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Short communication

Revision of *Phryssonotus burmiticus* (Diplopoda, Polyxenida, Synxenidae) in mid-Cretaceous amber from Myanmar

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ABSTRACT

Phryssonotus burmiticus (Cockerell, 1917) was the first formally described millipede species in the mid-Cretaceous amber from northern Myanmar. Although it has been reassigned and redescribed several times, critical characters for a reliable placement of the species remain elusive. Here we provide detailed morphological characters of *P. burmiticus* on the basis of six well-preserved adults (five males, one female) and nine juveniles. The species has many similarities to extant species in many aspects, including the number of ommatidia, the number and arrangement of sensory trichomes, morphology and arrangements of body trichomes, and features of the trunk appendages. It differs from extant species by assemblage of numbers of ommatidia and trichome B. The new morphological interpretation indicates a long-term morphological stasis in this peculiar millipede group.

1. Introduction

Myriapods are terrestrial arthropods with approximately homologous trunk segments and numerous pairs of walking appendages, which represent significant members of the soil macrofauna. Myriapoda comprises four living classes: Diplopoda (millipedes); Chilopoda (centipedes); Pauropoda and Symphyla (Minelli, 2011, 2015). The earliest fossil record of myriapods comes from the mid-Silurian, representing the oldest air-breathing terrestrial animals (Wilson and Anderson, 2004). A considerable variety of myriapod fossils have been reported from the Silurian to Carboniferous, especially the late Carboniferous, represented by the extinct taxa such as Archipolypoda, Arthropleuridea (Diplopoda) and Devonobiomorpha (Chilopoda). Numerous fossils mostly placed in extant taxa are described from the Cenozoic. In contrast, Permian and Mesozoic fossils are sparse and mostly poorly studied (Shear, 1998; Shear and Edgecombe, 2010; Edgecombe, 2011, 2015). Amber is an important source of Mesozoic and Cenozoic fossils, especially as a significant supplement of the Mesozoic compression fossils. Cockerell (1917) described the first Mesozoic myriapod, *Phryssonotus burmiticus* (Cockerell), from the mid-Cretaceous amber in northern Myanmar, but the holotype showed a very limited number of morphological characters, and the number of antennomeres was inaccurately identified. Nguyen Duy-Jacquemin and Azar (2004) described two new genera and two species of the bristle millipede family Polyxenidae from Lower Cretaceous Lebanese amber and made briefly comparisons with extant polyxenid genera, also mentioned was an unplaced *Phryssonotus* from the mid-Cretaceous French amber. Edgecombe and Minelli (2009) described *Buziniphilus antiquus*, the second documented Mesozoic geophilomorph, and identified the genus as a member of the crown-group Geophilomorpha. Bonato et al. (2014) described another new genus and species *Kachinophilus pereirai* from Burmese amber, which is remarkably close to some extant taxa. Recently, Liu et al. (2017) described two new species of the peculiar millipede order Siphoniulida, representing the first fossil record of the order. Both species are highly similar to living species of the taxa and can be placed in the extant genus *Siphoniulus*. Cenozoic myriapod fossils have been reported from the Eocene Baltic amber, and Miocene Chiapas and Dominican amber, and most of them can be assigned to extant families and even genera (i.e. Koch and Berendt, 1854; Bachofen von Echt, 1942; Hoffman, 1969; Shear,

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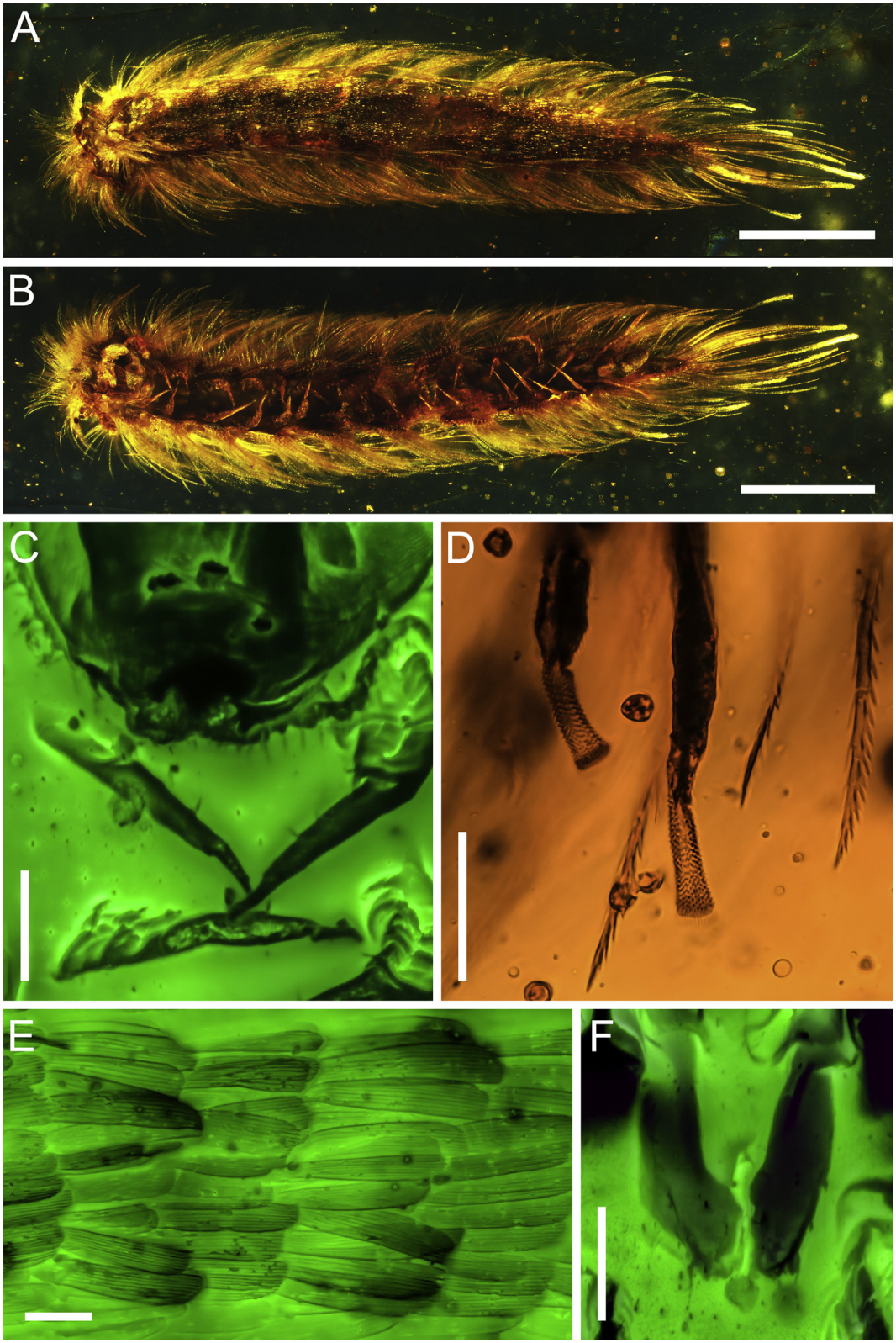

