessing the microrectangular ornamentation with microtrichiae. Scale bars: 0.25 mm (**a**, **b**), 0.5 mm (**c**), 120 µm (**d**, **e**)

Type locality. Ajka-Csingervölgy, appr. 1 km SE of the city Ajka (Bakony Mts, Hungary).

Horizon and age. Ajka Coal Formation, unknown shaft of the Ajka-Csingervölgy coal minery; Upper Cretaceous, Santonian (86.3–83.6 Ma).

Etymology. The name *santonicus* is derived from the Santonian age of the Ajka Coal Formation where the specimen originates from.

Differential diagnosis. Genus *Alienopterix* currently includes three valid species: *A. mlynskyi*, *A. ocularis* and *A. smidovae*. *Alienopterix santonicus* sp. n. clearly differs from all known species of the genus based on the combination of the following characters. Unlike in *A. santonicus* sp. n., epicranial sutures are visible in *A. mlynskyi*. Antennomeres of *A. mlynskyi* are less than two times as long as wide, while those of *A. santonicus* sp. n. are more than two times as long as wide. The species *A. ocularis* lacks the characteristic secondary structure of the forewing, while forewings of *A. santonicus* sp. n. are covered with microrectangular structures. Unlike *A. santonicus* sp. n., *A. ocularis* has a distinct, campaniform pronotum. Also, antennal segments of *A. ocularis* are subequal, while those of *A. santonicus* sp. n. are more than two times as long as wide. Antennal segments of *A. smidovae* are subequal and rich in short and

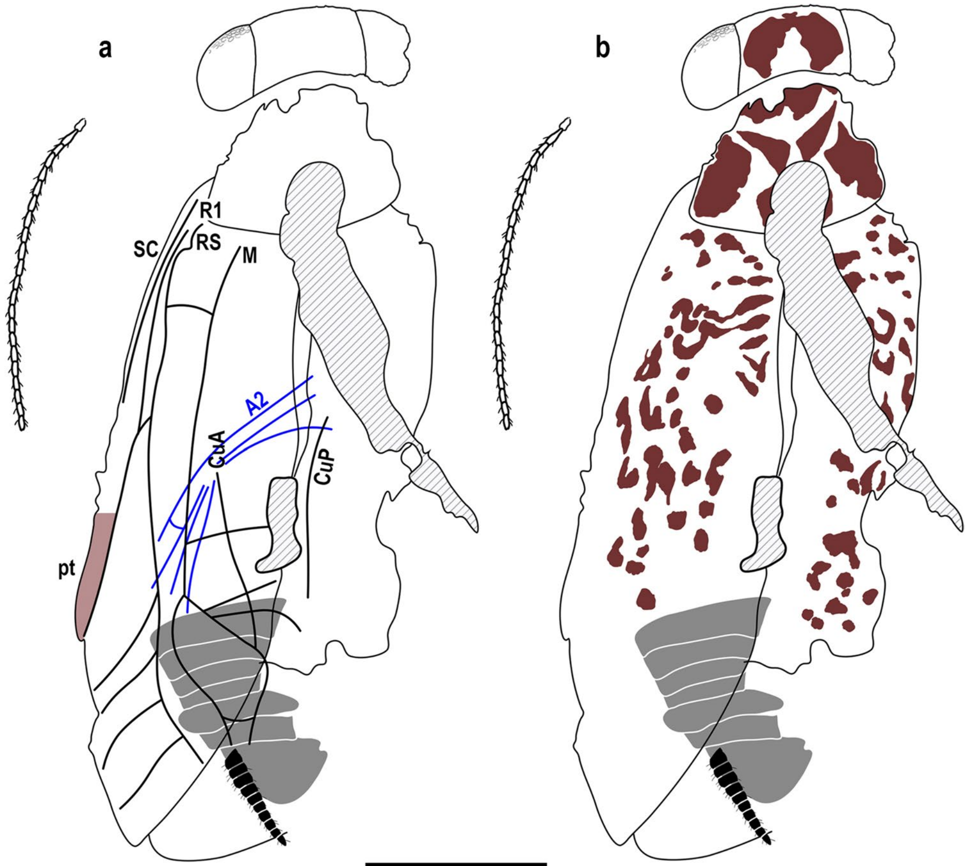

Fig. 4 *Alienopterix santonicus* sp. n., (SARA AT.10.24.1), holotype. Line drawing of the dorsal habitus showing the hindwing venation (**a**) and the disruptive maculate pattern (**b**). Scale bar: 0.5 mm

dense sensillae, while those of *A. santonicus* sp. n. are more longer than wide and comparatively sparse in sensillae.

