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# Two new luminous species of Neanuridae (Collembola) and the discovery of bioluminescence in the genus *Crossodonthina* Yosii

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## Abstract

This study describes two new luminous microarthoropod species, *Crossodonthina leodeus* **sp. nov.** and *Lobella lucifera* **sp. nov.**, and reports the discovery of bioluminescence in two previously described species, *Crossodonthina elegans* Kasai, Tanaka & Sawahata and *Crossodonthina laterisensillata* Ohira, Kataoka, Tanooka & Nakamori, from the tribe Lobellini (Collembola, Neanuridae, Neanurinae) in Asia. Identification keys to the species of both genera have been updated and taxonomic remarks on the genus *Cassagnaua* Özdikmen are provided. This study represents the first description of bioluminescent Collembola as new species, and the first report of bioluminescence in the genus *Crossodonthina* Yosii.

**Key words:** Asia, *Lobella* Börner, Lobellini, key to species, Japan

## Introduction

Collembola are microarthropods that are widely distributed across terrestrial habitats, and certain species have been reported to emit light (Allman 1851; Molisch 1904; Stammer 1935; Heidt 1936; Ohira *et al.* 2023). The Lobellini (Neanuridae: Neanurinae) are primarily distributed in Asia and Oceania (Cassagnau 1983), and within this tribe, only *Lobella sauteri* (Börner, 1906), *L. yambaru* (Tanaka & Hasegawa, 2010) and an unidentified species (*Lobella* sp.) have been reported to exhibit bioluminescence (Sano *et al.* 2019; Ohira *et al.* 2023). Here, we describe two new luminous species of Lobellini, *Crossodonthina leodeus* **sp. nov.** and *Lobella lucifera* **sp. nov.**, and report the discovery of bioluminescence in other two previously described species of the tribe, *Crossodonthina elegans* Kasai, Tanaka & Sawahata, 2023 and *C. laterisensillata* Ohira, Kataoka, Tanooka & Nakamori, 2022, all from Asia.

## Materials and Methods

### Sites of sample collection

Field-collected specimens or the wild-caught founders of laboratory-reared populations of each Collembola species were obtained from their respective type localities: *C. elegans* from Yonaguni, Yonaguni Island, Okinawa, Ryukyu Archipelago, Japan (24.4535°N, 122.9785°E, elevation 126 m); *C. laterisensillata* from Shirahama, Iriomote Island, Okinawa, Ryukyu Archipelago, Japan (24.3651°N, 123.7548°E, elevation 69 m); *C. leodeus* **sp. nov.** from Shimozato, Hirara, Miyako Island, Okinawa, Ryukyu Archipelago, Japan (24.7982°N, 125.2753°E, elevation 28 m); *L. lucifera* **sp. nov.** from Nishinakasone, Hirara, Miyako Island, Okinawa, Ryukyu Archipelago, Japan (24.8104°N, 125.3135°E, elevation 33 m); and *L. sauteri* from Bugenji, Yokohama, Kanagawa, Japan (35.4758°N, 139.6047°E, elevation 23 m).

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## Morphology and DNA barcoding

Collected Collembola were fixed in 99% ethanol. For morphological and molecular analyses, DNA was extracted prior to morphological examination, as described by Aoyama *et al.* (2015). In brief, the whole body of each specimen was boiled in buffer. For morphological studies, specimens were mounted between cover slips in Andre and Hoyer's fluid and examined under an optical microscope. If necessary, specimens were cleared in Nesbitt's fluid before mounting. Partial DNA sequences of the COI gene were obtained by direct Sanger sequencing, as described by Ohira *et al.* (2023), with primers modified from Folmer *et al.* (1994), Nakamori (2013), Hou *et al.* (2014), Aoyama *et al.* (2015) and Potapov *et al.* (2017). Uncorrected pairwise distances (*p*-distances) among the sequences of different specimens were estimated using MEGA X software (Kumar *et al.* 2018).

Since no DNA barcodes were previously available for the two new species and *C. elegans*, they are provided in the present study. Specimen information for the two new species is given in the descriptions below. For *C. elegans*, three specimens collected on 6 September 2023 from Yonaguni, Yonaguni Island, Okinawa (24.4535°N, 122.9785°E), served as voucher specimens. Voucher specimens for DNA barcoding were deposited at the National Museum of Nature and Science in Tsukuba, Japan (institution code: NSMT) under numbers NSMT-Ap 709, 711, 712, 718, 721, 722, 727–729. The nucleotide sequence data reported here are available at the International Nucleotide Sequence Database (INSD), under accession numbers LC857138–LC857146.

The terminology and abbreviations used here follow Deharveng (1979, 1981, 1983), Deharveng & Weiner (1984), Greenslade & Deharveng (1990, 1991), Hüther (1962), Luo & Chen (2010) and Smolis (2008), as indicated below.

General morphology: Abd.—abdominal segments; Ant.—antennal segments; Cx—coxa; Fe—femur; Scx—subcoxa; T—tibiotarsus; Th.—thoracic segments; Tr—trochanter; VT—ventral tube; x—labial organ.

Groups of chaetae: Ag—antegenital; Fu—furcal; hr—thin chaetae on the posterior edge of anal valves; Ve—ventroexternal; Vea—ventroexternoanteriores; Vec—ventroexternocentrales; Vei—ventroexternointernales; Vel—ventroexternolaterales; Vem—ventroexternomediales; Vep—ventroexteroposteriores; Vi—ventrointernal; Vl—ventrolateral.

Tubercles: An—antennal; Cl—clypeal; De—dorsoexternal; Di—dorsointernal; Dl—dorsolateral; Fr—frontal; L—lateral; Oc—ocular; So—subocular.

Types of chaetae: i—median ordinary chaeta on Ant. IV; M—macrochaetae; Me—mesochaetae (up to approximately one-third of the length of large macrochaetae); mi—microchaetae (up to approximately one-third of the length of large mesochaetae); ms—microsensilla; or—subapical organ of Ant. IV; s—sensory chaetae (sensilla, long and thin); S—thick, blunt, curved sensory chaetae on Ant. IV; sgd and sgv—dorsal and ventral guard sensilla of the Ant. III sensory organ, respectively.

## Light-emitting capacity test

The two new species and *C. laterisensillata* were tested for their capacity to emit light in response to stimuli. Specimens of each species were collected from their respective type localities mentioned above (23 specimens collected on 10 May 2023 and tested on 19 May 2023 for *C. leodeus* **sp. nov.**; 9 specimens collected on 16 January 2024 and tested on 29 January 2024 for *C. laterisensillata*; 22 specimens collected on 10 May 2023 and tested on 22 May 2023 for *L. lucifera* **sp. nov.**). Sampling, handling and light-emitting ability tests were performed as described by Ohira *et al.* (2023), with some modifications. In brief, to stimulate Collembola, the test container accommodating a single specimen was vibrated using audio equipment, and slammed against a desk. In the present study, blowing on the specimen about three times was added as a stimulus. During stimulation, emission of light was checked by naked eye in a dark room. Then, the Collembola were fixed in 99.5% ethanol and mounted on glass slides in Hoyer's fluid. The species and sex were determined under a microscope.

## Measurement of the bioluminescence spectrum

The bioluminescence spectrum of single living specimens was measured for *C. elegans*, *C. laterisensillata*, *C.*

*leodeus* **sp. nov.**, *L. lucifera* **sp. nov.** and *L. sauteri*. Prior to measurement, live specimens were placed in individual polystyrene containers (58 mm in diameter, 21 mm in height, with a polyethylene snap lid) with a moistened substrate (consisting of a mixture of activated charcoal and plaster of Paris in deionised water at the bottom), or in a polypropylene container (24 mm in diameter, 48 mm in height, with a polyethylene screw cap), with moistened filter paper (23 mm in diameter; Whatman, GE Healthcare Life Sciences) with 180 μL of deionised water at the bottom and kept in constant darkness at 20°C for at least 1 day. Single living specimens were transferred into 0.2 mL plastic tubes using an aspirator and the bioluminescence spectrum was measured immediately using a spectrometer (LumiFL SpectroCapture, AB-1850; Atto, Tokyo, Japan) for 1 min. The background-subtracted spectrum data were smoothed using the loess function in R (R Core Team 2020) with the default settings, except that span was set to 0.1, meaning that 10% of the data points were used for local fitting.

Laboratory-reared specimens were used for the two species of *Lobella* Börner, 1906. The source of the laboratory population of *L. sauteri* was the same as described previously (Ohira & Nakamori 2025). A laboratory population of *L. lucifera* **sp. nov.** was derived from 12 post-identified specimens collected at the type locality on 12–13 December 2023. The populations were fed plasmodia of *Fuligo septica* (L.) (for collection records, see Ohira *et al.* 2023), as described by Kataoka & Nakamori (2020). Spectra of 12 and 11 specimens were measured for *L. lucifera* **sp. nov.** and *L. sauteri*, respectively.

For the three species of *Crossodonthina* Yosii, 1954, field-collected specimens from their respective type localities, as mentioned above, were used. For *C. elegans*, the spectra of five specimens collected on 8–9 October 2024 were measured on 11 October 2024 (three were collected on 9 October) and 15 October 2024 (one was collected on 8 October and one was collected on 9 October). For *C. laterisensillata*, the spectra of nine specimens collected on 16 February 2024 were measured on 5 April 2024. For *C. leodeus* **sp. nov.**, the spectra of eight specimens collected on 24 April 2024 were measured on 30 April 2024.

After measurement, the specimens were fixed in ethanol and mounted on glass slides, and species and sex were examined under a microscope.

### Bioluminescence imaging

The bioluminescence of Collembola was photographed using an iPhone 13 camera (Apple Inc., Cupertino, CA, USA) with a macro lens (Apexel Technology Co. Ltd., Shenzhen, China) as described by Ohira & Nakamori (2025). Specimens for imaging were obtained from the field (respective type localities) for *C. elegans*, *C. laterisensillata* and *C. leodeus* **sp. nov.** (collected on 9 October, 16 January and 24 April 2024, respectively) or from the abovementioned laboratory populations of *L. lucifera* **sp. nov.** and *L. sauteri*. Bright-field images of live specimens were also taken; for *C. elegans*, *C. laterisensillata*, and *C. leodeus* **sp. nov.**, these specimens were collected from the field (respective type localities) on 9 October 2024, 16 January 2024 and 11 December 2023, respectively; for *L. lucifera* **sp. nov.** and *L. sauteri*, specimens were from the same laboratory populations.

