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Beyond Wallace: a new lineage of *Chrysorthenches* (Lepidoptera: Yponomeutoidea: Glyphipterigidae) reveals a journey tracking its host-plants, *Podocarpus* (Pinopsida: Podocarpaceae)

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A northward trans-Wallacean radiation is demonstrated for *Chrysorthenches*, a member of the *Orthenches* group. Here we review *Chrysorthenches* and allied genera resulting in a generic transfer of *Diathryptica callibrya* to *Chrysorthenches* and two new congeners: ***C. muraseae* Sohn & Kobayashi sp. nov.** from Japan and ***C. smaragdina* Sohn sp. nov.** from Thailand. We review morphological characters of *Chrysorthenches* and allied genera, and find polyphyly of *Diathryptica* and the association of the *Orthenches*-group with Glyphipterigidae. These findings were supported in a maximum likelihood phylogeny of DNA barcodes from ten yponomeutoids. We analysed 30 morphological characters for 12 species of *Chrysorthenches*, plus one outgroup, via a cladistic approach. The resulting cladogram redefined two pre-existing *Chrysorthenches* species-groups and identified one novel lineage: the *C. callibrya* species-group. We review the host associations between *Chrysorthenches* and Podocarpaceae, based on mapping the working phylogenies. Our review suggests that ancestral *Chrysorthenches* colonized *Podocarpus* and later shifted to other podocarp genera. Biogeographical patterns of *Chrysorthenches* show that they evolved long after the Podocarpaceae radiation. Disjunctive trans-Wallacean distribution of the *C. callibrya* species-group is possibly related to the tracking of their host-plants and the complicated geological history of the island-arc system connecting Australia and East Asia.

ADDITIONAL KEYWORDS: Gondwana – Lepidoptera – phylogenetics – plant/insect interaction – taxonomy – Wallace's Line.

INTRODUCTION

Wallace's Line, or more appropriately Wallacea, is a transitional zone between the Asian and Australian biota (Wallace, 1860). The validity of such a zone has been cited as a conceptual hallmark in biogeography (Mayr, 1944). However, trans-Wallacean radiation is more frequent than previously thought (Simpson, 1977) and it has been reported in many organisms, including the gekkonid genus *Gehyra* (Heinicke *et al.*, 2011), plants (Truswell *et al.*, 1987) and beetles (Tanzler *et al.*, 2014). These examples show that Wallacea is porous, although some studies continue to verify the importance of the concept (e.g. Keast, 1983; Clode & O'Brian, 2001).

Many lepidopterans are strong fliers; thus, they may be little affected by biogeographic barriers such as Wallacea. In support of this assumption, recent biogeographic studies have reported faunal exchanges between Asia and Australia in birdwing butterflies (Condamine *et al.*, 2015), *Taractrocera*-group butterflies (De Jong, 2001), Sphingidae (Beck *et al.*, 2006) and the pyralid genus *Vitessa* (Buchsbaum *et al.*, 2014). Overall, such phenomena have been observed exclusively in large moths and butterflies that possess strong dispersal powers. Nearly all of these examples

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have demonstrated southward dispersal from Asia to Australia. In the present study, the yponomeutoid genus *Chrysorthenches* Dugdale, 1996 is identified as a rare case among micromoths that has penetrated the Wallacea zone as it has dispersed northward. This unusual distributional pattern seems to be related to the biogeography of their host-plants and to the dynamic history of Indo-Australian geography.

Chrysorthenches once belonged to a heterogeneous genus, *Orthenches* Meyrick, 1885. Later, it was separated from others by Dugdale (1996) who recognized that they form a distinct group based on, for example, conifer feeding. Further, he suggested a collective group that he referred to as the '*Orthenches*-group' that would include *Chrysorthenches*, the remaining *Orthenches* species, and a few undescribed taxa. The systematic definition of the *Orthenches*-group remains premature, as it may include other possible lineages not traditionally considered; for example, *Stachyotis* Meyrick (Sohn, 2014). Currently, *Chrysorthenches* is comprised of ten species that are distributed exclusively in New Zealand and Tasmania. Monophyly of *Chrysorthenches* was supported by the presence of nine apomorphies (Dugdale, 1996): one from adult antennae, seven from the male genitalia and abdominal termina, and one from larvae. The adults of *Chrysorthenches* resemble those of the large genus, *Argyresthia* (Argyresthiidae), but these genera belong to separate families. For species with known biologies, the larvae of *Chrysorthenches* are leaf-tiers, shoot borers or leaf-miners in two coniferous families: Cupressaceae and Podocarpaceae (Dugdale, 1996).

Murase (2005) surveyed the lepidopteran pests on *Podocarpus macrophyllus* (Thunb.) Sweet, a popular ornamental conifer, locally referred to as 'Inumaki', 'Maki' or 'Kusamaki'. During this study, a curious species of micromoths, whose systematic position could not be determined, was observed. The first author (JCS) noted a remarkable resemblance between the undescribed species and the Australian plutellid *Diathryptica callibrya* Turner, 1923 and recorded another new species, allied to *D. callibrya*, from Thailand. Moreover, the authors of the present study recognized similarities between *D. callibrya* and *Chrysorthenches*. These findings prompted a question regarding the disjunct distribution of *Chrysorthenches* in the Australasian, Oriental and East Asian regions as to whether it is based on vicariance, dispersal or both. Dugdale (1996) suggested that larval studies are crucial for clarifying the systematic position of the *Orthenches*-group. To assist in that clarification, we describe the larvae and pupae of a new species of *Chrysorthenches* from Japan. Based on the new information included in the present study, we are exploring the following issues: (1) the systematic position and biodiversity of *Chrysorthenches*, (2) the identification of a new lineage within *Chrysorthenches*, based on a cladistics approach, (3) the evolution of the Podocarpaceae–*Chrysorthenches* associations and (4) the trans-Wallacean radiation of the *Chrysorthenches callibrya* species-group.

MATERIAL AND METHODS

Taxon sampling

Adult specimens (Figure 1A–D) for morphological observation were obtained from the following institutional collections:

ANIC – Australian National Insect Collection, Canberra, Australia.
NHMUK – Natural History Museum, London, UK.
OPU – Entomological Laboratory, Osaka Prefecture University, Osaka, Japan.
USNM – National Museum of Natural History, Washington, DC, USA.

Larval nests and pupal cocoons of *Chrysorthenches* from Japan were collected on the branches of *Podocarpus macrophyllus* by Ms Masumi Murase from Nogawa, Wakayama City, Wakayama Prefecture, Japan, on 15 May 2014 and by the second author (SK) in June 2017 and 2018 from Imai, Soni-mura, Uda-gun, Nara Prefecture, Japan. Some of the collected larvae and pupae were preserved in absolute alcohol for morphological observation. The rest of the larvae were reared with their nests in plastic cups (420 ml: 129 mm in diameter at top and 60 mm in depth) containing wet cotton at 20 ± 5 °C under a photoperiod condition in the laboratory of 13–16L (light hours): 8–12D (darkness hours). In addition, we examined the dry, pinned specimens of the adult moths in the OPU collection, prepared by Dr T. Saito, Ms Masumi Murase and Mr Seiichiro Koshino. Photographs of larval nests were taken primarily in the field using an OLYMPUS μ1060 digital camera (Olympus Corp., Tokyo, Japan). Some nests were scanned using an EPSON GT7400 scanner (Seiko Epson Corp., Nagano, Japan).

Genitalia slides were prepared according to Clarke (1941), except that chlorazol black and Euparal resin were used for staining and permanent mounting, respectively. Larval specimens were dissected following instructions in Stehr (1987) and kept in glycerin for examination. External morphology of adults was observed using a stereoscope (Leica L2, Leica Microsystems, Wetzlar, Germany). Slide specimens were examined using a compound microscope (Leica DM-500). Adults and their genitalia were photographed with a digital camera (Nikon D30, Nikon Corp., Tokyo, Japan) attached to a light box or a

microscope. Larval characters were illustrated by the third author (YY). The larval and pupal specimens for scanned electron microscope (SEM) were dried and sputter-coated with a 60:40 mixture of gold-palladium. The SEM photographs were obtained using Leica Seteroscan 440 (Leica Microsystems), installed in the Scanning Electron Microscopy Laboratory, USNM, and a Hitachi SU1510 (Hitachi Ltd., Tokyo, Japan) with a lanthanum hexaboride (LaB6) cathode source at an accelerating voltage of 15 kV in OPU. Terms for wing venation, genitalia, larvae and pupae follow Wootton (1979), Klots (1970), Stehr (1987) and Mosher (1916), respectively. Thoracic and abdominal segments of larval and pupal specimens are abbreviated as 'T' and 'A', respectively. The names of host-plants follow an online database, the World Checklist of Selected Plant Families (https://wcsp.science.kew.org/), which includes a curated and reviewed list of gymnosperms.

Verbatim label data were provided only for primary types. The pipe marks ('|') in the label data indicate line breaks. The contents in brackets are additional information given by the authors. The 'GSN' and 'WSN' in the collecting data stands for 'genitalia slide number' and 'wing slide number', respectively.

Morphological data preparation

A morphological data matrix (Table 1) was constructed using ASADO v.1.61 (www.diversityoflife.org/winclada), a bridge program to WinClada (Nixon, 2002). Our taxon-set comprises a total of 13 species, including ten ingroup taxa used in Dugdale (1996), two additional species of *Chrysorthenches* and an outgroup, *Orthenches chlorocoma* Meyrick, 1885. Morphological characters were sampled likewise from Dugdale (1996) with two corrections (character # 12 and 24) and two additions (character # 26 and 30). The final morphological dataset comprises 30 characters: four adult external morphologies, 15 from the male genitalia and abdominal segment VIII, nine from the female genitalia and two from the larvae. All encoded characters were non-additive and equally weighted. Missing and inapplicable data were encoded as '-'. Data matrix is available as a nexus file in the Supporting Information Appendix S1.

DNA data preparation

DNA barcodes were obtained from GENBANK (www.ncbi.nlm.nih.gov/genbank) for nine species of yponomeutoids and from the previous experiments by the first author (JCS) for one species ('CL67' in Sohn *et al.*, 2013). Accession numbers of all these sequences are provided in Supporting Information, Table S1. A *COI* sequence for the 'CL67' was obtained following the procedures in Regier (2008) for DNA extraction, polymerase chain reaction (PCR), PCR primer sets and DNA sequencing. See Sohn *et al.* (2013) for the details of experimental condition. The collected DNA barcodes were aligned and edited using GENEIOUS v.11.1.4 (Biomatters Ltd.).

Phylogenetic analyses

Maximum parsimony (MP) analyses for the morphological data matrix were conducted using ASADO program with NONA v.2.0 (Goloboff, 1999) implemented. The following commands were used: hold 1000, hold/100, mult*1000, max* and mswap+. The resulting cladograms were rooted by an outgroup and examined using unambiguous, fast (=ACCTRAN) and slow (=DELTRAN) character optimizations. Confidence of the tree topologies was estimated by jackknifing (JK) and Bremer support, using WinClada and TNT v.1.5 (Goloboff *et al.*, 2008), respectively.

A phylogenetic tree for the aligned DNA barcodes was constructed under a maximum likelihood criterion, using a default setting for RAxML-HPC Blackbox (Stamatakis, 2014) through the CIPRES Science Gateway website (www.phylo.org). Confidence was estimated by bootstrapping (BP) implemented in RAxML with 1000 resampling sets. The resulting trees were visualized using FigTree v.1.4.3 (Rambaut, 2015) with a root at the divergence between ingroups and an outgroup, the diamondback moth *Plutella xylostella* (Linnaeus, 1758).

Biogeography

Cladistic biogeography of *Chrysorthenches* was deduced using the divergence-vicariance analysis (DIVA v.1.1: Ronquist, 1996). Four general distribution areas were considered: New Zealand, Tasmania, eastern Australia and East Asia. The most parsimonious tree from our cladistic analysis for 12 species of *Chrysorthenches* and an outgroup was used as an input tree for the DIVA analysis. Optimization parameters were set as default: no limitation in maximum area, bound = 250, hold = 100, weight = 1.000 and age = 1.000.

Host association

Host-plant records of *Chrysorthenches* were obtained from Dugdale (1996) with additions from the present study. The classification of gymnosperms follows Christenhusz *et al.* (2011) and higher phylogenetic relationships of host-plants follows Lu *et al.* (2014) and Quiroga *et al.* (2016). A phylogeny of *Podocarpus* follows Knopf *et al.* (2012). Distributional information of *Podocarpus* species came from the IUCN Red List (https://www.iucnredlist.org).

RESULTS

SYSTEMATIC ACCOUNTS

SUPERFAMILY YPONOMEUTOIDEA STEPHENS, 1829

FAMLY GLYPHIPTERIGIDAE STAINTON, 1854

GENUS *CHRYSORTHENCHES* DUGALE, 1996

Chrysorthenches Dugdale, 1996: 34. Type species: *Orthenches porphyritis* Meyrick, 1886, by original designation.

Dugdale (1996) defined *Chrysorthenches* in relation to *Orthenches* and suggested the following apomorphies for the former genus: (1) in the male genitalia, the gnathos and socii absent; (2) the anellus as a spinulose sheath and often with strong apical thorns; (3) the vinculum plus saccus T-shaped; (4) the posterior margin of the saccus convex; (5) the male phallus uniformly cylindrical; (6) the male sternum VIII with a V-shaped lobe (Fig. 2G); (7) the male tergopleural lobe arising obliquely and fused dorsally (Fig. 2G, arrow); and (8) the larval abdominal segment VII with spiracle and seta SD1 on a common pinaculum or scobinate field.

Two additional characters: the presence of the antennal scape with pecten, but no awning, and the valva of the male genitalia with an outer tuft of specialized scales or setae distally, were suggested as apomorphies for *Chrysorthenches* by Dugdale (1996). These were excluded from this study as proposed from our cladistics analysis. With our additions, *Chrysorthenches* comprises 13 species in three species-groups.

CHRYSORTHENCHES CALLIBRYA SPECIES GROUP

Description: Head – Vestiture of vertex appressed but rough around temporal area. Antenna filiform in both sexes, two-thirds as long as forewing costa. Labial palpus slightly ascending, 4× longer than antennal scape; second labial palpomere with ventrodistally denser scale tuft; third palpomere longest. Maxillary palpi three-segmented, as long as antennal scape. Temporal and occipital areas with piliform scales.

Thorax – Forewing narrow, greenish; venation (Fig. 1F) with Sc reaching margin slightly before middle of costa; R arising from near basal two-fifths of radius; Rs_{1-3} reaching margin above apex; Rs_1 arising from anterior margin of accessory cell near basal two-fifths, slightly divergent from R; Rs_2 slightly convergent to Rs_1; Rs_2 and Rs_3 basally separate, divergent; Rs_3 and Rs_4 slightly divergent; Rs_4 reaching margin right below apex; M_2 parallel to M_1 and M_3; CuA_1 and CuA_2 sinuous, close to each other at middle; CuP vestigial as fold in basal five-seventhes; basal fork of 1A+2A near one-third of the length. Hindwing venation (Fig. 1F) with Sc+R_1 reaching margin at middle of costa; Rs reaching margin above apex; M stem vestigial in basal five-sixths; M_1 slightly close to Rs at middle; M_1 and M_2 slightly divergent in distal half; M_2 nearly parallel to M_3; M_3 and CuA_1 divergent; CuA_1 parallel to CuA_2; CuP present; 1A+2A sinuous, close to CuP at distal one-third, with basal fork one-eighth of length; 3A straight.

