TAXONOMY, PHYLOGENY AND EVOLUTION OF EGG-POWDERING BEHAVIOR ASSOCIATED TRAITS IN *MOLOMEA* CHINA, 1827

(INSECTA: HEMIPTERA: CICADELLIDAE)

Beatriz Macharet Camisão de Vasconcelos

Dissertação de Mestrado apresentada ao Programa de Pós-graduação em Biodiversidade e Biologia Evolutiva, Instituto de Biologia, Universidade Federal do Rio de Janeiro, como parte dos requisitos necessários à obtenção do título de Mestre em Biodiversidade e Biologia Evolutiva.

Orientadora: Profa. Dra. Daniela M. Takiya

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"Nothing in Biology makes sense except in the light of Evolution"
Theodosius Dobzhansky, 1973

"What makes things baffling is their degree of complexity, not their sheer size…a star is simpler than an insect"
Martin Rees, 1999

"Science never pursues the illusory aim of making its answers final, or even probable. Its advance is, rather, towards the infinite yet attainable aim of ever discovering new, deeper, and more general problems, and of subjecting its ever tentative answers to ever renewed and ever more rigorous tests. The wrong view of science betrays itself in the craving to be right; for it is not his possession *of knowledge, of irrefutable truth, that makes the man of science, but his persistent and recklessly critical* quest *for truth"*
Karl Popper, 1959

ABSTRACT

TAXONOMY, PHYLOGENY AND EVOLUTION OF EGG-POWDERING BEHAVIOR ASSOCIATED TRAITS IN *MOLOMEA* CHINA, 1827 (INSECTA: HEMIPTERA: CICADELLIDAE)

Beatriz Macharet Camisão de Vasconcelos

Advisor: Dr. Daniela M. Takiya

The twenty three known species of *Molomea* China are recorded from Argentina, Brazil, Ecuador, Paraguay and Peru. The identification of the species and the only taxonomic key to the genus are based on characters of the male, and the female terminalia was never studied in detail. Females of *Molomea* cover the incisions made in the plant tissue for oviposition with brochosomes, and this behavior is associated with two dimorphic features that are not always found in species among the genus. The aim of this study was to propose and discuss phylogenetic hypothesis for the species of *Molomea* based on morphological and molecular data, to describe the female terminalia, to provide a taxonomic key for males and females and also to discuss the patterns of gains and losses of the dimorphic characters related to the egg-powdering behavior in *Molomea*. A new species of *Molomea* from Rio de Janeiro, Brazil, is described and illustrated. Two females of *Molomea* that probably belong to two new species of the genus are described and illustrated. The type specimens of *M. alternata,* and *M. laminata* were described and illustrated, as the syntypes of *M. vermiculata,* which was found to belong to a different genus. The males of *M. guttuata* and *M. infulata*, known only from female types, are described and illustrated. A polymorphism of the male genitalia was illustrated and discussed. A comparative study of the female terminalia is showed. Eighty-three morphological characters were coded and the parsimony and Bayesian analyses found the genus monophyletic. The molecular analyses of four genes (16S, COI, COII and H3) individually and combined with maximum likelihood, and Bayesian inference obtained similar results, however the parsimony analyses of the same datasets obtained different topologies. Neither of the tree approaches supported

the monophyletism of *Molomea*. The morphological and molecular datasets were also analyzed together with parsimony, maximum likelihood and Bayesian inference, what helped to solve the relationships of some internal branches. The efficiency of the molecular data is discussed. The two dimorphic characters associated with the egg-powdering behavior were optimized on the most parsimonious trees, and it was found that the region with distinctly concentrate setae on female forewing originated at least seven times inside the genus, while the elongate setae on female hindtibia was a characteristic already found in the ancestral of the genus that was lost independently three times inside *Molomea*. A S-DIVA analysis was performed and it was found that the losses and gains of these two dimorphic characters in *Molomea* cannot be related to shifts to major phytogeographical regions.

RESUMO

TAXONOMIA, FILOGENIA E EVOLUÇÃO DOS CARACTERES ASSOCIADOS AO COMPORTAMENTO DE OVIPOSIÇÃO EM *MOLOMEA* CHINA, 1927 (INSECTA: HEMIPTERA: CICADELLIDAE)

Beatriz Macharet Camisão de Vasconcelos

Orientadora: Dr. Daniela M. Takiya

As 23 espécies de *Molomea* China, 1927 estão distribuídas na Argentina, Brasil, Equador, Paraguai e Peru. A identificação das espécies e a única chave taxonômica para o gênero são baseadas em caracteres dos machos, sendo a terminália feminina nunca estudada com detalhes. Fêmeas de *Molomea* cobrema s incisões feitas no tecido vegetal para oviposição com brocossomos, e esse comportamento está associado a dois caracteres dimórficos que não estão presentes em todas as espécies do gênero. O objetivo do estudo foi propor e discutir hipóteses de relação filogenética para as espécies de *Molomea* com base em dados morfológicos e moleculares, descrever a terminália feminina, fornecer uma chave taxonômica para machos e fêmeas, além de discutir os padrões de ganho e perda dos caracteres dimórficos ligados ao comportamento de oviposição em *Molomea.* Uma nova espécie de *Molomea* do Rio de Janeiro, Brasil, é descrita e ilustrada. Duas fêmeas de *Molomea* que provavelmente pertencem a duas novas espécies do gênero são descritas e ilustradas. Os tipos de *M. alternata,M. laminata* e *M. vermiculata* são descritos e ilustrados. Os machos de *M. guttulata* e *M. infulata,* antes conhecidas apenas por fêmeas, são descritos e ilustrados. Um polimorfismo da genitália masculina é ilustrado e discutido. Um estudo comparativo da terminália feminina é apresentado. Oitenta e três caracteres morfológicos foram codificados e as análises de parcimônia e inferência bayesiana recuperaram o gênero monofilético. As análises de quatro genes (16S, COI, COII e H3) individualmente e combinados com máxima verossimilhança e inferência bayesiana obtiveram resultados bastante semelhantes, no entanto, as análises moleculares de parcimônia obtiveram topologias diferentes. Nenhum dos três métodos recuperou o

monofiletismo de *Molomea*. Os dados morfológicos e moleculares foram analisados em conjunto com parcimônia, verossimilhança e inferência bayesiana, o que ajudou a resolver relacionamentos internos em alguns ramos. A eficiência dos dados moleculares é discutida. Os dois caracteres dimórficos associados ao comportamento de oviposição foram otimizados nas árvores mais parcimoniosas da morfologia e foi observado que a região com cerdas distintamente concentradas nas asas das fêmeas surgiu pelo menos sete vezes dentro do gênero, enquanto que as cerdas alongadas nas tíbias posteriores das fêmeas já estavam presentes no ancestral do gênero e foram perdidas independentemente três vezes dentro de *Molomea*. Uma análise com S-DIVA foi feita e observou-se que os ganhos e perdas dos dois caracteres dimórficos não podem ser associados a mudanças de regiões fitogeográficas.

SUMARY

LIST OF ILLUSTRATIONS

LIST OF ABREVIATIONS

ACRONYMS OF INSTITUTIONS:

AMNH: American Museum of Natural History, New York, USA.

BMNH: The Natural History Museum, London, England.

CAS: California Academy of Sciences, San Francisco, USA.

CMNH: Carnegie Museum of Natural History, Pittsburgh, USA.

CNC: Canadian National Collection of Insects, Arachnids and Nematodes, Ottawa, USA.

DZRJ: Departamento de Zoologia, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil.

DZUP: Coleção Pe. Jesus Santiago Moure, Universidade Federal do Paraná, Curitiba, Brazil.

FSMC: Florida Museum of Natural History, Gainesville, USA.

INHS: Illinois Natural History Survey, Champaign, USA.

IFNU: Ivan Franko National University, Lviv, Ukraine.

MMBC: Moravian Museum, Brno, Czech Republic.

MNHP: Muséum national d'Histoire naturelle, Paris, France.

MNRJ: Museu Nacional, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil.

MPEG: Museu Paraense Emílio Goeldi, Belém, Brazil.

MZSP: Museu de Zoologia, Universidade de São Paulo, São Paulo, Brazil.

NCSU: North Carolina State University, Raleigh, USA.

NMW: Naturhistorisches Museum Wien, Viena, Austria.

OSU: Ohio State University, Columbus, USA.

SEMC: Snow Entomological Museum, Lawrence, USA.

SMF: Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt, Germany.

UFRRJ: Universidade Federal Rural do Rio de Janeiro, Seropédica, Brazil.

UKL: University of Kentucky, Lexington.

USNM: United States National Museum, Washington D.C., USA.

ZMHB: Museum für Naturkunde der Humboldt-Universität, Berlin, Germany.

OTHER ABREVIATIONS:

CI: Consistency index.

L: Length of the tree.

RI: Retention index.

LIST OF TABLES

1. INTRODUCTION

In the last five decades, taxonomy has witnessed a great revolution, which started with Hennig's work (1966) and incorporated since then many new technologies. A few approaches to the theoretical basis and methodology of systematics have emerged, but only the phylogenetic approach succeeded in coupling a biological theory with a robust method (Bernardi, 1997 *in* Amorim, 2002; Simpson & Cracraft, 1995). Currently the world is facing a biodiversity crisis, which has uplifted systematics to one of today's most important sciences (Simpson & Cracraft, 1995), due to our great need to know the species diversity before it is lost. Since the publication of *Systema naturae* (Linnaeus, 1735), many species have been described and named based on the binomial system, but the task of knowing the true diversity of the world is far from being complete. There are approximately 1 million species of insects described so far, but this number may reach 10 or 30 million species according to some estimates (Erwin, 1982; 1983), which demonstrate how poor is our understanding of these animals.

Hemiptera *sensu* lato is one of the five megadiverse orders of insects and the largest order of non-holometabolous insects, including approximately 89,000 species around the world (Rafael, 2012). This number, however, is probably underestimated, and the true diversity of the order may be more than 180,000 species (Hodkinson & Casson 1991). The oldest known fossil of the order is from the Permian (290-250 m.y.a.) and the great diversity of the group may be related to the radiation of the Angiosperm plants on the Mesozoic period, because two entire suborders are mostly phytophagous (Grimaldi & Engel, 2005). The monophyly of the group is supported by molecular data (Cryan & Urban, 2011) and also by three main morphological features: the loss of maxillary and labial palps; the structure of the sucking beak, with mandibular and maxillary stylets lodged in a long labial rostrum; and forewings with the anterior axillary foldline forming a fork (Kirstensen, 1991; Yoshizawa & Saigusa, 2001).

Hemiptera comprises four suborders, Heteroptera, Coleorrhyncha, Sternorrhyncha and Auchenorrhyncha (Cryan & Urban, 2011). The latter includes more than 40,000 species of phytophagous insects and its monophyly has been debated by several authors (Hamilton, 1981; Kirstensen, 1991; Campbell *et al.*, 1995; von Dohlen & Moran, 1995; Sorensen *et al.*, 1995). However, recent studies have recovered the

monophyly of the suborder based on morphological data and a larger molecular dataset (Yoshizawa & Saigusa, 2001; Cryan & Urban, 2011). Synapomorphies supporting the group are the complex tymbal acoustic system located at the base of the abdomen, the aristate antennal flagellum, and the reduction of the proximal median plate of forewings (Grimaldi & Engel, 2005; Yoshizawa & Saigusa, 2001).

It is traditionally divided in two infraorders, Fulgoromorpha and Cicadomorpha. The former comprises only one superfamily, Fulgoroidea, with 20 families and around 9,000 species (Wilson, 2005). Cicadomorpha comprises around 35,000 species and is divided in 3 superfamilies, Cercopoidea, Cicadoidea and Membracoidea (Dietrich, 2005). Membracoidea comprises five families, including Cicadellidae, which includes more than 22,000 species distributed all over the world, divided in approximately 1,000 genera (Ross, 1957; Oman *et al.*, 1990; Forero, 2008). Cicadellidae is thus the largest family of Hemiptera and one of the ten largest families of insects (Ross, 1957 *apud* Takiya, 2007). Species included in this family can be distinguished by the following characters (Deitz *et al.*, 1993): mesothorax with the anepisternum and the katepisternum separated by a suture, pronotum not reaching scutellar suture, scutellum not strongly produced dorsally, and mesepisternum without a hook-shaped process dorsally.

Cicadellidae currently comprises 43 subfamilies (Dietrich, 2006), including Cicadellinae, which corresponds to approximately 9% of the whole diversity of Cicadellidae with 350 genera and approximately 3,100 species (Mejdalani, 1998; Dietrich, 2006). It is one of the most diverse subfamilies of Neotropical forests (Mejdalani, 1998, Dietrich & Wallner, 2002), and its members can be distinguished by the following features (Young, 1968): ocelli on crown, usually much closer to the posterior margin; proepisternum exposed; frontogenal sutures almost always extending over crown and reaching ocelli; body usually not depressed dorsoventrally; forewings with external margin of the inner apical cell parallel to the longitudinal axis of the wing; and hindtibiae with four regular rows of well-developed macrosetae. The size of specimens can vary from 3 mm to 22 mm, and species can be very colorful (Mejdalani, 1998).

All Cicadellinae feed preferentially on xylematic fluid and therefore are potencial vectors of phytopathogens transmitted through the sap, such as the bacterium *Xylella fastidiosa*, responsible for many diseases that affect economically important crops, such as grapevines, citrus, alfalfa, coffee, almond, peach, and some ornamental plants (Redak *et al.*, 2004). Therefore, the study of the evolution of the genera of this

group is very important not only from a theoretical point of view, but also as a contribution to future studies of pest management.

Cicadellinae includes two tribes, Cicadellini and Proconiini (Young, 1968, 1977). The former comprises around 250 genera and 2,000 species found in all zoogeographical regions, with higher diversity in Neotropical areas (Mejdalani, 1998; Takiya & Cavichioli, 2005). Proconiini comprises 56 genera and around 360 species restricted to the New World (Young, 1968; Cavichioli & Sakakibara, 1989; Godoy, 2005; Rakitov & Godoy, 2005; Carvalho *et al*., 2011). The only phylogenetical hypothesis for the Cicadellinae was proposed by Takiya (2007) based on morphological and molecular data, but it was never published. In this study, Proconiini was not recovered as a monophyletic grouping and seems to be divided in two monophyletic groups named in unpublished thesis as the "true" Proconiini, sister to all remainder Cicadellinae and the Oncometopiini, related to a paraphyletic Cicadellini.

Placed in Oncometopiini (*sensu* Takiya, 2007) is the genus *Molomea* China, 1927. It is similar to *Oncometopia* Stål, 1869 and *Tapajosa* Melichar, 1924 (Young, 1968) and can be distinguished from those by the frons with distinct muscular impressions, male pygofer more projected posteriorly, and subgenital plates extremely short, not attaining midlength of pygofer (Young, 1968). *Molomea fatalis* was the last species described for the genus (Bonfils & Perthuis, 1992), which now comprises 23 species recorded from Argentina, Brazil, Ecuador, Paraguay and Peru (Young, 1968; Bonfils & Perthuis, 1992).

The specific identification and the sole taxonomic key available for the genus are based exclusively on characters of the male genitalia. Male genitalia structures were illustrated with detail by Young (1968) in his revision of the Proconiini tribe for all the species known at that point, except six: *M. guttulata* (Melichar, 1925) and *M. infulata* (Melichar, 1925), known only from female holotypes; *M. novarae* Schröder, 1959 and *M. zikani* Schröder, 1960, which had the aedeagus illustrated on their original descriptions; and *M. laminata* (Signoret, 1855) and *M. vermiculata* (Signoret, 1855), whose types were not studied by the author. Based on the male genitalia, Young (1968) pointed out that *M. alternata*, *M. lineiceps*, *M. novarae*, and *M. zikani* formed a difficult group to identify specifically.

On the other hand, the shape of the female abdominal sternite VII was described and illustrated for only eight species, and the internal female terminalia was never thoroughly studied. Females have been associated to conspecific males based on color

pattern (which is rarely dimorphic in Cicadellinae) and/or based on the locality where it was collected. Since two species are known only by the females, it is highly important to find morphological characters in the female terminalia that are useful for taxonomic identification.

There has been no attempt to propose a phylogenetic hypothesis for the genus until now. Takiya (2007) included four species of *Molomea* in a phylogenetic study of the tribe using morphology and molecular data, but the sister group of the genus was not strongly recoveres. Most of the trees obtained in this study show *Molomea* in a politomy with *Tretogonia* spp., and *Tapajosa rubromarginata*.

Fourteen genera of the Proconiini, including *Molomea*, cover the incisions made in the plant tissue for oviposition with brochosomes (Rakitov, 2004), proteinaceous particles produced by specialized regions of the Malpighian tubules (Day & Briggs 1958). The majority of the Cicadellidae can produce brochosomes, which are spherical and secreted after the moult to recover the insect body and probably help to protect the animal against the excess of water (Rakitov 2004). Differently from integument brochosomes, egg-brochosomes are elongate particles and its use in oviposition seems to be a specialized behavior of only a few species (Rakitov, 2004). The most recent phylogenetic study of the group (Takiya, 2007) found that this specialization seems to have appeared only once, but it was lost independently at least five times. Females that are ready to oviposit secret a brochosome suspension released from the anus, which is transferred to the forewings with the hindlegs. Droplets of the suspension dry and form a pair of hard pellets (Rakitov, 2004; Hix, 2001). Females then powder the oviposition site by scraping the pellets with the hindlegs (Hix, 2001). This behavior is called egg-powdering behavior (Rakitov, 2004), and is associated with two dimorphic features: presence of areas with modified setae on the forewings of females to facilitate the anchoring of the brochosomes and elongate setae on the hindtibiae of the females for the powdering of eggs (Rakitov, 2004). Nevertheless, these two modifications are not always found in species that have this behavior and there are species that no longer behave like that, but still have the morphological features associated to it (Rakitov 2004). Until now this behavior was never observed in any species of *Molomea*, as in the majority of the species of the other thirteen genera. However, it can be assumed that the powdering of eggs with brochosomes is performed by many species of *Molomea* since many females individuals deposited in collections have brochosome pellets over their forewings. The behavior is believed to be ancestral in the genus (Takiya, 2007), but the

morphological features associated with it are very variable among the species of *Molomea* (Rakitov, 2004). Studying the evolution of those characters can contribute to the understanding of patterns of loss and acquisition of complex morphological features.

2. GOALS

This study aims to contribute to the general knowledge of the diversity and evolution of the genus *Molomea.* Specific goals are to:

1. Describe new species and previously unknown males of *Molomea*;
2. Describe the female terminalia of species of the genus;
3. Describe morphological characters useful for the phylogenetic reconstruction of the genus;
4. Propose phylogenetic relationship hypotheses based on morphological and molecular data;
5. Test the monophyly of the genus;
6. Elucidate the evolution of the morphological features associated with the egg-powdering behavior inside *Molomea*.

3. MATERIAL & METHODS

3.1. TAXON SAMPLING

Approximately 400 specimens of twenty-three species of *Molomea*, including three new species were analyzed in this study. Material studied was collected during expeditions promoted by Laboratório de Entomologia, Instituto de Biologia, UFRJ, and also by loans from the following twenty collections (Table 1):

Representatives of only three species of *Molomea* were not available for study in the laboratory, namely *M. laminata* (Signoret, 1855), *M. vermiculata* (Signoret, 1855), and *M. zikani* Schröder, 1960, and those were examined during a visit to the collections SMF and ZMHB (Table 2).

Specimens of ten *Molomea* species were available for DNA extraction and amplification (Table 2). The material was recently collected and preserved in ethyl alcohol 93-100%.

Outgroups for the phylogenetic analyses were selected based on the Cicadellinae phylogeny (Takiya, 2007), and include representatives of four genera of Oncometopiini, one Proconiini, and one of Cicadellini for the morphological study (Table 2) and three representatives of each group were selected for the molecular study (Table 3).

Table 1: Acronym, institution and country of the collections from which the material was borrowed.

Acronym	Collection	City and Country
AMNH	American Museum of Natural History	New York, USA.
BMNH	The Natural History Museum	London, England
CAS	California Academy of Sciences	San Francisco, USA
CMNH	Carnegie Museum of Natural History	Pittsburgh, USA
CNC	Canadian National Collection of Insects, Arachnids and Nematodes	Ottawa, USA
DZRJ	Departamento de Zoologia, Universidade Federal do Rio de Janeiro	Rio de Janeiro, Brazil
DZUP	Coleção Pe. Jesus Santiago Moure, Universidade Federal do Paraná	Curitiba, Brazil
FSMC	Florida Museum of Natural History	Gainesville, USA
INHS	Illinois Natural History Survey	Champaign, USA
MNHP	Muséum national d'Histoire naturelle,	Paris, France
MNRJ	Museu Nacional, Universidade do Rio de Janeiro	Rio de Janeiro, Brazil
MPEG	Museu Paraense Emílio Goeldi	Belém, Brazil
MZSP	Museu de Zoologia, Universidade de São Paulo	São Paulo, Brazil
NCSU	North Carolina State University	Raleigh, USA
NMW	Naturhistorisches Museum Wien	Viena, Austria
OSU	Ohio State University	Columbus, USA
SEMC	Snow Entomological Museum	Lawrence, USA
UFRRJ	Universidade Federal Rural do Rio de Janeiro	Seropédica, Brazil
UKL	University of Kentucky	Lexington, USA
USNM	United States National Museum	Washington D.C., USA

3.2. CHARACTERS FOR PHYLOGENETIC ANALYSES

3.2.1. MORPHOLOGICAL CHARACTERS

Stereoscopic and optical microscopes were used for observation, illustration, and photography of the specimens. Terminology employed in this study for the morphology of the head follows Hamilton (1981), and for the rest of the body follows Young (1968, 1971) and Mejdalani (1998). Terminology for female terminalia follows Hill (1970) and Zahniser & Dietrich (2006), and for the chaetotaxy follows Rakitov (1997). Techniques for preparation of genital structures were described by Oman (1949). The dissected parts are stored in microvials with glycerin attached to the insect's pin.

Characters were selected from the external morphology, and male and female terminalia. Primary homology hypotheses (de Pinna, 1991) were proposed by the construction of a data matrix using the software Mesquite 2.7.5 (Maddison & Maddison 2009). Characters were coded after careful examination of specimens, except characters of male genitalia of *M. zikani*, which were coded based on bibliography, since the type specimen examined was only available for observation of the external morphology. Character construction follows a reductive approach to avoid concealing homoplasies (Wilkinson, 1995).

3.2.2. MOLECULAR CHARACTERS

Four molecular markers were used in this study, the nuclear gene subunit H3 of histone, and three mitochondrial genes, subunit 16S of rDNA and subunits I and II of the cytochrome oxidase. They were used in previous studies with Auchenorrhyncha (Dietrich *et al.*, 1997; Takiya, 2007; Paladini, 2012) and were already sequenced for seven species of *Molomea* (see Table 2, Takiya, unpublished data). A modified protocol of the extraction kit DNeasy Blood & Tissue Kit (QIAGEN) was used for DNA extractions (see Appendix I), using only the hindleg and associated muscles, without the maceration of the specimen. Amplification of molecular markers by PCR (Polymerase chain reaction) follows the protocols described in Takiya (2007, see Appendix II) and were conducted on an automatic thermal cycler (Veriti ,Applied Biosystems). Primer sequences are described in Table 4. PCR products were checked by submitting them through a 1% agarose gel electrophoresis to verify if DNA fragments were successfully amplified and if the product obtained had the expected size. Purification and sequencing of successful products were made by Macrogen (South Korea) using a capillary

sequencer with capacity to read up to 1,100 pair bases. Electropherograms of the resulting forward and reverse strands were aligned and edited using the software Geneious R6 (Biomatters, 2013) in order to obtain a consensus sequence. A BLAST (Basic Local Alignment Search Tool) search of the consensus sequences against the GenBank database was made in order to check if there was any contamination. Multiple alignment of the edited sequences was conducted using ClustalX (Larkin *et al*. 2007) available on the package MEGA 5.2 (Koichiro *et al.*, 2012), with gap opening and extension costs of 50 and 30 for the 16S gene and 15 and 6.6 for the remaining genes. Protein coding genes were translated to aminoacid sequences to check if they were correctly edited and the correct reading frame.

3.3. PHYLOGENETIC ANALYSES

Unrooted diagrams were built using the optimality criteria of Parsimony, Maximum Likelihood and Bayesian inference.

Parsimony analyses of the morphological dataset was performed on PAUP* with a heuristic search with 1,000 replicates of random starting trees and the algorithm TBR (tree bisection and reconnection) for branch-swapping. Characters were treated as unordered and had equal weights.

Adequate models of evolution of the DNA sequences for the probabilistic analyses were selected using the software jMODELTEST (Posada, 2008) based on the Akaike Information Criterion or AIC (Akaike, 1974), which simultaneously compares all the possible models and chooses the one with the smallest information loss (Lemey *et. al.* 2009). The model GTR+I+G was selected for the four genes analyzed.

Bayesian inference was performed using MrBayes 3.2.2 through the portal CIPRES Science Gateway (Miller *et al.*, 2010) for the morphological and molecular data combined and individually. Each analysis was made with two independent runs of 1,000,000 generations and four chains and trees were sampled every 500 generations. Maximum Likelihood analyses were performed using GARLI 2.0 (Zwickl, 2006) through the website of the Lattice Project (Bazinet & Cummings 2008) for the molecular dataset with 1,000 replicates. Each partition of the combined matrices was analyzed under their own evolutionary model chosen on both probabilistic methods, including the morphological dataset, which was modeled under the MK2 model of Lewis (2001).

Clade support was calculated with non-parametric bootstrap with 1,000 pseudo-replicates under parsimony (same search strategy as described above in PAUP*) and maximum likelihood (same search strategy as described above in GARLI) and Bayesian posterior probabilities.

3.4. EVOLUTION OF EGG-POWDERING BEHAVIOR ASSOCIATED TRAITS

Morphological characters associated with the egg-powdering behavior were optimized on the maximum likelihood tree based on the combined morphological and molecular data using Parsimony and Maximum Likelihood methods with the software Mesquite 2.7.5 (Maddison & Maddison 2009) to understand the multiples losses and origins of those characters among the species of the genus.

To test whether losses of these dimorphic characters in *Molomea* were related to shifts to major phytogeographical regions in South America, ancestral areas were reconstructed on the maximum likelihood tree based on the combined analysis, but ancestral areas were calculated using all post-burnin trees recovered from the Bayesian analysis of the same dataset, in an approach named S-DIVA (Yu *et al.*, 2010). S-DIVA analyses were run in RASP 2.1 (Yu *et al.*, 2011) based on pre-defined distributional areas based on ecological systems of South America (Navarro *et al.*, 2003) determined by plotting the collecting localities of specimens studied on QuantumGis 2.0.1 on top of a georeferenced layer of Navarro *et al.*, 2003. The analysis was performed with max areas equal 2.

Table 2: Terminal species included in the morphological analysis, with respective depository institutions of the material studied.

Species	Depository of material
Outgroups	
Versigonalia ruficauda (Cicadellini)	DZRJ
Diestostemma ptolyca (Proconiini)	DZRJ
Tretogonia cribata (Oncometopiini)	DZRJ
Tapajosa fulvopunctata (Oncometopiini)	DZRJ
Oncometopia facialis (Oncometopiini)	DZRJ
Oncometopia nigerrima (Oncometopiini)	DZRJ
Ingroup	
M. alternata (Signoret, 1855)	DZUP, MNRJ, MPEG, OSU
M. biimpressa (Signoret, 1855)	DZRJ, MZSP
M. cincta (Signoret, 1854)	CNC, MPEG, MZSP NCSU, UFRRJ
M. confluens (Melichar, 1925)	DZUP
M. consolida Schröder, 1959	AMNH, CMNH, DZRJ, DZUP, INHS, MNRJ, MPEG, NCSU
M. consorta (Melichar, 1925)	NCSU
M. exaltata (Melichar, 1925)	INHS, USNM
M. fatalis Bonfils et Perthuis, 1992	CAS, FSMC, INHS, MPEG
M. flavolimbata (Signoret, 1854)	DZUP
M. guttulata (Melichar, 1925)	
M. hamleti (Distant, 1908)	AMNH, DZRJ, DZUP, MNRJ, MZSP
M. infulata (Melichar, 1925)	
M. insignis (Distant, 1908)	MNRJ
M. laminata (Signoret, 1855)	ZMHB*
M. lineiceps Young, 1968	DZRJ, DZUP, UKL
M. magna (Walker, 1851)	AMNH, MNRJ, MZSP, NCSU, NMW, SEMC
M. malkini Young, 1968	DZUP
M. novarae Schröder, 1959	DZRJ
M. personata (Signoret, 1854)	AMNH, DZRJ, MZSP NCSU, NMW
M. vermiculata (Signoret, 1855)	ZMHB*
M. virescens (Distant, 1908)	CNC, DZUP, INHS, MNRJ, MPEG, NCSU, USNM
M. xanthocephala (Germar, 1821)	MNRJ, MZSP NCSU, NMW
M. zikani Schröder, 1960	SMF*

*Specimens studied at these institutions belong to the type-series.

Table 3: Species with DNA markers used for reconstructing the phylogeny of *Molomea*. Representative specimens of species in bold had the DNA extracted during this work. Voucher specimen numbers are followed by depositary institutions in parenthesis and refer to sequences that are unpublished. X, sequences obtained. -, sequences not obtained.

