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Short communication

A new Cretaceous cockroach with heterogeneous tarsi preserved in Burmese amber (Dictyoptera, Blattodea, Corydiidae)

Xin-Ran Li [a, b], Diying Huang [a, c, *]

[a] State Key Laboratory of Palaeobiology and Stratigraphy, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing 210008, Jiangsu, China
[b] University of Science and Technology of China, Hefei 230026, Anhui, China
[c] Center for Excellence in Life and Paleoenvironment, Chinese Academy of Sciences, Nanjing 210008, China

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ABSTRACT

Here we describe a new corydiid cockroach, *Nodosigalea burmanica* gen. et sp. nov., from the middle Cretaceous Burmese amber. The well-preserved specimens exhibit a typical habitus of Corydiidae, and are characterized by nodulous pronotum, distinct wing venation and unique tarsi, the hind ones of which have different ventral structures from the fore- and midlegs. The combination of adhesive fore- and midtarsi and propulsive hindtarsi suggests a particular life style of the new genus. The phylogenetic position of the new genus within Corydiidae, however, is uncertain.

1. Introduction

Members of Corydiidae (=Polyphagidae) are sometimes called sand cockroaches or desert cockroaches. Their pronota and tegmina are often pilose, and the flat (i.e. not fanwise folded) vannus characterizes the family, although this character should be plesiomorphic for cockroaches (but see a case of derived flat vannus in Grandcolas and Deharveng, 2007), in contrast to the reduced one in Nocticolidae (or Nocticolinae in Corydiidae), or fanlike ones in other winged families of crown cockroaches (Roth, 2003). Corydiidae, nesting "Nocticolidae", are sister to the remaining crown cockroaches and termites (Djernæs et al., 2015; Legendre et al., 2015; Wang et al., 2017), and their history was estimated to start in the Triassic-Jurassic boundary (Wang et al., 2017), Triassic (Djernæs et al., 2015), or latest Permian (Legendre et al., 2015). Triassic might be more plausible because some of the fossils used for calibration in the other two estimations are not justified (Evangelista et al., 2017). A phylogenomic study (Misof et al., 2014) suggested that Dictyoptera *sensu stricto* (mantises, crown cockroaches and termites) started at the Triassic-Jurassic boundary; according to this study, Corydiidae may start in the Jurassic.

Seventeen cockroach fossils were recorded under Corydiidae (Table 1), the earliest ones come from Cretaceous. Unfortunately, eight species are too poor to consider in classification, six of which are represented by isolated tegmen or tegmina. The wings of cockroaches bear abundant plesiomorphies and homoplasies (Evangelista et al., 2017), and tegminal venation is variable even within one species (Ross, 2012); therefore taxonomic studies on extant taxa do not rely much on the tegmen unless the latter bears unique characters. In contrast, many fossil cockroaches are described from isolated tegmen or tegmina, most of which cannot reliably characterize the genera or species. The type specimens of two genera described from Ypresian (Cenozoic) Fushun ambers (Hong, 2002) are, though well preserved, of dubious inclusion in Corydiidae. The specimens, which are nymphs, cannot distinguish these genera from other cockroach families; therefore the credibility of these genera remains to be confirmed. There is a shortage of reliable records of early Corydiidae, and our new materials from Cretaceous Burmese ambers constitute essential records of the evolutionary history of Corydiidae.

* Corresponding author. State Key Laboratory of Palaeobiology and Stratigraphy, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing 210008, Jiangsu, China.
E-mail addresses: ConlinMcCat@gmail.com (X.-R. Li), dyhuang@nigpas.ac.cn (D. Huang).

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Table 1
Fossil species purported to be of Corydiidae

