Mesozoic 001 (3): 223–234
https://www.mapress.com/mz/

Article

ISSN 3021-1859 (print edition)
MESOZOIC
ISSN 3021-1867 (online edition)

https://doi.org/10.11646/mesozoic.1.3.3
http://zoobank.org/urn:lsid:zoobank.org:pub:DBCF803B-72E3-46ED-A27D-DE26FAB866A2

A new species of Heterochordeumatidae (Myriapoda: Diplopoda: Chordeumatida) from mid-Cretaceous Burmese amber

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Abstract

A new species of millipede from the family Heterochordeumatidae, *Heterochordeuma liae* **sp. nov.**, is described from mid-Cretaceous Burmese (Kachin) amber. The detailed morphological characteristics of this species are provided based on the examination of 14 specimens, primarily utilizing confocal laser scanning microscopy. This new species can be confidently assigned to the extant genus *Heterochordeuma* due to its extended and polydesmidan-like paranota, 32 body rings in male and distinctive curved anterior gonopods, modified coxites 9, and leg-pair 10. A comprehensive comparison with extant species is also presented.

Keywords: Mesozoic, Myanmar, millipede, *Heterochordeuma*, taxonomy

Introduction

The family Heterochordeumatidae is a small and unusual group of millipedes belonging to the superfamily Heterochordeumatoidea within the order Chordeumatida. It is distinguished from other members of the superfamily by the presence of elongate, broad, polydesmidan- or platydesmid-like paranota (Shear, 2000; Enghoff *et al*., 2015). Currently, extant heterochordeumatids comprise only three genera and six species, all found in Southeast Asia (Shear, 2000, 2012; Enghoff *et al*., 2015). To date, no fossil members of this family have been described, with only unidentified specimens reported from mid-Cretaceous Burmese (Kachin) amber (Wesener & Moritz, 2018). The genus *Heterochordeuma* Pocock, 1893, includes four extant species, which are exclusively distributed in Myanmar and Sumatra (Shear, 2000; Enghoff *et al*., 2015). This genus is differentiated from others by its 32 body rings in males, curved anterior gonopods, modified coxites of the 10th body segment, and unmodified femora of the third leg pair (Shear, 2000; Enghoff *et al*., 2015).

The mid-Cretaceous Burmese (Kachin) amber from the Hukawng Valley in Kachin State harbors a diverse array of protists, fungi, plants, invertebrates, and vertebrates (Ross, 2019). The geological setting and details of this amber deposit have been explored in studies by Zherikhin & Ross (2000), Grimaldi (2002), Cruickshank & Ko (2003), and Ross *et al*. (2010). Although fossil myriapods are generally rare, they are abundant in Burmese amber, particularly diplopods (Wesener & Moritz, 2018). To date, 12 genera and 16 species of Myriapoda have been described from this amber. Aside from one species each of Geophilomorpha and Symphyla, 14 species in 10 genera of Diplopoda have been documented (*e.g*., Liu *et al*., 2017; Jiang *et al*., 2019; Moritz & Wesener, 2019, 2021; Stoev *et al*., 2019; Ross, 2019, 2021, 2023; Su *et al*., 2021, 2022, 2023, 2024).

We describe a new fossil species of Heterochordeumatidae based on 14 individuals preserved in Kachin amber. This new species can be confidently assigned to the extant genus *Heterochordeuma* Pocock.

Material and methods

This study was based on 14 newly discovered specimens entombed in mid-Cretaceous Burmese amber, which originated from a locality near Noije Bum (26°20′N, 96°36′E), Hukawng Valley, Kachin State, northern Myanmar (Yin *et al*., 2018), with an age close to the Albian-Cenomanian boundary (Shi *et al*., 2012; Mao *et*

Submitted: 12 Jul. 2024; accepted by Z. Feng: 13 Sept. 2024; published: 26 Sept. 2024

al., 2018). All specimens are deposited in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, China.

The amber pieces containing the inclusions were cut and shaped manually with a handheld engraving tool and a razor blade, and polished using emery paper of different grit sizes, rare earth polishing powder, and diatomite mud (Azar *et al*., 2003). Observations were made and photographs were taken using a Zeiss Axio Zoom V16 stereo microscope and a Zeiss Axio Imager 2 light microscope with a digital camera attached. Widefield fluorescence images (green background) were captured with a Zeiss Axio Imager 2 light microscope combined with a fluorescence imaging system. Confocal laser scanning microscopy (CLSM) images (cyan or multi-colour background) were obtained with a Zeiss LSM710 microscope with 5× and 10× objectives, using the 488 nm Argon laser excitation line (Cai & Huang, 2014; Fu *et al*., 2021; Li *et al*., 2023).

The classification and nomenclature of characters were based on Silvestri (1895), Hoffman (1963), Shear (2000, 2012), and Enghoff *et al*. (2015).

Systematic palaeontology

Class Diplopoda de Blainville *in* Gervais, 1844
Subclass Helminthomorpha Pocock, 1887
Order Chordeumatida Pocock, 1894
Suborder Heterochordeumatidea Shear, 2000
Superfamily Heterochordeumatoidea Pocock, 1894
Family Heterochordeumatidae Pocock, 1894
Genus *Heterochordeuma* Pocock, 1893

Type species. *Heterochordeuma doriae* Pocock, 1893

Heterochordeuma liae sp. nov.

Material. Holotype: NIGP175104, a well-preserved adult male (Fig. 1, 2). Paratypes: NIGP175105–NIGP175107, one poorly-preserved adult male (Fig. 3, 4), one well-preserved adult female (Fig. 5, 6), one moderately-preserved specimen of unknown sex (Fig. 7). Additionally, 10 females or sex-undetermined specimens were studied.

Etymology. Specific named for our colleague Dr Juan LI. She pasted away during the field work in Tibet, July of 2023.

Diagnosis. The head is slightly broader than the collum. The anterior gonopods are elongated and relatively slender, with a noticeable enlargement and a long seta on the medial part. The coxa of the posterior gonopods features a strong, straight branch, and the telopodite femora are markedly swollen, bearing a distinct projection with a seta at the apex. In males, the 10th leg pair is reduced, with telopodites comprising two articles; the distal article is longer than it is wide.

