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Two new species of the bristle millipede genus *Pauropsxenus* (diplopoda, Polyxenidae) in mid-Cretaceous Burmese amber

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ABSTRACT

Two new species of the bristle millipede family Polyxenidae, *Pauropsxenus extraneus* sp. nov. and *Pauropsxenus extraneus* sp. nov., are described from the mid-Cretaceous Burmese amber. They can be confidently placed in the extant genus *Pauropsxenus* (Polyxenidae) based on a set of critical characters. In additions, the morphological similarity of hooked caudal trichomes shared by the new species and extant counterparts may suggest a similar defensive function. Our discovery indicates that a prey-predator relationship between polyxenids and other soil animals has already been established in the Cretaceous period.

1. Introduction

The diplopod subclass Penicillata and its single order Polyxenida, generally known as bristle millipedes, are the sister-group to all other extant diplopod taxa (Blanke & Wesener, 2014), they possess unique morphological characters represented by soft, uncalcified cuticle and specific trichomes on head, each segment, and telson (Enghoff et al., 2015). Polyxenidae is the largest family of Polyxenida, currently comprising 22 genera and over 100 species (Millibase, 2018) found in all continents except Antarctica. The family differs from other polyxenid families by 11 segments with 13 pairs of legs, mostly eyed and pigmented, gnathochilarium with outer palps, tergite with rows of barbate trichomes ending with a cluster on each side instead of scale-shaped trichomes, and hooked trichomes present on telson commonly arranged in two clusters (Enghoff et al., 2015). Condé divided the family into four subfamilies in his manuscript mainly by features of telson, the presents of ommatidia and pigmentation and the presents of pseudoarticulad sensilla on gnathochilarium (Condé; Nguyen Duy-Jacquemin, 2008): Polyxeninae, Monographinae, Macroxeninae, and Hypogexeninae. Polyxenids, mainly feed on algae from bark (Hopkin & Read, 1992; Kime & Golovatch, 2000), are well accepted by having a subcortical habitat. They can be also commonly found in litter layers (e.g. Meidell, 1970). Their specific caudal trichomes are used as physical defense against predators (Eisner et al., 1996).

Polyxenidae fossils are very rare and confined to amber. 5 species of *Polyxenus* Latzel have been reported by Koch & Berent (1854) from the Eocene Baltic amber: *P. conformis* Koch & Berendt (1854), *P. ovalis* Koch & Berendt (1854), *P. caudatus* Menge (1854), *P. colurus* Menge (1854), and *P. lophurus* Menge (1854). However, the descriptions of these species are too brief to confidently attribute them to the genus *Polyxenus* or even the family Polyxenidae. Bachofen von Echt (1942) briefly described polyxenid fossils (*Polyxenus* sp.) from the Baltic amber. Nguyen Duy-Jacquemin & Azar (2004) described 2 new genera and 2 species (*Electroxenus jezzinensis* Nguyen Duy-Jacquemin & Azar, 2004; *Libanoxenus hammanaensis* Nguyen Duy-Jacquemin & Azar, 2004) from the Early Cretaceous amber of Lebanon, and both are very close to the extant genera of Polyxenidae. They represent the oldest records of

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0195-6671/

Penicillata. Fossils from other families of Polyxenida including *Phryssonotus burmiticus* (Cockerell, 1917) (reviewed by Rasnitsyn & Golovatch, 2004 and Su et al., 2019) from Burmese amber, an unidentified *Phryssonotus* from Lebanese amber (Nguyen Duy-Jacquemin & Azar, 2004) and an unidentified *Lophoproctus* from Dominican amber (Santiago-Blay & Poinar, 1992).

In the present paper, we describe 2 new species of Polyxenidae from the mid-Cretaceous Burmese amber based on 40 individuals. The new species can be confidently put in Polyxenidae and the extant genus *Pauropsxenus* Silvestri, 1948.

2. Material and methods

The material described here derived from amber deposits in the Hukawng Valley of northern Myanmar. The mining was done at a hill named Noije Bum, near Tanai. An overview of the amber deposit and its geological settings was made by Zherikhin & Ross (2000), Grimaldi et al. (2002) and Ross et al. (2010). The recent list of taxa described or recorded from Burmese amber was made by (Ross, 2019a, b; 2020). U–Pb zircon dating constrained the Burmese amber to a maximum age of 98.79 ± 0.62 Ma, which is equivalent to the Late Cretaceous (earliest Cenomanian; Shi et al., 2012). Recent studies of the pholadid borings (Smith & Ross, 2017) and marine animals symbiotic with or adhere to Burmese amber suggest the age of Burmese amber may be close to the Albian and Cenomanian boundary (Mao et al., 2018).

A total of 40 individuals were included in the present study. All specimens were prepared, including cut with a razor blade and polished with sand papers with different grain sizes and with diatomite mud (Sidorchuk & Vorontsov, 2018). All specimens are housed in the Nanjing Institute of Geology and Palaeontology (NIGPAS), Nanjing, China. Observations and photographs were taken using a Zeiss Discovery V16 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, or using a Zeiss LSM 710 confocal laser scanning microscope (CLSM). Classification and phrases of characters are based on Condé & Nguyen Duy-Jacquemin (2008), Enghoff et al. (2015), and MilliBase (2018). Identification of the stage of juveniles is based on Condé (1962).

3. Systematic palaeontology

Class: Diplopoda de Blainville in Gervais (1844)
Subclass: Penicillata Latreille, 1831
Order: Polyxenida Verhoeff, 1934
Superfamily: Polyxenoidea Lucas, 1840
Family: Polyxenidae Lucas, 1840

Genus: ***Pauropsxenus*** Silvestri, 1948
Type species
Pauropsxenus vilhenae Silvestri (1948)

Pauropsxenus ordinatus sp. nov.

Zoobank LSID:
urn:lsid:zoobank.org:act:C50C7773-9298-4A24-BBA5-D04B5B984810.

Etymology
Derived from the Latin *ordinatus*, means ordered, in reference to the regularly arranged tergal trichomes.

Studied material
Holotype: NGIP168231, a completely preserved adult male. Paratype: NGIP168232, a well-preserved adult female; NGIP168233 juvenile of stage V, well-preserved. Additional material: NGIP168233–NGIP168240: 1 relatively well-preserved adult female, 3 moderately preserved sex-undetermined adults, 1 poorly preserved sub-adults; 2 juveniles of stage V, moderately preserved.

Diagnosis
5 ommatidia on each side; 3 basiconic sensilla on antennal article VI, 2 located anteriorly, the intermediate one longest and located most posteriorly; antennal article VII with 2 basiconic sensilla and a setiform sensillum; trichomes on the posterior vertex of head only arranged in 1 row on each side, 1–2 caudally pointed trichome located middle-posterior to the row; tergal trichomes arranged in 2 rows along the posterior edge of tergite, posterior rows without medial gap; tarsus II with a thick spine; penes of the male cylindrical in shape, apparently longer and slenderer than vulvae of the female.