Genus and species	Age	Locality	Preservation of holotype or syntypes	Reference	Credibility
Cretaholocompsa Martínez-Delclòs, 1993				Martínez-Delclòs, 1993	good in Corydiidae (close to Holocompsinae according to Evangelista et al., 2017)
[a]*C. montsecana* Martínez-Delclòs, 1993	Barremian	Montsec Range, Spain	head, pronotum, forelegs, tegmina; in lime mudstone	Martínez-Delclòs, 1993	as above
Vitisma Vršanský, 1999				Vršanský, 1999	good in Corydiidae
V. occidentalis Vršanský and Ansorge, 2001	Barremian	Montsec Range, Spain	tegmina; in lime mudstone	Vršanský and Ansorge, 2001	good in genus, poor for itself
V. orientalis Vršanský, 2005	Barremian	Sharin-Gol, Mongolia	tegmen; in coal quarry	Vršanský, 2005	good in genus, poor for itself
[a]*V. rasnitsyni* Vršanský, 1999	Aptian	Baissa, Russia	leg almost lost, no abdomen; in marl/siltstone	Vršanský, 1999	good
V. diffusa Vršanský, 2003	Aptian	Bon Tsagaan, Mongolia	tegmen; in siliciclastic rock	Vršanský, 2003	good in genus, poor for itself
Netherea Vršanský and Anisyutkin, 2008				Anisyutkin et al., 2008	poor in Corydiidae
[a]*N. haatika* Vršanský and Anisyutkin, 2008	Turonian	Gerofit, Israel	tegmen; in shale	Anisyutkin et al., 2008	as above
Ergaula Walker, 1868					living genus
E. atica Vršanský and Anisyutkin, 2008	Turonian	Gerofit, Israel	tegmen; in shale	Anisyutkin et al., 2008	poor in Corydiidae, poor for itself
E. stonebut Vršanský et al., 2013	Danian	Belaya Gora, Russia	tegmen; in siliciclastic rock	Vršanský et al., 2013	poor in Corydiidae, poor for itself
Dromocites Hong, 2002				Hong, 2002	poor in Corydiidae
[a]*D. guchengziensis* Hong, 2002	Ypresian	Fushun, China	almost complete nymph; in amber	Hong, 2002	uncertain
D. orbiculigastralatus Hong, 2002	Ypresian	Fushun, China	almost complete nymph; in amber	Hong, 2002	uncertain
Testudiblatta Hong, 2002				Hong, 2002	poor in Corydiidae
[a]*T. xilutianensis* Hong, 2002	Ypresian	Fushun, China	almost complete nymph; in amber	Hong, 2002	uncertain
Paralatindia Saussure, 1868					living genus
P. saussurei Scudder, 1890	Ypresian-Lutetian	Green River, Wyoming	unrecognizable; in diatomite/shale	Scudder, 1890	poor in Corydiidae
Homoeogamia Burmeister, 1838					living genus
H. ventriosa Scudder, 1876	Priabonian	Florissant, Colorado	last five segments of abdomen; in shale	Scudder, 1890	poor in Corydiidae
Proholocompsa Gorochov, 2007				Gorokhov, 2007	good in Corydiidae
[a]*P. fossilis* (Shelford, 1910)	Priabonian	Kaliningrad, Russia	complete; in amber	Shelford, 1910; Gorokhov, 2007	good
Paraeuthyrrhapha Anisyutkin, 2008				Anisyutkin, 2008	excellent in Corydiidae
[a]*P. groehni* Anisyutkin, 2008	Priabonian	Kaliningrad, Russia	complete; in amber	Anisyutkin, 2008	as above
Holocompsa Burmeister, 1838					living genus
H. abbreviate Gorochov and Anisyutkin, 2007	Burdigalian/ Langhian	Dominica	complete; in amber	Gorokhov, 2007	good
H. nigra Gorochov and Anisyutkin, 2007	Burdigalian/ Langhian	Dominica	almost complete; in amber	Gorokhov, 2007	good

[a] Type species of the genus.

2. Material and methods

The ambers are from deposits in the Hukawng Valley of northern Myanmar (see Grimaldi et al., 2002, fig. 1), currently considered to be of the earliest Cenomanian age (Shi et al., 2012), Albian-Cenomanian boundary (Rasnitsyn et al., 2016), or Albian (Ross et al., 2010), more likely late Albian. Specimens are deposited in Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences.

Ambers were filed with abrasive papers and polished with polishing powder. Normal photos were taken with a Canon 5D camera, a Zeiss SteREO Discovery V20 stereoscope, or a Zeiss AxioZoom V16 stereoscope, green ones were taken with a Zeiss AXIO Imager Z2 microscope; stacked using CombineZP software (by Alan Hadley); and optimized using Photoshop CS6.

Morphological terminology largely follows Roth (2003); venational terms follow Snodgrass (1935), with further interpretations by Smart (1951) and Li and Wang (2017) as a frame of reference. The unit of measurement is millimetre. Measurements of tarsomeres are taken from the lateral midline. This publication and nomenclatural acts herein were registered in ZooBank, and the LSID for this paper is urn:lsid:zoobank.org:pub:E603A53E-75E7-4D0E-ACA7-1E06FBB60FCC.

