A single common ancestor for praying mantids, termites, cave roaches and umenocoleoids

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In the evolution of praying mantids, eusocial termites, cave cockroaches and the beetle/ant/bee/wasp-mimicking umenocoleoids, at a single Early Cretaceous diversification point (127 Ma) each lacked hierarchical structure, and independent explosive radiations are revealed. Adult male, female and individuals of unidentified sex of new cockroaches (Corydioidea, Fractaliidae fam. n.) sharing all the most important autapomorphies of these four major groups (raptorial legs, nuptial flight-related breaking sutura, hardened forewings and specialised cerci) represent a lineage of their common relatives supported by phylogenetic trees. Immature individuals suggest they were autochthonous to the source forests. They originate from the "tropical" Myanmar amber (70- 98 Ma) and Upper Jurassic "subtropical" sedimentary rocks from Kazakhstan and Germany (151; 151 Ma) with supporting data from new most primitive representatives of predatory lineages from Lebanese "subtropical" and Taimyr "polar" ambers (ca. 127; 86 Ma).

- fossil insect - Mesozoic amber - Cretaceous - Blattaria= Blattodea= Isoptera= Mantodea - burmite -

Lack of hierarchical structure in the evolution of major cockroach lineages was the most surprising discovery based on representative adults preserved in the amber fossil record: beetle and hymenopteran mimicking Umenocoleidae and Alienopteridae were instead shown to have radiated explosively after initial origination (Vršanský et al. 2018a). The same pattern, related to explosive reductions, was observed in cave cockroaches of the family Nocticolidae (Sendi et al. 2019, Sendi 2021) and in eusocial cockroaches including termites (Vršanský et al. 2019d, Song et al. 2021). This concept, the hypothesis of reduction rings with constructive compensations also explains higher diversity in tropics disregarding higher metabolism. Organisms can fix to more diverse habitats based on plants - which can evolutionary cope and diversify keeping partially functional with more numerous reductions due to higher energy input, especially in early successive series. In environments with low energy input, most of plant gene reductions result in insufficient production and extinction. Explosive radiation is also revealed here in the basalmost praying mantodeans ("M" in figs. 1-2). Notably, all these explosions occurred simultaneously at the 127 Ma diversification point, and all main cockroach lineages originated at one of 7 such periodic diversification points (Vršanský et al. 2017). The main problem remained of how these four major corydioid lineages originating at 127 Ma diversification point were connected earlier in history. Discovery of adult male and female of a new taxon in Myanmar amber and Solnhöfen and Karabastau sediments demonstrate that these 4 major cockroach (including termite and mantis) lineages had a single shared common ancestor about 25 million years before the respective "explosions" took place, and evidence double-peak origination near the J/K boundary. Hi-res phylogenetic analysis reveals that this connection was also explosive and not hierarchical, and is in concordance with general insect genus level (Sepkoski & Labandeira 1993) and cockroach family level data (Vršanský et al. 2017), which also both show a double peak at J/K. Thus changes to the gross insect pattern and the phylogenies of major cockroach groups at J/K probably reflect abiotic changes near this most distinct terrestrial diversification point.

Materials and methods

Specimens were photographed using a Leica M205 C binocular microscope and Leica DFC295 camera, immersed in agave syrup to neutralise light distortion and combined using CombineZP software (edited in Adobe Photoshop CS5). The drawings were made using CorelDrawX7 software. Detailed measurements of all visible segments were made using a micrometer scale and a Leica M205 C binocular microscope. The locality of two specimens preserved in amber is situated in the North Myanmar, which has produced 525 families, 777 genera and 1013 insect species (Ross, 2018; Guo et al., 2017; Ross et al., 2010; Nicholson et al., 2015; Dlussky, 1996a; 1996b; Ross & York, 2000; Rasnitsyn & Ross, 2000) and today 102 orders with hexapods, arachnids, centipedes, millipedes, crustaceans, onychophorans, molluscs, nematodes, annelids, amphibians, reptiles, theropods, protists, plants and fungi. U-Pb dating of zircons from the matrix which surrounds the amber have placed Burmite at 98.79 ± 0.62 Ma (Cenomanian) (Shi et al. 2012). Chemistry and inclusions within burmite point to a coniferan source, most probably a Metasequoia-like tree, with additional presence of diverse angiosperms (Daza et al., 2016). Deposition. Specimens are deposited under SNM Z numbers (Slovak National Museum in Bratislava), PIN (Paleontological Institute, Russian Academy of Sciences, Moscow) and LU (Lebanese University, Beirut). We calculated the most parsimonious trees in PAUP* 4.0b8 (Swofford

2003) using a heuristic search, 10 random addition taxon replicates, the accelerated transformation optimalization algorithm (ACCTRAN), as well as the three bisection-reconnection branch-swapping (TBR) algorithm (characters unordered, 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.

Results

chresmodids)

Systematic palaeontology

Order: Blattaria Latreille, 1810 = Blattodea Brunner von Wattenwyl, 1882 Superfamily: Corydioidea Saussure, 1864 (this superfamily comprise also termites, mantodeans and

Family: Fractaliidae Vršanský et Hinkelman, fam. n.