Fig. 1. *Phryssonotus burmiticus* (Cockerell, 1917), NIGP167288, adult male. **A**. dorsal view; **B**. ventral view; **C**. ventral view of the head; **D**. right legs 16, 17 terminating in hairy pads; **E**. scale-shaped dorsal trichomes; **F**. short conical penis located on the second pair of coxal plates. **A**, **B** under reflected light; **D** under transmitted light; **C**, **E**, **F** using CLSM. Scale bars: 200 μm in **A**, **B**; 50 μm in others.

1981; Santiago-Blay and Poinar, 1992; Scheller and Wunderlich, 2004; Edgecombe et al., 2012; Riquelme et al., 2014a, b).

The Burmese amber comes from the Hukawing Valley in northern Myanmar. The amber mine is located at a hill named Noije Bum, near Tanai. An overview of the amber deposit and its geological settings was made by Zherikhin and Ross (2000), Grimaldi et al. (2002), Cruickshank and Ko, 2003, and Ross et al. (2010). Recent U-Pb dating using zircons separated from the amber matrix show a maximum age of 98.79 ± 0.62 Ma (earliest Cenomanian, Shi et al., 2012). Only 3 species of millipedes have been reported from Burmese amber, including a bristle millipede (Cockerell, 1917) and two species of Siphoniulida (Liu et al., 2017).

