Phylogeny, character evolution and species diversity in Crambinae, Heliothelinae and Scopariinae

DISSERTATION
zur Erlangung des akademischen Grades

DOCTOR RERUM NATURALIUM
(Dr. rer. nat.)

vorgelegt
dem Bereich Mathematik und Naturwissenschaften
der Technischen Universität Dresden

von

M. Sc. Théo Antonin Baptiste Léger

geboren am 02.01.1989
in Lausanne, Schweiz

eingereicht am 10. Januar 2020
Die Dissertation wurde in der Zeit von 09/2014 bis 12/2019 an den Senckenberg Naturhistorischen Sammlungen Dresden angefertigt.

The time will come I believe, though I shall not live to see it, when we shall have very fairly true genealogical trees of each great kingdom of nature

Charles Darwin, letter to T. H. Huxley, 26 September 1857
Darwin Correspondence Project, "Letter no. 2143",
https://www.darwinproject.ac.uk/letter/DCP-LETT-2143.xml

1. Gutachter
Prof. Dr. Christoph Neinhuis
Lehrstuhl für Botanik,
Fakultät Mathematik und
Naturwissenschaften
Technische Universität Dresden
Dresden, Deutschland

2. Gutachter
Prof. Dr. Niklas Wahlberg
Systematic Biology Group
Faculty of Science
Lund University
Sölvegatan 37, Lund
Schweden

Declaration

Erklärung gemäß § 5.1.5 der Promotionsordnung

Hiermit versichere ich, dass ich die vorliegende Arbeit ohne unzulässige Hilfe Dritter und ohne Benutzung anderer als der angegebenen Hilfsmittel angefertigt habe; die aus fremden Quellen direkt oder indirekt übernommenen Gedanken sind als solche kenntlich gemacht. Die Arbeit wurde bisher weder im Inland noch im Ausland in gleicher oder ähnlicher Form einer anderen Prüfungsbehörde vorgelegt.

Berlin, 14. Januar 2020

Théo Léger

Acknowledgements

This work would not have been possible without the help and support from various people. I want to express my sincere gratitude to Matthias Nuss and Bernard Landry for introducing me to the fabulous group that represent Pyraloidea and to the thrilling field of research that is systematics. Matthias Nuss supervised me for five years and suggested most of the projects presented here. I appreciated the liberty I was given in the realisation of my projects and enjoyed our discussions that sharpened my scientific reasoning. Huge thanks goes to Bernard Landry from the Muséum d'histoire naturelle de Genève (MHNG) for suggesting and co-supervising my phylogenetic work on the Crambinae and Scopariinae. I am very thankful to my thesis director Christoph Neinhuis for accepting to supervise my work and guide me through the administrative standards of the Technische Universität Dresden (TUD).

The supportive and entertaining atmosphere at the Senckenberg Museum für Tierkunde (SMTD) greatly contributed to the accomplishment of my work. As my closest colleague, I am thankful to Richard Mally who co-authors two of the papers presented here and set up the protocols in the lab for the Lepidoptera section during his time at the SMTD. Also, having him alongside when collecting, setting moths and escaping earthquakes during our fieldtrip to Mount Kinabalu was a much appreciated and memorable experience. Special thanks are given to Manuela Bartel and Christian Kehlmaier who provided great help with lab work. Furthermore, I am indebted to Christian Schmidt, Francesca Vegliante, Franziska Bauer and Klaus Dieter-Klass for our entomological discussions and to Loreen Knöbel and Melita Vamberger for our entertaining lunch breaks.

For their help concerning field expeditions, I am grateful to Dr. Stephen Sutton, Prof. Charles Vairappan (Institute for Tropical Biology and Conservation), Ching Y. Chung (Sabah Biodiversity Centre), the staff of the Sabah Parks and Peter Achleiner (Borneo, Malaysia); Clemente, Inocêncio José, Miguel Bungo (Universidade Kimpa Vita, Ndalatando), José Lau (Universidade Kimpa Vita, Uíge), Christoph Neinhuis, Thea Lautenschläger, Christin Heinze (TUD) (Angola); Ashley Field, Daren Crayn, David Rentz and the staff of the Australian Tropical Herbarium (James Cook University, Cairns), Christoph Neinhuis and Sarah Wagner (TUD) (Queensland, Australia). David Lees and Geoff Martin from the Natural History Museum (London, UK), as well as my friends Claire Monari and Jonty Forrester are thanked for the help and entertainment graciously offered during my tight-budget stay in London. Moreover, I am really indebted to all the people who provided material for molecular investigations.

I am thankful to the Senckenberg Gesellschaft für Naturforschung, the Muséum d'histoire naturelle de Genève and the Museum für Naturkunde Berlin for providing funds, as well as all other temporary employers that helped bridging the gaps.

Also, I want to thank Patrick Schmitz who, on a night of May 2010, gave a presentation on endemic aquatic moths of Hawaii at "la Datcha", the student local at the University of Geneva. That talk left me bewildered and with one thing on my mind: "That's what I want to do!". I also thank my friends from Dresden, Geneva and elsewhere for the leisure time beside PhD work, eventhough my interest for tiny dull moths remain obscure for most of them up until now. Last but not least, I thank my parents and my sister for always being supportive of my passions and endeavours.

Abbreviations

Institutions
BMNH: British Museum of Natural History, London BORN: Borneensis, Institute for Tropical Biology and Conservation, Kota Kinabalu, Malaysia
ITBC: Institute for Tropical Biology and Conservation, Kota Kinabalu, Malaysia
MHNG: Muséum d'histoire naturelle de Genève, Switzerland
SMTD: Senckenberg Museum für Tierkunde Dresden
TUD: Technische Universität Dresden

Scientific terms
BI: Bayesian Inference
bp: base pair
BS: Bootstrap support
ESS: Effective Sample Size
GTR: General Time Reversible
MCMC: Markov Chain Monte Carlo
ML: Maximum likelihood
pp: posterior probability

Phylogenetic groups CAMMSS clade: clade comprising the Crambinae, Acentropinae, Midilinae, Musotiminae, Schoenobinae and Scopariinae, as of Regier et al. (2012)
OG clade: clade comprising the Odontiinae and Glaphyriinae, as of Regier et al. (2012).
PS clade: clade comprising the Pyraustinae and Spilomelinae, as of Regier et al. (2012).
non-PS clade: clade comprising the Odontiinae, Glaphyriinae, Crambinae, Acentropinae, Midilinae, Musotiminae, Schoenobinae and Scopariinae as of Regier et al. (2012).

Genes
CAD: carbamoyl-phosphate synthetase 2, aspartate transcarbamylase, and dihydroorotase
COI: cytochrome oxydase subunit I
DDC: dopa decarboxylase
EF-1a: Elongation Factor I alpha
GAPDH: glyceraldehyde-3-phosphate dehydrogenase
IDH: isocitrate dehydrogenase
MDH: cytosolic malate dehydrogenase
rps5: ribosomal protein S5

Abstract

Pyraloidea is one of the largest superfamilies of Lepidoptera comprising 15 955 described species. The monophyly of the group was suggested by the presence of a tympanal organ in the first abdominal segment; it has been confirmed later by molecular data. This group is divided into Pyralidae (5750 species in 5 subfamilies) and Crambidae (10 205 species in 14 subfamilies). The work presented here provides new insights on the phylogeny and evolution of morphological and ecological characters of the Crambinae and Scopariinae, as well as the first phylogenetic placement, host plant record, and taxonomic work on the Heliothelinae.

Crambinae (2,047 species) and Scopariinae (577 species) were previously recovered as sister groups in a molecular phylogenetic analysis of three and two species respectively, while Heliothelinae (50 species) have never been investigated in a phylogenetic framework. The morphology-based classification divided Scopariinae into 24 genera and Crambinae into 9 tribes and 176 genera, while Heliothelinae comprised the two tribes Heliothelini and Hoploscopini. Analyses of a six-gene dataset including 110 taxa with Maximum Likelihood and Bayesian Inference confirm the monophyly of Crambinae as well as Scopariinae, while no support was found for the position of Heliothelinae. Phylogenetic results demonstrate that Scopariinae were oversplit at the generic level by traditional classification, with five genera found nested within, and consequently synonymized with the two species-rich genera *Eudonia* and *Scoparia*. *Anarpia*, recovered as the basal-most lineage of Scopariinae, occurs in the Mediterranean region, in contrast to the remaining Scopariinae found in temperate regions and wet tropical montane forests. In Crambinae, our revision of the tribal classification leads to two synonymizations, one reinstatement as well as the description of a new tribe. Furthermore, several genera are confidently assigned to a tribe for the first time and two are synonymized with *Microcrambus*. Ancestral character reconstructions for 27 morphological characters provide new apomorphies for several clades and reveal several modifications of the female oviscapt associated with the behavior of laying adhesive or non-adhesive eggs, the latter being associated with the use of Pooidae as host plants.

Inclusion of a greater number of taxa and genes comprising all subfamilies of Crambidae supports the polyphyly of Heliothelinae. Heliothelinae s. str. are sister to Scopariinae, while Hoploscopinae are sister to (Heliothelinae+Scopariinae)+Crambinae. Heliothelinae s. str. occur in xerothermic habitats and larvae of *Heliothela wulfeniana* are recorded as miners in Violaceae. In contrast, Hoploscopinae occur in montane rainforests of the Oriental and Austral-Asian regions. Field observations on Mount Kinabalu and subsequent studies of the material collected provided the first host plant record for *Hoploscopa* and highlighted a high proportion of undescribed species in this genus. Following an iterative approach combining morphology and DNA barcoding from museum specimens, twenty-six new species of *Hoploscopa* – among which eight from Mount Kinabalu – are described here, and re-descriptions are provided for the 15 hitherto described species. Genetic diversity among different islands highlighted by the species delimitation analysis and the estimated thirty further undescribed species from museum collections make *Hoploscopa* an example of the largely unexplored pyraloid fauna in the tropics. The con-

fined distribution and the high species diversity in *Hoploscopa* makes it an ideal model-group for phylogeographical investigations.

Zusammenfassung

Mit 15.515 beschriebenen Arten sind die Zünslerfalter (Pyraloidea) eine der artenreichsten Gruppen der Lepidoptera. Die Monophylie der Gruppe wurde durch das Vorhandensein eines gepaarten Tympanalorgans in den ersten zwei abdominalen Segmenten begründet und durch molekulargenetische Analysen bestätigt. Pyraloidea sind unterteilt in Pyralidae (5.408 Arten in fünf Unterfamilien) und Crambidae (10.107 Arten in 14 Unterfamilien). Die hier vorgelegte Arbeit liefert neue Kenntnisse über die Phylogenie und Evolution morphologischer und ökologischer Merkmale der Crambinae und Scopariinae sowie zur larvalen Morphologie und Ernährungsweise, Phylogenie und Taxonomie der Heliothelinae.

In stammesverwandtschaftlichen Untersuchungen der vergangenen Jahre stellte sich heraus, dass die Crambinae (2.047 Arten) und die Scopariinae (577 Arten) Schwestergruppen sind. Die Heliothelinae hingegen waren bisher nie Gegenstand phylogenetischer Untersuchungen. Morphologisch sind die Scopariinae in 24 Gattungen und die Crambinae in 176 Gattungen, verteilt auf neun Triben, klassifiziert, während die Heliothelinae zwei Triben beinhalten: Heliothelini und Hoploscopini. Unsere phylogenetischen Maximum Likelihood – und Bayes-Analysen, basierend auf einem sechs Gene umfassenden Datensatz für 110 Taxa, bestätigen die Monophylie sowohl der Crambinae als auch der Scopariinae, während die Heliothelinae nicht als Monophylum gestützt sind. Einige Gattungen der Scopariinae wurden in der Vergangenheit in zu viele Untergruppen aufgeteilt. So enthalten zum Beispiel die beiden artenreichen Gattungen *Eudonia* und *Scoparia* fünf ehemalige Gattungen, die inzwischen synonymisiert wurden. *Anarpia*, die als Schwester zu allen anderen Scopariinae gefunden wurde, kommt in der Mittelmeerregion vor, während alle anderen Scopariinae vorwiegend in gemäßigten Zonen und tropischen Bergwäldern verbreitet sind. Die Triben-Klassifikation der Crambinae wird im Licht unserer Ergebnisse revidiert, wobei wir zwei Triben synonymisieren, eine Tribus wieder etablieren und eine neue Tribus beschreiben. Mehrere Crambinae-Gattungen werden zum ersten Mal einer Tribus zugewiesen. In der Analyse 27 morphologischer Merkmale fanden wir neue Synapomorphien für einige Kladen. Eine der Schlüsselerkenntnisse ist, dass innerhalb der Crambinae die Entstehung nicht-klebender Eier mit einigen Modifikationen des weiblichen Oviskapts sowie mit einem Wechsel der Nahrungspflanzen hin zu Pooideae einherging.

Die phylogenetische Analyse eines größeren, zehn Gene umfassenden Datensatzes mit Vertretern aller Crambidae-Unterfamilien zeigt auf, dass die Heliothelinae ein Polyphylum darstellen: Heliothelini s. str. sind Schwester zu den Scopariinae, während Hoploscopini eine völlig eigene Entwicklungslinie ist, die als eigenständige Unterfamilie angesehen werden sollte. Heliothelinae s. str. kommen in xerothermen Zonen vor, und ihre Larven fressen an Violaceae. Hoploscopinae hingegen sind in den tropischen Bergwäldern Südostasiens und Australasiens verbreitet. Feldarbeit und anschließende Laboranalysen erbringen den ersten Nachweis der Nahrungspflanzen – Farne – für die Gattung *Hoploscopa* und deuten auf eine große unbeschriebene Artendiversität in dieser Gattung hin. Sechsundzwanzig *Hoploscopa*-Arten – davon acht vom Mount Kinabalu – werden anschließend anhand morphologischer Befunde und dann-Barcoding als neu beschrieben.

Weitere 15 Arten werden wiederbeschrieben. Die hohe genetische Divergenz zwischen morphologisch ähnlichen Arten auf verschiedenen Inseln sowie dreißig weitere in Museumssammlungen auf ihre wissenschaftliche Beschreibung wartende Arten sind Anlass für zukünftige Untersuchungen. Die Arten der Gattung *Hoploscopa* erweisen sich durch ihre Diversität und ihre geographisch enge Verbreitung als eine geeignete Objekte für weitergehende phylogeographische Studien.

Contents

1 Phylogeny, tribal classification and character evolution in Crambinae and Scopariinae (Lepidoptera: Pyraloidea) 17

2 Refining the phylogeny of Crambidae with complete sampling of subfamilies (Lepidoptera, Pyraloidea) 39

3 Discovery of another fern-feeding group of moths: the larvae of Hoploscopini (Insecta: Lepidoptera: Pyraloidea) from Borneo. 59

4 Twenty-six new species of *Hoploscopa* (Lepidoptera, Crambidae) from South-East Asia revealed by morphology and DNA barcoding. 69

5 Conclusion and outlook 167

Appendix A Phylogeny, tribal classification and character evolution in Crambinae and Scopariinae (Lepidoptera: Pyraloidea) 175

Appendix B Refining the phylogeny of Crambidae with complete sampling of subfamilies (Lepidoptera, Pyraloidea) 229

Appendix C Twenty-six new species of *Hoploscopa* (Lepidoptera, Crambidae) from South-East Asian revealed by morphology and DNA barcoding. 239

Introduction

Pyraloidea, a major lineage of Lepidoptera

Pyraloidea, also commonly known as snouth-moths, represent with 15 515 described species one of the major lineages of Lepidoptera. This number is exceeded in the Lepidoptera only by Gelechioidea, Geometroidea and Noctuoidea (Regier et al., 2012). The presence of a tympanal organ formed by the invagination of the ventral part of the first two abdominal segments is the most striking apomorphy of the group (Munroe & Solis, 1998). These structures allow to detect echo-locatiing bats (Fenton & Fullard, 1981), and serve as acoustic communication devices (Greenfield & Weber, 2000; Nakano et al., 2008; Spangler, 1988). Tympanal organs evolved independently in other Lepidoptera lineages (Geometridae, Noctuidae) (Minet & Surlykke, 2003). The scaled proboscis has also been proposed as an apomorphy for the group, but is also observed in Choreutoidea and Gelechioidea (Minet, 1991). The deltoid posture at rest and the antennae directed backwards in many species also help to recognize this group. The wingspan of the moths range from less than 10 mm (e.g. *Microcausta* spp) to 120 mm (*Myelobia* spp). Wing pattern and shape provide several species a camouflage on grasses or rocks (see Scopariinae on Fig. 1), while few species arbour an aposematic wing pattern or imitate jumping spiders (see Musotiminae and Spilomelinae on Fig. 1) (Munroe, 1991). A representation of the diversity of forms found in the Crambidae is given on Fig. 1.

Pyraloid moths are encountered on all continents (except Antarctic) in a variety of habitats ranging from tropical forests to grasslands and montane habitats (Munroe & Solis, 1998). Few species of Phycitinae are encountered in deserts (Munroe & Solis, 1998). The Acentropinae are found in aquatic habitats where the immatures develop under water. Colonisation and subsequent radiations on distant oceanic islands are observed in some genera (e.g., *Eudonia*, *Mestolobes*, *Udea*) (Mally & Nuss, 2011; Nuss, 1999; Nuss et al., 1998; Zimmerman, 1958).

