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Dissertação de Mestrado

Interações entre uma espécie de *Palaeomystella* (Lepidoptera: Momphidae) indutor de galha em *Tibouchina sellowiana* (Melastomataceae) e um gênero e espécie nova de Lepidoptera que utiliza a galha: cecidofagia, inquilinismo ou cleptoparasitismo?

Fernando Albuquerque Luz

Porto Alegre, Fevereiro de 2014

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Dissertação de Mestrado apresentada ao Programa de Pós-Graduação em Ecologia, do Instituto de Biociências da Universidade Federal do Rio Grande do Sul, como parte dos requisitos para obtenção do título de Mestre em Ecologia.

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"Creio no riso e nas lágrimas como antídotos contra o ódio e o terror".

Charles Chaplin

"Há uma grandeza nesta visão da vida, com os seus vários poderes originalmente soprados em algumas formas, ou em apenas uma; e enquanto este planeta foi girando na sua órbita, obedecendo à lei fixa da gravidade, intermináveis formas, belas a admiráveis, a partir de um começo tão simples, evoluíram e continuam a evoluir."

Charles Darwin

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Resumo

As galhas são alterações no tecido vegetal das plantas, induzidas principalmente por insetos, ácaros, helmintos e vírus galhadores. Estes tecidos por serem altamente nutritivos atraem outros organismos para consumir tais recursos; além disso, o próprio indutor também apresenta seus inimigos naturais, criando assim, nestes sistemas, complexas interações, que pouco são abordadas na literatura de galhas. Os insetos constituem-se no principal grupo de organismos indutores de galha. Apesar da alta diversidade do grupo ser relatada, ela é pouco conhecida; ou seja, uma grande minoria dessa diversidade foi descrita para a ciência. Sendo assim, no Capitulo I desta Dissertação, descrevemos três novas espécies de lepidópteros galhadores associados com espécies de *Tibouchina* (Melastomataceae) no Brasil, com descrições das larvas, pupas e adultos, além da história de vida e suas relações filogenéticas. As três novas espécies pertencem ao gênero *Palaeomystella* (Momphidae), usando como hospedeiras *T. asperior*, *T. fissinervia* e *T. sellowiana*. Nesta última planta, foi encontrado outro lepidóptero interagindo com o indutor, cujo estudo resultou o Capitulo II da Dissertação, que teve como objetivos: (1) descrever uma nova espécie de microlepidóptero, (2) identificar que guilda pertence esta nova espécie, (3) descobrir porque estas galhas mudam sua coloração e (4) estudar a variação na abundância estacional das populações do indutor e do ocupante da galha. Tivemos como resultados: (1) descreve-se uma nova espécie de Gellechidae; (2) trata-se de um cleptoparasita, pois mata o indutor da galha para usufruir dos recursos utilizados por ele, (3) a galha muda de coloração, do verde para o vermelho, devido a sua maturação, e não a presença do cleptoparasita e (4) a variação nas densidades do indutor e do cleptoparasita seguem um padrão predador/presa, correspondente à interação consumidor/recurso.

Palavras-chave: Galhadores, Gellechioidea, *Tibouchina*, Guildas associadas á galhas.

Abstract

Galls are changes in plant tissue of plants, induced mainly by insects, mites, helminthes and viruses. Their tissues are highly nutritious, attracting other organisms for consumption. Moreover, the inducer also has its natural enemies, thus creating in such systems, complex interactions that have been little explored in the gall literature. Insects constitute the main group of gall-inducing organisms. Despite their high diversity, a large minority of this diversity has been described. Thus, in Chapter I of this Msc. Thesis, we describe the larva, pupa and adults of three new cecidogenous species of Lepidoptera associated with species of *Tibouchina* (Melastomataceae) in Brazil. Data on life history and a phylogenetic analysis are also provided. The three new species belong to the genus *Palaeomystella* (Momphidae), using as host *T. asperior*, *T. fissinervia* e *T. sellowiana*. In the latter plant, it was found another lepidopteran interacting with the inducer, whose study resulted in the Chapter II that aimed: (1) to describe a new genus and a new species of this microlepidoptera; (2) to identify the guild this new species belong to; (3) to find out why these galls change color, and (4) to determine the seasonal variation in the abundance of such populations. The new taxon corresponded to kleptoparasitic Gellechidae that kills the gall inducer to take advantage of the gall resources. The galls change from green to red due to their maturation, and not by the presence of kleptoparasite. Variation in density of the inducer and kleptoparasite followed a prey/predator pattern corresponding to the consumer/resource interaction.

Key-words: Cecidogenous moths, Gellechioidea; *Tibouchina*, guilds associate to galls.

Sumário

Introdução*

Indutores de galha

Galhas são alterações no tecido vegetal em resposta à alimentação ou outro estímulo induzido por organismos, como insetos, ácaros, vírus, entre outros (Dreger-Jaufret & Shorthouse 1992). Os insetos são o grupo mais representativo de indutores de galha (Maia & Fernandes 2004) e são considerados um grupo cosmopolita de herbívoros especialistas, que formam uma guilda diferenciada (Espirito-Santo & Fernandes 2007).

Os lepidópteros são um grupo com poucos galhadores conhecidos. Até o ano de 2005, eram reconhecidos 352 indutores de galha desta ordem de insetos, distribuídos em 20 famílias, dentre estas, Gelechiidae, considerada a mais representativa. A maioria dos lepidópteros galhadores são univoltinos, formando galhas uniloculares e tem seu ciclo sincronizado com a fenologia da planta (Miller 2005).

Várias hipóteses sobre a riqueza de insetos galhadores são conhecidas (e.g., Fernandes 1992, Fleck and Fonseca 2007, Mendonça Jr. 2002). Na concepção de Fernandes (1992), famílias botânicas com maior número de espécies e plantas com complexidade arquitetônica possuem maior riqueza de galhadores. Espirito-Santo & Fernandes (2007) fizeram uma estimativa para a diversidade de galhadores, e estimaram um número de 132,930 indutores de galha para todo o mundo, fauna essa, pouco conhecida, e com muitas espécies a serem descritas.

Guildas associadas a galhas

As galhas servem de recurso não só para seus indutores, mas também para predadores, parasitóides, sucessores, simbiontes, cecidófagos, inquilinos e

cleptoparasitas (Mani 1964, Fernandes et al 1987, Sanver & Hawkins 2000, Sugiura et al 2004, Morris et al 2000) estes três últimos casos recebem pouca atenção da literatura.

Estas outras guildas associadas ao sistema planta-indutor podem interagir tanto com o galhador quanto com a galha, formando uma rede complexa de interações (Sugiura & Yamazaki, 2009)

Os galhadores podem ser considerados como engenheiros de microhábitats, visto que as galhas por eles induzidas são estruturas conspícuas, muitas vezes rígidas externamente e de tamanho considerável, que no mínimo podem oferecer abrigo para pequenos invertebrados. Assim, podem ser exploradas por outros herbívoros ou onívoros, que não se alimentam diretamente do galhador (Sanver & Hawkins, 2000). De uma maneira geral, estes organismos são conhecidos como sucessores ou inquilinos.

Predadores e parasitóides, são os principais responsáveis pela mortalidade dos indutores de galha. Os predadores conhecidos são pássaros e outros insetos (Craig et al 2007) e, dentre os parasitóides, muitas vespas são conhecidas por atacarem os imaturos de indutores de galha (e.g Stone et al 2002).

Sucessores são organismos que utilizam a galha após a saída do indutor e os simbiontes são, na maioria, fungos que estão associados com os galhadores (Mani 1964).

Inquilinos e cecidófagos são organismos incapazes de produzir sua própria galha, mas se alimentam destes tecidos induzidos por um galhador (Mani 1964).

O cleptoparasitismo é o roubo do recurso (galha) por outro organismo, ocasionando no afugentamento ou morte do galhador (Mound & Morris 2000)

Os termos inquilinismo, cleptoparasitismo e cecidófagos muitas vezes são confusos e contraditórios na literatura de galhas.

Inquilinismo versus cleptoparasitismo versus cecidofagia

Destas três guildas associadas, o inquilinismo é o mais estudado. De acordo com Ronquist (1994), os inquilinos não podem induzir galhas, e acabam se instalando em galhas produzidas pelos indutores. Quando na presença do indutor, podem ser letais ou não para estes, dependendo se eles modificam o tecido vegetal e/ou criam seu próprio compartimento (Sanver & Hawkins 2000), ou simplesmente, por consumir o recurso previsto para o indutor.

A respeito do efeito de inquilinos sobre os indutores de galha estudados por László & Tóthmérész (2006), foi constatado que inquilinos aumentam a sobrevivência de indutores de galha, mas este resultado provavelmente se deve ao fato de que o inquilino não modifica o tecido da galha. No caso estudado por Noort (2007), em que cinipídeos inquilinos modificam o tecido da galha induzido por um lepidóptero, acabam sendo letais para este último.

A distinção entre inquilinos e predadores/parasitas, muitas vezes, não é muito clara, porém, os inquilinos são muito comuns em galhas e podem ser componentes chave em estudos com foco de comunidades de galhadores (Sanver & Hawkins 2000). Cinipídeos inquilinos de galhas de outros cinipídeos são os inquilinos mais estudados (Ronquist 1994, Sanver & Hawkins 2000, Abe and Wachi 2011). A associação de inquilinismo entre grupos taxonômicos próximos foi tratada por Ronquist (1994) como *"Agastoparasitism"*.

Maia et al. (2008) mostraram que os Lepidoptera destacaram-se como a segunda ordem de insetos mais freqüente como inquilinos de galhas, ocorrendo em 13 morfotipos em uma área de restinga no estado de São Paulo. Miller (2005) relata que o inquilinismo ocorre em 9 ou mais famílias de Lepidoptera, dentre elas os próprios gelequídeos (conforme descrito acima, um dos principais indutores de galhas).

Inquilinos entram no “domicilio” do indutor, mas não tem como propósito matá-lo. A interação em que ocorre o afugentamento ou a morte do indutor é conhecida como Cleptoparasitismo.

O Cleptoparasitismo ocorre em vários grupos de animais (Iyengar 2008), especialmente em aves (e.g. Brockmann & Barnard 1979). Podemos dizer que o cleptoparasitismo é o roubo de qualquer tipo de recurso produzido ou adquirido por outro organismo. (Iyengar 2008).

No contexto das galhas, os cleptoparasitas são organismos que usurpam do domicilio, roubando o recurso para si (Morris 2000). Essa definição no contexto dos galhadores é muito pouco explorada, sendo encontrados apenas trabalhos com espécies de tripses australianos (e.g. Bono 2007, Mound & Morris 2000). Sendo assim, pouco se sabe da interação desses organismos com os indutores.

Os cecidófagos são organismos exclusivamente fitófagos (Caltagirone 1964), eles coexistem com o indutor, apenas matando-o quando consumido todo o recurso disponível para o indutor (Myiatake et al 2000, Sugiura & Yamazaki 2009). Os cecidófagos da ordem Lepidoptera raramente matam o indutor das galhas, ao contrário de Coleoptera que na maioria das vezes são letais (Sugiura & Yamazaki 2009)

A maioria dos cecidófagos da ordem Lepidoptera, como dito anteriormente, não matam o indutor, os letais são aqueles que deterioram os tecidos da galha, resultando na morte do indutor (Sugiura & Yamazaki 2009)

Alguns trabalhos já demonstraram a diferença entre inquilinos e cecidófagos (Mani 1964, Sugiura et al 2006, Sugiura & Yamazaki 2009). Mani (1964) sugere que os inquilinos evoluíram esse hábito de galhadores ancestrais e cecidófagos evoluíram isso independentemente. Além de que inquilinos conseguem modificar o tecido da galha

(Noort 2007) enquanto cecidófagos alimentan-se do tecido original, tanto interna quanto externamente (Sugiura & Yamazaki 2009)

Para Bono (2007) tanto cleptoparasitas quanto inquilinos são considerados parasitas, pois implicam custos reprodutivos para o hospedeiro. Mound & Morris (2000) estudaram trips cleptoparasitas de outros trips, galhadores ou construtores de domicílio, porém apenas relataram que os Cleptoparasitas matam os indutores de galha, ao contrário de trips inquilinos que não causam distúrbio ao galhador.

De acordo com nosso conhecimento, não existem na literatura, trabalhos que tratem, no contexto de galhas, a distinção do termo cecidófago e cleptoparasita.

As Melastomataceae e seus galhadores

As Melastomataceae são conhecidas por serem hospedeiras de muitos insetos indutores de galha, destacando-se Lepidoptera (Tavares 1917, Houard 1933, Becker & Adamski 2008). Dentre os insetos indutores de galhas, Cecidomyiidae (Diptera) é a mais conhecida e o grupo de galhadores predominante em todas as regiões do mundo (Espirito-Santo & Fernandes 2007). Maia & Fernandes (2004) estudaram galhadores em 30 famílias botânicas, e Cecidomyiidae foi o táxon predominante entre os indutores de galha, exceto em Melastomataceae, onde lepidópteros foram os indutores mais comuns. Em adição, em um estudo realizado em Minas Gerais por Carneiro et al (2009), Melastomataceae foi a segunda família de plantas com maior número de espécies hospedeiras e também a segunda em número de galhadores, sendo encontrado o maior número de lepidópteros galhadores nestas plantas.

Becker and Adamski (2008) descreveram três novas espécies de micro-lepidópteros associados a três espécies de Melastomataceae no Brasil. Os resultados indiretamente obtidos por Vecchi (1999) a respeito sugerem que existem dezenas de

espécies adicionais, indutoras de galhas nessa família botância, ainda desconhecidas para a ciência.

Dinâmica Populacional

A dinâmica populacional de galhadores está intimamente ligada à fase fenólogica da planta hospedeira (Price et al 1987); normalmente existe um sincronismo entre a emergência dos adultos do galhador e a produção de novos meristemas pela planta, visto que a indução das galhas (hiperplasia e/ou hipertrofia celular) dependem da diferenciação e desenvolvimento dos tecidos (Dreger-Jaufret & Shorthouse 1992).

A dinâmica entre consumidor - recurso segue o padrão de que a população consumidora é limitada pelo suprimento de alimento da população recurso e essa é controlada pela densidade da população consumidora (Townsend et al 2006). Porém, apesar de conhecidas as dinâmicas correspondentes entre consumidor - recurso (e.g. predador/presa, patógeno/hospedeiro), não se tem um conhecimento de como se comporta a relação galhador – inquilino/cleptoparasita/cecidófago, se a mesma segue um padrão consumidor-recurso.

Sendo assim, esta dissertação está estruturada em dois capítulos, que correspondem a dois artigos, o primeiro com descrição de três novas espécies de lepidópteros galhadores em Melastomataceae. O segundo contempla a descrição de um microlepidóptero que utiliza uma galha induzida em *Tibouchina sellowiana*, com considerações sobre a que guilda pertence esse organismo, porque que essas galhas mudam de coloração, bem como é determinada a variação estacional na densidade dos dois organismos envolvidos na interação.

* Introdução formatada segundo revista Zookeys.

Capitulo1. Taxonomy, life-history and phylogenetic relationships of three new cecidogenous *Palaeomystella* Fletcher (Lepidoptera, Momphidae) associated with *Tibouchina* Aubl. (Melastomataceae) in the Atlantic Rain Forest[1]

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Abstract. Neotropical melastomes host a variety of morphotype galls that are known to be induced primarily by the larval stage of momphid moths. However, only a few have been properly associated with the inducer identity at the species level, as most of them remain undescribed. Male, female, pupa, larva, and galls, of three new cecidogenous species of *Palaeomystella* Fletcher (Lepidoptera, Momphidae) using such plants are herein described and illustrated with the aid of optical and scanning electron microscopy. They include *Palaeomystella* "*A*" sp.n., *P.* "*B*" sp.n. and *P.* "*C*" sp.n. that are associated respectively with *Tibouchina sellowiana* (Cham.) Cogn., *T. asperior* (Cham.) Cogn. and *T. fissinervia* (Schrank & Mart. ex DC.) Cogn. (Melastomataceae) in the Atlantic Rain Forest, Brazil. Data on life-history and a preliminary analysis of mitochondrial DNA sequences including related species are also provided. Results pointed out to the existence of still uncovered taxonomic diversity and considerable variation not only on gall morphology but also on larval and pupal life-styles among these momphid species. Last instar can stay inside and thus pupating within galls that either remain fixed to the plant (*P.* "*C*") or that fall to the soil (*P.* "*A*"). Alternatively, they can leave the gall before, moving out from the plant to pupate within a cocoon made of attached leaves in the litter (*P.* "*B*").

Keywords. momphines, momphid moths, plant galls, melastome plants, Neotropical region.

Introduction

Cecidogeny have evolved independently in at least 20 microlepidopteran families, mostly located within the Gelechioidea. Although accounting to only a few hundred species, the majority of such moths have been associated to their gall morphotype only, as most are still waiting for taxonomic description at the specific level (Miller 2005).

This is the case for the Neotropical Melastomataceae, which hosts a variety of morphotype galls that are known to be induced primarily by Lepidoptera. In this case, even the family identity of the corresponding gall-inducers remained for a long time uncertain (*e.g*. Tavares 1917, Houard 1933, Lima 1945), being only recently associated with the momphine lineage, as a subfamily of Coleophoridae (Becker, 1999), and herein treated as Momphidae (sensus Kaila 2011, Nieukerken *et al*. 2011). Only four of such species have been described, all belonging to *Palaeomystella* Fletcher, 1940 (Becker 1999; Becker and Adamski 2008). The type-species (*P.chalcopeda* Meirick), to which only the female holotype is known has not been associated to any gall morphotype yet (Becker 1999). The other three (*P. tibouchinae, P. oligophaga and P. henriettiphila*) that were described by Becker and Adamski (2008) induce galls on *Tibouchina* Aubl. and *Macairea* DC. species that are distributed in the Cerrado biome, Central Brazil (the first two species) and on a *Henriettea* DC. species, found in Northeast Brazil (last momphine species). As result, until recently in the related literature as for example in botany and ecology related papers, these and other similar gall morphotypes appear as induced either by unidentified or erroneously identified Lepidoptera (*e.g*. Gonçalves-Alvim et al. 1999, Maia and Fernandes 2004, Carneiro et al. 2009, Santos et al. 2011, Bena and Vanin 2013, Ferreira and Isaias 2013, Isaias et al. 2013, Vecchi et al. 2013). These aspects raise the urgent need for carrying out alfa taxonomic work with this specialized moth lineage, in association with description of gall morphotype they induce.

Furthermore, the majority of the gall morphotypes (ca. 30) that are known to be induced by unidentified lepidopteran larvae in Brazil have been originally described not to the area mentioned above, but from the Atlantic Rain Forest (Rio de Janeiro State), mostly on *Tibouchina* species (Tavares 1917, Houard 1933). In fact, this is one of the

most diverse genus within the Melastomaceae that occur in such a biome, accounting to ca. 137 species in Southern and South Brazil, to where most are endemic (Goldenberg et al. 2012, Guimarães 2014). Although now substancially reduced and fragmented, the Atlantic Rain Forest is still associated with one the greatest diversity of plants and animals on earth, known as extremily rich in endemism (for a general description and discussion, see Morellato and Haddad 2000, Myers et al. 2000, Carnaval et al. 2009). Thus, as already pointed out for this biome by Brito et al. (2013) regarding expected diversity of leaf miner moths in general, it is expected that several species of cecidogenous momphine moths associated with Melastomataceae await there for description, given the high level of host specificity usually found for the gall-inducing insects in general.

In the course of an ongoing survey on the diversity of microlepidopterans in the Atlantic Rain Forest, Brazil, we found recently three momphid species associated with galls induced on three different *Tibouchina* species that are distributed in Bahia (one morphotype) and Rio Grande do Sul (two morphotypes). A comparison made between their inducers and type material showed not only their generic affinity with *Palaeomystella*, but also indicated they have diagnosable, stable characters that make them distinct, and thus new species are herein proposed. We describe and illustrate the last instar larva, pupal and adult stages of these new species, and provide characterization of their life history, including a general description of their galls. We also present a preliminary phylogenetic inference based on mitochondrial DNA sequences, including additional members of the genus.

Materials and Methods

Adults used in the study were reared from galls in small plastic vials under controlled abiotic conditions (14 h light / 10 h dark; 25 ± 2 ºC) in the Laboratório de Morfologia e Comportamento de Insetos, Departamento de Zoologia, Universidade Federal do Rio Grande do Sul (UFRGS), Porto Alegre city, Rio Grande do Sul State (RS), Brazil, from March 2012 to October 2013. Galls were field-collected with either later instar larvae or pupae inside, on shoots of *Tibouchina sellowiana* (Cham.) Cogn. (São Francisco de Paula municipality, RS), *T. asperior* (Cham.) Cogn. (Santo Antônio da Patrulha municipality, RS) and *T. fissinervia* (Schrank & Mart. ex DC.) Cogn. (Camacãn municipality, Bahia State) plants. Immature stages were obtained by dissecting additional galls. They were fixed in Dietrich´s fluid and preserved in 75% ethanol. For DNA analyses, they were preserved in 100% EtOH at -20°C.

For gross morphology studies, the specimens were cleared in a 10% potassium hydroxide (KOH) solution and slide-mounted in either glycerin jelly or Canada balsam. Observations were made with the aid of a Leica® M125 stereomicroscope. Structures selected to be drawn were previously photographed with an attached Sony® Ciber-shot DSC-H10 digital camera. Then, vectorized line drawings were made with the software CorelPhotoPaint® X4, using the corresponding digitalized images as a guide. At least five specimens were used for the descriptions of each life stage. Measurements were made with an attached ocular micrometer; values are presented as mean $\pm$ standard deviation unless noted otherwise.

For scanning electron microscope analyses, 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 phylogeny. Total genomic DNA was purified from larvae tissue using Qiagen DNA Blood and Tissue Kit to investigate (i) monophyly of *P.* "*A*", *P.* "*B*" and *P.* "*C*" and (ii) reconstruct phylogenetic relationships within *Palaeomystella*. For comparison, two pupae of *P. oligophaga* Becker & Adamski, that came from a population of *Macairea radula* (Bonpl.) DC. located in Brasilia, DF, were also used for DNA extraction (Table 1).We amplified through polymerase chain reaction (PCR) the mitochondrial gene cytochrome *c* oxidase subunit I (*CO-I*), including 660 base pairs (bp), using the universal primers LCO1490 (5'-ggtcaacaaatcataaagatattgg-3') and HCO2198 (5'-taaacttcagggtgaccaaaaaatca-3'), following conditions proposed by Folmer et al. (1994). PCR products were treated with Exonuclease I and FastAP Thermosensitive Alkaline Phosphatase (Thermo Scientific), sequenced using the BigDye chemistry and analysed on an ABI3730XL (Applied Biosystems Inc.) 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. All data generated in this study were deposited in GenBank under the accession numbers KJ188233- KJ188249 (Table 1). A phylogenetic tree was reconstructed in order to test our hypothesis of monophyletic status for the three *Palaeomystella*: *P.* "*A*", *P.* "*B*" and *P.* "*C*". In addition, we investigated the internal relationship of these taxa within *Paleomystella* and among other species. We thus used the unique currently recognized taxa (*P. oligophaga*) as well as undescribed species (*Palaeomystella* sp.1 and *Palaeomystella* sp. 2), in order to cover the most diversity of the genus as possible (Table 1). Accordingly, we obtained variants that match exactly

the region previously sequenced in a representative taxa of the sister group of Momphidae (genus *Mompha*) downloaded from the Genbank and incorporated in our analysis as outgroup (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 the GTR [General Time-Reversible] (Rodríguez et al. 1990) model of sequence evolution. We used four independent runs of 10 million generations and a burn in period of 100,000 (the first 1000 trees were discarded); the remaining trees were summarized in TreeAnnotator 1.6.2 (Drummond and Rambaut 2007) and used to infer a maximum a posteriori consensus tree. Posterior probabilities 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 figtree/). We also analyzed the evolutionary distance using Kimura 2-parameters (K2P) model (Kimura 1980) procedure, with 1000 of bootstrap replication, between groups defined as: 1) outgroup (*Mompha conturbatella*); 2) *Palaeomystella* sp. 1; 3) *Palaeomystella* sp. 2; 4) *P.* "*A*"; 5) *P.* "*C*"; 6) *P.* "*B*"; 7) *P. oligophaga*.

Museum collections. Abbreviations of the 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.

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, Camacãn, Bahia.

Results

Palaeomystella "*A*" Moreira and Becker, new species

Figs. 1A-B, 2-4, 11A-C, 12A-C

Diagnosis. Although showing congeneric affinity, *P.* "*A*" has morpholological features that in conjunction make it different from all known *Palaeomystella* species, as follows: 1) male, with genitalia having the upper section of valve narrowing distally, forming a single process that bends medially; 2) pupa, with cremaster short and apically rounded, with four pairs of setae; 3) galls, of fusiform type, with external surface without conspicuous pubescence, bearing a few longitudinal carena, induced on stem of the *T. sellowiana* apical branches.