Locality and horizon. Noije Bum near Tanai, Hukawng Valley, Kachin State of northern Myanmar; upper Albian to lower Cenomanian (mid-Cretaceous).

Description. Body length 4.6–5.0 mm, maximum width of mid-body metazonites 0.85–0.98 mm. 32 body rings in adult males and females; no distinct size difference between sex (Figs 1A, B, 3A, B, 5A–D, 7A, B).

Head large, sparsely setose. 7–10 ommatidia (Figs 2C, 6D, 8A, B) can be observed on each side, the number remains questionable due to observation angles or preservations. Antennae (Figs 1C, D, F, 2C, 3C, 5E, 6C, 7C, 8A) long and slender, moderately setose, with seven elongate antennomeres; each antennomere bears a strong and elongate seta with relatively obvious socket; antennomere 3 and 5 prominently longer than others.

Collum (Figs 1C, F, 2C, 5E, 6C, D) small, sub-oval shaped, slightly narrower than head, lateral edge round to acute; with three pairs of transversely arranged macrochaetae, two pairs located dorsally on medial part, one pair located dorsolaterally near lateral edge. Microtrichia slender, arranged sparsely. Tergite fused with pleurite, with distinct dorso-medial suture (Figs 5G, H, 6E, 7E, 8E, F). Prozonite (Figs 1H, 2E, 5H, 6E, 7E, 8E, F) slightly narrower than metazonite, with orderly arranged polygon texture. Metazonite (Figs 1H, 2E, 5G, H, 6E, 7D, E, 8E, F) convex, with three pairs of transversely arranged macrochaetae: two pairs located on medial part, one pair located near lateral edge of paranota. Dorsal surface of metazonite covered with sparse and slender microtrichia; posterior edge of metazonite with a row of slightly stouter microtrichia. Paranota (Figs 1C, F–H, 2A, E, 5G, 6E, 7D, E, 8E) strongly developed, slightly wing-like and recurved; anterior and posterior margin with small, densely arranged spine-like microtrichia; anterior paranotal notch poorly to moderately developed, sometimes smooth and obscure (*e.g*., Figs 2E, 7D). Defensive glands absent. Pleurite with scale-like structures or spines. Sternite not visible. Common legs slender, moderate in length, with seven podomeres, sparsely setose; femora of leg-pair 3 normal.

Telson (Figs 2B, F, 3G, H, 4F, 6A, B, F, G, 7F) short with a pair of well-developed spinnerets; spinneret setae elongate. Valves oval-shaped, with 2–3 pairs of thin setae.

Gonopods modified from the 8th and 9th leg-pairs; leg-pair 10 of males significantly modified. Anterior gonopods (Figs 8C, D) limb-like, bend posteriorly, latero-posteriorly passing coxites 9; medial part seems slightly enlarged, may bears a long seta and several short setae. Posterior gonopods femora (Figs 1G, 2D, 3E, F, 4C–E) rounded and strongly swollen, with several thin setae on