Zoobank code: 42765F69-9A50-4679-BF47-5AB7AA015AE2

Type genus and species. *Fractalia articulata* Hinkelman et Vršanský, gen. et sp. n.

Composition: *Fractalia articulata* Hinkelman sp. n.; *Fractalia aristovi* Vršanský, sp. n.; undescribed *Fractalia* sp. from lithographic limestone of Eichstätt in Germany (specimens 4310 and 4817 *"Lithoblatta lithophila* Germar, 1839" trifoss.com).

Differential diagnosis: Fractaliidae fam. n. differs from other cockroach families, except termites, in having a forewing breaking suture, from termites in having the body and hindwings completely covered by elytrised forewings, pronotum with partially concave anterior margin, large number of tibial spurs and all 6 legs "raptorial", mantodean–like. Hind wing standard primitive umenocoleoid (long Sc, slightly curved R1 with few branches, pterostigma overlapping up to nearest intercalary; Rs simplified (3–5), branched M; CuA with numerous branches; CuP simple or with two veins at margin; A1 branched, its field wide).

Description: as for *F. articulata,* extended in diagnosis of *F. aristovi*.



Figure 1 Illustrations of dinosaur age cockroaches from Myanmar (a-e, g) and Lebanese ambers (h) and Kazakhstan sedimentary rock (f, i). **a-d** *Fractalia articulata* sp. n. holotype SNM Z 38677 in ventral view, detail of foreleg, detail of midleg and dorsal views; **e** additional material SNM Z 38877 in ventral and dorsal views; f *Fractalia aristovi* sp. n. holotype PIN 1789/ 73; **g** *Ocelloblattula margarita* sp. n. holotype SNM Z 38669 in dorsal and ventral views; **h** *Pseudomantina occisor* sp. n. holotype LU810CD in dorsal and ventral views; **i** *Pseudomantina nigroalba* sp. n. holotype PIN 2554/49 photo and line drawing; **I** A 50% majority-rule bootstrap consensus tree with bootstrap values and age; **m** Phylogenetic network with bootstraps along edges (>50% with red highlight).

Remarks: Structure of the hindwing with wide main (black) veins and thinner (brown) intercalaries, sharply curved clavus and wide cercus place this species within Corydioidea. This species differs from Liberiblattinidae and Blattulidae (and from termites) in having elytrised forewings and from Umenocoleoidea by its very short antennal and cercal sensilla, basally protruding pronotum and unusually distinct clavus. Corydiidae s. str. lack an externally protruding female ovipositor. Similarities with mantids include numerous femoral spines set in two rows, differentiated and long, some of them movable. Their characteristic forewing breaking suture is otherwise unique to termites, while hindwing is insufficiently visible to appreciate the presence of sutura.

Derivation of name: *Fractalia articulata* is partially derived from the Latin words "*fractus*" which means "broken" and "*articulata*" which means "jointed" and refers to the characteristic crazed pattern on the forewings. The species name "*aristovi*" honours our colleague and friend Danilo Aristov (DSc).

Stratigraphic range: Kimmeridgian–Cenomanian Geographic range: Laurasia

Fractalia Hinkelman et Vršanský, gen. n. Zoobank code: 78B2D854-95B0-4D16-AA59-546CF2E98047

Differential diagnosis: monotypic: as for family. **Description:** as for *F. articulata,* with the reservation that 'A' might be simplified in the second species, *F. aristovi.*

Type species: Fractalia articulata sp. n.

Fractalia articulata Hinkelman, sp. n. (figs 1AE, 2E, 3) Zoobank code: 38B4F4FE-699A-407A-B461-4103C2EB20EF

Holotype/ additional material: SNM Z 38677 /SNM Z 38877 (not made a paratype, since public display of type material is not permitted in the Slovak National Museum), complete female holotype and male adults. Noije Bum Village, Tanaing Town, Myanmar; Cenomanian Cretaceous amber.

Diagnosis: Forewing with 'A' branched.

