

Description, molecular phylogeny, and natural history of a new kleptoparasitic species of gelechiid moth (Lepidoptera) associated with Melastomataceae galls in Brazil

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The male, female, pupa and larva of a new species of Gelechiidae (Lepidoptera), *Locharcha opportuna* Moreira and Becker, are described and illustrated with the aid of optical and scanning electron microscopy. A preliminary analysis of mitochondrial DNA sequences including members of related lineages is also provided. The immature stages are associated with galls induced by a species of *Palaeomystella* Fletcher (Lepidoptera: Momphidae) on *Tibouchina sellowiana* (Cham.) Cogn. (Melastomataceae), endemic to the Atlantic Rainforest. Larvae are kleptoparasitic, usurping the gall internal space and thereafter feeding on the internal tissues. By determining the variation in population density of both species and following gall development individually throughout ontogeny under field conditions, we demonstrated that the kleptoparasite completes its life cycle inside galls induced by *Palaeomystella*, where pupation occurs. The variation in seasonal abundance of the kleptoparasite is tied to that of the cecidogenous species, with their corresponding peaks in density occurring sequentially.

<http://zoobank.org/urn:lsid:zoobank.org:pub:525F6D52-8CE1-47D1-A0D9-78B564DF5565>

Keywords: Neotropical region; Atlantic Rainforest; melastome galls; momphid moths; kleptoparasitism

Introduction

Cecidogenous insect species are known as ecosystem engineers (Sanver and Hawkins 2000), because the galls that they induce are used as a resource not only by themselves but also by other guilds (Mani 1964). They may form very complex, multitrophic-level systems including predators, parasitoids, cecidophagous, inquiline and kleptoparasites, among other insects, such as successors who may use the empty galls for shelter. Although well known for other biological systems (e.g. Iyengar 2008; Litman et al. 2013), the kleptoparasites in particular have been little studied in the context of insect galls, except for those induced by Thysanoptera (Morris et al. 2000; Mound and Morris 2000; Bono 2007). They are known to feed on the gall tissues, after invading the

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gall and usurping the cecidogenous species (e.g. Morris et al. 2000). Contrary to the inquilines, which may change substantially both the shape and size of the galls that they invade, by inducing either similar (Brooks and Shorthouse 1988) or different tissues (Van Noort et al. 2007) from the cecidogenous insects, kleptoparasites do not induce development of new tissues but simply feed on those that were induced to develop by their precursors. Unlike cecidophagous insects that are exclusively phytophagous and mobile, and thus may feed on the external portion of more than one gall (e.g. Caltagirone 1964), kleptoparasites are omnivorous and relatively sedentary, usually feeding on the internal portions of a single gall during ontogeny. However, in the literature on galls induced by Lepidoptera in particular, the meaning of such terms is confused; in general, the use of kleptoparasitism has been neglected (e.g. Miller 2005; Sugiura and Yamazaki 2009), with the exception of Ito and Hattori (1983), and cecidophagy has been used in some cases as a synonym of inquilinism (e.g. Caltagirone 1964; Miller 2005; Bená and Vanin 2013), and thus needs to be revised. According to Miller (2005), lepidopterans belonging to at least nine families are found within this poorly defined feeding group.

The fauna associated with galls induced by Lepidoptera in general is still little known, even regarding the cecidogenous group, which includes a few hundred species belonging to c.20 families, most within the Gelechioidea. Most of these species await description, as they are known only from their gall morphotype (for a review, see Miller 2005). In the Neotropical region these gall morphotypes are commonly found in Melastomataceae (e.g. Tavares 1917; Houard 1933; Lima 1945). However, only six of them have been recently associated with the cecidogenous species, all belonging to the genus *Palaeomystella* Fletcher (Momphidae) (Becker and Adamski 2008; Luz et al. 2014). More precise knowledge of this fauna will require additional effort including intensive studies, since the presence of other feeding groups, such as inquilines, cecidophages insects and kleptoparasites may lead to misidentification of species and their corresponding biological functions in the gall system, if any. This is particularly true when species of different feeding groups belonging to closely related lineages are present at the same time in these complex, multi-trophic gall systems.

As a case study, herein we describe the larva, pupa and adults of a new species of kleptoparasitic gelechiid moth belonging to the genus *Locharcha* Meyrick, associated with a fusiform gall induced by *Palaeomystella fernandesi* Moreira & Becker (Lepidoptera: Momphidae) that was described in Luz et al. (2014), on *Tibouchina sellowiana* (Cham.) Cogn. (Melastomataceae) in southern Brazil. We also carried out a preliminary analysis of mitochondrial DNA sequences, including members of related lineages. By following the development of galls individually throughout ontogeny under field conditions, we determined the life history of the kleptoparasite in comparison with the cecidogenous species, taking into account variations in gall colour and size. In addition, through monthly estimates of the density of galls on *T. sellowiana* plants, together with dissection of field-collected galls in the laboratory, during 14 months, we determined concomitantly the variation in the seasonal abundance of both the cecidogenous and kleptoparasitic moths.

Materials and methods

Taxonomy

Specimens used in the study were reared in small plastic vials under controlled abiotic conditions (14 h light/10 h dark; $25 \pm 2^\circ\text{C}$) in the Laboratório de Morfologia e

Comportamento de Insetos, Departamento de Zoologia, Universidade Federal do Rio Grande do Sul (UFRGS), Porto Alegre city, state of Rio Grande do Sul (RS), Brazil, from March 2012 through April 2013. They came from galls induced by *Palaeomystella fernandesi* Moreira & Becker (Lepidoptera: Momphidae), which were described elsewhere (Luz et al. 2014). These galls were field-collected with either late-instar larvae or pupae inside, developed on shoots of *Tibouchina sellowiana* (Cham.) Cogn. from a population existing at CPCN Pró-Mata, São Francisco de Paula, RS, Brazil. Immature stages were obtained from additional dissected galls. They were fixed in Dietrich's fluid and preserved in 75% ethanol.

For gross morphology descriptions, the specimens were cleared in a 10% potassium hydroxide (KOH) solution and slide-mounted in either glycerine jelly or Canada balsam. Observations were performed with the aid of a Leica® M125 stereomicroscope (Wetzlar, Germany). Structures selected to be drawn were previously photographed with an attached Sony® Cyber-shot DSC-H10 digital camera (Tokyo, Japan). Vectorized line drawings were then made with the software Corel Photo-Paint® X3, using the corresponding digitized images as a guide. At least five specimens were used for the descriptions of each life stage or instar. Measurements were made with an attached ocular micrometer.

For scanning electron microscope analyses, additional specimens were dehydrated in a Bal-Tec® CPD 030 critical-point dryer (Pfäffikon ZH, Switzerland), mounted with double-sided tape on metal stubs, and coated with gold in a Bal-Tec® SCD 050 sputter coater. They were examined and photographed in a JEOL® JSM 5800 scanning electron microscope (Tokyo, Japan) at the Centro de Microscopia Eletrônica (CME) of UFRGS.

Nomenclature follows Stehr (1987) for the larva, Patočka and Turčani (2005) for the pupa, and Lee and Brown (2008) for the adults.

Molecular analysis

High-quality DNA was purified from larval tissue, using the organic method of cetyl trimethyl ammonium bromide (CTAB) from three specimens (Table 1). Amplification was performed through a polymerase chain reaction (PCR) for a 621-base pair (bp) segment of the mitochondrial gene cytochrome *c* oxidase subunit I (*CO-I*), with the universal primers LCO1490 (5'-GGTCAACAAATCATAAAGATATTGG-3') and HCO2198 (5'-TAAACTTCAGGGTGACCAAAAAATCA-3'), following the program and conditions proposed by Folmer et al. (1994). Accordingly, we obtained variants that match exactly the region previously sequenced in related gelechiids deposited in the GenBank database and Barcode of Life DataBase. Aliquots of PCR products were treated with exonuclease I and FastAP thermosensitive alkaline phosphatase (Thermo Scientific, Waltham, MA, USA), sequenced using the BigDye chemistry and analysed on an ABI3730XL (Applied Biosystems, Waltham, MA, USA) at Macrogen (Seoul, Republic of Korea). Sequences were aligned and visually inspected using the algorithm Clustal X in MEGA 5 (Tamura et al. 2011) running in full mode with no manual adjustment. Data generated in this study were submitted to GenBank (ID 1693397) and are awaiting accession numbers (Table 1).

A phylogenetic tree was reconstructed in order to test our hypothesis of monophyletic status for the new species and also to infer its evolutionary relationships among specific genera within Gelechiinae. We thus incorporated all available taxa

Table 1. Specimens used to reconstruct the monophyletic status and phylogenetic relationships of *Locharcha opportuna*, using related genera.

Genus	Species	Voucher	GenBank accession numbers
Ingroup			
<i>Coleotechnites</i>			
	<i>C. atrupictella</i>	10-JDWBC-3951	HM865863
	<i>C. blastovora</i>	10-JDWBC-1056	HM862690
	<i>C. nr. coniferella</i>	UBC-2007-0871	FJ412324
	<i>C. floriae</i>	10-JDWBC-2714	HM864509
	<i>C. piceaella</i>	EE-725-93 P3	HM374090
	<i>C. quercivorella</i>	BIOUG:2006-ONT-0146	GU358080
	<i>Coleotechnites</i> sp.	Jflandry0789	GU095776
	<i>C. starki</i>	10-JDWBC-2912	HM864727
<i>Locharcha</i>			
	<i>L. opportuna</i>	LMCI 174-57_1	ID 1693397
		LMCI 174-57_2	ID 1693397
		LMCI 174-53_A	ID 1693397
Outgroup			
	<i>Exoteleia dodecella</i>	CNCLEP00024608	GU358112
	<i>Exoteleia pinifoliella</i>	JFL3 BIOUG: HLC-17153	GU358161
	<i>Recurvaria nanella</i>	CNCLEP00028723	GU358180

belonging to *Coleotechnites* (the putative sister lineage of the new taxa based on our preliminary findings) and rooted with the currently known related genera *Exoteleia* and *Recurvaria*, according to Karsholt et al. (2013) and Lee and Brown (2008) (Table 1).

