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Two new species of Siphonorhinidae (Myriapoda: Diplopoda: Siphonophorida) from mid-Cretaceous Burmese amber

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Abstract

Two new species of the millipede family Siphonorhinidae, *Siphonorhinus globosus* **sp. nov.** and *Siphonorhinus peculiaris* **sp. nov.**, are described from the mid-Cretaceous Burmese amber. Detailed morphological characters are provided on the basis of 22 specimens, mainly using confocal laser scanning microscopy. The new species can be confidently placed in the extant genus *Siphonorhinus* based on the head lacking a beak-like rostrum, antennae stout and elbowed; antennomeres 5 and 6 each with a field of basiconic sensilla, and gonopods leg-like, with apical podomere of posterior gonopod divided to two branches. A detailed comparison between the new and extant species is given.

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

Introduction

Siphonorhinidae is a small group in the millipede order Siphonophorida, famous for containing the leggiest animal in the world (*e.g.*, Marek *et al*., 2012, 2021). Alongside the family Siphonophoridae, this group is sometimes dubbed "taxonomist's nightmare" and is one of the least studied diplopods (*e.g.*, Read & Enghoff, 2009). Extant Siphonorhinidae, which contains six genera and 16 species mainly distributed in southeastern Asia, southern Africa, Madagascar, and western USA, are characterized by: (1) pyriform head not extended to form elongate beak-like rostrum; (2) antennae stout, usually elbowed; (3) antennomeres 5 and 6 each with field of basiconic sensilla; and (4) gonopods leg-like, with apical podomere of posterior gonopod divided into two or more branches (Enghoff *et al*., 2015; Siewald & Spelda, 2023). No fossil siphonorhinids have been described to date. Only un-identified specimens have been reported from mid-Cretaceous Burmese amber (Wesener & Moritz, 2018). *Siphonorhinus* Pocock, 1894 contains eight extant species occurring in southeastern Asia (Enghoff *et al*., 2015, Siewald & Spelda, 2023). It differs from the other genera by: (1) body size various; (2) coxae 1 fused with sterna; and (3) last podomere of posterior gonopod divided into two branches without spines (Enghoff *et al*., 2015).

The mid-Cretaceous Burmese amber from Hukawng Valley in Kachin State contains diverse groups of protists, fungi, plants, invertebrates, and vertebrates (Ross, 2019). An overview of the amber deposit and its geological setting was provided by Zherikhin & Ross (2000), Grimaldi (2002), Cruickshank & Ko (2003), and Ross *et al*. (2010). Fossil myriapods are rare but are abundant in Burmese amber, especially diplopods (Moritz & Wesener, 2018). To date, a total of 10 genera and 13 species of Myriapoda have been described from Burmese amber. Except for one species of Symphyla, 12 species in 7 orders and 9 genera of Diplopoda are documented (*e.g.*, Moritz & Wesener, 2018; Jiang *et al*., 2019; Ross, 2019, 2021, 2023; Su *et al*., 2021, 2022, 2023).

Here, we describe two new fossil species of Siphonorhinidae based on 22 individuals trapped in Burmese amber, both placed in the extant genus *Siphonorhinus* Pocock, 1894.

Material and methods

This study was based on 22 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

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Myanmar (Yin *et al*., 2018), with an age close to the Albian-Cenomanian boundary (Shi *et al*., 2012; Mao *et 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 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).

Classification and nomenclature of characters were based on Enghoff *et al*. (2015), Moritz & Parra-Gómez (2023), Siewald & Spelda (2023) and Wesener (2023).

Systematic palaeontology

Class Diplopoda de Blainville *in* Gervais, 1844
Subclass Helminthomorpha Pocock, 1887
Order Siphonophorida Newport, 1844
Family Siphonorhinidae Cook, 1895
Genus *Siphonorhinus* Pocock, 1894

Type species. *Siphonorhinus pallipes* Pocock, 1894

Siphonorhinus globosus sp. nov.

Material. Holotype: NIGP175073, a well-preserved adult male (Figs 1–3). Paratypes: NIGP175074–NIGP175076, one moderately-preserved adult male (Fig. 4), two moderately-preserved adult females (Figs 5–6). Additionally, 6 females or sex-undetermined specimens are studied.

Etymology. Named after the globoid head shape of the species.

Diagnosis. Head globoid, with small beak-like structure. Anterior gonopods with six podomeres, 6th podomere folded medial-ventrally, with elongate setae on margin. Posterior gonopods with seven podomeres, 7th podomere divided into two thin branches, with an extremely thin seta.

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

Description. Body elongated and flattened, length 5.6–6.9 mm in male, 4.7–10.6 mm in female, with up to 48 tergites, width of tergites nearly uniform, maximum width of mid-body metazonites *ca.* 0.58 mm.

Head moderately to densely setose; globoid to sub-globoid in shape (Figs 1C, D, 2A, 4C, 5C, D, 6C–F), anterior part without constriction; with a small, short beak-like structure (Figs 2B, 3E, 5D, 6E). Ommatidia absent. Antennae stout and setose, usually elbowed between antennomere 3 and 4; antennomere 5 and 6 strongly swollen; length of antennomere 6>5>4≈3≈2≈1>7. A field of 10–16 basiconic sensilla observed on antennomere 5 and 6, usually arranged in 2 rows (Figs 2C, 4E, F).

Collum relatively small, sub-oval shaped, only slightly overlaps posterior margin of head, setose and with small number of tubercles on lateral side (Figs 2A, 4C, 5C, 6D–F). Tergites, pleurites, and sternites free from each other, no medial suture on tergites. Prozonites slightly narrower than metazonites, with regularly arranged flattened tubercles (Figs 5C, 6D–F). Metazonite obviously convex, moderately to densely setose, only with tubercles on anterior and lateral margin (Figs 2A, 5C, 6D–F). Ozopores present from metazonite 5, round, located near lateral-posterior corner (Figs 3C, 5C, 6D–F). Paraterga absent. Pleurites rounded to sub-angular, covered with dense discoidal flat tubercles (Figs 2A, D, 3A, 4G–H). Sternites usually overlapped by pleurites. Spiracles columned, located lateral-anterior to coxae. Legs relatively short, consisting of six podomeres; a row of strong seta present on medial part of each podomere; tarsus tapering, longer than other podomeres; claw sharp, moderately curved (Figs 2D, 3B).

Telson round and large, with dense setae and tubercles. Hypoproct tiny, posterior margin smooth.

Gonopods (Figs, 3A, 4H) leg-like, modified from 9th and 10th leg-pairs. Anterior gonopods stout, with six podomeres, elbowed forward at 4th podomere; 5th podomere significantly short; 6th podomere longest in length, angled and folded medial-ventrally, with several elongate setae on margin. Posterior gonopods with seven podomeres; 1st to 6th similar in length; 7th podomere cone-shaped, tapered and divided into two thin branches, with an extremely thin seta.

Siphonorhinus peculiaris sp. nov.

Material. Holotype: NIGP175077, a well-preserved adult male (Figs 7–8). Paratypes: NIGP175078–NIGP175082, two well-preserved adult males (Figs 9–12), three moderately-preserved adult females (Figs 13–15). Additionally, 6 female or sex-undetermined specimens are studied.

