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Parasitic cockroaches indicate complex states of earliest proved ants

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Abstract

Myrmecophilous and termitophilous interactions likely contributed to the competitive advantage and evolutionary success of eusocial insects, but how these commensal and parasitic relationships originated is unclear due to absence of fossil records. New extinct cockroaches of the still living family Blattidae are reported here from the Cretaceous Myanmar amber (99 Ma) and are the earliest known inhabitants of complex ant nests, demonstrating that this specialised myrmecophily originated shortly after ant eusociality and appeared in the fossil record. Cretaceous stem aposematic Blattidae are known from the amber of Myanmar and Lebanon and we report them here also from the Syrian amber. Concurrent evolution suggests that the collective internal defence of early ants was weak and allowed infiltrations by numerous unrelated organisms, At the same time, the contemporary presence of ant mimicking myrmecomorphs suggests a need for strong external protection against visually hunting predators. Myrmecophily is supported by morphological adaptations (lack of wide fat body and feeding of adult male; short, fossorial legs; shortened cerci; oligomerised antenna; hairy surface structures) and camouflage behaviour, documented by sediment and own feces covering. Moreover the same piece of amber contains ants, ant mimics and other undescribed ant nest-visiting insects as syninclusions. Another species preserved along with two termites is a putative termitophile. Abundant comparatively large parasitic cockroaches influenced Mesozoic tropical forest ecosystems by affecting the early evolution of complex nests of eusocial insects. Rainforest rudiments in South Yunnan yielded observation of analogical still living, formally undescribed species.

Keywords Fossil insect · Mesozoic · Cretaceous amber · Myanmar · Syria · New genera · New species

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Introduction

Living ant colonies have sophisticated interactions with nest-inhabiting insects, with dozens of other non-ant species recorded in a single *Eciton burchellii* Westwood, 1842 nest (and totally about 300 species depending on this single species) (Rettenmeyer et al. 2011), or even in small *Crematogaster difformis* Smith, 1857 domatia of a single fern species (Inui et al. 2009). Likewise, the scope of potential of interactions in a termite nest is exemplified by 54 ant species inhabiting active and abandoned nests of three termite species; while one species inhabits external galleries of active termite nests regularly (Santos et al. 2010). While living associations of eusocial insects are well investigated, it is very hard and nearly impossible to study how these interactions with myrmecophilous and termitophilous (Cai et al. 2017a, b; Yamamoto 2017) commensals and parasites originated, mainly because of a non-existent fossil records (e.g., Vršanský et al. 2018a and Figs. 1, 2, 3 herein). An exception is the indirect evidence of termite gut endosymbionts (Poinar 2009a, b) and the recently documented record of parasitic rove-beetles, suggesting at least small ant nests (Yamamoto et al. 2016). Due to multiple gains and losses of the relevant adaptations, the evolutionary path that leads to myrmecophily in most lineages is unknown (Pierce et al. 2002). Recent ant and termite nest inhabiting cockroaches of the genera *Attaphila* Wheeler, 1900 (and *Myrmeblattina longipes* (Chopard, 1924) of the same source family Ectobiidae from Brazil; as well as *Myrmecoblatta wheeleri* Hebard, 1917 of Corydiidae) and *Tivia termitium* (Shelford, 1910 of the same family) have been considered to be nest parasites (Wheeler 1900; Chopard 1924; Rodríguez et al. 2013). The unrelated *Nocticola termitophila* Silvestri, 1946 was recorded from Vietnam (the family Nocticolidae is characteristic of caves), and *Pseudoanaplectina yumotoi* Roth, 1995 and an undetermined cockroach (Anaplectidae and Blattidae) from Borneo (Silvestri 1946; Roth 1995; Inui et al. 2009). These taxa may contribute to cleaning functions within the nest and thus may be rather mutualistic or even symbiotic. This was eventually the case of the larvae of the present species, but not an adult which lacks the fat-shaped body necessary for cleaning feeding.

In the course of the present research we observed communities of closely related cockroaches of the family Blattidae (2 undescribed species) associated with diverse small-population (n~ 200) *Polyrhachis illaudata* Walker, 1859 formicid ant nests. These cockroaches resemble the present fossil in general shape, size and coloration. Nevertheless, they are paradoxically less specialized and they lack dense setation. Thus we infer their specialisation was not necessary in rather small colonies of the present ants. They inhabit the internal spaces of active nests and freely trespass even through the main entrance, disregarded by the guards. In addition to ants, numerous other myrmecophiles were observed in the single two observation days and a night, namely beetles, flies and butterflies (Figs. 4, 5). This is a strong evidence for the weak internal protection of even the living ants. Additionally, the partially myrmecomorph and partially myrmecophilous spiders were hunting for guard ants exactly at the nest main entrance (Fig. 4o). Myrmecophilous beetle (Fig. 4n) also worth mentioning as it is camouflaged at distance, myrmecomorph in more close examination while aposematic when cornered.

Nowadays, Attaphilidae are highly specialized, using ant alates for transfers (true phoresis) within the nest and during nuptial flights to invade a new nest: transportation to new nests seems to be of secondary importance, as most queens die before founding a new nest (Bell et al. 2007). A more simple means of transmission can be found by walking along an ant odour trail and this behaviour has been documented previously (Bolívar 1905; Moser 1964). Therefore, the occurrence in amber of fossil cockroaches with the characteristic myrmecophilous adaptations, together with ants and ant-mimickers as syninclusions, provides rare evidence for the origin of sophisticated ecological interactions of early eusocial insects, which nowadays constitute a large portion (up to 20%) of the animal biomass in tropical terrestrial ecosystems. It is worth mentioning that the diversity in the Burmite is very high, surpassing even that of most recent rainforests, and we recorded 74 species of cockroaches among 531 specimens.

Methods

The specimens described here were collected from the Hukawng Valley of Kachin Province, Myanmar (Fig. 1 in Kania et al. (2015)). We follow the age determination as Early Cenomanian (98.8 ± 0.6 million years) as given by U-Pb dating of zircons from the volcanoclastic matrix of the amber (Shi et al. 2012). The Syrian sample was collected in the Bloudane area (Choufani et al. 2015). Three specimens

Fig. 1 Dinosaur-age nest-inhabiting myrmecophilous cockroach *Spinka fussa* sp. n. from Myanmar amber (**a, b, d**) with ant and ant-related syninclusions (Myanmar amber – 98 Ma); putatively termitophilous *Bimodala ohmkuhnlei* sp. n. holotype NIGP154996 (**c**); and aposematic Blattidae relative *Anenev asrev* sp. n. Holotype LU BL3BC from Syrian amber 130 Ma (**f**). (**a1–2**) SNHM BU-235; (**a5**), ant *Haidomyrmex*, (**a4**), Curculionidae and (**a3**), Pselaphidae as syninclusions; (**b3**) larva SNM Z 38601A - ant mimicking Alienopteridae as syninclusion; (**b4**) with μCT visualization of own "asphalt" feces apparent as a black glutinous mass including heterogeneities used for "dirt camouflage" and overlain pattern of aposematic signal; (**d, e**) male holotype SNM Z 38600; SNM Z 38604 miniature larva stage 3 or higher, with dirt camouflage. Arrows show degree of fecal camouflage on specimens. Red number is for the holotype. Drawing scales: 1 mm (rest in the text)
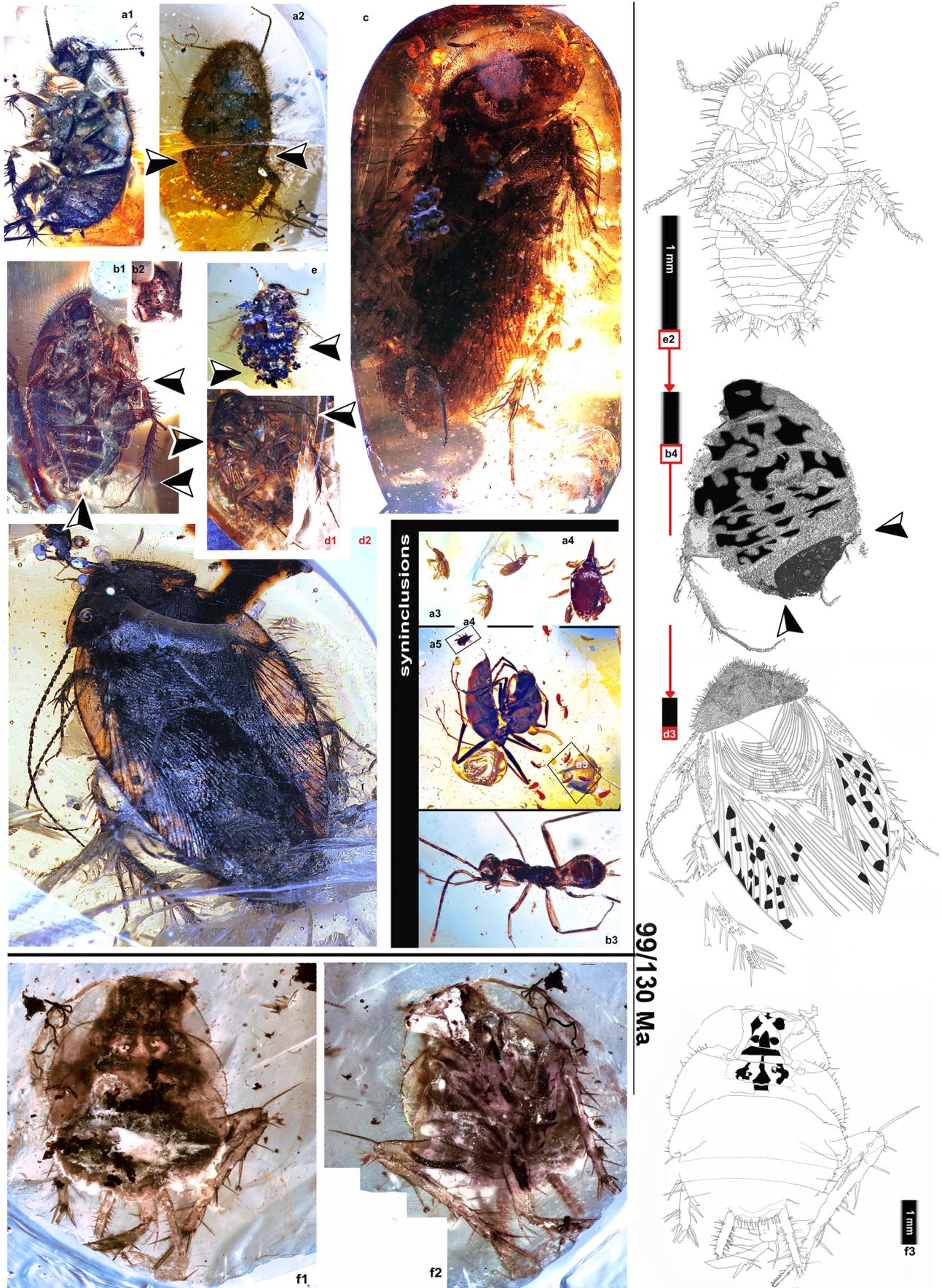
(prefix SNM Z) are deposited in the Slovak National Museum in Bratislava, one specimen (SNMS) is at the Staatliches Museum für Naturkunde Stuttgart, one specimen (NIGP) in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, one specimen (M) in Zhejiang Museum of Natural History, Hangzhou, one specimen (LV) in Dian Jiang Collection, Heshunzhen and one specimen (LU) in Lebanese University in Beirut.

Samples were collected directly at the site, at the rough transition market in Yunnan and obtained from traders (tested for genuity using UV light). Samples were polished using sequences of grid papers. For better visualization, maple sirup was added and coverslide glass attached. Determination is based on complex procedure of respective character analysis as well as life-long experience of authors.

Photomicrographic composites (ca. 40 individual focal planes digitally stacked using the free software Combine ZP) were taken using a Zeiss Stereo Discovery V16 microscope system and Zen software (Fig. 1c); LEICA MZ6 binocular loupe and LEICA EC3 camera (Fig. 1b, f); Canon 750D on tube lens connected with Mitutuyo objective and on a Leica Macroscope 420 (Fig. 1a, e) with incident and transmitted light used simultaneously, processed by Helicon Focus and combine ZP stacking softwares. The figures were prepared with CorelDraw X4 and Adobe Photoshop CS3. Microtomographic CT was performed using Phoenix v|tome|x L 240 with 180 kV nannofocus transmission X-ray tube (110 kV; 134 μA; 750 ms; voxel size 3.5 μm). Phoenix datosx 2 and VGStudio MAX 2.2 were used for reconstruction (2000 images; averaging 3; 1 skipped frame) and final visualization.

Living observations were performed in Xishuangbanna Tropical Botanical Garden, Mengla County, southern Yunnan Province, China (21°55′ N, 101°16′ E; 520 m a.s.l.), the northernmost rudiments of secondary tropical rainforest in SE Asia. This region is influenced by monsoon with wet season in summer and dry season in winter and early spring. The mean annual temperature and mean annual precipitation are 21.6 °C and 1557 mm, respectively; tree species in families including Moraceae, Lauraceae, Rubiaceae, Fabaceae, and Annonaceae are the most abundant, without a dominant species (Tang et al. 1999). Other myrmecomorphs from South China were also reported previously (Song and Li 2014; Yin 2018).

