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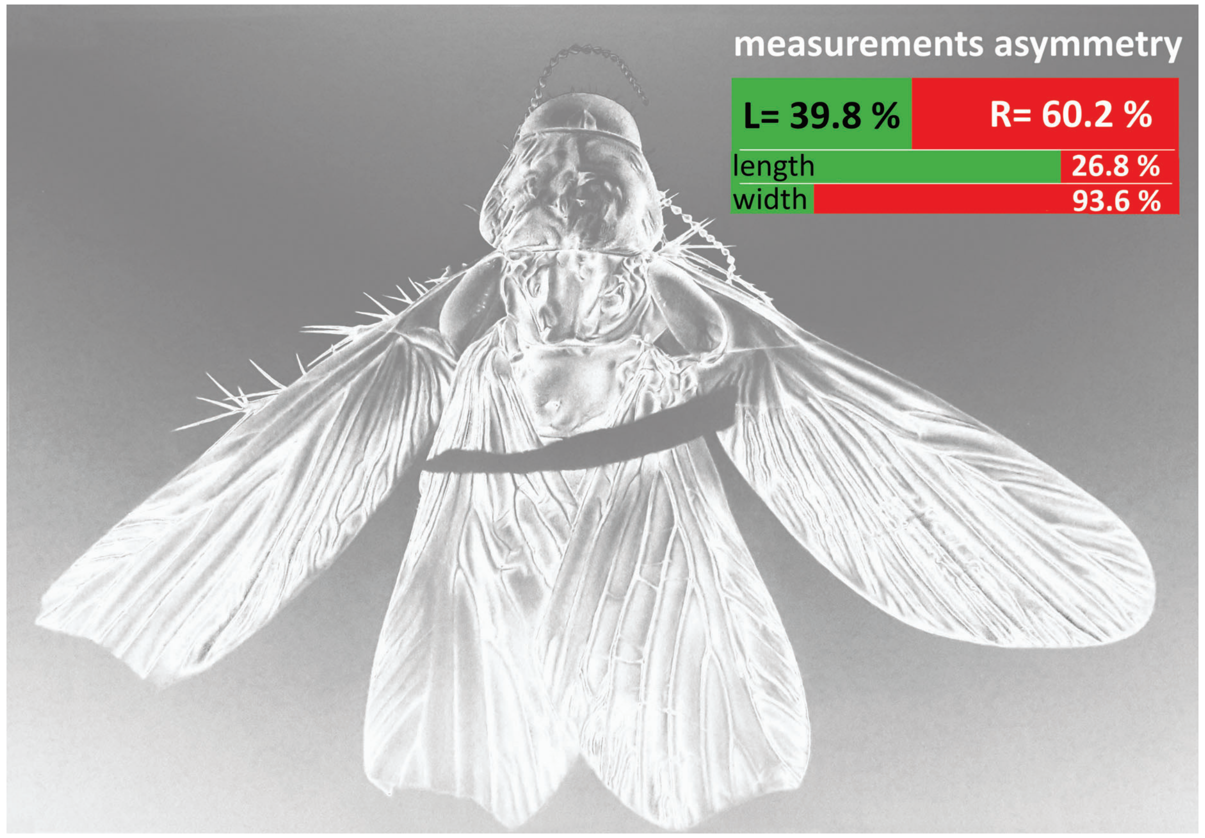

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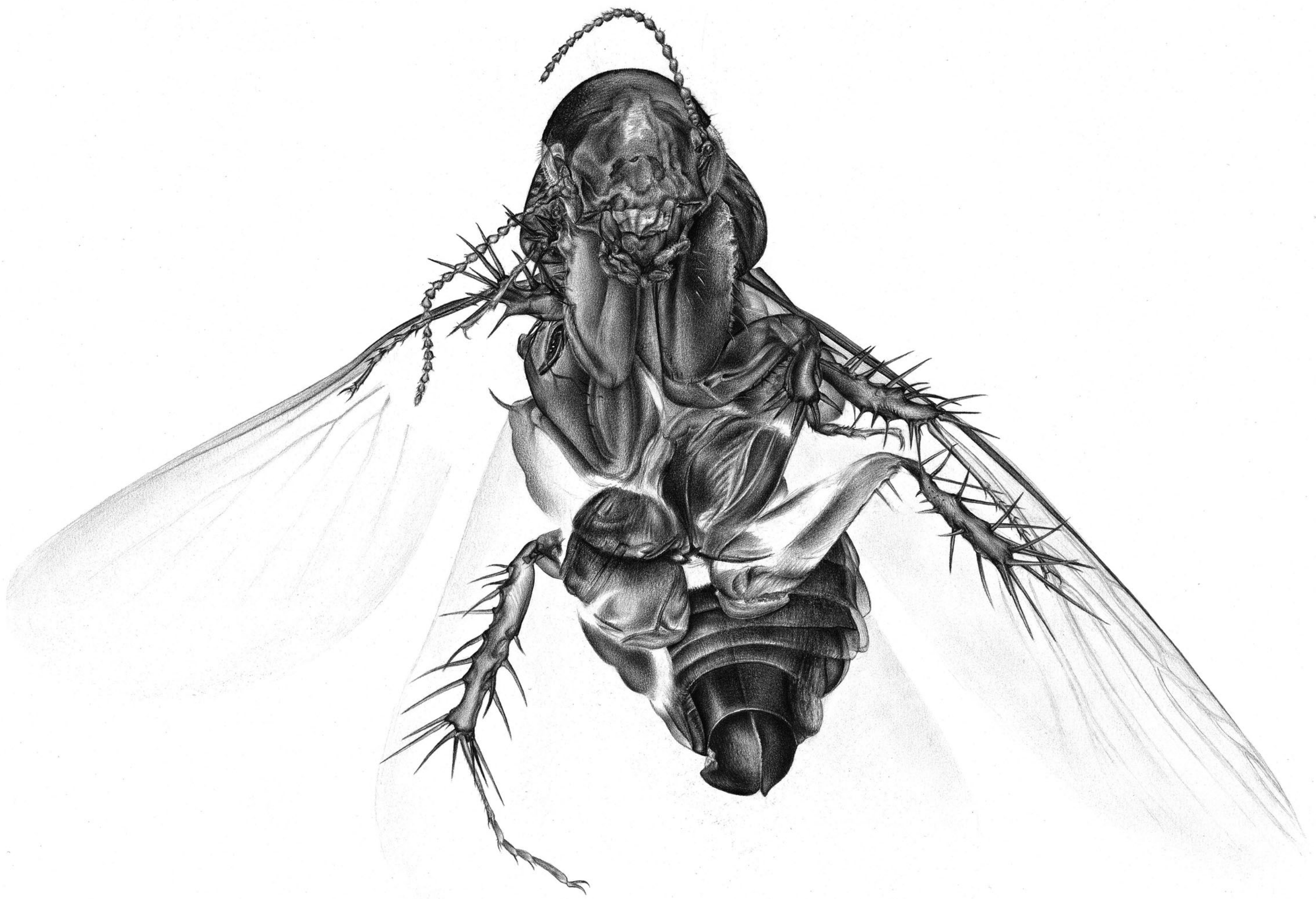

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EARLY WOOD-BORING ‘MOLE ROACH’ REVEALS EUSOCIALITY “MISSING RING”

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Front cover:
Dinosaur aged wood boring roach *Pabuonqed eulna* Vršanský, sp. n.
Holotype SNM Z 38683 (family type). Deposited in Slovak National Museum in Bratislava.

EARLY WOOD-BORING ‘MOLE ROACH’ REVEALS EUSOCIALITY “MISSING RING”

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The earliest eusociality of cockroaches is conserved in termites. New wood-boring mole “roaches” from Cretaceous Burmite belong to a new, most primitive, termite family Pabuonqedidae. Cockroach symplesiomorphies include hypognathous head concealed under pronotum/ paranotalia, regular wing venation, clavus, long cercal sensillae, carinated legs, unspecialized tarsi, cerci and mouthparts. Venation schemes, moniliform antennae and hexagonal feces ($n = 940$; $l/w_{ave} = 0.30/0.19$ mm) are termite synapomorphies. “Cracked” body surface and structure of forelegs are unique. Eusociality is indicated by 6 larvae preserved together, a larva amber-embedded inside a wood tunnel and nuptial-flight-related wing shedding sutures of adult females (one dealate). Nineteen syninclusions include a true termite, an archaeognathan bristletail, a wood boring caterpillar, 9 mites - one attached parasitic. The new species exhibits the first transitional form leading to true sociality. Mesozoic all-termite phylogeny reveals a basal (explosively-appearing) diversification “ring” resulting from general fluid Bauplan tunings to simple reductions from a single transitional taxon.

The transformation between truly social cockroaches and termites is documented by fossils[1,2] and molecules[3], and they are now considered as a single systematic unit. The direct linkage remains obscure, and cockroaches and termites may be polyphyletically related. We focus here on Cretaceous lineages, and disregard crown termites. The purpose of this study was to analyze the phylogeny of a new taxon placed in a separate family within Termitoidea[1,2]. Along with transitional taxa within cockroaches[4] it demonstrated that transitional forms are also common at the highest ranks, which is significant due to growing evidence for saltational hypotheses[5]. The here-revealed concept of apparently explosive principal diversifications also identify numerous “missing rings“, while transitional forms, earlier called “missing links“ s.s. represented by single species, remain untraceable in the fossil record due to their ephemeral duration. Analyses reveal a surprising evolutionary boom, and the disparity of forms is caused by simple reductions and consequent tunings, unbalanced by cryptic variability, of the general Bauplan of a single transitional form.

Systematic paleontology

Order Dictyoptera Latreille, 1829

= Blattaria Latreille, 1810 (conservative cockroaches; eusocial Socialidae; predatory Eadiidae, Manipulatoridae, Raphidiomimidae, Mutoviidae and certain Liberiblattinidae; parasitic Attaphilidae; cavernicolous Nocticolidae)
= Isoptera Brullé, 1832 (two lineages of eusocial cockroaches: Mastotermitidae, and all others)
(= Mantodea Burmeister, 1838 – one of the predatory cockroach lineages)

Superfamily Mastotermitoidea Silvestri, 1909

Family Pabuonqedidae fam. n.

See Supplementary Information for a full description of the new genus and species.

Type genus and species.
Pabuonqed eulna Vršanský, gen. et sp. n.

Differential diagnosis. Head hypognathous, globular; antennae moniliform; pronotum transverse and unexcavated; body wide, distinctly telescopic with cracked surface, cerci well-developed, with apparently 7 segments, with distinct long sensillae; forelegs burrowing, mole-like; wings unspecialized, rounded, Costal and Radial areas narrow; some hindwing veins not terminating at margin.

Pabuonqed Vršanský, gen. n.

Type species.
Pabuonqed eulna Vršanský, sp. n.

Derivation of name. The generic name is a random combination of letters. Gender: Feminine.
Differential diagnosis. As for family.

Pabuonqed eulna Vršanský, gen. et sp. n.

Derivation of name. The specific name is after Eulna, the female name.

Holotype. SNMZ 38683, a complete adult female, deposited in the Slovak National Museum in Bratislava.

Additional materials. SNMZ 38883, a complete adult female with detached wings (after nuptial flight). NIGP (preliminary number P0001), 6 complete immatures preserved in a single amber piece, deposited in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences; BA (preliminary number BA P0001), One complete immature preserved within a wood tunnel deposited in the Lingpoge Amber Museum in Shanghai.

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

Diagnosis. (figs. 1-5). As for genus, due to monotypy. For detailed description see SI1.

Morphologically the type species is a conservative cockroach with diagnostic termite traits. Large soil burrowing cockroaches Panesthiinae and Geoscapheinae have modified forelegs[6], although not as specialized as the new taxon, the very modified fossorial forelegs of which are here described as 'moling'. Burrowing is also present in the semisocial *Cryptocercus,* which bore in rotting wood without foreleg specialization, have concealed cerci and plesiomorphically filiform antenna. Soil and wood burrowing habits are phylogenetically connected[7]. The present small species resembles the truly wood-boring solitary cockroach genera *Bantua, Compsagis, Cyrtotria* and *Pilema* of the Blaberidae[8], though these all lack 'moling' forelegs and termite specializations. Their resemblances include elongation, coverage of the head, wide forewing veins under narrow fore margins and moniliform antennae, but the new taxon takes these adaptations further; shortened legs and a more pronounced thin habitus. Wood boring also occurs in the unrelated *Colapteroblatta* (Epilamprinae)[8,9]. Its reduced forewings result in an identical shape to the present species[10], while forewing scale rudiments were also preserved after wing shedding, suggesting their importance in protection inside wood. 'Moling' adaptations are unique, as well as the "cracked" structure of body surface. Wood nesting habits are also supported by the separately treated coprolites (Figs. 2F, 4).