The vannus of *A. santonicus* sp. n. is also unique. Although the vannus is not clearly preserved in any alienopterid, a veer-like pleated vannus is unknown for any Umenocoleoidea (although presumed; Vršanský, pers. comm.). The left hindwing also shows several deformities (see above). This is remarkable, as deformities occur in cockroaches from Early Cretaceous Lebanese amber (and other 127 Ma diversification points), while they were extremely rare among Late Cretaceous Myanmar amber cockroaches. This applies more to the hindwing, which bears the most of the aerodynamical weight during the stroke in this presumably well-flying organisms. Among Cretaceous Alienopteridae (and Umenocoleidae), hindwing deformities are barely known. During the whole Upper Cretaceous similar deformities were generally rare.

A. santonicus sp. n. can be distinguished from all other members of the genus by the unique maculate pattern of the dorsum—namely the pronotum and forewings.

Preservation. Body of the type specimen incomplete (length/ width 4.9/ 1.8 mm); all legs, most of the abdomen (except for seven posterior tergites and the left cercus), one of the antennae and a large part of the head including mouthparts are missing (Fig. 2a, b). Dorsally, a bubble covers the scutellum, part of the pronotum and the right forewing.

Discussion

Based on phylogenetic Bayesian network analysis, Alienopteridae experienced explosive radiation ~ 127 Ma (Vršanský et al. 2018). Until the present study, the genus *Alienopterix* was known to be indigenous to Myanmar: *A. mlynskyi*, *A. ocularis* and *A. smidovae* were discovered in the Late Cretaceous (Cenomanian) amber of Northern Myanmar (Vršanský et al. 2018, 2021b; Luo et al. 2022). Northern Myanmar amber is considered by some authors to be of Gondwanan origin (Poinar 2018). The discovery of *A. santonicus* sp. n. in the Santonian ajkaite amber expands the temporal and geographical distribution of the whole family and the genus as well. This genus also seems to occur in the Cretaceous ambers of Spain (L. Šmídová, unpublished observation) – thus the Mesozoic presence of Alienopteridae in Laurasia is fully validated.

Most cockroach species are regarded as omnivorous scavengers and detritivores (Sendi et al. 2020). However, according to Vršanský et al. (2018, 2021b) and Hinkelman (2020), alienopterids were most likely pollinators (of cycads, angiosperms and gymnosperms) and pollinivores. The depositional area of the Ajka Coal was characterized by swampy and lacustrine environments, dominated by angiosperms (Szabó et al. 2022a). Nonetheless, gymnosperms, in the form of Araucariaceae trunks are also reported from the formation (Rákosi L., unpublished reports; Bodor et al. 2013). As a pollinator life-style is tentatively suggested for *A. santonicus* sp. n., the species could have found a wide range of food sources and suitable habitats in the Ajka Coal swamp, thanks to the rich floral assemblage. Therefore, as a possible pollinator, *A. santonicus* sp. n. could have been playing an important role in the Ajka Coal ecosystem during the Santonian. For an artistic reconstruction of *A. santonicus* sp. n. see Fig. 5.

Metallic colouration and iridescence is fairly abundant among modern insects, including the extant cockroach genera *Eucorydia*, *Eustegasta*, *Melyroidea* and *Pseudoglomeris* (Shelford 1912; Li et al. 2018; Hinkelman et al. 2020; Yanagisawa et al. 2021). Fossil metallic cockroach species are extremely rare. This pattern occurs only in one immature cockroach from Taimyr amber (Vršanský 2019). Metallic colouration also occurs in the fossil genus *Alienopterix*. The dorsal surface of the forewings of *A. santonicus* sp. n. also bears rectangular (microrectangular) structures, built up by seemingly concave units. Similar forewing structures are present in *A. smidovae* and *A. mlynskyi*, and are also partially visible in *A. ocularis* (Vršanský et al. 2021b; Vršanský, pers. comm.). Following this similarity, a metallic colouration is proposed in *A. santonicus* sp. n. as well.

In order to confirm the metallic colouration of *A. santonicus* sp. n., various extant iridescent taxa of Coleoptera, Mantodea and Blattodea were investigated with scanning electron microscope. Different types of microscopic surface structures were captured, however, most of them appear different from those observed in Alienopteridae (Fig. 6a–l). However, the forewing of *Melyroidea magnifica* Shelford, 1912, a species with distinct, metallic colouration, possesses unique microrectangular structures (as it was presented by Hinkelman et al. 2020, Fig. 2h). The microornamentation of *M. magnifica* is built up by concave, hexagonal units, creating a honeycomb-like pattern (Fig. 6m–p). Identical structures were observed on the dorsal surface of the elytron of *Cicindela soluta* Dejean, 1822 (Coleoptera: Carabidae), a brigthly coloured and metallic predatory tiger beetle (Fig. 6q–t). This type of sculpting of the dorsal forewing surface is generally very similar to that of *A. santonicus* sp. n., further supporting its metallic colouration. Note that the similarities between the microornamenation of the forewings of *M. magnifica* and the elytra of *C. soluta* is may be due Müllerian mimicry in *Melyroidea* spp.