The new discovery mainly contributes to disparity of cockroach forms currently being reported from Myanmar amber (Poinar 1999, 2009a, b; Grimaldi and Ross 2004; Ross et al. 2010; Vršanský and Bechly 2015; Poinar and Brown 2017; Šmídová and Lei 2017; Bai et al. 2016, 2018; Vršanský and Wang 2017; Li and Huang 2018a, b; Gao et al. 2018; Podstrelená and Sendi 2018; Vršanský et al. 2018a, b; Kočárek 2018; Mlynský et al. 2018), which is higher than in all living rainforests taken together.

Results

Systematic paleontology

Order Blattaria Latreille, 1810 (Latreille 1810) = Blattodea Brunner von Wattenwyl, 1882 (Brunner von Wattenwyl 1882) = typified Blattida Latreille, 1810.

Family Blattidae Latreille, 1810 (Latreille 1810) (family–group priority name (ICZN coordination rule) for "Blattariae" Latreille, 1810 (Latreille 1810) – originally described as a family).

Type genus. *Blatta* Linnaeus, 1758 (Linnæus 1758)
Geographic range. Cosmopolitan.
Stratigraphic range. Lower Cretaceous of China, unconfirmed – (Lin 1980); Aptian Lower Cretaceous of Brazil, unconfirmed – (Vršanský 2002; Lee 2016); Lower Cretaceous amber of Syria: present discovery; Cenomanian – (Šmídová and Lei 2017; present discovery); Lower Barremian Lebanese amber – (Sendi and Azar 2017, confirmed) – Present.

Diagnosis (after Roth 2003). Male: with two simple, symmetrical, cylindrical, widely separated styles, each in the posterolateral corner of a symmetrical or weakly asymmetrical subgenital plate. Genitalia relatively complex. Female is plesiomorphic (like no other living cockroaches) with subgenital plate divided into a pair of valves by a longitudinal groove (bivalvular). Autapomorphy of Blattidae in respect to ancestral Mesoblattinidae is simply and only the intrusion of external ovipositor inside body cavity. Oviparous. Forewings are diagnostic in rich venation with intercalaries and eventually branched SC, HW with unreduced venation (plesiomorphies).

Spinka

Vršanský, Šmídová et Barna, gen. n.

Type species. *Spinka fussa* Vršanský, Šmídová et Barna, sp. n. described below, by monotypy.

Stratigraphical and chronological range. Indigenous to Cenomanian Myanmar amber.

Description. As for species.

Differential diagnosis. The taxon is categorized within Blattidae on the basis of close relationship with well investigated *Balatronis* Šmídová et Lei, 2017: the resemblance includes forewing venation (regular veins, but with irregularity in descending of RS; simplified SC, simple A and generally high number of veins), aposematic body coloration, claws with highly reduced arolia and Terminalia with styli. Dense setation cover is autapomorphic. Triangle-shaped pronotum is highly derived.

Systematic remarks. While there is a plethora of described (Šmídová and Lei 2017; Sendi and Azar 2017) and undescribed aposematic cockroaches known from the Cretaceous ambers (and precisely this pattern is observed in

closely related living *Neostylopyga rhombifolia* (Stoll, 1813) related to ant alert escape pheromone 6-methyl-5-hepten-2-one (Capinera 2008), it is impossible to precisely derive the present taxon from any certain species (the more rarely preserved with wings). The aposematic pattern of the present species is apparently in decline (low distinctness), and thus stating aposematic ancestor is rather safe. Such aposematic species are known among fossils only representing the stem family Blattidae, while some living representatives of other descendant family Blaberidae also share this pattern especially in the immature stage (see *Blaberus*). Blaberidae evolved only at KPg so it can be hypotethised that the stem for Blaberidae were namely among these colorful primitive Blattidae. They were symplesiomorphic with more primitive Blattidae in branched SC (certain Blaberidae can have simple SC, but those are highly derived and advanced) and eventually A (simple A of the present taxon explicitly excludes Mesoblattinidae and Blaberidae) and also the head shape with huge eyes and short labrum and mentum characteristic for Blattinae and early and primitive Blaberidae and not the proposed Mesoblattinidae (Vršanský et al. 2013). The morphological hiatus between Mesoblattinidae and Blattidae (resp. to Ectobiidae) is arbitrary (Wei and Ren 2013), so this inference is not principal at the present state of the knowledge. Categorization within Attaphilidae is excluded on the basis of absence of significant arolia (contrary is observed and most of the stages have arolia totally indistinct). Terminalia with styli are characteristic for Blattidae. Nevertheless, direct derivation of the present taxon from known Blattidae such as *Balatronis* is excluded based on generally high number of veins contrasting with the very small size. Venation is generally with regular distance among veins, except for secondary irregularity in descending of RS, which also excludes Mesoblattinidae and other Mesozoic groups, but can be ancestral for Olidae.

Derivation of name. *"spinka"* (*"špinka"* is Slovak for small dirt; *"spinká"* is "is sleeping", but *"spinka"* is also a paperclip) – refers to dirt and feces camouflage resting in amber. Gender feminine.
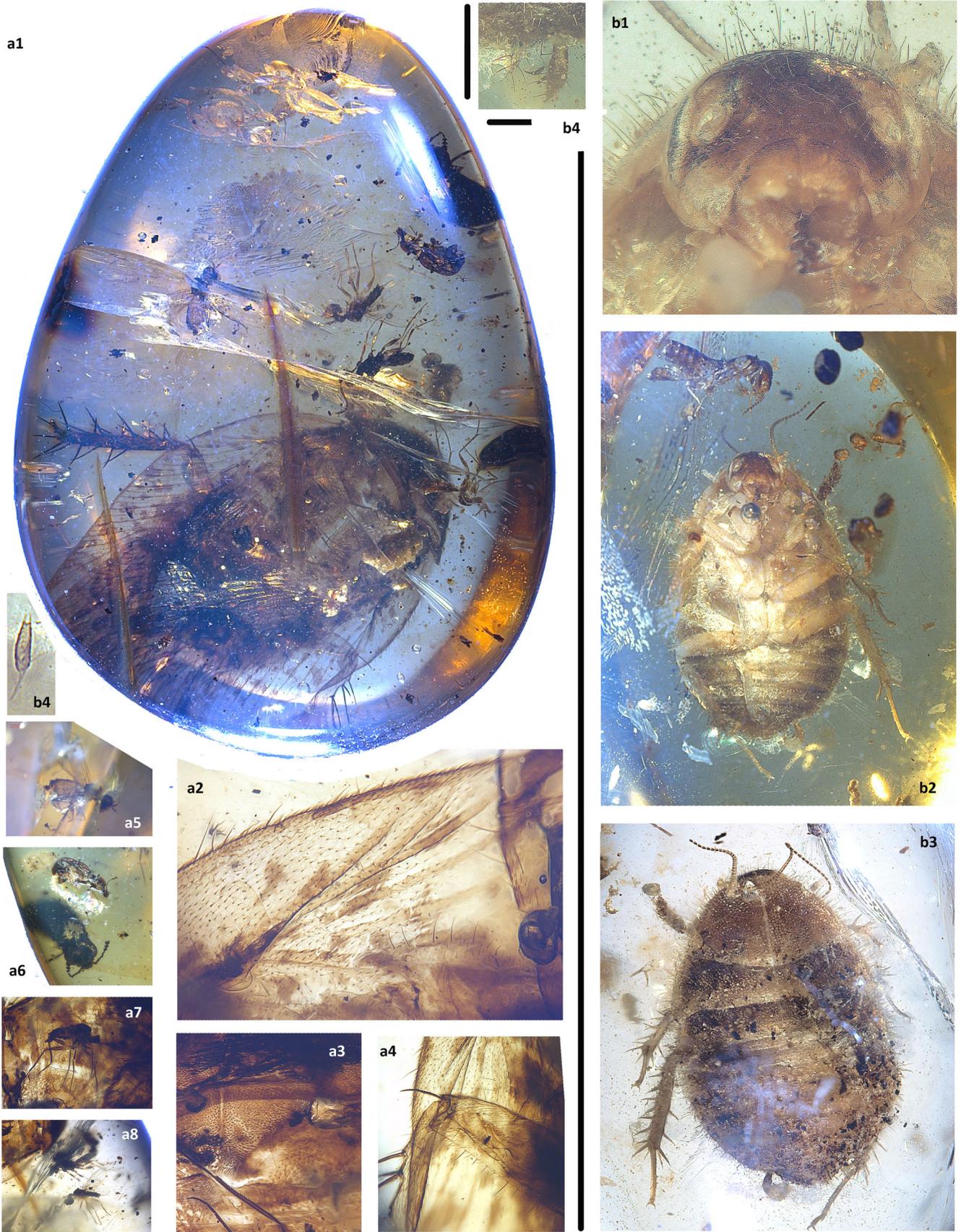
Spinka fussa

Vršanský, Šmídová et Barna, sp. n. (Figs.1a, b, d, e, 2a, 3a)

Description (based on male adult holotype herein; description of immatures below). The standard general cockroach morphotype (with hypognathous head and dorsoventrally flattened body) but densely covered with long and strong sensilla (haired, fuzzy). Small species, with overall head-abdomen tip length/ widest width 9.4/ 4.9 mm. Head standard, completely hypognathous and entirely hidden by pronotum (autapomorphy due to ant attacks); dark, length/ width 1.47/ 1.4 mm. Compound eye comparatively large, round, 0.49 mm in diameter, protruding beyond the head

outline. Two dark lateral ocelli of lentil-like, slightly prolonged shape present. Antenna filiform, covered with chaetica distributed in 2 (basal) - 7 (terminal) rows. Left scape 0.37 mm long, pedicel 0.10 mm long. Flagella of the left antenna lengths (segments 1st - 38th): 0.12/ 0.12/ 0.91/ 0.12/ 0.13/ 0.14/ 0.15/ 0.14/ 0.15/ 0.14/ 0.15/ 0.15/ 0.19/ 0.16/ 0.16/ 0.18/ 0.19/ 0.18/ 0.18/ 0.19/ 0.19/ 0.20/ 0.19/ 0.20/ 0.19/ 0.19/ 0.18/ 0.18/ 0.18/ 0.17/ 0.16/? /? / 0.17/ 0.16/ 0.15/ 0.14/ 0.12 mm. Right scape 0.38 mm, pedicel 0.15 mm long. Flagella of the right antenna lengths (segments 1st - 46th): 0.11/ 0.89/ 0.10/ 0.11/ 0.12/ 0.11/ 0.12/ 0.11/ 0.14/ 0.15/ 0.14/ 0.15/ 0.15/ 0.15/ 0.17/ 0.18/ 0.17/ 0.18/ 0.17/ 0.18/ 0.18/ 0.18/ 0.17/ 0.17/ 0.17/ 0.18/ 0.18/ 0.17/ 0.16/ 0.17/ 0.18/ 0.16/ 0.17/ 0.17/ 1.15/? /? /? / 0.14/ 0.14/ 0.13/ 0.14/ 0.13/ 0.12/ 0.11/ 0.10 mm. Maxillary palp terminal palpomere length/ width 0.35/ 0.1 mm. Pronotum triangular, densely covered with setae up to 0.25 mm long. The surface of the pronotum consists of uniform layer of small circle shaped depressions (~1600 dots/mm^2), also containing setae. Two light-colored, kidney-shaped maculas present. Forewings with irregular spots and numerous hair. Left wing length/ width 7.7/ 3.1 mm. Costal field short (reaching a third of the shortened wing) with long Costa reaching 2/3 of the wing length and with simple SC (with possible few soft branches ascending terminally). Veins thick 0.04 mm. Radial field wide, R bifurcating from the anteriormost part, with about 15–18 more or less straight branches meeting margin. M bifurcated only basally, CuA richly branched. CuP fluent, without sharp curvature, clavus with numerous simple anal veins (16). Forelegs (tibiae especially) extremely shortened. Left foreleg coxa length/ width 1.69/0.53 mm, femur 1.80/ 0.38 mm, tibia 0.67/ 0.20 mm, tarsi (1st-5th segment) 0.90/ 0.07, 0.18/ 0.07, 0.15/ 0.06, 0.13/ 0.11, 0.30/ 0.04 mm. Claws symmetrical, arolium very small (in immatures nearly invisible), with length 0.14 mm. Left mid leg coxa length/ width 2.11/ 0.72 mm. Femur 2.38/ 0.58 mm. Tibia length 1.71 mm. Tarsi (2nd- 5th segment): 0.37/ 0.08, 0.23/ 0.06, 0.13/ 0.08, 0.26/ 0.05 mm. Left hind leg femur length 0.64 mm. Tibia length 0.23 mm. Right foreleg coxa length 1.51 mm, femur length/ width 1.89/ 0.40 mm. Tibia length 1.49. Fifth tarsal segment length 0.39 mm. Right mid leg coxa length 2.84 mm, femur length/ width 2.41/ 0.57 mm. Tibia 1.70/ 0.28 mm. Tarsi (1st-5th segment): 1.28/ 0.09, 0.36/ 0.05, 0.23/ 0.05, 0.14/ 0.08, 0.27/ 0.04 mm. Right hind leg coxa length 2.60 mm; femur length/ width 2.70/ 0.70 mm. Tibia 2.67/ 0.35 mm; tarsi (3rd- 5th segment): 0.22/ 0.07, 0.13/ 0.07, 0.27/ 0.06 mm. The length of spine on leg about 0.05 mm.