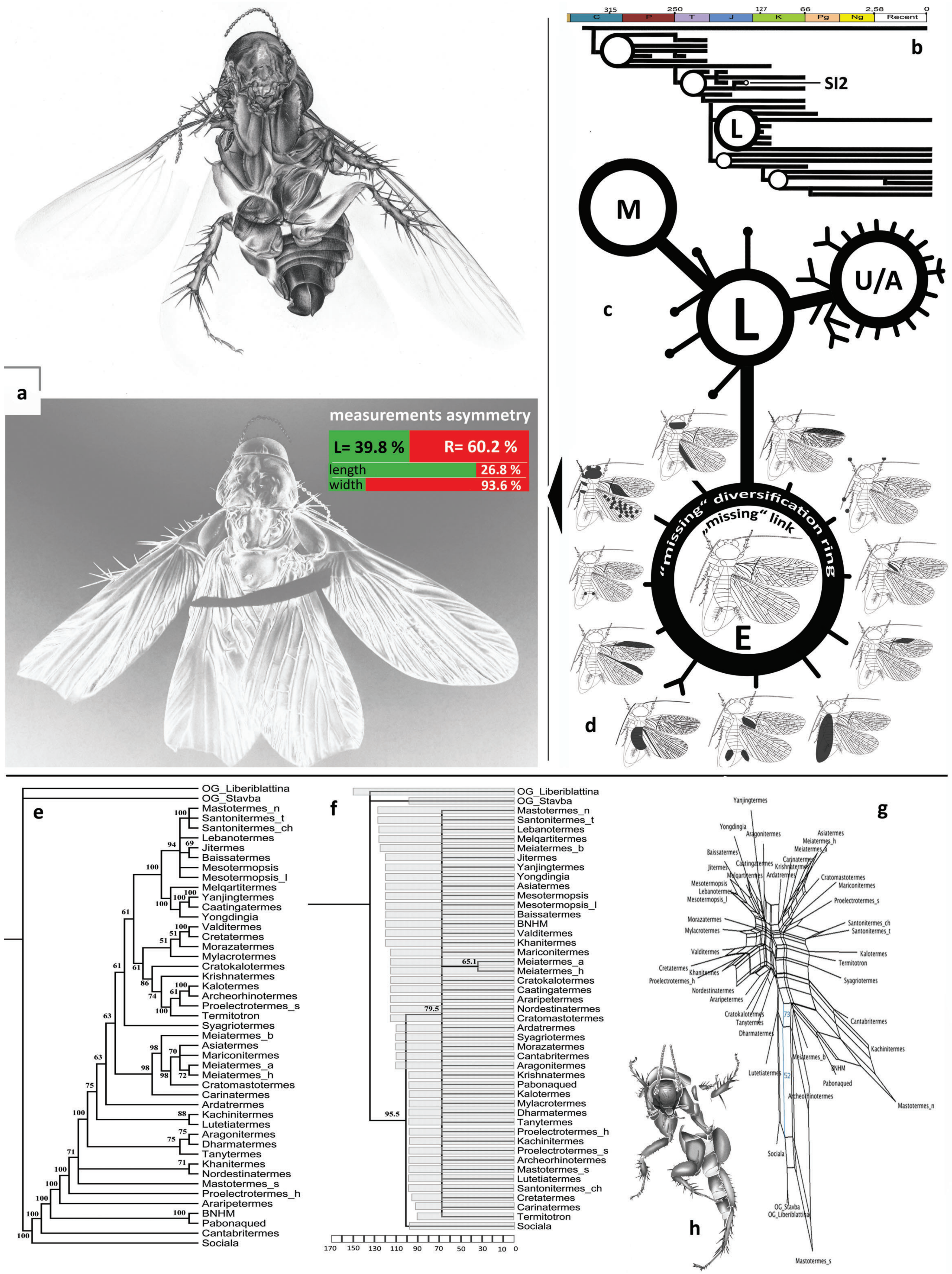
Convergence? So why does the present species not simply represent a primitive winged cockroach, such as Cryptocercidae? *Cryptocercus* has plesiomorphic filiform antenna and a derived morphology, but it cannot definitely be excluded as some termites have such traits (see SI2N). The molecular evidence and evidence from endosymbionts[11,12]; challenged by Boscaro et al. 2017[13], from 28SrRNA[11], SSU rDNAs[14] and mitochondria[11,15] unequivocally place *Cryptocercus* as a sister taxon to the true termites[16]. Fossils obscure this evidence, as all Triassic cockroaches appear to have possessed endosymbionts, and the topology of the phylogenetic tree always displays *Cryptocercus* as the most primitive. The sperm of *Cryptocercus* is typical for cockroaches, and differs from that of Mastotermites and Eutermites[17]. The present extinct taxon nevertheless may confirm this relationship, which would render living cockroaches polyphyletic. Cryptocercidae, with termites, nocticolids and mantodeans, derived from Liberiblattinidae, while all other living cockroaches derived from Mesoblattinidae. Egg cases are reduced in termites and modified in mantodeans, and *Mastotermes* and *Cryptocercus* have primitive oothecae[18] which were already developed in advanced Liberiblattinidae. Cockroach traits in new true termite species suggest the classification of *Cryptocercus* within termites is possible, further supported by the short genome characteristic for termites and not cockroaches[19].

Classification of the new species within a new termite family is based on the complex of body and wing morphological characters (and combinations), supported by its semihexagonal fecal pellets and a wood-inhabiting lifestyle revealed by morphology as well as preservation with wood debris and one immature individual inside a wood chamber. Maximum parsimony analysis reveals 61,047 equally parsimonious trees (540 steps). A 50% majority-rule consensus cladogram of these has a clear hierarchical structure (fig. 2 a). Bootstrap analysis left most relations statistically unsupported and most nodes collapsed into polytomies (fig. 2 b). All except *Sociala* are classified together (termites) in a large clade with 79.5% bootstrap support. Only two *Meiatermes* sp. formed a monophyletic group (bootstrap support 65.1%), whereas relationships among all the other taxa were not statistically supported. Network analyses corroborated this phylogeny (fig. 2 c). The star-like pattern of the network might indicate a rapid radiation of major clades (genera) and the mesh-like structure of the network reflects ancestrally polymorphic taxa[20]. Most of the taxa reveal a high diversification rate supported by numerous autapomorphies (long edges in the network). Bootstrap support values along the edges were lower than 50% in all taxa except for the two outgroup taxa.

Phylogenetic analyses are consistent with an intuitive diagram (fig. 1 d), with cockroach symplesiomorphies making bifurcations impossible, instead indicating an explosive termite radiation from a hypothetical transitional form, in this case a true "missing" link. The same pattern already occurs in Alienopteridae[21] (fig. 1 c) and mantodeans. All cockroach phylogeny consists exclusively of explosive radiations at all taxonomic units (fig. 1 b), and the only indigenous cockroach family known from any significant Lagerstatte (see SI3) reveals immediate explosion of form disparity. The association of reductions in this process is surprising: each studied taxon in the missing ring diversification has some plesiomorphic trait reduced. Thus the "creative" character of this explosive diversification and disparity of form phylogenetic pattern results exclusively from reductions, and consequent tuning to these losses (interrupted by cryptic variability, possibly as adaptive compromise sensu Rasnitsyn [22]). Homogenization of characters (see[5]) is unnecessary: major evolutionary radiations are triggered by simple initial reductions. A question remains of how this phylogenetic analogue of a phylotypic stage, a real missing link, originated and whether genome homogenization was required for its origin. It does not appear to have been necessary, creative and complicated; it seems to be caused by a single character, a breaking suture on the wings. This change might initially have been a trivial behavioral change linked to nuptial flight and nest founding in an already existing semisocial organization. Notably, this trait never reduced (with *Cryptocercus* losing all wings as a possible exception).

The missing ring pattern might explain general inconsistency in phylogenetic data of insects. While phylogenetic analysis of simpler protozoans reveal an index >0.95 (see[20]); in insects this number is often <0.8 (see[23]). This results from attempts to apply quantum logic to the matrix, mixing of data from parasites etc., i.e., epigenetic explanations. Explosive radiation as an exclusive pattern of branching explains synthetically at least the greatest proportion of this principal discrepancy.

Further ecological inferences. Bizarre roaches are characteristic of Burmite[24], including cranefly-like predators, taxa with heterogenou tarsi[25], bark camouflaged[26], aposematic[27], hymenopteran mimicking[21,28,29,30,31], ant nest parasites and undescribed forms. True termites[2] were also bizarre in Burmite. There are ~4,000 cockroaches and 9 cockroach-like termites known so far. The present taxon (like all known species) was also autochthonous and the immature stages preserved within the wood tunnel suggest the species' nests were situated in wood, as in the most primitive living termites. The probable origin of the wood is the amber producing tree



	Autapomorphic characteristic	Basalmost plesiomorphy
Lebanotermes veltzae	Specialised tarsi, long body, short head	**Normally developed R**
Mariconitermes talicei	**Elongated notum and head**	**Normal A**
Cratomastotermes wolfschwenningeri	**Pronotum short**, specialised tarsi	**Wide pronotum**
Ardatermes kudaludi	Modified pronotum, **4- segmented tarsi**	**Styli segmented**
Syagriotermes salomeae	Long wings, specialised tarsi, long body	Big arolia
Krishnatermes yoddha	Long wings	**Widely ascending R**
Pabonaqued eulna	**Mole, specialized R,** arolia missing	**Carination, full pronotum, hypognathy, standard CuA,** unspecialized tarsi
Proelectrotermes holmgreni	Elongated wings, long narrow CuA	Standard unspecialized tarsi with arolia, **tibial spination**, wide R, **intercalaries**
Santonitermes chloeae	Specialised tarsi, reduced cerci	**Wide R**
Archaeorhinotermes rossi	Irregular fully costalised veins including M	**Uniform sclerotisation of veins, no FW trichiae**
Mylacrotermes cordatus	Modified pronotum	**Rather big clavus,. long sensilla** on cerci
Miatermes bertrani	Costalised R, carved pronotum, prolonged head	**Filiform antenna**, intercalaries, fat body, uniform vein width
Cratokalotermes santanensis	**Irregular M**, reduced cerci	Original state of R (also R in hindwing)

Supplementary Table 1 (SI4) | **List of unique autapomorphies and symplesiomorphies which intuitively confirm impossibility of simple dichotomization pattern and unequivocally support explosive diversification of major termite taxa.** Text representation of figure 1D.

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(fig. 3 d; wood fragment undetermined). Amber producing and/or neighboring trees were autochthonous to both the fresh nest as well as the old nest. This is evidenced by the holotype preserved with complete wings (discarded immediately after reaching the "new nest"), while the female was preserved with wings already broken after the nuptial flight. The sample with 6 different immature specimens belongs to at two different stages, suggesting generation overlap and a (semi/eu) social way of life (*see*[8]). All 7 immatures are morphologically uniform and indicate morphologically undifferentiated castes. Forewing breaking sutures support true sociality, as they are characteristic of taxa with a single, nuptial flight by reproductive alates and the subsequent shedding of wings. 'Moling' legs combined with a narrow, telescopic body suggest that the species used tunnels made by other species and by themselves.