Species	Voucher specimen	Molecular Markers			
		COI	COII	16S rDNA	H3
OUTGROUP					
CICADELLINI					
Graphocephala coccinea (Foster, 1771)		AY869730	AY869789	AY869807	AY869763
Paromenia isabellina (Fowler, 1899)		AY869734	AY869782	AY869822	AY869759
Cicadella viridis (Linnaues, 1758)		AY869735	AY869786	AY869826	AY869760
PROCONIINI					
Diestostema excisum Schmidt, 1910		AY869733	AY869778	AY869817	AY869756
Proconosama alalia (Distant, 1908)		AY869742	AY869794	AY869812	AY869768
Paraulacizes irrorata (Fabricius, 1794)		AY869737	AY869788	AY869815	AY869762
ONCOMETOPIINI					
Oncometopia facialis	PR10 (INHS)	X	X	X	X
Tapajosa rubromarginata	PR91 (INHS)	X	X	X	X
Tretogonia cribata	PR13 (INHS)	X	X	X	X
INGROUP					
Molomea alternata	PR143 (INHS)	X	X	X	X
Molomea biimpressa	ENT1228 (DZRJ)	X	-	X	X
Molomea cincta	PR208 (INHS)	X	X	X	X
Molomea consolida	PR207 (INHS)	X	X	X	X
Molomea consorta	ENT1001 (DZRJ)	-	-	X	X
Molomea exaltata	PR144 (INHS)	X	X	X	X
Molomea fatalis	PR95 (INHS)	X	X	X	X
Molomea hamleti	ENT1034 (DZRJ)	-	-	X	X
Molomea infulata	ENT1003 (DZRJ)	X	X	X	X
Molomea lineiceps	PR206 (INHS)	X	X	X	X
Molomea magna	ENT1033	X	-	X	X

	(DZRJ)				
Molomea malkini	ENT1035 (DZRJ)	X	-	X	X
Molomea personata	ENT1230 (DZRJ)	X	X	X	X
Molomea virescens	PR29 (INHS)	X	X	X	X
Molomea xanthocephala	ENT1002 (DZRJ)	X	X	X	X
***Molomea* sp. 1**	ENT1036 (DZRJ)	X	-	X	X
***Molomea* sp. 2**	ENT1229 (DZRJ)	-	-	-	X

Table 4: Sequences of primers used for amplification and sequencing of molecular markers used for reconstructing the phylogeny of *Molomea*. Roles of genes in organisms from Lehninger (2000).

Molecular marker	Role in organism	Primer	Sequence (5'-3')	Reference
Cytochrome oxidase I	Part of the enzymatic complex IV of the respiratory chain, which reduces molecular oxygen to H_2O	C1 (R)	TTGATTTTTTGGTCAYCCWGAAGT	Takiya et al. 2006
		3014 (F)	TTCATTGCACTAATCTGCCATACTA	Takiya et al. 2006
Cytochrome oxidase II	Part of the enzymatic complex IV of the respiratory chain, which reduces molecular oxygen to H_2O	3037 (F)	TAGTATGGCAGATTAGTGCAATGAA	Takiya et al. 2006
		C2 (R)	CCRCAAATTTCWGARCATTGACCA	Takiya et al. 2006
Subunit 16S of rDNA	One of the structural components of the small subunit of ribosomes in prokaryotic cells	16S+ (F)	CCGGTYTGAACTCARATCA	Takiya et al. 2006
		16S- (R)	CRMCTGTTTAWCAAAAACAT	Takiya et al. 2006
Subunit H3 of Histona	One of the four subunits of the protein Histone, which together with DNA form the nucleosomes	HF (F)	ATGGCTCGTACCAAGCAGACGGC	Ogden & Whiting 2003
		HR (R)	ATATCCTTGGGCATGATGGTGAC	Ogden & Whiting 2003

4. RESULTS AND DISCUSSION

4.1.TAXONOMY OF THE GENUS *MOLOMEA* CHINA, 1927

The genus *Molomea* is redescribed below mostly based on Young (1968). Information added based on this study are marked with an asterisk (*).

***Molomea* China, 1927**

(Figure 1)

Molomea China, 1927 (nom. nov. for *Centrometopia* Melichar, 1925)
Centrometopides Strand, 1928 (nom. nov. for *Centrometopia* Melichar, 1925)
Centrometopia Melichar, 1925 (subgen. nov. of *Oncometopia* Say, 1859)

Additional literature citations:
Schröder, 1959; 1960: Description of new species and redescriptions.
Young, 1968. Revision of the genus.
Bonfils & Perthuis, 1992: Description of a new species.
Oman, Knight & Nielson 1990
McKamey, 2007: Catalogue.
Costa & Lozada, 2010: Catalogue.
Dellapé *et al.*, 2011: New records.
Paradell *et al.*, 2012: Catalogue.

Type-species: *Tettigonia personata* Signoret, 1854, by original designation.
External morphology: Head moderately produced, its median length varying from 0.2 to 0.7 times its interocular width, and from 0.1 to 0.5 times its transocular width*; anterior margin rounded, slightly truncate or slightly acute in dorsal aspect*; transition from crown to face without a carina; ocelli located on imaginary line between anterior eye angles, each equidistant from adjacent eye angle and median line of crown (rarely closer to adjacent eye angle); without an M-shaped elevation bordering posterior

Figure 1: Dorsal habitus of 22 species of *Molomea*. A, *M. alternata*, ♀, Brazil, MT; B, *M. biimpressa*, Brazil, MG; C, *M. cincta*, ♀, Brazil, MG; D, *M. confluens*, ♀, Brazil, RS; E, *M. consolida*, ♀, Brazil, MT; F, *M. consorta*; G, *M. exaltata*; H, *M. fatalis*; I, *M. flavolimbata*; J, *M. guttulata*; K, *M. hamleti*; L, *M. infulata*; M, *M. insignis*; N, *M. laminata*; O, *M. lineiceps*; P, *M. magna*; Q, *M.malkini*; R, *M. novarae*; S, *M. personata*; T, *M. vermiculata*; U, *M. virescens*; V, *M. xanthocephala*.

margin; without a longitudinal carina laterad of each ocellus; transverse shallow depression on crown; crown without pubescence. Lateral clypeal sutures extending onto crown and attaining ocelli. Antennal ledges protuberant in dorsal aspect, usually with a longitudinal depression, carinate or not dorsally in lateral aspect; anterior margins steeply declivous. Frontoclypeus strongly convex with distinct muscle impressions. Epistomal suture obscure. Face finely pubescent; anteclypeus not protuberant, its contour continuing profile of frontoclypeus. Pronotum width less than transocular width of head; lateral margins divergent anteriorly; surface usually rugose, with a pair of distinct broad shallow depressions near lateral margins at midlength; without pubescence; complete dorsopleural carina slightly arched downward in lateral view. Proepimeron with lower marginal area not depressed, its width greater than length. Mesoscutellum with or without transverse striations. Forewings with apical membrane; veins distinct and often elevated; texture of surface coriaceous and occasionally punctate; with only four apical cells, base of the third slightly more distal than base of the fourth; claval veins parallel; without an anteapical plexus of veins or anteapical supernumerary crossveins to costal margin. Hindwings at rest extending almost as far posteriorly as forewings; vein R2+3 incomplete (exception: *M. personata*). Hindlegs with femur setal formula 2:0:0, 2:1:0, 2:1:1 or 2:1:1:1; first tarsomere with length equal to or less than combined length of second and third tarsomeres (exception: *M. exaltata*).

Coloration*: The color pattern is very variable interspecifically. Species of *Molomea* have the background coloration of the dorsal surface of the body yellow to dark brown or black, and many species have colorful maculae over the crown, pronotum, mesonotum and forewings. Female sternite VII with color pattern variable interspecifically.

Male genitalia: Pygofer strongly produced posteriorly in lateral view; apex rounded, slightly acute or truncate in lateral view*; with numerous dispersed microsetae and a few interspersed macrosetae; without processes (exception: *M. biimpressa* and *M. flavolimbata*). Subgenital plates fused basally for a short distance; very short, not extending nearly as far posteriorly as pygofer midlength (exception: *M. hamleti*); basal portions concealed by valve; with dispersed microsetae and few interspersed macrosetae. Styles extending posteriorly to a variable distance compared to the apex of connective; with distinct preapical lobe (exception: *M. hamleti*); apex rounded. Conective Y-, U*-, T-shaped or as a transverse bar, usually with a dorsal median carina.

Aedeagus variable interspecifically, and processes length can be variable intraspecifically to a considerable degree in some species. Paraphyses absent.

Female terminalia*: Abdominal sternite VII with posterior margin approximately straight, with shallow median concavity or median projection, which can be triangular, subquadrate, or bifurcate, extending or not beyond lateral margins of the sternite. Internal abdominal sternite VIII membranous or sclerotized, with shape variable interspecifically. Valvulae I sculpturing with dorsal pattern concatenate and ventral pattern imbricate becoming concatenate near ventral margin. Valvulae II with 23 to 63 not continuous primary triangular teeth on dorsal margin, each bearing small denticles on the anterior and posterior margin; preapical region with denticles on ventral margin between apex and preapical prominence.

4.1.1. DESCRIPTION OF A NEW SPECIES OF *MOLOMEA*

A new species of *Molomea* is described below based on a single male specimen.

***Molomea* sp. nov.**

(Figure 2)

Type-locality: Parque Nacional da Serra dos Órgãos, Teresópolis, Rio de Janeiro, Brazil.

External morphology: Head with median length 0.4 times its interocular width, and 0.3 times its transocular width; anterior margin slightly truncate. Mesoscutellum without transverse striations. Forewings not punctate. Hindwings with vein R2+3 incomplete. Hindlegs with femoral setal formula 2:0:0; first tarsomere shorter than combined length of second and third tarsomeres. Other characters as described in generic description.

Coloration: Body dark brown dorsally and beige ventrally. Crown with six conspicuous yellow maculae, median anterior one rounded, median posterior one trapezoidal, lateral pair between eyes and ocelli, and lateral pair on anterior margin. Frons dark brown with median round yellow macula; beige laterally. Clypeus beige. Pronotum with one median round macula at anterior third and several other maculae of variable shapes and sizes, yellow. Mesonotum with scutum with three maculae, one median round pale macula and pair of yellow maculae at basolateral corners; scutellum with pale trapezoidal macula covering most of disk. Forewings with round yellow maculae.

Male genitalia: Pygofer with apex rounded. Subgenital plates extending posteriorly to midlength of pygofer; with dispersed microsetae and macrosetae. Styles extending posteriorly beyond apex of connective; without distinct preapical lobe. Connective U-shaped; with dorsal keel. Aedeagus with shaft with three pairs of apical processes, one of them multifurcate (only bifurcate at one side); preatrium well developed.

Notes: *Molomea* **sp. nov.** has a similar external coloration to *M. magna* (Walker, 1851) and *M. hamleti* (Distant, 1908), as they share the black lines delimiting conspicuous round markings on crown and a round median macula at mesoscutum. However, the new species can be distinguished from these and other *Molomea* by the longer

subgenital plates, connective with short stem, and aedeagus shaft with three pairs of apical processes, one of them multifurcate.

Material examined: Male holotype, “Parque Nacional | Serra dos Órgãos | Teresópolis – RJ| 30.VIII.1992| G. Mejdalani col.” (DZRJ).

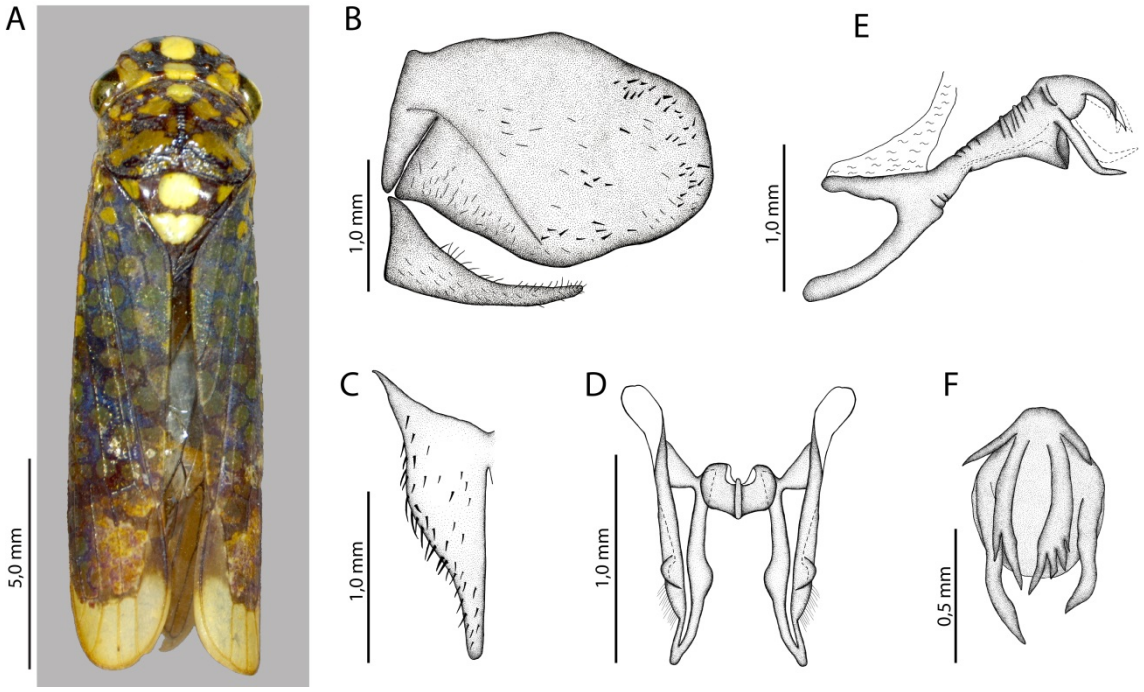

Figure 2: *Molomea* sp. nov., male holotype. A, Dorsal habitus; B, Pygofer and subgenital plates, lateral view; C, Subgenital plate, ventral view; D, Styles and connective, dorsal view; E, Aedeagus, lateral view; F, Aedeagus, caudal view.

4.1.2. UNIDENTIFIED FEMALES *OF MOLOMEA*

Three female specimens could not be identified. They might represent two new species of *Molomea*, but since there are no topotypical males available they will remain unnamed, but are described below. The two species were included in the morphology and molecular phylogeny, and their females are described below.

***Molomea* sp. 1**

(Figure 3)

Collecting locality: Alto Paraíso de Goiás, Goiás, Brazil.

External morphology: Anterior margin of head slightly acute. Mesoscutellum without transverse striations. Forewings not punctate. Hindwings with vein R2+3 incomplete. Hindlegs femoral setal formula 2:1:0; first tarsomere with shorter than combined length of second and third tarsomeres. Other characters as in generic description.

Coloration: Crown light purple With pair of thin longitudinal black stripes not delimiting distinct maculae. Frons light purple, with median black macula on inferior half. Clypeus black, continuous to black macula of frons; lateral margins pale. Pronotum dark brown with several reticulate small pale yellow macula; two pairs of bright yellow maculae, median pair at anterior half and larger lateral pair near margins. Mesoscutum light purple with three thin longitudinal dark stripes originating at anterior margin, two of them reaching lateral margins and median one reaching scutellar suture. Forewings dark brown; veins and reticulate maculae green. Thorax and abdomen with yellow longitudinal stripe over entire lateral of body. Ventral surface purple; with black maculae over the abdominal sternites. Female abdominal sternite VII with dark median macula, which a longitudinal stripe connecting the anterior and posterior margins of the sternite, which can be interrupted at midlength.

Female terminalia: Abdominal sternite VII (Figure 4B) posterior margin with median subquadrate projection, not extending beyond lateral margins. Internal abdominal sternite VIII sclerotized (Figure 4C). Valvulae I (Figure 4D) with microspines over bases in ventral view. Valvulae II (Figure 4E) with 24 primary teeth; teeth more than two times longer than higher.

Notes: This species is indistinguishable based on the external morphology and dorsal color pattern from *M. laminata*, as both of them have dark thin longitudinal stripes over crown, pronotum with reticulate brown stripes and two pairs of orange to yellow

maculae. However, these females can be distinguished from *M. laminata* female syntypes (see below) by the shape of the abdominal sternite VII, which has a subquadrate median projection at the posterior margin that does not extend beyond lateral margins, and a dark median longitudinal macula incomplete at middle third of sternite.

Material examined: Two females. 1 female, "BRASIL, GO, Alto Paraíso de Goiás | Santuário Raizama 14°11'50"S 47°49'48"W | sweep Santos, A. P. & Takiya, D. M." (DZRJ). 1 female, "BRASIL, GO, Alto Paraíso de Goiás | Santuário Raizama 26-30.X.2013 | 14°11'50"S 47°49'48"W sweep | Camisão, B. M., Gonçalves, C. G. | & Takiya, D. M." (DZRJ).

Molomea sp. 2

(Figure 4)

Collecting locality: 6 km NW San Ramón, Junín, Peru.

External morphology: Anterior margin of head slightly acute. Mesoscutellum without transverse striations. Forewings not punctate. Hindwings with vein R2+3 incomplete. Hindleg femoral setal formula 2:1:0; first tarsomere as long as combined length of second and third tarsomeres. Other characters as in generic description.

Coloration: Crown, pronotum, and ventral surface of the body, red. Mesonotum red, with apex pale. Forewings dark brown; basal half of clavus and basal third of corium, white. Female abdominal sternite VII with dark subquadrate macula with laterals attaining the two lateral thirds of the posterior margin but not the middle third. Pygofer with pair of basal round maculae slighty lighter than remainder surface, in ventral view.

Female terminalia: Abdominal sternite VII posterior margin with median triangular projection, not extending beyond lateral margins. Valvulae I with microspines over bases in ventral view. Vavulae II with 36 primary teeth on dorsal margin; teeth more than two times longer than higher; apex slightly rounded.

Notes: This species of *Molomea* is very different from the others, both in external coloration and shape of the female abdominal sternite VII.

Material examined: 1 female, “PERU: Junín, 6 km NW | San Ramón, 850m | 11°5'47"S75°23'34"W | 19 Oct 2002 | C.H.Dietrich & R.A.Rakitov”, (MUSM).

4.1.3. TYPE-SPECIMENS OF *MOLOMEA* STUDIED

A visit to the Museum für Naturkunde in Berlin (ZMNH) made possible the study of type-specimens of three *Molomea* species, and descriptions and notes on these specimens are given below.

***Molomea laminata* (Signoret, 1855)**

(Figure 5)

The original description of *Molomea laminata* is poor and ambiguous, and only the outline of the female abdominal sternite VII was illustrated previously by Schröder (1959). Other parts of female terminalia and male genitalia were never illustrated or described because the only specimen studied by Young (1968) in his revision of the genus was without the abdomen, and the author suggested that it could be conspecific with *M. flavolimbata*. Four syntypes of *M. laminata* (two males, one female, and the specimen without abdomen) were studied and the male and female genitalia were illustrated and described. One of the males examined had the genitalia a little damaged, so the other male was chosen as a lectotype.

Type-locality: Brazil.

External morphology: Head with median length between 0.6 to 0.8 times interocular width and 0.4 to 0.6 times transocular width; anterior margin slightly acute. Mesoscutellum without transverse striations. Forewings not punctate. Hindwings with vein R2+3 incomplete. Hindlegs femoral setal formula 2:0:0; first tarsomere as long as combined length of second and third tarsomeres. Other characters as in generic description.

Coloration: Crown, pronotum, and mesonotum purple. Crown with longitudinal thin dark stripes not delimiting distinct maculae. Pronotum with thin brown reticulate stripes; two pairs of orange to yellow maculae, median pair at anterior half and larger lateral pair near margins. Mesonotum with thin dark stripes not delimiting distinct maculae. Forewings dark green. Female abdominal sternite VII with dark longitudinal complete median stripe with width of approximately one third of sternite width, with a pale median macula at basal third.

Male genitalia: Pygofer with apex rounded; microsetae distributed over entire surface and few interspersed macrosetae. Subgenital plates not extending to midlength of pygofer. Styles extending posteriorly to connective apex; with distinct preapical lobe. Connective Y-shaped; with dorsal keel. Aedeagus shaft slender and approximately straight in lateral view; pair of basal processes bifurcate, each ramus with one to three basal spines and extending beyond apex of shaft.

Female terminalia: Abdominal sternite VII posterior margin with triangular median projection, extending beyond lateral margins. Internal abdominal sternite VIII sclerotized. Valvulae I with microspines over bases in ventral view. Valvulae II with 23 primary teeth; teeth more than two times longer than higher; apex slightly rounded.

Notes: The male genitalia of *M. laminata* is very similar to *M. alternata*, as both of them share the aedeagus shaft slender and straight, and basal processes bifurcate. However, *M. laminata* can be distinguished by more slender and not very arcuate basal processes rami, which additionally have spines at their bases (spines are absent in *M. alternata*).

Material examined: Syntypes, 2 males, 1 female, 1 without abdomen. 2 males: “Brasil | V. Alfers | N: 6572”, “Zool. Mus. Berlin”, “Syntype” (ZMHW). Female, “Brasil | V. Alfers | N: 6572”, “Zool. Mus. Berlin”, “18”, “Photographed by NMGW | Entom. | image no. E003196”, “Protographed by NMGW | Entom. | image no. E003197”, “Syntypus” (ZMHW). Specimen without abdomen, “Laminata Sign.”, “Nr. 6572 | Brasil, V. Olf.”, “Syntypus”, “Zoolog. Museum Berlin”, “6572”, “Bras. V. Olf.” (ZMHW).

Molomea alternata (Signoret, 1855)

(Figure 6)

The original description of *M. alternata* is also very poor and ambiguous, and did not include any illustrations. Schröder (1960) redescribed the species, but only included illustrations of the aedeagus, in both lateral and caudal view. In the revision of the genus, Young (1968) included illustrations of the aedeagus, in lateral view, of two distinct non-type specimens from Chapada, Brazil, with considerable variation in basal processes length, which he considered intraspecific variation. The male lectotype of *M. alternata* was illustrated and described.

Type-locality: Brazil.

External morphology: Head with median length 0.5 times its interocular widh and 0.3 times its transocular width; anterior margin rounded. Mesoscutellum without transverse striations. Forewings not punctate. Hindwings with vein R2+3 incomplete. Hindlegs femoral setal formula 2:1:0; first tarsomere as long as combined length of second and third tarsomeres. Other characters as in generic description.

Coloration: Head, pronotum, and mesonotum yellow. Crown with pair of thin longitudinal black stripes not delimiting distinct maculae. Pronotum with several dark reticulate maculae. Mesonotum with pair of thin and short longitudinal stripes originating on anterior margin and one dark inverted T-shaped macula over the scutum-scutellar suture. Forewings dark green; veins dark.

Male genitalia: Pygofer apex rounded; macrosetae close to apical margin and microsetae distributed over entire surface. Subgenital plates not extending to midlength of pygofer. Styles extending posteriorly slightly beyond connective apex; with distinct preapical lobe. Connective Y-shaped; with dorsal keel. Aedeagus shaft slender, slightly curved anteriorly in lateral view; pair of basal processes bifurcate extended to apex of shaft in lateral view.

Notes: See notes of *M. laminata*.

Material examined: Male lectotype, “ Alternata Sign.”, “Lecto | Typus” , “*Molomea* | *alternata* (Sign) | Heinz Schröder det.”, “nm. 6520 | Brasil V. Olf.”, “Zoolog. Museum | Berlin”, “6520”, “Bras. V. Olf.” (ZMHW).

Tettigonia vermiculata Signoret, 1855

(Figure 7)

This species was originally described in the genus *Tettigonia*, and was later transferred to *Amblyscarta* (Tribe Cicadellini) by Z. P. Meltcalf in 1964. The original description is very short and ambiguous, and does not include any illustrations. In his revision of cicadellines, Young (1968) did not study the type-specimens, however, he implicitly transferred the species to *Molomea*, based on specimens that were identified by C. Berg, which were conspecific to *M. consolida*. Young (1968) also suggests that these species should probably be synonymized in the future. Male and female syntypes were studied, and are described and illustrated below.

It was confirmed that the species actually belongs to the genus *Versigonalia* of the tribe Cicadellini because of the following set of characteristics: male pygofer with pair of internal anteapical processes; long subgenital plates, extended posteriorly to apex of pygofer; styles with apex narrow, without conspicuous preapical lobe; and aedeagus with shaft broad and bisinuate in lateral view, with apex rounded.

Type-locality: Brazil.

External morphology: Head with median length between 0.5 to 0.6 times interocular width and between 0.3 and 0.4 times transocular width; ocelli located slightly behind line between anterior eye angles. Forewings with membrane including first apical cell entirely and apex of the remaining ones; with 5 apical cells. Other characters as in generic description by Young (1977).

Coloration: Crown, pronotum, and forewings brown; with dull yellow to white reticulate maculae. Mesonotum pale; with pair of dark triangular maculae over basolateral region.

Male genitalia: Pygofer with processes arising anteapically; macrosetae distributed at apical third; apex angulate. Subgenital plates extending posteriorly beyond pygofer apex; with uniseriate macrosetae and microsetae on lateral margin. Styles with apex narrowed and truncate, directed ventrally . Connective Y-shaped. Aedeagus in lateral view with shaft broad; apex round.

Female terminalia: Abdominal sternite VII posterior margin with projection truncate and slightly concave, extending posteriorly beyond lateral margins. Internal abdominal

sternite VIII membranous with pair of lateral sclerotized regions. Valvulae II with well developed teeth on dorsal margin.

Notes: *Tettigonia vermiculata* can be distinguished from the other two valid species of *Versigonalia* by the following features: (1) male pygofer with apex acute and macrosetae at apical third; (2) styles with apex narrow and truncate in dorsal view; (3) aedeagus in lateral view with apical half of shaft narrowed and apex rounded, with basal constriction becoming broadened transversally at median region in caudal view; (4) female abdominal sternite VII with posterior margin with median projection truncate and slightly concave, extending posteriorly beyond lateral margins; (5) female internal abdominal sternite VIII membranous, with pair of lateral sclerotized regions; and (6) valvulae II of the ovipositor with well-developed teeth.

For this species to be transferred to *Versigonalia*, a new name must be proposed to replace the younger homonym *Versigonalia vermiculata* Young, 1977.

Material examined: Syntypes, 1 male, 1 female. 1 male, “Vermiculata Sign.”, “syntype | Tettigonia | vermiculata | Signoret, 1855”, “Bras. v. Olf.”, “6624” (ZMHW). Female, “25 | syntype”, “Brasil | V. Alfers | n. 6624”, “Zool. Mus. Berlin”, “Photographed by NMGW | Entom. | Image no. E003165”, “Photographed by NMGW | Entom. | Image no. E003166” (ZMHW).

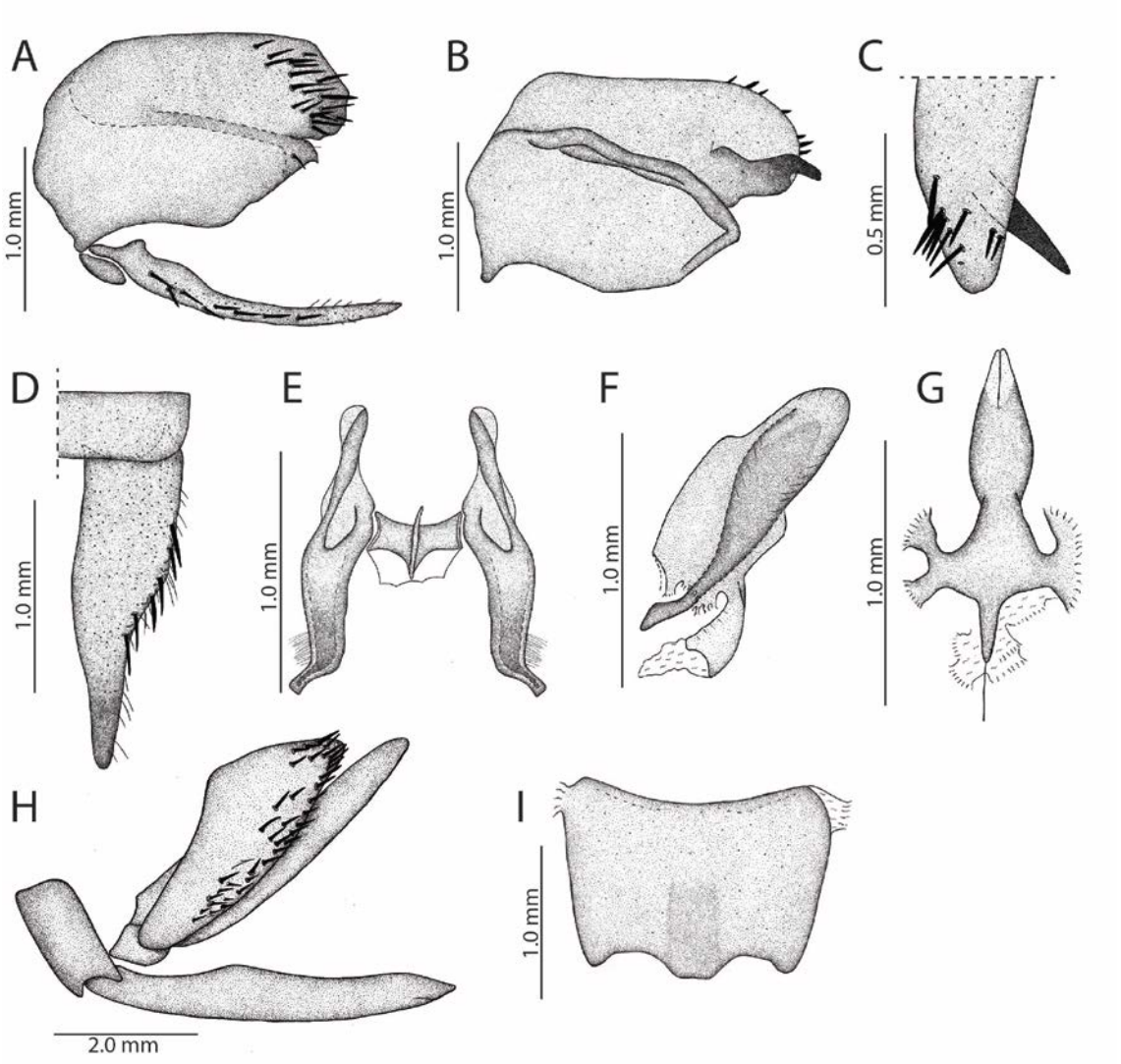

Figure 7: *Tettigonia vermiculata*, syntypes. A, I-K, Female syntype. B-H, Male syntype. A, Dorsal habitus; B, Pygofer, valve and subgenital plates, lateral view; C, Pygofer lobe, internal surface; D, Pygofer, apex, dorsal view; E, Subgenital plate and valve, ventral view; F, Styles and connective, dorsal view; G, Aedeagus, lateral view; H, Aedeagus, caudal view; I, Pygofer, sternite VII, and gonoplac, lateral view; J, Abdominal sternite VII, ventral view; K, Base of valvulae I, ventral view.