Larval host plants span from mosses (e.g., Scopariinae), lichens (e.g., some Glaphyriinae), ferns (e.g., Musotiminae), monocotyledons (e.g., Crambinae, Midilinae and Schoenobiinae), to dicotyledons (e.g., Spilomelinae, Pyraustinae) (Munroe & Solis, 1998). Feeding habits include leaf miners or leaf rollers as well as stem- or root borers (Munroe & Solis, 1998). Non-phytophagous feeding habits include detritophagy (e.g., *Euchromius*) or coprophagy (e.g., *Cryptoses*, *Parachma*; Bradley, 1982; Hayden, 2012). Few cases of inquilinism are observed with ants (e.g., *Niphopyralis*), bees or wasps (e.g., some Glaphyriinae), as well as sloths (e.g., *Cryptoses* spp.) (Dyar, 1908a; Munroe & Solis, 1998). Several taxa are pests on crops (e.g., *Chilo*, *Diatraea*, *Eoreuma*, *Loxostege*, *Ostrinia*, *Rupela* spp.), stored products (e.g., *Ephestia kuehniella*, *Plodia interpunctella*), bamboo (*Myelobia* spp.), various fruits or vegetables (*Deanolis*, *Leucinodes*, *Neoleucinodes* spp.) (Capinera, 2001; Khan et al., 1991; Landry et al., 2015; Mally et al., 2015; Montilla et al., 2013; Zhang, 1994). Others are pest of ornamental ferns (Musotiminae), aquatic plants (Acentropinae) or lawn (some Crambini).

Figure 1: Moths of the Crambidae family. 1. Acentropinae (*Nymphula nitidulata*, © P. Sansum). 2. Cathariinae (*Catharia pyrenaealis*, © L. Mikonranta). 3. Crambinae (*Agriphila geniculea*, © F. Bauer). 4. Cybalomiinae (*Ptychopseutis sp.*, © R. Kendrick). 5. Glaphyriinae (*Glaphyria fulminalis*, © L. Prosperi). 6. Heliothelinae: Heliothelini (*Heliothela ophideresena*, © D. Hobern). 7. Heliothelinae: Hoploscopini (*Hoploscopa sp.*, © L. Gabrielsen). 8. Lathrotelinae (*Sufetula sp.*, © M. Ng Fu Chuan). 9. Linostinae (*Linosta centralis*, © G. Kunz). 10. Midilinae (*Midila quadrifenestra*, © B. Dupont). 11. Musotiminae (*Ambia sp.*, © Itchydogimages, Flickr.com). 12. Odontiinae (*Cynaeda dentalis*, © I. Ustyantsev). 13. Pyraustinae (*Pyrausta aurata*, © D. Hobern). 14. Schoenobiinae (*Donacaula forficella*, © P: Kitchener). 15. Scopariinae (*Scoparia ambigualis*, © P. Boissel). 16. Spilomelinae (*Nevrina procopia*, © L. Lai).

Pest species like *Chilo supressalis*, *Ostrinia nubilalis* (Crambidae), *Ephestia kuehniella*, *Galleria mellonella*, *Plodia interpunctella* (Pyralidae) have been repeatedly used in research on behavior, development, ecology, genomics or population genetics (selected publications: Beck et al., 2011; Dopman et al., 2004; Dopman et al., 2010; Ellis et al., 1997; Janzen et al., 2009; Segar et al., 2017; Siaussat et al., 2008; Thomas et al., 2003; Vogel et al., 2011; Yamamura et al., 2006; Yin et al., 2014)

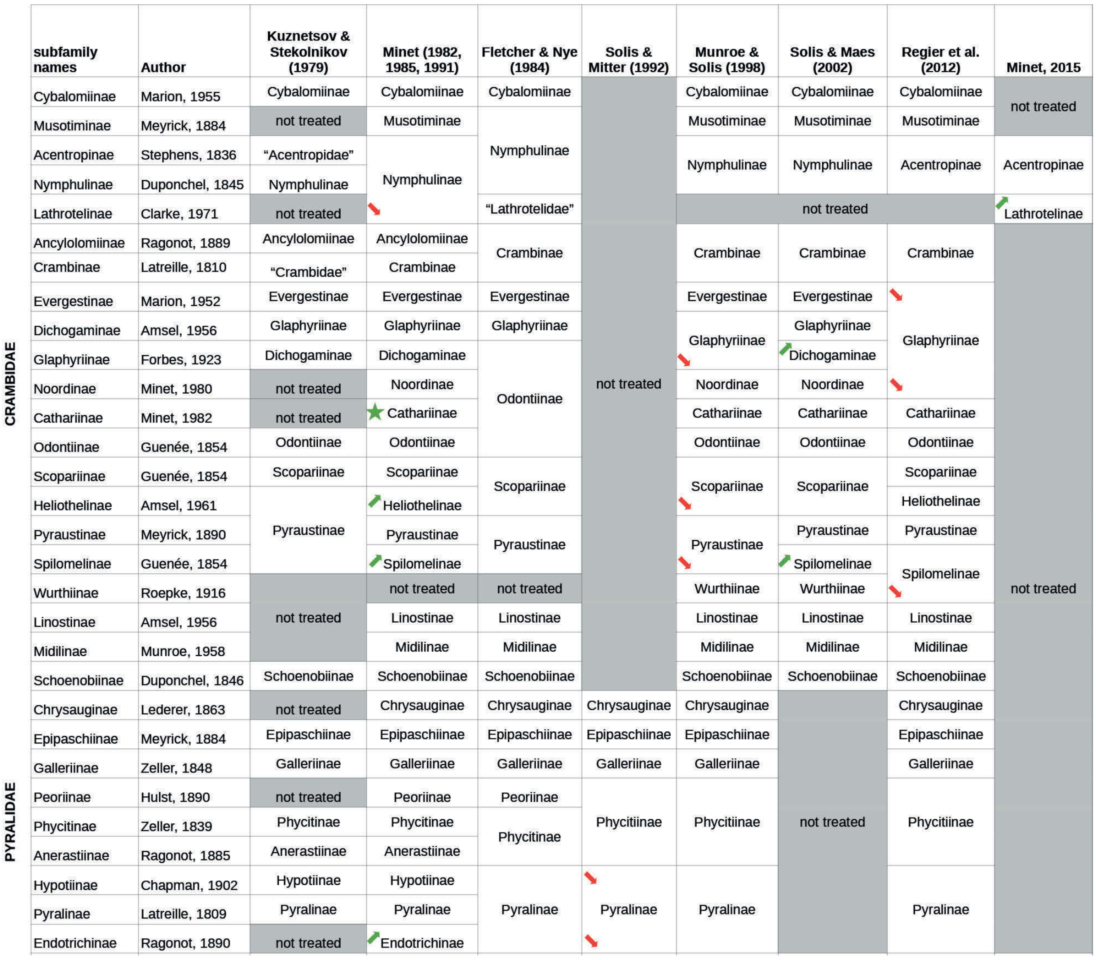
History of the systematics of pyraloid moths

The systematic classification of Pyraloidea dates back to the origin of Linnean systematics with the description of *Pyralis* by Carl Linnaeus, along with other species misplaced in *Geometra* and *Tinea* (Linnaeus, 1758). Several groupings were proposed in the early 19th century, some of them lasting until today (e.g., Crambinae Latreille, 1810). Systematic studies during the 19th century were mainly based on the examination of external features such as the labial palpi, antennae, wing pattern and venation. The second half of the 19th century saw several authors working on pyraloid moths. Guenée (1845, 1854) and Meyrick (1878, 1884, 1885, 1890) paved the way toward a classification of pyraloid moths. Classification and keys to family groups were proposed by Meyrick (1890). Hampson (1896, 1897, 1898, 1899) further elaborated on this classification. Other notable workers of this time include Ragonot (1887, 1888, 1889, 1891, 1891), Walker (1859), Zeller (1848, 1848, 1863), followed at the beginning of the 20th century by American entomologists Dyar (1908, 1908), Dyar & Heinrich (1927).

The beginning of the 20th century saw the first works in Lepidoptera including the use of genitalic characters (1909, 1914). Chapman (1912) is among the first authors to use this technique in Pyraloidea. The widespread use of genitalia dissections in the second half of the century brought a considerable amount of new characters providing further insights in pyraloid diversity. Major taxonomic revisions were undertaken at this time among others by Bleszynski (e.g., 1964, 1965, 1970, 1970), Gaskin (e.g., 1972, 1975), Marion (e.g., 1952, 1954, 1954, 1955, 1955, 1957, 1959, 1959), and Munroe (e.g., 1970, 1972, 1974, 1976). The morphology of the tympanal organs was used for the first time by Börner (1925) to highlight two distinct groups in Pyraloidea, and the first work dedicated to the morphology of tympanal organs is that of Kennel & Eggers (1933). Extensive investigations of the structure of the tympanic organs were performed by Minet (1982, 1985) in order to define pyraloid subfamilies. First hypotheses on phylogenetic relationships within Pyraloidea appear in the 1970's, following the phylogenetic concepts introduced by Hennig (1950). Putative relationships are presented in numerous works, however without proper phylogenetic analyses. For instance, Roesler (1978) suggested several characters for phylogenetic reconstruction, and Kuznetsov and Stekolnikov (1979) presented a phylogeny based on characters of the male genitalia. Larval morphology provided further characters to formulate hypotheses of phylogenetic relationships in Pyraloidea (Passoa, 1985; Yoshiyasu, 1985). The first phylogenetic analysis based on morphological characters was that of Solis and Mitter (1992). This analysis – the first of that kind for pyraloid moths – disentangled the relationships among the five Pyralidae subfamilies. The phylogeny of the Crambidae published ten years later by Solis and Maes (2002), however, encountered mitigated success in resolving relationships among the subfamilies of this group. Further morphology-based phylogenies were published on few subfamilies, e.g., on Crambinae (Landry, 1995) or Schoenobiinae (Martínez, 2010). An overview of the treatment of the family-groups across major works of the late 20th century is presented on figure 2.

A third major step in the history of research on Lepidopteran systematics was brought by the development of molecular methods that enabled to test morphology-based classification with molecular characters (Cho et al., 2011; Kawahara & Breinholt, 2014; Mutanen et al., 2010; Regier et al., 2009, reviewed by Mitter et al., 2017). The first molecular phylogenies of Lepidoptera confirmed the monophyly of Crambidae and Pyralidae and provided few insights into their inner relationships (Cho et al., 2011; Mutanen et al., 2010; Regier et al., 2009).

Figure 2: Table summarizing the treatment of most family-group names by major systematic and phylogenetic works on Pyraloidea published after 1970. A green arrow indicates rehabilition of a name, while a red arrow indicates its synonymization. The green star represents a new description.

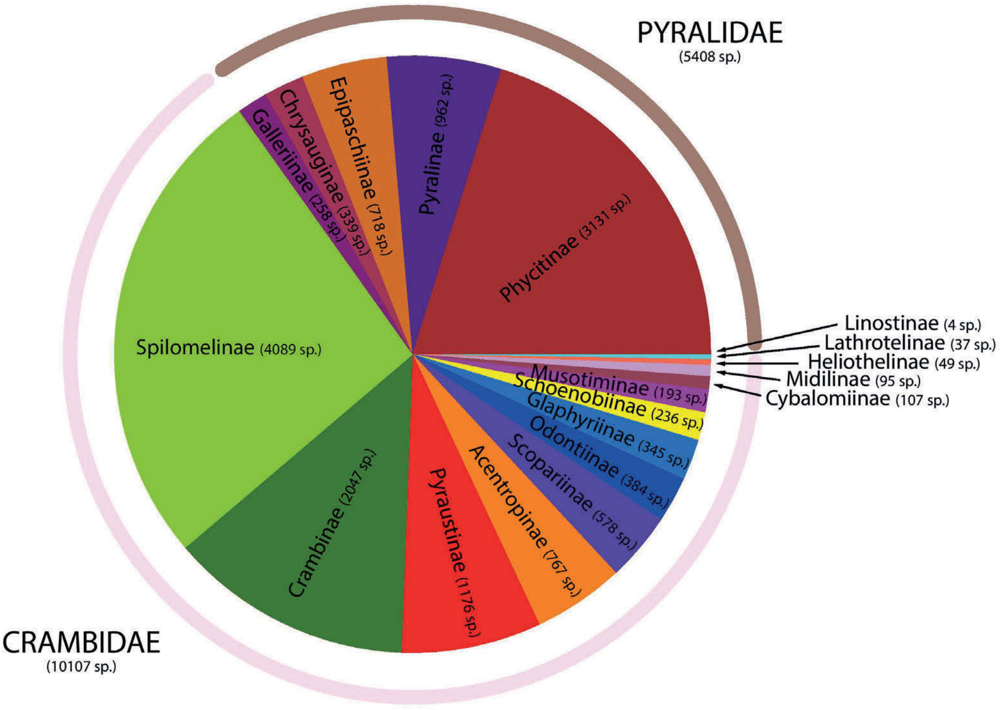


	subfamily names	**Author**	**Kuznetsov & Stekolnikov (1979)**	**Minet (1982, 1985, 1991)**	**Fletcher & Nye (1984)**	**Solis & Mitter (1992)**	**Munroe & Solis (1998)**	**Solis & Maes (2002)**	**Regier et al. (2012)**	**Minet, 2015**
CRAMBIDAE	Cybalomiinae	Marion, 1955	Cybalomiinae	Cybalomiinae	Cybalomiinae	not treated	Cybalomiinae	Cybalomiinae	Cybalomiinae	not treated
	Musotiminae	Meyrick, 1884	not treated	Musotiminae	Nymphulinae		Musotiminae	Musotiminae	Musotiminae	
	Acentropinae	Stephens, 1836	“Acentropidae”	Nymphulinae			Nymphulinae	Nymphulinae	Acentropinae	Acentropinae
	Nymphulinae	Duponchel, 1845	Nymphulinae							
	Lathrotelinae	Clarke, 1971	not treated	↘	“Lathrotelidae”		not treated			↗ Lathrotelinae
	Ancylolomiinae	Ragonot, 1889	Ancylolomiinae	Ancylolomiinae	Crambinae		Crambinae	Crambinae	Crambinae	not treated
	Crambinae	Latreille, 1810	“Crambidae”	Crambinae						
	Evergestinae	Marion, 1952	Evergestinae	Evergestinae	Evergestinae		Evergestinae	Evergestinae	↘	
	Dichogaminae	Amsel, 1956	Glaphyriinae	Glaphyriinae	Glaphyriinae		Glaphyriinae	Glaphyriinae	Glaphyriinae	
	Glaphyriinae	Forbes, 1923	Dichogaminae	Dichogaminae	Odontiinae		↘	↗ Dichogaminae		
	Noordinae	Minet, 1980	not treated	Noordinae			Noordinae	Noordinae	↘	
	Cathariinae	Minet, 1982	not treated	★ Cathariinae			Cathariinae	Cathariinae	Cathariinae	
	Odontiinae	Guenée, 1854	Odontiinae	Odontiinae			Odontiinae	Odontiinae	Odontiinae	
	Scopariinae	Guenée, 1854	Scopariinae	Scopariinae	Scopariinae		Scopariinae	Scopariinae	Scopariinae	
	Heliothelinae	Amsel, 1961	Pyraustinae	↗ Heliothelinae			↘		Heliothelinae	
	Pyraustinae	Meyrick, 1890		Pyraustinae	Pyraustinae		Pyraustinae	Pyraustinae	Pyraustinae	
	Spilomelinae	Guenée, 1854		↗ Spilomelinae			↘	↗ Spilomelinae	Spilomelinae	
	Wurthiinae	Roepke, 1916	not treated	not treated	not treated		Wurthiinae	Wurthiinae	↘	
	Linostinae	Amsel, 1956		Linostinae	Linostinae		Linostinae	Linostinae	Linostinae	
	Midilinae	Munroe, 1958		Midilinae	Midilinae		Midilinae	Midilinae	Midilinae	
	Schoenobiinae	Duponchel, 1846	Schoenobiinae	Schoenobiinae	Schoenobiinae		Schoenobiinae	Schoenobiinae	Schoenobiinae	
PYRALIDAE	Chrysauginae	Lederer, 1863	not treated	Chrysauginae	Chrysauginae	Chrysauginae	Chrysauginae	not treated	Chrysauginae	
	Epipaschiinae	Meyrick, 1884	Epipaschiinae	Epipaschiinae	Epipaschiinae	Epipaschiinae	Epipaschiinae		Epipaschiinae	
	Galleriinae	Zeller, 1848	Galleriinae	Galleriinae	Galleriinae	Galleriinae	Galleriinae		Galleriinae	
	Peoriinae	Hulst, 1890	not treated	Peoriinae	Peoriinae	Phycitiinae	Phycitiinae		Phycitiinae	
	Phycitinae	Zeller, 1839	Phycitinae	Phycitinae	Phycitinae					
	Anerastiinae	Ragonot, 1885	Anerastiinae	Anerastiinae						
	Hypotiinae	Chapman, 1902	Hypotiinae	Hypotiinae	Pyralinae	↘	Pyralinae		Pyralinae	
	Pyralinae	Latreille, 1809	Pyralinae	Pyralinae		Pyralinae				
	Endotrichinae	Ragonot, 1890	not treated	↗ Endotrichinae		↘				

The first phylogenetic study dedicated entirely to Pyraloidea is that of Regier et al. (2012). Their analysis of up to 19 nuclear genes is a significant milestone on the systematic of the group and represent the latest state of knowledge. Much concordance was found with the study of Solis & Mitter (1992) for phylogenetic relationships within Pyralidae, except for the positions of the Phycitinae and Pyralinae which are reversed, while relationships found within Crambidae were at odds with those presented by Solis & Maes (2002). A phylogeny based on mitochondrial genomes and including five Crambidae and three Pyralidae subfamilies was published a year later (Ye et al., 2013). DNA barcoding represent another major finding brought by the molecular methods. The discovery of this 654bp-fragment of the mitochondrial COI gene to serve as standard molecular marker for species delimitation revolutionized the field of systematics, ecology and conservation (Hebert et al., 2003; Hebert & Gregory, 2005). DNA barcoding is highly effective in species identification in Lepidoptera, with an estimated success rate lying over 98% (Huemer et al., 2014). This method allowed the discovery of overlooked species in Pyraloidea (e.g., Mally et al., 2016; Mally et al., 2018; Yang et al., 2012). It also opened new perspectives to rapidly capture the species diversity of poorly known regions (e.g., Lees et al., 2014; Lopez-Vaamonde et al., 2018).