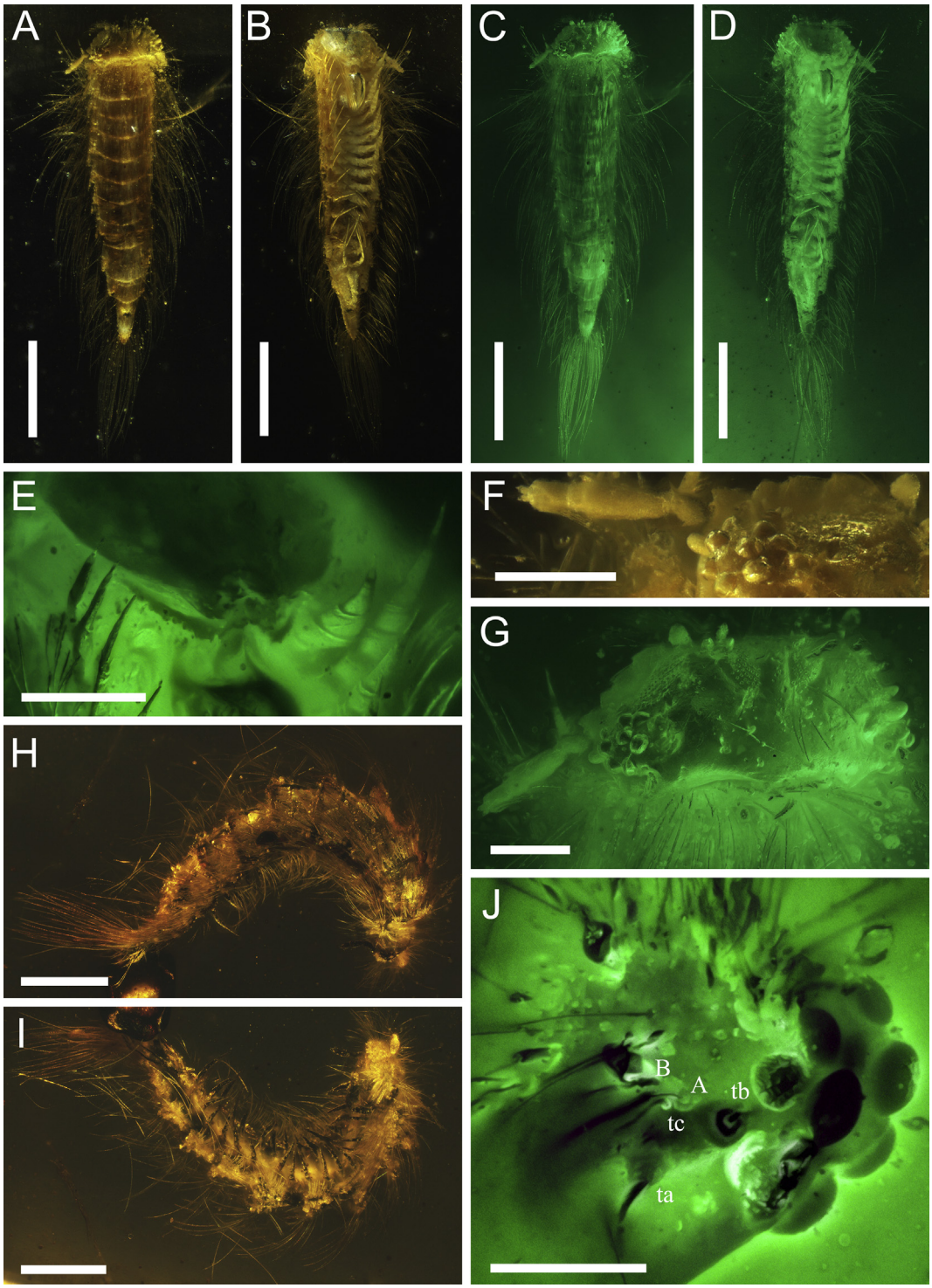

Fig. 2. *Phryssonotus burmiticus* (Cockerell, 1917), **A**–**G** NIGP167289, adult male. **A**, **C**. dorsal view; **B**, **D**. ventral view; **E**. ventral view of the gnathochilarium palps; **G**. dorsal view of the head; **F**. left ommatidia and antennae; **H**–**J** NIGP167290, adult male. **H**. dorsolateral view; **I**. ventrolateral view; **J**. ommatidia, trichobothria (***ta***, ***tb***, ***tc***), long barbate trichome (***A***) and short barbate trichome (***B***) on right side of the head. **A**, **B**, **F**, **H**, **I** under reflected light; **C**, **D**, **E**, **G** under green fluorescence; **J** using CLSM. Scale bars: 500 μm in **A**–**D**, **H**, **I**; 100 μm in **E**, **F**, **G**; 50 μm in **J**.

The millipede genus *Phryssonotus* is a significant member of the bristle millipede subclass Penicillata, characterized by soft uncalcified cuticle, 12 segments and 17 pairs of legs (although *P. brevicapensis* has only 11 tergites and 15 pairs of legs), long and thin barbate trichomes all along the lateral sides of the body and telson, two transverse rows of striated scale-shaped trichomes on each tergite except the collum, a row of sensory trichomes near the anterior trichobothrium, female vulva enlarged as strong, cylindrical ovipositors, and terminations of the last two pairs of legs modified as palettes (Condé and Nguyen Duy-Jacquemin, 2008; Enghoff et al., 2015). *Phryssonotus* contains 7 extant species: *P. platycephalus* (Lucas, 1846), from North Africa, Sicily and Spain; *P. orientalis* (Silvestri, 1900) from Uruguay; *P. capensis* (Silvestri, 1923) from South Africa, Mozambique, Madagascar and Papua New Guinea; *P. novaehollandae* (Silvestri, 1923) from Australia; *P. chilensis* (Silvestri, 1948) from Chile; *P. cubanus* (Silvestri, 1948) from Cuba; and *P. brevicapensis* Nguyen Duy-Jacquemin et al., 2011 from South Africa. *Phryssonotus* usually occurs in leaf litter and under tree bark, and is generally considered as feeding on algae (Hopkin and Read, 1992; Short and Huynh, 2009). *Phryssonotus* was first described from Eocene Baltic amber as *Lophonotus hystrix* Menge, 1854. Scudder (1885) assigned it to *Phrssonotus*, a new genus. Silvestri (1900) established another genus *Synxenus* including six extant species but it was later synonymized with *Phryssonotus* (Condé, 1954).

Phryssonotus burmiticus was first briefly described by Cockerell (1917) and was originally placed in *Polyxenus* Latreille, 1802/1803. It was then transferred to the family Synxenidae (Condé and Nguyen Duy-Jacquemin, 1963) and the extant genus *Phryssonotus* (Nguyen Duy-Jacquemin and Geoffroy, 2003). Rasnitsyn and Golovatch (2004) redescribed *Phryssonotus* based on a restudy of the holotype and 60 additional juveniles but they provided limited further details. Critical characters of *Phryssonotus*, such as the number of the ommatidia, numbers and arrangements of sensory trichomes near the eye hill, the detailed character of body trichomes, and features of trunk appendages, remained largely elusive. Here we provide additional morphological details of *P. burmiticus* based on our new materials.

Table 1
Measurements of *Phryssonotus burmiticus* (Cockerell, 1917).