Description

Adult (Figs. 1E-F). Male and female similar in size and color. Small moth with forewing length varying from 4.68 to 6.11 mm (n = 7). *Head* (Fig. 1F): Frons and vertex white cream; labial palpus mostly dark brown, basal segments porrect, terminal segment slightly angled upwards; antennae dark brown; proboscis yellowish brown. *Thorax*: Tegula and mesonotum white cream; legs dark brown. Forewing (Figs. 1E,

2A): lanceolate, with 13 veins; L/W index ~ 5.1; dorsally covered mostly by dark brown scales; with three inter-connected clear areas, which form a longitudinal S-like band; one proximal, rounded, in the anal area, made of light cream scales, followed by a short a stripe aligned in cubital area, made of white cream scales, and a third, also rounded and fainted, in the cell, made of light cream scales; a tenue, U-shaped band of light gray scales contours the tornus; 3 raised scale tufts bearing light gray scales, located posteriorly to cubitus, 1 in anal area, 1 in line with midcell, and 1 near tornal area; fringes dark brown; most covered by dark brown scales ventrally; retinaculum subcostal; discal cell closed, ~ 0.8x length of forewing; ending near one fifth of wing margin; Sc ending ca. middle anterior margin; R 5-branched; R_1 ending near one third of wing margin; R_5 and R5 stalked ca.1/2 distance from the cell apex; M 3-branched; CuA 2-branched; CuP weak proximally and not stalked with 1A+2A that is well developed, extending more than half the length of posterior margin. Hindwing (Fig. 2A): extremily lanceolate, with 9 veins; L/W index ~ 7.2, ~ 0.8 forewing in length; scales dark brown on both sides; fringes dark brown; frenulum a single acanthus on male, with two parallelside acanthi on female; $Sc+R_1$ ending ca. 1/2 anterior margin; Rs ending circa 1/5 anterior margin; M 3-branched, M_1 and M_2 stalked from remnant chorda of cell from point beyond base of Rs; CuA 2-branched, with CuA_1 stalked to M3; CuP weakly sclerotized, ending 1/3 posterior margin; 1A+2A well developed, ending near basis of posterior margin. *Abdomen* (not showed): scales pale brown, intermixed with gray scales; terga covered with transverse irregular rows of spiniform setae; eighth sternum (Fig. 2C) anteriorly expanded medially by a short lobe, associated to a subtriangular sternite.

Male genitalia (Figs. 2B, D-G). Uncus narrow, separated from tegumen by a narrow membranous area, distally rooflike and laterally setose (Fig. 2F); tegumen narrow; vinculum widened ventrally; fultura superior a flat, rounded plate; aedeagus tubiform, parallelsided, moderately long, slightly wider basally (Fig. 2G); vesica bearing a few stout and short, spinelike setae; juxta (Fig. 2D) attached to distal portion of aedeagus, longer than wide, with two small, parallel pointed projections centro-anteriorly and deeply concave distally; valva (Fig. 2B) covered by several long setae, divided near one third from the basis, forming a lower finger-like portion and an upper, wider and palmate portion that narrows ventro-distally, ending as a medially bent process; costa of dorsal portion bearing several stout, medium sized spines (Fig. 2E).

Female genitalia (Fig. 2H). Anal papillae connected dorsally, narrowed distally and setose; anterior apophyses with arms slightly curved, similar in length to posterior apophyses; sterigma divided into a bandlike tergum and a distally bilobed sternum, shallowly and widely emarginate medially; ostium bursae of small size, wider than long; ductus bursae membranous, shorter than corpus bursae, with ductus seminalis inserted distally; corpus bursae an elongate sac, with no sclerotizations on inner wall.

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 on *Tibouchina sellowiana* (Cham.) Cogn. (Melastomataceae): LMCI 174, 26.III.2012, by G.R.P. Moreira, F.A. Luz and P. Pollo; LMCI 210, 7-9.III.2013 by G.R.P. Moreira, F.A. Luz and L.T. Pereira. HOLOTYPE: ♂ (LMCI 210-56), donated to DZUP (29.409). PARATYPES: 2♀♀ (LMCI 174-161 and 162), donated to DZUP (29.410 and 29.411); 1♂ (LMCI 174-157) with genitalia in

glycerin (GRPM 50-51), 1♀ (LMCI 174-158), donated to MCTP (????? and ?????, respectively).

Other specimens examined. With the same collection data, deposited in LMCI. Adults, dried and pinned: 2 ♂♂ (LMCI 174-159 and 210-49), 1 ♀ (LMCI 174-160), 1 ♀ (LMCI 174-163) with genitalia in glycerin (GRPM 50-52). Adults, fixed in Dietrich and preserved in 70% ethanol: 1♂ (LMCI 174-165), 3♀♀ (LMCI 174-164, 166 and 167). Slide preparations, mounted in Canada balsam: genitalia, 3 ♂♂ (GRPM 50-29, 47 and 48), 1 ♀ (GRPM 50-28); wings, 2 ♂♂ (GRPM 50-45 and 50), 1 ♀ (GRPM 50-46); larvae, 2 last instars (GRPM 50-49). Immature stages, fixed in Dietrich's fluid and preserved in 70% ethanol: 8 last instar larvae (LCMI 174-52); 7 pupae (LMCI 174-168, 169 and 223; and, 210-16); 10 galls (LMCI 174-47 to 49, 174-217 to 222, and 210-15). In tissue collection, nine larvae (LMCI 174-50 and 56) fixed and preserved in 100% ethanol, under -20°C.

Etymology. *Palaeomystella "A"* is named …

Immature stages

Last larval intar (Fig. 3). Body length varying from 3.51 to 7.01 mm (n = 6). Cecidogenous, endophyllous, semiprognathous and tissue-feeder. Head, thorax and abdomen with setae well developed. *Head* (Fig. 3A, C-D): brownish, with two middle-dorsal lighter areas; smooth, with shallow ridges; labrum shallowly notched; frons higher than wide, extending ca. three-fourth epicranial notch; six stemmata arranged in C-shaped configuration. Chaetotaxy (Fig. 3A): A group trisetose; L group unisetose; P group bisetose; MD trisetose; C group bisetose; F group unisetose; AF group bisetose; S group trisetose; SS group trisetose. A1, A3, P1 and S2 about equal in length, longest

setae on head; C1, C2, F1, A2, AF2, L1 intermediate in length; AF1 shorter; MD1-3 very reduced and aligned to each other. Antenna two-segmented. Mandibles broad with four teeth, and one seta on the outer surface; labium broad, with two-segmented palpus and spinneret parallel sided; maxilla prominent.

Thorax and Abdomen (Fig. 3B-D): Prothoracic shield light brown, divided longitudinally by slightly marked, unpigmented area; anal plate brownish. Thoracic legs slightly pigmented. Prolegs on A3-A6 and A10 of equal size; crochets in a circle, uniserial and uniordinal. Thorax chaetotaxy: T1 with D group bisetose, both located on the dorsal shield, D1 shorter than D2; XD group bisetose, with similar length and both on the dorsal shield; SD bisetose, lateraly on the dorsal shield; L group bisetose, 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, median-transversally alined; D2 and SD1 similar in length, and longer than D1 and SD2 respectively; L trisetose, L3 posterior to L1-L2, with similar length to L1; SV unisetose; V unisetose. Abdomen chaetotaxy: D group bisetose; A1-9 with D2 slightly longer than D1, and A10 with D1 longer than D2; SD group bisetose, A1-7 with SD1 slightly longer than SD2 and A10 with SD2 longer than SD1, SD2 absent in A9; A1-8 with L group bisetose, L1 longer than L2, L2 absent in A9; A1-8 with SV group bisetose, SV1 slightly shorter than SV2, SV1 absent in A9; V group unisetose.

Pupa (Figs. 4A-C, 11A-C). Length varying from 4.42 to 6.11 mm (n = 5). Body elongate oval in dorsal and ventral views, widest and dorsally raised in the mesothoracic region. Integument weakly melanized, mostly smooth, with a few micro-setae, scattered dorsally. Frontoclypeal suture not evident. Labrum U-shaped. Labial palpi long; antennae arched anteriorly and separate, approximate and parallel posteriorly to distal

margins of maxillae, surpassing the apical margin of forewings; maxillae extending distally between sclerites of midlegs; femora of midleg not fused distally; femora of foreleg extending beyond the widest part of labial palpi. Cremaster (Fig. 11A-C) short and apically rounded, with four pairs of setae; one latero-basally, another latero-dorsally and two latero-distally located.

Host Plant. Melastomataceae: *Tibouchina sellowiana* (Cham.) Cogn. It is a small three (from 3 to 6 m high) found in the forests located on the coastal mountains of southern Brazil, where it is endemic. It ranges in distribution from the states of Minas Gerais to Rio Grande do Sul, usually flowering during April-May (Souza 1986, Guimarães 2014).

Distribution. *Palaeomystella* "*A*" is known only from the type locality, the Dense Umbrophilous Forest (= Brazilian Atlantic Rain Forest *sensu stricto*) portions of the CPCN Pró-Mata, São Francisco de Paula Municipality, RS, Brazil.

Life history (Figs. 12A-C). Gall of the fusiform type varying in length from 6.0 to 18 mm; n = 12), induced on stem of *T. sellowiana* apical branches (Fig. 12A). Without conspicuous pubescence, bearing a few longitudinal carena on surface and changing gradually with age from green to violet. They are common on *P. sellowiana* plants at the type locality, during Summer and Spring. Most of them house a specialized kleptoparasitic gelechiid moth, whose complex natural history is described in detail elsewhere (Luz et al. 2014). Those that are free from kleptoparasite fall from the host plant to the ground later in larval ontogeny, the cecidogenous development being completed in the soil. Pupation occur inside the gall, within a cylindric, longitudinally disposed cocoon made of tied white silk. The adults emerge supposedly after the winter.

Emergence occur through a rounded operculum, built and sealed by the last larval instar on the gall wall (Fig. 12B), before pupation. The pupal exuvium remains in the cocoon, inside the gall.

Palaeomystella "*B*" Moreira and Becker, new species

Figs. (1C-D, 5-7, 11D-F, 12D-F)

Diagnosis. It is closest to *P*. "*fissinervia*", sharing with this species a pronounced palmate upper section of male valve and bladelike female signa. These characteristics make them different from all *Palaeomystella* species, except from *P. oligophaga*. This species, however, has the forewings with R_4 - R_5 fused and hindwing with M_1 and M_2 stalked from remnant chorda of the cell (Becker & Adaminski 2008). *P*. "*B*" differs from *P*. "*C*", by having: 1) adults, with body covered with pale brown scales interspersed by pale brown scales tipped with dark brown ones; 2) males, with latero-anterior margin of sternum eight deeply concave; distal portion of valve upper section narrower; juxta as long as wide, and anteriorly slightly concave; 3) females, with signa having inward projection long, fine and curve; 4) pupa, with cremaster tubular, dorsally directed, bearing latero-apically a pair of anteriorly curved spines; 5) galls, of globoid type with external surface covered with short spine-like projections, induced on terminal buds of *T. asperior* plants.

Description

Adult (Figs. 1E-F). Male and female similar in size and color. Small moth with forewing length varying from 4.81 to 5.59 mm (n = 5). *Head* (Fig. 1F): Frons pale brown; vertex with pale brown scales tipped with dark brown; labial palpus with scales pale brown tipped with dark brown, basal segments porrect, terminal segment slightly

angled upwards; antennae with scales pale brown tipped with dark brown; proboscis yellowish brown.

Thorax: Tegula and mesonotum with pale brown scales tipped with dark brown, posterior ones having more pale brown; prothoracic and meso-thoracic legs dark brown; metathoracic legs pale brown, having tibia and tarsum intermixed with scales darkbrown. Forewings (Figs. 1E, 2A): lanceolate in shape, with 13 veins; L/W index ~ 4.5; dorsally covered by pale brown scales, intermixed with scattered, pale brown scales tipped with dark brown, and with longitudinally aligned groups of brown scales; a narrow, ill-defined, dark-brown streak bisects wing longitudinally from base to tornus; 3 raised scale tufts located posterior to cubitus, 1 wider in anal area, made of black gray scales, 1 in line with midcell, and 1 near tornal area; fringes pale brown, interspersed by a few pale brown scales tipped with dark brown; tornal area with two bands of pale brown scales tipped with black brown; most uniformely covered by dark brown scales ventrally; retinaculum subcostal; discal cell closed, ~ 0.7x length of forewing; ending near one fifth of wing margin; Sc ending ca. middle anterior margin; R 5-branched; R_1 ending near one third of wing margin; R_5 and R5 stalked ca. 1/4 distance from the cell apex; M 3-branched; CuA 2-branched; CuP weak proximally and not stalked with 1A+2A that is well developed, extending more than half the length of posterior margin. Hindwing (Fig. 2A) extremily lanceolate, with 9 veins; L/W index ~ 6.4, ~ 0.8 forewing in length; scales light brown on both sides; fringes pale brown; frenulum with a single acanthus on male, and with two acanthi on female, proximal one anteriorly divergent, and the distal, parallelside to the wing anterior margin; Sc+R_1 ending ca. 1/2 anterior margin; Rs ending circa 1/5 anterior margin; M 3-branced, M_1 and M_2 stalked , near Rs; CuA 2-branched, with CuA_1 stalked to M3; CuP weakly sclerotized ending 1/3 posterior margin; 1A+2A well developed, ending near basis of posterior margin.

Abdomen (not showed): scales pale brown intermixed with grey scales; terga covered with transverse irregular rows of spiniform setae. Eighth sternum (Fig. 5C) anteriorly expanded medially by a slender, shaply pointed lobe, associated to a subtrapezoidal sternite.

Male genitalia (Figs. 5B, D-F). Uncus narrow, separated from tegumen by a narrow membranous area, laterally setose (Fig. 5F); tegumen narrow, widened dorsally; vinculum widened ventrally; fultura superior a short, flat plate; aedeagus tubiform, curved ventrally, short, slightly wider basally (Figs. 5F, E); vesica bearing several stout, spinelike setae; juxta (Fig. 5D) attached to distal portion of aedeagus, wider than long, with slightly concave anterior margin and pointed distally; valva (Figs. 5B) covered by several long setae, divided near one third from the basis, forming a lower, wider finger-like portion and an upper, narrowly based, longer palmate portion.

Female genitalia (Figs. 5 G,H). Anal papillae connected dorsally, setose (Fig. 5G); anterior apophyses with arms sligtly shorter in length than posterior apophyses; sterigma divided into a bandlike tergum and a distally bilobed sternum, shallowly emarginate medially; ostium bursae of median size, wider than long; ductus bursae membranous longer than corpus bursae, with ductus seminalis inserted medially; corpus bursae an elongate sac, bearing two narrow and curved, bladelike signa that are connected to transversally elongate, rounded plates located in the wall (Fig. 5H).

Type material. BRAZIL: Antonio Malta´s farm, Coxilha das Lombas, 30°02`13``S; 50°36`30``W, 17m, Santo Antônio da Patrulha municipality, RS, Brazil. Adults preserved dried and pinned, reared by the senior author from galls induced on *Tibouchina asperior* (Cham.) Cogn. (Melastomataceae), LMCI 211, 12.III.2013, by

G.R.P. Moreira, F.A. Luz and S. Bordignon. HOLOTYPE: ♂ (LMCI 211-12), donated to DZUP (29.412). PARATYPES: 1♀, 1♀ (LMCI 211-14 and 06) with genitalia in glycerin (GRPM 50-43 and 44), donated to DZUP (29.413 and 29.414, respectively).

Other specimens examined. Adults, dried and pinned, with the same collection data, deposited in LMCI under the following accession numbers: 2 ♂♂ (LMCI 211-07 and 10); 1 ♀ (LMCI 211-11). Slide preparations, mounted in Canada balsam: genitalia, 2 ♂♂ (GRPM 50-38 and 39), 1 ♀ (GRPM 50-40); wings, 1 ♂ (GRPM 50-36), 1 ♀ (GRPM 50-37); larvae, 2 last instars (GRPM 50-41 and 42). Immature stages, fixed in Dietrich's fluid and preserved in 70% ethanol: 6 last instar larvae (LCMI 211-17 to 22); 3 pupae (LMCI 211-5, 9 and 26); 6 mature, intact galls (LMCI 211-25). In tissue collection, six larvae (LMCI 211-8) fixed and preserved in 100% ethanol, under -20°C.

Etymology. *Palaeomystella "B"* is named …

Immature stages

Last larval intar (Fig. 6). Body length varying from 4.94 to 9.88 mm (n = 5). Cecidogenous, endophyllous except prior pupation, semiprognathous and tissue-feeder. Body subcilyndrical, whitish cream, changing to red before pupation. Head, thorax and abdomen with setae well developed. *Head* (Fig. 3A, C-D): light brownish, interposed by two pairs of middle-dorsal darker areas; smooth, with shallow ridges; labrum shallowly notched; frons higher than wide, extending ca. three-fourth epicranial notch; six stemmata arranged in C-shaped configuration. Chaetotaxy (Fig. 3A): A group trisetose; L group unisetose; P group bisetose; MD trisetose; C group bisetose; F group unisetose; AF group bisetose; S group trisetose; SS group trisetose. A1, A3, P1 and S2 about equal

in length, longest setae on head; C1, C2, F1, A2, AF2, L1 intermediate in length; AF1 absent; MD1-3 very reduced and alined to each other. Antenna two-segmented. Mandibles broad with four teeth, and one seta on the outer surface; labium broad, with two-segmented palpus, the distal one minute; spinneret parallel sided; maxilla prominent.

Thorax and Abdomen (Fig. 3B-D): Prothoracic shield and anal plate slightly marked by irregular, small light brown blots. Thoracic legs also scarcely pigmented. Prolegs on A3-A6 and A10 of equal size; crochets in a semi-circle, uniserial and uniordinal. Thorax chaetotaxy: T1 with D group bisetose, both located on the dorsal shield, D1 shorter than D2; XD group bisetose, with similar length and both on the dorsal shield; SD bisetose, lateraly on the dorsal shield; L group bisetose, 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, median-transversally alined; D2 and SD1 similar in length, and longer than D1 and SD2 respectively; L trisetose, L3 posteriorly, with similar length to L1; SV unisetose; V unisetose. Abdomen chaetotaxy: D group bisetose; A1-9 with D2 slightly longer than D1, and A10 with D1 longer than D2; SD group bisetose, A1-7 with SD1 slightly longer than SD2 and A10 with SD2 longer than SD1, SD2 absent in A9; A1-8 with L group trisetose, L1 longer than L2, L1 and L2 absent in A9; A1-8 with SV group trisetose, SV3 absent in A7-9; V group unisetose.

Pupa (Figs. 7A-C, 11D-F). Length varying from 5.59 to 6.76 mm (n = 3). Body elongate in dorsal and ventral views, slightly wider in the thoracic region. Integument light ambar, mostly smooth, with a few micro-setae, scattered dorsally. Frontoclypeal suture not evident. Labrum U-shaped. Labial palpi long; antennae arched anteriorly and separate, approximate and parallel posteriorly to distal margins of maxillae, reaching the

apical margin of forewings; maxillae extending distally between sclerites of midlegs; femora of midleg not fused distally; femora of foreleg extending beyond the widest part of labial palpi. Cremaster (Fig. 11D-F) long, tubular, dorsally directed, bearing latero-apically a pair of distally conspicuous, anteriorly curved spines.

Host Plant. Melastomataceae: *Tibouchina asperior* (Cham.) Cogn. It is a shrub (from 0.5 to 1 m high) found in humid grassland areas, endemic to the states of Santa Catarina and Rio Grande do Sul (Souza 1986, Guimarães 2014). At Coxilha das Lombas, where the southern most portions of lowland Dense-Umbrophilous Atlantic Forest occur, they are common on boarder of forest fragments that are located on poorly drained, swampy areas, associated with formation of lagoons and also influenced by sand dunes.

Distribution. *Palaeomystella* "B" is known only from the type locality, the fragments of lowland Dense-Umbrophilous Atlantic Forest of Coxilha das Lombas, Santo Antônio da Patrulha municipality, Rio Grande do Sul, Brazil.

Life history (Figs. 12D-F). *Palaeomystella "B"* induces a small, delecate gall of the globoid type (maximum diameter varying from 5.2 to 7,28 mm; n = 7) on *T. asperior* distal stem buds. At the type locality, they occur in a few number per plant. They vary in color from green to reddish, being convered by several short, spine-like projections. Little is known about life-history of this cecidogenous species. In the rearings, mature last larval instar invariabily made a lateral orifice by chewing the gall wall (Fig. 12E), and moved straight to the plastic pot botton where promptly start building a cocoon by tying together with silk small peaces of dried leaves that were offered, and where thus pupation occurred (Fig. 12D). The adult leaves the cocoon throught a slit made in the

terminal end, the pupal ecdises remaining inside. Specimens that pupated under laboratory during the Summer emerged as adult in the next Fall season.

Palaeomystella "*C*" Becker and Moreira, new species

Figs. (1E-F, 8-10, 11G-I, 12G-I)

Diagnosis. It is closest to *P*. "*B*", sharing with this species a pronounced palmate upper section of male valve and a bladelike female signa. As already mentioned, these characteristics make them different from all *Palaeomystella* species, except from *P. oligophaga*. This species, however, has the forewings with R_4 - R_5 fused and hindwing with M_1 and M_2 stalked from remnant chorda of the cell (Becker & Adamski 2008). *P.* "*C*" differs from *P*. "*B*", by having: 1) adults, with body covered by pale brown scales tipped with brown and brown scales; 2) males, with latero-anterior margin of sternum eight anteriorly expanded medially by a stout, rounded lobe; distal portion of valve upper section wider; juxta longer than wide, and anteriorly convex; 3) females, with signa having inward projections shorter, straight and stout; 4) pupa with cremaster slightly bifurcated and porteriorly directed, with a latero-apically located pair of blunt spines; 5) galls of rosette type, induced on stem of *T. fissinervia* apical branches, causing terminal leaves to become shorter and clustered together, and forming a cylindric chamber inside.

Lima (1945) showed for an unidentified species of *Tibouchina* in Rio de Janeiro state the same type of gall, and associated it to an unidentified species of *Walshia* Clemens (Cosmopterigidae). However, the wing and genitalia illustrations provided by him led Becker & Adamski (2008) to conclude such species was congeneric to *Palaeomystella* species desbribed by them. In fact, such illustrations are very similar

to those provided herein for *P*. "*C*", thus suggesting that specimens used by Lima (1945) are conspecifics to those used in this study.

Description

Adult (Figs. 1E-F). Male and female similar in size and color. Small moth with forewing length varying from 7.02 to 9.23 mm (n = 8). *Head*: Frons pale brown; vertex with pale brown scales tipped with brown (Fig. 1F); labial palpus pale brown, basal segments porrect, terminal segment slightly angled upwards; antennae brown; proboscis yellowish brown. *Thorax*: Tegula and mesonotum (Fig. 1F) with brown scales tipped with dar brown, posterior ones having more pale brown; prothoracic and meso-thoracic legs dark brown; metathoracic legs pale brown, having tibia and tarsum intermixed with scales darkbrown. Forewings (Figs. 1E, 2A): lanceolate in shape, with 13 veins; L/W index ~ 4.4; dorsally covered by brown scales, intermixed with dark brown scales tipped with black, and pale brown scales; a narrow, ill-defined, dark-brown streak bisects wing longitudinally from base to a brown, subapical, crescent-shaped marking, demarcated distally with dark gray scales; 3 raised scale tufts located posterior to cubitus; 1 in anal area, 1 in line with midcell, and 1 near tornal area; fringes pale brown; most uniformely covered by dark brown scales ventrally. Retinaculum subcostal; discal cell closed, ~ 0.7x length of forewing; ending near one fifth of wing margin; Sc ending ca. 1/3 anterior margin; R 5-branched; R_1 ending near 1/4 of wing margin; R_5 and R5 stalked ca. 1/2 distance from the cell apex; M 3-branched; CuA 2-branched; CuP weak proximally and not stalked with 1A+2A that is well developed, extending more than half the length of posterior margin. Hindwing (Fig. 1E, 2A): extremily lanceolate, with 9 veins; L/W index ~ 5.4, ~ 0.84 forewing in length; scales light brown on both sides; fringes pale brown; frenulum a single acanthus on male, with two parallelside acanthi

on female; $Sc+R_1$ ending ca. 1/2 anterior margin; Rs ending near end of anterior margin; M 3-branched, with M_1 and M_2 stalked near Rs; CuA 2-branched, with CuA_1 stalked to M3; CuP weakly sclerotized ending 1/2 posterior margin; 1A+2A well developed, ending near basis of posterior margin. *Abdomen* (not showed): scales pale brown intermixed with grey scales; terga covered with transverse irregular rows of spiniform setae. Eighth sternum (Fig. 8C) anteriorly expanded medially by a stout, rounded lobe, associated to a subtrapezoidal sternite.

Male genitalia (Figs. 8 B, D-F). Uncus narrow, separated from tegumen by a narrow membranous area, laterally setose (Fig. 8F); tegumen narrow; vinculum widened ventrally; fultura superior a short, flat plate; aedeagus tubiform, curved ventrally, short, slightly wider basally (Fig. 8E); vesica bearing several stout, spinelike setae; juxta (Fig. 8D) attached to distal portion of aedeagus, as long as wide, with convex basal margin and pointed distally; valva (Fig. 8B) covered by several long setae, divided near one third from the basis, forming a lower, wider finger-like portion and an upper, narrowly based, longer palmate portion.