Contemporary workers of the Western hemisphere include Agassiz, Hayden, Landry, Mally, Nuss, Solis (selected works: Agassiz, 2012; Hayden, 2011; Landry, 1995, 2003, 2016; Landry & Roque-Albelo, 2006, 2008; Nuss, 1998, 1999; Solis & Adamski, 1998; Solis & Metz, 2011, 2016). The recent body of literature also shows a net increase of works from authors based in Asia (Liu et al., 2019; selected publications: Chen et al., 2006c, Chen et al., 2006b, 2006, 2002, 2007, 2010; Li et al., 2002; Singh et al., 2019b, 2019). Global revisions are available for subfamilies Linostinae (Munroe, 1959), Midilinae (Munroe, 1970) and Scopariinae (Nuss, 1999). Regional faunas are available for North-America (Munroe, 1972, 1974, 1976) and the Palearctic region (Amsel et al., 1965, Slamka, 2008), while a checklist is available for the Neotropical fauna (Munroe, 1995). The database GlobIZ, standing for Global Information Zünslerfalter, was started in 2003 by Nuss and colleagues with the goals of inventorying all taxonomic names of Pyraloidea and the related bibliography, and promoting systematic work on the group (Nuss et al., 2003–2019). To date, molecular studies focussing on relationships within subfamilies are available for Pyraustinae and Spilomelinae (Mally et al., 2019), as well as Acentropinae (Tsai, 2013). Subfamilies recognized by different authors are summarized on Fig. 2, and the fifteen Crambidae and five Pyralidae subfamilies currently recognized are displayed on Fig. 3.

Figure 3: Pie chart displaying species diversity for all Pyraloidea subfamilies



Understanding evolution patterns in Crambinae, Heliothelinae and Scopariinae

The Crambinae are classified into 156 genera and 9 tribes, and the Scopariinae into 24 genera (Nuss et al., 2003–2019). The phylogeny of the Crambinae inferred from 45 morphological characters for North American genera highlighted two new tribes and confirmed two others as monophyletic (Landry, 1995). However, this work could not provide conclusions on the status of other tribes (e.g., the Argyriini), and other taxa, such as *Diatraea* or *Epina*, could not be assigned to any tribe. Also, the reconstruction of the relationships within the species-rich tribe Crambini resulted in a large polytomy (Landry, 1995). Crambinae and Scopariinae were found to represent sister groups in the study of Regier et al. (2012). However, the three and two taxa sampled respectively for each of the two subfamilies only represent a tiny fraction of the diversity of these groups. The Scopariinae include two large genera, *Eudonia* and *Scoparia*, containing 87 percent of the described species with 263 and 242 species respectively. *Micraglossa* comes far behind as the third most species-rich genus with 15 described species, while the remaining 21 genera include ten or less species and were mostly described to accommodate unique species exhibiting morphological peculiarities. Possible relationships between scopariine genera were presented by Nuss (2003) – although these were not based on a formal phylogenetic analysis. The Heliothelini, inhabiting xerothermic habitats of the Old World, and the Hoploscopini, found in montane rain forests of South-East Asia and Australasia, have been grouped into Heliothelinae based on the presence of an inwardly directed spine in the corpus bursae of the female genitalia regarded as a putative synapomorphy (Nuss, 1998). Some authors included Heliothelinae into the Scopariinae (Hannemann, 1964; Leraut, 1980; Munroe & Solis, 1998; Solis & Maes, 2002), while others recognized them as a separate subfamily (Nuss, 1998). Species diversity is thought to be strongly underestimated in the South-East Asian genus *Hoploscopa*, with sixteen species currently described, but another 70 yet undescribed (Robinson et al., 1994).

The classification within the three subfamilies introduced above rely merely on topological concepts and was never tested with molecular characters. Goal of this dissertation are as follows:

1. Test whether Crambinae, Heliothelinae and Scopariinae represent monophyletic groups, or if one is subordinate to the others.

2. Investigate evolution of morphological and ecological patterns in these groups in the light of the phylogenetic backbone.

3. Explore the diversity of the genus *Hoploscopa* by mean of morphology and DNA barcoding to highlight potential new species.

Bibliography

Agassiz, D. J. (2012). The Acentropinae (Lepidoptera: Pyraloidea: Crambidae) of Africa. *Zootaxa*, *3494*, 1–73.

Amsel, H. G., Reisser, H., & Gregor, F. (1965). *Microlepidoptera Palearctica* (Georg Fromme & Co). Wien.

Beck, J., Brehm, G., & Fiedler, K. (2011). Links between the environment, abundance and diversity of Andean moths. *Biotropica*, *43*(2), 208–217. doi:10.1111/j.1744-7429.2010.00689.x

Bleszynski, S. (1964). Revision of the world species of the family Crambidae (Lepidoptera). Part 2. Genera: *Pseudocatharylla* Blesz., *Classeya* Blesz., *Pseudoclasseya* Blesz. and *Argentochiloides* Blesz. *Acta Zoologica Cracoviensia*, *9*(11), 683–760.

Bleszynski, S. (1965). Crambinae. In *Microlepidoptera Palearctica* (Georg Fromme & Co, Vol. 1). Wien.

Bleszynski, S. (1970a). A revision of the world species of *Chilo* Zincken (Lepidoptera: Pyralidae). *Bulletin of the British Museum*, *25*(4), 101–195, pls 1–5.

Bleszynski, S. (1970b). New genera and species of tropical Crambinae (studies on the Crambinae, Lepidoptera, Pyralidae, Part 48). *Tijdschrift voor entomologie*, *113*, 1–26.

Börner, C. (1925). 22. Ordn. Lepidoptera, Schmetterlinge. In *Fauna von Deutschland, 3. verbesserte Auflage. – Fauna von Deutschland, ein Bestimmungsbuch unserer heimischen Tierwelt* (Quelle and Meyer, pp. 358–387). Leipzig.

Bradley, J. D. (1982). Two new species of moths (Lepidoptera, Pyralidae, Chrysauginae) associated with the three-toed sloth (Bradypus spp.) in South America. *Acta Amazonica*, *12*(3), 649–656.

Capinera, J. (2001). *Handbook of vegetable Pests* (Academic Press). Elsevier.

Chapman, T. (1912). On the British (and a few Continental) species of *Scoparia*, Hw. *Transactions of the Entomological Society of London*, 501–518, pls. 35–44.

Chen, F., Song, S., & Wu, C. (2006a). A review of genus *Cirrhochrista* Lederer in China (Lepidoptera: Pyralidae: Schoenobiinae). *Oriental Insects*, *40*, 97–105.

Chen, F., Song, S., & Wu, C. (2006b). A review of the genus *Parapoynx* Hübner in China (Lepidoptera: Pyralidae: Acentropinae). *Aquatic Insects. International Journal of Freshwater Entomology*, *28*(4), 291–303.

Chen, F., Song, S., & Wu, C. (2006c). A review of the genus *Scirpophaga* Treitschke, 1832 in China (Lepidoptera: Pyralidae). *Zootaxa*, *1236*, 1–22.

Chen, F., Song, S., & Wu, C. (2007). A review of the genus *Paracymoriza* Warren in China (Lepidoptera: Crambidae: Acentropinae). *Aquatic Insects. International Journal of Freshwater Entomology*, *29*(4), 263–283.

Chen, F., Wu, C., & Xue, D. (2010). A review of the genus *Elophila* Hübner, 1822 in China (Lepidoptera: Crambidae: Acentropinae). *Aquatic Insects. International Journal of Freshwater Entomology*, *32*(1), 35–60.

Cho, S., Zwick, A., Regier, J. C., Mitter, C., Cummings, M. P., Yao, J., … Parr, C. (2011). Can Deliberately Incomplete Gene Sample Augmentation Improve a Phylogeny Estimate for the Advanced Moths and Butterflies (Hexapoda: Lepidoptera)? *Systematic Biology*, *60*(6), 782–796. doi:10.1093/sysbio/syr079

Dopman, E. B., Bogdanowicz, S. M., & Harrison, R. G. (2004). Genetic mapping of sexual isolation between e and z pheromone strains of the European Corn Borer (*Ostrinia nubilalis*). *Genetics*, *167*, 301–309.

Dopman, E. B., Robbins, P. S., & Seaman, A. (2010). Components of reproductive isolation between North American pheromone strains of the European Corn Borer. *Evolution*, *64*(4), 881–902.

Dyar, H. G. (1908a). A Pyralid inhabiting the fur of the living Sloth (*Cryptoses choloepi*, n. gen. and sp.) *Proceedings of the Entomological Society of Washington*, *9 (1907)*, 142–144.

Dyar, H. G. (1908b). A review of the North American Pyralinae. *Proceedings of the Entomological Society of Washington*, *10*, 96–102.

Dyar, H. G. & Heinrich, C. (1927). The American moths of the genus *Diatraea* and allies. *Proceedings of the United States National Museum, Washington*, *71*(19), 1–48, pls 1–20.

Ellis, W. N., Donner, J. H., & Kuchlein, J. H. (1997). Recent shifts in phenology of Microlepidoptera, related to climatic change (Lepidoptera). *Entomologische Berichten*, *57*, 66–72.

Fenton, M. B. & Fullard, J. H. (1981). Moth hearing and the feeding strategies of bats: Variations in the hunting and echolocation behavior of bats may reflect a response to hearing-based defenses evolved by their insect prey. *American Scientist*, *69*(3), 266–275.

Gaskin, D. E. (1972). Revision of New Zealand Diptychophorini (Lepidoptera: Pyralidae: Crambinae). *New Zealand Journal of Science*, *14 (1971)*(4), 759–809.

Gaskin, D. E. (1975). Revision of the New Zealand Crambini (Lepidoptera: Pyralidae: Crambinae). *New Zealand journal of zoology*, *2*(3), 265–363.

Greenfield, M. D. & Weber, T. (2000). Evolution of ultrasonic signalling in wax moths: Discrimination of ultrasonic mating calls from bat echolocation signals and the exploitation of an antipredator receiver bias by sexual advertisement. *Ethology Ecology & Evolution*, *12*(3), 259–279.

Guenée, M. A. (1845). Essai sur une nouvelle classification des Microlépidoptères et catalogue des espèces européennes. – (ser. 2) 3. *Annales de la Société Entomologique de France, Paris*, *(ser. 2) 3*, 105–192, 297–344.

Guenée, M. A. (1854). Deltoïdes et Pyralites. In *Histoire Naturelle des Insectes. Species Général des Lépidoptères* (Vol. 8, Vols. 8, pp. 1–448). Paris: Roret.

Hampson, G. F. (1896). On the classification of the Schoenobiinae and Crambinae, two subfamilies of moths of the family Pyralidae. *Proceedings of the Zoological Society of London.* 897–974.

Hampson, G. F. (1897). On the classification of two subfamilies of moths of the family Pyralidae: The Hydrocampinae and *Scoparia*nae. *Transactions of the Entomological Society of London*, 127–240.

Hampson, G. F. (1898). A revision of the moths of the subfamily Pyraustinae and family Pyralidae. Part i. *Proceedings of the General Meetings for Scientific Business of the Zoological Society of London*, *4*, 590–761, pls 49–50.

Hampson, G. F. (1899). A revision of the moths of the subfamily Pyraustinae and family Pyralidae. Part II. *Proceedings of the General Meetings for Scientific Business of the Zoological Society of London*, *1*, 172–291.

Hannemann, H. J. (1964). Kleinschmetterlinge oder Microlepidoptera II. Die Wickler (s.l.) (Cochylidae und Carposinidae). Die Zünslerartigen (Pyraloidea). In *Die Tierwelt Deutschlands* (Vol. 50). Jena: Gustav Fischer.

Hayden, J. E. (2011). Revision of *Cliniodes* Guenée (Lepidoptera: Crambidae: Odontiinae). *Annals of Carnegie Museum, Pittsburgh*, *79*(4), 231–347.

Hayden, J. E. (2012). Revision of *Odilla noralis* Schaus and transfer of Erupini to Midilinae (Lepidoptera: Crambidae). *Annals of Carnegie Museum*, *80*(4), 309–322. doi:10.2992/007.079.0401

Hebert, P. D. N., Cywinska, A., Ball, S. L., & Dewaard, J. R. (2003). Biological identifications through DNA barcodes. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *270*(1512), 313–321. doi:10.1098/rspb.2002.2218

Hebert, P. D. N. & Gregory, T. R. (2005). The Promise of DNA Barcoding for Taxonomy. *Systematic Biology*, *54*(5), 852–859. doi:10.1080/10635150500354886

Hennig, W. et al. (1950). Grundzuge einer theorie der phylogenetischen systematik.

Huemer, P., Mutanen, M., Sefc, K. M., & Hebert, P. D. N. (2014). Testing DNA Barcode Performance in 1000 Species of European Lepidoptera: Large Geographic Distances Have Small Genetic Impacts. *PLOS ONE*, *9*(12), 1–21. doi:10.1371/journal.pone.0115774

Janzen, D. H., Hallwachs, W., Blandin, P., Burns, J. M., CADIOU, J.-M., Chacon, I., … Espinoza, B. (2009). Integration of DNA barcoding into an ongoing inventory of complex tropical biodiversity. *Molecular Ecology Resources*, *9*, 1–26.

Kawahara, A. Y. & Breinholt, J. W. (2014). Phylogenomics provides strong evidence for relationships of butterflies and moths. *Proceedings of the Royal Society B: Biological Sciences*, *281*(1788), 20140970. doi:10.1098/rspb.2014.0970

Kennel, J. & Eggers, F. (1933). Die abdominalen Tympanalorgane der Lepidopteren. *Zool. Jahrb. Anat. Orttog.* (57), 1–104.

Khan, Z. R., Litsinger, J. A., Barrion, A. T., Villanueva, F. F. D., Fernandez, N. J., & Taylo, L. D. (1991). *World Bibliography of Rice Stem Borers: 1794-1990.* Manila, The Philippines: IRRI.

Kuznetsov, V. I. & Stekolnikov, A. A. (1979). Classification and phylogenetic relationships of the families and subfamilies of the Pyraloidea (Lepidoptera) of the palearctic fauna with regard to functional morphology of the male genitalia. *Trudy Institute Zoological Leningrad*, *82*, 43–74 (in Russian).

Landry, B. (1995). *A phylogenetic analysis of the major lineages of the Crambinae and of the genera of Crambini of North America (Lepidoptera:Pyralidae)* (Memoirs on Entomology International). Gainesville: Associated Publishers.

Landry, B. (2003). Revision of the Neotropical genus *Micrelephas* (Lepidoptera: Pyralidae: Crambinae). *Tropical Lepidoptera, Gainesville*, *11*(1), 13–27.

Landry, B. (2016). Taxonomic revision of the Spilomelinae (Lepidoptera, Pyralidae s. l.) of the Galápagos Islands, Ecuador. *Revue suisse de zoologie, Genève*, *123*(2), 315–399. doi:10.5281/zenodo.155309

Landry, B., Maes, J., Passoa, S., & Léger, T. (2015). Description of a new species of *Myelobia* Herrich-schäffer (Lepidoptera, Pyralidae s.l., Crambinae) from Nicaragua feeding on cultivated bamboo, *Guadua aculeata* Rupr. ex e. Fourn. (Poaceae). *Journal of Research on the Lepidoptera*, *48*, 65–81.

Landry, B. & Roque-Albelo, L. (2006). The Acentropinae and Musotiminae (Lepidoptera, Pyralidae) of the Galápagos Islands, Ecuador. *Zootaxa*, *1354*, 45–56.

