Zootaxa 3557: 1–19 (2012)
www.mapress.com/zootaxa/

Article

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

urn:lsid:zoobank.org:pub:6E0C880F-D6B3-4C70-AD62-D020662E8C1A

Revalidation of *Oliera* Brèthes (Lepidoptera: Cecidosidae) based on a redescription of *O. argentinana* and DNA analysis of Neotropical cecidosids

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Abstract

Larvae of *Oliera argentinana,* Brèthes 1916 (Lepidoptera: Cecidosidae) were rediscovered inducing spindle-shaped galls enclosed within swollen stems of *Schinus* (Anacardiaceae) in central Argentina and Rio Grande do Sul, the southernmost state of Brazil. Male, female, immature stages, and plant galls of *O. argentinana* are redescribed, using optical and scanning electron microscopy. The genus *Oliera* Brèthes, 1916, previously a junior synonym of *Cecidoses* Curtis, 1835, is revalidated, by comparing morphological characteristics within the family and through an analysis of mitochondrial (COI) DNA sequences, including putative members of the four Neotropical cecidosid genera. Information on preliminary Cecidosidae phylogeny and taxonomy is also provided.

Key words: Gall moths, *Schinus*, Anacardiaceae, Neotropics

Introduction

Cecidosidae comprise a small group of ancient, poorly known moths found in austral South America, South Africa, and New Zealand. With the exception of the recently described *Xanadoses nielseni* Hoare & Dugdale, 2003, which is a bark-miner of several New Zealand bark trees, all are gall-makers on Anacardiaceae (Pellmyr & Leebens-Mack 1999). In South America, they are represented by four genera; *Dicranoses* Kieffer & Jörgensen, 1910 with two species; and the monotypic *Cecidoses* Curtis, 1835, *Eucecidoses* Brèthes, 1916, and *Oliera* Brèthes, 1916 (Davis 1998; Hoare & Dugdale 2003). Their galls have been reported from populations located in Chile, Argentina, Uruguay, and Southern Brazil, all associated with *Schinus* (*e.g*., Curtis 1835; Kieffer & Jörgensen 1910; Tavares 1915; Brèthes 1916; Jörgensen 1917; Wille 1926; Houard 1933; Biezanko *et al*. 1957; Biezanko 1961; Becker 1977; Núñez & Sáiz, 1994; Sáiz & Núñez 1997).

Apart from the detailed work carried out by Wille (1926) on the gall morphology and life history of *Cecidoses eremita* Curtis, there exists little knowledge on cecidosid biology. Taxonomic studies on South American species are largely restricted to their original descriptions provided by Curtis (1835), Kiefer & Jörgensen (1910), and Brèthes (1916). Becker (1977) and Parra (1998) proposed *Eucecidoses* and *Oliera* as synonyms of *Cecidoses*, respectively. However, these synonymies have not been universally adopted due to the lack of information on their phylogeny and possible confusion related to the life history and identity of *Oliera argentinana* Brèthes (Davis 1998; Hoare & Dugdale 2003). The present study addresses these questions, with emphasis on the latter.

Accepted by J.-F Landry: 23 Oct. 2012; published: 21 Nov. 2012

Originally Brèthes (1916), based on material from Argentina, described the gall induced by *O. argentinana* as restricted to feeding under the bark of terminal branches, without developing an external, fruit-like chamber. Based on material from Chile, Parra (1998) re-described the gall of what he identified as *Cecidoses argentinana* (Brèthes) as bearing a short stalk with a chamber protruding externally on the branch. Parra did not study the type material of *O. argentinana*, which led him to misidentify the species and to describe a different taxon under that name. During our survey of Cecidosidae in southern South America over the last five years, we have collected and reared abundant gall material that consistently corresponds to the original description of Brèthes (1916). Our findings contrast with those of Parra (1998) from both gross morphology and fine structural details regarding the larva, pupa, and adult stages of the gall inducer, in addition to the differing gall morphology.

This study is the first of a planned series on the phylogeny and taxonomy of Neotropical cecidosids. Using both optical and scanning electron microscopy, we confirm the original identity of *O. argentinana*, and provide detail descriptions and illustrations of the gall, larva, pupa, and adult male and female. By comparing morphological characteristics within the family and by conducting an analysis of mitochondrial (COI) DNA sequences of all putative members of the four known Neotropical cecidosid lineages, we provide support for re-validation of the genus *Oliera* and make a preliminary assessment of the putative monophyly of the Cecidosidae.

Materials and Methods

Collecting and rearing. *O. argentinana* specimens used in the study were reared from galls in transparent plastic bags at room temperature in Laboratório de Morfologia e Comportamento de Insetos, Departamento de Zoologia, Universidade Federal do Rio Grande do Sul (UFRGS), Porto Alegre city, Brazil. They were collected from small sections of apical branch cuttings gathered from *Schinus polygamus* plants in Caçapava do Sul and Canguçu municipalities, State of Rio Grande do Sul, Brazil. Last instar larvae and pupae were obtained by dissecting developed galls under a stereomicroscope. For morphological studies, specimens were fixed with Dietrich´s fluid and preserved in 75% ethanol. For DNA analyses, they were preserved in 96% EtOH at –20°C.

Morphology. For observations on gross morphology, specimens were cleared in a 10% potassium hydroxide solution (KOH) and slide-mounted either in glycerin jelly or Canada balsam. At least five specimens were used for the descriptions of each life stage. Selected structures were observed with the aid of a Leica® M125 stereomicroscope, and photographed with a Sony® DSC-H10 digital camera. Vectorized line drawings were made with the software CorelDraw® X4, using the corresponding digital images as a guide. Measurements were made with an attached ocular micrometer; values are presented as mean $\pm$ standard deviation unless noted otherwise.

For scanning electron microscope examination, specimens were dehydrated in a Bal-tec® CPD030 critical-point dryer, mounted with double-sided tape on metal stubs, and coated with gold in a Bal-tec® SCD050 sputter coater. They were examined and photographed in a JEOL® JSM5800 scanning electron microscope at the Centro de Microscopia Eletrônica (CME) of UFRGS.

Molecular analysis. Total genomic DNA was extracted from larval tissue using the CTAB method (Doyle & Doyle 1987). In addition to *O. argentinana,* other Neotropical cecidosids [*Dicranoses congregatella* (Brèthes), *Eucecidoses minutanus* Brèthes*, Cecidoses eremita* Curtis and an additional taxon not yet assigned to any cecidosid species, and herein referred as Cecidosidae sp.] were incorporated in the analysis in order to assess phylogenetic relationships among lineages. Species of Prodoxidae [*Greya variabilis* Davis & Pellmyr, *Prodoxus aenescens* Riley and *Tetragma gei* Davis & Pellmyr] and Adelidae (*Adela septentrionella* Walsingham), both sister lineages of Cecidosidae (Peelmyr & Leebens-Mack 1999) were used as outgroups, and the corresponding sequences downloaded from GenBank (Table 1). Cecidosid specimens from different localities (Argentinean and Brazilian populations) were surveyed to amplify part of the mitochondrial gene cytochrome oxidase I (COI—626 bp) using primers and conditions described by Folmer *et al*. (1994). PCR products were purified using Exonuclease (GE Healthcare Inc.) and Shrimp Alkaline Phosfatase (SAP), sequenced with a BigDye chemistry and analyzed on an ABI3730XL (Applied Biosystems Inc.). Chromatograms obtained from the automatic sequencer were read and sequences were assembled using the software CodonCode Aligner (CodonCode Corporation). All sequences have been deposited in GenBank (Table 1).

TABLE 1. Specimens used to reconstruct the phylogenetic relationships of Neotropical cecidosids.

Taxa	Voucher*	Locality	Genbank Acession Number
ADELIDAE			
Adela septentrionella	PLIC 05.62	USA	EU884115
CECIDOSIDAE			
Cecidoses eremita	-	Argentina: Neuquén	U04881
	LMCI 10-13-1	Brazil: Canguçu	GQ305452
	LMCI 10-13-3	Brazil: Canguçu	GQ305454
	LMCI 10-13-4	Brazil: Canguçu	GQ305453
	LMCI 10-13-5	Brazil: Canguçu	GQ305455
	LMCI 163-1A	Argentina: Mendoza	JQ783125
	LMCI 163-1B	Argentina: Mendoza	JQ783126
Dicranoses congregatella	LMCI 5-10	Brazil: Canguçu	GQ305456
	LMCI 163-11A	Argentina: San Luis	JQ783127
	LMCI 163-11B	Argentina: San Luis	JQ783128
Eucecidoses sp.	LMCI 14-40	Brazil: Curitiba	GQ305446
	LMCI 14-41	Brazil: Curitiba	GQ305445
	LMCI 14-42	Brazil: Curitiba	GQ305444
	LMCI 14-43	Brazil: Curitiba	GQ305443
	LMCI 14-44	Brazil: Curitiba	GQ305442
Eucecidoses minutanus	LMCI 163-21A	Argentina: Mendoza	JQ783129
	LMCI 163-21B	Argentina: Mendoza	JQ783130
	LMCI 163-21C	Argentina: Mendoza	JQ783131
	LMCI 163-21D	Argentina: Mendoza	JQ783132
Oliera argentinana	LMCI 6-11	Brazil: Canguçu	GQ305448
	LMCI 6-12	Brazil: Canguçu	GQ305451
	LMCI 6-13	Brazil: Canguçu	GQ305450
	LMCI 11-33	Brazil: Caçapava do Sul	GQ305447
	LMCI 11-34	Brazil: Caçapava do Sul	GQ305449
	LMCI 163-13A	Argentina: Mendoza	JQ783133
Cecidosidae sp.	LMCI 163-14A	Chile: Rungue	JQ783134
	LMCI 163-14B	Chile: Rungue	JQ783135
PRODOXIDAE			
Tetragma gei	-	USA: Asotin, WA	AF150913
Prodoxus aenescens	-	USA: Tulare, CA	AF150915
Greya variabilis	-	USA: Clallam, WA	AF150909

* PLIC = Pellmyr Lab Insect Collection; LMCI = Laboratório de Morfologia e Comportamento de Insetos

Phylogenetic trees were constructed using both distance (Neighbor-joining; NJ) and maximum likelihood (ML) in the softwares PAUP * 4.0b2a (Swofford 1999) and PHYML 3.0 (Guindon *et al*. 2010), respectively. The program JMODELTEST (Posada 2008) was used to estimate the substitution model GTR + G [General Time-Reversible model (Rodríguez *et al*. 1990), with gamma distribution (G)] for ML according to the Akaike Information Criterion (AIC). Monophyly-confidence limits were assessed with the bootstrap method (Felsenstein 1985) at 50% cut-off after 1000 bootstrap iterations. For comparison, we also conducted Maximum Parsimony (MP) analyses in PAUP*, using a heuristic search with TBR branch swapping. The consensus tree was calculated

using 50% majority rule, and confidence in branches was assessed by bootstrapping with TBR branch swapping (1000 replicates). We also analyzed the genetic distance using Kimura 2-parameters model (Kimura 1980) procedure, with 1000 of bootstrap replication, between groups defined as: Adelidae (n=1), *Cecidoses* (n = 6), Cecidosidae sp. (n =2), *Dicranoses* (n = 3), *Eucecidoses* (n = 8), *Oliera* (n = 6), and Prodoxidae (n = 3).