SNM Z 38601 (the specimen is categorized within this species on the basis of small size, dense setation, characteristic head with huge protruding eye-part of the head (but not eyes), short antenna and appendages, aposematic coloration and nearly lacked arolium). Small wingless cockroach with ovoid overall shape of body, covered by

prominent setae, antennae long approximately as half of body length, strongly reduced cerci, thick legs with prominent tibial spination. Body 5.31 mm long, 3.3 mm wide. Pronotum 1.31 mm long, 2.4 mm wide (approximate width, half of pronotum obscured), subtriangular with strongly rounded cranial and lateral sides, caudal side slightly convex in the middle. Covers the head completely. Strongly covered by medium sized setae and thick long setae. Setae on top of mesonotum, metanotum and abdomen are significantly shorter, thick long setae are positioned only on lateral sides. Dorsal side of thorax and abdomen has ornamentation of light and dark areas, being least prominent on pronotum. Coloration of pronotum mostly dark, with lighter areas around cranial edge, in caudolateral areas and smaller areas around the middle (pronotum not fully visible). Mesonotum with a large lighter butterfly shape light area in the middle having two dark maculae positioned anterolaterally and one macula centrocaudally. Metanotum has similar pattern but the light area is disconnected by the darker maculae inside which are connected to each other and in the side connected to the rest of darker colored metanotum. Tergites of abdomen have centrally a light area with dark

macula craniocentrally. Ventral side of the body dark colored. Head 1.2 mm long, 1 mm wide; dark colored, covered with long thick setae, eyes positioned laterally far from each other.

Forelegs with spines on ventral side of femora and thick longer setae, tibiae with long thick setae and thick spines; forelegs are significantly shorter than middle and hind legs. Left forecoxa l = 1.08 mm, right forecoxa length 1.1 mm; left foretrochanter l = 0.34 mm, w = 0.36 mm, right foretrochanter l = 0.33 mm, w = 0.14 mm, left forefemur l = 0.89 mm, w = 0.29 mm, right forefemur l = 1.13 mm, w = 0.25 mm; left foretibia l = 0.46 mm, w = 0.18 mm, right foretibia l = 0.45 mm, w = 0.18 mm; 1st left tarsomere l = 0.24 mm, 1st right tarsomere l = 0.37 mm; 2nd left tarsomere l = 0.11 mm, 2nd right tarsomere l = 0.12 mm; 3rd left tarsomere l = 0.07 mm, 3rd right tarsomere l = 0.1 mm; 4th left tarsomere l = 0.11 mm, 4th right tarsomere l = 0.09 mm, 5th left tarsomere l = 0.21 mm, 5th right tarsomere l = 0.19 mm. Middle legs with one thick terminal spike on femora, and numerous thick long spines on tibiae. Coxae not well visible to be properly measured. Left middle trochanter l = 0.49 mm, w = 0.23 mm, right middle trochanter l = 0.51 mm, w = 0.22 mm; left middle femur l = 1.3 mm, w = 0.46 mm, right middle femur l = 1.18 mm, w = 0.4 mm; left middle tibia l = 0.88 mm, w = 0.18 mm, right middle tibia l = 0.97 mm, w = 0.19 mm; left 1st tarsomere l = 0.6 mm, right 1st tarsomere l = 0.6 mm; left 2nd tarsomere l = 0.14 mm, right 2nd tarsomere l = 0.18 mm; left 3rd, 4th and 5th tarsomeres in not good position to be measured, 3rd right tarsomere l = 0.11 mm,

Fig. 3 Dinosaur-age ant nest-inhabiting myrmecophilous cockroach *Spinka fussa* sp. n. (**a** SNM Z 38600) and putatively termitophilous *Bimodala ohmkuhnlei* sp. n. (**b**, NIGP L007), both from Myanmar amber. Line drawings of the male holotypes, ventral and dorsal views

4th right tarsomere l = 0.1 mm, 5th right tarsomere l = 0.23 mm. Hind legs are the longest, femora have small spines on ventral side and one long terminal spine, tibiae bear numerous long thick spines. Left trochanter l = 0.64 mm, w = 0.23 mm, right trochanter l = 0.56 mm, w = 0.32 mm; left femur l = 1.43 mm, w = 0.5 mm, right femur l = 1.39 mm, w = 0. 49 mm; left tibia l = 1.68 mm, w = 0.18 mm, right tibia l = 1.47 mm, w = 0.23 mm; left 1st tarsomere l = 0.9, right 1st tarsomere l = 0.78 mm; left 2nd tarsomere l = 0.27 mm, right 2nd tarsomere l = 0.21 mm; left 3rd tarsomere l = 0.17 mm, right 3rd tarsomere l = 0.17 mm; left 4th tarsomere l = 0.13 mm, right 4th tarsomere l = 0.14 mm; left 5th tarsomere l = 0.25 mm, right 5th tarsomere l = 0.21 mm.

SNHM BU-235 (the specimen is categorized within this species on the basis of small size, dense setation, characteristic head with huge protruding eye-part of the head (but not eyes), short antenna and appendages, aposematic coloration and nearly lacked arolium). Small wingless roach with ovoid body 5.5 mm long and 3.08 mm wide, densely covered by distinct setae. Head ovoid, inflated, 1.03 mm long, around (not in the best position for measurement) 0.93 mm wide, with very big eyes which are on the top of head near each other and occupy almost the whole lateral area of head. Frons densely covered by long distinct setae similarly as the pronotum. Antennae with mostly uniform short flagellomeres (still bigger length than width). Pronotum with narrower front, rounded and wide caudolateral angles and concave caudal edge, l = 1.9 mm, w = 2.45 mm. Densely covered by distinct setae which are longer around the frontal and lateral edge. Mesonotum wingless with distinct caudally oriented caudolateral edges and distinct central furrow; l (in the middle) = 0.78 mm, w = 3 mm; densely covered by distinct setae, longest around the lateral edges. Metanotum wingless with distinct caudally oriented caudolateral edges and distinct central furrow; l (in the middle) = 0.68 mm, w = 3.08 mm; densely covered by distinct setae, but having longer setae around the lateral edges. Abdomen wide, l = 2.08 mm, w = 2.83 mm, densely covered by shorter setae on the top of dorsal side, but longer setae around lateral edges. Abdominal sternites cover by mostly short but also longer setae. Cerci appear to be 7-segmented, wide at the base and more or less regularly narrowing distad; left cercus l = 0.35 mm, w = 0.11 mm; right cercus l = 0.38 mm, w = 0.11 mm. Bearing long setae which with their length distinctly exceed both length and width of cercomeres. Forecoxae with long distinct setae, both of them not enough visible to be measured. Foretrochanteri covered by long distinct setae. Left foretrochanter l = 0.6 mm, w = 0.2 mm; right foretrochanter l = 0.45 mm, w = 0.18 mm. Forefemora with concave dorsal and ventral side, covered by distinct long setae, anteroventral ridge bears row of numerous small thin spines, posteroventral ridge with 7 short moderately thick spines, in between these two rows and laterally from them several extremely long

setae, which exceed the width of femur, dorsal side with one large terminal spine. Left forefemur not measurable, right forefemur l = 0.1 mm, w = 0.23 mm. Foretibiae short and distinctly thick, covered by very long thin setae, distally from the middle of its length bears a large thick serrated spine with prominent base, distal end bears 6 large spines of the same look. Left foretibia not measurable, right foretibia l = 0.48 mm, w = 0.2 mm. Foretarsi with medium sized setae. 1st left tarsomere l = 0.35 mm, 1st right tarsomere l = 0.4 mm; 2nd left tarsomere l = 0.1 mm, 2nd right tarsomere l = 0.1 mm; 3rd left tarsomere l = 0.1 mm, 3rd right tarsomere l = 0.1 mm; 4th left tarsomere l = 0.09 mm, 4th right tarsomere l = 0.09 mm; 5th left tarsomere l = 0.2 mm, 5th right tarsomere l = 0.18 mm. Middle coxae covered by long distinct setae. Left middle coxa l = 1.2 mm, w = 0.55 mm; right middle coxa length not measurable, w = 0.63 mm. Middle trochanteri covered by long distinct setae. Left middle trochanter not measurable, right middle trochanter l = 0.38 mm, w = 0.23 mm. Middle femora covered by long distinct setae, dorsally at distal end one large terminal spine. Left middle femur length not measurable, w = 0.43 mm; right middle femur l = 1.25 mm, w = 0.38 mm. Middle tibiae covered by long distinct setae, along their length with several long thick spines, most of them at dorsal side, distal end with 6 large, thick terminal spines. Left middle tibia l = 0.95 mm, width not measurable; right middle tibia l = 0.83 mm, w = 0.23 mm. Middle tarsi with medium sized setae and numerous small spines. 1st left tarsomere l = 0.68 mm, 1st right tarsomere l = 0.7 mm; 2nd left tarsomere l = 0.18 mm, 2nd right tarsomere l = 0.18 mm; 3rd left tarsomere not measurable, 3rd right tarsomere l = 0.13 mm; 4th and 5th tarsomeres of both middle legs not measurable; hind coxae covered by distinct long setae; hind trochanteri covered by distinct long setae (measurement impossible). Hind femora with long distinct setae and one distinct terminal spine at dorsal side. Left hind femur not well measurable, right hind femur l = 1.35 mm, w = 0.43 mm. Hind tibiae with long distinct setae and several long thick spines mostly positioned dorsally, 6 positioned terminally. Left hind tibia l = 1.63 mm, width not measurable; right hind tibia l = 1.28 mm, w = 0.18 mm. Hind tarsi with shorter setae and numerous short small spines. 1st left tarsomere l = 0.88 mm, 1st right tarsomere l = 0.9 mm; 2nd left tarsomere l = 0.3 mm, w = 0.28 mm; 3rd left tarsomere l = 0.18 mm, 3rd right tarsomere l = 0.15 mm, 4th left tarsomere not measurable, 4th right tarsomere l = 0.13 mm; 5th left tarsomere not measurable, 5th right tarsomere l = 0.25 mm.

SNM Z 38604 (the specimen is categorized within this species on the basis of small size, dense setation, characteristic head with huge protruding eye-part of the head (but not eyes), short antenna and nearly lacked arolium; the aposematic coloration is barely visible). Extremely small (2.61 mm long, 1.48 mm wide) wingless roach with dorsal and lateral sides of its body covered by long setae,

short antennae and shorter legs. Head 0.51 mm long, 0.59 mm wide, completely covered with pronotum dorsally covered by long setae, eyes positioned laterally away from each other, antennal pits distinct, maxillar palps distinct but their length does not reach the length of the head. Antennae short (around 0.8–0.9 mm long) left with 10 antennomeres, right with 13 antennomeres, bearing setae with length similar to flagellomeres, even exceeding the shorter flagellomeres. Scapus elongate, pedicel around half of scapus length, flagellomeres short but length always exceeds width, club-like, 1st flagellomere larger than pedicel, 2nd, 3rd and 4th flagellomeres are the shortest. Pronotum semi-circular, 0.71 mm long, 1.19 mm wide, its surface covered by long distinct setae. Mesonotum 0.34 mm long, 1.44 mm wide, covered by long setae, most distinct on lateral sides, wingless. Metanotum 0.26 mm long, 1.48 mm wide, covered by long setae, most distinct on lateral sides, wingless. Abdomen short ovoid, l = 1.28 mm, w = 1.34 mm, dorsally covered by long setae, on ventral side few setae near the caudal margin of last four sternites. Cerci (only right one complete and in a well measurable position) 9-segmented, 0.41 mm long, in the basal half (cercomeres 1–3) more or less uniform thickness (maximal width 0.07 mm) transitions between them very mild, cercomere 4 slightly thinner at its base, narrowing distad, from distinctly thinner cercomere 5 to cercomere 9 are the cercomeres getting thinner (cercomere 8 and 9 width less than 0.01 mm), ceromere 5 short, cercomere 6 even shorter, cercomeres 7–9 elongate, while cercomere 8 and 9 are slightly shorter than cercomere 7. Setae on cerci not many, long, distinctly exceeding both length and width of cercomeres. Stylli distinct with few long setae, segmented but segmentation in many parts poorly visible, left stylus seems to be 4-segmented, right stylus 4-segmented (it is probable that these numbers and the drawing of segmentation of stylli is incorrect), segments seem to have always bigger length than width. Both are terminated by a very small spike. Legs rather short with thick tibiae bearing thick spines, all tarsi terminated by pair of hooked claws. Right forecoxa l = 0.53 mm, w = 0.19 mm, left forecoxa not measurable. Foretrochanteri have a ventroterminal process. Left foretrochanter l = 0.16 mm, w = 0.06 mm, right foretrochanter l = 0.18 mm, w = 0.08 mm. Forefemora with anteroventral and posteroventral rows of small spines and a large thick anteroterminal spine. Left forefemur l = 0.46 mm, w = 0.12 mm; right forefemur l = 0.47 mm, w = 0.11 mm. Foretibiae short, club-like, distinctly widening distad, covered by smaller setae and several larger seta/spines from which the 5 terminal spikes are the largest. Left foretibia l = 0.26 mm, max w = 0.09 mm; right foretibia l = 0.26 mm, w = 0.09 mm. Foretarsi covered by medium-sized setae. Left foretarsus l = 0.32 mm (1st tarsomere l = 0.12 mm, 2nd tarsomere l = 0.05 mm, 3rd tarsomere l = 0.04 mm, 4th tarsomere max l = 0.6 mm, 5th tarsomere l = 0.1 mm); right foretarsus length = 0.31 mm (1st tarsomere l = 0.1 mm, 2nd tarsomere l = 0.43 mm, 3rd tarsomere l = 0.04 mm, 4th tarsomere l = 0.04 mm, 5th tarsomere l = 0.12 mm). Middle coxa only right one visible (l = 0.6 mm, w not measurable). Middle trochanter wide, left partially obscured, right l = 0.24 mm, w = 0.16 mm. Middle femora with almost parallel ventral and dorsal margin, setae distributed mostly around ventral margin, prominent thick dorsoterminal spine present. Left mid femur partially covered by other leg, therefore full measurements cannot be made; right mid femur l = 0.54 mm, w = 0.16 mm. Middle tibiae widening in basal third but keeping more or less same width in the rest of their length; covered by shorter setae and bearing several long spikes, most of them positioned at dorsal edge and terminally. Left middle tibia l = 0.44 mm, w = 0.11 mm; right middle tibia l = 0.47 mm, w = 0.1 mm. Middle tarsi covered by medium sized setae. Left middle tarsus l = 0.36 mm (1st tarsomere l = 0.18 mm, 2nd tarsomere l = 0.05 mm, 3rd tarsomere l = 0.04 mm, 4th middle tarsomere l = 0.06 mm, 5th middle tarsomere l = 0.08 mm); right middle tarsus l = 0.47 mm (1st tarsomere l = 0.19 mm, 2nd tarsomere l = 0.08 mm, 3rd tarsomere l = 0.03 mm, 4th tarsomere l = 0.07 mm, 5th tarsomere l = 0.13 mm). Hind coxae large, only length of right hind coxa measurable, l = 0.55 mm. Hind trochanteri. Left hind trochanter l = 0.21 mm, w = 0.13 mm; right hind trochanter l = 0.22 mm, w = 0.12 mm. Hind femora with convex dorsal side and sinusoid ventral side, longer thick setae along ventral and dorsal margin. Left hind femur partially obscured, its dimensions estimation: l = 0.7 mm, w = 1.7 mm; right hind femur l = 0.57 mm, w = 0.18 mm. Hind tibiae covered with medium sized setae, ventral margin with few thin spines, dorsal margin with several long thick spines, at distal end five large thick terminal spines. Left tibia l = 0.63 mm, w = 0.11 mm, right hind tibia l = 0.67 mm, w = 0.09 mm. Hind tarsi covered by medium-sized setae. Left hind tarsus l = 0.64 mm (1st tarsomere l = 0.35 mm, 2nd tarsomere l = 0.1 mm, 3rd tarsomere l = 0.05 mm, 4th tarsomere l = 0.5 mm, 5th tarsomere l = 0.11 mm); right hind tarsus l = 0.56 mm (1st tarsomere l = 0.28 mm, 2nd tarsomere l = 0.09 mm, 3rd tarsomere l = 0.08 mm, 4th tarsomere l = 0.06 mm, 5th tarsomere l = 0.1 mm).