Landry, B. & Roque-Albelo, L. (2008). The Glaphyriinae (Lepidoptera: Pyralidae) of the Galápagos Islands, Ecuador, with keys to the Neotropical species of *Hellula* Guenée. *Tijdschrift voor Entomologie, 's Gravenhage*, *151*, 193–203. doi:10.1163/22119434-900000264

Lees, D. C., Kawahara, A. Y., Rougerie, R., Ohshima, I., Kawakita, A., Bouteleux, O., … Lopez-Vaamonde, C. (2014). DNA barcoding reveals a largely unknown fauna of Gracillariidae leaf-mining moths in the Neotropics. *Molecular Ecology Resources*, *14*(2), 286–296. doi:10.1111/1755-0998.12178

Leraut, P. (1980). Liste systématique et synonymique des Lépidoptères de France, Belgique et Corse. *Alexanor and Bulletin de la Société entomologique de France*, *Supplement*, 1–334.

Li, H. M., Li, H.-H., & Wang, S. X. (2002). Catalogue of the Crambinae of China (Lepidoptera: Pyraloidea, Pyralidae). *Shilap. Revista de Lepidopterologia, Madrid*, *30*(117), 49–76.

Linnaeus, C. (1758). *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis.* (Laurentii Salvii). Holmiae.

Liu, Y., Dietrich, C., Braxton, S., & Wang, Y. (2019). Publishing trends and productivity in insect taxonomy from 1946 through 2012 based on an analysis of the Zoological Record for four species-rich families. *European Journal of Taxonomy*, (504). doi:10.5852/ejt.2019.504

Lopez-Vaamonde, C., Sire, L., Rasmussen, B., Rougerie, R., Wieser, C., Allaoui, A. A., . . . Lees, D. C. (2018). DNA barcodes reveal deeply neglected diversity and numerous invasions of micromoths in Madagascar. *Genome*, (999), 1–14. doi:10.1139/gen-2018-0065

Mally, R., Hayden, J. E., Neinhuis, C., Jordal, B. H., & Nuss, M. (2019). The phylogenetic systematics of Spilomelinae and Pyraustinae (Lepidoptera: Pyraloidea: Crambidae) inferred from DNA and morphology. *Arthropod Systematics & Phylogeny*, *77*(1), 141–204. doi:10.26049/ASP77-1-2019-07

Mally, R., Huemer, P., & Nuss, M. (2018). Deep intraspecific DNA barcode splits and hybridisation in the *Udea alpinalis* group (Insecta, Lepidoptera, Crambidae) – an integrative revision. *ZooKeys*, (746), 51–90. doi:10.3897/zookeys.746.22020

Mally, R., Korycinska, A., Agassiz, D. J., Hall, J., Hodgetts, J., & Nuss, M. (2015). Discovery of an unknown diversity of *Leucinodes* species damaging Solanaceae fruits in sub-saharan Africa and moving in trade (Insecta, Lepidoptera, Pyraloidea). *Zookeys*, *472*(117). doi:10.3897/zookeys.472.8781

Mally, R. & Nuss, M. (2011). Molecular and morphological phylogeny of European *Udea* moths (Insecta: Lepidoptera: Pyraloidea). *Arthropod Systematics & Phylogeny*, *69*(1), 55–71.

Mally, R., Segerer, A. H., & Nuss, M. (2016). *Udea ruckdescheli* sp. n. from Crete and its phylogenetic relationships (Pyraloidea, Crambidae, Spilomelinae). *Nota lepidopterologica*, *39*, 123. doi:10.3897/nl.39.9090

Marion, H. (1952). Ebauche d'une classification nouvelle des Pyraustidae. *Revue française de Lépidoptérologie, Paris*, *13*, 260–270.

Marion, H. (1954a). Révision des Pyraustidae de la faune française (suite). *Revue française de Lépidoptérologie, Paris*, *14*, 181–188, 221–227.

Marion, H. (1954b). Révision des Pyraustidae de la faune française. Introduction. *Revue française de Lépidoptérologie, Paris*, *14 (1953)*, 123–128, pl.1.

Marion, H. (1955a). Révision des Pyraustidae de la faune française (suite). *Revue française de Lépidoptérologie, Paris*, *15*(3), 181–188, 221–227.

Marion, H. (1955b). Révision des Pyraustidae de la faune française (suite). *Revue française de Lépidoptérologie, Paris*, *15*(3), 41–58, 41–58.

Marion, H. (1957). Révision des Pyraustidae de la faune française (suite). *Revue française de Lépidoptérologie, Paris*, *16*, 60–63.

Marion, H. (1959a). Révision des Pyraustidae de la faune française (suite). *Alexanor*, *1*(4), 103–110.

Marion, H. (1959b). Révision des Pyraustidae de la faune française (suite). *Alexanor*, *1*(1), 15–22, pl. 1.

Martínez, E. L. (2010). *A revision of the new world species of Donacaula Meyrick and a phylogenetic analysis of related Schoenobiinae (Lepidoptera: Crambidae)* (Doctoral dissertation, Mississippi State University, Mississippi).

Meyrick, E. (1878). Description of Australian Micro-Lepidoptera. i. Crambites. *Proceedings of the Linnean Society of New South Wales*, *3*, 175–216.

Meyrick, E. (1884). On the classification of the Australian Pyralidina. *Transactions of the Entomological Society of London*, 61–80, 277–350.

Meyrick, E. (1885). On the classification of the Australian Pyralidina. *Transactions of the Entomological Society of London*, 421–456.

Meyrick, E. (1890). On the classification of the Pyralidina of the European fauna. *Transactions of the Entomological Society of London*, 429–492, pl. 15.

Minet, J. (1982). Les Pyraloidea et leurs principales divisions systématiques (Lep. Ditrysia). *Bulletin de la Société entomologique de France*, *86*, 262–280.

Minet, J. (1985). Étude morphologique et phylogénétique des organes tympaniques des Pyraloidea. 2- Pyralidae, Crambidae, première partie. (Lepidoptera, Glossata). *Annales de la Société entomologique de France*, (21), 69–86.

Minet, J. (1991). Tentative reconstruction of the ditrysian phylogeny (Lepidoptera: Glossata). *Insect Systematics & Evolution*, *22*(1), 69–95.

Minet, J. & Surlykke, A. (2003). Auditory and sound producing organs. pp. 289–323. – in: Kristensen, n. p., Lepidoptera, moths and butterflies. volume 2: Morphology, physiology, and development. – in: M. Fischer, – Walter de Gruyter, Berlin. In *Handbook of Zoology. Volume IV Arthropoda: Insecta, Part 36.* (Walter de Gruyter, pp. 289–323). Berlin.

Mitter, C., Davis, D. R., & Cummings, M. P. (2017). Phylogeny and Evolution of Lepidoptera. *Annual Review of Entomology*, *62*(1), 265–283. doi:10.1146/annurev-ento-031616-035125

Montilla, A. E. D., Solis, M. A., & Kondo, T. (2013). The tomato fruit borer, *Neoleucinodes elegantalis* (Guenée)(Lepidoptera: Crambidae), an insect pest of neotropical solanaceous fruits. *CABI*, *3*(137).

Munroe, E. (1959). Revision of the genus *Linosta* Möschler (Lepidoptera: Pyralidae) with characterization of the subfamily Linostinae and a new subfamily. *The Canadian Entomologist, Ottawa*, (91), 485–488.

Munroe, E. (1970). Revision of the subfamily Midilinae (Lepidoptera: Pyralidae). *Memoirs of the Entomological Society of Canada, Ottawa*, *102*(74), 1–94.

Munroe, E. (1972). Pyraloidea, Pyralidae comprising subfamilies Scopariinae, Nymphulinae. In *The Moths of America north of Mexico* (E. W. Classey and R. B. D. Publications Inc., Vol. 13.1.A & 13.1.B, pp. 1–134, 135–250). London.

Munroe, E. (1974). Pyraloidea, Pyralidae comprising the subfamily Evergestinae. In *The Moths of America north of Mexico* (Vol. 13.1.C, 251–304, pls 1–13, A–K, pp. xv–xx). London: E.W. Classey and R.B.D. Publications Inc.

Munroe, E. (1976). Pyraloidea Pyralidae comprising the subfamily Pyraustinae tribe Pyraustini (part & conclusion). In *The Moths of America north of Mexico* (E.W. Classey Ltd. and The Wedge Entomological Research Foundation, 1–78, 79–150, pls 1–4, A–H., pls 5–9, J–U, pp. xiii–xvii.). London.

Munroe, E. (1991). Transfer of *Aulacodes eupselias* Meyrick to Pyraustinae, with notes on *Marasmia* Lederer and on cataclystiform wing patterns in the family Crambidae (Lepidoptera: Pyralidae). *Occasional Papers, Bishop Museum*, *31*, 122–130.

Munroe, E. (1995). Crambidae (Crambinae, Schoenobiinae, Cybalomiinae, Linostinae, Glaphyriinae, Dichogaminae, Scopariinae, Musotiminae, Midilinae, Nymphulinae, Odontiinae, Evergestinae, Pyraustinae). In *Atlas of Neotropical Lepidoptera. Checklist: Part 2. Hyblaeoidea – Pyraloidea - Tortricoidea 3* (pp. 34–79). Gainesville: Association for Tropical Lepidoptera & Scientific Publishers.

Munroe, E. & Solis, M. A. (1998). The Pyraloidea. In *Lepidoptera, Moths and Butterflies. Volume 1: Evolution, systematics, and biogeography* (de Gruyter, Vol. IV Arthropoda: Insecta, pp. 233–256). Handbook of Zoology. Berlin.

Mutanen, M., Wahlberg, N., & Kaila, L. (2010). Comprehensive gene and taxon coverage elucidates radiation patterns in moths and butterflies. *Proceedings. Biological Sciences*, *277*(1695), 2839–2848. doi:10.1098/rspb.2010.0392

Nakano, R., Skals, N., Takanashi, T., Surlykke, A., Koike, T., Yoshida, K., ... Ishikawa, Y. (2008). Moths produce extremely quiet ultrasonic courtship songs by rubbing specialized scales. *Proceedings of the National Academy of Sciences*, *105*(33), 11812–11817. doi:10.1073/pnas.0804056105

Nuss, M. (1998). The Scopariinae and Heliothelinae stat. rev. (Lepidoptera: Pyraloidea, Crambidae) of the Oriental Region - a revisional synopsis with descriptions of new species from the Philippines and Sumatra. *Nachrichten des entomologischen Vereins Apollo*, *suppl. 17*, 475–528.

Nuss, M. (1999). Revision der Gattungen der Scopariinae (Lepidoptera: Pyraloidea, Crambidae). *Nova Supplementa Entomologica, Berlin*, *13*, 3–151.

Nuss, M. (2003). *Afroscoparia* – a new genus of Scopariine from southern Africa (Insecta: Lepidoptera: Pyraloidea: Crambidae). *Entomologische Abhandlungen*, *61*(1), 109–115.

Nuss, M., Karsholt, O., & Meyer, M. (1998). A taxonomic revision of the Scopariinae from the Macaronesian Region (Lepidoptera: Pyraloidea: Crambidae). *Entomologica Scandinavica*, *28*(4), 509–551.

Nuss, M., Landry, B., Mally, R., Vegliante, F., Tränkner, A., Bauer, F., ... Speidel, W. (2003–2019). Global Information System on Pyraloidea. - www.pyraloidea.org.

Passoa, S. (1985). *Taxonomy of the larvae and pupae of economically important Pyralidae in Honduras* (Doctoral dissertation, University of Florida).

Pierce, F. N. (1909). Genitalia of the group Noctuidae of the Lepidoptera of the British Islands An Account of the Morphology of the Male Clasping Organs. *Nature*, *80*(246). doi:10.1038/080246c0

Pierce, F. N. (1914). *The genitalia of the group Geometridae of the Lepidoptera of the British Islands: An account of the morphology of the male clasping organs and the corresponding organs of the female* (FN Pierce). Liverpool.

Ragonot, E. L. (1887). *Diagnoses of North American Phycitidae and Galleriidae* (Ragonot). Paris.

Ragonot, E. L. (1888). *Nouveaux genres et espèces de Phycitidae & Galleriidae*. Paris: Ragonot.

Ragonot, E. L. (1889). Phycitidae and Galleriidae of North America. Some new species and a general catalogue. *Entomologica Americana*, *5*(6), 113–117.

Ragonot, E. L. (1891a). Essai sur la classification des Pyralites. *Annales de la Société Entomologique de France, Paris*, *(ser. 6) 10*, 435–546, pls 5, 7, 8.

Ragonot, E. L. (1891b). Essai sur la classification des Pyralites (suite). *Annales de la Société Entomologique de France, Paris*, *60*(1), 15–114.

Regier, J. C., Mitter, C., Solis, M. A., Hayden, J. E., Landry, B., Nuss, M., ... Cummings, M. P. (2012). A molecular phylogeny for the pyraloid moths (Lepidoptera: Pyraloidea) and its implications for higher-level classification. *Systematic Entomology*, *37*(4), 635–656. doi:10.1111/j.1365-3113.2012.00641.x

Regier, J. C., Zwick, A., Cummings, M. P., Kawahara, A. Y., Cho, S., Weller, S., ... Parr, C. (2009). Toward reconstructing the evolution of advanced moths and butterflies (Lepidoptera: Ditrysia): An initial molecular study. *BMC Evolutionary Biology*, *9*(1), 280. doi:10.1186/1471-2148-9-280

Robinson, G. S., Tuck, K. R., & Shaffer, M. (1994). *A field guide to the smaller moths of South-East Asia*. London: Natural History Museum.

Roesler, R. U. (1978). Die Wertigkeit von Merkmalen bei phylogenetischen Untersuchungen am Beispiel der Pyraloidea. *Nota lepidopterologica*, *1*(3), 99–105.

Segar, S. T., Volf, M., Isua, B., Sisol, M., Redmond, C. M., Rosati, M. E., . . . Novotny, V. (2017). Variably hungry caterpillars: Predictive models and foliar chemistry suggest how to eat a rainforest. *Proceedings. Biological sciences*, *284*(1866). doi:10.1098/rspb.2017.1803

Siaussat, D., Bozzolan, F., Porcheron, P., & Debernard, S. (2008). The 20-hydroxyecdysone-induced signalling pathway in g2/m arrest of *Plodia interpunctella* imaginal wing cells. *Insect biochemistry and molecular biology*, *38*(5), 529–539. doi:10.1016/j.ibmb.2008.01.001

Singh, N., Chandra, K., Kirti, J. S., & Ranjan, R. (2019a). A new species of the genus *Toccolosida* Walker, 1863 from India (Lepidoptera: Pyralidae: Pyralinae). *Zootaxa*, *4656*(1), 189–192. doi:10.11646/zootaxa.4656.1.12

Singh, N., Kirti, J. S., Singh, H., & Ranjan, R. (2019b). Two new genera for the *Botyodes* species complex (Lepidoptera: Pyraloidea: Crambidae). *Zootaxa*, *4623*(2), 387–395. doi:10.11646/zootaxa.4623.2.12

Slamka, F. (2008). Crambinae & Schoenobiinae. In *Pyraloidea of Europe (Lepidoptera)* (Vol. 2). Bratislava.

Solis, M. A. & Adamski, D. (1998). Review of the Costa Rican Glaphyriinae (Lepidoptera: Pyraloidea: Crambidae). *J. N.Y. Entomol. Soc. 106*, 1–55.

Solis, M. A. & Maes, K. (2002). Preliminary phylogenetic analysis of the subfamilies of Crambidae (Pyraloidea: Lepidoptera). *Belgian Journal of Entomology*, *4*, 53–95.

Solis, M. A. & Metz, M. A. (2011). Male genital homology based on musculature originating from the tegumen in snout moths (Lepidoptera: Pyraloidea). *Arthropod structure & development*, *40*(5), 435–448. doi:10.1016/j.asd.2011.03.005

Solis, M. A. & Metz, M. A. (2016). An illustrated guide to the identification of the known species of *Diatraea* Guilding (Lepidoptera, Crambidae, Crambinae) based on genitalia. *Zookeys*(565), 73–121.

Solis, M. A. & Mitter, C. (1992). Review and preliminary phylogenetic analysis of the subfamilies of the Pyralidae (sensu stricto) (Lepidoptera: Pyraloidea). *Systematic Entomology*, *17*, 79–90.

Spangler, H. G. (1988). Moth hearing, defense, and communication. *Annual review of entomology*, *33*(1), 59–81.

Thomas, Y., Bethenod, M.-T., Pelozuelo, L., Frérot, B., & Bourguet, D. (2003). Genetic isolation between two sympatric host-plant races of the European Corn Borer, *Ostrinia Nubilalis* Hubner i. Sex pheromone, moth emergence timing, and parasitism. *Evolution*, *57*(2), 261–273.