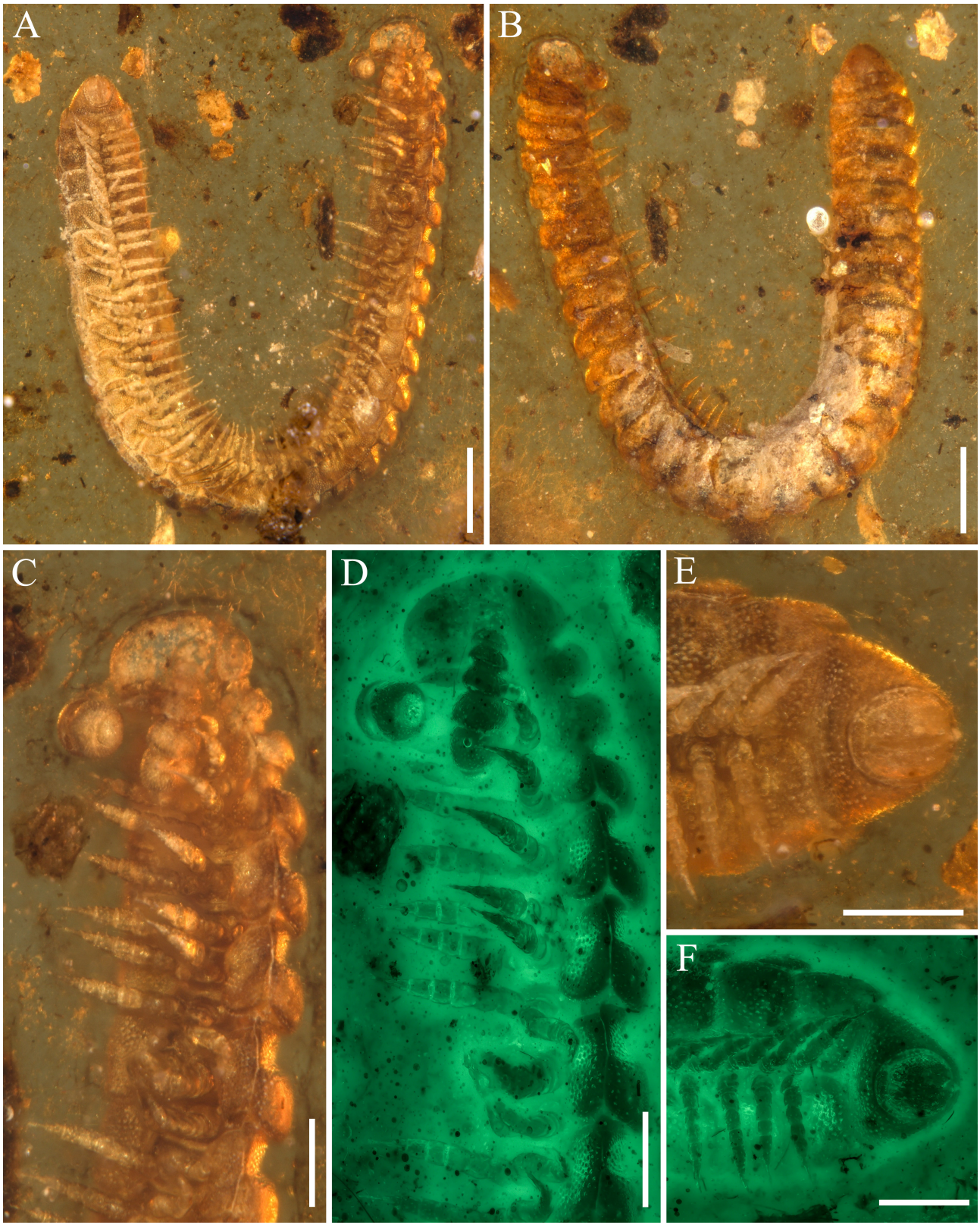

FIGURE 1. Adult male of *Siphonorhinus globosus* **sp. nov.**, holotype (NIGP175073). **A**, Ventral view. **B**, Dorsal view. **C**, **D**, Ventral view of head and anterior body part. **E**, **F**, Ventral view of telson. **D**, **F** under green epifluorescence. Scale bars: 0.5 mm in **A**, **B**; 0.2 mm in others.

Etymology. Named after the unusual arrangement of ozopores.

Diagnosis. Head of typical siphonorhinid form. Ozopores starting from tergite 3 in male and tergite 6 in female. Metazonites of male with more developed tubercles. Anterior gonopods with six podomeres, 6th

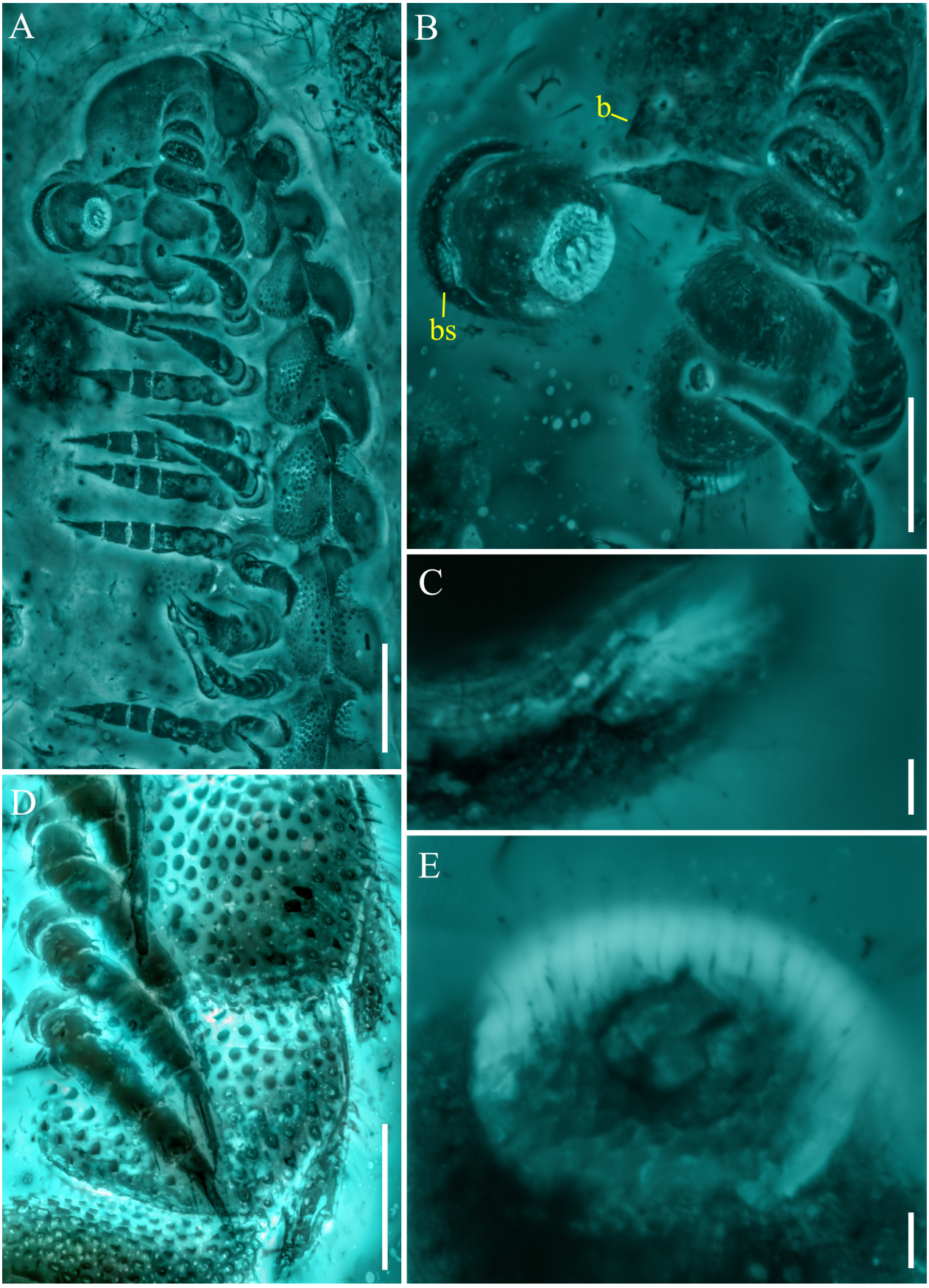

FIGURE 2. Adult male of *Siphonorhinus globosus* **sp. nov.**, holotype (NIGP175073), detailed structures under CLSM. **A**, Ventral view of head and anterior body part. **B**, Detail structures of head and antennae. **C**, Basiconic sensilla on antennomere 5. **D**, Detail structures of last 3 leg-pairs and last 2 pleurites. **E**, Detail structures of antennomere 7. Abbreviations: b, beak-like structure on anterior part of head; bs, basiconic sensilla. Scale bars: 200 μm in **A**; 100 μm in **B**, **C**; 10 μm in **D**, **E**.

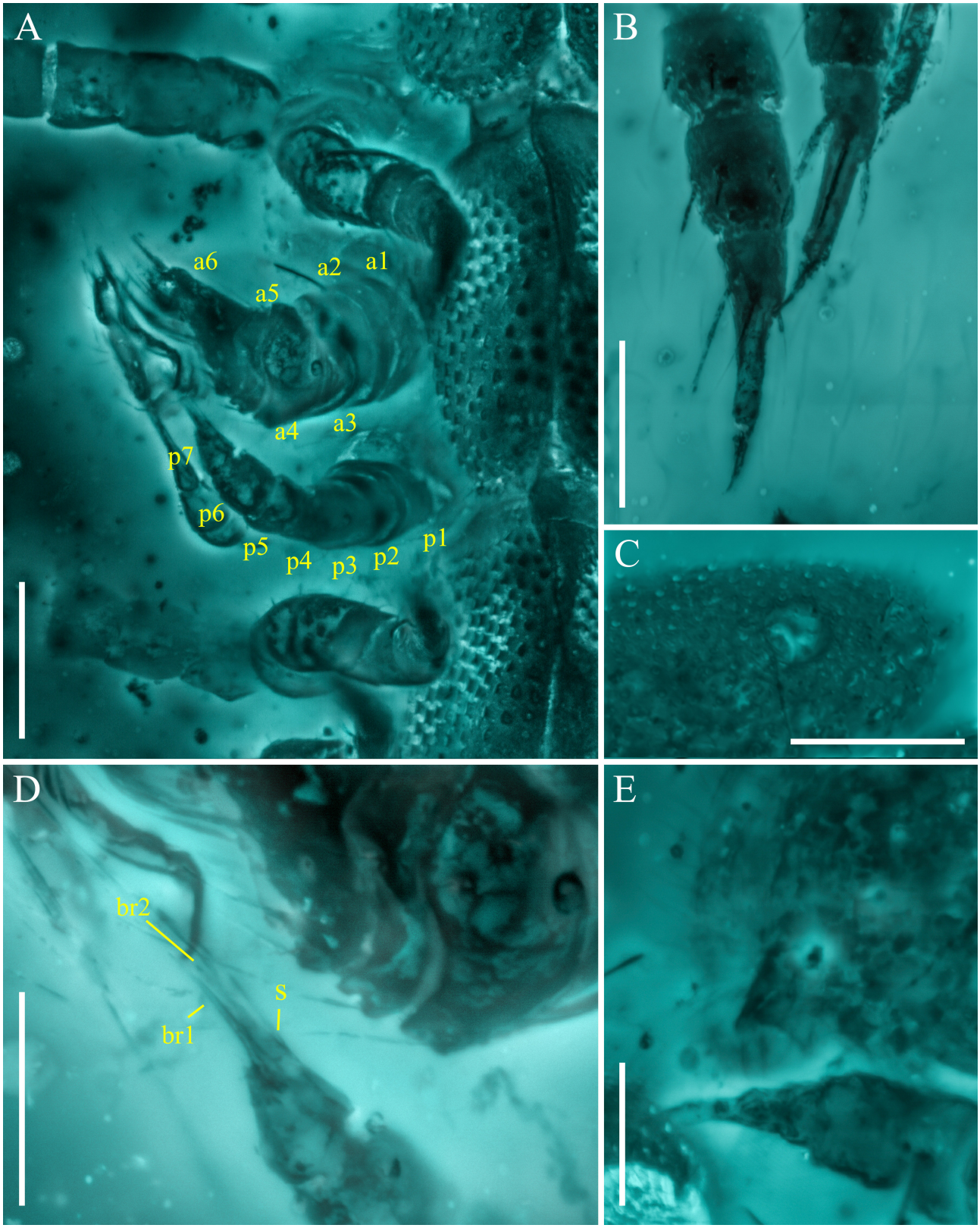

FIGURE 3. Adult male of *Siphonorhinus globosus* **sp. nov.**, holotype (NIGP175073), detail structures under CLSM. **A**, Details of gonopods. **B**, Details of postfemur, tibia and tarsus. **C**, Detailed view of ozopore. **D**, Details of posterior gonopod podomere 7. **E**, Detailed view of beak-like structure on anterior part of head. Abbreviations: a1–a6, podomeres of anterior gonopds; br1, br2, branches of posterior gonopod podomere 7; p1–p7, podomeres of posterior gonopds; s, seta on posterior gonopod podomere 7. Scale bars: 50 μm.