Female genitalia (Fig. 8G,H). Anal papillae connected dorsally, setose (Fig. 8H); anterior apophyses with arms similar in length to posterior, slightly curved apophyses; sterigma divided into a bandlike tergum and a distally bilobed sternum, deeply and narrowlly emarginate medially; ostium bursae of small size, wider than long; ductus bursae membranous longer than corpus bursae, with ductus seminalis inserted medially; corpus bursae an elongate sac, bearing two stout and stright, bladelike signa that are connected to crescent- plates located in the wall (Figs. 8G).

Type material. BRAZIL: Reserva Serra Bonita, 15°23'30''S, 39º33'57''W, 832m, Camacãn Municipality, Bahia (BA), Brazil. Adults preserved dried and pinned, reared by G.R.P. Moreira from galls induced on *Tibouchina fissinervia* (Schrank & Mart. ex DC.) Cogn. (Melastomataceae): LMCI 209, 17-23.II.2013 and LMCI 230, 15-21.X.2013, by G.R.P. Moreira; HOLOTYPE: ♂ (LMCI 230-05), donated to DZUP (29.415). PARATYPES: 1♂ (LMCI 209-31), 1♀ (LMCI 230-20), donated to DZUP (29.416 and 29.417, respectively); 1♂ (LMCI 230-06), 2 ♀♀ (LMCI 230-09 and 22) donated to VOB (?????, ????? and ?????, respectively) .

Other specimens examined. Adults dried and pinned, collected on light traps, at the type locality, deposited in VOB: 1 ♂ (VOB 144730), -.VIII.2009, by F.L. Santos; 1 ♂ (VOB 146783, with genitalia mounted on slide), -.IX.2010, by V.O. Becker. Additional specimens, with the same collection data as the type material, deposited in LMCI: adults dried and pinned, 6 ♂♂ (LMCI 230-07, 15, 16, 17 and 21; LMCI 230-08, with genitalia in glycerin GRPM 50-57) and 6 ♀♀ (LMCI 230-10, 11, 12, 18 and 19; LMCI 230-23 , with genitalia in glycerin GRPM 50-58). Slide preparations, mounted in Canada balsam: adults, 1 ♂ (GRPM 50-54), 1 ♀ (GRPM 50-55); wings, 1 ♂ (GRPM 50-53); larvae, 2 last instars (GRPM 50-56). Immature stages, fixed in Dietrich's fluid and preserved in 70% ethanol: 5 last instar larvae (LCMI 209-13 and 14, and 230-2); 6 pupae (LMCI 209-7, 11, 18, and 230-1); 12 dissected galls (LMCI 209-21 and 22, 230-3 and 4). In tissue collection, six larvae (LMCI 209-06) fixed and preserved in 100% ethanol, under -20°C.

Etymology. *Palaeomystella "C"* is named …

Immature stages

Last larval intar (Fig. 6). Body length varying from 7.28 to 11.7 mm (n = 4). Cecidogenous, endophyllous, semiprognathous and tissue-feeder. Body subcilyndrical, whitish cream, turning into light yellowish before pupation. Head, thorax and abdomen with setae well developed.

Head (Fig. 3A, C-D): uniform dark brown,with two conspicuous unpigmented, with irregularly shaped area along ecdisial line; smooth, with shallow ridges; labrum shallowly notched; frons higher than wide, extending ca. three-fourth epicranial notch; six stemmata arranged in C-shaped configuration. Chaetotaxy (Fig. 3A): A group trisetose; L group unisetose; P group bisetose; MD trisetose; C group bisetose; F group unisetose; AF group bisetose; S group trisetose; SS group trisetose. A1, A3, P1 and S2 about equal in length, longest setae on head; C1, C2, F1, A2, AF2, L1 intermediate in length; AF1 absent; MD1-3 very reduced and alined to each other. Antenna two-segmented Mandibles broad with four teeth, and one unequal seta on the outer surface; labium broad, with two-segmented palpus, the distal minute; spinneret parallel sided; maxilla prominent.

Thorax and Abdomen (Fig. 3B-D): Prothoracic shield and anal plate irregularly marked by dark brown. Thoracic legs light brown. Prolegs on A3-A6 and A10 of equal size; crochets in a circle, uniserial and uniordinal. Thorax chaetotaxy: T1 with D group bisetose, both located on the dorsal shield, D1 shorter than D2; XD group bisetose, with similar length and both on the dorsal shield; SD bisetose, lateraly on the dorsal shield; L group bisetose, 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, median-transversally alined; D2 and SD1 similar in length, and longer than D1 and SD2 respectively; L trisetose, L3 posterior to L1-L2, with similar length to L1; SV

unisetose; V unisetose. Abdomen chaetotaxy: D group bisetose; A1-9 with D2 slightly longer than D1, and A10 with D1 longer than D2; SD group bisetose, A1-7 with SD1 slightly longer than SD2, A10 with SD2 longer than SD1, SD2 absent in A9; A1-8 with L group bisetose, L1 longer than L2, L2 absent in A9; A1-8 with SV group trisetose, SV3 absent in A7-9; V group unisetose.

Pupa (Figs. 10A-C, 11G-I). Length varying from 6.37 to 8.84 mm (n = 5). Body elongate oval in dorsal and ventral views, widest in the thoracic region. Integument light ambar, mostly smooth, with a few micro-setae, scattered dorsally. Frontoclypeal suture not evident. Labrum U-shaped, weakly defined. Labial palpi long; antennae arched anteriorly and separate, approximate and parallel posteriorly to distal margins of maxillae, surpassing the apical margin of forewings; maxillae extending distally between sclerites of midlegs; femora of midleg not fused distally; femora of foreleg extending beyond the widest part of labial palpi. Cremaster (Fig. 11G-I) short, slightly bifurcated and porteriorly directed, bearing a latero-apically located pair of blunt spines.

Host Plant. Melastomataceae: *Tibouchina fissinervia* (Schrank & Mart. ex DC.) Cogn. It is a three up to 20m high found in the Atlantic Rain Forest, to where it is endemic, varying in distribution from Bahia to São Paulo State (Freitas 2011). At Serra Bonita reserve, they are relatively common at higher altitudes, growing expontaneouly on open areas and along trail sides.

Distribution. *Palaeomystella* "*C*" is known only from the type locality, preserved fragments of Atlantic Rain Forest at Serra Bonita reserve, Camacãn municipality, BA, Brazil.

Life history (Figs. 12G-I). Gall of the rosette type (maximum internal length varying from 18 to 31 mm; n = 6), induced on *T. fissinervia* growing shoots, causing terminal leaves to become shorter and clustered together (Fig. 12 G). They are green in color, becoming progressively darkish during senescence, after emergence of the cecidogenous moth. A cylindric shaped chamber is formed inside the gall (Fig, 12H), where larval development and pupation occur. Mature last larval instar builds near the middle of the chamber a brown-colored, tied silk-made gate, consisting of two convex, laterally open doors (Fig. 12 I). Then, it constructs a very flimsly silk-made cocoon at the proximal sector of the chamber, where pupation occurs. During emergence, by pressuring on the concave side, the adult opens the doors, crossing the gate and leaving the chamber distally through the flimsy, basally attached terminal leaflets of the gall. The pupal ecdises remains inside the proximal sector of the chamber. At the type locality, they occur scarcely among *T. fissinervia* trees, ocasionaly in groups of a few per plant. Under laboratory conditions, mature galls collected in the Spring season had the adults emerging ca. 15 days later.

Molecular phylogeny. A total of 660 nucleotide sites were analyzed within *Palaeomystella spp.* from different host plants, in which 211 (32%) were variable. According to our phylogenetic hypothesis, all species were recovered as monophyletic lineages within the *Palaeomystella* group of Momphidae in both methods of inference (BI and ML) with full branch supported (Fig. 13). Regarding internal relationships, *P. "B"* was placed as sister of *P. "C/fissinervia"* with strong posterior probability (= 1) and bootstrap (=100). On the other hand, *P. "A"* was more distantly related, however, with low branch support (< 0.8, posterior probability; < 70, bootstrap). Despite of the strong internal statistical branch support of the three new lineages of momphids, the

external relationships for *Palaeomystella* were poorly resolved (i.e., position of clades), and even the monophyly of the genus lack a statistical support. *Mompha* was used to root the tree, but its position as a sister clade of *Palaeomystella* was absent of support (Fig. 13). The evolutionary divergence observed between comparisons of pair of species was markedly high, showing greater genetic variation in this group of momphids (Table 2), particularly between clades (Fig. 13). An average of 18% (± 3%) of K2P differences was found between species of *Palaeomystella*, ranging from 14 (± 2%) to 24% (± 3%). The maximum divergence observed among clades was 20%, found between *P. "A"* and the clade formed by *P. "B"* + *P. "C"* + *Paleomystella* sp. 1 (Fig. 13). The genetic divergence within *Palaeomystella* (ca. 18%) was greater than between this genus and *Mompha* (16%).

Discussion

As already pointed out by Becker & Adamski (2008) for the other congeneric members, it is almost certain that species described herein belong to the Momphidae lineage. They are, however, tentatively placed within *Palaeomystella* Fletcher, based upon shared characteres on genitalia and monophyly found on preliminary molecular analysis carried out in this study. They differ from the type-species *Palaeomystella chalcopeda* Meyrick, since in all cases female genitalia have anterior and posterior apophyses similar in length. As illustrated by Becker (1999), the posterior apophyses almost double in length the anterior ones in *P. chalcopeda*. Thus, the male genitalia, immature stages and galls, if any, of the type species of *Palaeomystella* Fletcher remain unknown, which turns difficult to make a decision about its taxonomic status. Genetic variability that was found herein at the generic level (maximum distance among *Palaeomystella* clades = 20 %; average among species = 18 %), by using a

few putative species, strongly suggest that there are several gaps in diversity on the analysis. This pattern results in part from low collection efforts and reduced number of taxonomic studies within this lineage in the area. Alternatively, the result obtained could be associated with the single marker used. Although DNA barcoding is not the most suitable loci used to make broad inferences on phylogenetic relationships (Müller et al. 2013), we can still reveal a scenario of monophyletic status and diversity at genetic level using this molecular evidence (see Lee et al. 2013). The use of more gene loci could be an alternative to shed light into the phylogenetic relationships at species level, and the status of *Palaeomystella* at generic level. In other families of microlepidoptera, more loci have been used to solve phylogenetic problems at different taxonomic levels, as for example in Gracillariidae (Kawahara et al. 2011) and Gelechiidae (Kaila et al. 2011). Such effort might still be not entirely enough in our case. We are dealing with a greater, unknown diversity, as we can observe in the significantly different lineages found; and, at the same time, trying to solve phylogenetic relationships below the generic level. In other words, we suggest putting strong efforts first on sampling, and improving at least a few more loci, in order to better understand the relationships within this group of momphids.

As already mentioned, diversity of moth-induced melastome galls are in fact much greater. We have several species belonging to this group, in addition to those two included in the molecular analyses conducted here, awaiting for description in our collection. Furthermore, contrary to what we expected, species herein described are not only similar from a gross morphology perspective but share several morphological characteristic at the fine scale with those belonging to *Mompha* Hübner. For example, male valva divided into two sections and female bursa having bladelike signa are also found within the latter genus (e.g. Hodges 1998, Wagner et al. 2004). Pupal cremaster

presenting spines, similar to those described in this study are also found among the paleartic species of *Mompha* (*e.g*. Patočka and Turčani 2005). Contrary to what is known for two species of *Palaeomystella* that were proposed by Adamski and Becker (2008), all species we described here are bisetose regarding the prothoracic L group setae, a characteristic of *Mompha* species (Stehr 1987, Wagner et al. 2004). Unlike to what they found, we did not detect reduction on number of setae in the anal plate either. Thus, generic status of species described in this study may chance in the future, pending upon description of additional taxa, further studies on phylogeny, and taxonomic revision of the family. A decision concerning this matter at this time would be precipitate in our view, as *Mompha* is similarly a poorly known genus, having species that are difficult to collect and a wide variation of feeding habits (including cecidogenous one), and thus several are either undescribed or lack apropriate taxonomic description to allow comparison; also, DNA sequences for a few species are available, and similar to *Palaeomystella*, present wide range of evolutionary divergence (4-14%) (for discussion, see Emery et al. 2009).

Our study illustrates further variation on gall morphotypes known for a long time to exist among Melastomataceae galls (Tavares 1917, Houard 1933), confirming that they are associated with different species of Lepidoptera inducers. At least two of the galls herein described may have appeared before in the literature, but none of them has been accurately associated to any cecydogenous species. The fusiform type induced by *Palaeomystella "A"* on *T. sellowiana* is showed by Toma and Mendonça (2013) in a gall survey they carried out at the type locality, as being induced by an unidentified Gellechioidea. As already mentioned, depending upon the time of year, most of such galls are associated in the field with a specialized kleptoparasitic gelechiid moth, to which the cecidogenous species may be confounded (Luz *et al*.,

submitted). Galls similar to the rosette type induced by *Palaeomystella "C"* in *T. fissinervia* were illustrated by Tavares (1917), that were reproduced by Houard (1933) for *Tibouchina* sp. in Rio de Janeiro State. Lima (1945) showed for an unidentified species of *Tibouchina* also in Rio de Janeiro the same type of gall, but as already mentioned, he erroneously associated it to an unidentified species of *Walshia* Clemens (Cosmopterigidae). Furthermore, galls of the same rosette type as those of *P.* "*C*", having induction associated to unidentified species of Lepidoptera were showed by Maia & Fernandes (2004) on *Miconia theizans* (Bonpl.) Congn. occurring in Minas Gerais State, and by Santos et al (2011a, 2012) and Isaias et al. (2013) on *Henriettea succosa* (Aubl.) DC. located in Pernambuco State. Further studies should be conducted to determine whether such galls are induced by *P. "C"* or closely related species.

Our results also demonstrate the existence of considerable variation in life history styles for the pupal stage of *Palaeomystella* species, which should be taken into account in future studies. That is, last instar larvae may remain endophylous until pupation either in sessile (*P. "C"*) or dehicent (*P. "A"*) galls, or leave them to pupate in the litter (*P. "B"*). Although varying little in the general integumentary morphology, their pupae show considerable variation in size and shape of the cremaster, which may thus provide usefull characters for species identification beyond. Unfortunately, the other known *Palaeomystella* species (Becker and Adamski 2008) were not described under the scanning electron microscope, and thus not allow comparison. These structures are supposedly used to anchor the pupa laterally to the cocoon / pupal chamber. They have likely evolved in conjuction with the habit of molting to the adult stage in the pupation site, which has apparently first appeared in the Lepidoptera evolution within the Gellechioidea (e.g. Powell 1973, Becker 1982).

On the other hand, preliminary observations we made suggest that the striking changes in general body coloration acquired later on in the last larval stage of *P. "B"* and *P. "C"* is related to the gall tissue color ingested before pupation; this would thus limit the use of such character from a taxonomic perspective to that ontogenetic phase only. However, some of the fixed interspecific variation in color regarding the head, prothoracic shield and anal plate may be useful and should be explored further. There is variation among species regarding chaetotaxy that may be also proving to be useful in the future to identify different lineages within *Palaeomystella*. For example, in addition to variation on number of setae described by Adamski and Becker (2008) for the prothoracic L group and anal plate, we herein detected numeric variation in chaetotaxy also on the head (AF1 seta), thorax and abdomen (SD setae).

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FIGURE LEGENDS

Figure 1. Spread right wings (left column), head and thorax in detail (right column) of pinned *Palaeomystella* species, dorsal view: **A-B** *P. "A/sellowiana"*; **C-D** *P. "B/asperior"*; **E-F** *P. "C/fissinervia"*. Scale bars = 2, 0.5, 2, 0.5, 2 and 0.5 mm, respectively.

Figure 2. *Palaeomystella* "*A/sellowiana*" adult morphology: **A** wings; **B** male valva, meso-lateral view; **C** male eight sternum, ventral view; **D** juxta, ventral; **E** ventral spines of the valva upper section in detail (rectangular area showed in **B**), meso-lateral view; **F** male genitalia, lateral view; **G**, aedoeagus, lateral view (asterisk indicates furca); **H,** female genitalia, lateral view. Scale bars = 1mm; 200, 200, 100, 50, 200 and 200 µm; 0.5 mm, respectively.

Figure 3. *Palaeomystella* "*A/sellowiana*" last larval instar: **A** cephalic chaetotaxy, frontal view; **B** thoracic and abdominal chaetotaxy, lateral view; **C** head and prothoracic shield in detail, dorsal view; **D** body, lateral view. Scale bars = 50µm, 1mm, respectively.

Figure 4. *Palaeomystella* "*A/sellowiana*" pupa, in dorsal (**A**), ventral (**B**) and lateral (**C**) views, respectively. Scale bar = 1 mm.

Figure 5. *Palaeomystella* "*B/asperior*" adult morphology: **A** wings; **B** male valva, meso-lateral view; **C** male eight sternum, ventral view; **D** juxta, ventral; **E** aedoeagus, lateral view (asterisk indicates furca); **F** signum, internal view; **G** male genitalia, lateral view; **H** female genitalia, lateral view. Scale bars = 1mm; 200, 200, 100, 200, 200 and 100 µm; 0.5 mm, respectively.

Figure 6. *Palaeomystella* "*B/asperior*" last larval instar: **A** cephalic chaetotaxy, frontal view; **B** thoracic and abdominal chaetotaxy, lateral view; **C** head and prothoracic shield in detail, dorsal view; **D** body, lateral view. Scale bars = 50µm, 1mm, respectively.

Figure 7. *Palaeomystella* "*B/asperior*" pupa, in dorsal (**A**), ventral (**B**) and lateral (**C**) views, respectively. Scale bar = 1 mm.

Figure 8. *Palaeomystella* "C*/fissinervia*" adult morphology: **A** wings; **B** male valva, meso-lateral view; **C** male eight sternum, ventral view; **D** juxta, ventral; **E** aedoeagus, lateral view (asterisk indicates furca); **F** signum, internal view; **G** male genitalia, lateral view; **H** female genitalia, lateral view. Scale bars = 1mm; 200, 250, 50, 200, 200 and 100 µm; 0.5 mm, respectively.

Figure 9. *Palaeomystella* "*C/fissinervia*" last larval instar: **A** cephalic chaetotaxy, frontal view; **B** thoracic and abdominal chaetotaxy, lateral view; **C** head and prothoracic shield in detail, dorsal view; **D** body, lateral view. Scale bars = 50µm, 1mm, respectively.

Figure 10. *Palaeomystella* "*C/fissinervia*" pupa, in dorsal (**A**), ventral (**B**) and lateral (**C**) views, respectively. Scale bar = 1 mm.

Figure 11. Scanning electron micrographs of *Palaeomystella* species pupal cremaster, in dorsal view (left column), apical process in detail (central column) and lateral (right column) view: **A-B** *P.* "*A/sellowiana*"; **C-D** *P.* "*B/asperior*"; **E-F** *P.* "*C/fissinervia*". Scale bars = 100, 20, 200, 100, 20, 200, 100, 20, 200 µm, respectively.

Figure 12. Galls of *Palaeomystella* species: **A-C** *P.* "*A/sellowiana*"; **D-F** *P.* "*B/asperior*"; **G-I** *P.* "*C/fissinervia*". **A** gall on *Tibouchina sellowiana,* general view; **B** operculum (pointed by arrow) made by last instar larva on gall surface before pupation; **C** pupal cocoon in a dissected gall (seta points to the operculum showed in **B**); **D** gall on *Tibouchina asperior*, general view; **E** exit hole made by last larval instar on gall surface; **F** pupal cocoon constructed in between two leaves, uncovered by pulling them apart (direction pointed by setae); **G** gall on *Tibouchina fissinervia*, general view; **H** longitudinally dissected gall, showing internal chamber (arrow indicates position of

pupal gate); **I** internal chamber in detail, showing the pupal gate (asterisk). Scale bars = 1, 0.2, 0.4, 1, 0.5, 0.4, 1, 1, 0.2 cm, respectively.

Figure 13. Bayesian inference tree of *Palaeomystella*, based on 660 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) (see material and methods); those located below represent percentage of evolutionary divergence between clades.Asterisk indicates support < 0.80/60 for BPP and ML, respectively.

Table 1. Specimens used in this study to reconstruct the phylogenetic relationships of *Paleomystella* new species based on cytochrome oxidase subunit I sequences.

Genus	Species	Voucher	GenBank accession numbers
Ingroup			
Palaeomystella			
	P. oligophaga	LMCI 234-1A	KJ188233
		LMCI 234-1B	KJ188234
	Palaeomystella sp. 1	LMCI 211-4A	KJ188235
		LMCI 211-4B	KJ188236
	Palaeomystella sp. 2	LMCI 174-25	KJ188237
		LMCI 174-26	KJ188238
		LMCI 174-27	KJ188239
	P. "*C/fissinervia*"	LMCI 209-6A	KJ188240
		LMCI 209-6B	KJ188241
	P. "*B/asperior*"	LMCI 211-8A	KJ188242
		LMCI 211-8B	KJ188243
	P. "*A/sellowiana*"	LMCI 174-50A	KJ188244
		LMCI 174-50B	KJ188245
		LMCI 174-56	KJ188246
Outgroup			
Mompha			
	M. conturbatella	10-JDWBC-1043	HM862677

Table 2. Estimates of evolutionary divergence between sequences based on 660 base pairs of cytochrome oxidase *c* subunit I (*CO-I*) gene using Kimura 2-parameter model. Average number (± 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 three new *Palaeomystella* species described in this study (marked in bold), two undescribed taxa (sp. 1 and sp.2), one currently recognized taxa (*P. oligophaga*) and the outgroup (*Mompha*).

	1.	2.	3.	4.	5.	6.
1. *Mompha conturbatella*						
2. *Palaeomystella* sp. 1	0.18±0.02					
3. *Palaeomystella* sp. 2	0.20±0.02	0.23±0.03				
4. *P.* "*A/sellowiana*"	**0.21±0.02**	**0.23±0.02**	**0.24±0.03**			
5. *P.* "*C/fissinervia*"	**0.18±0.02**	**0.22±0.03**	**0.20±0.03**	**0.22±0.03**		
6. *P.* "*B/asperior*"	**0.16±0.02**	**0.24±0.03**	**0.20±0.03**	**0.21±0.03**	**0.14±0.02**	
7. *P. oligophaga*	0.14±0.02	0.18±0.02	0.25±0.03	0.17±0.02	0.19±0.02	0.16±0.02