Specimen number	Stadium	Sex	BL	CL	HW	BSW
NIGP167287	X(adult)	male	2.34	0.63	0.39	0.33
NIGP167288	X(adult)	male	2.47	0.60	>0.40	>0.36
NIGP167289	X(adult)	male	1.70	0.64	0.37	0.32
NIGP167290	X(adult)	male	2.36	0.69	?	?
NIGP167291	X(adult)	male	2.45	x	0.48	0.42
NIGP167292	X(adult)	female	2.53	0.65	0.54	0.58
NIGP167293	IX(subadult)	?	2.40	0.78	?	?
NIGP167294	IX(subadult)	female	>2.24	x	0.55	0.44
NIGP167295	VIII	?	2.55	0.67	0.56	0.50
NIGP167296	VIII	female	2.55	x	0.57	0.60
NIGP167297	VII	female	>1.60	x	0.40	0.33
NIGP167298	VI	?	1.98	0.56	0.59	0.57
NIGP167299	VI	?	1.86	0.58	0.45	0.41
NIGP167300	III	–	0.66	0.32	0.31	0.24
NIGP167301	?	?	>1.25	x	?	?

BL, body length (without cephalic and caudal trichomes); **CL**, length of caudal trichomes; **HW**, width of head (measuring between ocular fields); **BSW**, width of the broadest tergites. Identification of the stadium according to Condé (1962), Short and Huynh (2006).

2. Material and methods

The fossil specimens described here come from amber deposits in the Hukawng Valley in northern Myanmar. An overview of the amber deposit and its geological settings was made by Zherikhin

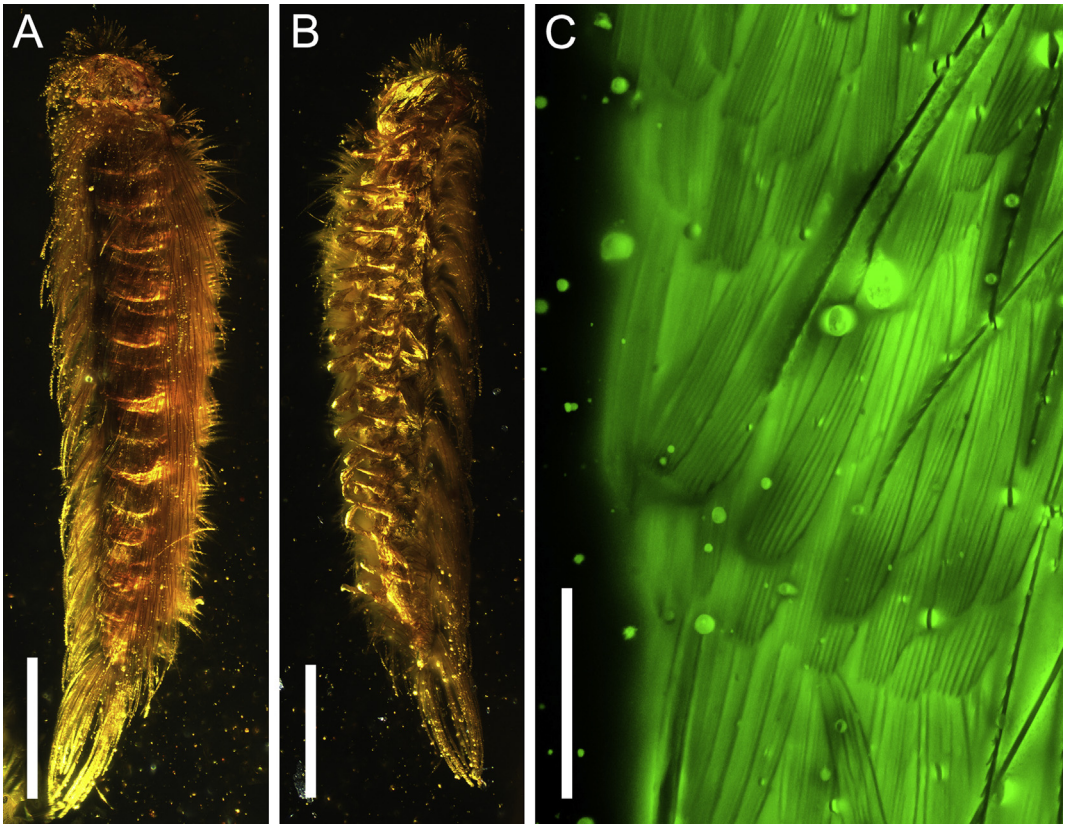

Fig. 3. *Phryssonotus burmiticus* (Cockerell, 1917), NIGP167288, adult male. **A**, dorsolateral view; **B**. ventrolateral view; **C**. dorsal trichomes. Scale bars: 500 μm.

and Ross (2000), Grimaldi et al. (2002) and Ross et al. (2010). A total of 15 individuals are included in the present study: 5 well-preserved adult males, 1 well-preserved adult female, 2 moderately preserved subadults and 7 well-preserved to poorly preserved juveniles. The material has been prepared, including cut with a razor blade and polished with sand paper of different grain sizes and polished with diatomitic mud.

Observations and photographs were taken using a Zeiss Discovery V20 stereo microscope, a Zeiss Axio Imager 2 light microscope and a Zeiss LSM 710 confocal laser scanning microscope with digital cameras attached. Photomicrographs with green background are taken using green fluorescence as light source attached to a Zeiss Axio Imager 2 light microscope and a Zeiss LSM 710 confocal laser scanning microscope. All materials are deposited in the Nanjing Institute of Geology and Palaeontology, Nanjing.