4.1.4. DESCRIPTIONS OF UNDESCRIBED MALES OF *MOLOMEA*

Currently, two valid *Molomea* species are only known based on female holotypes deposited at the Moravian Museum at Brno (MMBC) *M. guttulata* (Melichar, 1925) and *M. infulata* (Melichar, 1925), both from Peru. Additional males and females??? were identified based on photographs of these specimens made available by Dr. Mike Wilson (National Museum and Galleries, Cardiff, United Kingdom) and Dr. Igor Malenovsky (Moravian Museum, Brno, Czech Republic). Descriptions of the external morphology, male genitalia, and female terminalia of these species are given below.

***M. guttulata* (Melichar, 1925)**

(Figure 8)

Male genitalia: Pygofer (Figure 8B) with apex acute. Subgenital plates (Figure 8B, 8C) not extending posteriorly as far as midlength of pygofer. Styles (Figure 8D) extending posteriorly beyond apex of connective; with distinct preapical lobe. Connective V-shaped; with dorsal keel. Aedeagus (Figure 8E, 8F) shaft simple; with pair of slender basal processes, parallel in caudal view, originating in a common stem. Anal tube (Figure 8E, 8F) segment X ventral region with long and robust setae.

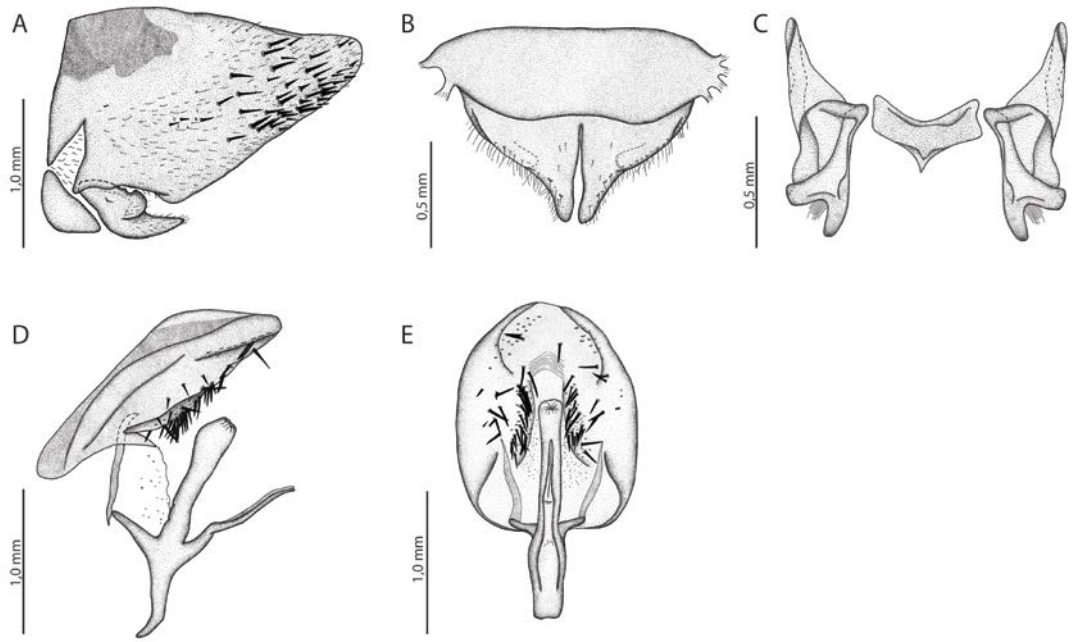

Figure 8: *Molomea guttulata*. A-F, male. Head, pronotum, and mesonotum, dorsal view; B, Pygofer, valve, and subgenital plates, lateral view; C, Valve and subgenital plates, ventral view; D, Styles and connective, dorsal view; E, Aedeagus and segment X of anal tube, lateral view; F, Aedeagus and segment X of anal tube, caudal view.

M. infulata (Melichar, 1925)

(Figure 9)

Male genitalia: Pygofer with apex slightly acute. Subgenital plates (Figure 9B, 9C) not extending posteriorly as far as midlength of pygofer. Styles extending posteriorly to apex of connective; with distinct preapical lobe. Connective T-shaped; with dorsal keel. Aedeagus shaft long and slender; without processes, but with pair of lateral apical short flanges; apex with cuticular denticles; preatrium connected to connective by membranous dorsal structure. Anal tube with pair of long basolateral processes, sharp and curved inwardly; pair of short apicolateral processes, sharp and curved inwardly.

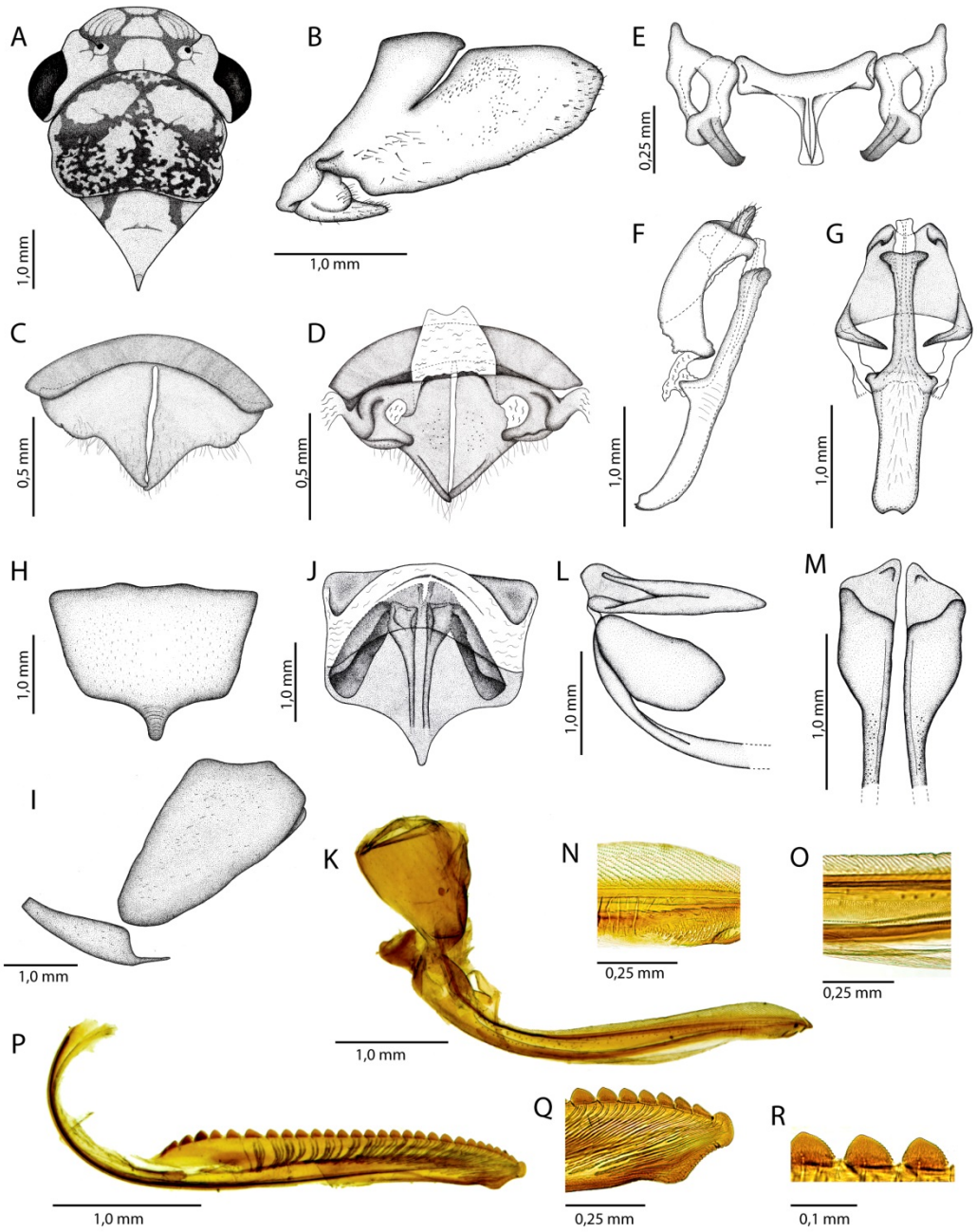

Figure 9: *Molomea infulata*. A, Head, pronotum, and mesonotum, dorsal view; B, Pygofer, valve, and subgenital plates, lateral view; C, Valve and subgenital plates, ventral view; D, Styles and connective, dorsal view; E, Aedeagus and segment X of anal tube, lateral view; F, Aedeagus and segment X of anal tube, caudal view.

4.1.5. POLYMORPHISM IN THE MALE GENITALIA

Species of *Molomea* were known to show some degree of intraspecific variability of the male aedeagus, which was illustrated by Young (1968). However, this author did not address this issue. Based on the study of several male specimens collected from the same or nearby localities in Brazil that agree in external morphology, coloration, and all other genitalia structures, it was possible to detect a great intraspecific polymorphism in the length of basal processes rami of the aedeagus of two species. Both species have simple and slender invariable aedeagus shaft and pair of basal bifurcate processes, which can vary in relative length of rami, in lateral view.

Males of *M. alternata* can vary in relation to the distance of which each ramus extends relative to one another and and also relative to the shaft. The rami can also have additional projections.

Males of *M. malkini* usually have the dorsal ramus of basal processes small and rounded at the apex, but it can be more slender and extend to variable distances relative to the ventral rami, which is usually slender and longer than dorsal ramus. However, the ventral ramus can also extend to variable distances relative to the shaft.

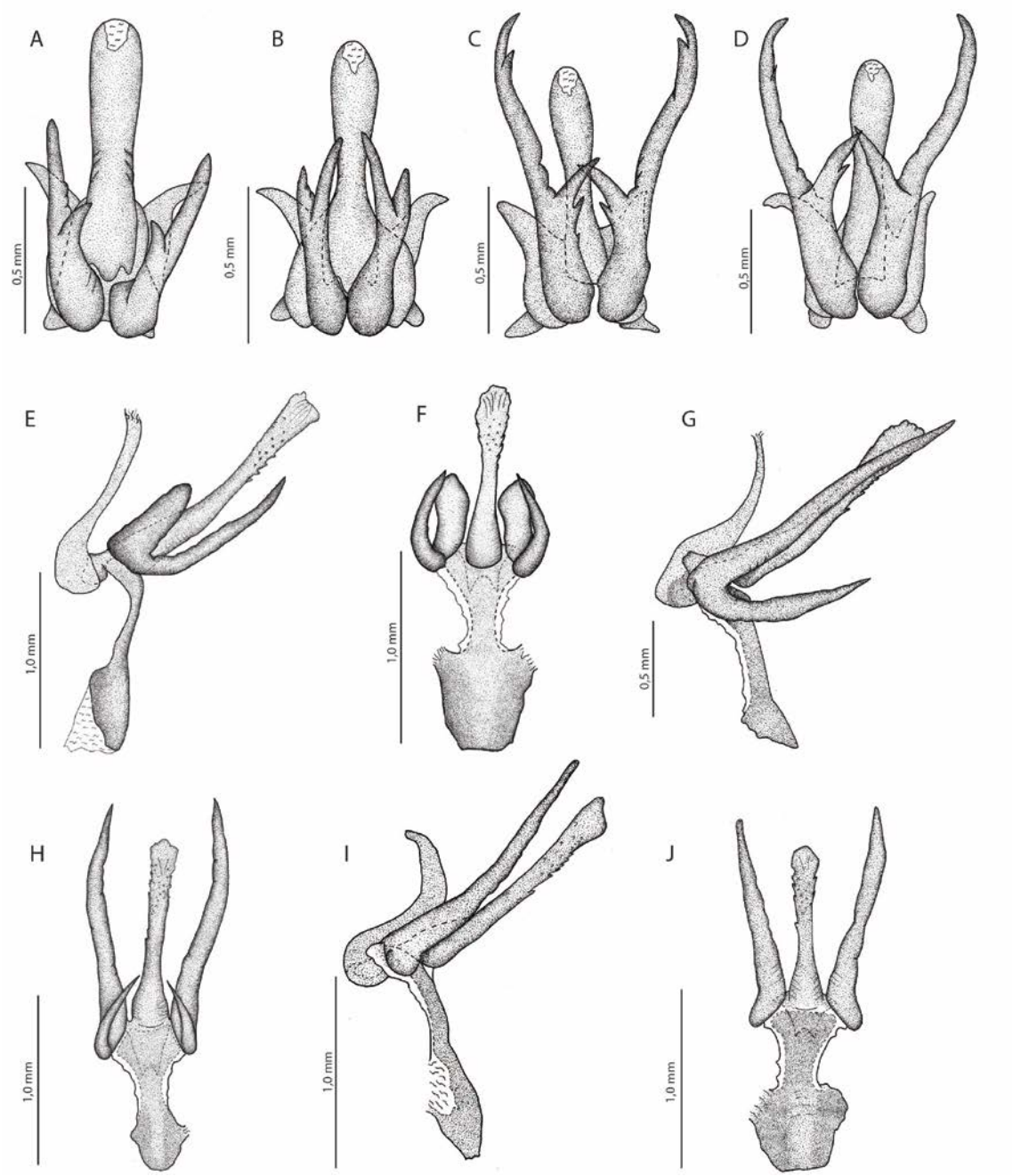

Figure 10: Polymorhism of the male genitalia. A-D, *M. alternata*. E-J, *M. malkini*.

4.1.6. COMPARATIVE MORPHOLOGY OF THE FEMALE TERMINALIA

The female terminalia morphology appears to be very useful to identify species of *Molomea*. The abdominal sternite VII is highly variable interspecifically in its shape and color pattern. Its posterior margin can be approximately rectilinear, concave mesally, or projected mesally. This median projection, when present, may be triangular or subquadrate, and it can extend beyond the lateral margins, or not. Many species have a complete or incomplete median longitudinal dark stripe, with variable width, while other species do not have any dark macula over the surface of the sternite.

The internal abdominal sternite VIII is also variable interspecifically. It can be completely membranous, or sclerotized to different degrees. The overall shape also appears to be specific. Furthermore, the connection between the sternite VIII and anterior margins of the bases of valvulae I of the ovipositor is usually sclerotized, with micro-sculpturing in some species.

The valvifers I have thin and long setae distributed on the posterior margin, and the shape is highly variable. On the other hand, valvulae I have setae on the shaft, and sculpturing with dorsal pattern concatenate and ventral pattern imbricate becoming concatenate near ventral margin, and imbricate at apex, in all species studied.

The valvifers II have a small region with robust setae near the articulation with the valvulae, but its shape is highly conserved. Valvulae II have the apex rounded, forming a conspicuous lobe or not, or acute. *Molomea* species have 23 to 63 primary teeth at dorsal margin, and although most range between 20 and 40 teeth, there are three species, *M. insignis*, *M. fatalis*, and *M. personata*, that have an average of 57, 48, and 58 teeth, respectively. The exact number can vary between individuals of the same species. The shape of the primary teeth is subtriangular in all species, with the proportion between length and height variable between species, but *Molomea fatalis* is the only species with teeth higher than longer. Denticles are present over the primary teeth and ventral margin of the preapical region.

4.1.7. TAXONOMIC KEY FOR MALES AND FEMALES OF *MOLOMEA*

A dichotomous key is given below based on characters of the coloration, male and female terminalia for all valid species of *Molomea* considered herein.

1. Forewings with transversal dark stripe over anteapical cells and dark macula near apex of clavus 2

1'. Forewings without dark stripe over anteapical cells and dark macula near apex of clavus 3

2. Crown with pair of longitudinal dark stripes delimiting one median pale macula between ocelli; male connective stem very short relative to rami length; female abdominal sternite VII with posterior margin completely dark .....

..... *M. personata* (Signoret)

2'. Crown without median pale macula; male connective stem longer than rami; female abdominal sternite VII with posterior margin black only mesally .... *M. insignis* (Distant)

3. Pronotum with transverse broad yellow stripe along posterior margin.....

.....*M. cincta* (Signoret)

3'. Pronotum without transverse yellow stripe 4

4. Crown with longitudinal and transversal black stripes delimiting conspicuous pale maculae 5

4'. Crown without conspicuous maculae delimited by black stripes 14

5. Crown with broad black stripes delimiting an inverted T-shaped light yellow macula between ocelli; male aedeagus with pair of thin basal processes produced anteriorly and

curved posterodorsally, longer than shaft in lateral view; female abdominal sternite VII with dark lateral margins ..... *M. confluens* (Melichar)

5'. Crown with narrow black stripes delimiting maculae of other shapes; male aedeagus with processes not as above or without basal processes; female abdominal sternite VII without dark lateral margins 6

6. Crown with single posterior median macula trapezoidal 7

6'. Crown with posterior median macula divided in three 10

7. Mesoscutum with a light yellow basal median round macula; forewings with round yellow or dark maculae 8

7'. Mesoscutum without a light yellow basal median round macula; forewings without round maculae ..... *M. infulata* (Melichar)

8. Mesoscutellum with pair of light yellow maculae; forewings with pairs of larger yellow maculae at posterior third of clavus and at corium near apex of clavus .... *M. magna* (Walker)

8'. Mesoscutellum with single light yellow macula; forewings without pairs of larger yellow maculae 9

9. Forewings with round dark maculae; male aedeagus with pair of apical processes; female abdominal sternite VII with median concavity on posterior margin and with median complete longitudinal black stripe ..... *M. hamleti* (Distant)

9'. Forewings with round yellow maculae; male aedeagus with two pairs of apical processes; female unknown ..... *Molomea* **sp. nov**.

10. Mesoscutellum with single light median macula .....*M. zikani* Schröder

10’. Mesoscutellum with pair of light maculae 11

11. Male aedeagus with single process on posteroventral margin of shaft and pair of basal processes; female abdominal sternite VII with longitudinal dark median macula ..... *M. lineiceps* Young

11. Male aedeagus without shaft process, but with pair of basal processes; female abdominal sternite VII not as above 12

12. Crown with purple maculae; mesoscutum with pair of purple maculae; male pygofer with dorsal processes; membrane connecting aedeagus to anal tube with small and thin setae; female abdominal sternite VII posterior margin without median projection .....
.....*M. biimpressa* (Signoret)

12’.Crown with yellow maculae; mesoscutum with four to six yellow maculae; male pygofer without dorsal processes; membrane connecting aedeagus to anal tube with long and robust setae; female abdominal sternite VII with posterior margin with median projection 13

13. Pronotum, mesonotum, and forewings black with yellow maculae .....
.....*M. guttulata* (Melichar)

13’. Pronotum with yellow spots on anterior third and pale spots at posterior two-thirds; mesonotum with black stripes delimiting large yellow maculae; forewings with pale spots.....*M. novarae* Schröder

14. Crown with longitudinal black stripes, not delimiting round maculae 15

14’. Crown without longitudinal black stripes, color usually uniform.....18

15. Pronotum with median pair of yellow to orange maculae at anterior third.....16

15’. Pronotum without median pair of yellow to orange maculae at anterior third 17

16. Pronotum with pair of lateral yellow to orange maculae near lateral margins.....

.....*M. laminata* (Signoret)

16’. Pronotum without lateral pair of yellow to orange maculae.....

.....*M. flavolimbata* (Signoret)

17. Mesoscutum with pair of dark lines bordering round maculae at basolateral areas; male aedeagal shaft thin and approximately straight, with apical microspines; female abdominal sternite VII with median complete longitudinal black stripe, with pale heart-shaped macula on anterior half.....……..*M. malkini* Young

17’. Mesoscutum without pair of dark lines at basolateral areas; male aedeagal shaft robust and slightly curved anteriorly, without apical microspines; female abdominal sternite VII with median complete longitudinal black stripe .....*M. alternata* (Signoret)

18. Pronotum pale and uniformly-colored.....*M. exaltata* (Melichar)

18’. Pronotum dark, uniformly-colored or not 19

19. Pronotum dark, with two pale maculae covering most of anterior third.....

..... *M. consorta* (Melichar)

19’. Pronotum completely dark, or with small pale spots at anterior third 20

20. Pronotum with narrow dark stripe along posterior margin; male aedeagal shaft without apical processes; female abdominal sternite VII with lateral margins strongly produced posteriorly, posterior margin deeply concave..... *M. xanthocephala* (Germar)

20’. Pronotum without dark stripe along posterior margin; male aedeagal shaft with apical pair of processes; female abdominal sternite VII with lateral margins not strongly produced, posterior margin with median triangular projection 21

21. Male aedeagal shaft with pair of basal and apical processes; female abdominal sternite VII with median complete longitudinal dark stripe .....*M. consolida* Schröder

21’. Male aedeagal shaft with pair of apical processes, but without basal processes; female abdominal sternite VII without median complete longitudinal dark stripe 22

22. Crown with dark three-lobed macula between ocelli; male aedeagal shaft robust, slightly curved anteriorly at midlength in lateral view; female abdominal sternite VII posterior margin with shallow concavities laterad of median projection.....
.....*M. fatalis* Bonfils & Perthuis

22’. Crown without dark macula between ocelli; male aedeagal shaft slender, approximately straight in lateral view; female abdominal sternite VII posterior margin without concavities laterad of median projection..... *M. virescens* (Distant)

4.1.8. LIST AND DISTRIBUTION OF SPECIES OF *MOLOMEA*

An up to date list and distributional records of valid species of Molomea are given below. New records based on studied specimens herein are marked in bold.

Molomea alternata (Signoret, 1855). Brazil: **BA, DF, GO, MG**, MT, **PA**.

Molomea biimpressa (Signoret, 1855). Brazil: **MG, RJ**.

Molomea cincta (Signoret, 1854). **Argentina**; Brazil: **GO, MA, MS,** MT**, PA, PB, SP**; **Bolivia**; **Paraguay**.

Molomea confluens (Melichar, 1925) Brazil: **PA,** RS.

Molomea consolida Schröder, 1959. Argentina; Brazil: **AC, AM, ES, GO**, **MA**, MT, **MS, MG**, PA, **PR,** RS**, RO**, SC, SP; Ecuador; Paraguay; **Peru**.

Molomea consorta (Melichar, 1925). Brazil: PA; **Ecuador**; Peru.

Molomea exaltata (Melichar, 1925). Brazil: PA; Peru.

Molomea fatalis Bonfils & Perthuis, 1992. **Brazil**: AC, PA, RO; Ecuador; **Peru**.

Molomea flavolimbata (Signoret, 1854). Argentina; Brazil: **GO**, PR, RS, SC, SP, PA, MT.

Molomea guttulata (Melichar, 1925). **Bolivia**; Peru.

Molomea hamleti (Distant, 1908). Brasil: MG, **PR, RJ, RS, SC, SP**.

Molomea infulata (Melichar, 1925). **Brazil: AM, PA**; **Bolivia**; Peru; **Venezuela.**

Molomea insignis (Distant, 1908). Brazil: RS, **SC**.

Molomea laminata (Signoret, 1855). Brazil: **GO**.

Molomea lineiceps Young, 1968. Argentina; Brazil: ES, **GO, MG, MT**, RS, SC, **SP**; Paraguay; **Uruguay**.

Molomea magna (Walker, 1851). Brazil: ES, MG, **PR**, RJ, RS, **RO**, SC, SP; Paraguay.

Molomea malkini Young, 1968. Brazil: ES, **GO**, MT.

Molomea novarae Schröder, 1959. Brazil: RJ.

Molomea personata (Signoret, 1854). Brazil: ES, RJ, SC, RS, **SP**.

Molomea virescens (Distant, 1908). **Brazil**: RO; Bolivia; **Colombia**; Ecuador; Peru.

Molomea xanthocephala (Germar, 1821). Brazil: **MG**, PR, **RJ**, RS, SC, SP, ES.

Molomea zikani Schröder, 1960. Brazil: MG.

4.2. PHYLOGENETIC ANALYSIS

4.2.1. MORPHOLOGY-BASED PHYLOGENY

4.2.1.1. MORPHOLOGICAL MATRIX

A total of 83 morphological characters were coded for 31 terminal taxa in a matrix shown in Figure 11. Of the thirty-three characters from the external morphology, fifteen are related to color pattern, eleven characters were from the head, and twenty-two from the thorax. In addition, twenty-five were scored from the female terminalia and twenty-five from male genitalia. Seven characters are non-informative to the parsimony analysis.

Figure 11: Morphological matrix of *Molomea* with 31 terminal taxa and 83 characters.