## Results

### Taxonomy

### Family Neanuridae Börner, 1901

### Subfamily Neanurinae Börner, 1901

### Tribe Lobellini Cassagnau, 1983

### Genus *Crossodonthina* Yosii, 1954

***Crossodonthina laterisensillata* Ohira, Kataoka, Tanooka & Nakamori, 2022**
[Japanese name: Fuchimi-akahusa-ibotobimushi]
Figs 1B, 1G, 2; Table 1

**Type locality**. Shirahama, Iriomote Island, Okinawa, Ryukyu Archipelago, Japan.

**Material examined.** Specimens collected from the type locality: 1 male, 3 females, Shirahama, Iriomote Island, Okinawa, Ryukyu Archipelago, Japan (24.3651°N, 123.7548°E, alt. 69 m) on 5 September 2023 by Ohira, A., Nakamori, T. and Takaesu, R. (one female deposited in the National Museum of Nature and Science, Tsukuba, Japan as voucher specimen; NSMT-Ap 730); 6 males, 3 females collected on 16 January 2024 by Ohira, A. and Nakamori, T.

**Remarks.** The presence of hr microchaetae on the anal valve was not described in the original description, but 2–3 and 3 hr microchaetae were present on each ventral anal valve and dorsal anal valve, respectively, in all specimens examined (Fig. 2, Table 1).

**TABLE 1.** *Crossodonthina laterisensillata*—Chaetae on abdominal sterna.

| Abdominal segment | Number of chaetae per group | | | |
|---|---|---|---|---|
| Abd. I | VT: 4 | | | |
| Abd. II | Ve: 4 | | | |
| Abd. III | Ve: 4 | Fu: 3 | | |
| Abd. IV | Vei: 1 | Vec: 2 | Vel: 4 | Vl: 5 |
| Abd. V | Ag: 3 | Vl: 1 | | |
| Abd. VI | Ve: 14–15 | hr (ventral): 2–3 | hr (dorsal): 3 | |

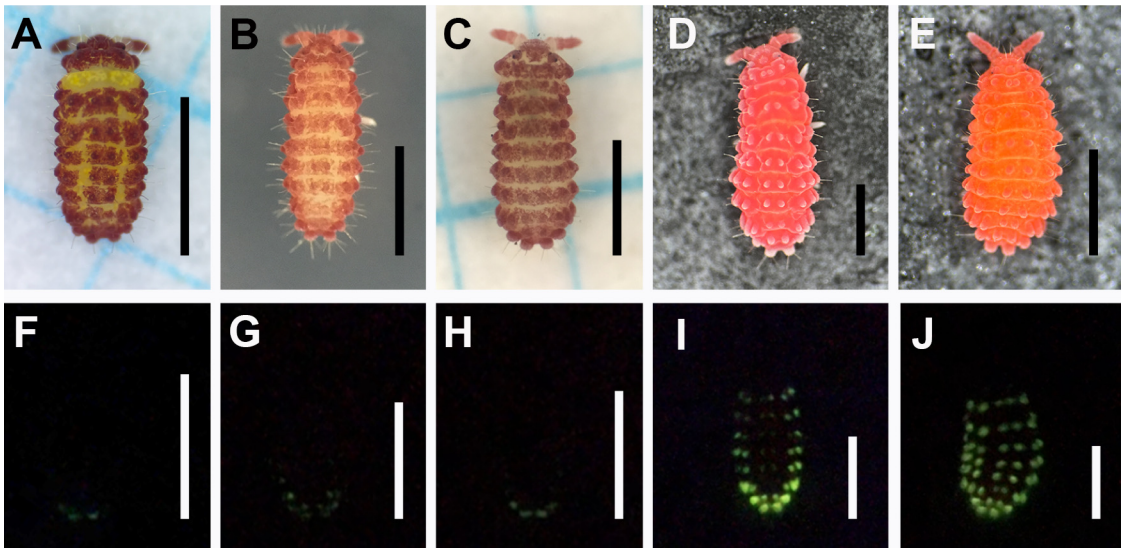


**FIGURE 1.** Living studied Collembola and bioluminescence: **A–E**, living specimens observed under bright-field conditions; **F–J**, bioluminescence observed under dark-field conditions. **A** and **F**, *Crossodonthina elegans* (NSMT-Ap 731 and NSMT-Ap 732, respectively); **B** and **G**, *Crossodonthina laterisensillata* (NSMT-Ap 733 and NSMT-Ap 734, respectively); **C** and **H**, *Crossodonthina leodeus* **sp. nov.** (NSMT-Ap 735 and NSMT-Ap 736, respectively); **D** and **I**, *Lobella lucifera* **sp. nov. E** and **J**, *Lobella sauteri*. Scale bars: 1 mm. The specimens photographed under bright-field and dark-field conditions are not the same individuals.

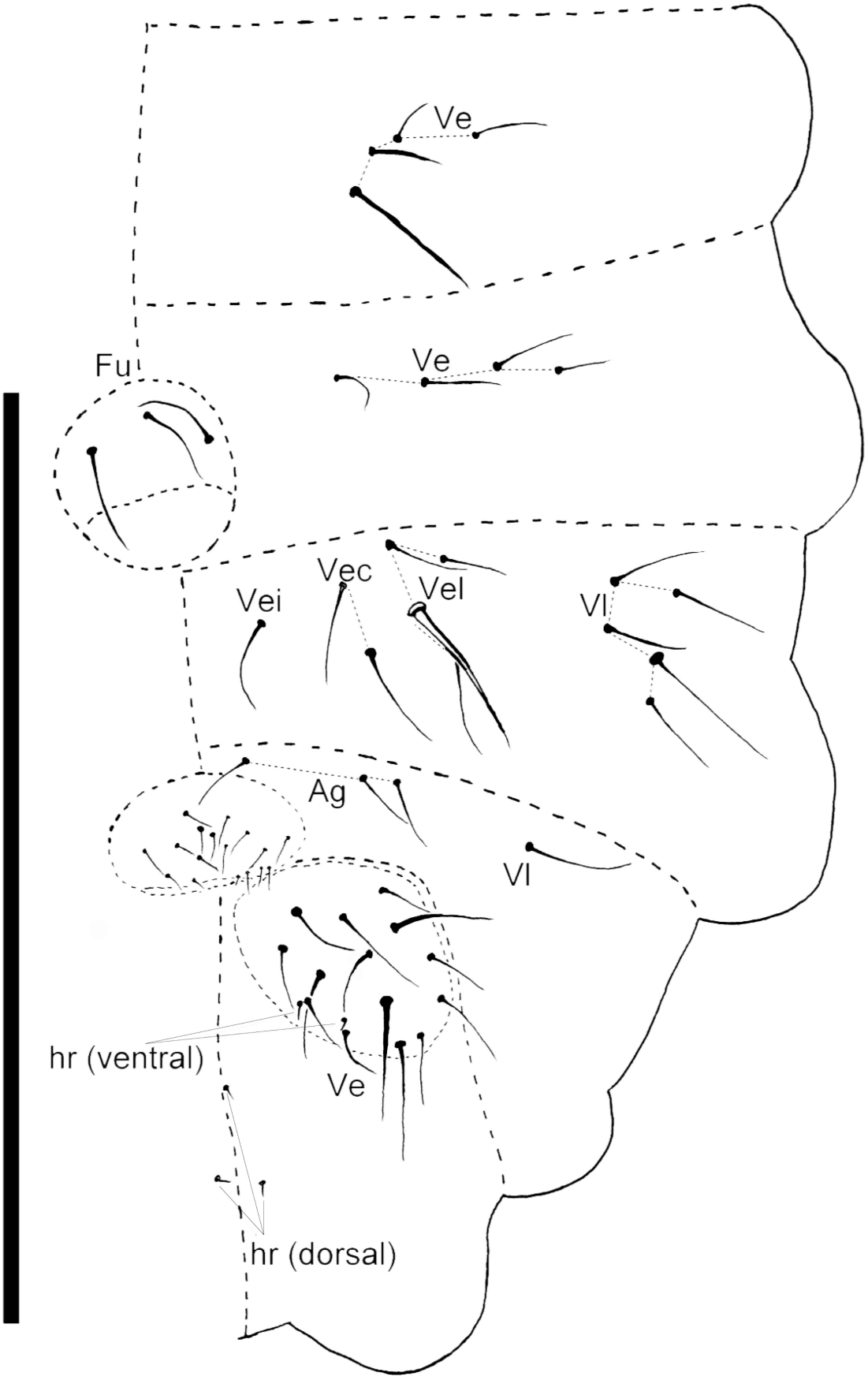


**FIGURE 2.** *Crossodonthina laterisensillata* sterna of Abd. II –VI. Abbreviations, see text. Scale bars: 500 μm. NSMT-Ap 730.

***Crossodonthina leodeus* sp. nov.**
[Japanese name: Shishigami-aka-ibotobimushi]
Figs 1C, 1H, 3–5; Tables 2–5

**Material examined.** Holotype: female, collected at Kamamamine Park, Shimozato, Hirara, Miyako Island, Okinawa, Ryukyu Archipelago, Japan (24.7982°N, 125.2753°E, elevation 28 m) on 10 May 2023 by Ohira, A., Nakamori, T. and Takaesu, R. Deposited in the National Museum of Nature and Science, Tsukuba, Japan (NSMT-Ap 717).