Description
Adult male (Fig. 1). Body length 1.7 mm without cephalic and caudal trichomes; width between ommatidia clusters 0.4 mm; average length of caudal trichomes 0.6 mm.
Head: flatten, covered with rows of trichomes anteriorly; posterior of vertex with a row of 9 + 9 trichomes on each side, 1 trichomes located middle-posteriorly and pointed backwards (Fig. 1C). 5 ommatidia on each side, with 3 dorsal, 1 anterior-lateral, 1 posterior-lateral; 3 trichobothrium almost in equal size arranged in a triangle near ommatidia clusters (Fig. 1D). Antenna with 8 articles; article VI most elongate, L/W about 1.65 (Fig. 1E). 3 basiconic sensilla and on article VI: the intermediate one (i) longest, located most posteriorly, the 2 anterior sensilla (a1, a2) nearly in same size; setiform (s) and coeloconic sensilla (c) not clearly visible, a coeloconic sensillum (c) may presents between the anterior basiconic sensillum (a) and the intermediate sensillum (i) (Fig. 1G). Article VII with 2 basiconic sensilla, the outer one (a) slightly longer and thinner; 1 setiform sensillum (s) located anteriorly between the two basiconic sensilla (Fig. 1F). 4 sensitive cones on the apex. Gnathochilarium palps with lateral expansion; sensilla on palps not pseudoarticulated; outer palps elongate, about 4 times as long as middle palps; 10 sensilla visible on the right outer palp.
Trunk: 11 tergites and 13 pairs of legs. Collum small, with a cluster of trichomes on each side and 4 rows of tergal trichomes; the anterior 3 rows with 2 + 2/3 + 3 trichomes, a small medial gap presents on each row; 8 sub-fusiform trichomes on the most posterior row, slightly different in shape from anterior trichomes (subclavate) and slightly shorter, without a medial gap (Fig. 1C). Tergites II–IX with 2 rows of trichomes located near the posterior margin, ending with clusters laterally (Fig. 1I), numbers of trichomes in clusters reduced in tergite VIII and IX; the anterior row with a large medial gap, 4–7 trichomes on each side of the gap; 14–18 trichomes on the posterior row, without median gaps, arranged along the posterior edge of tergite; shape and size of these trichomes similar to the collum. An oval cluster of trichomes presents on each pleurites from segments II–XI, relatively longer and thicker than tergal trichomes. Legs consisting of 8 podomeres except leg-pairs 1 and 2 which with 6 and 7 podomeres; tarsus II with a thick spine; one seta is visible on each of the other podomeres. Penes located near second coxa significantly large, cylindrical shaped; the apex of both sides might be slightly damaged (Fig. 1H).
Telson: 2 clusters of caudal trichomes closely aligned to each other; ornamental trichomes damaged; hooked trichomes commonly with 5 aligned hooks pointing anteriorly on distal part; single barbs on stem; apical multi-hooks not present (Fig. 1J).

Adult female (Fig. 2). Body length 2.0 mm without cephalic and caudal trichomes; width between ommatidia clusters 0.5 mm; average length of caudal trichomes 0.7 mm. Vulvae short, oval in

