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Designation of a new family group name, Tonzidae fam. nov., for the genus *Tonza* (Lepidoptera, Yponomeutoidea), based on immature stages of *Tonza citrorrhoa*

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Abstract. The systematic position of *Tonza* Walker, 1864 is re-evaluated, based on the characteristics of immature stages and DNA barcodes. Larvae and pupae of *Tonza citrorrhoa* Meyrick, 1905 are described and illustrated for the first time. Larvae of this species form a loose web among the leaves and branches of the host plant, *Putranjiva matsumurae* Koidz. (Putranjivaceae Endl.). The immature stages of *Tonza* exhibit four unique apomorphies including: in the larva, the prolegs on A5 and A6 absent, and the seta L2 on the A1–A8 very small; in the pupa, four minute knobs are positioned in the middle portion on abdominal segments V and VI; while its caudal processes possess a W-shaped spine with numerous minute spines. These characteristics clearly distinguish *Tonza* from other yponomeutoid families and hence, we propose a new family group name, Tonzidae Kobayashi & Sohn fam. nov., for the genus *Tonza*. Existing DNA barcode data suggest a relationship with Glyphipterigidae Stainton, 1854. The family level status of Tonzidae fam. nov. provides a hypothesis that needs to be tested with larger molecular data.

Keywords. Adenosma, Bedelliidae, DNA barcoding, *Putranjiva matsumurae*, leaf webber.

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Introduction

Tonza Walker, 1864 is a small genus of moths from Australia and Asia (Sri Lanka, Taiwan, Japan, and Solomon Is.). This genus was originally assigned to Plutellidae Guenée, 1845 (Walker 1864). Since then, the majority of authors (e.g., Common 1990; Heppner 1992) has followed the original assignment. However, no previous publications provided convincing evidence supporting the plutellid association of *Tonza*.

Recently, Kobayashi *et al.* (2015) recorded *T. citrorrhoa* Meyrick, 1905 from Japan and described the wing venation and genital structures of *Tonza* for the first time. Furthermore, they reevaluated the previously suggested association of *Tonza* with Plutellidae. The diagnostic characters of *Tonza* include: antenna almost the same length as forewing; forewing with only three radial plus radial sector veins; in the male genitalia, both uncal processes and the socii present; in the female genitalia, lamella antevaginalis strongly sclerotized. These morphological features of *Tonza* along with absence of ocelli clearly disputed its plutellid association and seemed to associate *Tonza* with the yponomeutoid family Attevidae Bruand, 1850 (Kobayashi *et al.* 2015). However, a formal family transfer was pending until the immature stages of *Tonza* became known.

In this paper, the immature stages of *Tonza* are described for the first time for *T. citrorrhoa* from Japan with photographs and drawings: the later instar larvae, pupae and life history. We propose a new family group name, Tonzidae Kobayashi & Sohn fam. nov., for the genus *Tonza* and discuss its relationships with other yponomeutoid families, based on larval and pupal morphology.

Material and methods

Larvae were collected from spinnings among the leaves and branches of *Putranjiva matsumurae* Koidz. by the third author (M. Kimura) in April, 2016 on Yonaguni Is., Okinawa Prefecture. Those were taken to the lab and reared in plastic cups (420 ml: 129 mm in top diameter and 60 mm in depth) containing wet cotton on the bottom. The cups were maintained in the laboratory at 20 ± 5ºC and at 13–16L:8–12D photoperiodic conditions. Some samples were preserved in 99% ethanol for DNA sequencing. Emerged adult specimens were preserved in the Osaka Prefecture University (OPU). Some samples of the larvae, the pupae and the adults were dried and sputter-coated with a 60:40 mixture of gold-palladium for scanning electron microscope (SEM). SEM photographs were taken using a Hitachi SU1510 (Hitachi Ltd., Tokyo, Japan) with a lanthanum hexaboride (LaB6) cathode source at an accelerating voltage of 15 kV. For genital dissections, the whole abdomen was removed, macerated for 3–4 min in 10% aqueous KOH, and brushed in 70% ethanol to remove residual scales and soft parts. Genitalia were then stained in acetocarmine for 1–2 h, dehydrated in a series of 70–100% ethanol and mounted in Canada balsam on a glass slide. For the observations of larval structure, the alcohol-fixed larvae were macerated for 5–6 min in 10% aqueous KOH and the right lateral side of the body was opened up, followed by removal of residual inner soft parts in 70% ethanol. The larval surface skin was then stained and mounted using the same methods as the genitalia. Larvae of *Atteva aurea* Fitch, 1856 were collected by the fourth author (JCS) and *Scythropia crataegella* Linnaeus, 1767 was obtained from Dr. Ian Sims (UK). Nomenclature for genitalia follows Sohn & Nishida (2011). Nomenclature for larval characters follows Stehr (1987). Scientific names of plants follow the Plant List (www.theplantlist.org).

Table 1. Sampling information and GenBank accession numbers.

Species name	Family name	Collection country	GenBank accession no. COI	Sequence length (bp)
Tonza citrorrhoa Meyrick, 1905	Tonzidae fam. nov.	Japan	LC310893	686
Ortenches epiphricta Meyrick, 1907	Plutellidae	Australia	HQ922367	658
Plutella xylostella Linnaeus, 1758	Plutellidae	Korea	DQ076411	681
Saridoscelis kodamai Moriuti, 1961	Yponomeutidae	Japan	KF492103	657
Swammerdamia pyrella Villers, 1789	Yponomeutidae	Finland	KT782599	658
Yponomeuta cagnagellus Hubner, 1813	Yponomeutidae	Finland	KT782553	658
Zelleria haimbachi Busck, 1915	Yponomeutidae	Canada	KT148240	658
Ypsolopha parallela Caradja, 1939	Ypsolophidae	Korea	KF523860	658
Glyphipterix equitella Scopoli, 1763	Glyphipterigidae	Denmark	KT782432	658
Orthotelia sparganella Thunberg, 1788	Glyphipterigidae	Norway	KX048240	657
Atteva albiguttata Zeller, 1873	Attevidae	Australia	HQ922342	658
Atteva aurea Fitch, 1856	Attevidae	Canada	GU013569	665
Atteva hysginiella Wallengren, 1861	Attevidae	Ecuador: Galapagos Is.	HM034104	658
Atteva zebra Duckworth, 1967	Attevidae	Costa Rica	GU692470	658
Prays autocasis Meyrick, 1907	Praydidae	Australia	JF840378	658
Prays fraxinella Bjerkander, 1784	Praydidae	Germany	KX044853	658
Prays ruficeps Heinemann, 1854	Praydidae	Germany	KX044999	658
Heliodines tripunctella Walsingham, 1892	Heliodinidae	USA	KF492395	658
Bedellia somulentella Zeller, 1847	Bedelliidae	Canada	KT139550	658
Scythropia crataegella Linnaeus, 1767	Scythroplidae	Germany	KX046825	658
Caloptilia belfrageella Chambers, 1875	Gracillariidae	Canada	KJ165583	658
Phyllocnistis citrella Stainton, 1856	Gracillariidae	USA	KF919121	658
Roeslerstammia erxlebella Fabricius, 1787	Roeslerstammiidae	Italy	JN307285	658

Molecular analysis

The DNA barcode region (658 bp), a part of the mitochondrial cytochrome c oxidase subunit I (COI) gene, was chosen for sequencing. This marker has been popularly used for inferring the relationships among closely related moth species and populations (Brown *et al.* 1994) One emerged adult of *T. citrorrhoa* was preserved in 99% ethanol for DNA sequencing (voucher no. SK-097). Total genomic DNA was extracted from the mid- and hind legs. Polymerase chain reaction (PCR) was carried out to obtain the DNA barcode region, using the primer LCO1490 (fwd) (5'-ggt caa caa atc ata aag ata ttg g-3') and HCO2198 (rev) (5'-taa act tca ggg tga cca aaa aat ca-3') (Folmer *et al.* 1994) in a thermal cycler C1000 (Bio-Rad, Hercules City, CA, USA) under the following conditions: initial 120 s denaturation at 94°C, and 39 alternating cycles of 15 s at 94°C for denaturation, 30 s at 52°C for annealing, and 60 s at 72°C for extension. PCR products were purified, after that they were sequenced using an automated DNA sequencer (ABI Prism 3100; Applied Biosystems, Foster City, CA, USA). The sequences were aligned using MEGA6 (Tamura *et al.* 2013) and Geneious v. 10.1.3 (Kearse *et al.* 2012). The aligned data were analyzed using RAxML installed in the CIPRES portal (https://www.phylo.org/). The outgroup sequences were obtained from GenBank (https://www.ncbi.nlm.nih.gov/genbank/) and accession numbers are shown in Table 1. A new sequence is deposited in DNA Data Bank of Japan (DDBJ) (accession no. LC310893).

Abbreviations

NHMUK = Natural History Museum, Department of Zoology (Formerly the British Museum [Natural History] or BMNH), London, United Kingdom.
USNM = National Museum of Natural History, Smithsonian Institution, Washington DC, USA.

Results

Class Hexapoda Blainville, 1816
Order Lepidoptera Linnaeus, 1758
Superfamily Yponomeutoidea Stephens, 1829

Family **Tonzidae** Kobayashi & Sohn fam. nov.
urn:lsid:zoobank.org:act:3E5EB9E2-2A60-4D77-94C5-6F02A7A92F44
Figs 1–13

Type genus

Tonza Walker, 1864.

Diagnosis

Adult. Maxillary palpi three-segmented; ocelli and chaetosema absent (Fig. 8C–D); antennae slightly longer than or same length as forewing (Fig. 1); forewings with slightly protruding apex and tornus; forewing termen oblique or concave; only two radial sector veins present, RS1 on apex and RS2 on termen (Kobayashi *et al.* 2015; Fig. 1F); in the male genitalia (Kobayashi *et al.* 2015; Fig. 2A–D), uncus small with a pair of long processes; socii with long terminal setae; valva elongate with several small spines and plate arising from middle to base of valva; in the female genitalia (Kobayashi *et al.* 2015; Fig. 2E), lamella antevaginalis sclerotized, covering sternite VIII; antrum slender; inception of ductus seminalis at the middle of corpus bursae (after Kobayashi *et al.* 2015).

Mature larva (based on *T. citrorrhoa*). Seta L2 on A1–A8 very small (Fig. 6C–D); Seta D1 of A9 segment markedly more slender than D2 (Fig. 6E); A3, A4 and A10 with the ventral prolegs absent for A5 and A6 (Fig. 4A, G).

Pupa. Vertex with triangular frontal process (Fig. 10A–D); dorsum of A2–A9 without spines (Fig. 7B–C); four minute knobs postioned in the middle portion on A5 and A6 (Fig. 10C–F); lateral side of abdomen with protuberances at spiracles (Fig. 7B); A10 furcate with Y-shaped caudal processes, slightly

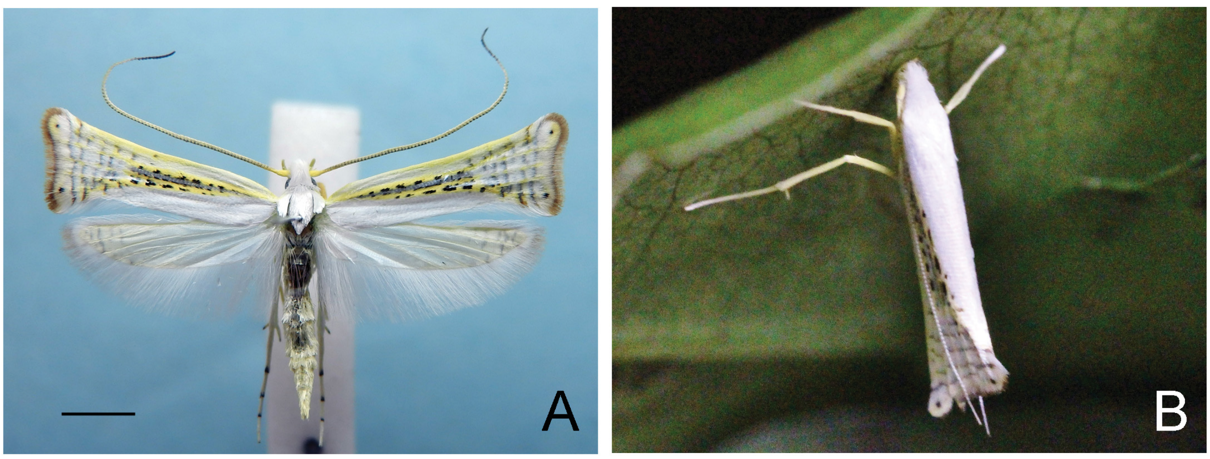

Fig. 1. Female adult of *Tonza citrorrhoa* Meyrick, 1905 (OPU-IN-LE 2018IV0005), host: *Putranjiva matsumurae* Koidz., from Yonaguni Is., Okinawa Pref., Japan. **A**. Adult specimen. **B**. Resting posture of adult, dorso-lateral view. Scale bar: 2 mm.