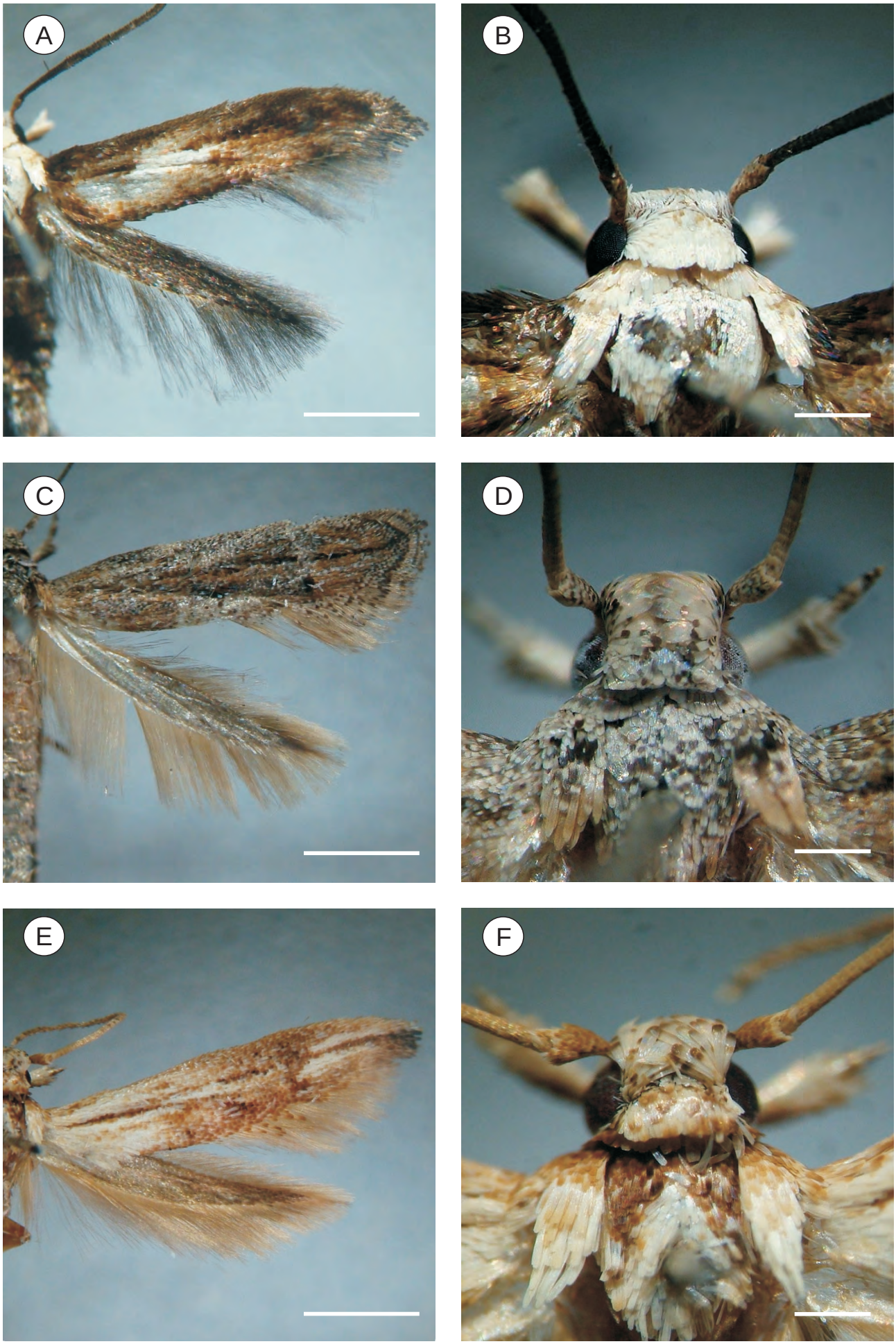


Fig. 1 - Luz et al

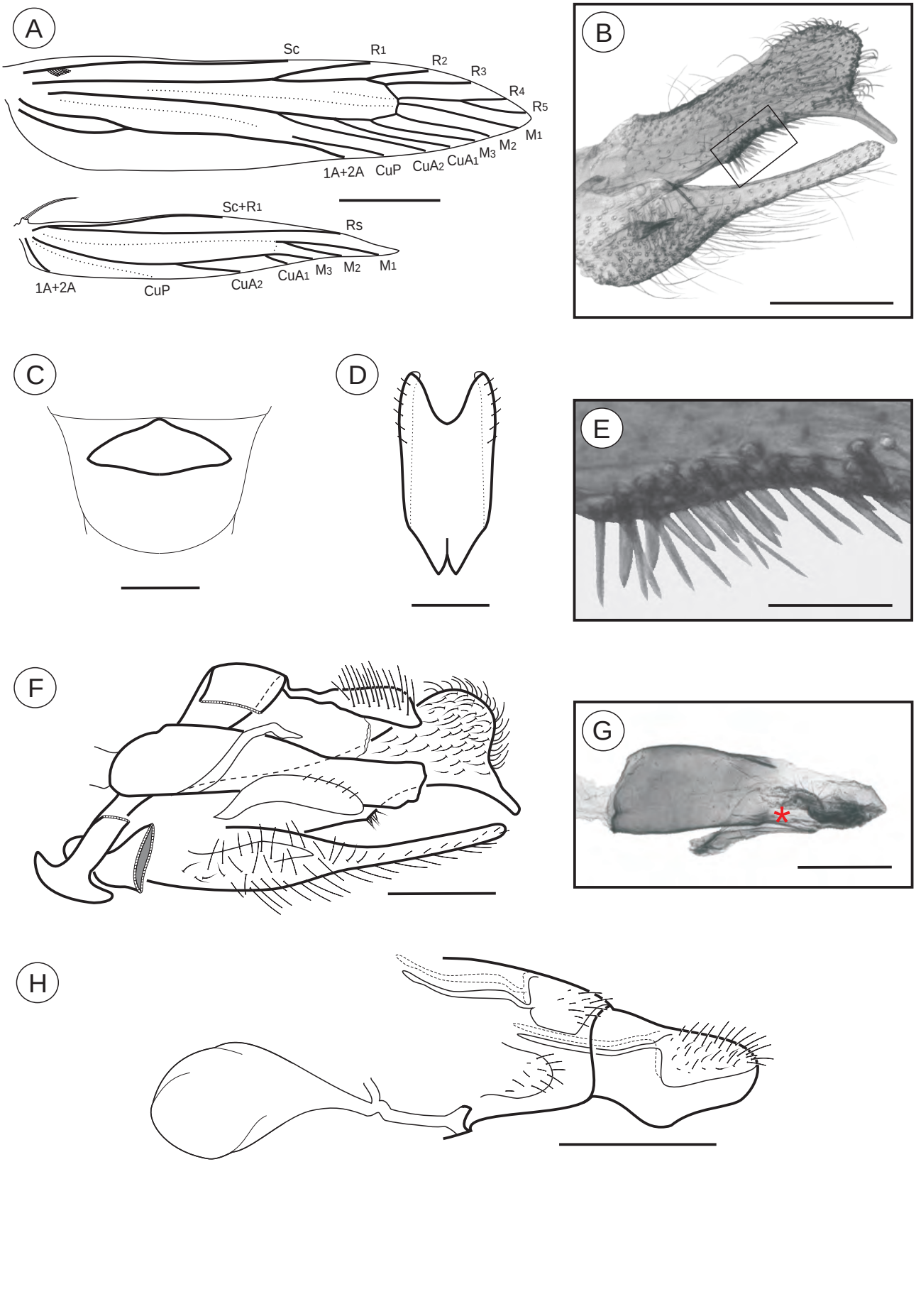


Fig. 2 - Luz et al

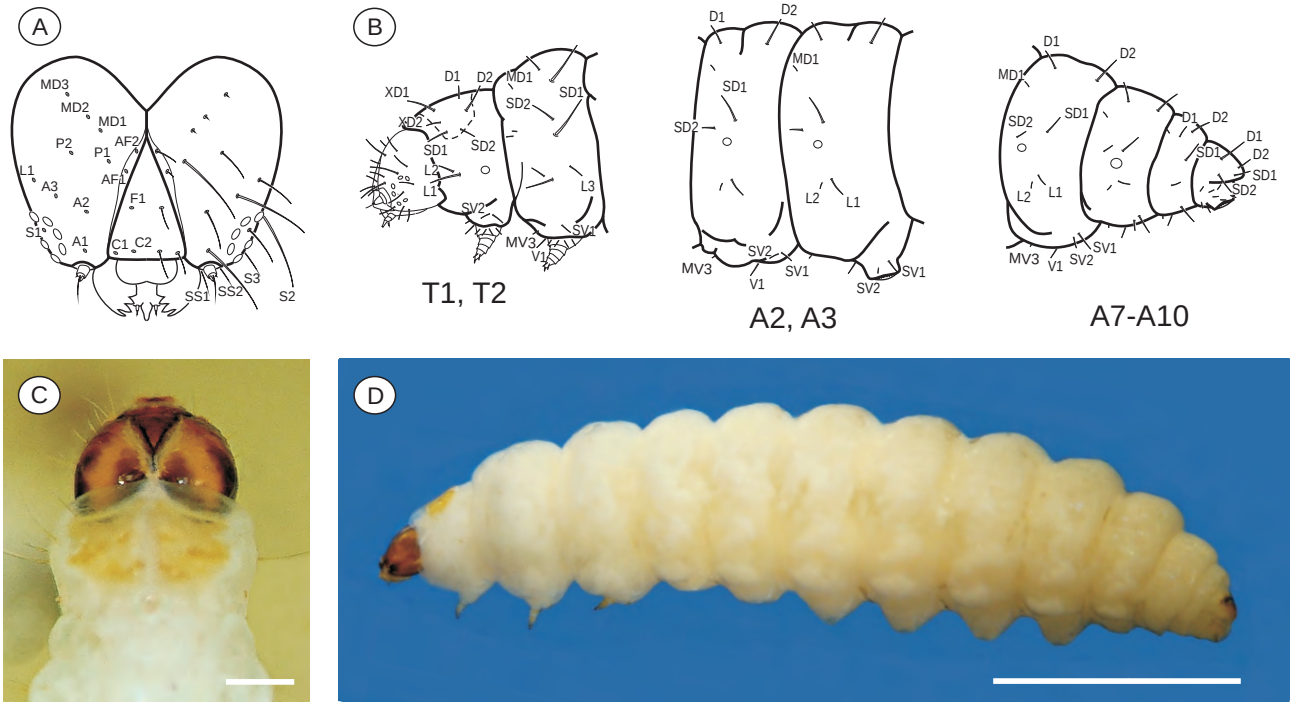


Fig. 3 - Luz et al

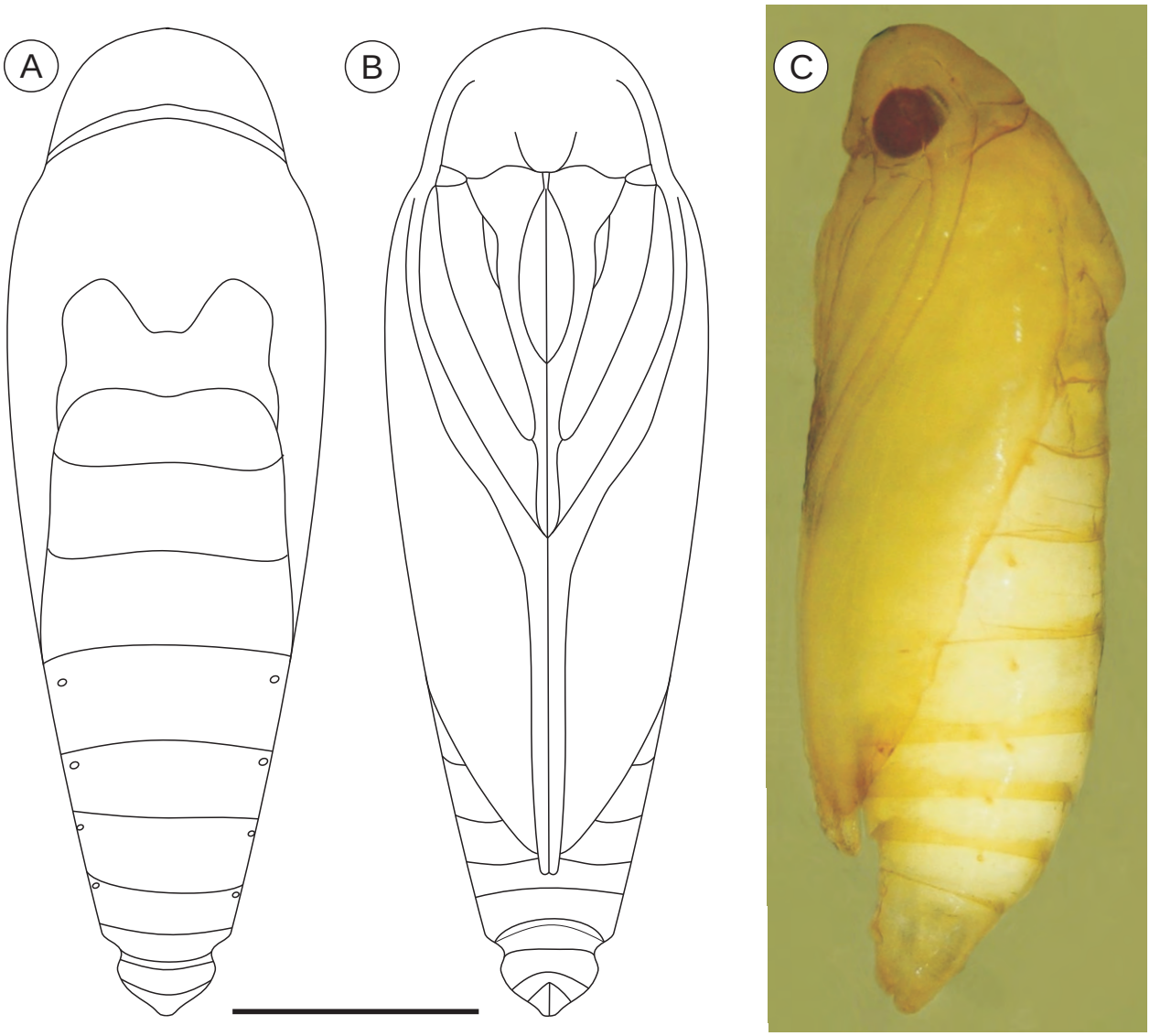


Fig. 4 - Luz et al

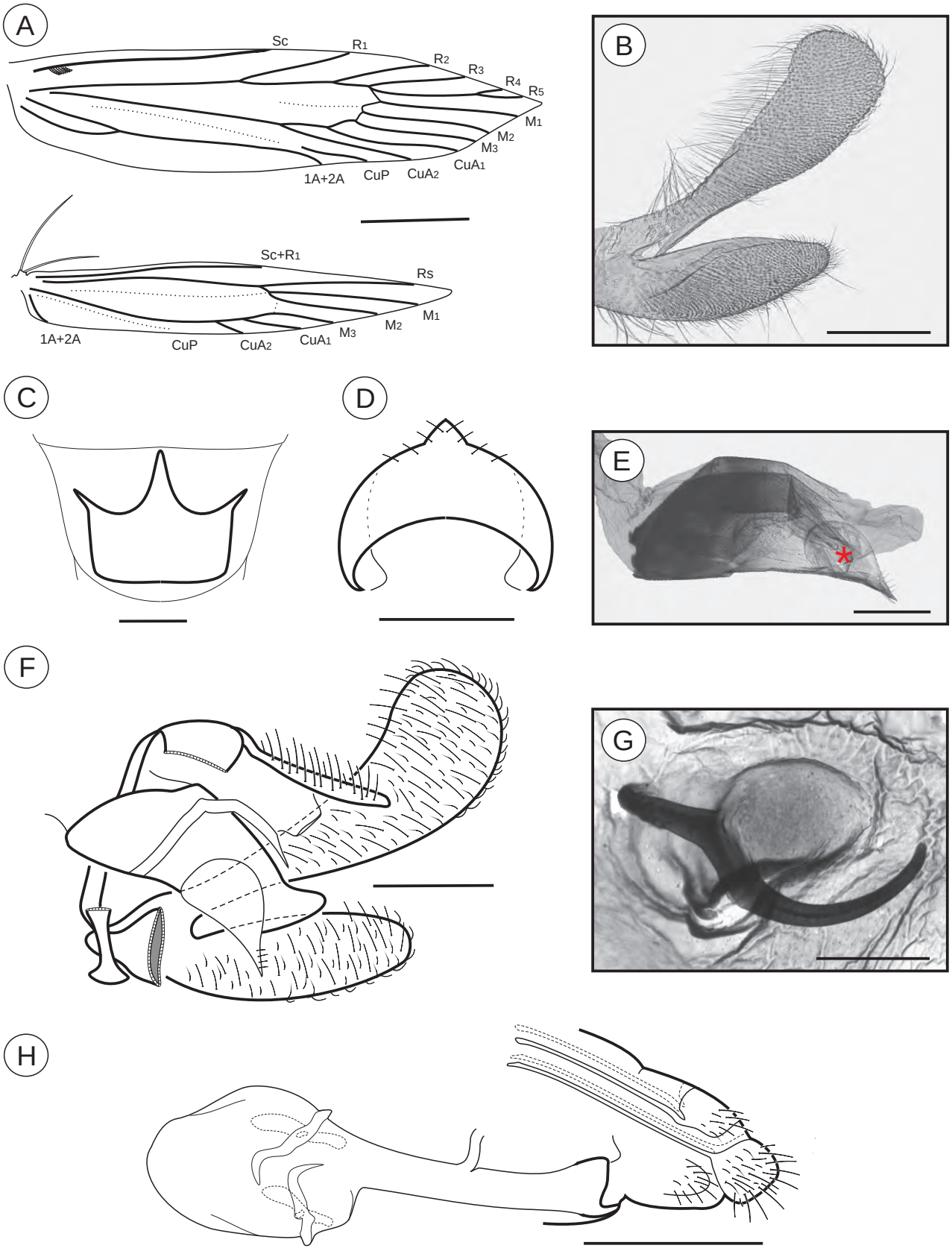
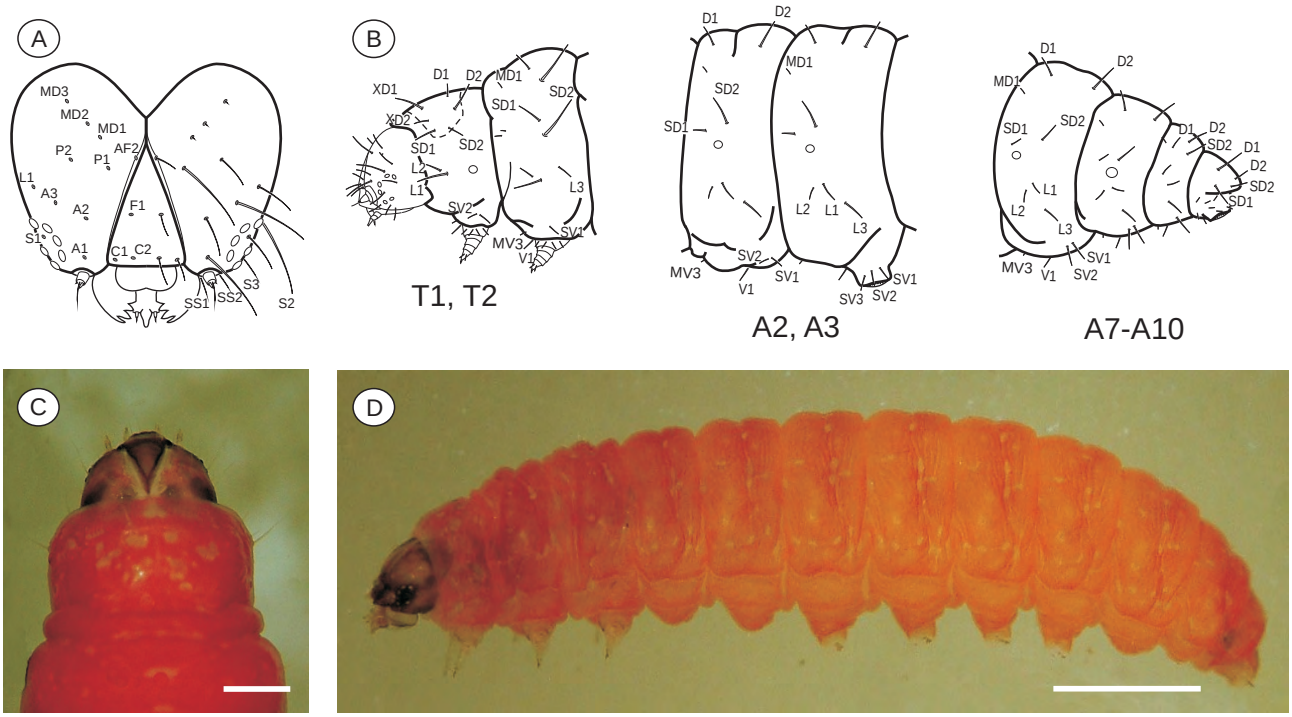


Fig. 5 - Luz et al



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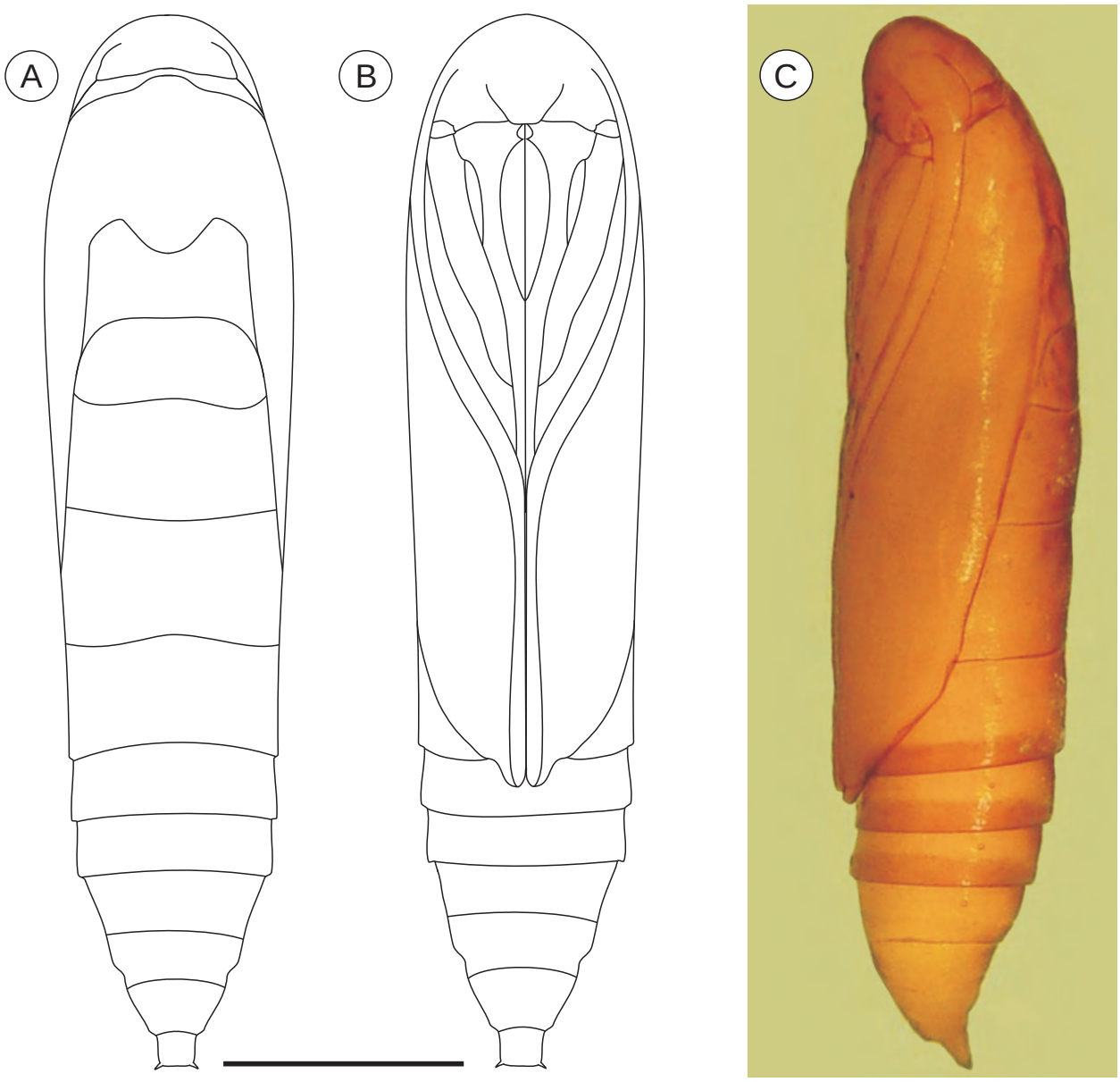