Life inside wood is non-banal. Pre-Cenozoic damage to living wood was unknown. Certain dinosaurs fed on living wood, but insect primary lignin decomposition is an advanced and sophisticated trait: it is one of the unique adaptations of termites and ancestral Mesozoic cockroaches. Their characteristic hexagonal feces have antifungal properties and provide nest sanitation through defecation[32]. 940 fecal pellets up to 1.3 mm long and 0.19 mm (on average) wide in the additional sample suggest the wood tunnels were filled with them. Their mostly uniform size distribution suggests wood chambers contained predominantly immature individuals. With coeval preservation of a sample

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Figure 1 | **Illustrations of *Pabuonqed eulna* sp. n. and phylogenetic scheme of all cockroaches – a** ventral and dorsal views of the wood boring mole "roach", the most primitive known termite from Myanmar amber; female adult **holotype** SNM Z 38683. Scale 1mm. **b** diagrammatic representation of family-level cockroach phylogeny with diversifications restricted to diversification "missing" rings; **c** major rings (Liberiblattinidae = L; Umenocoleidae/ Alienopteridae = U/A with indicated species[21] and mantodean ring = M; the single-family ring represents Fuziidae – see SI3), with marked family offshoots; **d** detail on eusocial diversification "missing" link and "missing" ring with cockroach symplesiomorphies shaded – they evidence explosive radiation instead of fluently branching (relevant Cretaceous species numbers from SI6, clockwise: 38, 28, 19, 32, 41, 35, 20, 22, 27, 33, 26); e A 50% majority-rule consensus tree. Numbers indicate percentage of clade occurrence among 61 047 most parsimonious trees; **f** A 50% majority-rule bootstrap tree with values. Scale in Mya; **g** Phylogenetic network with bootstraps along edges (>50% shown; on the basis of SI6); **h paratype** preserved inside wood tunnel BA P0001 line drawing.

inside a wood tunnel, this is the first direct evidence of any wood feeder. Thus the evidence from Barremian cheirolepidacean conifer wood of a boring filled with hexagonal coprolites from the Isle of Wight[33] might be associated with a primitive termite like the one described herein. Abandoned Cretaceous termite tunnels with pellets 0.75 mm long and 0.5 mm wide are also known from Texas[34] and Patagonia[35] in a fossil cycad stem. An additional immature specimen (SMNS BU 14: fig. SI2 n) representing another related new family ("cracked" surface, carinated, but without 'moling' legs) is also preserved with hundreds of fecal pellets of a comparable size (ca. 0.25/ 0.18 mm; fig. SI2 o). Most of the feces are preserved along with mycetal hyphae (fig. SI2 m). Diverse protosymbiosis established between termites and their symbionts during the Burmite time in a true termite[36] cannot be discerned due to the impossibility of cutting specimens. A diversity of mutualistic protists was already known during the times of formation of Burmite[37].

In addition to hexagonal feces and wood debris, 17 **syninclusions** (figs. SI2) occur, as well as an attached hematophagous mite. Among the syninclusions of the holotype, a large advanced true termite is especially distinct (fig. SI2 d). The opaque character of the amber piece full of debris and the presence of the archaeognathan (fig. SI2 e) and rove beetle (fig. SI2 i) both of which may be associated with nesting activity of other insects, suggest that the present species and/or the termite were not preserved incidentally, and that the holotype sample may represent part of a nest or its near surroundings. Two non-biting midges (fig. SI2 gh) often swarm on tree trunks and are frequent in amber. Other syninclusions were flies of the family Mycetophilidae (fig. SI2 f), 2 different diapriids of the subfamily Belytinae (figs. SI2 fj): hymenopterans parasitizing Mycetophilidae, possibly an associated bibiomorph. Seven different mites (2 Prostigmata, 2 Mesostigmata, Oribatida and 3 incertae sedis (fig. 3 segments K and O); fig. 1 c) and a pseudoscorpion (occurs undocumented in the margin, fig. 3 segment A) of the NIGPAS specimen suggest a high diversity of mites in the Burmite forests, but they are not unequivocally indicative of termite nests, as they can also occur in such diversity in rotting wood or litter (or as cockroach parasites[38]). A wood boring caterpillar and a beetle also occur. BA P0001 sample contains an undetermined, non-indicative psocopteran. These data support the uniqueness of Burmite[39], and the presence of more disparity of cockroach forms in this amber than in all extant rainforests of the world combined.

Transitional form ("missing link"). The present species documents a peculiar pattern, of amber species being earlier-derived than coeval organisms preserved in sediments[40]. It is by far the most superficially conservative among 52 Cretaceous termite species known from sediments, as well as compared to a 27 million year older termite from Chernovskie Kopi. Morphologically, it is apparently the ecological transitional form among the ancient semisocial *Cryptocercus* and the earliest eusocial termites. As eusociality with multigenerational organization (in "civilizations") is one of the most important innovations in the history of life[41] (while associated morphological changes are missing among key innovations of insects[42]), it places this discovery among the principal transitional forms of history. The general problem of transitional taxa has been a contentious topic since early Darwinian times and the subsequent discovery of *Archaeopteryx*. The modern synthesis expects gradual evolution and occurrence of transitional taxa, are, due to the fragmentary nature of the fossil record, usually missing. Epigenetic hypotheses invoke a saltational nature of phylogeny and thus the principal absence of "missing links". 110,000 fossil cockroaches provide a source of data for testing. We demonstrate here the missing ring on the cockroach-termite transition, and by surveying existing data[21,43] we see that this pattern is identical in the Liberiblattinidae-Umenocoleidae/Alienopteridae transition and in another 7 (in total, 9 of 15; unrecorded are only transitions to indigenous Fuziidae, Latiblattidae, Skokidae and Eadiidae and also to a living Corydiidae) family-level transitions (Phyloblattidae/Liberiblattinidae and Phyloblattidae/Caloblattinidae and Phyloblattidae/"Volziablattidae": *Sobytie tungusicum*; Liberiblattinidae/ Mantodea: *Santanmantis axelrodi*; Liberiblattinidae/ Blattulidae: *Eublattula*; Caloblattinidae/Raphidiomimidae: *Fortiblatta cuspicolor*; Mesoblattinidae/Ectobiidae: *Hispanoblatta sumptuosa*; Mesoblattinidae/ Blaberidae: *Morphna paleo;* Mesoblattinidae/Blattidae*: Balatronis lebanensis*). All originate from a diversification "missing ring", but none is a true missing link. Especially interesting is *Sobytie tungusicum* which reveals transitional characters to 3 different families, and really might represent a true missing link. Additionally it was preserved directly at the P/T boundary, where diversification was expected. Due to the explosive character of the diversifications and parallel reductions, hiatus-based taxonomy experiences a serious problem.

We coin the term **"missing rings"** for this general pattern, referring to a transitional or intermediate ring. Precisely, the phylogenetic analysis reveals the cockroach-termite true "missing link" was a never a single documented species (fig. 2 c) due to explosive diversification, and not "saltational" evolution. Consequently we observe a "missing ring" consisting of numerous species (here 14 of 45 known Mesozoic taxa), each bearing at least one unique symplesiomorphy (with a hypothetical transitional form; fig. 1 d). The success of ring representatives results in a "missing links s.l." fossil record. This pattern was unrecognized until now, and also in umenocoleid/alienopterid, fuziid (fig. SI3) and

Figure 2 | ***Pabuonqed eulna* sp. n. – a wood boring mole roach and the most primitive known termite. Cenomanian Cretaceous Myanmar amber. a** Female alate holotype **SNM Z 38683** head, ventral and dorsal views; **b** Female adult post-nuptial flight alate with wings detached along sutures SNM Z 38883, ventral view, dorsal view, general habitus, 'moling' foreleg, terminalia with externally protruding ovipositor, head, general habitus; **c** Five of six different immature individuals preserved in a single amber piece NIGP P0001, foreleg details under different preservation within the same amber specimen, syninclusions (6 mites, a beetle, a caterpillar), immature terminalia with cerci and distinct styli; **d** Immature individual BA P0001 preserved inside a tunnel of undetermined wood, general habitus with detail of 'moling' foreleg, externally protruding ovipositor with huge cercus, syninclusion (psocopteran).

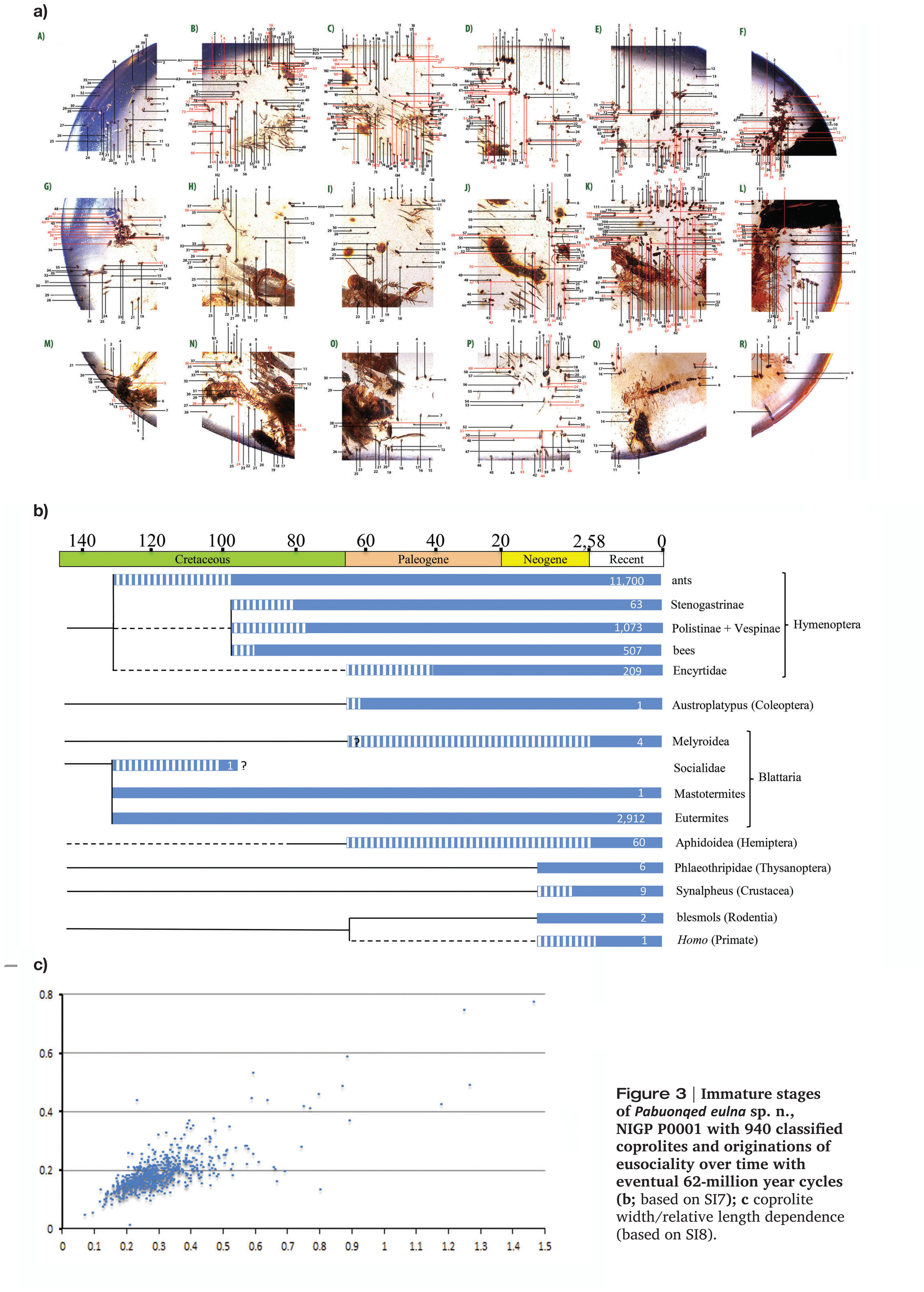

Figure 3 | **Immature stages of *Pabuonqed eulna* sp. n., NIGP P0001 with 940 classified coprolites and originations of eusociality over time with eventual 62-million year cycles** (**b**; based on SI7); **c** coprolite width/relative length dependence (based on SI8).

predatory cockroach transitions[21,44]. All family-rank diversifications are rudiments of such explosions, while it is impossible to prove this pattern at the species level. Nevertheless, intuitively, living forest insects with numerous closely related species suggest it might be valid at lower levels too. So we explain the phylogeny, at least within cockroaches, as a decay of an analogue of an obscure phylotypic stage at the phylogenetic level. Explosive radiation thus also explains why missing links s.l. are so numerous. The origin and genetic character of this explosively radiating "missing link state", i.e., strictly transitional taxon in linear logic, remain obscure. The size of the missing ring is linked to how long species can cope with accumulating reductions.

The **general pattern of eusociality that originated over the zoological system and over time** (fig. 3 b) can be explained if its origin is restricted to three diversification periods, 127, 66, 3.9 Ma, corresponding to 62-million year periodic mutations[43]. Alternatively, up to seven periods were involved. Low sample size (n = 18) and problems with dating of terrestrial sedimentary fossils prevents use of sophisticated correction analytic tools[45], so other originations of eusociality outside this periodicity cannot be excluded.

Supplementary Information is available in the online version of the paper.

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Author Contributions P.V. designed research, collected data, performed the systematic part and together with M.B. wrote the paper. T.B., X.L., X.R., F.X., J.L. and P.V. collected the material; L.V. polished samples, prepared line drawing, made measurements and complex evaluation of NIGP P0001; I.K. performed photodocumentation, drew illustrations and provided (SNMZ holotype and additional material) measurements and description; J.L. documented CNU collection. Ľ.V. and L.Š. collected literature; M.K and T. K performed phylogenetic analyses. J.H. provided eusociality review. All authors commented on the MS.