Description (for measurement details see SI2): Elongated–broad, red to brownish cockroach 6.50– 7 mm long and 1.25– 1.95 mm wide. Body is dorsoventrally flattened. Mesoscutellum is indistinct. Pronotum transverse, vaulted and as wide as abdomen, widest at base, with posterior central extension and transparent edge 1.71 mm long and 1.50 mm wide with sparse, short surface sensilla. Head globular, hypognathous, unmodified, partially covered by pronotum. Frontal field is narrow with vertex exposed. Sensilla on head are short and sparse. Head does not appear strongly mobile. Parietal and interanntenal ridges are indistinct. Eyes are large, wide, symmetrical, protruding sideways and pale in colour, width/ length 0.25/ 0.11 mm. Eye facets are small (0.05 mm) and pale in colour without sensilla. Ocelli are not observed. Maxillary palps are generally short 0.46–0.91 mm long and 0.18-0.33 mm wide, 5-segmented with one very large palp 0.75 mm long and 0.14 mm wide present on specimen 1. Terminal palpomeres are enlarged and oval in shape. Sensilla on maxillary palps are indistinct. Labial palp short. Mandibles are large, clypeus distinctly visible. Antennae filiform and short with 38 segments, apparently orientated forwards rather than sideways. Antennal sockets are small with proximal antennomeres appearing more conical. Each antennal segment 0.03-0.14 mm wide and 0.05-0.15 mm long covered with 8-10 short diversified, small dense sensilla. Antennomeres are cylindrical in shape and uniform. Left antenna is 3.38 mm long, right antenna 3.74 mm with distal antennomeres apparently missing. Scape is 0.29-0.37 mm long and 0.12 mm wide. Pedicle is apparently short, 0.13 mm long and 0.12 mm wide. Both pedicle and scape are wider than other antennomeres, while scape appears rather small. Forewing and hindwing appear equal in length, with subquadrate tegmina. Forewings 3.90- 5.18 mm long and 0.95- 1.25 mm wide, sclerotized, partially transparent and translucent with characteristic crazed surface pattern, fully covering abdomen. Cup-like supporting cells, the so called bunky are absent. Forewings appear triangular to ellipsoidal in shape without sensillary fovea. Forewing breaking regular, pronounced and extending sutura longitudinally. Longitudinal and posterior ridge of forewing visible. Sensilla on forewings are present but sparsely distributed. Venation is distinct with rich intercalaries and cross-veins in both forewings and hindwings. Apex appears membranous. Intercalaries wide both on forewing and hindwing. Pseudovein and diagonal kink are absent and vannus is not reduced. Veins and intercalaries on forewing appear wide, dark and thick. Costal field is long and narrow. Forewing Sc short (short as clavus), slightly curved and branched into 2 veins. Radial field is narrow and extending apically, richly branched RS (12 veins) and nearly R1.

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Figure 2 Dinosaur age cockroaches from Myanmar (a, b, e), Taimyr (c) and Lebanese ambers (d) and Kazakhstan sedimentary rock (f). **ab** Ocelloblattula margarita sp. n. holotype SNM Z 38669 head detail and dorsal and ventral views; **c** Ocelloblattula sp. PIN 3730/ 51; **d** *Pseudomantina occisor* sp. n. holotype LU810CD in dorsal and ventral views; **e** Fractalia articulata sp. n. holotype SNM Z 38677 in dorsal view, details of head, ovipositor, tibial spur, raptorial foreleg cercus; **f** Fractalia aristovi sp.n. holotype PIN 1789/ 73.

Veins show a constant regular distance from each other. M is straight, narrow and rich with one branch consistently fused to R. CuP is sharply curved and long. CuA contains 6 or more veins. Forewing A is branched. Clavus normally developed and comparatively short. Hindwing lacks fan-like pleating. R is sporadically branched with RS long but not strongly sigmoidal. Hindwing R1 is differentiated but with indistinct branches. Hindwing M is indistinct while CuA branches are simple. Clavus is convex while A1 and precostal field are indistinct. Posterior overlapping margin ridge appears indistinct. Pterostigma indistinct. All legs except the very short forelegs, appear to be comparatively long and raptorial, with long spines. Carination is full. Tibiae are extremely well equipped with long spines, some of which are serrated. Leg sensilla are sparse. Procoxae appear elongated and foreleg spines are very short, wide and asymmetrical. Trochanter short, curved and without sensilla. Femora appear strong with well developed, strongly curved terminal spines and a shorter one on the apex of the hind margin. Profemoral brush absent. Long spines ventromedially on proximal part of profemur show regular distribution and are set in two rows. Some spines apparently movable, preserved in unaligned positions. Forecoxae narrow, 0.95- 1.00 mm long and 0.55- 0.75 mm wide. Forefemur robust, 0.65– 0.95 mm long and 0.19– 0.30 mm wide, with up to 8 long, very strong movable spines set in two rows. Right forefemoral spines 1-2 length 0.11/ 0.09 mm, left forefemoral spines 1-8 length 0.07/ 0.10/ 0.18/ 0.11/ 0.11/ 0.12/ 0.10/ 0.06 mm and 0.02-0.07 mm wide. Both forefemora with a terminal spine up to 0.40 mm long. Foretibiae equal in length to forefemur, 0.71–0.75 mm long and 0.12 mm wide with up to 11 strong spines. Right foretibial spines 1-11 length 0.25/ 0.13/ 0.24/ 0.32/ 0.25/ 0.06/ 0.05/ 0.07/ 0.06/ 0.07/ 0.06 mm, left foretibia spines 1-10 length 0.20/ 0.23/ 0.12/ 0.21/ 0.10/ 0.11/ 0.12/ 0.22/ 0.38/ 0.12 mm. Foretarsi 5-segmented, 0.48- 0.85 mm long and 0.02- 0.06 mm wide, with small, short sensilla visible. Midcoxae up to 1.10 mm long and 0.90 mm wide. Midfemur up to 1.77 mm long and 0.50 mm wide with a 0.65 mm long and curved terminal spur on the femorotibial joint. Midfemoral spines 7, long, very strong and set in two rows. Right midfemoral spines 1–7 length 0.13/ 0.12/ 0.12/ 0.10/ 0.11/ 0.12/ 0.14 mm and 0.02–0.04 mm wide. Left midfemoral spines 1–6 length 0.13/ 0.13/ 0.14/ 0.08/ 0.08/ 0.07 mm and 0.02- 0.04 mm wide. Some of the spines are movable. Midfemoral spines differentiated into 2 types, type 1 being straight to curved long spines and type 2 short, curved, set