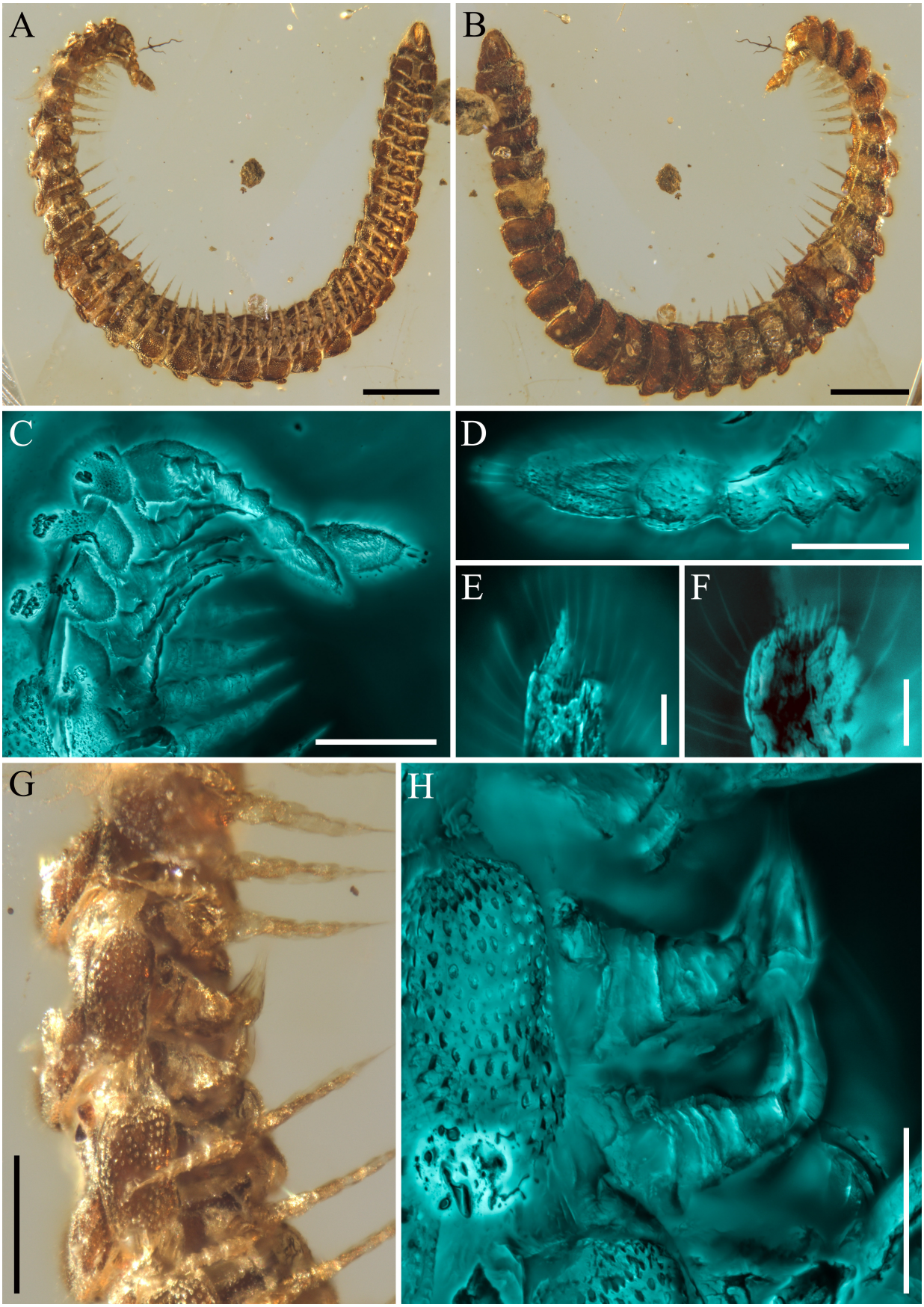

FIGURE 4. Adult male of *Siphonorhinus globosus* **sp. nov.**, paratype (NIGP175074). **A**, Ventral view. **B**, Dorsal view. **C**, Detailed view of head. **D**, Details of the right antenna. **E**, Basiconic sensilla on antennomere 5. **F**, Basiconic sensilla on antennomere 6. **G**, lateral view of gonopods. **H**, Details of gonopods. **C**–**F**, **H** under CLSM. Scale bars: 500 μm in **A**, **B**; 200 μm in **C**, **G**; 100 μm in **D**, **H**; 20 μm in **E**, **F**.

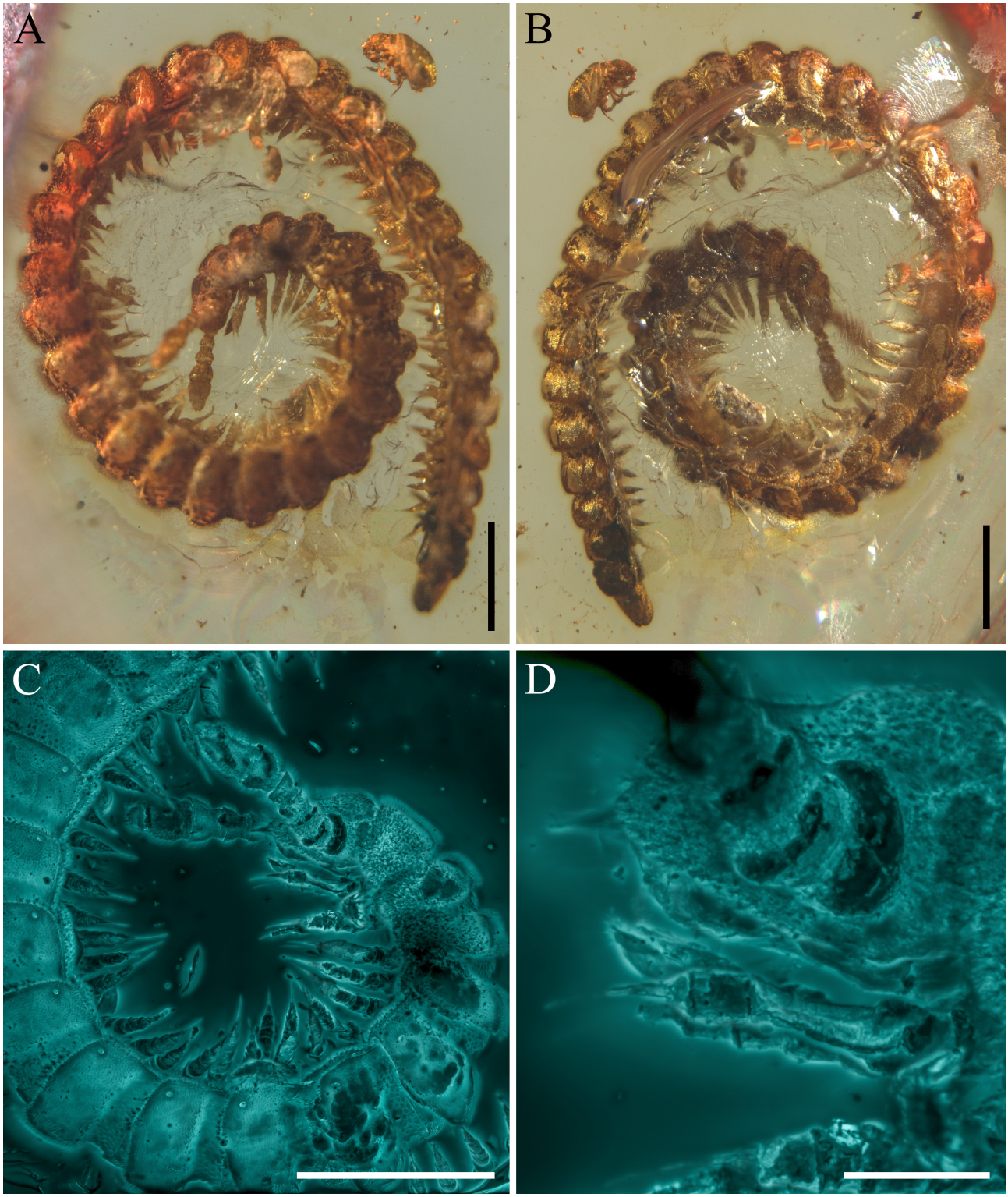

FIGURE 5. Adult female of *Siphonorhinus globosus* **sp. nov.**, paratype (NIGP175075). **A**, **B**, Overall view under bright field. **C**, Detailed view of head and anterior body part. **D**, Detailed view of head and the beak-like structure on anterior part of head. **C**, **D** under CLSM. Scale bars: 0.5 mm in **A**–**C**; 0.2 mm in **D**.

podomere folded medially, with elongate setae on margin. Posterior gonopods with seven podomeres, 7th podomere divided into elongate branch and spine-like branch, without seta or special modifications.