Museum collections. Abbreviations of Institutions from which specimens were examined are:

DZUP Coll. Padre Jesus S. Moure, Departamento de Zoologia, Universidade Federal do Paraná, Curitiba, Paraná, Brazil

LMCI Laboratório de Morfologia e Comportamento de Insetos, Universidade Federal do Rio Grande do Sul, Porto Alegre, Rio Grande do Sul, Brazil.

MACN Museu Argentino de Ciencias Naturales "Bernardino Rivadavia", CONICET, Buenos Aires, Argentina.

Results

Oliera argentinana Brèthes, 1916

Figs. (1–10)

Material examined. Data are listed as they are found in the labels. Lectotype: ♂, B. Aires, Argentina, 25 XI. 915, J. B., pinned, genitalia on slide 4477, D. R. Davis (MACN) [present designation]. Guaritas, Caçapava do Sul, Rio Grande do Sul (RS), Brazil, 30°50'15"S, 53°30'04"W, November 2007, G.R.P.Moreira & G.L. Gonçalves colls., 7♀♀, 8♂♂, pinned (LMCI 11-3-24 to 38), reared from galls collected on *Schinus polygamus*. With the same collection data: 1♀, 2♂♂, pinned (LMCI 11-3-39 to 41), donated by the senior author to DZUP (DZ 22.349, 22.359 and 22.369); near 50 galls (LMCI 11-3), 6 dissected adults (LMCI 11-3-21) and 23 pupae (LMCI 11-3-22), fixed and stored in 96% ethanol. Rincão da Ronda, Canguçu, RS, Brazil, 31°05'58''S, 52°52'06''W, October 2007, G.R.P.Moreira coll., 22 last instar larvae (LMCI 6-1 to 15; 6-20; 6-21) and 8 pupae (LMCI 6-18, 6-19), fixed and stored in 96% ethanol. With the same collection data, September 2007, 10 larvae (LMCI 5-3), fixed and stored in 96% ethanol. Quebrada N. Estación Aforadora, Luján de Cuyo, Mendoza, Argentina, 32°53'40''S, 69°13'49''W, September 24, 2011, G. San Blas coll., 2 larvae and 1 pupa (LMCI 163-13), dissected from galls on *Schinus fasciculatus*, fixed and stored in 96% ethanol.

Other cecidosid examined. *Dicranoses congregatella*: Rincão da Ronda, Canguçu, RS, Brazil, 31°05'58''S, 52°52'06''W, November 11, 2007, 3♀♀, 1♂, pinned (LMCI 6-31 to 34), G.R.P.Moreira coll., reared from galls collected on *Schinus polygamus*. With the same collection data, July 20, 2007, several galls (LMCI 3-13), 10 larvae (LMC 3-1 to 10), fixed and stored on ethanol 96%; September 9, 2007, 9 last instar larvae (LMCI 5-4), 43 pupae (LMCI 5-5; 5-6), fixed in Dietrich´s fluid and stored in ethanol 70%. Vila de Palmas, Bagé, RS, Brazil, 30°58'55''S, 53°37'10''W, November 17, 2007, G.R.P. Moreira & G.L.Gonçalves colls., 16 pupae (LMCI 12-33-1 to 16), dissected from galls collected from *S. polygamus*, fixed and stored in ethanol 96%. Av. Los Nogales y La Quinta, El Chorrillo Juana Koslay, San Luis, Argentina, 33°17'8''S, 66°15'32'W, October 10, 2009, G. San Blas coll., 4 larvae (LMCI 163-7), dissected from galls on *Schinus johnstonii*, fixed and stored in 70% ethanol. Frente Reserva Florofaunística Merlo, San Luis, Argentina, 32°21'22'S, 64°57'33'W, October 21, 2009, G. San Blas coll., 6 pupae (LMCI 163-11), dissected from galls on *Schinus johnstonii* fixed and stored in 70% ethanol. *Cecidoses eremita*: Rincão da Ronda, Canguçu, RS, Brazil, 31°05'58''S, 52°52'06''W, March 27, 2005, 2♀♀, 1♂, pinned (LMCI 2-13 to 15), G.R.P.Moreira coll., reared from galls collected on *Schinus polygamus* (Cavanilles) Cabrera. With the same collection data, November 15, 2007, 22 last instar larvae (LMC 10-13-1 to 21). Morro Maximiano, Eldorado do Sul, RS, Brazil, 30°10'47''S, 51°23'33''W, March 13, 2007, G.R.P. Moreira & G.L.Gonçalves colls., 4 last instar larvae (LMCI 16-44), 20 pupae (LMCI 16-45), fixed in Dietrich´s fluid and stored in ethanol 70%. Potrerillos, Cerca Estación Aforadora, Luján de Cuyo, Mendoza, Argentina, 32°55'08''S, 69°14'34''W, November 14, 2009 (LMCI 163-1; 2 larvae) and March 18, 2010 (LMCI 163-3; 1 pupa), G. San Blas coll., dissected from galls on *Schinus fasciculatus*, fixed and stored in 96% ethanol. *Eucecidoses* sp.: Parque Passaúna, Campo Comprido, PR, Brazil, 25°27'42''S, 49°22'54''W, February 22, 2008, G.R.P. Moreira, O.S. Ribas, E. Carneiro & L. Beltrami colls., 34 last instar larvae (LMCI 14-52; 14-53), dissected from galls collected on *Schinus engleri*, fixed in

Dietrich´s fluid and stored in ethanol 70%. With the same collection data, March 20, 2010, G.R.P. Moreira & E. Carneiro, 11 dissected adults (LMCI 80-75); near 80 galls, (LMCI 80-76), fixed and stored in ethanol 96%. *Eucecidoses minutanus*: Las Compuertas, Las Heras, Mendoza, Argentina, 33°02'28''S, 69°03'03''W, October 26, 2011, G. San Blas & G.R.P. Moreira colls., 29 pupae (LMCI 163-20 to 22), dissected from galls collected on *S. fasciculatus*, fixed and stored in 96% ethanol. Playa Hotel Villavicencio, Las Heras, Mendoza, Argentina, 32°31'39''S, 69°00'53''W, May 1, 2011, G. San Blas coll., 4 larvae (LMCI 163-4), dissected from galls collected on *S. fasciculatus*, fixed and stored in 70% ethanol. Cecidosidae sp. Tiltil, Rungue, Chile, 33°00'30''S, 70°53'51''W, October 12, 2011, G. San Blas, G. Flores & R. Carrara colls., 3 larvae (LMCI 163-14), dissected from galls collected on *Schinus polygamus* fixed and stored in 96% ethanol.

Diagnosis. Unlike adults of other Neotropical cecidosids, which have pale forewings and labial palpi either reduced or absent, those of *O. argentinana* have the body covered with uniform, shiny copper-colored scales and 2-segmented labial palpi, among other differences of genital structures. The pupa is characterized by possessing a cephalic, five-pointed frontal process (gall cutter), and a single large spine on the last abdominal tergum. Pupae of other Neotropical cecidosids have either single (*C. eremita* and *E. minutanus*) or three-pointed (*D. capsulifex* and *D. congregatela*) gall cutters. The larva is distinguished by having a uniform yellowish brown head, associated with a subretangular frontoclypeus that extends to the apex of the epicranial notch, and unpigmented ecdysial lines that delimit the posterior adfrontal enlarged areas, absent in the other Neotropical cecidosids. The gall is unique among cecidosids by being enclosed within swollen terminal branches of *Schinus* plants, without developing an external, fruit-like chamber that is characteristic for other gall-maker species.

Male adult (Figs. 1A–4)

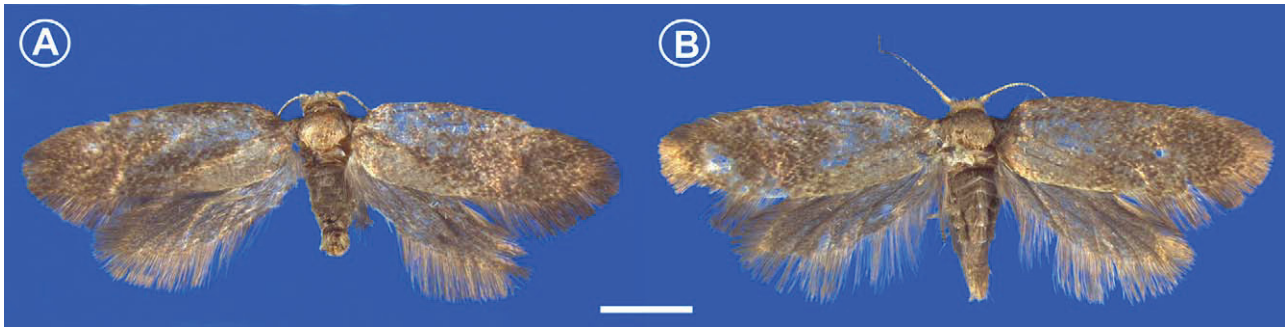

FIGURE 1. *Oliera argentinana* adults: (A) male; (B) female. Scale bar = 1.5 mm.