3. Systematic palaeontology

Class Diplopoda de Blainville in Gervais, 1844
Subclass Penicillata Latreille, 1831
Order Polyxenida Verhoeff, 1934
Superfamily Synxenoidea Silvestri, 1923
Family Synxenidae Silvestri, 1923

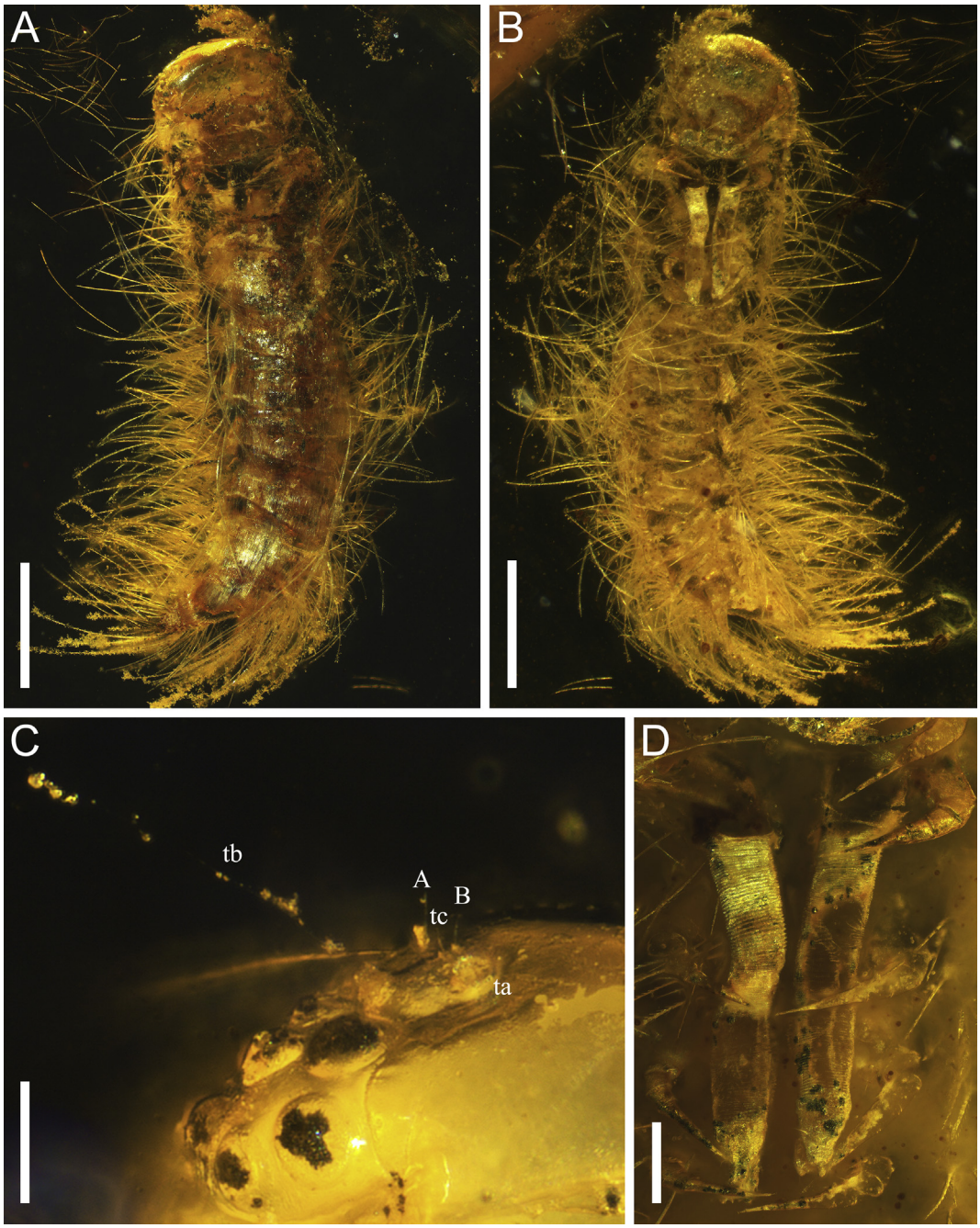

Fig. 4. *Phryssonotus burmiticus* (Cockerell, 1917), NIGP167292, Adult female. Under reflective light. **A**. dorsal view; **B**. ventral view; **c**. insertion of trichobothria (***ta***, ***tb***, ***tc***), long barbate trichome (***A***) and short barbate trichome (***B***) on left side of the head. **D**. ventral view of the vulvae located on the second pair of coxal plates. Scale bars: 500 μm in **A**, **B**; 50 μm in **C**, **D**.

Genus *Phryssonotus* Scudder, 1885
[= *Synxenus* Silvestri, 1900; *Kubanus* Attems, 1926; *Koubanus* Attems, 1928; *Schindalmonotus* Attems, 1928; *Lophonotus* Menge, 1854, preoccupied, non Stephens, 1829; *Kaubanus* (sic) Attems, 1929, misprint by Jones (1937); *Schindelmonatus* (sic) Attems, 1929, misprint by Jones (1937)]
Type species: *Phryssonotus hystrix* (Menge, 1854)

Phryssonotus burmiticus (Cockerell, 1917)
1917 *Polyxenus burmiticus* Cockerell, p. 40–41, fig. 1.
1954 *Polyxenus burmiticus* Conde, p. 75.
1963 *Polyxenus burmiticus* Conde & Jacquemin, p. 69
1978 *Polyxenus burmiticus* Zherikhin, p. 114.
2000 *'Polyxenus' burmiticus* Ross & York, p. 15.
2000 *Polyxenus burmiticus* Ross & York, fig. 18.
2003 *Phryssonotus burmiticus* Nguyen Duy-Jacquemin & Geoffroy, p. 101.