The metallic colouration of *A. santonicus* sp. n. is possibly related to its suggested pollinator life-style. Numerous important pollinator insect taxa are widely known to have iridescent metallic colouration (e.g., Jameson and Ratcliffe 2002; Jákl 2011; O'Neill et al. 2008 and references therein). Moreover, vivid metallic colouration of insects was previously interpreted as camouflage (Thayer 1909; Cott 1940; Kjernsmo et al. 2020).

The disruptive camouflage body pattern of *A. santonicus* sp. n. is very similar to that of the fossil umenocoleid *Cratovitisma bechlyi* Podstrelená in Podstrelená and Sendi (2018), from the Late Cretaceous Myanmar amber. Both species bear a similar, bow-like pattern between the eyes, which is posteriorly followed by more and more irregularly arranged maculae. This type of disruptive colouration is

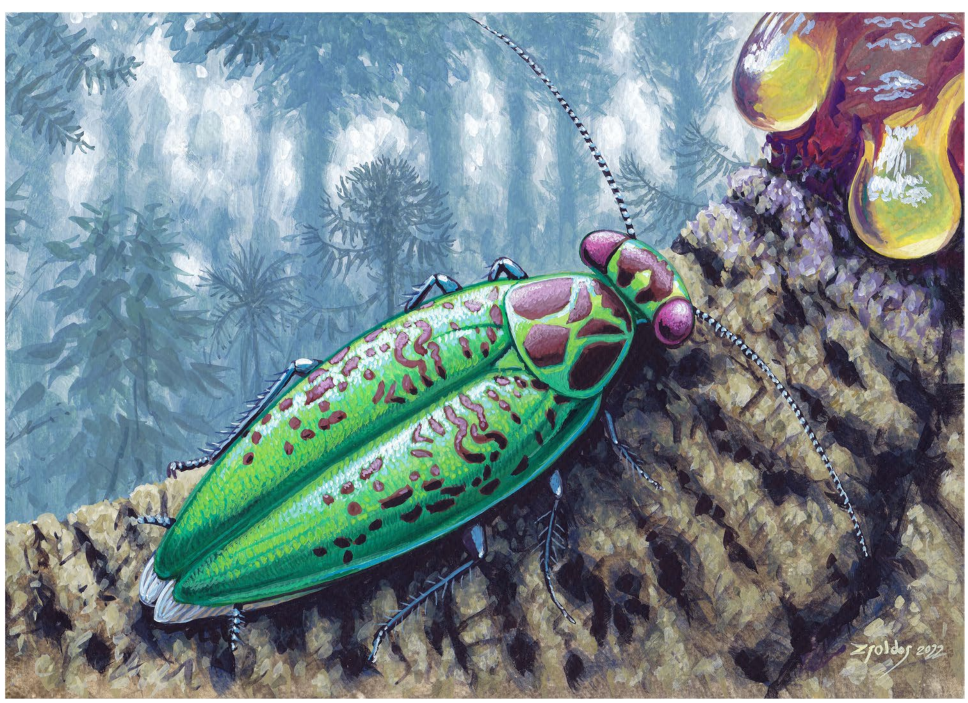

Fig. 5 Artistic reconstruction of *Alienopterix santonicus* sp. n., with hypothetical greenish-reddish colouration (artwork by Márton Zsoldos)