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

Description. Body elongated, length 5.8–8.3 mm in male, 6.3–13.3 mm in female, with up to 55 tergites, width

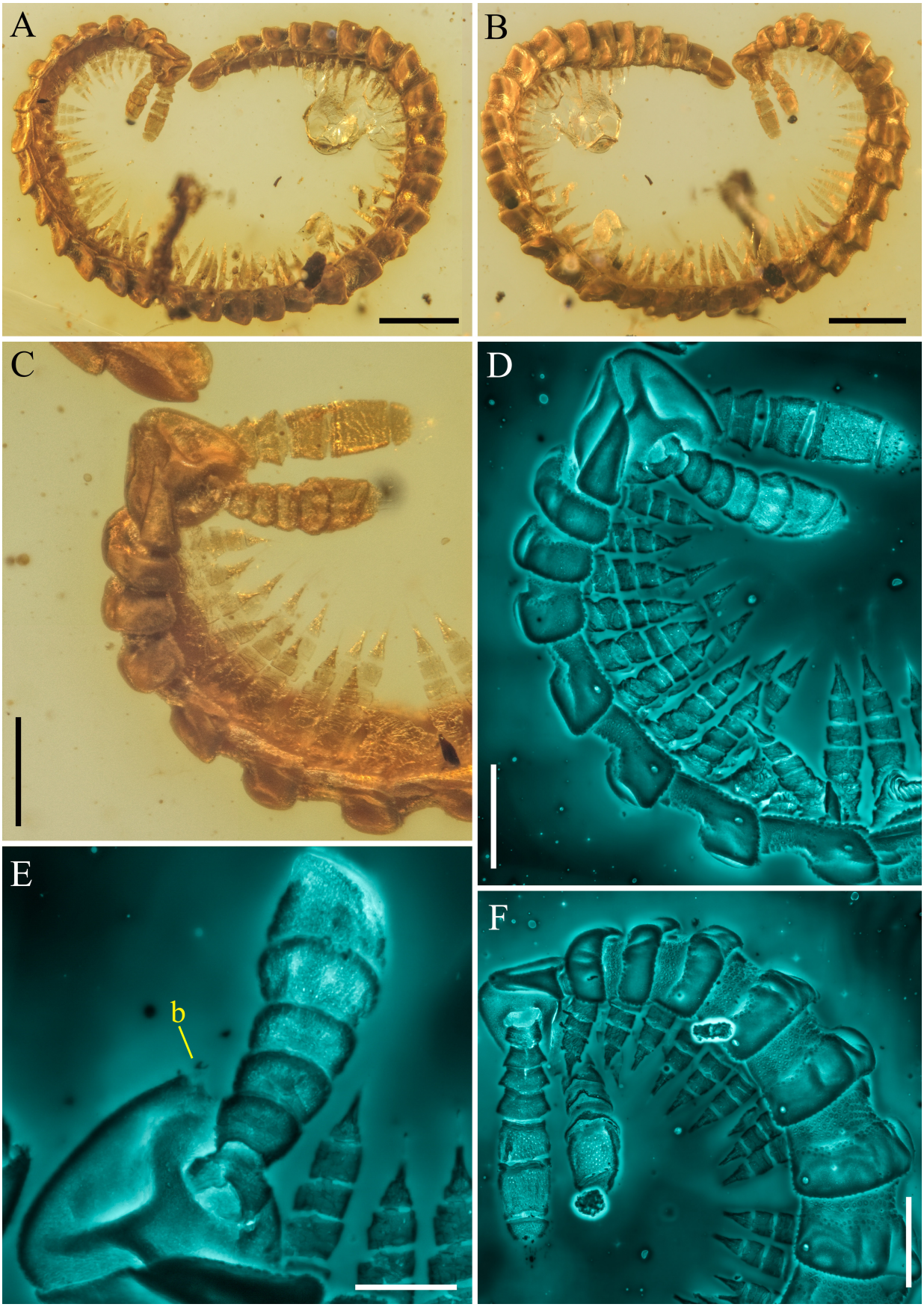

FIGURE 6. Adult female of *Siphonorhinus globosus* **sp. nov.**, paratype (NIGP175076). **A**, **B**, Lateral overall view under bright field. **C**, **D**, **F**, Details of head and anterior body part. **D**, Details of head. **D**–**F** under CLSM. Abbreviations: b, beak-like structure. Scale bars: 0.5 mm in **A**, **B**; 0.2mm in **C**, **D**, **F**; 0.1 mm in **E**.

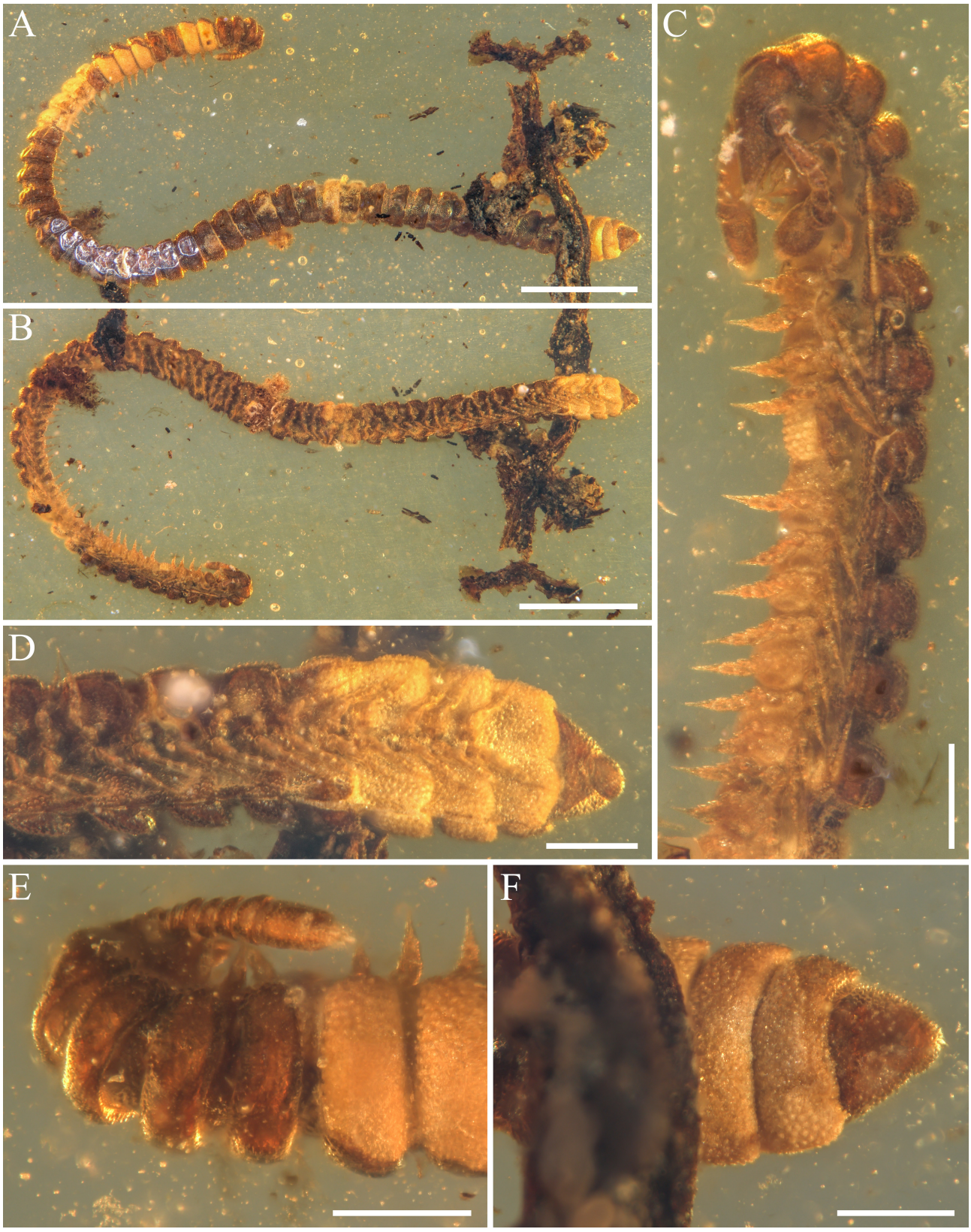

FIGURE 7. Adult male of *Siphonorhinus peculiaris* **sp. nov.**, holotype (NIGP175077). **A**, Dorsal view. **B**, Ventral view. **C**, Ventral view of head and anterior body part. **D**, Ventral view of posterior body part and telson. **E**, Dorsaled view of head collum and tergite 2–5. **F**, Dorsal view of telson. Scale bars: 1 mm in **A**, **B**; 0.2 mm in others.

of tergites nearly uniform, maximum width of mid-body metazonites *ca.* 0.52 mm. Female individuals slightly larger than male.