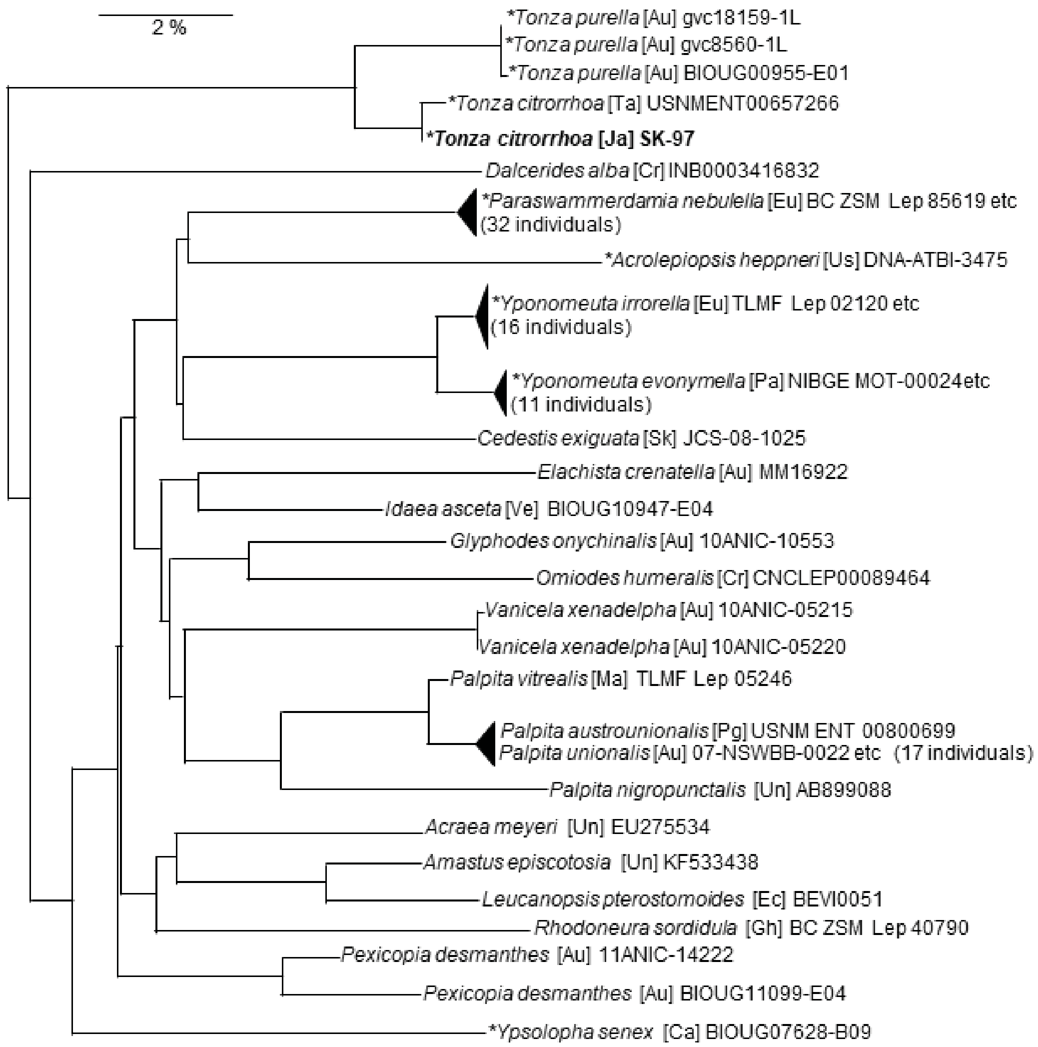

Fig. 2. A tree estimated by neighbor-joining analysis under Kimura's two-parameter distance model using DNA barcode sequence, retrieved from BOLD identification system (IDS). Branch lengths are proportional to distances. Sequence with ID started from "SK-" is obtained from the present study, and the others are from the BOLD database. The letters within square brackets refer to the collection site of specimens as follows: Au = Australia; Ca = Canada; Cr = Costa Rica; Ec = Ecuador; Eu = Europe; Gh = Ghana; Ja = Japan; Ma = Macedonia; Pa = Pakistan; Pg = Papua New Guinea; Sk = South Korea; Ta = Taiwan; Un = Unknown; Us = United States; Ve = Venezuela. Asterisks show the superfamily Yponomeutoidea.

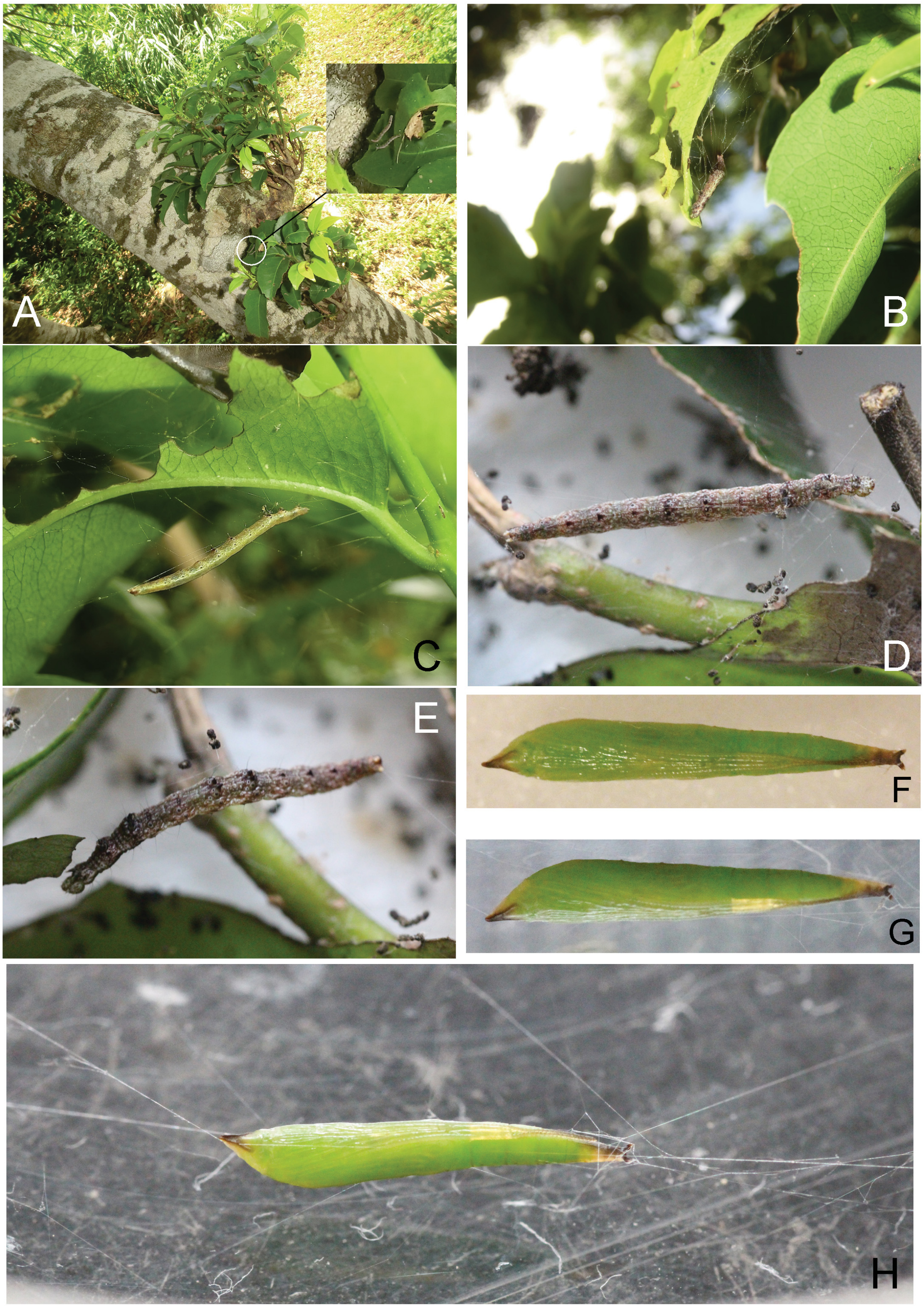

Fig. 3. Larvae and pupae of *Tonza citrorrhoa* Meyrick, 1905 on *Putranjiva matsumurae* Koidz. **A**. Tree of hostplant and larval webs. **B**. Later larva forming web on young leaves. **C**. Later larva, lateral view. **D**. Mature larva, dorsal view. **E**. Same, ventral view. **F**. Pupa, ventral view. **G**. Same, lateral view. **H**. Pupa at the joint of some cross silken threads, lateral view.

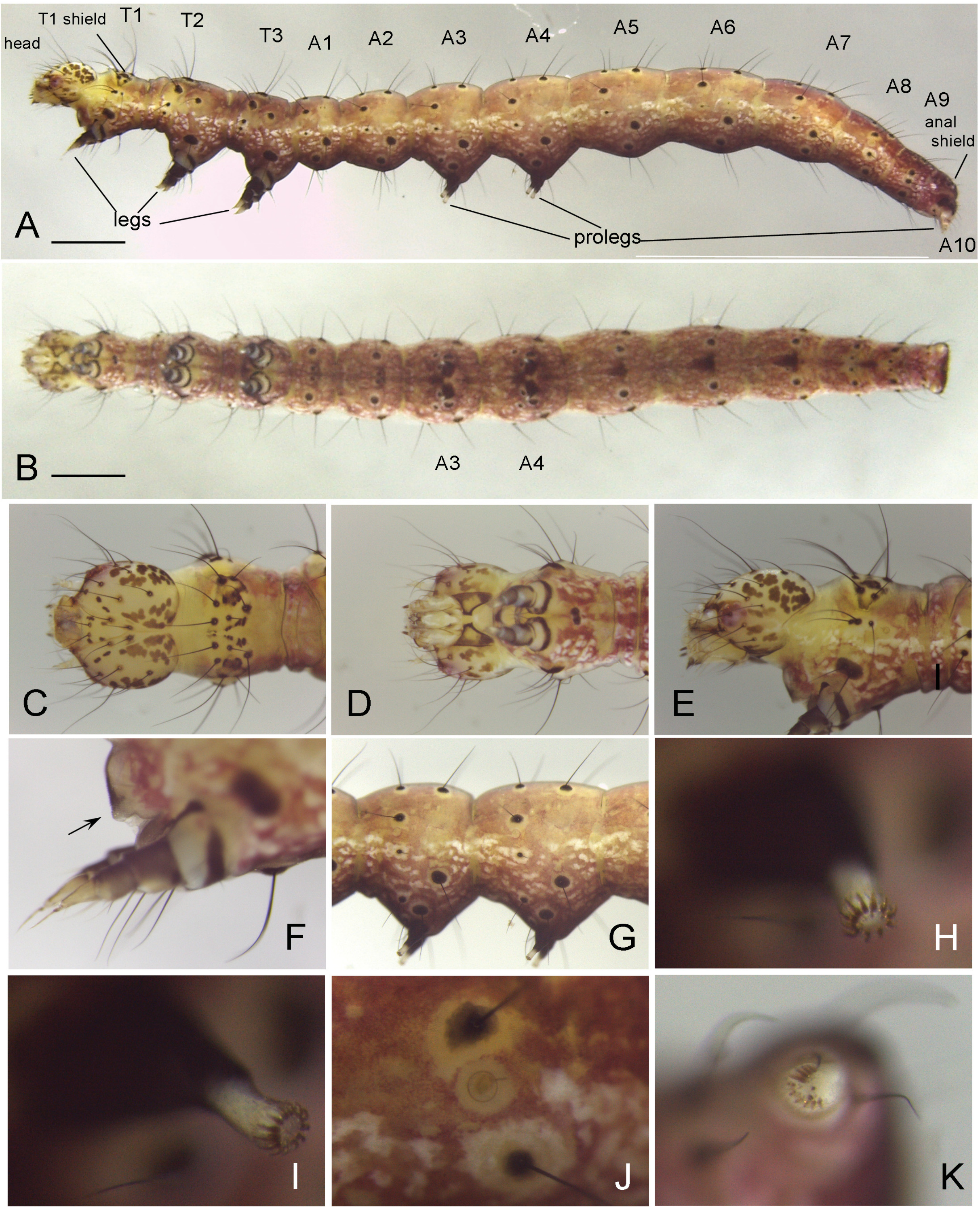

Fig. 4. Mature larva of *Tonza citrorrhoa* Meyrick, 1905 (OPU-IN-LE2018IV0031|SK600). **A**. General, lateral view. **B**. Same, ventral view. **C**. Head and prothorax, dorsal view. **D**. Same, ventral view. **E**. Same, lateral view. **F**. Jugular glands, lateral view. **G**. A3, 4. **H**. Proleg on abdominal segment 3. **I**. Same, on abdominal segment 4. **J**. Spiracle on abdominal segment 8. **K**. Anal proleg, ventral view. Scale bar: 1 mm.