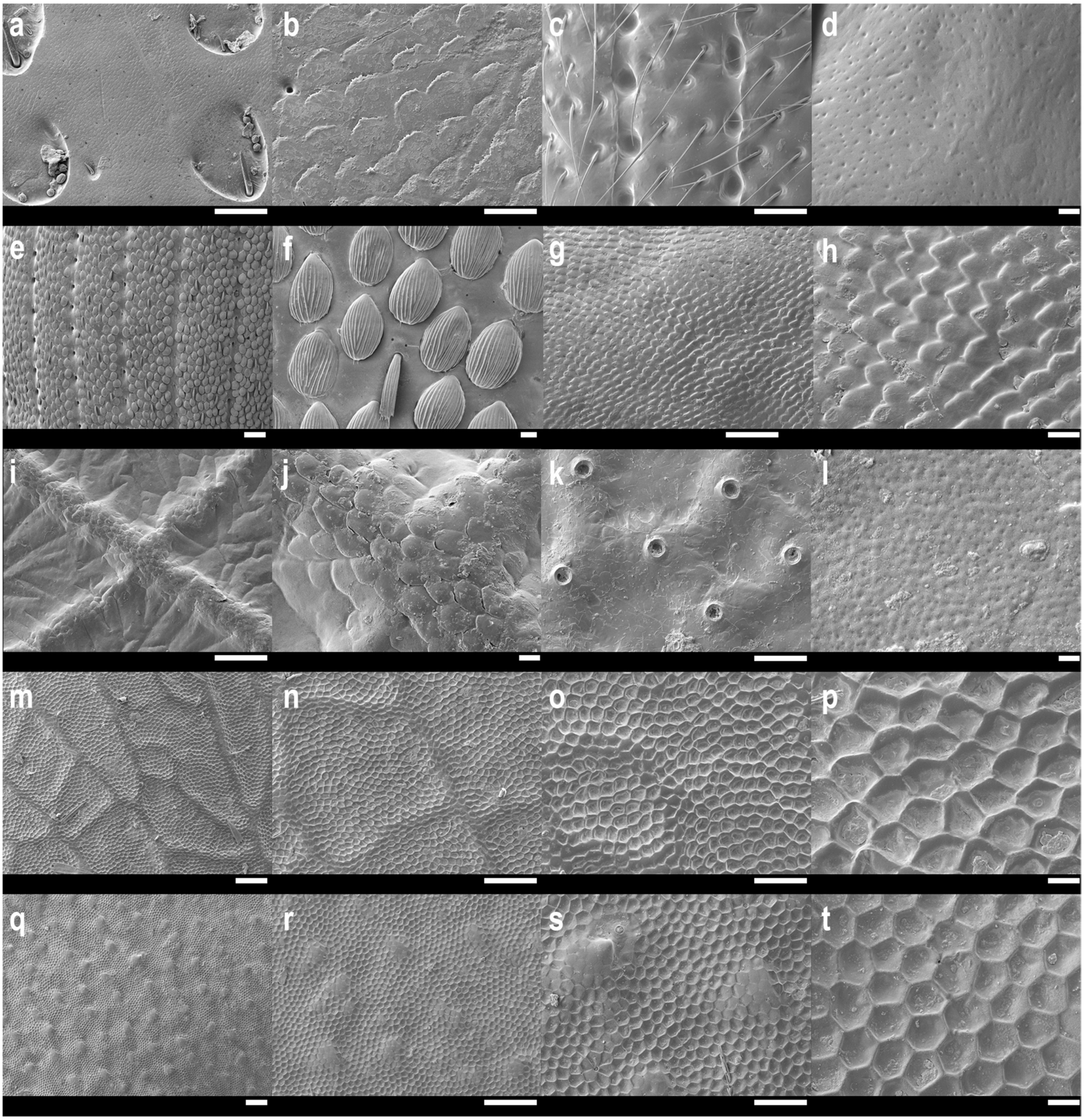

Fig. 6 SEM images of wing surface microstructures of various iridescent insect taxa. **a**, **b** *Cetonia aurata* (Linnaeus, 1761), elytron (Hungary, Budapest). **c**, **d** *Limoniscus violaceus* (Müller, 1821), elytron (Hungary, Bajót). **e**, **f**: *Polydrusus formosus* (Mayer, 1779) (Hungary, Ajka). **g**, **h** *Carabus* (*Morphocarabus*) *scheidleri* Panzer, 1799, yellow morphotype (Hungary, Pilisszentlélek). **i**, **j** *Metallyticus splendidus* Westwood, 1835, female forewing (bred in captivity, native to Asia). **k**, **l** *Eucorydia yasumatsui* Asahina, 1971, female forewing (bred in captivity, native to Asia). **m-p** *Melyroidea magnifica* Shelford, 1912, female forewing (Equador, Puyo; USMNH 2,039,895). **q-t** *Cicindela soluta* Dejean, 1822, elytron (Hungary, Székesfehérvár). Scale bars: A, C, E, I, M, N, Q, R: 100 µm (**a**, **c**, **e**, **i**, **m**, **n**, **q**, **r**), 50 µm (**g**, **k**, **o**, **s**), 10 µm (**b**, **f**, **h**, **j**, **p**, **t**), 1 µm (**d**, **l**)

extremely rare in cockroaches, and reflects a specific bark niche in (sub)tropical forests (Podstrelená and Sendi 2018). Additionally bark-related life-style also increases the chance for being trapped in amber (Azar 2007).

Alienopterix santonicus sp. n. most likely benefited from its iridescent and disruptive colouration, which served as camouflage. Such metallic colouration might have served to confuse visually hunting predators, giving *A. santonicus* sp.

n. a significant survival advantage if it was recognized on the bark surface or on flowers. Combination of iridescent (structural) and patterned (true colours) is highly unusual and as an advanced trait might be documented for the first time in history. Unfortunately and counterintuitively none of these colours can be identified with confidence at the present.

Acknowledgements Three anonymous reviewers and the managing editor are thanked for their helpful and constructive comments. The authors are extremely grateful to Peter Vršanský, Jan Hinkelman and Hemen Sendi for their enthusiastic help during the preparation of the manuscript. We thank Győző Széll, Tamás Németh, László Nádai, György Fiam, Péter Véninger and Gábor Varga for providing important prepared insect specimens for SEM analysis. Klára Palotás and László Makádi (SARA) are thanked for their technical assistance. We thank the Department of Palaeontology of the Eötvös Loránd University for the support during preparation of the amber stone specimens and data analysis. The Smithsonian National Museum of Natural History (Washington, DC) is acknowledged for providing a specimen of *Melyroidea magnifica* for SEM investigations. This research was supported by the MTA-ELTE Lendület Dinosaur Research Group (Grant No. 95102), National Research, Development and Innovation Office (NKFIH K 116665, K 131597, PD 130190, FK 130627).