Tsai, L.-Y. (2013). *Phylogeny of the genus Parapoynx (Lepidoptera: Crambidae: Acentropinae) with special reference to the evolution of host utilization* (Master Thesis, Institute of Biological Sciences National Sun Yat-sen University). Retrieved from etd.lis.nsysu.edu.tw

Vogel, H., Altincicek, B., Glöckner, G., & Vilcinskas, A. (2011). A comprehensive transcriptome and immune-gene repertoire of the lepidopteran model host *Galleria mellonella*. *BMC genomics*, *12*(1), 308. doi:10.1186/1471-2164-12-308

Walker, F. (1859). Pyralides. – List of the Specimens of Lepidopterous Insects in the Collection of the British Museum, London. *17, 18, 19*, 255–508, 509–798, 799–1036.

Yamamura, K., Yokozawa, M., Nishimori, M., Ueda, Y., & Yokosuka, T. (2006). How to analyze long-term insect population dynamics under climate change: 50-year data of three insect pests in paddy fields. *Population Ecology*, *48*(1), 31–48. doi:10.1007/s10144-005-0239-7

Yang, Z., Landry, J.-F., Handfield, L., Zhang, Y., Alma Solis, M., Handfield, D., ... Hebert, P. D. N. (2012). DNA barcoding and morphology reveal three cryptic species of *Anania* (Lepidoptera: Crambidae: Pyraustinae) in North America, all distinct from their European counterpart. *Systematic Entomology*, *37*(4), 686–705. doi:10.1111/j.1365-3113.2012.00637.x

Ye, F., Shi, Y., Xing, L., Yu, H., & You, P. (2013). The complete mitochondrial genome of *Paracymoriza prodigalis* (Leech, 1889)(Lepidoptera), with a preliminary phylogenetic analysis of Pyraloidea. *Aquatic insects*, *35*(3), 71–88. doi:10.1080/01650424.2014.948456

Yin, C., Liu, Y., Liu, J., Xiao, H., Huang, S., Lin, Y., ... Li, F. (2014). ChiloDB: A genomic and transcriptome database for an important rice insect pest *Chilo suppressalis. Database*, *2014*. doi:10.1093/database/bau065

Yoshiyasu, Y. (1985). A systematic study of the Nymphulinae and the Musotiminae of Japan (Lepidoptera: Pyralidae). *Scientific Report of Kyoto Prefectural University, Agriculture*, *37*, 1–162.

You, P., Li, H., & Chen, K. (2002). Catalogue of the Nymphulinae and Musotiminae of China (Lepidoptera: Pyralidae). *Fauna of China*, (4), 37–64.

Zeller, P. C. (1848a). Die Gallerien und nackthornigen Phycideen. *Isis von Oken, Leipzig*, (8–10): (8) 569–618, (9) 641–691, (10) 721–754.

Zeller, P. C. (1848b). Exotische Phyciden. *Isis von Oken, Leipzig*, 857–890.

Zeller, P. C. (1863). *Chilonidarum et Crambidarum genera et species* (Wiegandt & Hempel). Meseritz & Berlin.

Zhang, B. C. (1994). *Index of Economically Important Lepidoptera* (CAB International). Wallingford, Oxon.

Zimmerman, E. C. (1958). *Insects of Hawaii, vol. 7: Macrolepidoptera.* University of Hawaii Press, Honolulu, HI.

Manuscript authorship and personal contribution

Chapter 1. Phylogeny, tribal classification and character evolution in Crambinae and Scopariinae (Lepidoptera: Pyraloidea). Systematic Entomology 44(4), 757-776. DOI: 10.1111/syen.12353

Authors: Théo Léger, Bernard Landry & Matthias Nuss.
Status: published
Personal contribution:

- conception of the study along with B. Landry and M. Nuss
- generation of dataset
- analysis of dataset
- preparation of the figures
- writing of the manuscript

Chapter 2. Refining the phylogeny of Crambidae with complete sampling of subfamilies (Lepidoptera, Pyraloidea)

Authors: Théo Léger, Richard Mally, Christoph Neinhuis & Matthias Nuss.
Status: manuscript
Personal contribution:

- generation of the dataset along with R. Mally
- analysis of the dataset
- preparation of the figures
- writing of the manuscript

Chapter 3. Discovery of another fern-feeding group of moths: the larvae of Hoploscopini (Insecta: Lepidoptera: Pyraloidea) from Borneo. Raffles Bulletin of Zoology 65: 100–108.

Authors: Richard Mally, Théo Léger, Charles S. Vairappan, Stephen Sutton & Matthias Nuss
Status: published
Personal contribution:

- generation of the COI barcode sequences for conspecific Hoploscopa specimens
- pictures of specimens
- preparation of the figures of the chaetotaxy
- minor role in the writing of the manuscript

Chapter 4. Twenty-six new species of *Hoploscopa* (Lepidoptera, Crambidae) from South-East Asia revealed by morphology and DNA barcoding. Zookeys, in press.

Authors: Théo Léger, Christian Kehlmaier, Charles S. Vairappan & Matthias Nuss
Status: submitted and accepted
Personal contribution:

- conception of the study along with M. Nuss
- generation of the molecular dataset
- analysis of the molecular dataset
- dissections and mounting of genitalia
- preparation of the figures
- writing of the manuscript

Chapter 1

Phylogeny, tribal classification and character evolution in Crambinae and Scopariinae (Lepidoptera: Pyraloidea)

Systematic Entomology (2019), DOI: 10.1111/syen.12353

Phylogeny, character evolution and tribal classification in Crambinae and Scopariinae (Lepidoptera, Crambidae)

THÉO LÉGER[1], BERNARD LANDRY[2] and MATTHIAS NUSS[1]

[1]Senckenberg Museum für Tierkunde Dresden, Königsbrücker Landstr., Dresden, Germany and [2]Muséum d'histoire naturelle, Route de Malagnou, Genève, Switzerland

Abstract. Crambinae (2047 spp.) and Scopariinae (577 spp.) are two major groups of pyraloid moths with a worldwide distribution. Their larvae feed predominantly on Poales and Bryophyta, with many cereal crop pests. We present the first molecular phylogeny of the two groups based on five nuclear genes and one mitochondrial gene (total = 4713 bp) sampled for 58 crambine species representing 56 genera and all tribes, 33 scopariine species representing 12 genera, and species in several other crambid lineages. Maximum likelihood and Bayesian analyses of the molecular data resolve suprageneric relationships in Crambinae and Scopariinae, whereas relationships between these and other subfamilies remain ambiguous. Crambinae and Scopariinae are each recovered as monophyletic groups, and Erupini, formerly regarded as an ingroup of Midilinae, is recovered as a possible sister group of Crambinae. The tree topology suggests the following two major changes within Crambinae: Prionapterygini Landry **syn.n.** of Ancylolomiini Ragonot **stat. rev.** and Myelobiini Minet **syn.n.** of Chiloini Heinemann. Argyriini Munroe is monophyletic after the transfer of *Pseudocatharylla* Bleszynski and *Vaxi* Bleszynski to Calamotrophini. Crambini, Diptychophorini and Haimbachiini are monophyletic after the exclusion of *Ancylolomia* Hübner, *Euchromius* Guenée, *Micrelephas* Dognin and *Miyakea* Marumo from Crambini, as well as *Microchilo* Okano from Diptychophorini. Euchromiini **tribe n.** is described for *Euchromius*. *Microcramboides* Bleszynski **syn.n.** and *Tortriculladia* Bleszynski **syn.n.** are synonymized with *Microcrambus* Bleszynski. In Scopariinae, *Caradjaina* Leraut **syn.n.** and *Cholius* Guenée **syn.n.** are synonymized with *Scoparia* Haworth, and, in addition, *Dasyscopa* Meyrick **syn.n.**, *Dipleurinodes* Leraut **syn.n.** and *Eudipleurina* Leraut **syn.n.** are synonymized with *Eudonia* Billberg. *Micraglossa melanoxantha* (Turner) (*Scoparia*) **comb.n.** is proposed as a new combination. We analysed 27 morphological characters of wing venation, tympanal organs, male and female genitalia, as well as host plant data and egg-laying behaviour. The ancestral character-state reconstructions confirmed previous apomorphies and highlighted new apomorphies for some of the newly recovered clades. The derived, nonadhesive egg-dropping behaviour is found to have evolved at least twice in Crambinae and is associated with the use of Pooideae as host plants.

This published work has been registered in ZooBank, http://zoobank.org/urn:lsid:zoobank.org:pub:1A84282D-930A-4C32-8340-D681BFF27A12.

Correspondence: Théo Léger, Senckenberg Museum für Tierkunde Dresden, Königsbrücker Landstr, Dresden, Germany. E-mail: theo.leger@outlook.com

Introduction

With about 15 500 species, Pyraloidea is one of the most diverse superfamilies of Lepidoptera. The Crambinae (2047 species) and the Scopariinae (577 species) together account for about 18% of described pyraloid species (Nuss *et al.*, 2019). The Crambinae typically have elongated forewings that provide them with camouflage on grasses, while the Scopariinae generally exhibit a greyish wing pattern matching that of rocks and tree trunks where they rest during the day. The Crambinae and Scopariinae are encountered worldwide, with the Scopariinae being more diverse in tropical mountain areas and islands (Munroe & Solis, 1998). The majority of Crambinae larvae are known to feed upon grasses (Poaceae). Many species of *Chilo* Zincken, *Coniesta* Hampson, *Diatraea* Guilding and *Eoreuma* Ely are recognized as economically important pests of various crops, including maize, millet, rice, sorghum and sugarcane, and a few species of Crambini referred to as sod webworms are pests of lawns in North America (Hill, 1987, 2008; Khan *et al.,* 1991; Capinera, 2001). The majority of Scopariinae larvae, as well as some species of the crambine genera *Agriphila* Hübner, *Catoptria* Hübner, *Chrysoteuchia* Hübner, *Gadira* Walker, *Glaucocharis* Meyrick and *Platytes* Guenée feed on mosses (Munroe & Solis, 1998; Goater *et al.*, 2005; Slamka, 2008; Glime, 2017). Other larvae have been reported to feed on Cyperaceae, various dicotyledons (Robinson *et al.*, 2010), on dried leaves (Millière, 1868), and on lichens for two species of *Eudonia* Billberg (Nuss in Goater *et al.*, 2005). Crambinae larvae are either stem borers (Chiloini, Haimbachiini), root feeders or ground-living leaf feeders (many Crambini) (Munroe & Solis, 1998). Crambinae females are reported to glue their eggs onto their host plant in the Haimbachiini (*Coniesta*, *Eoreuma*, *Xubida* Schaus), *Argyria* Hübner, *Calamotropha* Zeller, *Chilo* and *Myelobia* Herrich-Schäffer (Peterson, 1963; Youm & Gilstrap, 1994; Legaspi *et al.*, 1997; Landry *et al.*, 2015), whereas most Crambini drop nonadhesive eggs while perched or during a slow, undulating flight (Ainslie, 1930; Peterson, 1963; Matheny & Heinrichs, 1972; Marshal, 1988; Ponomarev, 2016).

The Crambinae were historically split into two groups, the ‘Ancylolomiidae’ and the ‘Crambidae’ (designating here all Crambinae except Ancylolomiini) (Ragonot, 1888), a classification followed by Forbes (1920), who recorded the two groups as subfamilies of Pyralidae. The subsequent attempt towards a classification of the Crambinae was made by Bleszynski, who recognized a *Chilo* complex, including *Chilo*, *Diatraea* and *Myelobia*, and an *Acigona* Hübner (synonym of *Haimbachia* Dyar) complex (Bleszynski, 1966). The Crambinae were later divided into the following tribes: Chiloini (Klots, 1970), Diptychophorini and Crambini (Gaskin, 1972, 1975), Argyriini (Klots, 1983), Ancylolomiini and Myelobiini (Minet, 1982). Gaskin also used the name Calamotrophini (Gaskin, 1988) for the genus *Calamotropha* but he did not describe the tribe. The first phylogenetic analysis of the group was based on 45 morphological characters and highlighted two new tribes – the Haimbachiini and the Prionapterygini – and confirmed the monophyly of the Crambini and the Diptychophorini (Landry, 1995). Landry’s work was mostly restricted to North American taxa and failed to recover the relationships among the tribes or to assign some genera to a given tribe. The Crambinae are currently classified into 176 genera (Nuss *et al.*, 2019). The Scopariinae genera were reviewed by Nuss (1999), and possible relationships within the group were presented by the same author (Nuss, 2003), but the subfamily has never been analysed phylogenetically. The current classification divides the Scopariinae into 24 genera, with *Eudonia* Billberg (263 species) and *Scoparia* Haworth (242 species) making the bulk of their diversity (Nuss *et al.*, 2019). *Hoploscopa* Meyrick was described in Scopariadae (now Scopariinae) and *Heliothela* Guenée in Hercynidae (now Odontiinae). The latter was placed by Amsel (1961) in its own subfamily, the Heliothelinae, which was later supported by Minet (1982) and Nuss (1998). The latter author considered the spine in the corpus bursae of the female genitalia to be a synapomorphy of the group, in which he also placed *Hoploscopa*. Other authors either treated the Heliothelinae as subgroup of the Scopariinae (Hannemann, 1964; Leraut, 1980; Robinson *et al.*, 1994), or synonymized it with the Scopariinae (Munroe & Solis, 1998). The Erupini constitute another tribe whose phylogenetic relationships to other Crambidae lineages are not clear. *Erupa* Walker was placed in the Schoenobiinae (Bleszynski, 1966), then moved to the Crambinae (Lewvanich, 1981). Munroe (1995) introduced the tribe Erupini to accommodate *Erupa*, *Lancia* Walker, *Neerupa* Hampson and *Schoenerupa* Hampson, and placed the tribe in the Crambinae. Most recently, Hayden (2012) transferred the Erupini to the Midilinae.

The wing venation provides characters that have been used widely (Ragonot, 1888; Forbes, 1920; Dyar & Heinrich, 1927; Shibuya, 1928; Okano, 1962; Bleszynski, 1964, 1966, 1970a; Klots, 1970; Landry, 1995) to define and segregate groups within the Crambinae: forewing vein R_{S4} is either ‘free’, i.e. connected to the end of the cell, or stalked with $R_{S2} + R_{S3}$; the hindwing cell is either ‘open’ or ‘closed’ by a cross-vein; the base of hindwing M_1 is either adjacent or fused to $Sc + R$, or it originates near the middle of the cell. The variation in male genitalia structures, such as the pseudosaccus, the gnathos tip, the coecum penis, and the papillae anales in female genitalia, were recognized as key to understanding the phylogeny of the Crambinae (Okano, 1962; Bleszynski, 1966, 1970a; Klots, 1970; Landry, 1995), but the lack of well-resolved phylogenies impeded investigations of the evolution of these structures.

Regier *et al.* (2012) found the Crambinae and the Scopariinae to be sister groups in the first molecular phylogeny of the Pyraloidea. However, their study did not include Erupini and Heliothelinae, while Crambinae and Scopariinae were only represented by three and two species respectively, raising the question of whether both groups would remain monophyletic when analysing a more diverse taxon sampling. We present here the first molecular phylogenetic analysis based on five nuclear markers and one mitochondrial marker, including a large sampling of Crambinae and Scopariinae, along with Erupini and Heliothelinae, in order to: (i) decipher the evolutionary relationships within these groups and, accordingly, to revise the classification; (ii) infer the evolution of morphological characters and identify potential apomorphies; (iii) understand the evolution of nonadhesive egg-laying behaviour and host plant use.

Material and methods

Taxon sampling

Samples were collected by light-trapping or during the daytime with a net and preserved either in a dried condition or in alcohol (see Table S1 for all relevant information). A number of specimens were obtained from colleagues (see Acknowledgements). Specimens were identified based on wing pattern and genitalia, and identifications were cross-checked by blasting the COI barcode sequence against the 'All Barcode Records' of the 'Current Database' on the Identification Engine in BOLD (http://boldsystems.org/; Ratnasingham & Hebert, 2007). Fifty-eight species representing 56 of the 176 genera and all tribes of Crambinae, as well as 33 species representing 12 of the 24 genera of Scopariinae were selected. Additionally, *Erupa* sp. (Erupini), *Heliothela wulfeniana* (Scopoli) (Heliothelinae) and *Hoploscopa* sp. (Hoploscopini) were included. Published DNA sequences for 13 additional taxa were also included (Mutanen *et al.*, 2010; Kawahara & Breinholt, 2014), including all subfamilies of the Crambidae except for the Cybalomiinae, the Lathrotelinae and the Linostinae. Correct identifications of specimens was proofed on BOLD for all samples except for MM07046 [*Hellula undalis* (Fabricius)] for which no COI barcode sequence was available. *Patania ruralis* (Scopoli), *Syllepis* cf. *marialis* (Spilomelinae) and *Anania hortulata* (Linnaeus) (Pyraustinae) were chosen as outgroups because the clade including the Pyraustinae and the Spilomelinae was highlighted as a sister group to all other Crambidae subfamilies (Regier *et al.*, 2012).