Holotype. Complete adult male. SNM Z 38600. Deposited in Slovak National Museum.

Type locality. Hukawng valley mines, Myanmar.

Type horizon. Cenomanian Upper Cretaceous.

Derivation of name. After *"fussa"* (Latin for Fuss, referring to activities among ants causing "fuss"). Also see fuzzy habitus.

Character of preservation. One very small immature (? stage 3), 2 larger immatures (? stages 6, 7), 2 adults, one male - one female. All preserved in ideally transparent (with debris and particles) amber piece with yellow hue.

Phylogenetically annotated character list; numbered are characters based on Vršanský et al. (2018a): 0- plesiomorphy, 1- apomorphy.

Orientation of head (0) hypognathous; (1) orthognathous ((0) orthognathous; (1) prognathous or subprognathous (slightly inclined) according to Bai et al. (2016). Hypognathous is an original state in Blattaria; orthognathous in *Alienopterus* like in living cockroach *Melyroidea*, Mantodea (Grimaldi 2003; Wieland 2013*)*, most *Ponopterix* (Lee 2016), *Manipulator* (Vršanský and Bechly 2015); homoplastically in Mantophasmatodea (Baum et al. 2007), and most other groups of Polyneoptera; derived prognathous state in some other orders but also in predatory Raphidiomimidae (Vishniakova 1973; Wipfler et al. 2011; Liang et al. 2018) is not present in the present lineage and is disregarded herein. 60.

Head (0) standard, (1) modified. Head is extremely conservative in living cockroaches (exceptionally orthognathous in *Melyroidea*) and little variability, except for predatory Manipulatoridae, Eadiidae and Raphidiomimidae (and Mantodeans) (Vishniakova 1973; Vršanský 2009; Vršanský and Bechly 2015; Liang et al. 2018), is characteristic also for Mesozoic cockroaches. The head underwent drastic changes (to-orthognathy) in the transition to beetle-like habits (while no such change occurred in other beetle-like lineages like Diplopteridae or Anaplectidae) (Vršanský et al. 2016; Barna et al. unpublished) and further in certain Alienopteridae (up to prognathous state in Grant) in seriously modified unlike in any other Dictyoptera. 61.

Head oval/ globular (1) absent, (0) present. Head is globular in most stem Liberiblattinidae and also in most primitive Vitisma and primitive Jantaropterix (Vršanský 1999, 2002, 2009) and thus is regarded as plesiomorphic at the level of Umenocoleoidea. Within Blattoidea it is synapomorphic with Blattinae and Blaberidae. 59.

Parietal ridge s. str. (0) absent, (1) present. Such a ridge is present in certain Umenocoleoidea, extant Mantodea (Leverault 1936; Wipfler et al. 2011, 2012), and Grylloblattodea (Walker 1931; Bai et al. 2016). It does not occur in other groups of Polyneopterea (Wipfler et al. 2011) such as *Manipulator*. The condition in *Santanmantis* (although new specimens seems to possess it (Hörnig et al. 2013)) and most extinct mantises (Grimaldi 2003; Vršanský 2003; Wieland 2013; Vršanský and Bechly 2015; Li and Huang 2018b) is uncertain. 2.

Eyes protruding laterally (1) present, (0) absent. Eyes slightly protruding from the head outline are characteristic for advanced cockroaches including Mesozoic groups (validated for Fuziidae; Vršanský 2009). Significant protrusion is

autapomorphy of advanced Umenocoleoidea (absent in most primitive Umenocoleoidea, but synapomorphy with mantodean is excluded; slight lateral protrusion is characteristic for all studied umenocoleoids). 71.

Ocelli (0) present, (1) absent ((0) absent, (1) present according to Bai et al. 2016). Ocelli are present in stem cockroaches (Vršanský 2008; Anisyutkin and Gorochov 2008) and also in the most primitive mantodeans (Vršanský 2002; Grimaldi 2003: Fig. 3; Delclós et al. 2016), but not in other known predatory cockroaches. The reverse polarity would be correct regarding the more distant derivation (from Palaeozoic cockroaches). 3.

Ocelli (1) lentiform, (0) diffuse or plain. Ocelli are primitively structured in standard cockroaches (25). Autapomorphy of Umenocoleoidea, homoplasic with Mantodeans. Plain in the present taxon. 68.

Ocelli very large (1) present, (0) absent. Autapomorphy of some Umenocoleoidea. Homoplasically can occur in certain mantodeans. Ocelli of Mesozoic standard cockroaches (including Blattulidae, Caloblattinidae, Mesoblattinidae and Raphidiomimidae) are small (Vršanský 2008). Ocelli are not especially large, although in *Balatronis libanensis* Sendi et Azar, 2017 they are very large, but not lentiform, but only as maculas. 69.

Number of ocelli (0) three, (1) two. See above. Of living lineages only *Balatronis libanensis* possessed 3 ocelli, in the form of macula (Sendi and Azar 2017). 4.

Ocelli (1) in one line, (0) in triangle. Symplesiomorphy of *B. libanensis*, ocelli are in one line in advanced Alienopteridae. 67.

Interantennal ridge (0) present, (1) absent ((0) absent, (1) present according to Bai et al. 2016). The interantennal ridge connects the antennal sockets of the two sides. It is present in certain Alienopteridae, in extant Mantodea (Wieland 2013; see also Leverault 1936; Grimaldi 2003; Wipfler et al. 2011, 2012), in *Ambermantis* (Grimaldi 2003), in *Jantaromantis* (Vršanský 2002), and in Odonata (Blanke et al. 2012). The reverse polarity is due to the plesiomorphic presence in Umenocoleoidea and stem Liberiblattinidae and in higher level it would be correct. 5.

X-shaped median apodeme of frontal region (0) absent, (1) present. Absent in Mantodea (Wipfler et al. 2012; Wieland 2013: Figs. 68–70, 74–77) and also in most other groups of Polyneoptera (Wipfler et al. 2011). Present in Mantophasmatodea (Baum et al. 2007). Disregarded due to absence in adult fossils, although an alienopterid immature seem to have it indicated. All other unpublished adults do not have it.

Gula (0) absent, (1) present. Absent in *Alienopterus* like in extinct and extant Mantodea (Wieland 2013; Hörnig et al. 2013) and most other groups of Polyneoptera (Wipfler et al. 2011). Present in Embioptera, Dermaptera and Zoraptera (Rähle 1970; Beutel and Gorb 2006). Disregarded due to absence of evidence and presence on all Blattaria.

Antenna sensilla fine (1), (0) normal. Sensillar apparatus on antenna is family-specific in cockroaches (Vršanský et al. 2001), but this pattern (regular, not very dense normal size sensilla) is identical in Mesoblattinidae and Blattidae. 63; 114.

Antennal length (0) of comparable length than body, (1) shorter than body. Modification to live with ants. Long in all cockroaches including Umenocoleidae, *Alienopterus* and *Vcelesvab*, like in most other groups of Polyneoptera (e.g., Wipfler et al. 2011; Beutel et al. 2014). The original length consideration (very short in Ephemeroptera and Odonata) is modified here as the stem group Umenocoleidae has already a very long antenna identically as in primitive alienopterids *Alienopterus* and *Vcelesvab*. 9.

Lacinia (0) free, (1) in galeal cavity. Autapomorphy of dictyopterans (Wipfler et al. 2012).

Antenna (0) filiform, (1) **other**. Antenna is filiform and filamentous in nearly all cockroaches including type *Alienopterus* (Bai et al. 2016). Moniliform antenna is exceptionally present here and in termites. 62.

Palp (0) elongate, (1) short. Plesiomorphy at the level of order. Palp reduces only among Mesozoic Umenocoleoidea and some stem Liberiblattinidae, but surprisingly not here (as other appendages are reduced). 66.

Secondary (anterior) mandibular joint (0) gliding device, (1) ball-and-socket joint. A secondary mandibular articulation is present as a ball-and socket joint in Odonata and neopteran groups with normally developed mandibles. Also in the present fossil.

Number of maxillary palpomeres (0) five, (1) less than five ((0) more than five, (1) five, (2) less than five according to Bai et al. 2016). Four are present in *Alienopterus* (see Fig. 6a, Bai et al. 2016), unlike in other groups of Polyneoptera (e.g., Wipfler et al. 2011, 2012) including extant Mantodea (Wieland 2013), *Manipulator* (Vršanský and Bechly 2015) and *Ambermantis* (Grimaldi 2003; condition in *Ambermantis* unclear; in *Burmantis* 5-state was validated in Delclós et al. 2016 and Li and Huang 2018a, b. Palps are four-segmented in *Ponopterix* (clearly visible in a single specimen, which might be a developmental error or incomplete regeneration after damage) and *Jantaropterix* (Vršanský 2003 – and in many unpublished amber records of this genus). Five-segmented palp is present in stem cockroaches. 11.

Accessory anterior tentorial bridge (leading to "perforated corpotentorium") (0) absent, (1) present. The presence of an accessory anterior tentorial bridge is a characteristic feature of Dictyoptera (Hudson 1945; Klass and Eulitz 2007).

Neck (1) elongate, (0) short. Symplesiomorphy. Neck is elongate in *Teyia* and *Manipulator*. 74.

Paired lateral cervical sclerites (0) absent, (1) present. These sclerites are distinctly developed in like in most other groups of Polyneoptera (Walker 1931; Klass and Ehrmann 2003; Wieland 2006).

Mesoscutellum (0) not present as a defined part of the mesonotum, (1) present as a defined part of the mesonotum. Present in all Aienopteridae but missing in Mantophasmatodea and Grylloblattodea (Beutel and Gorb 2006), present also in all beetle-like cockroaches and some special forms such as Olidae. 20.

Forewings, length relative to length of hindwings (in unfolded condition) (0) of similar length or longer, (1) at most half as long as the hindwing. Short in most Alienopteridae (unique autapomorphy within Mesozoic cockroaches; a single collected Mesozoic (and none Palaeozoic) cockroach other than Alienopteridae (none Umenocoleidae) has reduced forewing length although forewing reduction is common in living cockroaches). This state is homoplasically common in Dermaptera (Giles 1963; Haas 2006), Phasmatodea (Bradler 2003: Fig. 16.1b) (and very common in e.g., beetles).

Wings covering the body entirely (1), partially (0). Related to need of total protection of body parts, likely only during some periods during the short visits of nests.

Forewing with secondary irregular venation in area RS ascending (1), venation regular (0). Synapomorphy with advanced cockroaches. Venation became regular during the Triassic in the *Volziablatta*-group and reversed to irregularity only at KPg (the present taxon is exceptional).

Pronotum strongly 3D (1) present, (0) absent. Autapomorhy related to protection against ants.

Pronotum widest at base (0) present, (1) absent. This state is ancestral for Umenocoleoidea and pronota widest in the center are present only in strongly derived taxa within Umenocoleoidea, but also in earliest proved Blattidae (*Balatronis*). In spite of this, pronotum widest at base is considered here for ancestral. 119.

Paranotalia (1) partially reduced, (0) fully developed. Paranotalia are plesiomorphically well developed (at the level of the order). Paranotalia are absent in advanced Umenocoleoidea and some other groups. 78.