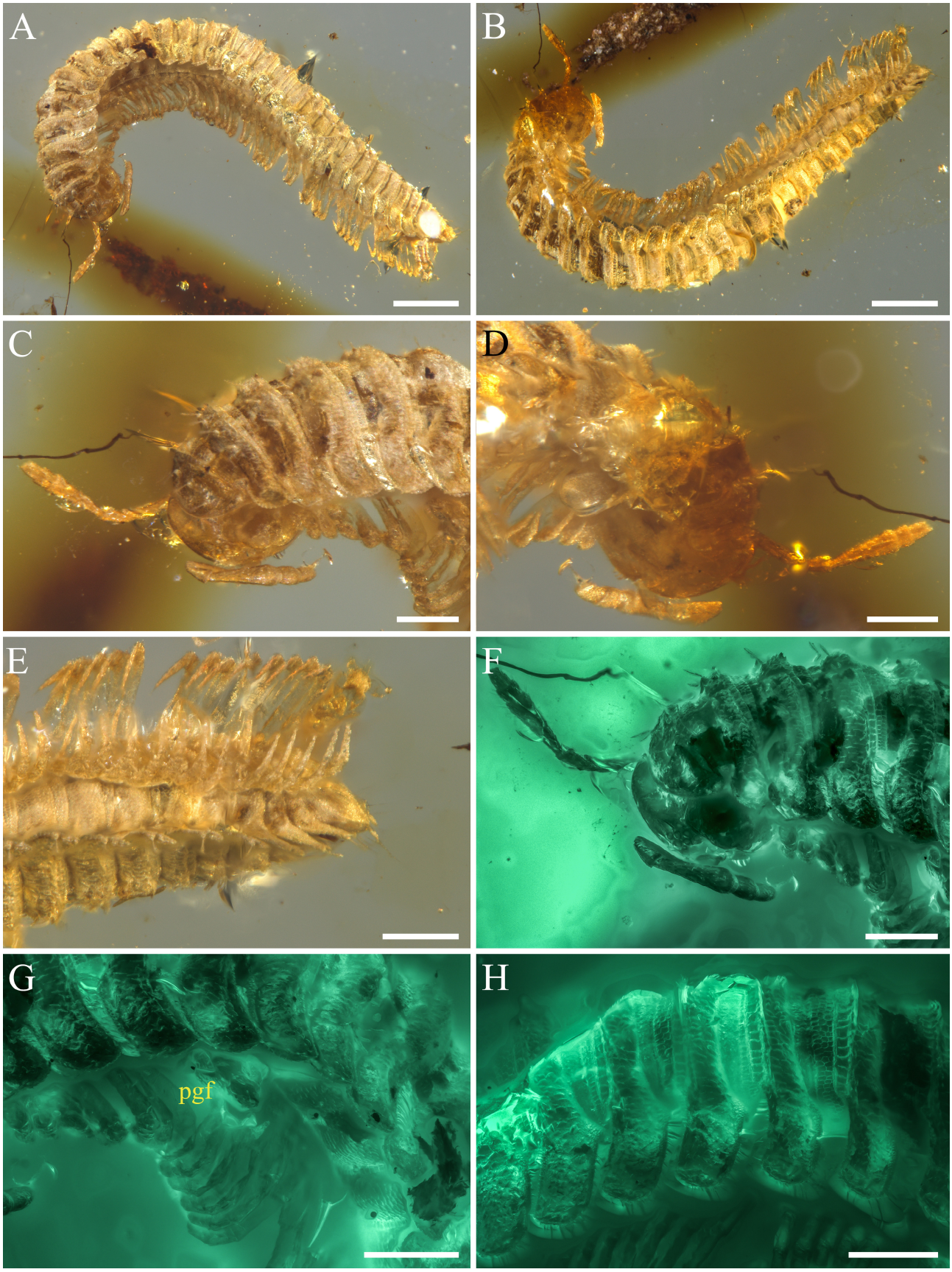

FIGURE 1. Adult male of *Heterochordeuma liae* **sp. nov.**, holotype (NIGP175104). **A**, **B**, Lateral overall view. **C**, **D**, **F**, Lateral view of head. **E**, Lateral view of telson. **G**, Lateral view of body-rings 3–10, showing the position of posterior gonopod femora. **H**, Dorsal-lateral view of body-rings 8–13. **F**–**H** under green fluorescence. Abbreviations: pgf, femora of posterior gonopod telopodites. Scale bars: 0.5 mm in **A**, **B**; 0.2 mm in others.

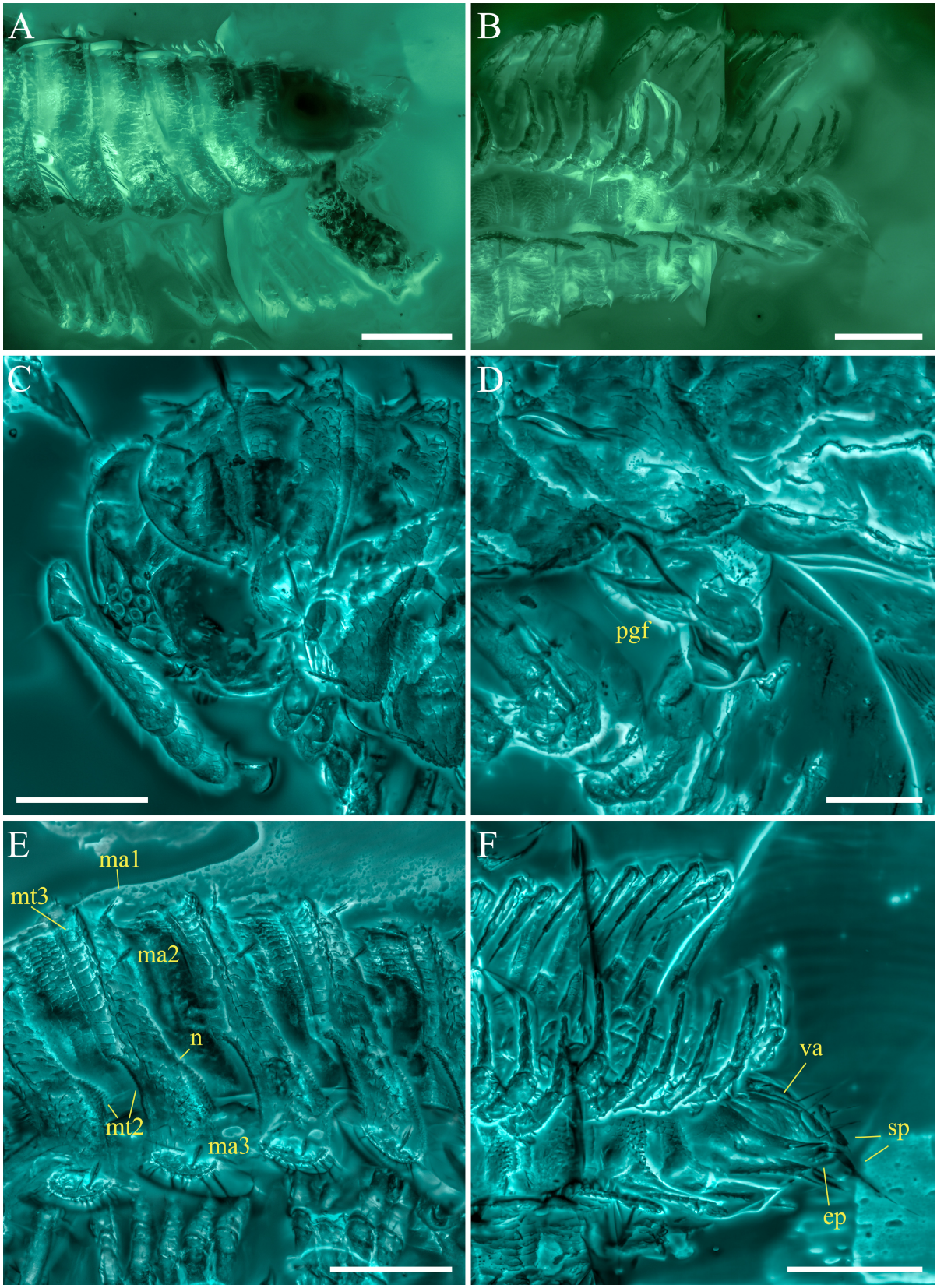

FIGURE 2. Adult male of *Heterochordeuma liae* **sp. nov.**, holotype (NIGP175104). **A**, Dorsal-lateral view of telson. **B**, Ventral-lateral view of telson. **C**, Detail structures of head. **D**, Detail structures of posterior gonopods femora. **E**, Detail structures of body-rings 11–14. **F**, Detail structures of posterior body part and telson. **A**, **B** under green fluorescence, others under CLSM. Abbreviations: ep, epiproct; ma1–3, metazonal macrochaetae; mt2, microtrichia on paranotal margin; mt3, microtrichia on posterior edge of metanonite; n, paranotal notch; pgf, femora of posterior gonopod telopodites; sp, spinnerets; va, anal valves. Scale bars: 100 μm in **D**; 200 μm in others.