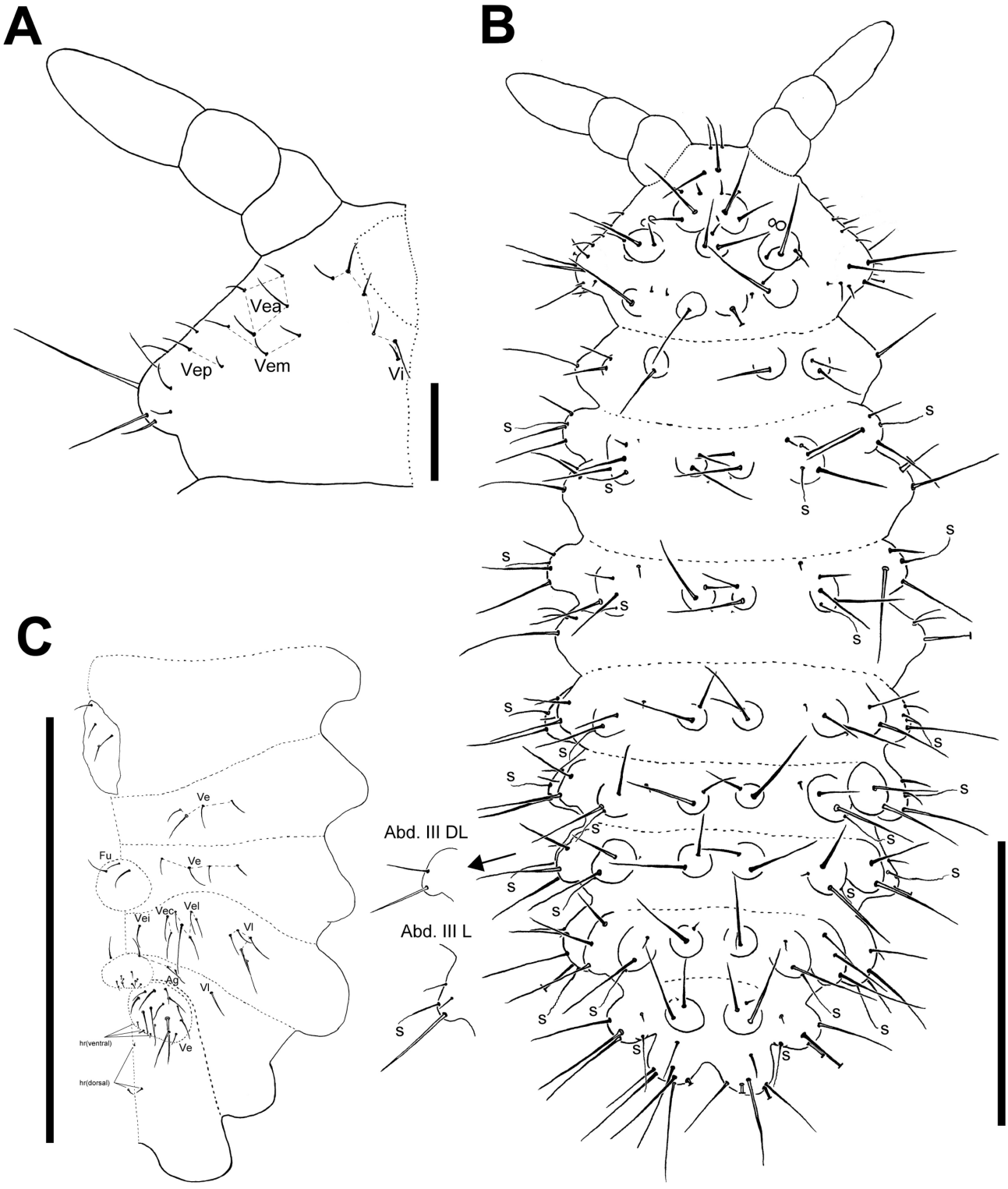


**FIGURE 3.** *Crossodonthina leodeus* **sp. nov.**: **A**, ventral chaetotaxy of the head; **B**, dorsal chaetotaxy of the body; **C**, sterna of Abd. I–VI. Abbreviations, see text. Scale bars: A, 100 μm; B–C, 500 μm. A–B, NSMT-Ap 717; C, NSMT-Ap 724.

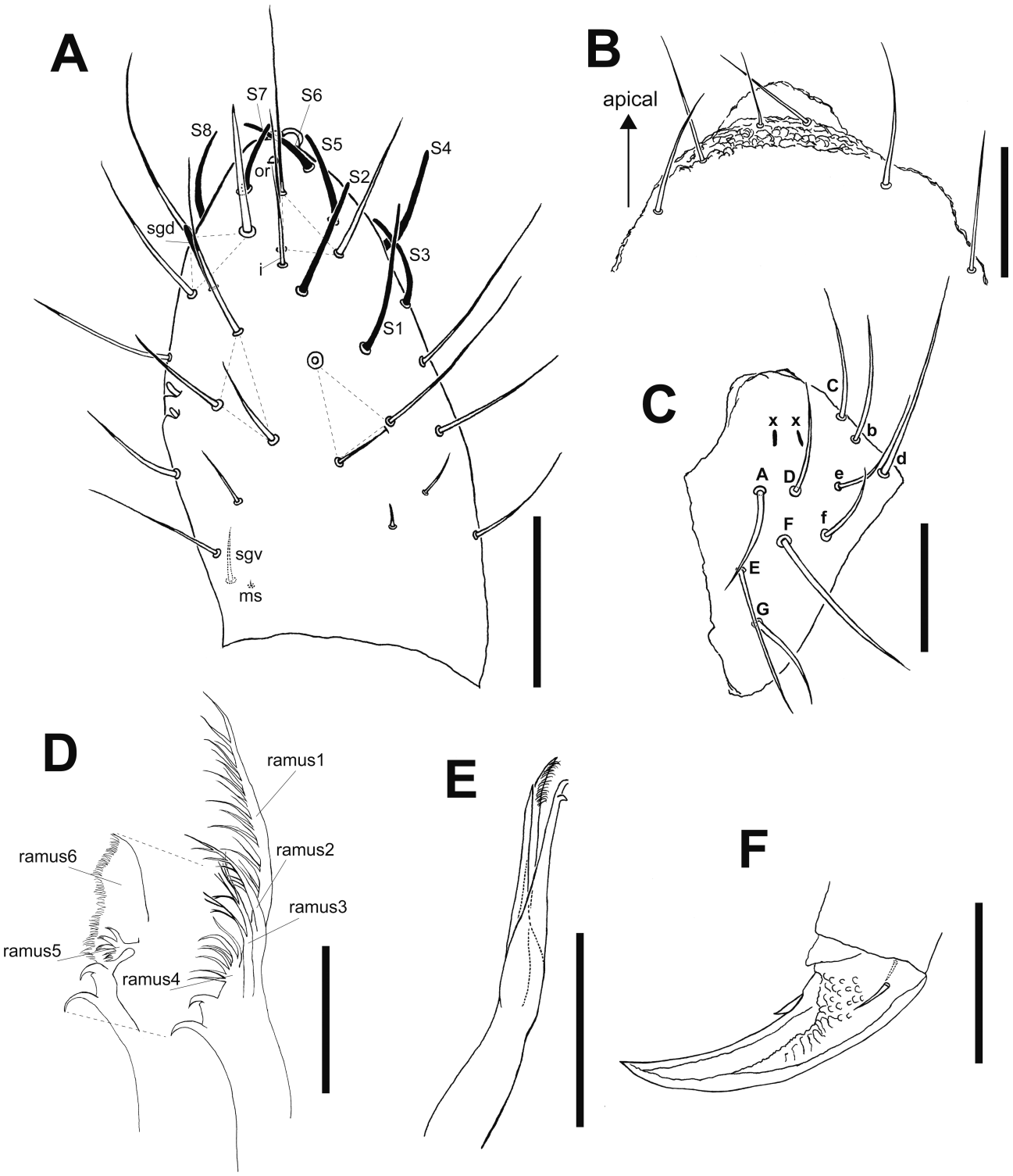


**FIGURE 4.** *Crossodonthina leodeus* **sp. nov.**: **A**, Ant. III–IV; **B**, labrum; **C**, labium; **D**, mandible; **E**, maxilla; **F**, hind claw. Scale bars: A–F, 50 μm. A, NSMT-Ap 723; B NSMT-Ap 717; C, NSMT-Ap 718; D, NSMT-Ap 725; E, NSMT-Ap 726; F, NSMT-Ap 719.

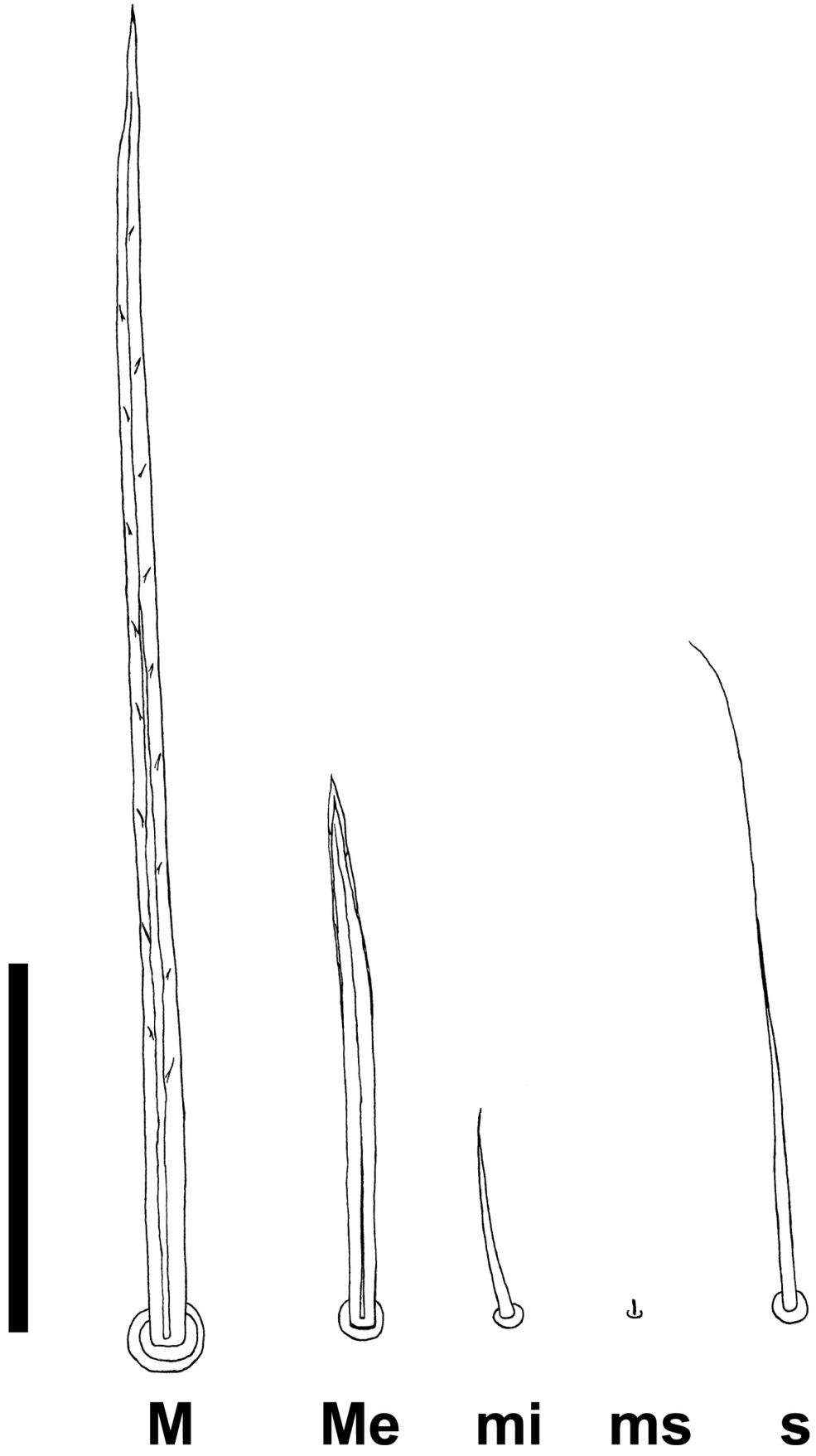


**FIGURE 5.** *Crossodonthina leodeus* **sp. nov.** types of chaetae (NSMT-Ap 720). M, macrochaetae; Me, mesochaetae (up to approximately one-third the length of large macrochaetae); mi, microchaetae (up to approximately one-third the length of large mesochaetae); ms, microsensilla; s, sensory chaetae (sensilla; long and thin). Scale bar: 50 μm.

Paratypes: 2 males, 7 females, collected at Kamamamine Park, Shimozato, Hirara, Miyako Island, Okinawa, Ryukyu Archipelago, Japan (24.7982°N, 125.2753°E, elevation 28 m) on 10 May 2023 by Ohira, A., Nakamori, T. and Takaesu, R. Deposited in the National Museum of Nature and Science, Tsukuba, Japan (NSMT-Ap 718–726; INSD accession numbers LC857141–LC857143 for COI gene).