Forewing length 4.2 ± 0.3 mm (n = 5).Wings, body, and other appendages uniformly of a shiny copper to reddish brown color (Fig. 1). *Head*: Frons and vertex smooth with sutures weakly developed (Fig. 2A); vestiture consisting of a pair of latero-dorsal scale tufts curved forward over frons (Fig. 3A). Frons covered by dense, piliform hairs (Figs. 2A, B). Scales slender, lamellar, suberect, and scattered over labrum, maxillary, and labial palpi (Fig. 3D). Eyes (Figs. 2A, 3A) large (interocular index varying from 0.95 to 1.25; n = 4). Antennae short (varying from 0.52 to 0.56 length of forewing; n = 4); scape smooth except for medium dense pecten; flagellum filiform, with slender scales scattered only over dorsal half (Fig. 3A); ventral half with elongate sensilla ca. 0.7x length of flagellomere (Fig. 3C). Labrum greatly reduced (Fig. 3D). Pilifers absent. Mandibles (Fig. 3E) reduced to minute, sclerotized stubs. Haustellum (Fig. 3G) reduced to minute lobes. Maxillary palpi (Fig. 3G) 3-segmented, distal one reduced. Labial palpi (Fig. 3F) 2-segmented, and short (circa 2/3 eye width in length).

Thorax: Anterior arms of laterocervical sclerites (Fig. 2D) long and slender, with apex dilated. Metafurca (Figs. 2B,C) with slender, elongate postero-dorsal apophyses free from secondary arms;, antero-dorsal apodemes absent. Wings (Fig. 2E) lanceolate; microtrichia reduced in number; accessory cell present; retinaculum absent. Wing coupling (Fig. 2F) consisting of ~15 frenular scales arising in two to three irregular rows near base of costa; Sc ending near midpoint of wing margin, radius with 5 free branches, M 3-branched, CuA 2-branched, CuA1 and M3 well separated from each other basally, CuP faint distally and not stalked with 1A+2A. Hindwing: ~ 2/3 forewing in length; Sc and R stalked and ending distally to midpoint of wing margin, Rs unbranched, M 3-branched, M1 and M2 well separated, CuA 2-branched, CuA1 and M3 well separated, CuP faded, not stalked with 1A+2A. Legs (Figs. 2G) with spurs 0-2-4; epiphysis present. Tibial length proportion (anterior / medium / posterior legs) ~ 0.5/0.7/1.0.

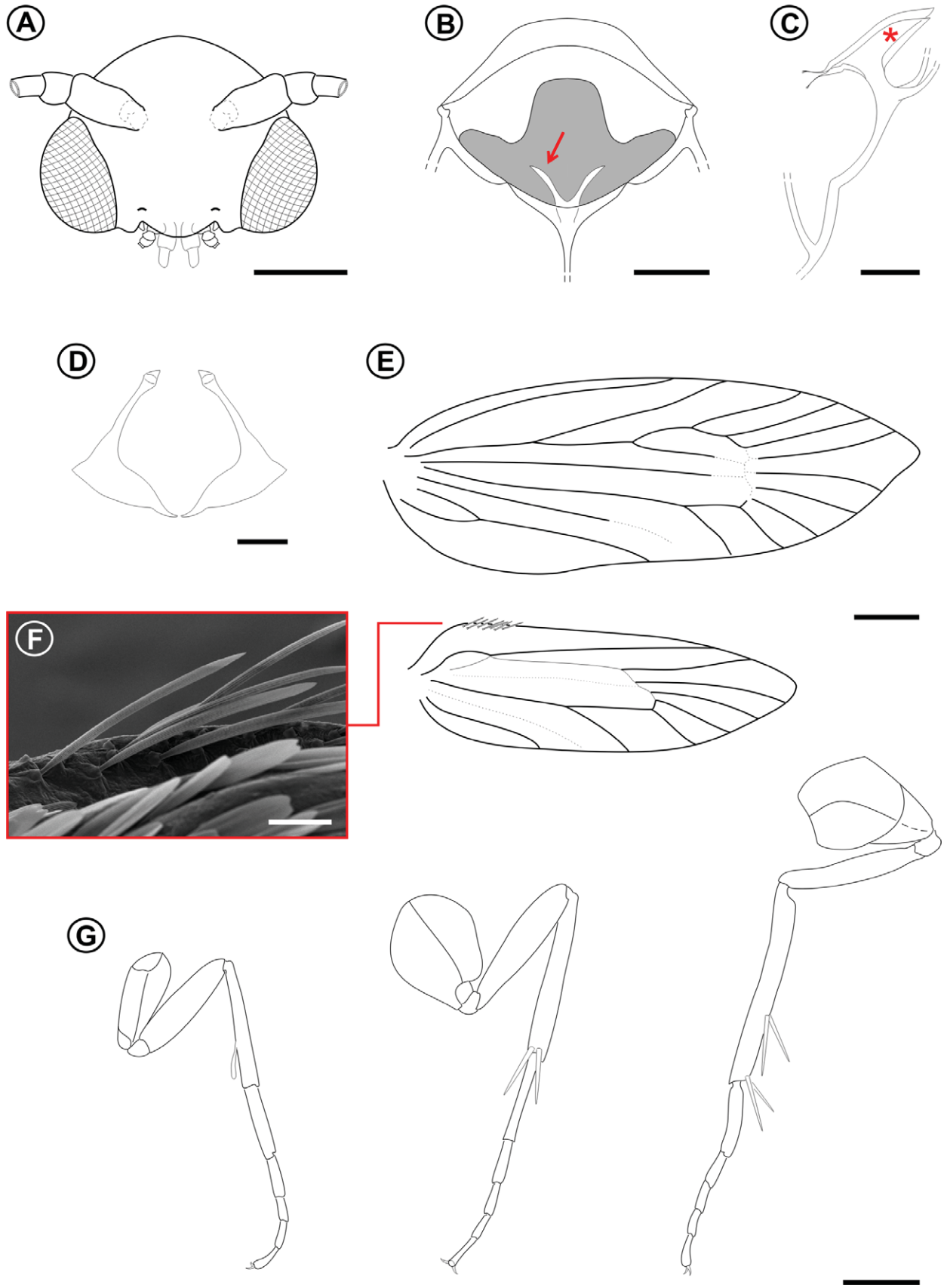

FIGURE 2. *Oliera argentinana* adult morphology: (A) female head, anterior view; (B) metathoracic furcasternum, posterior view (closed arrow points to furcal apophysis); (C) metathoracic furcasternum in detail, lateral view (asterisk indicates left furcal apophysis); (D) lateral cervical sclerites, anterior view; (E) fore- and hind wing venation; (F) detail of frenular scales; (G) fore-, median- and hindlegs, from left to right, respectively. Scale bars = 0.25mm, 0.25mm, 0.1mm, 0.1mm, 0.5 mm, 40µm, 0.5mm, respectively.

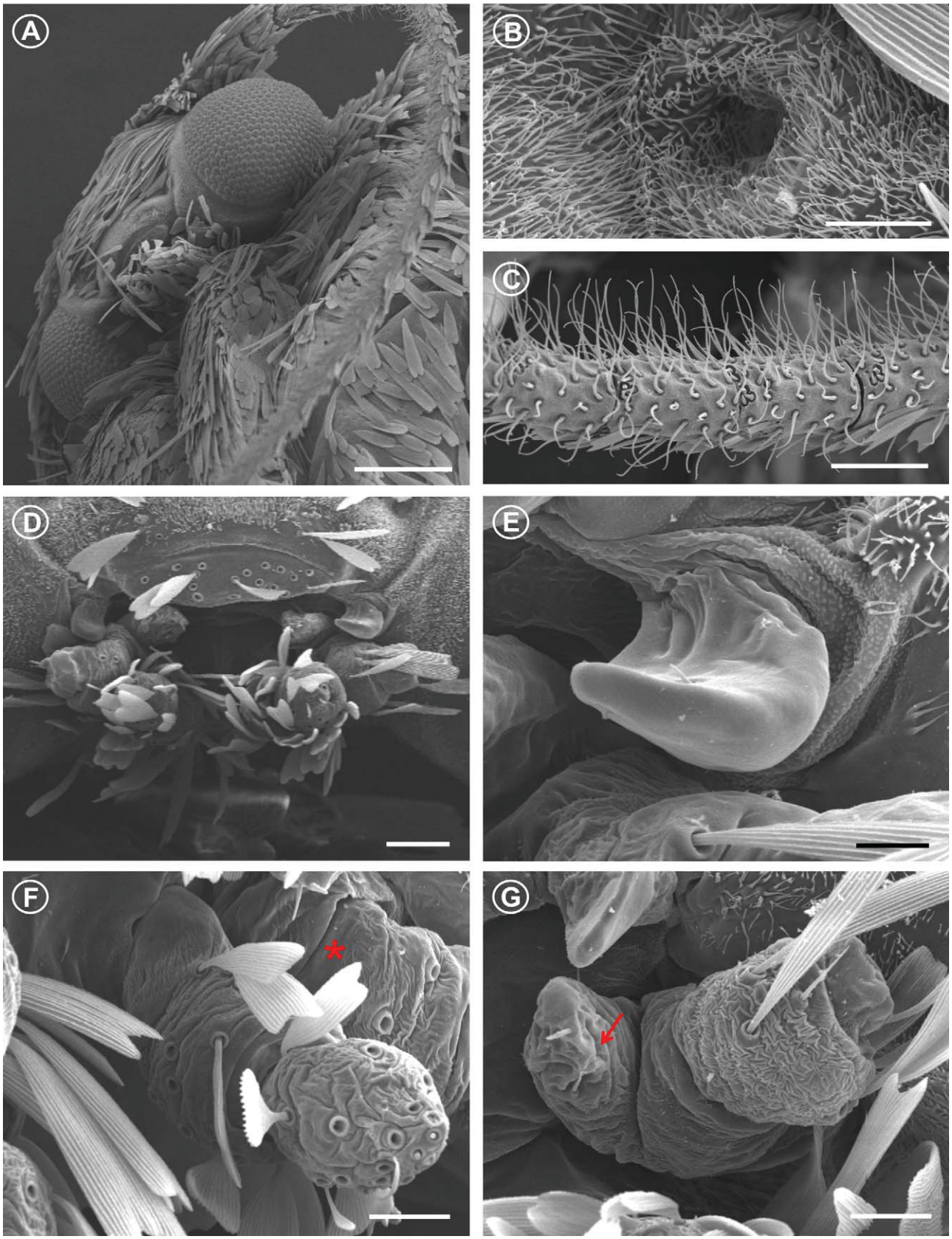

FIGURE 3. Scanning electron micrographs of *Oliera argentinana* adult head: (A) Head, antero-ventral view; (B) right tentorial pit, anterior view; (C) antennal flagellomeres, ventral view; (D) buccal appendages, anterior view; (E) left mandible, anterior view; (F) left labial palpus, anterior view (asterisk indicates left maxillar palpus); (G) left maxilla, antero-median view (arrow indicates haustellum). Scale bars = 200, 10, 50, 50, 10, 20, 20 µm, respectively.