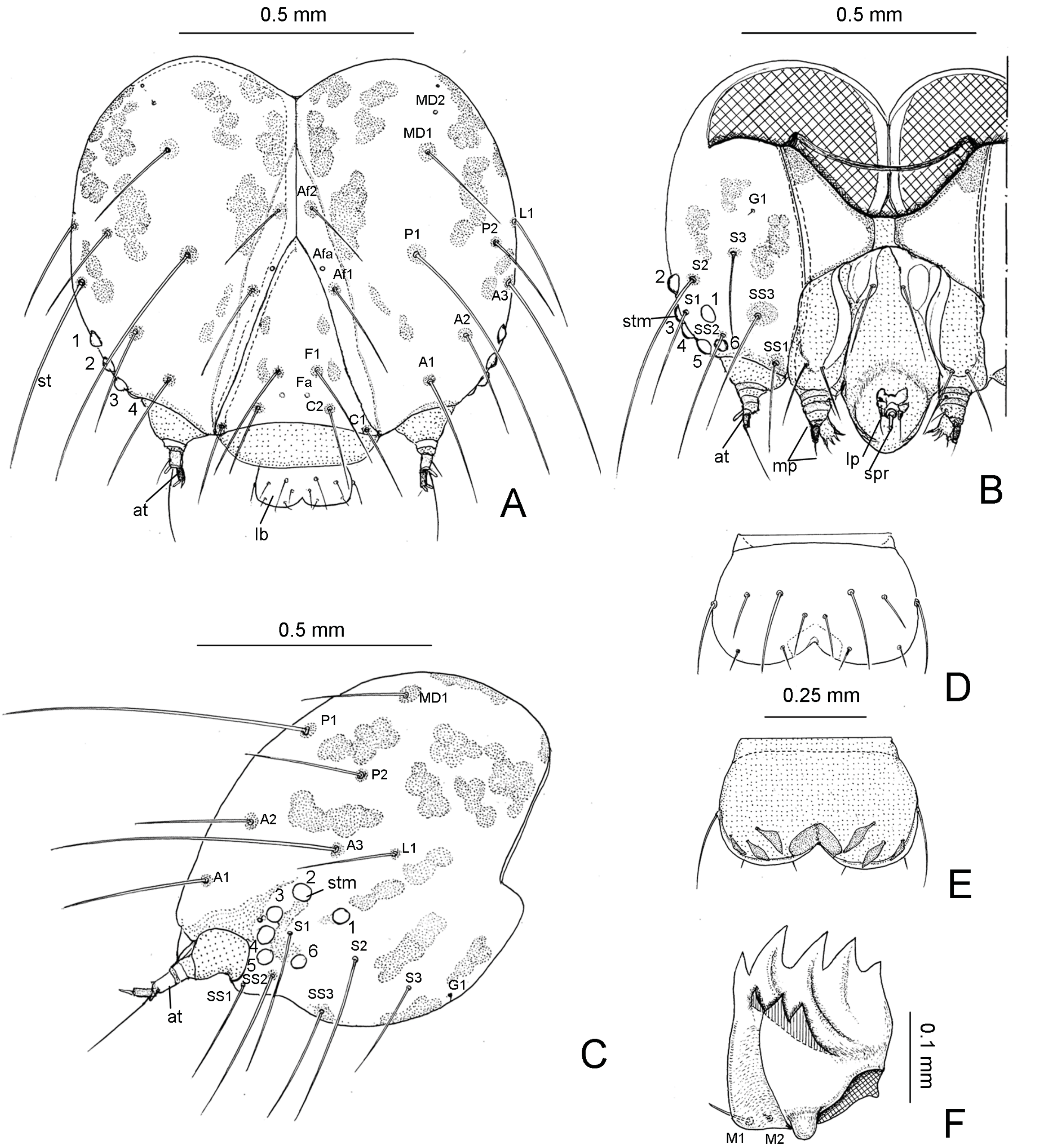

Fig. 5. Mature larval head of *Tonza citrorrhoa* Meyrick, 1905 (OPU-IN-LE2018IV0031|SK600, 0025|SK603, 0026|SK604). **A**. Head capsule, frontal view. **B**. Same, rear view. **C**. Same, lateral view. **D**. Labrum, frontal view. **E**. Same, rear view. **F**. Mandible, inner view. Abbreviations: A1, A2, A3 = anterior setae; Af1, Af2 = adfrontal setae; Afa = pore between setae Af1 and Af2; at = antenna; C1, C2 = clypeal setae; F1 = frontal seta; Fa: pore on the frons; L1 = lateral seta; lb = labium; lp = labial palpus; M1, M2 = mandibular setae; MD1, MD2 = microdorsal setae; MG1 = microgenal seta; mp = maxillary palpus; P1, P2 = posteriodorsal setae; S1, S2, S3 = stemmatal setae; spr = spinneret; SS1, SS2, SS3 = substemmatal setae; stm = stemma.

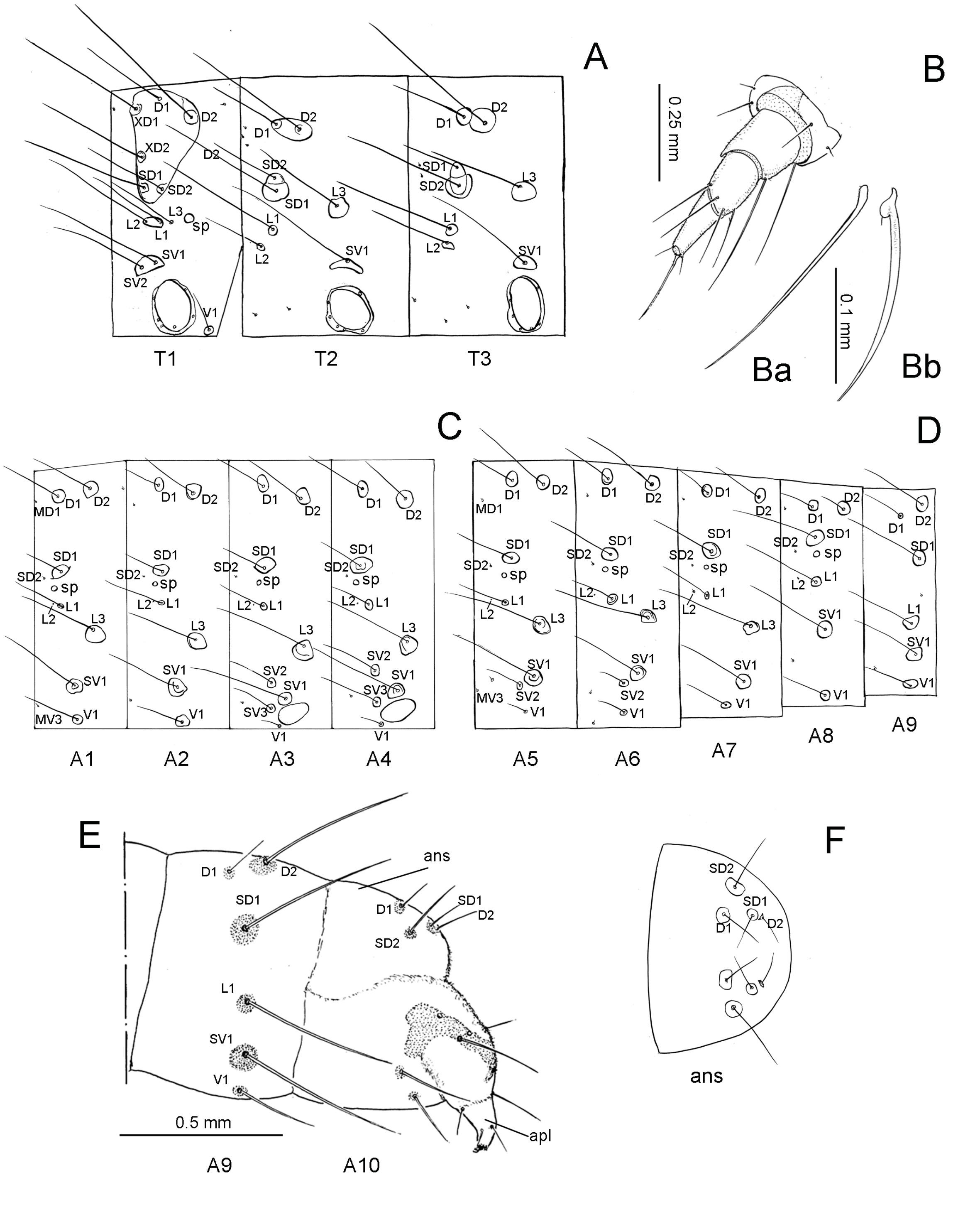

Fig. 6. Mature larval thorax and abdominal segment of *Tonza citrorrhoa* Meyrick, 1905 (OPU-IN-LE2018IV0031|SK600, 0025|SK603, 0026|SK604). **A**. Thorax segment 1–3. **B**. Thoracic leg on thorax segment 1. **C**. A 1–4. D. A5–9. **E**. A9–10. **F**. Anal shield. Abbreviations: ans = anal shield; apl = anal proleg; Ba = claw, lateral view; Bb = same, frontal view; D1, D2 = dorsal setae; L1, L2, L3 = lateral setae; MD1 = microdorsal seta; MV3 = microventral seta; SD1, SD2 = subdorsal setae; sp = spiracle; SV1, SV2, SV3 = subventral setae; V1 = ventral seta; XD1, XD2 = XD group, dorsal setae on the anterior margin of the T1.

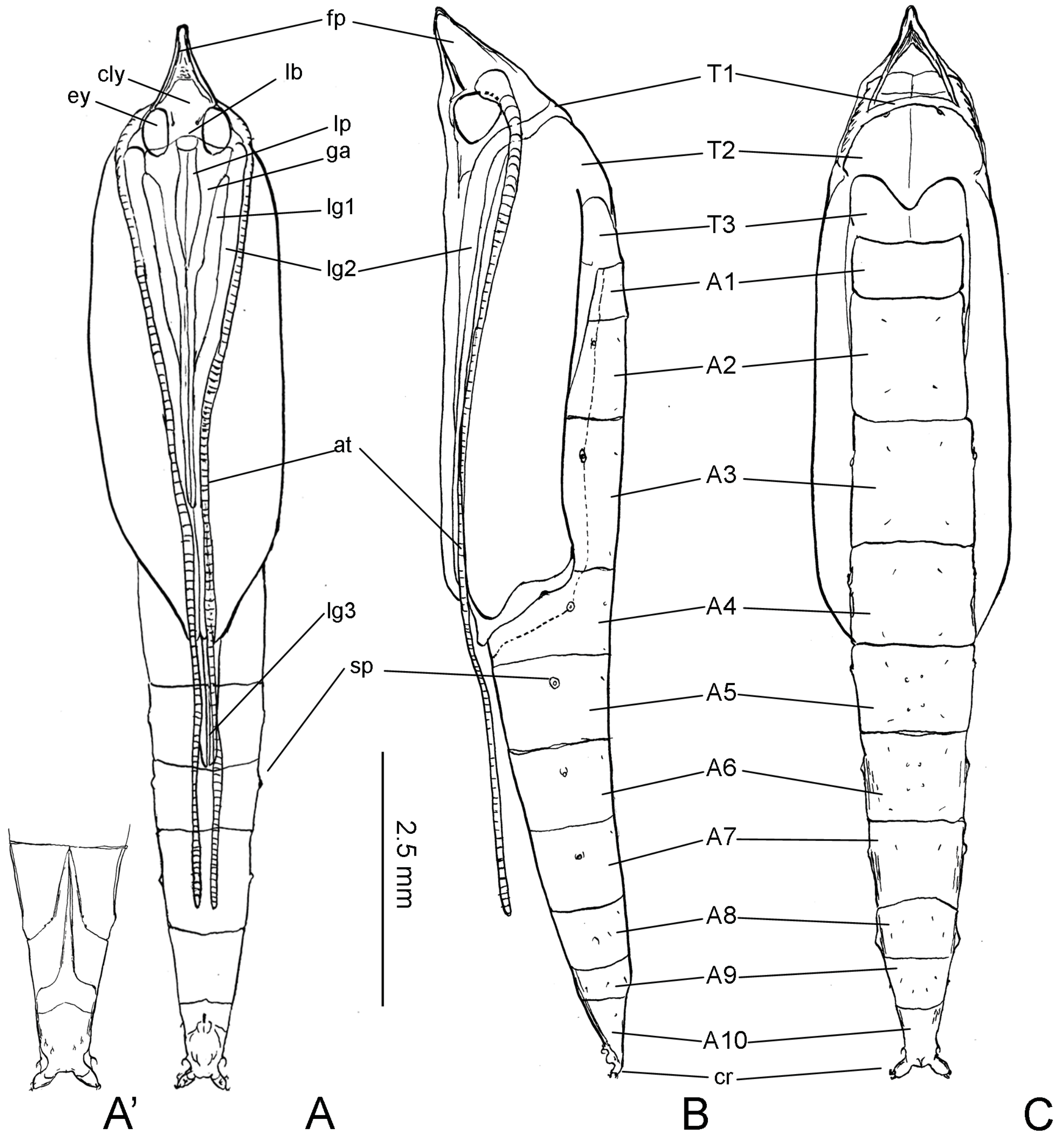

Fig. 7. Pupa of *Tonza citrorrhoa* Meyrick, 1905 (OPU-IN-LE2018IV0018–0024). **A**. Male, ventral view. **A'**. A7–10 of female. **B**. Lateral view. **C**. Dorsal view. Abbreviations: at = antenna; cly = clypeus; cr = cremaster; ey = eye; fp = frontal process; lb = labrum, labial palpus; lg 1 = foreleg; lg 2 = midleg; lg 3 = hindleg; pr = proboscis.