	10										20										30										40			
Diestostemma ptolyca	0	0	0	0	0	-	0	0	-	0	0	0	0	0	0	0	0	0	-	0	0	-	0	0	0	0	0	0	0	0	0	0	-	0	0	0
Versigonalia ruficauda	0	0	0	0	0	-	0	0	-	1	0	0	1	0	1	1	0	0	-	0	0	-	0	0	0	0	1	0	0	0	1	0	0	0	0	0	1	1	-	-
Tretogonia cribata	0	1	1	1	0	-	0	0	-	0	0	0	0	0	0	0	0	0	-	0	0	-	0	0	0	0	1	0	1	0	0	0	0	0	0	0	-	1	-	-
Tapajosa fulvopunctata	1	1	1	0	0	-	0	-	-	0	1	0	1	0	1	1	0	0	-	0	0	-	0	0	0	1	1	0	1	1	-	1	0	1	1	0	-	1	-	-
Oncometopia nigerrima	0	1	0	1	0	-	0	0	-	0	1	0	0	1	0	1	0	0	-	0	0	-	0	0	1	0	1	1	1	0	0	?	0	1	0	1	-	1	-	-
Oncometopia facialis	0	1	1	0	0	-	0	0	-	0	1	0	1	0	0	0	0	0	-	0	0	-	0	0	1	1	1	0	1	1	-	1	0	1	0	0	-	1	-	-
Molomea alternata	0	1	1	0	1	0	0	0	-	0	0	0	1	1	1	1	0	0	-	0	0	-	0	0	0	1	1	0	1	0	0	1	0	0	1	0	0	0	0	1
Molomea biimpressa	0	1	1	1	1	0	1	1	2	0	0	1	1	1	1	1	0	1	1	1	1	1	0	0	0	1	1	0	0	1	-	1	0	1	1	0	1	1	-	-
Molomea cincta	0	1	1	1	1	0	0	0	-	0	0	0	1	1	0	1	0	1	1	1	1	0	0	0	0	1	1	0	1	0	1	0	0	0	1	0	-	0	0	1
Molomea confluens	0	1	1	1	1	1	1	1	1	0	0	1	1	1	1	1	0	1	1	0	0	-	0	0	1	1	1	0	1	1	-	1	0	1	1	0	1	0	1	0
Molomea consolida	0	1	1	1	0	-	0	0	-	0	0	0	1	1	1	1	0	0	-	1	0	-	0	0	0	1	1	0	1	0	0	1	0	0	1	0	1	0	0	0
Molomea consorta	0	1	1	1	0	-	0	0	-	0	0	0	1	1	1	1	0	0	-	0	0	-	0	0	1	1	1	0	1	0	1	1	0	0	0	0	-	0	0	0
Molomea exaltata	0	1	1	1	0	-	0	0	-	0	0	0	1	1	0	1	0	0	-	0	0	-	0	0	1	1	1	0	0	0	1	1	0	0	1	0	-	1	-	-
Molomea fatalis	0	1	1	1	0	-	0	0	-	0	0	0	1	1	0	1	0	0&1	0	0&1	0	-	0	0	0	1	1	0	1	0	1	1	0	0	0	0	-	0	0	0
Molomea flavolimbata	0	1	1	1	1	0	0	0	-	0	0	1	1	1	1	1	0	1	0	1	1	1	0	0	0	1	1	0	0	0	1	1	1	1	0	0	1	1	-	-
Molomea guttulata	0	1	1	0	1	0	1	1	2	0	0	0	1	1	1	1	0	1	2	1	1	1	0	0	1	1	1	0	1	0	0	1	0	0	0	0	1	0	2	0
Molomea hamleti	0	1	1	1	1	0	1	1	0	0	0	0	1	1	1	1	0	1	0	1	1	0	0	0	0	1	1	0	1	0	0	1	0	0	1	0	0	1	-	-
Molomea infulata	0	1	1	1	1	0	1	1	0	0	0	0	1	1	1	1	0	1	0	1	1	0	0	0	1	1	1	0	1	1	-	1	0	0	0	0	1	0	0	0
Molomea insignis	0	1	1	1	0	-	0	0	-	0	0	0	1	1	0	1	1	0	-	0	0	-	1	1	0	1	1	0	0	0	0	0	0	0	0	0	1	0	0	1
Molomea laminata	0	1	1	0	1	0	0	0	-	0	0	1	1	1	1	1	0	0	-	0	0	-	0	0	0	1	1	0	1	1	0	1	1	0	0	0	1	0	0	1
Molomea lineiceps	0	1	1	0	1	0	1	1	2	0	0	0	1	1	1	1	0	1	2	1	1	1	0	0	0	1	1	0	1	0	0	1	1	0	0	1	0	-	0	1	0
Molomea magna	0	1	1	1	1	0	1	1	0	0	0	0	1	1	1	1	0	1	0	1	1	1	0	0	1	1	1	0	0	0	0	1	1	0	0	1	0	0	1	0
Molomea malkini	0	1	1	0	1	0	0	0	-	0	0	1	1	1	1	1	0	0	-	1	0	-	0	0	1	1	1	0	1	0	0	1	0	0	0	0	1	0	0	0
Molomea novarae	0	1	1	0	1	0	1	1	2	0	0	0	1	1	1	1	0	1	2	1	1	1	0	0	?	1	1	0	0	0	?	0	?	?	?	?	0	1	?
Molomea personata	0	1	1	1	1	0	1	0	-	0	0	0	1	1	0	1	1	1	0	0	1	0	1	1	0	1	1	0&1	0	0	1	1	0	0	0	0	0	0	0	1
Molomea virescens	0	1	1	1	0	0	0	0	-	0	0	0	1	1	1	1	0	0	-	0	0	-	0	0	0	1	1	0	0	0	1	1	0	0	0	0	-	0	0	0
Molomea xanthocephala	0	1	1	1	0	0	0	0	-	0	0	0	1	1	1	1	0&1	0	-	0	0	-	0	0	0	1	1	0	1	0	0	1	0	0	0	1	-	0	1	1
Molomea sp. nov.	0	1	1	1	1	0	1	1	0	0	0	0	1	1	1	1	0	1	0	1	1	0	0	0	?	1	1	0	1	0	0	?	0	?	?	?	?	?	?	?
Molomea sp. 1	0	1	1	0	1	0	0	0	-	0	0	1	1	1	1	1	0	0	-	0	0	-	0	0	0	1	1	0	1	0	0	0	1	0	0	0	1	0	1	1
Molomea sp. 2	0	1	1	0	0	0	0	0	-	0	0	0	1	1	0	1	0	0	-	0	0	-	0	0	0	1	1	0	1	0	0	1	0	0	0	0	-	0	0	1
Molomea zikani	0	1	1	0	1	0	1	1	2	0	0	0	1	1	1	1	0	1	2	1	1	0	0	0	?	1	1	0	?	?	?	?	?	?	?	?	0	-	0	1	0

Figure XX: Continuation.

	50										60										70										80									
Diestostemma ptolyca	0	-	-	-	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Versigonalia ruficauda	1	0	1	1	1	2	0	-	0	0	1	2	2	2	0	0	1	1	0	0	0	1	0	1	0	0	0	0	0	1	0	1	0	0	-	-	-	-	0	2	0	0	0
Tretogonia cribata	0	-	-	-	-	0	0	1	1	0	1	1	2	3	1	1	1	0	0	0	0	0	0	0	1	1	0	0	0	1	0	1	0	0	0	1	0	1	0	1	0	0	0
Tapajosa fulvopunctata	0	-	-	-	-	1	0	-	1	1	0	1	2	3	1	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0	1	0	0	3	0	0	0	0
Oncometopia nigerrima	0	-	-	-	-	0	1	0	0	0	0	0	2	3	1	1	1	0	1	2	0	0	0	1	1	1	0	0	0	0	0	1	1	0	1	1	0	1	0	1	0	0	0
Oncometopia facialis	0	-	-	-	-	0	1	0	0	0	0	1	0	3	1	1	1	1	1	0	0	1	0	1	1	1	0	0	0	0	0	1	1	0	0	0	1	-	0	1	0	0	0
Molomea alternata	1	0	1	1	0	0	1	0	1	0	0	1	2	3	1	1	1	0	0	0	1	1	0	1	1	0	0	0	0	1	0	0	0	0	1	0&1	0	1&3	1	1	0	0	0
Molomea biimpressa	1	0	1	0	1	0	0	0	1	1	0	1	2	3	1	1	1	0	0	0	1	0	0	1	1	0	0	0	1	0	1	1	0	0	1	1	0	1	1	0	0	0	0
Molomea cincta	0	-	-	-	-	0	1	1	1	0	0	1	2	3	1	1	1	0	0	0	1	1	0	1	1	0	0	0	0	1	0	1	0	0	1	0	0	0	1	0	0	0	0
Molomea confluens	1	0	1	0	1	0	1	0	1	0	0	1	2	3	1	1	1	0	0	0	1	1	0	1	1	1	0	0	0	1	0	1	0	0	1	0	0	3	0	0	0	0	0
Molomea consolida	1	0	1	1	0	0	1	1	1	0	0	1	2	3	1	1	1	0	0	0	1	1	1	1	1	0	0	0	0	1	0	0	0	0	1	1	1	2	0	0	0	0&1	0
Molomea consorta	0	-	-	-	-	0	1	1	0	0	0	1	2	3	1	1	1	0	0	1	1	1	0	1	1	0	0	0	0	1	0	1	0	0	1	0	0	1	1	0	0	0	0
Molomea exaltata	0	-	-	-	-	0	1	1	0	1	0	1	0	3	1	1	1	0	0	0	1	0	0	1	1	1	0	0	0	1	0	0	0	1	-	-	-	-	1	0	0	0	0
Molomea fatalis	1	0	1	1	-	1	1	1	1	0	0	1	1	1	1	1	1	0	0	0	1	1	1	1	1	1	0	0	0	1	0	0	0	1	-	-	-	-	0	0	0	0	0
Molomea flavolimbata	1	0	1	1	1	0	1	0	1	1	0	1	2	3	1	1	1	0	0	0	1	0	0	1	1	1	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0	0	0
Molomea guttulata	1	0	1	1	-	0	0	1	2	1	0	1	0	3	1	1	1	1	0	0	1	0	0	1	1	1	0	0	0	1	0	0	1	0	0	1	1	0	1	0	1	0	0
Molomea hamleti	1	0	0	1	0	0	1	1	1	1	0	1	0	3	1	1	1	1	0	0	0	1	0	1	0	0	0	0	0	1	0	0	1	1	-	-	-	-	0	0	0	0	0
Molomea infulata	0	-	-	-	-	1	1	0	1	1	0	1	0	3	1	1	1	1	0	0	1	1	1	1	1	0	0	1	0	1	0	1	1	0	1	1	0	1	1	0	0	1	1
Molomea insignis	1	0	1	1	1	0	1	1	1	0	0	1	0	1	1	1	1	0	0	0	1	1	0	1	1	1	0	0	1	0	0	1	0	0	1	1	0	1	1	0	0	0	0
Molomea laminata	1	0	1	1	-	0	1	1	1	1	0	1	2	3	1	1	1	0	0	0	1	1	1	1	1	0	0	0	0	1	0	1	0	0	1	0	0	1	0	0	0	0	0
Molomea lineiceps	1	1	0	1	-	0	1	1	2	1	0	1	0	3	1	1	1	1	0	0	1	1	1	1	1	0	1	1	0	1	0	1	1	0	0	0	0	3	0	0	0	0	1
Molomea magna	1	0	0	1	1	1	1	1	0	1	0	1	0	3	1	1	1	0	0	0	1	1	0	1	1	0	0	1	0	0	1	1	1	1	-	-	-	-	0	0	0	0	0
Molomea malkini	1	0	1	1	1	0	1	0	1	1	0	1	2	3	1	1	1	0	0	0	1	1	1	1	1	0	0	1	0	1	1	1	1	0	1	0&1	0	3	0	0	0	0	0
Molomea novarae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	1	1	0	1	1	1	0	0	0	1	1	0	1	0	1	1	1	1	0	1	1	0	1
Molomea personata	1	0	1	1	0	0	1	1	1	0	0	1	0	1	1	1	1	0	0	0	1	0	0	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0
Molomea virescens	0	-	-	-	-	1	1	1	1	0	0	1	0	3	1	1	1	0	0	0	1	0	0	1	1	1	0	0	0	1	0	0	0	1	-	-	-	-	1	0	0	0	0
Molomea xanthocephala	0	-	-	-	-	0	1	0	1	0	0	1	0	3	1	1	1	0	0	0	1	0	0	1	1	1	0	0	0	1	1	1	0	0	1	0	0	3	0	1	0	0	0
Molomea sp. nov.	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	0	0	0	1	0	1	0	1	0	0	0	0	1	1	-	-	-	-	0	0	0	0	0
Molomea sp. 1	1	0	1	1	-	0	1	0	1	1	0	1	2	3	1	1	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Molomea sp. 2	1	1	-	-	-	0	1	1	1	1	0	1	2	3	1	1	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Molomea zikani	0	-	-	-	-	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	1	?	?	?	?	?	?	?	0	1	0	1	?	0	0	0	0	0	?	0	0	0	?

4.2.1.2. MORPHOLOGICAL CHARACTERS

HEAD

1. Transition from crown to frons in lateral view, angle: (0) right or obtuse; (1) acute; (CI= 1.00; RI= 0.00).

2. Frons, pubescence: (0) mostly glabrous; (1) conspicuously pubescent; (CI= 1.00; RI= 1.00).

3. Frons, texture of the integument: (0) smooth; (1) rugose or granulose; (CI= 0.50; RI= 0.50).

4. Crown, shape of anterior margin in dorsal view: (0) acute or round; (1) truncate; (CI= 0.17; RI= 0.58)

The anterior margin of the crown truncate is a homoplastic apomorphy of groups B (*M. virescens, M. exaltata, M. fatalis, M. insignis, M. personata*) (Figure 12), and D (*M. cincta, M. confluens, M. biimpressa, M. flavolimbata, M. lineiceps, M. zikani, M. guttulata, M. novarae, M. hamleti, Molomea* sp. nov., *M. infulata, M. magna*), but changed to acute or round in the ancestor of group F (*M. lineiceps, M. zikani, M. guttulata, M. novarae, M. hamleti, Molomea* sp. nov., *M. infulata, M. magna*) and changed another time back to truncate in group J (*M. hamleti, Molomea* sp. nov., *M. infulata, M. magna*).

5. Crown, disk, coloration: (0) without longitudinal stripes; (1) with pair of longitudinal black stripes; (CI= 0.25; RI= 0.77).

Longitudinal black stripes on crown are a homoplastic apomorphy of groups A (*M. laminata, M. malkini*, and *Molomea* sp. 1) and D.

6. Crown, pair of longitudinal black stripes, width: (0) thin; (1) extremely wide; (CI= 1.00; RI= 0.00).

Wide stripes are an autapomorphy of *M. confluens.*

7. Crown, region close to apex of crown, coloration: (0) without transversal stripe; (1) with transversal black stripe; (CI= 0.33; RI= 0.80).

The transversal black stripe near apex of crown is a homoplastic apomorphy of the group E and it was lost in *M. flavolimbata*.

8. Crown, region between ocelli, coloration: (0) with transversal black stripe, delimiting a posterior median macula; (1) without black stripe; (CI= 0.50; RI= 0.89).

The transversal black stripe between ocelli is a homoplastic apomorphy of group E and it was lost in *M. flavolimbata*.

9. Crown, coloration, posterior median macula delimited by transversal black stripe between ocelli, shape: (0) trapezoidal; (1) inverted T-shape; (2) subdivided in three; (CI= 1.00; RI= 1.00).

The inverted T-shape is an autapomorphy of *M. confluens*. The macula subdivided in three is a non-homoplastic apomorphy of group E, but changed back to trapezoidal in group J.

10. Crown, antennal ledges in dorsal view: (0) prominent; (1) not prominent; (CI= 1.00; RI= 0.00).

11. Crown, pubescence: (0) without pubescence; (1) conspicuously pubescence; (CI= 1.00; RI= 1.00).

The crown without pubescence is a symplesiomorphy of *Molomea.*

THORAX

12. Pronotum, posterior region of the anterior third, coloration: (0) without round distinct maculae; (1) with pair of small round maculae arranged transversally; (CI= 0.50; RI= 0.80).

The pair of small maculae at the anterior third of pronotum is a homoplastic apomorphy of groups A and G.

13. Pronotum, lateral margins: (0) parallel or convergent anteriorly; (1) divergent anteriorly; (CI= 0.33; RI= 0.00).

14. Pronotum, anterior half in dorsal view: (0) without concavities; (1) with distinct lateral concavities; (CI= 0.50; RI= 0.75).

Distinct lateral concavities are a synapomorphy of *Molomea* and appear independently in *Oncometopia nigerrima*.

15. Pronotum, posterior third, coloration: (0) uniform; (1) with small maculae that may fuse; (CI= 0.17; RI= 0.44).

The presence of small maculae at posterior third of pronotum is a homoplastic synapomorphy of groups A and E.

16. Pronotum, posterior third, sculpturing: (0) punctate; (1) smooth; (CI= 0.33; RI= 0.0).

The posterior third of pronotum punctate is a symplesiomorphy of *Molomea*.

17. Pronotum, posterior margin, coloration: (0) concolorous to anterior two-thirds; (1) with a dark thin stripe along entire margin; (CI= 1.00; RI= 1.00).

The thin dark stripe along the posterior margin of pronotum is a homoplastic apomorphy of group C.

18. Mesonotum, median region of scutum, coloration: (0) without macula; (1) with distinct macula, divided or not; (CI= 0.50; RI= 0.92).

The distinct macula on scutum is a homoplastic apomorphy of group D.

19. Mesonotum, median macula of scutum, division: (0) single macula; (1) divided in two; (2) divided in four or six; (CI= 0.50; RI= 0.60).

The median macula of scutum divided in four or six is a non-homoplastic apomorphy of group F that fused back to a single macula in group J.

20. Mesonotum, basolateral region of scutum, coloration: (0) without macula; (1) with a light macula; (CI= 0.250; RI= 0.750)

The basolateral region of scutum with light macula is a homoplastic apomorphy of group D that was lost by *M. confluens*.

21. Mesonotum, scutellum, coloration: (0) without distinct macula; (1) with distinct macula, divided or not; (CI= 0.33; RI= 0.81).

The distinct macula on scutellum is a homoplastic apomorphy of group D that was lost by *M. confluens*.

22. Mesonotum, macula of scutellum: (0) single macula; (1) divided in two; (CI= 0.33; RI= 0.60).

The scutellum with macula divided in two is a homoplastic apomorphy of groups H and I.

23. Forewings, anteapical cells, coloration: (0) concolorous to the rest of wing; (1) with transversal dark stripe; (CI= 1.00; RI= 1.00).

The transversal dark stripe over the anteapical cells is a non-homoplastic apomorphy of group C.

24. Forewings, apical region of the clavus, coloration: (0) concolorous to the rest of clavus; (1) with dark macula; (CI= 1.00; RI= 1.00).

The dark macula over the clavus is a non-homoplastic apomorphy of group C.

25. Forewings, costal setae on females, distribution: (0) uniformly distributed; (1) distinctly concentrated; (CI= 0.14; RI= 0.25).

This is one of the two dimorphic characters associated to the egg-powdering behavior, and it will be further discussed later in this work.

26. Forewings, costal margin, shape: (0) concave; (1) rectilinear; (CI= 0.50; RI= 0.50).

Rectilinear costal margin is a symplesiomorphy of *Molomea*.

27. Forewings, sculpturing: (0) punctate; (1) not punctate; (CI= 0.50; RI= 0.00).

Forewings not punctate is a symplesiomorphy of *Molomea.*

28. Hind wings, vein R2+3, extension: (0) incomplete; (1) complete; (CI= 0.50; RI= 0.00).

Vein R2+3 complete is a homoplastic apomorphy of *M. personata*.

29. Metepimeron, surface projection: (0) not projected; (1) with longitudinal folded shelf-like projection; (CI= 0.17; RI= 0.50).

The shelf-like projection of the projected metepimeron is a homoplastic synapomorphy of groups B, H, *M. novarae*, and *M. magna.*

30. Hind legs, femoral setal formula, anteapical seta(e): (0) present (2:1:0) (1) absent (2:0:0); (CI= 0.17; RI= 0.00).

31. Hind legs, femoral setal formula, seta basad to the anteapical seta(e): (0) absent (2:1/2:0); (1) present (2:1:1); (CI= 0.20; RI= 0.56).

The basal seta is a homoplastic apomorphy of groups B and D and was lost secondarily independently by *M. insignis*, and groups I and K.

32. Hind legs, tibia, distal setae of the anteroventral row on females, length in relation to more basal setae: (0) subequal; (1) distinctly longer; (CI= 0.25; RI= 0.40).

This is the second dimorphic character associated to the egg-powdering behavior, and will be further discussed later in this work.

33. Hind legs, tarsomere I, plantar chaetotaxy: (0) biseriate; (1) multiseriate; (CI= 0.50; RI= 0.50).

FEMALE TERMINALIA

34. Pygofer, apex, shape: (0) rounded or slightly acute; (1) truncate; (CI= 0.50; RI= 0.80)

The truncate apex of pygofer is a homoplastic synapomorphy of group G.

35. Pygofer, coloration in ventral view: (0) uniform color pattern; (1) with dark maculae of variable sizes; (CI= 0.14; RI= 0.33).

Dark maculae on pygofer are a homoplastic synapomorphy of group D that were lost independently at least three times inside the group.

36. Abdominal sternite VII, length: (0) not extending posteriorly beyond the tergite VIII in ventral view; (1) produced posteriorly beyond tergite VIII in ventral view; (CI= 0.50; RI= 0.00).

Sternite VII produced posteriorly beyond tergite VIII is a homoplastic autapomorphy of *M. xanthocephala.*

37. Abdominal sternite VII, dark stripe along anterior margin, extension: (0) along entire margin: (1) restricted to the median portion; (CI= 0.25; RI= 0.00)

38. Abdominal sternite VII, median region of posterior margin: (0) with projection; (1) without projection; (CI= 0.20; RI= 0.50).

Sternite VII with a posterior median projection is a homoplastic synapomorphy of *Molomea* that was lost secondarily independently by *M. exaltata*, *M. hamleti*, and group H.

39. Abdominal sternite VII, shape of projection on median region of posterior margin: (0) triangular; (1) subquadrate; (2) bifurcate; (CI= 0.40; RI= 0.50).

The median projection bifurcate is an autapomorphy of *M. guttulata*, and a subquadrate projection is a homoplastic apomorphy of group E, that was changed back to triangular in *M. infulata.*

40. Abdominal sternite VII, length of median projection of posterior margin: (0) produced posteriorly beyond lateral margins; (1) not produced posteriorly beyond lateral margins; (CI= 0.20; RI= 0.43).

The median projection not produced posteriorly beyond lateral margins is a homoplastic apomorphy of group H.

41. Abdominal sternite VII, color pattern: (0) uniform color; (1) with dark macula of variable shape and size; (CI= 0.17; RI= 0.55)

The dark macula over the sternite VII is a homoplastic apomorphy of the groups A, C, and E that was lost independently by *M. infulata* and *M. zikani.*

42. Abdominal sternite VII, dark macula, length: (0) long, forming a stripe connecting the anterior and posterior margins; (1) short, not connecting both margins; (CI= 0.50; RI= 0.00).

43. Abdominal sternite VII, median region of dark macula: (0) extremely thin; (1) broader; (CI= 0.50; RI= 0.50).

A broad median region of the dark macula is a homoplastic apomorphy of the groups B, H and J.

44. Abdominal sternite VII, posterior third of dark macula relative to the median third, width: (0) abruptly narrowed ; (1) uniformly narrowed or broadening; (CI= 0.50; RI= 0.00).

45. Abdominal sternite VII, posterior margin: (0) with thin dark stripe extending on the entire length of the margin; (1) without dark stripe; (CI= 0.33; RI= 0.33)

46. Abdominal sternite VIII, degree of sclerotization: (0) completely sclerotized; (1) completely or greatly membranous; (1) with some sclerotized regions; (CI= 0.40; RI= 0.25)

Sternite VIII completely or greatly membranous is a homoplastic apomorphy of the group L.

47. Abdominal sternite VIII, connection to bases of valvulae I: (0) membranous; (1) sclerotized; (CI= 0.25; RI= 0.40)

A sclerotized connection of the sternite VIII to bases of valvulae I is a homoplastic apomorphy of *Molomea* that was independently lost by *M. biimpressa* and *M. guttulata*.

48. Abdominal sternite VIII, width: (0) more than 2.5 times wider than long; (1) less than 2 times wider than long; (CI= 0.14; RI= 0.40)

A narrower sternite VIII is a homoplastic apomorphy of groups B and D, and it changed to a wider one independently in group G and *M. infulata.*

49. Valvula I, shape of the anterior margin of bases, in ventral view: (0) approximately straight; (1) oblique; (2) rounded; (CI= 0.33; RI= 0.43).

50. Valvula I, sculpturing of base: (0) smooth or slightly rugose; (1) with cuticular micro-spines; (CI= 0.20; RI= 0.67).

The cuticular micro-spines are a homoplastic apomorphy of groups A and E that was lost by *M. confluens*.

51. Valvula I, sculpturing of dorsal region of shaft: (0) concatenate; (1) strigate; (CI= 0.50; RI= 0.00).

52. Valvula I, sculpturing of ventral region of shaft: (0) concatenate; (1) imbricate, becoming concatenate close to ventral margin; (2) strigate; (CI= 0.67; RI= 0.00).

53. Valvula II, dorsal margin, length of primary teeth relative to its height: (0) longer for distance shorter than two times its height; (1) shorter; (2) longer than two or more times its height; (CI= 0.33; RI= 0.64)

Primary teeth of valvula II shorter than two times its heigth is a homoplastic apomorphy of groups B and F. Primary teeth higher than long is an autapomorphy of *M. fatalis.*

54. Valvula II, dorsal margin, number of primary teeth: (0) more than 90; (1) between 50 and 60; (2) around 10 teeth; (3) between 20 and 45 teeth; (CI= 1.00; RI= 1.00)

Valvula II with 50 to 60 primary teeth is a homoplastic apomorphy of group C.

55. Valvula II, dorsal margin, primary teeth: (0) continuous; (1) separate at base; (CI= 1.00; RI= 1.00)

56. Valvula II, ventral margin: (0) without preapical prominence; (1) with preapical prominence; (CI= 1.00; RI= 1.00)

57. Valvula II, ventral margin, apical region, sculpturing: (0) without denticles; (1) with denticles; (CI= 1.00; RI= 0.00)

58. Valvula II, shape of apex: (0) acute or slightly rounded; (1) largely rounded, forming a distinct lobe; (CI= 0.25; RI= 0.40)

The round apex of valvula II is a homoplastic synapomorphy of group F that was secondarily changed back to slightly rounded in *M. magna.*

MALE GENITALIA.

59. Pygofer, basal portion of ventral margin: (0) without pair of processes; (1) with pair of processes; (CI= 1.00; RI= 1.00)

60. Pygofer, shape of apex: (0) rounded or slightly acute; (1) forming an angle, directed ventrally; (2) subquadrate; (CI= 1.00; RI= 0.00)

The angulate apex of pygofer is an autapomorphy of *M. consorta.*

61. Subgenital plates, length relative to pygofer: (0) reaching or extending beyond midlength of pygofer; (1) not reaching midlength of pygofer; (CI= 0.50; RI= 0.86)

Subgenital plates not extending beyond midlength of pygofer is a homoplastic synapomorphy of *Molomea* that was lost by group K.

62. Subgenital plates, external margin, dorsal view: (0) with small lobe near apex of style; (1) without such lobe; (CI= 0.11; RI= 0.27)

Subgenital plates without a small lobe is a homoplastic apomorphy of groups A and D and was lost independently by group H, *M. guttulata*, and *Molomea* sp. nov.

63. Styles, length relative to the apex of connective: (0) extending posteriorly beyond apex of connective; (1) not extending posteriorly to apex of connective; (CI= 0.20; RI= 0.20)

Styles not extending posteriorly to apex of connective is a homoplastic apomorphy of group A.

64. Styles, direction of the apex: (0) parallel or subparallel to the plane of the rest of the style; (1) curved ventrally; (CI= 0.33; RI= 0.00)

Apex of styles curved ventrally is a symplesiomorphy of *Molomea.*

65. Styles, preapical lobe: (0) indistinct; (1) distinct; (CI= 0.33; RI= 0.50)

The indistinct preapical lobe is a homoplastic apomorphy of group K.

66. Connective, length of shaft relative to the width of the arms: (0) as long or longer ; (1) shorter than; (CI= 0.13; RI= 0.46)

Shaft of connective as long as or longer than width of arms is a homoplastic apomorphy of groups A and D, and was secondarily independently changed to shorter by *M. confluens*, *M. flavolimbata*, *Molomea* sp. nov. and group I.

67. Connective, direction of arms in dorsal view: (0) divergent; (1) both perpendicular to the shaft; (CI= 1.00; RI= 0.00)

Perpendicular arms of the connective is an autapomorphy of *M. lineiceps.*

68. Aedeagus, connection between pre-atrium and subgenital plates, styles, and connective: (0) through a simple membrane; (1) through a dorsal membranous structure folded over preatrium; (CI= 0.25; RI= 0.25)

The membranous structure covering the pre-atrium is a homoplastic apomorphy of group L.

69. Aedeagus, shape of dorsal margin of shaft in lateral view: (0) not forming small basal lobe; (1) with a small basal lobe; (CI= 0.50; RI= 0.00)

The small basodorsal lobe of the shaft is a homoplastic autapomorphy of *M. insignis* and *M. biimpressa.*

70. Aedeagus, shape of anterior margin of shaft in lateral view: (0) strongly concave; (1) weakly concave or straight; (CI= 0.17; RI= 0.44)

The strongly concave anterior margin is a homoplastic apomorphy of groups C and H.

71. Aedeagus, anteapical region of shaft, sculpturing: (0) without spines; (1) with cuticular spines; (CI= 0.20; RI= 0.33)

Cuticular spines over the anteapical region of shaft is a homoplastic apomorphy of groups H and L.

72. Aedeagus, apex of the shaft: (0) produced as a pair of apical processes; (1) without projection; (CI= 0.13; RI= 0.42).

Apex of shaft of aedeagus produced as a pair of apical processes is a homoplastic apomorphy of groups B (lost in *M. insignis*) and E (lost in *M. falvolimbata* and groups I and J, but reacquired by *M. magna*).

73. Aedeagus, pre-atrium: (0) short and inconspicuous; (1) long and conspicuous; (CI= 0.33; RI= 0.78).

A long pre-atrium is a homoplastic apomorphy of group F.

74. Aedeagus, basal region, projection: (0) produced as paired basal processes; (1) without processes; (CI= 0.33; RI= 0.67).

Aedeagus without basal processes is a homoplastic apomorphy of groups B and J, and processes were secondarily reacquired by group C.

75. Aedeagus, pair of basal processes: (0) originating from a single stem; (1) separated from base; (CI= 0.20; RI= 0.33).

Pair of basal processes originating from a single stem is a homoplastic apomorphy of group F that was lost by *M. novarae.*

76. Aedeagus, length of the pair of basal processes: (0) longer, exceeding the apex of the shaft; (1) subequal or shorter than the shaft; (CI= 0.17; RI= 0.17).

The length of the pair of basal processes subequal or shorter than the shaft is a homoplastic apomorphy of group I.

77. Aedeagus, shape of the pair of basal processes: (0) curved; (1) approximately straight; (CI= 025; RI= 0.25).

The approximately straight basal processes is a homoplastic apomorphy of group I.

78. Aedeagus, direction of the rami of the basal processes in caudal view: (0) parallel or subparallel; (1) widely divergent; (2) convergent from base; (3) divergent at base, converging in apical half; (CI= 0.27; RI= 0.11)

79. Aedeagus, ventral region: (0) without pair of apodemes; (1) with pair of apodemes; (CI= 0.17; RI= 0.44).

Ventral region of aedeagus with a pair of apodemes is a homoplastic apomorphy of groups B and H, and they secondarily are lost in *M. fatalis*)

80. Segment X of anal tube, caudoventral margin, shape: (0) convex; (1) bilobada; (2) rectilinear; (CI= 0.33; RI= 0.20).

81. Anal tube, setae on ventral region of segment X: (0) thin and small; (1) long and robust; (CI= 1.00; RI= 1.00).

Long and robust setae appear are a non-homoplastic sinapomorphy of group I.