3. Systematic palaeontology

Order Dictyoptera
Suborder Blattodea
Family Corydiidae

Genus ***Nodosigalea*** gen. nov.
(urn:lsid:zoobank.org:act:339E7440-766B-4A22-847D-601CDBB12516)
Type species: *Nodosigalea burmanica* sp. nov.

Etymology. *Nodos*-, full of knots; *galea*, helmet, feminine; referring to the pronotum full of tubercles.
Diagnosis (male only). Head: totally concealed under pronotum; eyes large and long, in contact at vertex; ocelli large and bulging; clypeus swollen. Thorax: pronotum with dense tubercles, each of which bears a hair; apices of tegmen and hindwing free of veins; tegmen with several mediocubital veins that are incomplete at both ends; anteroventral margin of forefemora with a row of even spinules (type C according to Roth, 2003), terminating with one large spine (thus type C1); anterodorsal termination of mid- and hindfemora with a spine. Plantulae present at four proximal tarsomeres in fore- and midtarsi, whilst those tarsomeres in hindleg with paired ventral spines instead; claws symmetrical, not specialized; arolium moderate in size. Abdomen: cercus moniliform; subgenital plate (sternum 9) symmetrical, with two similar styli.

Species included. *Nodosigalea burmanica* gen. et sp. nov. described herein.
Taxonomic placement. The simple, flat folding of the hindwing excludes the new genus from Blattoidea and Blaberoidea. The spination type (C1) is widely distributed among Corydiidae. Whether or not it belongs to Corydiidae depends on the female ovipositor, which distinguishes between stem and crown cockroaches. However, females are unavailable in the present study. Nevertheless, the habitus and head morphology (mainly ocelli and clypeus) are typical of Corydiidae.

Nodosigalea burmanica gen. et sp. nov. (Figs. 1–3)
(urn:lsid:zoobank.org:act:2277741E-B8FD-4F5A-87F4-EB38FFB2582E)

Holotype. A male adult preserved in amber, almost complete, apices of antennae and left tegmen, and left midleg except coxa lost, NIGP168022.
Paratype. A male adult preserved in amber, shrunken and deformed, almost complete with apices of legs lost, NIGP168023.
Etymology. Type locality, Myanmar, also known as Burma.
Description. Measurements are of holotype, unless indicated otherwise. Body length 8.6 (holotype) –9.7 (paratype), overall length including wings 11.6 (holotype) –12.3 (paratype). Head (Figs. 1B, 2C): width including eyes 1.4, length from upper margin of eyes to lower margin of labrum 1.7; eyes height 1.2; ocellar diameter