Funding Open access funding provided by Eötvös Loránd University.

Declarations

Competing interests The authors of the paper declare that they have no known competing financial interests or personal relationships that could have influence the present work.

References

Azar D (2007) Preservation and accumulation of biological inclusions in Lebanese amber and their significance. C R Palevol 6(1):151–156

Bai M, Beutel RG, Klass KD, Zhang W, Yang X, Wipfler B (2016) †Alienoptera – a new insect order in the roach-mantodean twilight zone. Gondwana Res 39:317–326

Bai M, Beutel RG, Zhang W, Wang S, Hörnig M, Gröhn C, Yan E, Yang X, Wipfler B (2018) A new cretaceous insect with a unique cephalo-thoracic scissor device. Curr Biol 28:438–443. https://doi.org/10.1016/j.cub.2017.12.031

Barna P, Šmídová L, Coutiño José MA (2019) Living cockroach genus *Anaplecta* discovered in Chiapas amber (Blattaria: Ectobiidae: *Anaplecta vega* sp.n.). PeerJ 7:e7922. https://doi.org/10.7717/peerj.7922

Bodor ER, Baranyi V (2012) Palynomorphs of the Normapolles group and related plant mesofossils from the Iharkút vertebrate site, Bakony Mountains (Hungary). Cent Eur Geol 55(3):259–292

Bodor ER, Rákosi L, Baranyi V, Barbacka M (2013) Plant mesofossil based environmental reconstruction of the vicinity of Iharkút (the Bakony Mts. Hungary). In: Green Planet 400 million years of terrestrial floras: Symposium on the occasion of the 70th birthday of Han (Johanna H. A.) van Konijnenburg van Cittert Leiden, Netherlands, p 22

Bodrogi I, Fogarasi A, Yazikova EA, Sztanó O, Báldi-Beke M (1998) Upper Cretaceous of the Bakony Mts. (Hungary): sedimentology, biostratigraphy, correlation. Zbl Geol Paläontol 1(11/12):1179–1194

Borkent A (1997) Upper and Lower Cretaceous biting midges (Ceratopogonidae: Diptera) from Hungarian and Austrian amber and the Koonwarra Fossil Bed of Australia. Stuttg Beitr Naturk B 249:10

Chen SC, Tian CC (1973) A new family of Coleoptera from the lower cretaceous of Kansu. Acta Entomol Sin 16(2):169–178

Chen T, Liu S, Lei X, Chen L (2019) A new cockroach (Insecta: Blattaria: Blattulidae) from the Lower Cretaceous Laiyang Formation of China. Cretac Res 101:17–22

Chen X-Y, Zhang H-C, Shi X (2021) A new species and genus of Alienopteridae (Blattodea) from mid-Cretaceous amber of northern Myanmar. Zootaxa 4941(4):zootaxa.4941.4.7. https://doi.org/10.11646/zootaxa.4941.4.7

Cott HB (1940) Adaptive Coloration in Animals. Methuen & Co., Ltd., London

Császár GH, Góczán F (1988) A Bakony felső-kréta kőszénkutatás és kőszén láp vizsgálat. [in Hungarian: Upper Cretaceous coal prospecting and peat bog studies in the Bakony Mts]. Magyar Állami Földtani Intézet Évi Jelentése 1986-ról:155–178

Grimaldi DA, Engel MS, Nascimbene PC (2002) Fossiliferous cretaceous amber from myanmar (Burma): Its rediscovery, biotic diversity, and paleontological significance. Am Mus Novit 3361:1–71

Gutiérrez E, Pérez-Gelabert DE (2000) Annotated checklist of hispaniolan cockroaches. Trans Am Entomol Soc 126(3/4):423–446

Haas J (1983) Senonian in the transdanubian central range. Acta Geol Hung 26:21–40

Hantken M (1878) A magyar korona országainak széntelepei és szénbányászata. Légrády, Budapest

Hinkelman J (2020) Earliest behavioral mimicry and possible food begging in a Mesozoic alienopterid pollinator. Biologia 75:83–92. https://doi.org/10.2478/s11756-019-00278-z

Hinkelman J, Vršanská L (2020) A Myanmar amber cockroach with protruding feces contains pollen and a rich microcenosis. Sci Nat 107(13):1–19. https://doi.org/10.1007/s00114-020-1669-y