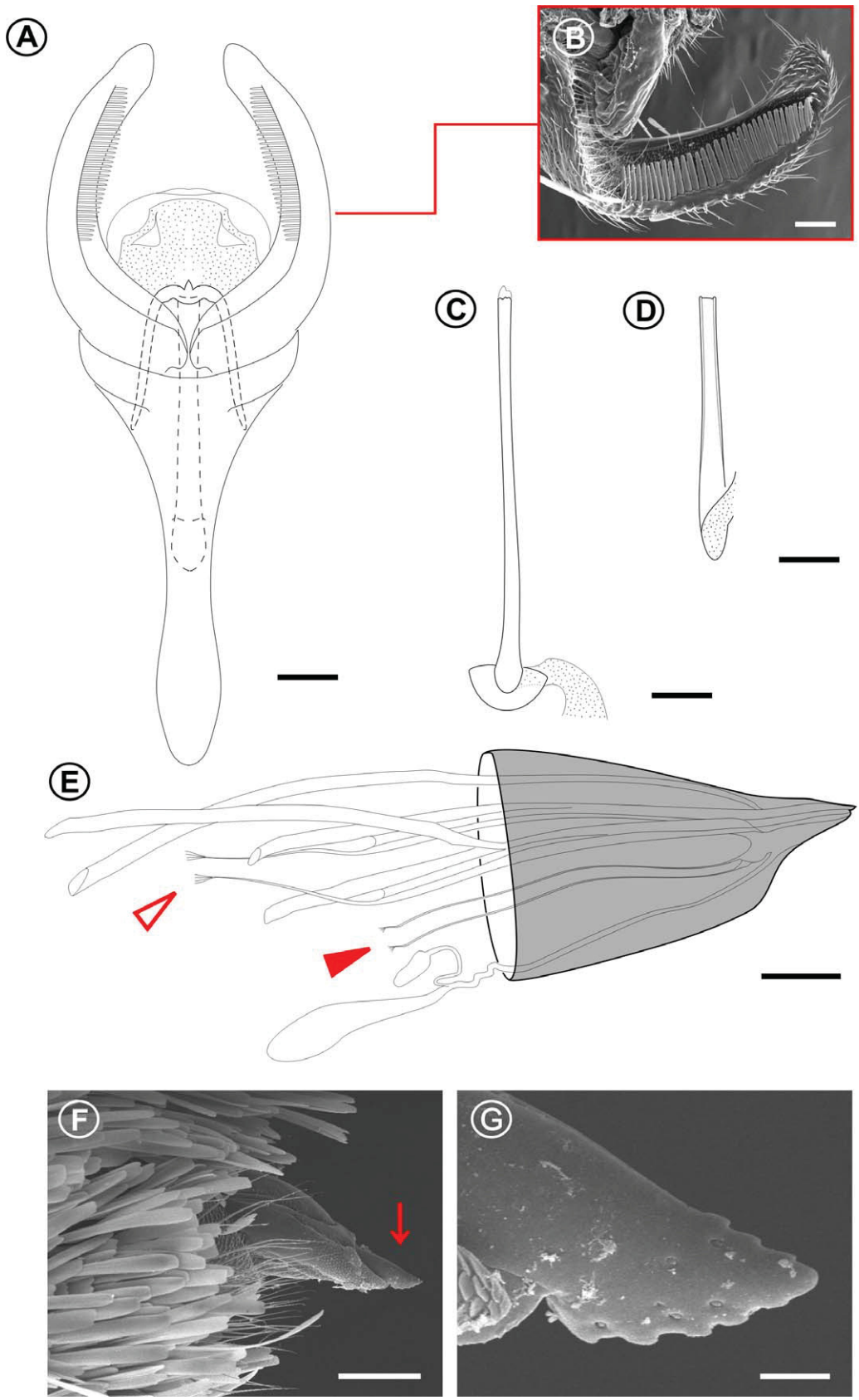

FIGURE 4. Genital morphology of *O. argentinana* on light and scanning electron microscopy: (A) male genitalia, ventral view (aedeagus omitted); (B) scanning electron micrograph of male right valve, median view; (C) juxta, dorsal view; (D) aedeagus, dorsal view; (E) female genitalia, lateral view (open and closed arrows indicate the apodemes of posterior apophysis and cloaca, respectively); (F) scanning electron micrograph of female ovipositor, lateral view; (G) detail of ovipositor apex (enlarged area indicated by arrow in F). Scale bars = 0.1mm, 50 µm, 0.1mm, 0.1mm, 0.25mm, 100 µm, 10 µm, respectively.

Abdomen: Sternum 2 with broad, U-shaped caudal rim; tergosternal connection absent, as in *C. eremita* (Davis 1998).

Male genitalia (Figs. 4A–C)**.** Uncus shallowly bilobed. Socii consisting of a pair of oval setigerous lobes. Valva (Fig. 4B) long and slender, with an elongate pectinifer along ventral margin extending ~ half length of valva. Vinculum Y-shaped. Aedeagus (Fig. 4D), simple, slender and tubular, rosette-like shaped anteriorly; vesica without cornuti. Juxta (Figs. 4C) elongate (~ 2/3 aedeagus length), slender, slightly spatulate distally, not divided but encircling aedeagus caudally. Saccus stout and tubular, with anterior apex slightly capitate.

Female adult (Figs. 1B–4)

Similar to male; abdominal sternum7 with caudal margin rounded, as in *C. eremita* (Davis 1998).

Female genitalia (Figs. 4E–G). Anterior apophyses long, extending beyond abdominal segment 5. Posterior apophyses fused distally. Apex of ovipositor (Figs. 4F,G) compressed and sagittate; ventral ridge with minute serrations. Cloaca with two apodemes that extend beyond abdominal segment 7. Spermatheca without lateral lagena; caudal part of ductus spermatheca not coiled. Vestibulum without sclerotized structures; ductus and corpus bursae membranous; signum absent.

Immature stages

Last instar larva (Figs. 5–7). Body length = 3.2±0.17 mm; head capsule width = 0.7±0.8 mm; n = 5. Prognathous, with chewing mouthparts; body cylindrical, covered with microtrichia; primary setae reduced.

Head dorsal (5B–C, 6A) yellowish brown, ~ 2x broader than high , with convex lateral margin; frontoclypeus well marked by pigmented adfontral sutures (Fig. 5B), subretangular in shape posteriorly, extending to apex of epicranial notch; ecdysial lines unpigmented, delimiting two semicircular, posteriorly located adfrontal areas. Head ventral (Fig. 5C) with well marked, slightly divergent hypostomal ridges; hypostomal lobes subtriangular; basistipes and postmentum areas unpigmented. Stemmata absent; antennae (Fig. 6C) reduced; labrum (Fig. 6B) bilobed, with three pairs of small setae on distal margin; mandible (Fig. 6D) well developed with four cusps along distal margin and one small seta basally on external surface; maxilla (Fig. 6E) with palpus and galea poorly developed; spinneret (Fig. 6F) tubular, equal in length to maxillary palpus; labial palpus (Fig. 6F) one-segmented, with well developed apical seta. Chaetotaxy consisting of 13 pairs of setae: F group unisetose; C group bisetose; AF group bisetose; A group trisetose; P group unisetose; L group unisetose; S group trisetose.

Thorax and abdomen (Figs. 5, 7) white; prothoracic shield (Figs. 5B) consisting of pair of irregularly shaped, yellowish brown areas; A1–7 with well developed calli, centrally on posterior margin of terga; thoracic legs reduced to circular, unsegmented tubercles (Fig. 7C, D); prolegs absent; circular spiracles without elevated peritreme (Fig. 7E) laterally on T1, A1–8. Abdominal segment 10 (Fig. 7F) composed of three lobes, one dorsal and two lateral. Thoracic and abdominal setae reduced in number and size. T1 with 7 pairs of setae; SD group bisetose; L group bisetose; V group bisetose. T2–3 with 4 pairs of setae; SD group unisetose; SV unisetose; V group bisetose. A1–9 with 2 pairs of setae; SD and L, unisetoses. A10 with 4 pairs of setae; SD unisetose; SV bisetose; V unisetose.

Pupa (Figs. 8, 9). Length = 3.723±0.102 mm; n = 6. Yellowish brown, becoming dark brown near adult emergence (Fig. 10F); head with frontal processes (Figs. 9A,B) used for cutting the gall chamber wall, formed by five large spines, grouped into two parallel rows: dorsalmost row with three apical processes, middle process blunt, lateral ones acute, ventralmost row with two smaller, pointed processes; frons and lateral portion of vertex with two pairs of setae each; antennae narrow, long, apex near forewing apex; prothorax a narrow transverse band between head and mesothorax; hindwings concealed by forewings, reaching sternum A6; metathoracic legs reaching beyond forewing apex, on segment A7; tergaT2–3 with a pair of latero-dorsal setae. Abdominal segments covered by microtrichia; A2–8 with a transverse band of spines (Figs. 9E, F), near anterior margin of terga; tergum A10 with anteriorly directed, acute process on posterior margin (Fig. 9G). Setae arranged in three rows (dorsal, supra- and subspiracular); one dorsal pair on segments A1–8; one supra-spiracular pair on segments A2–8; three subspiracular pairs on segments A3–7, one pair on A8–9; spiracle circular (Fig. 9D), without elevated peretreme laterally on A2–8, spiracle on A8 greatly reduced.