Fig. 7 - Luz et al

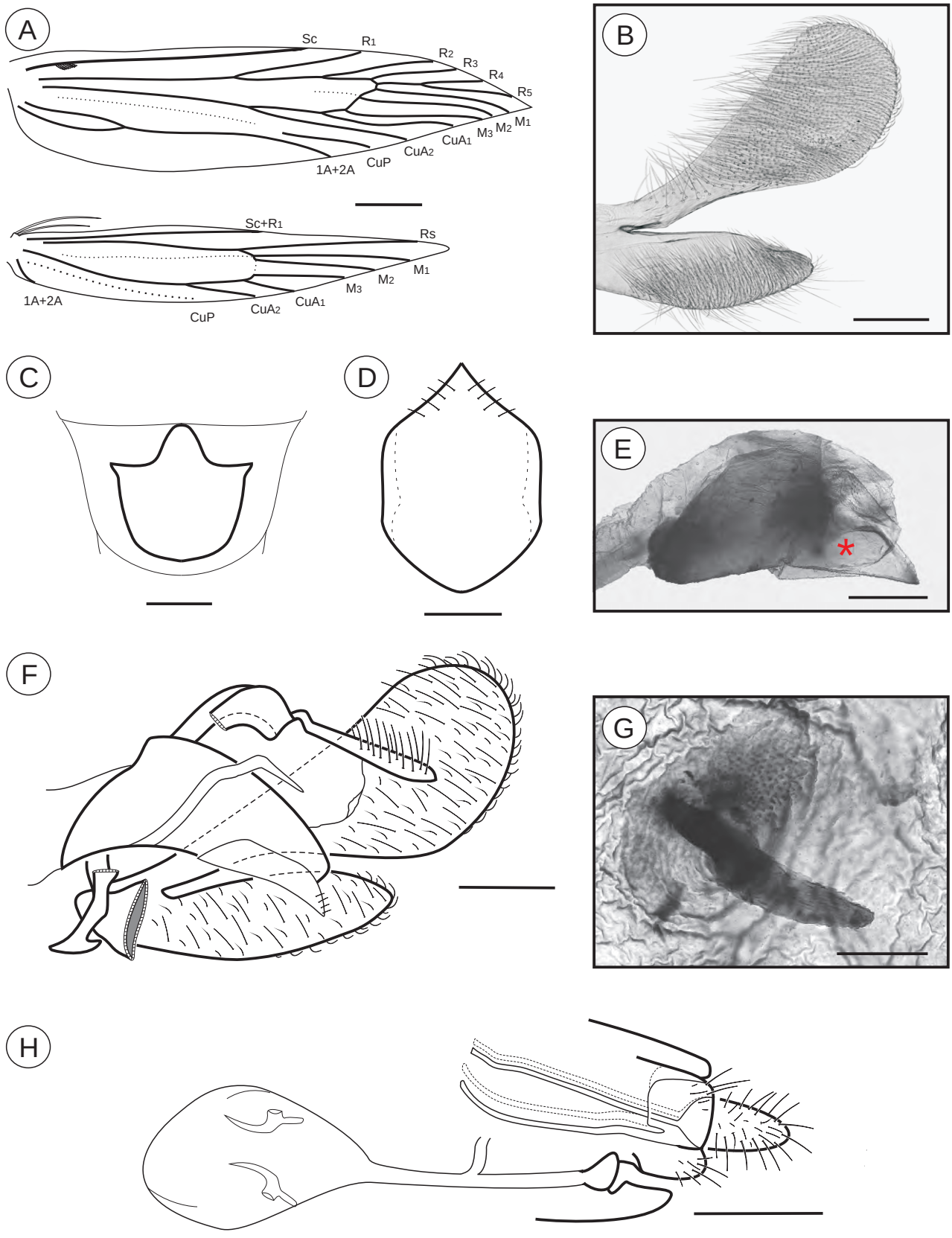

Fig. 8 - Luz et al

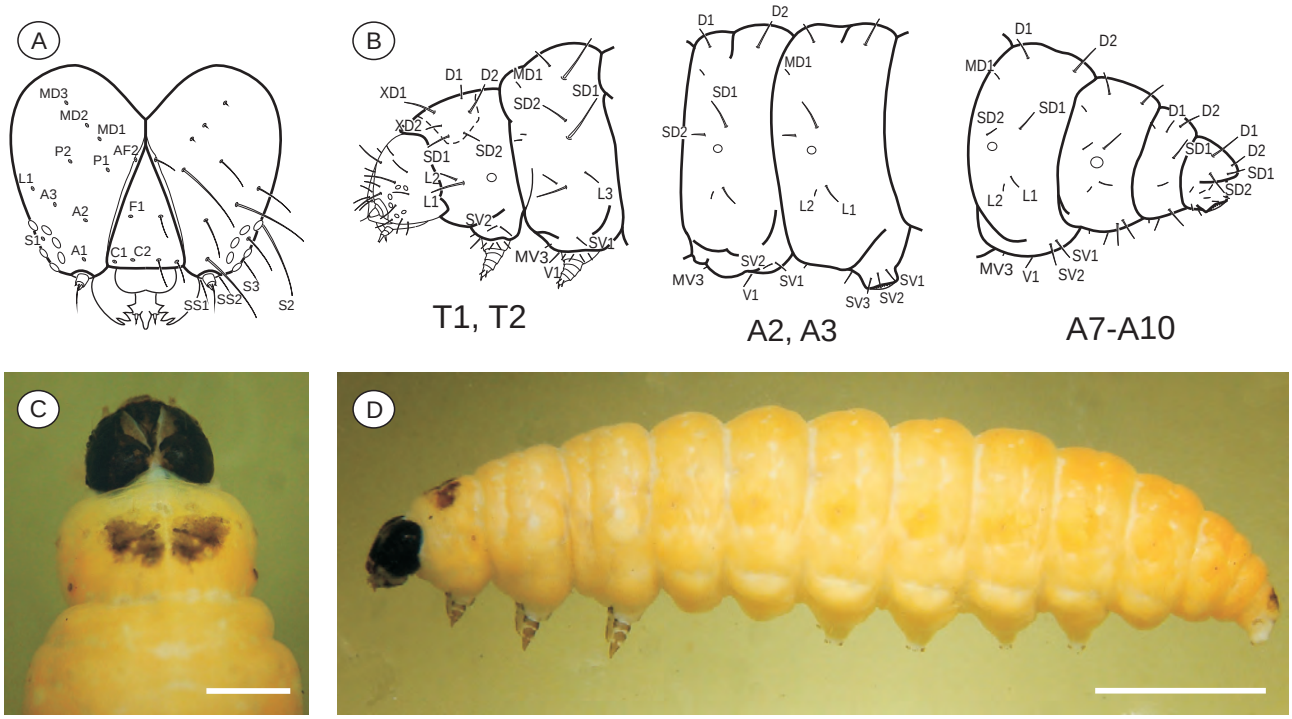

Fig. 9 - Luz et al

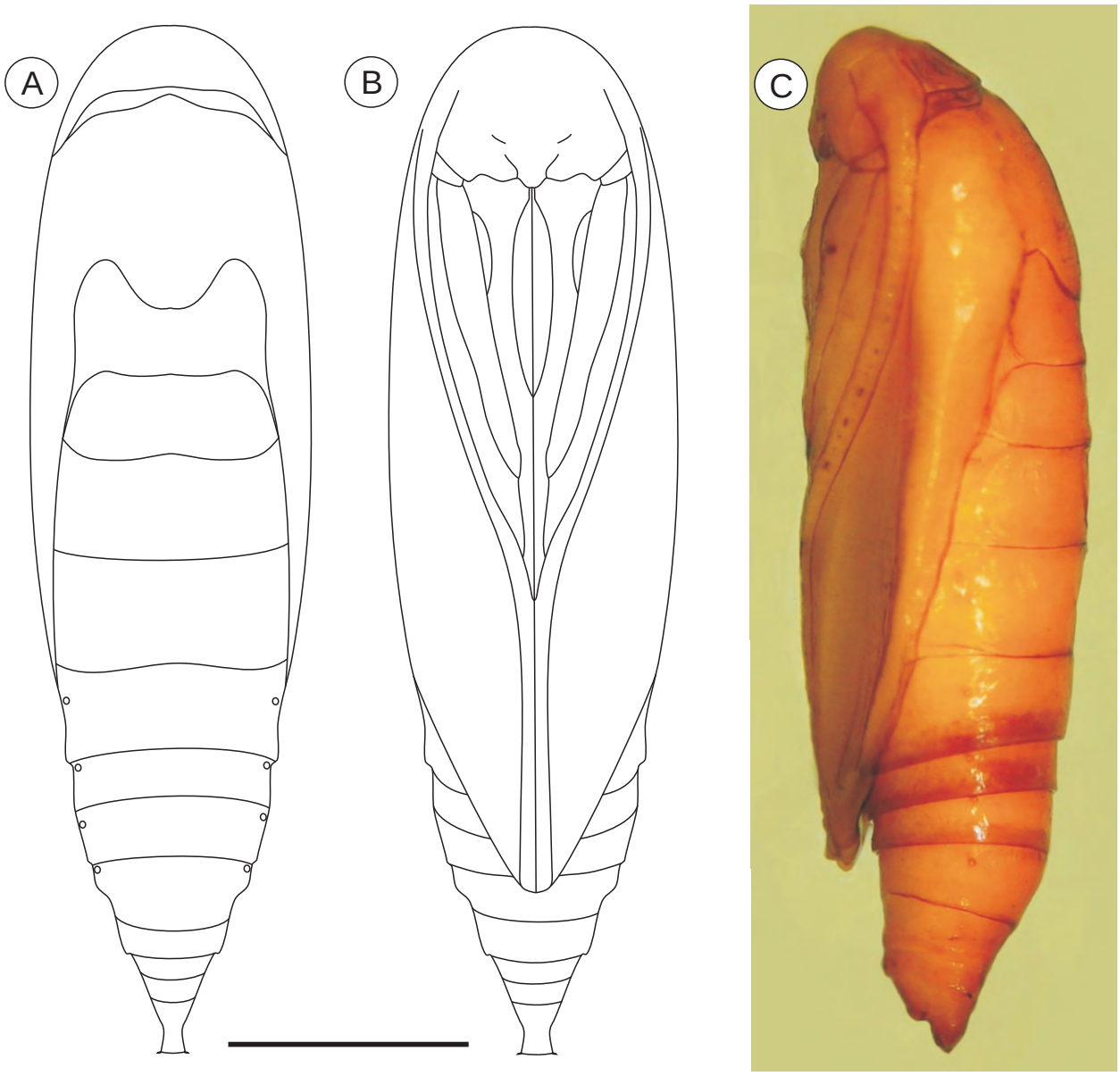

Fig. 10 - Luz et al

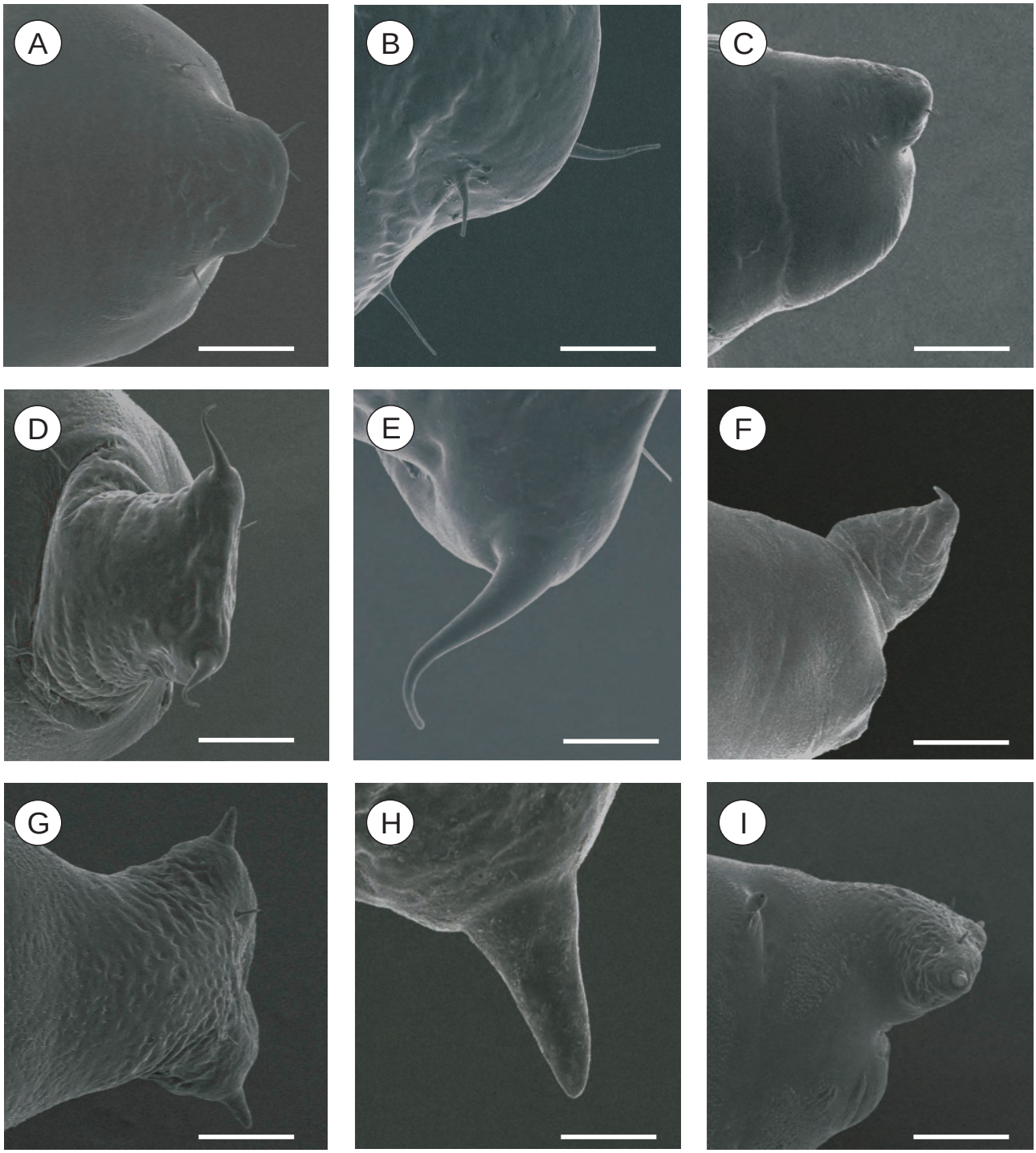

Fig. 11 - Luz et al

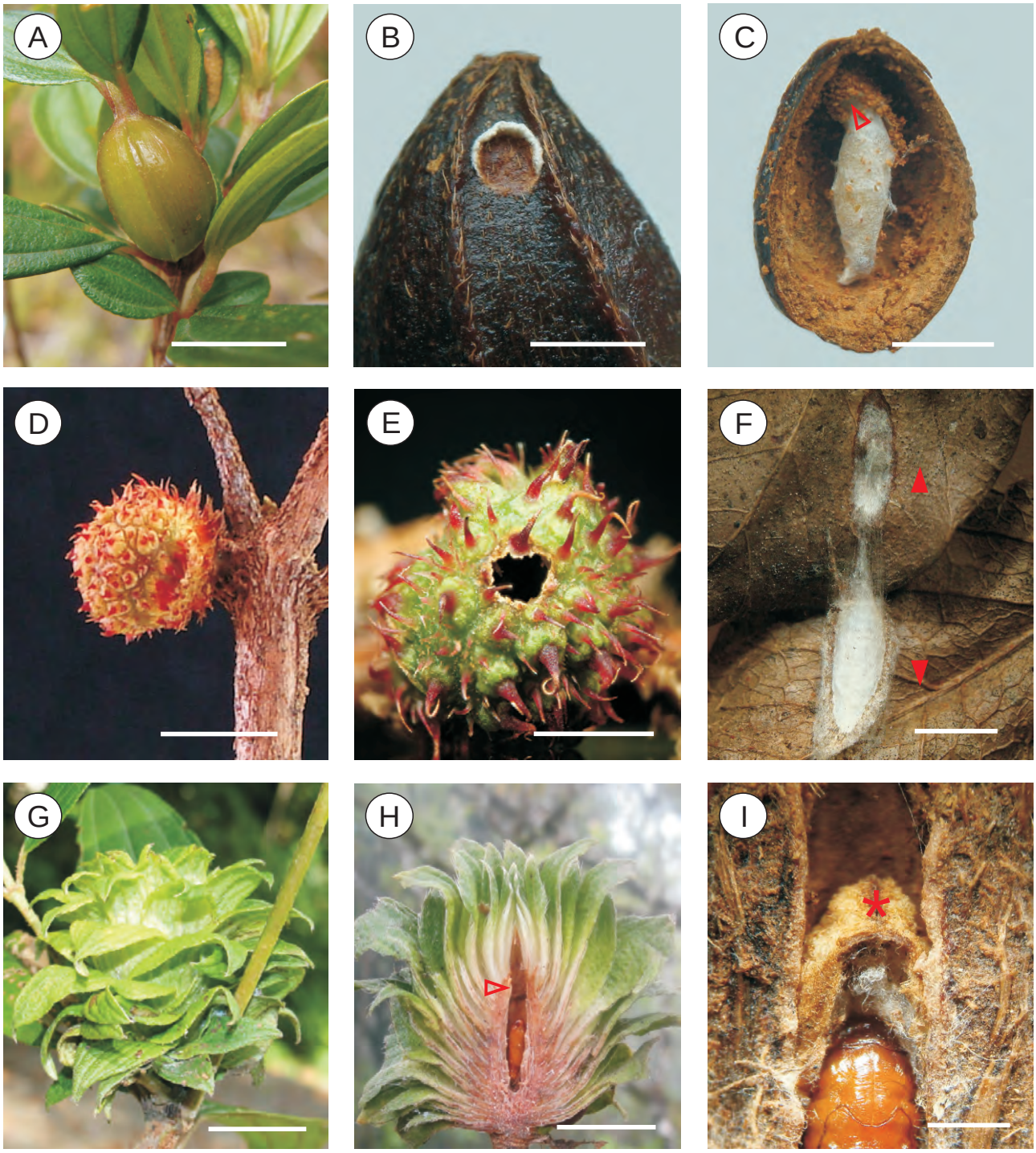

Fig. 12 - Luz et al

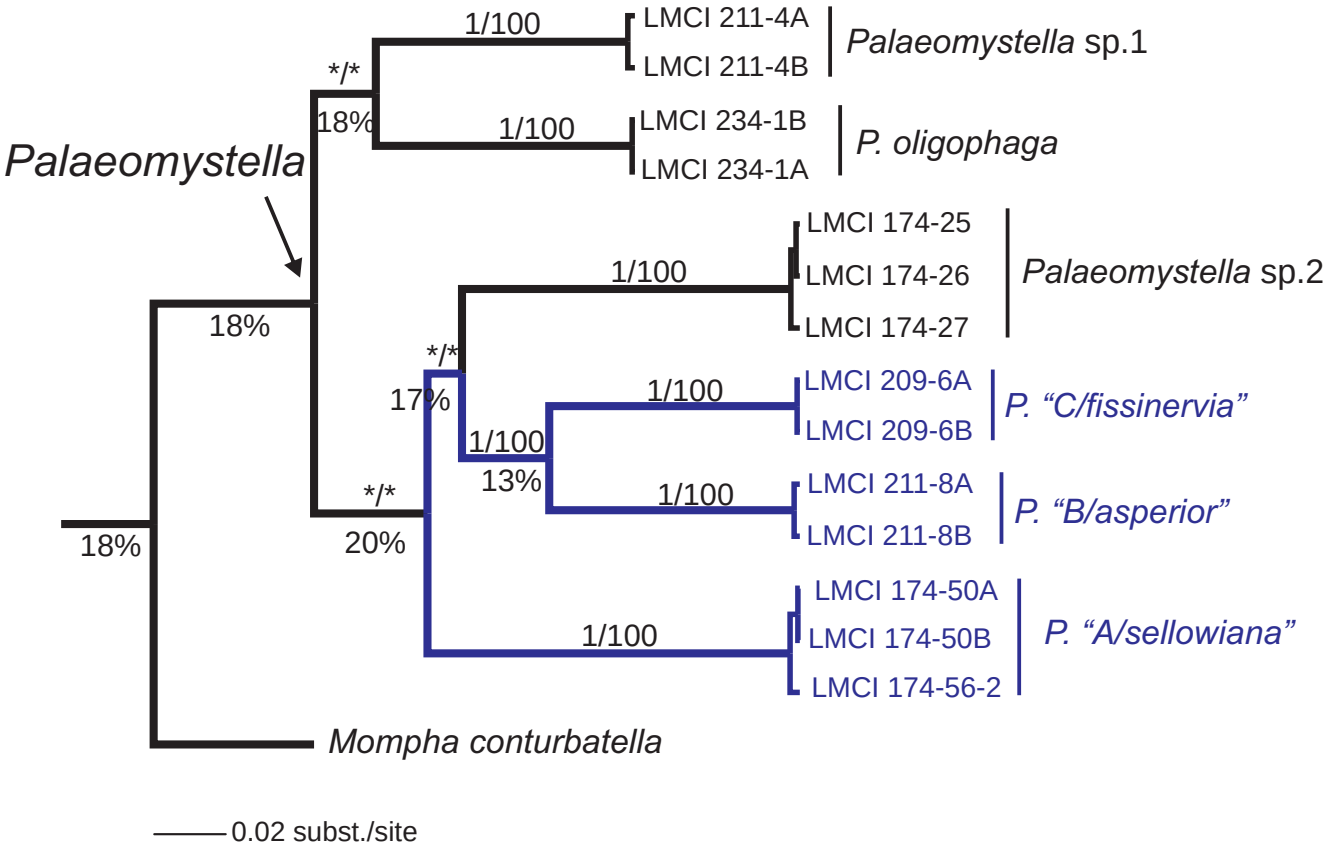

Fig. 13 - Luz et al

Capitulo2. Natural history, molecular phylogeny and taxonomy of a new genus and species of kleptoparasitic gelechiid moth associated with Melastomataceae galls

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Abstract. Male, female, pupa and larva of a new genus and species of Gelechiidae (Lepidoptera), *Genus species* gen.n., sp.n. Moreira and Becker from Southern Brazil 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 *Palaeomystella* Fletcher (Lepidoptera: Momphidae) species on *Tibouchina sellowiana* (Cham.) Cogn. (Melastomataceae) endemic to the Atlantic Rain forest. Larvae are kleptoparasitic, usurping the gall and thereafter feeding upon the internal tissues that were induced to develop by the cecidogenous species. By determining variation in populational density of both species and following gall development individually throughout ontogeny under natural conditions, we demonstrated that the kleptoparasite is sedentary, completing the life-cycle inside a given *Palaeomystella* gall, where pupation occurs. Galls change in color from green to violet as they grow, those of greater size and violet been mostly attacked. Variation in seasonal abundance of the kleptoparasite is tied to that of the cecidogenous species, corresponding peaks in density occurring subsequently (during Summer and Fall, respectively). Galls free from attack of kleptoparasite fall from the trees later in ontogeny, the cecidogenous species completing development inside, in the soil. In contrast, those attacked by *G. sp.n.* stay attached to the plant and can predominate in numbers, which may turn difficult identification of the true gall inducers in the field. Thus, by using an integrative framework, including morphological descriptions in association with molecular, behavioural and ecological analyses, we clarified such a specialized interaction between *G. sp.n.* and such *Palaeomystella* species, which could be also applied to characterize the taxonomy and life history of other kleptoparasitic moths and beyond.

Keywords. Neotropical region, Atlantic Rain Forest, melastome galls, momphid moths, kleptoparasitism.

Introduction

Cecidogenous insect species are known as ecosystem engeneers (Sanver and Hawkins 2000), as galls they induce are used as a resource not only by themselves but also by other guilds (Mani 1964). They may account for very complex, multitrofic-level systems including predators, parasitoids, cecidophagous, inquilines and kleptoparasites, among other insects, such as sucessors who may use empty galls for sheltering. Although well known for other biological systems (e.g. Ivengar 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 upon the gall tissues, after invading the gall and usurp the cecidogenous species (e.g. Morris et al., 2000). Contrary to the inquilines who may change substantially both the shape and size of the galls they invade, by inducing similar (Brooks and Shorthouse, 1988) or different tissues (Noort el al. 2007) from the cecidogenous, kleptoparasites do not induce development of new tissues, just feeding on those that were induced to develop by their precursors. Unlike cecidophagous 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 of the internal portions of a single gall during ontogeny. However, in the literature of 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, Benᅠá & Vanin 2013), and thus need to be reviewed. According to Miller (2005), lepidopterans belonging to at least nine families are found within this poorly defined feeding guild.

Fauna associated with galls induced by Lepidoptera in general is in fact still poorly known, including those of the cecidogenous guild which account to a few hundred species belonging to ca. 20 families, most located within the Gelechioidea. The greater number of such species await for description, as they are known only by their gall morphotype (for a revision, see Miller 2005). In the Neotropical region these gall morphotypes are commonly found in Melastomaceae (*e.g.* Tavares 1917, Houard 1933, Lima 1945). 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). Furthermore, knowledge of such fauna may demand additional efforts, by carrying out intensive studies, since the presence of other guilds, such as inquilines, cecidophagous and kleptoparasites may lead to misidentification of species and corresponding biological function in the gall-system, if any. This is particularly true when species of different guilds belonging to close related lineages are present at the same time in such complex, multitrophic gall-systems.

As a case study, we herein described first the larva, pupa and adults of a new genus and species of kleptoparasitic gelechiid moth, associated with a fusiform gall induced by a *Palaeomystella* Fletcher (Lepidoptera: Momphidae) species 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. Then, by following development of galls individually throughout ontogeny under field conditions, we determined the life history of the kleptoparasite in comparison to the cecidogenous species, taking into account variation in gall color and

size. In addition, by estimating monthly the density of galls on *T. sellowiana* plants in association with dissection of field-collected galls in laboratory, during fourteen months, we determined concomitantly variation in seasonal abundance of both cecidogenous and kleptoparasitc 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 ± 2 ºC) in the Laboratório de Morfologia e Comportamento de Insetos, Departamento de Zoologia, Universidade Federal do Rio Grande do Sul (UFRGS), Porto Alegre city, Rio Grande do Sul State (RS), Brazil, from March 2012 to April 2013. They came from galls induced by a *Palaeomystella* Fletcher species (Lepidoptera: Momphidae) that was described elsewhere (Luz et al. 2014). Such galls were field-collected with either later instar larvae or pupae inside on shoots of *Tibouchina sellowiana* (Cham.) Cogn. from a population existing at CPCN Pró-Mata, São Francisco de Paula municipality, 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 glycerin jelly or Canada balsam. Observations were performed with the aid of a Leica® M125 stereomicroscope. Structures selected to be drawn were previously photographed with an attached Sony® Ciber-shot DSC-H10 digital camera. Vectorized line drawings were then made with the software CorelPhotoPaint® X3, using the corresponding digitalized 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® 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.

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 larvae tissue using the organic method of Cetyl Trimethyl Ammonium Bromide (CTAB) from three specimens (Table 1). Amplification was performed through 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 program and conditions proposed by Folmer et al. (1994). Accordingly, we obtained variants that match exactly the region previously sequenced in related gelechids deposited in Genbank database and BOLD. Aliquots of PCR products were treated with Exonuclease I and FastAP Thermosensitive Alkaline Phosphatase (Thermo Scientific), sequenced using the BigDye chemistry and analysed on an ABI3730XL (Applied Biosystems Inc.) 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 waiting for accession numbers (Table 1)

A phylogenetic tree was reconstructed in order to test our hypothesis of monophyletic status for *G. sp.n.*. We thus also incorporated all available taxa belonging

to *Coleotechnites* (supposedly the sister of *G. sp.n.*) and rooted with the currently known related genera *Exoteleia* and *Recurvaria*, according to 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. We used four independent runs of 10 million generations and a burn in period of 10,000 (the first 1000 trees were discarded); 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 figtree/). Finally, we analyzed the evolutionary distance between the same pairs of taxa used in the phylogenetic analysis (including outgroups) using Kimura 2-parameters (K2P) model (Kimura 1980) procedure, with 1000 of bootstrap replication.

Museum collections. Abbreviations of the 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.

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, Camacãn, Bahia.

Populational studies. Galls were monthly sampled from April 2012 to May 2013 an additional population of *Tibouchina sellowiana* existing at the type locality. The CPCN Pró-Mata corresponds to a 4,500 ha reserve of Atlantic Rain Forest, presenting portions of Dense Umbrophilous Forest (= Brazilian Atlantic Rain Forest *sensu stricto*) intermixed with fragments of *Araucaria* forests and grasslands. *T. bouchina* plants are common in the area, mainly along the trails located on higher altitudes (Mello 2006).