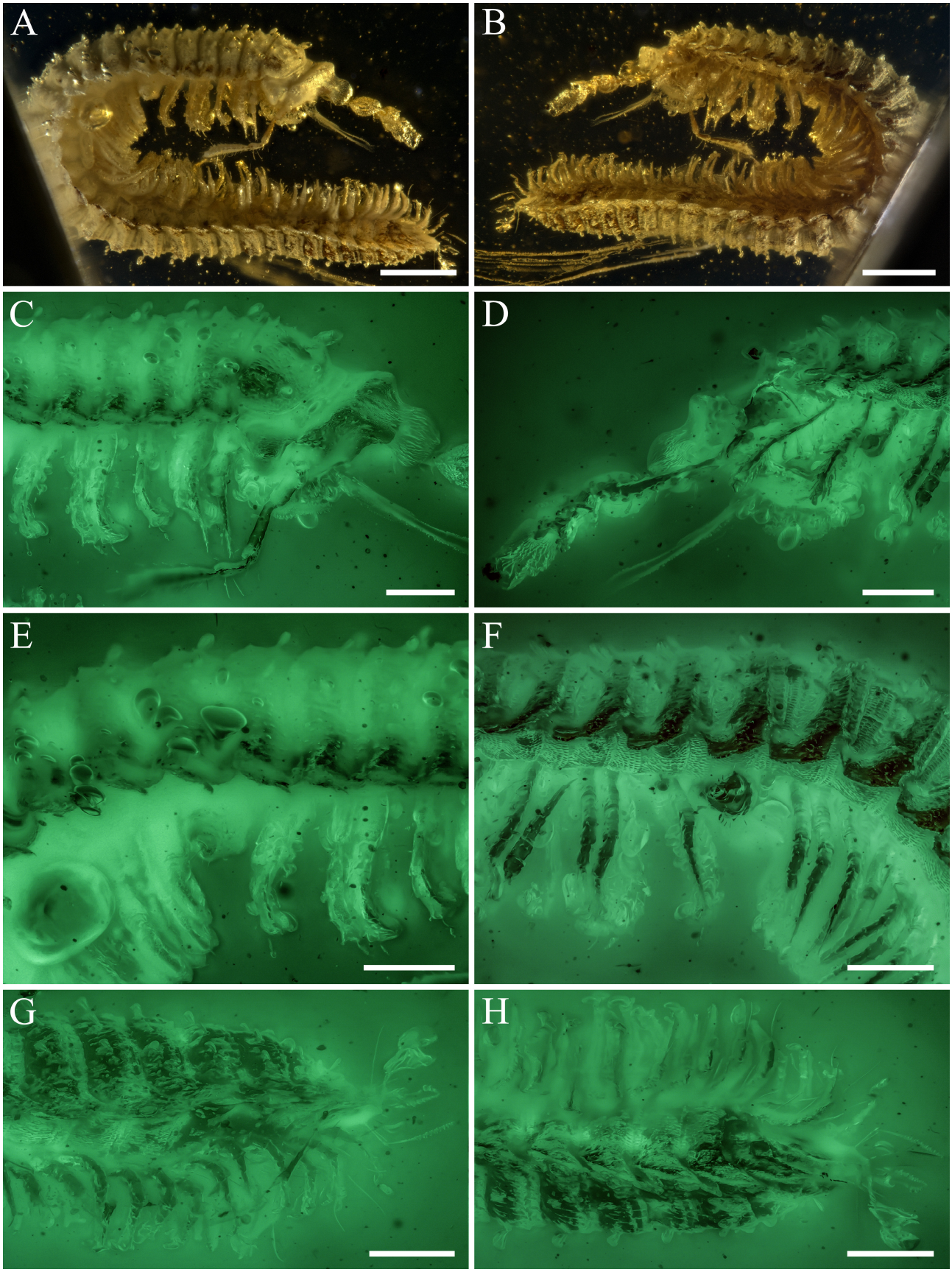

FIGURE 3. Adult male of *Heterochordeuma liae* **sp. nov.**, paratype (NIGP175105). **A**, **B**, Lateral overall view. **C**, **D**, Lateral view of head. **E**, **F**, Lateral view of body-rings 4–11, showing the position of posterior gonopod femora. **G**, **H**, Lateral view of telson. **C**–**H** under green fluorescence. Scale bars: 0.5 mm in **A**, **B**; 0.2 mm in others.