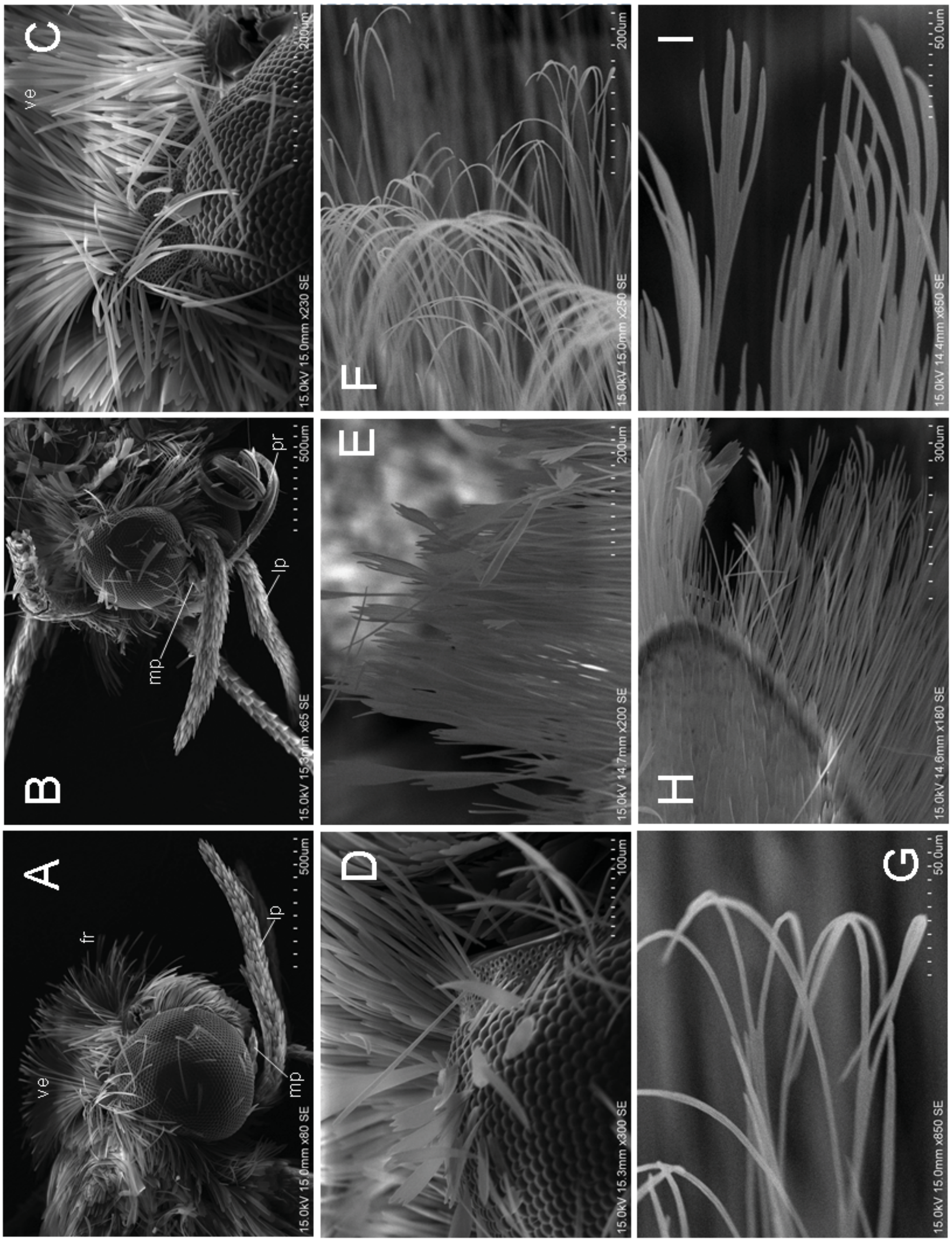

Fig. 8. Scanning electron micrographs (SEMs) of the adult of *Tonza citrorrhoa* Meyrick, 1905 (A, C = OPU-IN-LE2018IV0033, unsexed; B, E–I = 0034, male). A–D. Head. E–I. Cilia. **A**. Right side, lateral view. **B**. Left side, lateral view. **C–D**. Vertex and eye. **E**. Apical cilia on forewing. **F–G**. Cilia of dorsum on hindwing. **H–I**. Apical cilia on hindwing.

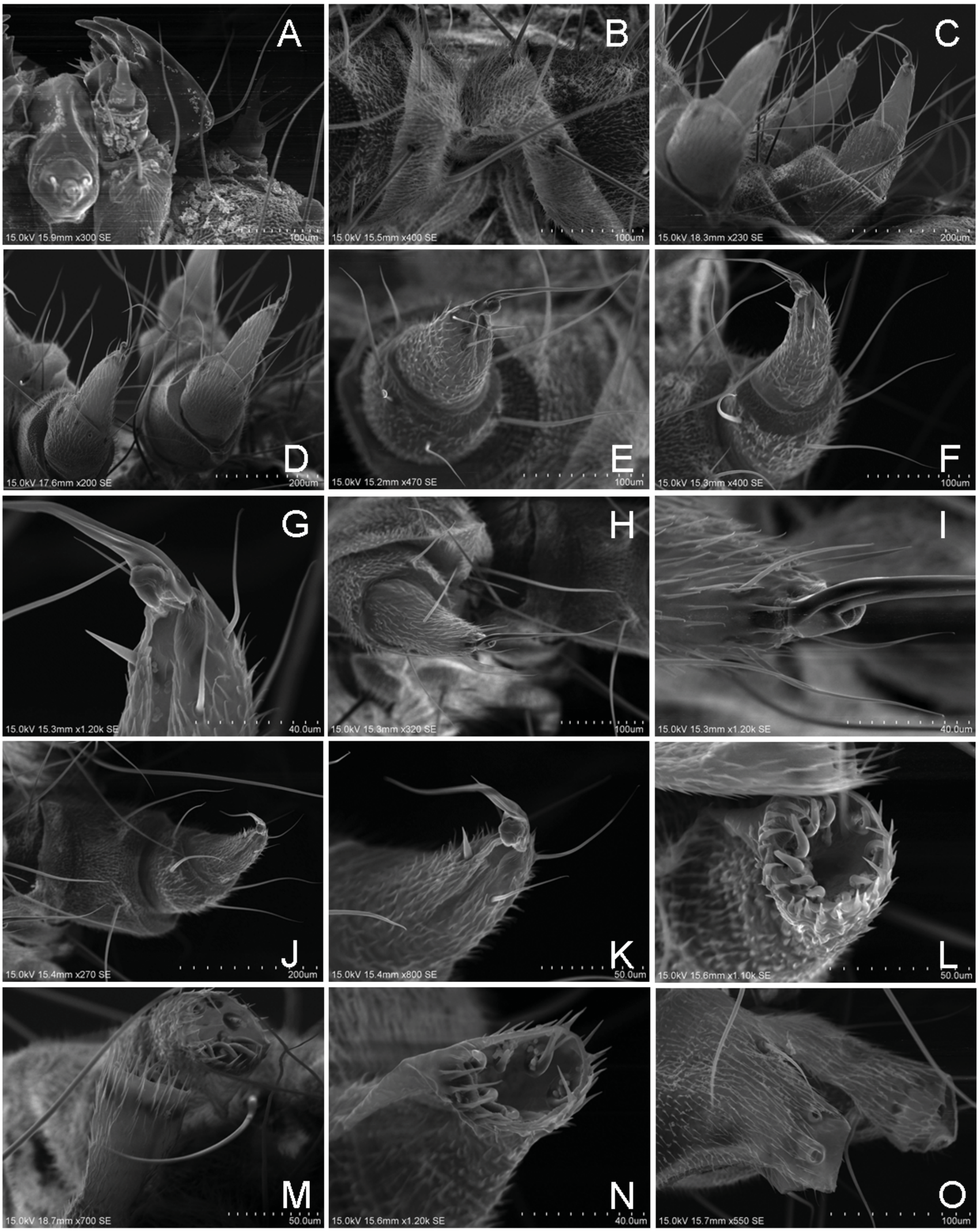

Fig. 9. SEMs of the mature larval structure of *Tonza citrorrhoa* Meyrick, 1905 (OPU-IN-LE2018IV0035|SK543). **A**. Mandible and maxillary palpus. **B**. Jugular gland-like structure. **C**. Prothoracic legs. **D**. Meso- and metathoracic legs. **E**. Right mesothoracic leg. **F**. Left mesothoracic leg. **G**. Same, base of claw. **H**. Right metathoracic leg. **I**. Same, base of claw. **J**. Left metathoracic leg. **K**. Same, claw and tarsus. **L–M**. Crochets of proleg on A3. **N**. Same on A4. **O**. Crochets of anal prolegs.

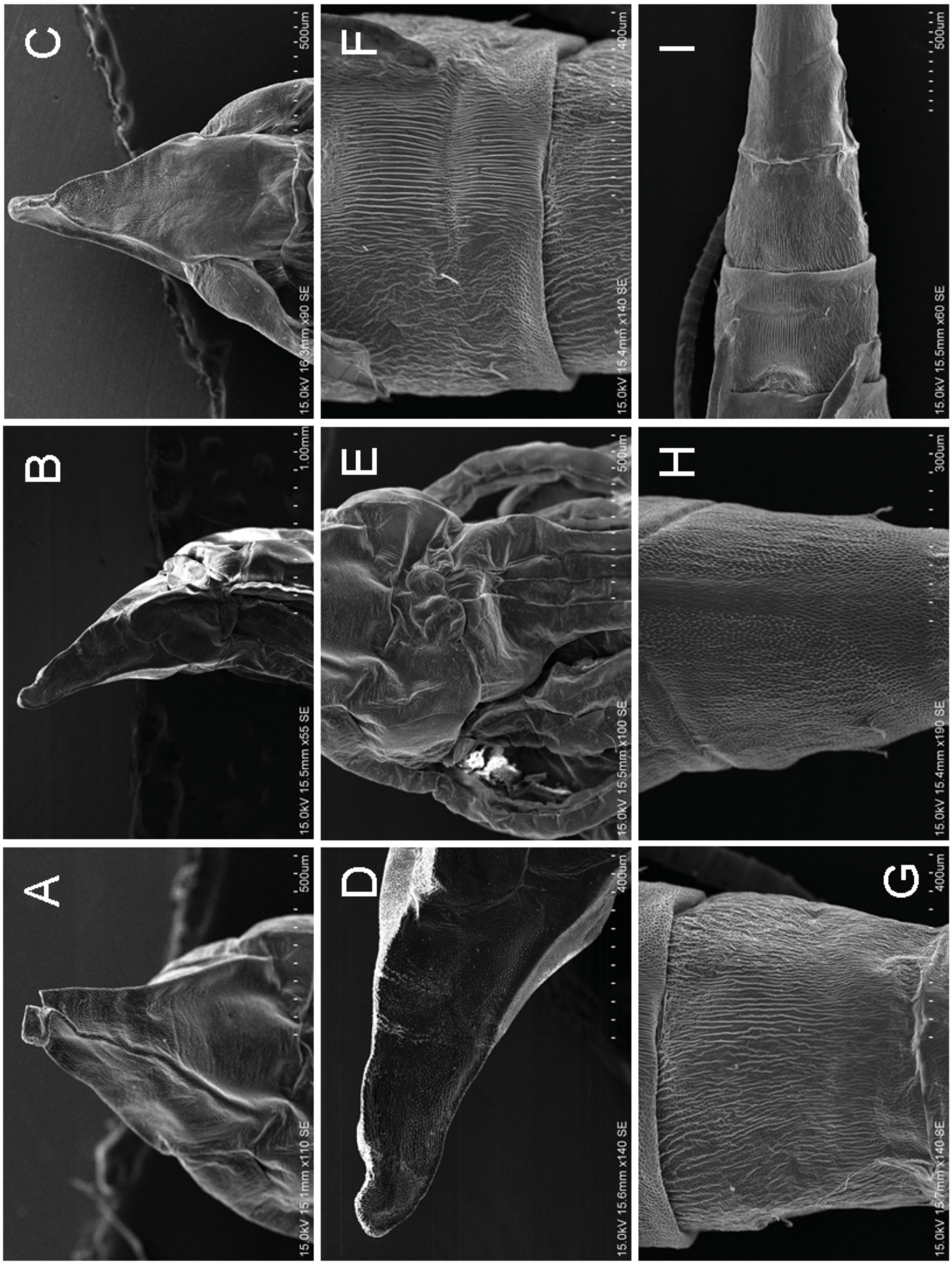

Fig. 10. SEMs of the pupal head and abdomen of *Tonza citrorrhoa* Meyrick, 1905 (OPU-IN-LE2018IV0018–0020). **A**. Frontal process, ventral view. **B**. Head, lateral view. **C**. Frontal process, dorsal view. **D**. Same, lateral view. **E**. Face, ventral view. **F**. A5, ventral view. **G**. Setae of abdominal tergum 6. **H**. Same, A7. **I**. A5–A7, dorsal view.