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Methods

The amber insects were obtained from the amber mine located near Noije Bum Village, Tanaing Town. The U-Pb dating of zircons from the volcanoclastic matrix of the amber gave a maximum age of 98.8 ± 0.6 million years[46]. However, multiple lines of evidence, including the high degree of roundness of the amber and the presence of bivalve borings on the surface, suggest that the amber was most likely reworked before deposition in the volcanoclastic matrix, which implies that the age of the amber should be somewhat older than the matrix.

Depository. A specimen (NIGP P0001, six immature specimens in a single amber piece) is deposited in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences; one immature (BA P0001) is deposited in the Lingpoge Amber Museum in Shanghai (specimen available for study by contacting F.X.); holotype/adult females SNMZ 38683/ 38883 are at the Slovak National Museum in Bratislava.

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

Network analysis. Most parsimonious trees were computed in PAUP* 4.0b8 using a heuristic search, 10 random addition taxon replicates, the accelerated transformation algorithm (ACCTRAN) as well as the three bisection-reconnection branch-swapping (TBR) algorithm. ACCTRAN pushes evolutionary transformation of a character down the tree as far as possible, favoring reversals over parallelisms when the choice is equally parsimonious[47]. TBR generates more neighbor trees during heuristic search than other traditionally used swapping algorithms[48]. Characters were treated as 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 (neighbor-net algorithm - 49) with bootstrap analysis (1000 replicates) in effect. This approach can infer and simultaneously depict all possible evolutionary trajectories present in the dataset[50]. *Cratocalotermes novalolindensis* and *Huaxitermes huangi* are deleted due to representation of either fore- or hindwings.

Supplementary Information 1

Pabuonqed eulna **VRŠANSKÝ, sp. n.**

Derivation of name. The specific name is after Eulna, the female name.

Holotype. SNMZ 38683, a complete adult, deposited in the Slovak National Museum in Bratislava.

Additional material. SNMZ 38883; NIGP P0001, 6 complete immatures preserved in a single amber piece, deposited in the Nanjing Institute of Geology and Paleontology, Chinese Academy of Sciences; BA P0001, a complete immature preserved within a wood tunnel deposited in the Lingpoge Amber Museum in Shanghai.

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

Description. Holotype (Figs. 1, 2a).

Preservation. The polished amber is drop-shaped, 35.84 mm long, nearly 26.26 mm in width with a maximum thickness of 6.43 mm. Weight is 3.594 g. The color is honey brown, and the transparency is somewhat reduced due to many small particles, feces, remains of plants and insects. Other than the material examined, it contains 9 complete insects (see "syninclusion" section). The holotype, cca 5 mm long from head to abdomen, occurs in the wider part of the amber in the upper corner.

The individual is complete, except the left hind tarsus is nearly completely absent, and the distal edges of both hind wings and a small distal part of the left front wing, caused by manipulation of the sample. Numerous white clots, crystals and air bubbles complicate measurement of the insect's ventral side. Small air bubbles are present at the frons, mouth and antennae, larger bubbles under the basal parts of the wings, and the largest bubble is in the central part of the body from the front coxae to the hind trochanters. A light fuzz of white clots predominantly covers parts of the body such as the mouthparts, parts of the limbs, antennae and spines. This may be caused by secreted water rather than fungi (although the paratype shows the same preservation, and these structures may represent fungi). This suggests that during solidification of the amber, the specimen was positioned with the head upwards. The right cercus is entirely missing, the left one retains only 3 segments. It is remarkable that all the cerci of the paratype are preserved, considering that it is a mated female post nuptial flight. Stipes, galea, paraglossa and mandibular teeth cannot be observed visually.

Position: Head, thorax and abdomen are in a subplanar position. Left antenna is arcuate, bending above the head. Right antenna is directed towards the front legs on the same side, covering them in ventral view except two spines, and in the other half it bends below 50 degrees and parallel to the body. Right front and middle legs are pressed forward to the body and head, with only tarsi and tibiae protruding. Left front and middle legs are in similar positions, more open and not pressed towards the head or body. Hind legs are free "hanging" along the abdomen. In dorsal view, all legs are covered by wings except a few front and middle tibial spines and part of the right middle tarsus. Front wings are directed from the body at about 45°. They are flat and in a horizontal position relative to the body, only the left one is angled down slightly towards the ventral side of the body. Hind wings are directed to the rear, completely covering the abdomen, right hind tibia and tarsus. The right wing is located above the left one and overlaps ¼ of its surface. Edges of the left hind wing are bent inward. Abdomen is slightly twisted to the ventral side, but mostly straight. The greatest length is 7.318 mm from left antenna to the edge of the hind wing and the maximum wingspan is 9.88 mm.

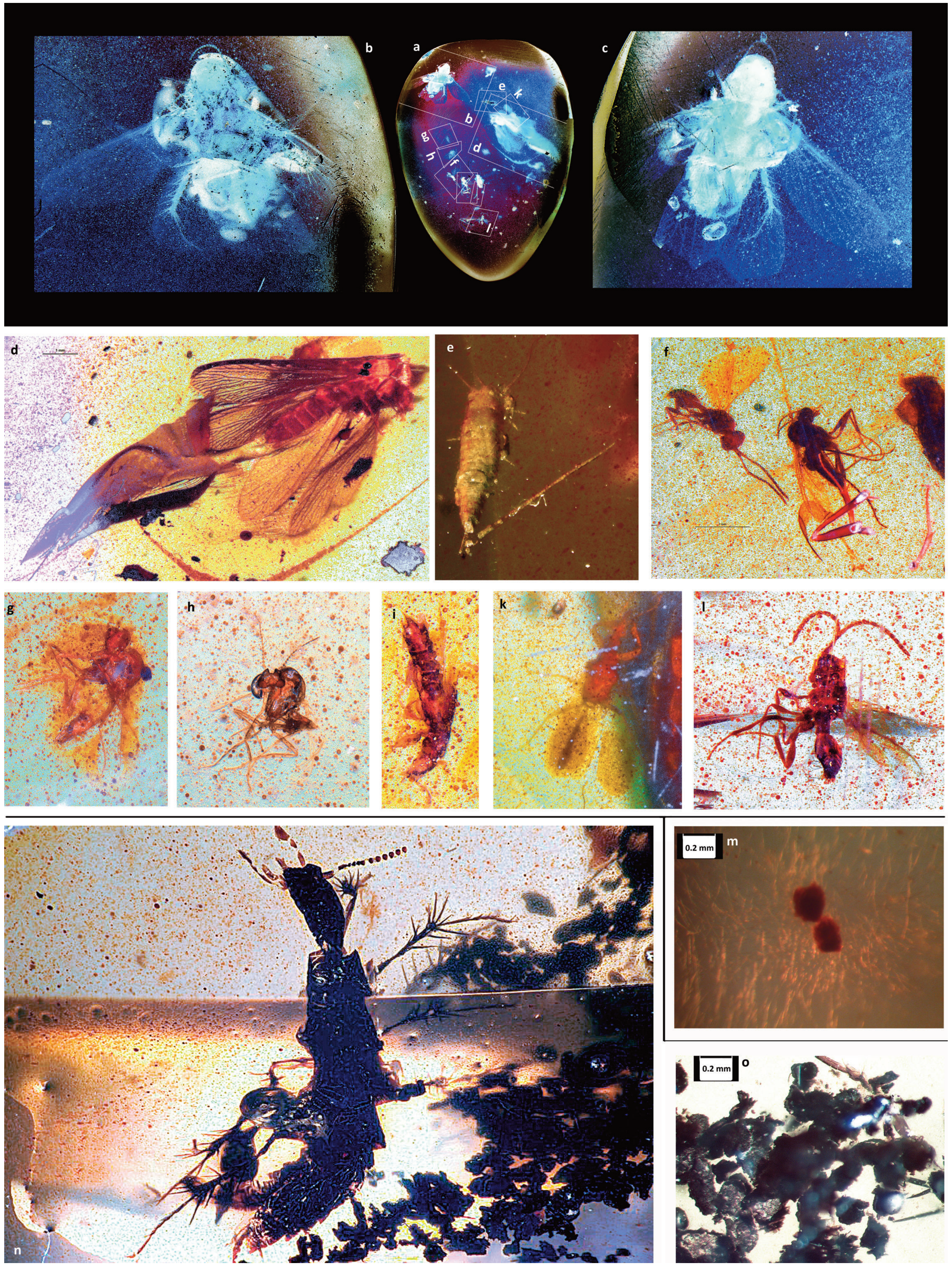
Exoskeleton and color: This fossil is characterized by strong shades of brown, except the more transparent thinner exoskeleton of the proximal leg segments, which are honey to ocher colored. Antennae are the same color, but the thicker parts of the segments are darker brown. The thickest layer of the exoskeleton covers the head, pronotum, abdomen and distal parts of the legs. This dark shade of brown can even look brown-red in parts of the head, pronotum and abdomen. Spines can even be brown-black. It is unclear whether these are the natural colors, because the paratype is almost entirely black.

Measurements: see SI5.

Head: Head large, spherical, lentiform with a circular contour. The length is 1.3962 mm including oral apparatus. Maximum width is 1.3143 mm, width of epicranium is 1.1999 mm and frons is wide 0.9048 mm. Clypeus measurements are 0.169 mm high and 0.4524 mm wide, and clypeus bordered by a transparent, colorless margin. Labrum is 0.1846 mm high and 0.3068 mm wide. Minimum distance between genae is 0.8801 mm and height of recognizable gena is 0.2522 mm. Spacing between the clypeus and the bottom part of the jaw is 0.5759 mm.
Antennae are very short and wide, moniliform. The right antenna is 2.03 mm long and left is 1.961 mm. Both consist of 23 antennomeres. Scapus and pedicel are longer than other antennomeres, 0.14 mm on average, cylinder shaped, while the right one seems larger (length of left scapus was calculated as ascending under 45° degree). Width of antennomeres is on average 0.09 mm, only the left pedicel is markedly thinner, approximately 0.06 mm. The first segment after the pedicel is smaller, spherical and the same on both sides. Middle segments are skewed drop-shaped, with distinct short funnel stems on their bases. Length of antennomeres varies from 0.05 to 0.1 mm and width from 0.05 to 0.08 mm; there is a tendency towards increased size towards the middle of the antennae, a slight reduction in the middle, and another wave of increase followed by a gradual reduction towards the tips of the antennae. Six terminal antennomeres are bell-shaped. The last antennomere is 0.087 mm long and 0.05 mm wide, longer compared to the preceding ones, and cylindrical. The width of the antennomeres gradually decreases towards the ends of the antennae, with small oscillations from 0.09 mm to 0.05 mm except for the mentioned third antennomere. Sensillary covering is very thin, sensillae 0.03 mm long on average.
The compound eyes are lentiform, protruding beyond the outline of the head, situated on the sides behind the bases of antennae. Eyes are large, almost the same on both sides, cca 0.5 mm in height and 0.1 mm in width. They are without coloration, clear bounded the same as ocelli but ocelli are lighter, even blue, located above the antennal pit and halfmoon-shaped. Height is cca 0.14 mm and width 0.1 mm. The central ocellus resembles a very large diffuse stain.

The visible part of the left mandible is 0.364 mm long. The width is symmetrically similar about 0.12 mm. The first segment of the right maxillary palp is not visible. The second is short, 0.09 mm on both sides. Next three right maxillary palp segments seem to be of the same length cca 0.03 mm and width, 0.1 mm. The last segment is wider. The most proximal segment on the left side is longer, cca 0.128 mm but thinner than the second one. The last three segments tend to gradually protract to the distal segment, 0.0348 mm long. It is also the widest one, with value 0.1105 mm. Sensillar cover is thin, short but dense, covering all segments (due to contamination they are indistinct, and seem longer and denser on the last segments).

Labial palps of three segments look the same. The proximal segment is the shortest one, around 0.09 mm, middle ones are 0.2 mm long and the right



last segment is a little longer than the left one, with length 0.2886 mm. Width around 0.06 mm, almost the same for all.
Neck very short.