Phylogenetic reconstructions were based on two methods: Bayesian inference (BI), implemented in BEAST 2.0 (Drummond et al. 2012) and maximum likelihood (ML), run in PHYML 3.0 (Guindon et al. 2010). In BI, a relaxed uncorrelated lognormal clock was used together with no fixed mean substitution rate and a Yule prior on branching rates, using the GTR (general time-reversible; Rodríguez et al. 1990) model of sequence evolution. Four independent runs of 10 million generations and a burn-in period of 10,000 (the first 1000 trees were discarded) were used; the remaining trees were summarized in TreeAnnotator 1.6.2 (Drummond and Rambaut 2007) and used to infer a maximum a posteriori consensus tree. Bayesian posterior probabilities (BPP) were used as an estimate of branch support. For ML, the program jModeltest (Posada 2008) was used to estimate the substitution model GTR + G, with gamma distribution (G) according to the Akaike information criterion. Monophyly-confidence limits were assessed with the bootstrap method (Felsenstein 1985) at 60% cut-off after 1000 bootstrap iterations. Trees were visualized and edited in FigTree 1.3.1 (<http://tree.bio.ed.ac.uk/software/201/>). Finally, we analysed the evolutionary distance between the same pairs of taxa used in the phylogenetic analysis (including outgroups) using the Kimura 2-parameters (K2P) model (Kimura 1980) procedure, with 1000 bootstrap replications.

Museum collections

Abbreviations of the institutions from which specimens were examined are as follows. **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; **MCNZ**: Museu de Ciências Naturais, Fundação Zoobotânica do Rio Grande do Sul, Porto Alegre, Rio Grande do Sul, Brazil; **MCTP**: Museu de Ciências e Tecnologia da Pontifícia Universidade Católica do Rio Grande do Sul, Porto Alegre, Rio Grande do Sul, Brazil; **VOB**: Coll. Vitor O. Becker, Reserva Serra Bonita, Camacan, Bahia.

Population studies

From April 2012 through May 2013, galls were collected monthly from an additional population of *T. sellowiana* existing at the type locality. The CPCN Pró-Mata is a 4500 ha reserve of Atlantic Rainforest, with portions of Dense Umbrophilous Forest (= Brazilian Atlantic Rainforest *sensu stricto*) intermixed with fragments of *Araucaria* Forest and grasslands. *Tibouchina sellowiana* plants are common in the area, mainly along the trails located at higher altitudes (Mello 2006).

To determine the variation in density and colour of galls, a total of 160 randomly selected plants (ranging from 1 to 2 m tall) that were located and mapped along two trails were surveyed (for a corresponding map, see Supplementary material, Figure 1S). From these plants, 140 individuals were mapped, randomly sorted and marked initially to be sampled every month (10 plants per occasion). On each occasion, these plants were inspected and any galls present were collected and brought to the laboratory to measure their size and colour, followed by dissection. These plants were sampled only once during the study, and are hereafter termed 'destructive samples'. The additional 20 *T. sellowiana* plants were used to evaluate changes in colour and size of the galls. Their galls were individually marked and on each sampling occasion they were photographed, until their fate was determined in the field (hereafter termed 'non-destructive samples'). The phenology of the plants was determined concomitantly.

In both field and laboratory conditions, galls were photographed with a Sony® Cyber-Shot DSC-H10 digital camera. To correct for lighting conditions, we used a WhiBal® (Michael Tapes Design, Melbourne, FL, USA) white balance reference card. Gall size and colour (RGB pattern) were determined from the corresponding digital images, using the software AxioVision® Rel. 4.8 (http://www.zeiss.com/microscopy/en_de/downloads/axiovision.html). Dissections were performed with the aid of a Leica® M125 stereomicroscope, in order to determine the presence of immature stages of either the cecidogenous insect or the kleptoparasite, or both. Empty, old galls were discarded after dissection. Measurements were made with an ocular micrometer attached to the stereomicroscope (for corresponding data on larval capsule width, see Supplementary material, Table 1S).

Statistical analyses

Data for colour and size of galls, and size of larval instars were evaluated for homogeneity of variance and normal distribution, assessed respectively by Bartlett

and Kolmogorov–Smirnov tests. The data for gall size and green intensity passed the tests, and then were linear-regressed. The data obtained for size of larval instars were not normally distributed, and were then compared by nonparametric Kruskal–Wallis test, followed by Dunn’s multiple comparison tests. The parametric and nonparametric tests were performed by using the software PAST v.2.08 (<http://folk.uio.no/ohammer/past/>), following criteria described by Zar (1999) and Conover (1980), respectively.

Systematic account

Family **GELECHIIDAE** Stainton

Subfamily **GELECHIIDAE** Sattler

Tribe **Teleiodini** Piskunov

Genus ***Locharcha*** Meyrick

Type species ***Locharcha emicans*** Meyrick by monotypy

Locharcha opportuna Moreira and Becker, new species
(Figures 1–8)

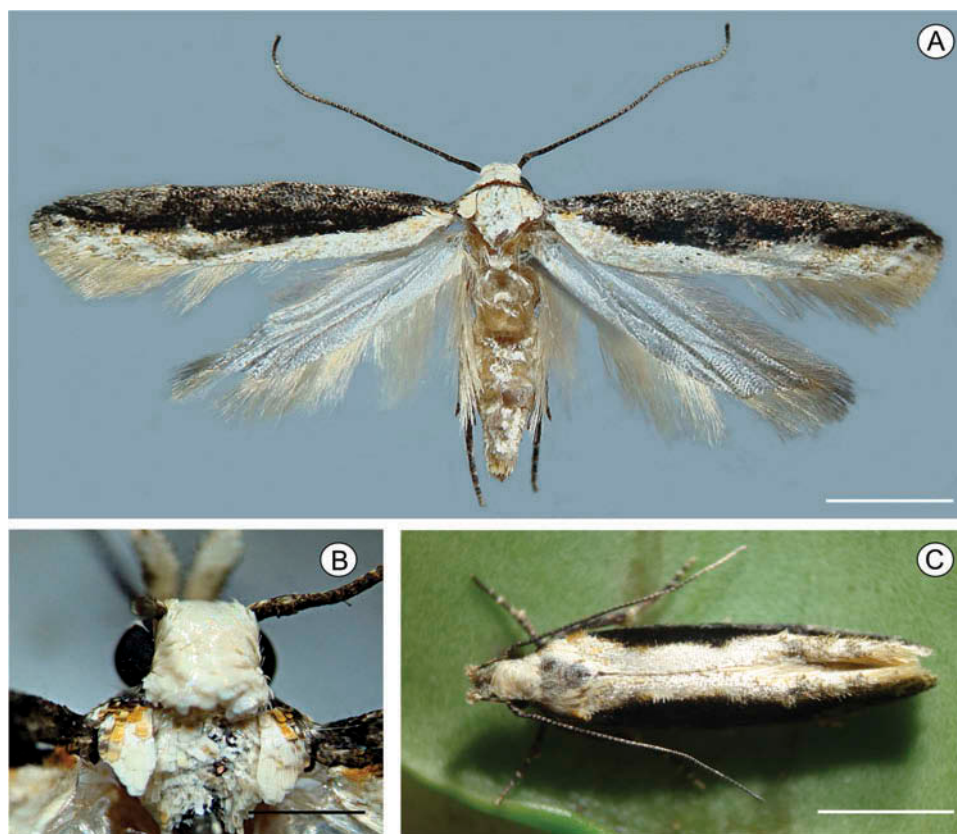


Figure 1. *Locharcha opportuna* adult, dorsal view: (A) wings spread, pinned; (B) head and thorax, in detail; (C) wings folded, on *Tibouchina sellowiana* leaf. Scale bars = 2, 1 and 2 mm, respectively.

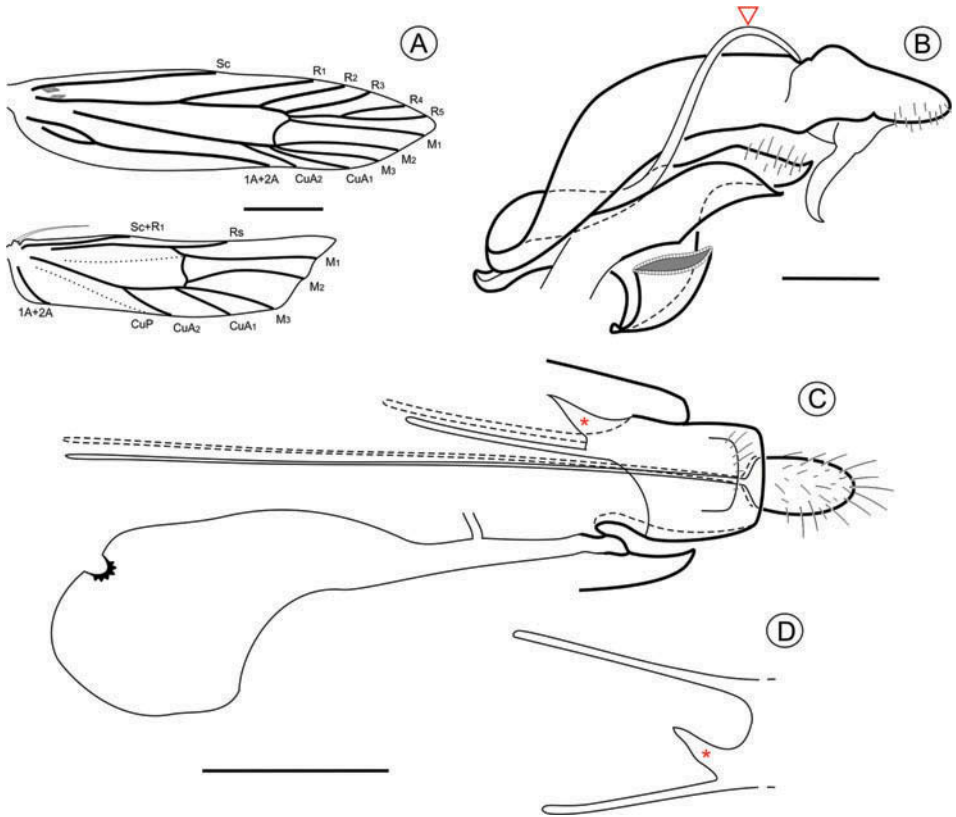


Figure 2. *Locharcha opportuna* adult morphology: (A) wings; (B) male genitalia (arrow indicates glandiductor), lateral view; (C) female genitalia, lateral view; (D) detail of tergal process (asterisk), dorsal view. Scale bars = 1, 0.2 and 0.5 mm, respectively.