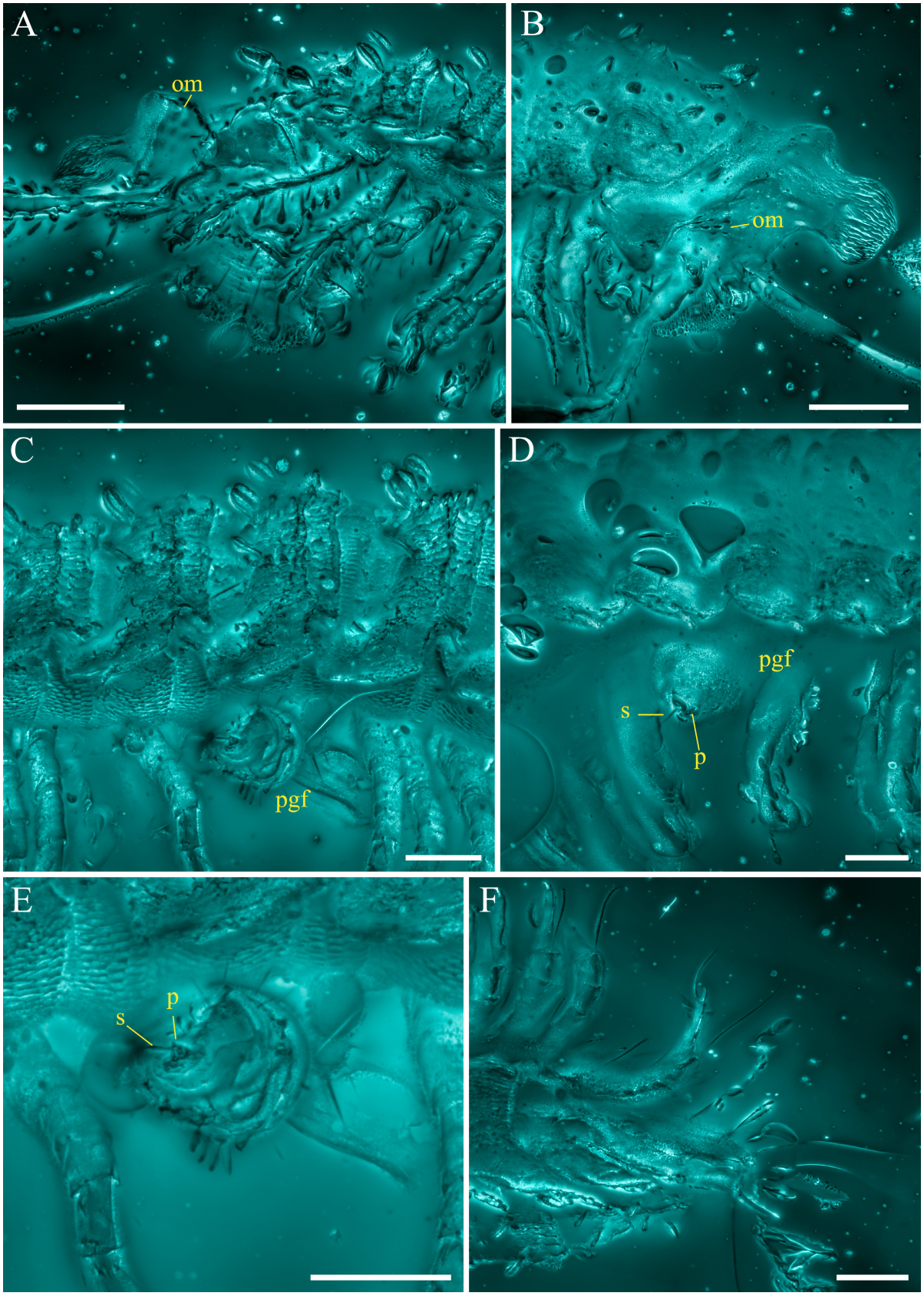

FIGURE 4. Adult male of *Heterochordeuma liae* **sp. nov.**, paratype (NIGP175105), detail structures under CLSM. **A**, **B**, Detail structures of head. **C**, Detail structures of right posterior gonopod femora. **D**, Detail structures of left posterior gonopod femora. **E**, Enlarged view of right posterior gonopod femora. **F**, Detail structures of telson. Abbreviations: om, ommatidia; p, projection on apex of posterior gonopod femora; pgf, femora of posterior gonopod telopodites; s, seta on apex of posterior gonopod femora. Scale bars: 200 μm in **A**, **B**; 100 μm in others.