To determine variation in density and color of galls, a total of 160 randomly selected plants (range from 1 to 2 m tall) that were located and mapped along of two trails were surveyed (for a map, see Suplementary material – Fig. 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, such plants were searched for the presence of galls that were collected and brought to the laboratory for measuring their size and color, followed by dissection. These plants were sampled only one time during the study, being thereafter called destructive samples. The additional 20 *T. sellowiana* plants were used to evalute changes on color and size of galls. They had

their galls individually marked and photographed each occasion until their fate being determined in the field (thereafter called non-destructive samples). Phenology of plants was determined concomitantly.

On both field and laboratory conditions, galls were photographed with a digital camera Sony® Cyber-shot DSC-H10. To correct for lighting conditions, we used a WhiBal® white balance reference card. Gall size and color (RGB pattern) were determined from the corresponding digital images, using the software AxioVision® Rel. 4.8. Dissections were performed with the aid of a Leica® M125 stereomicroscope, to determine the presence immature stages of either the cecidogenous or kleptoparasite, or both. Empty, old galls were discharged from samples after dissection. Measurements were made with an attached ocular micrometer (for data on larval capsule width, see Supplementary material – Table 1S).

Statistical analyses. The results for color and size of galls, and size of larval instars were evaluated for homogeneity of variance of data, assessed by Bartlett test, and for normal distribution of the data by the Kolmogorov–Smirnov test. Those on gall size and green intensity passed the test, and then were linear regressed. The data obtained for size of larval instars were not normally distributed, and were compared by nonparametric Kruskal–Wallis test, followed by Dunn's multiple comparison tests. These parametric and nonparametric tests were performed by using the software PAST v.2.08, following criteria described Zar (1999) and Conover (1980), respectively.

Results

Taxonomy

Genus Moreira and Becker, gen.n.

Figs. 1-7

Type species. *Genus species* Moreira and Becker, sp. nov. by present designation.

Diagnosis. A gelechiid lineage with larvae, pupae and adults having clear affinity with the Teleiodini (sensus Lee and Brown 2008). It is close to *Coleotechnithes* Chambers by sharing males with strongly assymetrical valve and hindwings with hair pencils at base of anal, and females with a single spiny, wedge shaped signum. *G. sp.n.* differs from those of *Coleotechnithes*, however, by several characteristics, as follows: 1) forewings, with veins R_4 stalked to R_5, and M_2 stalked to M_3; 2) hindwings, with vein R_5 separate from M_1, and M_2 separeted from M_3; 3) males without hair pencil on anal region of hindwings; 4) females, with anterior margin of sterigma asymmetric in shape, projecting anteriorly on the left side, on both tergum and sternum. Also, by having a kleptoparasitic habit, associated with galls.

Description

Adult (Figs. 1E-F). Male and female similar in size and color. Small moth with forewing length varying from 5.33 to 7.15 mm (n = 8). *Head* (Fig. 1F): Vestiture moderately smooth. Eye relatively large, rounded; vertical diameter ~ subequal interocular distance across frons. Ocellus absent. Antenna filiform, long, greater thal half forewing in length; flagellomeres completely encircled by single, dense row of slender scales. Clypeus with ventral margin broadly truncate.. Pilifers well developed, triangular.Proboscis anteriorly scaled, elongate, ~ 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*: Forewing (Figs. 1E, 2A): lanceolate, with 12 veins; L/W index ~ 4.3; retinaculum subcostal, with secondary, adjacent subradial setae on females; discal cell closed, ~ 0.63x length of forewing; Sc ending ca. middle anterior margin; R 5-branched; R_1 ending near two third of wing margin; R_4 and R_5 stalked ca.1/2 distance from the cell apex; R_{4+5} and M_1 separate; M 3-branched; M_2 and M_3 stalked near cubitus; CuA 2-branched; 1A+2A forked basally, extending more than half the length of posterior margin. Hindwing (Fig. 2A): with 9 veins, with a parallelside hair pencil at base of anal area; L/W index ~ 4.4, ~ 0.76 forewing in length; frenulum a single acanthus on male, with two parallelside acanthi on female; discal cell closed, ~ 0.63x length of forewing; Sc+R_1 ending ca. one third anterior margin; Rs ending circa two third anterior margin; M 3-branched, with M_1, M_2 and M_3 separate; CuA 2-branched, CuA_1 and CuA_2 separate; CuP weakly sclerotized, ending one third posterior margin; 1A+2A well developed, ending near basis of posterior margin. Legs with tibial spur pattern 0-2-4; epiphysis present. *Abdomen* (not showed): pregenital segments unmodified.

Male genitalia (Figs. 2B, 3A-E). Uncus (Fig. 3A) small, subtrapezoidal, subequal in lenght with gnathos and with distal margin setose; tegumen dome shaped, basal width / length ratio ca. 0.45; gnathos (Fig. 3B) hook shaped; costal part of left valve (Fig. 3C) with bulbous base and distal part slender, long and curved; in locus (Fig. 2B), the distal part directs first to the right side, and then above, contouring the tegumen dorsally; saccular part of valve absent; right valve not detected; siccae (Fig. 3D) symmetric, curved mesally and setose, with the aedeagus anchored mesally; phallic fulcrum

cyllindric (Figs. 3D,E), median sized, with distal margin ventrally pointed; vesica without cornuti;saccus not developed.

Female genitalia (Figs. 2C-E, 3F-G). Anal papillae (Figs. 2C, 3F) laterally compressed, forming a narrow terminal, setose lobe; apophyses posteriores ca. 3x length of apophyses anteriores; sterigma (Figs. 2D, E) with anterior margin asymmetric in shape, projecting anteriorly on the left side, on both tergum and sternum; the latter deeply and narrowly emarginated medially, bearing the ostium bursae on anterior portion, that is thus located on the left ventral side; ductus bursae membranous, shorter than corpus bursae, with ductus seminalis inserted medially; corpus bursae an elongate sac, having the wall covered by small, stout spines and bearing anteriorly, a single spiny, wedge shaped, centrally constricted signum (Fig. 3G).

Etymology. The generic name is derived from …

Genus species **Moreira & Becker, sp.n.**

Figs. 1-7

Diagnosis. As discussed for the genus.

Description. Adult (Fig.). *Head*. Frons and vertex mostly white cream; labial palpus most with scales white cream tipped with dark gray, basal segments, terminal segments slightly angled upwards, with proximal portion white cream; antennae dark gray; proboscis yellowish brown, with scales white cream tipped with dark gray.

Thorax. Tegula and mesonotum mostly white cream, mottled by sparse yellowish scales; the former with dark gray scales anteriorly; prothoracic and mesothoracis legs mostly dark gray; metathoracic legs clearer, mostly covered with scales white cream tipped with dark gray. Forewings: dorsally covered by dark gray scales along anterior

portion and with cream white scales on posterior margin, forming two wide, irregularly shaped, longitudinal bands; the latter, mottled with yellowish scales; ventrally covered by darkish gray scales; fringe uniformelly yellowish. Hindwings: light gray on both sides; fringe mostly light gray and yellowish on anterior and posterior margins, respectively. *Abdomen*. Mostly covered by white cream scales.

Male genitalia (Figs. 2B, 3A-E). As described for genus.

Female genitalia (Figs. 2C-E, 3F-G). As described for genus.

Etymology. The specific name is derived from ...

Type material. BRAZIL: Centro de Pesquisas e Conservação da Natureza Pró-Mata (CPCN Pró-Mata; 29º29'16''S, 50º10'60''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* "*A*" Moreira & Becker on *Tibouchina sellowiana* (Cham.) Cogn. (Melastomataceae): LMCI 174, 26.III.2012, by G.R.P. Moreira, F.A. Luz and P. Pollo; LMCI 210, 7-9.III.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 (??.???, ????? and ?????, respectively); 1♂ (LMCI 174-187), 2♀♀ (LMCI 174-41 and 176), donated to MCTP (??.???, ????? and ?????, respectively); 1♂ (LMCI 210-64), 2♀♀ (LMCI 174-194 and 196), donated to VOB (??.???, ????? and ?????, 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 glycerin GRPM 50-24), 5 ♀♀ (LMCI 174-185, 188, 195, 210-46; 174-171, with genitalia in glycerin GRPM 50-25). Adults, fixed in Dietrich´s fluid, preserved in 70% ethanol: 2 ♂♂ (LMCI 174-206 and 207, with genitalia in glycerin GRPM 50-68 and 69, respectively); 2 ♀♀ (LMCI 174-210 and 211, with genitalia in glycerin 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); larvae, 2 last instars (GRPM 59-66 and 67). Immature stages, fixed in Dietrich's fluid and preserved in 70% ethanol: 12 last instar larvae (LCMI 174-55); 9 pupae (LMCI 174-216); 6 dissected galls (LMCI 174-217 to 222). In tissue collection, nine larvae (LMCI 174-53 and 57) fixed and preserved in 100% ethanol, under -20^{o}C.

Immature stages

Last larval intar (Figs. 4,5). 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 (Fig. 4C), smooth (Fig. 5A); frons subequal in high and width, extending ca. one-half epicranial notch (Fig. 4A,C); labrum (Fig. 5B) shallowly notched, with six pairs of setae of unequal size; six stemmata (Fig. 5C) arranged in C-shaped configuration. Chaetotaxy (Fig. 4A): 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 (Fig. 5D) two-segmented; mandibles (Fig. 5B) broad, with four teeth and two

unequal setae on the outer surface; labium (Fig 5E) with two-segmented palpi, each bearing a seta; first segment ca. 8x the second in length; spinneret parallel sided; maxilla (Fig. 5F) prominent.

Thorax and Abdomen (Fig. 3B-D): Prothoracic shield (Fig. 4A) dark brown, divided longitudinally by slightly marked, unpigmented area; anterior and posterior half of mesotoracic, metatoracic and abdominal segments white and violet, respectively, giving a longitudinally banded aspect to the larva (Fig. 4D); pinacula small, fuscous; anal plate (Fig. 4D) dark brown; anal fork black, with three major pair of prongs ; thoracic legs (Fig. 4D) dark brown, with a pair of broad bladelike setae (Fig. 5G) ventrolaterad to terminal claw. Prolegs (Fig. 5I) on A3-A6 and A10 of equal size; crochets in a biordinal, uniserial circle, mesal penellipse. Thorax chaetotaxy: T1 with D group bisetose, both located on the dorsal shield, D1 shorter than D2; XD group bisetose, with similar length and both on the dorsal shield; SD bisetose, lateraly 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, with similar length to L1; SV unisetose; V unisetose. Abdomen chaetotaxy: D group bisetose; A1-9 with D2 slightly longer than D1, and A10 with D1 and D2 with similar size; A1-8 with SD group unisetose, A10 with SD1 and SD2 of similar size; L group trisetose; A1-8 with SV group bisetose, SV1 slightly shorter than SV2, SV1 absent in A9; V group unisetose.

Pupa (Figs. 6, 7). Length varying from 5.2 to 6.24 mm (n = 8). Body elongate oval in dorsal and ventral views, widest in the mesothoracic region; vertex rounded; frontoclypeal suture weakly defined, concave medially; labrum U-shaped, labial palpi minutely exposed; maxillary palpi short, not extending beyond anterior margin of eye;

maxillae extending distally between sclerites of midlegs; antennae meeting mesially and reaching the apical margin of forewings; apices of metathoracic legs large, with distal part wider than antenna. Integument weakly melanized, with a few micro-setae scattered dorsally on cephalic region (Fig. 7A,B) and abdomen, and on anterior portion of abdominal segments. Abdominal terga mostly covered with stout spine-like microtrichia (Fig. 7C). Thoracic and abdominal spiracles rounded, with elevate peritreme (Fig. 7B); spiracle A8 partially closed. Sternum A6 with a pair of pseudopodium scars (Fig. 7E); the scars on A5 are hidden by the overlying wing. Abdominal segment A7 posteriorly marginated by several aligned groups of short, stout setae (Figs. 7B, D). Abdominal segments A8-10 partially fused, with caudal cremaster bearing a few, long and stout, distally coiled setae (Figs. 7F,G).

Molecular phylogeny. A total of 621 nucleotide sites were analysed, in which 150 (24%) were variable. According to our phylogenetic hypothesis, *G. sp.n.* was recovered as monophyletic in both methods of inference (BI and ML), with high support values (Fig. 8). Because topologies were identical, we decided to present only one (BI). *G. sp.n.* was placed as sister of *Coleotechnites* with strong BPP and bootstrap support values (0.98 and 88, respectively) (Fig. 8). The evolutionary divergence observed between comparisons of pair of species range from 2 to 13% (± 1%) (Table 2). The distance between the new lineage described herein and *Coleotechnites* was 11% (Fig. 8). Similarly, the divergence between *G. sp.n.* and outgroups (*Recurvaria* and *Exoteleia*) was ca. 12% (± 1%). Finally, the K2P distances within *Coleotechnites* indicate that such group also presents a significant diversity, evidenced by the range of distances (2-8% ± 1%) (Table 2).

Distribution. "*Genus species*" gen. n, sp. n. is known only from the type locality, the Dense Umbrophilous Forest (= Brazilian Atlantic Rain Forest *sensu stricto*) portions of the CPCN Pró-Mata, São Francisco de Paula Municipality, Rio Grande do Sul, Brazil. As already mentioned, it occurs in association with fusiform galls (Fig. 9A) 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 laboratory demontrated that field-collected galls having intact walls (Figs. 9E,H) usually carry inside a larva of *Palaeomystella*, which can be differentiate from those of *G. sp.n.* by presenting cream white bodies (Fig. 9B), among other morphological characteristics. Additional such galls left to develop in laboratory showed that pupation of the cecidogenous larva occurs inside, within a tied, silk-made cocoon. Prior to pupation in this case, the last larval instar builds an operculum (Fig. 9D) through which the adult emerges. However, none of such galls were collected attached to *T. sellowiana* plants during systematic sampling. Individual observations on such galls under field conditions, on host plant belonging to the non-destructive sampling group demonstrated that in fact they are dehiscent, later in ontogeny falling to the ground (Fig. 9C) where the cecidogenous development is completed. Searching for them on the soil surrounding *T. sellowiana* trees resulted in collection of many of such operculated galls.

On the other hand, dissections also showed that galls having open, rounded orifices on the wall (Fig. 9E) usually carry a larva of *G. sp.n.* (Fig. 9F) inside. Additional such galls left to develop in laboratory showed these larvae are residents, live alone within such 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-made cocoon that is generally covered with faecal pellets (Fig. 9G). By following each gall throughout ontogeny in the non-destructive samples we found that, contrary to the former, this modified gall morphotype does not fall to the ground, staying attached to *T. sellowiana* trees for months. They progressevily dry out, turning into black after *G. sp.n.* emergence, and are then frequently used as shelter by small arthropod such as Collembola and Acari.

From the total of 512 galls dissected in laboratory, 164 (32.05%) had intacted walls, carrying larva of the cecidogenous inside, 169 (33.0%) had orifices on it and thus bearing *G. sp.n.* larva/pupa inside: the remaining galls had unidentified immatures of either parasitoid wasps (19.92%), predator tripses (9.96%) or cecidophagous curculionids (5.07%). None gall had alive larvae of both inducer and *G. sp.n.* living together inside, but dead bodies and exuvia (head capsules) of the former were found in a few galls presenting alive larva of the latter. None gall was found with two or more larvae of *G. sp.n.* either.

Within the continuous from green to violet coloured galls found in the field (Fig. 10A), green galls that were dissected had predominantly cecidogenous larva inside, and the violet ones, *G. sp.n.* (Fig. 10B). The smallest size of field collected galls had no larvae of the latter inside (Fig. 10C). We also found a significative correlation between gall size and color by taken all such galls into account, the green density decreasing and violet increasing with the increase of size (Fig. 10D).

Variation in frequency of different instars in relation to gall size color revealed that early instars (II and III) of the cecidogenous species were found inside green galls and, the later ones (IV), in a color spectrum varying from green to violet (Fig. 11A). We

suppose galls having first instar larvae of the cecidogenous were not detected while sampling in this study due their very small size. Head capsule exuvia for the first instar were frequently found inside those carrying second instar inside, and that accounted for the smallest gall size sampled. On the other hand, larvae of the kleptoparasite from all instar were found primarily on violet galls (Fig. 11B).

Galls bearing either cecidogenous or kleptoparasite inside varied in number from 57 (April 2012) to 3 (August 2012) per occasion (average $\pm$ standard deviation = 23.78 – 4,36 per occasion), which correspond to7.12 and 1.5 per plant per occasion, respectively (= 4.49 $\pm$ 2.00 galls per plant per occasion). Young, small galls bearing cecidogenous larvae inside start appearing during early Spring (September) with the sprouting of *T. sellowiana* trees, reaching a clear density peak during next Fall, which coincides with the florewing season (April) (Fig. 12). The existence of a second, shorter density peak during October, suggest there may occur two generations per year, which should be further investigated. Variation in abundance of the kleptoparasite followed that of the cecidogenous, the corresponding density peaks occurring subsequently.

Discussion

Taxonomy. Male genitalia in gelechiid moths can be very specialized by reduction, modification and asymmetry; however, females in general have the ostium bursae ventro-mesial, rarely located laterally or dorsally (Hodges 1999). As far as we are concerned, strongly modified female sterigma as herein described for *Genus species* gen.n., sp. n. may have evolved *de novo* within the Teleiodini, and should be further investigated. On the other hand, modifications on male valvae such as those described herein have been reported to other teleiodinids, including the close related lineage formed by *Recurvaria* Haworth, *Exoteleia* Wallengren and *Coleotechnites* Chambers

(Lee and Brown 2008). In the latter species, valva are strongly asymetrical, the right one been reduced (Hodges and Stevens 1978; Lee and Brown 2008). We could not detect any indication for the presence of the right valve in the genitalia herein studied, which may have been either fused with genitalic structures or losted. However, as described by Ponomarenko (2008), these highly modified structures are glandular in nature, what she called "glandiductors". Also, they may not be homologous to any part of the valva, which thus would have been fused to other genitalic structures. The rounded, proximal basis of such structures is secretory in nature and the sclerotized, slender distal portion bear an opening at the apex; we confirm such a description for the material herein studied. Ponomarenko (2008) concluded then that such genital glands could be considered as a basal synapomorphy for the subfamily Gelechiinae, and thus limiting the corresponding taxonomic use at the generic level.

Genetic distances resulting from molecular phylogenetic analyses gave support to our hypothesis that "*G. species nov.*" is a distinct genus. We found evolutionary distances values similar to those observed between *Coleotechnite*s and outgroup (*Recurvaria* and *Exoteleia*), correspondending to a generic level of divergence, i.e. ca. 10 % (for threshold discussion in Lepidoptera, see Wiemers and Fiedler 2007). Particularly in this group of gelechids, the interspecific variation exceeds intraspecific variation by at least one order of magnitude. Furthermore, we found that the new genus is closer related to *Coleotechnites* when compared to *Recurvaria* and *Exoteleia*. *Coleotechnites* was previously known as closely related to teleiodinid genera existing in the Asia, Europe, and North America (Lee and Brown 2008).

G. sp.n. has wing venation similar to those of *Exoteleia* species, differing in the hindwing pattern, M2 and M3 being connate in the latter. Furthermore, male valva are symetrical and female bursa lacks signum in *Exoteleia* species (Lee and Brown 2008).

Similarities found on larval and pupal stages, such as the maxillae longer than prothoracic legs and rows of setae on posterior margin of abdominal segment A7, also suggest that *G. species* is closest to *Coleotechnites*. *Exoteleia* species 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 methoracic legs are narrower than the antennae; they are wider than the antennae in *Coleotechnites* and *G. sp.n.*. Contrary to postulated by Lee and Brown (2008) and Adamski et al. (2010), and in accordance to what was herein described, the abdominal segment VII in *Coleotechnites* pupae are marginated by setae caudally; in fact, these structures are also present in *Recurvaria* but absent in *Exoteleia* species (Patočka and Turčani 2005). As discussed bellow, kleptoparasitic life styles have been described for other gelechiid genera, but as far as we known, not for *Coleotechnites* or closely related lineages. Additional collections we made in Atlantic Rain Forest indicate the existence of at least a second, undescribed species congeneric to *G. species*, presenting the same life style.

Life-history and Seasonal abundance. In conjuction, results demonstrated that *T. sellowiana* galls are induced only by *P. "A"*, and that *G. sp.n.* is a kleptoparasite. Behavioral observations confirmed the latter feeds upon tissues induced to develop by the former. The absence of *G. sp.n.* on the smallest field-collected galls demonstrated that this species enters the systems later in gall ontogeny. Additional observations made in laboratory by the senior author suggest oviposition occurs on or near the gall, the larva entering the gall immediately after hatching, which should be better explored. Presence of dead bodies and head capsules of *P. "A"* inside, indicates the kleptoparasite kills the cecidogenous larvae after entering the gall. As reported by

Caltagirone (1964), for a kleptoparasitic cosmopoterigid on galls induced by *Pontania* (Hymenoptera: Tenthredinidae) on *Salix* (Salicicaceae), larva may prey on any insect encountered in the gall, which should be examined for the case studied herein. The presence of only one larva within a given gall in most cases demonstrates *G. sp.n.* has a solitary habit. Furthermore, presence of head capsule exuvia of the same instar, as thus belonging to different larvae was niglegeable which does suggest *G. sp.n.* larva uses a single gall during ontogeny, and have low mobility, if any.

There was no indication galls change either color, size or shape due the presence of kleptoparasite inside, as is the case for other cecidogenous species when attacked by inquilines (e.g. Noort et al. 2007) and parasitoids (e.g. Dias et al. 2013). The existence of negative correlation between gall size and green color, when both gall types were included in the analysis, free and attacked of kleptoparasite, demonstrates that changes in color in this case is a phenomenon tied to additional factors related to gall ontogeny, whose underlyning mechanisms remain unknown. Changes in color from green to violet such as found on *P. "A*" galls have been associated in several plant parts and tissues to 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 the violet colour of galls may be also envolved with protection of inducers from natural enemies, which does not seem to be the case for the system herein study. Thus, *G. sp.n.* may choose violet galls, either for being more attractive to females during oviposition or for bearing greater amounts of resource since they are older and bigger; these hypotheses are not mutually excludent, and should be further tested.

As expected, *P. "A"* galls start increasing in numbers during Spring, with the new grown shoots of *T. sellowiana* trees, since gall induction depends on host-tissue reactivity (Raman 1994; Yukawa 2000). The great number of gall attacked (ca. half in

total field-collected galss; almost all 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. "A"* galls. An attack index of ca. 30 percent was reported by Hawkins and Goeden (1994) for other 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 *G. sp.n.* responds accordingly to 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 carrying out studies with 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 a kleptoparasitic habit in galls induced by a momphid Lepidoptera in Melastomataceae. It differs primarily from other guilds, such as inquilinism, as the kleptoparasite larva does not coexiste with the cecidogenous one in a given gall; there is no production of new tissues in this case. The kleptoparasite takes the gall environment over and feeds thereafter internaly upon the tissues induced to develop by the former, without changing the external shape and size of the gall. It does not qualify within the cecidophagy guild either, since it has low mobility, usually attacking only one gall internaly, where the life-cycle is completed, and may be also carnivorous.

There are many methodological, taxonomic and ecological implications related to this complex interaction, starting with the potential misidentification of the true gall inducer (Miller 2005), since in this case later instar of cecidogenous species may occur in lower numbers, as their galls are dehicent, completing the development in the soil. 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 and life-history of other kleptoparasitic moths and beyond.

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FIGURE LEGENDS

Figure 1. *G. sp.n.* adult, dorsal view. **A** wings spread, pinned; **B** head and thorax, in detail; **C** wings folded, on leaf *Tibouchina sellowiana* leaf. Scale bars = 2, 1 and 2 mm, respectively.

Figure 2. *G. sp.n.*adult morphology: **A** wings; **B** male genitalia (arrow indicate glandiductor), lateral view; **C** female genitalia, lateral view; **D**, **E** female sterigma, in dorsal and ventral views, respectively. Scale bars = 1, 0.2, 0.5 and 0.5 mm, respectively.

Figure 3. Genital morphology of *G. sp.n.* under light and scanning electron microscopy: **A** uncus, dorsal view; **B** gnathos, lateral view; **C** left valve (= glandiductor) detached from uncus, lateral view; **D** sicae with anchored aedoeagus (pointed by arrow), latero-posterior view; **E** dissected aedoeagus (asterisk indicates everted vesica), lateral view; **F** female papilla annalis, lateral view; **G** female signum, internal view. Scale bars = 100, 50, 100, 100, 200, 100 and 200 µm, respectively.

Figure 4. *G. sp.n.* 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 = 50µm and 1mm, respectively.

Figure 5. Scanning electron micrographs of *G. sp.n.*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, latero-anterior view; **G** distal portion of mesothoracic leg, postero-lateral view (arrow indicates spatulate seta); **H** prothoracic spiracle, lateral view; **I** pseudopodium abdominal A6, meso-ventral view. Scale bars = 200, 100, 100, 20, 20, 20, 20, 20, 100 µm, respectively.

Figure 6. *G. sp.n.*pupa, in dorsal (**A**), ventral (**B**) and lateral (**C**) views, respectively. Scale bar = 1 mm.