Type material

BRAZIL: Centro de Pesquisas e Conservação da Natureza Pró-Mata (CPCN Pró-Mata; 29°29'16"S, 50°10'60"W; 925 m), São Francisco de Paula Municipality, Rio Grande do Sul State (RS), Brazil. Adults preserved dried and pinned, reared by the senior author from galls induced by *Palaeomystella fernandesi* Moreira & Becker (Lepidoptera: Momphidae) on *Tibouchina sellowiana* (Cham.) Cogn. (Melastomataceae): LMCI 174, 26 March 2012, by G.R.P. Moreira, F.A. Luz and P. Pollo; LMCI 210, 7–9 March 2013 by G.R.P. Moreira, F.A. Luz and L.T. Pereira. HOLOTYPE: ♂ (LMCI 210–189), donated to DZUP (29.418). PARATYPES: 1 ♂ (LMCI 210–45), 2 ♀♀ (LMCI 174–179 and 193), donated to DZUP (29.419, 29.420 and 29.421, respectively); 1 ♂ (LMCI 174–180), 2 ♀♀ (LMCI 174–40 and 210–57), donated to MCNZ (81.904, 81.905 and 81.906, respectively); 1 ♂ (LMCI 174–187), 2 ♀♀ (LMCI 174–41 and 176), donated to MCTP (36.227, 36.228 and 36.229, respectively); 1 ♂ (LMCI 210–64), 2 ♀♀ (LMCI 174–194 and 196), donated to VOB.

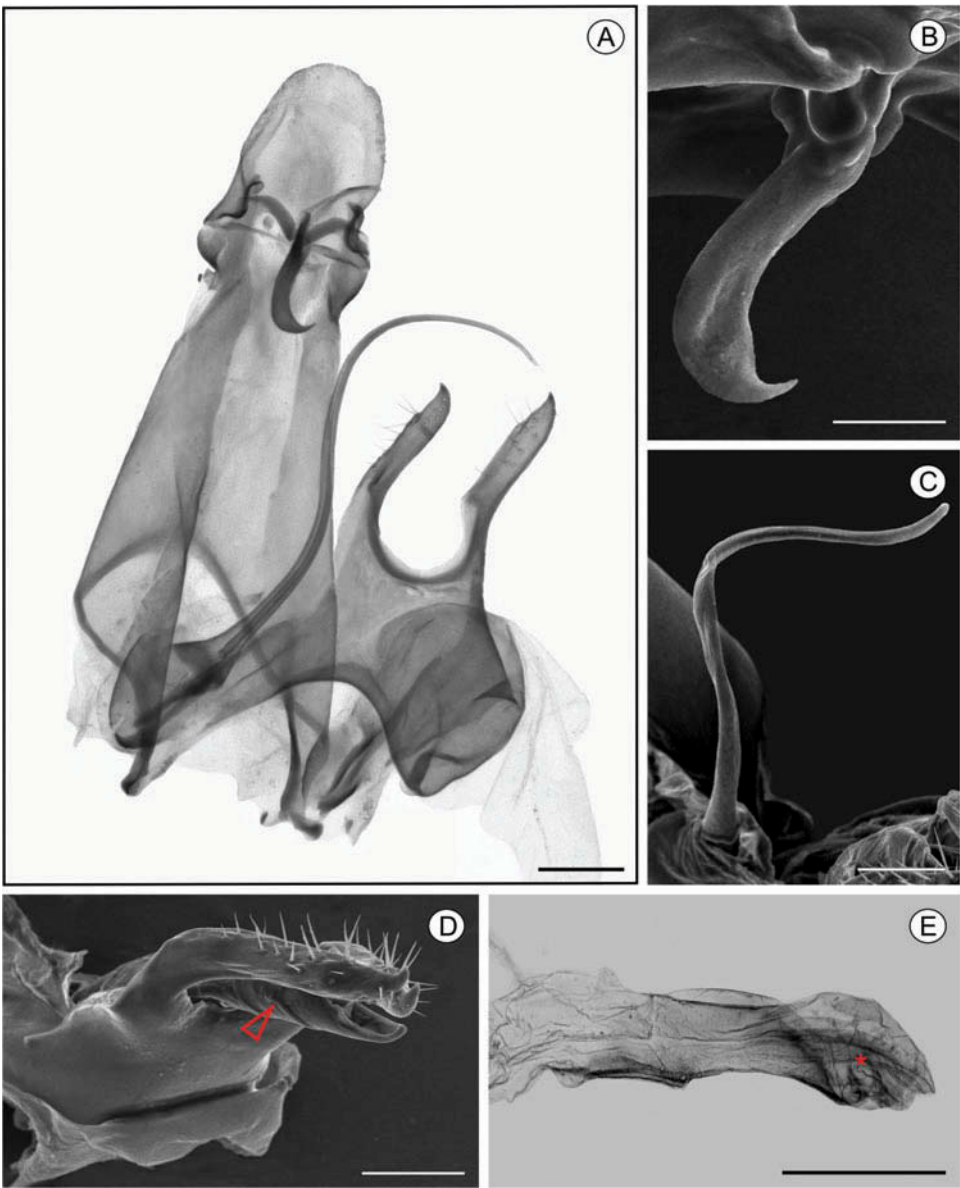


Figure 3. Male genital morphology of *Locharcha opportuna* under light and scanning electron microscopy: (A) genitalia (aedeagus removed), oblique view (slide preparation GRPM 50–63); (B) gnathos, lateral view; (C) left valve (= glandiductor) detached from tegumen, lateral view; (D) sicae with anchored aedeagus (pointed by arrow), lateroposterior view; (E) dissected aedeagus (asterisk indicates everted vesica), lateral view. Scale bars = 1 mm, 50, 100, 100, 200 μm, respectively.

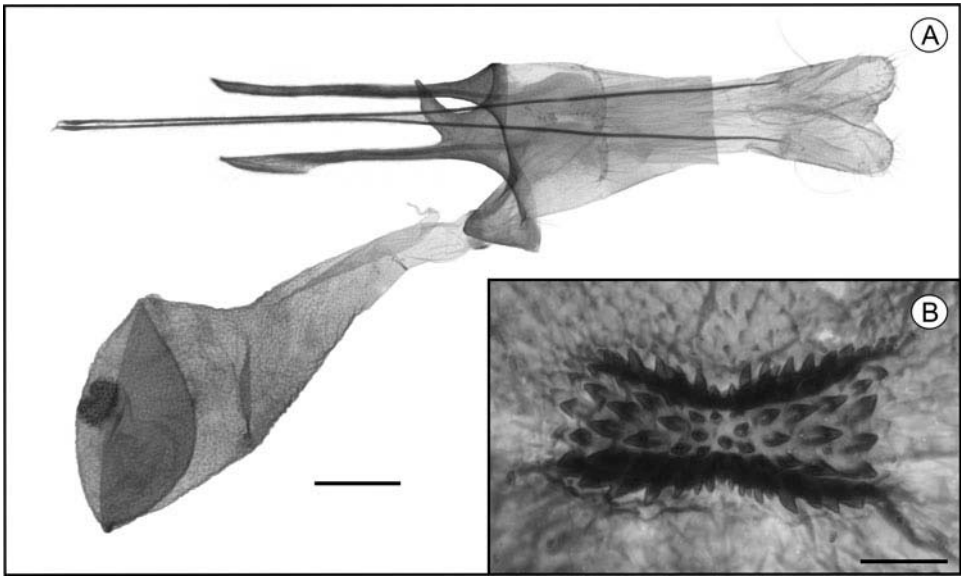


Figure 4. Female genital morphology of *Locharcha opportuna* under light microscopy: (A) genitalia, oblique view (slide preparation GRPM 50–65); (B) female signum, internal view. Scale bars = 250 and 500 μ m, respectively.

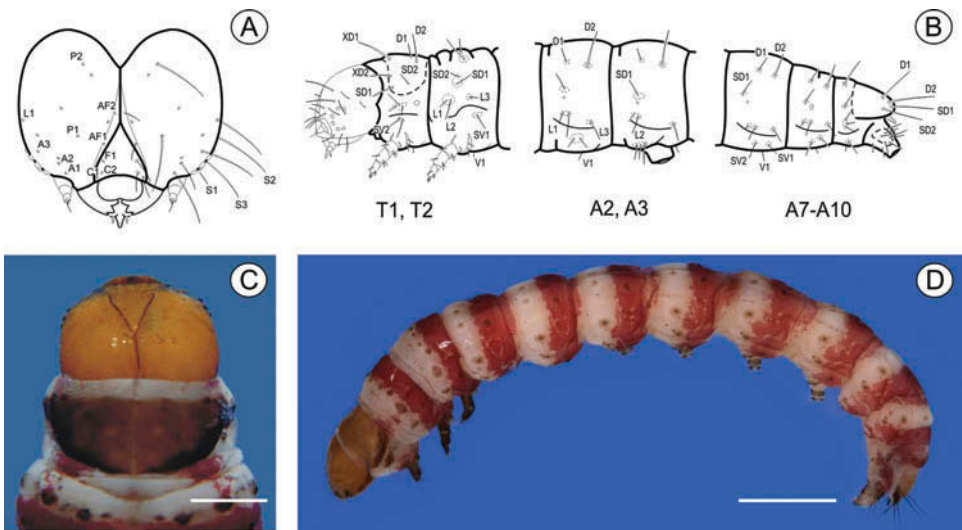


Figure 5. *Locharcha opportuna* last larval instar: (A) head chaetotaxy, frontal view; (B) thoracic and abdominal chaetotaxy, lateral view; (C) head and prothoracic shield, dorsal view; (D) body, lateral view. Scale bars = 50 μ m and 1 mm, respectively.