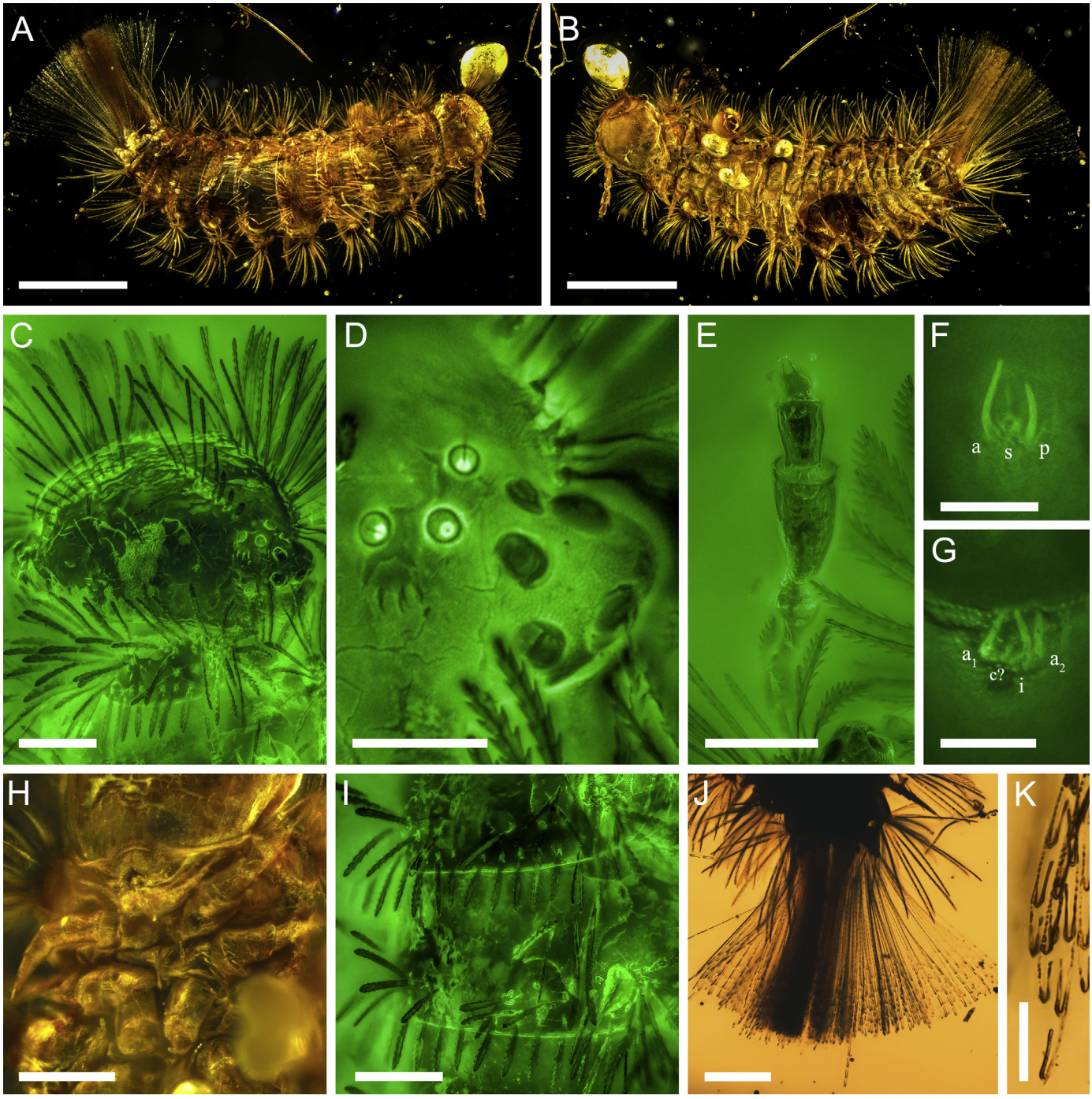

Fig. 1. *Pauropsxenus ordinatus* sp. nov., holotype, NGIP168231, adult male. **A**, dorsal view; **B**, ventral view; C, dorsal view of the head; **D**, ommatidia and trichobothria on the right side; **E**, article VI-VIII of the right antenna; **F**, sensilla on antennal article VII; **G**, sensilla on antennal article VI; **H**, ventral view of the mouth part and penes; **I**, tergal trichomes of tergite II-III; **J**, ventral view of the caudal trichomes; **K**, hooks of the hooked caudal trichomes. **A**, **B**, **H** using reflective light; **C**, **E**, **I** using green fluorescence; **D**, **F**, **G** using CLSM; **J**, **K** using transmission light. Abbreviations: **a**, $\mathbf{a_1}$, $\mathbf{a_2}$, anterior basiconic sensilla; **p**, posterior basiconic sensilla; **i**, intermediate basiconic sensilla; **s**, setiform sensilla; **c**, coeloconic sensilla. Scale bars: **A**, **B** 500 μm; **C**, **E**, **I** 100 μm; **D**, **K** 50 μm; **F**, **G** 20 μm; **J** 200 μm. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

shape, located near the second pair of coxae (Fig. 2C). Hooked trichomes on telson with 3–4 hooks.

Sub-adult. Abnormally small in size, body length 0.9 mm, average length of caudal trichomes 0.4 mm 11 tergites and 13 pairs of legs. Hooked trichomes on telson with 4–5 hooks.

Juvenile of stage VI. Body length 1.4–1.8 mm, average length of caudal trichomes 0.4–0.6 mm 5 ommatidia. Trichomes on posterior of vertex 9 + 9, with 1–2 caudally pointed trichomes posteriorly on each side. Hooked trichomes on telson with 4–5 hooks.

Juvenile of stage V (Fig. 3). Body length 1.0 mm, average length of caudal trichomes 0.4 mm 5 ommatidia; 1 row of 8 + 9 trichomes with 1 + 2 caudally-pointed trichomes on posterior of vertex (Fig. 3D). 8 tergites with 8 pairs of legs. Telson with 2 clusters of hooked trichomes closely aligned to each other; hooked trichomes with 6–7 aligned hooks (Fig. 3C); several linear arranged

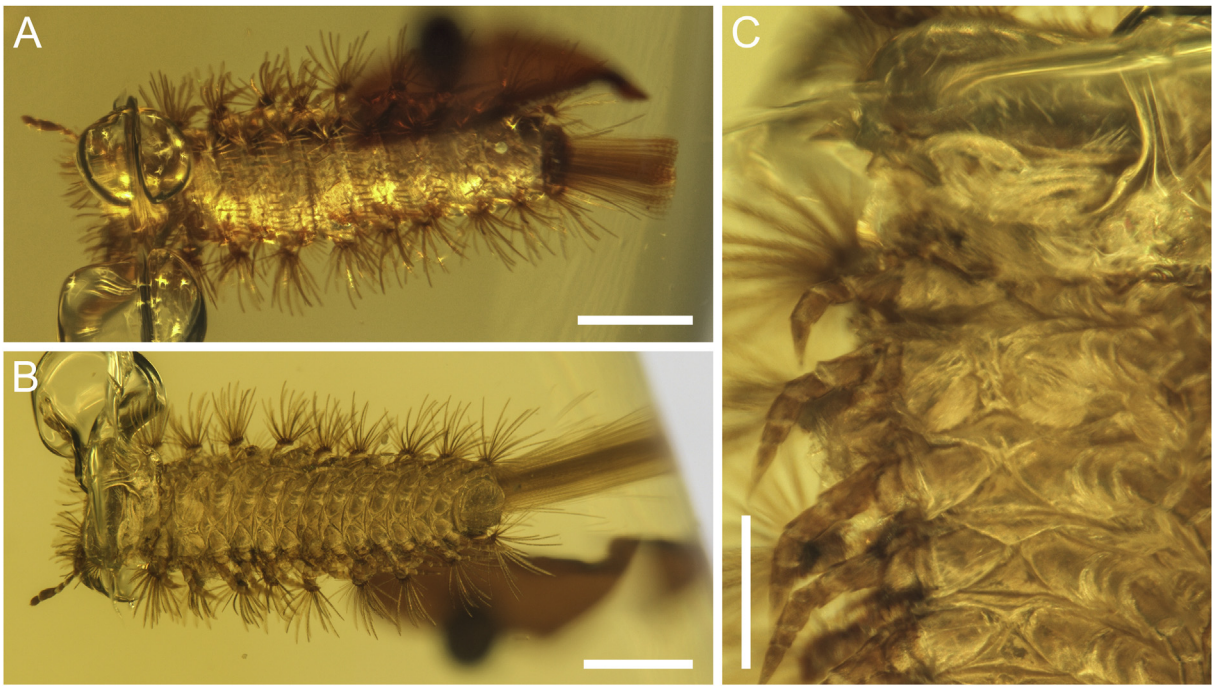

Fig. 2. *P. ordinatus*, paratype, NGIP168232, adult female, under normal light. **A**, dorsal view; **B**, ventral view; **C**, enlargement of vulvae. Scale bars: **A**, **B** 500 μm; **C**, 200 μm.

short barbate trichomes and 2 + 2 long barbate trichomes located dorsal to the hooked trichomes clusters; some short barbate trichomes are also visible on ventral edge of the clusters; numbers and insertion of these ornamental trichomes are not clear.

Pauropsxenus extraneus sp. nov.

Zoobank LSID:
urn:lsid:zoobank.org:act:9BB3142E-4516-4DFE-A001-1279B42A6643.

Etymology
Derived from the Latin *extraneus*, means strange, in reference to the 4 ommatidia and the special shape of penis that are unusual in *Pauropsxenus*.

Studied material
Holotype: NGIP168241, a well-preserved adult male. Paratype: NGIP168242–NGIP168243, 2 well-preserved adult females; NGIP168244, a well-preserved sub-adult female. Additional material: NGIP168245–NGIP168255: 2 relatively well-preserved adult females; 4 moderately preserved sex undetermined adults; 2 relatively well-preserved sub-adult males; 1 moderately preserved sub-adult female; 2 juveniles of stage V, moderately preserved. Additional with 6 poorly preserved specimens.