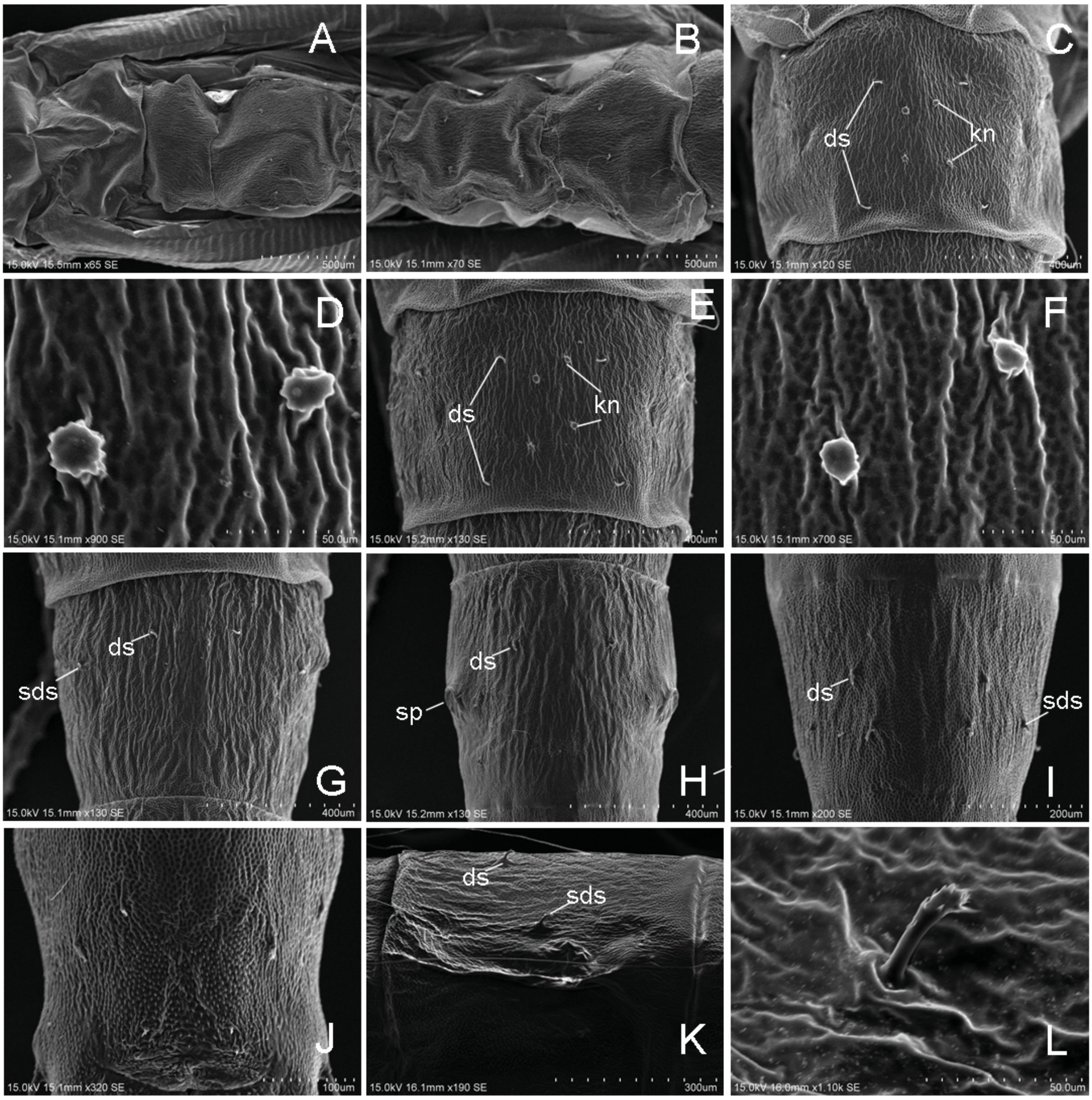

Fig. 11. SEMs of pupal abdomen of *Tonza citrorrhoa* Meyrick, 1905 (OPU-IN-LE2018IV0018 -0020). A–J. Dorsal view. K–L. Lateral view. **A**. A1–A2. **B**. A3–A4. **C**. A5. **D**. Anterior two minute knobs on A5. **E**. A6. **F**. Anterior two minute knobs on A6. **G**. A7. **H**. A8. **I**. A9. **J**. A10. **K**. A10. **L**. Subdorsal seta of A10. Abbreviations: ds = dorsal seta; kn = knob; sds = subdorsal seta; sp = spiracle.

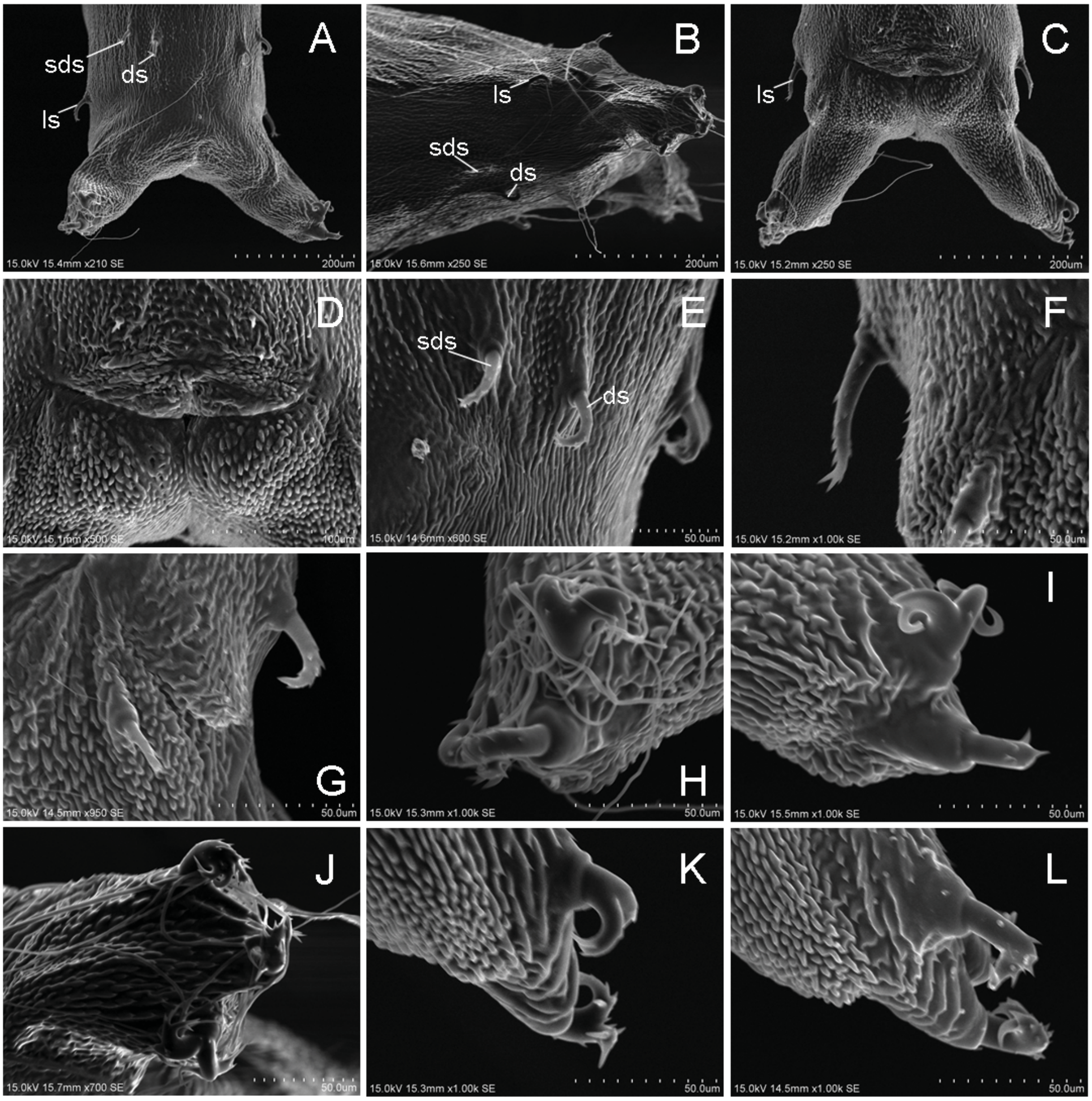

Fig. 12. SEMs of pupal abdominal segments A9–A10 of *Tonza citrorrhoa* Meyrick, 1905 (OPU-IN-LE2018IV0018 -0020). **A**. Ventral view. **B**. Lateral view. **C**. Dorsal view. **D**. Middle portion of A10. **E**. Ventral setae of A9. **F**. Lateral seta of A10. **G**. Dorsal setae of A10. **H**. Apical setae of right process of cremaster, ventral view. **I**. Same, left process. **J**. Left process of cremaster, lateral view. **K**–**L**. Apical setae of right process of cremaster, dorsal view. Abbreviations: ds = dorsal seta; ls = lateral seta; sds = subdorsal seta; svs = subventral seta; vs = ventral seta.

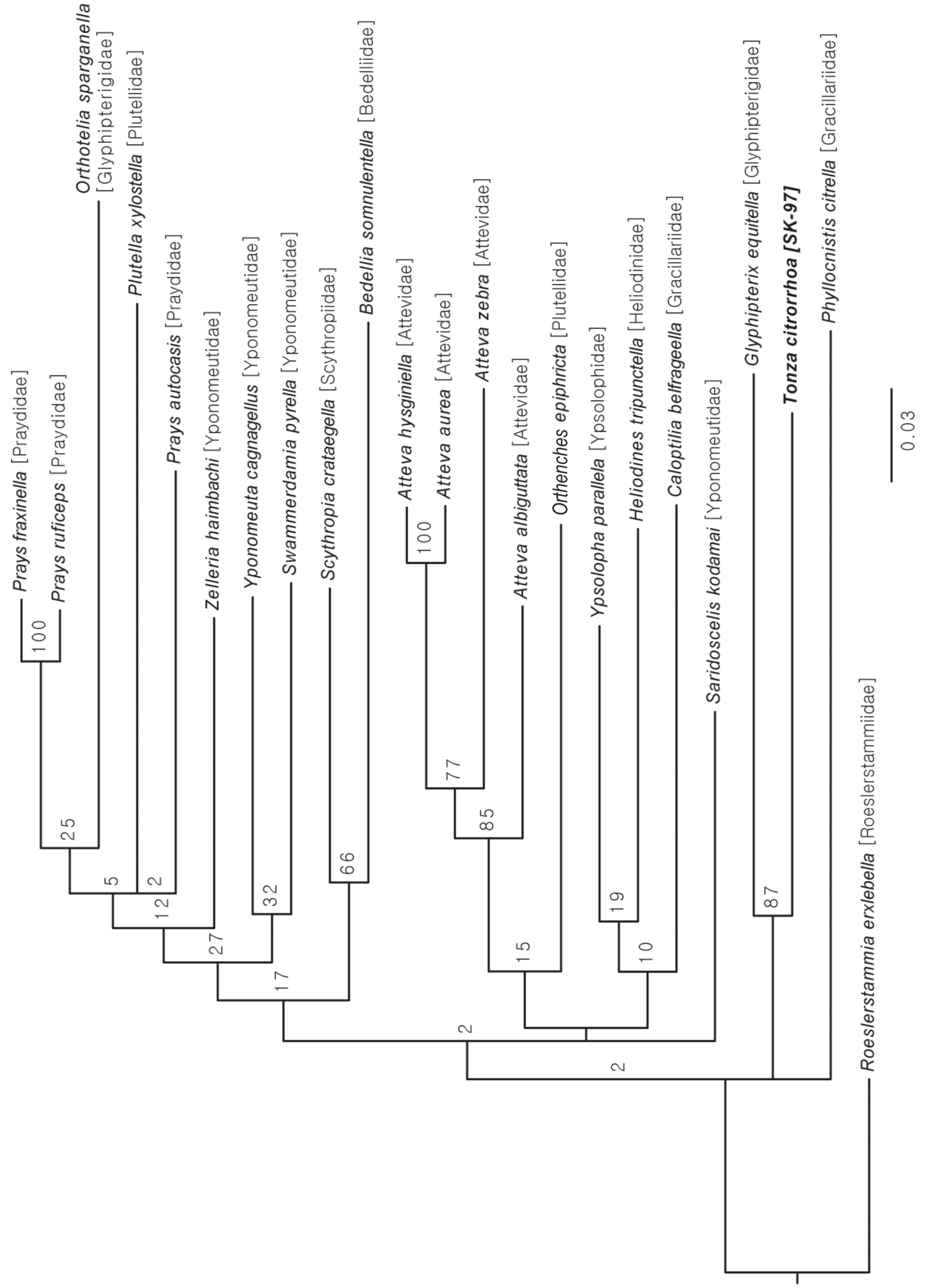

Fig. 13. Maximum Likelihood tree of 23 yponomeutoid/gracillarioid species based on the DNA barcoding region. Numbers on nodes indicate bootstrap support values. *Tonza citrorrhoa* Meyrick, 1905 is indicated in bold.

rolled on ventral side; three pairs of spiny hooked setae from apex of caudal processes (Fig. 12), the hook furcate as a pair of W-shaped spines with numerous minute spines (Fig. 12G–L).

Genus ***Tonza*** Walker, 1864

Tonza Walker, 1864: 1011 – Kobayashi *et al.* (2015: 68–69) (redescription). Type species: *T. purella* Walker, 1864.

Diagnosis

For the adult: see description for the family and see Kobayashi *et al.* (2015).