Male genitalia (Fig. 2A–F, H) – Uncus elongate, bifid apically; tuba analis broad, sparsely setose apically; subscaphium densely setose; tegumen subrectangular, setose laterally. Valva obovate or subrectangular, densely hairy, with large, sparsely-setose; membranous disc basally, sparsely setose. Anellus densely spinulate. Saccus elongate, digitate, enlarged subapically. Phallus slightly sinuous, broadened basally, opening obliquely at apex, with needle-like and spiniform cornuti; carina strongly sclerotized, spiniform; vesica with a needle-like cornutus, a spinulate, digitate cornutus and five spiniform cornuti (Fig. 2D–F).

Female genitalia (Fig. 3A, B) – Ovipositor telescopic; papillae anales with setose, digitate protrusions dorsoapically. Abdominal segment IX with a pair of setose lobes ventrally. Ductus bursae slender, entirely sclerotized. Ductus seminalis arising on accessory sac of corpus bursae. Corpus bursae with accessory sac at middle; signum absent.

KEY TO THE SPECIES-GROUPS OF *CHRYSORTHENCHES*

1. Ductus bursae in female genitalia narrow and entirely sclerotized; larval mesothoracic L1 and L2 setae on separate pinacula ..... *C. callibrya* species-group
- Ductus bursae in female genitalia partly sclerotized or entirely membranous; larval mesothoracic L1 and L2 setae on same pinaculum 2
2. Ductus seminalis entirely sclerotized; ductus bursae shorter than corpus bursae ..... *C. argentea* species-group
- Ductus seminalis partly sclerotized; ductus bursae longer than or as long as corpus bursae ..... *C. porphyritis* species-group

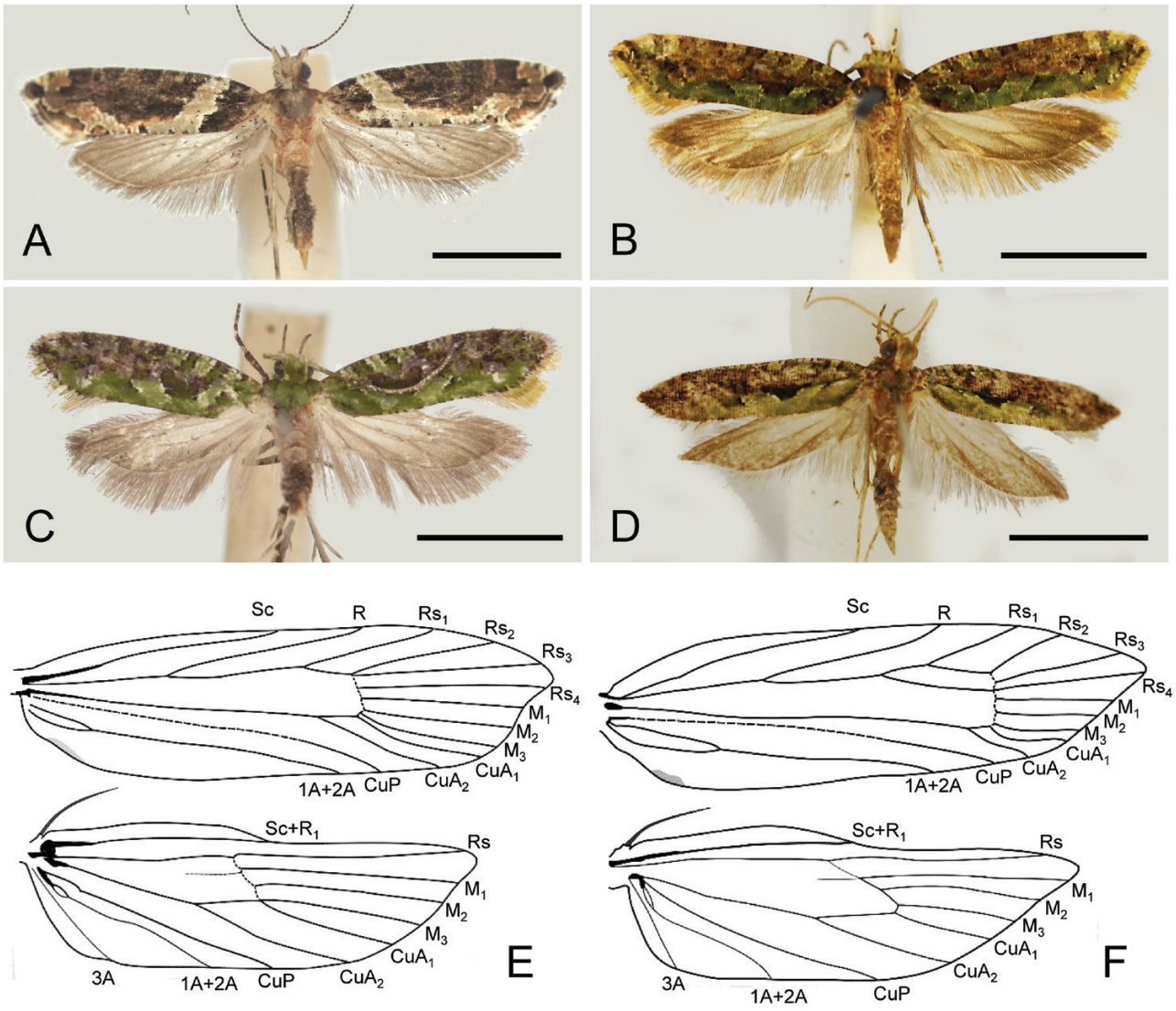

Figure 1. Adults of *Chrysorthenches* and *Diathryptica*. A, *D. proterva*, male, ANICF957-10. B, *C. callibrya*, lectotype. C, *C. muraseae*, holotype. D, *C. smaragdina*, holotype. E, Wing venation of *D. proterva*. F, Wing venation of *C. muraseae*. Scale bars = 3 mm.

Distribution: Eastern Australia, Thailand and Japan.

Host-plants: Podocarpaceae – *Podocarpus*.

Remarks: Chrysorthenches callibrya (Turner, 1923), the focal species of *C. callibrya* species-group, was originally associated with an Australian genus *Diathryptica*. This species was compared with the type species of *Diathryptica*, *D. proterva* Meyrick, 1907 and both species showed several differences in generic level. Further, *C. callibrya* shares five characters with *Chrysorthenches* and they include the presence of a chorda on the forewing; the male genitalia without the gnathos and socii and with the valva divided into a proximal and a distal piece; the male pleural lobes fused dorsally; and the trophic association with conifers. Our *COI* phylogeny also agrees a separation of *C. callibrya* from *Diathryptica* (Supporting Information, Fig. S1).

CHRYSORTHENCHES CALLIBRYA (TURNER, 1923), COMB. NOV.

(FIGS 1B, 2A, D, G, 3A)

Diathryptica callibrya Turner, 1923: 172. Type locality: Australia, Queensland, National Park.

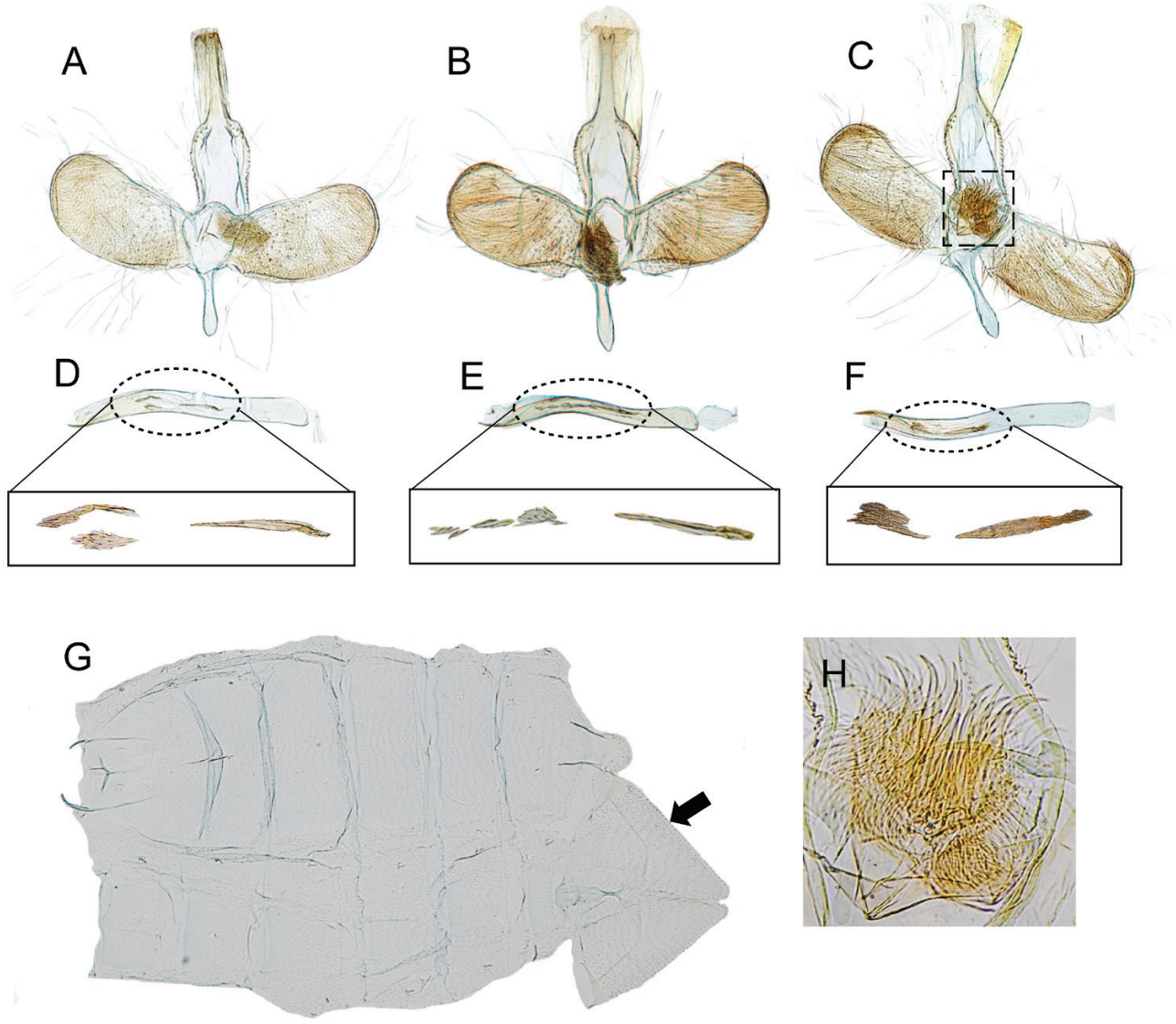

Figure 2. Male genitalia and abdomen of *Chrysorthenches*. A–C, genital capsule. D–F, phallus, inset = close-up of cornuti corresponding dotted ellipse. A, D, *C. callibrya*, ANIC-20627. B, E, *C. muraseae*, USNM-115161. C, F, *C. smaragdina*, BM-32892. G, sternites (top side) and tergites (bottom) *of C. callibrya*, ANIC-20627, arrow indicating pleural lobes. H, Close-up of spinulate anellus of *C. smaragdina*, corresponding dotted box of 2C.

Diagnosis: Chrysorthenches callibrya is similar to *C. lagarostrobi* Dugdale, 1996 and *Diathryptica proterva* (Fig. 1A) in the forewing markings, but these species have different ground colour on the forewings (green in *C. callibrya* vs. brown in *C. lagarostrobi* and *D. proterva*).

Redescription: Adult (Fig. 1B): Head – Vertex dark yellowish green, with greenish orange piliform scales on temporal area; frons dark yellowish green. Antenna with scape pale greenish orange, with piliform scales of awning anteriorly; flagellum dark yellowish green, sparsely intermixed with white scales; most flagellomeres with dark purplish brown whorls distally. Maxillary palpus dark brown, tinged with white apically. Labial palpus 4× longer than antennal scape; first palpomere dark purplish brown on outer surface, pale orange on inner surface; second palpomere 2.3× longer than first palpomere, dark yellowish green, sparsely intermixed with dark brown scales on outer surface, pale orange on inner surface, white apically; third palpomere 2.2× longer than second palpomere, greenish orange, intermixed with dark brown scales apically and ventrally.

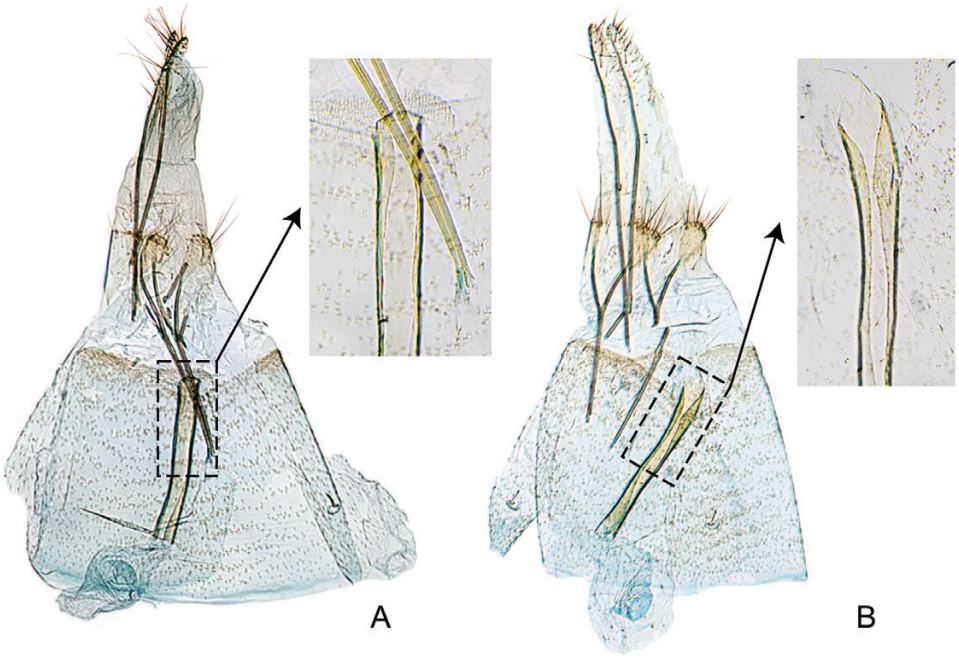

Figure 3. Female genitalia and abdominal segment VIII of *Chrysorthenches*. A, *C. callibrya*, ANIC-20637. B, *C. muraseae*, USNM-115162. Inset = close-up of dotted box area on corresponding figure.

Thorax – Patagium dark yellowish green, intermixed with dark brownish brown scales medially; tegula dark yellowish green, tinged with dark brown basally and apically; mesonotum dark yellowish green dark yellowish green, tinged with dark brown medially; mesoscutellum dark purplish brown. Foreleg with coxa and femur dark brown; tibia and tarsomeres dark brown, with white ring distally. Midleg with coxa and femur pale greyish orange, densely intermixed with dark brown scales; tibia and tarsomeres dark brown, with white ring distally. Hindleg with coxa pale greyish orange, densely intermixed with dark brown scales; femur and tibia lustrous, grey, tinged with greyish orange dorsally; tarsomeres dark greyish brown, with pale greyish yellow ring distally. Forewing length 4.8–5.5 mm, dark brown costally, brown medially, dark yellowish green dorsally and terminally; basal six costal strigulae pale greenish grey; distal one strigula white with dark brown spot at centre; fasciae pale greenish grey, bordered with white, and then with black; subbasal and median fasciae bar-like; postmedian patch round, with black spot at centre; tornus and dorsal two-thirds of termen with alternation of white spots and black bars; posterior margin with short, black strigulae; fringe dark yellowish green, sparsely intermixed with dark purplish green scales. Hindwing pale brownish grey, paler to base; fringe pale brownish grey. Abdomen – Dorsal area pale brownish grey darker posteriorly; ventral area pale greyish orange, intermixed with greyish orange scales laterally.