Gall (Fig. 10). Spindle-shaped, enclosed within swollen stems (Figs. 10A, B) on the host plant terminal branches. Larval chamber elliptical in shape (maximum diameter = 3.8±0.15mm; n = 6), transversally located in relation to the stem axis (Figs. 10C–E); with an external shallow wall, formed as an expansion of the wood tissue, under the bark. Unlike other Neotropical cecidosids, an operculum is lacking. With the advent of pupation, a progressive necrosis and eventual death of the external bark tissue of the gall occur which results in a thinning of

the outer wall of the chamber (Fig. 10F). With the action of the frontal process and body contortions, the pupa opens an irregular, lateral orifice (Fig. 10G). By continuing these movements and anchoring the body laterally with its abdominal spines, the pupa pushes itself partially out of the gall. During this process, the anterior portion of the exuvia is split, allowing adult emergence. In most cases after adult emergence, the anterior part of the pupal exuvium (head and thorax) is found protruding to the outside, while the posterior third remains in the chamber (Fig. 10H). After emergence, the outer wall of the chamber eventually collapses, with the empty galls appearing as small craters on the host plant stem surface (Fig. 10I).

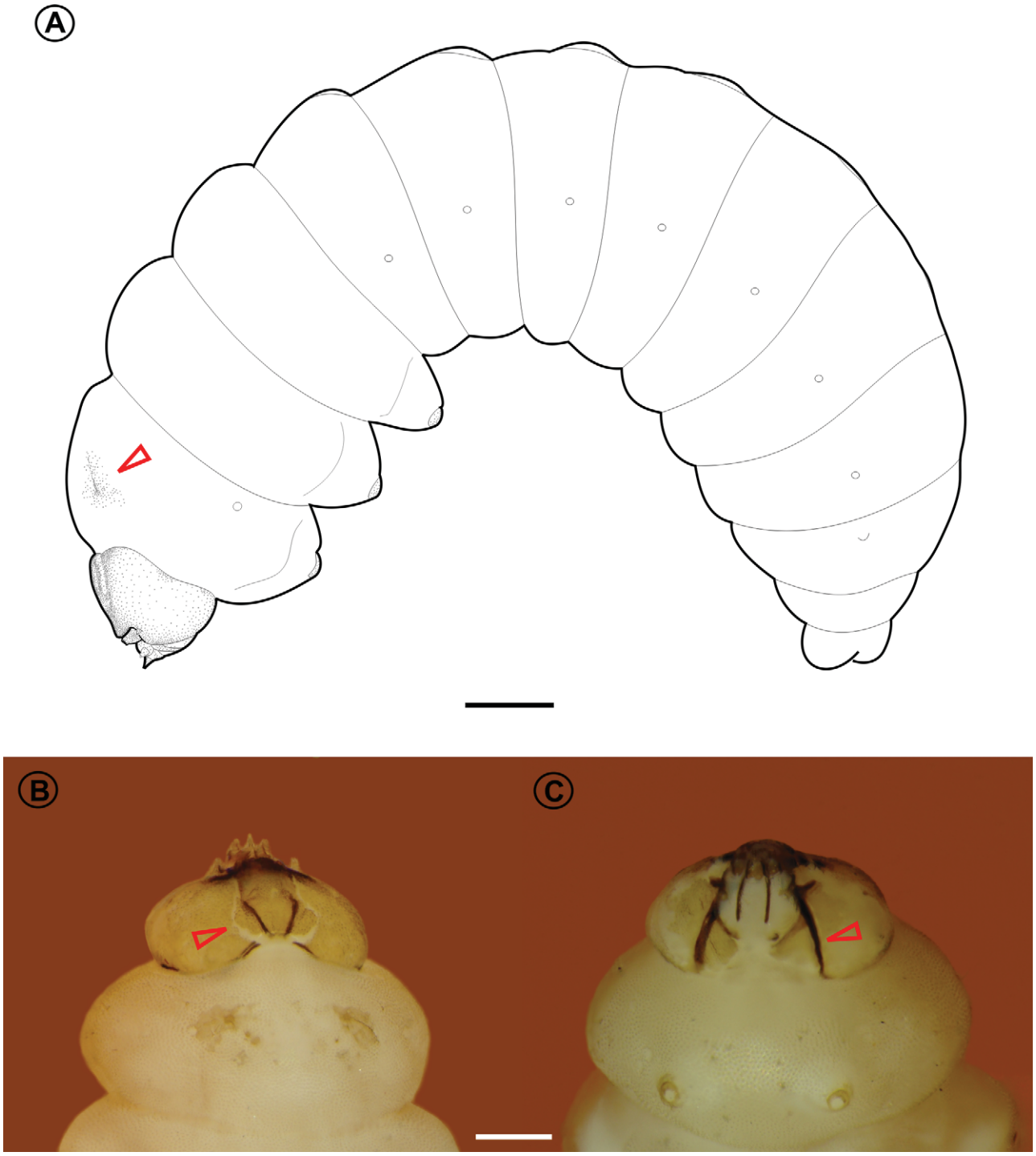

FIGURE 5. *O. argentinana* last larval instar on light microscopy: (A) larva, lateral view (prothoracic plate is indicated by arrow); (B) head and prothorax, dorsal view (arrow indicates the ecdisial line); (C) head and prothorax, ventral view (arrow indicates the hypostomal ridge). Scale bars = 0.3, 0.25, 0.25 mm, respectively.

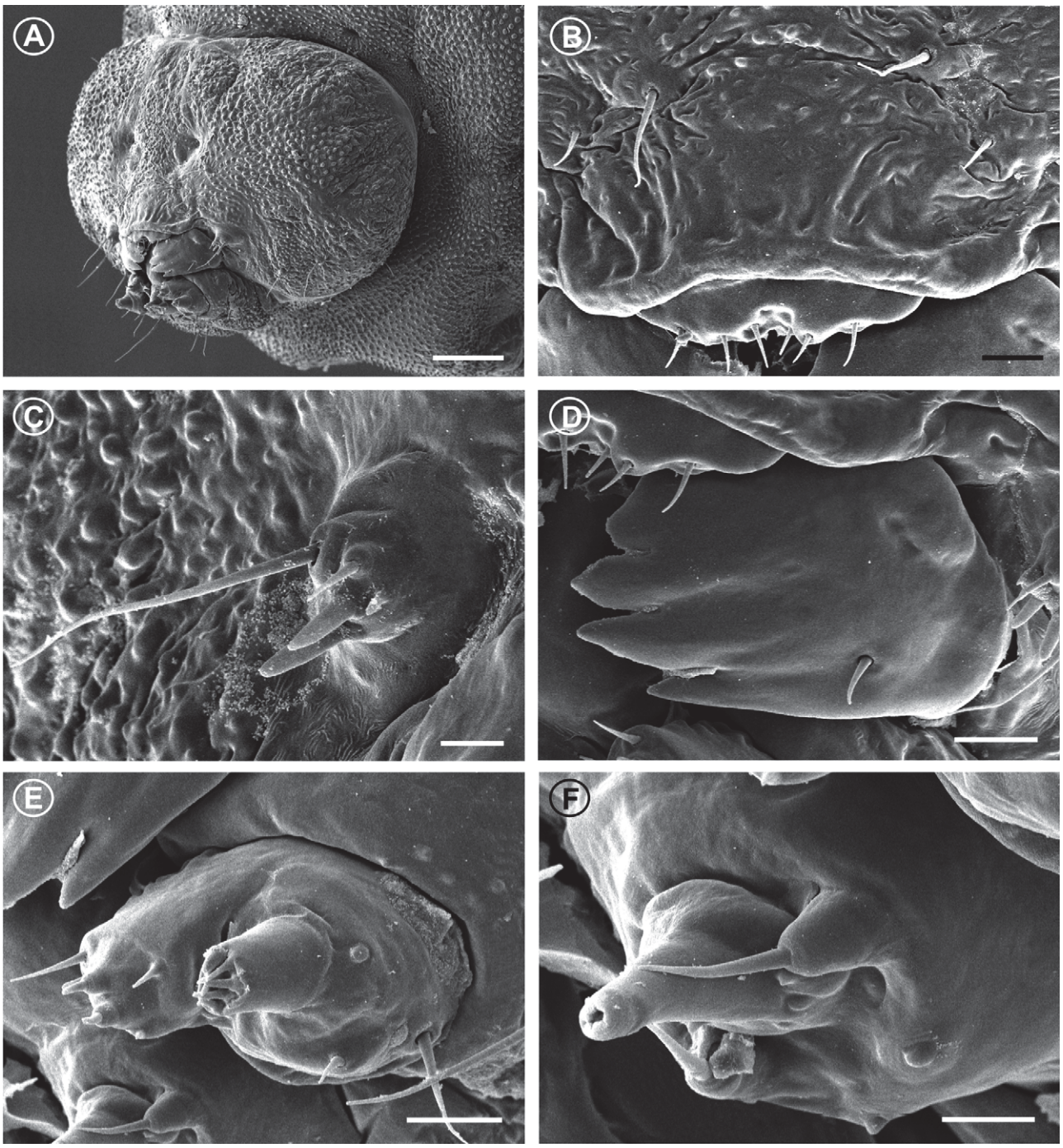

FIGURE 6. Head morphology of *O. argentinana* last larval instar on scanning electron microscopy: (A) Head, antero-lateral view; (B) clypeus and labrum, anterior view; (C) right antenna, anterior view; (D) left mandible, anterior view; (E) left maxilla, antero-lateral view; (F) labium and spinneret, antero-lateral view. Scale bars = 100, 20, 10, 20, 20, 10 μm, respectively.

Host plant. In Rio Grande do Sul (RS) state, Brazil, *O. argentinana* galls have been found on plants identified in most Brazilian herbaria as *Schinus polygamus* (*sensu* Cabrera 1938; Fleig 1987, 1989). The identity of such plants should be taken with caution because the taxonomy of the South American species of *Schinus* is controversial and in need of revision (for a discussion, see Barkley 1957, Burckardt & Basset 2000, and Steibel & Troiani 2008). According to Barkley (1957), records of *S. polygamus* from Uruguay might pertain to *S. fasciculatus*, which may also be true for those from the southern part of RS. According to that author, the distribution of *S. polygamus* is restricted to Chile. In Mendoza, Argentina, such galls are in fact found on *S. fasciculatus*, as already mentioned.