**Other materials examined.** Four males and five females, collected at Kamamamine Park, Shimozato, Hirara, Miyako Island, Okinawa, Ryukyu Archipelago, Japan (24.7982°N, 125.2753°E, elevation 28 m) on 10 May 2023 by Ohira, A., Nakamori, T. and Takaesu, R. Two males and six females, collected at Kamamamine Park, Miyako Island, Okinawa, Ryukyu Archipelago, Japan (24.7982°N, 125.2753°E, elevation 28 m) on 24 April 2024 by Nakamori, T.

**Diagnosis.** Eyes 3+3, black. Cephalic chaeta O present. The sgd displaced apically, close to i on Ant. IV. Mandible head consisting of 6 rami and 3 basal teeth. Maxilla head consisting of 3 stylets. Labrum granulated, chaetal formula 2/2, 2. Labium with 10 chaetae and 2 x. Head Oc with 3 chaetae. Lateral sensilla present on tubercles Dl on Th. II and III, and on L on Abd. I–IV.

**Description.** Body length about 1.5–2.2 mm. Colour red in living specimen (Fig. 1C) and white in alcohol. Eyes 3+3, black (Fig. 3B). Postantennal organ absent. Antennae shorter than head. Ant. III and IV dorsally fused (Fig. 4A). Ant. I and II with 9 and 11 chaetae, respectively. Ant. III organ with 5 sensory chaetae, including sgd, sgv, ms and 2 finger-like rods in separate pits. The sgd displaced apically, close to i. Ant. IV with trilobed apical bulb, dorsal chaetotaxy with 8S and i (Fig. 4A). Mandible head consisting of 6 rami and 3 basal teeth (Fig. 4D): five rami of flagellum (Fig. 4D): the largest one (ramus 1) twice as long as the smaller two (rami 3 and 4), with simple (rarely bifurcated) cilia; medium one (ramus 2) slightly longer than the smaller two (rami 3 and 4), with simple (rarely bifurcated) cilia; 2 smaller ones (rami 3 and 4) multiply branched; the smallest one (ramus 5) with simple and bifurcated cilia; basal ramus (ramus 6) as fringed lamella. Medial tooth much smaller than the other two. Maxilla head consisting of 3 stylets: inner one with 2 minute apical teeth, middle one fringed, outer one needle-shaped (Fig. 4E). Labrum granulated, chaetal formula 0/2, 2 (Fig. 4B). Boundary between labrum and prelabral area not distinct. Labium with 10 chaetae and 2 x (Fig. 4C).

Cephalic tubercles and chaetotaxy. Cephalic area with 12 separate tubercles. Chaetotaxy of dorsal head as in Fig. 3B. Tubercle Cl with 4 chaetae, An with 4 chaetae, Fr with 3 chaetae (O-chaeta present), Oc with 3 chaetae, Di with 2 chaetae, De with 2 chaetae, area between De and L with 1–2 microchaetae and Dl+L+So with 11–16 chaetae (Fig. 3B, Table 2). Ventral chaetotaxy of the head as in Fig. 3A and Table 3.

Body tubercles and chaetotaxy. Th. I–Abd. VI without unpaired tubercles. Tubercles Di on Th. I and II not distinct. Tubercles Di on Th. III and Abd. I–V distinct. Th. I with 3+3 tubercles (Di, De, Dl). Th. II–Abd. IV with 4+4 tubercles, respectively (Di, De, Dl, L). Abd. V dorsally with 2+2 tubercles (Di, De+Dl); tubercle L ventrally situated (Fig. 3B). Abd. VI with 1+1 tubercles. Body dorso-lateral chaetotaxy as in Fig. 3B and Table 4. Sensory chaetae on the body acuminate, long and smooth; macrochaetae slightly serrated (Fig. 5). Formula of s and ms on half terga of Th. II–Abd. V as 2+ms, 2/2, 2, 2, 2, 1. Tubercles De with s on Th. II–Abd. IV. Each tubercle De+Dl on Abd. V with 1 sensory chaeta. Lateral sensilla present on tubercles Dl on Th. II–III and on L on Abd. I–IV. Ventral chaetotaxy of Abd. I–Abd. VI as in Fig. 3C.

Appendages. Chaetotaxy of legs, ventral tube and furcular remnant as in Table 5. Tibiotarsi I–III with 19, 19 and 18 chaetae, respectively. Unguis with 1 inner tooth, unguiculus absent (Fig. 4F). Ventral tube with 4+4 chaetae. Furcula absent. Furcular remnant with 3 chaetae. Genital plate with 16–42 chaetae (male: 18–26; female: 16–42). Each ventral anal valve with 14–15 Ve chaetae and 3 hr microchaetae. Dorsal anal valve with 3 hr microchaetae (Fig. 3C).

**Etymology.** The name *leodeus*, as a Latin noun, is derived from the Latin nouns *leo* (lion) and *deus* (god). The species was named after the Shisa, Okinawan guardian lions. Shisa are regarded as traditional amulets and guardian deities in Okinawa Prefecture. The park where they were collected has a huge Shisa monument, so the name was derived from the guardian deity.

**Ecology.** This species was found in leaf litter in forests. The species emitted light when stimulated (Fig. 1H).

**DNA barcoding.** The *p*-distances for the COI gene within *Crossodonthina leodeus* **sp. nov.** (3 sampled individuals) were 0.000. No COI gene sequences with >93% identity to the new species were found in the GenBank or BOLD databases. The *p*-distances of the COI gene between *C. leodeus* **sp. nov.** and other congeneric species, i.e., *C. elegans* (LC857144–LC857146; present study), *C. laterisensillata* (LC612526–LC612528; Ohira *et al.* 2023), *Crossodonthina nipponica* Yosii, 1954 (LC715144–LC715145; Ohira *et al.* 2023), collected from their respective

type localities, were 11.7%–11.8%, 8.2%–8.9% and 19.6%, respectively. In addition, the *p*-distance between *C. leodeus* **sp. nov.** and an undescribed *Crossodonthina* species collected from Okinawa Island (LC760484–LC760485; Ohira *et al.* 2023) was 17.3%.

**Remarks.** *Crossodonthina leodeus* **sp. nov.** is similar to *Crossodonthina tridentiens* Yue & Yin, 1999 in having well-defined tubercles and De tubercles fused to Dl tubercles on Abd. V, but the new species can be distinguished from the latter by having additional sensory chaetae on tubercles L of Abd. I–IV and 6 rami on the mandible (no additional sensory chaetae on tubercles L of Abd. I–IV and 4 rami on the mandible in *C. tridentiens*). *Crossodonthina leodeus* **sp. nov.** is also similar to *C. laterisensillata* from Iriomote Island and *Crossodonthina tiantongshana* Xiong, Chen & Yin, 2005 in mouthpart structures and in tergal sensory chaeta formula. However, it differs from *C. laterisensillata* by having chaetae Di2 on Abd. IV as microchaetae (mesochaetae in *C. laterisensillata*). Furthermore, the new species is genetically distinct from *C. laterisensillata*, with a *p*-distance of 8.2%–8.9% in the COI gene. *Crossodonthina leodeus* **sp. nov.** also differs from *C. tiantongshana* by having an unguis with an inner tooth without basal denticules and 3-branched maxillae consisting of 1 bidentate, 1 fringed and 1 needle-shaped stylet, while *C. tiantongshana* has an unguis with an inner tooth, with 1–3 tiny basal denticules and 4-branched maxillae consisting of 1 tridentate, 1 fringed and 2 needle-shaped stylets (Luo & Chen 2010).

A non-luminous congeneric species currently under taxonomic examination has been collected from Okinawa (*Crossodonthina* sp. of Ohira *et al.* 2023; voucher specimen numbers, NSMT-Ap 628–629; INSD accession numbers of DNA barcodes, LC760484–LC760485). This species resembles *C. nipponica* in lacking additional sensory chaetae on tubercles L of Abd. I–IV. This information was not provided in the previous study and is presented here. In contrast, the species described here possesses additional sensory chaetae on tubercles L of Abd. I–IV, distinguishing it from both *C. nipponica* and the Okinawan species of *Crossodonthina*.

**TABLE 2.** *Crossodonthina leodeus* **sp. nov.**—Dorsal tubercles and chaetotaxy of the head.

| Tubercle | Number of chaetae | Types of chaetae | Chaetae labels |
|---|---|---|---|
| Cl | 2 | M | F |
| | 2 | Me | G |
| An | 2 | M | B |
| | 2 | mi | E |
| Fr | 2 | M | A |
| | 1 | Me | O |
| Oc | 1 | M | Ocm |
| | 2 | mi | Oca, Ocp |
| Di | 1 | M | Di1 |
| | 1 | mi | Di2 |
| De | 1 | M | De1 |
| | 1–2 | mi | De2 |
| Dl+L+So | 3 | M | |
| | 3–5 | Me | |
| | 3–10 | mi | |

**TABLE 3.** *Crossodonthina leodeus* **sp. nov.**—Ventral chaetotaxy of the head.

| Group | Number of chaetae |
|---|---|
| Vi | 6 |
| Vea | 4 |
| Vem | 3 |
| Vep | 2 |

**TABLE 4.** *Crossodonthina leodeus* **sp. nov.**—Dorsal tubercles and overall chaetotaxy of the trunk.

| Segment | Di | De | Dl | L |
|---|---|---|---|---|
| Th. I | 1M | 2M | 1M | |
| Th. II | 2M+1mi | 2M+1Me+1s+1mi | 2M+1Me+1s+1ms | 1M+2Me |
| Th. III | 2M+1mi | 2M+1Me+1s+1mi | 2M+1Me+1s | 1M+2Me |
| Abd. I | 2M | 2M+1s+1mi | 2M | 1M+1s+2mi |
| Abd. II | 2M | 2M+1s+1mi | 2M | 1M+1s+2mi |
| Abd. III | 2M | 2M+1s+1mi | 2M | 1M+1s+2mi |
| Abd. IV | 1M+1Me | 1M+1s+1mi | 2M+1Me | 3M+1Me+1s+1mi |
| Abd. V | 2M+1mi | 3M+1mi+1s | | |
| Abd. VI | 7M | | | |

**TABLE 5.** *Crossodonthina leodeus* **sp. nov.**—Chaetae on legs and abdominal sterna.

| Leg or abdominal segment | Number of chaetae | | | | |
|---|---|---|---|---|---|
| Leg I | Scx: 0 | Cx: 3 | Tr: 6 | Fe: 13 | T: 19 |
| Leg II | Scx: 2 | Cx: 7 | Tr: 6 | Fe: 12 | T: 19 |
| Leg III | Scx: 2 | Cx: 8 | Tr: 6 | Fe: 11 | T: 18 |
| Abd. I | VT: 4 | | | | |
| Abd. II | Ve: 4 | | | | |
| Abd. III | Ve: 4 | Fu: 3 | | | |
| Abd. IV | Vei: 1 | Vec: 2 | Vel: 4–5 | Vl: 5 | |
| Abd. V | Ag: 3 | Vl: 1 | | | |
| Abd. VI | Ve: 14–15 | hr (ventral): 3 | hr (dorsal): 3 | | |