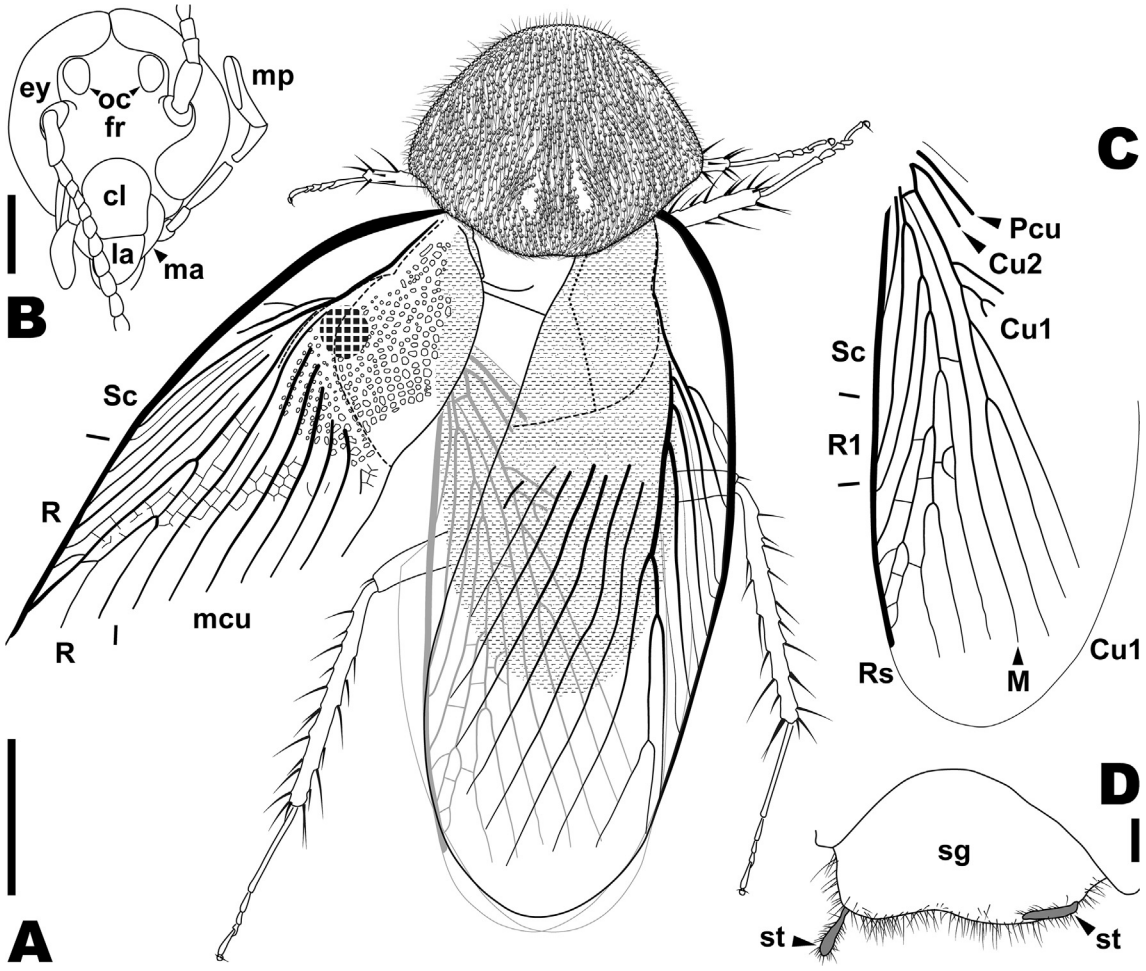

Fig. 1. *Nodosigalea burmanica* gen. et sp. nov., holotype. **A.** Dorsal habitus with hindwings drawn in grey; dot-dash shading, covered body part; grid shading, obstacle; dashed line, furrow; to the left of the dotted line on right tegmen is smooth, and the right is punctate. **B.** Head, ventral view. **C.** Left hindwing detached from inset A. **D.** Subgenital plate, ventral view. Abbreviations: cl, clypeus; ey, eye; fr, frons; la, labrum; ma, mandible; mp, maxillary palpus; oc, ocelli; sg, subgenital plate; st, stylus. Scale bars: A, 2 mm; B, 0.5 mm; D, 0.2 mm.