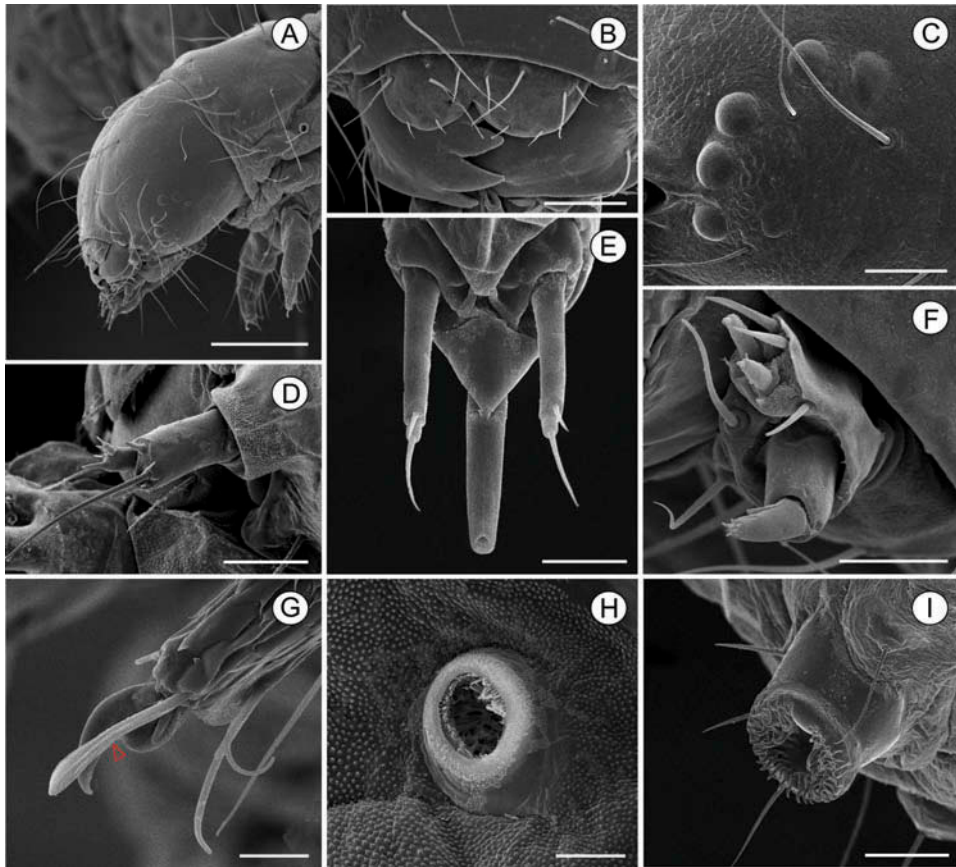


Figure 6. Scanning electron micrographs of *Locharcha opportuna* last larval instar: (A) head and prothorax, lateral view; (B) labrum and mandibles, frontal view; (C) stemmata; (D) antenna, lateral view; (E) labium and spinneret, ventral view; (F) maxilla, anterolateral view; (G) distal portion of mesothoracic leg, posterolateral view (arrow indicates spatulate seta); (H) prothoracic spiracle, lateral view; (I) pseudopodium abdominal A6, mesoventral view. Scale bars = 200, 100, 100, 20, 20, 20, 20, 20, 100 μm , respectively.

Other specimens examined

With the same collection data, deposited in LMCI. Adults, dried and pinned: 6 ♂♂ (LMCI 174–174, 177, 182, 191, 210–62; 174–170, with genitalia in glycerine GRPM 50–24), 5 ♀♀ (LMCI 174–185, 188, 195, 210–46; 174–171, with genitalia in glycerine GRPM 50–25). Adults, fixed in Dietrich's fluid, preserved in 70% ethanol: 2 ♂♂ (LMCI 174–206 and 207, with genitalia in glycerine GRPM 50–68 and 69, respectively); 2 ♀♀ (LMCI 174–210 and 211, with genitalia in glycerine GRPM 50–70 and 71, respectively). Slide preparations, mounted in Canada balsam: genitalia, 1 ♂ (GRPM 50–63), 2 ♀♀ (GRPM 50–64 and 65); wings, 2 ♂♂ (GRPM 50–59 and 60), 2 ♀♀ (GRPM 50–61 and 62); 2 last-instar larvae (GRPM 59–66 and 67). Immature stages, fixed in Dietrich's fluid and preserved in 70% ethanol: 12 last-instar larvae (LMCI 174–55); 9 pupae (LMCI 174–216); 6 dissected galls (LMCI 174–217 to

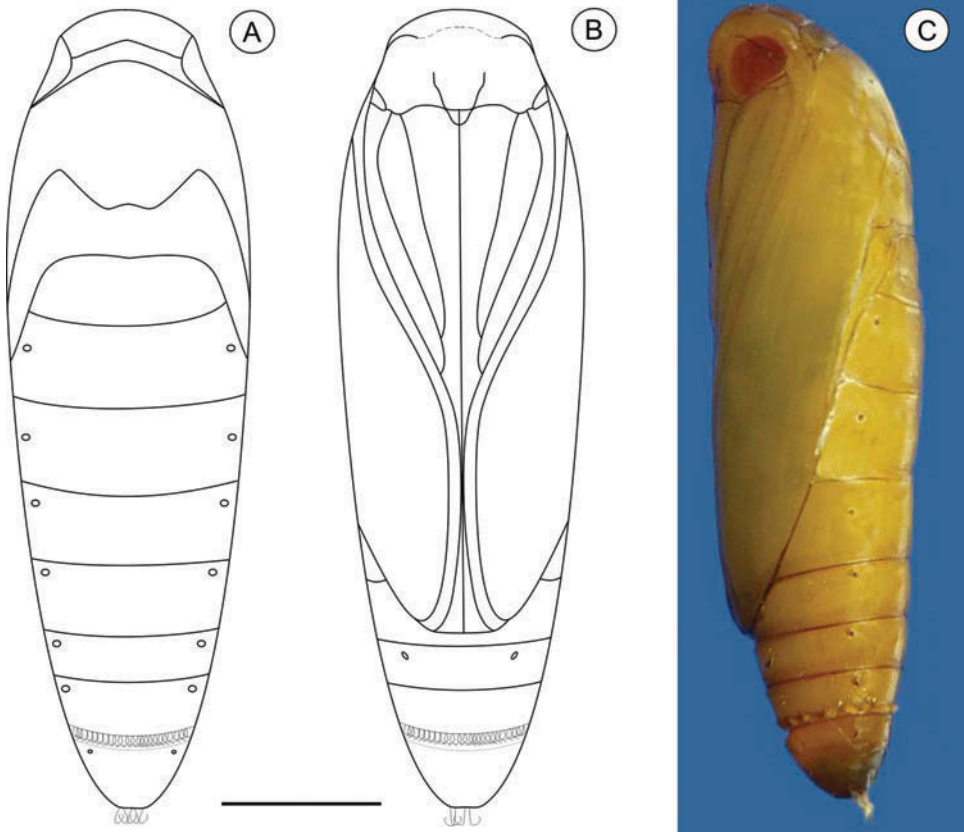


Figure 7. *Locharcha opportuna* pupa, in dorsal (A), ventral (B) and lateral (C) views, respectively. Scale bar = 1 mm.

222). In tissue collection, nine larvae (LMCI 174–53 and 57) fixed and preserved in 100% ethanol, at -20°C .

Diagnosis

A gelechiid lineage with larvae, pupae and adults having a clear affinity with the Teleiodini (*sensu* Lee and Brown 2008). It is assigned to the (formerly) monotypic genus *Locharcha* Meyrick, in having males with very similar wing venation patterns, and a strongly asymmetrical valva associated with a dome-shaped tegumen (Clarke 1969). *Locharcha opportuna* differs from *L. emicans* Meyrick in having a different wing colour pattern, uncus subtrapezoidal, tegumen longer than wide, and saccus not developed.

It is close to *Coleotechnites* Chambers, sharing males with an asymmetrical valve, and females with a single spiny, wedge-shaped signum. *Locharcha opportuna* differs from the species of *Coleotechnites* in several characteristics: (1) fore wings with veins

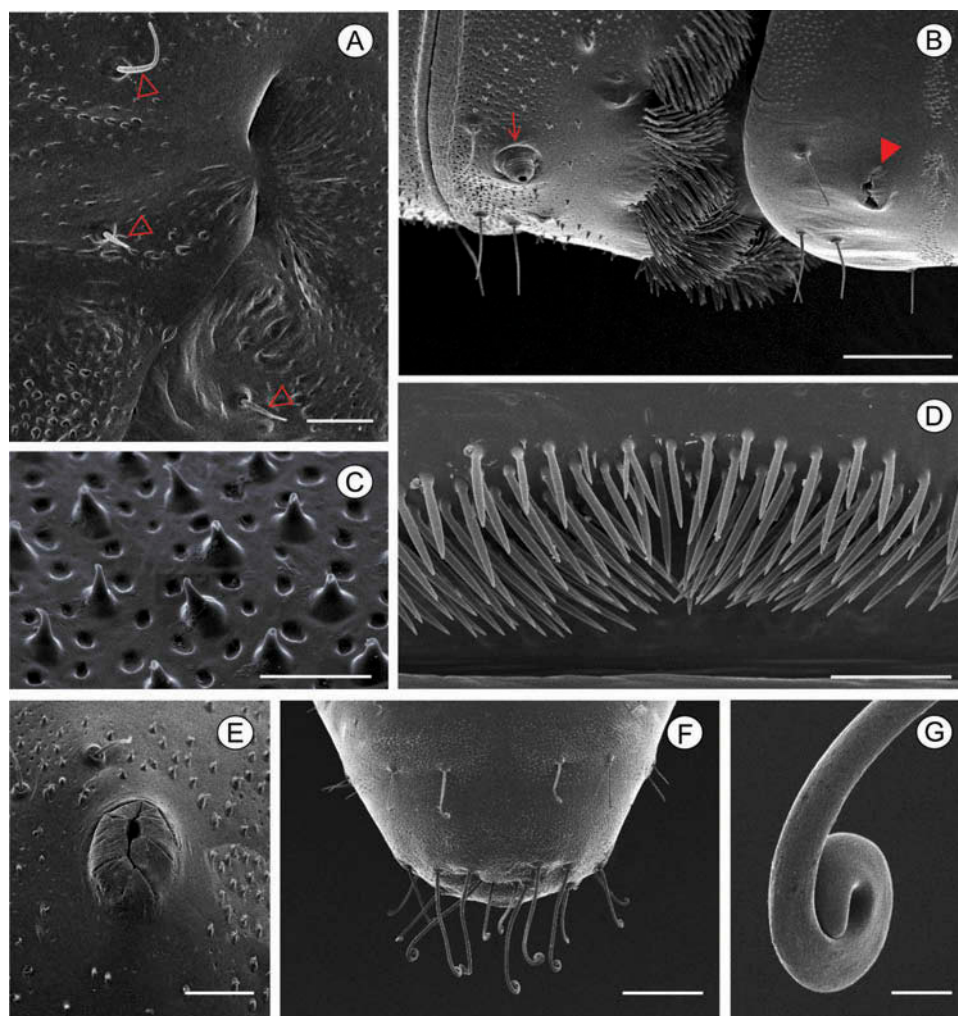


Figure 8. Scanning electron micrographs of *Locharcha opportuna* pupa: (A) clypeal and mandibular areas (open arrows indicate microsetae), ventral view; (B) abdominal segments seven and eight (small arrow and arrow head indicate abdominal spiracles seven and eight, respectively), laterodorsal view; (C) microtrichia of abdominal segment A5, dorsolateral view; (D) setae of seventh abdominal segment posterior margin, dorsal view; (E) pseudopodium scar of abdominal segment A6, ventral view; (F) distal portion of abdomen, dorsal view; (G) apical portion of cremaster seta, dorsolateral view. Scale bars = 50, 100, 10, 20, 50, 100, 10 μm , respectively.