82. Anal tube, apical region, projection: (0) without processes; (1) with pair of lateral processes; (CI= 1.00; RI= 0.00).

83. Anal tube, basal region, projection: (0) without processes; (1) with pair of lateral processes; (CI= 0.333; RI= 0.00).

4.2.1.3. MAXIMUM PARSIMONY ANALYSIS

Sixty most parsimonious trees were found with L=296, CI=0.32 and RI=0.52, and their strict consensus tree is showed below (Figure 12). *Molomea* appears as a monophyletic group in all most parsimonious trees, but without any clade support.

Another analysis was conducted based on this dataset, but excluding the two characters related to the egg-powdering behavior (characters 25 and 32) to evaluate if there are significant changes in the topology. Seventy-six most parsimonious trees were found (L=284, CI=0.33, RI=0.51) and their strict consensus was exactly the same obtained for the previous analysis.

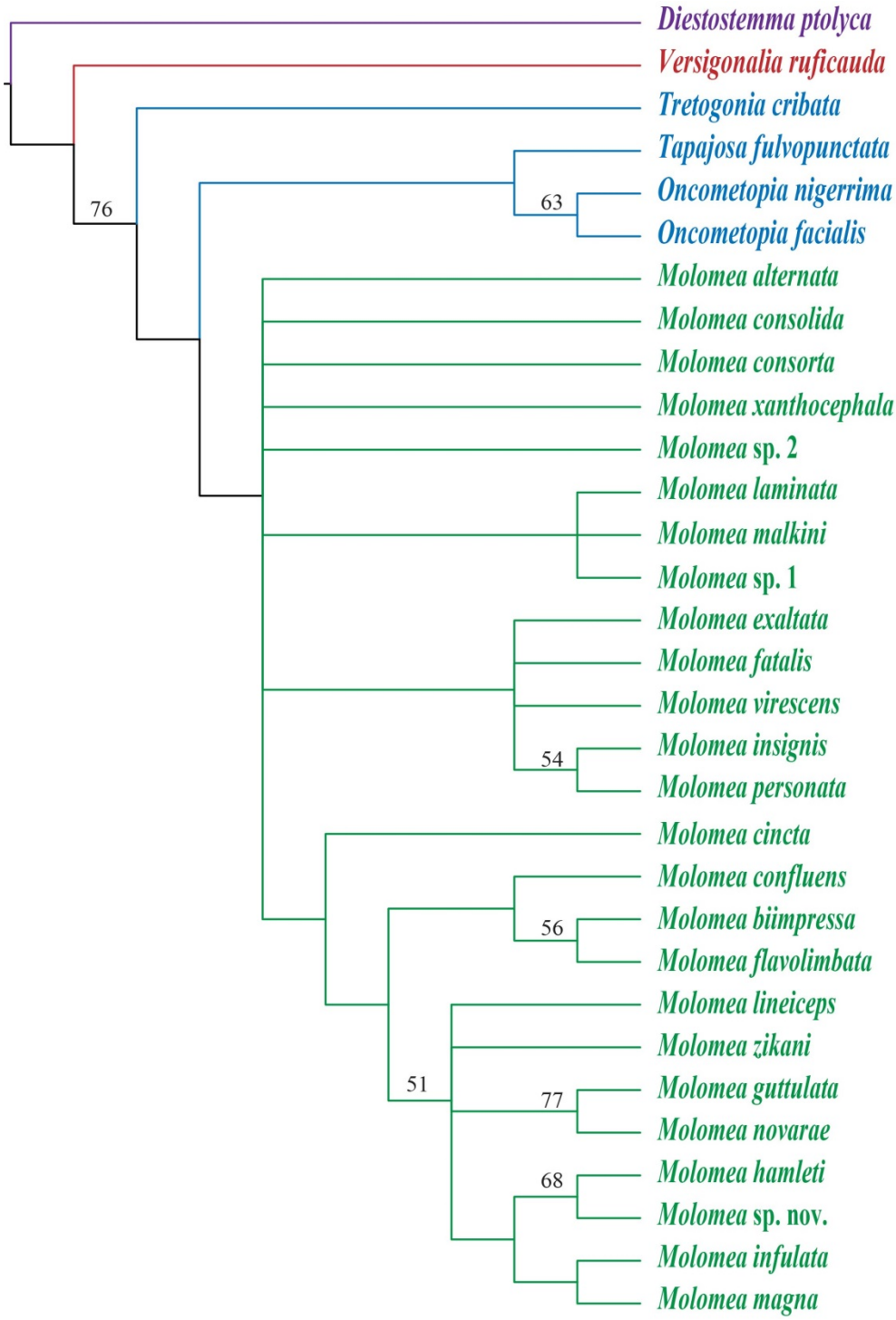

Figure 12: Strict consensus of the 60 most parsimonious trees (L=296, CI=0.32, RI=0.52) obtained with the analysis of the morphological dataset of *Molomea*. Numbers above branches are bootstrap values. Species colored in purple is a Proconiini; red is a Cicadellini; in blue are Oncometopiini. The genus *Molomea* is in green.

Morphological characters were optimized in all sixty most parsimonious trees and the result is showed in Figure 13. Only apomorphies of non-ambiguous optimization found for branches present in all trees are showed.

Four synapomorphies were recovered for the genus *Molomea*, all of them homoplastic: (1) anterior half of pronotum with distinct lateral concavities (char. 14[1]); (2) posterior margin of female abdominal sternite VII with median projection (3) sclerotized connection of female abdominal sternite VIII with base of valvula I; and (4) males with subgenital plates not extending beyond midlength of pygofer.

Twelve groups were identified in the parsimony morphological analysis and are discussed below (group names in Fig. 12):

GROUP A: *M. malkini, M. laminata*, and *Molomea* sp. 1.

All three species share the following eight homoplastic apomorphies: (1) pair of longitudinal black stripes on crown; (2) pair of small round maculae arranged transversally at posterior region of the anterior third of pronotum; (3) small maculae at posterior third of pronotum; (4) dark macula over female abdominal sternite VII; (5) base of valvulae I with cuticular micro-spines; (6) male subgenital plates without small lobe near the apex of style; (7) styles not extending posteriorly beyond apex of connective; and (8) shaft of connective as long as or longer than width of arms.

GROUP B: *M. exaltata, M. fatalis, M. insignis, M. personata*, and *M. virescens.*

Species of this group share the following homoplastic apomorphies: (1) anterior margin of crown truncate; (2) metepimeron without a shelf-like projection (regained by *M. fatalis*); (3) presence of seta basad to the anteapical seta on hind femur (lost by *M. insignis*); (4) female sternite VIII length shorter than two times its width; (5) primary teeth of valvula II length shorter than two times its height (except *M. fatalis*); (6) aedeagal shaft with pair of apical processes (lost by *M. insignis*); (7) ventral region of aedeagus without processes (present in *M. insignis* and *M. personata*); and (8) aedeagus with pair of ventral apodemes (lost by *M. fatalis*).

This group comprises group C.

GROUP C: *Molomea insignis* and *M. personata.*

Species of this group are the only species of the genus with forewings colored with a transversal dark stripe over anteapical cells and a dark macula over apex of

clavus, and they share the following homoplastic apomorphies: (1) thin dark stripe along the posterior margin of pronotum; (2) dark macula over sternite VII; (3) 50 to 60 primary teeth on dorsal margin of valvula II; (4) anterior margin of shaft of aedeagus strongly concave; and (5) pair of basal processes on aedeagus.

GROUP D: *M. biimpressa, M. cincta, M. confluens, M. flavolimbata, M. guttulata, M. hamleti, M. infulata, M. lineiceps, M. magna, M. novarae, M. zikani*, and *Molomea* sp. nov.

Species of this group share the following eleven homoplastic apomorphies: (1) anterior margin of crown truncate; (2) pair of longitudinal black stripes on crown; (3) distinct macula on scutum; (4) basolateral region of scutum with light macula; (5) distinct macula on scutellum; (6) macula of scutellum divided in two (except in *M. biimpressa, M. flavolimbata, M. lineiceps, M, guttulata, M. novarae*, and *M. magna*); (7) absence of seta basad to anteapical seta on hind femur (reacquired by *M. guttulata, M. novarae, M. hamleti*, and *Molomea* sp. nov.; (8) dark maculae on female pygofer (lost by *M. flavolimbata, M. guttulata* and *M. infulata*); (9) female abdominal sternite VIII shorter than 2 times its wider than long (lost by *M. biimpresa, M. confluens, M. flavolimbata* and *M. infulata*); (10) male subgenital plates without small lobe near the apex of style (reverted on *M. biimpressa, M. flavolimbata, M. guttulata* and *Molomea* sp. nov.); and (11) length of shaft of connective sub-equal or greater than width of arms (except for *M. confluens, M. flavolimbata, M. guttulata, M. novarae*, and *Molomea* sp. nov.).

GROUP E: *M. biimpressa, M. confluens, M. flavolimbata, M. guttulata, M. hamleti, M. infulata, M. lineiceps, M. magna, M. novarae, M. zikani,* and *Molomea* sp. nov.

Species of this group share the six following homoplastic apomorphies: (1) transversal black stripe near apex of crown (except *M. flavolimbata*); (2) transversal black stripe between ocelli (except *M. flavolimbata*); (3) small maculae at posterior third of pronotum; (4) median projection of posterior margin of sternite VII subquadrate (except in *M. guttulata* and *M. infulata*); (5) dark macula on female abdominal sternite VII (lost by *M. infulata* and *M. zikani*); and (6) base of valvula I with cuticular micro-spines (lost by *M. confluens*).

This group is divided in two main groups, F and G.

GROUP F: *M. guttulata, M. hamleti, M. infulata, M. lineiceps, M. magna, M. novarae, M. zikani*, and *Molomea* sp. nov.

These species share the following six homoplastic apomorphies: (1) anterior margin of crown acute or round (except for *M. hamleti, M. infulata, M. magna* and *Molomea* sp. nov.); (2) primary teeth of valvula II shorter than two times its height; (3) apex of valvula II largely rounded (lost by *M. magna*); (4) pre-atrium of aedeagus long and conspicuous; (5) pair of basal processes of aedeagus originating from a single stem; (6) aedeagus without ventral apodemes.

This group comprises groups I and J.

GROUP G: *M. biimpressa, M. confluens,* and *M. flavolimbata.*

Species of this group are the only *Molomea* with a truncate apex of the female pygofer. They also share the following three homoplastic apomorphies: (1) pair of small maculae at anterior third of pronotum; (2) abdominal sternite VII longer than 2.5 times its width; (3) shaft of connective shorter than width of the arms (except for *M. biimpressa*).

This group comprises group H.

GROUP H: *M. biimpressa* and *M. flavolimbata.*

The two species included in this group share the following homoplastic apomorphies: (1) scutellum with macula divided in two; (2) metepimeron not projected; (3) posterior margin of female abdominal sternite VII without projection; (4) male subgenital plates with small lobe near apex of style; (5) anterior margin of shaft of aedeagus strongly concave; (6) apex of shaft of aedeagus without projections; and (7) aedeagus with pair of ventral apodemes.

GROUP I: *M. guttulata* and *M. novarae.*

Species in this group are the only in the genus with long and robust setae on ventral region of segment X of anal tube. They also share the following seven homoplastic apomorphies: (1) scutellum with macula divided in two; (2) seta basad to the anteapical seta of hind femur absent; (3) female pygofer with uniform color pattern; (4) shaft of connective shorter than width of arms; (5) aedeagal shaft with pair of apical processes; (6) pair of basal processes of aedeagus subequal or shorter than shaft; and (7) pair of basal processes of aedeagus approximately straight.

GROUP J: *M. hamleti*, *M. infulata*, *M. magna*, and *Molomea* sp. nov.

These four species share the following seven homoplastic apomorphies: (1) anterior margin of crown truncate; (2) trapezoidal posterior median macula on crown; (3) single macula over scutum; (4) median region of the dark macula on the female sternite VII extremely narrow; (5) with dorsal membranous structure covering the pre-atrium and connected to the subgenital plates, styles, and connective (lost by *M. hamleti*); (6) aedeagal shaft with pair of apical processes (lost in *M. magna*); and (7) ventral region of aedeagus without processes.

This group is divided in two groups, K and L.

GROUP K: *M. hamleti* and *Molomea* sp. nov.

These are the only species of *Molomea* with subgenital plates reaching the midlength of pygofer. They also share the absence of seta basad to the anteapical seta at the hind femur, which is a homoplastic apomorphy.

GROUP L: *M. infulata* and *M. magna*.

These species share the following two homoplastic apomorphies: (1) female internal sternite VIII completely or greatly membranous; and (2) anteapical region of shaft of aedeagus with cuticular spines.

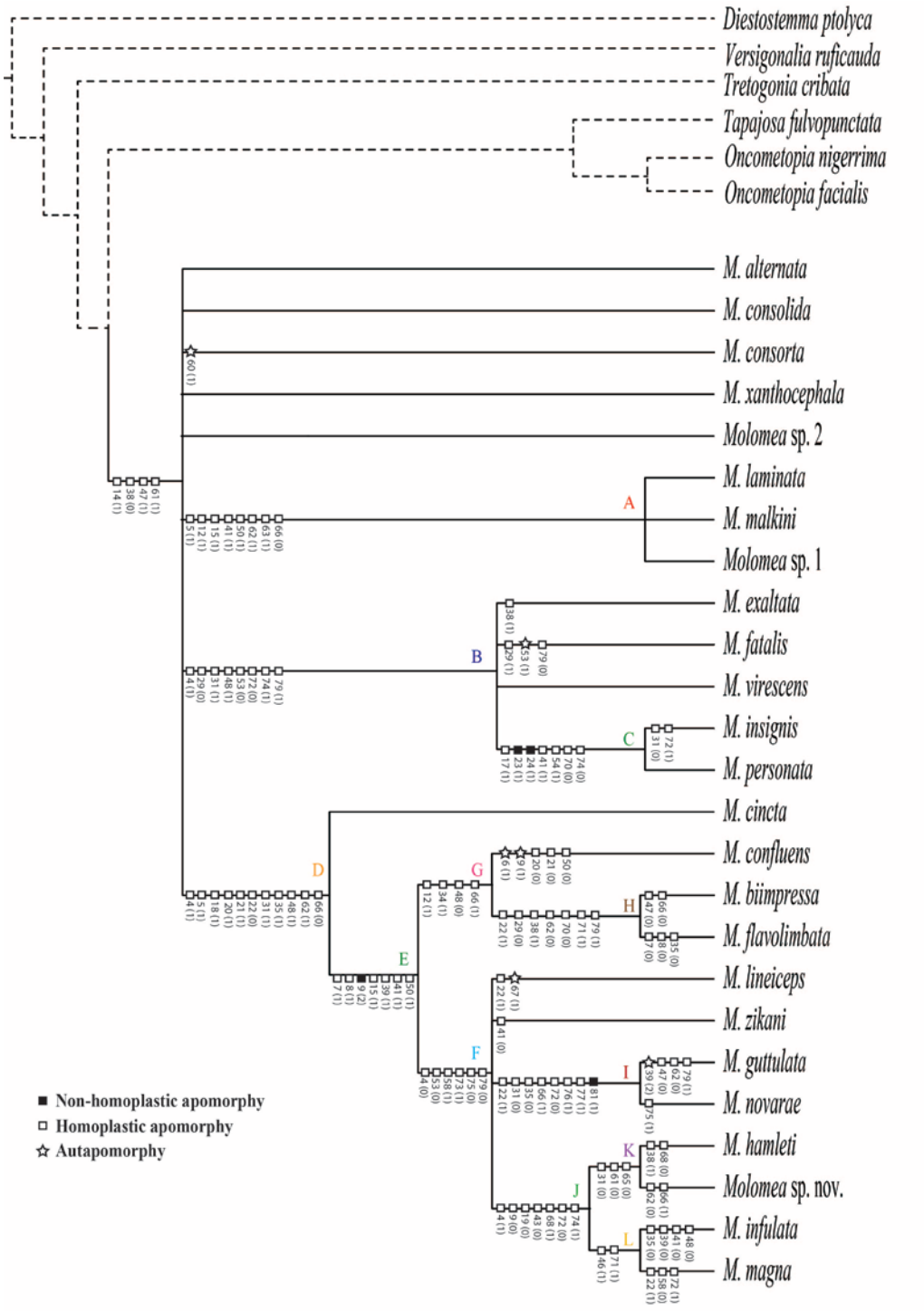

Figure 13: Strict consensus of sixty most parsimonious trees showing character state changes of the morphological dataset of *Molomea*. Character optimization was made using parsimony and all most parsimonious trees. Only non-ambiguous apomorphies found for the branches recovered in all trees are showed. Dashed branches lead to outgroups. White squares represent homoplastic synapomorphies. Black squares represent non-homoplastic synapomorphies. Stars represent autapomorphies.

4.2.1.4. BAYESIAN INFERENCE

The analysis of the morphological dataset with Bayesian inference (BI) also recovered a monophyletic *Molomea*, with an extremely low clade support (Figure 14). The consensus tree is also greatly polytomous, but some of the clades within *Molomea* that were recovered in the parsimony analysis were also found.

Groups C, I, J, K, and L and their internal relationships were identical in both parsimony and Bayesian analyses. Group B (in Figure 12) recovered with parsimony was not recovered by BI, Groups A, D, F and G were also recovered in the Bayesian analysis, but with different internal relationships. Internal relationships of Group A were only recovered in the Bayesian analysis, but with low support, where *Molomea* sp. 1 was recovered as sister to *M. laminata* with clade support of 60, and *M. malkini* appears as sister group to this clade. A basal polytomy for Group D was found with BI. The basal polytomy of Group F found in the parsimony analysis was resolved in part in the Bayesian analysis with the clade *M. lineiceps* + *M. zikani* with low support. *Molomea biimpressa* was recovered as sister to *M. confluens* within Group G, contrary to Group H from the parsimony analysis. Groups B and E were collapsed in the BI analysis.

It is noticeable that bootstrap values for parsimony were smaller than the values of Bayesian posterior probability. This disparity was already expected, since posterior probabilities seem to be overinflated and too liberal in comparison to bootstrap values that tend to be a little more conservative (Suzuki *et al.*, 2002) and, therefore, less susceptible to strongly support a false phylogenetic hypothesis (Douady *et al.*, 2003). A support of 75% bootstrap should be considered good, but posterior probabilities values should be over 95% to be considered as a robust support for the clade (Pereira, 2012 *in* Matioli, 2012).

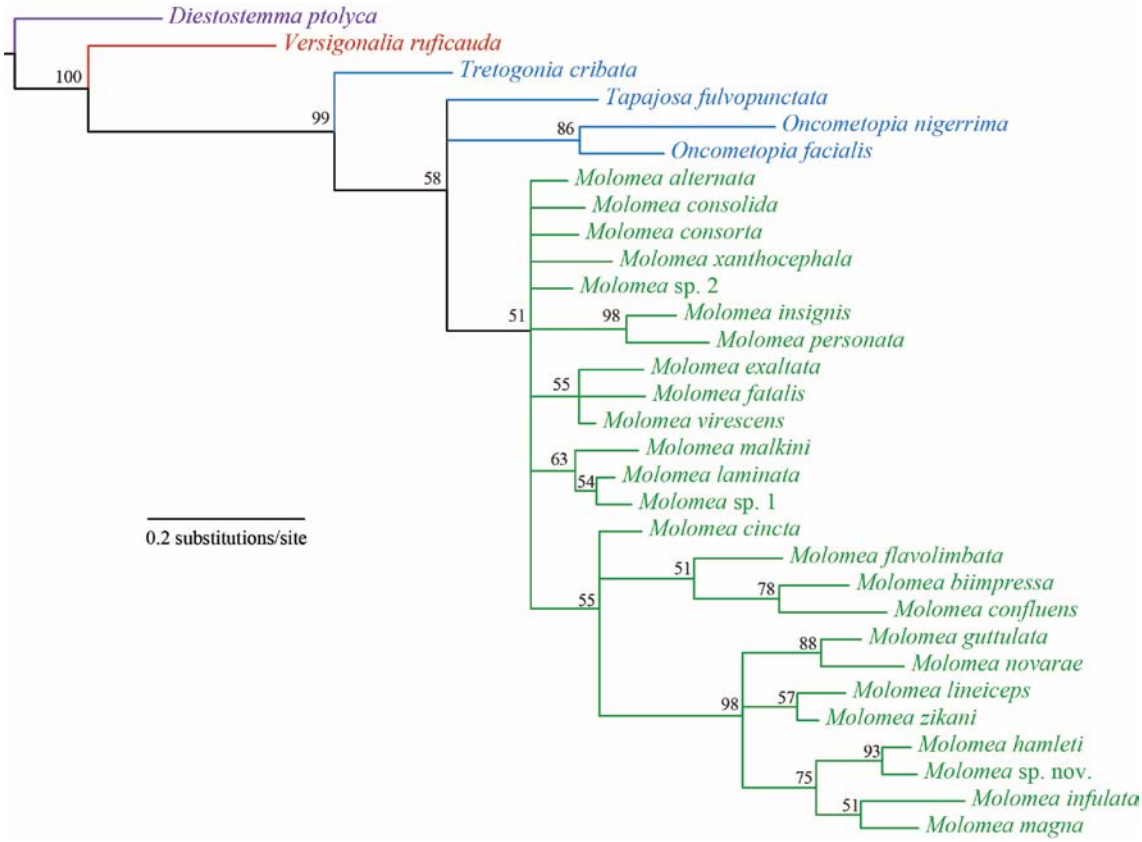

Figure 14: Majority-rule consensus of post-burnin trees found with Bayesian inference of the morphological dataset of *Molomea* (average lnL: -1064.59). Numbers above branches are posterior probabilities of clades.

4.2.2. MOLECULAR PHYLOGENY

All trees obtained were rooted on the "true" Proconiini based on a recent phylogeny (Takiya, 2007). Table 4 summarizes the information of the four genes used based on individual alignments shown in Appendix III. Hyper-variable regions of the gene 16S was excluded from initial analyses, but results were not topologically improved. Therefore, the complete alignment of the gene was used in all analyses in this study.

Table 4: Statistics of each gene alignment used to recover the phylogeny of *Molomea*. Models of molecular evolution were selected with AIC criterion. Length of the sequences in base pairs. *P* is the value of the qui-square test of homogeneity of base frequencies (calculated with PAUP*).

Gene	**Model of evolution**	**Length (bp)**	**Number of taxa**	**Variable sites (%)**	**Informative sites (%)**	***P***
COI	GTR+Γ+I	752	23	337 (45)	254 (34)	1.00
COII	GTR+Γ+I	564	19	269 (48)	182 (32)	1.00
16S	GTR+Γ+I	506	25	249 (49)	178 (35)	1.00
H3	GTR+Γ+I	336	26	87 (26)	62 (18)	1.00
Combined	-	2158	26	942 (44)	676 (31)	-

4.2.2.1. MAXIMUM LIKELIHOOD ANALYSES

Maximum Likelihood (ML) analyses were conducted for each gene separately and for four genes combined. The trees obtained are showed below with values of bootstrap above branches. Independent gene trees are very different topologically from another in both out- and ingroup relationships. Overall, very few branches had good statistical support.

The genus was recovered as monophyletic only in the individual analysis of the gene COII, which is the smallest molecular dataset. For the other three genes and the combined dataset with the four genes, the genus appears para- ou polyphyletic.

Furthermore, analyses of individual genes did not recover any of the groups found in morphological analyses, except for one. Group F from the morphological analyses was also recovered with molecular data, considering that in molecular datasets there were no representatives of *M. guttulata*, *M. novarae*, and *M. zikani*. This group appears in the 16S ML tree (*Molomea* sp. nov. not included) and in the combined tree (Fig. XX), but the internal relationships are different from those found with morphological characters. On the other hand, the combined molecular dataset strongly supports two alternative groups in the combined analyses that were corroborated by two individual genes studied:

ALTERNATIVE GROUP M (98% bootstrap in combined analysis): *M. infulata* and *M. lineiceps*.

This group is included in Group F and was recovered independently in analyses of COII and 16S (51% bootstrap).

ALTERNATIVE GROUP N (82% bootstrap in combined analysis): *M. virescens* and *M. exaltata*.

This group was recovered independently in analyses of COII and 16S (76% bootstrap).

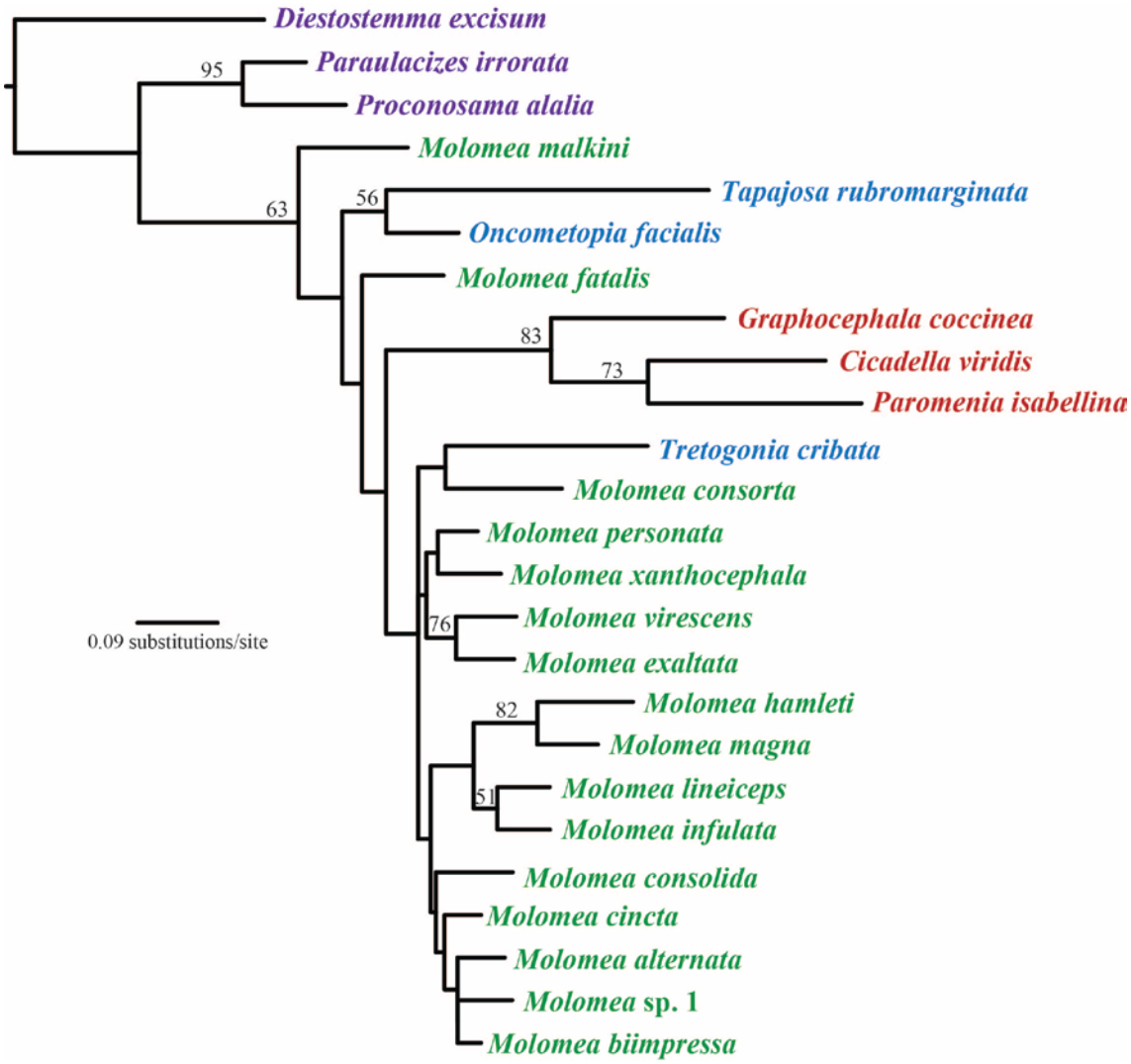

Figure 15: Best maximum likelihood tree for the gene 16S of *Molomea* (LnL: -4210.6785) using the GTR+I+G model. Numbers above branches are bootstrap values. Species colored in purple are Proconiini, red are Cicadellini, and blue are Oncometopiini. The genus *Molomea* is in green.