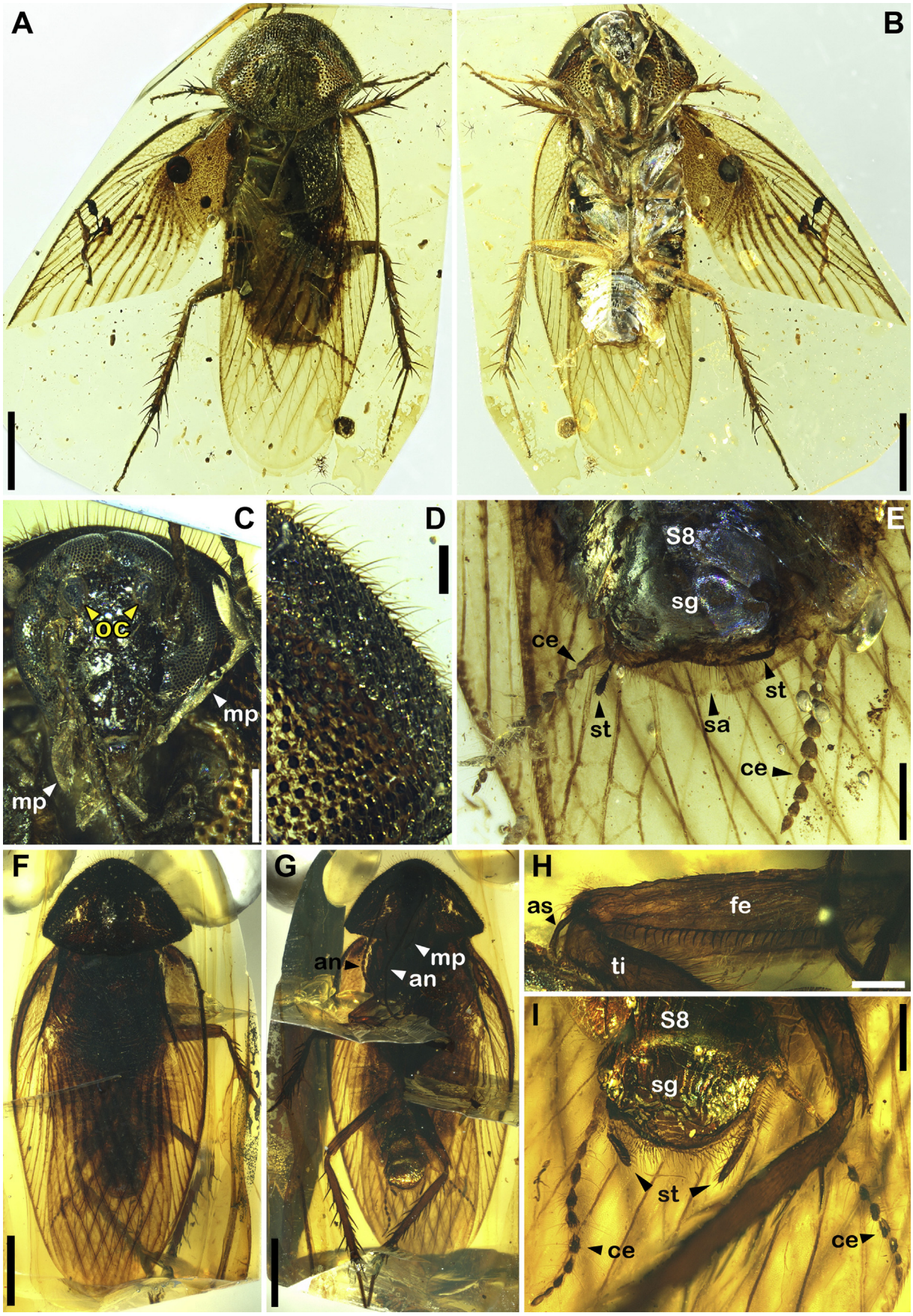

Fig. 2. *Nodosigalea burmanica* gen. et sp. nov. **A**–**E.** Holotype. **C.** Head, ventral view. **D.** Detail of pronotum, showing tubercles and hairs. **E.** Terminalia, ventral view. **F**–**I.** Paratype. **H.** Right forefemur, anterior view. **I.** Terminalia, ventral view. Abbreviations: an, antenna; as, apical spine; ce, cercus; fe, femur; mp, maxillary palpus; oc, ocelli; S8, sternum 8; sa, supra-anal plate; sg, subgenital plate; st, stylus; ti, tibia. Scale bars: A,B,F,G, 2 mm; C,E,I, 0.5 mm; D, 0.25 mm; H, 0.2 mm.