Figure 7. Scanning electron micrographs of *G. sp.n.* pupa: **A** , clypeal and mandibular areas (open arrows indicate microsetae), ventral view; **B** abdominal segments seven and eight (seta and closed arrow indicate abdominal spiracles seven and eight, respectively), latero-dorsal view; **C** microtrichia of abdominal segment A5, dorso-lateral view; **D** setae of seven 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, latero-dorsal view. Scale bars = 50, 100, 10, 20, 50, 100, 10 µm, respectively.

Figure 8. Bayesian inference tree of 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 percentage of evolutionary divergence between clades.Asterisk indicates support < 0.80/60 for BPP and ML, respectively.

Figure 9. Galls induced by *Palaeomystella* "*A"*on *Tibouchina sellowiana* plants, free from (A-D) and attacked by (E-H) the kleptoparasite *G. sp.n.*. **A** general aspect of two young, green galls habiting 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 soil, bearing a cecidogenous later instar larva; **D** operculum (indicate by closed arrow) made by a last instar of cecidogenous larva on dehiscent gall before pupation, external view; **E** violet gall habiting by a kleptoparasite larva, as indicated by the presence of two orifices (pointed by open arrows); **F** dissected gall showing a kleptoparasite larva inside; **G** dissected gall showing a kleptoparasite pupal coccon inside (covered by larval fecal pellets, indicated by asterisk); **H** empty old gall, left

attached to a *T. sellowiana* plant after the kleptoparasite emergence. Scale bars = 4, 2, 2, 2, 4, 4, 4, 4 mm, respectively.

Figure 10. Variation in colour and size among galls induced by *Palaeomystella "A"* 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 (closed bars; total = 155 individuals) and kleptoparasite (open bars; total = 163 individuals) inside in relation to gall green density and size, respectively; **D** linear regression between size and intensity of green color on galls ($y = 0.67x + 8.77$, $R^2 = 0.152$, $p < 0{,}0001$, n = 348).

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

Figure 12. Seasonal abundance of cecidogenous (*Palaeomystella "A"*, dashed line) and kleptoparasite (*G. sp.n.* , solid line) larvae in galls (total = 164 and 169 individuals, respectively) induced on *Tibouchina sellowiana* plants at CPCN Pró-Mata, from April 2012 to June 2013. Arabic numbers from 1 to 14 represent 30-days sampling intervals. Upper horizontal bars indicate host plant phenological phases: red, flowering; green, fruiting; blue, dormancy; black, shooting.

Table1. Specimens used to reconstruct the monophyletic status and phylogenetic relationship of the *G. sp.n.* using related genera.

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

Table 2. Estimates of evolutionary divergence between sequences based on 621 base pairs of cytochrome oxidase I (COI) gene using Kimura 2-parameter model. Average number (± 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 genus (in bold), 8 species of *Coleotechnites* and 2 outgroups (*Exoteleia* and *Recurvaria*).

	1.	2.	3.	4.	5.	6.	7.	8.	9.	10.
1. *C. quercivorella*										
2. *C.* sp.	0.05±0.01									
3. *C. piceaella*	0.07±0.01	0.03±0.01								
4. *C. florae*	0.04±0.01	0.06±0.01	0.06±0.01							
5. *C. starki*	0.04±0.01	0.06±0.01	0.07±0.01	0.05±0.01						
6. *C. blastovora*	0.04±0.01	0.07±0.01	0.07±0.01	0.04±0.01	0.06±0.01					
7. *C. atrupictella*	0.04±0.01	0.07±0.01	0.08±0.01	0.06±0.01	0.07±0.01	0.06±0.01				
8. *C. coniferella*	0.07±0.01	0.02±0.01	0.04±0.01	0.06±0.01	0.06±0.01	0.08±0.01	0.08±0.01			
9. **Gen. nov**	**0.08±0.01**	**0.10±0.01**	**0.11±0.01**	**0.08±0.01**	**0.09±0.01**	**0.09±0.01**	**0.09±0.01**	**0.10±0.01**		
10. *Exoteleia*	0.10±0.01	0.12±0.01	0.12±0.01	0.10±0.01	0.11±0.01	0.10±0.01	0.11±0.01	0.12±0.01	**0.11±0.01**	
11. *Recurvaria*	0.11±0.01	0.13±0.01	0.13±0.01	0.11±0.01	0.12±0.01	0.12±0.01	0.11±0.01	0.13±0.01	**0.13±0.01**	0.12±0.01

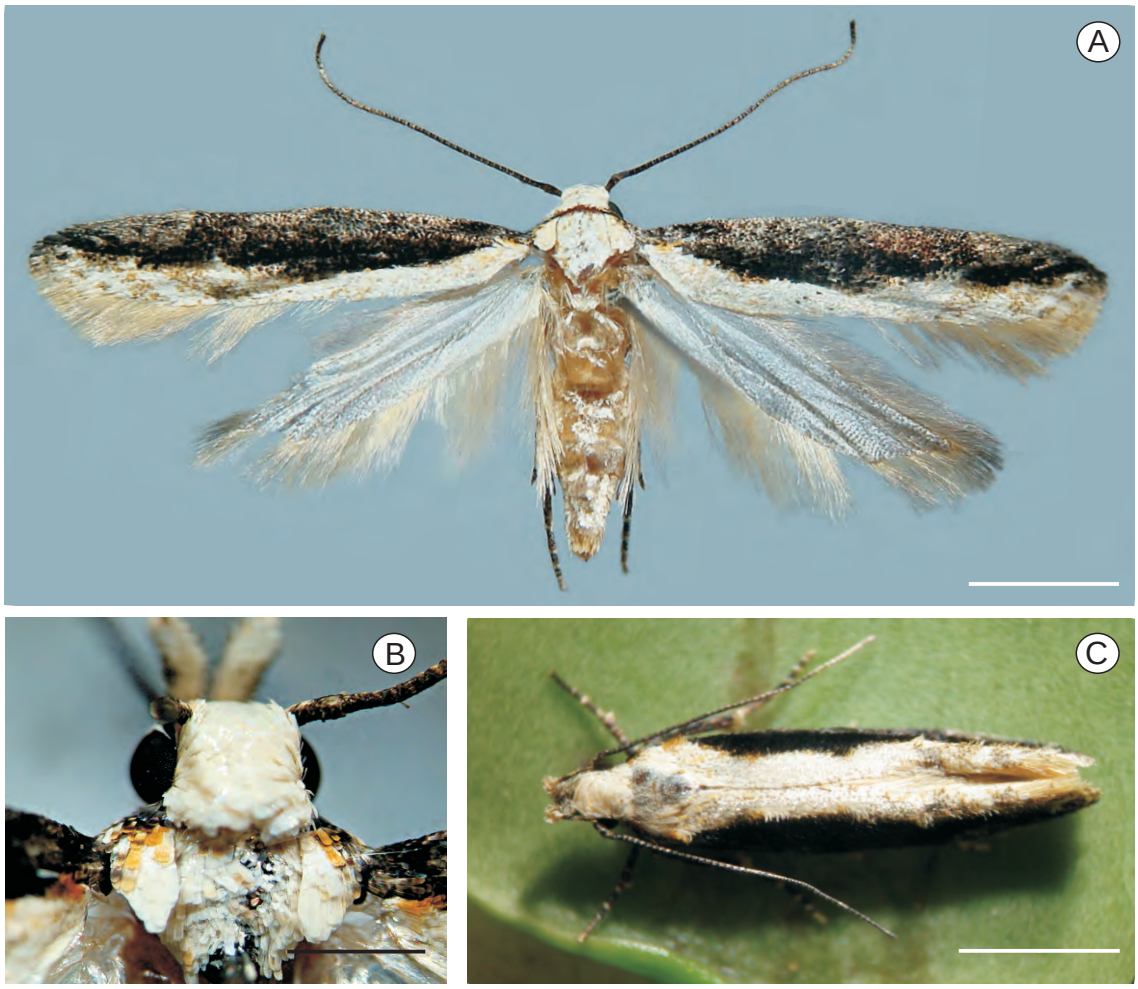
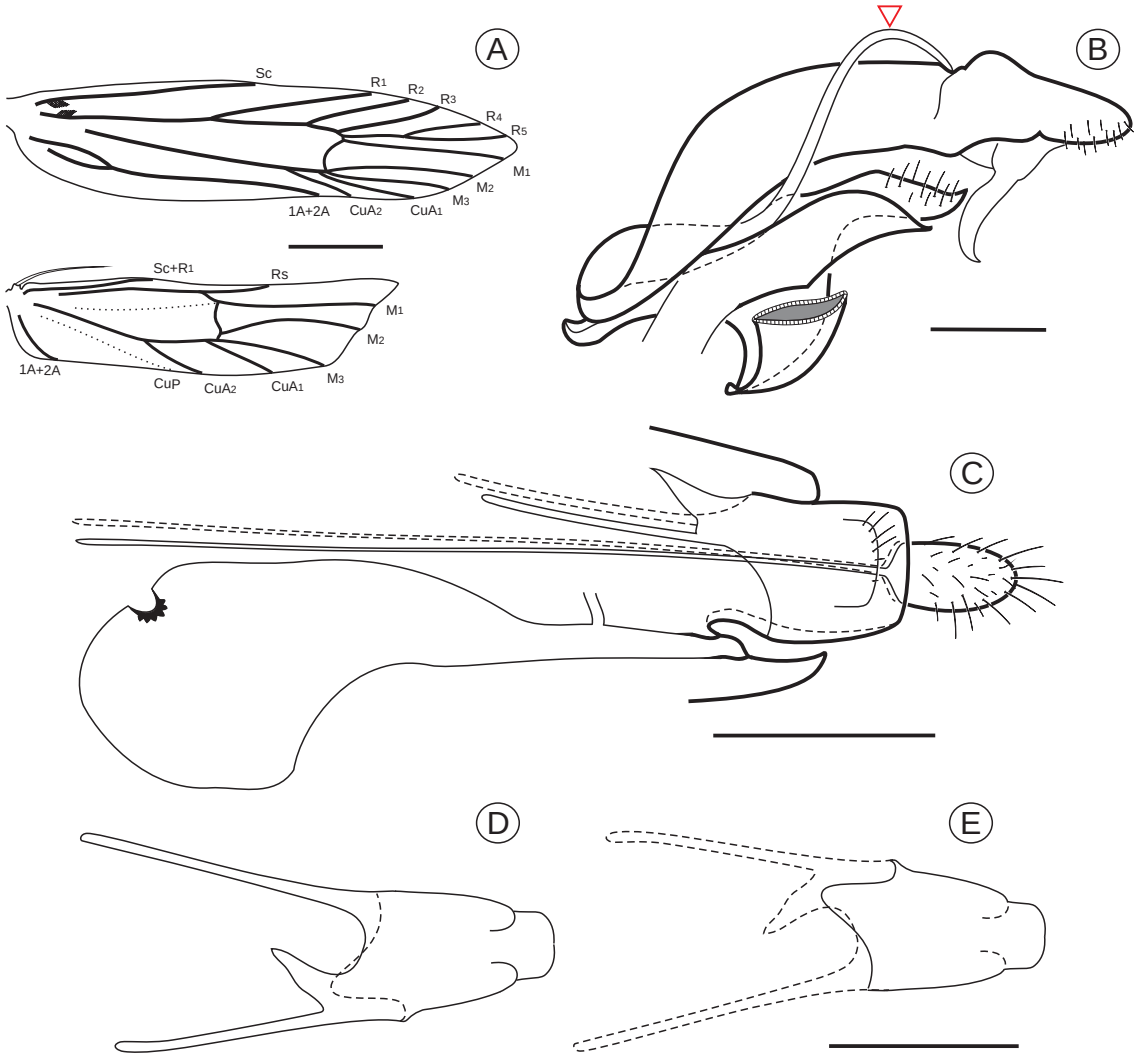


Fig. 1 - Luz et al



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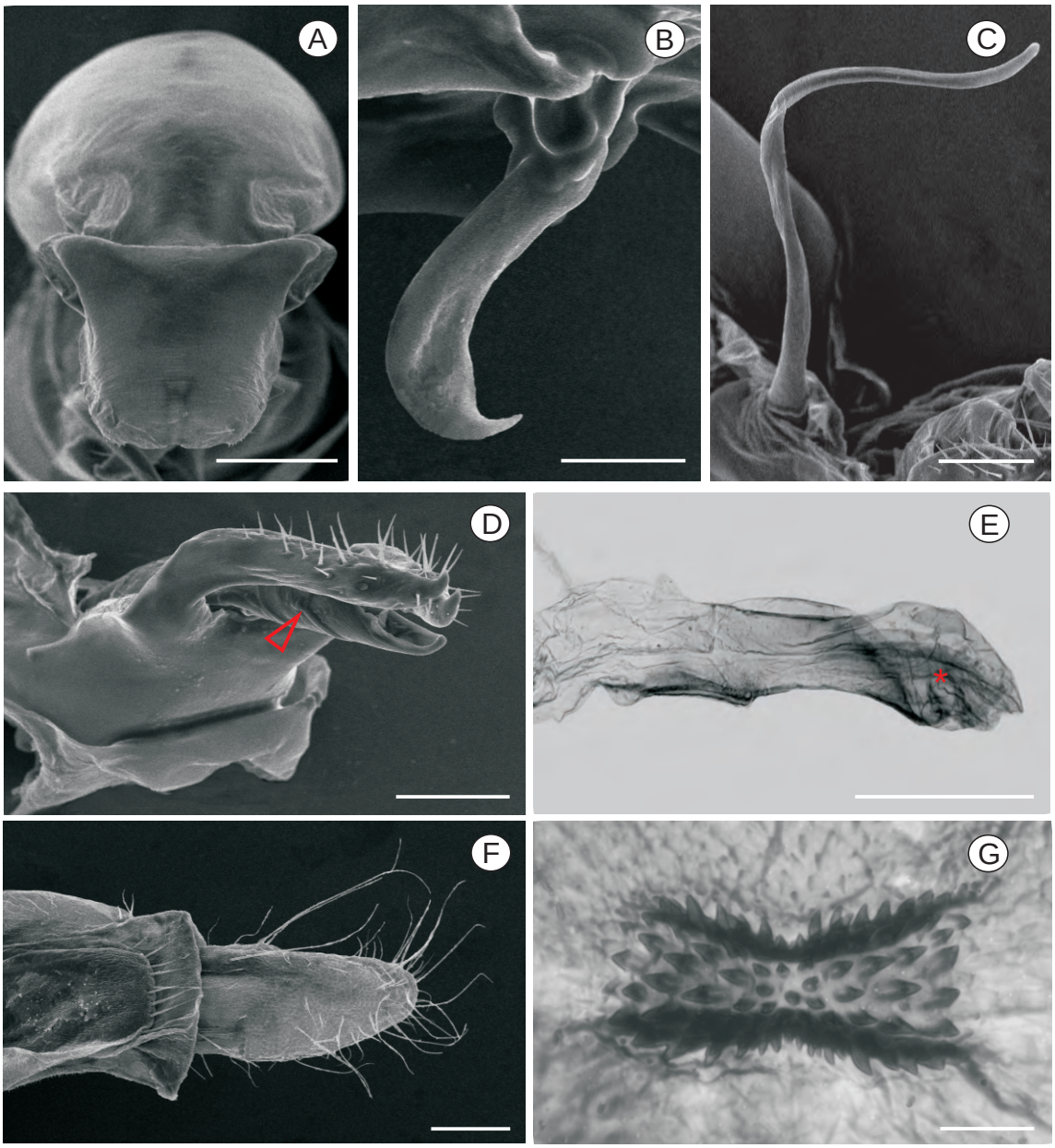

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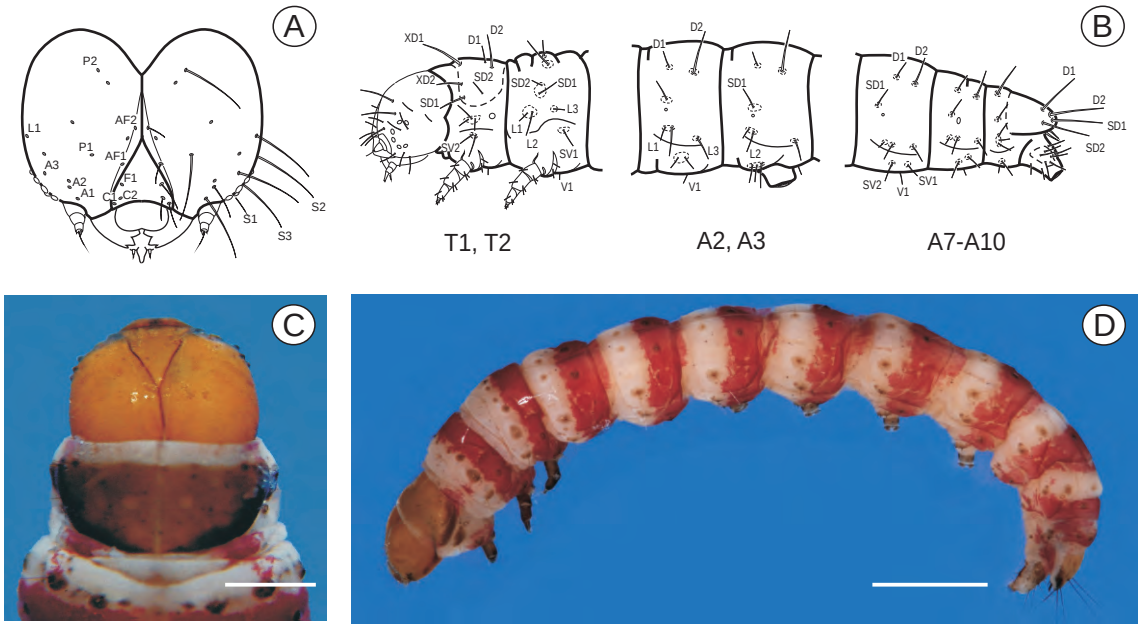

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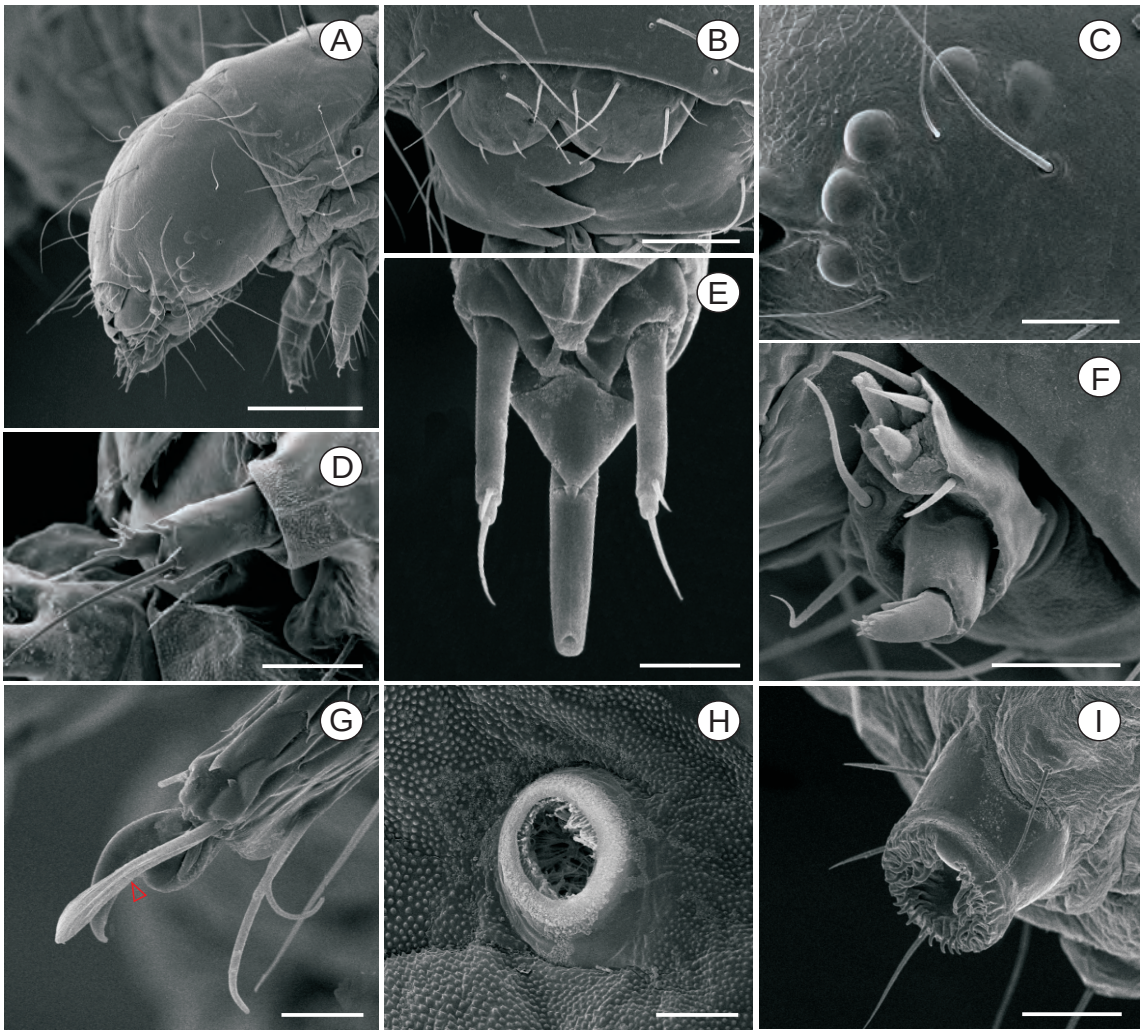

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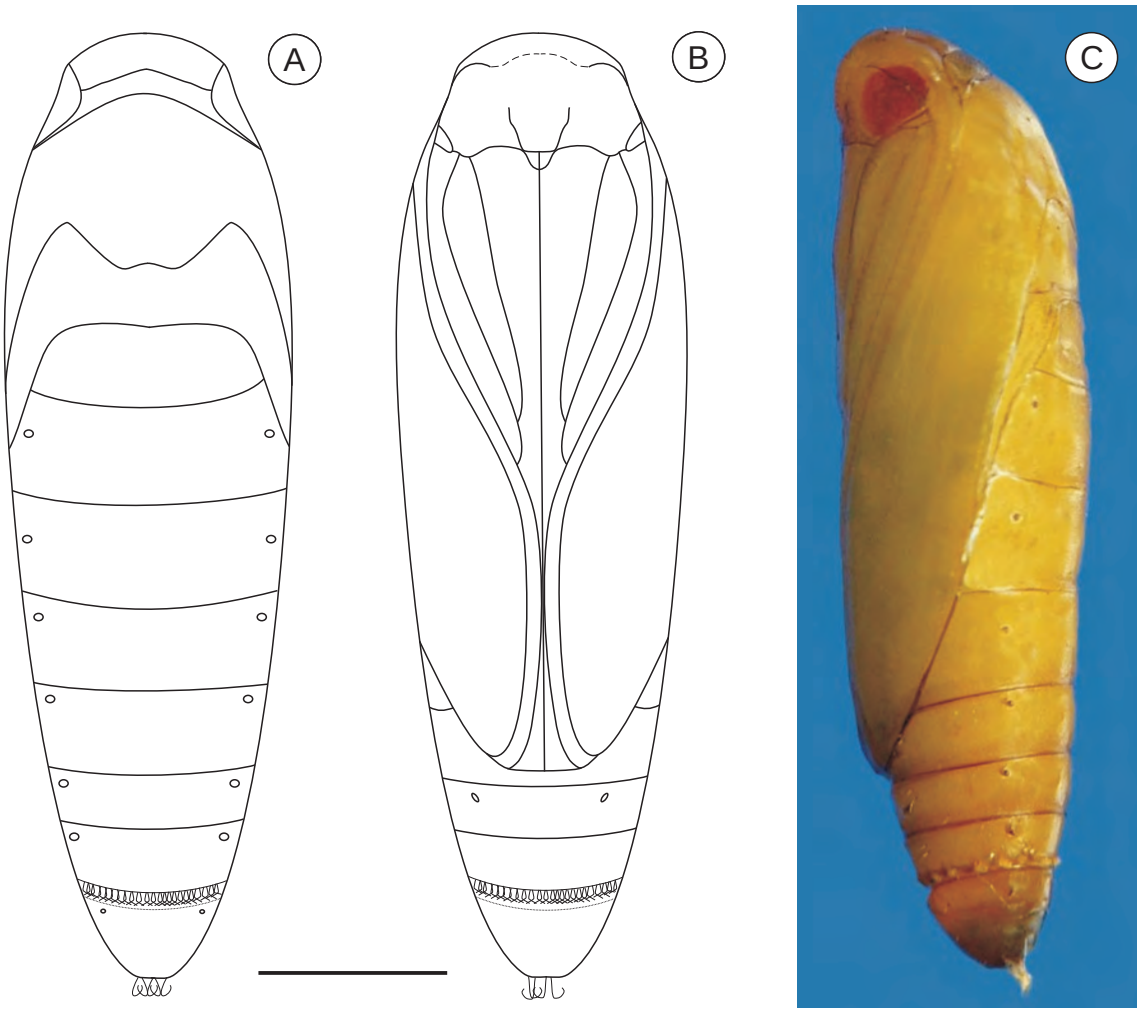