Diagnosis
At least 4 ommatidia on each side; 3 basiconic sensilla, antennal article VI, the inner two located posteriorly, the intermediate one thickest; antennal article VII with 2 basiconic sensilla; trichomes on the posterior vertex of head forming 1 dense row with 2–5 trichomes located posteriorly; tergal trichomes arranged in 3–4 rows fused with tergal clusters on each side, the posterior row of trichomes longer and more slender than *P.ordinatus*, arranged along the edge of tergal clusters, a large medial gap presents on each tergite.1 thick spine on tarsus II. Penes of the male cylindrical shaped with sharp apex, apparently longer and slenderer than vulvae of the female.

Description
Adult male (Fig. 4). Body length 2.7 mm without cephalic and caudal trichomes; width between ommatidia clusters 0.6 mm; average length of caudal trichomes 0.8 mm.
Head flatten, covered with rows of trichomes anteriorly, anterior trichomes denser than *P. ordinatus*; posterior of vertex with 1 row of 14 + 12 trichomes and 3 + 3 trichomes sparsely arranged posterior to the row (Fig. 4E). 4 ommatidia visible, including 1 anterior-dorsal, 1 dorsal, 1 posterior-lateral, and 1 posterior; 3 trichobothrium almost in equal size arranged in a triangle near ommatidia (Fig. 4F). Antenna with 8 articles; L/W of the article VI about 1.6; 4 sensitive cones on the apex. Gnathochilarium palps with lateral expansion, sensilla not pseudoarticulated; outer palps about twice as long as inner palps; 17–19 sensilla visible on outer palps, 16–20 sensilla visible on inner palps (Fig. 4D).
Trunk with 11 tergites and 13 pairs of legs. Collum small, with two dense clusters of trichomes widely separated from each other without connection. 3–4 rows of trichomes arranged irregularly on posterior part of tergite II–V, fused with lateral tergal clusters on each side, with large medial gaps, giving the appearance of two oblate oval clusters each tergite (Fig. 4H); posterior row with 10–12 trichomes on each side, arranged along the edge of the cluster, located slightly far from posterior edge of tergite, these trichomes are more elongate than *P. ordinatus*; tergites VI–X damaged. An oval cluster of trichomes presents on each pleurites, relatively longer and thicker than tergal trichomes. Legs consisting of 8 podomeres except leg–pairs 1 and 2 which with 6 and 7 podomeres; tarsus II with a thick spine. Penes located near the second pair of coxae, large, with cylindrical shaped base and cone shaped apex (Fig. 4G).
Dorsal part of the telson damaged. 2 closely aligned clusters of hooked trichomes can be observed, commonly with 3–4 aligned hooks pointing anteriorly on distal part, and single barbs on stem; apical multi-hooks not present (Fig. 4C).

Adult female (Figs 5–6). Body length 2.1–2.4 mm excluding cephalic and caudal trichomes; width between ommatidia clusters

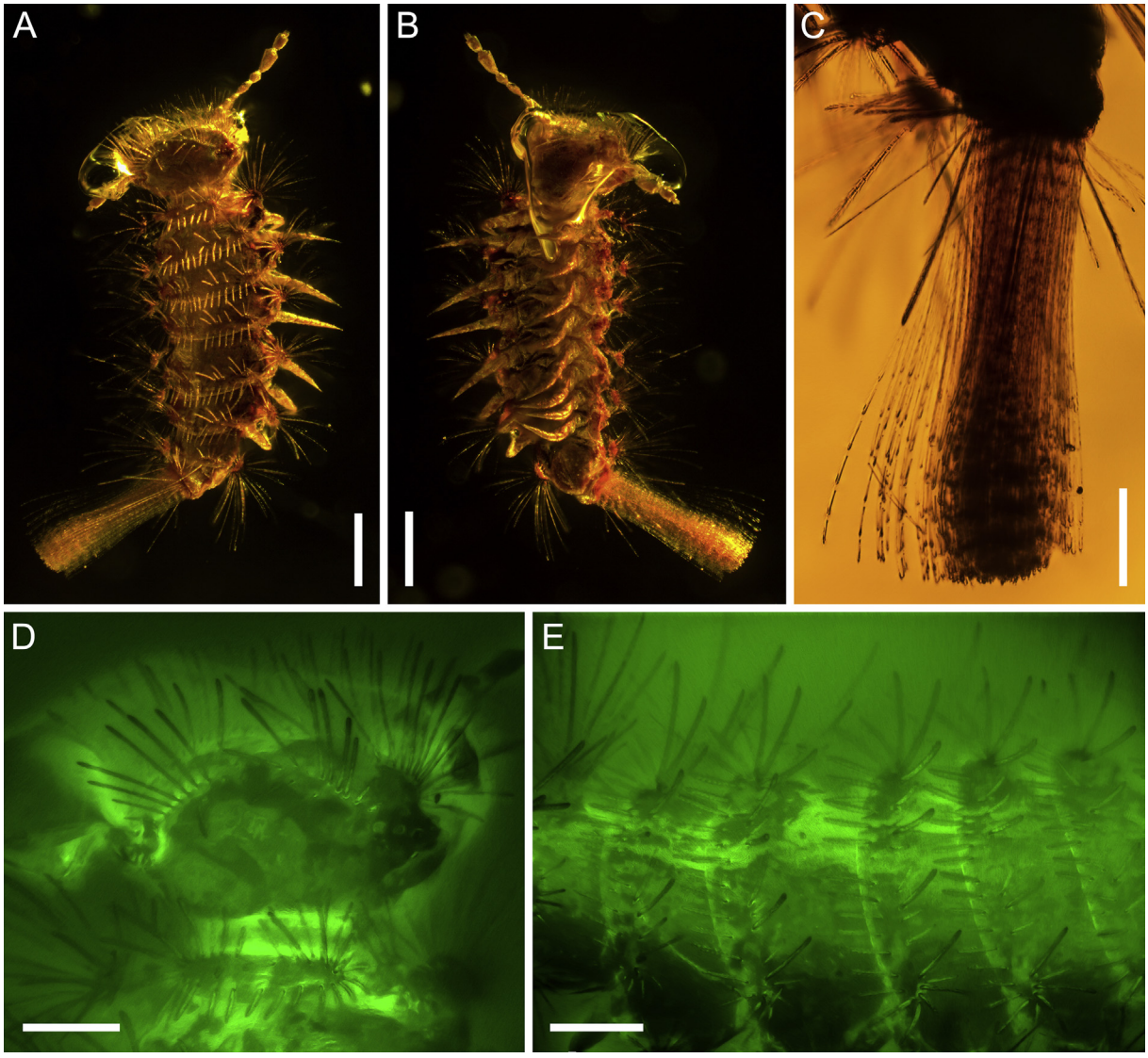

Fig. 3. *P. ordinatus*, paratype, NGIP168233, juvenile of stage V. **A**, dorsal view; **B**, ventral view; **C**, ventral view of the caudal trichomes; **D**, dorsal view of the head; **E**, tergal trichomes of tergite II-VII. **A**, **B** using reflective light; **C**, using transmission light; **D**, **E** using green fluorescence. Scale bars: **A**, **B** 200 μm; **C**, **D**, **E** 100 μm. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