Male genitalia (Fig. 2A, D) – Uncus as long as tegumen; setose area of tuba analis one-quarter of its length. Valva obovate, round apically; costa slightly concave at basal three-fifths; sacculus narrow, half as long as ventral margin of valva. Vinculum converging medially; saccus two-thirds as long as uncus. Phallus (Fig. 2D) with needle-like cornutus one-seventh the length of phallus; spinulate, digitate cornutus one-third as long as needle-like cornutus; elongate, spinose cornutal zone.

Female genitalia (Fig. 3A) – Papillae anales as long as abdominal segment IX; apophyses posteriores same length of apophyses anteriores. Ductus bursae of even width, 1.3× longer than corpus bursae. Corpus bursae elliptical.

Types: Lectotype (designated here) – male, 'LECTOTYPE | *Diathryptica* | *callibrya* | Turner, 1923 | desig. by' (red label), 'National Pk | B. 3-4000 ft | Q. 21-12-21', '*Diathryptica* | *callibrya* Turn. | TYPE' (hand-writing), 'ANIC | genitalia slide | No 20627'; paralectotype – male, same data as lectotype. All types in ANIC.

Additional material: AUSTRALIA: (New South Wales) 1♂, Border Ranges National Park, Antarctic Beech Picnic Area (22.22S 153.06E, elev. 1000 m), 9 February 1999 (ED Edwards), ANIC; 3♂, 1♀, Robertson (14.35S, 150.35E), 5 December 1980 (IFB Common), (GSN) ANIC-20637 (♀), ANIC; 1♀, Mt. Keira, 7 March

1967 (IFB Common), ANIC; 1♀, 29 November 1971 (V. J. Robinson), ANIC; 1♀, Barren Grounds Fauna Research area, 22 November 1971 (V. J. Robinson), ANIC. (Queensland) 1♂, Mt. Glorious (27.19S, 152.45E, elev. 640 m), 1–3 November 1994 (IFB common), ANIC; 1♂, Lamington National Park, Binna Burra (Tallawalla), *Nothofagus* forest (28.13S, 153.11E), 4 November 1984 (E. D. Edwards), ANIC; 12♂, 9♀, 1/2km WSW of Mt. Bellenden-Ker, Centre Peak (17.16S, 145.51E, elev. 1560 m), 3–6 November (E. D. Edwards), ANIC; 1♀, 11 km SSE of Eungella, rainforest (21.12S, 148.32E), 9 October 1983 (I. F. B. Common), ANIC.

Distribution: Australia (New South Wales, Queensland).

Host-plants: Possibly *Podocarpus lawrencei* Hook.f., Podocarpaceae (adult association).

Remarks: Turner (1923) described *Chrysorthenches callibrya* (*Diathryptica callibrya* auct.) based on two specimens. The genitalia of a 'Kosciusko' female illustrated in Dugdale (1996) are nearly identical with those of *C. callibrya*. The female was also found from a locality within a distributional range of *C. callibrya*. It is likely that it belongs to *C. callibrya*. Dugdale's specimens of *C. callibrya* were collected by sweeping on *Podocarpus*, hinting their host-plants.

CHRYSORTHENCHES MURASEAE SOHN & KOBAYASHI, SP. NOV.

(FIGS 1C, F, 2B, E, 3B, 4–14)

lsid:urn:lsid:zoobank.org:act:829DA7A5-9E03-4697-8F1A-C5AEA04EE078

Diagnosis: Chrysorthenches muraseae is nearly indistinguishable from *C. callibrya* in external appearance, but differs from the latter in having the broader sacculus in the male genitalia, the shorter spiniform cornuti in the male phallus and the oblique caudal end of the antrum in the female genitalia (truncate end in *C. callibrya*).

Description: Adults (Figs 1C, 14F–H). Head – Vertex vestiture dark yellowish green; frons dark yellowish green. Antenna with scape dark yellowish green, mottled with white at anterior distal end, pecten pale brown; first flagellomere dark brown, second to fourth dark yellowish green, fifth to eighth orange, mottled with white and dark brown; remainders dark brown, mottled with white. Maxillary palpus dark brown, mottled with pale orange, white apically. Labial palpus with first segment half as long as second, dark brown, mottled with pale orange; second segment dark yellowish green, mottled with dark brown on exterior side, pale orange on interior side; third segment 1.5× longer than second, dark brown, sparsely mottled with dark orange, pointed apically.

Thorax – Patagium dark yellowish green; tegula dark yellowish green, mottled with dark brown marginally; mesonotum dark yellowish green, dark brown anterior marginally; mesoscutellum dark brown, intermixed with yellowish green anteriorly. Foreleg with coxa dark brown, tinged with pale brown ventrally with yellowish green scale covering basally; femur dark brown, tinged with brownish grey dorsally; tibia and tarsomeres dark brown with a narrow white band terminally. Midleg with coxa pale brownish grey; femur dark brown, tinged with dark orange dorsodistally; tibia dark brown, with white band at middle and distal end; each tarsomere dark brown, with a white band distally. Hindleg with coxa dark brown; femur pale brownish grey, tinged with dark brown ventrally; tibia and tarsomeres dark brownish grey, with white band distally; tibia with tufts of spiniform scales ventrally. Forewing length 5.0–6.1 mm (average = 5.7 mm, sample numbers = 7), narrow, costal and dorsal margins almost parallel, termen oblique, apex obtuse, dark brown, intermixed with purplish grey in central area, suffused with dark yellowish green broadly in dorsal area and basal third of costal area; fasciae greenish grey, bordered with white and then with black, five fasciae on costa, only two of which reach to dorsum, viz. oblique subbasal line and medially angled antemedian line; two costal strigulae as paired white dots in preapical area; fringes brownish grey, intermixed with greyish green and pale orange. Hindwings fuscous, paler to base; fringes yellowish grey.

Abdomen – Terga grey, sparsely intermixed with dark brownish grey; sterna yellowish grey.

Male genitalia (Fig. 2B, E) – Uncus as long as tegumen, broadened in basal one-quarter; setose area of tuba analis one-quarter of its length. Valva obovate, broadly round apically; costa slightly concave at distal one-quarter; sacculus one-third as long as ventral margin of valva, broadened at middle; membranous disc broadly round along distal margin, half as long as valva. Vinculum U-shaped; saccus as long as uncus, subtriangular apically. Phallus (Fig. 2E) with needle-like cornutus one-quarter the length of phallus; spinulate, digitate cornutus one-eighth as long as needle-like cornutus; a zone of spinose cornuti in various size.

Female genitalia (Fig. 3B) – Papillae anales as long as abdominal segment IX; apophyses posteriores 2× longer than apophyses anteriores. Ductus bursae of even width in anterior three-quarters, slightly broadened in posterior quarter, with oblique cleavage near ostium bursae, 2× longer than corpus bursae. Corpus bursae globular.

Larvae (Figs 4–7, 13). Body length 7.5–8.8 mm (mean: 8.0 mm, $N = 5$). Integument colour varying from yellow

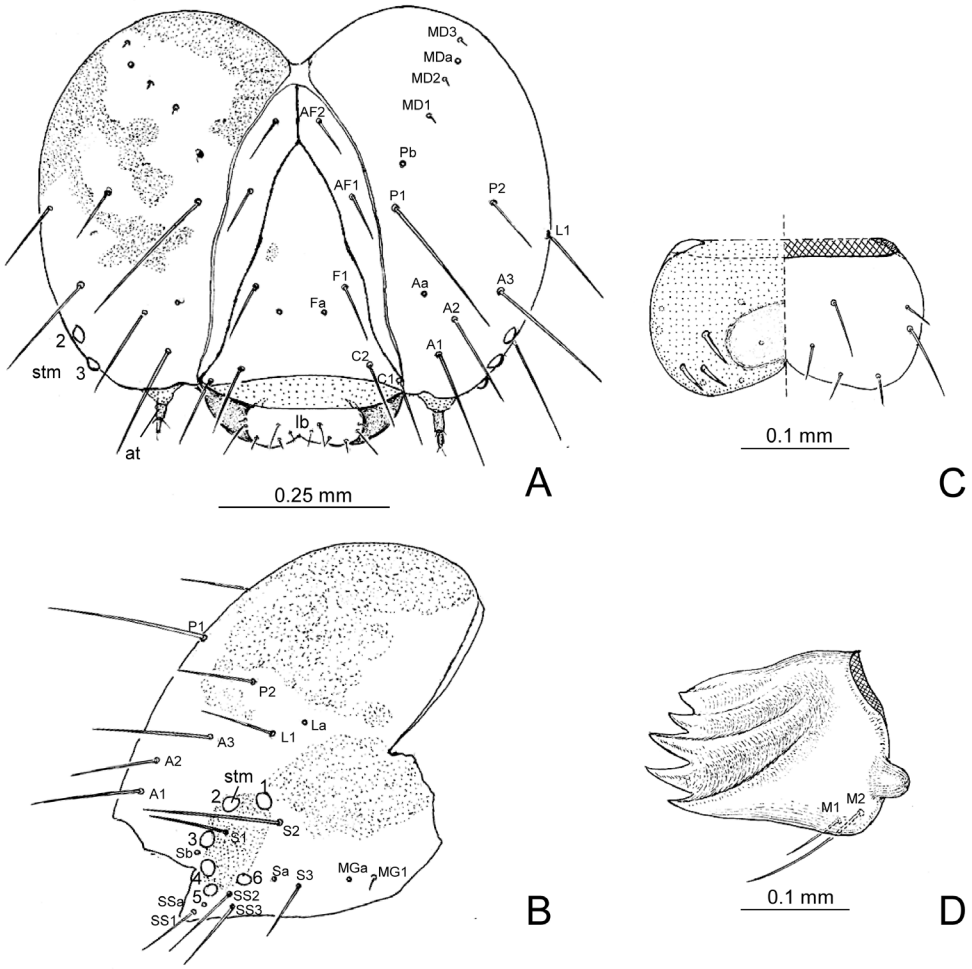

Figure 4. Mature larval head of *Chrysorthenches muraseae*. A, head capsule, frontal view. B, head capsule, lateral view. C, labrum, frontal (right) and backside (left). D, mandible, inner view.

to pale yellowish green (Fig. 13D, E), turning to red dark brown to fuscous in full mature larva (Fig. 13I, J). Pinacula conspicuous, brown in coloration (Fig. 5A).

Head – Hypognathous. Head capsule marked with some brown patches (Fig. 4A), 0.67–0.80 mm in width (mean 0.75 mm, $N = 6$). Front clypeus wide, extending a half to epicranial notch. Mandible about 0.3 mm in length, with two large teeth, three smaller teeth, with seta M2 longer than seta M1 (Fig. 4D). Six stemmata arranged in an arc except for stemmata 1 and 6; S1 more posterior and S6 ventrad (Fig. 4A, B). Spinneret (Fig. 7B) typical in Lepidoptera.

Cranial setae (Fig. 4A, B) – Seta MD1 minute; A1, A2 and A3 as triangle with A2 most distant from stemmata; P1 below Af2–P2 line; Afa and Pa absent.

Thorax (Fig. 5B) – T1 shield sclerotized, brown, marked with dark brown patches. D1 and D2 approximated on T2 and T3; SD1 and SD2 approximated on T2 and T3; L-group trisetose, L1, L2, and L3 on a same pinaculum on T1 and separated on T2 and T3; SV1 and SV2 on a same pinaculum on T1 and SV2 absent on T2 and T3; Seta V1 (Fig. 6B) on separate pinacula on T1 and on outer margin of coxal sclerite on T2 and T3. Thoracic legs fuscous; tarsus brown; each claw short, pale brown, slightly curved to inner side.

Abdomen (Fig. 5C–F) – D1 above level of D2; SD2 small a same pinaculum of SD1; spiracle and SD1 approximated on A1 and A7 (Figs 5C, 6E), on a same pinaculum on A8 (Figs 5D, 6G); L-group trisetose on A1–8, bisetose on A9; SV-group bisetose on A1, A2 and A7, trisetose on A3–6, unisetose on A8 and A9; anal shield brown. Prolegs short, almost same length of width of proleg base; crochets uniordinal, arranged in a circle, being usually 17 in number, with asymmetrical, incomplete inner series of crochets, being four, sometimes two (Figs 5G, 6C, D, 7E). Crochets on anal prolegs arranged in semicircle, open posteriorly, uniordinal, *c*. 20 in number, with a short, uniordinal series of six to eight crochets posteriorly in addition to anterior series (Figs 5F, 7F).

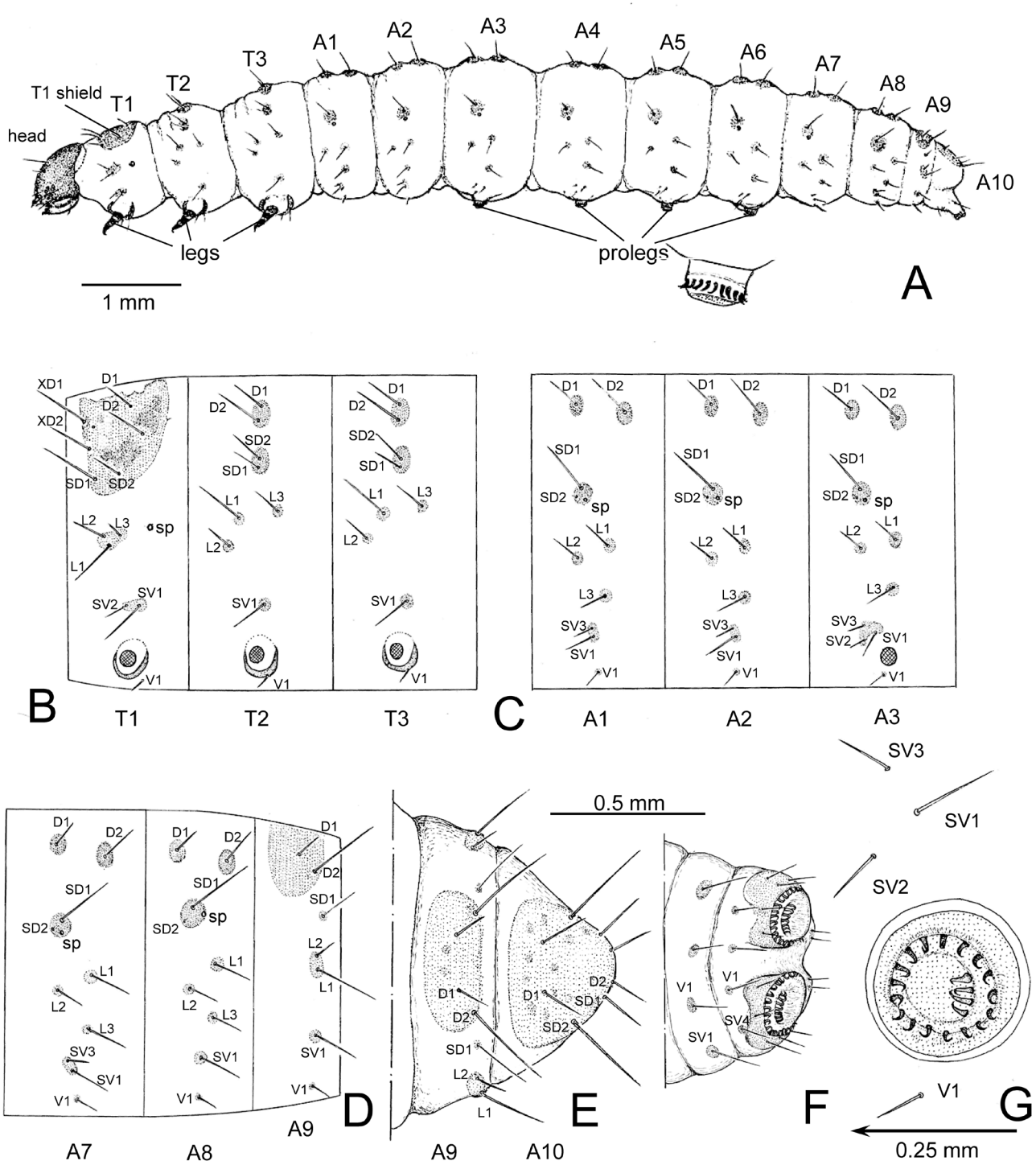

Figure 5. Mature larval thoracic and abdominal segments of *Chrysorthenches muraseae*. A, lateral view of whole larva, inset = close-up of proleg, lateral view. B, setal map of thoracic segments T1–3.C, setal map of A1–3. D, setal map of A7–9. E, setal map of abdominal segments A9–10. F, proleg on A3, arrow indicating direction from ventral to dorsal side.