R_4 stalked to R_5 , and M_2 stalked to M_3 ; (2) hind wings with vein R_5 separate from M_1 , and M_2 separate from M_3 ; (3) males without hair pencil in anal area of hind wings; (4) females with anterior margin of sterigma asymmetrical, projecting anteriorly as a process on the left side.

Description

Adult (Figures 1–4). Male and female similar in size and colour. Small moth, with fore wing length varying from 5.33 to 7.15 mm ($n = 8$). *Head* (Figure 1B): Frons and vertex mostly cream-white; labial palpus mostly with cream-white scales tipped with dark grey, terminal segments angled slightly upward; antennae dark grey; proboscis yellowish brown. Vestiture moderately smooth. Eye relatively large, rounded; vertical diameter subequal to interocular distance across frons. Ocellus absent. Antenna filiform, longer than half fore wing; flagellomeres completely encircled by single, dense row of slender scales. Clypeus with ventral margin broadly truncate. Pilifers well developed, triangular. Proboscis ~ length of labial palpus. Maxillary palpus short, smoothly scaled, 4-segmented, bent anteriorly and upward. Labial palpi three-segmented, long, bent anteriorly and upward; ratio of segments from base ~1.0: 3.4: 3.4. *Thorax*: Tegula and mesonotum mostly cream-white, mottled with sparse yellowish scales; tegula with dark-grey scales anteriorly; prothoracic and mesothoracic legs mostly dark grey; metathoracic legs lighter, mostly covered with cream-white scales tipped with dark grey. *Fore wings* (Figures 1A, 2A): dorsally covered with dark-grey scales along anterior portion and with cream-white scales on posterior margin, forming two wide, irregularly shaped, longitudinal bands; the cream-white band, mottled with yellowish scales; ventrally covered by darkish-grey scales; fringe yellowish; lanceolate, with 12 veins; L/W index ~ 4.3; retinaculum subcostal, with secondary, adjacent subradial setae in female; discal cell closed, ~ 0.63× length of fore wing; Sc ending circa middle anterior margin; R 5-branched; R₁ ending near two-thirds of wing margin; R₄ and R₅ stalked $c.1/2$ distance from the cell apex; R₄₊₅ and M₁ separate; M 3-branched; M₂ and M₃ stalked near cubitus; CuA 2-branched; 1A +2A forked basally, extending more than half length of posterior margin. *Hind wings* (Figures 1A, 2A): light grey on both sides; fringe mostly light grey and yellowish on anterior and posterior margins, respectively; with 9 veins, with a parallel-sided hair pencil at base of anal area; L/W index ~ 4.4, ~ 0.76 fore wing in length; frenulum a single acanthus in male, with two parallel-sided acanthi in female; discal cell closed, ~ 0.63× length of fore wing; Sc+R₁ ending at circa one-third of anterior margin; Rs ending circa two-thirds of anterior margin; M 3-branched, with M₁, M₂ and M₃ separate; CuA 2-branched, CuA₁ and CuA₂ separate; CuP weakly sclerotized, ending at one-third of posterior margin; 1A +2A well developed, ending near basis of posterior margin. Legs with tibial spur pattern 0–2–4; epiphysis present. *Abdomen*: Mostly covered by cream-white scales; pregenital segments unmodified.

Male genitalia (Figures 2B, 3A–E). Uncus (Figure 3A) small, subtrapezoidal, subequal in length to gnathos and with distal margin setose; tegumen dome-shaped, basal width/length ratio $c.0.45$; gnathos (Figure 3B) falcate; costal part of left valva (Figure 3C) with bulbous base and distal part slender, long and curved; in locus (Figure 2B), the distal part directed first to the right, and then upward, contouring the tegumen dorsally; saccular part of valve absent; right valve not detected; siccae (Figure 3D) symmetrical, curved mesally and setose, with the aedeagus anchored mesially; phallic fulcrum cylindrical (Figures 3D, E), middle-sized, with distal margin ventrally pointed; vesica without cornuti; saccus not developed.

Female genitalia (Figures 2C, D, 4A, B). Anal papillae laterally compressed, forming a narrow terminal, setose lobe; apophyses posteriores $c.3\times$ length of apophyses anteriores; sterigma with anterior margin asymmetrical; tergum projecting anteriorly on the left side as a pointed process (Figures 2D, E, 4A); sternum deeply and narrowly emarginated medially, bearing the ostium bursae on anterior, rounded portion, located on the left ventral side; ductus bursae membranous, shorter than corpus bursae, with ductus seminalis inserted medially; corpus bursae an elongate sac, wall covered by small, stout spines and bearing anteriorly a single spiny, wedge-shaped, centrally constricted signum (Figure 4B).

Etymology. From the Latin *opportunus* [= opportunist]; feminine.

Immature stages

Last larval instar (Figures 5, 6). Body length varying from 3.9 to 5.72 mm ($n = 7$). Endophyllous, semiprognathous and tissue-feeder. Head, thorax and abdomen with setae well developed. *Head*: light brown (Figure 5C), smooth (Figure 6A); frons subequal in height and width, extending to circa one-half epicranial notch (Figure 5A, C); labrum (Figure 6B) shallowly notched, with six pairs of setae of unequal size; six stemmata (Figure 6C) arranged in C-shaped configuration. Chaetotaxy (Figure 5A): A group trisetose; L group unisetose; P group bisetose; C group bisetose; F group unisetose; AF group bisetose; S group trisetose; SS group trisetose. A1, A3, P1, P2, S2 and S3 about equal in length, longest setae on head; C1, C2, F1, A2, AF2, L1 intermediate in length; AF1 shorter. Antenna (Figure 6D) two-segmented; mandibles (Figure 6B) broad, with four teeth and two unequal setae on outer surface; labium (Figure 6E) with two-segmented palpi, each bearing a seta; first segment $c.8\times$ longer than second segment; spinneret parallel-sided; maxilla (Figure 6F) prominent.

Thorax and abdomen (Figure 5B–D). Prothoracic shield (Figure 5C) dark brown, divided longitudinally by indistinct, unpigmented area; anterior and posterior half of mesothoracic, metathoracic and abdominal segments white and violet, respectively, giving a banded appearance to the larva (Figure 5D); pinacula small, fuscous; anal plate (Figure 5D) dark brown; anal fork black, with three major pairs of prongs; thoracic legs (Figure 5D) dark brown, with a pair of broad bladelike setae (Figure 6G) ventrolateral to terminal claw. Prolegs (Figure 6I) on A3–A6 and A10 of equal size; crochets in a biordinal, uniserial circle, mesial penellipse. Thorax chaetotaxy: T1 with D group bisetose, both located on the dorsal shield, D1 shorter than D2; XD group bisetose, similar in length and both on the dorsal shield; SD bisetose, laterally on the dorsal shield; L group trisetose, L1 longer than L2; SV group bisetose, posteroventral to L2, SV1 slightly longer than SV2; V group unisetose. T2 and T3 with D and SD groups bisetose; SD2 shorter than SD1; L trisetose, L3 posterior to L1–L2, similar in length to L1; SV unisetose; V unisetose. Abdomen chaetotaxy: D group bisetose; A1–A9 with D2 slightly longer than D1, and A10 with D1 and D2 similar in size; A1–A8 with SD group unisetose, A10 with SD1 and SD2 similar in size; L group trisetose; A1–A8 with SV group bisetose, SV1 slightly shorter than SV2, SV1 absent in A9; V group unisetose.

Pupa (Figures 7, 8). Body elongate-oval in dorsal and ventral views, varying from 5.2 to 6.24 mm ($n = 8$) in length, widest in mesothoracic region; vertex rounded; frontoclypeal suture weakly defined, concave medially; labrum U-shaped, labial palpi barely exposed; maxillary palpi short, not extending beyond anterior margin of eye; maxillae extending distally between sclerites of midlegs; antennae meeting mesially and reaching apical margin of fore wings; apices of metathoracic legs large, with distal part wider than antenna. Integument weakly melanized, with a few microsetae scattered dorsally on cephalic region (Figure 8A) and abdomen, and on anterior portion of abdominal segments. Abdominal terga mostly covered with stout spine-like microtrichia (Figure 8C). Thoracic and abdominal spiracles rounded, with elevated peritreme (Figure 8B); spiracle A8 partially closed. Sternum A6 with a pair of pseudopodium scars (Figure 8E); the scars on A5 are hidden by the overlying wing. Abdominal segment A7 posteriorly fringed with several aligned groups of short, stout setae (Figure 8B, D). Abdominal segments A8–A10 partially fused, with caudal cremaster bearing a few long, stout, distally coiled setae (Figure 8F, G).