0.6–0.7 mm; average length of caudal trichomes 0.7–1.1 mm 4 ommatidia visible on each side, including 2 dorsal, 1 posterior-lateral, and 1 posterior (Fig. 5D). A row of 10 + 10–17 + 17 trichomes with 2+2–2+5 posteriorly located trichomes on posterior of the vertex (Figs 5C, 6F). 3 basiconic sensilla on the antennomere VI: 1 located anteriorly, 2 located posteriorly; the anterior one (a) smallest, the intermediate one (p_1) longest and thickest; setiform (s) or coeloconic sensilla (c) not clearly visible, a coeloconic sensillum (c) may presents outer to the anterior basiconic sensillum (a) (Fig. 6D). Article VII with 2 basiconic sensilla, almost in same size; setiform (s) and coeloconic sensilla (c) not clearly visible (Fig. 6D). 14 lamellar teeth on anterior margin of labrum (Fig. 5E). Outer palps of the gnathochilarium more elongate than holotype, about 3.5 times as long as inner palps; 10–14 sensilla on outer palps, 13–16 sensilla on inner palps (Fig. 5E). Vulvae located near the second pair of coxae, significantly small, oval in shape (Fig. 5G). Telson with 2 clusters of hooked trichomes closely aligned to each other; hooked trichomes with 3–7 aligned hooks (Figs 5H, 6I); barbate trichomes on telson not clearly visible due to the disturbance of hooked trichomes and body trichomes.

Sub-adult (Fig.7). Body length 1.3–1.5 mm; average length of caudal trichomes 0.6 mm 4 ommatidia on each side, including 1 anterior, 1 lateral, 1 dorsal, 1 posterior–lateral (Fig. 7D). Trichomes on posterior of vertex 10 + 10–12 + 12, with 2–3 trichomes posteriorly on each side (Figs 7D, E). 10 tergites with 12 pairs of legs. Hooked trichomes on telson with 3–5 hooks, more than 10 linear arranged short barbate trichomes and 2 + 2 long barbate trichomes located dorsal to the hooked trichomes clusters (Fig. 7F).

Juvenile of stage V. Body length 1.6–2.2 mm, average length of caudal trichomes 0.7–0.8 mm. Trichomes on posterior of vertex 8 + 8, with 2 caudally-pointed trichomes posteriorly on each side. Hooked trichomes on telson with 4–5 hooks.

4. Discussion

The new species described here are convincingly placed within the family Polyxenidae by a combination of the following features: 11 segments with 13 pairs of legs, rows of barbate trichomes ending

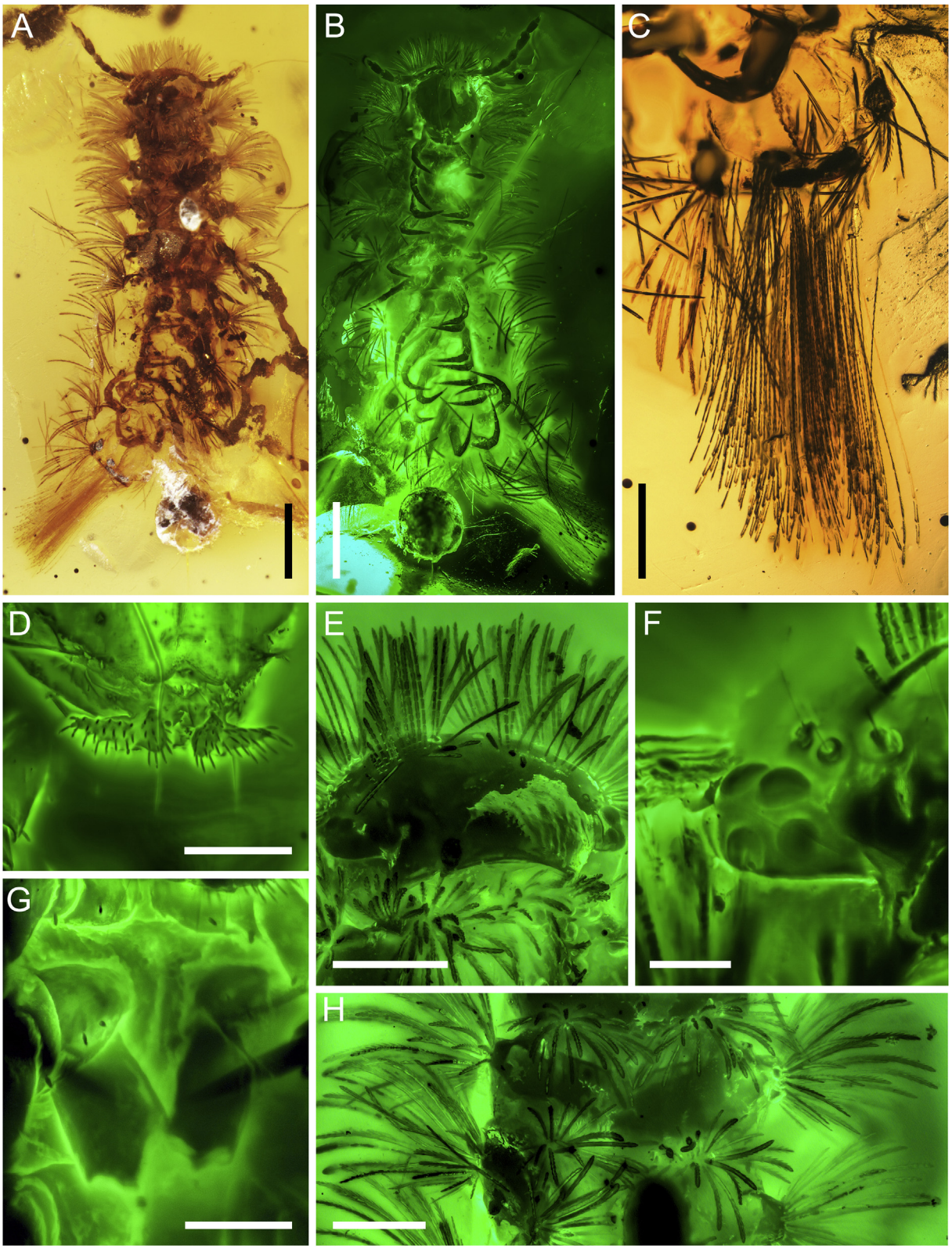

Fig. 4. *Pauropsxenus extraneus* sp. nov., holotype, NGIP168241, adult male. **A**, dorsal view; **B**, ventral view; **C**, ventral view of the caudal trichomes; **D**, enlargement of the mouth part; **E**, dorsal view of the head; **F**, ommatidia and trichobothria on the left side **G**, enlargement of the penes; **H**, tergal trichomes of tergite II, III. **A**, **C** using normal light; **B**, **E**, **H** using green fluorescence; **D**, **F**, **G** using CLSM. Scale bars: **A**, **B** 500 μm; **C**, **E**, **H** 200 μm; **D**, **G** 100 μm, **F** 50 μm. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