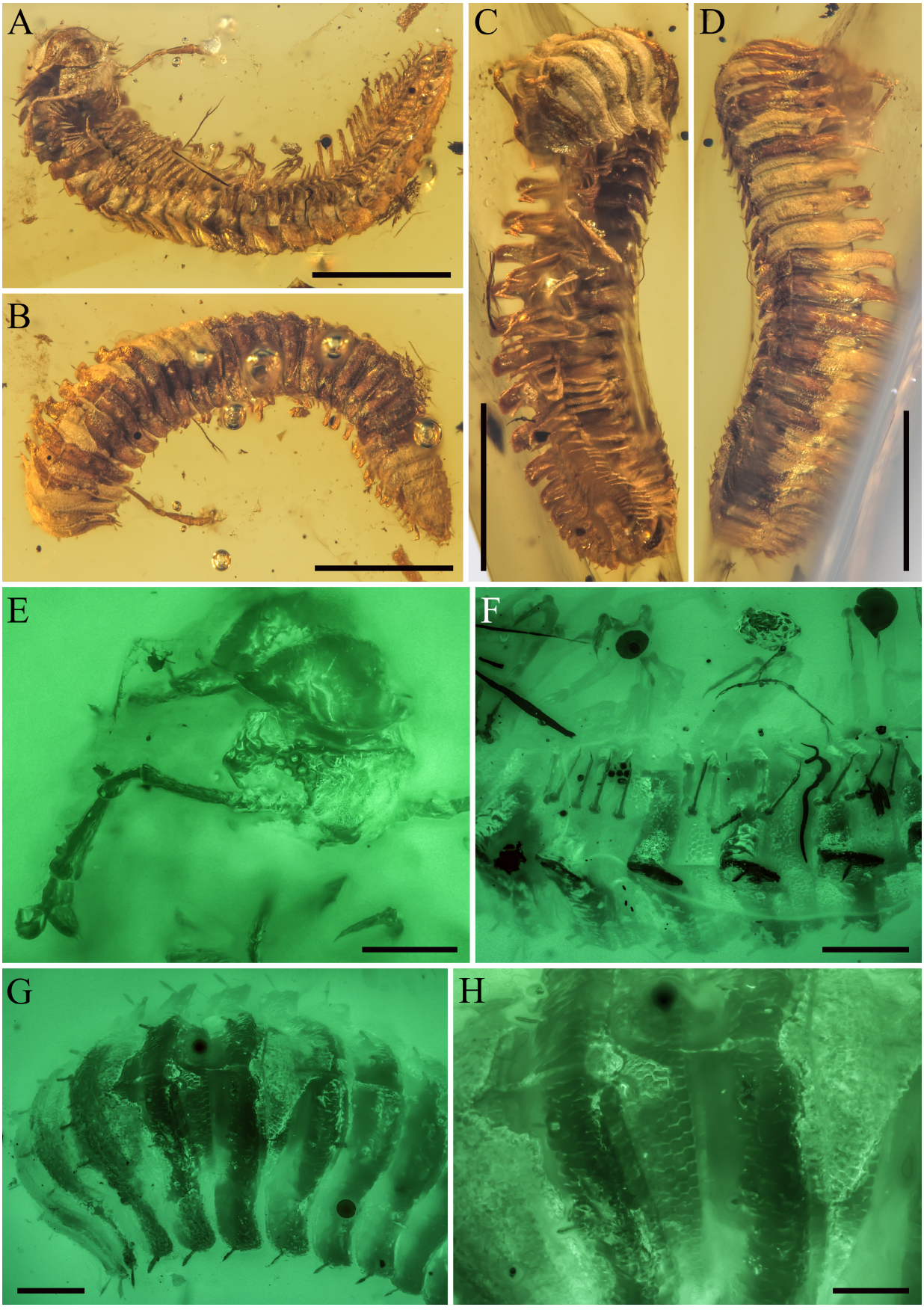

FIGURE 5. Adult female of *Heterochordeuma liae* **sp. nov.**, paratype (NIGP175106). **A**, **C**, Ventral-lateral overall view. **B**, **D**, Dorsal-lateral overall view. **E**, Dorsal-lateral view of head. **F**, Lateral view of body-rings 4–11. **G**, Dorsal-lateral view of body-rings 4–11. **H**, Enlarged view of body-rings 7, 8. **E**–**H** under green fluorescence. Scale bars: 1 mm in **A**–**D**; 0.2 mm in **E**, **F**; 0.1 mm in others.

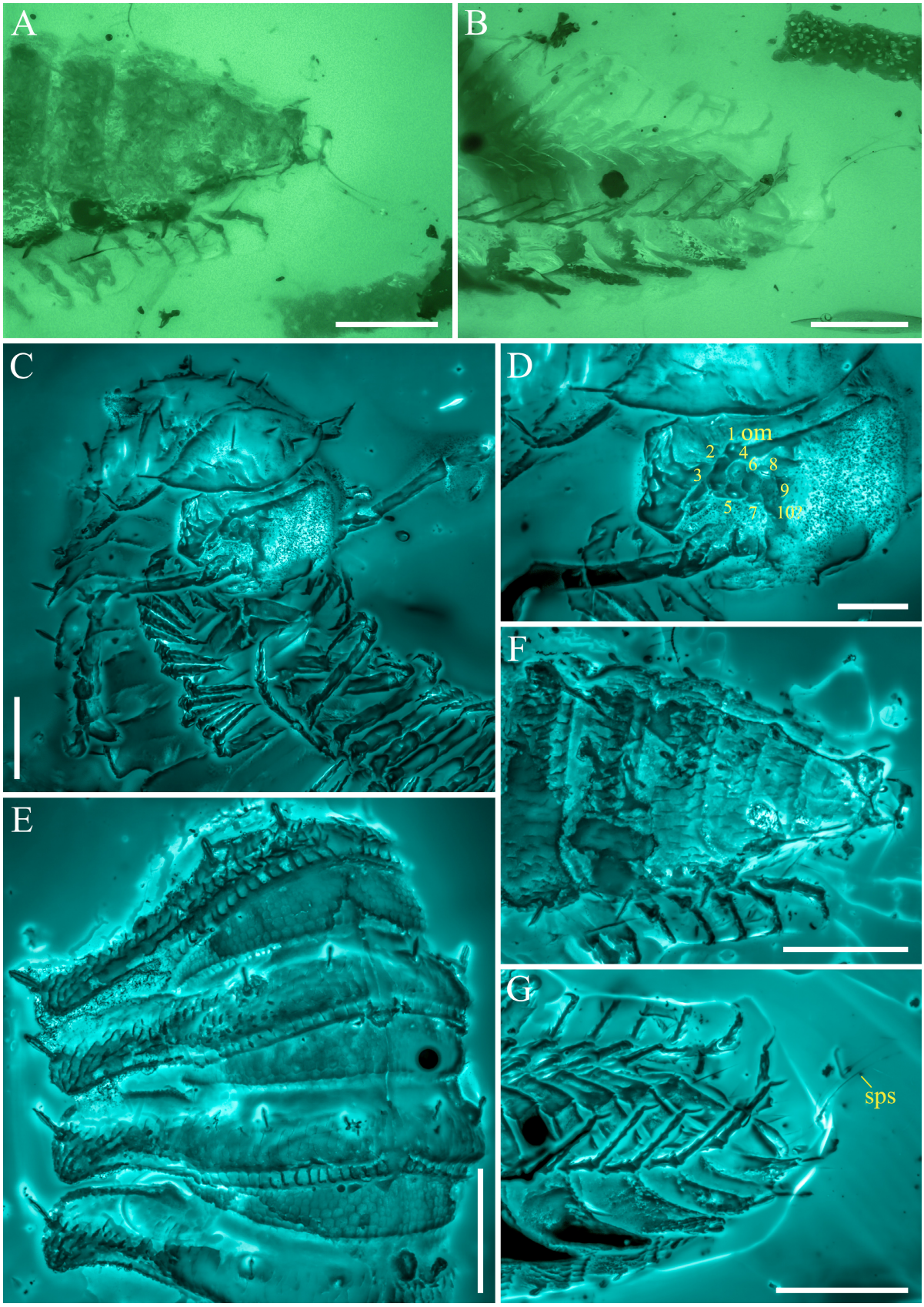

FIGURE 6. Adult female of *Heterochordeuma liae* **sp. nov.**, paratype (NIGP175106). **A**, Dorsal-lateral view of telson. **B**, Ventral-lateral view of telson. **C**, Detail structures of head and anterior body part. **D**, Enlarged view of head, showing the estimate number of ommatidia. **E**, Detail structures of tergites 5–8. **F**, **G**, Detail structures of posterior body part and telson. **A**, **B** under green fluorescence, others under CLSM. Abbreviations: om, ommatidia; sps, spinneret setae. Scale bars: 100 μm in **D**; 200 μm in others.