Hinkelman J, Vršanský P, Garcia T, Tejedor A, Bertner P, Sorokin A, Gallice GR, Koubová I, Nagy Š, Vidlička Ľ (2020) Neotropical *Melyroidea* group cockroaches reveal various degrees of (eu)sociality. Sci Nat 107:39. https://doi.org/10.1007/s00114-020-01694-x

Hinkelman J (2021) *Cuniculoblatta brevialata* gen. et sp. n., the second case of brachyptery from Cretaceous North Myanmar amber. Palaeontogr Abt A 321(1–6):97–107. https://doi.org/10.1127/pala/2021/0104

Jákl S (2011) Description of seven new taxa of Cetoniinae from Indonesia (Coleoptera: Scarabaeidae). Acta Entomol Mus Natl Pragae 51(2):535–550

Jameson ML, Ratcliffe BC (2002) Series Scarabaeiformia Crowson 1960 (= Lamellicornia), superfamily Scarabaeoidea Latreille 1802. In: Thomas MC, Skelley PE, Frank JH, Arnett RH (eds) American beetles, vol 2. CRC Press, Boca Raton, pp 1–81

Kjernsmo K, Whitney HM, Scott-Samuel NE, Hall JR, Knowles H, Talas L, Cuthill IC (2020) Iridescence as camouflage. Curr Biol 30:551–555. https://doi.org/10.1016/j.cub.2019.12.013