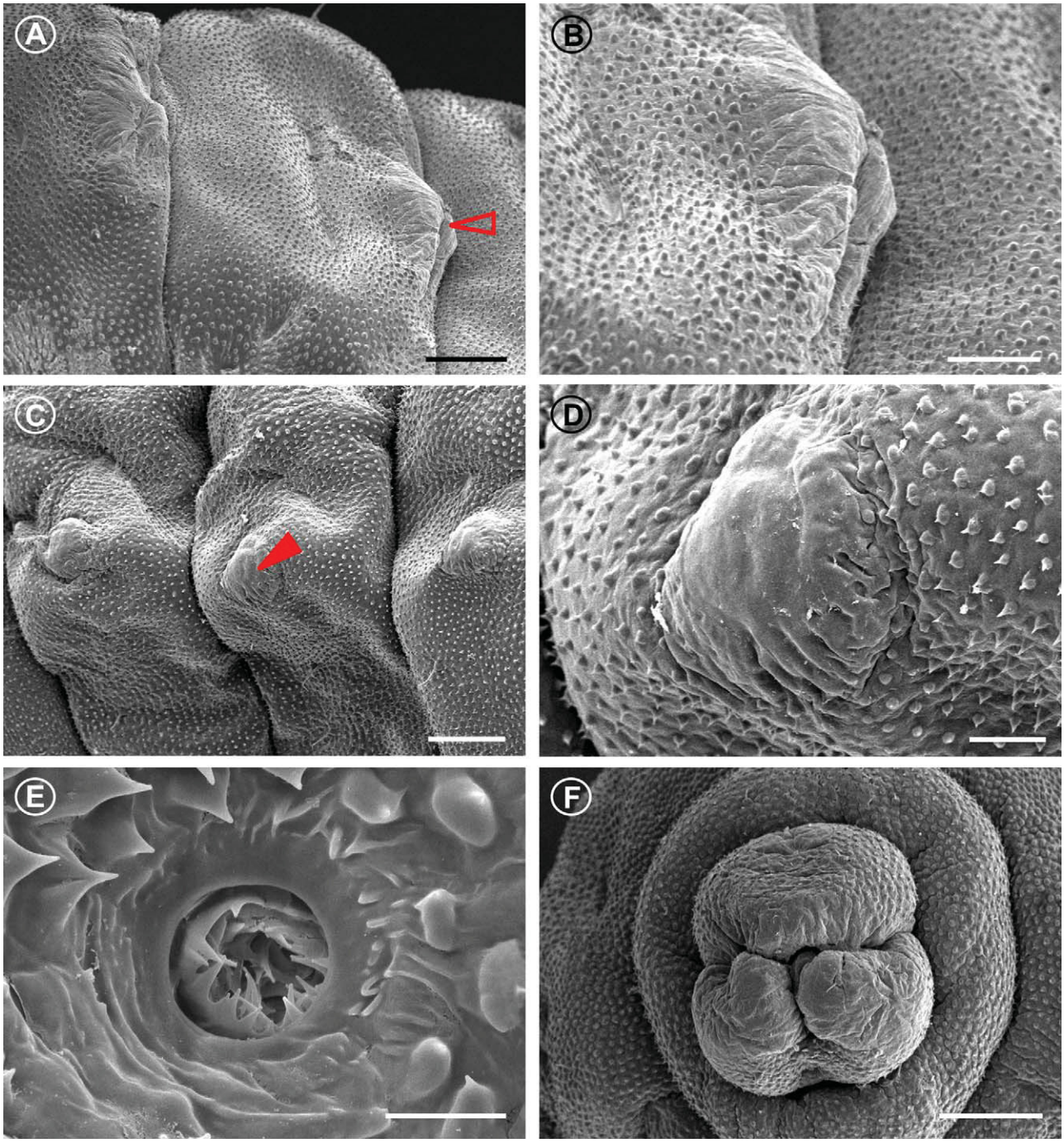

FIGURE 7. Thoracic and abdominal morphologies of *O. argentinana* last larval instar on scanning electron microscopy: (A) first and second abdominal segments, latero-dorsal view (arrow points to dorsal calli); (B) detail of the callus on A2; (C) left thoracic pleura, lateral view (arrow points to unsegmented tubercles, reminiscent of thoracic legs); (D) Detail of the mesothoracic leg rudiment; (E) spiracle from second abdominal segment, lateral view; (F) abdominal segment A10, posterior view. Scale bars = 100, 50, 100, 25, 10, 100 µm, respectively.

Distribution. In general, Neotropical cecidosids are rarely represented in insect collections. *Oliera argentinana* was originally described from material collected in the Buenos Aires province, Argentina (Brèthes 1916). The species was recently collected further west in the Argentinean province of Mendoza, where apparently it is rare. It has been found further east by the first author in the Southeastern Highlands of Rio Grande do Sul state, Brazil. It was not listed by Biezanko *et al*. (1957) from Uruguay, possibly due to inadequate collecting. Thus, the meager distributional data available suggest that *O. argentinana* occurs primarily within the Pampa province of the Chacoan subregion (*sensus* Morrone 2006).

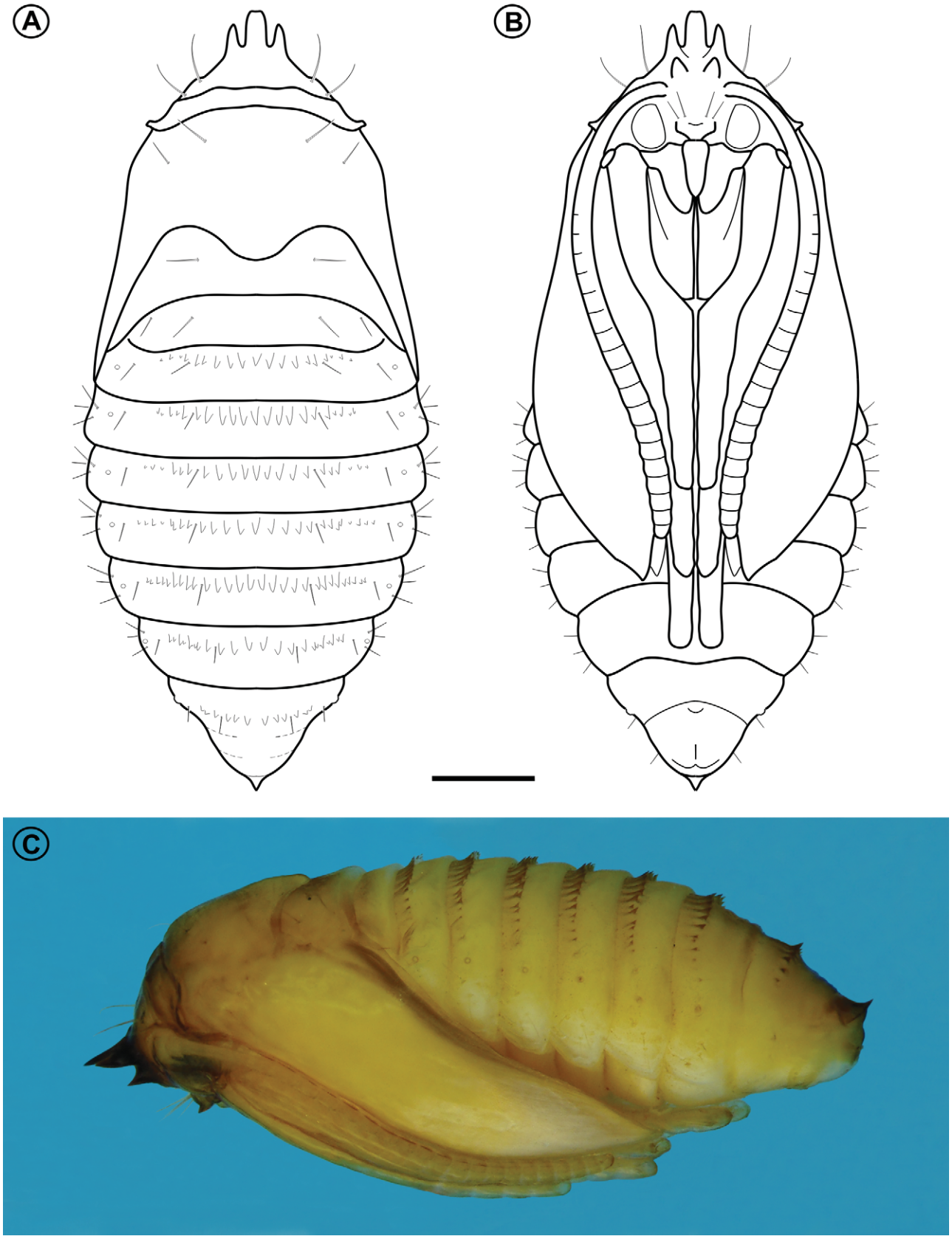

FIGURE 8. *O. argentinana* pupa on light microscopy. (25) dorsal view; (26) ventral view; (C) lateral view. Scale bar = 0.50 mm.