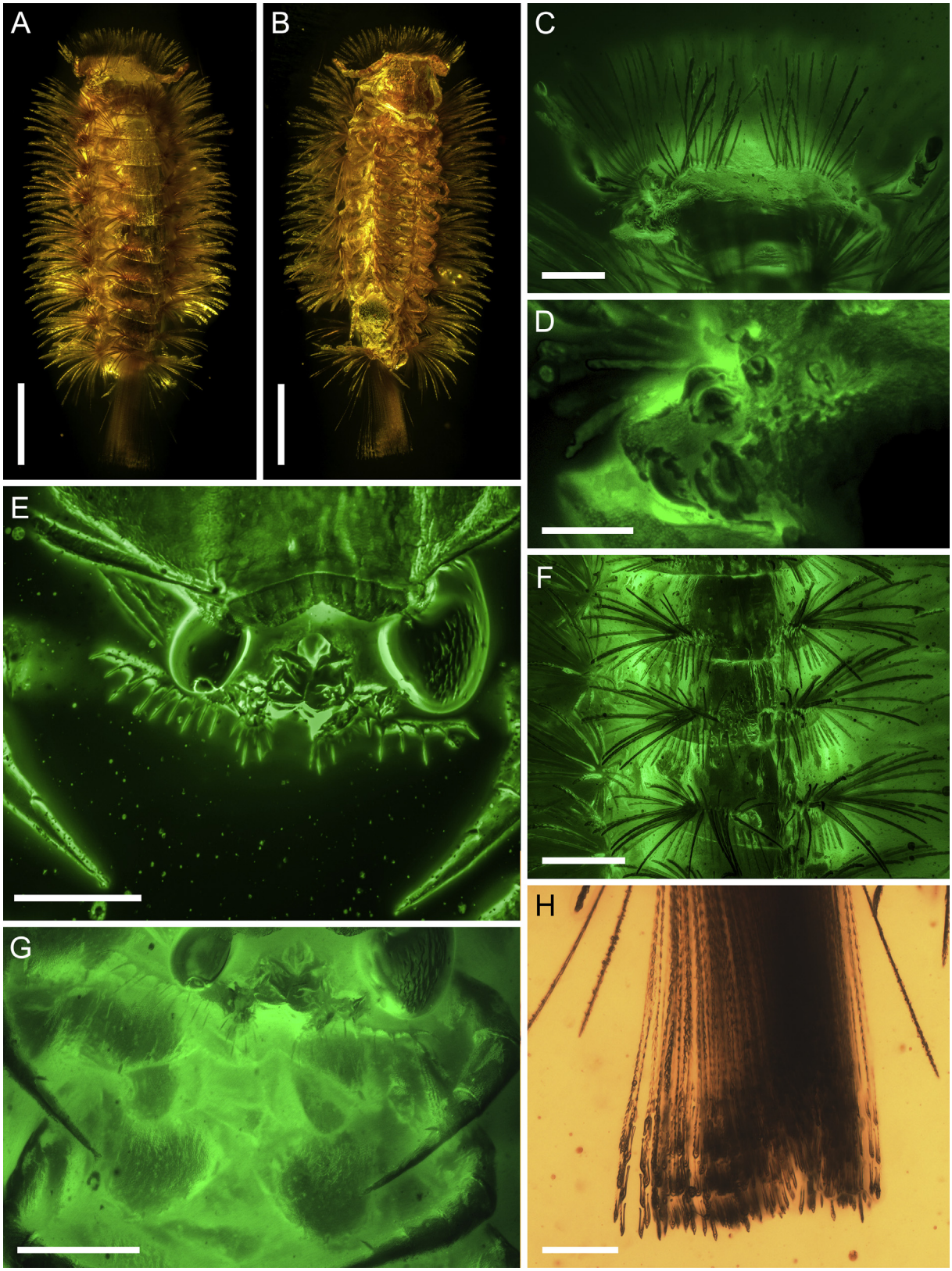

Fig. 5. *P. extraneus*, paratype, NGIP168242, adult female. **A**, dorsal view; **B**, ventral view; **C**, article VI-VIII of the left antenna; **D**, sensilla on antennal article VII; **E**, sensilla on antennal article VI; **F**, dorsal view of the head; **G**, enlargement of the mouth part; **H**, tergal trichomes of tergite IV-VII; **I**, ventral view of the caudal trichomes. **A**, **B** using reflective light; **C**, **F**, **G**, **H** using green fluorescence; **D**, **E** using CLSM; **I** using transmission light. Abbreviations: **a**, anterior basiconic sensilla; **p**, $\mathbf{p_1}$, $\mathbf{p_2}$, posterior basiconic sensilla; **c**, coeloconic sensilla. Scale bars: **A**, **B** 500 μm; **C**, **G**, **I** 100 μm; **D**, **E** 20 μm; **F**, **H** 200 μm. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