Molecular work

Dried specimens collected less than 2 years prior to DNA extraction were considered for PCR. DNA was extracted from abdomens following a nondestructive method (Knölke *et al.*, 2004) with the NucleoSpin Tissue kit (Macherey-Nagel, Germany) according to the manufacturer's protocol. Abdomens from alcohol-preserved specimens were dried 24 h before extraction to remove ethanol. Standard primers from Wahlberg & Wheat (2008) in combination with universal T3 and T7 tails were used to amplify six genes – carbamoyl-phosphate synthetase 2, aspartate transcarbamylase, and dihydroorotase (CAD), cytochrome oxydase subunit I (COI), glyceraldehyde-3-phosphate dehydrogenase (GAPDH), isocitrate dehydrogenase (IDH), cytosolic malate dehydrogenase (MDH) and ribosomal protein S5 (rps5) – giving a 4710 bp dataset in total (see Table S1 for respective gene length). Nested primers were designed from gene alignments by eye and with GENEFISHER2 (Giegerich *et al.*, 1996; bibiserv.cebitec.uni-bielefeld.de/genefisher2/) and were subsequently checked for melting temperature, 3′ complementarity, self-annealing and potential hairpin formation on the online platform of OLIGOCALC (www.basic.northwestern.edu/biotools/OligoCalc.html) (Table S2). BIO-X-ACT Short DNA Polymerase (Bioline, U.K.) was used following the PCR protocol of Wahlberg & Wheat (2008) with minor optimizations (Table S3). Hi-Spec Additive (Bioline) was added to samples with lower yields. PCR programmes from Wahlberg & Wheat (2008) with the annealing temperature optimized for each primer set or the TouchDown PCR programme (Regier, 2007) were used (Table S4). Amplification success was checked by electrophoresis on 1% or 2% agarose gels subsequently stained with ethidium bromide and visualized under UV light. For PCR products with weak or multiple bands, bands of interest were excised from the gel and DNA was extracted using the PCR clean-up gel extraction kit from Macherey-Nagel. Alternatively, the 'gel-picking' method was used (Decker, 2003): the band of interest was briefly touched with a sterilized toothpick, which was used to inoculate a new PCR and reamplified. PCR products were cleaned by adding 0.3 μL ExoSAP-IT (Affymetrix, Cleveland, Ohio, U.S.A.) and 1 μL H_2O to 10 μL of PCR product, and we then followed the manufacturer's protocol. Cleaned PCR products were sequenced forward by Macrogen (South Korea) or alternatively at the SMTD on a 3730 DNA Analyzer (Applied Biosystems, U.S.A.) using the T7 sequencing primer or PCR primers. Reverse sequencing with the T3 sequencing primer or PCR primers was performed for poor-quality samples.

DNA sequences processing

Sequences were aligned by eye and trimmed to first codon position on PHYDE 0.9971 (Müller *et al.*, 2005). Single-gene datasets were concatenated with help of a bash script. Gene sequences of conspecific samples sharing identical COI barcode were concatenated for the following species: *Chilo quirimbellus* Bleszynski (LEP1576 and LEP1577), *Eudonia mercurella* (Linnaeus) (LEP109 and LEP2677), *Heliothela wulfeniana* (LEP550 and LEP837), *Pseudocatharylla argenticilia* (Hampson) (LEP1905 and LEP1906) and *Urola nivalis* (Drury) (LEP2671 and LEP2672). Illumina transcriptome reads of *Myelobia smerintha* (Hübner) from Kawahara & Breinholt (2014) were retrieved from the Dryad depository and searched for the genes of interest with reciprocal BLAST using gene sequences of *C. quirimbellus* and *Diatraea saccharalis* (Fabricius), with subsequent identification of orthologues done under RAXML. The six gene sequences were concatenated into a 4710 bp dataset with 17.8% of missing data. The alignment of the DNA sequences was straightforward with no insertion or deletion detected, with the exception of the CAD gene of *Thaumatopsis pexella* (Zeller) (Crambinae) being one codon longer. Sequencing success and GenBank reference numbers are reported in Table S1. Codon saturation for each third codon position was visualized by plotting the substitution rate between each pair of taxa on the branch length separating them (Klopfstein *et al.*, 2013). The best-scoring RAXML tree calculated from the standard concatenated dataset was used in order to compare substitution rates for each gene and codon position with a reference branch length. Substitution rate plots revealed saturation of the COI third position at deep relationships of the phylogenetic tree (Fig. S1). Two datasets were thus analysed, the whole dataset (conc6genes) and one with the COI third codon position deleted (conc6genes_COI1 + 2). Unless otherwise mentioned, the conc6genes is implicitly considered.

Partitioning

The best partition scheme was searched for on the dataset prepartitioned per gene and codon position (total = 18 subsets) using PARTITIONFINDER (Lanfear *et al.*, 2017). Greedy algorithms (Lanfear *et al.*, 2012) for the models GTR, GTR+G and GTR+I+G with the corrected Akaike information criterion model selection approach were used. The best partition scheme that was found contained 16 character sets, with the first codon position of CAD and IDH merged into one character set and the second codon position of GAPDH and rps5 merged into another character set.

Phylogenetic analyses

Maximum likelihood (ML) analyses were performed using RAXML (Stamatakis, 2006) with the GTR + G evolution model. Branch support was assessed by performing 1000 bootstrap replicates using the GTRCAT approximation. The best-partitioning scheme found with PARTITIONFINDER was used. Bayesian inference (BI) analyses were performed with MRBAYES (Huelsenbeck & Ronquist, 2001), with the dataset partitioned following the best PARTITIONFINDER model and nst = 6, rates = gamma, revmatpr = dirichlet (1,2,1,1,2,1) (prior assumption of twice as many transitions as transversions), ratepr = variable, brlenspr = unconstrained: exponential (1.0) applied. While the parameters revmat, tratio, statefreq, shape, pinvar were set unlinked, other parameters were left unchanged. Two independent runs were done on 100 mio generations, each with three heated and one cold chain. Good mixing of the Markov chains Monte Carlo (MCMC) was estimated by visualizing the effective sample size (ESS) for all parameters on TRACER (Rambaut *et al.*, 2018), with ESS > 200 indicating sufficient sampling. Posterior trees produced before reaching the log-likelihood plateau were discarded from the sampling. The consensus tree was generated with TREEANNOTATOR from the BEAST package (Bouckaert *et al.*, 2014). The ML and BI analyses were run on the CIPRES portal (Miller *et al.*, 2010).

Identification of rogue taxa

Taxa flagged as 'rogues' appear at different and often contradictory positions in phylogenetic trees, thereby affecting the stability of a topology (Wilkinson, 1994; Aberer *et al.*, 2013). ROGUENAROK (Aberer *et al.*, 2013) was used to identify rogue taxa from the complete taxon sample with the following options: majority-rule search, support optimized, maximum dropset size = 2, algorithm = ROGUENAROK. The ROGUENAROK analysis returned *Hellula undalis* (Glaphyriinae) and *Microchilo* cf. *elgrecoi* (Crambinae) as the two most unstable taxa among the bootstrapped trees (respective scores, 1.15556 and 1.18611) and were removed from the final taxon sampling. Six further *Eudonia* species, three *Scoparia*, one *Caradjaina* Leraut and two species of *Microcrambus* Bleszynski, as well as *Microcramboides meretricellus* Bleszynski and *Tortriculladia* cf. *pentaspila* recovered within *Microcrambus*, were removed from the final taxon sampling to limit the sampling to one or few representatives per genus.

Character evolution

Dissection and slide-mounting methods follow Landry (1995). Ratios of structures were measured with an eyepiece micrometer. Male and female specimens used for morphological investigations were associated based on wing pattern and COI barcode sequence. Twenty-seven characters analysed by Landry (1995) and Nuss (2003) were investigated. These comprise the wing venation, tympanal organs, and male and female genitalia. Additional information on characters was retrieved from the following papers: Bleszynski (1963, 1965, 1966), Clarke (1965), Gaskin (1975), Landry (1995) and Song *et al.* (2009). Wing venation nomenclature follows Wootton (1979). The characters were coded in a morphomatrix using MESQUITE (Maddison & Maddison, 2017) (Table S5) and illustrated using Adobe ILLUSTRATOR CS6 (Fig. 1).

Ancestral character states were estimated with the *ace* function of the R package APE (Paradis *et al.*, 2004) using ML (Pagel, 1994) for discrete characters, and with the *fastAnc* function of the PHYTOOLS package in R (Revell, 2012) using ML and tree rerouting (Felsenstein, 1985) for continuous characters (scripts available as Files S1 and S2, respectively). These packages were used in previous publications for reconstructing character evolution in plants (Soltis *et al.*, 2013; Landis *et al.*, 2018; Spriggs *et al.*, 2018) and animals (Tingle *et al.*, 2017; Irisarri *et al.*, 2018). Minor modifications of the source code of the 'ace' function as suggested by Emmanuel Paradis (personal communication) were done to take uncertain character states (coded '?') into account (File S3). The best RAXML tree of the molecular data was used as input file. The 'ER' (equal rates) model was chosen for the 'ace' analyses. Ancestral continuous character states were mapped using the 'contMap' function of the PHYTOOLS package. The phylogenetic signal for continuous traits was estimated with the PHYTOOLS function 'phylosig' (Revell, 2012) using Pagel's λ (Pagel, 1999) and Blomberg's K (Blomberg *et al.*, 2003) methods.

Records of egg adhesiveness and larval life habits were retrieved from the literature and the Lepiforum website (www.lepiforum.de), and host plant records were retrieved from the literature and the HOST database (Robinson *et al.*, 2010) (Table S7). Information associated with congeneric species was used for species for which character traits were missing in order to incorporate the maximum amount of information for these traits. Due to the scarcity of the information record, these traits were not formally analysed like morphological characters.

Results

Phylogenetic relationships

The ML and BI analyses of conc6genes and conc6genes_COI1+2 delivered similar topologies except for the placement of *Donacoscaptes* Zeller, *Eudonia truncicolella* (Stainton) and *Heliothela*, but none of these conflicting placements were supported by either of the analyses (BS < 70). The 'CAMMSS clade', including the Acentropinae, Crambinae, Midilinae, Musotiminae, Schoenobiinae and Scopariinae, was recovered as monophyletic, with Erupini, Heliothelini and Hoploscopini also included [bootstrap support (BS) = 92, posterior probability (PP) = 1; Fig. 2]. Heliothelinae was not supported as monophyletic. *Heliothela* was sister to the Crambinae and Scopariinae in the ML analysis of conc6genes, whereas it is recovered as the most basal lineage of the CAMMSS clade in the BI of conc6genes as well as in the ML and BI analyses of conc6genes_COI1+2. However, none of the analyses provided good support for these placements. *Hoploscopa* was sister to the Musotiminae in all analyses, but only the BI analyses provided good support for this topology (PP = 0.98 in analyses of both datasets). The sister-group relationship between Scopariinae and Crambinae + *Erupa* was not supported in the ML analyses, but was weakly and strongly supported in the BI of conc6genes (PP = 0.96) and conc6genes_COI1+2 (PP = 1.00; Fig. S3).

The Scopariinae (Heliothelinae excluded, following Nuss, 1998) were found to be monophyletic (BS = 100, PP = 1.00). *Anarpia* Chapman was found sister to all remaining Scopariinae, which form four major well-supported clades: (i) *Helenoscoparia* Nuss, *Gesneria* Hübner, *Cosipara* Munroe and an unidentified Scopariinae; (ii) *Micraglossa* Warren; (iii) *Scoparia*, including *Caradjaina* Leraut **syn.n.**, *Cholius* Guenée **syn.n.**; and (iv) *Eudonia*, including *Dasyscopa* Meyrick **syn.n.** and *Dipleurinodes* Leraut **syn.n.** Relationships among *Antiscopa* Munroe, *Micraglossa* and *Eudonia* + *Scoparia* are ambiguous. Weak evidence was found for *Micraglossa* as sister to *Eudonia* + *Scoparia* in the analyses of the conc6genes dataset (BS < 70, PP = 0.93), but analyses of conc6genes_COI1+2 provided better support for this topology (BS = 75, PP = 0.98). The two species-rich genera *Eudonia* and *Scoparia* are recovered as sister groups.

The Erupini, represented here only by *Erupa*, are sister to the Crambinae, a position not supported in the ML analysis but well supported in the Bayesian analysis (PP = 0.99). The Crambinae were recovered as monophyletic with strong support in all analyses (Fig. 2). The Diptychophorini were recovered as monophyletic, with *Diptychophora* Zeller, *Glaucocharis* and *Microcausta* Hampson sister to *Gargela* Walker, a genus

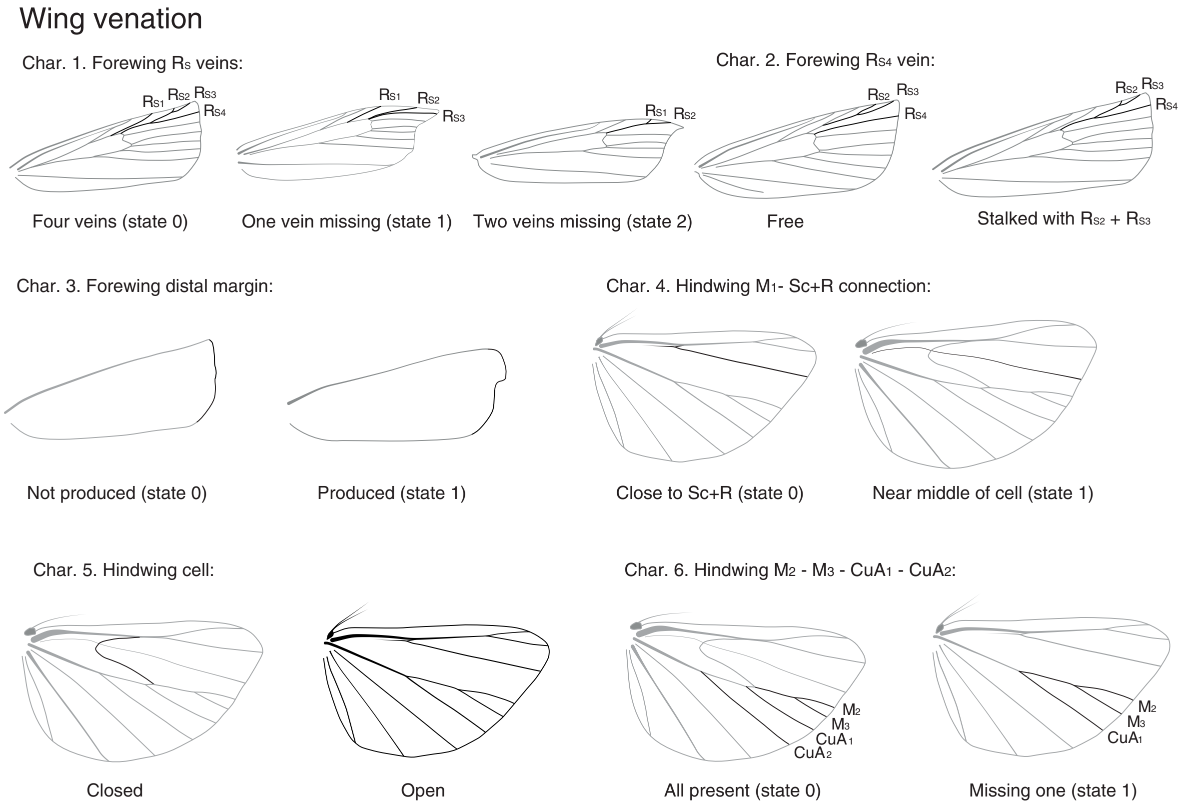


Fig. 1. List of the 27 morphological characters studied. State polarization reflects what is thought to be the derived state.