Kočárek P (2019) *Alienopterella stigmatica* gen et sp. nov.: the second known species and specimen of Alienoptera extends knowledge about this Cretaceous order (Insecta: Polyneoptera). J Syst Palaeontol 17(6):491–499. https://doi.org/10.1080/14772019.2018.1440440
Koubová I, Mlynský T (2020) Two new mid-Cretaceous dictyopterans (Umenocoleidae: Vitisminae) from northern Myanmar exemplify taphonomic bias. AMBA Projekty 10(1):1–16
Kováčová Z (2022) Two new cockroaches (Insecta: Vitisma, Nuurcala) from the Lower Cretaceous sediments of Shar-Tologoy in Mongolia. Biologia. https://doi.org/10.1007/s11756-022-01145-0
Kozma K (1991) Az ajkai szénbányászat története. [in Hungarian: History of the coal mining at Ajka]. Veszprémi Szénbányák Kiadó, Veszprém, p 531
Li X-R, Wang L-L, Wang Z-Q (2018) Rediscovered and new perisphaerine cockroaches from SW China with a review of subfamilial diagnosis (Blattodea: Blaberidae). Zootaxa 4410(2):251–290. https://doi.org/10.11646/zootaxa.4410.2.2
Li JX, Zhao XD, Gao YP, Wang B, Xiao CX (2020) Cockroach *Stavba jarzembowskii* sp. nov. (Blattaria: Liberiblattinidae) from mid-Cretaceous Burmese amber. Cretac Res 115:e104531. https://doi.org/10.1016/j.cretres.2020.104531
Li X-R (2019) Disambiguating the scientific names of cockroaches. Palaeoentomology 2(4):390–402. https://doi.org/10.11646/palaeoentomology.2.4.13
Liang JH, Shih CK, Ren D (2019) Blattaria – Cockroaches. Chapter 7. In: Ren D, Shih CK, Gao T, Yao Y, Wang Y (eds) Rhythms of Insect Evolution: Evidence from the Jurassic and Cretaceous in Northern China. John Wiley & Sons Ltd, Hoboken, pp 91–112. https://doi.org/10.1002/9781119427957.ch7
Luo C, Beutel RG, Engel MS, Liang K, Li L, Li J, Xu C, Vršanský P, Jarzembowski EA, Wang B (2022) Life history and evolution of the enigmatic Cretaceous-Eocene Alienopteridae: a critical review. Earth-Sci Rev 225:103914. https://doi.org/10.1016/j.earscirev.2021.103914
McKay IJ (2007) A new genus of the cockroach family Umenocoleidae from Cretaceous deposits at Orapa. Botswana Palaeontol Afr 42:127
Mlynský T, Wu H, Koubová I (2019) Dominant Burmite cockroach *Jantaropterix ellenbergeri* sp. n. might laid isolated eggs together. Palaeontogr Abt A 314(1-3):69–79. https://doi.org/10.1127/pala/2019/0091
O'Neill KM, Fultz JE, Ivie MA (2008) Disribution of adult Cerambycidae and Buprestidae (Coleoptera) in a subalpine forest under shelterwood management. Coleopt Bull 62(1):27–36
Ősi A, Apesteguía S, Kowalewski M (2010) Non-avian theropod dinosaurs from the early Late Cretceous of central Europe. Cretac Res 31:304–320. https://doi.org/10.1016/j.cretres.2010.01.001
Ősi A, Bodor ER, Makádi L, Rabi M (2016) Vertebrate remains from the Upper Cretaceous (Santonian) Ajka Coal Formation, western Hungary. Cretac Res 57:228–238. https://doi.org/10.1016/j.cretres.2015.4.014
Oyama N, Hirokazu Y, Takuya I (2021) New cockroach assemblage from the Lower Cretaceous Kitadani Formation. Fukui. Japan Palaeontogr Abt A 321(1–6):37–52
Podstrelená L, Sendi H (2018) *Cratovitisma* Bechly, 2007 (Blattaria: Umenocoleidae) recorded in Lebanese and Myanmar ambers. Palaeontogr Abt A 310(3–6):121–129. https://doi.org/10.1127/pala/2018/0076
Poinar G Jr (2018) Burmese amber: evidence of Gondwanan origin and Cretaceous dispersion. Hist Biol 31:1304–1309. https://doi.org/10.1080/08912963.2018.1446531
Poinar G (2022) *Supella dominicana*, a new species of cockroach (Blattida: Ectobiidae) with developed spermatids in Dominican amber. Biologia. https://doi.org/10.1007/s11756-022-01271-9
Poinar G Jr, Brown AE (2017) An exotic insect *Aethiocarenus burmanicus* gen. et sp. nov. (Aethiocarenodea ord. nov., Aethiocarenidae fam. nov.) from mid-Cretaceous Myanmar amber. Cretac Res 72:100–104. https://doi.org/10.1016/j.cretres.2016.12.011
Schneider JW, Werneburg R (2006) Insect biostratigraphy of the Euramerican continental Late Pennsylvanian and Early Permian. Geol Soc Spec Publ 265:325–336
Sendi H (2021) Diverse Liberiblattinidae (Insecta: Blattaria) from Lebanese and North Myanmar amber document allometric modifications near lowest size limit. Palaeontogr Abt A 321(1–6):127–148. https://doi.org/10.1127/pala/2021/0108
Sendi H, Hinkelman J, Vršanská L, Kúdelová T, Kúdela M, Zuber M, van de Kamp T, Vršanský P (2020) Roach nectarivory, gymnosperm and earliest flower pollination evidence from cretaceous ambers. Biologia 75:1613–1630. https://doi.org/10.2478/s11756-019-00412-x
Shelford RWC (1912) Mimicry amongst the Blattidae; with a revision of the genus *Prosoplecta* Sauss., and the description of a new genus. Proc Zool Soc 82:358–376. https://doi.org/10.1111/j.1469-7998.1912.tb07022.x
Siegl-Farkas Á, Wagreich M (1996) Correlation of palyno- (spores, pollen, dinoflagellates) and calcareous nannofossil zones in the Late Cretaceous of the Northern Calcareous Alps (Austria) and the Transdanubian Central Range (Hungary). Advances in Austrian-Hungarian Joint Geological Research, Budapest, pp 127–135
Siegl-Farkas Á (1988) Az Ajkai Kőszén Formáció palynosztratigráfiája és fejlődéstörténete. In: Magyar Állami Földtani Intézet Évi Jelentése 1986-ról, pp 179–209
Šmídová L (2021) New genus and species of the families Olidae and Corydiidae (Corydioidea, Blattodea) from mid-Cretaceous Kachin amber. Palaeontogr Abt A 321(1–6):61–70. https://doi.org/10.1127/pala/2021/0117
Šmídová L, Lei X (2017) The earliest amber-recorded type cockroach family was aposematic (Blattaria: Blattidae). Cretac Res 72:189–199. https://doi.org/10.1016/j.cretres.2017.01.008
Solórzano-Kraemer MM (2007) Systematic, palaeoecology, and palaeobiogeography of the insect fauna from Mexican amber. Palaeontogr Abt A 282(1–6):1–133
Szabó J (1871) Az ajkai kőszéntelep a Bakonyban. (in Hungarian: The coal deposits of Ajka in the Bakony Mountains). Földtani Közlöny 1:124–130
Szabó M, Hammel JU, Harms D, Kotthoff U, Bodor E, Novák J, Kristóf K, Ősi A (2022a) First record of the spider family Hersiliidae (Araneae) from the Mesozoic of Europe (Bakony Mts, Hungary). Cretac Res 131:105097. https://doi.org/10.1016/j.cretres.2021.105097
Szabó M, Kundrata R, Hoffmannova J, Németh T, Bodor E, Szenti I, Prosvirov AS, Kukovecz Á, Ősi A (2022b) The first mainland European Mesozoic click-beetle (Coleoptera: Elateridae) revealed by X-ray micro-computed tomography scanning of an Upper Cretaceous amber from Hungary. Sci Rep 12(1):24. https://doi.org/10.1038/s41598-021-03573-5
Szabó M, Brazidec M, Perrichot V, Szenti I, Kukovecz Á, Ősi A (2022c) A unique record of the Late Cretaceous of East-Central Europe: The first fossil wasps (Hymenoptera: Bethylidae, Spathiopterygidae) from the ajkaite amber (Bakony Mts., western Hungary). Cretac Res 139:105314. https://doi.org/10.1016/j.cretres.2022.105314
Tan J (1980) Geological history of insects. Acta Zootax Sin 5:1–12
Tasnádi Kubacska A (1957) Magyar ősgyanta (Hungarian fossil resin). Élet és Tudomány 1957
Thayer GH (1909) Concealing-coloration in the animal kingdom: an exposition of the laws of disguise through color and pPattern: being a summary of Abbott H. Thayer's discoveries. Macmillan