Pupae (Figs 8–11, 14A–E). Body length 4.9–5.3 mm; maximum diameter 1.4–1.5 mm. Overall shape short, cylindrical. Head and abdomen brown; thorax dark brown. Frons with a decumbent tooth (Figs 8A, B, 9A, B). Prothoracic spiracle on anteriorly projecting process (Fig. 9C, D). Dorsum of A5–A10 with seta D1

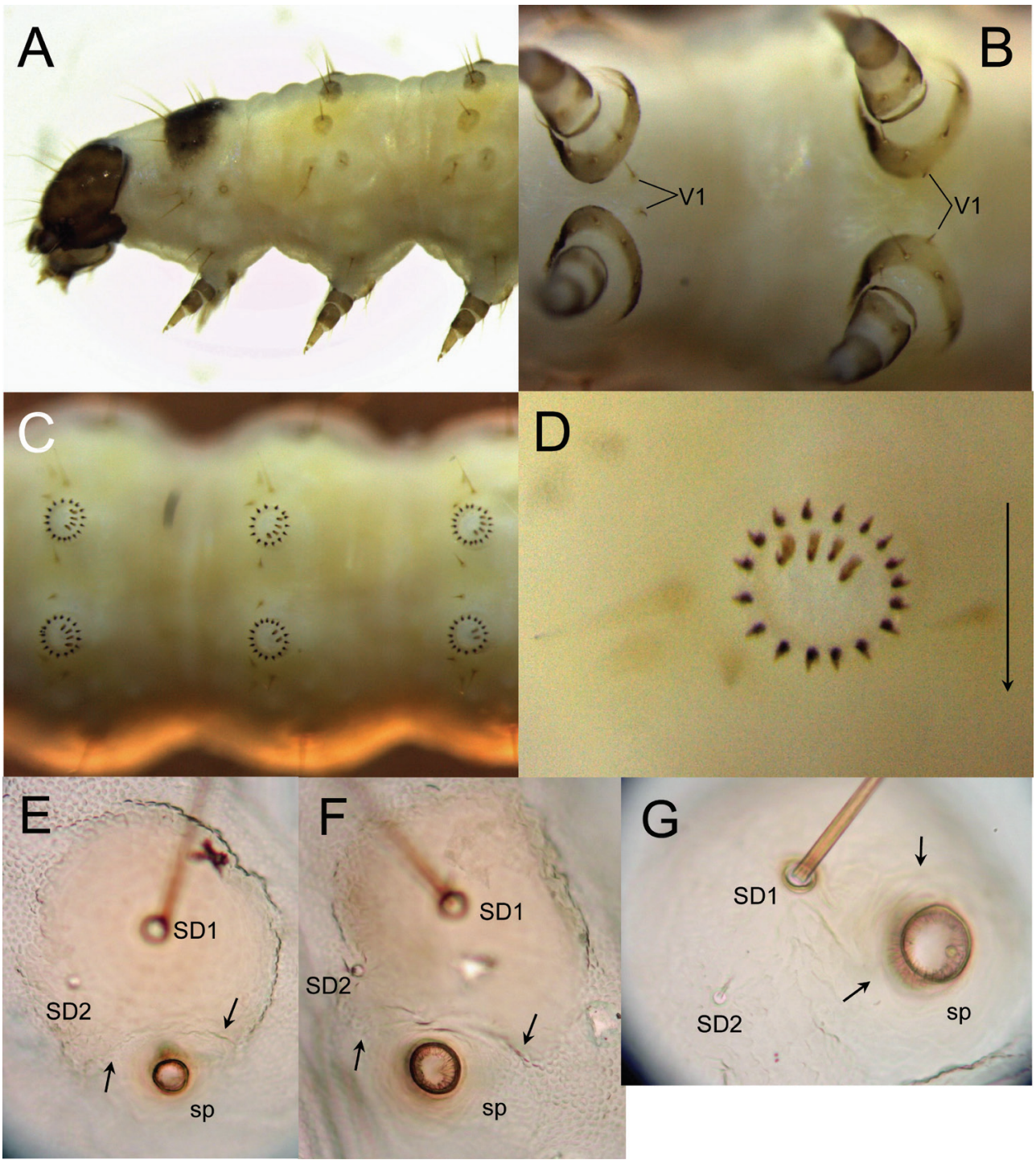

Figure 6. Mature larva of *Chrysorthenches muraseae*, specimen ID 1862-05. A, head and thorax, lateral view. B, thoracic legs on T1 and T2. C, prolegs on A4–A6. D, close-up of proleg on A4, arrow indicating direction from caudal to frontal side. E–G, close-up of subdorsal setae and spiracle (E, A1; F, A4; G, A8).

on a thorn, SD1, L1 and L2; lateral side of abdomen with protuberances at spiracles (Fig. 10); a small posteriorly projecting process on a spiracle; A10 with a pair of small caudal spines with a long slender hooked seta on middle in ventral side; two pairs of spines and a pair of two long slender hooked setae on dorsal side; three pairs of long slender setae on ventral side (Figs 11, 14E).

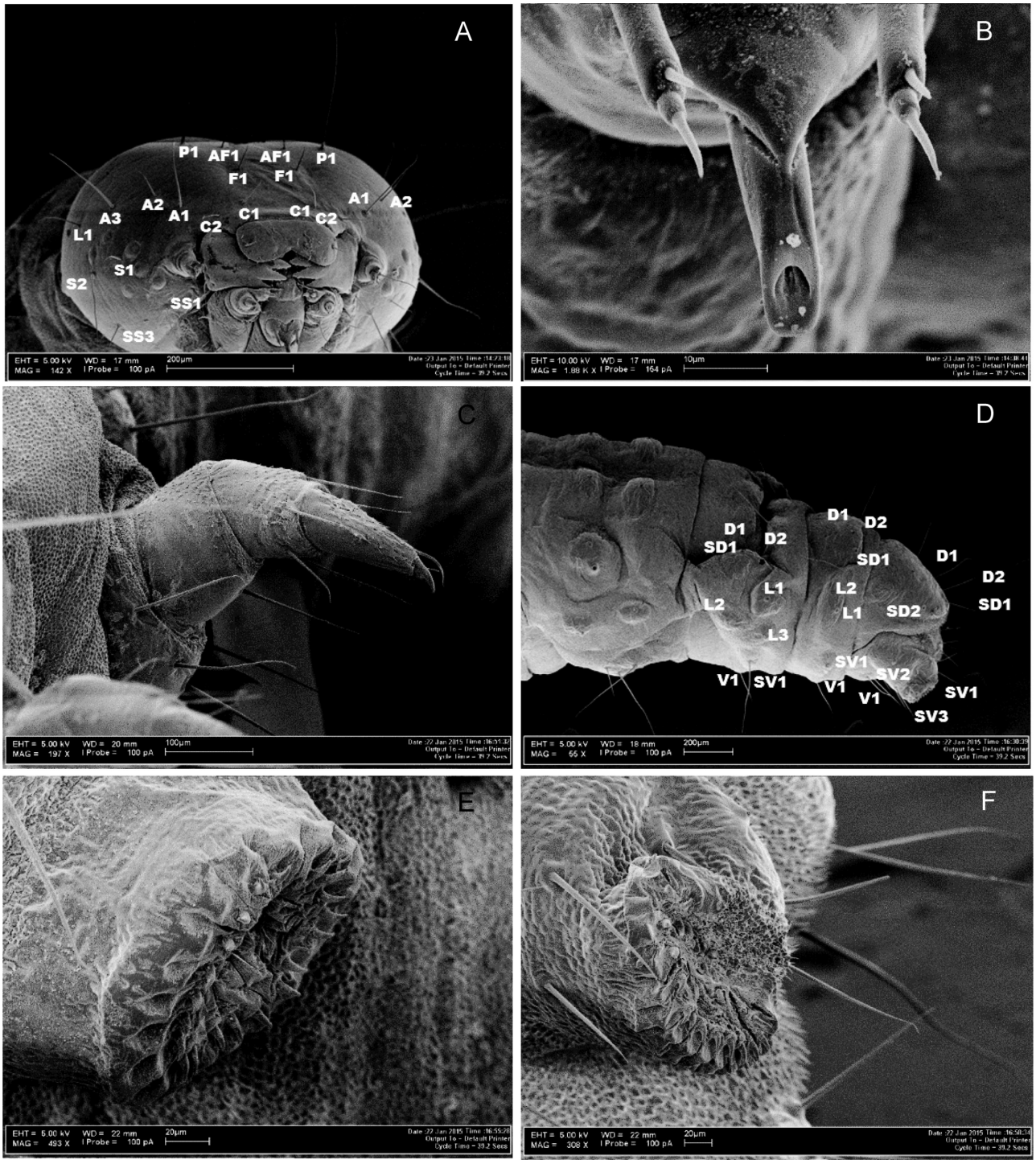

Figure 7. SEM photographs of mature larvae of *Chrysorthenches muraseae*. A, ventrofrontal view of head. B, spinneret and labial palpi. C, thoracic leg on T3. D, A7–9. E, crochet on proleg on A3. F, left anal leg.

Types: Holotype – Male, 'HOLOTYPE | *Chrysorthenches* | *muraseae* | Sohn & Kobayashi' (red label with black marginal lines), 'Japan Honsyu | Wakayama | Natisan | T.Kodama', 'Bred f. [Japanese] | of Inumaki [in Japanese] | 26/VI. 1957 em[ergence]', 'Issiki | Collection | 1972', deposited in USNM. Paratypes (21♂, 32♀, 2 unsexed) – JAPAN: (Mie Pref.) 2♂, 3♀, Kinki region, 'Ise Osugidani', 9.vi.1952 (S. Issiki), bred from *Podocarpus macrophyllus*, emerged on 28–29.vi.1952, (GSN) USNM-115161 (♂),

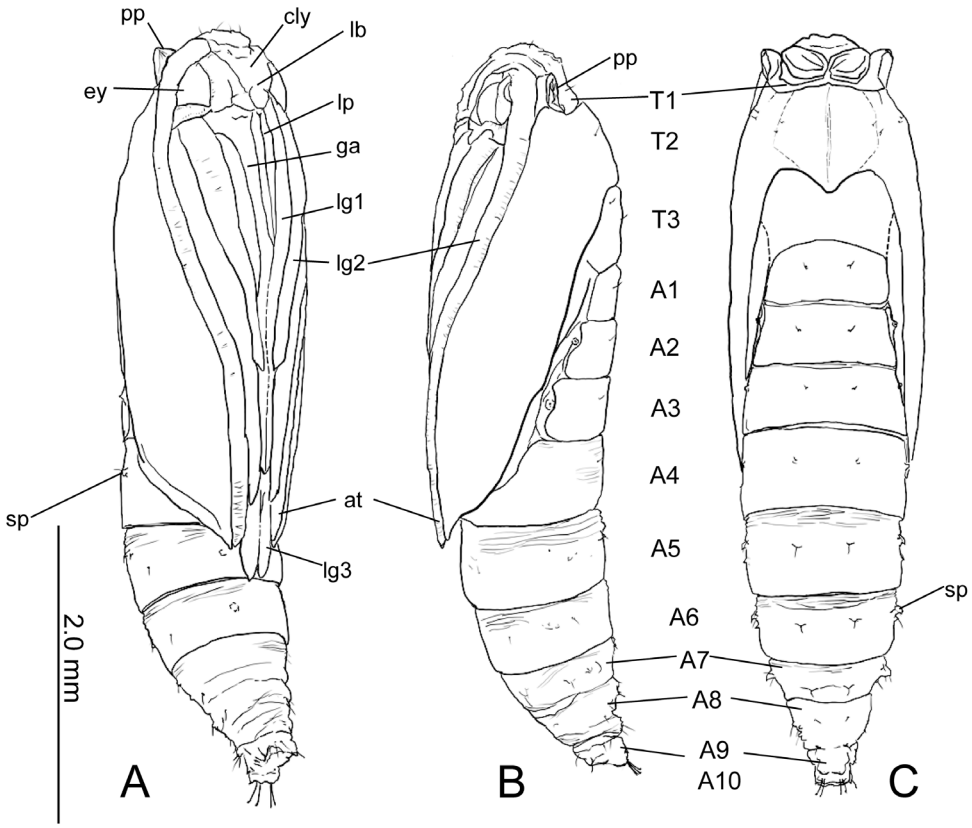

Figure 8. Pupa of *Chrysorthenches muraseae*. A, ventrolateral view. B, lateral view. C, dorsal view. Abbreviations: at, antenna; cly, clypeus; ey, eye; ga, galea; lb, labrum; lg 1, foreleg; lg 2, midleg; lg 3, hindleg; sp, spiracle; pp, projecting process on T2.