FW venation (0) traceable, (1) absent. Plesiomorphy at the level of order. Tend to reduce with degree of elytrization. Venation is fully traceable in the present taxon.

Clavus (0) distinct, (1) indistinct. Plesiomorphy at the level of order. Tend to reduce with degree of elytrization. 88.

Clavus sigmoidal (1) present, (0) absent. Clavus is sigmoidal in *Umenocoleus* and *Umenopterix* and homoplasically in *Anaplecta* sp. from Mexican amber (Barna et all., submitted). 89.

Anal veins numerous (1), standard (0). Autapomorphy of the present taxon.

Legs (1) very short, (0) standard. Legs are of normal length in stem Blattidae (Šmídová and Lei 2017; Sendi and Azar 2017).

Legs extremely short (1) present, (0) absent. Autapomorhy (homoplasically) related to ant-habits.
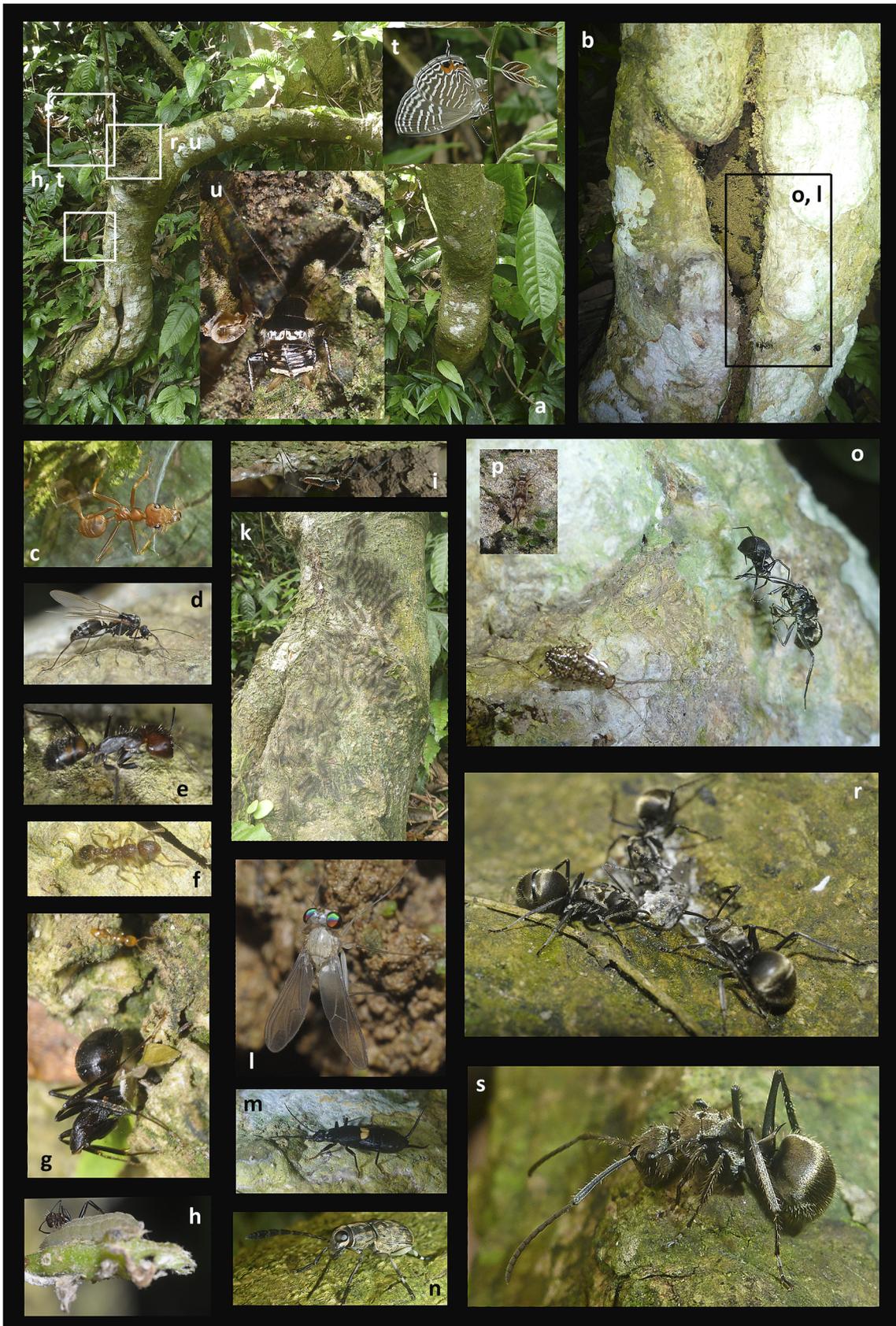
Fig. 4 *Polyrhachis illaudata* (Formicidae) ant nest with two blattid myrmecophilous cockroaches on *Diospyros nigrocortex* (Ebenaceae), tropical rainforest rudiments in Xishuanbanna Tropical Garden, Yunnan Province, China. (**a**) general view with *Magnolia henryi* (Magnoliaceae) in center and with location of arthropods indicated by rectangles; (**b**) detail on the nest main entrance with indication of the position of predatory myrmecophilous and at the same time myrmecomorph spider (Theridiidae - o) directly near the main entrance. (**c-h**), ant species occurring near the main entrance *Oecophylla smaragdina, Camponotus aner, Camponotus* sp., *Tetramorium* sp., *Camponotus* sp. 1; 2 with *Arhopala pseudocentaurus*; (**i**) spider with a web near main entrance; (**k**) mass of caterpillars (Lithosinae) with against ant-protecting spicules; (**l**) fly (Dolichopodidae) emerging from pupa within the atrium of the main entrance; (**m**) earwig *Labidura sp.* (Labiduridae); (**n**) beetle camouflaged from distance, ant-mimicking from medium distance and aposematic at contact (Anthribidae); (**o**) immature stage of a myrmecophilous cockroach (Blattidae); (**p**) bug; major nest ants feeding on damaged fungi-attacked ootheca of unknown, possibly this myrmecophilous cockroach, (**r**), (**s**) main ants; (**t**) myrmecophilous butterfly *Jamides alecto* (Lycaenidae) laing eggs on ant-nest branch; (**u**), second species immature stage of myrmecophilous cockroach (Blattidae). September 26–27, 2017, night and day

Number of tarsomeres (0) five, (1) less than five. Character disregarded herein due to standard occurrence of 5-segmented tarsi in all cockroaches including aleinopterids and standard occurrence of 4-segmented tarsi in damaged individuals (Vršanský 2002). 25.

Carination (1) reduced, (0) present. Most cockroaches plesiomorphically possess rich carination of legs. This character is autapomorphically reduced in Umenocoleoidea except *Jantaropterix*-group (Vršanský 2003). 97.

Carination (1) very rich, (0) standard. Autapomorphy of the present taxon – the high passive protection is unlikely the single cause for extensive carination. Probably related to moling in nests.

Discoidal spines ventromedially on proximal part of profemur (0) absent, (1) present ((0) absent, (1) present according to Bai et al. 2016). Absent in all non-dictyopteran Polyneoptera, all extant Blattodea, and in *Jersimantis, Burmantis,* and *Ambermantis* (Grimaldi 2003). Present in all extant Mantodea including *Chaeteessa* and *Metallyticus* (Wieland 2013). This character was meanwhile proved for *Santanmantis* (Hörnig et al. (2017) and also recorded in Mesozoic mantodeans (Xia et al. 2015; Li and Huang 2018a, b), Manipulatoridae and numerous other Mesozoic cockroaches of diverse families (such as Mesoblattinidae - Hörnig et al. 2017 corrected interpretation by Lee 2016 and also *Liberiblattina*). 49.

Orientation of ultimate tarsomere (0) not distinctly bent upwards, (1) distinctly bent upwards. Distinctly bent upwards in most Alienopteridae like in Mantophasmatodea (Beutel and Gorb 2008). Unclear in *Santanmantis* (reconstructed as bent by Hörnig et al. 2017).

Size of anterior terminal tibial spine of protibia (Tt1) relative to Tt1 spine of mesotibia (Grimaldi 2003: char. 17) (1) subequal, (0) distinctly smaller ((0) subequal, (1) distinctly

larger, (2) distinctly smaller according to Bai et al. 2016). The spines are subequal in size in most Polyneoptera including Blattodea, *Manipulator* (Vršanský and Bechly 2015: Fig. 1D) and *Alienopterus*. In the known Mantodea, including most fossil taxa (Grimaldi 2003), the protibial Tt1 is larger, only in *Chaeteessa* it is distinctly smaller (Wieland 2013: Fig. 278, arrow in Figs. 418–422). The character is unclear in *Santanmantis* (Grimaldi 2003; Hörnig et al. 2013). Also subequal in Mantophasmatodea and Grylloblattodea. The reverse polarity is used due to early derivation of *Vitisma* and *Jantaropterix* and ancestral outgroup *Liberiblattina* (with shorter protibial Tt1). It is shorter apparently also in blattid lineage. 23.

Posterior part of apical mesotibial margin with a notch and an accessory lobe adjoining it ventrad (0) absent, (1) present. This character is poorly documented across insects; detailed data are only available for Dictyoptera and selected members of some other polyneopteran orders (Klass et al. 2009). The presence of a notch and an accessory lobe is documented for *Chaeteessa* and *Metallyticus* (Klass et al. 2009) and for *Burmantis* (Grimaldi 2003: Fig. 9e). Some Alienopteridae show the notch. Absence is known for the blattodeans *Periplaneta* and *Ectobius* (Klass et al. 2009) and for the Orthoptera, Mantophasmatodea, and Grylloblattodea (Klass et al. 2009; Bai et al. 2016). The notch is apparently absent in early Blattidae and Olidae. 51.

Anterior terminal tibial spine of protibia (Tt1) placed on a projection of the apical tibial margin (formation of tibial claw) (0) present, (1) absent ((0) absent, (1) present according to Bai et al. 2016). In most Polyneoptera the Tt1 spines of the protibia (as far as Tt1 spines can be identified) are placed on a part of the apical tibial margin that projects not at all or only a little – the same condition as for the Tt1 of the meso- and metatibiae. This condition has also been documented for *Burmantis* and *Jersimantis* (Grimaldi 2003: Figs. 8, 14, 15) and is also present in *Alienopterus*. Only in all extant mantodeans (Wieland 2013) and at least in *Ambermantis, Burmantis* and *Jantarimantis* among the fossil ones (Grimaldi 2003: Fig. 3b, c) the part of the tibial apex that bears Tt1 forms an elongate projection; the projection and spine Tt1 form the tibial claw. Also indicated in *Santanmantis* (Grimaldi 2003; Hörnig et al. 2013, 2017). Due to the presence of this structure in certain Alienopteridae, basal umenocoleid *Vitisma* and also in stem Liberiblattinidae, the polarity is reversed. 47.

Euplantulae (0) absent, (1) present. Tarsal euplantulae are present in all studied Umenocoleoidea and also stem Liberiblattinidae, like in most groups of Polyneoptera (Beutel and Gorb 2006), but it is unclear whether they are present in *Manipulator* with slender tarsomeres (Vršanský and Bechly 2015: Fig. 1D and unpublished). Unclear in *Santanmantis, Jersimantis, Burmantis* and *Ambermantis*, but present in Jantarimantidae (Vršanský 2002) and Juramantidae.

Fig. 5 *Polyrhachis illaudata*
(Formicidae) ant nest with blattid
myrmecophilous cockroaches on
Lauroceratus zippeliana
(Rosaceae), tropical rainforest
rudiments in Xishuanbanna
Tropical Garden, Yunnan
Province, China. (**a**) An ant nest
with about 300 individuals; (**b**)
Dalpada oculata bug
(Pentatomidae); (**c**) immature
individual of a myrmecophilous
cockroach (Blattidae). September
26–27, 2017, night and day

This character greatly varies in cockroaches, and is absent in the present taxon. 26.

Arolium (0) absent, (1) present. Present in most cockroaches (absent only in some extremely derived Mesozoic and living cockroaches), in Mantophasmatodea (Beutel and Gorb 2008) and most other polyneopteran groups (Matsumura et al. 2015). Absent in extant Mantodea (Beutel and Gorb 2008; Wieland 2013), present in *Jantarimantis* (Vršanský 2002), *Santanmantis* (Grimaldi 2003; Grimaldi and Engel 2005: Fig. 7.98), *Juramantis, Jersimantis, Burmantis* and *Ambermantis*. 27.

Size of arolium (0) not enlarged and not pan-shaped, (1) enlarged and pan-shaped. Enlarged and pan-shaped in Mantophasmatodea and Phasmatodea-Timematidae (Beutel and Gorb 2008; Matsumura et al. 2015) and homoplasically in some Alienopteridae and Umenocoleidae. This character might be related to contact with ants, sometimes even regarded for related to their phoresis (referenced below). Absent in the present taxon. 28.

Arolium big (1) present, (0) absent. Autapomorhy of Alienopteridae. This charater become less obvious with the

immature stages (in early instar extremely well developed possibly due to phoresis (see analogical character and function in living ant nest parasitizing Attaphilidae – Gurney 1937). No big arolium is present in *Spinka*. 96.

Claw (1) asymmetrical, (0) symmetrical. Standard, suggesting no specific phoresis-related adaptations. 99.