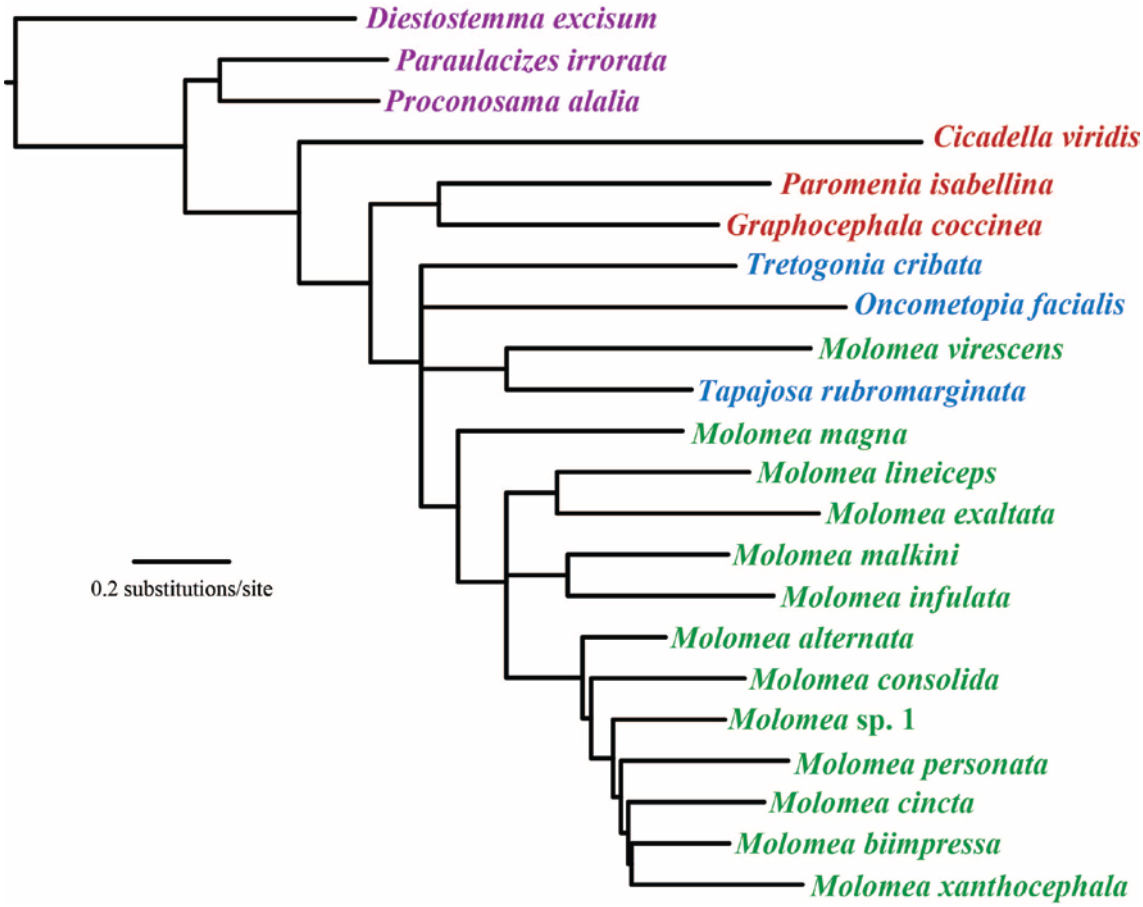

Figure 16: Best maximum likelihood tree for the gene COI of *Molomea* (lnL: -:6180.1433) using the GTR+I+G model. Numbers above branches are bootstrap values. Species in purple are Proconiini; species in red are Cicadellini; species in blue are Oncometopiini. The genus Molomea is in green.

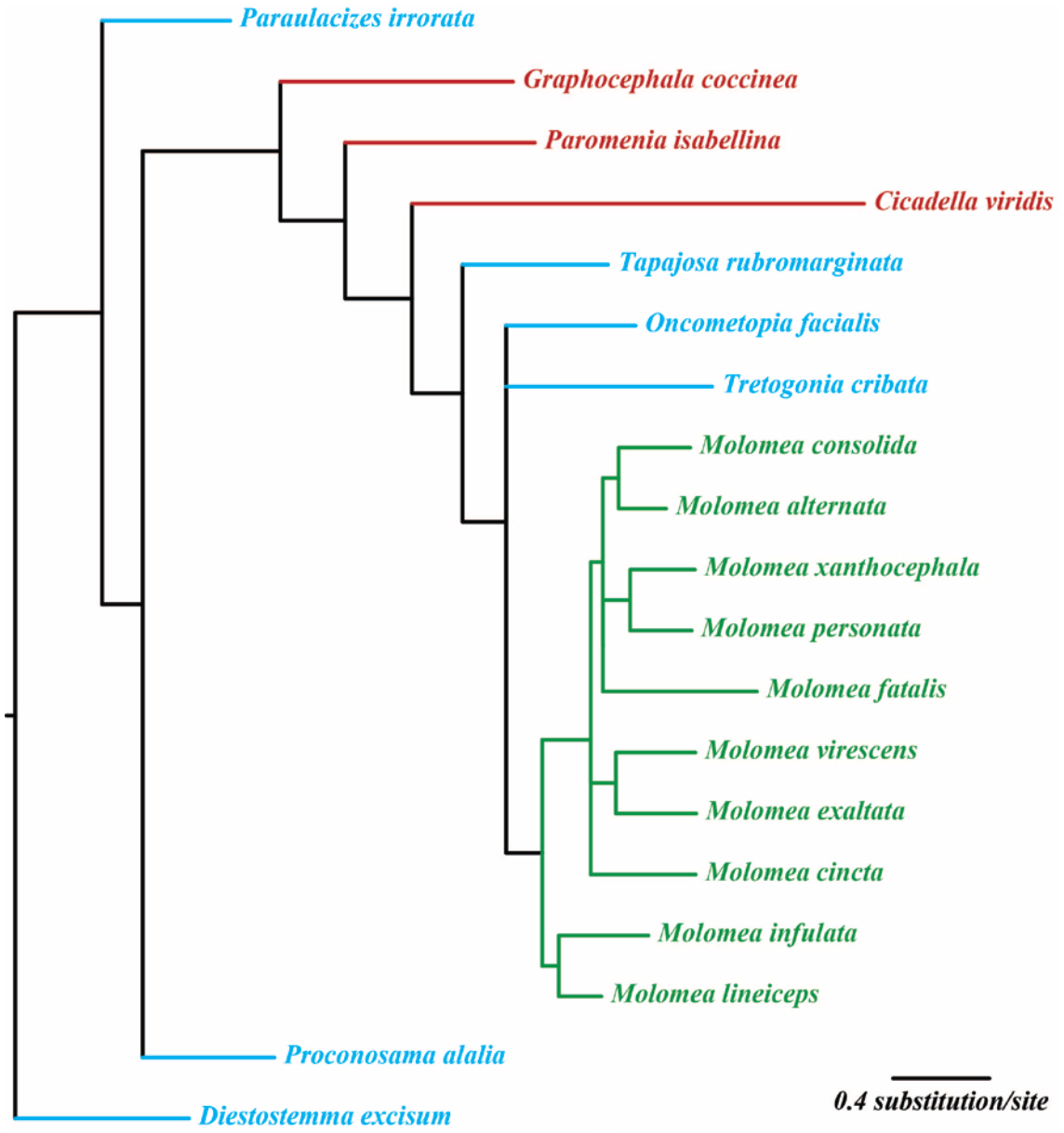

Figure 17: Best tree obtained with maximum likelihood for the gene COII (LnL: -4042.492) using the GTR+I+G model. Numbers above branches are bootstrap values. Species in purple are Proconiini; species in red are Cicadellini; species in blue are Oncometopiini. The genus *Molomea* is in green.

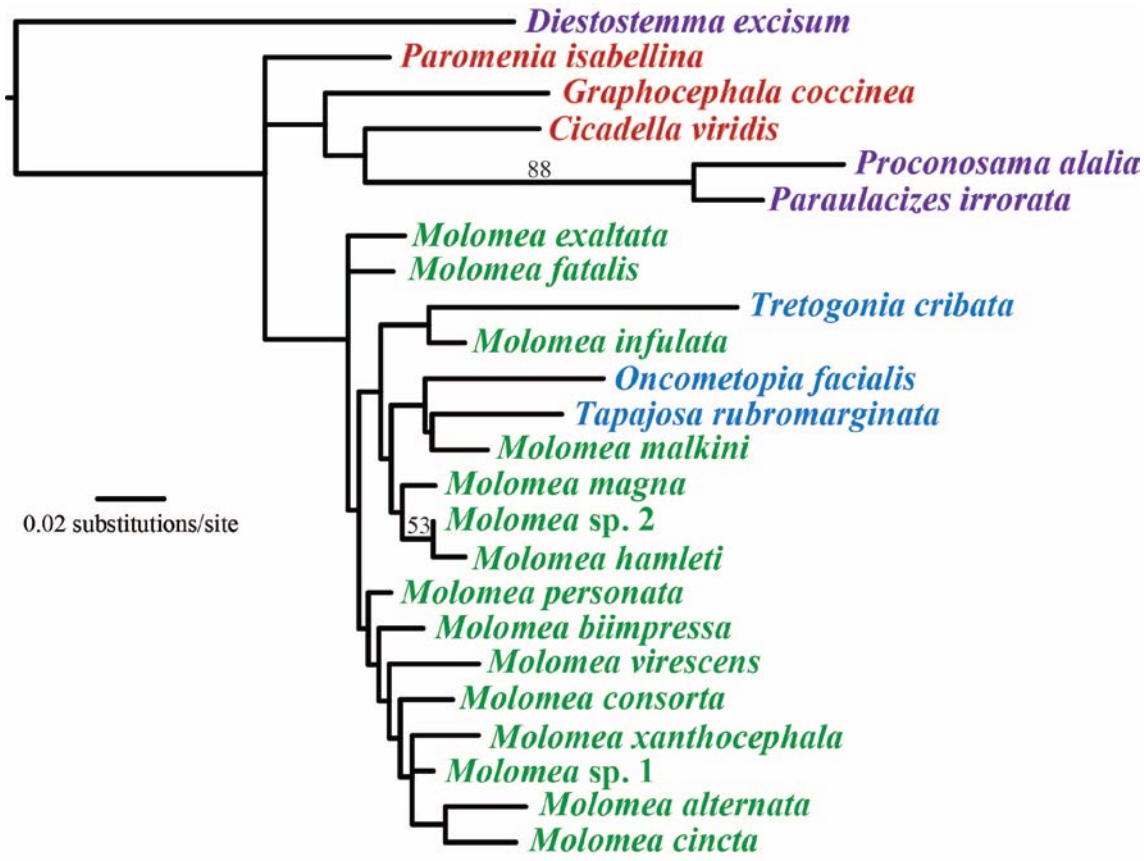

Figure 18: Best maximum likelihood tree for the gene H3 (lnL: -1660.536) using the GTR+I+G model. Numbers above branches are bootstrap values. Species colored in purple are Proconiini, red are Cicadellini, and blue are Oncometopiini. The genus *Molomea* is in green.

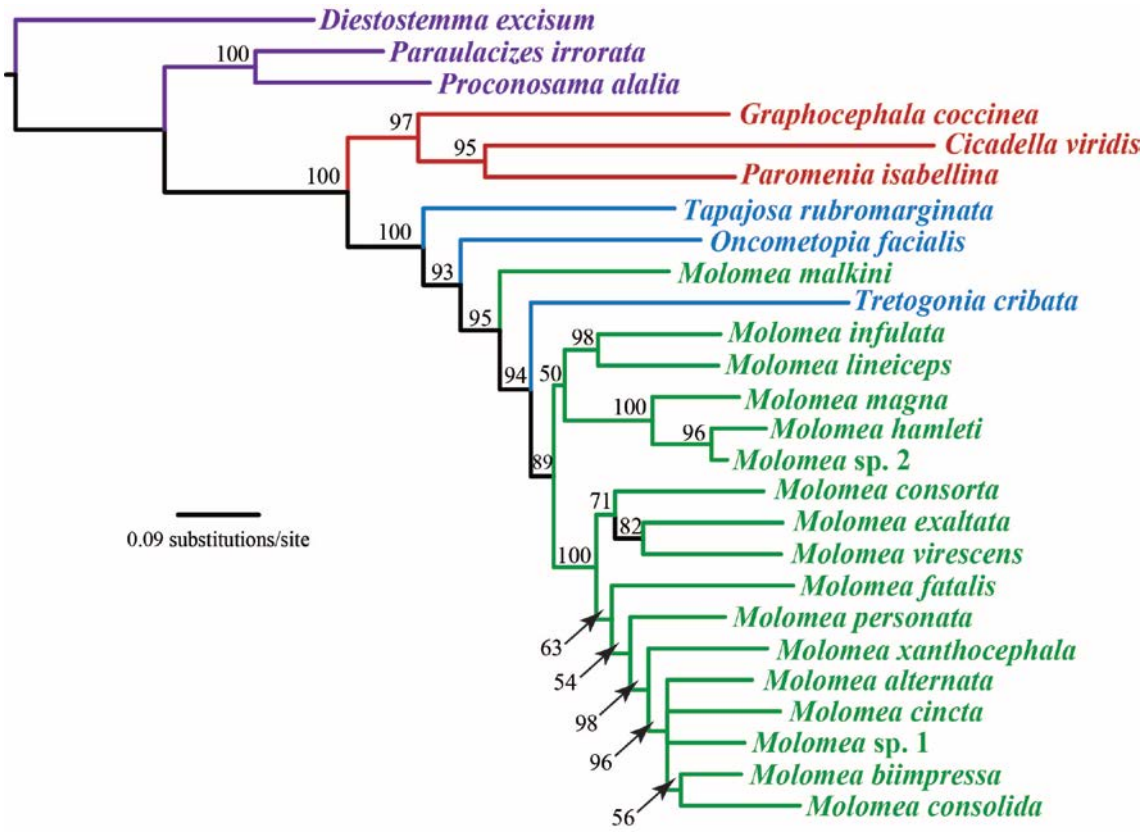

Figure 19: Best tree obtained with maximum likelihood for the four genes combined (16S, COI, COII and H3) using the GTR+I+G model for each partition (LnL: -6180.1433). Numbers above branches are bootstrap values. Species in purple are Proconiini; species in red are Cicadellini; species in blue are Oncometopiini. The genus *Molomea* is in green.

4.2.2.2. BAYESIAN INFERENCE

Bayesian inference analyses were also conducted for each gene separately and for the four genes combined, with *burnin* of 10% of the trees (total of 101 trees). The results are showed below (Figures 20-25) with posterior probability for clade support. Results are very similar to those recovered with maximum likelihood, but with more polytomies.

Molomea appears as monophyletic only in the analysis of COII, being recovered in a large polytomy with members of Oncometopiini in the analysis of COI and H3, Oncometopiini and Cicadellini in the analysis of 16S, and with *Tretogonia* nested within in the combined dataset analysis.

Identical to the ML analyses, Group F was the only group of the morphological analysis that appears in the Bayesian inference analyses of the molecular data. This group appears in the 16S tree and in the combined tree. Additionally, the strongly supported groups M and N are also recovered with the same individual and combined datasets.

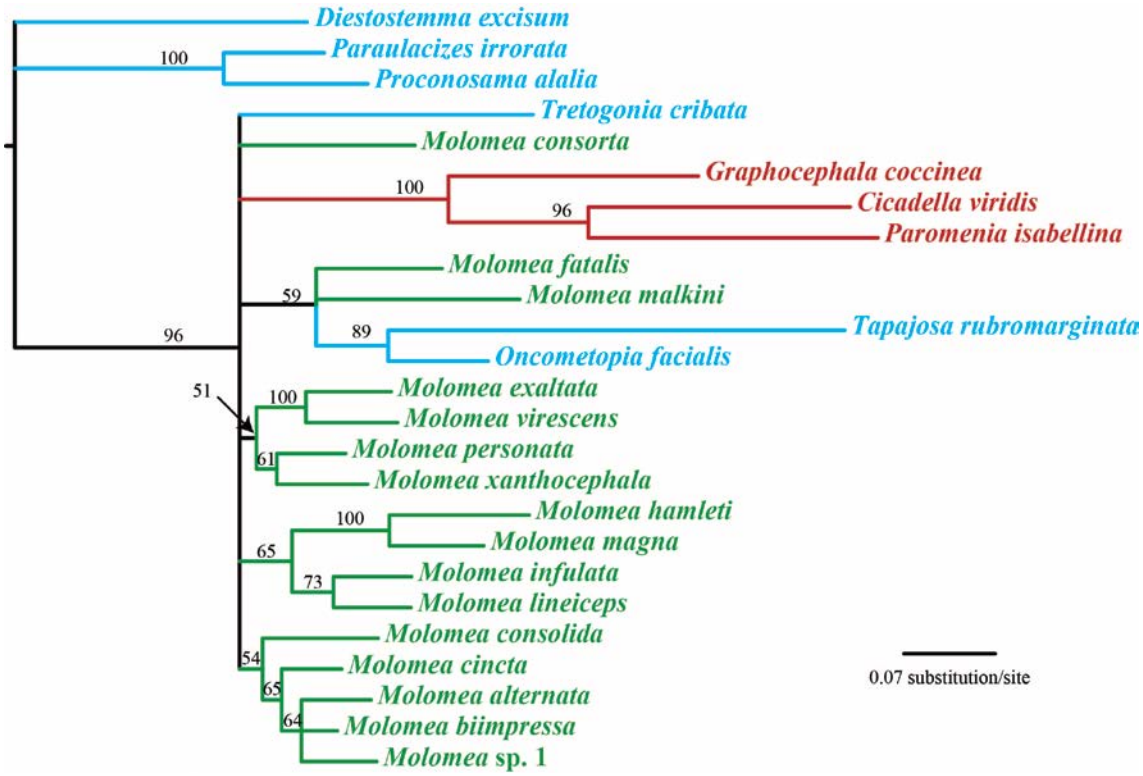

Figure 20: Bayesian consensus tree for the gene 16S of *Molomea* (lnL: -4235.520) using the GTR+I+G model. Numbers above branches are posterior probabilities. Species colored in purple are Proconiini, red are Cicadellini, and blue are Oncometopiini. The genus *Molomea* is in green.

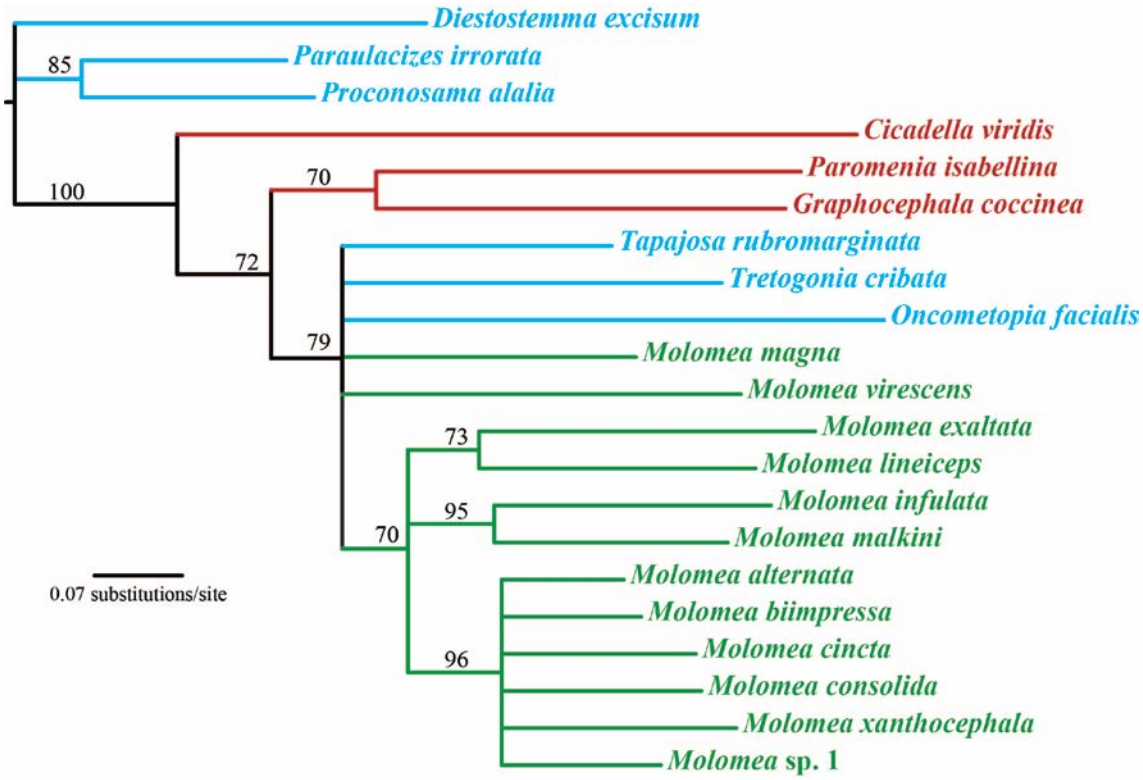

Figure 21: Consensus tree obtained with Bayesian inference for the gene COI (LnL: -6030.040) using the GTR+I+G model. Numbers above branches are posterior probabilities. Species in purple are Proconiini; species in red are Cicadellini; species in blue are Oncometopiini. The genus *Molomea* is in green.

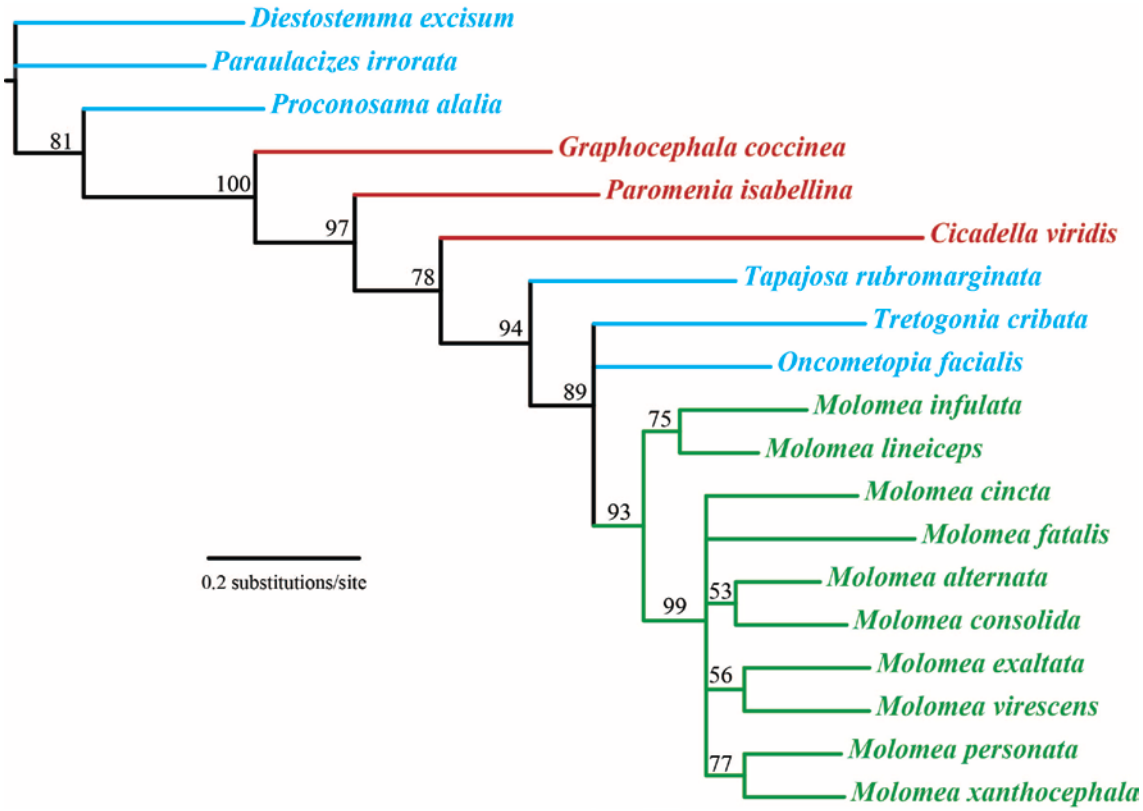

Figure 22: Consensus tree obtained with Bayesian inference for the gene COII (LnL: -4064.152) using the GTR+I+G model. Numbers above branches are posterior probabilities. Species in purple are Proconiini; species in red are Cicadellini; species in blue are Oncometopiini. The genus *Molomea* is in green.

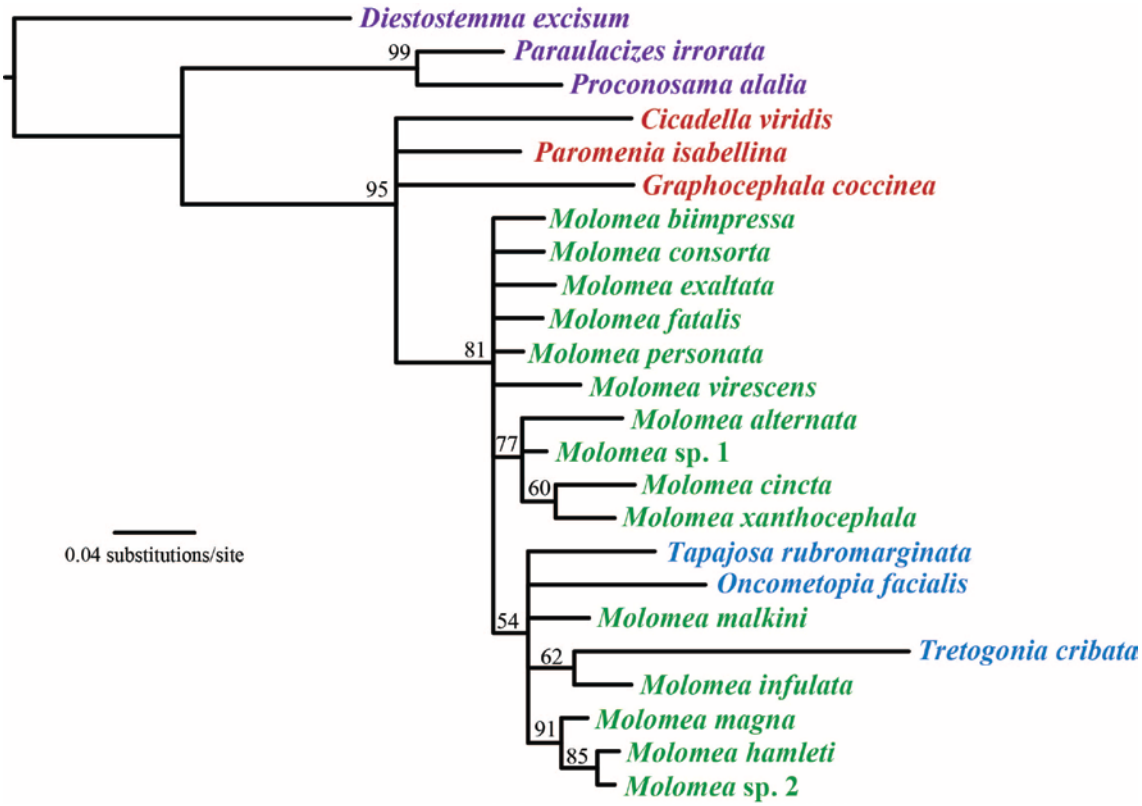

Figure 23: Consensus tree obtained with Bayesian inference for the gene H3 (LnL: -1682.530) using the GTR+I+G model. Numbers above branches are posterior probabilities. Species in purple are Proconiini; species in red are Cicadellini; species in blue are Oncometopiini. The genus *Molomea* is in green.

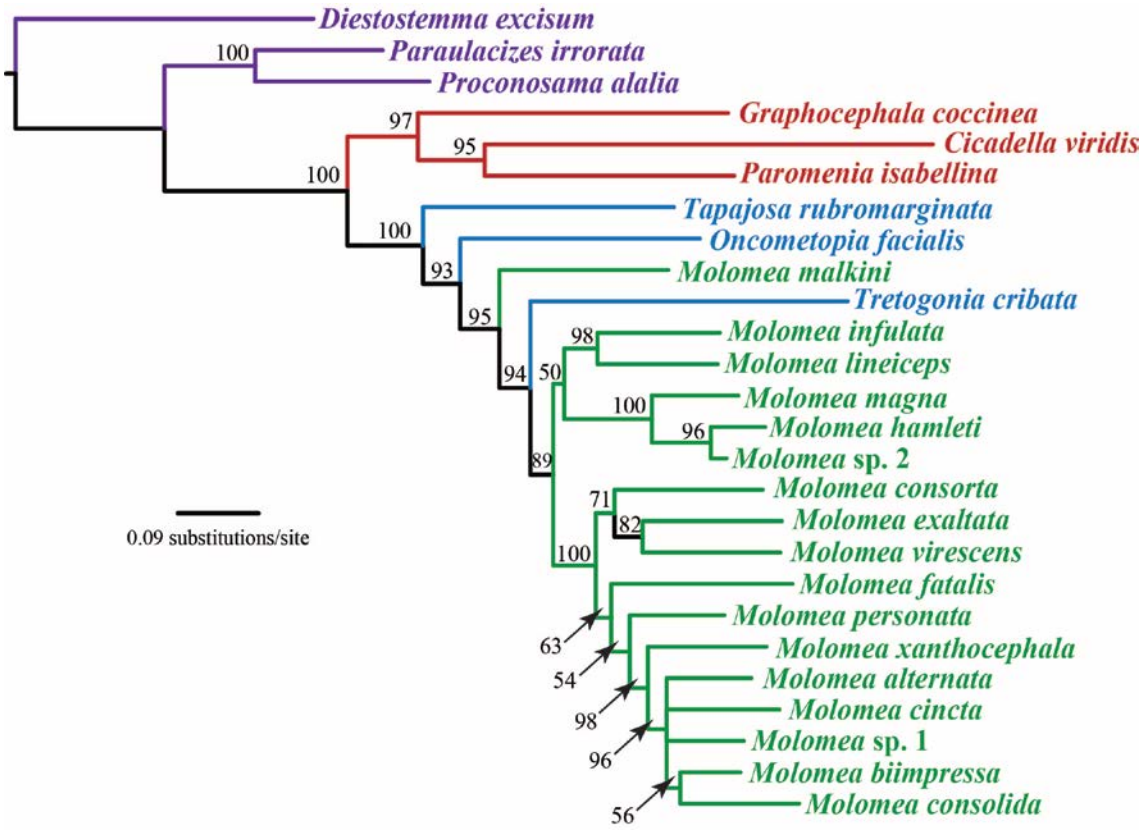

Figure 24: Consensus tree obtained with Bayesian inference for the four genes combined (16S, COI, COII and H3) using the GTR+I+G model for each partition (LnL: -16382.06). Numbers above branches are posterior probabilities. Species in purple are Proconiini; species in red are Cicadellini; species in blue are Oncometopiini. The genus *Molomea* is in green.