(WSN) SJC-W068, USNM. (Nara Pref.) 1♀, Yamato, 16.v.1920 (S. Issiki), (GSN) USNM-115162, USNM; 1♂, 2♀, Uda-gun, Soni-mura, Imai, Oku-Kochi-Sanso, 17.vi.2017 (larva), bred from spun leaves of *Podocarpus macrophyllus*, emerged on 7–8.vii.2017 (S. Kobayashi), OPU-IN-LE2018IV0043–0045, OPU; 2♂, 2♀, 2 unsexed, same locality, 2.vi.2018 (larva), bred from spun leaves of *Podocarpus macrophyllus*, emerged on 28.vi.–9.vii.2018 (S. Kobayashi), specimen-ID1862-02, 08, 13, 14, 19, 23, OPU; 2♂, Kamikitayama, Mt. Odaigahara, Type VIB, 15.vii.2004 (light trap) (T. Hirowatari, K. Ikeuchi, N. Yamamoto, B. W. Lee, K. Yamada, S. Takaki, K. Tateiwa), OPU-IN-LE2018IV0058, 0059; 1♂, same locality and data except Type III, OPU-IN-LE2018IV0060; 1♂, Type VIB, 16.viii.2004 (light trap) (K. Ikeuchi, B. W. Lee, Y. Nishinaka, K. Yamada, H. Mizukawa, S. Takaki, K. Tateiwa), OPU-IN-LE2018IV0061; 3♀, Type VI ['Shinoyō'(=Conifer forest)], 18.vii.2006 (light trap) (T. Hirowatari, N.H. Ahn, C.W. Huang, N. Yamamoto), OPU-IN-LE2018IV0062–0064; 2♂, same data and collectors, except Type V ['Kōyō'(=Broad leaf forest)], OPU-IN-LE2018IV0065–0067; 1♀, Type V ['Kōyō'(=Broad leaf forest)], 13.ix.2006 (light trap) (same collectors), OPU-IN LE2018IV0067. (Osaka Pref.) 1♀, Kishiwada, Izumi-Katuragisan (foot), 13.xi.2004 (T. Saito), OPU-IN-LE2018IV0056, OPU; 1♂, Izumi, Butsunami, 27.vi.1997, host: *Podocarpus macrophyllus*, 29.vi.1997 (Y. Nasu), OPU-IN-LE2018IV0057, OPU. (Shizuoka Pref.) 1♀, Tokai region, Izu Peninsula, Ito, 27.xi.1975 (S. Issiki), USNM. (Wakayama Pref.) 3♂, 6♀, same data as holotype, spun top leaves of *Podocarpus macrophyllus*, emerged on 24–29.vi.1957, (GSN) USNM-96488 (♂), SJC-649 (♀), USNM; 2♂, 2♀, Wakayama-shi, Nogawa, 26.v.1997, from spun leaves of *Podocarpus macrophyllus*, emerged on 14–18.vi.1997 (M. Murase), OPU; 1♂, 3♀, Nogawa, 29.v–2.vi.1978 (S. Kosino), OPU; 2♂, 5♀, Susami-cho, Esuzaki, 4.vi.2000 (larva), host: *Podocarpus macrophyllus*, 22.vi.2000 (T. Saito), OPU-IN-LE2018IV0046–0052, OPU; 1♂, 2♀, Same locality and host-plant,17.v.–5.vi.2002 (T. Saito), OPU-IN-LE2018IV0053–0055, OPU.

Additional material: Adults (in 99% ethanol) – JAPAN: (Nara Pref.) 2 unsexed, Uda-gun, Soni-mura,

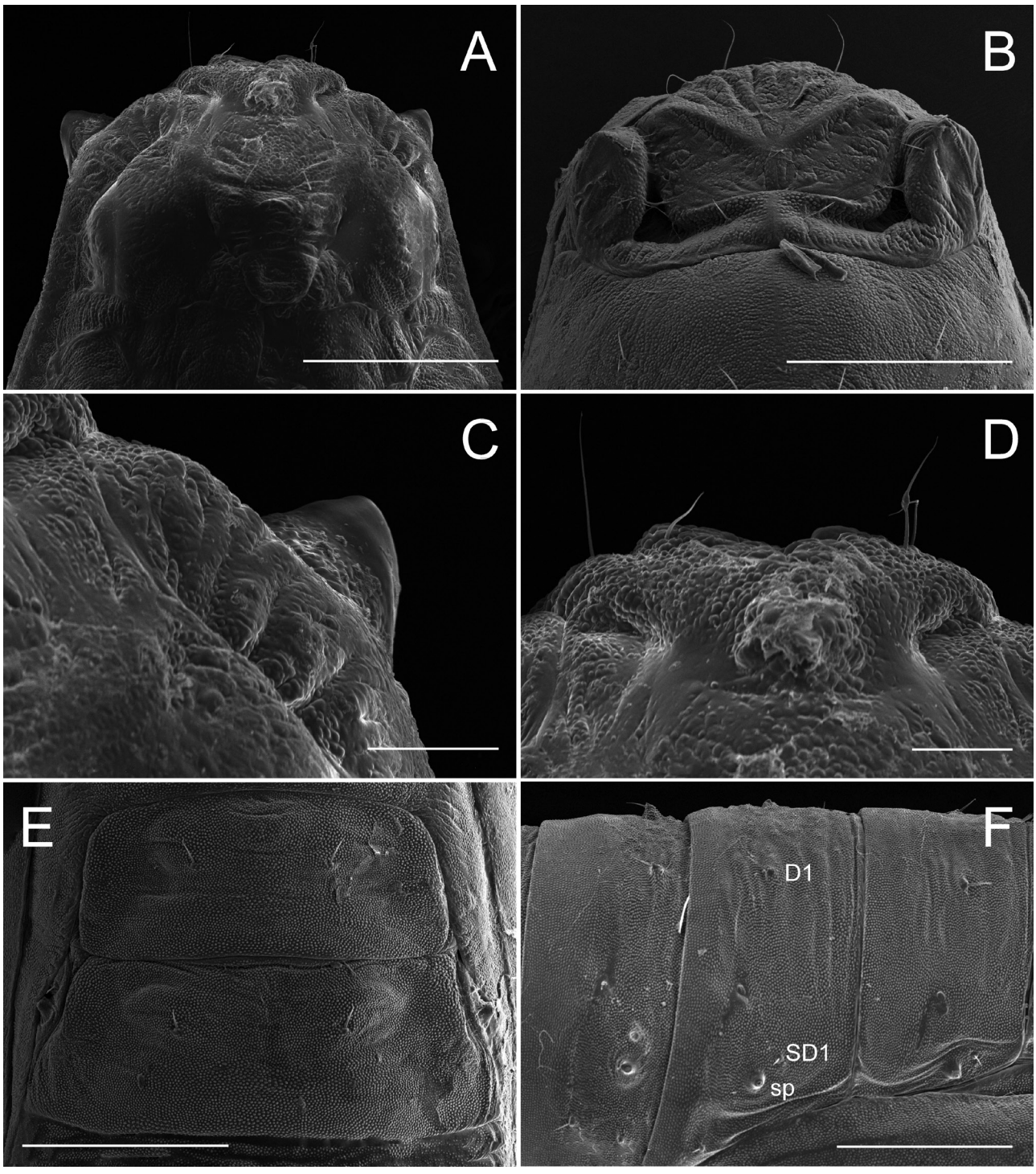

Figure 9. SEM photographs of pupal head and abdomen of *Chrysorthenches muraseae*. A, head, ventral view. B, head, dorsal view. C, projecting process on T2. D, vertex, dorsal view. E, A1–2, dorsal view. F, A2–4, lateral view. Scale bars: 500 μm (A, B, E, F); 100 μm (C, D).

Imai, Oku-Kochi-Sanso, 17.vi.2017 (larva) bred from spun leaves of *Podocarpus macrophyllus*, emerged on 7&11.vii.2017 (S. Kobayashi), SKD-108/OPU-IN-LE2018IV0074, SKD-110, OPU; 3 unsexed, same locality and host-plant, 2.vi.2018 (larva), emerged on 3.vii.2018 (S. Kobayashi), 1862-06/

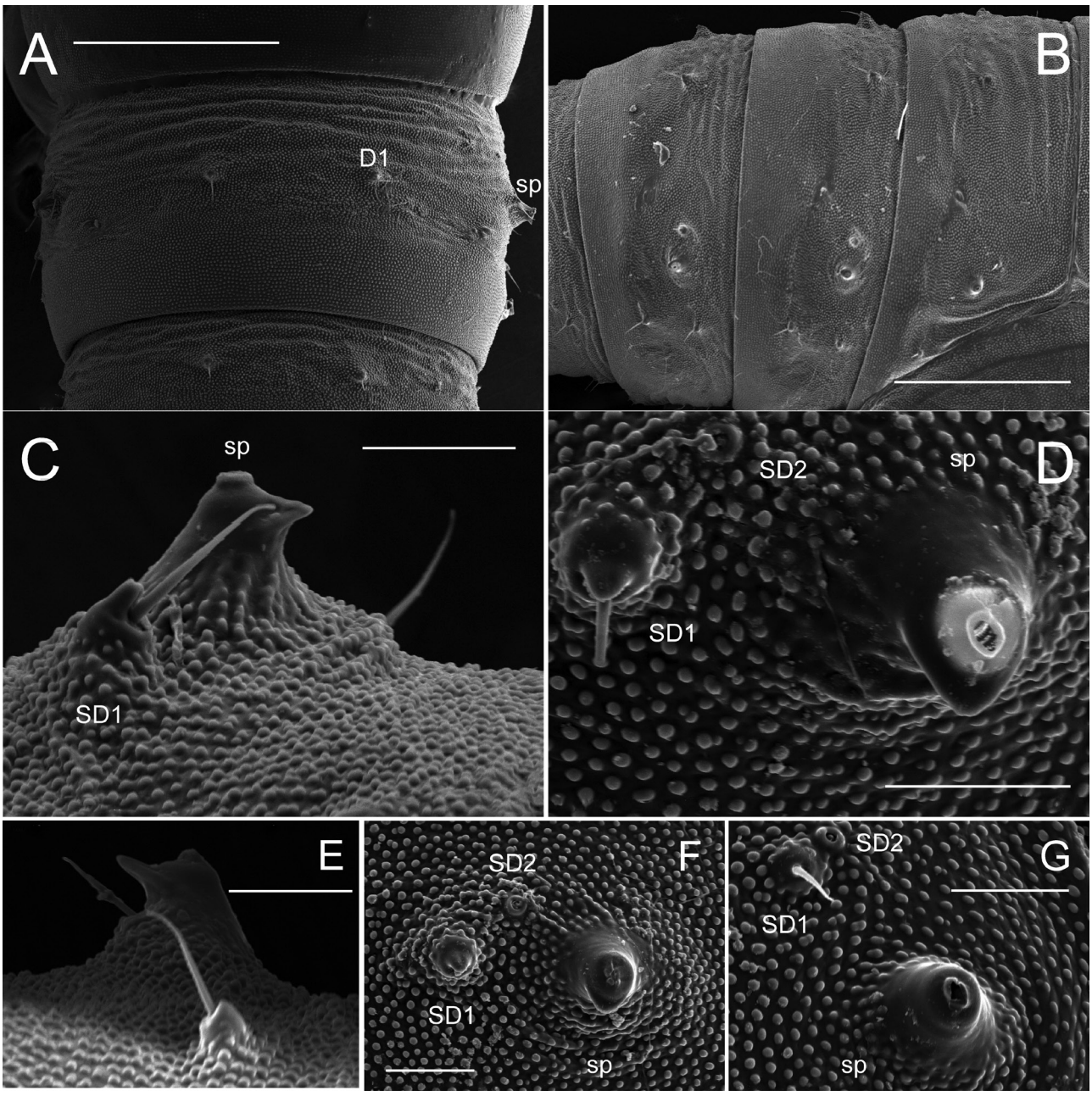

Figure 10. SEM photographs of pupal abdomen of *Chrysorthenches muraseae*. A, A6, dorsal view. B, A4–6, lateral view. C–E, spiracle on A6 (C, dorsal view; D, lateral view; E, ventral view). F, spiracle on A7, lateral view. G, spiracle on A8, frontal view. Scale bars: 500 μm (A, B), 50 μm (C–G).

SKD-120/ OPU-IN-LE2018IV0075, 1862-09/ SKD-121/ OPU-IN-LE2018IV0076, 1862-20/ SKD-122/ OPU-IN-LE2018IV0077, OPU; 1♂, 1♀, 3 unsexed, Kamikitayama, Mt. Odaigahara, Type VII, 18–19.x.2017 (Box light trap) (S. Ueda, K. Ikeuchi, S. Kobayashi, R. Matsumoto, S. Hirai, M. Haraguchi, M. Yamamoto, Y. Watanabe), OPU-IN-LE2018IV0068–0071, 0073/SKD-112 in 99% ethanol, OPU. Larvae (in 99% ethanol) – JAPAN: (Nara Pref.) 4 exuviae, Uda-gun, Soni-mura, Imai, Oku-Kochi-Sanso, 17.vi.2017 (larva), bred from spun leaves of *Podocarpus macrophyllus*, 7–8.vii.2017 (S. Kobayashi), SKD-113, OPU; 6 unsexed, same locality and host-plant, 2.vi.2018 (larva), 8.vi.2018, 1862-01/ SKD-115, 1862-10/SKD-116, 1862- 16/SKD-117, 1862-17/SKD-118, 1862-18/SKD-119. Pupae (in 99% ethanol) – JAPAN: (Nara Pref.) 3 unsexed, 1 exuvia, Uda-gun, Soni-mura, Imai, Oku-Kochi-Sanso, 17.vi.2017 (larva) bred from spun leaves of *Podocarpus macrophyllus*,

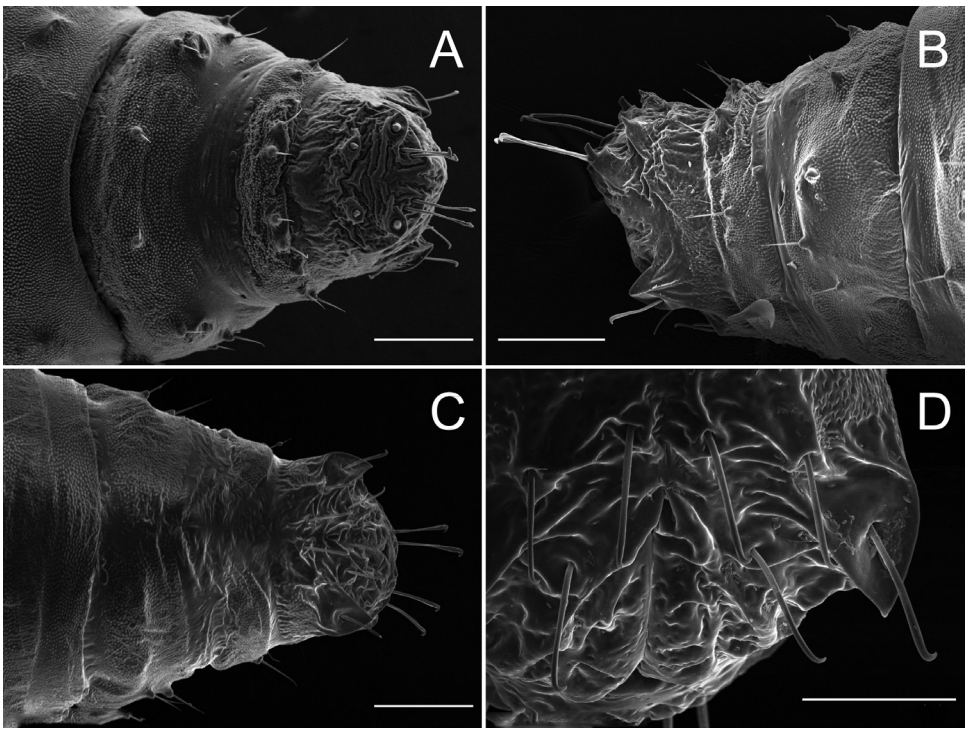

Figure 11. SEM photographs of pupal A8–A10 of *Chrysorthenches muraseae*. A, ventral view. B, lateral view. C, dorsal view. D, right portion of A10, ventral view. Scale bars: 500 μm (A–C), 100 μm (D).

8.vii.2017 (S. Kobayashi), SKD-109, OPU.

Distribution: Japan (Honshu, Shikoku).

Etymology: The species epithet is dedicated to Ms Masumi Murase, who provided valuable information, collected specimens of this species and donated them to us.

Host-plants: Podocarpus macrophyllus (Thunb.) Sweet., Podocarpaceae.