Pronotum: Fully developed, transverse, with fully developed short paranotalia, oval, expanding towards body. Maximum measurements are 1.222 mm in height and 1.742 mm wide. More or less in horizontal plane with body, with edges slightly bent inside, especially at sides, covering cca 2/3 of head in ventral view. Disc of pronotum not distinct.
Wings: Membranous net–veined wings are heteronome, with distinct intercalaries and sporadic cross-veins and reticulations. Forewings are narrower and longer, hind wings are shorter and drop shaped with round apices. All are near-flat, with a wavy surface furrowed by veins and crossveins (seen at certain angles of light). Right and left wing overhang the pronotum outline by 4.513 and 5.609 mm respectively. Length of front left forewing is 5.79 mm and width 1.978 mm. Hind wing is 4.645 mm long and 2.495 mm wide. Right forewing is 5.428 mm long and 1.635 mm wide. Hind wing is 4.504 mm long and 1.361 mm wide. Measured lengths of veins R1. M and anal area on left front wing are 3.743 mm, 4.337 mm a 1.14 mm; 3.535 mm, 4.123 mm a 1.068 mm long on right side. Forewing with entirely costalized fore margin. Subcosta is simple, Radius limited to 2(R)-3(L) branches. Media is expanded with anterior offshoots, amounting to 10(R) veins at margin. Cubitus normally developed, with 8 veins at margin. Two branches are fused on the left side. Clavus distinct, very short and partially sclerotized. Anal veins indistinct. Base of the wing very narrow, causing somewhat triangular shape of the forewing.

Hindwing is oval, with round apex (destroyed during polishing as the specimen was at the very edge of the amber piece). Sc simple. R1 limited to a single branch, in the right wing fused to Subcosta. RS distinct, straight, with 5 veins reaching margin. M is missing. CuA well developed, branched (on left side secondarily), with 7-8 veins at margin; CuP simple. A1 present at remigium. Vannus indistinct.

Legs: Diversification between front, middle and hind legs is distinct. Protraction from front to hind legs prevails at the expense of the width. Legs are armed with very long and thick spines and spurs. They are also long on hind legs. The most significant difference seems to be the presence of rudiments of an arolium on the middle legs, apparently missing on other legs.

Front legs are fossorial, shorter and more compact compared to others (right femur and tibia; and tarsus on left leg was not measured due to position). Left coxa is longer and thinner than the right one. Maximum values are 1.277 mm long and 0.676 mm wide. The left femur is 0.84 mm long and 0.428 mm wide, and the left tibia is 0.577 mm long and 0.234 mm wide. Tibia here is flatter than on the other legs. Although the spines are not as long as others but more massive, and they can be flat (especially from the base to the middle part). The longest 0.203 mm front leg spine is localized on the left leg and 0.042 mm wide. The spurs are shortest here. They increase in number to 6 to 7 to the end of the tibiae, and since tibiae are flatter they are more in one plane. Spurs are densely covered with a minute fuzz, the bases becoming thinner followed by a distinct hump, regularly tapering to a sharp tip. Section round but flat, with sparse (< 8) helical ridges distally. Tarsi are very long, robust, 5 segmented. Tarsomeres unspecialized. The first fore segment is half as long as that on other legs (cca 0.3 mm) but on other legs was long and thin in the center. Whole tarsi are cca 0.77 mm long. The maximum width measured on the distal segments with spines is 0.065 mm, and minimum width is 0.046 mm measured on the thinnest middle part of the first segment. Tarsus spines probably grow in pairs from the dorsal side, and are symmetrical diverging to the sides, not remote from the surface. They are mostly 0.086 mm long, and cca 0.01 mm wide. Terminal tarsomere is most massive here and the largest measured values are on the left leg. Length is 0.199 mm and width 0.072 mm. This part spreads distally in width to a triangular cross section. Claws are with length 0.133 mm and width 0.02 mm. They are widely spaced, and lack arolia and pulvilli.

Figure SI2 (4) |**Adult female *Pabuonqed eulna* sp. n. alate** holotype **SNM Z 38683 (a-c) and immature of an undescribed family SMNS BU 14 (n). a-c** dorsal, ventral views and the whole piece detail in true colors standardized to remove yellow hue of the amber; **d-l** syninclusions (a termite; an archaeognathan bristletail; Diapriidae/Belytinae with Mycetophilidae/ Leiinae; 2 chironomids; Staphylinidae/ Osoriinae; enicocephalid bug; Diapriidae/ Belytinae), **m, o** fecal pellets, most with mycetal hyphae**.** Scale 1mm.

Segments of middle legs are markedly longer and thinner, except for the coxa which is only measurable on the right leg and is 1.013 mm long and 0.653 mm wide. Femur (visible part) is 0.502 mm long (measurement is complicated by position of legs and central large bubble). (Visible) part of left tibia, is 0.833 mm long and 0.214 mm wide. Right one is around the same width, and measured length is markedly less (the base is not visible). It is flattened in the wider distal part, but not as much as in front legs. The longest spine was measured on the left tibia, it is 0.411 mm long and 0.046 mm wide. On the right, it is 0.332 mm long and 0.071 mm wide. Spurs still do not form a perfect rosette shape, because of flattening of the tibiae, but they are not in one plane as on the front legs. The longest left leg spurs are 0.6 mm long and 0.043 mm wide. The left tarsus also dominates over the right, is 1.086 mm long and 0.06 mm wide (segment with spine), 0.041 mm (thinnest part). The right tarsus is 1.03 mm long and width is 0.066 mm - 0.03 mm. Single tarsomeres were easily measured on both sides. Spine on tarsus is of approximately the same length on the left and right, is 0.06 mm long and 0.01 mm wide. Area bearing claws is 0.186 mm long and wide 0.071 mm on the right. Although left leg reveals fewer measurements but they are of the same shape and construction with regard to the claw area. Left claw is 0.13 mm long, 0.016 mm wide and right one is 0.092 mm long and just a little wider. They grow at the end of the last segment of the tarsus from a very thin structure, unlike the front legs, and because of this reduction appear more fragile on both sides. Between the claws is a localized oblong structure. A probable arolium rudiment is narrow with small bump at the end. It is 0.053 mm long on the right leg, 0.047 mm on the left, and its width is the same, 0.024 mm. For this reason, the claws are more arcuately diverging to the sides and are not as straight as on other legs without arolia.

(Measuring the hind coxae and femora was complicated by the large bubble. Therefore, the measurements given for the coxae are probably slightly inaccurate). Length is 1.177 mm, width could not be measured on the left leg, and right coxa is 1.068 mm long, 0.875 mm wide. The trochanter is the shape of two drops, separated by wider parts, and adjoins the joint of the coxa and femur. They are comparatively strong. The two parts are at an angle of approximately 90ºto each other, and have sharp ends. The end of the horizontal part is chipped on the left side, and the upper is obscured by the central bubble. Maximum dimensions of the right trochanter are 0.422 mm in height and 0.527 mm in horizontal length. Only the right femur could be measured, and it is 1.52 mm long and 0.521 mm wide. Tibiae are clearly visible on both sides, and have a more regular oblong shape, not as flat as on the other legs. The left one is 1.289 mm long and dominates (length calculated under 35° degrees), right one is 1.269 mm long and their width is around the same, 0.22 mm. Overall, the longest spine, 0.546 mm, and 0.052 mm wide was found on the left leg. On the right spines are 0.472 mm long and 0.4 mm wide. Also the longest spurs are situated at the end of the left tibia, 0.829 mm long but just 0.34 mm wide, supporting the above mentioned view that elongation can be at the expense of width. Six to seven spurs are arranged in a radial rosette around the base of the tarsus. The right tarsus is 1.29 mm long and 0.064 wide (maximum), 0.03 mm (minimum). The first proximal thin segment is 0.7 mm. The spine from one of the segments is 0.083 mm in length and of the same width, just 0.01 mm. Claws are 0.13 mm long and 0.016 mm wide, at the end of the tarsus, which is also narrowed and appears less straight. No arolium rudiment was observed. The area with claws was approximately 0.189 mm long, as on middle legs but is thinner, 0.061 mm.

Abdomen: The tergal gland is apparent as a dark spot under the hind wings. The abdomen is comparatively less oblate, the last segments are significantly thicker. There is a longitudinal white furrow in the central axis of the subgenital plate and an ovipositor is present. The last segment is the highest, 0.574 mm, in the axis with a maximum width of 0.608 mm. The surface is smooth close to the axis, and gently wavy and rough towards the sides and narrows to the tip of the plate. The penultimate sternum is the highest, 0.33 mm and 0.889 mm wide (including lateral extensions of the terga). The other sternal surface is in the same trend as on the subgenital plate, smooth around the axis and furrowed on the sides. The following sterna are lower because of the position of the abdomen. S7 is 0.111 mm high, S6 is 1.36 mm and the last measurable S5 is 1.73 mm high. The width of the sterna is not measured exactly after S7 (due to the air bubble on the right side): S7 is cca 1.267 mm wide, S6 cca 1.748 mm, and S5 is not measurable. Ovipositor is external, extremely short and robust. Cerci multisegmented, wide and long, styli apparently absent.

SNMZ 38883 – a complete adult female with wings shed after nuptial flight (this specimen is categorized into the present species on the basis of combination of hypognathous head and moniliform antenna, ‘moling’ forelegs, complete pronotum, abdomen surface structure).

Character of preservation. The polished piece of amber is oval, 12.32 mm long, and 10.95 mm wide, a maximum thickness of 4.47 mm. The weight of the sample is 0.342 g. It is a light honey color, and its transparency is excellent, clean without small particles. Ventral measuring of the paratype reveals a length of 6.608 mm from the head to the end of the cerci with the center located approximately in the center of the sample, slightly skewed to the right.

The individual lacks wings (female forewings are partially detached after the nuptial flight), left antennae after 15th segment (16th if we consider the third segment consisting of two segments), left middle and right hind leg both from third segment of tarsus. The left hind leg is missing from the trochanter, with all of the femur, probably resulting from crafting of the sample; part of the tibia appears close above the middle left tibia. Large air bubbles make measurements complicated on the front tibiae and right ventral part of head, the dorsal body and especially a thin layer of bubble, excluding the legs. Also, close above the right antennal pit and ocellus is a flat flake of white debris or mineral matter. White clots cover the body parts with small sensillary cover, such as the mouthparts, and predominantly fuzzy parts of the legs, antennae and spines (not as much as on the holotype).

T2/ T3 right side has a parasitic white mite (parasite: body 0.145 mm long, head 0.057 mm, width is 0.097 mm and front to hind legs length is 0.077, 0.054, 0.051 mm).

The dark color and corrugation of the exoskeleton suggests that the individual dried out post burial. Stipes, galea, paraglossa and mandibular teeth are not visible.

Position: Head, thorax and abdomen are in a subplanar position. Right antenna consists of 15 - 16 segments (for comparison with the holotype, we fused two putatively separate very small segments to reveal 23 comparable overall antennae segments as in the holotype and other termites), directly laterally descending from head to side and is subtly sigmoidally curved. Left complete antenna is straighter, and in the other half bends below 50º degrees and turns subvertically.

Fore coxae are parallel to the central axis, femora directed perpendicular to sides. Right fore leg continues parallel to the body and left to the middle coxae. Middle and hind legs are in a more open position, while femora converge on the right side and middle tibia and tarsus are closer to the abdomen. Middle femur is pressed under the front left femur and tibia, tarsi continue nearly directly to side. Remaining part of hind left leg occurs close above the distal part of the middle left tibia. Abdomen is twisted to the upper left in dorsal view, distally to the ovipositor and cerci.

Exoskeleton and color: The specimen is characterized by a darker brown color, except the more transparent thinner exoskeleton of the proximal legs segments, which is dark brown-red colored like the abdomen in ventral view. The same antennae, but the thinner distal parts of the segments, appear lighter brown, as does the ovipositor. The thickest layer of cuticle covering the head, pronotum, distal parts of legs and spines is darker brown and might appear black. It is unclear whether these represent the original colors, because of postburial drying and the fact that the holotype is lighter.

Measurements: see SI5.

Head: Head is large, spherical, lentiform with circular contour. The length 1.376 mm including oral apparatus. Maximum width 1.209 mm, width of epicranium 1.093 mm and frons are wide 0.855 mm. Clypeus 0.172 mm long and 0.45 mm wide, delimited with transparent surface of light honey color to almost colorless (measurements complicated by air bubble). Labrum is 0.765 mm long and 0.274 mm wide and is lighter in color. Minimum distance between genae is 0.956 mm, and length of recognizable gena is 0.253 mm. Spacing between clypeus and bottom part of jaw is 0.446 mm. Antennae very short and wide, moniliform. Right antenna is 2.476 mm long and consists of 23 segments (if we count connected segments 3 and 4 separately, then 24 segments) and left segments from 15th - are absent. Scape and pedicel are longer, 0.195 and 0.161 mm on the right antennae and 0.215, 0.108 mm on the left, cylindrical, right pedicel seems wider: 0.086 mm. Width of other antennomeres is 0.04 mm on average. The first 2-3 segments are smaller, intertwined so it is harder to recognize them (especially on the right). Middle segments are skewed drop shaped, with distinct short funnel stems on base. Length of segments decreases distally and vary from 0.133 to 0.08 mm on average, and width from 0.05 to 0.08 mm, progressively increasing to middle segments and then gradually reducing towards the end. Last four segments of the right antennae are preserved together, they are lighter, circular and smaller (length 0.07 to 0.06 mm on average, width 0.068 to 0.065mm). The last one is cylindrical, just 0.05 mm wide. Sensillar cover is very thin, long 0.044 mm on average and the longest measured sensilla chaetica is 0.057 mm long.