4.2.2.3. PARSIMONY ANALYSES

Parsimony analyses were performed for each gene separately.

The analysis of the gene 16S found seventeen most parsimonious trees, and the strict consensus is showed below (Figure XX). It did not recover the same relationships as the analysis of maximum likelihood and Bayesian inference for this gene. *Molomea consorta* appears as sister group to the clade that includes all the *Molomea* (except of *M. fatalis*) and also *Tretogonia cribata* and *Oncometopia facialis*. The latter species appears as sister group of *M. malkini* with low clade support, and the position of *M. fatalis* is uncertain. *Molomea personata* appears as sister group of *Tretogonia cribata*, with no clade support.

The analysis of the gene COI retained ten most parsimonious trees, and the strict consensus (Figure XX) is different from the ML and Bayesian analyses. *Molomea lineiceps* was recovered as sister group of the Cicadellini species *Graphocephala coccinea*, and this group appears as sister group of a clade formed by all the other *Molomea* and also *Tretogonia cribata* and *Paromenia isabellina*.

The analysis of the gene COII found only one most parsimonious tree. The outgroup *Tretogonia cribata* was recovered as sister group of *M. consolida*, which appeared as sister group of *M. alternata* on the ML and Bayesian analyses. The latter species appears as sister group of *M. fatalis.*

The analysis for the gene H3 retained 5,920 most parsimonious trees and the strict consensus recovered only the clade formed by *M. hamleti, M. magna* and *Molomea* sp. 2, with low branch support, but it did not recover the internal relationships of this clade.

Clearly the results found are not compatible to the ones found with the probabilistic methods. The parsimony analysis is a method that infers a phylogeny by calculating how many times a certain event has happened. The tree with the smallest number of these events is considered the most parsimonious tree and therefore the best tree to reflect the phylogeny of a given group. This method has been largely applied to morphological data. However, some authors argue that it can be misleading when applied to molecular data particularly if the sequences are subject to many homoplasies (Felsenstein, 1978). Probabilistic methods consider a model of evolution that can incorporate substitution rates and other parameters (Pereira *et al.* 20012 in Matioli, 2012). Therefore, it is not unusual to obtain different topologies using both parsimony and probabilistic methods.

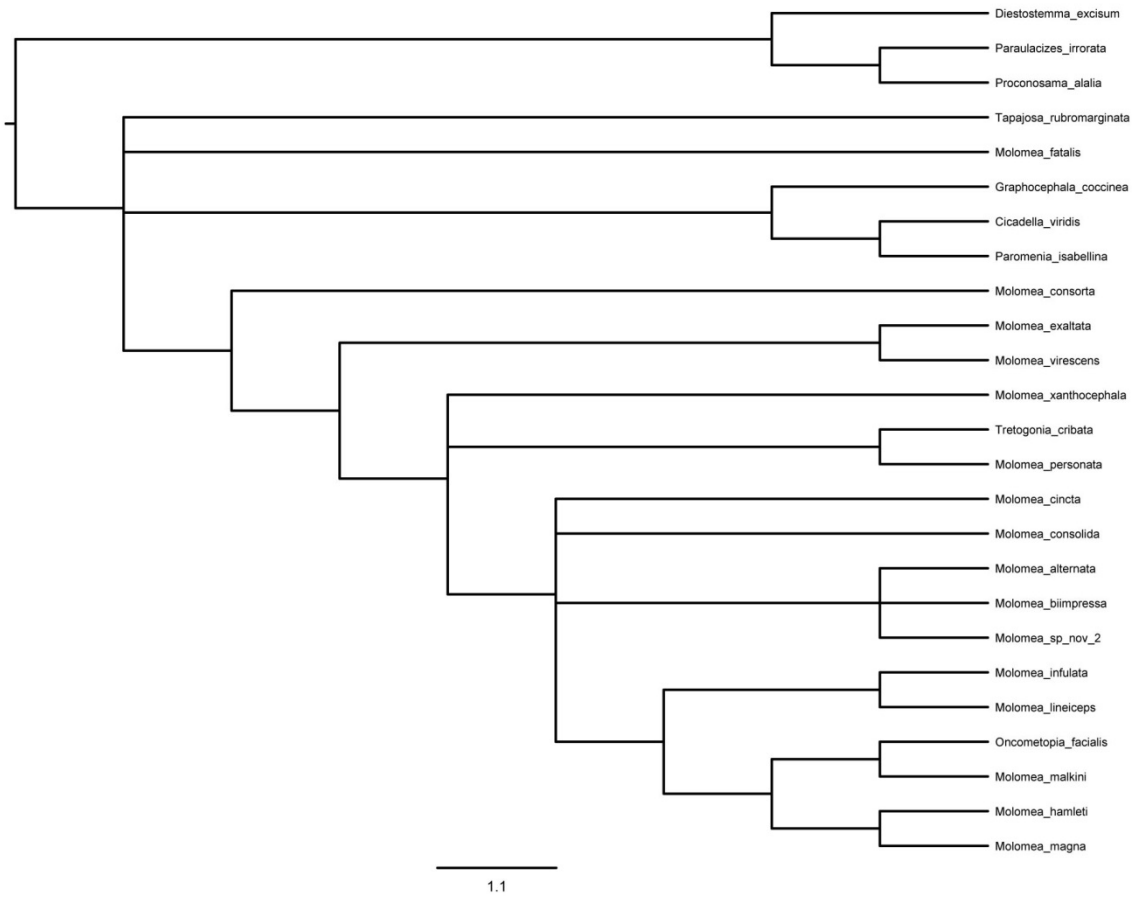

Figure 25: Strict consensus of 17 most parsimonious trees obtained for the gene 16S of *Molomea* (L=889). Numbers above branches are bootstrap values. Species colored in purple are Proconiini, red are Cicadellini, and blue are Oncometopiini. The genus *Molomea* is in green.

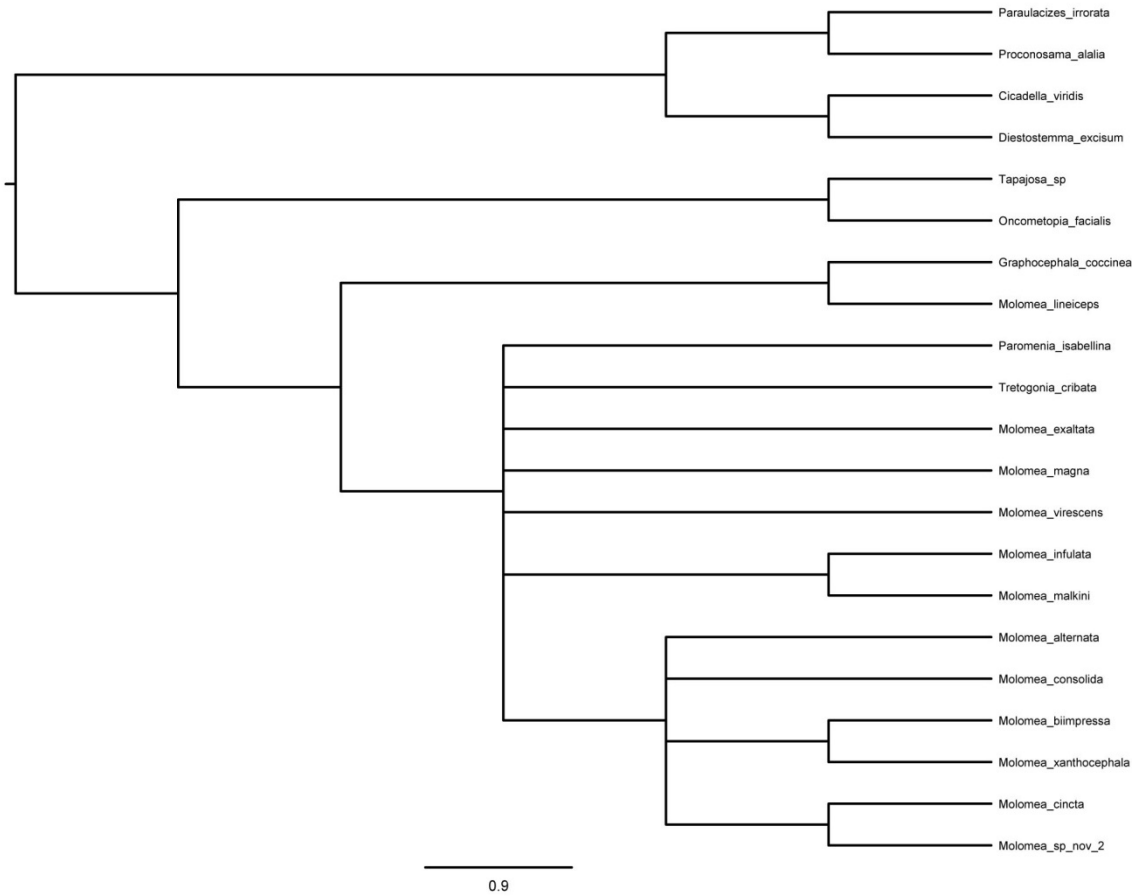

Figure 26: Strict consensus of 10 most parsimonious trees obtained for the gene COI. Numbers above branches are bootstrap values. Species in purple are Proconiini; species in red are Cicadellini; species in blue are Oncometopiini. The genus *Molomea* is in green.

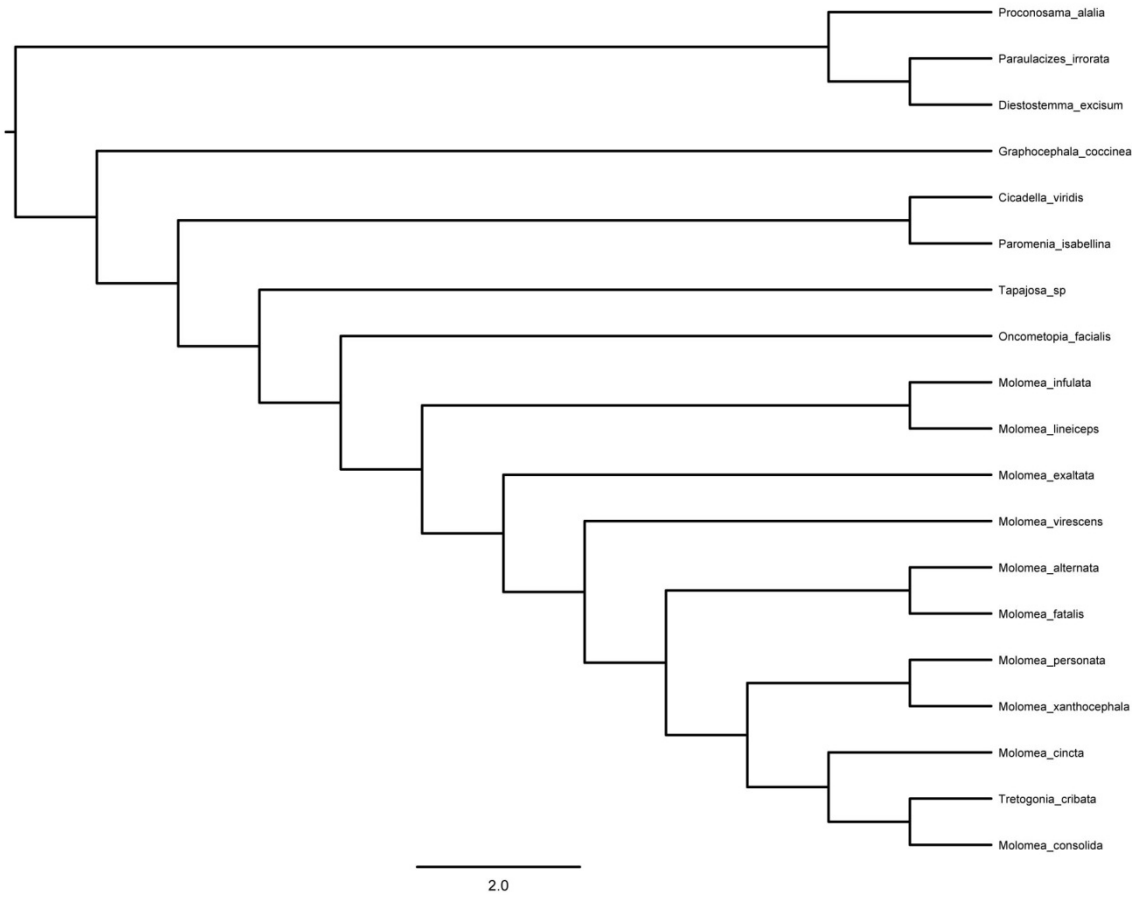

Figure 27: Most parsimonious tree obtained for the gene COII of *Molomea*. Numbers above branches are bootstrap values. Species colored in purple are Proconiini, red are Cicadellini, and blue are Oncometopiini. The genus *Molomea* is in green.

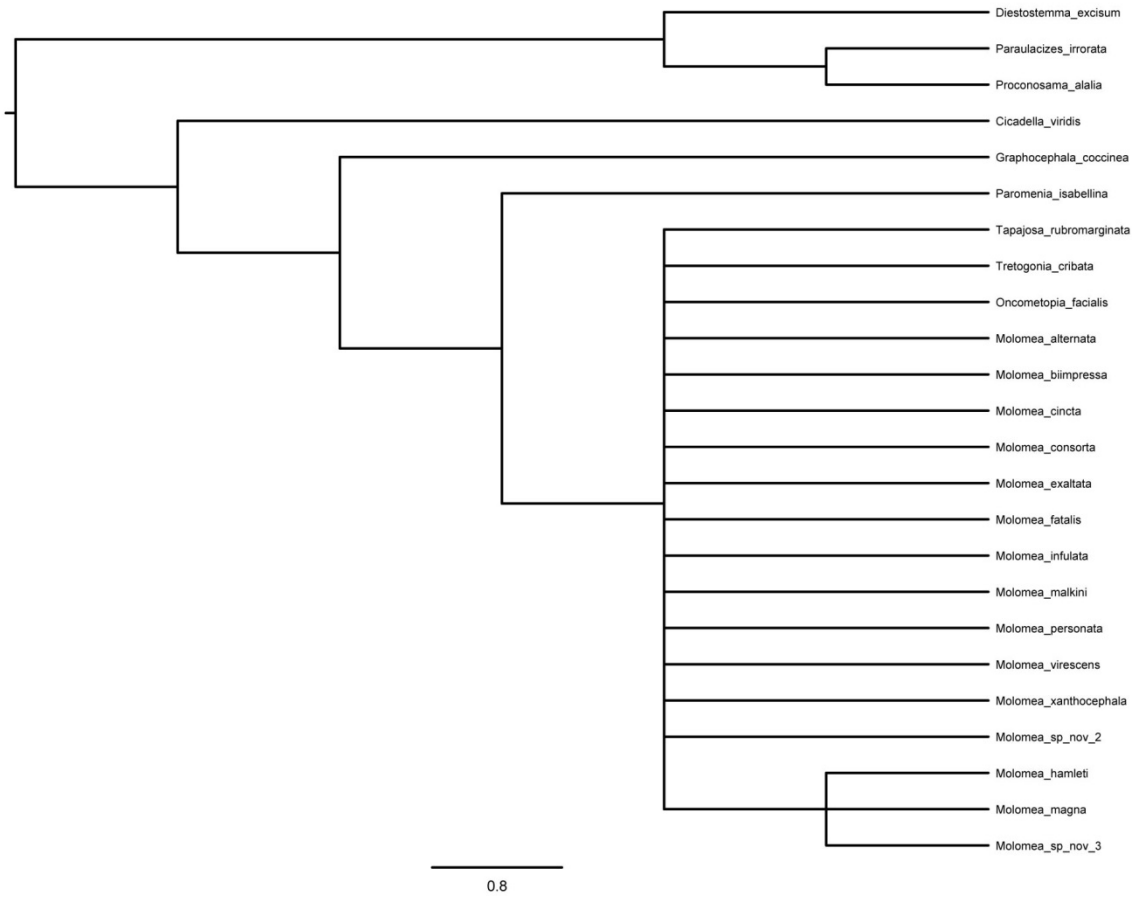

Figure 28: The most parsimonious tree obtained for the gene H3.Numbers above branches are bootstrap values. Species in purple are Proconiini; species in red are Cicadellini; species in blue are Oncometopiini. The genus *Molomea* is in green.

4.2.3. COMBINED DATA

The combined dataset of morphological and molecular characters was analyzed using parsimony, ML, and BI. Trees obtained are showed below (Figures 29-31).

The parsimony analysis found twenty-seven most parsimonious trees, and the genus is recovered as monophyletic (Figure XX). Groups C, H, I and K of the morphological analyses were the only ones found.

The Bayesian analysis did not recover *Molomea* as monophyletic, with *Tretogonia cribata* in a polytomy with internal clades of the genus (Figure XX). It recovered groups C, F, I and K but with different internal relationships.

Alternative Group N, *Molomea virescens* + *M. exaltata*, is recovered in all combined dataset analyses. *Molomea insignis* + *M. personata* (Group C) were recovered as sister groups in all analyses based on the morphology datasets and combined datasets. *Molomea insignis*, however, was not available for DNA extraction, and in the molecular analyses *M. personata* was recovered as sister to *M. xanthocephala.* The latter was not found to be related to Group C in the morphological analyses, so the inclusion of molecular data of *M. insignis* could help to solve the relationship of these three species.

The new species of *Molomea* is recovered as the sister group of *M. hamleti*. This result was already expected since the morphology of males of both species is really similar. They are the only species of *Molomea* with subgenital plates reaching the midlength of pygofer and with indistinct pre-apical lobe of styles. Unfortunately, female and molecular data were not available to corroborate this relationship, because the only specimen of *Molomea* sp. nov. known is a rather old pinned male.

The most problematic species is *M. malkini*. It appears as sister group of *M. infulata* in some molecular analyses, while in others the species is not most closely related to other *Molomea,* and the morphological analyses places is as related to *M. malkini, M. laminata,* and *Molomea* sp. 2.

Further efforts to collect fresh material and new attempts to obtain DNA from pinned specimens may help elucidate the relationships among species of *Molomea*. Additionally, more genes will be included in the analyses, which could help solving the uncertain position of some taxa and increasing clade support. Attempts to obtain males and females that were not available for the morphological study, especially with new collecting efforts, will also help improve the phylogenetic analyses.

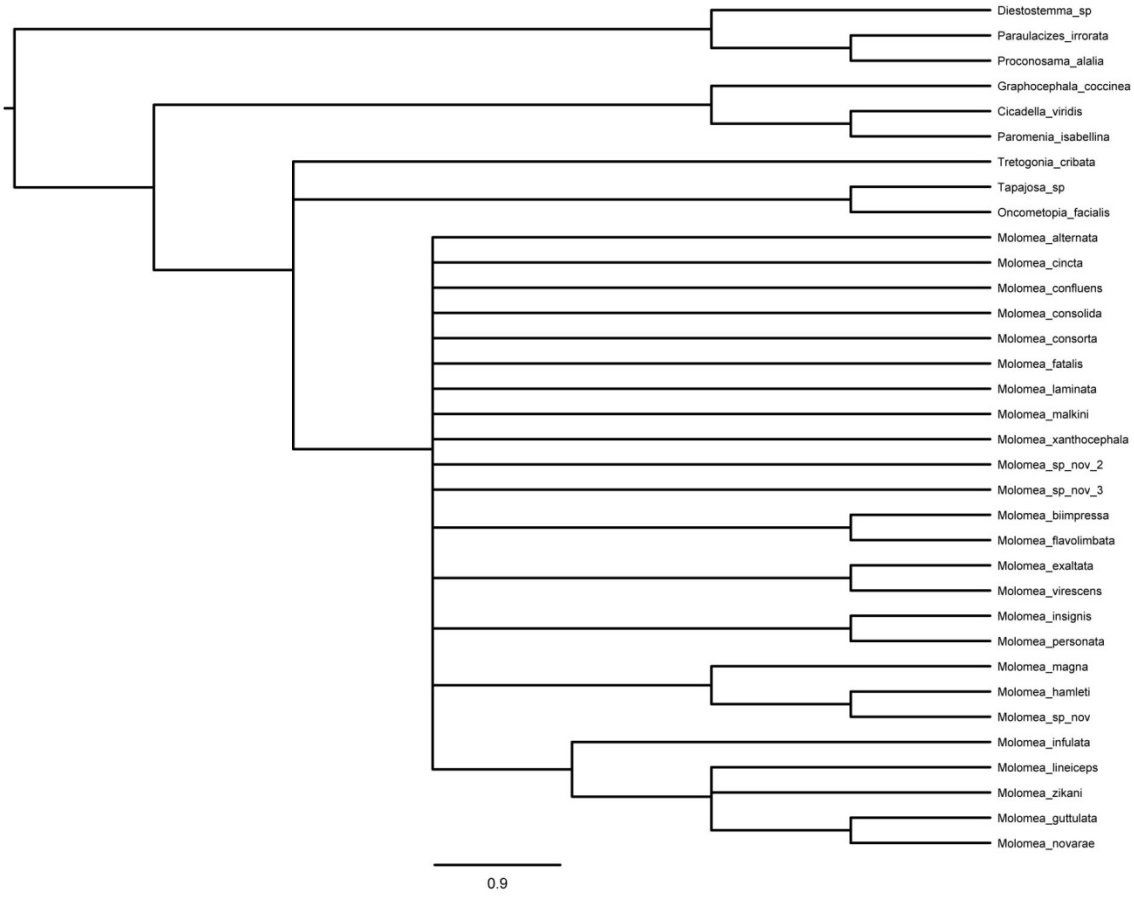

Figure 29: Strict consensus of 27 most parsimonious trees for the combined dataset of morphology, 16S, COI, COII and H3. Numbers above branches are bootstrap values. Species in purple are Proconiini; species in red are Cicadellini; species in blue are Oncometopiini. The genus *Molomea* is in green.

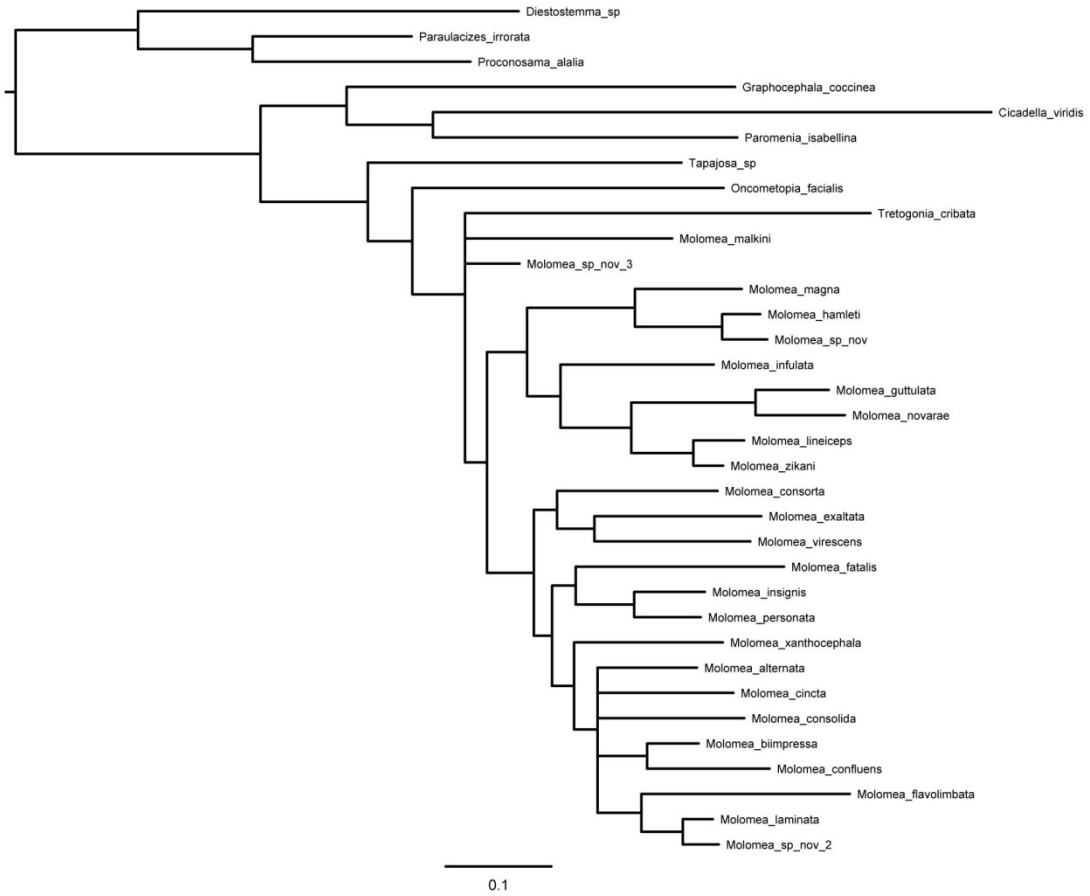

Figure 30: Majority-rule Bayesian consensus tree for the combined dataset of morphology, 16S, COI, COII and H3 using the MK2 model for the morphological and GTR+I+G model for each of the molecular partitions (lnL: -17407.24). Numbers above branches are posterior probabilities. Species in purple are Proconiini; species in red are Cicadellini; species in blue are Oncometopiini. The genus *Molomea* is in green.

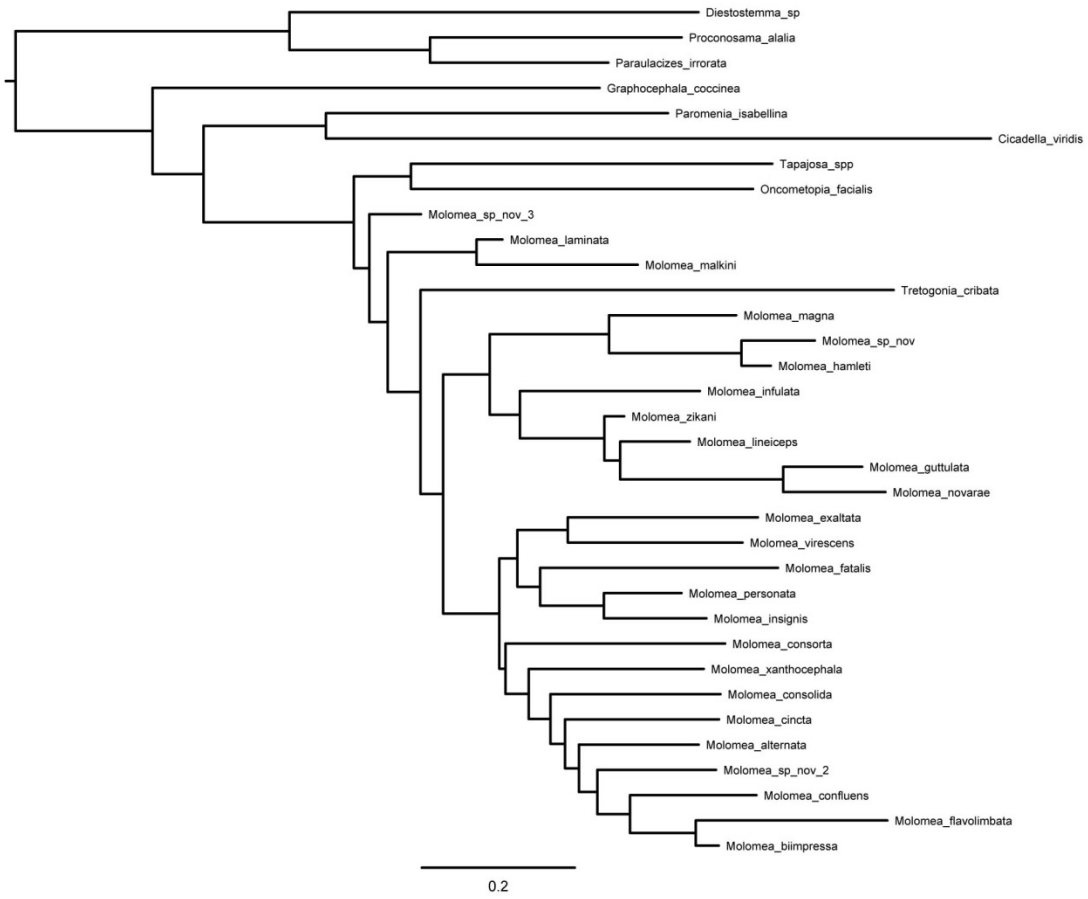

Figure 31: Best tree obtained for the combined data set (morphology, genes 16S, COI, COII and H3) using the GTR+I+G model for the molecular partitions and the MK2 model for the morphological partition (LnL: -17299.2648). Numbers above branches are bootstrap values. Species in purple are Proconiini; species in red are Cicadellini; species in blue are Oncometopiini. The genus *Molomea* is in green.