Remarks: The existence of *C. muraseae* has been known in Japan for over ten years, but it remained unidentified (Murase, 2005) or misidentified as a gelechiid species (Manabe, 2018, electronic source). The larvae of *C. muraseae* spun the apical pieces of shoots and live inside (Murase, 2005). We observed that the larvae of *C. muraseae* in June in Kinki region construct their nests with unspread young leaves spun (Fig. 12A, C–I). They leave frass inside the nests or sometimes eject it through holes (Fig. 12A, 13A-C, F-H). There is only one larva in each nest on a shoot. The pupal cocoons of *C. muraseae* are situated outside of the larval nests, usually on the surface of nearby leaves. The white cocoons are 5.0–6.8 mm in length and *c.* 2.0 mm in maximum width, covered with larval frass (Fig. 14A). Unexpectedly, we found the larval nests of *Lobesia aeolopa* Meyrick, 1907 (Tortricidae) on *Podocarpus* similar to those of *C. muraseae*. Differing from *C. muraseae* pupating within cocoon, the pupae of *L. aeolopa* stay exposed.

CHRYSORTHENCHES SMARAGDINA SOHN, SP. NOV.

(FIGS 1D, 2C, F, H)

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Diagnosis: This new species is similar to *C. callibrya* in the male genitalia, but differs from the latter in having the subrectangular valva (obovate in *C. callibrya*) and the subtriangular apex of the saccus (digitate in *C. callibrya*).

Description: Adult (Fig. 1D). Head – Vertex yellowish green, with greenish orange piliform scales on temporal and occipital areas; frons yellowish green. Antenna with scape yellowish green; flagellum pale greyish green, intermixed with dark brown scales basally and distally. Maxillary palpus with first palpomere dark brown; second and third palpomeres dark brown, tinged with pale greenish grey apically. Labial palpus with first palpomere yellowish green on outer surface, pale orange on inner surface, tinged

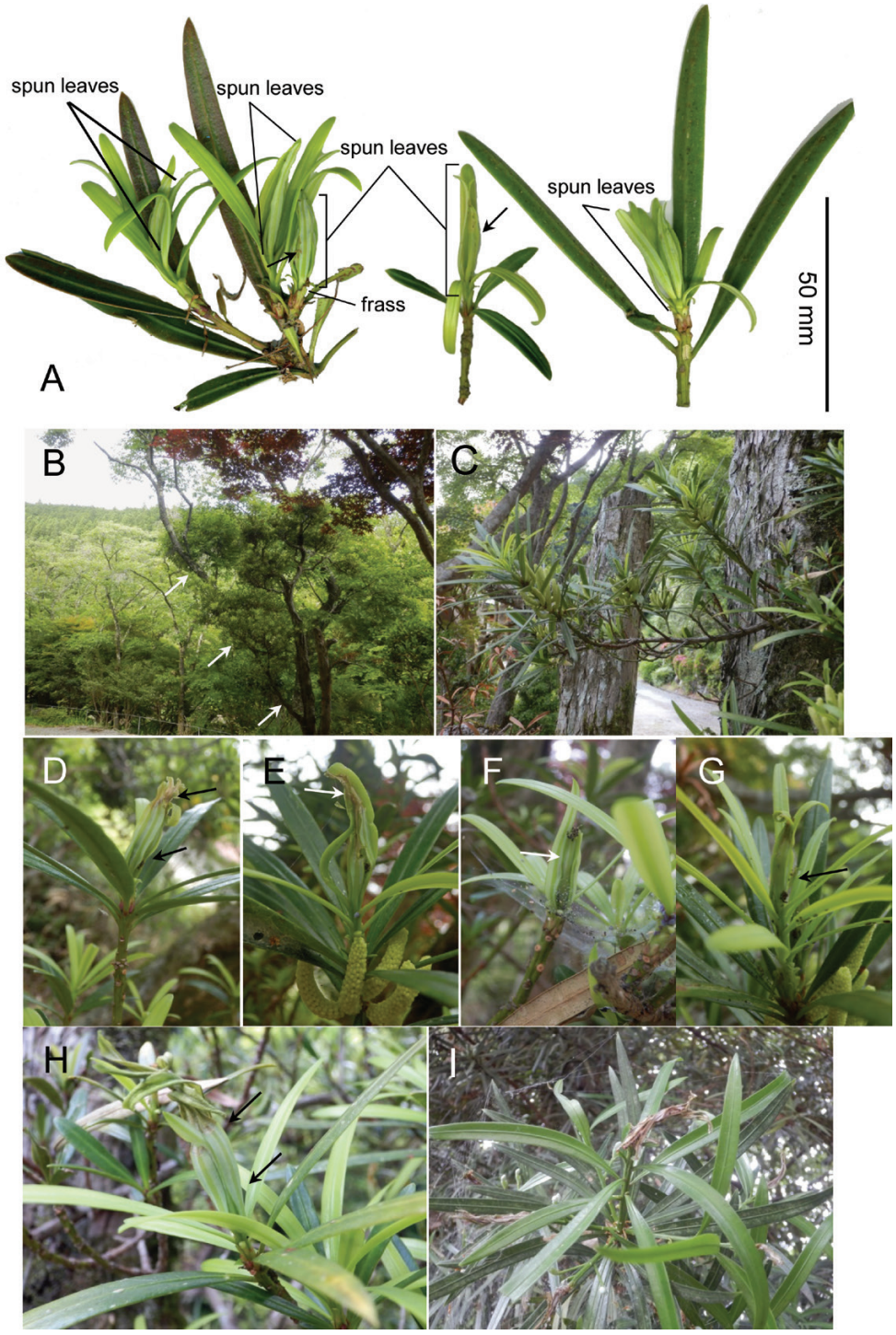

Figure 12. Habitat and feeding habit of *Chrysorthenches muraseae* on *Podocarpus macrophyllus*. A–H, Oku-Kochi-Sanso, Imai, Soni, Nara Prefecture. I, Osaka Prefecture University, Sakai, Osaka Prefecture. A, spun leaves of *Podocarpus macrophyllus*, arrows indicating holes to eject frass. B, habitat and host-plant trees (arrows). C, D, fresh shoots and spun leaves (arrows). E–H, developing stages of spun leaves (arrows). I, Old spun leaves.

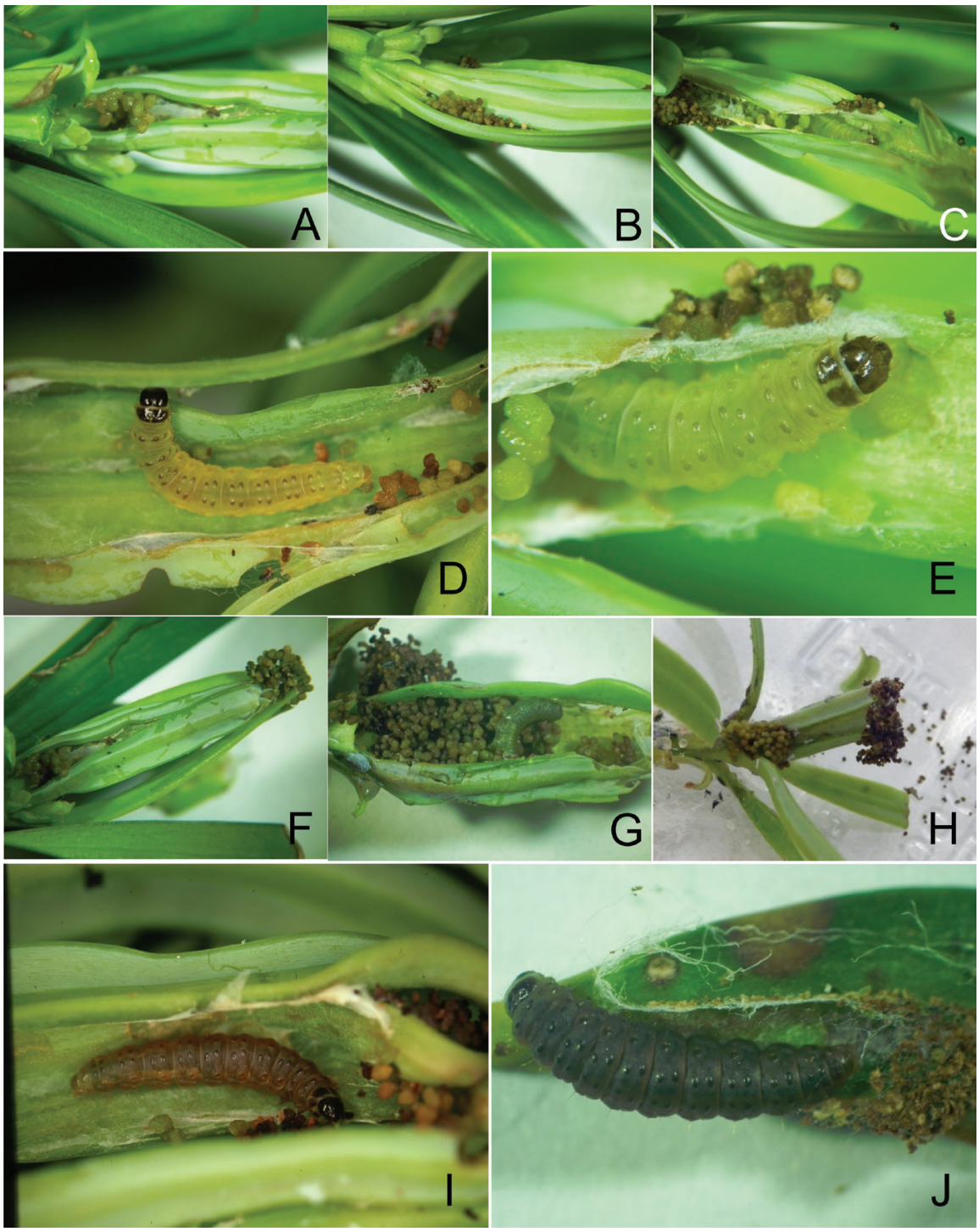

Figure 13. Spun leaves and larvae of *Chrysorthenches muraseae* on *Podocarpus macrophyllus*. A–C, F, H, spun leaves with larval frass. D, E, mature larva. F–I, spun leaves with final instar larva. G, I, inside of spun leaves with final instar larva. J, final instar larva on the cocoon.

with dark brown dorsally; second palpomere 2× longer than first palpomere, dark brown, mottled with yellowish green on outer surface, pale orange on apex and inner surface; third palpomere 2.2× longer than second palpomere, dark brown on outer surface, pale orange on inner surface.

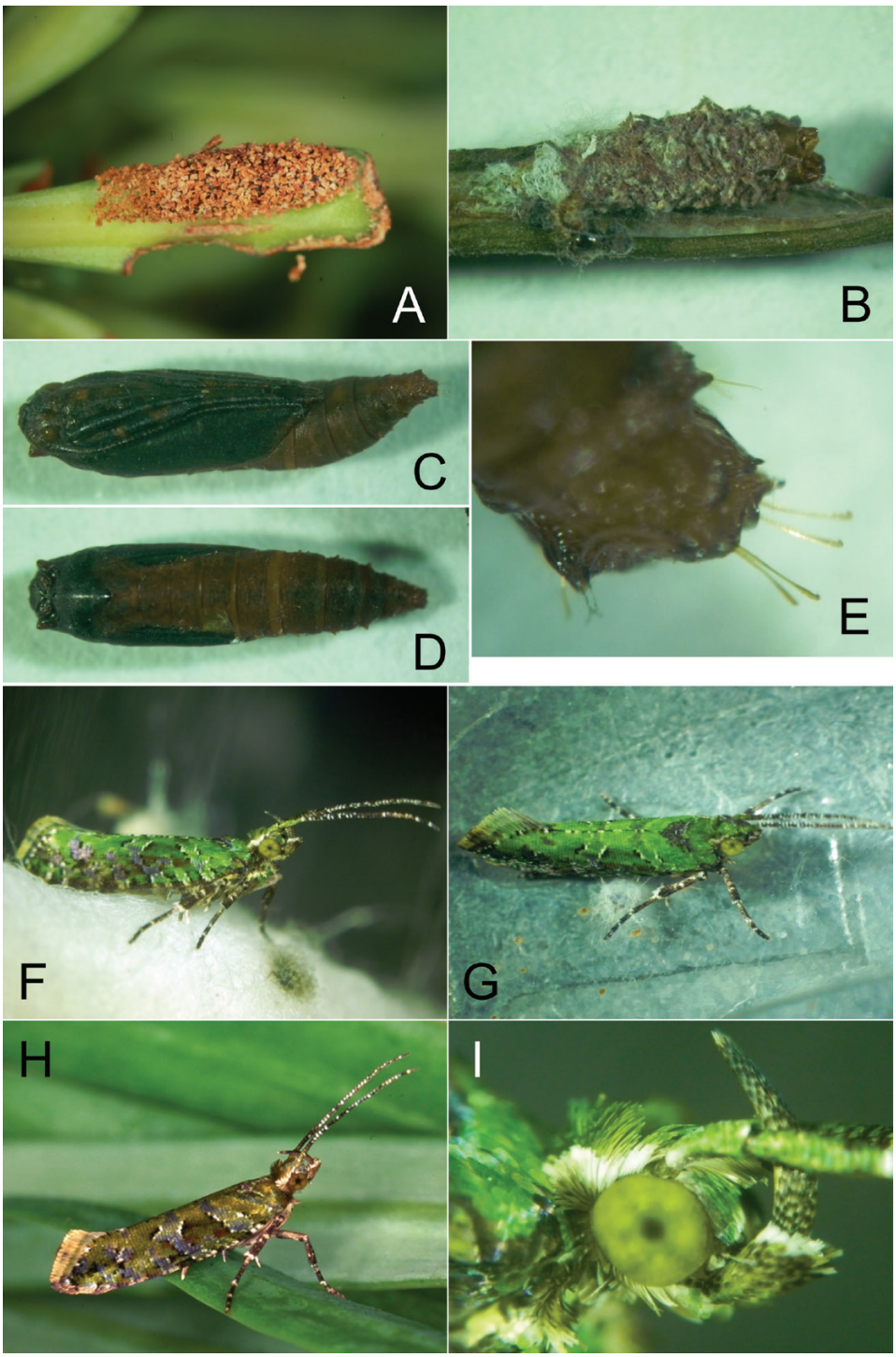

Figure 14. Cocoons, pupae, and resting adults of *Chrysorthenches muraseae*. A, pupal cocoon on leaf surface of *Podocarpus macrophyllus*. B, cocoon with pupal exuvia. C, pupa, ventrolateral view. D, pupa, dorsal view. E, cremaster on A10, ventrolateral view. F–H, resting posture of adult (F, H, lateral view; G, dorsal view). I, close-up of adult head, lateral view.

Thorax – Patagium dark yellowish green, tinged with dark brownish green medially; tegula dark purplish brown; mesonotum dark greenish grey, intermixed with dark brown scales anterolaterally; mesoscutellum dark brown. Foreleg with coxa dark greyish brown; femur dark brown; tibia and tarsomeres

dark brown, with pale orange ring distally. Midleg with coxa and femur pale orange, intermixed with dark greyish brown scales; tibia and tarsomeres dark brown dorsally, pale orange ventrally, with pale orange ring distally. Hindleg with coxa and femur pale greyish orange, sparsely intermixed with brownish grey scales; tibia and tarsomeres dark brownish grey, with pale orange ring distally. Forewing length 5.2 mm (sample number = 1), dark brown, tinged with yellowish green narrowly along costal area and broadly along dorsal area; apical area dark greenish brown; costal strigulae dark brown, irregularly intermixed with small white bars; subbasal and median fascia bar-like, yellowish green, bordered with pale greyish green, and then with black; dorsal margin with dark brown strigulae; fringe pale greyish green. Hindwing greyish brown, paler to base; fringe brownish grey.