## Identification key to the species of *Crossodonthina**

1 Eyes 2+2 . . . . . 2
- Eyes 3+3 . . . . . 6
2 Tubercle Oc with 2 chaetae . . . . . *C. hainana* Xiong, Chen & Yin, 2005 (China)
- Tubercle Oc with 3 chaetae . . . . . 3
3 Tubercles Di fused on Abd. V . . . . . *C. bidentata* Luo & Chen, 2009 (China)
- Tubercles Di separated on Abd. V . . . . . 4
4 Mandible with 1 basal tooth . . . . . *C. montana* Lee & Kim, 1990 (Taiwan)
- Mandible with 2 or more basal teeth . . . . . 5
5 Mandible with 2 or more basal teeth. Eyes black. . . . . *C. langshanensis* Hu, Jiang C. & Jiang J.G., 2019 (China)
- Mandible with 5 basal teeth. Eyes unpigmented . . . . . *C. quadridentata* Jiang & Wang, 2024 (China)
6 Cephalic O chaeta absent . . . . . 7
- Cephalic O chaeta present . . . . . 8
7 Four cephalic tubercles, 2 Di and 2 De, fused into a single median structure . . . . . *C. altamontana* Yoshii, 1981 (Malaysia)
- Four cephalic tubercles, 2 Di and 2 De, not fused with each other . . . . . *C. formosana* Yosii, 1965 (Taiwan)
8 Tubercles Di, De, Dl on Th. I with 3, 2, 3 chaetae, respectively . . . . . *C. radiata* (Salmon, 1941) (New Zealand)
- Tubercles Di, De, Dl on Th. I with 1, 2, 1 chaetae, respectively . . . . . 9
9 Tubercles De and Dl fused on Abd. V . . . . . 10
- Tubercles De and Dl separated on Abd. V . . . . . 12
10 An additional sensory chaeta present on tubercle L of Abd. IV. . . . . *C. leodeus* **sp. nov.** (Japan)
- An additional sensory chaeta absent on tubercle L of Abd. IV . . . . . 11
11 Di2 chaetae on Th. II–Abd. V as microchaeta. Body tubercles poorly developed: Di tubercles on Th. I–Abd. IV reduced. . . . . *C. koreana* Yosii & Lee, 1963 (Korea & Japan)
- Di2 chaetae on Th. II–Abd. V as macro- or mesochaeta. Body tubercles spherical . . . . *C. tridentiens* Yue & Yin, 1999 (China)
12 De2 chaetae on head as macrochaeta . . . . . *C. alatoserrata* Yosii, 1965 (Taiwan)
- De2 chaetae on head as microchaeta or absent . . . . . 13
13 An additional sensory chaeta present on tubercle L of Abd. IV. . . . . 14
- An additional sensory chaeta absent on tubercle L of Abd. IV . . . . . 15
14 An additional sensory chaeta present on tubercle L of Abd. I–III . . . . . *C. acuminata* Jiang & Wang, 2021 (China)

- An additional sensory chaeta absent on tubercle L of Abd. I–III ..... *C. nipponica* Yosii, 1954 (Japan)
15 An additional sensory chaeta present on tubercle L of Abd. I–III ..... 16
- An additional sensory chaeta absent on tubercle L of Abd. I–III ..... 18
16 Maxillary head with cilia. Macrochaeta pointed. Dorsal side of Th. I red in living specimen ..... 17
- Maxillary head without cilia. Macrochaeta blunt. Dorsal side of Th. I yellow or white in living specimen ..... *C. elegans* Kasai, Tanaka & Sawahata, 2023 (Japan)
17 Mandible with 3 rami and 5 basal teeth. Unguis inner tooth often with 1–3 tiny basal denticules ..... *C. tiantongshana* Xiong, Chen & Yin, 2005 (China)
- Mandible with 6 rami and 3 basal teeth. Unguis inner tooth without basal denticules ..... *C. laterisensillata* Ohira, Kataoka, Tanooka & Nakamori, 2022 (Japan)
18 Five chaetae (4+s) on tubercle De of Th. II. Eyes black ..... *C. choui* Jiang & Zhang, 2012 (China)
- Four chaetae (3+s) on tubercle De of Th. II. Eyes unpigmented ..... *C. clavata* Jiang & Wang, 2021 (China)

*This key is partially based on Luo & Chen (2009), Jiang & Wang (2021) and Kasai *et al.* (2023).

## Genus *Lobella* Börner, 1906

### *Lobella lucifera* sp. nov.

[Japanese name: Akahoshi-aka-ibotobimushi]
Figs 1D, 1I, 6–8; Tables 6–9

**Material examined.** Holotype: male, collected at Nishinakasone, Hirara, Miyako Island, Okinawa, Ryukyu Archipelago, Japan (24.8104°N, 125.3135°E, elevation 33 m) on 10 May 2023 by Ohira, A., Nakamori, T. and Takaesu, R. Deposited in the National Museum of Nature and Science, Tsukuba, Japan (NSMT-Ap 709; INSD accession number LC857139 for COI gene).

Paratypes: 3 males, 3 females and 1 unknown, collected at Nishinakasone, Hirara, Miyako Island, Okinawa, Ryukyu Archipelago, Japan (24.8104°N, 125.3135°E, elevation 33 m) on 10 May 2023 by Ohira, A., Nakamori, T. and Takaesu, R. Deposited in the National Museum of Nature and Science, Tsukuba, Japan (NSMT-Ap 710–716; INSD accession numbers LC857138 and LC857140 for COI gene).

**Other materials examined.** One male, two females, collected at Nishinakasone, Hirara, Miyako Island, Okinawa, Ryukyu Archipelago, Japan (24.8104°N, 125.3135°E, elevation 33 m) on 10 May 2023 by Ohira, A., Nakamori, T. and Takaesu, R.

**Diagnosis.** Eyes 3+3, black. Apically displaced sgd, close to i on Ant. IV. Mandible tridentate with the apical tooth subdivided into 3 toothlets. Maxilla styliform. Labrum chaetal formula 2/2, 2. Labium with 10 chaetae and 2 x. Cephalic O chaeta present, head Oc with 3 chaetae, De with 2 chaetae. De of Abd. II and III with 4 chaetae. Th. I–Abd. VI lacking unpaired tubercles. Sensory chaeta present on tubercle L of Abd. IV. Di of Abd. V with 3 chaetae, including 1 microchaeta. Tubercle De separated from tubercle Dl on Abd. V. Tubercle Di of Th. II and III with 3 chaetae each. Unguis with 1 inner tooth.

**Description.** Body length approximately 2.5–3.1 mm. Colour bright red in living specimen (Fig. 1D) and white in alcohol. Eyes 3+3, black (Fig. 6B). Postantennal organ absent. Antennae shorter than head. Ant. III and IV dorsally fused (Fig. 7A). Ant. I and II with 7 and 11 chaetae, respectively. Ant. III organ with 5 sensory chaetae, including sgd, sgv, ms and 2 finger-like rods in separate pits. Apically displaced sgd, close to i, Ant. IV with trilobed apical bulb, dorsal chaetotaxy with 8 S and i (Fig. 7A). Mandible thin and tridentate with the apical tooth subdivided into 3 toothlets (Fig. 7D). Maxilla head consisting of 2 stylets: one with 2–3 minute apical teeth (Fig. 7E). Labrum granulated, chaetal formula 0/2, 2 (Fig. 7B). Labium with 10 chaetae and 2 x (Fig. 7C).

Cephalic tubercles and chaetotaxy. Cephalic area with 14 separate tubercles. Chaetotaxy of dorsal head as in Fig. 6B. Tubercle Cl with 4 chaetae, An with 4 chaetae, Fr with 3 chaetae (O chaeta present), Oc with 3 chaetae, Di with 2 chaeta, De with 2 chaetae, Dl with 4 chaetae, L+So with 11–15 chaetae (Fig. 6B, Table 6). Ventral chaetotaxy of the head as in Fig. 6A and Table 7.

Body tubercles and chaetotaxy. Th. I–Abd. VI lacking unpaired tubercles. Th. I with 3+3 tubercles (Di, De, Dl). Th. II–Abd. IV with 4+4 tubercles, respectively (Di, De, Dl, L). Abd. V dorsally with 3+3 tubercles (Di, De, Dl). Abd. VI with 1+1 tubercles. Body chaetotaxy as in Fig. 6B and Table 8. Sensory chaetae on the body acuminate, long and smooth; macrochaetae rough, sheathed and apically rounded (Fig. 8). Formula of s on half terga of Th.

II–Abd. V as 2+ms, 2/1, 1, 1, 2, 1. Sensilla present on tubercles De on Th. II to Abd. V and tubercles Dl on Th. II to III. Lateral sensilla present on tubercle L on Abd. IV. Ventral chaetotaxy of Abd II –VI as in Fig. 6C.