Occurrence. Mid-Cretaceous (*ca.* 99 Ma) amber from the village of Tanai, Hukawing Valley, northern Myanmar.
Diagnosis. (revised after Rasnitsyn and Golovatch, 2004).

Body small (ca. 2.3 mm), caudal trichome to body length radio slightly larger than other cogeners; eye with 10 ommatidia with 1 trichome B on each side; margins of the two median clusters of cephalic trichomes with grooves.

Description.

Adult male (NIGP167287-167291, Figs. 1, 2, 3):
Body length without cephalic and caudal trichomes 1.70 mm–2.47 mm; lengths of caudal trichomes 0.60 mm–0.69 mm (see Table 1 for details).
Head: 10 ommatidia on each side (Figs 2f, 2g, 2j), 3 tricho-bothria arranged in triangle on each side near ommatidia, the frontal one presenting shortest and thinnest sensory hair while the posterior two presenting larger frustum bases, a distinctively elongate trichome (tirchome A) and 1 short barbate trichome (trichome B) adjacent to trichobothrium c (Fig. 2j). Antennae with 8 articles; antennomere 6 elongate, length to width ratio about 3, 3 times as long as antennomere 7; antennomere 8 short, bearing 4 sensillae with sturdy base on the apex (Figs 2f, 2g). Insertion of cephalic trichomes in 4 distinct areas, the paramedical clusters with distinct groove on margin (Fig. 2g). Gnathochilarial palps combining elongate outer palps and oval inner palps, with acicular sensilla on ventral side, about 21 sensilla visible on outer palps (Figs 1c, 2e).
Trunk: 12 tergites (including collum and telson) and 17 pairs of legs in adult, the 5th or 6th tergite widest. Collum small, with 2 oval clusters of long barbate trichomes. Tergites II–XI covered with short striated scale-shaped trichomes, arranged in 2 overlapping rows on each tergite (Figs 1e, 3c). A group of elongate trichomes on each pleurite. Legs short, 8 articles except the first pair and the last two pairs; tarsus II elongate, with a seta on middle area (Figs 1c, 2e); each of the other articles apparently bearing a soft seta which sometimes cannot be observed. 16th and 17th leg-pairs with 7 articles but slightly longer than other leg-pairs, terminating with hairy pads other than claws (Fig. 1d). Penis located on the second pair of coxal plates, relatively poorly preserved or cannot be observed in our specimens, short and conical in shape (Fig. 1f). Coxal glands not visible.
Telson: Small, elongate, cone-shaped, about 0.25 mm in length, covered by one transverse row of scale-shaped trichomes, with elongate barbate trichomes on lateral edge and distal part.
Adult female (NIGP167292, Fig. 4):
Body length without cephalic and caudal trichomes 2.53 mm; lengths of caudal trichomes 0.65 mm (see Table 1 for details).
Large and elongate vulvae on the second pair of coxal plates. Vulva cylindrical, unarticulated, reaching at least 5th leg-pairs, with fine transverse wrinkles on about 5/6th area of vulva, distal part without wrinkles (Fig. 4c). Other characters similar to male individuals.

Other individuals:
NIGP167293 (Fig. 5a), subadult, sex undetermined, 12-segmented with 16 pairs of legs.