Male genitalia (Fig. 2C, F, H) – Uncus slightly concave apically, gradually broadened basally; setose area of tuba analis one-quarter of its length. Valva subrectangular; costa nearly straight in basal two-thirds, slightly curved in distal third; sacculus narrow, one-third as long as ventral margin of valva; membranous disc obliquely round, half as long as valva. Vinculum U-shaped; saccus as long as uncus, slightly narrowed at middle, narrowly round apically. Anellus densely spinose (Fig. 2H). Phallus (Fig. 2F) with broad, needle-like cornutus one-sixth the length of the phallus; spinulate, digitate cornutus two-sevenths as long as the needle-like cornutus; elongate, spinose cornutal zone.

Type: Holotype – 'HOLO- | TYPE' (round label with red edges), 'HOLOTYPE | *Chrysorthenches* | *smaragdina* | Sohn' (red label with black marginal lines), 'N. THAILAND: 1640–1685 m | Nan, Doi Phu Kha NP, | km 33.8 to 34.4, | 26–30.xii.1991', 'B. M. ♂ | Genitalia slide | No. 32892', deposited in NHMUK.

Distribution: Thailand.

Etymology: The epithet is derived from the Greek σμαράγδι, '*smarágdi*', emerald, referring to the broad green patch on the forewing of this new species.

Phylogenetics

Our cladistic analyses of the morphological characteristics of 13 yponomeutoids resulted in a single most parsimonious tree (Fig. 15A: tree length = 74, Ci = 67, Ri = 68). The resulting tree recovers strong support (Fig. 16: JK support = 100, Bremer support = 5) for the monophyly of *Chrysorthenches* against the outgroup, *Orthenches chlorocoma*. The backbone of the tree is divided into two clades. One clade corresponds to the *C. callibrya* species-group (including *C. callibrya* and *C. muraseae*) and is recovered as monophyletic (Fig. 16: JK support = 95, Bremer support = 4). The monophyly of the *C. callibrya* species-group is defined by one unambiguous character (Fig. 15A). The other clade is divided into two subclades, but the supports are weak.

Biogeography

Optimal reconstruction of our DIVA analysis requires two dispersals (Fig. 15B). The result shows three possible scenarios for the ancestral distribution of *Chrysorthenches*: all areas covering (1) New Zealand–Tasmania–eastern Australia–East Asia, (2) New Zealand–eastern Australia–East Asia or (3) Tasmania–eastern Australia–East Asia. The *Chrysorthenches callibrya* species-group branched off from the ancestors and dispersed to East Asia. Subsequently, the *C. porphyritis* species-group diverged and occupied New Zealand and Tasmania. The *Chrysorthenches argentea* species-group radiated within New Zealand.

DISCUSSION

Family association

Affinities between *Chrysorthenches* and *Orthenches* were suggested by Dugdale (1996) who designated the *Orthenches*-group for those two genera. The *Orthenches*-group was defined by Dugdale (1996) based on one synapomorphy: the presence of a unisetose SV setal group on the larval abdominal segment IX. However, not all the members of the group have been examined for that character due to scant larval descriptions (Dugdale, 1996). In the present study, we examined the larvae of *C. muraseae* and observed that they exhibit the synapomorphy of the *Orthenches*-group. That finding strengthens the phylogenetic value of the character defining the group.

The systematic status of the *Orthenches*-group remains poorly understood. Dugdale (1996) suggested its association with Plutellidae, based on larval and pupal characteristics. However, the *Orthenches*-group does not share the synapomorphy for Plutellidae proposed by Kyrki (1984): i.e. the presence of a gnathal process surrounding the anal tube. Sohn *et al.* (2013) recovered an unidentified species of the *Orthenches*-group from South America ('CL67' in their phylogeny) that was nested in a glyphipterigid subfamily, Orthoteliinae. This suggests that the *Orthenches*-group, including *Chrysorthenches*, belong to the subfamily.

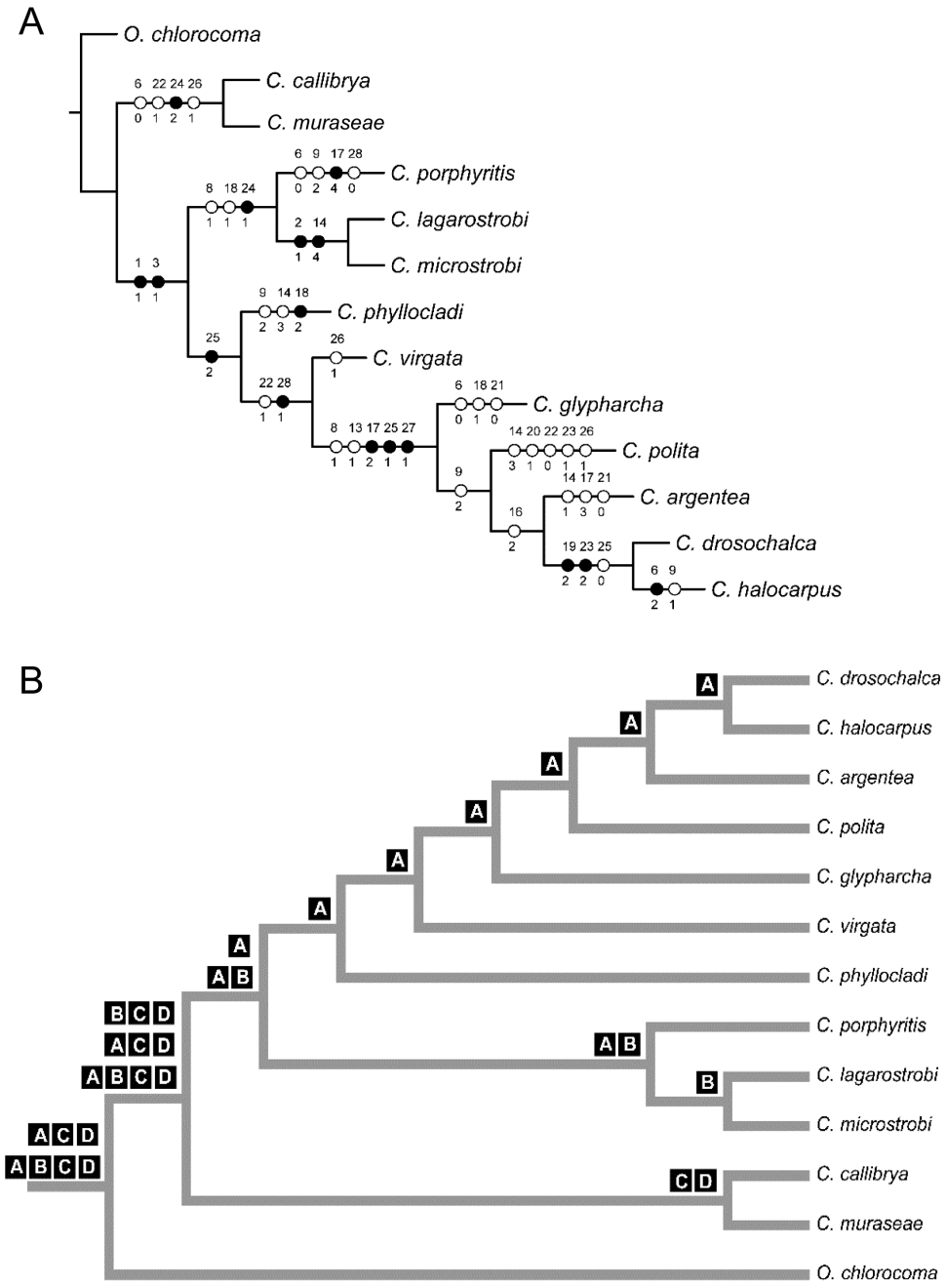

Figure 15. Most-parsimonious cladogram of *Chrysorthenches*. A, optimized character state changes over the most parsimonious tree for 12 species of *Chrysorthenches* and one outgroup, circles on nodes and branches indicating unambiguous character changes: numbers above circles = character numbers in Table 1; numbers in circles = character states. B, result of DIVA analysis over the most parsimonious tree for 12 species of *Chrysorthenches* and one outgroup, letters in black boxes representing four general areas: A = New Zealand; B = Tasmania; C = eastern Australia; and D = East Asia.

Our *COI*-based maximum likelihood tree of ten yponomeutoids also supported their association with Glyphipterigidae (Supporting Information, Fig. S1), although usefulness of one-locus phylogeny for family association is often limited. The Orthoteliinae have been redefined with the addition of putative yponomeutoids, formerly associated with Plutellidae, from the Southern Hemisphere (Heppner, 2005).

Table 1. Morphological characters and character states coded for cladistics analyses. Changes from Dugdale (1996) are indicated in brackets

1:	antennal scape: (0) with awning and pecten; (1) with pecten only.
2:	maxillary palpi: (0) four-segmented; (1) one-segmented.
3:	subtegular tuft: (0) narrow, sinuous; (1) broad, straight.
4:	forewing chorda: (0) present, long; (1) present, short; (2) absent.
5:	uncus: (0) long, linear; (1) short, broad or absent.
6:	apex of uncus: (0) bifid, (1) unifid.
7:	gnathos and socii: (0) present; (1) absent.
8:	anellus: (0) trough-like with paired lateral sclerites; (1) a single spinulate sheath; (2) sheath divided transversely into proximal and distal parts.
9:	spinulation on anellus: (0) absent; (1) uniformly spinulate; (2) with apical outstanding spinules.
10:	vinculum and saccus: (0) V- or U-shaped; (1) T-shaped.
11:	posterior margin of saccus: (0) straight or concave; (1) convex.
12:	[modified] lobe on male sternum VIII: (0) paired; (1) single, V-shaped.
13:	valva structure: (0) undivided; (1) divided transversely at right angle to costa; (2) divided obliquely.
14:	outer scale-tuft of distal part of valva: (0) absent; (1) setose; (2) comprising broad persistent scales; (3) comprising scales and one seta; (4) as line of scales.
15:	phallus shape: (0) basally swollen; (1) uniformly cylindrical.
16:	apex of phallus: (0) simple; (1) with a ventral mesal process; (2) with lateroventral process.
17:	apical carina of phallus: (0) absent; (1) acuminate; (2) acute; (3) hooked; (4) with a thorn patch.
18:	number of cornuti: (0) four or more; (1) two or three; (2) one; (3) none.
19:	tergopleural lobe: (0) arising perpendicularly, separate dorsally; (1) arising obliquely, largely fused dorsally.
20:	sterigma: (0) sunken; (1) on a papilla.
21:	antrum: (0) parallel-sided or barrel-shaped; (1) funnel-shaped.
22:	ductus seminalis: (0) arising dorsally; (1) arising ventrally.
23:	ductus bursae: (0) tubular; (1) sinuous, furrowed; (2) cumuloid, furrowed, wider than corpus bursae; (3) gradually widened to corpus bursae.
24:	[modified] sclerotization of ductus bursae: (0) unsclerotized; (1) partly sclerotized; (2) entirely sclerotized.
25:	length of ductus bursae: (0) longer than corpus bursae; (1) equal to corpus bursae; (2) shorter than corpus bursae.
26:	[added] inception of ductus seminalis: (0) on ductus bursae; (1) on corpus bursae.
27:	appendix bursae on corpus bursae: (0) absent; (1) present.
28:	signum: (0) single; (1) double; (2) absent.
29:	larval spiracle VIII: (0) separate from seta SD pinacula or scobinate zone; (1) included on SD pinacula or scobinate zone.
30:	[added] larval thoracic L1 and L2 seta: (0) on same pinaculum; (1) on separate pinacula.

Generic association

Chrysorthenches callibrya was originally combined with *Diathryptica* (type species: *D. proterva*) by Turner (1923). In the present study, we examined the type species of *Diathryptica* and found three major differences: the chorda of the forewing, the division of the male valva and the sclerotization of the ductus bursae in the female genitalia. The *C. callibrya* species-group includes *C. callibrya* and two allied new species. These three species share the diagnostic characteristics of *Chrysorthenches* as proposed by Dugdale (1996), including, in both sexes, the lack of a dense awning of scales on the antennal scape, the long apical segment of the labial palpus, the lack of socii and gnathos, the presence of a V-shaped mesal lobe on the male sternum VIII, and the absence of a sclerotized costa on the membranous distal part of the valva in the male genitalia. In addition, our examination of the larvae of *C. muraseae* revealed four characteristics associating it with *Chrysorthenches*: (1) seta V1 on the meso- and metathorax present at the ventral edge of each coxa, (2) a spiracle on abdominal segment VIII on the SD1 pinaculum, posterior to the SD1 seta, (3) abdominal segments VII and VIII with one SV seta and (4) abdominal segment IX with setae D1 and D2 on the same broad pinaculum. These shared characteristics justify a generic transfer of *Diathryptica callibrya* to *Chrysorthenches* and the assignment of the two new

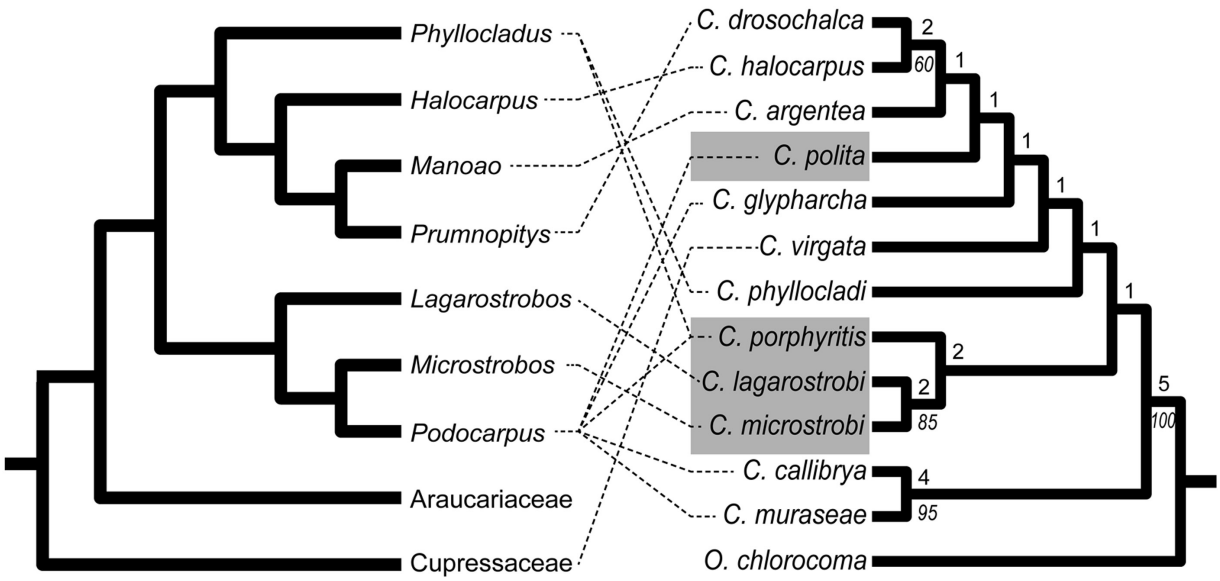

Figure 16. Host associations between *Chrysorthenches* and conifers. Left and right trees represent the latest working phylogenies of Podocarpaceae and *Chrysorthenches*, respectively. Host associations are indicated by dotted lines. Numbers above and below nodes of right tree indicate the Bremer supports and the bootstrapping supports (only >50 shown), respectively. Shaded boxes show the members of the '*porphyritis*' lineage *sensu* Dugdale (1996).

species mentioned in this study to the same genus. The former finding was also consistent with our *COI* phylogeny result (Supporting Information, Fig. S1).