Antennal pit resembles a large circular depression with raised edges approaching the ocelli, 0.171 to 0.153 mm wide.

The compound eyes are lentiform, kidney shaped, protruding beyond the head outline, situated on the sides behind the base of the antenna, large, 0.594 mm in height on the left, measurement on the right complicated by the mentioned white matter. The width is reduced because of preservation, and appears to have a light brown rim poorly visible on the holotype. Left ocelli lighter, nearly colorless, located above the antennal pit, halfmoon-shaped. Height is cca 0.548 mm and width 0.065 mm. Right and central ocellus are indistinct because of dirt and air bubble.

Mandibles are massive, left one predominates, 0.58 mm long and 0.226 mm wide. The right mandible is 0.447 mm long and 0.147 mm wide. Unlike in the holotype, the fuzzy surface is possible to observe here, as well as on the genae.

First maxillary palpomeres indistinct). The first palpomeres are 0.03 mm long and 0.021 mm wide (both sides). The next segments gradually protract to distal segment. Second right segment is 0.075 mm long and 0.065 mm wide, (left 0.0785/ 0.032 mm). Third seems much bigger on the left too, 0.132 mm long and 0.054 mm wide (0.1183/ 0.046 mm on the right). The right penultimate segment is longer, 0.1798 mm and 0.044 mm wide (0.1387 and 0.046 mm on the left) and the last segment is a protracted triangular shape, as well, its length is 0.232 mm with width 0.094 mm (0.1787/ 0.081 mm on the left). Sensillar cover is thin, short but dense, covering all segments (due to contamination they are indistinct, and seem longer and denser on the last segments). Labial palps indistinct. Neck short.

Pronotum: fully developed, transverse, with fully developed short paranotalia, oval, expanding towards body. Plane more less in horizontal position with body, with edges slightly bent inside, especially at the point of contact with head, and crinkled on the sides. It covers cca 2/3 of head in ventral view. Maximum measurements are 1.506 mm length and 1.884 mm wide. Central disc of pronotum 1.167 mm and 1.111 mm wide, distinct. Central longitudinal furrow distinct, 0.626 mm long in the center. An obscure large shield shaped structure arises from the pronotal anterior margin directed towards head, 0.215 mm long and 0.989 mm wide.

Thorax and wings: Forewings were detached along the breaking suture, so only the base remains; wing section is 0.275 mm wide (apparently not perpendicularly). Clavus is distinct, but no anal veins were traced. Wings are missing.

Legs: Diversification between front, middle and hind legs is as distinct as in the holotype. The same trend of protraction from front to hind legs prevails, with decreasing width. This trend is made apparent by comparing left and right parts of the body. Legs are armed with very long, thick spines and spurs, which are also long on hind legs. The most significant difference, except the length and shape of the segments between the front and the other legs, seems to be the shape of the claws at the end of the tarsi on the front legs compared with the holotype. Arolium rudiments occur on all preserved complete tarsi, and look different on the front and middle legs (shaped like that of the holotype, preserved on the middle legs only). Distinct differences from the holotype are the appearance of fore procoxal processes, trochanters clearly visible on all legs, the first fore tarsomere shorter, coxae and sensillae longer (possibly related to overall size).

Front legs fossorial, shorter and more compact than other legs. Left coxa is longer and thinner than the right one (as in holotype), 1.452 mm long and 0.676 mm wide. Procoxal processes appear on the inner parts of the front coxae, and are of the same length 0.688 mm, the width (0.306 mm on the right and 0.142 mm on the left) is different due to the position of the right coxa, which suggests a slight twisting of the right coxa. The trochanters are similar, on average 0.4 mm long and 0.18 mm wide. The right femur is 1.067 mm long and 0.362 mm wide, the left is slightly smaller. The left tibia is 0.642 mm long, right 0.571 mm but much wider, 0.236 mm wide. The tibia here is flatter than on the other legs (description as for the holotype). Although the spines are not as long as the others, they are more massive and they can be flat (especially from the base to the middle part). The longest front leg spine, 0.335 mm, is localized on the right leg and is 0.046 mm wide. The spurs are shortest here. They are present in smaller numbers at the ends of the tibiae, and because the tibiae are flatter, they are in more than one plane. The spur surface is densely covered with medium short chaetae, the bases might be thinner, followed by a hump and regularly tapering to a sharp tip. Section round but locally flat with sparse ($<$ 8) helical ridges distally. Tarsi massive, long, 5-segmented. Tarsomeres unspecialized. The first segment is shorter than on the other legs or on holotype (cca 0.248 mm) but on other legs is long and thin in the center. Entire tarsi (measured in all cases without claws) are cca 0.4 mm long. The maximum width measured of the distal segments with spines is 0.062 mm, and minimum width is 0.038 mm measured at the thinnest middle part of the first segment. Tarsal spines are in pairs, probably arising from the dorsal side, and diverge symmetrically to the sides. The measurable ones are 0.035 mm long and cca 0.01 mm wide. The part with claws is most massive here and the largest measured values are 0.121 mm in length and 0.182 mm in width. This part does not spread distally in width to a triangular cross section as it does in the holotype, where the arolium relicts are also absent. The claws are largest and widest, with length 0.124 mm and width 0.036 mm. Arolium rudiments are 0.038 mm long and 0.018 mm wide.

Middle legs are markedly longer and thinner. The right coxa is 1.159 mm long and 0.747 mm wide and left is 1.345 mm long, 0.669 mm wide. The right trochanter is much longer 0.675 mm (left is 0.474 mm), the width is 0.267 mm (left is 0.247 mm). Left femur is 1.381 mm long (right 1.129 mm) and 0.476 mm wide (right 0.687 mm). The right tibia is slightly bigger, 1.162 mm long and 0.292 mm wide. The longest spine was measured on the left tibia, it is 0.402 mm long and 0.079 mm wide. On the right it is long 0.292 mm and 0.061 mm wide. The longest left leg spur is 0.542 mm long and 0.043 mm wide. The only tarsus is the right one, is 1.147 mm long and wide 0.062 mm (segment with spine), 0.039 mm (thinnest part). The spine on the tarsus is longer on the right, is 0.07 long mm and 0.017 mm wide. The area holding the claws is 0.28 mm long and 0.049 mm wide on the right. The claw is 0.29 mm long, 0.011 mm wide. The whole tarsus segments including the claws looks more fragile (probably has lost last three segments on the remaining legs). Arolium looks more complete and its 0.049 mm wide and claws are very small 0.029 mm and thin.

Only the hind left coxa is measurable due the position of the bubble and the middle right leg. It is 1.715 mm long and 0.957 mm wide. The right trochanter is 0.554 mm long and 0.224 mm in width. Only the right femur is measurable and is 1.309 mm long and 0.747 mm wide. Tibia are visible on both sides. The right one is 1.79 mm long and 0.233 mm in width, the remains of the left one is 0.223 mm long and its width is 0.167 mm. Overall, the longest spine is 0.607 mm long and 0.07 mm wide and is on the right leg. On the left the spine is 0.465 mm long and 0.036 mm wide. Also the longest spur is situated at the end of right tibia, 0.649 mm long but just 0.056 mm wide, supporting width compensation. Spurs and spines are arranged in a radial rosette around the tarsus base, but appear to be less open than in the holotype. The length of the whole tarsi are not measurable, but the width of the right one is 0.074 (max), 0.054 mm (min) wide and the left width is 0.062 (max) and 0.075 mm (min). The first proximal visible segments has even 0.85 mm on average on both sides, and the right second is 0.223 mm long and 0.17 mm on the left. A spine from one of the right segments is 0.066 mm long and 0.016 mm wide, on the left 0.045 mm long and 0.011 mm wide.

Abdomen: Dorsoventrally flattened, wide. Segments are longitudinally wrinkled. Surface is covered by a thin layer of air bubbles, visible in dorsal view. Ventral view shows abdomen length 2.631 mm. Externally protruding ovipositor is robust, 0.672 mm long at. The base is 0.576 mm wide. Subgenital plate is 0.493 mm long and 0.872 mm wide. Four sterna can be measured: S2 to S5. They are 0.275 mm, 0.256 mm, 0.25 mm and 0.499 mm long and 1.32 mm, 1.562 mm, 1.722 mm, 1.952 mm wide. The central axis furrow is not as distinct as on holotype.

Ovipositor is partially covered dorsally by subgenital plate, and by layer of semi-transparent laminated matter. Visible part is 0.58 mm in long and 0.612 mm wide proximally. Sensilla chaetica is distinct (in contrast to holotype), sparse, thin (width cca 0.006 mm) but long. The longest measured ovipositor sensilla is 0.157 mm long. Subgenital plate (T8) measurements as appearing is 0.195 mm long and 1.237 mm wide (damaged on right side). The longest sensilla here is 0.194 mm long.

Cerci multisegmented, fuzzy. Last segment is moniliform. The right cercus is 0.4 mm long, 0.171 mm wide on the base and 0.109 mm on the distal part. Sensilla here is 0.333 mm long. The left cercus appears longer, 0.429 mm, 0.175 mm wide on the base, 0.089 mm distally and sensilla 0.369 mm long.

Terga measurements T7 (0.345 mm long, 1.655 mm wide), T6 (0.315/ 1.789 mm), T5 (0.32/ 1.92 mm), T4 (0.35/ 2.035 mm), T3 (0.42/ 2.001 mm), T2 (0.31/ 1.737 mm) and the most proximal T1 is uncovered due to forewing remnants (0.908/ 1.447 mm).

BA P0001 (figs. 1 h, 2 d). This immature specimen is categorized into the present species on the basis of combination of hypognathous head and moniliform antenna, complete pronotum, 'moling' forelegs, abdomen surface structure.

NIGP P0001 ABCDEF (figs. 2 c, 3 a, 4 m; weight 11.6 g). These immature individuals are categorized into the present species on the basis of combination of hypognathous head and moniliform antenna, complete pronotum, 'moling' forelegs, abdomen surface structure**.** Sample was used for coprolite analysis (fig. 3 c).

Phylogenetically annotated character (n= 170) list

[106 corresponding characters of Engel et al. 2009 are in square brackets]

Head hypognathous - **plesiomorphy** at the level of the order (earliest Blattaria s.str.); unique trait within termites [9]

Head large - **plesiomorphy** at the level of the advanced Liberiblattinidae; head becomes smaller in elongated forms and large termites

Head globular - **symplesiomorphy** at level of certain advanced Liberiblattinidae (*Leptolythica*), and presumed earliest eusocial liberiblattinids as well as the most primitive know social cockroaches, the Socialidae; present also in some undescribed Umenocoleidae (some *Vitisma* spp. from Myanmar amber)

Head not elongated - **plesiomorphy** at the level of the order Blattaria; head is prognathous and extremely elongated in some undescribed termites and cockroaches from Myanmar amber. Prognathous also in numerous predatory Raphidiomimidae

Head entirely concealed by pronotum - **plesiomorphy** at the level of the order (earliest Blattaria s.str.); unique trait within termites [31]

Head smooth - **plesiomorphy** at the level of the order Blattaria. See character below!

Head with groove lines - **autapomorphy** of females or a cast

Head densely covered with setae - **autapomorphy** of eusocial cockroaches/termites; homoplasically this trait occurs in ant and termite nest-inhabiting cockroaches (Attaphilidae; all known Cretaceous Blattidae - *Balatronis, Spinka*; Olidae), and in most Corydoidea and desert species

Setae covering head fine - **autapomorphy** of eusocial cockroaches/termites; homoplasically this trait occurs in ant and termite nest-inhabiting cockroaches (Attaphilidae; all known Cretaceous Blattidae - *Balatronis, Spinka*; Olidae)

Head sensilla extremely long - **autapomorphy**

Y-shaped coronal ecdysial cleavage line in imago absent: - **plesiomorphy** at the level of the order Blattaria. It is present in *Mariconitermes talicei, Meiatermes araripena* and in advanced termites [17]

Eyes fully developed in immature stages – **plesiomorphy** at the level of the order (earliest Blattaria s.str.)