longitudinally and pointed medially. Both types are set in two rows. Midtibiae strong, longer than midfemur, up to 1.50 mm long and 0.22 mm wide and extremely rich in spines (ca. 9-15) up to 0.48 mm long. Midtarsi 5segmented, up to 1.21 mm long and 0.08 mm wide, with short spines and dense short sensilla, unspecialized. Terminal tarsomere slightly enlarged and conical. Hindcoxae up to 1.40 mm long and 0.90 mm wide. Hindfemora strong, up to 1.83 mm long and 0.52 mm wide with up to 0.77 mm long and curved terminal spine on the femorotibial joint. Hindfemoral spines ca. 10, very strong, long and set in two rows with both types present. Right hindfemoral spines 1-10 length 0.12/ 0.14/ 0.22/ 0.20/ 0.25/ 0.18/ 0.20/ 0.12/ 0.21/ 0.19 mm and 0.02- 0.06 mm wide. Left hindfemur spines 1–5 length 0.20/ 0.18/ 0.13/ 0.26/ 0.14 mm and 0.02-0.06 mm wide. Some spines movable. Hindtibiae very long and strong, up to 2.30 mm long and 0.22 mm wide, extremely rich in spines (ca. 13-16) up to 0.62 mm long. Hindtarsi 5-segmented, up to 1.95 mm long and 0.25 mm wide, with short but strong spines. Tarsal claws sharp, curved and symmetrical without distinct arolium. Pulvilli absent on all tarsomeres. Abdomen is segmented with 7 abdominal segments 0.42-0.53 mm long and 0.90–1.95 wide, fully covered by wings. Cercus is curved, 0.70 mm long and 0.01-0.16 mm wide, with heterogenous and asymmetrical segments, quadrate in shape. Cercus is 8-segmented with densely distributed strong and very diversified sensilla ranging from short to long, and some curved. Huge terminal cercomere present, with long cercal filaments missing. Ovipositor is preserved, segmented, symmetrical, of short type and slightly protruding.

Fractalia aristovi Vršanský, sp.n.

Zoobank code: 617D3D24-DB49-41C9-948C-7A9F3015AB4F

Holotype: PIN 1789/73; head, pronotum, and all wings with a fragment of the abdomen.

Type locality: Karatau, Kazakhstan **Type horizon**: Upper Jurassic Karabastau Formation

Diagnosis: A simplified, anal branches reduced in number. Hindwing of more–or–less standard liberiblattinid/ umenocoleoid venation, with long Sc, slightly sigmoidally curved R1 with few branches and with pterostigma overlapping up to nearest intercalary; RS simplified to a few branches (3–5), possibly fused

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Figure 3| New dinosaur age cockroaches *Fractalia articulata* sp. n. from Myanmar amber. a holotype SNM Z 38677 in ventral and dorsal views; b additional material SNM Z 38877 in ventral and dorsal views; and syninclusions

with branched M; CuA with numerous branches; CuP simple or with two veins at margin; A1 branched, its field wide.

Description: Head extremely large, globular (threequarters width of pronotum), with very large, distinct clypeus; pronotum round, with short paranotalia and dark anterior coloration. Body standard, wide. Right forewing (5.5 mm long) overlapping left forewing in posterior third; both forewings with sharp apex, venation indistinct but at least intercalaries present; Sc as long as clavus, branched (3-4); R and CuP sharply curved; clavus distinct. Hindwing as long as forewing (i.e., hindwing apex not covered by forewing apex), with distinct intercalaries, extremely wide costal field; Sc with a single vein at margin; R with 3-4 branches, branches not dichotomized and pterostigma reaching intercalaries; RS reduced to 3–5 branches (posteriormost vein hardened), and possibly fused with 1-3 M; CuA (6-8) with extremely wide anteriormost branches and secondary branches; CuP not branched; A1 branched, located in remigium in a very wide field.

Superfamily Corydioidea Saussure, 1864 Family Liberiblattinidae Vršanský, 2002

Type species. *Liberiblattina ihringovae* Vršanský, 2002.

Composition: see Vršanský (2002), Martin (2010), Barna (2014), Vršanský et al. (2018a, 2018b, 2019), Chen et al. (2020), Li et al. (2020), Sendi (2021).

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

Diagnosis (modified after Vršanský, 2002). Main veins and intercalaries wide. Forewing with regular venation with terminal dichotomisation limited to the clavus. SC field narrow with SC long and branched. R field narrow with R ending prior to wing apex. M and Cu sigmoidal, M reaching wing apex. CuP strongly curved. Anal veins branched mostly in apical third. Tarsi with large arolia.

Pseudomantina Sendi et Vršanský, gen.n. Zoobank code: 47B5554C-7C0D-44EF-88C4-F48DE8BCBFFA

Type species. Pseudomantina occisor Sendi, sp.n.

Composition: Type species and *P. nigroalba* Vršanský, sp.n.