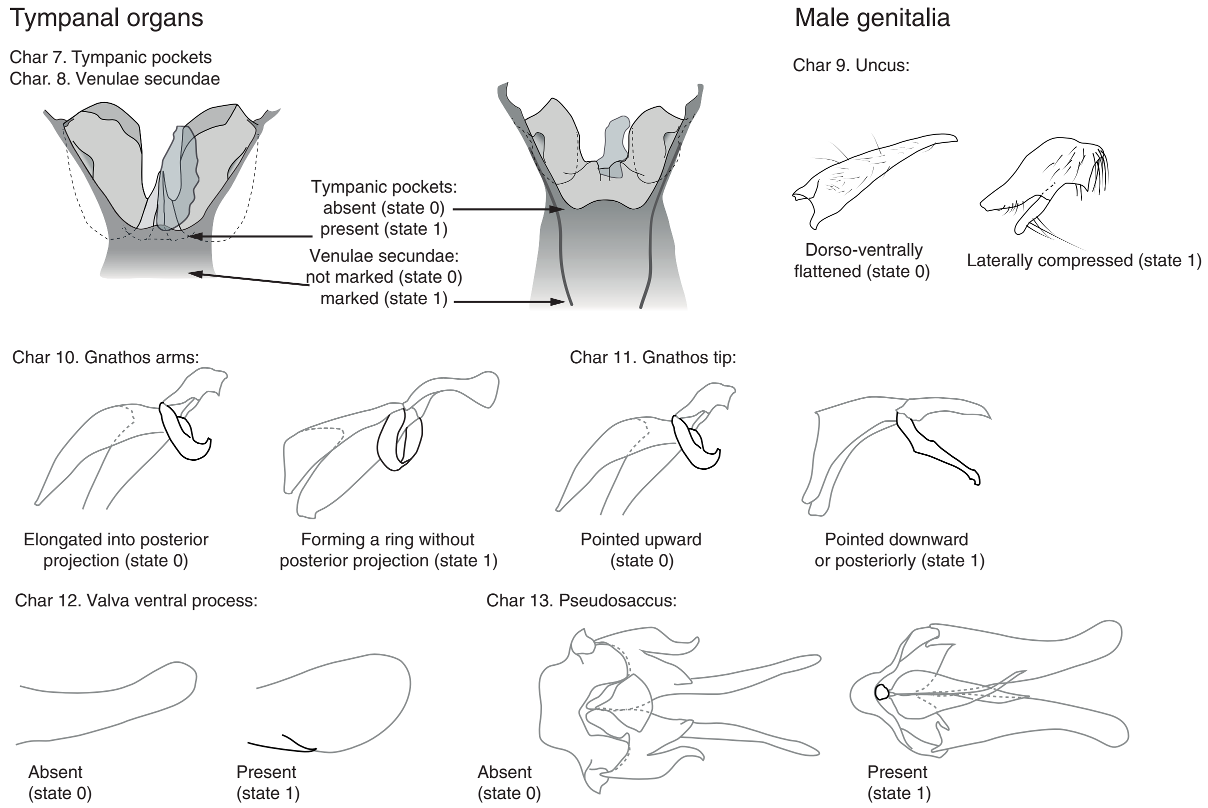


Fig. 1. Continued.

formerly unplaced to tribe (Song *et al.*, 2009). The Diptychophorini are sister to all remaining Crambinae, which form a well-supported monophyletic group, here referred to as the 'narrow winged clade'. *Microchilo* Okano, so far placed in Diptychophorini, has been recovered in our analyses within the 'narrow winged clade' (Fig. S2). There is a basal dichotomy between the Ancylolomiini + Chiloini and all remaining narrow-winged crambines, but the sister-group relationship between the Ancylolomiini and the Chiloini was only supported by the BI analysis (PP = 0.99). In the Ancylolomiini **stat. rev.**, *Ancylolomia* Hübner is nested within the Prionapterygini **syn.n.** (*Mesolia* Ragonot, *Prionapteryx* Stephens, *Pseudoschoenobius* Fernald), and *Prionotalis* Hampson is consistently found as sister group to the rest of the Ancylolomiini in all topologies, with moderate (PP = 0.97) and strong support (PP = 0.99) in the BI of conc6genes and conc6genes_COI1+2 respectively. The Chiloini were well supported in all analyses (BS = 99, PP = 1.00). The New Zealand *Gadira* and the Australian *Hednota* Meyrick form a monophyletic clade sister to *Chilo* + *Diatraea* + *Myelobia*. The East-Palearctic *Miyakea* Marumo, formerly placed in the Crambini (Nuss *et al.*, 2019), and the Hawaian *Orthomecyna* Butler form a well-supported monophyletic group (BS = 96, PP = 1.00) sister to the 'open cell clade'. The latter clade, including the Argyriini, Calamotrophini **stat. rev.**, Crambini, Euchromiini **tribe n.**, Haimbachiini, as well as *Catharylla* Zeller and *Micrelephas* Dognin was consistently recovered in all analyses (BS = 98, PP = 1.00). *Argyria*, *Catharylla*, *Urola* Wakler (part of the Argyriini) and *Micrelephas* – formerly placed in the Crambini (Landry, 2003) – form with the Haimbachiini a monophyletic clade (BS = 81, PP = 1.00), sister to the 'R_{S4} stalked clade'. The Argyriini sensu Munroe (1995), defined on the basis of the snow-white colour of the wings, are polyphyletic with *Argyria* and *Urola*, as well as *Catharylla*, belonging to one clade along with *Micrelephas* and the Haimbachiini, whereas *Pseudocatharylla* Bleszynski and *Vaxi* Bleszynski belong to the Calamotrophini. The Haimbachiini were recovered as monophyletic with strong support in all analyses (BS = 100, PP = 1.00). The 'R_{S4} stalked clade' includes the Calamotrophini, Crambini and Euchromiini (BS = 98, PP = 1.00), with the clade including *Euchromius* and the Calamotrophini found sister to the Crambini. *Euchromius*, formerly placed in the Crambini (Landry, 1995), is sister to the Calamotrophini, which includes *Calamotropha*, *Pseudocatharylla* and *Vaxi* (BS = 98, PP = 1.00). The Crambini (*Ancylolomia*, *Euchromius, Micrelephas* and *Miyakea* excluded) are monophyletic (BS = 100, PP = 1.00), with *Platytes* recovered as the most early diverging lineage. *Agriphila* and *Catoptria* form a sister clade to the remaining Crambini. Two major groups are observed in the remaining Crambini, the *Crambus* group (BS = 100,

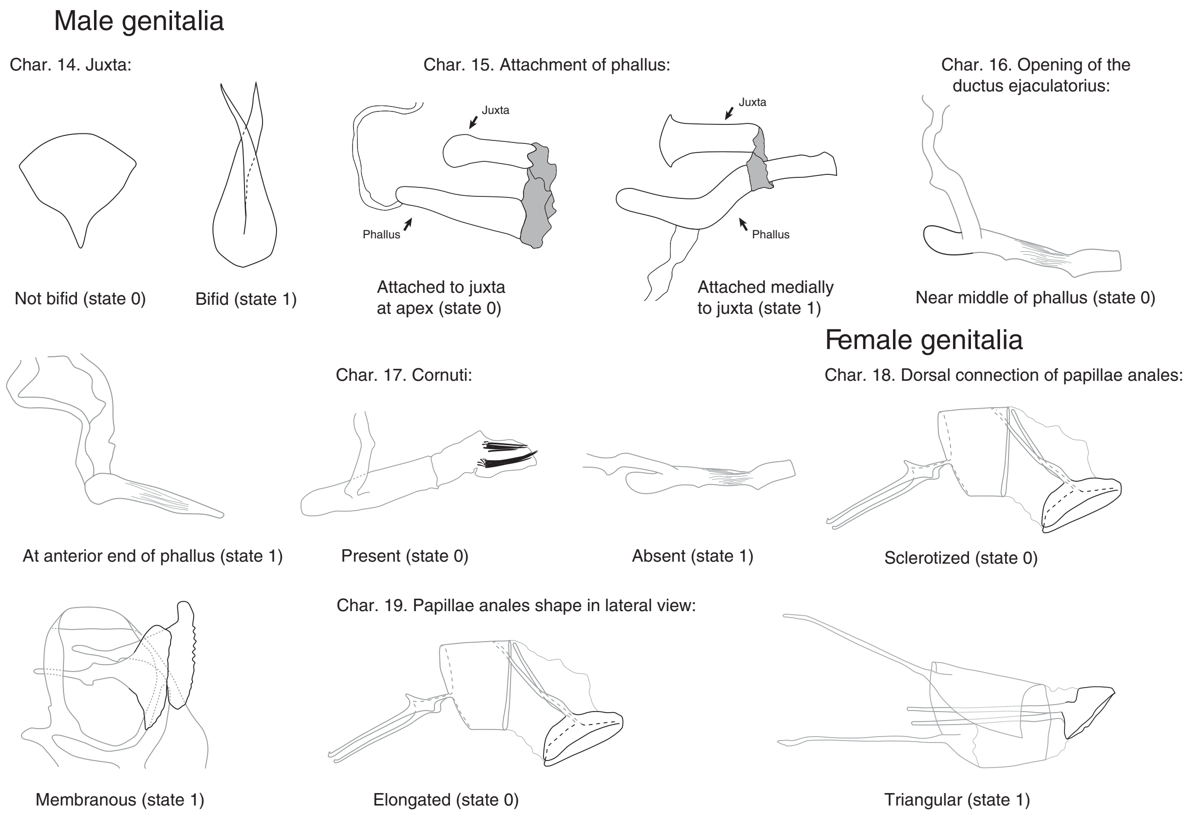


Fig. 1. Continued.

PP = 1.00) and the *Pediasia* group (BS = 75, PP = 1.00). Relationships within the *Crambus* group are well resolved, while basal relationships among the genera of the *Pediasia* group remain ambiguous. In the *Crambus* group, *Microcramboides* **syn.n.** and *Tortriculladia* **syn.n.** fall within *Microcrambus* (Fig. S2).

Evolution of morphological traits

Wing venation. Wing venation provides several characters varying in Crambinae, whereas no variation is observed in Scopariinae. Reduction in the number of veins in the forewing, with loss of the R_{S4} vein, and in the hindwing, with loss of one of the M_2–M_3 vein, is observed in 12 genera, five of them showing reductions in both the forewing and hindwing. Six of these genera belong to Crambini alone: *Culladia* Moore (one forewing R vein missing), *Fernandocrambus* Aurivillius, *Neoculladia* Bleszynski, *Novocrambus* Amsel, *Platytes* (one forewing R vein, one hindwing M vein missing), and *Raphiptera* Hampson (forewing CuA_2, two forewing R veins, and one hindwing M vein missing (Landry, 1995)). Species of *Euchromius* and *Microcrambus* are also reported missing one vein (Landry, 1995). Vein loss is found in several very small moths (< 7 mm in *Microcausta*, *Neoculladia*, *Novocrambus* and *Raphiptera*) and is associated with the narrowing of the wings or the reduction in size of the moths (Landry, 1995; Polilov, 2015).

The forewing R_{S4} vein is connected to the cell in all *Euchromius* species (R. Schouten, personal communication), *Platytes ornatellus* Leech, and *P. vobisne* Dyar, but missing in *P. alpinella* Hübner (Landry, 1995; Kirpichnikova, 1999), and stalked with $R_{S2} + R_{S3}$ in the Calamotrophini and in all Crambini sampled. Forewing vein R_{S4} stalked to $R_{S2} + R_{S3}$ (Fig. 1, character 2) is reconstructed as the most probable ancestral state in the Calamotrophini ($P = 0.9$; Table S6) and for the node including all Crambini sister to *Platytes* ($P = 0.992$), whereas no support for the R_{S4} vein stalked as the ancestral state of the R_{S4} clade was found ($P = 0.526$). The hindwing M_1 stem well separated from the Sc + R vein (character 4; Fig. 1) is reconstructed as the most probable ancestral state of the Crambinae ($P = 0.87$; Fig. 3) and constitutes a new apomorphy for the subfamily. The M_1 stem is closer to the Sc + R vein in the clade including *Chilo*, *Diatraea* and *Myelobia* and in the 'open cell clade'. In the latter, the hindwing cell is of the 'open' type, i.e. without a vein connecting the base of M_1 and M_2 (Fig. 1, character 5). The ancestral character reconstruction supports one origin of this trait in the open cell clade (Fig. 3), with the closed cell in *Calamotropha*, and the open cell in *Glaucocharis* (Diptychophorini) representing homoplasies.

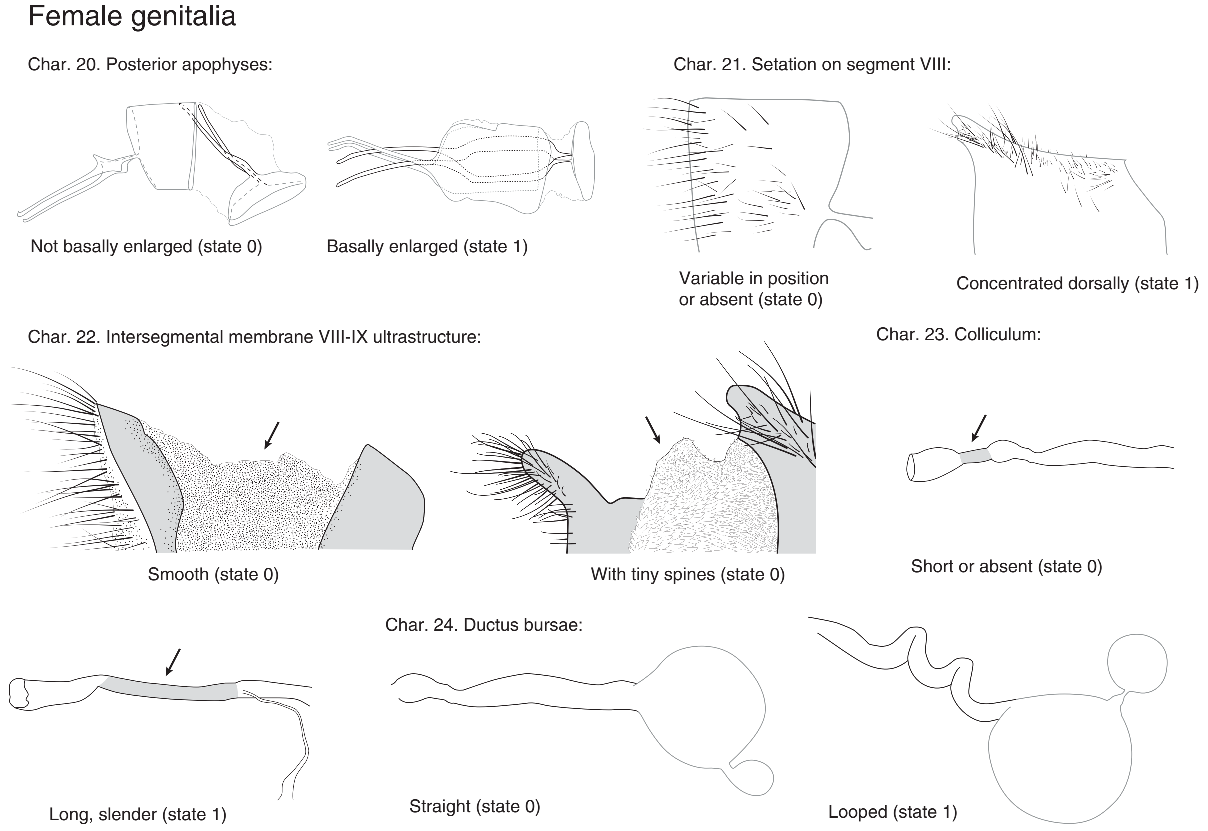


Fig. 1. Contined.

Tympanal organs. Two characters of the tympanal organs were investigated. Presence and absence of tympanic pockets (Fig. 1, character 7) are homoplastic. In the Crambidae, they are observed in the two Spilomelinae included here and in the Crambinae. Within the Crambinae, they are absent in Diptychophorini (but present in *Microcausta*), *Myelobia* + *Diatraea*, *Orthomecyna*, Haimbachiini and *Neoculladia* + *Novocrambus*. The ancestral character-state reconstruction revealed the presence of tympanic pockets as the ancestral state for the 'narrow winged clade' ($P = 0.99$). Strongly sclerotized venulae secundae (Fig. 1, character 8) are observed in *Helenoscoparia* (Scopariinae), and in Chiloini, Haimbachiini, *Calamotropha* and some Crambini (Crambinae). They are also found in *Acentria* Stephens (Acentropinae), *Erupa*, *Evergestis* Hübner (Glaphyriinae), *Patania* Moore (Spilomelinae) and *Schoenobius* Duponchel (Schoenobiinae), and are thus strongly homoplastic.