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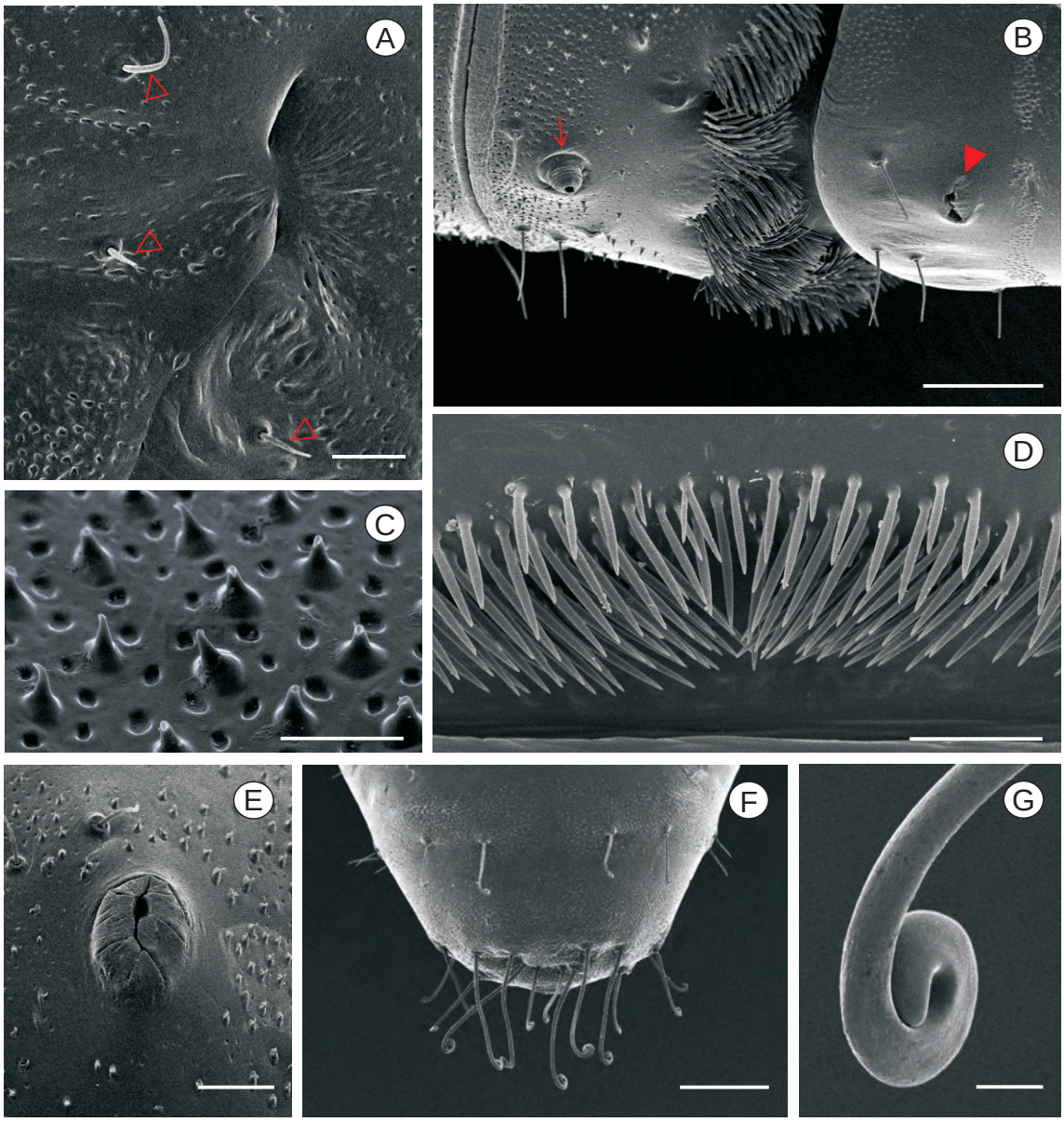

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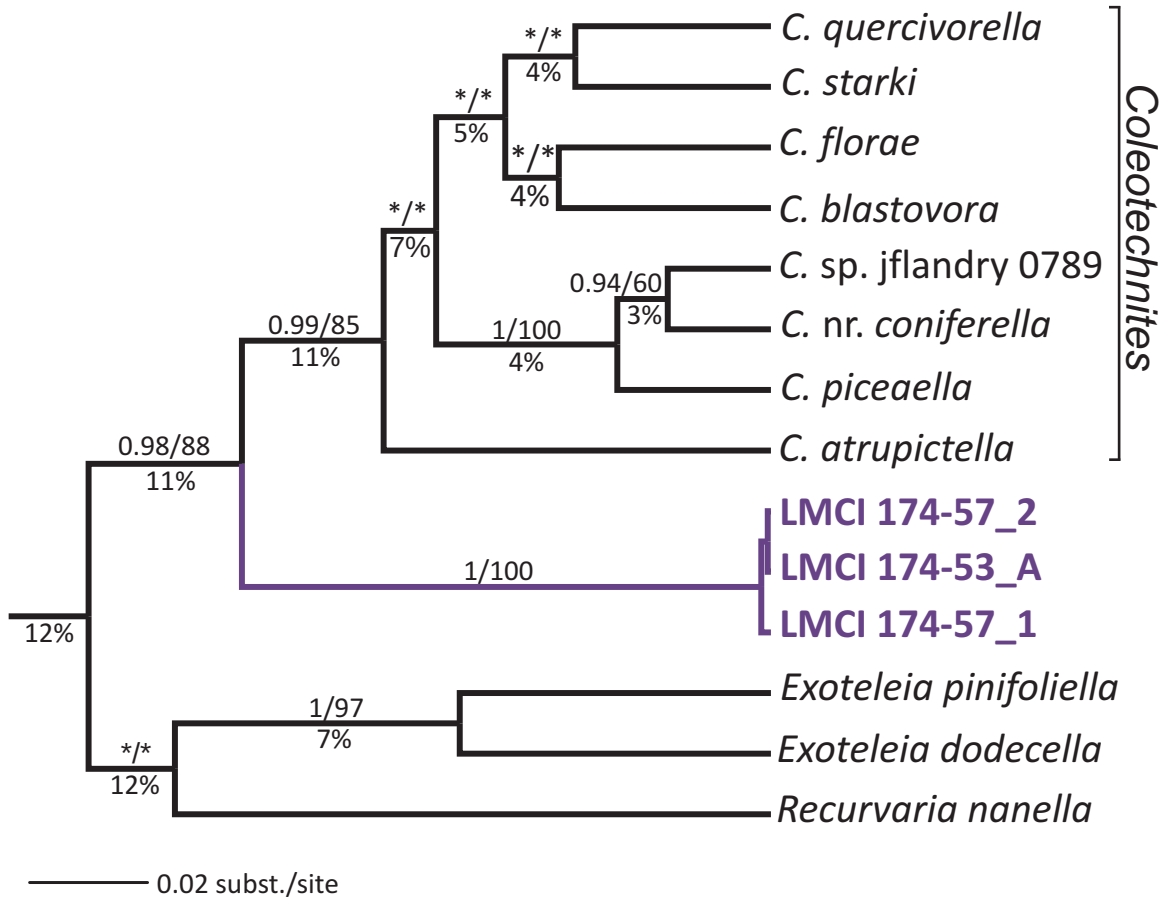

Fig. 8 - Luz et al

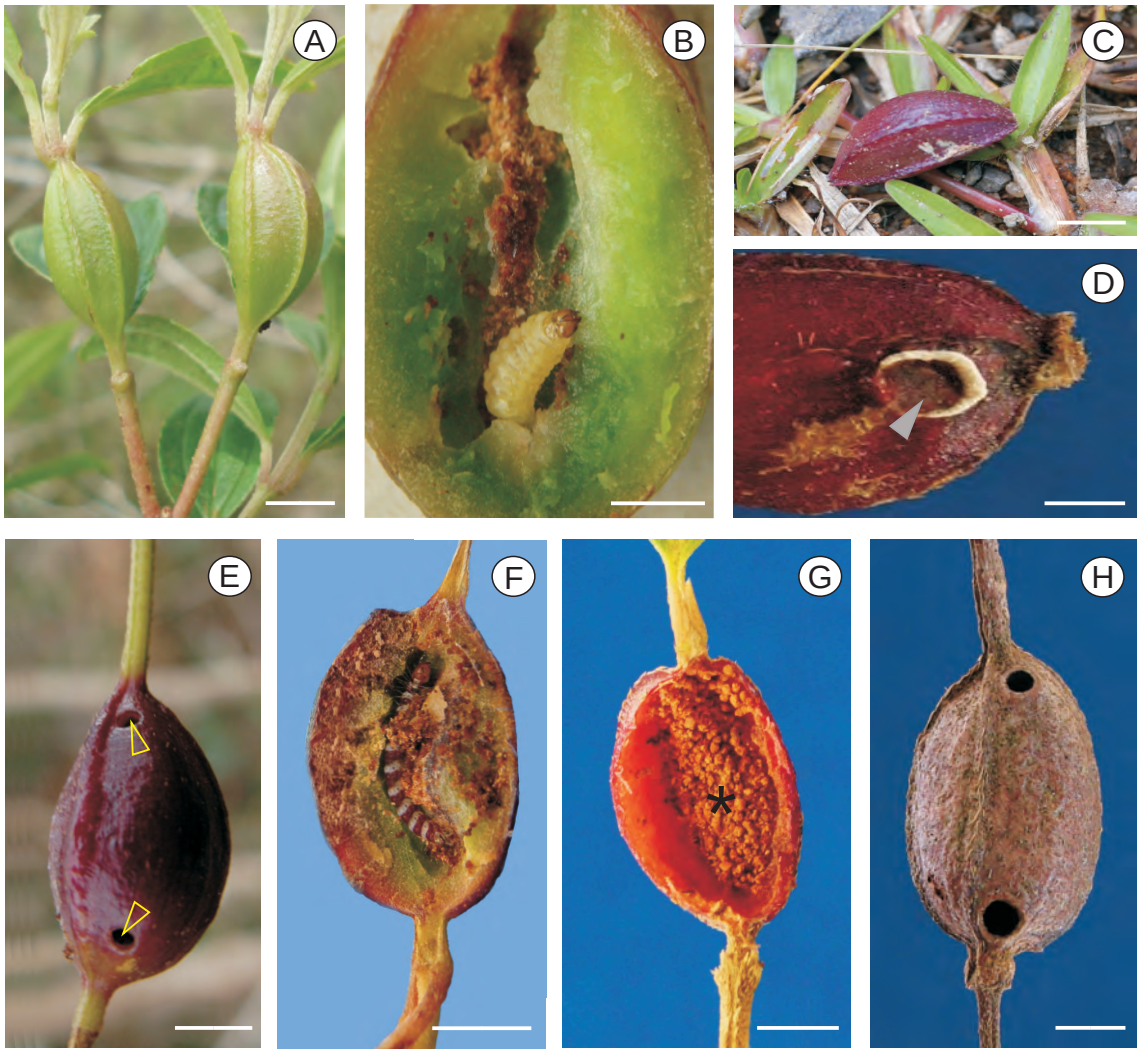

Fig. 9 - Luz et al

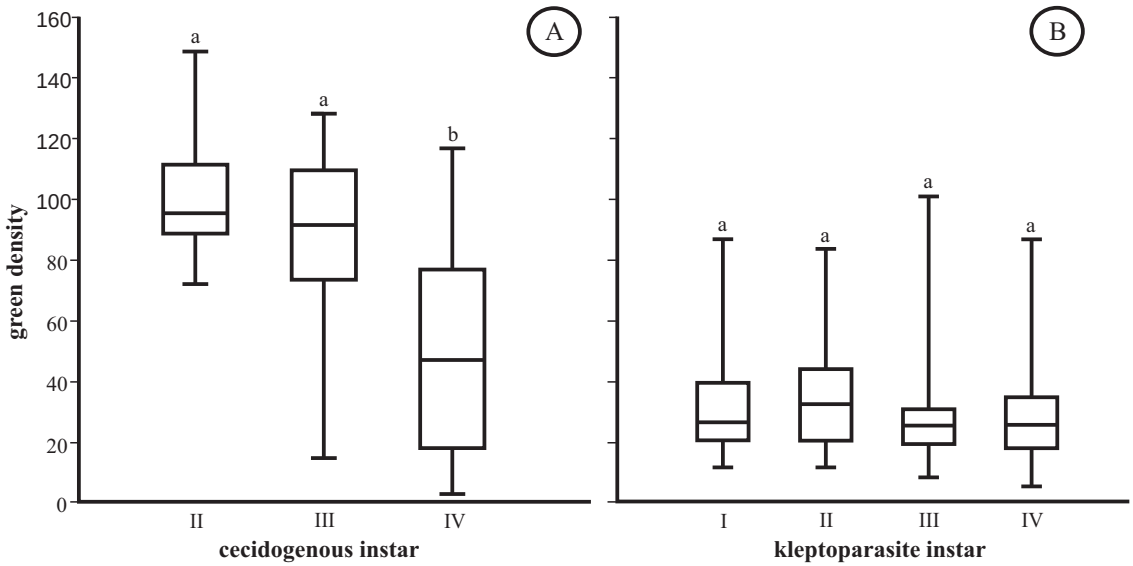

Fig. 10 - Luz et al

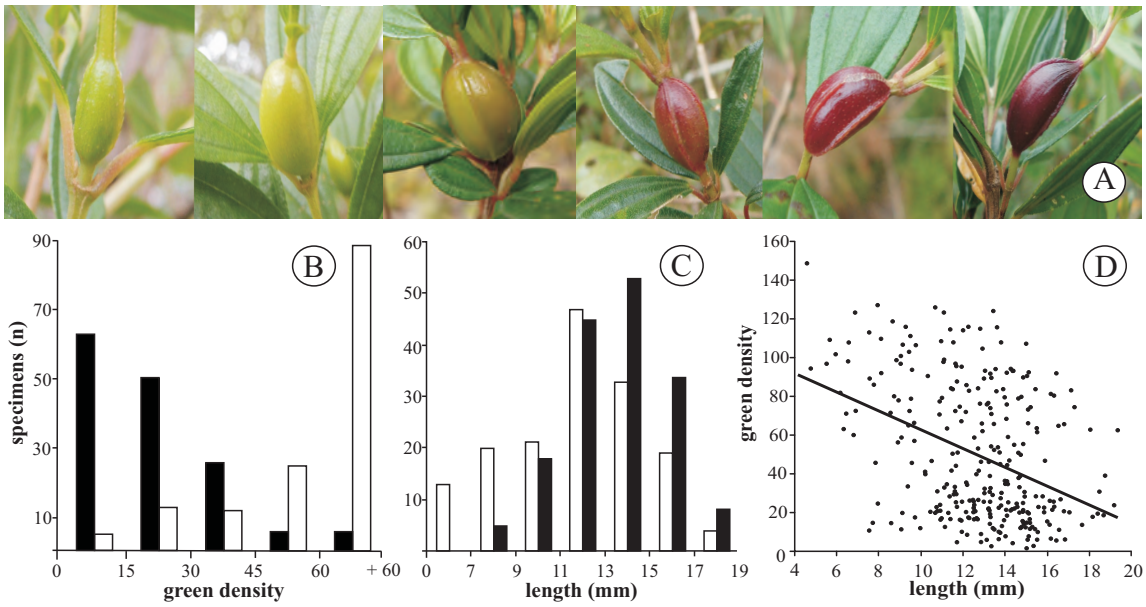

Fig. 11 - Luz et al

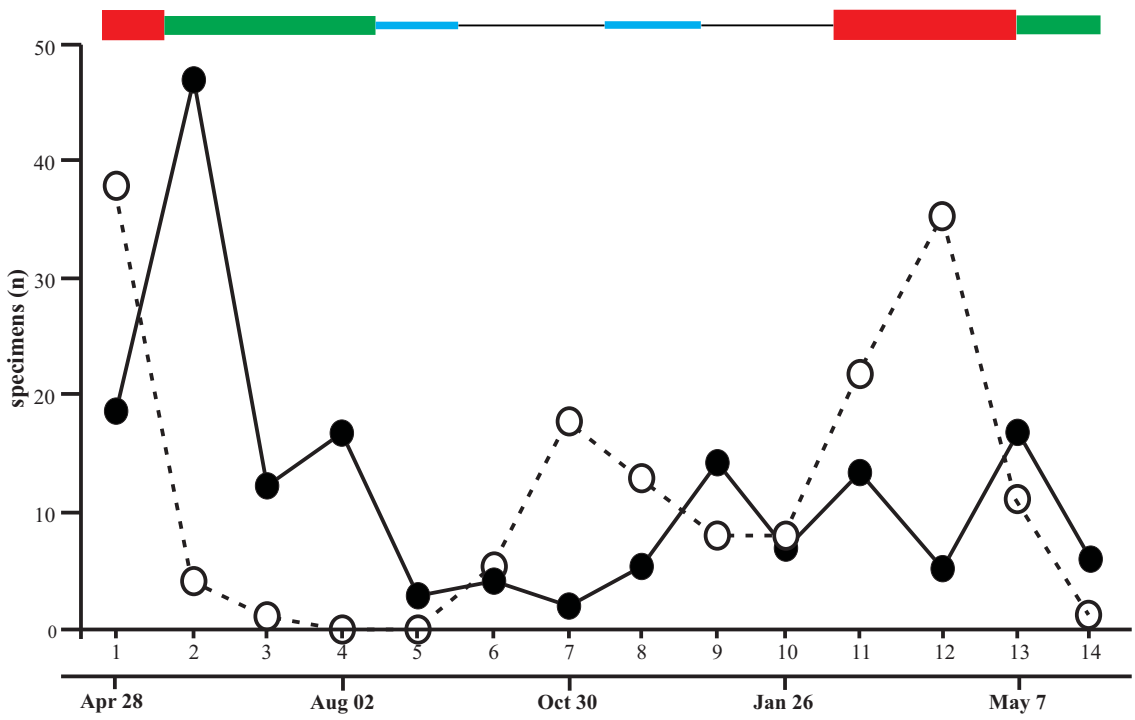

Fig. 12 - Luz et al

Supplementary Material

Figure 1S. Schematic representation of study area on GoogeEarth image. Trails are represented by yellow lines. Red dots correspond to plants belonging to the "destructive sampling" group. Numbers associated with white dots represent plants belonging to the "non-destructive sampling" group. Open arrow indicates CPCN Pró-Mata administration building office (29°28'51.7"S, 50°10'27.5"W; 925m). Lake is indicated by asterisk.

Table 1S. Variation in head capsule width of *Palaeomystella* 'A' an *Genus species* gen. n. sp. n. used to identify instars. Asterisk indicate measures were performed on head capsule exuvia.

Species	Instar	Head capsule (mm)			
		mean ± SE	range	growth rate	n
Palaeomystella **"A"**	I	0.091 ± 0.0035	0.095 – 0.084	-	3*
	II	0.220 ± 0.0061	0.190 – 0.260	2.41	10
	III	0.444 ± 0.0021	0.409 – 0.493	2.02	81
	IV	0.655 ± 0.0041	0.588 – 0.735	1.47	64
Genus species **gen. n. sp. n.**	I	0.228 ± 0.0071	0.168 – 0.283	-	25
	II	0.399 ± 0.0077	0.300 – 0.472	1.75	35
	III	0.608 ± 0.0100	0.504 – 0.693	1.52	28
	IV	0.870 ± 0,0063	0.745 – 0.945	1.43	55

Considerações Finais

As Melastomataceae possuem uma associação com lepidópteros indutores de galha, além das três espécies descritas nesse trabalho; ou seja, provavelmente muitas outras desconhecidas para ciência devem existir. Os resultados sugerem que o gênero ***Palleomystela*** apresenta uma alta diversidade, ainda desconhecida, com forte associação principalmente a o gênero ***Tibouchina***, mais diverso na região. As espécies aqui descritas diferem morfologicamente tanto no estágio imaturo quanto adultos. Suas galhas também são diferentes, bem como suas histórias de vida também.

A nova espécie que utiliza a galha induzida por uma espécie de ***Palleomystela*** galhadora em ***T. sellowiana***, pertence também a um novo gênero. Apresenta o hábito cleptoparasita, pois invade a galha, mata o indutor para desfrutar dos recursos produzidos por ele, que neste caso é a galha.

Inicialmente, acreditávamos que as galhas mudassem de colaração, na presença de outro organismo, levando em conta o efeito deste (conceito de fenótipo extendido). Porém, concluímos que a mudança de coloração nesta galha em ***T. sellowiana*** está relacionada com a idade da galha, mudando progressivamente de verde para violeta ao longo da ontogênese.

Por se tratar de um cleptoparasita, que preda o indutor, a interação relativa à variação na densidade populacional das espécies de ***Palleomystela*** (indutor) e desse segue um padrão similar ao ciclo predador-presa, já conhecido (Hassell 1978; Varley et al 1973).

O cleptoparasitismo até o momento não foi contextualizado no sistema de galhas em geral. Mani (1964) e Sugiura & Yamazaki (2009), por exemplo, ao revisarem as

guildas associadas às galhas não incluíram o cleptoparasitismo. Sendo assim, ao final dessa dissertação, adicionamos tal componente (Figura 1).

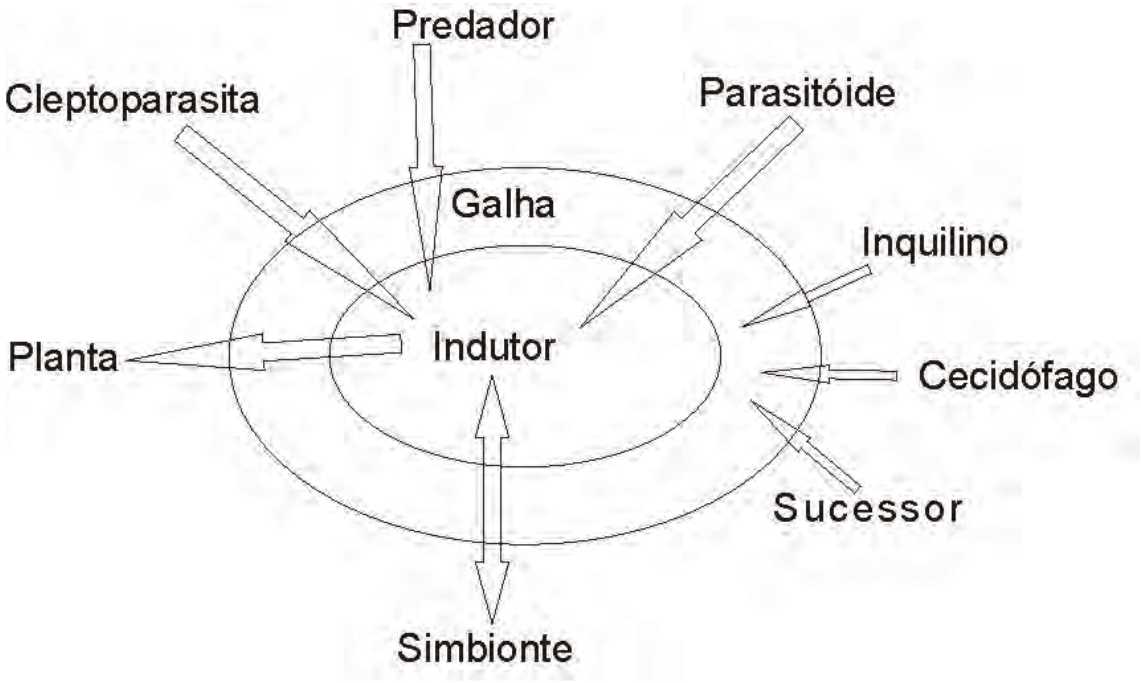

Figura 1. Guildas de organismos associados às galhas e aos indutores de galha em geral (modificada de Sugiura & Yamazaki 2009)

Na Tabela 1, trazemos uma compilação de dados da literatura mais resultados obtidos neste trabalho, que nos permitem diferenciar as três interações abordadas na dissertação.

Por fim, inferimos que as interações entre planta/ galhador/ terceiro nível trófico são muito complexas e pouco estudadas em nosso meio. Assim, muito se tem a descobrir nestes sistemas, desde a identidade destes organismos, sua história de vida até padrões complexos em comunidades.

Tabela 1 – Características importantes de cada interação que podem ser utilizadas para diferenciá-las.

traits	inquilinismo	cecidofagia	cleproparasitismo	source
Hábito Alimentar	São exclusivamente fitófagos	São exclusivamente fitófagos.	Apresentam hábitos de onívoria.	Caltagirone 1964; Noort et al 2007; Mound & Morris 2000.
Coexistência com o Indutor	Coexistem, se não houver modificação do tecido.	Coexistem, mas podem ser letais.	Não coexistem.	Sanver & Hawkins 2000; Myiatake et al 2000; Mound & Morris 2000.
Produção de Novos Tecidos	Estimula a produção de novos tecidos quando do mesmo grupo taxonômico, e quando de grupo diferente modifica o tecido.	Não modificam o tecido nem o fenótipo da galha	Não modificam o tecido nem o fenótipo da galha	Brooksand & Shorthouse 1997; Ronquist 1994; Noort et al 2007; Sugiura & Yamazaki 2009; Bono 2000; Presente estudo.
Relação de parentesco com o Indutor	Inquilinos têm relação filogenética próxima com o indutor	Cecidófagos não apresentam relação filogenética próxima ao indutor	Podem apresentar uma relação	Mani 1964; Sugiura & Yamazaki 2009. Presente estudo.
Motilidade	Sedentários	Alta	Baixa	Stone et al 2002; Sugiura & Yamazaki 2009; Presente estudo.

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