Eyes in immature stages large, not circular, kidney-shaped – **plesiomorphy** at the level of the order (earliest Blattaria s.str.); unique trait within termites [(20)]

Eyes in adults kidney-shaped – **plesiomorphy** at the level of the order (earliest Blattaria s.str.); unique trait within termites [20]

Eyes in adults small – **autapomorphy**; eyes undergo reduction in numerous living cockroach lineages (no fossil with reduced eyes is known) especially in cave species (Nocticolidae), but the reduction usually results in a circular or elongated shape, no kidney-shape is preserved

Eyes in adults protruding beyond lateral margin of head – **plesiomorphy** at the level of the order (earliest Blattaria s.str.); unique trait within termites [94]

Lateral ocelli present - **plesiomorphy** at the level of the order Blattaria [18]

Lateral ocelli extremely developed – **synapomorphic with Neoisoptera** [95]

Central ocellus present – **plesiomorphy** at the level of the order (earliest Blattaria s.str.); unique trait within termites, unless fontanelle is not a central ocellus remnant [4]

Central ocellus very small – **autapomorphy** (partial reduction of a unique trait); homoplasically reduction of central ocellus takes place in the lineage leading to all living cockroaches and in numerous extinct fossil lineages (at the genus level), but such small central ocellus remained undocumented

Frontal gland developed into distinct fontanelle – **autapomorphy** [8]

Antenna moniliform – **autapomorphy** of true termites (*Sociala* has filiform antenna)

Antenna short – **autapomorphy** of eusocial cockroaches/termites

Antenna with few segments – **autapomorphy** of eusocial cockroaches/termites; homoplasically this trait occurs in ant and termite nest-inhabiting cockroaches (Attaphilidae, filiform; all known Cretaceous Blattidae - *Balatronis, Spinka*, both filiform; Olidae, bipectinate) [1]

Apex of imago flagellum untapered – **plesiomorphy** at the level of the order (earliest Blattaria s.str.) [3]

Antennal sensilla comparatively long and dense – **autapomorphy of termites**

Mandible strong, massive, wide, not pinzeta-like – **plesiomorphy** at the level of the order (earliest Blattaria s.str.)

Marginal teeth of left mandible three or more – **autapomorphy** [11]

Subsidiary tooth of right mandible present – **autapomorphy** [12]

Notch between first and third marginal teeth present – **plesiomorphy at unknown level** [21]

Mandibular excavation between apical and first marginal teeth absent – **plesiomorphy at unknown level** [22]

Lacinial teeth of maxilla apical – **plesiomorphy at unknown level;** one tooth is subapical in some termites [this state is unknown in *P. eulna* and characters are attributed into matrix exclusively based on 13]

Palp short - **plesiomorphy** at the level of the order Blattaria. Palp is extremely long in *Sociala*, probably due to palpal manipulation or "antennation"

Palp extremely short – **synapomorphy with *T. vendeense* and others**

Palp 5 - segmented - **plesiomorphy** at the level of the order Blattaria

Clypeus high (long) - **plesiomorphy** at the unknown level (probably of the order Blattaria)

Anterior margin of postclypeus convex - **plesiomorphy** at the unknown level (probably of the order Blattaria) [reversely polarized 93]

Postclypeal furrow absent - **plesiomorphy** at the unknown level (probably of the order Blattaria) [14]

Neck short - **plesiomorphy** at the level of the order (earliest Blattaria s.str.); neck is elongated only in *Manipulator*

Head with pronotum and mesonotum not protruded - **plesiomorphy** at the level of the order Blattaria; It is elongated in *Mariconitermes.*

Pronotum fully developed - **plesiomorphy** at the level of the order (earliest Blattaria s.str.); pronotum partially reduces in numerous termites

Pronotum with paranotalia fully developed - **plesiomorphy** at the level of the order (earliest Blattaria s.str.); paranotalia reduce in numerous termite lineages and some bizarre cockroaches (Umenocoleoidea: Umenocoleidae, Alienopteridae)

Pronotal posterolateral corners of imago broadly arched - **plesiomorphy** at the level of the order (earliest Blattaria s.str.) [28]

Pronotum transverse - **plesiomorphy** at the level of the order (earliest Blattaria s.str.)

Pronotal posterior margin of imago rounded - **plesiomorphy** at the level of the order (earliest Blattaria s.str.) [29]

Pronotal anterior margin of imago concave - **plesiomorphy** at the level of the order (earliest Blattaria s.str.) [32]

Pronotum densely covered with setae - **autapomorphy** of eusocial cockroaches/termites; homoplasically this trait occurs in ant and termite nest-inhabiting cockroaches (Attaphilidae; all known Cretaceous Blattidae - *Balatronis, Spinka*; Olidae), and in most Corydoidea and desert species

Setae covering pronotum fine - **autapomorphy** of eusocial cockroaches/termites; homoplasically this trait occurs in ant and termite nest-inhabiting cockroaches (Attaphilidae; all known Cretaceous Blattidae - *Balatronis, Spinka*; Olidae)

Pronotum unmodified - **plesiomorphy** at the level of the order Blattaria; pronotum is frequently modified in termites, very rarely in cockroaches

Pronotum shape regular - **plesiomorphy** at the level of the order (earliest Blattaria s.str.); it is frequently carved in termites

Pronotum not very wide - **synapomorphy with advanced termites**; it is wide, but modified in *Cratomastotermes wolfschwenningeri*

Pronotum shape somewhat quadrate - **autapomorphy**

Pronotum shape somewhat converging towards apex – **synapomorphy with primitive termites** [30]

Pronotum with distinct disc - **plesiomorphy** at the level of the order (earliest Blattaria s.str.)

Pronotum without central ridge - **plesiomorphy** at the level of the order Blattaria. Ridge is present in *Mariconitermes talicei, Meiatermes araripena* and in advanced termites

Pronotal wings undeveloped - **symplesiomorphic** at the level of the order (earliest Blattaria s.str.) and above

Wings not especially long - **plesiomorphy** at the level of the order Blattaria; wings are frequently long in advanced and some Mesozoic termites.

Sclerotization of veins uniform - **plesiomorphy** at the level of the order Liberiblattinidae; vein become differentiated in all other termites, but not in *Sociala* and partially in *A. rossi* [55]

Forewing fully developed - **plesiomorphy** at the level of the order (earliest Blattaria s.str.); homoplasically FW becomes reduced both in borers, burrowers (common trait) and open-living cockroaches (less common) [46]

FW membranous - **plesiomorphy** at the level of the order (earliest Blattaria s.str.)

FW membrane transparent - **plesiomorphy** at the level of the order (earliest Blattaria s.str.)

FW (and HW) membrane microsetulose setae present - **synapomorphy of Mastotermitoidea, Eutermites and *Sociala*** [50]

FW (and HW) membrane smooth - **plesiomorphy** at the level of the order (earliest Blattaria s.str.); membrane is nodulose or pimplate in some termites [59]

FW base diverging, triangular with narrow base - **synapomorphy** of Mastotermitoidea and Eutermites, *Sociala* has base more or less normally wide [62]

FW apex shape round, nearly globular - **symplesiomorphy** at the level of earliest eusocial cockroaches; this trait rarely homoplasically occur over the cockroach system, and reduces back to the original state (somewhat sharp apex) in numerous termites

FW clavus delimited - **plesiomorphy** at the level of the order (earliest Blattaria s.str.); this trait reduced in all termites except Mastotermitoidea (present in Sociala) [71]

FW clavus partially sclerotised - **synapomorphy with *Krishnatermes yoddha***

FW clavus not elytrised completely **- plesiomorphy** at the level of the order Blattaria; it is entirely sclerotized in *Krishnatermes yoddha*

FW clavus as long as basal sutura **- plesiomorphy** at the level of the order termites, present in *Krishnatermes* and *Mastotermes*, but shorter in *Meiatermas* [65]

FW clavus small - **synapomorphy** of Mastotermitoidea, *Sociala* has clavus normally developed

FW anal veins other than in standard cockroaches - **synapomorphy** of termites; only *Sociala* has unmodified A

FW anal veins indistinct - **synapomorphy** of termites; only *Mariconitermes talicei* has A distinct (and also *Sociala*)

FW anal veins modified - **synapomorphy** of termites *except Mariconitermes talicei*

FW radial fracture present - **autapomorphy** of eusocial cockroaches/termites [60]

FW breaking basal cleavage sutura present - **autapomorphy** of eusocial cockroaches/termites [52]

FW breaking sutura distinct anteriorly - **autapomorphy** of termites

FW veins thick - **synapomorphy of Corydoidea at the level of earliest Liberiblattinidae**

FW veins extremely thick - **synapomorphy of Mastotermitoidea**, *Sociala* has veins thick, but not extremely

FW regular intercalaries present - **plesiomorphy** at the level of Phyloblattidae

FW cross-veins absent - **autapomorphy** of eusocial cockroaches/termites; homoplasically this trait rarely occurs in small species (Nocticolidae, new family from Myanmar amber) [54]

FW venation regular - **plesiomorphy** at the level of Phyloblattidae; venation is regular also in Socialidae, but not in termites (neither in Mastotermitoidea)

FW venation simplified – **plesiomorphy at level of Liberiblattinidae;** also in *Sociala* and all termites, *Mastotermes* rich venation seems secondary [(72)]

FW reticulations present (CuA/P area) – ***synapomorphy of mastotermites;*** absent in *Sociala* [61]

FW reticulations rare – **plesiomorphy at level of Liberiblattinidae**

FW costal field narrow - **symplesiomorphy** at level of Liberiblattinidae

FW radial field narrow, FW partially costalised (R, RS ascending in sharp angle, branched) - **synapomorphy of Mastotermitoidea**, **Eutermites and *Sociala***

FW not fully costalized (C+Sc+R and Rs not extremely close and simple and parallel) - **plesiomorphy** at the level of the order (earliest Blattaria s.str.) [67]

FW subcosta extremely short, reaching only about a fourth of the wing length – **synapomorphy of termites except *Mariconitermes, Cratomastotermes* and *Sociala*;** no homoplasies, likely related with the clavus reduction

FW radial veins ascending sharply - **synapomorphy** of eusocial cockroaches/termites (including *Sociala*)

FW radial veins ascending extremely sharply - **synapomorphy with most primitive termites, *Cratomastotermes, Meiatermes* and *Mariconitermes*;** paradoxically eusocial cockroaches and more advanced termites retained more primitive character of more or less normally ascending R; this trait likely related to fusion of RS with M

FW radial veins present - **plesiomorphy** at the level of the order (earliest Blattaria s.str.) [45]

FW radial veins greatly simplified - **synapomorphy with primitive termite *Mariconitermes talicei***

FW R short, not reaching apex - **synapomorphy with primitive termite *Mariconitermes talicei*.** In *Sociala* it is also plesiomorphically near apex [42, 70]

FW "radius sector" undifferentiated - **autapomorphy** [73]

FW medial vein present - **plesiomorphy** at the level of the order (earliest Blattaria s.str.) [48]

FW medial vein richly branched - **plesiomorphy** at the level of the order (earliest Blattaria s.str.) [69]

FW M with ascending (in addition to descending) veins reaching apex - **synapomorphy with *Mariconitermes talicei* and *Meiatermes araripena*** [69- originally this character refer to RS, we interpret this branch as ? although both branched might become fused]

FW cubitus anterior standard - **plesiomorphy** at the level of the order Blattaria; CuA is running and densely branching along posterior margin in *Meiatermes araripena* and some advanced termites

FW cubital area short and narrow - **autapomorphy** *of Sociala and termites, possibly inherited from unknown Liberiblattinidae* [44]

FW cubitus posterior curved sharply - **synapomorphy** of advanced Liberiblattinidae within Corydioidea [63]

FW apical margin meeting or overlapping HW - **plesiomorphy** at the level of the order (earliest Blattaria s.str.); termite scales are usually well-separated [49]

Hindwing present - **plesiomorphy** at the level of the order (earliest Blattaria s.str.) [47]

Hindwing fully developed - **plesiomorphy** at the level of the order (earliest Blattaria s.str.)

HW basal cleavage absent - **plesiomorphy** at the level of the order (earliest Blattaria s.str.)[53]

HW membranous - **plesiomorphy** at the level of the order (earliest Blattaria s.str.)

HW membrane transparent - **plesiomorphy** at the level of the order (earliest Blattaria s.str.)