Stratigraphic range. Late Jurassic (Kimmeridgian) – Lower Cretaceous (Barremian)

Geographic range. Laurasia and Gondwana, circumtropical

Description. As for *Pseudomantina occisor*, with the reservation that species can be down to 7 mm small as in some specimens of *P. nigroalba*.

diagnosis: Differs Differential from most Liberiblattinidae in having 'SC' simplified, and from possibly related Ocelloblattula, Kridla, Habroblattula and Svabula in possessing simplified coloration restricted to anterior forewing margin, having more elongate forewing (and not round at apex at least in P. nigroalba) and in more pronounced raptorial leg carination. Most similar taxon, Svabula Vršanský, 2005 known from sediments of Semen and Sharin-Gol (Russia and Mongolia) and from Myanmar amber, differs in having more wide wings with wide radial area, shorter 'SC' and more limited coloration.

Systematic remarks. Head triangular with large ocelli, all three pairs of legs raptorial, long SC and branched A allow classification within the predatory Liberiblattinidae. At the same time, the posterior extension of the pronotum, simplified SC, numerous cross veins in the anal area associated with characteristic coloration place the genus in the complex *Huablattula, Ocelloblattula, Kridla, Habroblattula* and *Svabula,* currently categorized within Blattulidae. Large eye facets might indicate partially crepuscular and/or nocturnal habitats.

Derivation of name. *Pseudomantina* is derived from *pseudos* (Greek for false) and *mantina* (Latin for mantis).

Pseudomantina occisor Sendi, sp.n. (Figs. 1h) Zoobank code: 235DD773-11C1-4539-8376-BD01B3914322

Holotype. 810CD. Deposited in the Lebanese University, Beirut, Lebanon.

Type locality. Hammana/Mdeyrij, Lebanese amber **Type horizon**: Barremian Lower Cretaceous

Description. Length from the head to the tip of the abdomen, and width 6.41/ 3.78 mm. Head subtriangular, large (1.63/ 2.15 mm). Exposed vertex of head visible. Ocelli well developed, and central ocellus (0.20 mm in diameter) positioned slightly beneath lateral ocelli (0.29 mm in diameter). Compound eyes large, round, pale (1.31/ 0.87 mm), with hexagonal

ommatidia (0.01 mm in diameter), laterally positioned and somewhat protruding beyond the head outline. Chewing mouthparts extremely large (0.87 mm long). Interantennal ridge (0.58 mm) visible. Frons (0.93/ 2.03 mm) appears somewhat depressed centrally, clypeus (0.44/ 0.87 mm) almost as long as labrum (0.52/ 0.29 mm). Antennae very thin, filiform, with large antennal socket (0.35/ 0.44 mm). Pedicel large (0.47/ 0.15 mm), almost 3 times as long as flagellomeres (0.17/ 0.06 mm). Flagellomeres almost homogenous, each bearing a short sensilla chaetica (0.07 mm long). Maxillary palps 5-segmented (0.20/ 0.03; 0.21/ 0.04; 0.22/ 0.04; 0.20/ 0.04; 0.21/ 0.03 mm) with distal part somewhat truncated. Left labial palp 4-segmented (0.27/ 0.2/ 0.13/ 0.09 mm long). Maxillary palps 4 segmented (0.33/ 0.24/ 0.24/ 0.33 mm long). Pronotum (2.33/ 2.79 mm) with large angulate lobe posteriorly and complex, almost symmetrical coloration, except the translucent paranota. Forewing (1.63 mm wide) membranous, right forewing folded over left one, and without melanised veins. CuP sigmoidal. CuA with at least 4 visible veins, some posterior forked. A curved with at least 5 visible veins. Pale elongated maculae visible between A veins. Forelegs slender in comparison with mid- and hindlegs. Fore femur (1.60/ 0.17 mm) bearing 7 spines (0.23 mm long) on medial with posterior notch. Medial of tibia (1.74/ 0.23 mm) with 5 semierect spines (0.52 mm long). Tarsus 5-segmented bearing dense chaetica with large pulvilli (up to 0.14 mm long) on each segment anteriorly. Basitarsus elongated (0.73/0.08 mm), 2nd (0.26/ 0.12 mm), 3rd(0.25/ 0.13 mm), 4th (0.26/ 0.12 mm) tarsi reduced and 5th tarsus shorter (0.29/ 0.09 mm) than basitarsus. Arolium large (0.14 mm in diameter), enclosed by symmetrical claw (0.11 mm long). Mesocoxa triangular, robust (1.60/ 1.34 mm) with small membrane (0.8/ 0.8 mm) covered by several sensilla, trochanter rounded (0.52 mm in diameter), right femur (3.05/ 0.73 mm) somewhat robust, tibia (0.26 mm wide) bearing large spines (up to 0.38 mm long). Right metacoxa triangular, robust (1.74/ 1.45 mm), trochanter rounded (0.53 mm in diameter), femur (3.00/ 0.75 mm) with huge genicular spine (1.04 mm long), and proximal part of tibia (0.27 mm wide) visible, bearing large spines (up to 0.42 mm long).