Body (0) fat, (1) reduced. Plesiomorphy at the level of order. Body in N-fixing cockroaches loses fat (and *Blattabacterium*) only during changed diet such as in Nocticolidae (but surprisingly remain fixed in predatory Eadiidae and Raphidiomimidae, and in somewhat transitional form also in Manipulatoridae and Mantodea). Homoplasy of advanced pollen-feeding Alienopteridae. 109.

Cercus short (0) absent, (1) present. Cercus can be shortened also in other ant-related taxa such as in immatures of Cryptocercidae (the hidden state in adults results from fixation, and is not the living state) and Attaphilidae (**Scudder 1862**; Wheeler 1900). 111.

Cerci (0) present, (1) reduced. Cerci are reduced only in ant-related cockroaches.

Cerci: (0) segmented, (1) unsegmented. The cerci are segmented in all cockroaches except Attaphilidae, in Mantodea, Grylloblattodea and other polyneopteran groups. They are one-segmented in Mantophasmatodea, Orthoptera, Phasmatodea, Odonata, Dermaptera and Zoraptera (Klass and Ehrmann 2003; Mashimo et al. 2014). Segmented, although reduced in the present taxon.

Cercus extremely short (0) absent, (1) present. Autapomorphy. Homoplasic with of certain Alienopteridae. 112.

Styli with extremely long filaments (1) absent, (0) present. Autapomorphy.

Styli (1) present, (0) absent. Styli are plesiomorphically present in Caloblattinoidea, Blattulidae and Liberiblattinidae (Vršanský 2002, 2003) and are missing in all other studied Mesozoic-living cockroaches.

Whole body densely covered with hard sensilla (0) absent, (1) present. Autapomorphy (homoplasic with Alienopteridae, which have fine sensilla).

Hindwing vannus (0) large, (1) small ((0) small, (1) large according to Bai et al. 2016). Large in all Mesozoic cockroaches including stem Umenocoleidae, *Alienopterus* and most Alienopteridae. (small in derived genus *Mimimio)* like in most other groups of Polyneoptera with developed wings (Bai et al. 2016). Reverse polarity would work in earlier, Palaeozoic derivation of the family. 37.

Hindwing (HW) distinctly overlapping body (1) absent, (0) present. HW overlaps body in most cockroaches including stem Liberiblattinidae and also primitive Umenocoleoidea (and also the present taxon).

HW (1) fenestrate, (0) standard. HW is fenestrate in certain Umenocoleoidea (probably due to aerodynamics replacing the

forewings stroke) and in Diplopteridae (see Vršanský et al. 2016). 100.

Hindwing membrane (0) **transparent**, (1) dark. HW membrane is plesiomorphically transparent in fossil cockroaches (and very rarely locally dark in certain Alienopteridae). 86.

Forewing with coloration pattern maculated (0) present, (1) absent. All known representatives of the stem family Blattidae are maculated, thus this character is regarded for plesiomorphic at the level of stem Blattidae.

Bimodala

Šmídová, gen. n.

Type species. *Bimodala ohmkuhnlei* Šmídová, sp. n. described below, by monotypy.

Description. As for species.

Stratigraphical and chronological range. Indigenous to Cenomanian Myanmar amber.

Derivation of name. Stochastical combination of letter partially alluding to *bis* and *modus* (Latin for two states referring to two different types of sense organs). Gender feminine.
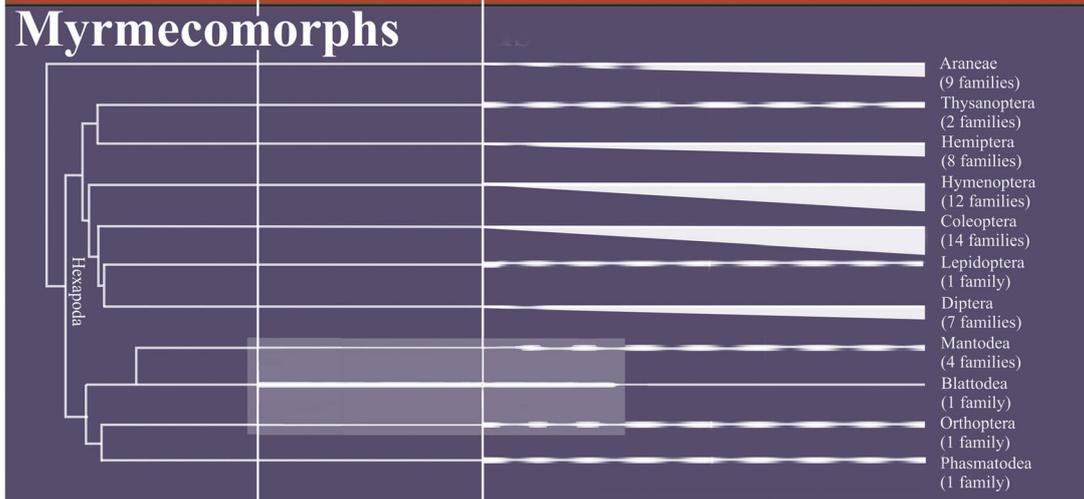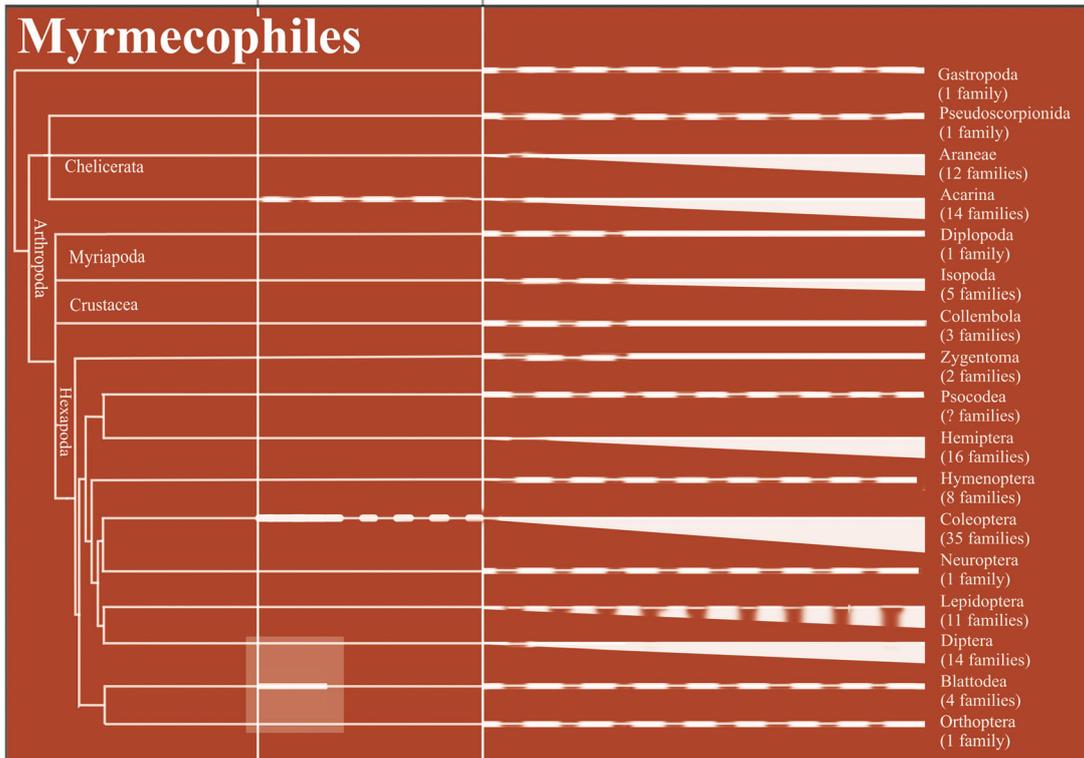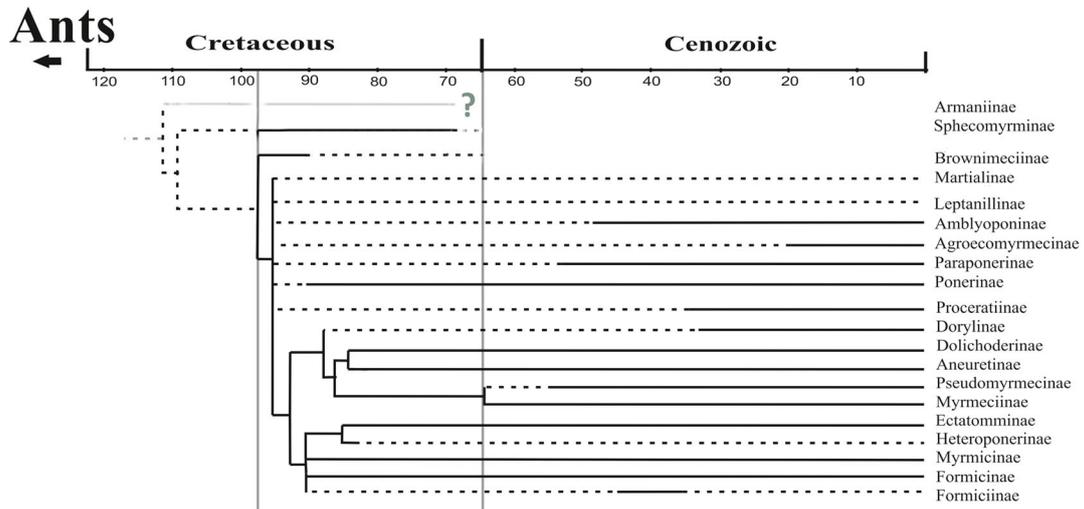
Differential diagnosis. Differs from closely related *Spinka* in the shape of pronotum and modality of hairs on it. The triangular-like shape of *Spinka* is more pronounced, with the narrower edges, meanwhile the edges of *Bimodala* are curvy and the apex of pronotum is orbicular. Also, the difference between the lengths of two types of hairs is greater in *Spinka*. Forewing CuP is sharply curved, clavus is somewhat sclerotized in contrast to standard in *Spinka*.

Systematic remarks. The new genus can be categorised within Blattidae on the basis of a close resemblance with *Spinka*, namely forewing with patchy coloration, reduced venation with greatly reduced Sc, great number of long hairs on the marginal part of the pronotum and thick femora and tibiae covered with lot of hairs. Its genitalia with asymmetrical genital plate and right genital hook suggest it is a male and confirms the placement. The irregular venation with great distances among veins in medial area, then compressed veins in the cubital area and sclerotisation of clavus show tendency further expressed in the Olidae Vršanský et Wang, 2017 (see also Li and Huang 2018a).

Bimodala ohmkuhnlei

Šmídová, sp. n. (Figs.1c, 2 b, 3b, c)

Description (based on male adult holotype herein; description of immatures below): The total body length (anterior edge of the pronotum-posterior edge of the wing) 10.9 mm, width 5.6 mm. Wing length 8.40 mm. The width of the left/ right wing 3.75/ 2.80 mm (as preserved), the left wing overlaps the right wing. Pronotum subtriangular, length/

Ants

Cretaceous   Cenozoic

120 110 100 90 80 70 60 50 40 30 20 10

Armaniinae
Sphecomyrminae
?

Brownimeciinae
Martialinae
Leptanillinae
Amblyoponinae
Agroecomyrmecinae
Paraponerinae
Ponerinae
Proceratiinae
Dorylinae
Dolichoderinae
Aneuretinae
Pseudomyrmecinae
Myrmeciinae
Ectatomminae
Heteroponerinae
Myrmicinae
Formicinae
Formiciinae

Myrmecophiles

Arthropoda

Chelicerata

Gastropoda
(1 family)
Pseudoscorpionida
(1 family)
Araneae
(12 families)
Acarina
(14 families)
Diplopoda
(1 family)

Myriapoda

Crustacea

Isopoda
(5 families)
Collembola
(3 families)
Zygentoma
(2 families)
Psocodea
(? families)
Hemiptera
(16 families)
Hymenoptera
(8 families)
Coleoptera
(35 families)
Neuroptera
(1 family)
Lepidoptera
(11 families)
Diptera
(14 families)
Blattodea
(4 families)
Orthoptera
(1 family)

Hexapoda

Myrmecomorphs

Hexapoda

Araneae
(9 families)
Thysanoptera
(2 families)
Hemiptera
(8 families)
Hymenoptera
(12 families)
Coleoptera
(14 families)
Lepidoptera
(1 family)
Diptera
(7 families)
Mantodea
(4 families)
Blattodea
(1 family)
Orthoptera
(1 family)
Phasmatodea
(1 family)

Fig. 6 Phylogenetic tree of ants and review of myrmecophiles and myrmecomorphs. Pale rectangles show present discoveries. Solid lines represent confirmed fossil records of all three groups (EDNA fossil insect, and Fossilworks (for non-insects) databases both active September 09, 2017; http://edna.palass-hosting.org; http://fossilworks. org), dotted lines expected occurrences (dotted line falling into solid one means extinction and independent repeated origin in the same order), grey are unconfirmed "ants". Phylogenetic tree is after Ward (2007); Brady et al. (2014); Barden and Grimaldi (2016) with modified Proceratiinae, Dolichoderinae, Ectatomminae and Formiciinae). Myrmecomorphy based on list (McIver and Stonedahl 1993), myrmecophili (Witte et al. 2002, 2008; Hölldobler and Wilson 1990)). Except for putative evidence of beetles (Yamamoto et al. 2016; Poinar and Fanti 2016), pre-K/Pg occurrence of any ant-related taxon is unconfirmed (mites expected)

width 2.45/ 4.15 mm. It has dark area in the central part, around 0.5 mm from the anterior edge and almost reaching the edges on the lateral sides. The sensilla chaetica are of two sizes; 0.40 and 0.05 mm long. The short sensilla stem from the dark dot (ø = 0.017 mm) and cover the whole surface of pronotum. The density of dots (and therefore sensilla) is ~120/ mm². The long sensilla are more sporadic and grow predominantly in the proximity of the edges of pronotum.