Molecular phylogeny. A total of 621 nucleotide sites were analysed, of which 150 (24%) were variable. In accordance with our phylogenetic hypothesis, *Coleotechnites* was recovered as monophyletic in both methods of inference (BI and ML), with high support values (Figure 9). Because the topologies were identical, we decided to present only one (BI). *Locharcha opportuna* was placed as a sister lineage of the *Coleotechnites* species included in the analyses, with strong BPP and bootstrap support values (0.98 and 88, respectively) (Figure 9). The evolutionary divergence observed between comparisons of pairs of species ranged from 2 to 13% ($\pm 1\%$) (Table 2). The distance between the new lineage described herein and *Coleotechnites* was 11% (Figure 9). Similarly, the divergence between *L. opportuna* and the out-groups (*Recurvaria* and *Exoteleia*) was $c.12\%$ ($\pm 1\%$). Finally, the K2P distances within *Coleotechnites* indicate that this group also shows significant diversity, as evidenced by the range of distances ($2\text{--}8\% \pm 1\%$) (Table 2).

Distribution. *Locharcha opportuna* is known only from the type locality, the Dense Umbrophilous Forest (= Brazilian Atlantic Rainforest *sensu stricto*) portions of the CPCN Pró-Mata, São Francisco de Paula, Rio Grande do Sul, Brazil. As already mentioned, it occurs in association with fusiform galls (Figure 10A) induced by a species of *Palaeomystela* Fletcher (Lepidoptera, Momphidae) on the terminal branches of *Tibouchina sellowiana* (Cham.) Cogn. (Melastomataceae), which is described elsewhere (Luz et al. 2014).

Life history and seasonal abundance. Dissections in the laboratory demonstrated that field-collected galls having intact walls usually contain a larva of *Palaeomystella*, which can be differentiated from those of *L. opportuna* by their cream-white bodies (Figure 10B), among other morphological characteristics. Additional galls of this type left to develop in the laboratory showed that pupation of the cecidogenous larva occurs inside, within a tied-silk cocoon. Prior to pupation in this case, the last larval instar builds an operculum (Figure 10D) through which the adult emerges. However, none of these galls was collected attached to *T. sellowiana* plants during systematic sampling. Observations of individual galls under field conditions, on host plants belonging to the non-destructive sampling group, demonstrated that in fact they are

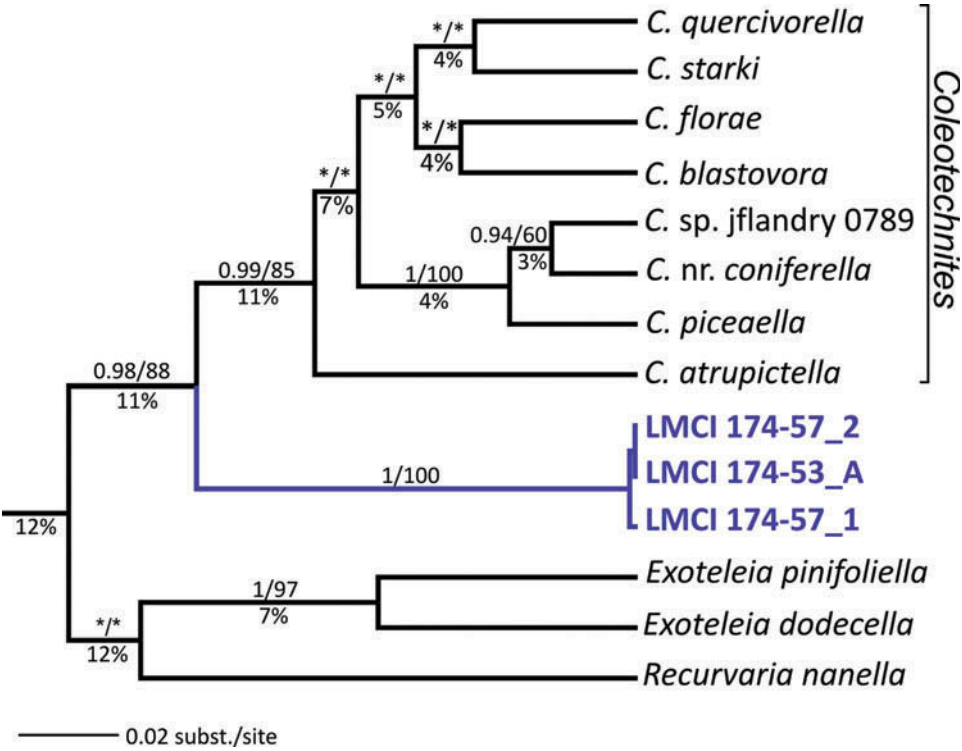


Figure 9. Bayesian inference tree for the new genus, based on 621 bp of the mitochondrial cytochrome oxidase c subunit I gene (CO-I). Numbers above branches indicate support values > 0.8/60 for Bayesian posterior probability (BPP)/bootstrap – for maximum likelihood (ML); those located below represent the percentage of evolutionary divergence between clades. Asterisk indicates support < 0.80/60 for BPP and ML, respectively.

dehiscent, later in ontogeny falling to the ground (Figure 10C), where the cecidogenous larva completes its development. Searches for them on the ground near *T. sellowiana* trees resulted in collection of many of these operculated galls.

The dissections also showed that galls having open, rounded orifices in the wall (Figure 10E) usually contained a larva of *L. opportuna* (Figure 10F). Additional galls of this type left to develop in the laboratory showed that these larvae are residents and live solitarily within these galls, feeding intensively on tissues induced to develop by the *Palaeomystella* species. They use the wall orifices to discharge their faeces. Dissection also showed that pupation in this case occurs inside the gall, within a tied-silk cocoon that is generally covered with faecal pellets (Figure 10G). By following each gall throughout ontogeny in the non-destructive samples, we found that, in contrast to the galls containing the *Palaeomystella* larvae, this modified gall morphotype does not fall to the ground, but remains attached to *T. sellowiana* trees for months. They progressively dry out, turning black after the *L. opportuna* emerge, and are then frequently used as shelters by small arthropods such as collembolans and acarines.

Table 2. Estimates of evolutionary divergence between sequences, based on 621 base pairs of the cytochrome oxidase I (*COI*) gene using the Kimura 2-parameter model. Mean number ($\pm$ standard error) of base substitutions per site over all sequence pairs between groups obtained by a bootstrap procedure of 1000 replicates is shown. The analysis involved the new species (in bold), eight described species of *Coleotechnites* and two outgroups (*Exoteleia* and *Recurvaria*).

	1.	2.	3.	4.	5.	6.	7.	8.	9.
1. <i>C. quercivorella</i>									
2. <i>Coleotechnites</i> sp.	0.05 $\pm$ 0.01								
3. <i>C. piceaella</i>	0.07 $\pm$ 0.01	0.03 $\pm$ 0.01							
4. <i>C. floriae</i>	0.04 $\pm$ 0.01	0.06 $\pm$ 0.01	0.06 $\pm$ 0.01						
5. <i>C. starki</i>	0.04 $\pm$ 0.01	0.06 $\pm$ 0.01	0.07 $\pm$ 0.01	0.05 $\pm$ 0.01					
6. <i>C. blastovora</i>	0.04 $\pm$ 0.01	0.07 $\pm$ 0.01	0.07 $\pm$ 0.01	0.04 $\pm$ 0.01	0.06 $\pm$ 0.01				
7. <i>C. atrupictella</i>	0.04 $\pm$ 0.01	0.07 $\pm$ 0.01	0.08 $\pm$ 0.01	0.06 $\pm$ 0.01	0.07 $\pm$ 0.01	0.06 $\pm$ 0.01			
8. <i>C. coniferella</i>	0.07 $\pm$ 0.01	0.02 $\pm$ 0.01	0.04 $\pm$ 0.01	0.06 $\pm$ 0.01	0.06 $\pm$ 0.01	0.08 $\pm$ 0.01	0.08 $\pm$ 0.01		
9. <i>Locharcha opportuna</i>	0.08 $\pm$ 0.01	0.10 $\pm$ 0.01	0.11 $\pm$ 0.01	0.08 $\pm$ 0.01	0.09 $\pm$ 0.01	0.09 $\pm$ 0.01	0.10 $\pm$ 0.01	0.11 $\pm$ 0.01	
10. <i>Exoteleia</i>	0.10 $\pm$ 0.01	0.12 $\pm$ 0.01	0.12 $\pm$ 0.01	0.10 $\pm$ 0.01	0.11 $\pm$ 0.01	0.10 $\pm$ 0.01	0.12 $\pm$ 0.01	0.12 $\pm$ 0.01	0.12 $\pm$ 0.01
11. <i>Recurvaria</i>	0.11 $\pm$ 0.01	0.13 $\pm$ 0.01	0.13 $\pm$ 0.01	0.11 $\pm$ 0.01	0.12 $\pm$ 0.01	0.12 $\pm$ 0.01	0.13 $\pm$ 0.01	0.13 $\pm$ 0.01	