Head sparsely setose or without seta on labrum part, moderately setose on other area; conic-pyriform in shape, without special extension or structure (Figs 7C, 8C, 9C,

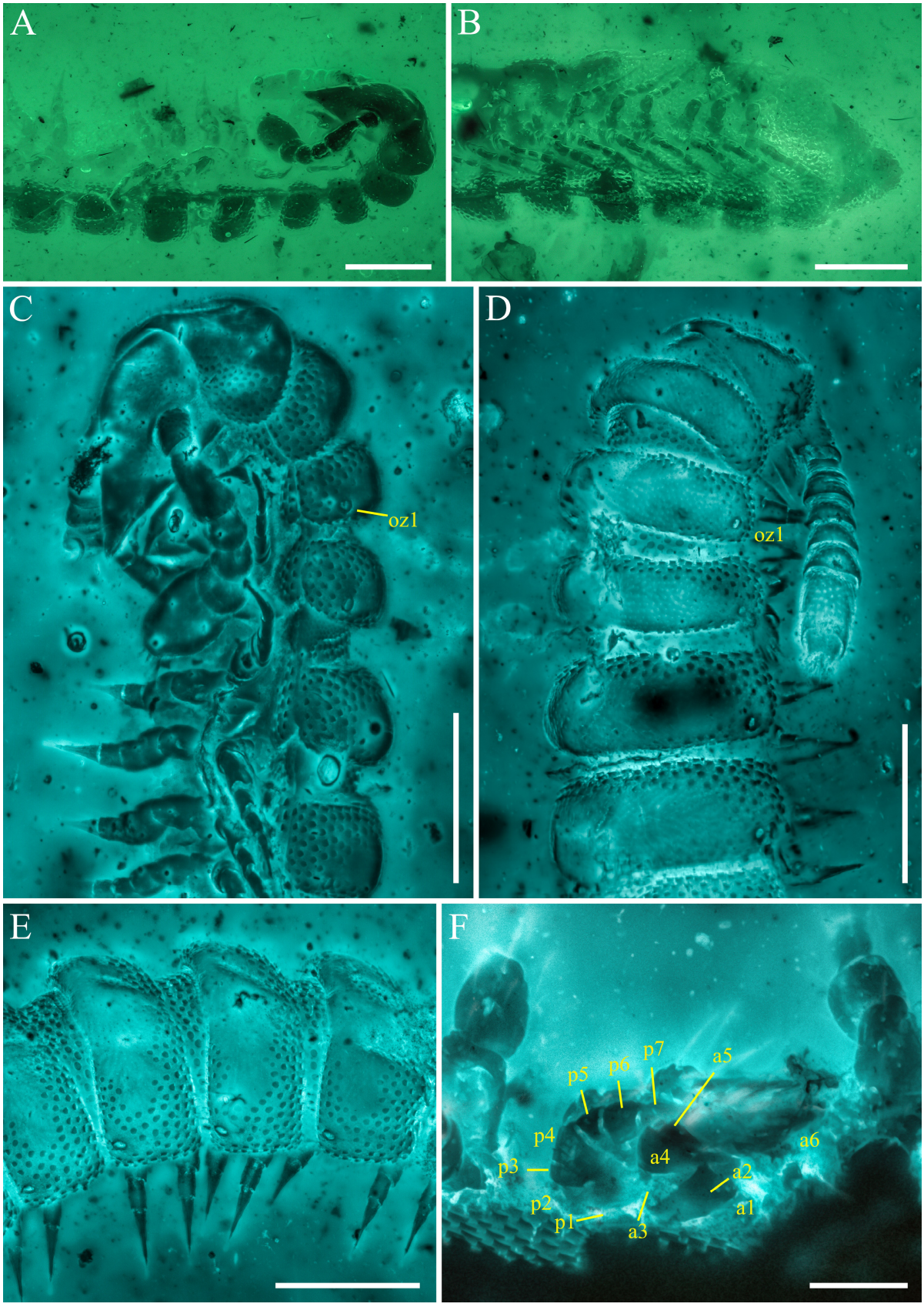

FIGURE 8. Adult male of *Siphonorhinus peculiaris* **sp. nov.**, holotype (NIGP175077). **A**, Ventral view of head and anterior body part. **B**, Ventral view of posterior body part and telson. **C**, Details of head and anterior body part, ventral view. **D**, Details of head and anterior body part, dorsal view. **E**, Details of tergite 16–19. **F**, Details of gonopods. **A**, **B** under green fluorescence, **C**–**F** under CLSM. Abbreviations: a1–a6, podomeres of anterior gonopds; oz1, the first present ozopore; p1–p7, podomeres of posterior gonopds. Scale bars: 50 μm in **F**; 200 μm in others.

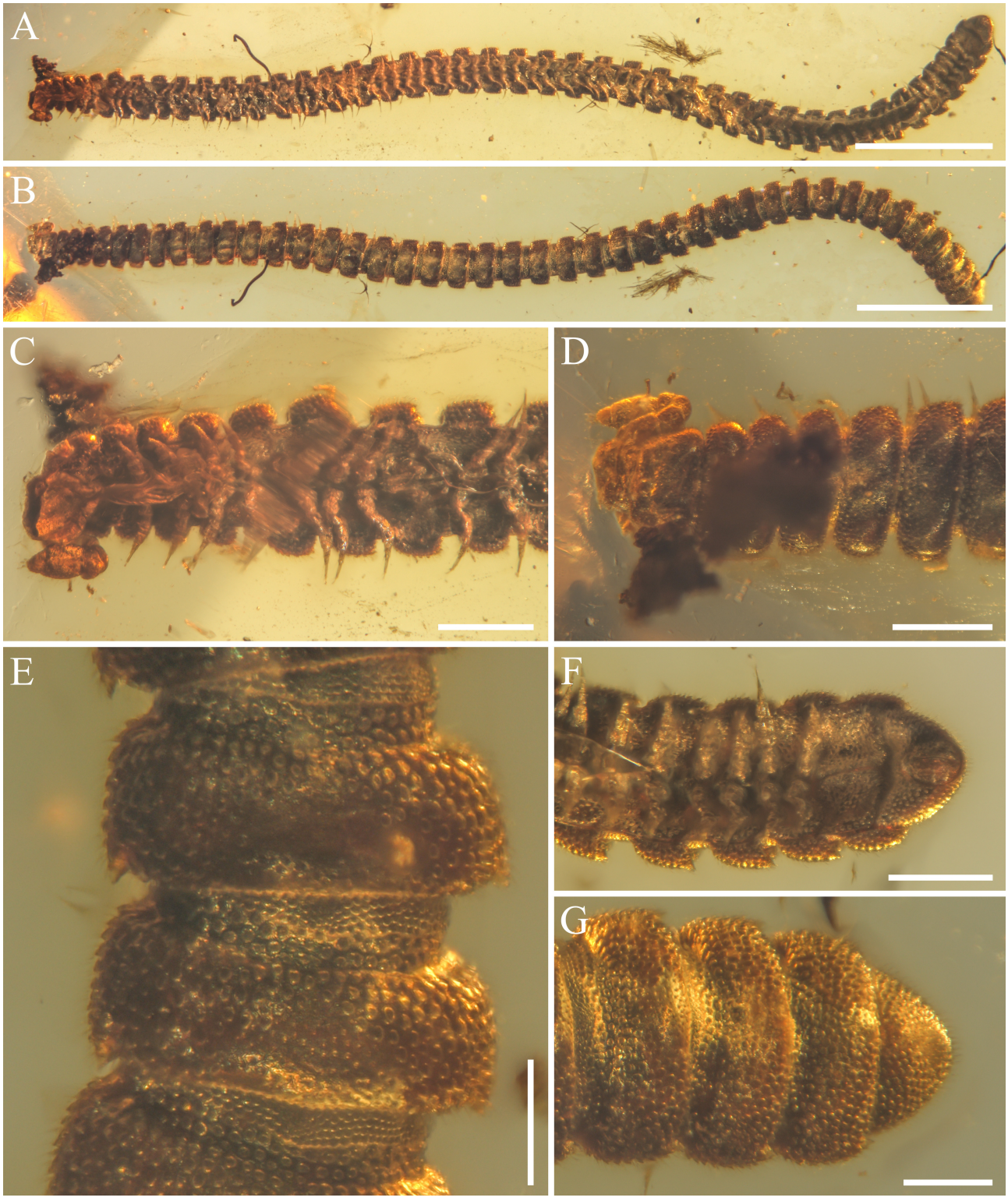

FIGURE 9. Adult male of *Siphonorhinus peculiaris* **sp. nov.**, paratype (NIGP175078). **A**, Ventral view. **B**, Dorsal view. **C**, Ventral view of head and anterior body part. **D**, Dorsal view of head and anterior body part. **E**, Dorsal view of tergite 36–38. **F**, Ventral view of telson. **G**, Dorsal view of telson. Scale bars: 1 mm in **A**, **B**; 0.2 mm in **C**, **D**, **F**; 0.1 mm in **E**, **G**.

D, 10A, B, F, 11C, 12A, 13F, 14E–H, 15E). Ommatidia absent. Antennae stout and moderately setose, usually elbowed at antennomere 4; antennomere 5 and 6 strongly swollen; length of antennomere 6>2≥5≈4≈3>1≈7. A field of 12–16 basiconic sensilla observed on antennomere 5 and 6, usually arranged in 2–3 rows (Fig. 12D, E, F).

Collum relatively large, sub-oval shaped, obviously overlap posterior margin of head, moderately setose (Figs