Wings wider in the posterior part. The C covered with setae, reaching 8/ 9 of wing length. 13 R, the anteriormost and the posteriormost branched, all of them with intercalaries. Min. 6 M, simple, branched anteriorly. Min. 6 CuA, bifurcated anteriorly, with intercalaries. CuP curved acutely. Dark, rough clavus covered with dots (ø 0.05 mm) indicating position of A. A simple. The area between veins and veins themselves has numerous sensilla chaetica. The wings have dark irregular maculas, ranging from 0.16 mm to 0.63 mm in diameter.

The forefemora with two rows of spinules. The left forecoxa with coloration, length/ width 1.56/ 0.78 mm. Femur 2.1/ 0.34 mm. Tibia −/ 0.22 mm. The right forecoxa 1.75/ 0.66 mm. Femur 2.20/ 0.25 mm. Tibia with 7 spurs, 0.53/ 0.22 mm. The left midleg femur 2.5 mm long. Tibia with 14 spurs, 1.72/ 0.5 mm. First tarsomere 1.19 mm long. The right midleg coxa 2.81/ 0.84 mm. Femur 2.66/ 0.34 mm. Tibia with 14 spurs, 1.40/ 0.44 mm. The first tarsomere 1.16 mm long. The left hindleg femur 2.50/ 0.78 mm. Tibia 3.13/ 0.34 mm. The right hindfemur 2.53/ 0.75 mm. Tibia with 20 spurs, 2.91/ 0.31 mm.

Each leg segment rich in hairs. Each tarsomere has 4 spinules on its posterior side. Femora with terminal spike and two lines of hairs growing more densely than in the rest of their surface. Spurs are usually around 0.8 mm long, with comb-like structure on the proximal side, more frequent in the posterior part of tibia. The spur length increases posteriorly. The arolium with symmetrical claws, claw 0.014 mm long. Trochanteri well-pronounced.

The length between terminalia and posterior end of the wing 2 mm. The width of cercus 0.14 mm. Cercomeres globular with long hairs. The posteriormost preserved cercomere

length 0.16 mm, the subsequent cercomeres length 0.18, 0.14, 0.13, 0.09, 0.07 mm. The right phallomere with genital hook of width 0.14 mm.

Holotype. Complete adult male. NIGP154996. Deposited in Nanjing institute for Geology and Paleontology.

Type locality. Hukawng valley mines, Myanmar.

Type horizon. Cenomanian Upper Cretaceous.

Character of preservation. One adult male and putatively one large (?preimaginal) immature stage, both preserved in transparent (with debris and particles) amber piece with yellow hue. Head missing, parts of tentorium left. Pronotum complete, with all the hairs and rims with no visible damage. It is bent in 45° to the left in respect of the body axis. Wings are cut in the posterior and latero-posterior part, in the shape resembling a bite (ø 1.4 mm) from a predator. A costal area of the wing is bent downwards. Thoracical ventrites missing, forelegs consist of: coxa, trochanter, femur and tibia. Left midleg with trochanter, femur, tibia, first tarsomere and small part of the second tarsomere. The right midleg with femur, tibia and first two tarsomeres. The right hindleg with coxa, trochanter, femur, tibia, the first, the second, part of the third and the fifth tarsomere, and arolium. The left hindleg with posterior part of coxa, trochanter, femur and tibia. Abdominal part consisting of 6 damaged sternites. Incomplete cercus with 6 cercomeres of one cercus and right phallomere detached.

LV 777 (the specimen is putatively categorized within this species on the basis of larger size, absence of body coloration and termites as syninclusions). Large (7.9 mm long, 5.2 mm wide) wingless roach with dorsal and lateral sides of its body covered by long setae, short antennae and shorter legs. Head 1.4 mm long, 1.37 mm wide, completely covered with pronotum dorsally covered by long setae, eyes (0.74 long, 0.14 mm wide) positioned laterally away from each other, antennal pits distinct, maxillary palps distinct but their length does not reach the length of the head. Antennae short (around 0.098 mm wide). Mandible width 0.93 mm. Palpomeres ? / 0.361/ 0.373/ 0.218 mm long. Pronotum 2.58 mm long, 4.06 mm wide, its surface covered by long distinct setae. Mesonotum 0.86 mm long, 5.1 mm wide, covered by long setae, most distinct on lateral sides, wingless. Metanotum 1.06 mm long, 5.1 mm wide, covered by long setae, most distinct on lateral sides, wingless. Abdomen short ovoid, w = 0.55 mm, dorsally covered by long setae. Cerci 0.64 mm long, central cercomeres (totally 1–10) widest (0.17 mm). Setae on cerci not many but long, distinctly exceeding both length and width of cercomeres. Styli massive, with long and strong setae, segmented but segmentation in many parts poorly visible, right stylus 4 segmented, segments seem to have always bigger length than width. Both are terminated by a very small spike. Legs rather short with thick tibiae bearing thick spines, all tarsi terminated by pair of hooked claws distant ca. 0.2 mm. Right forecoxa l=

1.5 mm, w = 0.79 mm, left forecoxa not measurable. Forefemora with anteroventral and posteroventral rows of small spines and a large thick anteroterminal spine (0.27 mm long). Left forefemur l = 1.36 mm, w = 0.18 mm; right forefemur l = 1.67 mm, w = 0.34 mm. Middle coxa only right one visible (l = 1.49 mm, w = 0.71 mm). Middle femora with almost parallel ventral and dorsal margin, setae distributed mostly around ventral margin, prominent thick dorsoterminal spine present. Left mid femur l = 1.8 mm, w = 0.6 mm; right mid femur l = 1.36 mm, w = 0.49 mm. Middle tibiae widening in basal third but keeping more or less same width in the rest of their length; covered by shorter setae and bearing several long spikes, most of them positioned at dorsal edge and terminally. Left middle tibia l = 1.13 mm, w = 0.31 mm. Hind right coxae large, l = 1.6 mm, w = 0.72 mm. Hind femora with convex dorsal side and sinusoid ventral side, longer thick setae along ventral and dorsal margin. Left hind femur l = 1.94 mm, w = 0.63 mm; right hind femur l = 2.1 mm, w = 0.56 mm. Hind tibiae covered with medium sized setae, ventral margin with few thin spines, dorsal margin with several long thick spines, at distal end five large thick terminal spines (0.44 mm). Left tibia l = 2.48 mm, w = 0.37 mm. Hind tarsi covered by medium-sized setae. Right hind tarsus l = 2.06 mm (1st tarsomere l = 1.28 mm, 2nd tarsomere l = 0.33 mm, 3rd tarsomere l = 0.16 mm, 4th + 5th tarsomere l = 0.38 mm).

Derivation of name. After Dr. Dr. Christoph Öhm-Kühnle, a kind donator of Burmite specimens.

Anenev

Vršanský, Oružinský, Sendi, Choufani, El-Halabi et Azar, gen. n.

Type species. *Anenev asrev* Vršanský, Oružinský, Sendi, Choufani, El-Halabi et Azar, sp. n., by monotypy.

Description. As for species.

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

Diagnosis. The present taxon can be cathegorized within the family Blattidae on the basis of close relation with *Balatronis* Šmídová et Lei, 2016 (Lebanese and Myanmar ambers; aposematic coloration, styli, long cerci with numerous segments and short sensilla), but is autapomorphic in extremely wide nota and elongated head and extremities (homoplastic with Caloblattinoidea).

Anenev asrev

Vršanský, Oružinský, Sendi, Choufani, El-Halabi et Azar, sp. n. (Fig. 1f).

Description. Preimaginal instar of the immature individual. Head completely concealed under pronotum, heavily deformed with distinct equilateral triangular shape

with concave profile, approximately 1.30 mm each side. Left compound eye large: 0.31/ 0.41 mm. Antenna filiform, with at least 13 segments, approximately 0.04/ 0.03 mm wide, densely covered by sensilla chaetica 0.009 mm long. Left maxillary palp 0.83 mm long (segments 1–4 ca. 0.34/ 0.5; 0.16/ 0.05; 0.15/ 0.05; 0.18/ 0.08 mm) and densely covered by sensilla chaetica 0.026 mm long, larger than those on antenna. Body wide, spherical with sophisticated coloration pattern. Pronutum length/ width 0.79/ 2.26 mm (mesothorax 0.68/ 1.58 mm; 1/2.44 mm; methathorax 1/ 2.44 mm; abdomen 0.75/ 1.86 mm). Fore- and hind wing buds slightly elongated without visible venation, transparent and densely covered with chaetica (0.07 mm long) on sides. Left forewing 1.12/ 0.49 mm, right forewing 1.16/ 0.51 mm, left hind wing 1.14/ 0.54 mm and right hindwing 1.18/ 0.47 mm. Extremities cursorial, robust, with strong spurs alternated by smaller chaetica. Femoral spur extremely well developed, very long, strong and curved. Foreleft tibia 1.06/ 0.11 mm, foreright femur 0.98/ 0.21 mm, left tarsus fragment on 0.03 mm width. Mid right femur 0.56/ 0.16 mm, mid tibia fragment 0.10 mm. Mid right trochanter 0.42/ 0.31 mm tibia 1.12/ 0.08 mm, mid left femur 0.90/ 0.18 mm, mid left tarsus 0.03 mm wide. Right hind leg: coxa 1.08/ 0.4 mm, trochanter 0.2/0.16 mm, femur 0.98/ 0.21 mm, tibia 1.06/ 0.11 mm, tarsus fragment 0.03 mm wide. Left hind leg: coxa 0.9/ 0.4 mm, trochanter 0.42/ 0.29 mm, femur 0.90/ 0.18 mm, tibia 1.12/ 0.08 mm, tarsus fragment 0.03 mm wide. Robust cerci without visible segmentation, but densely covered with medium length tiny chaeta. Left cercus 1.02/ 0.12 mm; right 0.7/ 0.14 mm; left stylus 0.12/ 0.02 mm; right 0.12/ 0.02 mm.

Holotype. LU BL3BC. Deposited in the Lebanese University.

Type locality. Zarzar lake, Bloudane area, Syria.

Type horizon. Lower Cretaceous.

Character of preservation. One complete preimaginal nymph.

Derivation of name. After **Alliance Short Range Enforcement Vessel.** An anagram with meaning "venena versa "(Latin for reversed poison) – alluding to the species representing the earliest aposematic and likely a toxic insect.

Discussion

Morphological evidence for myrmecophily in the present fossils includes small size combined with unique, extremely dense setation of the entire surface of the body. Life in ant-nests also tends to be associated with the reduction of all appendages (also shortened legs while their tarsi are paradoxically standard), especially with the reduction and invagination of cerci and shortening of the antennae, which is also

visible in the fossils. Notable morphological structures in myrmecophilous roaches are enlarged arolia, which are an adaptation for clinging to hosts in modern groups, like *Attaphila* (Gurney 1937). While arolia are large in ant-mimicking Alienopteridae, they are nearly or entirely reduced in the new taxa described here. Therefore, phoresis seems to have originated later in their evolutionary history, along with further miniaturization. Fossorial forelegs are also an adaptation for making tunnels in decaying wood, most probably directly in nests. All formally described living myrmecophile cockroaches have at least partially reduced wings (Bell et al. 2007), while wings are fully developed in newly described *Spinka fussa*. Apparently in this primitive myrmecophile, the wings would serve as protection, but this also suggests a free adult life style (supported with absence of fat body and thus probably absent feeding of adult). The coloration suggests camouflage for life on associated bark (a lifestyle recorded in living undescribed winged Blattidae, but without this coloration (Inui et al. 2009)), similarly as some other Burmite cockroaches (Podstrelená and Sendi 2018). Paradoxical combination of a plant camouflage and insect-insect mimicry (or an aposematic signal) in a single individual also occurs in several living species of the family Membracidae. The fossorial legs of this type are known in an undescribed woodborer from the same locality, supporting bark nest location. A crystalline mineral particle on the smallest larva contributing to its camouflage is thus obscure and would rather indicate a ground nest. The large, protective forewings have hair and possess a transparent membrane, suggesting that these myrmecophilous cockroaches could move freely between different ant nests by active flight. This is supported by lack of the wide fat body of the adult male suggesting an exclusively dispersal function of this stage. It is interesting that the larvae possess rudiments of aposematic coloration, known in a single closely related extinct genus, with *Balatronis cretacea* Šmídová et Lei, 2017 from Myanmar amber (Šmídová and Lei 2017) and *B. lebanensis* from Lebanese amber (Sendi and Azar 2017), but common in descendant lineages of Blattidae - *Euzosteria, Leptozosteria, Polyzosteria* and even in the direct descendant *Neostylopyga* (Capinera 2008). It is very probable that this pattern in an ant-associated but not ant-mimicking species evolved as a response to (yet unknown) ant-predators. In fact, this aposematic coloration pattern today is associated with the ant-escaping alert allomone 6-methyl-5-hepten-2-one (alarm pheromone for ants and defence pheromone for *Neostylopyga rhombifolia*) (Capinera 2008). While *B. cretacea* is one of the most common cockroaches in Myanmar amber, the coloration in the present species is matte and nearly impossible to discern. We interpret this darkening as a consequence of a life spent inside nests, where contrast coloration became

unnecessary. Paradoxically, wood-inhabiting species (and those found within wood) usually do not lose pigment and usually have poisons in the cuticle that serve as defence (see benzoquinone in *Diploptera* resulting in teneral females exclusively being capable of fertilization (Eisner 1958)).