HW reticulations present – **synapomorphy with mastotermites;** reticulations are absent in *Sociala* [58]

HW reticulations pigmented – **autapomorphic** [58]; reticulations are secondary

HW reticulations rare – **symplesiomorphy at the level of termites**

HW shape round, nearly globular - **symplesiomorphy** at the level of earliest eusocial cockroaches; this trait rarely homoplasically occur over the cockroach system, and reduces back to the original state (somewhat sharp apex) in numerous termites

HW with distinct vannus - **plesiomorphy** at the level of the order (earliest Blattaria s.str.); this trait reduces in termites except Mastotermitoidea [56]

HW venation strictly regular – ***symplesiomorphy*** at the level of Liberiblattinidae

HW venation complete - **plesiomorphy** at the level of order s.l.

HW venation simple - **synapomorphy with advanced Liberiblattinidae and all eusocial dictyopterans;** rich venation of *Mastotermes* is secondary

HW intercalaries distinct – ***symplesiomorphy*** at the level of Phyloblattidae

HW cross-veins present - **plesiomorphy** at the level of Neorthroblattinidae

HW cross-veins sporadic (2) – **synapomorphy of eusocial dictyopterans;** reduction is due to non-repeated nuptial flight and wing shedding

Some HW veins not ending at margin – this deformity is **not a diagnostic character**, although such fusions and incomplete venation patterns are characteristic for termites due to impoverished flight activity and is rare in active cockroaches

HW subcostal area short, reaching a third of the wing – **synapomorphy** of advanced Liberiblattinidae and all descendant Corydioidea; this trait has reversal in numerous lineages (within Umenocoleidae, Blattulidae, Liberiblattinidae and living taxa)

HW subcostal area narrow – **symplesiomorphy** at the level of Voltziablatta-group; trait with exceptions present in all Corydioidea

HW SC simple – **symplesiomorphy** at the level of Voltziablatta-group; trait with exceptions present in all Corydioidea

HW R1 fused with RS – **autapomorphy**; without homoplasies (except for possibly homoplasic *K. burmensis*)

HW R1 branches transversal – **symplesiomorphy** at the level of Voltziablatta-group; trait with exceptions present in all Corydioidea

HW radial area straight, R stem not vaulted – **symplesiomorphy** at the level of Voltziablatta-group; trait present in all Corydioidea except sigmoidal in Umenocoleoidea and Blattulidae

HW M absent - **synapomorphy with *Cratomastotermes*;** this trait is probably (paradoxically) present in other primitive termites as a synapomorphy, but HW was unpreserved; M is plesiomorphically preserved in all advanced termites [107]

HW CuA secondarily branched – **symplesiomorphy** at the level of Liberiblattinidae; CuA are obligatory simple in Umenocoleidae and Blattulidae

HW CuP simple; it is shortened (fusion, deformity) in left HW - **symplesiomorphy** at the level of Liberiblattinidae

HW A1 present in remigium [57] - **plesiomorphy** at the level of the order (earliest Blattaria s.str.); this trait seems to reduce in termites except Mastotermitoidea (at least this character was never preserved out of this group)

HW A1 branched basally [57] - **plesiomorphy** at the level of the order (earliest Blattaria s.str.); this trait is present also in advanced Liberiblattinidae

Foreleg fossorial – ***autapomorphy*** *without homoplasies*

Procoxal ventral keel present - **plesiomorphy** at the level of the order (earliest Blattaria s.str.) [39]

Legs fully carinated - **plesiomorphy** at the level of the order (earliest Blattaria s.str.); *Mastotermes* retained full, but shortened carination, lost in other termites [(40)]

Legs fully carinated with long setae - **plesiomorphy** at the level of the order (earliest Blattaria s.str.)

Tibial spurs smooth (but with helical ridges) or pimplate - **plesiomorphy** at the level of the order (earliest Blattaria s.str.); spurs are slightly pimplate to heavily serrate in numerous Cretaceous (rarely) and Cenozoic to living true cockroaches [33]

Tibial spurs asymmetrical, with one side flattened - **plesiomorphy** at unknown level (all known amber cockroaches); spurs are symmetrical in some termites [34]

Protibial apical spurs 3 or more - **plesiomorphy** at the level of the order (earliest Blattaria s.str.) [99]

Mesotibial apical spurs 5 or more - **plesiomorphy** at the level of the order (earliest Blattaria s.str.) [100]

Metatibial apical spurs 4 or more - **plesiomorphy** at the level of the order (earliest Blattaria s.str.) [101]

Tarsi pentamerous - **plesiomorphy** at the level of the order (earliest Blattaria s.str.) [35]

All tarsi unspecialized - **plesiomorphy** at the level of the order (earliest Blattaria s.str.); termites (unknown in *Sociala*) tarsi are specialized and also some Liberiblattinidae have tarsi specialized (with tarsal segments shortened and of similar length)

Numerous tarsomeres extremely shortened – **autapomorphy** of some termites

Metabasitarsomere longer than 3 times the width - **plesiomorphy** at the level of the order (earliest Blattaria s.str.) [36]

Arolia present - **plesiomorphy at the level of the Liberiblattinidae** and possibly earlier (earlier evidence is absent)

Arolia rudimentary - **synapomorphic** with termites; arolia are homoplasically reduced in numerous cockroach lineages including all Mesozoic Blattidae

Arolia extremely reduced - **autapomorphy;** loss of arolium is homoplasically present throughout Dictyoptera (e.g., all known Cretaceous Blat-

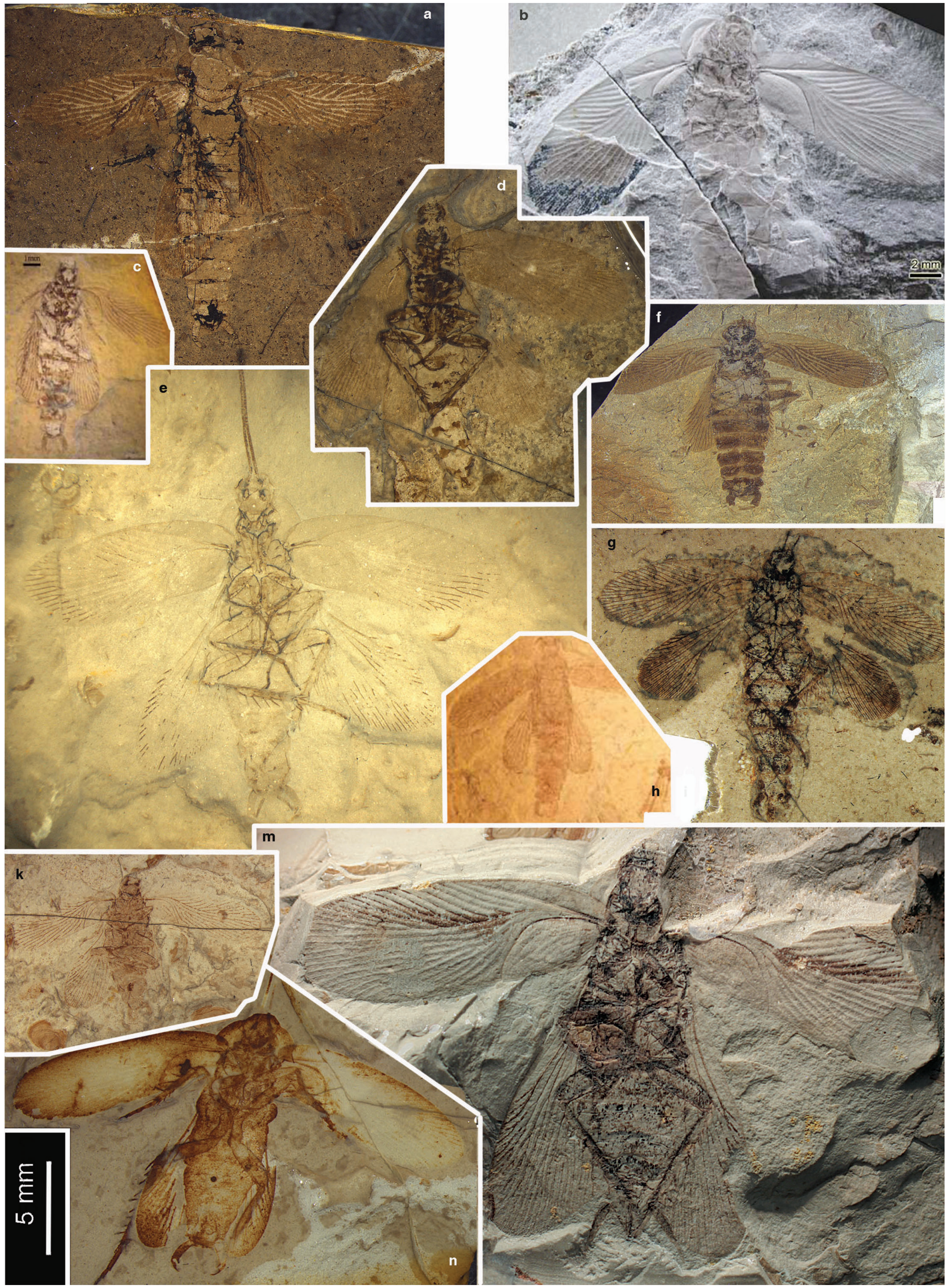


Figure SI3 (5) | **Huge diversity and disparity of forms of a single indigenous cockroach family, Fuziidae.**
The Middle Jurassic Daohugou Lagerstatte in Inner Mongolia, China. Collection of the Capital Normal University, Beijing.

tidae do not possess arolium); while arolia are retained in advanced true Cretaceous termites [37]

Pulvilli present – **symplesiomorphic at the level of advanced Liberiblattinidae;** pulvilli become lost along with the modification of tarsi in termites [38]

Pulvilli small – **autapomorphy**; homoplasically pulvilli reduce along the cockroach taxa

Forelegs with 'moling' adaptations - **autapomorphy;** no homoplasies among Dictyoptera

Tarsal claws symmetrical - **plesiomorphy** at the level of the order (earliest Blattaria s.str); claws become asymmetrical along the cockroach spectrum

Body fat - **plesiomorphy** at the level of the order (earliest Blattaria s.str); body of termites tend to reduce, exception is *Mastotermes*

Body exceptionally telescopic - **autapomorphy;** homoplastically occurs also in living *Compsagis*

Body nearly round in diameter - **autapomorphy;** homoplastically occurs also in living *Compsagis*

Female with externally protruding ovipositor - **plesiomorphy** at the level of the order (earliest Blattaria s.str.); absent in living cockroaches and termites present in ancestral Liberiblattinidae, unknown in Socialidae

Body surface "cracked" - **autapomorphy** (this character is present in all specimens and thus is not a post-burial artifact)

Sternal gland present - **plesiomorphy** at the level of the superfamily (occurs also in Caloblattinoidea derived from ancestral Phyloblattidae) [102-104 regarded herein as a single character due to common homeotic mixage of any structure position on body]

Male tergal gland present - **plesiomorphy** at the level of the Phyloblattoidea (probably), confirmed at the level of Caloblattinoidea (Fuziidae); unique trait within termites; homoplasically male tergal glands might reduce throughout the systematic spectrum of cockroaches

Cerci present - **plesiomorphy** at the level of the order (earliest Blattaria s.str.); occur in termites

Cerci multisegmented (4-) - **plesiomorphy** at the level of the order (earliest Blattaria s.str.); reduced in certain termites to 4 or 3 segments [75]

Cerci with less than 4-8 segments **- symplesiomorphy of primitive termites** (state unknown in *Sociala*); this trait homoplasically occur also in Umenocoleoidea (including Alienopteridae)

Cerci shortened, but normally wide **- plesiomorphy** at the level of the order (earliest Blattaria s.str.); termite cerci are narrow

Cerci not rudimentary - **plesiomorphy** at the level of the order (earliest Blattaria s.str.); termite cerci are rudimentary

Cerci without long sensillae - **autapomorphy** of termites (state unknown in *Sociala*)

Styli of immatures present- **plesiomorphy** at the level of the order (earliest Blattaria s.str.)

Immature styli 2-segmented- **plesiomorphy** at the level of the order (earliest Blattaria s.str.)

Styli of adult (including female) absent - **autapomorphy**; this trait is homoplasically lost in numerous cockroach and termite lineages. Styli are present in termite *Meiatermes hariolus* [74]

Social organization - **synapomorphy of termites, *Sociala,* mastotermites, and *Cryptocercus*** [(81)]

Eusocial organization – **autapomorphy of mastotermites**; possibly homoplasically developed by true termites with *Sociala* [81]

Societies living in wood – **symplesiomorphy at the level of earliest eusocial dictyopterans**; advanced termites can construct true nests [82]

Feces (semi)hexagonal **- synapomorphy of eutermites and mastotermites;** *Cryptocercus* has normally shaped feces; state is unknown in *Sociala*

Wood feeding [80] **- synapomorphy of eutermites and mastotermites;** unknown but expected for *Sociala*

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