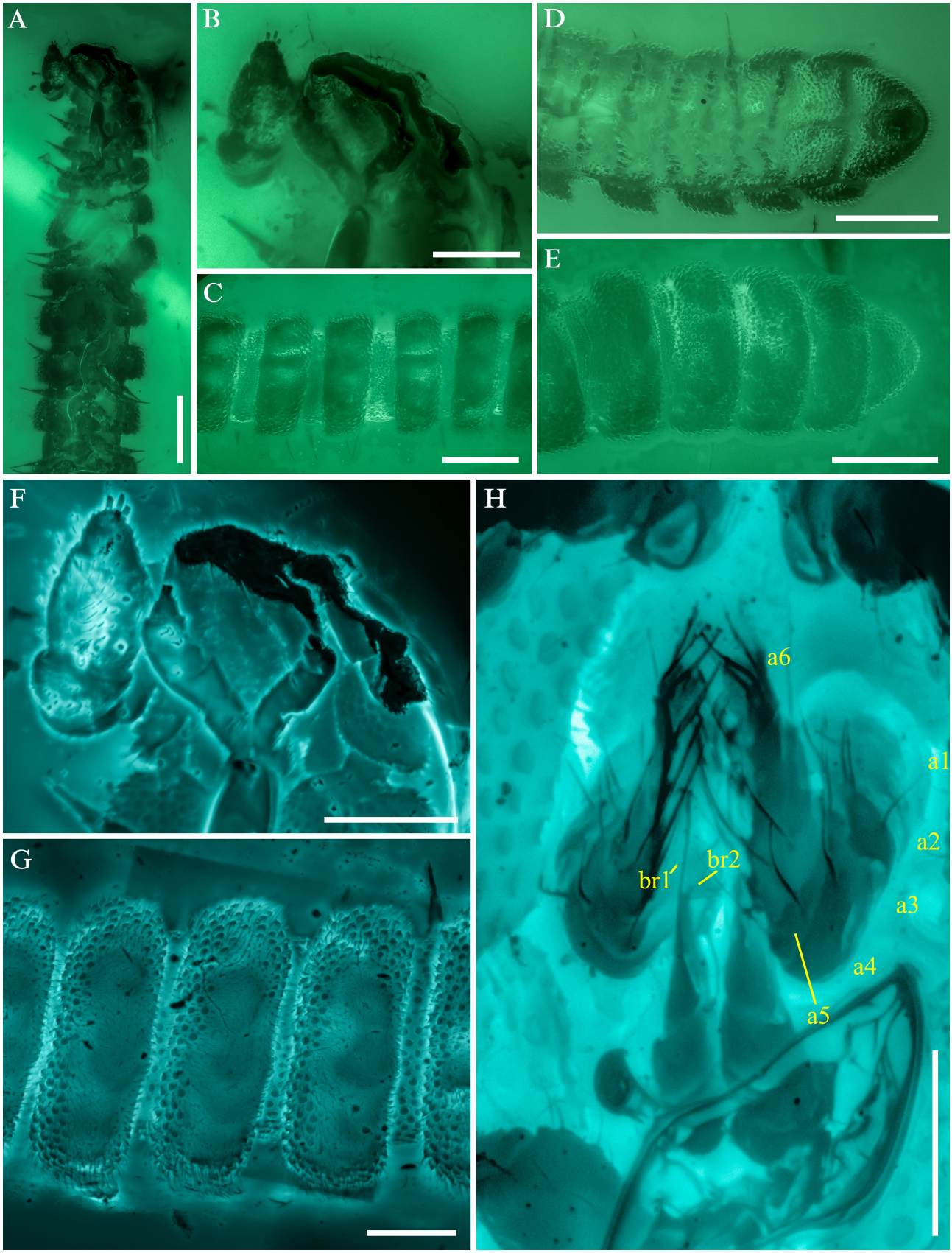

FIGURE 10. Adult male of *Siphonorhinus peculiaris* **sp. nov.**, paratype (NIGP175078). **A**, Ventral view of head and anterior body part. **B**, Detailed view of head. **C**, Dorsal view of tergite 9–13. **D**, Ventral view of posterior body part and telson. **E**, Dorsal view of posterior body part and telson. **F**, Details of head, ventral view. **G**, Details of tergite 5–7. **H**, Details of gonopods. **A**–**E** under green epifluorescence, **F**–**H** under CLSM. Abbreviations: a1–a6, podomeres of anterior gonopods; br1, br2, branches of posterior gonopod podomere 7. Scale bars: 200 μm in **A**, **C**–**E**; 100 μm in **B**, **F**, **G**; 50 μm in **H**.

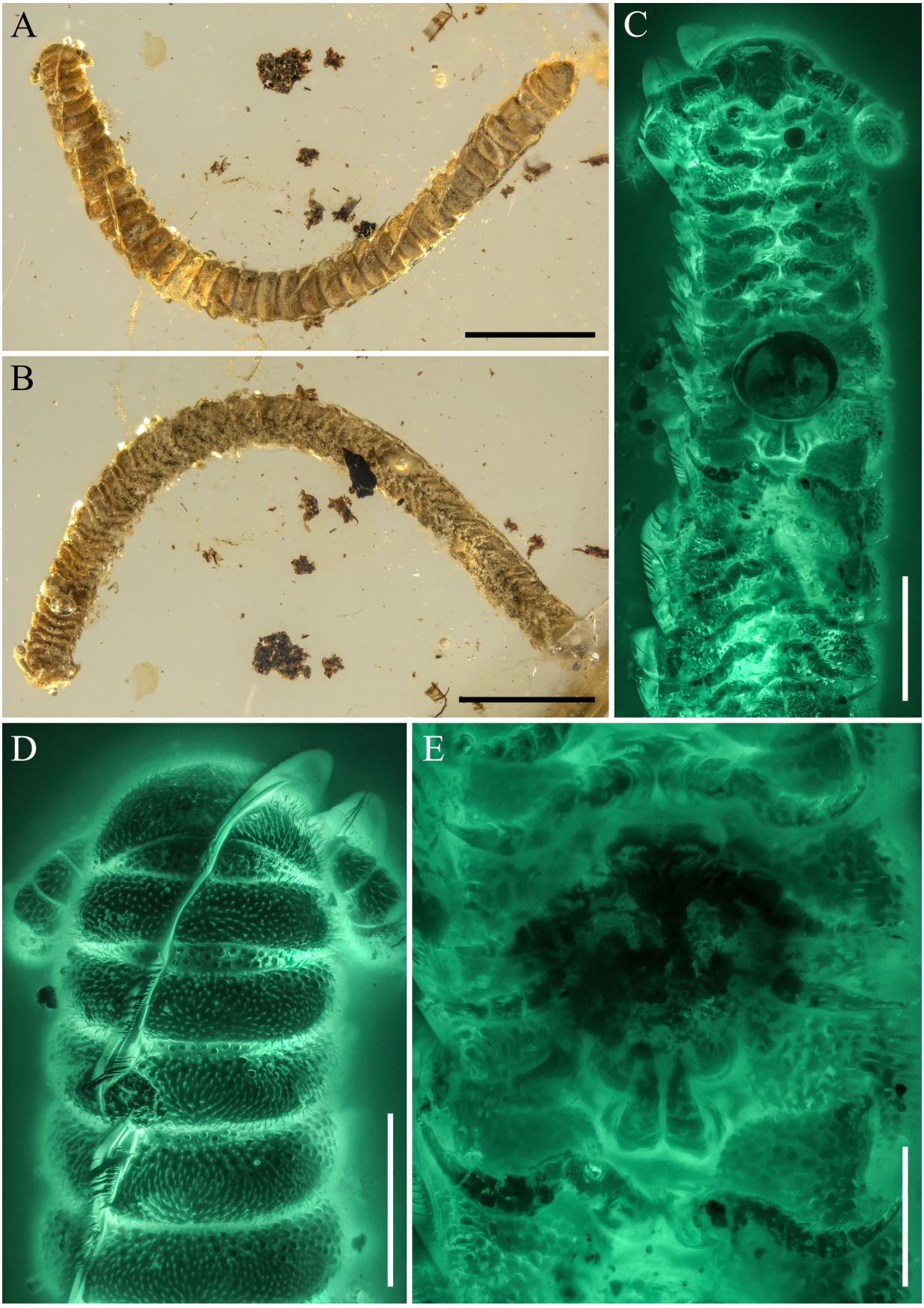

FIGURE 11. Adult male of *Siphonorhinus peculiaris* **sp. nov.**, paratype (NIGP175079). **A**, Dorsal view. **B**, Ventral view. **C**, Ventral view of head and anterior body part. **D**, Dorsal view of head and anterior body part. **E**, Ventral view of gonopods. **C**–**E** under green epifluorescence. Scale bars: 1 mm in **A**, **B**; 0.2 mm in **C**, **D**; 0.1 mm in **E**.