Supporting evidence for myrmecophily includes dirt camouflage, also found in the same deposit for other groups (antlions, bugs etc.), as a defence against ants (Wang et al. 2016). The present species *Spinka fussa* shows extensive camouflage with sediment and its own feces (covering all the dorsal part of the abdomen in specimen SNHN BU-235 and half of the ventral side and dorsal terminal part of specimen SNM Z 38601, and part of the dorsal side in the minute SNM Z 38604), present in all three larvae and the adult. The cockroach feces are black (in adult transparent), and unlike all the known studied fossil cockroaches it is sticky and viscous, containing a diversity of particle types. The feces wrap around the body, forms a film on the dorsal part of the abdomen and dries (Fig. 1a2). In adults this camouflage is visible from the ventral side, but unlike in larvae, it is entirely transparent. Additionally the adult male lacks the fat body characteristic for all cockroaches except *Nocticola* (Lo et al. 2007), suggesting lack of feeding of the adult stage as a similar diet would also be reflected in larvae with fat bodies. The body's dorsal surface is only covered with the wings. There might be film covering the ventral part of the body of the larvae (Fig. 1b1). In some specimens there is a distinct wide mass, which probably formed in a *post-mortem* defecation (Fig 1b4). It appears that some particles were eaten, not necessarily for digestion but for this "active" camouflage through their incorporation into the feces. The "clean" (dark, but entirely dry) dirt is present only in the smallest specimen, which includes debris, one small pale mineral particle and also dried fecal scales. The feces themselves are structured, containing small globular parts and also larger unidentified spheres (interesting anyway as living or fossil cockroach diets do not contain such particles, except for Nocticolidae, where they represent fungal spores - some of these fungi were proved to be pathogenic for insects (Behie et al. 2012; and a similar, cyanobacterian-based diet is recently recorded in caves – Smrž et al. 2013). To find evidence for these materials perhaps consumed by the ants themselves is impossible.

Supportive indirect evidence for myrmecophily can be found in the many syninclusions of ants and ant-mimics. SNM Z 38604 and NIGP154996 are too small (15/0.4; 15/10 mm) to include any other insect; SNM Z 38600 (10/8 mm) contains numerous unidentifiable insects as well as ant-nests collembolans. SNM Z 38601 (21/14 mm) contains an undetermined ant-mimicking alienopterid cockroach and SMNS BU-235 contains a *Haidomyrmex* ant adult, and Cepheniini (Staphylinidae: Scydmaeninae) beetles, which are occasionally found in ant nests, feeding on mites. Three semi-hexagonal

fecal droplets are also preserved in this sample, belonging to umenocoleid/ alienopterid cockroaches. Termites have easily identifiable hexagonal feces. This evidence, taken together, suggests that the resin flowed directly onto the ant-nest and/ or associated parts on the bark. In this respect, the syninclusions of the ant-mimics are even more significant than the ants themselves, as myrmecomorphy is effective only within ant nests or in close proximity. All five specimens are preserved in yellowish, transparent amber. The common occurrence of termites and ants in these inclusions further point to an early ecological relationship between these two eusocial groups, both found so commonly in modern rainforests.

While all *Spinka* specimens can be categorized with high degree of confidence within a single species based on autapomorphies (dense setation, specific aposematic coloration, huge specific eyes, shortened antenna and specifically reduced cerci and styli; dirt and feces camouflage) it is remarkable that each of the stages somewhat resemble general morphotypes of diverse living eusocial insect nest-associated parasitic cockroaches. While the adult is unique, the earliest preserved larva resembles *Attaphila* (Attaphilidae, but without arolia), while the latest stage resemble unrelated (Corydiidae) *Tivia termitium*. The medium larva closely resembles *Balatronis* (Blattidae, a specimen with a distinct aposematic pattern – paradoxically the dirt camouflage might have originally aimed to cover this color pattern). This refers to low specialization of this ancestral nest parasite.

An important ecological inference from the presence of myrmecophiles in the inclusions is that this type of combination is usually only known from more established ecosystems. Myrmecophilous lineages tend to be extremely rare (in contrast to myrmecophilous taxa, which are numerous) in modern faunas. Although there is low diversity of myrmecophiles (5 specimens of 1 species) in the inclusions, this is a group that tends to have lower potential for preservation in the fossil record. Due to eight myrmecophile lineages (the present one, undescribed Blattidae, *Attaphila*, *Nocticola*, *Myrmecoblatta, Myrmeblatta, Tivia*, *Pseudoanaplectina*) however, one can assume that the original diversity of myrmecophiles was high also because unrelated lineages (families Blattidae, Nocticolidae, Attaphilidae, Ectobiidae and Corydiidae) were able to avoid the defenses of the ants (against nest parasites). This is in sharp contrast to the very common myrmecomorphs, which suggest that ants were already very effective at protecting the nest against visually hunting predators. These notable differences in morphology and behaviour depend on whether an insect is primarily found outside or inside a nest and there are even documented examples of insects using ants inside the nest to get a safe passage out of the nest (Lachaud et al. 2015; Nehring et al. 2016).

Furthermore, the bark camouflage found on this new species might suggest that the host nests were located in the vicinity of tree trunks (such as *C. difformis* ant with cockroach

Pseudoanaplectiva yumotoi which are known to inhabit the domatia of epiphytic ferns). The preserved dirt camouflage suggests quite sophisticated behaviours in these early parasitic cockroaches. In addition, the number of known inclusions suggests that myrmecophilous cockroaches were abundant in the Myanmar amber forest, which likely existed for more than 20 Ma. Living *P. yumotoi* represent 20% ($n = 7279$) of all other insects in ant nests (Roth 1995), contrasting with less than 1% of ladybirds (Orivel et al. 2004) or about 3% each of any myrmecophilous species per colony (Witte et al. 2008). It is interesting to note that the same nests can include approximately 1% of another undescribed Blattidae (the only myrmecophilous representative of the family). This specimen is similar, but unrelated to the one recorded as a fossil (differing from *P. yumotoi* in lacking ant cuticular hydrocarbons) (Inui et al. 2009). Nevertheless, these blattid cockroaches were localized mainly on the outer edges of nests and sometimes outside them, escaping ant attacks by keeping away from the center of the nest and fleeing quickly (Inui et al. 2009). This lifestyle is consistent with the habitus and coloration of this new extinct species.

It is natural that cockroaches, which lived in areas of the future ant nests before, become immediately their commensals and/or parasites (taking into consideration the low level of internal ant protection). It could appear obscure as they belong to Blattidae absent in earlier sedimentary record. On the other hand, Blattidae are present in Syrian and Lebanese ambers, whose might originate from the pre-ant time period.

The roles that commensals and parasites play in host nests are diverse and include everything from simple cleaning functions and pathogen transfer, which can influence population control, through the exchange of genetic information (Gasmi et al. 2015) and the transfer of symbionts (common in termites). Attaphilidae possess nest-specific cues and are sometimes regarded as symbiotic (Pierce et al. 2002), while feeding either on detritus and/or fungi inside the nest, but they are also known to be fed by ant soldiers. The lack of an aggressive response in *Crematogaster difformis* Smith, 1857 workers (no biting and only 20% mandibular opening following antennation unlike 10–40% fatal biting) also suggests that workers identify these cockroaches as nest mates, or at least do not recognize them as intruders. Nevertheless, cockroaches might escape (Inui et al. 2009), avoid inspection and hide (Blanke et al. 2012), or cover themselves with dirt and/or their own feces (the present example). Previous work has shown that nearly half (47%) of tested workers showed aggressive behavior toward dead cockroaches (included extra-colony individuals) (Inui et al. 2009). Furthermore, modern semisocial primitive lineages of facultative ant-nests inhabitants, like *Cryptocercus,* cannot be considered parasitic at all (they are also very large compared to the ants, with sizes up to 40 mm), but will be attacked by ants when dead (observed in

C. relictus, 10,06,1997 in UNESCO BR Kedrovaja Paď Reserve, Russia; and *Cryptocercus*, 10, 06, 2006 UNESCO BR Baotianman, China). Finally, one of the decaying specimens is covered with possible mycelia of entomoparasitic *Entomopthora* ("bubbles" at Figs. 1b1-2), suggesting early fungal parasitism among nest-inhabiting insects.

Systematically, the new species and genera can be categorized within the cockroach family Blattidae (a single genus *Balatronis* in the fossil record) on the basis of a close relationship with already categorized members of the genus *Neostylopyga*. Numerous, at least 10 instar stages (?;?; 2.1;?;?;?; 5.3; 5.8;?;?, 7 mm adult (Fig. 2)) support this categorization (known fossil species have a low number of instars). *Spinka fussa* sp. n. and *Bimodala ohmkuhnlei* sp. n. are diagnostic for Blattidae in forewing, cercus and styli morphology. They differ from the closely related genus *Balatronis* Šmídová et Lei, 2017 known from the same deposit of Myanmar amber and also from the Lebanese amber in being densely covered with trichia, with significantly smaller size and in a higher number of instars. It is interesting that the same habitus was reached by representatives of the modern, unrelated myrmecophilous family Attaphilidae Bolívar, 1901 (*Attaphila* Wheeler, 1900) with 7 species in Texas, Central and South America (without fossil record). Concurrently, the same habit was also reached by the unrelated termitophilous *Tivia termitium* (Shelford, 1810) of the family Corydiidae Saussure, 1864 (genus in Africa and Near East; Australia and Indonesia). Although this species is wingless, it is remarkable that related winged and non-myrmecophilous *T. simulatrix* Walker, 1869 (holotype BNHM 876455; female BNHM 876456 small and oval pronotum) has the same habitus as the present adult including the punctuated coloration, but without the dense setation. The associated stem Blattidae new genus and species from Syrian amber is also described.

Origin calibrations Disregarding the specific lifestyle and ecology, present formal descriptions of cockroaches are significant systematically because fossil Blattidae (Cenomanian 98 Ma - Recent) were described only in 2017 (*Periplaneta succinica* Shelford, 1910, a possible Blattidae, was Cenozoic and destroyed in WWII) (Šmídová and Lei 2017; Sendi and Azar 2017). The family split from the Mesoblattinidae/ Ectobiidae lineage (fossil (Wei and Ren 2013) and molecular (Legendre et al. 2015) evidences) along with most living families after J/K (127 Ma) (Vršanský et al. 2017). Its earlier derivation revealed by strong molecular data (Wang et al. 2017) was based on extrapolation of the origin of fossil taxa and is unsupported by fossils (Evangelista et al. 2017). The divergence of cockroach clades with myrmecophiles is the basalmost divergence of major living lineages, either at J/K or hypothetically J1 (see Huber et al. 2003); split of the Ectobiidae/ Blattidae ancestors Mesoblattinidae from corydioid lineage) but not earlier.

Estimated ages for ant diversifications also need clarification, because as in the case of cockroaches, molecular analysis reveal a slightly earlier (139–158 Ma compared with 98 confirmed and considered here) time of origin (Moreau and Bell 2013) and a study based on fossils also expected insignificantly earlier origination time (110 Ma) (Barden and Grimaldi 2016). The earlier than 98 Ma fossil record of ants is nevertheless, very improbable as there are more than 400,000 fossil insect samples from the Early Cretaceous including about 10,000 samples from the Lebanese amber. None (including unpublished material) contains a proved ant. The extrapolation of their origin significantly deeper into history is also obscure as the most primitive "ants", the Armaniidae are also being disregarded because ants and Sphecomyrminae occur only from the Cenomanian (Barden and Grimaldi 2016). The latest reviews (Perrichot et al. 2016; Barden 2017) also did not validate earlier occurrences. Although most of the earliest (Myanmar and Maritime ambers) ants were solitary or living in small groups (Perrichot et al. 2016), rare aggregations of workers suggest comparatively large groups, but on their own they are not decisive for taxa in huge "cities" of crown ants (Barden and Grimaldi 2016). Therefore the discovery of the present parasites only able to live in big nests is far from banal.

To summarize (see Fig. 6), ants either originated earlier in the Early Cretaceous (at 127 Ma diversification point) and were extremely rare prior to their earliest record in the Cenomanian ambers (Myanmar; Charente Maritime) or the ant nests were highly sophisticated in structure early in their evolutionary history. This is exemplified by the discovery presented here of abundant ant-nest parasitizing (and ant and myrmecomorph syninclusions) cockroaches from Myanmar amber and recently reported ant-nest parasitizing rove-beetles (Yamamoto et al. 2016). These cockroaches were highly specialized in morphology (dense setation, reduced length of appendages) and dirt camouflage (including own-fecal material) and bearing the rudiments of aposematic coloration (the same associated with the presence of ant escape alert allomone in their living relative *Neostylopyga*). Fully winged adults suggest an active lifestyle in the adult stage and bark coloration (along with frequent deposition) probably indicates these ant nest were preserved directly on the stems of source trees or under their bark. These taxa additionally produced a new family, Olidae (Vršanský and Wang 2017).

Author's contribution We collected the material (S.E., P.M., D.A., L.J., W.H., B.T.); took the photographs (S.E., P.M., P.B., L.Š., P.V., X.R., X.L.), produced drawings (L.Š., P.B., P.V.), CT (P.B., L.Š., H.S.), descriptions and comparison (P.V., L.Š., P.B., H.S.); observations in the living ecosystem (P.V., T.S., W.D., T.B., X.S.); designed research (P.V.), wrote and edited the paper (P. V., G.B., D.A.) with contributions from all authors.

Compliance with ethical standards

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

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