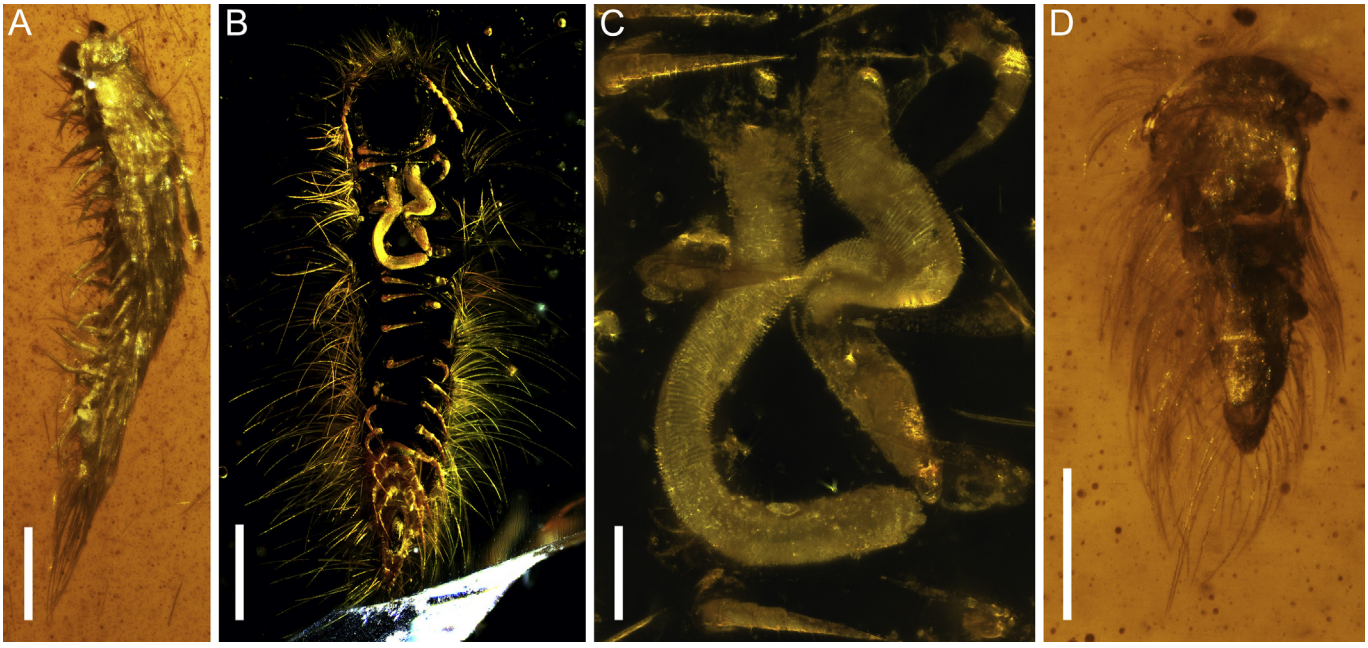

Fig. 5. *Phryssonotus burmiticus* (Cockerell, 1917). **A**. NIGP167293, subadult, sex undetermined, lateral view. **B**, **C**. NIGP167296, juvenile female of stage VIII: **B**. ventral view; **C**. ventral view of the vulvae. **D**. NIGP167300, juvenile of stage III, dorsal view. Scale bars: 100 μm in **C**; 500 μm in others.

NIGP167294, subadult, female, 12-segmented with 16 pairs of legs; the termination of last leg-pair modified as hairy pads; vulva strong, reaching 5th leg-pairs.
NIGP167295, juvenile of stadium VIII?, sex undetermined, poorly preserved, 11?-segmented, legs not visible.
NIGP167296 (Figs. 5b, 5c), juvenile of stadium VIII, female, 11-segmented with 14 pairs of legs; vulva strong, elongate, reaching 5th leg-pairs.
NIGP167297 (Fig. 6), juvenile of stadium VII, female, 10-segmented with 12 pairs of legs; 10 ommatidia on each side; vulva immature, cylindrical, reaching 3rd leg-pairs, less than half area of vulva with transverse wrinkles (Fig. 6c).
NIGP167298-99, juvenile of stadium VI, sex undetermined, relatively poorly preserved, 9-segmented with 10 pairs of legs.
NIGP167300 (Fig. 5d), juvenile of stadium III, relatively large head with small cone-shaped body, 6-segmented with 5 pairs of legs.
NIGP167301, only 13 pairs of legs and 7 segments preserved.

4. Discussion

Phryssonotus burmiticus is very similar to extant *Phryssonotus* species in the following features: eye with 10 ommatidia; the presence of 3 trichobothria, trichome A and 1 trichome B; cephalic