A checklist and distribution of the species of the genus *Tonza*

1. ***Tonza purella*** Walker, 1864

Distribution

Australia (Queensland; Moreton Bay, type locality; specimens including types in NHMUK and data on BOLD; Bold Index Number (BIN), BOLD:AAY2226).

Hostplants

Unknown.

2. ***Tonza citrorrhoa*** Meyrick, 1905

Distribution

India; Sri Lanka; China (Taiwan); Japan (Kagoshima, Okinawa); Indonesia, identity not certain; Philippines, identity not certain (Specimens in NHMUK, but not including the two syntypes, whereabouts unknown; USNM and data on BOLD).

Hostplants

Putranjiva matsumurae, Putranjivaceae Endl. (present study).

3. ***Tonza callicitra*** Meyrick, 1913

Distribution

Solomon Islands (Bougainville; type locality, types in NHMUK), New Guinea, New Ireland, New Britain, E. Sula: Mangole, Salomo Archipelago (Shortland I.).

Hostplants

Unknown.

Note

The genus is also found fairly widely in the palaeotropics, as well as in Indo-Australasia, in Africa, Madagascar (material in NHMUK and data on BOLD; BOLD:ACU1104) and on Réunion (J. Rochat & M. Bippus, pers. comm.).

Tonza citrorrhoa Meyrick, 1905
Figs 1–13

Tonza citrorrhoa Meyrick, 1905: 614 – Heppner (1992: 74) (species list) – Kobayashi *et al.* (2015: 69–72, figs 1–2).

Diagnosis

See Kobayashi *et al.* (2015: 69) and diagnosis of the family.

Material examined (4 ♂♂, 7 ♀♀, 10 unsexed)

JAPAN: 2 ♂♂, 5 ♀♀ adults, Ryukyus, Okinawa Prefecture, Mt. Kubura-dake, Yonaguni Is., 3–6 May 2016, M. Kimura leg. (host: *Putranjiva matsumurae*), 22 Apr. 2016 (larva) (OPU-IN-LE2018IV0003–0009); material in NHMUK, see above, has not been critically re-examined; 2 ♂♂, 2 ♀♀, 3 unsexed, pupae, same data as for preceding, but May 2016 (OPU-IN-LE2018IV0018–0022); 7 unsexed larvae, same data as for preceding, but May 2016 (OPU-IN-LE2018IV0026–0028|SK600, 0025|SK603, 0026|SK604, 0035|SK543(exuvia)).

Type locality

SRI LANKA: Hantane.

DNA barcodes

GenBank accession no. LC310893, voucher no. SK-097. BIN: BOLD:ACX8102, voucher no. USNMENT00657266.

Additional description

ADULT. Wingspan range 11.0–14.4 mm (mean 13.7 mm, n = 9): forewing length range 5.2–7.1 mm (mean 6.6 mm, n = 9).

MALE GENITALIA AND FEMALE GENITALIA. See Kobayashi *et al.* (2015: fig. 2).

MATURE LARVA (FIGS 4–6, 9). Range: 11.5–12.5 mm in length (mean 12.0 mm, n = 4). Integument varying from yellowish green to yellow in colouration, full mature larva yellow in colouration, marked with numerous purple blotches and white dots (Fig. 4). Pinacula conspicuous, dark brown in colouration (Fig. 4A, J). Primary setae long and secondary setae absent (Fig. 4A–E).

HEAD (FIG. 5). Hypognathous. Head capsule marked with numerous ochreous spots (Fig. 5A, C), 0.90–1.00 mm in width (mean 0.94 mm, n = 5). Frontclypeus wide, extending a half to epicranial notch. Mandible about 0.15 mm in length, with three large teeth, two smaller teeth, and three small teeth at inner portion, with M1 and M2 setae much shorter (Fig. 5F). Six stemmata arranged in an arc except for S1 and S6; S1 more posterior and S6 ventrad (Fig. 5A–C).

CRANIAL SETAE (FIG. 5A–C). MD1 very long; A1, A2 and A3 as obtuse triangle with A2 most distant from stemmata; P1 below Af2–P2 line; pore not found.

THORAX (FIG. 6A–B). T1 shield indistinct, yellow in colouration, marked with dark brown patches. Jugular gland (adenosma) absent, but like structure present ventrally on T1 (Fig. 4F), anterior to the legs and antero-medial to the long setae SV1 and SV2; the structure not eversible and a tubular or sacciform gland at inner side of body not found. D1 and D2 approximated on T2 and T3; SD1 and SD2 approximated on T2 and T3; L-group trisetose, L1 and L2 on the same pinacula on T1 and separated on T2 and T3; SV1 and SV2 on the same pinacula on T1 and on separate pinacula on T2 and T3; Seta V1 present on T1, absent T2 and T3. Thoracic legs pale ochreous to brown in colouration; pale brown claws elongate, slightly curved to inner side (Figs 4F, 6B).

Abdomen (Fig. 6C–F). D1 above level of D2 except for A9; SD2 very small, separated from pinaculum of SD1; L-group trisetose on A1–7, bisetose on A8 and unisetose on A9; L2 minute; SV-group trisetose on A3 and A4, bisetose on A5 and A6, unisetose on A1, A2, and A7–A9; Seta D1 of A9 segment markedly more slender than D2. Anal shield indistinct as in figure 6F. Prolegs present on A3, A4, and A10 (Fig. 4A, G). Ventral prolegs elongate, about 2× length of width of proleg base; crochets uniordinal, arranged in a circle, being usually 12 in number (Figs 4H–I, 9L–N). Crochets of the anal prolegs arranged in a semicircle (Fig. 4K).

Pupa (Figs 7, 10–12). General: long and slender, yellowish green in colouration, 10–11 mm in length, 1.0–2.0 mm in diameter. Maxillary palpi concealed (Fig. 10E). Dorsum of A2–A9 with two pairs of minute spiny setae from dorsal side (Figs 7B, C, 11). Other characters as for family diagnosis.

Distribution

INDIA: Khasia/Khasi Hills; Darmsala, Punjab; Coimbatore (NHMUK): new record. SRI LANKA: Colombo, Kandy, Bogawantalawa, Puttalam, Maskeliya, Bentota, Gulla, Dondanduwa, Hikkaduwa, Nawalatipiya (NHMUK): new record, Hantane [Hanthana] (Meyrick 1905). CHINA: Taiwan (Heppner 1992; USNM, on BOLD). JAPAN: Kagoshima Prefecture: Amai-Ohshima Is. (Seino 2016), Okinawa Pref.: Okinawa Is. (Kobayashi *et al.* 2015), Iriomote Is. (Umetsu 2016), Yonaguni Is.: [new record]. INDONESIA: Telawa, Java (NHMUK; abdomen missing, identity not certain but included among 13 identified specimens constituting Meyrick's collection); Sulawesi (NHMUK), identity not certain. PHILIPPINES (NHMUK): identity not certain.

Hostplants

Putranjivaceae: *Putranjiva matsumurae*: new larval hostplant record. The adult has been recorded feeding on 'Marygold flowers' [sic; *Tagetes* L., Asteraceae Bercht. & J. Presl] at Coimbatore, S. India (NHMUK).

Life history

The detailed biology of this species is unknown. The third author (Kimura) observed a number of late instar larvae on the young leaves of *Putranjiva matsumurae*. The larva is a leaf webber tying together several leaves loosely with silk threads (Fig. 3A–C). The full grown larva is suspended from the tree by a silk lifeline spun out from the head spinnerets. Pupation takes place at the intersection of some cross silken threads (Fig. 3H). A number of the mature larvae occurred on tall trees of the hostplant in Yonaguni Is., Okinawa Pref. (Fig. 3A). Young larvae were not found in our study. Given that no larval mine was observed, the young larvae are probably external feeders like the later instars.

Remarks

The resting posture of the adult moth with head end lowered and abdomen lifted is similar to certain Argyresthiidae, Ypsolophidae and several genera in Yponomeutidae (Fig. 1B). However, when at repose in nature the suspension may be different and rather unusual involving only the prothoracic and mesothoracic legs in contact with the lower surface of a leaf with the wing and body tending to hang vertically below a leaf. In this position, the antennae relatively long with respect to wing length may accentuate a potential false head-like appearance.

Leaf webbing larvae occur in several yponomeutoid families, Yponomeutidae, Scythropiidae, Plutellidae, Ypsolophidae (Ypsolophinae) and Attevidae (Sohn *et al.* 2013). However, larvae of *Tonza* form rather

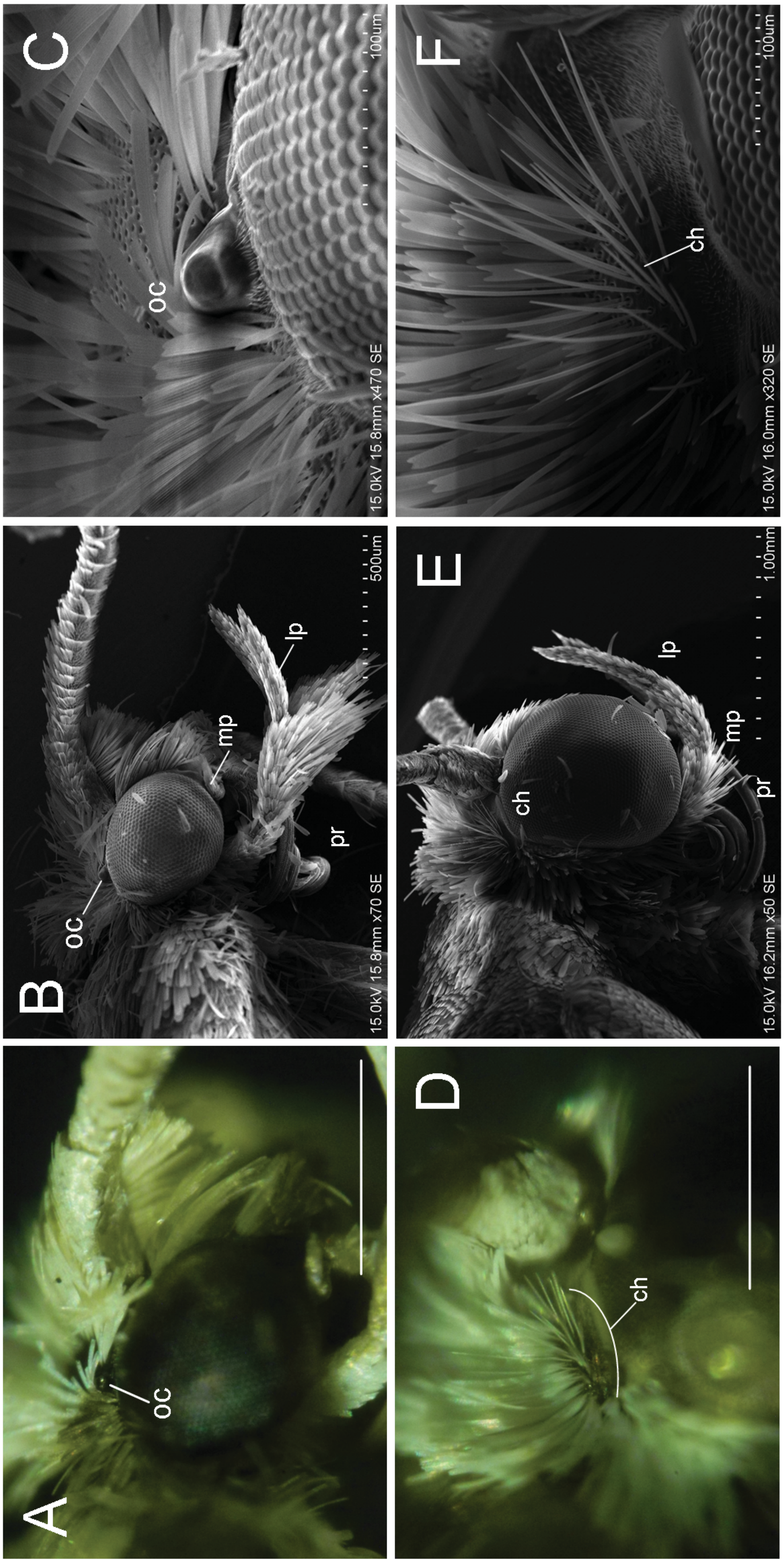

Fig. 14. Adult head of Yponomeutoidea moths. A–C. *Plutella xylostella* Linnaeus, 1758 (OPU-IN-LE2018IV0037), Plutellidae, from Japan. D–F. *Atteva* sp. [OPU-IN-LE2018IV0036], Attevidae, from Thailand. **A–B**, **E**. Head, lateral view. **C**. Ocellus. **D**, **F**. Chaetosema. Abbreviations: ch = chaetosema; lp = labial palpus; mp = maxillary palpus; oc = ocellus; pr = proboscis. Scale bar: 0.5 mm.

Table 2. Comparison of character states of larva, pupa and adult among new family Tonzidae fam. nov., and yponomeutid families. Reference: Kyrki (1984, 1990), Dugdale *et al.* (1998), Nasu *et al.* (2011), Sohn & Wu (2013). Larva: the present study; adult: after Kobayashi *et al.* (2015).