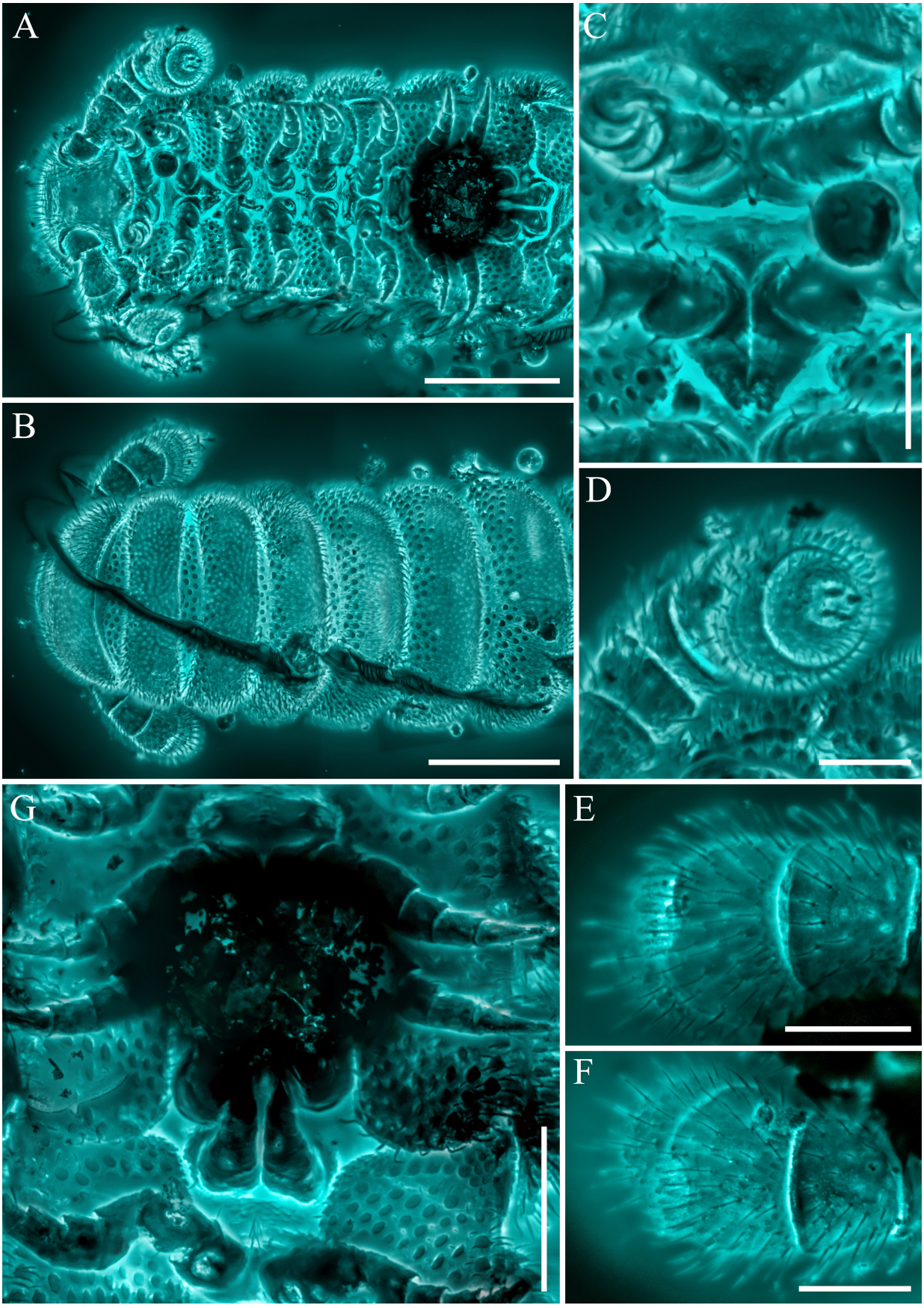

FIGURE 12. Adult male of *Siphonorhinus peculiaris* **sp. nov.**, paratype (NIGP175079). Detailed structures under CLSM. **A**, Ventral view of head and anterior body part. **B**, Dorsal view of head and anterior body part. **C**, Detailed view of leg-pair 1 and gonapophysis. **D**, Detailed view of the left antenna. **E**, Detailed view of antennomere 4 and 5 of the right antenna. **F**, Detailed view of antennomere 4 and 5 of the left antenna. **G**, Details of gonopods. Scale bars: 200 μm in **A**, **B**; 50 μm in others.

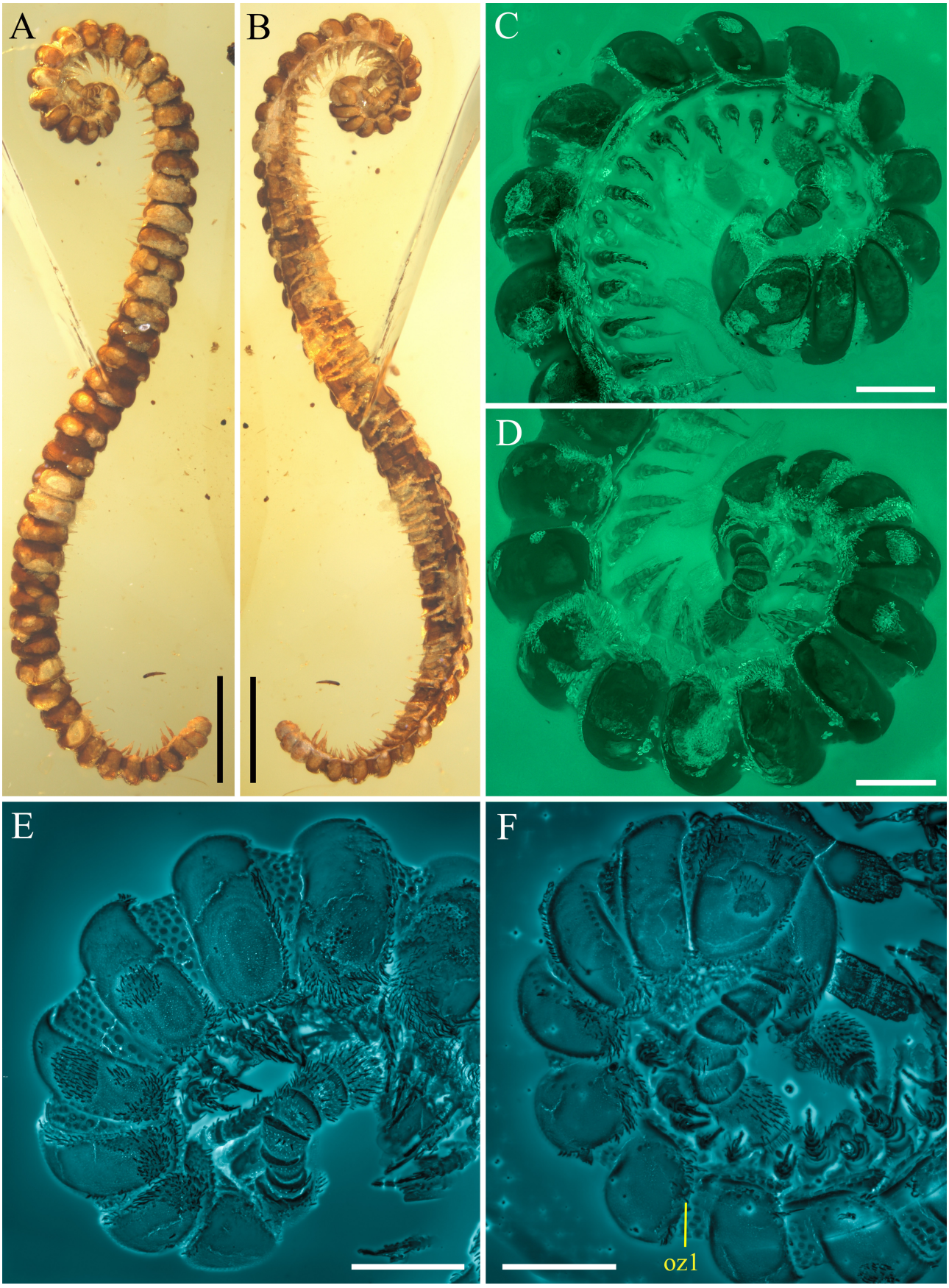

FIGURE 13. Adult female of *Siphonorhinus peculiaris* **sp. nov.**, paratype (NIGP175080). **A**, **B**, Lateral overall view under bright field. **C**–**F**, Details of head and anterior body part. **C**, **D** under green epifluorescence, **E**, **F** under CLSM. Abbreviations: oz1, first present ozopore. Scale bars: 1 mm in **A**, **B**; 0.2 mm in others.

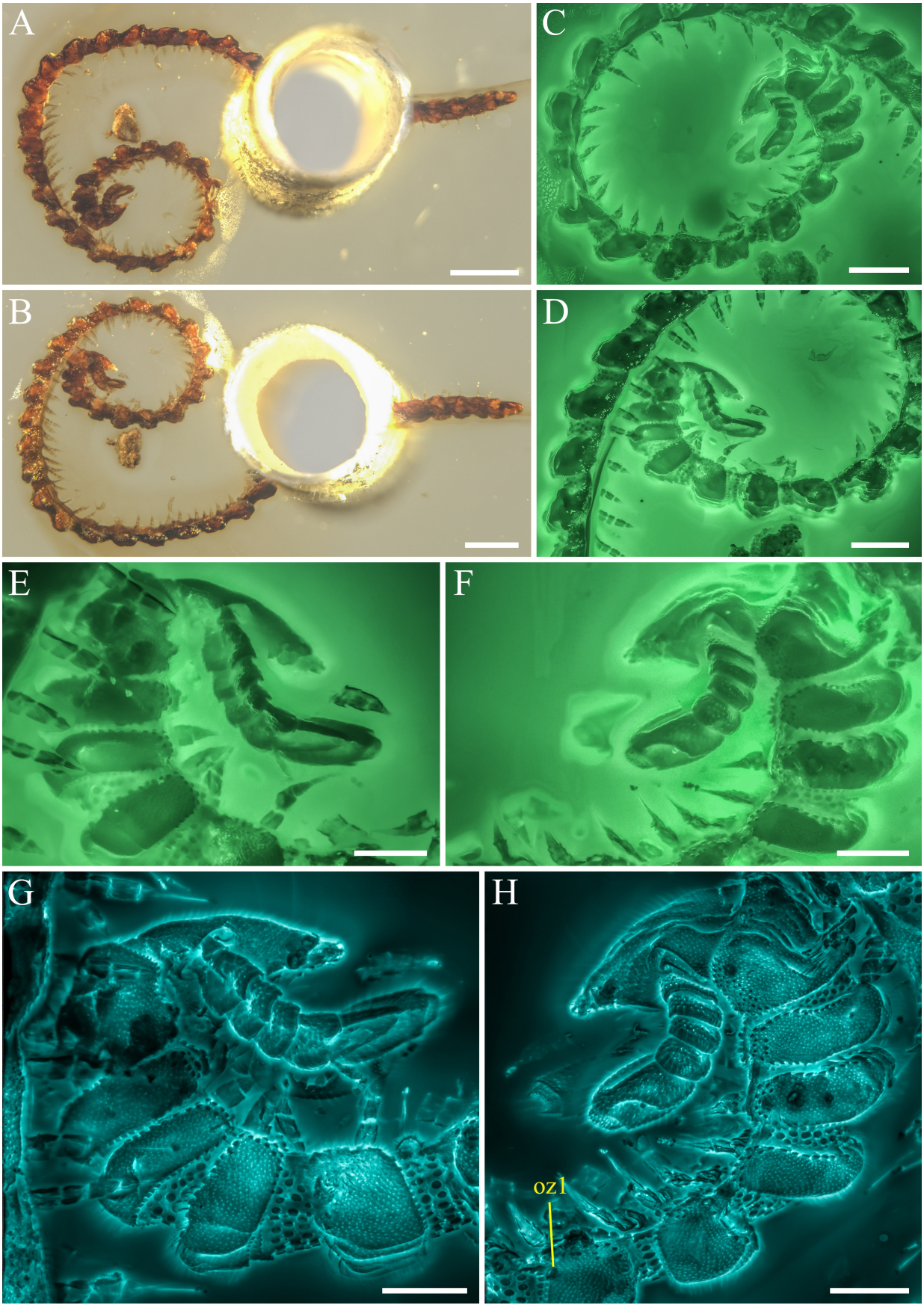

FIGURE 14. Adult female of *Siphonorhinus peculiaris* **sp. nov.**, paratype (NIGP175081). **A**, **B**, Lateral view. **C**, **D**, Lateral view of head and anterior body part. **E**, **F**, Lateral view of head, collum and tergite 2–4. **G**, Details of head, collum and tergite 2–5. **H**, Details of head, collum and tergite 2–6. **C**–**F** under green epifluorescence, **G**, **H** under CLSM. Abbreviations: oz1, the first present ozopore. Scale bars: 1 mm in **A**, **B**; 0.2 mm in **C**, **D**; 0.1 mm in others.