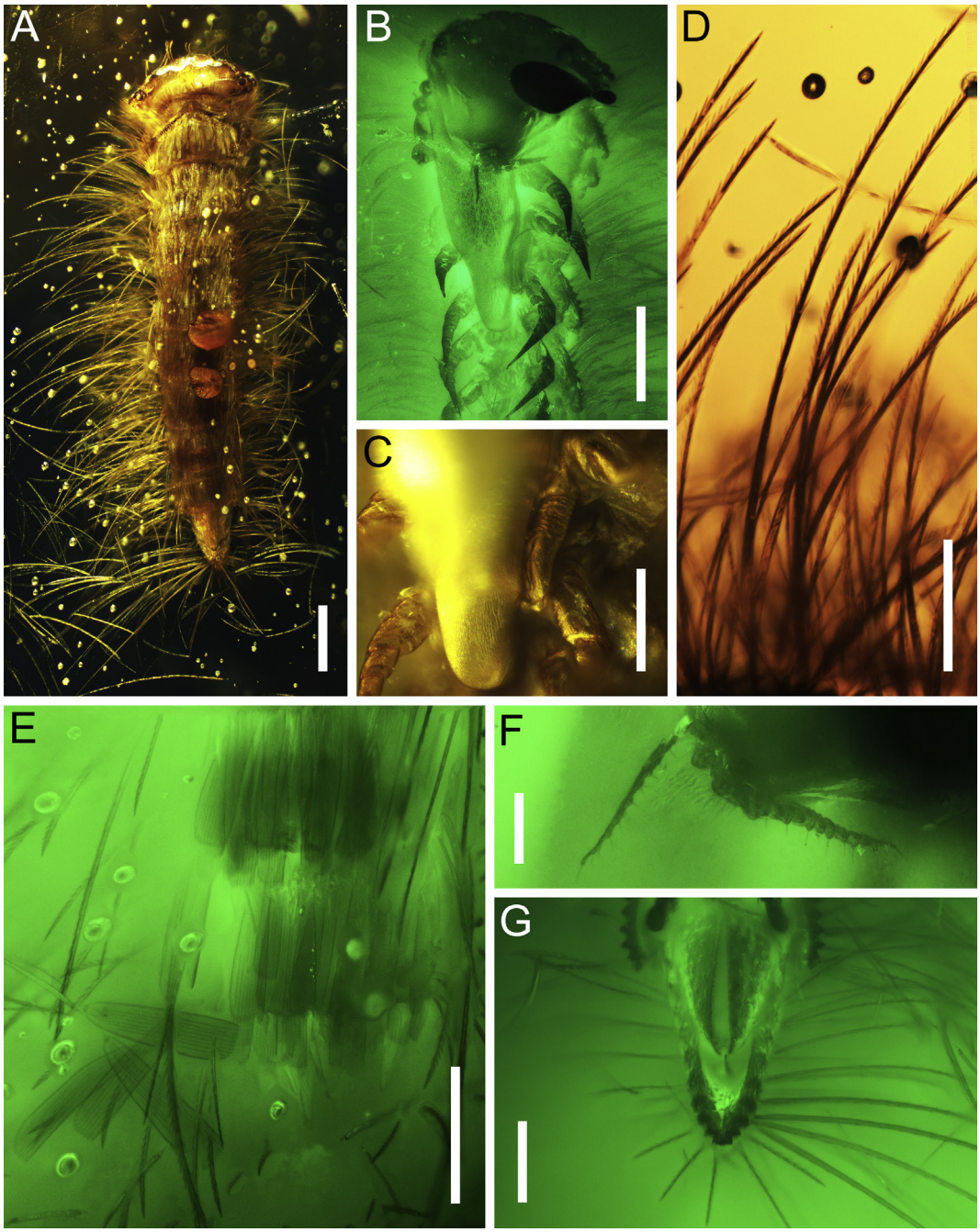

Fig. 6. *Phryssonotus burmiticus* (Cockerell, 1917), NIGP167297, juvenile female of stadium VII. **A**. dorsal view; **B**. ventral view of the head; **C**. ventral view of the immature vulvae; **D**. lateral barbate trichomes on the right side; **E**. scale-shaped dorsal trichomes; **F**. ventral view of the gnathochilarium palps; **G**. ventral view of the telson. **A**, **C** under reflected light; **B**, **E**–**G** under green fluorescence; **D** under transmitted light. Scale bars: 200 μm in **A**, **B**; 100 μm in **C**, **D**, **E**, **G**; 50 μm in **F**.

trichomes arranged in four areas; elongate outer palps and oval middle palps of gnathochilarium; proportion of the antennae; 4 sensillae on distal of the antenna; 12 tergites including collum and telson, 17 leg-pairs; long barbate lateral and caudal trichomes, scale-shaped dorsal trichomes; elongate antennomere 6 and tarsus II; and modified leg-pairs 16th, 17th; and positions and patterns of the short conical penis and large cylindrical vulva. No possible plesiomorphic characters are found in our specimens. Extant species of *Phryssonotus* have great similarity on their general characters. The only available identification key which provided by Silvestri (1923) is based on the number of ommatidia and the number of barbate trichomes near the anterior trichobothrium. *P. burmiticus* differs from other living species by having 10 ommatidia with 1 trichome B (Figs. 2j, 3d). *P. capensis* and *P. brevicapensis* also have 10 ommatidia but bear 5–6 and 5 trichome B (Silvestri, 1923; Nguyen Duy-Jacquemin, 2006). *P. platycephalus* and *P. orientalis* have 1 trichome B, but with 11 and 9 ommatidia (Silvestri, 1923; Vadell, 2010). Compared with extant species, *P. burmiticus* has a relatively smaller body-size but has slightly larger caudal trichome to body length ratio. In our adult specimens, the body length ranges from 1.70 mm to 2.53 mm, the body length of the holotype of *P. burmiticus* is 2.1 mm (Rasnitsyn and Golovatch, 2004). Most living species are 3.5 mm–4.5 mm in length, while only specimens of *P. novaehollandiae* from Barrow Island has smaller size ranging from 2.1 mm to 2.4 mm (Short and Huynh, 2009). The radio of caudal trichome length to body length is about 0.26–0.38 and extant species about 0.22–0.32 (Silvestri, 1900, 1923, 1948; Short and Huynh, 2006, 2009; Vadell, 2010). *P. burmiticus* also has special grooves on the margins of the two median clusters of cephalic trichomes, a character not mentioned in descriptions of modern species.

Other fossil species of *Phryssonotus* are only known as amber inclusions, including *P. hystrix* (Menge, 1854) from Eocene Baltic amber and an unidentified juvenile from the mid-Cretaceous amber of France (Nguyen Duy-Jacquemin and Azar, 2004). It is difficult to compare *P. burmiticus* with other fossil members due to the poor preservation and/or insufficient descriptions. However, according to those insufficient original descriptions, it is clear that these fossils display the modern appearance of *Phryssonotus* (Menge, 1854; Bachofen von Echt, 1942; Nguyen Duy-Jacquemin and Azar, 2004), indicating that the Late Cretaceous mass extinction may not have significantly impact on the genus. The litter and subcortical habitat may likely account for the bradytely of *Phryssonotus* through long geological time.

5. Concluding remarks

Our examination of new specimens provides detailed morphological structures of the bristle millipede *Phryssonotus burmiticus*, revealing great similarities between fossil and living *Phryssonotus* species. Together with the general appearances of other fossil *Phryssonotus*, we suggest a long-term morphological stasis in the genus from the mid-Cretaceous to the present. Therefore the major evolution of the genus or even the family Synxenidae may have happened before the Cretaceous.

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