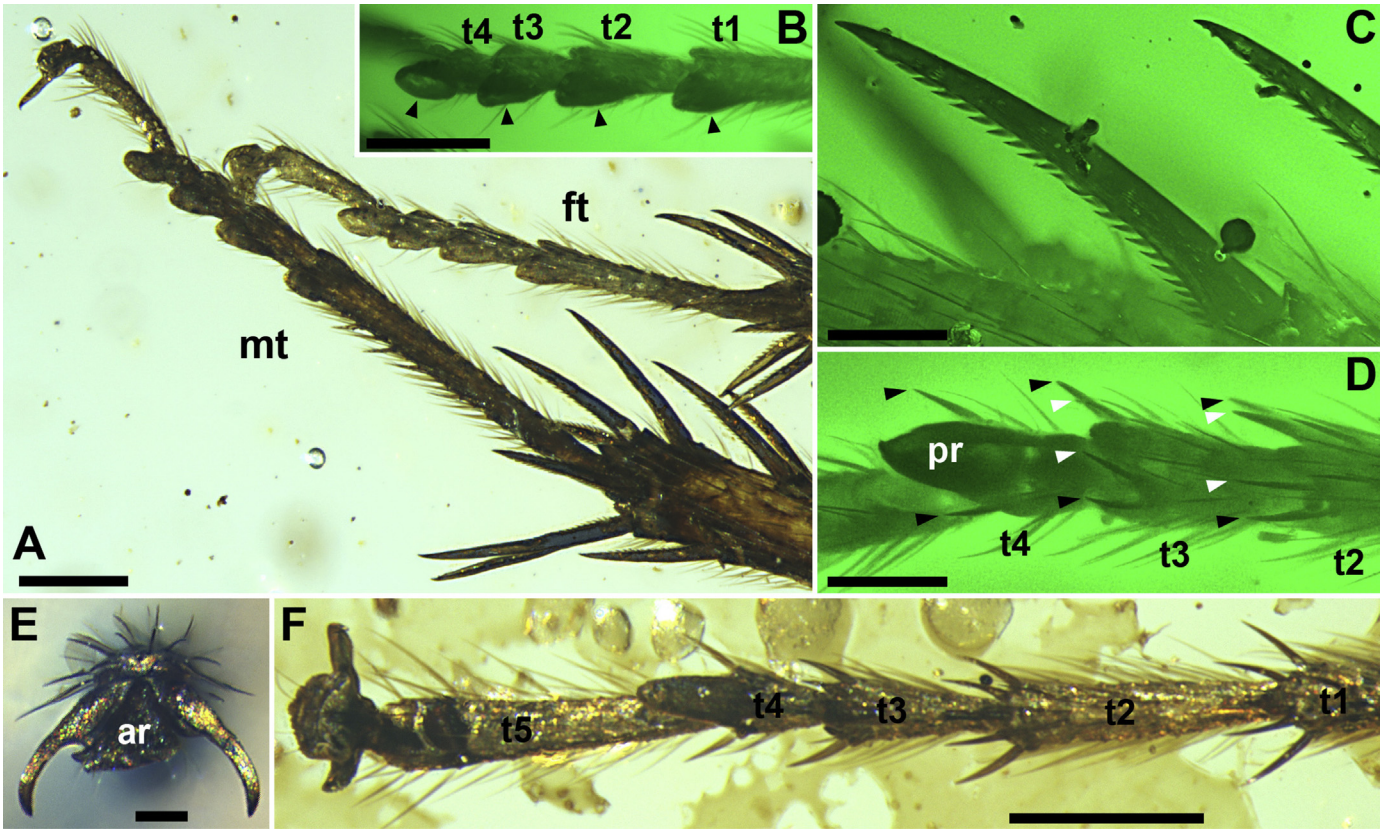

Fig. 3. *Nodosigalea burmanica* gen. et sp. nov. Leg details of the holotype. **A.** Fore- and midtarsus. **B.** Foretarsus with black arrowheads indicating plantulae. **C.** Tibial spine, showing serration; only one of the two rows is visible from this view. **D.** Hindtarsus with black arrowheads indicating outer pair of ventral spines and white ones for inner spines. **E.** Hind claws and arolium. **F.** Hindtarsus, ventral view. Abbreviations: ar, arolium; ft, foretarsus; mt, midtarsus; pr, process; t1–t5, tarsomere 1–5. Scale bars: A, 0.25 mm; B,F, 0.2 mm; C,D, 0.1 mm; E, 50 μm.

0.22–0.24; antennal length at least half of body length (apex not preserved); maxillary palpomere 1–5 lengths 0.11/0.14/0.38/0.26/0.48. Pronotum: length 3.8 and width 3.0, ratio 1.27; in posteromedial pronotum, tubercles and hairs are specially arranged, making room for a pair of smooth areas (Fig. 1A). Tegmen: length 9.2 and width 3.3, clavus length 3.4 and width 1.7, full of pits, veins invisible; costal vein not extending to wing apex, triangular prism-like, the outer surface perpendicular to wing plane and pilose; with seven mediocubital veins, the posteromost one extremely reduced (Fig. 1A). Hindwing: costal vein not extending to wing apex, pilose; Sc, R1, Rs and M with 1/1/9/1 terminal veinlets, only eight anterior veinlets complete (Fig. 1C). Leg: evenly setose, segments length (femur/tibia//tarsomere 1/2/3/4/5): foreleg 1.5–1.6/0.84–0.88//0.60/0.20/0.12/0.079/0.27, midleg 2.3/1.7//0.,84/0.22/0.14/0.091/0.31, hindleg 2.1–2.2/3.0//1.2/0.30–0.32/0.16–0.18/0.083–0.10 (+0.12 plantula?)/0.39–0.42. Tibiae with long spines, which bear two rows of serration on the inner surface (Fig. 3C). Plantulae present at four proximal tarsomeres in fore- and midtarsi (Fig. 3A,B), fourth tarsomere of hindleg with a pair of spines, and a long process which may be a large plantula, but the first through third tarsomeres apparently lack plantulae, two pairs of spines instead (Fig. 3D,F). Terminalia: hind margin of supra-anal plate (tergum 10) convex, setose, with a wide shallow incision medially (Fig. 2E); cerci length 1.4, with ten segments, and scattered long hairs (Fig. 2E,I). Hind margin of subgenital plate (sternum 9) concave, setose (Figs. 1D, 2E). Styli on the posterolateral margins of the plate (Figs. 1D, 2E,I), clavate, symmetrical, setose, length 0.25.