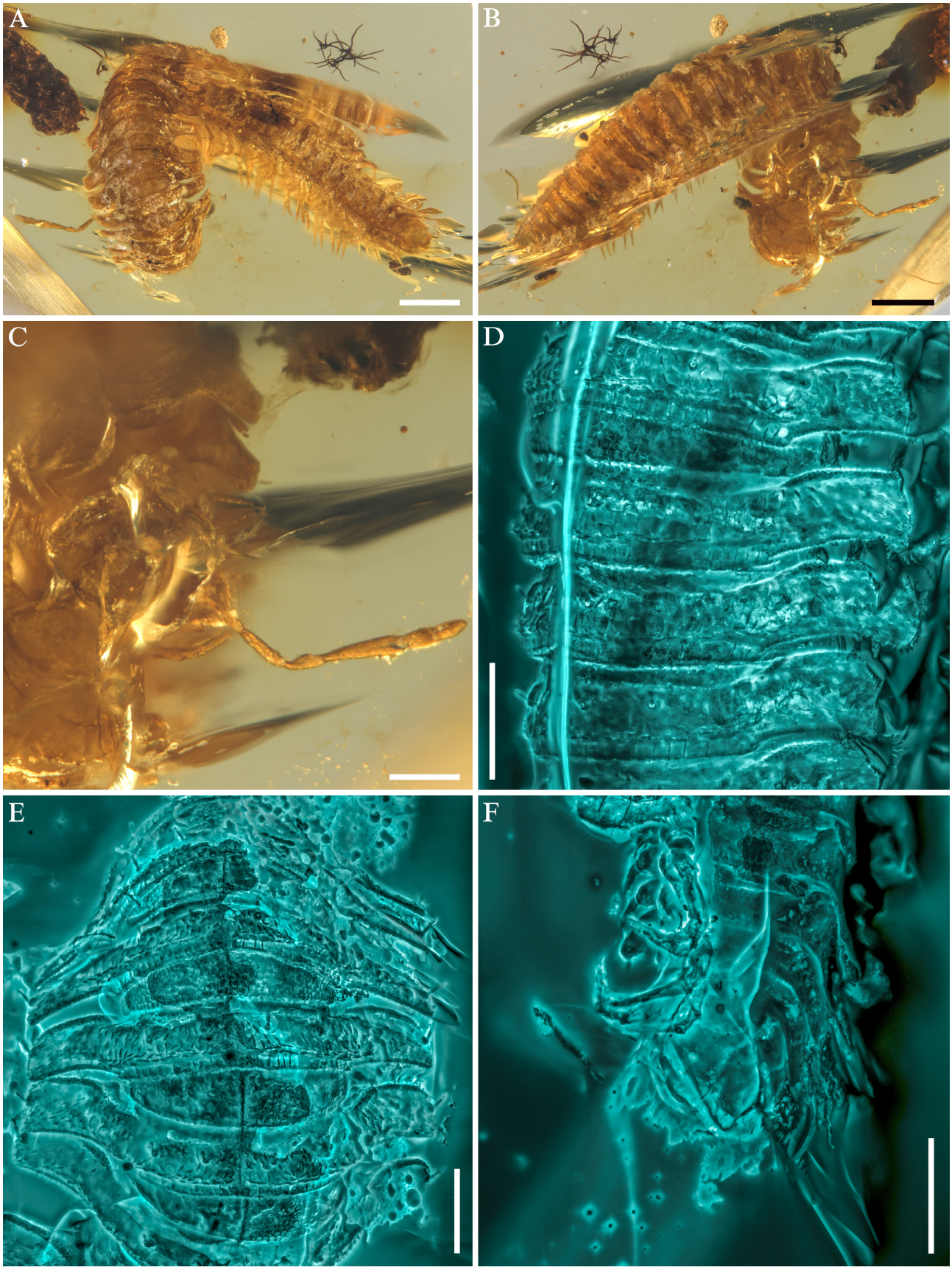

FIGURE 7. Adult *Heterochordeuma liae* **sp. nov.**, sex un-determined, paratype (NIGP175107). **A**, **B**, Overall view. **C**, Enlarged view of head. **D**, Dorsal-lateral view of body-rings 16–19. **E**, Dorsal view of body-rings 7–9. **F**, Ventral-lateral view of telson. **D**–**F** under CLSM. Scale bars: 0.5 mm in **A**, **B**; 0.2 mm in others.