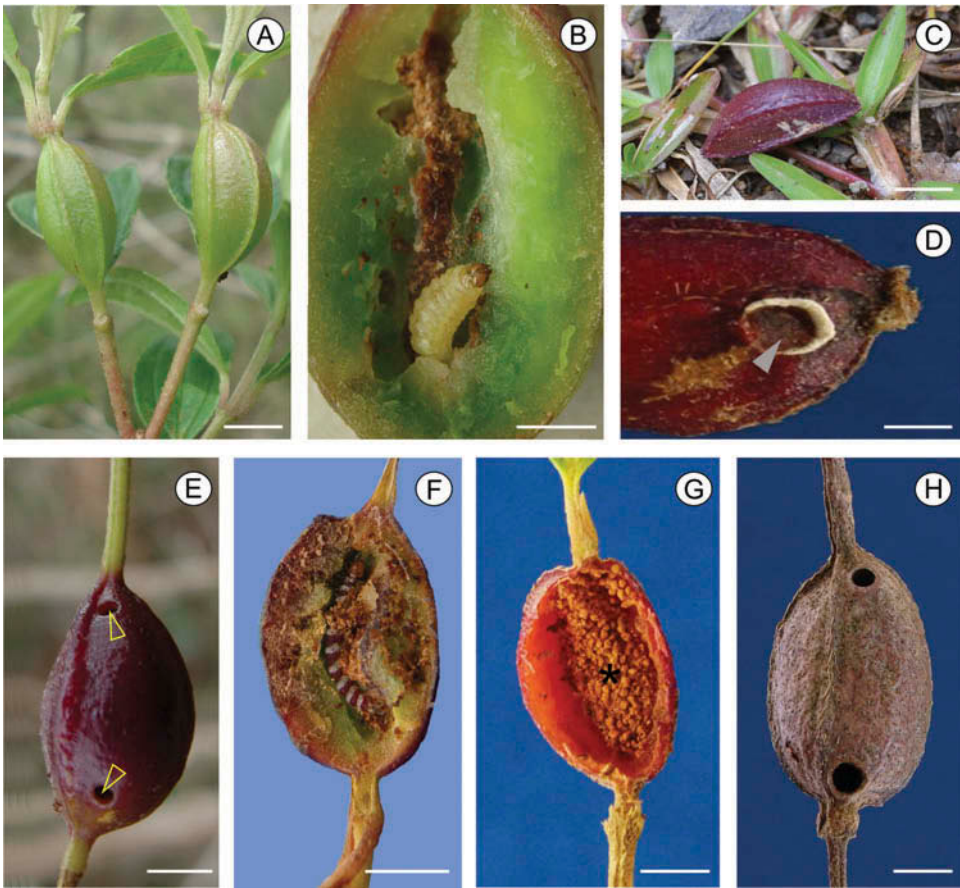


Figure 10. Galls induced by *Palaeomystella fernandesi* on *Tibouchina sellowiana* plants, free from (A–D) and attacked by (E–H) the kleptoparasite *Locharcha opportuna*. (A) general aspect of two young, green galls inhabited by cecidogenous larvae, as indicated by the absence of external orifices; (B) dissected gall showing a cecidogenous larva inside; (C) dehiscent, violet gall on the ground, bearing a cecidogenous late-instar larva; (D) operculum (indicated by closed arrow) made by a last instar of the cecidogenous larva on a dehiscent gall before pupation, external view; (E) violet gall inhabited by a kleptoparasite larva, as indicated by the presence of two orifices (open arrows); (F) dissected gall showing a kleptoparasite larva inside; (G) dissected gall showing a kleptoparasite pupal cocoon inside (covered by larval faecal pellets, indicated by asterisk); (H) old, empty gall, left attached to a *T. sellowiana* plant after the kleptoparasite emergence. Scale bars = 4, 2, 2, 2, 4, 4, 4, 4 mm, respectively.

Of the total of 512 galls dissected in laboratory, 164 (32.05%) had intact walls, containing larva of the cecidogenous insect; 169 (33.0%) had orifices and thus contained a larva or pupa of *L. opportuna*: the remaining galls had unidentified immatures of either parasitoid wasps (19.92%), predator thrips (9.96%) or cecidophagous curculionids (5.07%). No gall contained living larvae of both the inducer and *L. opportuna* living together, but dead bodies and exuviae (head capsules) of the former

were found in a few galls that contained living larvae of the latter. The number of galls found with two or more larvae of *L. opportuna* was negligible.

The variation in the frequency of different instars in relation to gall size and colour revealed that early instars (II and III) of the cecidogenous species were found inside green galls, and the later ones (IV) in galls with a colour spectrum ranging from green to violet (Figure 11A). We presume that galls containing first-instar larvae of the cecidogenous species were not detected in our sampling because of their very small size. Head-capsule exuviae from the first instar were frequently found inside galls with a second instar inside, and these were the smallest galls sampled. In contrast, larvae of the kleptoparasite, from all instars, were found primarily in violet galls (Figure 11B).

Within the continuum from green to violet-coloured galls found in the field (Figure 12A), green galls that were dissected had predominantly cecidogenous larvae inside, and the violet ones contained *L. opportuna* (Figure 12B). The smallest field-collected galls contained no larvae of the latter (Figure 12C). We also found a significant correlation between gall size and colour; taking all the galls into account, the intensity of green decreased and the violet increased with the increase in the size of the galls (Figure 12D).

Galls containing either cecidogenous larvae or the kleptoparasite ranged in number from 57 (April 2012) to three (August 2012) per sampling occasion (mean $\pm$ standard deviation = 23.78 ± 4.36 per occasion), which correspond to 7.12 and 1.5 per plant per occasion, respectively ($= 4.49 \pm 2.00$ galls per plant per occasion). Young, small galls containing cecidogenous larvae began to appear during early spring (September) when the *T. sellowiana* trees began to sprout, and reached a

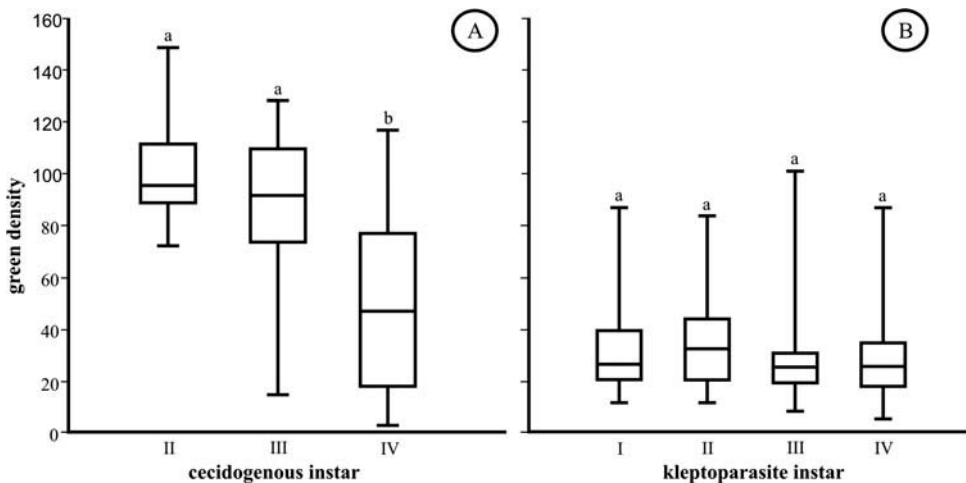


Figure 11. Variation in green colour intensity of *Tibouchina sellowiana* galls (median and corresponding quartiles) in relation to larval ontogeny, when considered the presence of larva either of the cecidogenous insect (A; = 10, 81 and 64 individuals, respectively, for instar II to IV) or the kleptoparasite (B; = 29, 38, 32, 64 individuals, respectively for instars I to IV) larvae inside. Bars followed by the same letter do not differ statistically (Kruskal–Wallis test, followed by Dunn’s multiple comparison tests).

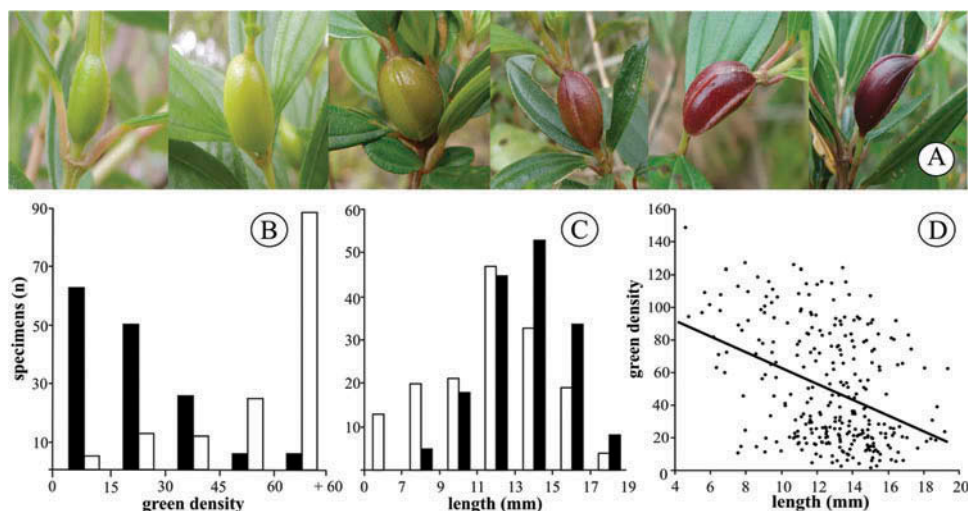


Figure 12. Variation in colour and size among galls induced by *Palaomystella fernandesi* on *Tibouchina sellowiana* plants, and corresponding use by either cecidogenous or kleptoparasite moths at CPCN Pró-Mata (April 2012 to June 2013). (A) Gradient from green- to violet-coloured for galls that were studied; (B, C) abundance of cecidogenous larvae (closed bars; total = 155 individuals) and kleptoparasite (open bars; total = 163 individuals) inside in relation to intensity of green colour and size of green galls, respectively; (D) linear regression between size and intensity of green colour on galls ($y = 0.67x + 8.77$, $R^2 = 0.152$, $p < 0.0001$, $n = 348$).

clear peak in density during the following autumn, which coincides with the flowering season (April) (Figure 13). The existence of a second, shorter density peak during October suggests that two generations may occur per year, and this possibility should be further investigated. The variation in abundance of the kleptoparasite followed that of the cecidogenous species, with the corresponding density peaks occurring in succession.