	LARVA								
	MD1 on head	P1 on head below Af2–P2 line	Cervical gland (adenosma)	D1 and D2 on T2–3	L-group on T1	L2 on abdomen	D1on A9 below D2	Prolegs	Crochets
Tonzidae fam. nov.	long	Yes	absent	same pinaculum	3	present	yes	A3, 4, 10	uniserial
Plutellidae (*Plutella* group)	short	Yes	absent	same pinaculum	3	present	yes/no	A3–6, 10	uniserial
Yponomeutidae	long	Yes	present	same pinaculum	3	present	yes	A3–6, 10	multiserial
Ypsolophidae	short	Yes	absent	same pinaculum	3	present	no	A3–6, 10	uniserial
Glyphipterigidae	short	Yes	absent	same, pinaculum undeveloped	2	present	no	A3–6, 10	uniserial
Argyresthiidae	short	Yes	absent	separate (pinaculum undeveloped)	3	present	no	A3–6	uniserial
Lyonetiidae	short	P2 absent	absent	separate (pinaculum undeveloped)	2	present	yes	A3–6, 10	uniserial
Attevidae	short	No	absent	same pinaculum	2	absent	yes	A3–6, 10	multiserial
Praydidae	short	No	absent	same pinaculum	3	present	yes	A3–6, 10	multiserial
Heliodinidae	short	Yes	absent	same pinaculum	3	present	yes/no	A3–6, 10	uniserial
Bedelliidae	short	Yes	absent	separate (pinaculum undeveloped)	3	absent (A1–A8)	yes	A3–6, 10	uniserial
Scythropiidae	long	Yes	absent	same pinaculum	3	present	no	A3–6, 10	multiserial

Table 2. (Continuation.)

	PUPA							
	General form	Frontal process	Labial palpus	Maxillary palpus	Thoracic spiracle	Cremaster	Cocoon	Lateral ridges on abdomen
Tonzidae fam. nov.	fusiform	present	present	small	present	present	absent	absent
Plutellidae (*Plutella* group)	fusiform	absent	present	large	present	absent	present	absent
Yponomeutidae	fusiform	absent	present	large	present	absent	present	present
Ypsolophidae	compact	absent	present	large	present	absent	present	absent
Glyphipterigidae	fusiform	present, small	present	large	present	absent	present	present
Argyresthiidae	compact	absent	present	large	absent	absent	present	absent
Lyonetiidae	fusiform (Lyonetiinae) compact (Cemiostominae)	present (Lyonetiinae)/ absent	present	small	absent	present	present	present
Attevidae	fusiform	absent	absent	small	present	present	absent	absent
Praydidae	compact	absent	absnet	small	present	absent	present	absent
Heliodinidae	compact	absent	present	large	present	absent	present	present
Bedelliidae	fusiform	present	absent	small	present	absent	absent	present
Scythropiidae	fusiform	present	present	small	absent	absent	absent	absent

Table 2. (Continuation.)

	ADULT								
	Ocelli	Chaetosema	No. of segments of maxillary palpus	2nd segment of labial palpus	Antenna compared with forewing	Scape of antennae	Pterostigma	No. of R veins on forewing	Transverse costa of A2 on forewing
Tonzidae fam. nov.	absent	absent	3	smooth	long (1.0–1.1 ×)	smooth	absent	3	present
Plutellidae (*Plutella* group)	present	absent	3	scale brush	short	smooth	present	5	present
Yponomeutidae	absent	absent	1–4	smooth	short	with scale flap or pecten	present	5	present
Ypsolophidae	present	absent	4	scale brush	short	with scale flap	present absent	5	absent
Glyphipterigidae	present	absent	4	smooth	short	smooth	present	5	present
Argyresthiidae	absent	absent	1	smooth	short	with pecten	present	5	present
Lyonetiidae	absent	absent	absent	absent	long (0.8–1.5 ×)	with eye-cap	absent	2–4	present/ absent
Attevidae	absent	present	3	smooth	short	smooth	absent	5	present
Praydidae	absent	absent	1	smooth	short	smooth	present	5	present
Heliodinidae	present	absent	2	smooth	short	smooth	absent	4	present
Bedelliidae	absent	absent	1	smooth	long (1.0 ×)	with pecten	absent	4	present
Scythropiidae	absent	absent	4	smooth	short	with pecten	present	5	present

Table 2. (Continuation.)

	ADULT						
					Male genitalia		
	Spiniform setae of tergum A2–A7	Sternite	Pleural lobes	Coremata	Uncus	Socii	Teguminal processes
Tonzidae fam. nov.	absent	normal	present	present	small with a pair of long processes	small with long terminal setae	large, with dense setae
Plutellidae (*Plutella* group)	absent	normal	present	present/ absent	absent	absent	sclerotized setose lobes
Yponomeutidae	present	sclerotized	present	present	semielliptical to oblong	long hairly lobe	absent
Ypsolophidae	absent	normal	present	present, long	small with short setae	oblong, rounded	absent
Glyphipterigidae	absent	forming conical lobe	absent	absent	absent	absent	absent
Argyresthiidae	absent	strongly sclerotized	present	present	oblong	small with special scales at apex	absent
Lyonetiidae	present/absent	forming processes‡	absent	present/ absent	absent	absent	absent
Attevidae	absent	sclerotized	present	present	small with a pair of short processes	slender with special scales	absent
Praydidae	absent	strongly sclerotized	present	present	absent	hairly process	absent
Heliodinidae	absent	normal	present	absent	absent	absent	absent
Bedelliidae	absent	normal	absent	absent	absent	absent	absent
Scythropiidae	absent	sclerotized	present	?	oblong	small with unscaled	absent

Table 2. (Continuation.)

	ADULT					
	Male genitalia			***Female genitalia***		
	Gnathos	Valva	Scape / cornutii / coecum of Aedeagus	Lamella postvaginalis (hairy humps)	Lamella antevaginalis	Signum
Tonzidae fam. nov.	absent	elongate with several process	absent / absent / absent	1, rounded	present	absent
Plutellidae (*Plutella* group)	narrow band	rounded	absent / present / present	2	absent	absent
Yponomeutidae	band	elongate, rounded	present / absent / present	2	absent	present
Ypsolophidae	long, forming ventral plate	rounded	absent / present / present	2	absent	present
Glyphipterigidae	absent	small, rounded	absent / absent / absent	2	absent	absent
Argyresthiidae	small band	rounded	absent / present / absent	1, rounded	absent	present
Lyonetiidae	A pair of small processes	rounded	absent / present / absent	absent	present	absent
Attevidae	developed with medial plate	elongate	absent / present / absent	1, rounded	absent	present
Praydidae	band	slender with process	absent / present / absent	2	absent	present
Heliodinidae	long, narrow band	elongate	absent / absent / absent	absent	absent	present
Bedelliidae	narrow band	rounded with small spine at apex	absent / absent / absent	absent	absent	present
Scythropiidae	band	rounded lobe	absent / present / absent	absent	present	absent

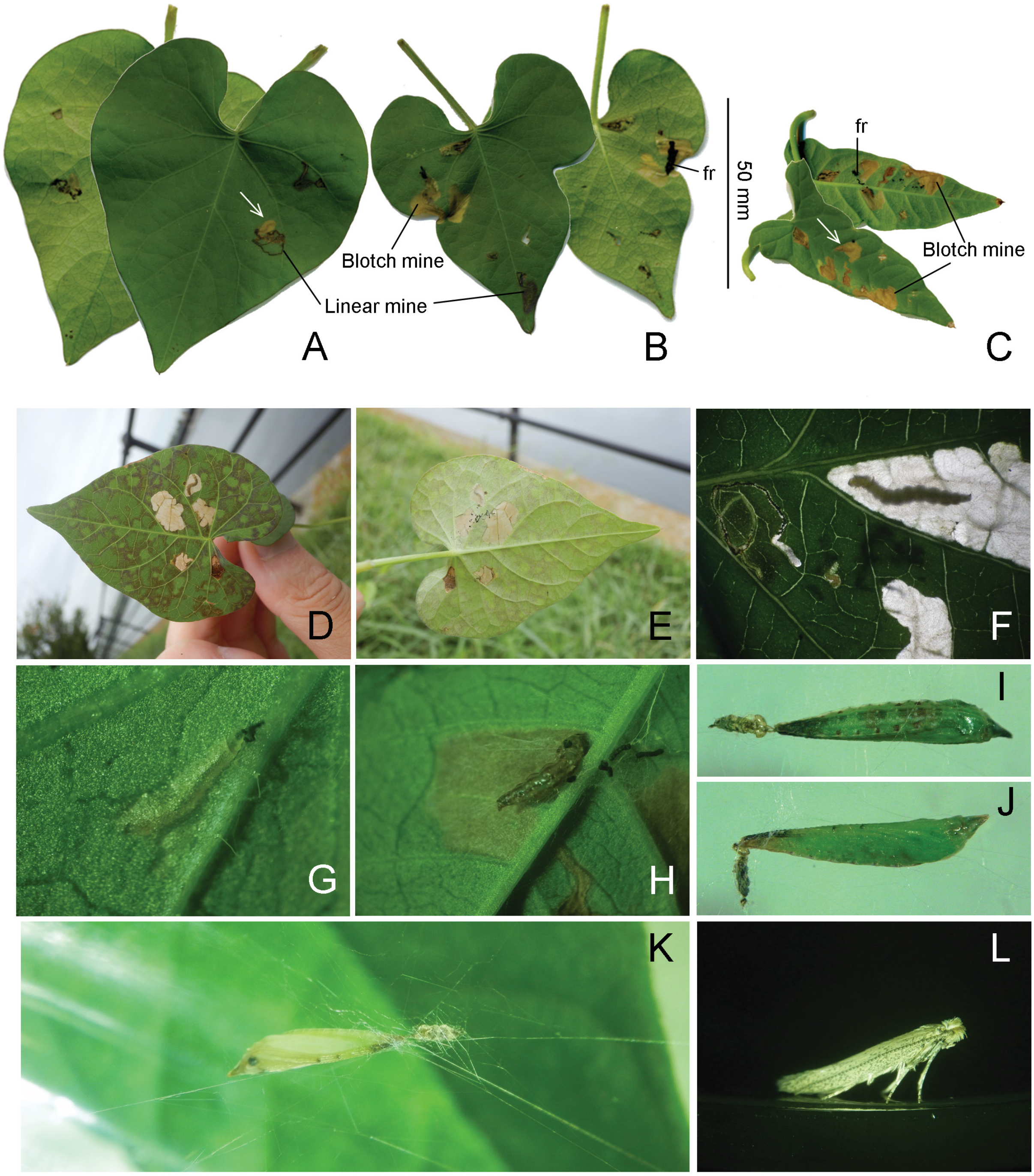

Fig. 15. Biology of *Bedellia somnulentella* Zeller, 1847, Bedelliidae Stainton, 1849, and its hostplants. A–B, D–L. *Ipomoea* sp. C. *Calystegia* sp. **A–C**. Leaves and mines. **D**. Blotch mines by later larva. **E**. Blotch mines and frass on abaxial side of leaf. **F**. Young larva and later larva. **G**. Later larva. **H**. Later larva forming new mine. **I**. Pupa, dorsal view. **J**. Lateral view. **K**. Pupa at the joint of some cross silken threads. Abbreviations: fr = frass.