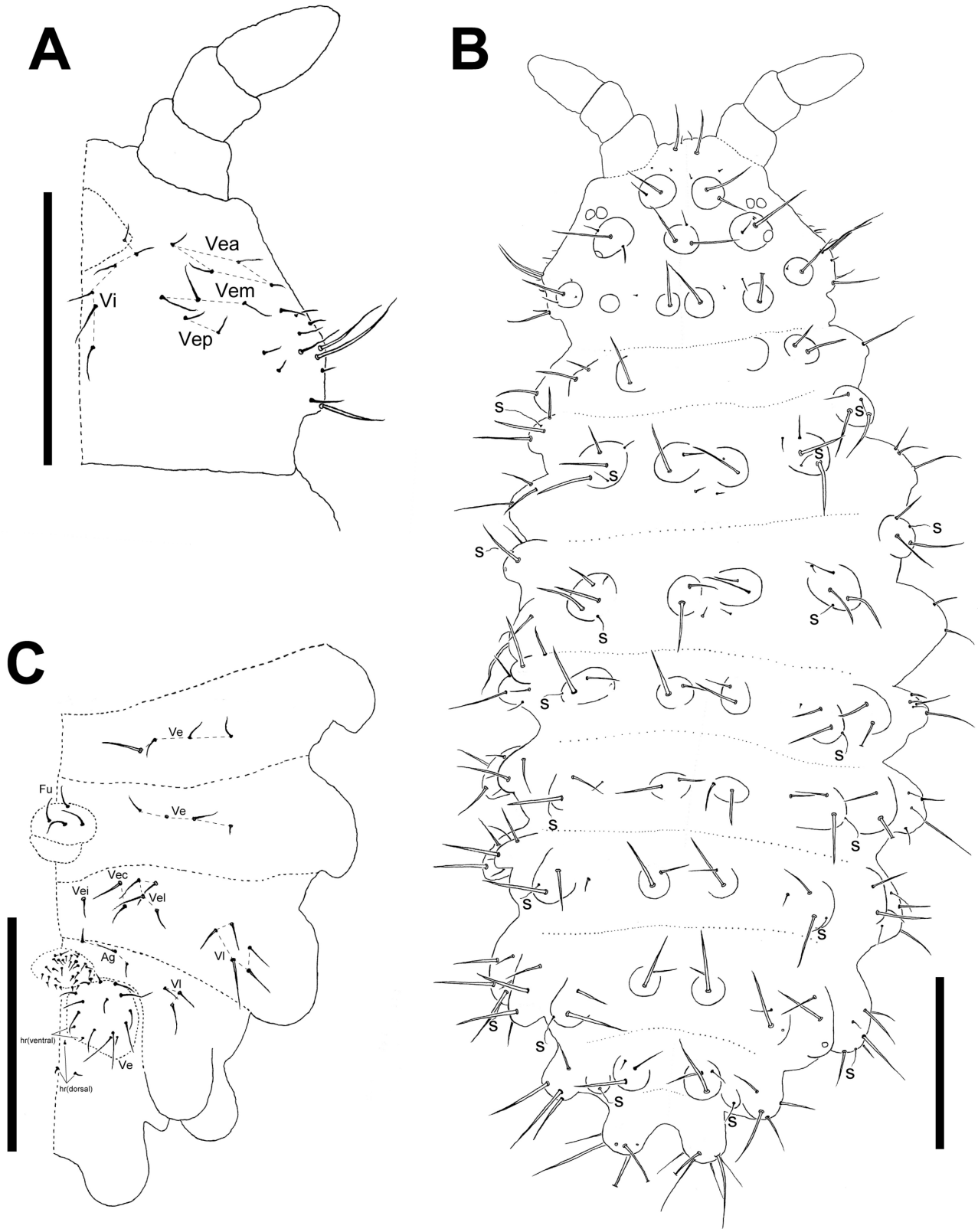


**FIGURE 6.** *Lobella lucifera* **sp. nov.**: **A**, ventral chaetotaxy of the head; **B**, dorsal chaetotaxy of the body; **C**, sterna of Abd. II –VI. Abbreviations, see text. Scale bars: A–C, 500 µm. A–C, NSMT-Ap 709.

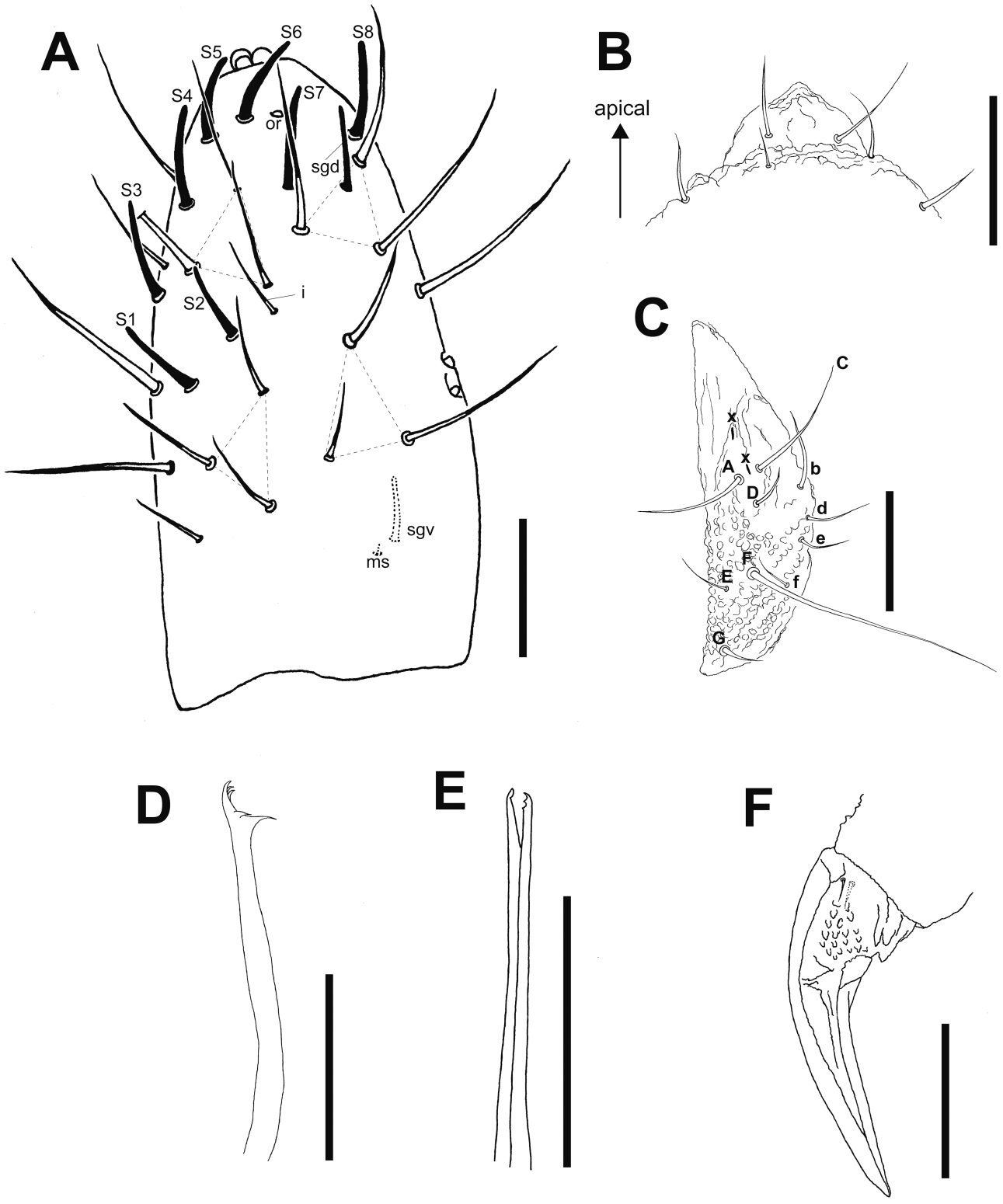


**FIGURE 7.** *Lobella lucifera* **sp. nov.**: **A**, Ant. III–IV; **B**, labrum; **C**, labium; **D**, mandible; **E**, maxilla; **F**, hind claw. Scale bars: A–F, 50 μm. A, NSMT-Ap 709; B–C, NSMT-Ap 712; D–E, NSMT-Ap 710; F, NSMT-Ap 712.

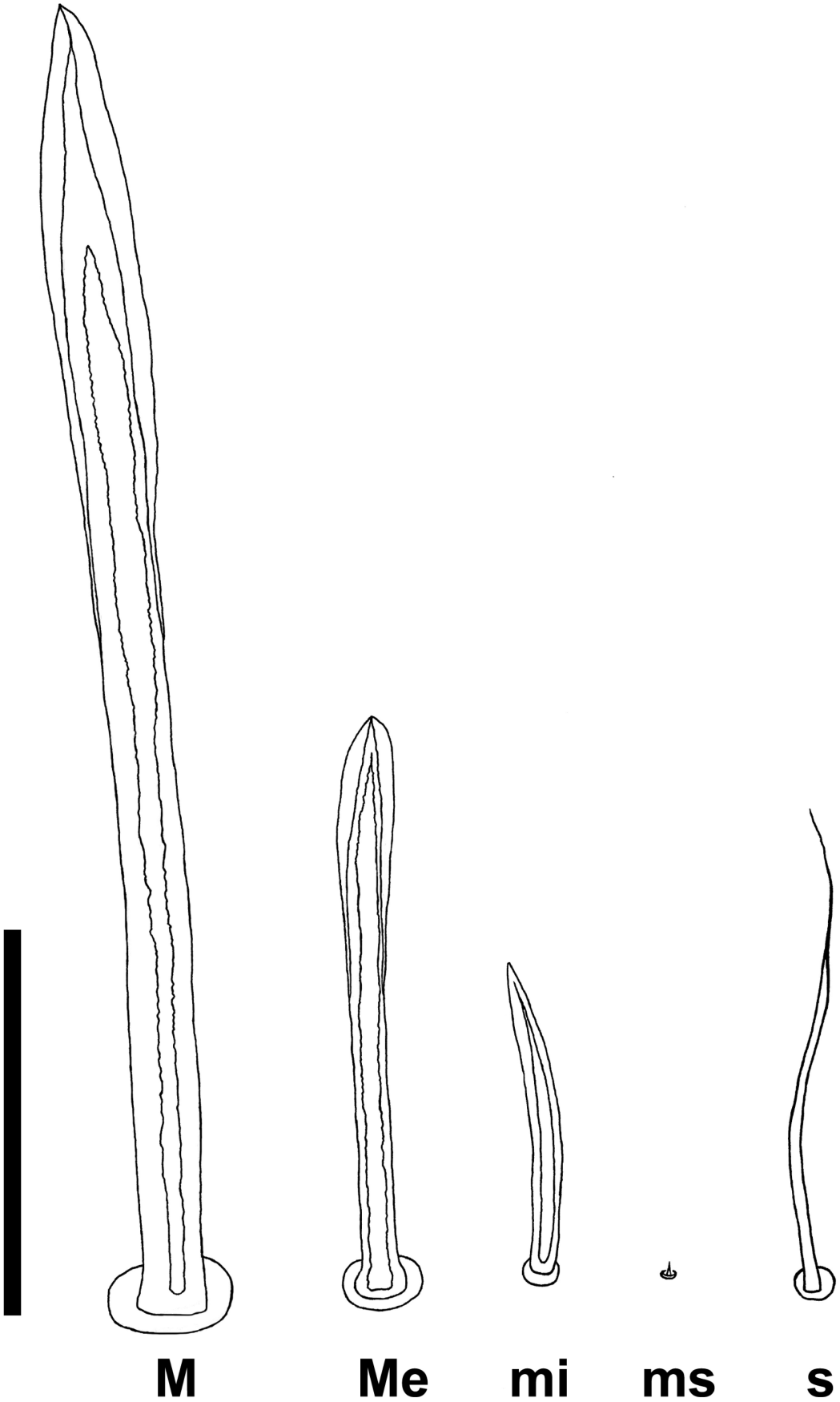


**FIGURE 8.** *Lobella lucifera* **sp. nov.** types of chaetae (NSMT-Ap 709). M, macrochaetae; Me, mesochaetae (up to approximately one-third the length of large macrochaetae); mi, microchaetae (up to approximately one-third the length of large mesochaetae); ms, microsensilla; s, sensory chaetae (sensilla; long and thin). Scale bar: 50 μm.