Character of preservation. Adult cockroach with preserved upper part of body; without preserved right labial palp or distal part of antennae. Only right foreleg is fully preserved (except procoxa), and in other legs all parts missing, except for the one described above. Only

proximal part of left protibia, right mesotibia, and right metatibia preserved. Body and wings underneath A veins, including abdomen with genitalia, cerci, styli missing. Amber piece is translucent. Syninclusion includes probably a fragment of small Diptera.

Derivation of name. From the Latin *occisor* (murderer) referring to the predacious mode of life of the specimen and species.

Pseudomantina nigroalba Vršanský, sp.n. (Figs. 1i) Zoobank code: 22F571F0-929B-4A0A-B021-F6A9E7E21552

Holotype: PIN 2554/49. Imprint of a completely articulated forewing 5.3 mm long.

Paratypes: 2997/1473, 515 (forewings); 2784/393 (hindwing).

Type locality: Karatau, Kazakhstan **Type horizon**: Karabastau Formation, Upper Jurassic

Differential diagnosis. Pale coloration in radial field narrower, small species forewing up to 7 mm.

Description: Forewing significantly elongated 5.3– 6.5 mm long with dark coloration in posterior halve. Costal field very narrow, Subcosta long simple, R (10–12) richly branched, M reduced to 3 short branches; CuA with 4–5 veins. Clavus narrow, short, with 5 anal branches, some of them dichotomise. Numerous cross-veins present in clavus (and also adjacent CuA) forming characteristic fenestrate structures of coloration.

Hindwing 7.5 mm long, SC simple, R1 and RS differentiated (3+5), media simpliefied to 3 branches, Cubitus with 4+1 veins, A1 3. Coloration similar as in hindwing, membrane dark witth pale anterior margin.

Derivation of name: from *nigrum et album* (Latin for black and white).

Character of preservation: 3 isolated forewings, one isolated hindwing.

Taphonomy: isolated forewings and also a hindwing might indicate short pre-depositional transport.

Genus: Ocelloblattula Anisyutkin et Gorochov, 2008

Stratigraphic range: Barremian to Cenomanian and possibly Santonian ambers.

Geographic range: circum(sub)tropical in Laurasia and Gondwana

Ocelloblattula margarita Koubová et Vršanský, sp. n. Zoobank code: E09782D8-733C-4D5C-BD63-9F4C82D47D0D

Holotype: SNM Z 38669, a complete adult male. Noije Bum Village, Tanaing Town, Myanmar; Cenomanian Cretaceous amber.

Differential diagnosis: Differs from the type species in having more narrow pronotum and in more restricted coloration.

Description: Head nearly globular, large, not fully concealed by pronotum, with huge eyes partially protruding beyond the eye outline. Facets small and numerous. Three small ocelli present. Antenna long filiform. Mandibles very long and narrow. Maxillary palps long, robust, 4- segmented. Labial palp thin and long, 3- segmented. Pronotum nearly globular, with posterior central extension. Legs moderately robust, with very robust and heavily posteriorly carinated femora (8+8 in forefemora; 7+6 in mid femora and 8+8 in hind femora). Terminal femoral spur extremely developed. Fore tibia with 8 spines. First tarsomere long, second and third subequal, fourth shortened but with extension. Claws symmetrical, arolium not distinct. Mid tibia with 13 spurs. Forewings with characteristic coloration, dark fields among cross-veins in the clavus and adjacent areas (similar also to Svabula) and with big pale central macula. Right wing overlaps the left one. Total number of veins (R) 34 including A. SC long simple and with narrow costal area. R slightly sigmoidally curved with 11 (R) –12 (L) veins meeting margin. M with 6 curved veins (visible on right forewing). CuA straight, with 5 veins. CuP sharply cut. A simple (6). Intercalaries and cross-veins present all over the membrane. Hindwings only partially visible below forewings, with wide veins and numerous intercalaries and cross-veins. Cerci moderately long, multisegmented (8) and narrow. Styli extremely long as long as cerci, segmented.

Derivation of name: From the Latin *margarita* (pearl).

Character of preservation: 1 complete adult male, with partially unpreserved antennae and right maxillary palp (2 segments preserved).

Discussion

Morphologically these new "fractaliids" show unique forewing sutura. The sutura is composed of two parts, one running along the 'R' main stem and the perpendicular connecting the terminal part of the

clavus with the anterior margin. This pattern is distinct and identical in both Myanmar and Karatau specimens, thus excluding incidental separation during growth or postburial deformation (Duncan et al. 2003). Wing detachment is unknown in extant and fossil cockroaches except for mutual detachment by different individuals (Bell et al. 2007). Termites shed their wings after mating and during establishment of new nesting sites after their nuptial flight (Martius et al., 1996) and the breaking sutura is their only stable and unique character. Raptorial legs are known in 9 independent cockroach lineages, but the presence of raptorial adaptations on all six legs is a character unique in a lineage leading directly to true mantodeans and the most primitive mantises (Anisyutkin & Gorochov 2008, Hörnig et al. 2013). It is also present in the specimens studied here. Unique heterogenous, asymmetrical cerci with terminal sensilla are characteristic for cave cockroaches and their epigeic ancestors (Sendi et al. 2019, Sendi 2021). The final autapomorphy within Mesozoic cockroaches are the elytrised forewings of Umenocoleoidea. 254 other most important supporting/ conflicting characters are provided in SI2.