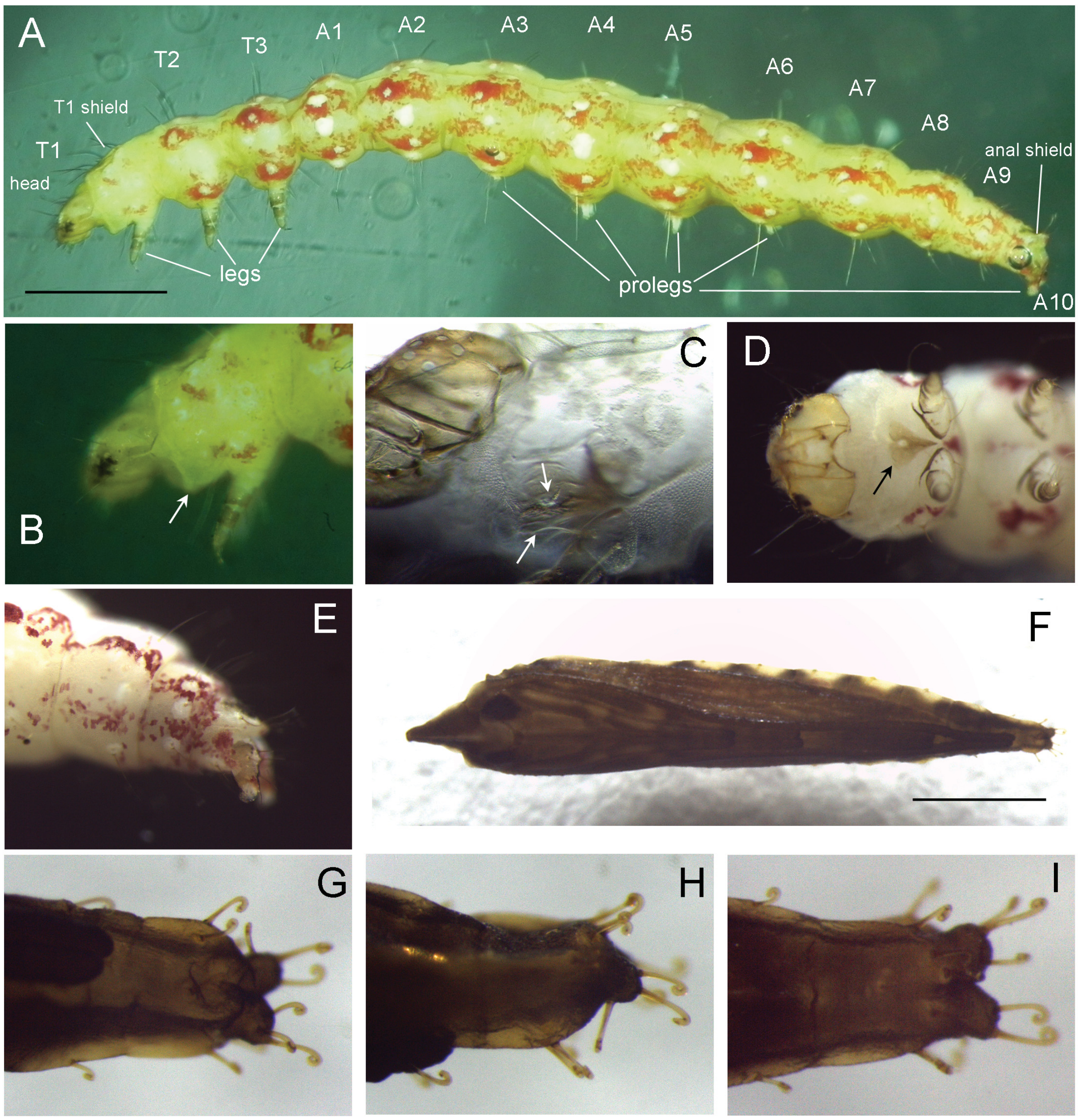

Fig. 16. Mature larva and pupa of *Bedellia somnulentella* Zeller, 1847. A–E. Mature larva (OPU-IN-LE2018IV0031|SK612, 0032|SK613). F–I. Pupa (OPU-IN-LE2018IV0038–0039). **A**. General, lateral view. **B**. Head and thorax, lateral view. **C**. Jugular gland-like structure, lateral view. **D**. Head and thorax, ventral view. **E**. A8–A10, lateral view. **F**. General, ventral view. **G**. Setae of A8–A10, ventral view. **H**. Lateral view. **I**. Dorsal view. Scale bars: 1 mm.

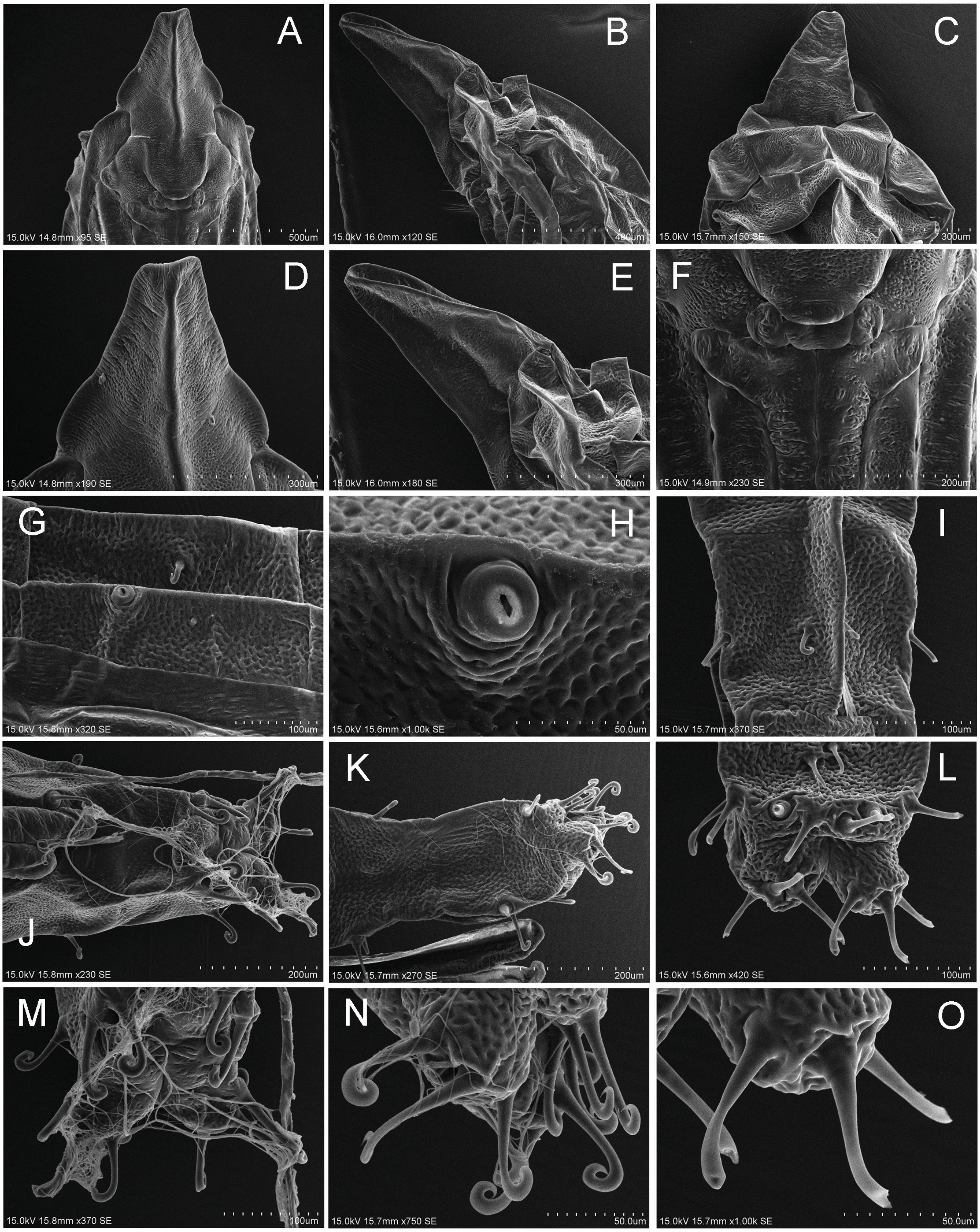

Fig. 17. SEMs of pupa of *Bedellia somnulentella* Zeller, 1847 (OPU-IN-LE2018IV0038–0039). **A**. Head, ventral view. **B**. Lateral view. **C**. Dorsal view. **D**. Frontal process, ventral view. **E**. Same, lateral view. **F**. Face, ventral view. **G**. Seta and spiracle of abdomen, lateral view. **H**. Spiracle. **I**. A7, dorsal view. **J**. A7–A10, dorsal view. **K**. Same, lateral view. **L**. Dorsal view. **M**. Setae of A10, ventral view. **N**. Same, lateral view. **O**. Dorsal view.

looser webs than other yponomeutoid leaf-webbers. We observed that the larvae move on silk threads using the claws of the thoracic legs and the prolegs, but cannot move on flat surfaces without silk.

Molecular analysis

The COI DNA barcoding region (COI-5P) was sequenced from a Japanese specimen of *Tonza*. We performed sequence comparison to check species variation for *T. citrorrhoa*, using the BOLD Identification System (IDS) from the BOLD website (http://www.barcodinglife.org/) [accessed 1 Jul. 2016]. The DNA barcode sequence of *T. citrorrhoa* (Fig. 2, sample ID: SK-97) was clearly distinguished from that of *T. purella* registered in BOLD with more than 3% pairwise divergence (Fig. 2) and to a sample from Madagascar belonging to BIN BOLD:ACU1104 by 2.91% pairwise divergence. The nearest neighbour of *T. citrorrhoa* in the BOLD database which is 0.35% pairwise divergent is a Taiwanese conspecific specimen (Fig. 2), which belongs to the same BIN (BOLD:ACX8102).

Figure 13 shows a maximum likelihood tree of the DNA barcoding region from 23 species of Yponomeutoidea and Gracillarioidea Stainton, 1854, including our sequence, SK-97. This tree based on a single locus could not resolve all the higher-level relationships within the groups, except for Attevidae Mosher, 1916 (85% bootstrapping support). The traditional sense of Plutellidae, which would comprise *Plutella* Schrank, 1802, *Orthenches* Meyrick, 1885, and *Tonza*, among other taxa not represented here, did not form a monophyletic group. Two species, *T. citrorrhoa* and *Glyphipterix equitella* Scopoli, 1763, were grouped together with 87% bootstrapping support.

Discussion

Morphology

Historically, the genus *Tonza* had been associated with Yponomeutidae (Philpott 1927, who also noted the four-segmented maxillary palp as an exception; Common 1966) or Plutellidae (Common 1990; Heppner 1992), until Kobayashi *et al.* (2015) discussed its similarities with and possible association to Attevidae based essentially on male genitalic features: the presence of uncal processes and socii and the shape of the pleural lobes in the abdomen. Kobayashi *et al.* (2015) also mentioned that the genitalia of *Stachyotis* Meyrick, 1905 are similar to those of *Tonza*. *Stachyotis* is another genus whose plutellid association was defined merely by superficial similarity (Sohn 2014). However, Table 2 shows many characteristics in the genitalia are homoplastic among yponomeutoids and thus their phylogenetic value needs to be carefully evaluated. Immature stages as well as molecular data may help in defining the systematic position of *Tonza*. Such information has not been available or analysed until the present study.

We examined the immature stages and some additional adult characters of *Tonza* and compared it with other yponomeutoids (Table 2, Fig. 14). Our examination supports the designation of a new family group name, Tonzidae fam. nov., for *Tonza*. Tonzidae fam. nov. is clearly distinguished from other families of Yponomeutoidea by larval prolegs absent on A5 and A6. Larvae of other families possess prolegs on A3–A6, while several families have reduced prolegs. For example, the prolegs on A3 and A6 of Bedelliidae are shorter than those on A4 and A5 (Fig. 16A). The larval proleg modifications are curious and might relate to locomotion on silk threads as mentioned above. Mature larvae of *Tonza* have a very long seta MD1 on the head. This character also occurs in Yponomeutidae (Yponomeutinae and Saridoscelinae) and Scythropiidae Friese, 1966. Yponomeutine larvae possess a cervical gland (adenosma) on T1 that has been presumed to be an exocrine organ producing a trail-pheromone, used for orientation and homing (Povel & Beckers 1982). This character is not found in other yponomeutoid groups, including *Tonza*. However, the larvae of *Tonza* and *Bedellia* (Bedelliidae) possess a gland-like structure ventrally on T1 (Figs 4F, 16B, D). Furthermore, an endocrine gland-like structure is found in the larvae of *Bedellia* inside the body (Fig. 16), but not in the larvae of *Tonza*.

The pupa of *Tonza* is also similar to that of Bedelliidae (Table 2, Fig. 15K) in having a triangular single frontal process on the head (Figs 10A–D, 16F, 17A–E). The larva of *Lyonetia* Hübner, 1825 (Lyonetiidae Stainton, 1854) forms a hammock-shaped cocoon similar to *Tonza* and Bedelliidae, but the pupa differs from the latter two in possessing two frontal processes on the head and straight setae on the cremaster (Ahn *et al.* 2004; Kobayashi 2015).

Molecular phylogeny

Unexpectedly, our ML tree showed a close relationship between *Tonza* and *Glyphipterix* (Glyphipterigidae: Glyphipteriginae) (Fig. 13). The multigene analyses by Sohn *et al.* (2013) supported the family Glyphipterigidae comprising three subfamilies, Glyphipteriginae, Acrolepiinae Heinemann , 1870, and Orthoteliinae Herrich-Schaffer, 1857. Our COI phylogeny failed to recover such relationships. *Tonza* may be related with Glyphipteriginae and in that case, suggest that it is a member of Glyphipterigidae. We, however, could not find any morphological characteristic associating *Tonza* with Glyphipterigidae. Our phylogeny based on a single gene was not sufficient to resolve the association of *Tonza* with Glyphipterigidae. This issue needs to be explored with a much larger molecular dataset that is currently under construction.

The larval and pupal morphological features of *Tonza* exclude its associations with all existing families in Yponomeutoidea. Therefore, we propose a new family group name, Tonzidae fam. nov., to accommodate these unique characteristics of *Tonza*. This hypothesis is now available for further phylogenetic testing using new data and any other existing members of this new taxon need to be searched for and examined. The family-level rank itself needs to be confirmed with a much larger molecular dataset that is currently under construction.

Host association

The hostplant relationship of *Tonza* uncovered from this study is novel for Yponomeutoidea. Putranjivaceae seems to be the only non-Brassicaceae plant lineage containing mustard oil glucosides, a convergence with Brassicaceae Burnett (Hall *et al.* 2002). It would therefore be interesting to check other members of the Indo-Australian genus *Putranjiva* Wall., as well as the more widely distributed *Drypetes* Vahl for larvae of *Tonza*, and also other members of this family (e.g., *Lingelsheimia* Pax). The new relationship gives a strong clue to discover early stages elsewhere in the World. Since *Tonza* is now removed from Plutellidae (a group like Pierinae Swainson, 1820 that has radiated on Brassicaceae), the ability to feed on plants with mustard oils (iso-thiocyanates: Puntambekar 1950) could be a symplesiomorphy or a convergence.

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