Our cladistic analysis supported the monophyly of the *C. callibrya* based on one synapomorphy, the entirely sclerotized ductus bursae (24:2 in Table 1), and three homoplastic characters: the bifid uncus (6:0 in Table 1), the ventrally arising ductus seminalis (22:1 in Table 1) and an enception of the ductus seminalis on the corpus bursae (26:1 in Table 1). The fast and slow character optimizations in the cladistics study recognized two additional synapomorphies: the presence of a short chorda on the forewing (4:1 in Table 1) and larval thoracic L1 and L2 setae arising on separate pinacula (30:1 in Table 1) (Supporting Information, Fig. S2). The larval features of *C. muraseae* differed from those of the *C. argentea* and the *C. porphyritis* species-groups in the presence of thin SD1 setae on the mesothorax and the abdominal segment VIII, and an SV setal group on abdominal segments I and II bisetose. These characters can also serve as synapomorphies of the *C. callibrya* species-group, but more information on larval characters is needed to confirm their phylogenetic value.

Our cladogram (Fig. 15A) for 12 species of *Chrysorthenches* differed from that presented by Dugdale (1996). The most critical dissimilarity was in the position of *C. polita* (Philpott, 1918), which was placed in the *C. argentea* species-group in our study but in the *C. porphyritis* species-group by Dugdale (1996). The positions of *C. glypharcha* (Meyrick, 1919) and *C. phyllocladi* Dugale, 1996 were also discordant between the two studies. All these differences may be the result of our modifications and additions of characteristics to the data matrix presented by Dugdale (1996). Thus, we analysed another data matrix (J. -C. Sohn, unpublished) that included the same character-set and coding as that used by Dugdale (1996). The analysis still resulted in a different cladogram from that described by Dugdale (1996), possibly due to the additions of *C. callibrya* and *C. muraseae*. In fact, the relationships among the species-groups in *Chrysorthenches* are ambiguous, because those depend on the characteristics of the ductus bursae and the ductus seminalis, which are membranous and thus versatile. In accordance with this ambiguity, the backbone relationships of *Chrysorthenches* were poorly supported by the results of our study (1–2 range in Bremer supports: Fig. 16). Thus, the phylogenetic relationships within *Chrysorthenches* need further attention.

PODOCARPACEAE ASSOCIATION

Chrysorthenches is distinguished from other lineages of the *Orthenches*-group by a trophic association with conifers. Larval host-plants are known for only nine of the 12 species in *Chrysorthenches* and for two congeners whose larval hosts were inferred from vegetation in which the adult moths were observed (Dugdale,

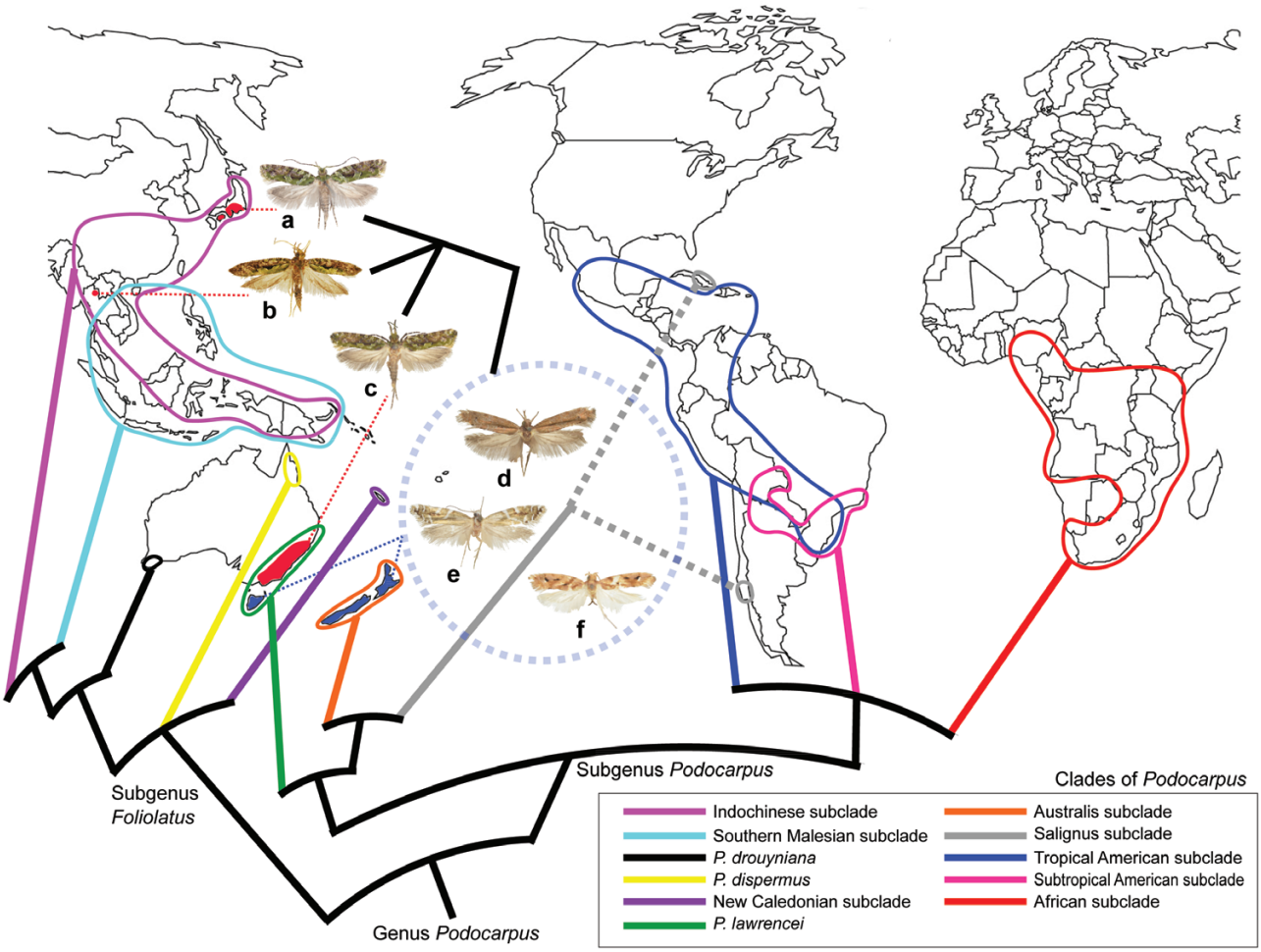

Figure 17. Biogeography of *Chrysorthenches* and *Podocarpus*. Cladogram of *Podocarpus* is redrawn from Knopf *et al.* (2012). Areas filled with colours are corresponding the distributional range of *C. callibrya* species-group (red) and two other species-groups (blue). Dotted lines connect the representative species of *Chrysorthenches* with their distributions: A, *C. muraseae*; B, *C. smaragdina*; C, *C. callibrya*; D, *C. porphyritis*; E, *C. glypharcha*; F, *C. virgata*.

1996). These records indicate that all species of *Chrysorthenches*, except for *C. virgata* (Philpott, 1920), which feeds on Cupressaceae, and *C. smaragdina*, whose larval hosts are unknown, are associated with Podocarpaceae. Among the Podocarpaceae, the majority of *Chrysorthenches* species utilize the largest genus of that family, *Podocarpus*. The members of the *C. callibrya* species-group seem also to be associated with *Podocarpus*. The host-plants of *C. muraseae* are reported from the present study, while an association of *C. callibrya* with *Podocarpus* could be inferred from Dugdale's (1996) field observation at Charlotte Pass, New South Wales, Australia. It is likely that *C. smaragdina* also feeds on *Podocarpus*, given the host associations of two other species in the same species-group and the occurrence of *Podocarpus* in Thailand.

Chrysorthenches utilize seven genera of Podocarpaceae and those genera are not necessarily closely related (Fig. 16). This may suggest that most, if not all, of their host associations have resulted from sequential colonization, not co-evolution, as Dugdale (1996) has already pointed out. Podocarpaceae-feeding species of *Chrysorthenches* were associated with only one or two plant genera, while *Podocarpus* was the genus on which most species of *Chrysorthenches* feed (Fig. 16). The *C. callibrya* species-group, earliest diverging in *Chrysorthenches*, also uses *Podocarpus* as a larval host. Taken together, these observations may suggest that ancestral *Chrysorthenches* colonized *Podocarpus* and later shifted to other podocarp genera. Among the *Podocarpus*-feeding *Chrysorthenches*, the New Zealand species are associated exclusively with the *Australis* subclade in the subgenus *Podocarpus*. On the other hand, the host-plants of the *C. callibrya* species-group belong to two *Podocarpus* subgenera (Fig. 17).

The trophic associations between *Chrysorthenches* and Podocarpaceae are noteworthy, given the limited numbers of insects that utilize these plants. Other than *Chrysorthenches*, few lepidopterans feed on Podocarpaceae and they include macroheterocerans such as Erebidae (Lymantriinae), Geometridae and Lasiocampidae and some microlepidopterans (Tortricidae, Gracillariidae, Lecithoceridae and Pyralidae) worldwide (Okelo, 1972; Singh *et al.*, 1978; Oku, 1979; Murase, 2005; Costa & Boscardin, 2014; Liu *et al.*, 2018). Most of these moths are generalist larval feeders, but *Makivora hagiyai* Oku, 1979 (Tortricidae) is a specialist on *Podocarpus*. *Chrysorthenches* are comparable to *Milionia* Walker, 1854 (Geometridae) in that all or nearly all members are associated with Podocarpaceae. Yasui (2001) found that *Milionia* were able to sequester the phytochemicals of *Podocarpus* for protection against predatory stink bugs. Like *Milionia*, the adults of *Chrysorthenches* are colourful, but it is unknown if they can also take advantage of a chemical defence system.

Biogeography and host–plant tracking

The high trophic fidelity of *Chrysorthenches* with Podocarpaceae hints that the radiation of *Chrysorthenches* may have been affected by the host-plants. Recent studies have suggested that Podocarpaceae originated in Gondwana during the Triassic–Jurassic periods (Biffin *et al.*, 2011; Rothwell *et al.*, 2012; Escapa *et al.*, 2013). Furthermore, Lu *et al.* (2014) estimated the origination of the extant podocarp genera to be in the Early Cretaceous. The largest genus of Podocarpaceae, *Podocarpus*, is one of the representative groups in the Antarctic flora that originated in the cold and wet climate of southern Gondwana (Page, 1990; Mill, 2003). Quiroga *et al.* (2016) dated the divergence of two subgenera of *Podocarpus* as within the Late Cretaceous–Early Palaeogene. The surviving lineages of Podocarpaceae radiated into the tropical regions, not earlier than 30 million years ago or the Late Eocene (Cernusak *et al.*, 2011).

Extant species of *Chrysorthenches* occur only in New Zealand, eastern Australia, Tasmania, South-East Asia and Japan (Fig. 17). The highest diversity among the *Chrysorthenches* species (eight of 13 total species) is observed in New Zealand. This, from the viewpoint of traditional dispersal biogeography, would suggest that New Zealand is the centre of origin for *Chrysorthenches*. However, the result of our DIVA analysis (Fig. 15B) favoured a broad distribution of ancestral *Chrysorthenches* that subsequently split according to palaeogeographical changes. Regarding their presence in Tasmania and Australia, the *Chrysorthenches*–conifer association may pre-date the opening of the Tasman Sea, which began about 80 million years ago (Molnar *et al.*, 1975). The distributional range of *Chrysorthenches* occupies only a small proportion of the distribution of Podocarpaceae. This difference may indicate that *Chrysorthenches* evolved long after the Podocarpaceae radiation that pre-dated the splitting of the Gondwanan subcontinents. Another, less plausible, explanation would be the extensive extinction of *Chrysorthenches*, except in the Australasian region. Direct evidence for this hypothesis does not exist to our knowledge, but a leaf-mine trace left by a larva that was presumed to belong to *Chrysorthenches* in Wilf *et al.* (2005) may indicate their existence on other Gondwana subcontinents until at least 52 million years ago.

The *Chrysorthenches callibrya* species-group differs from the other two congeneric species-groups as the distribution of the former is not restricted to the Australasian region (Fig. 17). Moreover, three species of the species-group have disjunctive distributions: eastern Australia for *C. callibrya*, Thailand for *C. smaragdina* and Japan for *C. muraseae*. Our cladogram recovered this species-group as the earliest diverging with respect to other *Chrysorthenches* (Fig. 17). This poses questions, such as: why have no members of the species-group been reported from west and north Australia, Papua New Guinea and other islands spanning the Wallacea zone? Further inventory of *Chrysorthenches* in the Australasian region may help to fill these gaps.

The collective distributional range of the *C. callibrya* species-group corresponds to that of the island arc system connecting Australia and East Asia. This island system has facilitated trans-Wallacean radiation in many organisms through faunal exchanges between Australia and Asia during 15–20 million years ago (Sklenarova *et al.*, 2013). The *C. callibrya* species-group may have followed this route, but their direction was distinctively northward, as reconstructed from our DIVA analysis (Fig. 15B). Most biogeographic studies in Australia and Asia have suggested southward dispersals (De Jong, 2001), although there are a few examples indicating northward radiations; for example, the plant family Proteaceae (Truswell *et al.*, 1987) and skipper butterflies of the *Taractrocera*-group (De Jong, 2001).

The *Chrysorthenches callibrya* species-group may have evolved as a result of their colonization of *Podocarpus* in the Cenozoic Era. Given the distributions of their sister groups, it would seem plausible that ancestors of the *C. callibrya* species-group evolved as one of the lineages resulting from the radiation of *Chrysorthenches* before the separation of New Zealand and Australia in the Middle–Late Cretaceous. In such a scenario, this lineage would have dispersed toward South-East Asia, as represented by the occurrence of *C. smaragdina* in Thailand. Such an event could

have happened only after the *Podocarpus* species had radiated into tropical Asia in the Late Eocene, about 30 million years ago (Cernusak *et al.*, 2011) and after the first opportunity for faunal exchange between Australia and Asia approximately 25 million years ago (De Jong, 2001). Consistent with these requirements, the emergence of host-plant clades for the *C. callibrya* species-group were estimated to occur in the Eocene–Oligocene periods (Quiroga *et al.*, 2016). Pre-existence of host-plants was a prerequisite for the *C. callibrya* species-group crossing the Wallacea zone, like other lepidopteran examples (Beck *et al.*, 2006). *Chrysorthenches muraseae* may represent the currently understood terminus of the sequential radiation for the *C. callibrya* species-group. It is known that the island arc system crossing the Wallacea zone reached Japan in the Late Miocene or in the Pliocene (De Jong, 2001).

Recent advances in biogeography allow the differentiation of dispersal from vicariance and the determination of possible divergence dates using molecular data (Trewick, 2000; Trewick & Wallis, 2001; Waters & Roy, 2004; de Queiroz, 2005). This type of approach would be necessary to better explain the curious distribution of *Chrysorthenches*.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's website:

Figure S1. The maximum likelihood tree for *COI* barcodes of ten yponomeutoids, numbers above nodes indicating bootstrapping supports.

Figure S2. The optimized character state changes over the tree in Figure 15A. A, fast optimization. B, slow optimization. Closed circles indicate synapomorphies; open circles indicate homoplasies and reversals. The numbers above and within circles denote the character numbers, shown in Table 1, and character states, respectively.

Table S1. Accession numbers of cytochrome oxidase subunit I (*COI*) sequences in GENBANK.

Appendix S1. Data matrix in nexus format for our cladistics analyses with the morphological characters of 13 yponomeutoids.