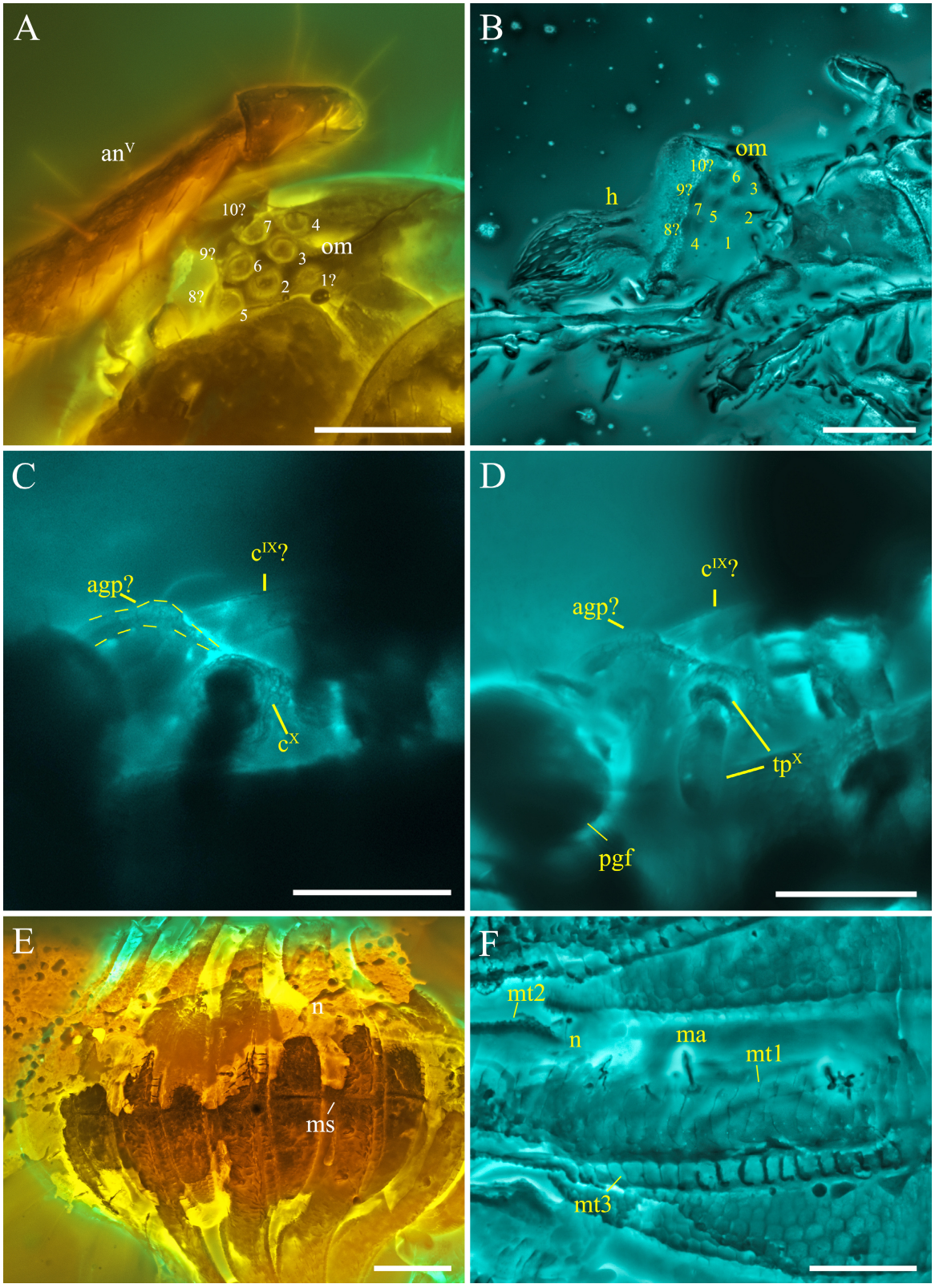

FIGURE 8. Detail features of ommatidia, gonopods and surface structures under CLSM. **A**, Ommatidia of adult male, holotype (NIGP175104). **B**, Ommatidia of adult male, paratype (NIGP175105). **C**, **D**, Detail structures of gonopods and leg-pair 10, dotted lines show the estimate shape of anterior gonopods. **E**, Tergites 7–9 of adult, paratype (NIGP175107). **F**, Enlarged view of tergite 7, adult female, paratype (NIGP175106). Abbreviations: agp, anterior gonopods; an^{V}, antennomere 5; c^{IX}, coxites of posterior gonopods; c^{X}, coxites of leg-pair 10; h, head; ma, metazonal macrochaetae; ms, medial suture; mt1, microtrichia on metanonite surface; mt2, microtrichia on paranotal margin; mt3, microtrichia on posterior edge of metanonite; n, paranotal notch; om, ommatidia; pgf, femora of posterior gonopod telopodites. Scale bars: 200 μm in **E**; 100 μm in others.

surface; apical part with a relatively strong seta located on projection; coxites not visible except a long stout straight branch (Fig. 8C, D), detail structures not available. Leg-pair 10 of males (Fig. 8C, D) small; telopodites only with two articles: a short sparsely setose article (basal) and a smooth rod-like article (apical), apical article much longer than basal article; coxites enlargement apparently absent.

Discussion

The new species described here can be confidently placed within the extant genus *Heterochordeuma* (Silvestri, 1895; Hoffman, 1963; Shear, 2000, 2012) based on the following combination of features: (1) a platydesmid-like body with a well-developed head and mouthparts, and the presence of ommatidia; (2) 32 body rings in both adult males and females; (3) tergites fused with pleurites, with a medial suture present; (4) metazonites with characteristic chordeumatidan macrochaetae and covered in microtrichia, and strongly developed, wing-like paranota; (5) femora of the third leg pair not swollen; (6) anterior gonopods curved posteriorly and laterally, embracing the posterior gonopod coxites; posterior gonopods with swollen femora and branches on the coxites; the 10th leg pair in males is greatly reduced, with telopodites consisting of two short articles; (7) a pair of prominent spinnerets on the epiproct. The extant genus *Pyrgeuma* Shear, 2012, though it may appear similar to the new species, lacks the enlarged coxites 10 and displays distinct differences, including having 30 body rings in adult males, erect anterior gonopods that do not extend past coxites 9, and metazonites with undetectable setae and densely developed microtrichia.

The new species can be distinguished from living *Heterochordeuma* species (Silvestri, 1895; Hoffman, 1963; Shear, 2000) by its relatively larger head and smaller collum, as well as its comparatively simpler anterior and basal posterior gonopod structures. Additionally, the swollen femora of the posterior gonopod telopodites bear a distinct projection with a seta at the apex, a feature not present or not mentioned in extant species. The prominent elongate apical article of the 10th leg pair may also differ from all known *Heterochordeuma* species, as it is notably longer than the basal article (which, based on the line drawings in Shear (2000), is either only slightly longer or roughly the same length). However, this feature may be questionable, as the structure was not observed directly. The absence of coxite 10 enlargements in the new species could be another major difference from extant species, although it is possible that this structure is obscured and therefore unobservable.

Given the characters and morphological comparisons discussed above, the new species from Kachin amber shows considerable similarity to extant species of *Heterochordeuma* in most features. This morphological resemblance suggests that the family Heterochordeumatidae has undergone bradytely from the mid-Cretaceous to the present. Consequently, it is likely that the origin of the family predates the Cretaceous period.

Acknowledgements

We thank two anonymous reviewers for their valuable comments on an earlier version of this work. This project was supported by the National Natural Science Foundation of China (41925008 and 42288201), and the Second Tibetan Plateau Scientific Expedition and Research project (grant no. 2019QZKK0706).

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