Vršanský P (2002) Origin and the early evolution of mantises. AMBA Projekty 6(1):1–16
Vršanský P (2003) Umenocoleoidea – an amazing lineage of aberrant insects (Insecta, Blattaria). AMBA Projekty 7(1):1–32
Vršanský P (2005) Mass mutations of insects at the Jurassic/Cretaceous boundary? Geol Carpath 56(6):473–781
Vršanský P (2008) New blattarians and a review of dictyopteran assemblages from the Lower Cretaceous of Mongolia. Acta Palaeontol Pol 53:129–136
Vršanský P (2009) Albian cockroaches (Insecta, Blattida) from French amber of Archingeay. Geodiversitas 31(1):73–98
Vršanský P (2010) Cockroach as the earliest eusocial animal. Acta Geol Sin 84:793–808
Vršanský P (2019) Santonian cockroaches from Yantardakh amber (Russia: Taimyr) differ in dominance. Palaeoentomology 2(3):297–307. https://doi.org/10.11646/palaeoentomology.2.3.15
Vršanský P (2020) Cockroaches from Jurassic sediments of the Bakhar Formation in Mongolia. SpringerBriefs Anim Sci. https://doi.org/10.1007/978-3-030-59407-7
Vršanský P, Vishniakova VN, Rasnitsyn AP (2002) Order Blattida Latreille, 1810. The cockroaches. In: Rasnitsyn AP, Quicke DLJ (eds) History of insects. Kluwer Academic Publisher, Dodrecht, pp 263–271
Vršanský P, Cifuentes-Ruiz P, Vidlička L', Čiampor F, Vega FJ (2011) Afro-Asian cockroach from Chiapas amber and the lost Tertiary American entomofauna. Geol Carpath 62(5):463–475. https://doi.org/10.2478/v10096-011-0033-8
Vršanský P, Oružinský R, Aristov D, Wei D-D, Vidlička Ľ, Ren D (2017) Temporary deleterious mass mutations relate to originations of cockroach families. Biologia 72(8):886–912. https://doi.org/10.1515/biolog-2017-0096
Vršanský P, Bechly G, Zhang Q, Jarzembowski EA, Mlynský T, Šmídová L, Barna P, Kúdela M, Aristov D, Bigalk S, Krogmann L, Li L, Zhang Q, Zhang H, Ellenberger S, Müller P, Gröhn C, Xia F, Ueda K, Vďačný P, Valaška L, Vršanská L, Wang B (2018) Batesian insect-insect mimicry- related explosive radiation of ancient alienopterid cockroaches. Biologia 73:987–1006. https://doi.org/10.2478/s11756-018-0117-3
Vršanský P, Hinkelman J, Koubová I, Sendi H, Kúdelová T, Kúdela M, Barclay M (2021a) A single common ancestor for praying mantids, termites, cave roaches and umenocoleoids. AMBA Projekty 11(1):1–16
Vršanský P, Sendi H, Hinkelman J, Hain M (2021b) *Alienopterix* Mlynský et al., 2018 complex in North Myanmar amber supports Umenocoleoidea/ae status. Biologia 76:2207–2224. https://doi.org/10.1007/s11756-021-00689-x
Wappler T, Vršanský P (2021) Cockroaches: masters of ancient non-aquatic ecosystems. Palaeontogr Abt A 321(1–6):1–2. https://doi.org/10.1127/pala/2021/0121
Wei D, Ren D (2013) Completely preserved cockroaches of the family Mesoblattinidae from the Upper Jurassic-Lower Cretaceous Yixian Formation (Liaoning Province, NE China). Geol Carpath 64(4):291–304. https://doi.org/10.2478/geoca-2013-0021
Weitschat W, Wichard W (2002) Atlas of Plants and Animals in Baltic Amber. Verlag Dr Friedrich Pfeil, Munich
Yanagisawa S, Hiruta SF, Sakamaki Y, Liao J-R, Shimano S (2021) Two new species of the genus Eucorydia (Blattodea: Corydiidae) from the Nansei Islands in Southwest Japan. Zool Sci 38(1):1–13. https://doi.org/10.2108/zs200048
Zhang ZJ, Schneider JW, Hong YQ (2012) The most ancient roach (Blattida): a new genus and species from the earliest Late Carboniferous (Namurian) of China, with discussion on the phylomorphogeny of early blattids. J Syst Palaeontol 11:27–40