Aut(syn)apomorphies/ conflicting characters:

MANTODEA - specialised head with large eyes (as in Umenocoleidae); posterior medial extension of pronotum; 3 pairs of raptorial legs; long cercus lacking long filaments (as in basal Umenocoleidae, termites and cave cockroaches)/ elytrised forewings not conflicting with stem predatory Liberiblattinidae and *Manipulator*; breaking sutura; heterogenous cerci with huge cercal terminal sensilla; standard, vaulted pronotum and short forelegs are plesiomorphies

ISOPTERA - breaking forewing sutura/ elytrised forewings (filiform antenna and wide HW intercalaries occur in basal Isoptera; head is very similar in *Sociala*); dense tibial spurs.

CAVE COCKROACHES - heterogenous cerci; huge terminal cercal sensilla/ ovipositor protrudes externally in Latindiinae and Nocticolidae; there are several Cenozoic lineages with elytra, but a single one in the Mesozoic; basal, epigeic, Nocticolidae tend to hardening of forewings; raptorial legs (short palps are plesiomorphic)

UMENOCOLEOIDEA - elytrised forewings ; long unspecialised tarsi; specialised head with big eyes; long cercus; simplified HW R1; partially concave pronotal fore margin/ raptorial legs (structure of leg is similar in Umenocoleidae and Alienopteridae, but femoral posterior spines are lost); overlapping wings CORYDIOIDEA S.STR. - serrated spurs; this character is further expressed in *Magniocula*/ raptorial legs, breaking sutura

LIBERIBLATTINIDAE - wide HW intercalaries/ lack of arolia, lack of central and possibly also lateral ocelli (not visible); simplified hindwings R1; partially concave pronotal fore margin; large transverse head.

The species can be systematically categorised within Corydioidea on the basis of hindwing structure with wide main (black) veins and thinner (brown) intercalaries, sharply curved clavus and wide cercus. It can be distinguished from Liberiblattinidae and Blattulidae (and from termites) by its elytrised forewings and from Umenocoleoidea by its very short antennal and cercal sensilla and distinct CuP. Corydiidae s.str. differ in lacking an externally protruding female ovipositor. Thus, autapomorphies (dense forewing venation and short sensilla, numerous leg spurs) and plesiomorphies at the same time exclude derivation within Liberiblattinidae (dense venation, short 'SC') and support erecting of the new family. Forewing hardening resulted in vein deforming M-R fusions (Vršanský et al. 2017).

Consequences of morphological adaptations and revealed phylogenetic patterns coincide with spurs, which originated via temporary duplication, as Fractalia is the genus with the greatest number of spurs. Spurs were duplicated and elongated, and subsequently differentiated and reduced. Especially in Umenocoleoidea, the reduction was prolonged to nearly totally reduced carination in advanced species both within Umenocoleidae and Alienopteridae (Ponopterix; Teyia). Posterior profemural carination was reduced before the emergence of the main stem of Umenocoleoidea - all umenocoleoids lack it, which enables their separation from basalmost mantodeans (otherwise difficult due to their extremely similar heads). Tracing consequences of other changes is impossible due to the lack of hierarchical structure of the phylogenetic trees including the four main groups under discussion. Hence, it is obscure whether the first transitional species derived from a beetle-like, predacious or eusocial ancestor. No group is supported within this dataset, although analysis with eliminated characters with too many question marks results in close relation of Fractalia with genus Stavba. Stavba was proved at least as stem for Nocticolidae and

temites and the real ancestor likely resembled predatory *Stavba* (with breaking sutura developed on some of the stages).

Amber cockroaches have been recorded in ambers from Lebanon (Vršanský, 2003; 2004; Anisyutkin & Gorochov, 2008), Jordan (Kaddumi, 2005), Taimyr (Vršanský, 2019), New Jersey (Vršanský, 2003), and France (Vršanský, 2009). Myanmar amber cockroaches show great diversity in forms and life habits, with like Manipulator modificaputis, predator Rhapidiomimula burmitica and Svabula spp. (Grimaldi & Ross, 2004; Vršanský & Bechly, 2015; Qiu et al., 2019b), beetle like Umenocoleidae (Mlynský et al., 2019; Podstrelená & Sendi, 2018; Ross et al., 2010; Vršanský et al, 2021; Luo et al., 2021), aposematic and bark Blattidae (Šmídová & Lei, 2017; Sendi & Azar, 2017; Šmídová, 2020), hymenopteran-mimicking Alienopteridae (Bai et al., 2016; 2018; Kočárek, 2018ab; Poinar & Brown, 2017; Vršanský et al., 2018, 2021; Hinkelman, 2020; Chen et al., 2021) and bizarre Olidae with bipectinate antennae (Vršanský & Wang, 2017; Li & Huang, 2018; Šmídová, 2021) and also standard decomposers (Šmídová et al., 2021; Hinkelman 2021ab; Sendi 2021b; Li & Huang, 2021). Within the superfamily Corydioidea, a cockroach with holoptic eyes is also remarkable (Qiu et al., 2019a). Other more typical cockroaches found in Burmite along with primitive ootheca (Gao et al., 2018; Hinkelman, 2019; Li & Huang, 2019) show evidence of parasitism by hairworms (Poinar, 1999) and pathogen transfer (Vršanský et al., 2019c). In general, the amber record frequently reveals groups with long branches, due to the stability of the amber producing environments.