Appendages. Chaetotaxy of legs, ventral tube and furcular remnant as in Table 9. Tibiotarsi I–III with 19, 19 and 18 chaetae, respectively. Unguis with 1 inner tooth. Unguiculus absent (Fig. 7F). Ventral tube with 4+4 chaetae. Furcula absent. Furcular remnant with 3–4 chaetae (Fig. 6C). Genital plate with 32–42 chaetae (male: 32–42; female: 32–42). Each ventral anal valve with 15 Ve chaetae and 2–3 hr macrochaetae (Fig. 6C). Dorsal anal valve with 3 hr microchaetae (Fig. 6C).

**Etymology.** The name *lucifera*, as a Latin adjective, is derived from another Latin adjective *lucifer* (bringing light), referring to the light-emitting ability of the species.

**Ecology.** This species was found in leaf litter and on dead wood. The species emitted light when stimulated (Fig. 1I). *Lobella lucifera* **sp. nov.** can be fed plasmodia of *F. septica* in the laboratory.

**DNA barcoding.** The *p*-distances for the COI gene within *L. lucifera* **sp. nov.** (4 individuals) were 0.0%. No COI gene sequences with >85% identity to the new species were found in the GenBank or BOLD databases. The *p*-distances of the COI gene between *L. lucifera* **sp. nov.** and other congeneric species, i.e., *Lobella monstrum* Ohira & Nakamori, 2023 (LC760502–LC760504; Ohira *et al.* 2023), *L. sauteri* (LC760492–LC760494; Ohira *et al.* 2023) and *L. yambaru* (LC760495–LC760497; Ohira *et al.* 2023), collected from their respective type localities, were 18.6%, 16.8% and 14.8%, respectively.

**Remarks.** *Lobella lucifera* **sp. nov.** is most similar to *L. sauteri* and *L. yambaru* according to the key of *Lobella* described by Ohira *et al.* (2023). However, the new species can be distinguished from them by having 1 of the 3 chaetae on Di tubercles of Abd. V as a microchaeta (2 of the 3 chaetae as microchaetae in *L. sauteri* and *L. yambaru*), and blunt macro- and mesochaetae (pointed in *L. sauteri* and *L. yambaru*).

**TABLE 6.** *Lobella lucifera* **sp. nov.**—Dorsal tubercles and chaetotaxy of the head.

| Tubercle | Number of chaetae | Types of chaetae | Chaetae labels |
|---|---|---|---|
| Cl | 2 | M | F |
| | 2 | mi | G |
| An | 2 | M | B |
| | 2 | mi | E |
| Fr | 2 | M | A |
| | 1 | Me | O |
| Oc | 1 | M | Ocm |
| | 2 | mi | Oca, Ocp |
| Di | 1 | M | Di1 |
| | 1 | mi | Di2 |
| De | 1 | M | De1 |
| | 1 | mi | De2 |
| Dl | 1 | M | |
| | 1 | Me | |
| | 2 | mi | |
| L+So | 3 | M | |
| | 3–5 | Me | |
| | 4–9 | mi | |

**TABLE 7.** *Lobella lucifera* **sp. nov.**—Ventral chaetotaxy of the head.

| Group | Number of chaetae |
|---|---|
| Vi | 6 |
| Vea | 4 |
| Vem | 3 |
| Vep | 2 |

**TABLE 8.** *Lobella lucifera* **sp. nov.**—Dorsal tubercles and overall chaetotaxy of the trunk.

| Segment | Di | De | Dl | L |
|---|---|---|---|---|
| Th. I | 1M | 1M+1Me | 1M | |
| Th. II | 1M+1Me+1mi | 2M+1Me+1s+1mi | 2M+1Me+1s+1ms | 2M+1Me |
| Th. III | 1M+1Me+1mi | 2M+1Me+1s+1mi | 2M+1Me+1s | 1M+2Me |
| Abd. I | 1M+1Me | 1M+1Me+1s+1mi | 1M+1Me | 1M+1Me+3mi |
| Abd. II | 1M+1Me | 1M+1Me+1s+1mi | 1M+1Me | 2M+3Me |
| Abd. III | 1M+1Me | 1M+1Me+1s+1mi | 1M+1Me | 2M+3mi |
| Abd. IV | 1M+1Me | 1M+1Me+1s | 2M+1Me | 3M+3Me+1s |
| Abd. V | 1M+1Me+1mi | 1s | 3M+1mi | |
| Abd. VI | 7M | | | |

**TABLE 9.** *Lobella lucifera* **sp. nov.**—Chaetae on legs and abdominal sterna.

| Leg or abdominal segment | Number of chaetae | | | | |
|---|---|---|---|---|---|
| Leg I | Scx: 0 | Cx: 3 | Tr: 6 | Fe: 13 | T: 19 |
| Leg II | Scx: 2 | Cx: 7 | Tr: 6 | Fe: 12 | T: 19 |
| Leg III | Scx: 2 | Cx: 8 | Tr: 6 | Fe: 11 | T: 18 |
| Abd. I | VT: 4 | | | | |
| Abd. II | Ve: 4 | | | | |
| Abd. III | Ve: 4 | Fu: 3–4 | | | |
| Abd. IV | Vei: 1 | Vec: 2 | Vel: 4 | Vl: 5 | |
| Abd. V | Ag: 3 | Vl: 3 | | | |
| Abd. VI | Ve: 15 | hr (ventral): 2–3 | hr (dorsal): 3 | | |

## Identification key to the species of *Lobella*

1 An additional sensory chaeta present on tubercle L of Abd. IV . . . . . 2
- An additional sensory chaeta absent on tubercle L of Abd. IV . . . . . 12
2 Tubercle De fused to tubercle Dl on Abd. V . . . . . 3
- Tubercle De separated from tubercle Dl on Abd. V . . . . . 4
3 Tubercle De of Abd. V with 5–6 chaetae. De of Abd. I–III with 2+s chaetae . . . . . *L. wayang* Yosii, 1976 (Indonesia)
- Tubercle De of Abd. V with 3 chaetae. De of Abd. I–III with 3+s chaetae . . . . . *L. kemiri* Suhardjono & Deharveng, 2001 (Indonesia)
4 Tubercle Di of Th. II and III with 3 chaetae . . . . . 5
- Tubercle Di of Th. II and III with 2 chaetae . . . . . 8
5 Cephalic O chaeta absent . . . . . *L. sandakanensis* Yoshii, 1981 (Malaysia)
- Cephalic O chaeta present . . . . . 6
6 Tubercle Di of Abd. V with 3 chaetae, including 2 microchaetae . . . . . 7
- Tubercle Di of Abd. V with 3 chaetae, including 1 microchaeta . . . . . *L. lucifera* **sp. nov. (**Japan)
7 Tubercle Oc of the head with 1 macrochaeta and 2 mesochaetae; the two mesochaetae longer than the diameter of the ocellus . . . . . *L. sauteri* Börner, 1906 (Japan)
- Tubercle Oc of the head with 1 macrochaeta and 2 microchaetae; the two microchaetae shorter than the diameter of the ocellus . . . . . *L. yambaru* (Tanaka & Hasegawa, 2010) (Japan)
8 Tubercle De of Th. I with 1 chaeta. Cephalic O chaeta absent . . . . . *L. setapauca* Gapud, 1970 (Philippines)
- Tubercle De of Th. I with 2 chaetae. Cephalic O chaeta present . . . . . 9
9 Tubercle Di of Th. I with 1 chaeta . . . . . 10
- Tubercle Di of Th. I with 2 chaetae . . . . . 11
10 Cephalic O chaeta as macrochaeta . . . . . *L. monocincta* Cassagnau & Deharveng, 1984 (Philippines)
- Cephalic O chaeta as macrochaeta . . . . . *L. bicincta* Cassagnau & Deharveng, 1984 (Philippines)
11 Tubercle L of Abd. V with 4 chaetae . . . . . *L. punctata* Cassagnau & Deharveng, 1984 (Philippines)
- Tubercle L of Abd. V with 5 chaetae . . . . . *L. bicolor* Cassagnau & Deharveng, 1984 (Philippines)
12 Tubercle De fused to tubercle Dl on Abd. V . . . . . *L. nana* Lee & Kim, 1990 (Taiwan)
- Tubercle De separated from tubercle Dl on Abd. V . . . . . 13
13 Tubercle Di reduced on Abd. III . . . . . *L. decipiens* Yosii, 1965 (Japan)

- Tubercle Di developed on Abd. III . . . . . 14
14 Tubercle Di reduced on Abd. IV . . . . . *L. mizunasiana* Yosii, 1956 (Japan)
- Tubercle Di developed on Abd. IV. . . . . 15
15 Cephalic O chaeta absent . . . . . *L. stachi* Yosii, 1956 (Japan)
- Cephalic O chaeta present . . . . . 16
16 Chaeta of tubercle Di on Th. I as microchaeta. Microchaeta of tubercle De not shifted between Di and De on Abd. I–III . . . . . *L. sokamensis* Deharveng & Weiner, 1984 (North Korea)
- Chaeta of tubercle Di on Th. I as mesochaeta. Microchaeta of tubercle De shifted between Di and De on Abd. I–III . . . . . *L. monstrum* Ohira & Nakamori, 2023 (Japan)

## Remarks on nomenclatural change

The genus *Cassagnaua* Özdikmen, 2009 was proposed as a substitute name for *Pectinura* Cassagnau, 1983 by Özdikmen (2009) and presently comprises only one species, *Cassagnaua hongkongensis* (Yosii, 1976), which was previously transferred from *Womersleya* Denis, 1948 by Cassagnau (1983). In this study, we transfer another species originally described under *Womersleya* to this genus, for which we propose the name *Cassagnaua formosana* (Lee & Kim, 1990) **comb. nov.**

The diagnostic characters of *Womersleya*, which is currently placed within the tribe Neanurini (Smolis & Paśnik 2020), include fusion of the Di and De tubercles on the head and fusion of the Di, De and Dl tubercles on Abd. V (Deharveng 1988). The type species, *Womersleya vicina* (Denis, 1934), has 2+2 unpigmented eyes. These characteristics, along with the importance of eye number in Neanuridae taxonomy, as emphasised by Jiang & Wang (2024), exclude the 3-eyed species *C. formosana* **comb. nov.** from *Womersleya*.

The attribution of *C. formosana* **comb. nov.** to the genus *Cassagnaua* requires an expansion of its definition, to include both species with dorsal tubercles on Abd. V, which are shifted laterally towards the Abd. VI in *C. hongkongensis*, or with tubercles in the normal position as in *C. formosana* **comb. nov.** In the original definition of *Cassagnaua*, the eyes were described as pigmented (Cassagnau 1983); however, the presence or absence of eye pigmentation in *C. formosana* **comb. nov.** was not specified in the original description by Lee & Kim (1990). The updated diagnosis of *Cassagnaua* is as follows:

**Diagnosis.** Eyes 3+3. Hypodermal blue pigment absent. Maxillae styliform; mandibles elongated into a comb-like shape, with a large basal tooth and 12–25 small teeth. Di and De tubercles on the head either well-defined and separated or reduced. Di tubercles separated from other dorsal tubercles on Abd. V. Dorsal tubercles on Abd. V either in their normal position or shifted laterally towards Abd. VI.