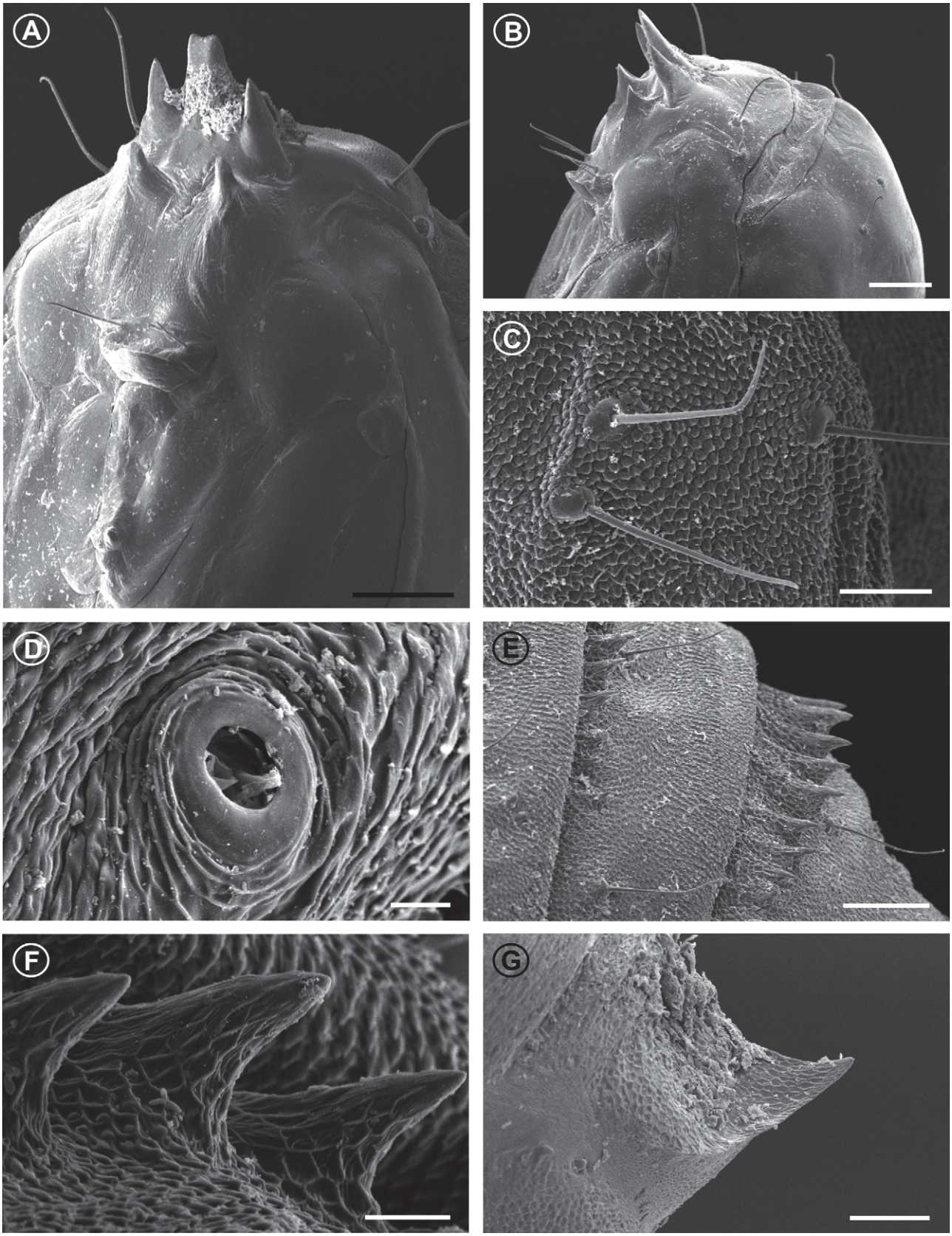

FIGURE 9. *O. argentinana* pupal morphology on scanning electron microscopy. (A) head, ventral view; (B) head, lateral view; (C) subspiracular setae from fourth abdominal segment, lateral view; (D) spiracle from third abdominal segment, lateral view; (E) abdominal terga A6 and A7, lateral view, showing tergal spine rows, located on anterior margin; (F) tergal spine rows in detail, latero-posterior view; (G) Single tergal spine, centrally located on posterior margin of segment abdominal A10, lateral view. Scale bars = 200, 200, 50, 10, 100, 20, 50 µm, respectively.

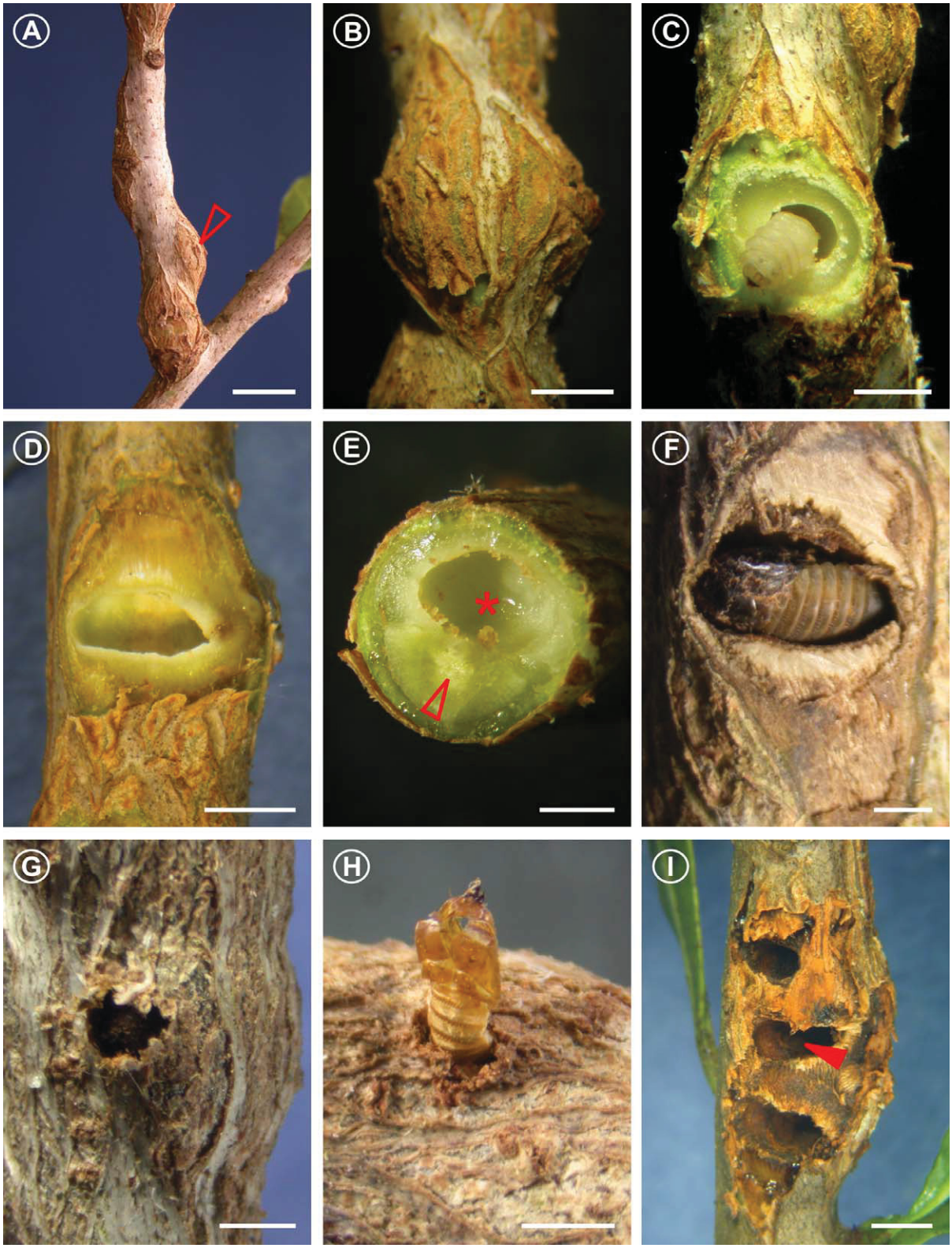

FIGURE 10. *O. argentinana* gall on *S. polygamus* branch: (A) apical branches showing lateral galls (indicated by arrow); (B) Detail of the stem bark surface on top of gall chamber; (C) superficially cut gall chamber of the same gall, showing a last instar larva; (D) a longitudinally cut gall, showing the transversal location of the gall chamber in relation to the stem axis; (E) transversal section of a stem through a gall chamber, showing its elliptical shape and location under bark (asterisk indicates gall chamber; arrow points to plant vessels); (F) longitudinally cut gall chamber showing a mature pupa inside; (G) the same gall, showing the pupal exit hole prior emergence; (H) pupal exuvia protruded from the gall exit hole, just after the adult emergence; (I) empty gall chambers (indicated by arrow) on branch after dehiscence of stem bark covering, later on, after adult emergence season. Scale bars = 6, 2, 2, 2, 2, 1, 1.5, 1.5, 2 mm, respectively.

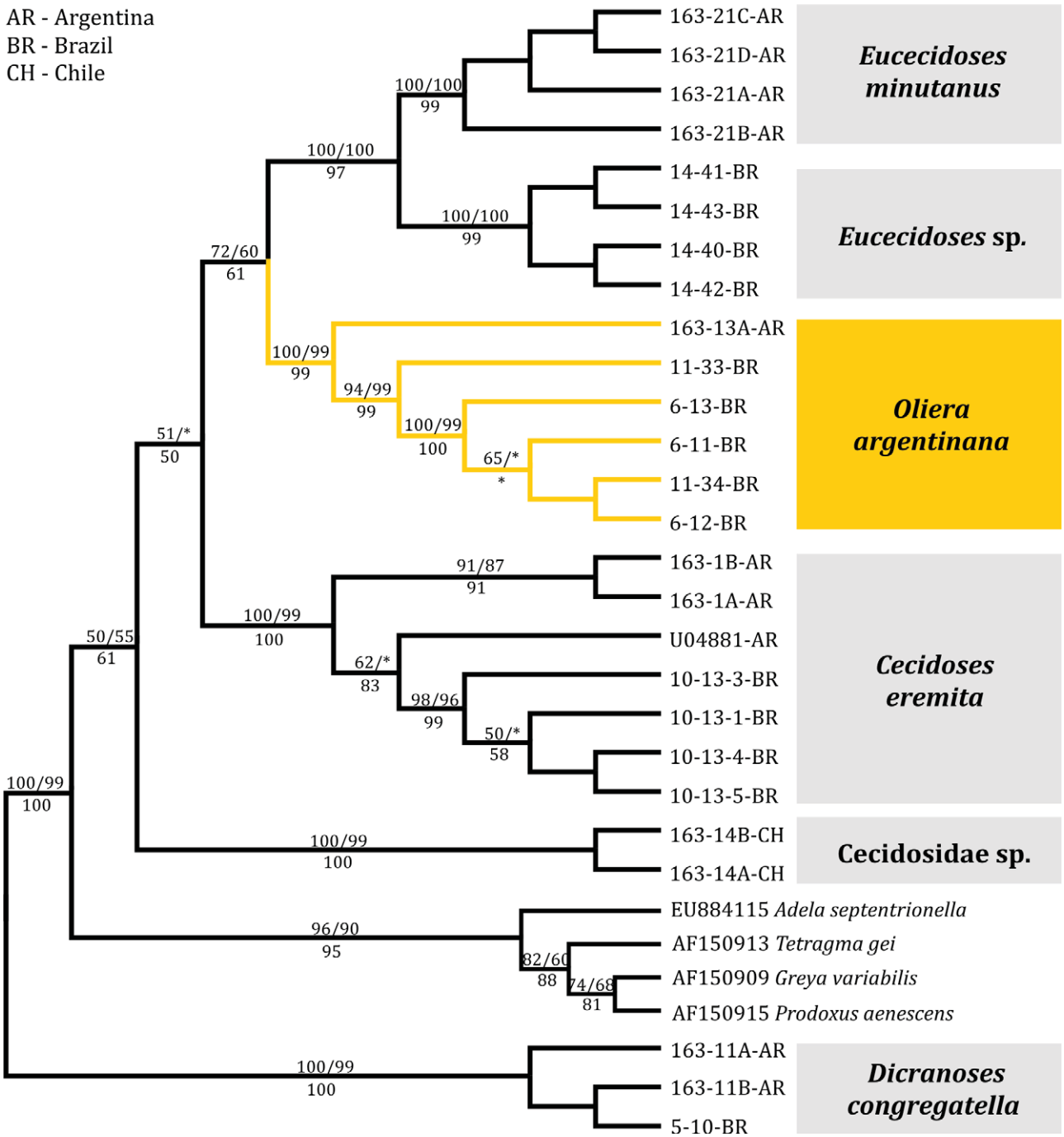

FIGURE 11. Maximum likelihood tree of Neotropical cecidosid species based on 626 bp of the mitochondrial marker cytochrome-c oxidase I gene [COI]). Numbers indicate bootstrap support higher than 50%: above branches, maximum likelihood/neighbour-joining; below branches, maximum parsimony. Asterisk indicates bootstrap values < 50%. Species of Prodoxidae (*Greya* + *Prodoxus* + *Tetragma*) and Adelidae (*Adela*) were used to root the tree according to the phylogeny proposed for Incurvarioidea (Peelmyr & Leebens-Mack 1999); see Table 1 and text for further description.