Discussion

Taxonomy

Male genitalia in gelechiid moths can be very specialized by reduction, modification and asymmetry; however, females in general have the ostium bursae ventromesial, rarely located laterally or dorsally (Hodges 1999). It is uncertain whether strongly modified female sterigma as here described for *Locharcha opportuna* sp. n. has evolved *de novo* within the Teleiodini, which should be further investigated. On the other hand, modifications in male valvae such as those described here have been reported for other teleiodinids, including the closely related genera *Recurvaria* Haworth, *Exoteleia* Wallengren, *Coleotechnites* Chambers (Lee and Brown 2008), and *Locharcha* Meyrick (Clarke 1969). In species of *Coleotechnites*, the valvae are strongly asymmetrical, with the right valve reduced (Hodges and Stevens 1978; Lee and Brown 2008). Similarly to the illustration provided by Clarke (1969) for *Locharcha emicans* Meyrick, we could not detect any indication of the presence of

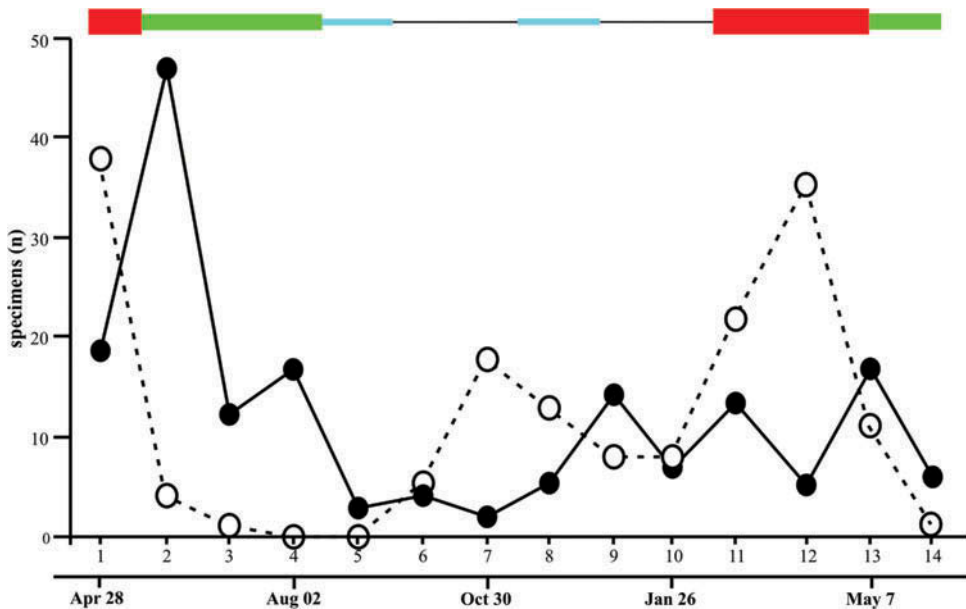


Figure 13. Seasonal abundance of cecidogenous (*Palaeomystella fernandesi*, dashed line) and kleptoparasite (*Locharcha opportuna*, solid line) larvae in galls (total = 164 and 169 individuals, respectively) induced on *Tibouchina sellowiana* plants at CPCN Pró-Mata, from April 2012 through June 2013. Arabic numbers from 1 to 14 represent 30-day sampling intervals. Upper horizontal bars indicate host plant phenological phases: red, flowering; green, fruiting; blue, dormancy; black, forming new shoots.

the right valve in the genitalia of *L. opportuna*, which may have been lost. However, as described by Ponomarenko (2008), these highly modified structures are glandular in nature, which she termed ‘glandiductors’. Also, they may not be homologous to any part of the valva, which thus would have been fused to other genital structures. The rounded, proximal basis of these structures is secretory in nature, and the sclerotized, slender distal portion has an opening at the apex; we confirm that this structure is present in the material studied here. Ponomarenko (2008) concluded that these genital glands could be considered as a basal synapomorphy for the subfamily Gelechiinae, thus limiting their taxonomic use at the generic level.

The genetic distances resulting from the molecular phylogenetic analyses gave further support to our hypothesis that *L. opportuna* is a distinct species. Furthermore, we found evolutionary distance values similar to those observed between *Coleotechnites* and the outgroup (*Recurvaria* and *Exoteleia*), corresponding to a generic level of divergence, i.e. *c.*10% (for a discussion of this threshold in Lepidoptera, see Wiemers and Fiedler 2007). Particularly in this group of gelechiids, the interspecific variation exceeds the intraspecific variation by at least one order of magnitude. We also found that the new species is more closely related to *Coleotechnites* than to *Recurvaria* and *Exoteleia*. *Coleotechnites* was previously recognized as closely related to teleiodinid genera existing in Asia, Europe, and North America (Lee and Brown 2008). However, it has not been compared with other related lineages existing in South America, such as the poorly known *Locharcha*

Meyrick and *Synactias* Meyrick. These are monotypic genera, whose wing-colour pattern and venation, and genitalia were illustrated by Clarke (1969). Unfortunately, the female of the type-species of the former (*L. emicans* Meyrick) is unknown, which prevents comparison for both sexes regarding the species described here. We also found similarities, for example in the wing colour pattern and aspects of the female genitalia (corpus bursae covered with small, stout spines), existing between *L. opportuna* and the type-species of the latter (*Synactias micranthis* Meyrick). In this case, the male is unknown, which again prevents further comparison. Thus, it is almost certain that the species described here belongs to the Teleiodini (sensu Lee and Brown 2008), but its generic status may change in the future upon revision of this group in the Neotropical region.

Locharcha opportuna has wing venation similar to those of species of *Exoteleia*, but differs in the hind wing pattern, M2 and M3 being connate in the latter. Furthermore, the male valvae are symmetrical and the female bursa lacks a signum in species of *Exoteleia* (Lee and Brown 2008). Similarities found in the larval and pupal stages, such as the maxillae longer than the prothoracic legs and rows of setae on the posterior margin of abdominal segment A7, also suggest that *L. opportuna* is closest to *Coleotechnites*. The species of *Exoteleia* have pupal maxillae shorter than the prothoracic legs; in *Recurvaria* and *Coleotechnites* these structures are longer than the prothoracic legs (Adamski et al. 2010). In *Recurvaria*, however, the caudal portion of the mesothoracic legs is narrower than the antennae; they are wider than the antennae in *Coleotechnites* and *L. opportuna*. Contrary to the suggestion of Lee and Brown (2008) and Adamski et al. (2010), and in accordance with the present description, the abdominal segment VII in *Coleotechnites* pupae are fringed with setae caudally; these structures are also present in *Recurvaria* but absent in species of *Exoteleia* (Patočka and Turčani 2005). As discussed below, kleptoparasitic lifestyles have been described for other gelechiid genera, but as far as we are aware, not for *Coleotechnites* or closely related lineages. Additional collections that we made in the Atlantic Rainforest indicate the existence of at least a second, undescribed species congeneric to *L. opportuna*, with the same lifestyle.

Life history and seasonal abundance

In conjunction, the present observations demonstrated that the galls of *T. sellowiana* are induced only by *Palaeomystella fernandesi*, and that *L. opportuna* is a kleptoparasite. Behavioural observations confirmed that the latter feeds upon tissues induced to develop by the former. The absence of *L. opportuna* in the smallest field-collected galls demonstrated that this species enters the systems later in gall ontogeny. Additional observations made in the laboratory by the senior author suggest that oviposition occurs on or near the gall, the larva entering the gall immediately after hatching, and this possibility should be better explored. The presence of dead bodies and head capsules of *P. fernandesi* inside the galls indicates that the kleptoparasite kills the cecidogenous larva after entering the gall. As reported by Caltagirone (1964), for a kleptoparasitic cosmopterigid on galls induced by *Pontania* (Hymenoptera: Tenthredinidae) on *Salix* (Salicaceae), the larva may prey on any insect encountered in the gall, and this possibility should be examined for the case studied here. The presence of only one larva within a gall, in most cases, demonstrates that *L. opportuna* has a solitary habit. Furthermore, the presence of head-capsule exuviae of the

same instar, which would of course belong to different larvae, was extremely rare, which suggests that the larva of *L. opportuna* uses a single gall during ontogeny, and has low, if any, mobility.

There was no indication that the galls change in colour, size or shape due to the presence of the kleptoparasite inside, as is the case for other cecidogenous species when attacked by inquilines (e.g. Van Noort et al. 2007) and parasitoids (e.g. Dias et al. 2013). The negative correlation between gall size and green colour, when both gall types (free and attacked by the kleptoparasite) were included in the analysis, demonstrates that in this case the colour change is a phenomenon tied to additional factors related to gall ontogeny, whose underlying mechanisms remain unknown. Changes in colour from green to violet such as found in *P. fernandesi* galls have been associated in several plant parts and tissues with the presence of anthocyanins, as a response to light stress (Gould et al. 1995; Chalker-Scott 1999; Barp et al. 2006). Inbar et al. (2010) suggested that the violet colour of galls may be also involved with protection of the inducers from natural enemies, which does not seem to be the case for the system studied here. Thus, *L. opportuna* may choose violet galls, either because they are more attractive to females during oviposition or because they contain larger amounts of resources since they are older and larger; these hypotheses are not mutually exclusive, and should be further tested.

As expected, *P. fernandesi* galls begin to increase in number during the spring, with the new growth of shoots of *T. sellowiana* trees, since gall induction depends on host-tissue reactivity (Raman 1994; Yukawa 2000). The large numbers of galls attacked (circa half of all field-collected galls; almost all of the galls during the density peaks in the first season) further indicate the existence of a high level of specialization for this kleptoparasitic species in relation to *P. fernandesi* galls. An attack index of c.30% was reported by Hawkins and Goeden (1984) for another kleptoparasitic gelechiid, associated with galls induced by *Asphondylia* (Diptera: Cecidomyiidae) on *Atriplex* (Chenopodiaceae) in southern California, USA. The increase in density, subsequently to that of the inducer, shows that *L. opportuna* responds according to the variation in density of the latter. The corresponding pattern may fit that known for predator/prey systems (e.g. Varley et al. 1973; Townsend et al. 2003), which should be confirmed by studies with a longer duration than that adopted here.

In summary, our study demonstrates with descriptive and quantitative data, as a case study for a new species of gelechiid, the existence of its kleptoparasitic habit in galls induced by a momphid lepidopteran in Melastomataceae. It differs primarily from other guilds, such as inquilines, as the kleptoparasite larva does not coexist with the cecidogenous larva in a given gall; there is no production of new tissues in this case. The kleptoparasite takes the gall environment over and feeds thereafter internally on the tissues that were induced to develop by the cecidogenous larva, without changing the external shape and size of the gall. It does not qualify within the cecidophage guild either, since it has low mobility, usually attacking only one gall internally, where it completes its life cycle; and may also be carnivorous.

There are many methodological, taxonomic and ecological implications related to this complex interaction. For example, potential misidentification of the true gall inducer should be taken into account, since in this case later instars of cecidogenous species may occur in lower numbers, as their galls are dehiscent, completing the development on the ground. Also, as galls bearing *L. opportuna* remain attached

longer to the host, the corresponding role of this kleptoparasitic species to indirectly enhance use by successor species in *P. fernandesi* galls should be investigated. Thus, our results not only clarified the specialized interactions existing in this peculiar momphid/gelechiid gall system, but also provided a solid integrative framework that could be applied to characterize the taxonomy, life history and ecology of other kleptoparasitic moths and beyond.

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Disclosure statement

No potential conflict of interest was reported by the authors.

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Supplemental material

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