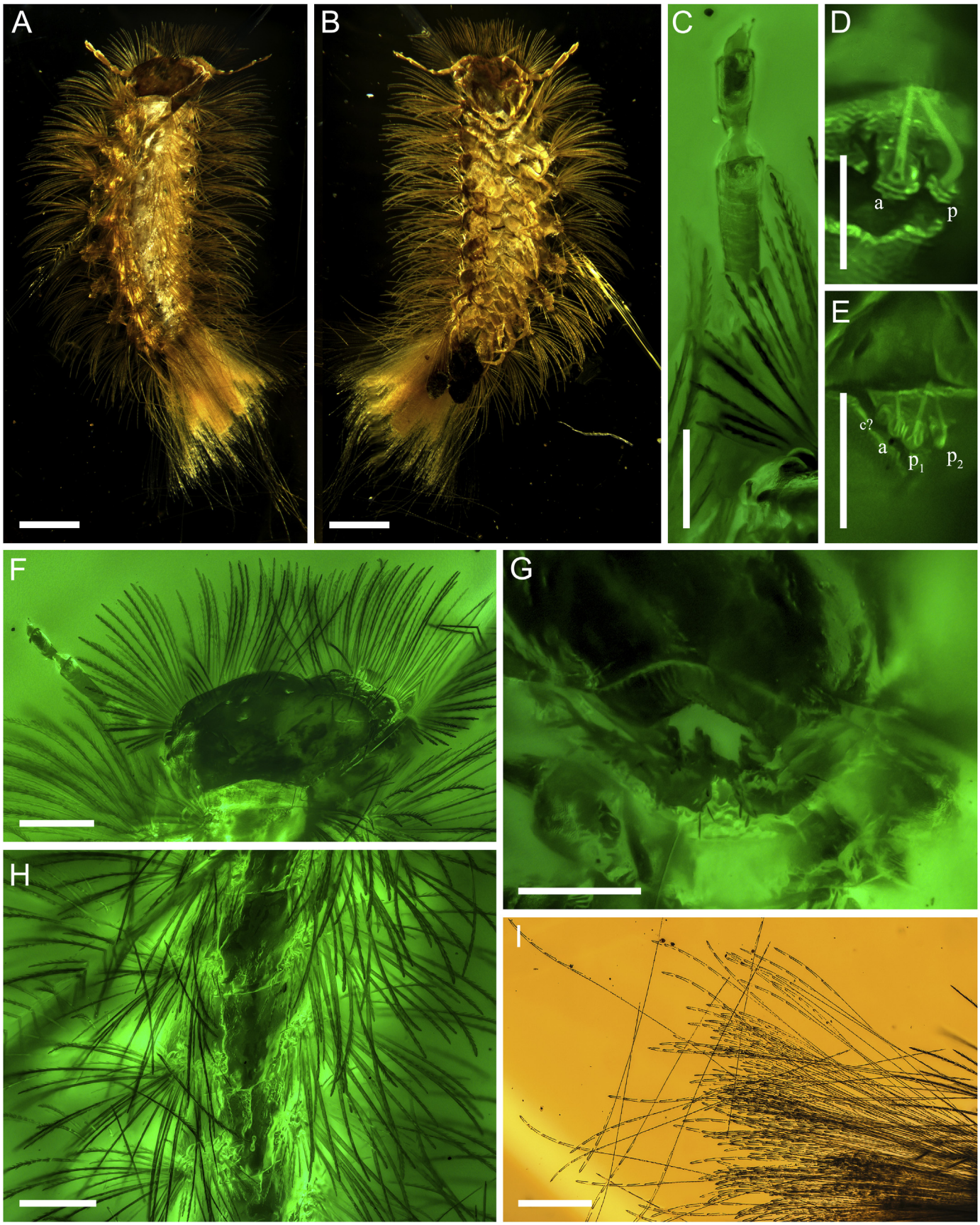

Fig. 6. *P. extraneus*, paratype, NGIP168243, adult female. **A**, dorsal view; **B**, ventral view; **C**, dorsal view of the head; **D**, ommatidia and trichobothria on the left side; **E**, enlargement of the mouth part; **F**, tergal trichomes of tergite IV-VI; **G**, enlargement of vulvae; **H**, ventral view of the caudal trichomes. **A**, **B** using reflective light; **C**, **F**, **G** using green fluorescence; **D**, **E** using CLSM; **H** using transmission light. Scale bars: **A**, **B** 500 μm; **C**, **E-H** 100 μm; **D** 50 μm. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