4.2.4. EFICIENCY OF THE MOLECULAR DATASET

Regarding the base composition of the four genes studied, there is a clear discrepancy between the three mitochondrial genes and the nuclear one. COI, COII, and 16S have more than 70% of A and T, while H3 has only 38% of A and T and about 62% of C and G (Table 6). None of the genes showed a significantly heterogeneity of base composition between the studied taxa (number of *P* in table 4).

Table 6: Percentage of bases for each gene alignment of *Molomea*.

Gene	Purines		Pyrimidines	
	A	**G**	**C**	**T**
COI	33.32%	14.51%	13.77%	38.4%
COII	37.13%	10.98%	13.13%	38.76%
16S	44,6%	7,6%	16%	31,8%
H3	22.68%	28.64%	33.07%	15.61%

The phylogenetic information of a gene may be calculated using different kinds of tests. The PTP (Permutation Tail Probability) test (Archie, 1989) implemented in PAUP* compares the score of the most parsimonious tree generated by the original dataset with the scores of the most parsimonious trees found after states have been randomly permuted within each character (Archie, 1989). This test was performed for the four genes individually, and showed that the values were all significant (P = 0.001), demonstrating that the most parsimonious trees found for the four original alignments were not within the distribution curve of the values of the trees after the randomization and, therefore, may have reliable phylogenetic information for parsimony analyses.

However, another approach to testing the phylogenetic signal of a molecular partition is looking at the amount of transitions and transversions as a way of searching for possible substitution saturation of the sequences. The three mitochondrial genes (COI, COII, and 16S) showed a higher rate of transversions than transitions (Table 7). COI and COII show rates of 43.45% and 47.63% of transitions, respectively, while 16S shows only 29.50% of transitions against 70.50% of transversions. The gene H3 was the only one with a higher amount of transitions, with 53.70% against 46.30% of transversions.

Table 7: Percentages of transitions (Ts) and transversions (Tv) for each gene alignment of *Molomea*.

Gene	Transitions		Transversions				Total	
	AG	CT	AC	AT	CG	GT	Ts	Tv
COI	17.04%	26.41%	7.13%	42.66%	1.7%	5.05%	43,45%	56,55%
COII	19.7%	27.93%	6.66%	38.56%	2.01%	5.14%	47.63%	52.37%
16S	10.52%	18.98%	11.98%	55.47%	0.44%	2.61%	29.5%	70.5%
H3	22.24%	31.47%	17.11%	5.92%	12.08%	11.19%	53.7%	46.3%

Sequences with higher transversion rates may be saturated, since the repair system of the DNA is much more sensible to detect transversions than transitions, resulting in a normally higher rate of transitions (Snustad & Simmons, 2000). Substitution saturation weakens the phylogenetic signal of the sequence, because the similarities between a pair of sequences may not be due to a common ancestor (Xia *et al.*, 2003). Plotting the number of transitions and transversions against the genetic divergence between sequences is a good way to evaluate their intrinsic rate and detect saturation (Schneider, 2007). Figures 32-35 show the saturation plots of the four genes, using the TN93 distance (Tamura & Nei, 1993), which assumes unequal base frequencies and different nucleotide substitution rates for purines and pyrimidines transitions.

The gene 16S shows a high degree of saturation (Fig. 32), since the rate of transversions (in green) is much higher than the number of transitions (in blue), which appear to have reached a plateau, demonstrating that the sequence is probably undergoing a significantly amount of saturation.

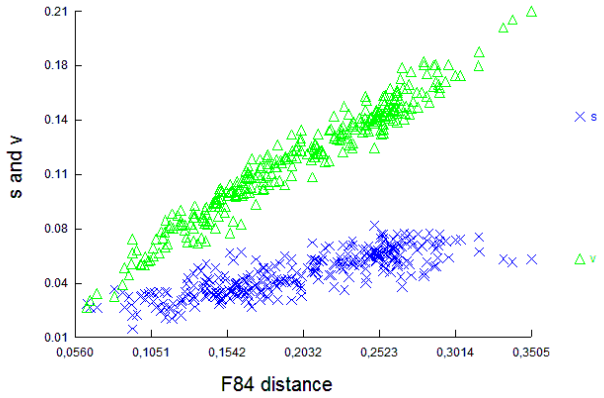

Figure 32: Saturation plot of the gene 16S with the number of transitions (blue X) and transversions (green triangles) versus the Kimura's two parameter distance.

The genetic code for aminoacid translation from DNA is called degenerated or redundant because a single amino acid can be coded by more than one codon (sequences of three nucleotides). A mutation on the third position of the codon is more likely to be neutral, since this position is the most redundant of the three. Hence, it can accumulate a greater amount of changes than the first and second positions without affecting the production of a protein (Snustad & Simmons, 2010) Therefore, the third position of the codons of the three protein-coding genes, COI, COII and H3, was analyzed separately. The gene COI show signs of saturation for all codon positions (Fig. 33), but it is especially strong in the third position of the codon, as expected. The COII also show signs of saturation of the second and third position of the codons, but the first position still shows a linear rate of transitions and transversions, transitions showing a higher rate than transversions. The only gene that appears not to undergo substitution saturation is the nuclear gene H3, however, it is not clear if the third position has a significant amount of saturation since the linear distributions of transversions and transitions coincide.

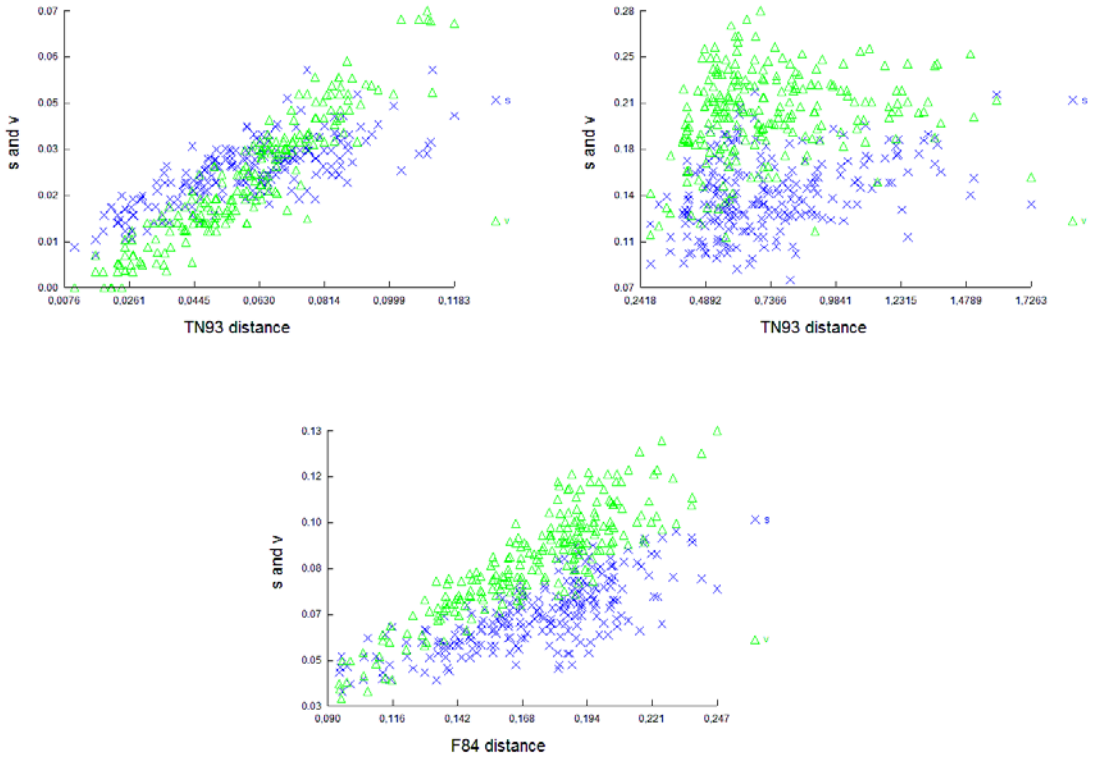

Figure 33: Saturation plot of the gene COI with the number of transitions (blue X) and transversions (green triangles) versus the TN69 distance. Plot A: First and second positions of the codons only. Plot B: Third position of the codons only. Plot C: The three positions analyzed together.

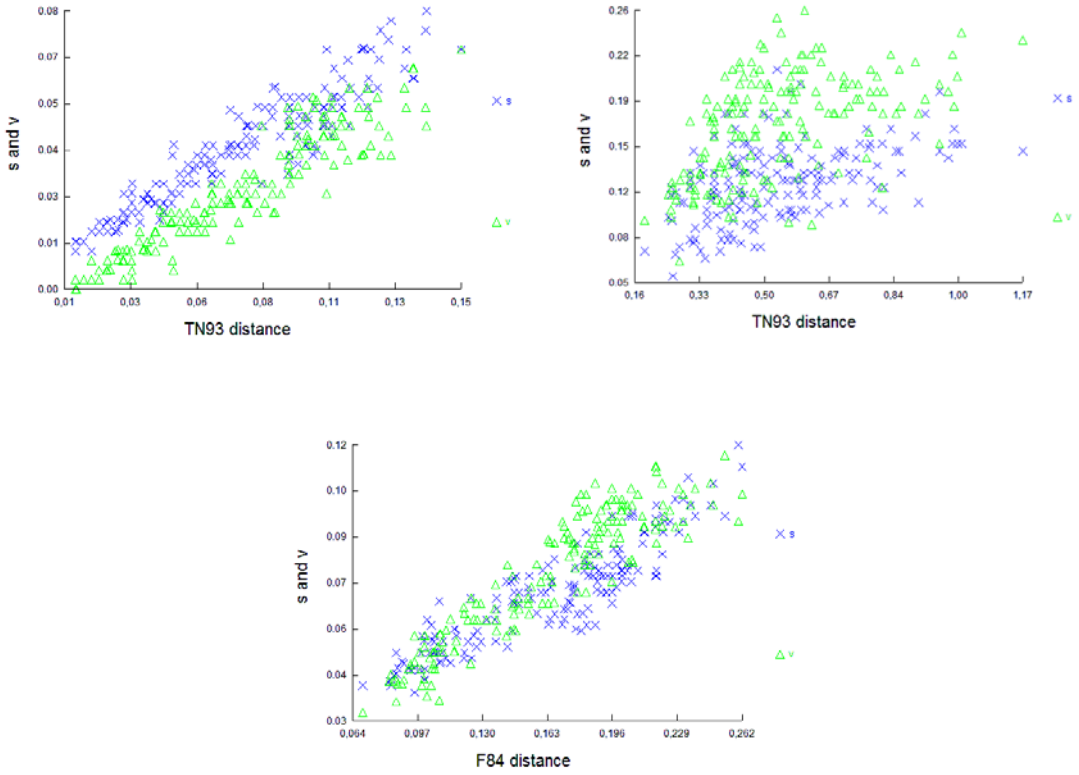

Figure 34: Saturation plot of the gene COII with the number of transitions (blue X) and transversions (green triangles) versus TN69 distance. Plot A: First and second positions of the codons only. Plot B: Third position of the codons only. Plot C: The three positions analyzed together.

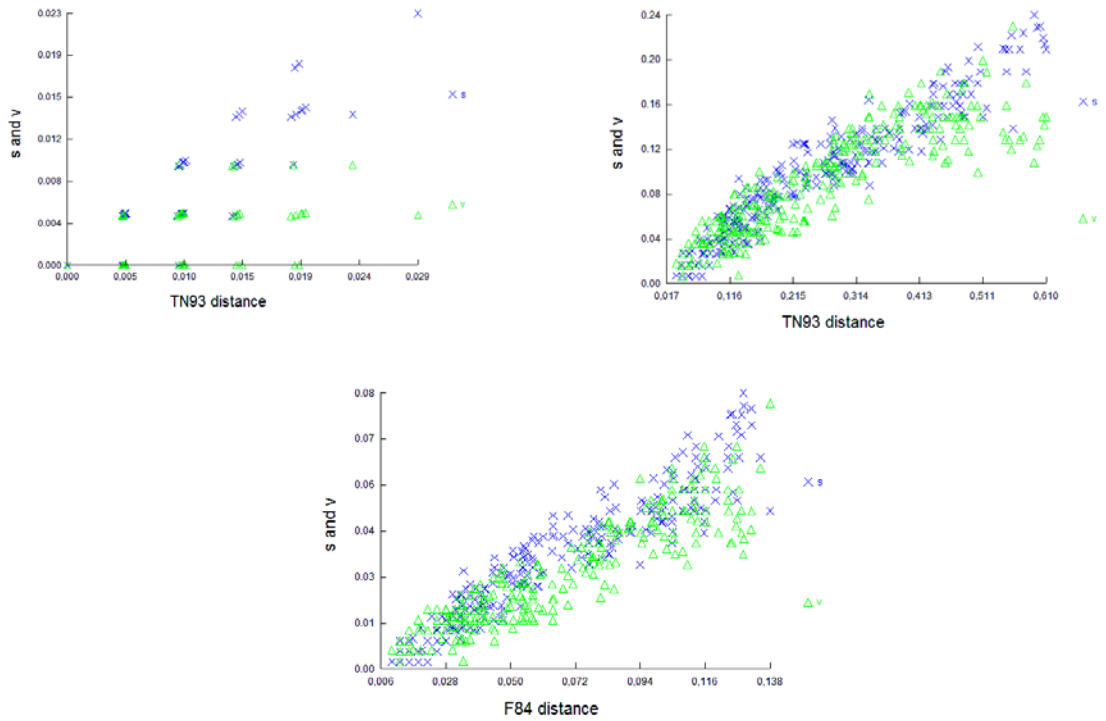

Figure 35: Saturation plot of the gene H3 with the number of transitions (blue X) and transversions (green triangles) versus the Kimura's two parameter distance. Plot A: First and second positions of the codons only. Plot B: Third position of the codons only. Plot C: The three positions analyzed together.

There are other tests available to test the amount of substitutions saturation of a DNA sequence and infer the quality of the phylogenetic information. The Xia's test (Xia *et al.*, 2003) is based on the entropy of the sequence, and compares the index of substitution saturation (Iss, calculated dividing the mean value of entropy by the full substitution saturation entropy of the sequence) to the critical index of substitution saturation (Iss.c) at which the sequences will begin to fail to recover the true tree for the group, both for symmetrical and asymmetrical topologies (Xia *et al.*, 2003). If Iss is significantly lower than Iss.c (P<0.01) than there is little saturation in the sequence. Results of the alignments studied herein are showed in Table 8.

Similarly to the saturation plot results, the gene 16S is apparently saturated in both symmetrical and extremely asymmetrical trees, making this gene a poor phylogenetic marker for this analysis. COI shows Iss values lower than Iss.c when the three positions of the codons are analyzed together. However, when only the third position is analyzed, there is significant signal for saturation (in symmetrical

topologies). The same happens with COII (in symmetrical topologies) and H3 (in both symmetrical and asymmetrical topologies), demonstrating that third codon positions of these genes may not contain reliable phylogenetic information and may be removed in future analyses.

Table 8: Xia's saturation test for genes and codon positions (pos) of sequences of *Molomea*. Iss: index of substitution saturation; Iss.c: critical index of substitution saturation; *P*: probability of the two-tailed test. When P>0.01, sequences show signs of saturation.

Gene	Iss	Symmetrical tree		Asymmetrical tree	
		Iss.c	***P***	**Iss.c**	***P***
COI	0.3083	0.7510	0.0000	0.5020	0.0000
COI pos1&2	0.1773	0.7138	0.0000	0.4637	0.0000
COI pos3	0.7034	**0.6323**	**0.0156***	0.3963	0.0000
COII	0.2198	0.7252	0.0000	0.4926	0.0000
COII pos1&2	0.1089	0.6848	0.0000	0.4550	0.0000
COII pos3	0.5395	**0.6029**	**0.0545***	0.4047	0.0001
16S	0.6055	**0.7150**	**0.0574***	**0.4456**	**0.0056***
H3	0.1470	0.6713	0.0000	0.4109	0.0000
H3 pos1&2	0.0467	0.6138	0.0000	0.3741	0.0000
H3 pos3	0.3631	**0.4793**	**0.0270***	**0.3463**	**0.7478***

Finally, based on the average value of the free parameters sampled during the Bayesian analyses of each gene partition (Table 9), alpha parameter values were all moderate. Gene H3 has the highest alpha, indicating that the rate of substitutions across sites is conservative, possibly a bias due to the high proportion of invariant sites.

Table 9: Average values of free parameters of the models of evolution for each gene sampled by the Bayesian inference: the six rate parameters (r (A-C) etc); the four nucleotide frequencies (pi (A)); the shape parameter of the Γ distribution of rate variation across sites (alpha); and the proportion of invariables sites (pinvar).

Parameter	Gene partition			
	COI	**COII**	**16S**	**H3**
r (A-C)	0.03148052	0.03326479	0.05778083	0.1223420
r (A-G)	0.2543192	0.2964992	0.2395895	0.2101128
r (A-T)	0.03493397	0.01288020	0.2038899	0.1616753
r (C-G)	0.1267848	0.2164302	0.01409368	0.02036329
r (C-T)	0.5262729	0.3936561	0.4579519	0.3350086
r (G-T)	0.02620863	0.04726953	0.02669420	0.1504980
pi (A)	0.4180264	0.4258703	0.4991617	0.2121917
pi (C)	0.08954130	0.08638344	0.1204571	0.3463631
pi (G)	0.07870812	0.06155404	0.06099978	0.2930755
pi (T)	0.4137242	0.4261922	0.3193814	0.1483696
alpha	0.4398832	0.4236929	0.5742377	0.9783009
pinvar	0.4436667	0.3893467	0.3076805	0.6090089

4.3. EVOLUTION OF THE EGG-POWDERING BEHAVIOR ASSOCIATED TRAITS IN *MOLOMEA*

Table 10 summarizes the information about the two morphological characters associated with the egg-powdering behavior, aswell as the presence of pellets of brochosomes over the female forewings, which is indicative of the behavior.

Table 10: Presence of the dimorphic characters and possibly of EPB (based on observation of females with brochosomes pellets on their wings) in *Molomea* species. Column "Forewings" refers to the presence of a region with distinctly concentrate setae on female forewings. Column "Hindtibiae" refers to the presence of elongate setae on hindtibiae of the females. Symbol "+" represents presence; "-" indicates absence; "?" indicates that the character could not be observed.

Species	Brochosome pellets	Forewings	Hindtibiae
M. alternata	+	-	+
M. biimpressa	-	-	+
M. cincta	-	-	-
M. confluens	-	+	+
M. consolida	+	-	+
M. consorta	-	+	+
M. exaltata	+	+	+
M. fatalis	+	-	+
M. flavolimbata	-	-	+
M. guttulata	-	+	+
M. hamleti	+	-	+
M. infulata	-	+	+
M. insignis	+	-	-
M. laminata	-	-	+
M. lineiceps	+	-	+
M. magna	+	+	+
M. malkini	+	+	+
M. novarae	?	?	?
M. personata	+	-	+
M. virescens	+	-	+
M. xanthocephala	-	-	+
M. zikani	-	?	?
***Molomea* sp. 1**	-	-	-
***Molomea* sp. 2**	-	-	+
***Molomea* sp. nov.**	?	?	?

The two dimorphic characters related to the egg-powdering behavior were optimized over the maximum likelihood tree obtained with the combined morphological and molecular datasets with likelihood and parsimony criterions on Mesquite 2.75 (Figure 36).

In a recent study (Takiya, 2007), the origin of the egg-powdering behavior was found to have appeared in the ancestral of Oncometopiini, and it was lost several times inside the group, and the associated traits originated after the origin of the behavior. Similarly, the ancestral of *Molomea* was likely to have the behavior, and it may have been lost independently inside the genus.

The presence of a region with distinctly concentrate setae on female forewings seems to have appeared independently seven times inside the genus (*M. malkini, M. magna, M. infulata, M. guttulata, M. consorta, M. exaltata,* and *M. confluens*). The ancestor of *Molomea* has 76% probability of not having this characteristic.

The presence of elongate setae on hindtibiae of the females is a much more conservative character and it seems to have a unique origin and three independent losses inside the genus (by *M. insignis, M. cincta* and *Molomea* sp. 1). This characteristic was already present in the ancestral of the genus *Molomea* (99.43% probability). These three species also lack the area with concentrate setae on female forewing. *Molomea insignis* is thought to still execute the behavior since egg-brochosomes over the forewings were found in dry specimens. Brochosome pellets were never reported for specimens of *M. cincta*, which is therefore believed to have lost the behavior. *Molomea* sp. 1 is known only from two female specimens, and both of them do not have pellets, indicating that this species too may have lost the behavior. These species are closely related to species that retain only the morphological trait of the hindtibia, what could indicate that the losses of the dimorphic characters may precede and maybe facilitate the loss of the behavior itself. However, there are species that retain one or both morphological traits and are thought to have lost the behavior (*M. infulata, M. guttulata, M. consorta, M. confluens*), suggesting that the loss of the characteristics and the behavior occur independently.

To test whether losses of these two dimorphic characters in *Molomea* were related to shifts to major phytogeographical regions in South America, the ancestral areas were calculated using the Bayesian trees found with the combined morphological and molecular datasets with the S-DIVA approach and the areas were reconstructed on

the best maximum likelihood tree found for the same datasets. The result is showed in figure 37.

There is no obvious correlation between losses and gains of the dimorphic characters and changes of phytogeographical regions. Of the seven species with a region with concentrate setae on forewings, four occur only in the Amazon Forest (*M. consorta, M. exaltata, M. guttulata,* and *M. infulata*), one occur only in the Brazilian Atlantic Forest (*M. confluens*), one only in the Cerrado Savanna (*M. malkini*), and *M. magna* occur in all three regions. The ancestral of each of the seven species was found in at least one of the areas the extant species occupy today. Brochosome pellets need to be anchored to the wing to avoid it to be scratched of as an unique piece (Rakitov, 2004). The anchorage is done by the forewing setae, which also help to enhance the adhesion of droplets of the brochosome suspension to the surface of the forewings (Rakitov, 2004). This characteristic may be important in very humid places, where the brochosomes take longer to dry and form the pellets. However, there are several other species found in the Amazonian and Atlantic forests that do not have this trait.

Regarding the elongate setae on hindtibiae, three species lost this trait: *M. insignis, M. cincta* and *Molomea* sp. 1. *Molomea insignis* is found in the Brazilian Atlantic Forest and *Molomea* sp. 1 is found in the Cerrado Savanna, while *M. cincta* is a widespread species, found in Cerrado, Atlantic Forest, Amazonia, Caatinga and Chaco steppes. The ancestral of these species did not suffer any change of phytogeographical region. These elongate setae are slightly curved and allow collecting a greater amount of brochosomes and also the application of it to a wider area (Rakitov, 2004). The elongate setae are also more flexible and therefore can brush the brochosomes pellets more gently (Rakitov, 2004).

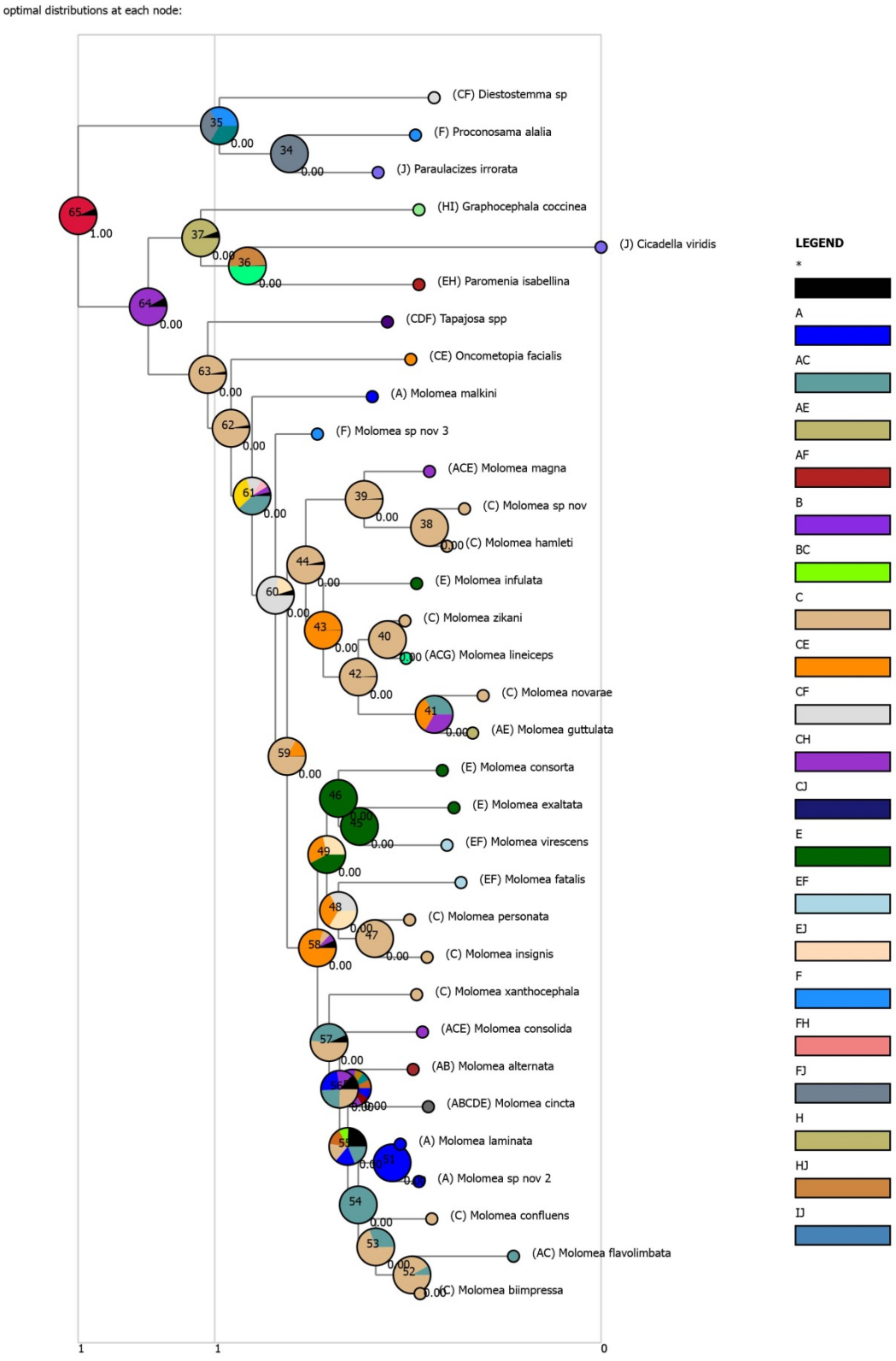

Figure 37: Ancestral areas reconstruction over the best maximum likelihood tree obtained for the morphological and molecular datasets combined.

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APPENDIX I: PROTOCOL FOR DNA EXTRACTION

DNA extraction with DNeasy Blood & Tissue Kit (Protocol modified from Qiagen, 2006)

1. Extract the hindleg and associated muscle and place it in a 1.5 or 2.0 ml microcentrifuge tube.
2. Add 180 µL of Buffer ATL.
3. Add 20 µL of Proteinase K. Mix thoroughly by vortexing and incubate at 55° for 48 hours.
4. Vortex for 15 seconds. Add 200 µL of Buffer AL and 200 µL of ethanol (96-100%) and vortex again.
5. Pipet the solution from step 4 including any precipitate into a mini spin column (*DNeasy Mini spin column* provided with the kit) placed in a 2 mL collection tube.
6. Centrifuge at 8,000 rpm for 60 s and discard flow-through and collection tube.
7. Place the column in a new 2 mL collection tube and add 500 µL of Buffer AW1.
8. Repeat step 6.
9. Place the column in a new 2 mL collection tube and add 500 µL of Buffer AW2.
10. Centrifuge at 14,000 rpm for 5 min and discard flow-through and collection tube.
11. Place the column in a clean 1.5 or 2.0 mL microcentrifuge tube and add 50 µL of Buffer AE directly onto the membrane.
12. Incubate at 70° for 5 min.
13. Centrifuge at 8,000 rpm for 1 min.
14. Keep the solution in the microcentrifuge tube in a freezer.
15. Repeat steps 11 to 14 in a new microcentrifuge tube to enhance the total amount of DNA obtained.

APPENDIX II: PCR PROTOCOL

PCR reaction (total volume of 25 μL):

- 5 μL of 10X Green Taq Buffer (PROMEGA)
- 13 μL of mH_2O3.5 μL of $MgCl_2$
- 25mM (PROMEGA)
- 0.5 μL of dNTP 2,5mM (Invitrogen)
- 1.0 μL of forward primer 10mM
- 1.0 μL of reverse primer 10mM
- 0.1 μL of Taq DNA polymerase (PROMEGA)
- 1.0 μl of DNA template.

Thermocycler program from Takiya (2007):

1. Initial denaturing at 94° C for 3 min;
2. 35 cycles of denaturing at 94° C for 1 min, annealing at 50° C for 1 min and extension at 72° C for 2 min;
3. Final extension period of 72° C for 7 min.
4. Cool down at 4° C on hold.