Remarks. The new genus is currently monotypic, therefore a diagnosis for *Nodosigalea burmanica* gen. et sp. nov. is unavailable. Nevertheless, we suggest the following characters of the new species to be considered in interspecific comparison in the future: the pair of smooth areas in the pronotum (Figs. 1A, 2A), and the seven free mediocubital veins in the tegmen, with the posteriormost vestigial. Although the venation pattern is variable within a species, the sparse veins tend to be conserved.

4. Discussion

Ambers allow us to investigate the morphology of cockroaches in a manner similar to extant specimens. While our materials preserve many details, it is still difficult to identify this new genus to a subfamily of Corydiidae. The subfamilial taxonomy of Corydiidae, unfortunately, is far from clear. According to Beccaloni (2014), 14 out of 40 genera of extant Corydiidae are not identified to subfamily, and 19 out of 26 classified genera are Corydiinae. From another perspective, the subfamilies of Corydiidae are based on wing venation (see Rehn, 1951), and thus immature and undefined, in contrast to other cockroach subfamilies that are delimited with oviposition behaviour and genitalia morphology (see McKittrick, 1964). Corydiidae remain insufficiently sampled even in recent phylogenetic studies (e.g. Legendre et al., 2015; Wang et al., 2017). Fossil Corydiidae will be more valuable when the taxonomy of extant taxa is more robust.

Nodosigalea gen. n. has a unique character set within Corydiidae, but some of the characters are similar to those of extant genera. The bulging ocelli and the swollen clypeus are typical of some larger species of Corydiinae (e.g. *Arenivaga* spp., see Hopkins, 2014). The nodulose pronotum is found in some corydiines (e.g. *Eucorydia*, see Qiu et al., 2017). These may suggest a close relationship to Corydiinae and even the inclusion in Corydiinae, but the wing venation

of *Nodosigalea* gen. n. is distinct from known forms as far as we know: it is much simpler than that of many corydiid genera and has a unique veinless apex (see Rehn, 1951), and simple forms (e.g. Holocompsini, see Gorokhov, 2007; Rehn, 1951) are far different from *Nodosigalea* gen. nov. The tarsi of *Nodosigalea* gen. n. and suchlike tarsal differentiation is rare among cockroaches. The tarsal plantulae in fore- and midlegs are adhesive devices that allow the cockroach to perch or forage on leaves, whilst the tarsal spines on hindlegs can help with rapid movement (Bell et al., 2007). This combination should play a vital role in the life history of *Nodosigalea* gen. n. Similar tarsi were found in *Pseudocalolampra inexpectata*, of which the proximal two hindtarsomeres have distal spines instead of plantulae (Anisyutkin, 2018). Although the phylogenetic position of *Nodosigalea* gen. n. within Corydiidae is currently uncertain, the new specimens should be more informative when more affinitive fossils are found and a robust systematics of Corydiidae is established.

5. Concluding remarks

Nodosigalea burmanica gen. et sp. nov., a cockroach of Corydiidae, is described from Burmese ambers. The fossils are well preserved, and allow detailed documentation. It is uncertain, however, which subfamily *Nodosigalea* belongs to. Identifying the new genus to a subfamily requires a robust taxonomy of Corydiidae. *Nodosigalea burmanica* gen. et sp. nov. is one of few known cockroaches that have differentiated locomotion features among tarsi.

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