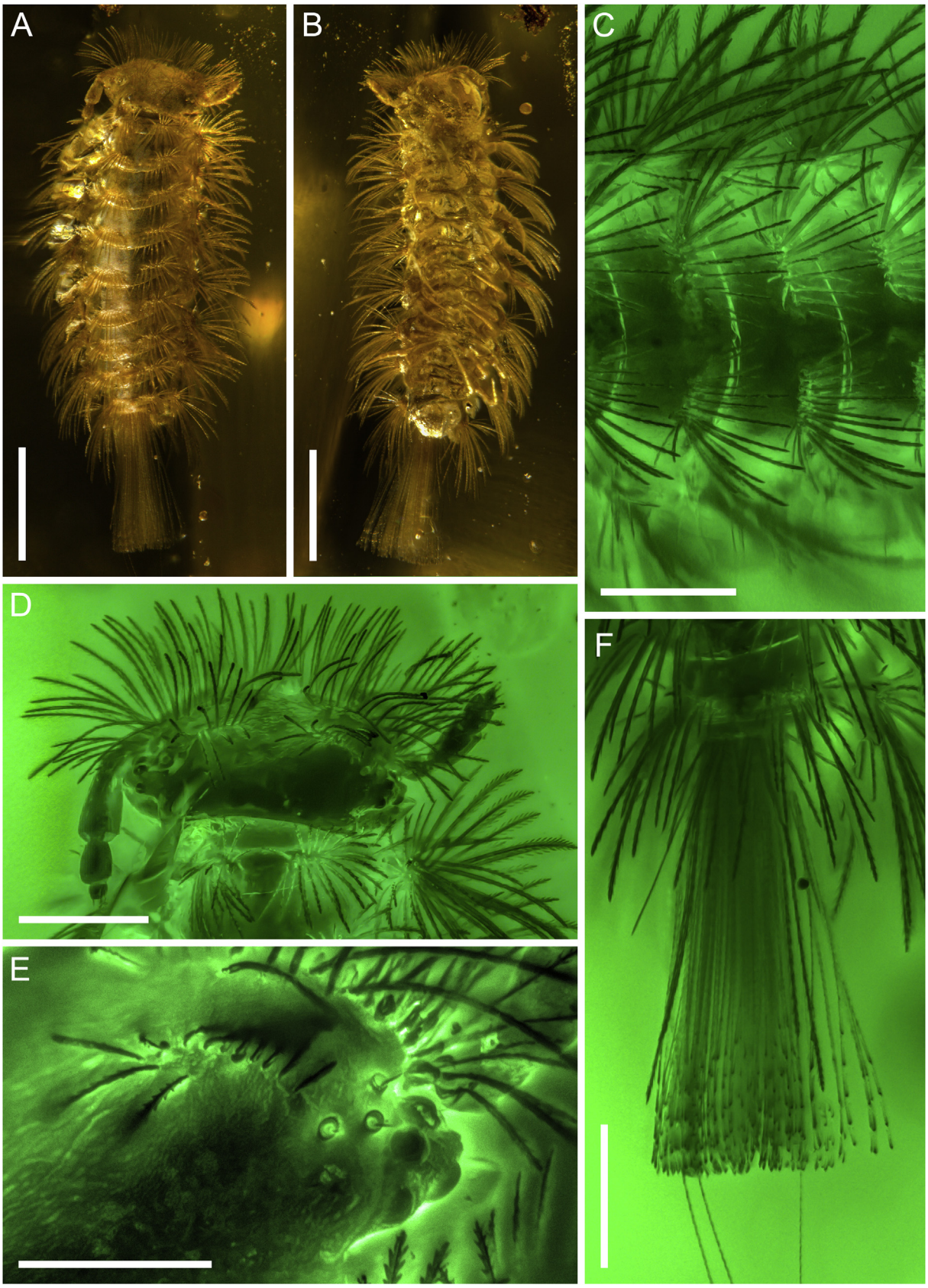

Fig. 7. *P. extraneus*, paratype, NGIP168244, sub-adult female. **A**, dorsal view; **B**, ventral view; **C**, tergal trichomes of tergite III-IV; **D**, dorsal view of the head; **E**, ommatidia, trichobothria and arrangement of trichomes on the right side. **F**, dorsal view of the caudal trichomes. **A**, **B** using reflective light; **C**, **D**, **F** using green fluorescence; **E** using CLSM. Scale bars: **A**, **B** 500 μm; **C**, **D, F** 200 μm; **E** 100 μm. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

with clusters on tergites, the presence of ommatidia, pigmentation and outer palps of gnathochilarium. Moreover, 3 basiconic sensilla on antennal article VI, 2 basiconic sensilla on antennal article VII, the closely aligned caudal trichomes forming an appearance of a single cluster, and 3–7 anteriorly facing hooks with barbate stem on hooked trichomes. Also, the absence of pseudoarticulated gnathochilarium palps and multiple hooks match the typical characters of the extant subfamily Monographinae Condé, 2008 (Condé & Nguyen Duy-Jacquemin, 2008; Enghoff et al., 2015). The only significant difference between the new species and extant polyxenids is the large, cylindrical shaped penes of the male (Figs 1H, 4G). Penes of extant polyxenids are relatively small, pyriform shaped with sharp apex. We consider that such a difference is not enough for establishing a new genus, and therefore assign them to the extant monographine genus *Pauropsxenus* Silvestri, 1948, based on the number of ommatidia and a spine on tarsus II. *Pauropsxenus* currently contains 3 species, mainly occurring in intertropical Africa (Angola, Gabon, Katanga, Uganda, Tanganyika, etc.), and they can be recognized by the presence of 5 ommatidia and a spine on tarsus II (Brölemann, 1920; Silvestri, 1948; Marquet & Condé, 1950; Attems, 1953; Nguyen Duy-Jacquemin & Condé, 1965; Enghoff et al., 2015; Millibase, 2018). Although there are only 4 ommatidia visible in *P. extraneus*, the arrangement of ommatidia in a female (Fig. 5D) may indicate the presence of an additional anteriorly located ommatidium. The 2 new species differ from other congeners by having a smaller number of trichomes only arranged in 1 row on the posterior part of the vertex; arrangements of the sensilla on anntenal article VI and VII; more elongate outer palps of gnathochilarium and cylindrical shaped penes of the male. Other species of *Pauropsxenus* usually have more than 30 trichomes, forming 3 or 4 irregular rows on the posterior part of the vertex, shorter outer palps of gnathochilarium and typical pyriform penes (Brölemann, 1920; Silvestri, 1948; Marquet & Condé, 1950; Attems, 1953; Nguyen Duy-Jacquemin & Condé, 1965). Moreover, *P. ordinatus* can be also recognized from other species by the arrangement of trichomes on tergites, whereas the arrangements of tergite trichomes of extant species are all similar to those of *P. extraneus*.

Compared with other described Mesozoic polyxenids (*Electroxenus* and *Lebanoxenus* Nguyen Duy-Jacquemin & Azar, 2004), the 2 new species differ from *Electroxenus* by 4–5 ommatidia, 3 basiconic sensilla on antennal article VI, 2 sensilla on antennal article VII (*Electroxenus* with 6–8 ommatidia, 4 or more basiconic sensilla on antennal article VI and 3 on VII; Nguyen Duy-Jacquemin & Azar, 2004), but with a similar large spine on tarsus II and similar type of caudal trichomes; differs from *Lebanoxenus* by 4–5 ommatidia, a large spine on tarsus II (8 ommatidia and a setae on tarsus II in *Lebanoxenus*; Nguyen Duy-Jacquemin & Azar, 2004). Polyxenids from the Eocence Baltic amber need restudies and further descriptions to compare with the 2 new species.

Given the characters and comparison discussed above, the new species are similar to the extant polyxenids in most characters. Together with fossils from Lebanese amber (Nguyen Duy-Jacquemin & Azar, 2004), we notice that the Cretaceous polyxenids bear great morphological similarities to the living taxa, which may indicate a similar living habitat and a feeding preference.

Extant polyxenids use their hooked caudal trichomes to defend themselves. These trichomes can be easily detached and can attach to predators by hooks and barbs in order to immobilize them (i.e. Eisner et al., 1996). Eisner et al. (1996) recorded the uses of hooked trichomes in modern polyxenids to defend themselves against ants: when being attacked, they brush their caudal trichomes against ants, causes numbers of hooked trichomes fasten to the ant, then move away and leave these hooked trchomes to entangle the ant; the ant will get furtherly entangled when it attempts to clean itself, sometimes even get killed when it is heavily entangled. The two new species have more than 120 hooked trichomes arranged in two caudally-located clusters, have barbate stem and 3–7 anteriorly facing hooks on apex; the hooks are slightly V-shaped, have much shorter width than length (Figs 1J, 3C, 4C, 5H, 6I, 7F). These features are all similar to the extant polyxenids (Monographiniae) and the detachment of these trichomes can be observed in our specimen (Fig. 6I), suggesting a similar function of the hooked trichomes in our fossil species. It may indicate that Cretaceous polyxenids were already developed their defensive system. A predator-prey relationship between polyxenids and other soil animals might have been established in the Cretaceous, but direct evidence such as the brushing behavior against predators and the attachment of these trichomes on predators are still required. A similar defensive function can be also found in Cretaceous dermestid larvae from Burmese amber (Poinar & Poinar, 2016).

5. Concluding remarks

In the present paper, 2 new species of the bristle millipedes, *Pauropsxenus extraneus* sp. nov. and *Pauropsxenus extraneus* sp. nov., are described in details from the mid-Cretaceous Burmese amber. The new species present great similarities to living polyxenids, are convincingly placed within the extant genus *Pauropsxenus*. The defensive caudal trichomes are also found in the new species, which indicate the Cretaceous polyxenids were already developed their defensive system, and the predator-prey relationship between polyxenids and other soil animals might have been established in the Cretaceous period.

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