Paleogeographically the new basal stem group Fractaliidae, from Karabastau of Kazakhstan, Myanmar amber and Solnhöfen of Germany, seems restricted to Laurasia. Major derived groups show a cosmopolitan distribution. Mantodeans occur also in Gondwana, starting from the Barremian, along with the most primitive predatory cockroaches in their lineage (Lebanese amber and later in the Albian Crato in Brazil; Lee 2016). Based on current distribution and molecular analyses, Nocticolidae were likely present in both supercontinents, but were so far found only in Myanmar amber (Sendi et al. 2019). Termites were cosmopolitan, but rare in Gondwana. Umenocoleidae were cosmopolitan, Alienopteridae derived from the

Running title: Mantid-termite shared relative

same stem after divergence of Jantaropterix (Vršanský et al. 2018a, Mlynský et al. 2019) and were restricted to Gondwana (Hinkelman 2019b), but in the Eocene occurred in North America. Respective localities also share subordinate taxa: five of 11 studied cockroach genera from the Lebanese amber in common with those of the Karabastau Formation of Kazakhstan. Solnhöfen preservational character is unsuitable for systematic conclusions: indigenous Lithoblatta, cosmopolitan Blattula (Bechly 2019). Myanmar amber shares most taxa with Lebanese amber, including the genera Cratovitisma, Perlucipecta, Jantaropterix, Ocelloblattula, Balatronis and an undescribed one. Perlucipecta also occurs in Taimyr amber, which otherwise differs in having exclusively liberiblattinids, and indigenous genera.

Taphonomy of Fractaliidae in amber reveals complete adults of both male and female, as well as an immature, suggesting that the taxon inhabited the immediate vicinity of the amber producing trees. At the same time it is another species (as all other formally described) represented by larvae. Two specimens differ in shape of the head, pronotum and forewings, which is due to the process of post-burial drying. All legs posteriorly oriented in both individuals are not stochastic, and along with small foreleg size, too small to capture prey from beyond, instead counterintuitively suggest posterior capture as proposed for Santanmantis individuals (Hörnig et al., 2013). Syninclusions of the holotype and paratype are an unidentified small beetle and a thrips. An adult Erythraeoidea (?Erythraeidae) mite is not an example of parasitism, which is restricted to larval forms (Konikiewicz & Mąkol, 2018). Both cockroach adults are preserved in opaque moderatesized orange amber pieces (0.66 and 0.68 g). Solnhöfen specimens are preserved as complete articulated adults including body. Presence of body (without tip of abdomen and legs) and hindwings in the Karabastau specimen also suggests only short transport prior to deposition, and can be a reason for shared species between Karabastau and ambers.

Explosive radiation as the main pattern of evolution, i.e., phylogeny and radiation without hierarchical structure, has recently been confirmed for all major groups of cockroaches. Only the main groups are recorded as fossils, so this pattern does not necessarily mean that explosive radiation works at the species level, and actually species by species molecular phylogeny of cockroach species seems hierarchical (Legendre et al., 2015). Explosive radiation was proposed and illustrated for bird evolution by one of the first evolutionary thinkers William Charles Linnaeus Martin (1798–1864) (fig. 65). This pattern has theoretical support in the rare plasticity of species which rarely but explosively radiate (Flegr 2013). Otherwise, species rarely evolve so fundamentally that genus or higher rank differences appear. In cockroaches, these principal changes are entirely restricted to 7 diversification peaks with periodicity 62 Ma (Vršanský et al. 2017); other insects are also reported to radiate explosively (Grimaldi, 1999; Rota-Stabelli et al., 2013). So what we observe here is the coeval explosive radiation of mantodeans, termites, umenocoleoids and cave cockroaches at 127-128 Ma diversification point, and an explosion at least 25 Ma earlier producing these main 4 groups and potentially also other unrecorded taxa.

Specifically, maximum parsimony does not contradict explosive radiation and does not reveal any structure in the data, instead revealing the entire polytomy. Surprisingly, this result is also obtained when outgroups from other superfamily were selected (Fig. 1I). Analyses yielded two equally parsimonious trees (662 steps, Fig. 11). No significant structure was recorded, except for a supported clade formed by two alienopterid taxa (Alienopterix ocularis and Formicamendax vrsanskyi), the rest of the tree remained polytomous, including the Jantaropterix from same superfamily Umenocoleoidea. This pattern also remained stable if Fractalia, representing species with a chimaeric distribution of characters, was excluded. Network analyses also showed two other groups (outgroup Magniocula and Ocelloblattula both from Corydioidea; and the living basal corydioids Gapudipentax and the basal termite Mastotermes) with bootstrap support greater than 50% (Fig. 1m).

Supplementary Information (measurement and character matrix) is available upon request

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