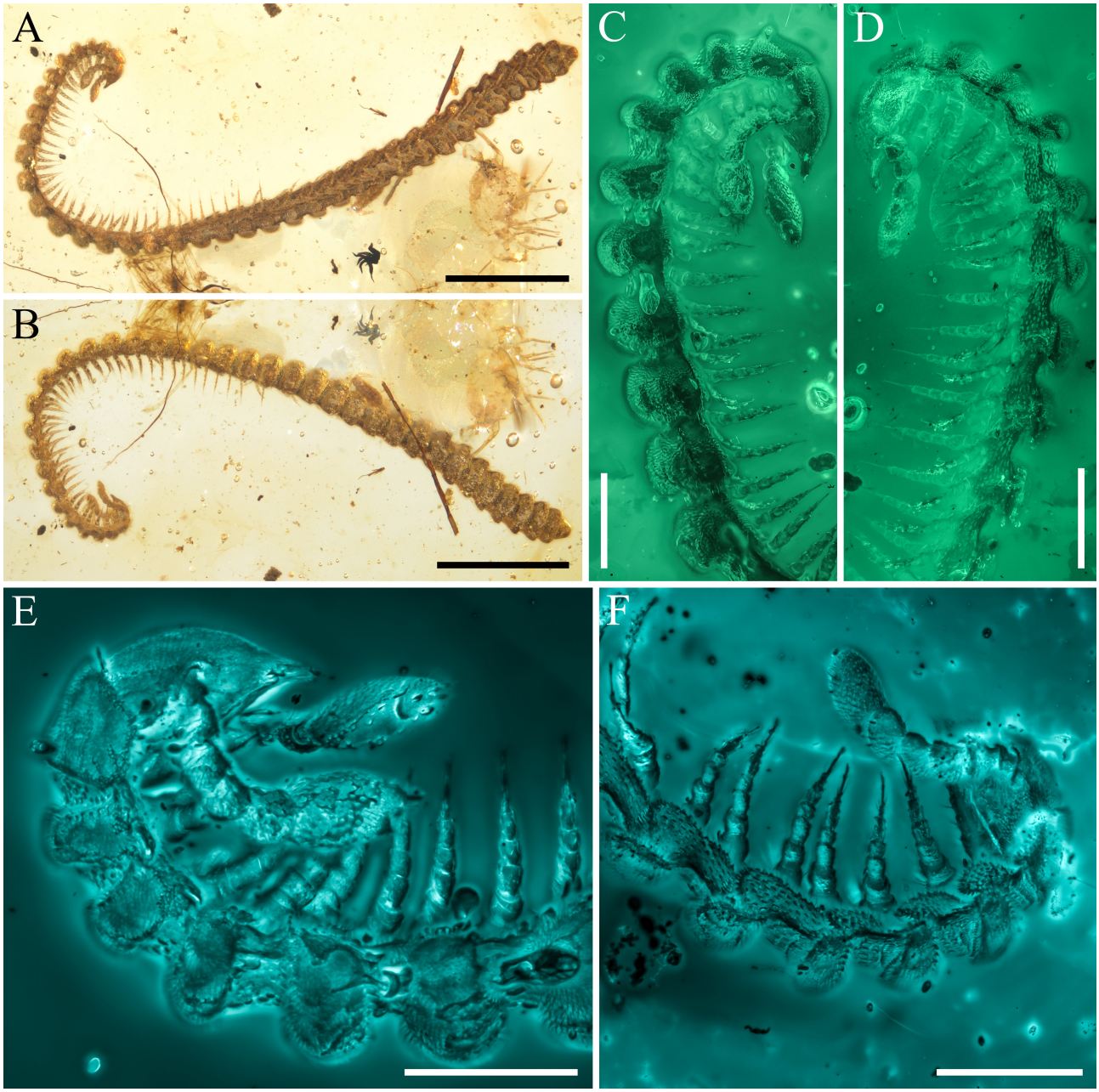

FIGURE 15. Adult female of *Siphonorhinus peculiaris* **sp. nov.**, paratype (NIGP175082). **A**, **B**, Lateral view under bright field. **C**, **D**, Lateral view of head and anterior body part. **E**, **F**, Details of head, collum and tergite 2–6. **C**, **D** under green epifluorescence, **E**, **F** under CLSM. Scale bars: 1 mm in **A**, **B**; 0.2 mm in others.

7C, E, 8C, D, 11D, 12B, 13F, 14F, H, 15C, E). Tergites, pleurites, and sternites free from each other, no medial suture on tergites. Prozonites slightly narrower than metazonites, with regularly arranged flattened tubercles (Figs 8E, 9E, 10C, 13E, 14G–H, 15E–F). Metazonite obviously convex, moderately setose. Male specimens with moderate-densely tubercles on metazonites except medial-posterior area (Figs 8D, E, 9D, E, G, 10C, E, G, 11D, 12B), female specimens only with a row of tubercles on metazonites margin (Figs 13C–F, 14G, H, 15E). Ozopores present from metazonite 3 in male (Fig. 8C, D), 6 in female (Figs 13F, 14H), round, located closer to posterior than lateral margin of metazonites. Paraterga absent. Pleurites rounded to subangular, covered with sparse setae and dense discoidal flat tubercles (Figs 8C, 12A, G). Sternites usually overlapped by pleurites. Spiracles columned, located lateral-anterior to coxae. Legs relatively short, consisting of 6 podomeres; each podomere with several sparsely arranged setae; tarsus tapering, longer than other podomeres; claw elongate, sharp, moderately curved. First leg-pairs slightly smaller than others, without any special modifications; coxae

of leg-pair 1 suspiciously fused with sterna (Fig. 12C). Coxae 2 in male with short, cone-shaped gonapophysis (Fig. 12C).

Telson round and large, with moderate-densely setae and tubercles. Hypoproct tiny, posterior margin smooth.

Gonopods (Figs 8F, 10H, 12G) leg-like, modified from 9th and 10th leg-pairs. Anterior gonopods stout, with six podomeres, elbowed forward at 4th podomere; 5th podomere shortest, 1st to 4th podomeres wider than others; 6th podomere longest in length, angled and folded medially, with several elongate setae on margin. Posterior gonopods with seven podomeres; 3rd podomere larger than others except last podomere; 7th podomere cone-shaped, tapered and divided into a significant elongate branch and a short spine-like branch, without visible seta.

Discussion

The two new species described here can be confidently placed in the extant *Siphonorhinus* (family Siphonorhinidae) based on the following combination of features: 1) head small, mouth part reduced, not extend into elongate rostrum; ommatidia absent; 2) antennae strongly swollen, usually elbowed at antennomere 4; antennomeres 5 and 6 each with a field of basiconic sensilla on each; 3) leg-pair 1 without special modification, coxae suspiciously fused with sterna; 4) gonopods modified from 9th and 10th leg-pairs; anterior gonopods with 6 podomeres, posterior gonopods with seven podomeres; last podomere of posterior gonopod divided into two branches. *Siphonorhinus globosus* **sp. nov.** bears an unusual beak-like structure on anterior part of head, but its feature differs greatly from the elongate beak-like rostrum of Siphonophoridae. The extant genus *Kleruchus* Attems, 1938 also has six anterior gonopod podomeres and seven posterior gonopod podomeres, but it has a strongly modified leg-pair 1, which is absent in the new species.

Siphonorhinus globosus **sp. nov.** differs from extant siphonorhinid species by its globoid head with a strange beak-like structure, fewer tubercles, and the absence of a ridge on metazonites. Additionally, the last anterior gonopod podomere is longer and folded medial-ventrally, while the last posterior gonopod podomere is cone-shaped with two thin branches and a seta.

Siphonorhinus peculiaris **sp. nov.** differs from extant species by the peculiar development of ozopores, fewer tubercles in female individuals, the longer and folded medial last anterior gonopod podomere, and the cone-shaped last posterior gonopod podomere with an elongated branch and a spine-like branch (*e.g.*, Pocock, 1894; Silvestri, 1895; Attems, 1930, 1936, 1938; Turk, 1948).

The two new species are distinct from each other in head shape and structure, collum size, tubercles on metazonites of male specimens, length of gonopod podomeres, and branches of the last posterior gonopod podomere. The extant *Siphonorhinus pellita* (Attems, 1930) has similar last posterior gonopod podomere branches to *S. globosus* **sp. nov.**, but its anterior gonopod has only five podomeres and with a shorter last podomere. *Siphonorhinus robusta* (Attems, 1938) has similar last posterior gonopod podomere branches to *S. peculiaris* **sp. nov.**, but it has a shorter and setose last anterior gonopod podomere. The arrangement of ozopores in *S. peculiaris* **sp. nov.** is not observed in any other known siphonorhinids (starting from tergite 5). However, it may be questioned to some extent, as male ozopores can only be observed in the holotype, and female ozopores are difficult to observe due to poor preservation. It is also possible that the male and female specimens represent different species, but the differences in their other characters are minimal, and it would be inappropriate to establish a new species without gonopod features.

Given the characters and morphological comparisons discussed above, the two new species from Burmese amber exhibit similarities with extant siphonorhinids in most features. This resemblance suggests bradytely within Siphonorhinidae from the mid-Cretaceous to the present day. Consequently, the origin of the family likely predates the Cretaceous period.

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