*Womersleya marhia* Baijal, 1958, originally described from India, is also likely to be transferred to *Cassagnaua* due to its possession of 3+3 eyes. However, as the status of some relevant characteristics of this species, like the morphology of the tubercles on the head and Abd. V, remain unclear, *W. marhia* is tentatively retained within *Womersleya* at this time.

Based on our notes, *Cassagnaua* includes the species listed in the identification key below, which possess sensory chaetae on the L tubercles of Abd. IV. Their well-developed mandibles and the presence of sensory chaetae on the L tubercles of Abd. IV suggest close affinity with one of the groups within *Crossodonthina*, which are characterised by having 3+3 eyes and sensory chaetae on the L tubercles of Abd. IV.

## Identification key to the species of *Cassagnaua*

1 Cephalic O chaeta absent. Dorsal tubercles on Abd. V shifted laterally towards the Abd. VI . . . . . *C. hongkongensis* (Yosii, 1976) (China)
- Cephalic O chaeta present. Tubercles on Abd. V in the normal position, not shifted laterally towards the Abd. VI . . . . . *C. formosana* (Lee & Kim, 1990) **comb. nov.** (Taiwan)

## Light-emitting capacity and *in vivo* bioluminescence spectrum

Light emission in response to stimuli and blinking was observed by eye in *C. laterisensillata*, *C. leodeus* **sp. nov.** and *L. lucifera* **sp. nov.** (Table 10, Fig. 1G–I). *Crossodonthina elegans* was not tested for light-emitting capacity but

imaging showed luminescence and blinking (Fig. 1F). The light was greenish, emitted from certain tubercles and strongest at the abdomen (Fig. 1). *In vivo* bioluminescence spectra showed peaks at around 520–550 nm (greenish) for all species examined, and at around 600–650 nm (reddish) for some specimens of *L. lucifera* **sp. nov.** and *L. sauteri* (Fig. 9). Light emission was observed for both sexes by eye and/or spectral measurement in all species examined (Table 10, Fig. 9).

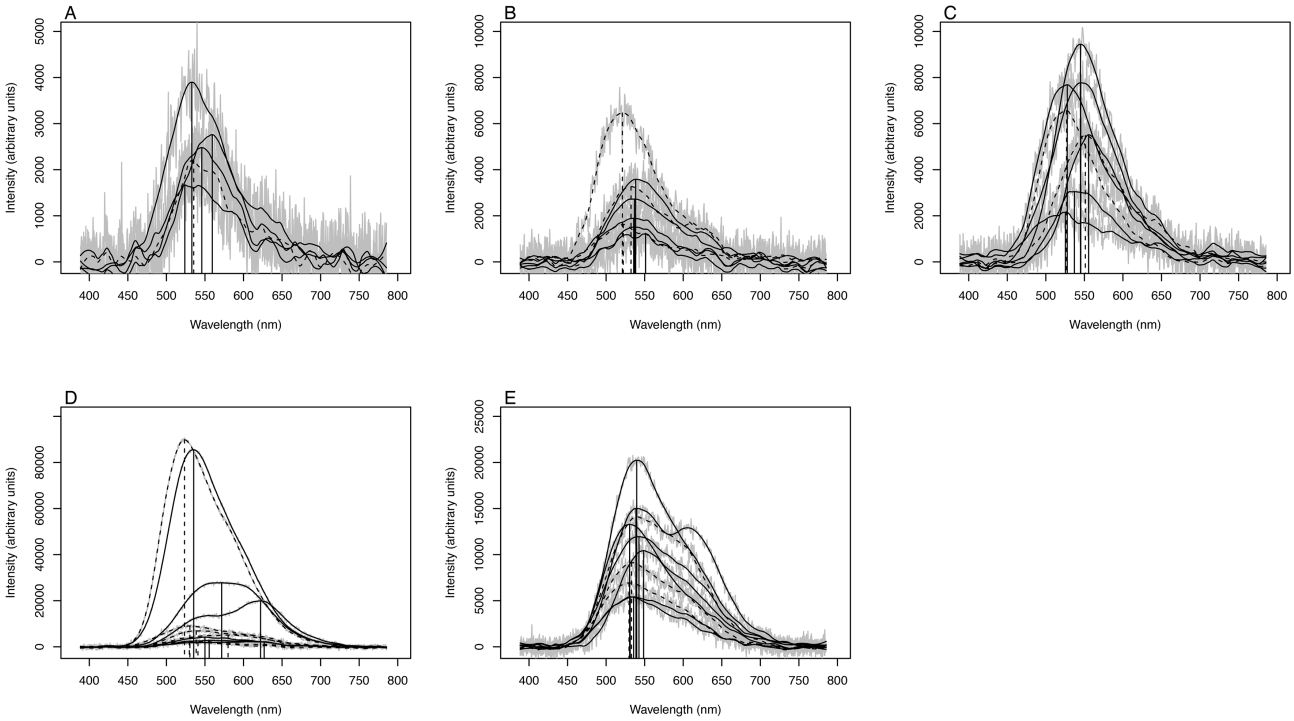


**FIGURE 9.** *In vivo* bioluminescence spectra of single individuals: **A**, *Crossodonthina elegans*; **B**, *Crossodonthina laterisensillata*; **C**, *Crossodonthina leodeus* **sp. nov.**; **D**, *Lobella lucifera* **sp. nov.**; **E**, *Lobella sauteri*. Grey lines represent the raw data, black solid and dashed lines represent smoothed data of females and males, respectively.

**TABLE 10.** Number of studied light-emitting individuals in the light-emitting capacity test.

| Species | Transportation period (d) | Standing period (d) | Number of light-emitting individuals (male/female/immature or unspecified) | | | | Total number examined (male/female/immature or unspecified) |
|---|---|---|---|---|---|---|---|
| | | | Sound | Slam on the desk | Breath | Total | |
| *Crossodonthina laterisensillata* | 6 | 7 | 3 (2/1/0) | 6 (5/1/0) | 6 (5/1/0) | 6 (5/1/0) | 9 (6/3/0) |
| *Crossodonthina leodeus* **sp. nov.** | 5 | 4 | 0 | 9 (3/6/0) | 9 (3/6/0) | 10 (3/7/0) | 23 (8/15/0) |
| *Lobella lucifera* **sp. nov.** | 5 | 7 | 0 | 19 (8/9/2) | 18 (8/9/1) | 19 (8/9/2) | 22 (9/9/4) |

## Discussion

The present study described two new bioluminescent microarthropod species and discovered bioluminescence in two previously described species from the tribe Lobellini. This is the first description of bioluminescence in a new Collembola species. The phenomenon of light emission from Collembola has been documented since 1851, but reports to date involved either unidentified or already known species (Allman 1851; Dubois 1894; Molisch 1904; Barber 1913; Heidt 1936; Sano *et al.* 2019; Ohira *et al.* 2023). It has been speculated that the bioluminescence observed in some cases may have originated from opportunistic microbial infections or microorganisms in the digestive tract (Handschin 1926; but see Stammer 1935; Heidt 1936). In contrast, all species examined exhibited

flickering light emission (*C. elegans*, *C. laterisensillata*, *C. leodeus* **sp. nov.** and *L. lucifera* **sp. nov.** in this study; *L. sauteri* in Ohira *et al.* 2023). Given that microorganisms are generally known to emit light steadily or with gradual variations (Nealson & Hastings 1979; Oliveira *et al.* 2015), the flickering pattern and stimulus-responsive luminescence observed in this study are unlikely to be of microbial origin. This suggests that the light is produced intrinsically by the Collembola. Observations of light emission in laboratory-reared populations of *Lobella* (*L. lucifera* **sp. nov.** and *L. sauteri* in this study) also support the hypothesis that the springtails themselves are the source of the light.

This is the first study to identify bioluminescence in the genus *Crossodonthina*. This discovery highlights a common feature among bioluminescent species within the tribe Lobellini: the presence of additional sensory chaetae on the lateral tubercles of the fourth abdominal segment. In *Lobella*, previous studies showed that bioluminescent species possess additional sensory chaetae (Ohira *et al.* 2023) and the present study adds another luminous species with the same characteristic. Furthermore, in *Crossodonthina*, while a congeneric species lacking these additional sensory chaetae did not emit light in a previous study (Ohira *et al.* 2023), all three species possessing these chaetae exhibited bioluminescence in the present study. The possibility that species possessing these additional sensory chaetae may exhibit bioluminescence was suggested previously (Ohira *et al.* 2023), and our study provides further evidence supporting this hypothesis. Whether the bioluminescence of species with these additional sensory chaetae is due to phylogenetic constraints, or ecological commonalities, remains an open question for future research. Species with unverified bioluminescence and possessing the (additional) sensory chaetae on the lateral tubercles of the fourth abdominal segment include members of the genus *Lobella* (*sauteri*-group of Ohira *et al.* 2023), *Crossodonthina* (at least *C. tiantongshana*, *C. choui* and *C. clavata*), *Cassagnaua* (*C. hongkongensis* and *C. formosana* **comb. nov.**) and other genera, such as *Hyperlobella* Cassagnau, 1988, *Paralobella* Cassagnau & Deharveng, 1984 and *Sulobella* Deharveng & Suhardjono, 2000. Investigations of these species will contribute to understanding this phenomenon. It is worth noting, however, that bioluminescent species without the additional sensory chaetae on the lateral tubercles have been documented outside the tribe Lobellini, such as *Vitronura giselae* (Gisin, 1950), *Vitronura kunigamiensis* Tanaka & Hasegawa, 2010 (Ohira *et al.* 2023) and *Neanura muscorum* (Templeton, 1836) (Molisch 1904; Stammer 1935; Heidt 1936).

All species examined were found to emit greenish light. This is consistent with previous studies measuring the bioluminescence spectra of Collembola. The peak wavelengths of the bioluminescence spectra of *L. sauteri* and *Lobella* sp. (at around 520 and 540 nm, respectively, as reported in Ohira *et al.* 2023 and Sano *et al.* 2019) fall within the range of peak wavelengths identified in this study. In *L. lucifera* **sp. nov.** and *L. sauteri*, additional peaks were also observed in the range 600–650 nm (reddish), which may have been attributable to the influence of red pigments present in these species. As living, moving individuals were used in this study, factors such as movement, flickering, body orientation and the presence of pigments or other molecules in the body could have influenced the measurements of light intensity and colour. Although the bioluminescence spectra were not measured, there were early reports of light emitted from *Lipura armata*/*Onychiurus armatus*—currently called *Protaphorura armata* (Tullberg 1869)—described as ‘bluish’ or ‘blue-green’ (Dubois 1886; Heidt 1936). Further studies are required to confirm this phenomenon and provide spectral measurements.

The ecological role of bioluminescence in Collembola remains unclear. Previous studies suggested that it may be involved in courtship behaviour (Sano *et al.* 2019) or as an aposematic signal to predators (Lloyd 1978; Ohira *et al.* 2023).


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