Life history. Little is known about the biology of *O. argentinana*. In southern Brazil, their galls have been collected occasionally, and concentrated primarily on a few hosts among *S. polygamus* plants within a given locality. They may, however, occur in dense concentrations on single plants and share the same host with other cecidosids, such as *C. eremita* and *D. congregatella*. In agreement with Brèthes (1916), our field collection dates indicate that the species is univoltine in Argentina and Southern Brazil, with adult emergence occurring from late Spring to early Summer (November / December).

Molecular phylogeny. A total of 626 nucleotide sites were analyzed, in which 262 sites were variable and 230 parsimony informative. Genetic divergence among major lineages tested, including cecidosid genera and outgroups, varied from 15 to 28% (Table 2). Distance, ML and MP analyses showed identical topology with different bootstrap supports (Fig. 11). *Oliera argentinana* was strongly supported as a monophyletic clade positioned within Cecidosidae and related to *Eucecidoses*. The node that joins *Oliera* + *Eucecidoses* was recovered either in distance, probabilistic or parsimony analyses, with bootstrap support higher than 60%. The clade *Oliera* + *Eucecidoses* is likely the sister group of *Cecidoses*. These three clades together represent the current status of Neotropical Cecidosidae (excluding *Dicranoses*). In addition, the resulting phylogeny indicated that *Dicranoses* is not closely related to the other cecidosid genera, because the Prodoxidae and Adelidae examined were positioned between these groups, thus leaving *Dicranoses* as an outgroup (Fig.11).

TABLE 2. Estimates of evolutionary divergence between sequences based on 626 base pairs of cytochrome oxidase I (COI) gene using Kimura 2-parameter model (Kimura 1980). Average number (± standard error) of base substitutions per site over all sequence pairs between groups, obtained by a bootstrap procedure of 1000 replicates are shown. The analysis involved 24 specimens belonging to five Neotropical cecidosid lineages and two outgroups (Prodoxidae and Adelidae).

	Oliera	*Dicranoses*	Cecidosidae sp.	*Cecidoses*	*Eucecidoses*	Prodoxidae
Oliera	-					
Dicranoses	0.26 ± 0.03	-				
Cecidosidae sp.	0.15 ± 0.02	0.25 ± 0.03	-			
Cecidoses	0.18 ± 0.02	0.28 ± 0.03	0.21 ± 0.03	-		
Eucecidoses	0.17 ± 0.02	0.25 ± 0.03	0.18 ± 0.03	0.21 ± 0.03	-	
Prodoxidae	0.25 ± 0.03	0.28 ± 0.03	0.25 ± 0.03	0.24 ± 0.03	0.25 ± 0.03	-
Adelidae	0.22 ± 0.03	0.24 ± 0.03	0.26 ± 0.03	0.22 ± 0.03	0.26 ± 0.03	0.18 ± 0.03

Discussion

Results found in the present study have relevant implications not only for the taxonomy and phylogeny of *O. argentinana* but also for the other supra-specific lineages of Neotropical Cecidosidae. They also suggest the existence of a greater diversity for the family in southern South America, which should be explored further.

In the original work of Brèthes (1916), the external morphology of the gall, larva, pupa and adult stage of *O. argentinana* were illustrated. Although lacking details, his general description gave three conspicuous characters that clearly separate this species from other described South American cecidosids: 1) gall formation restricted to under bark of terminal branches, without developing an external, fruit-like chamber; 2) pupa with a cephalic frontal process (gall cutter) formed by five large spines, grouped into two rows, with three spines in the anterior and two in the posterior row; 3) adult uniformly covered by reddish brown scales. Because the specimens we examined agree completely with these features, we conclude that the original description of the gall of *O. argentinana* presented by Brèthes (1916) is accurate. We complement it further with data from scanning electron microscopy and DNA sequences. The lectotype of *O. argentinana* is in poor condition; it is basically only a thorax on a pin with a slide of the damaged genitalia. But it shows clear diagnostic similarities, as for example the stout saccus and enlarged, semicircular anterior end of the aedeagus, which are most characteristic for *O. argentinana*.

The redescription presented by Parra (1998) of what was allegedly *C. argentinana* from Chile diverges markedly from the features presented above for Argentinean material. Parra described the gall as a chamber on a short stalk protruding externally from the plant stem, the frontal process of the pupa as truncated and conical, and the adult colour as varying from greyish to whitish-grey with scattered black scales on the forewings. In addition, the larva studied by Parra (1998) possessed two stemmata, structures that are absent in all known Neotropical Cecidosidae. Also, the pupa illustrated by him possessed conspicuous abdominal spines whose size, shape and arrangement are different from those known for the remaining species. Furthermore, the adult figured by Davis (1999), as *O. argentinana*, illustrated from material collected in Chile and supposedly conspecific with that examined by Parra (1998), has a 3-segmented labial palpi, contrary to what we described herein. The DNA analysis in this study included specimens from Chile

(treated here as Cecidosidae sp.), which morphologically are similar to the material studied by Parra (1998). Our results give further support to our hypothesis that Parra misidentified the species he studied, because such specimens arose not within the *Oliera* clade, but as a sister group of the *Eucecidoses* + (*Oliera* + *Eucecidoses*) clade (Fig.11). We conclude that the specimens studied by Parra (1998) and Davis (1999) belong to either one or two different cecidosid lineages, which will be treated elsewhere (San Blas, G. *et al*. in prep.).

Systematic position of *Oliera*. Results from both morphology and DNA do not support the proposition by Parra (1998) that *Oliera* is synonymous to *Cecidoses*. Instead, we found *Oliera* to be more closely related to *Eucecidoses*. Other species should be assigned to this genus with increased collecting efforts for Neotropical cecidosids. According to preliminary molecular results, not included in the present study, there are at least two additional congeneric species to *O. argentinana*, which are known only from the larval stage, collected recently in Chile and Brazil (San Blas, G. & Moreira, G.R.P., unpubl. data). Furthermore, our observations revealed that these genera present major, consistent morphological differences for most life stages (larva, pupa and adult). *Oliera argentinana* specimens have the following characteristics, which are not found on the other Neotropical cecidosids examined: 1) gall developing under the bark of terminal branches, without developing an external, fruit-like chamber; 2) larva with pronounced, posteriorly rectangular frontoclypeus with apex extended to the epicranial notch, associated with unpigmented ecdisial lines that delimit two semicircular, posteriorly located adfrontal areas; 3) pupa with cephalic frontal process composed of 5 separate individual processes, and last abdominal segment with a single, dorsal acute spine; and, 4) adult with 2-segmented labial palpi.

Phylogeny and systematic of Cecidosidae. Our study shows that genetic divergence among Neotropical cecidosid genera (> 20% in most cases) is nearly equal or greater than the divergence between them and the related adeloid families Prodoxidae and Adelidae, herein used as outgroups. Such results do not support the proposition of Becker (1977) regarding the synonymy of *Eucecidoses* with *Cecidoses*. Thus, we propose that *Eucecidoses* be re-instated as valid. We are in the process of revising *Eucecidoses*. Our preliminary results indicate a greater diversity of *Eucecidoses* species in southern Brazil than previously suspected.

Finally, our molecular analysis suggests that the family Cecidosidae (*sensu* Nielsen & Davis 1985; Davis 1999) may be paraphyletic. *Dicranoses congregatella* came out as the sister group of a cluster comprising species belonging to the Adelidae (*Adela*) and the Prodoxidae (*Tetragma* + *Greya* + *Prodoxus*), and not closely related to the clade of *Cecidoses* + (*Eucecidoses* + *Oliera*) as was initially expected. In addition, distance-based analysis revealed pairwise divergences among cecidosid lineages to be as high as those between Cecidosidae and the outgroups. The Prodoxidae is considered to be the sister group of Cecidosidae (Pellmyr & Leebens-Mack 1999; Hoare & Dugdale 2003). We plan to obtain additional DNA sequences, using more conserved gene markers and also to study *Dicranoses capsulifex* Kieffer & Jörgensen, 1916, the type species of *Dicranoses*, in order to test further the composition and phylogenetic relationships of the Cecidosidae.

Acknowledgements

Thanks are due to Arturo R. Alsina (MACN) for the loan of type material. We acknowledge the staff members of CME/UFRGS and Thales O. Freitas (UFRGS) for the use of facilities and assistance with scanning electron microscopy and molecular analyses. We are grateful to Abner Elpino-Campos, Kim R. Barão and Denis S. Silva (UFRGS) for their help on optical and scanning electron photography, and especially the latter for editing the plates. We also thank Eduardo Carneiro, Gabriel Mello and Olaf H. Mielke (UFPR) for their assistance with collecting cecidosids in Paraná state, Brazil. We are specially grateful to Jean François-Landry (Agriculture and Agri-Food Canada) for significant improvements on the final version of the manuscript made possible by his comments. We also wish to thank Wolfram Mey (University of Berlin) for suggestions that improved the earlier version of the manuscript. This study was financially supported in part by CNPq/ Brazil (project numbers 309676/ 2011-8 and 156153/2011-4, granted to GRPM and GLG, respectively).

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