Male genitalia. The tip of the gnathos in lateral view is either directed upwards, or posterad to downwards. In Scopariinae, it is directed downwards (Fig. 1, character 11), which represents the most probable ancestral state for the group ($P = 0.85$), but it is directed upwards in *Antiscopa*, *Helenoscoparia*, and upwards or posterad in *Eudonia*. A gnathos tip directed downwards or posterad is observed in *Calamotropha*, *Euchromius*, *Micrelephas*, *Ancylolomia*, *Prionotalis*, and in all Crambini where it is reconstructed as the most probable ancestral state ($P = 0.89$). The gnathos of *Mesolia*, *Prionapteryx* and *Pseudoschoenobius* is reduced to a ring without posterior extension. The pseudosaccus, a small sclerite nested between the antero-ventral angle of valvae and vinculum (Fig. 1, character 13), is observed in the Ancylolomiini + Chiloini clade and 'R_{S4} stalked clade'. The pseudosaccus was either gained once in the ancestor of the 'narrow-winged clade' with secondary losses in the clade including the Argyriini, *Catharylla*, *Micrelephas* and the Haimbachiini, as well as in *Miyakea* + *Orthomecyna*, or it is homoplasic, with two independent origins in the ancestors of the Ancylolomiini + Chiloini clade and the 'R_{S4} stalked clade'. The phallus is attached medially via the diaphragma to the juxta in all Crambinae (*Ancylolomia* and *Microchilo* excepted) and in *Musotima* Meyrick (Musotiminae) (Fig. 1, character 15), while it is attached apically in all Scopariinae and in other Crambidae subfamilies investigated here. The medial attachment of the phallus represents an apomorphy for the Crambinae, corroborating the findings of Landry (1995). The opening of the ductus ejaculatorius (Fig. 1, character 16) is situated in the anterior part of the phallus in all Ancylolomiini as well as in *Myelobia* + *Diatraea*, suggesting that this configuration evolved twice independently in Crambinae. A bifid juxta (Fig. 1, character 14) was observed in all Chiloini and was recovered as the most

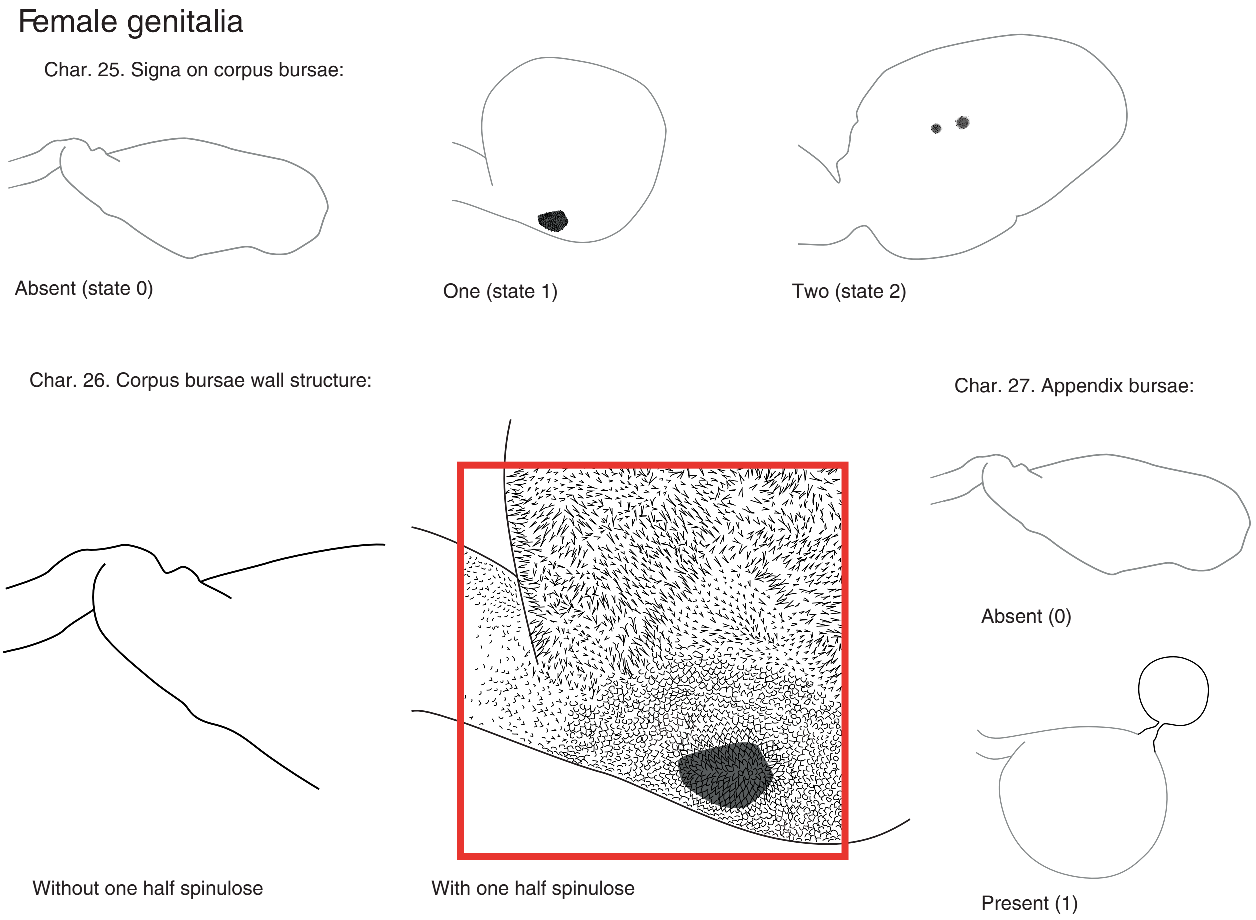


Fig. 1. Contined. [Colour figure can be viewed at wileyonlinelibrary.com].

probable ancestral state of the clade, but convergent, nonhomologous structures were observed in *Diptychophora*, *Gargela*, *Micrelephas* and *Vaxi*.

Female genitalia. An appendix bursae (Fig. 1, character 27) is present in *Eudonia* + *Scoparia*, with one secondary loss in *Scoparia luteolaris* **comb.n.** An appendix bursae was also observed in outgroups *Anania* Hübner (Pyraustinae) and *Syllepis* Poey (Spilomelinae). A gain of this feature in the ancestor of *Eudonia* + *Scoparia* was supported and represents a synapomorphy for this clade.

The presence of a signum (or signa) in the corpus bursae (Fig. 1, character 25) was reconstructed as the ancestral state in the Crambinae, with the absence of signum recovered as the most probable ancestral state of the ‘narrow-winged clade’ ($P = 0.99$). In the Crambini, *Platytes* species bear one or two signa, while only one signum is present in all *Agriphila* and *Catoptria* species. The presence of two signa was recovered as the most probable ancestral state of the *Crambus* group (Fig. 3) with moderate support ($P = 0.83$), with secondary losses of one signum in *Conocramboides* Bleszynski and both signa in *Microcrambus*. Few species of *Chrysoteuchia* and *Orocrambus* Purdie only have one signum. No signum is observed in the *Pediasia* group, with the exception of few species of *Chrysocrambus* Bleszynski and *Parapediasia* Bleszynski with one or two signa.

The female oviscapt is made of evertible segments VIII and IX + X and intersegmental membranes VII–VIII and VIII–IX. Segments IX + X are modified into papillae anales that sometimes help to fix the eggs to the substrate (Kristensen, 2004). A membranous dorsal connection of the papillae anales (Fig. 1, character 18) was observed in six different taxa (*Ancylolomia*, *Diptychophora*, *Euchromius*, *Gadira*, *Miyakea* and all Crambini), and represents the most probable ancestral state of Crambini ($P = 0.94$). The anterior and posterior apophyses are attachments for muscles responsible for the retraction of the eighth and ninth segments after oviposition (Kuznetsov & Stekolnikov, 2001; Kristensen, 2004). While the pattern of distribution of the posterior apophyses lengths did not show any phylogenetic signal [null hypothesis stating no correlation not significantly rejected under the λ method ($P = 0.063$) or the K method ($P = 0.238$)], phylogenetic signal was found for the lengths of the anterior apophyses [null hypothesis significantly rejected with the λ method ($P = 5.18 \times 10^{-9}$) and the K method ($P = 0.049$)], indicating a tendency to anterior apophyses reduction in the ‘open cell clade’ (Fig. 4).

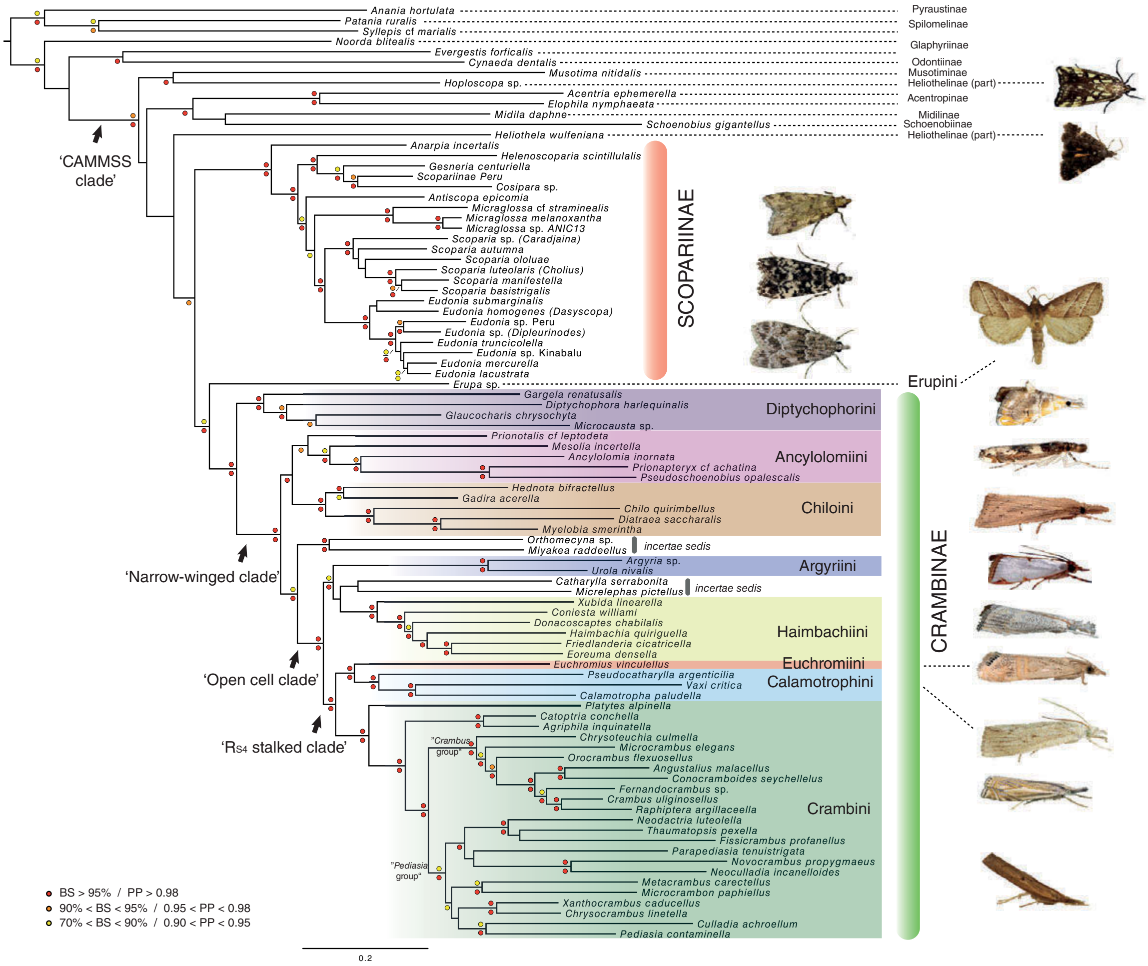


Fig. 2. Best-scoring maximum likelihood (ML) tree of the conc6genes dataset with best PARTITIONFINDER model applied. Filled circles above the nodes represent bootstrap support (BS) values from 1000 replicates, and filled circles below the nodes represent the posterior probability (PP) of the Bayesian analysis of the same dataset. Highlighted groups reflect the new classification adopted here. Species pictures (with photographers in brackets) from top to bottom are as follows: *Hoploscopa* sp. (T. Léger), *Heliothela ophideresana* (D. Hobern), *Micraglossa aureata* (jpmoth.org), *Scoparia exhibitalis* (D. Hobern), *Eudonia mercurella* (R. Coleman), *Erupa* sp. (T. Léger), *Glaucocharis* sp. (L. Shih), *Prionapteryx nebulifera* (L. Prosperi), *Diatraea saccharalis* (R. Gomes da Costa), *Argyria centrifugens* (Ian Morton), *Haimbachia squamulella* (P. Coin), *Euchromius ocelleus* (L. Hoy), *Calamotropha paludella* (D. Hobern), *Crambus lathoniellus* (F. Bauer), *Pediasia contaminella* (D. Hobern).

Discussion

Phylogenetic relationships

Our six-gene dataset recovered the monophyly of the Crambinae and the Scopariinae with strong support, with 60% of their inner relationships recovered with strong support (BS > 90%) and 19% with moderate support (70% < BS < 90%), while support for relationships among different subfamilies remained weak. *Erupa*, *Heliothela* and *Hoploscopa* were included for the first time in a molecular phylogeny. Our results do not support a close relationship between *Heliothela*, *Hoploscopa* and the Scopariinae, but low support in the backbone of the phylogeny precludes any definite statement concerning their positions. *Erupa* was consistently found as sister group to the Crambinae, though without support (BS < 70) in the ML analysis. Although the Crambinae and the Scopariinae were recovered as sister groups in Regier *et al.* (2012), the topology (Crambinae + *Erupa*) + Scopariinae was recovered here, but only with good support in the Bayesian analysis. The sister-group relationship Crambinae + Scopariinae shows an increase in bootstrap support (58% vs 88%) when *Erupa*, *Heliothela* and *Hoploscopa* are removed from our dataset (not shown), therefore resulting in a topology similar to that of Regier *et al.* (2012). The placement of *Erupa*, *Heliothela* and *Hoploscopa* with respect to Crambinae and Scopariinae remains uncertain and must be adressed in further studies with a greater number of genes and broader sampling of Crambidae.

Our phylogeny confirmed some of the tribes treated by Landry (1995) (e.g. the Diptychophorini, Haimbachiini), while others were found to be polyphyletic (Argyriini, Crambini). The snow-white colour of the forewing in *Argyria*, *Catharylla*,

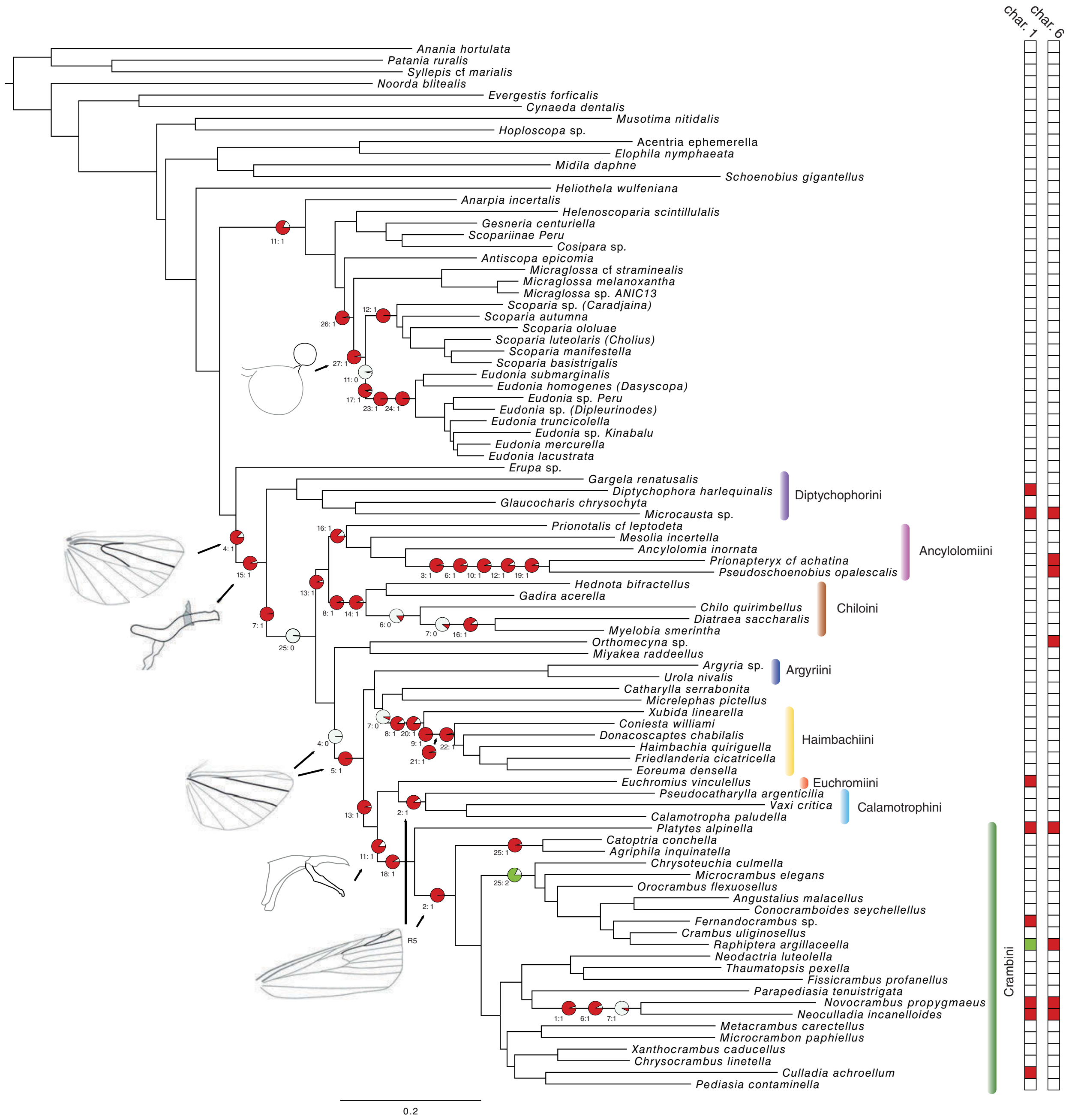


Fig. 3. Ancestral character-state reconstruction mapped on best-scoring maximum likelihood (ML) tree where change is most likely to have occurred. The ML probability of ancestral character state is represented as pie charts. Pies are colored as follows: white (state 0), red (state 1), green (state 2). States for characters 1 (forewing Rs veins) and 6 (hindwing $M_2 - M_3 - CuA_1 - CuA_2$) are displayed on the first and second columns on the right, respectively.

Urola and *Vaxi*, the gnathos pointing downwards or posterad, or the noncoalesced papillae anales in *Ancylolomia*, *Euchromius, Miyakea* and the Crambini were shown to be homoplastic. In other cases, genera erected for species displaying ‘odd’ features, e.g. yellow colour of forewing in *Cholius* **syn.n.** or row of hairs on hindwing A_1 vein in males of *Dasyscopa* **syn.n.**, were found to represent highly apomorphic characters within *Scoparia* or *Eudonia*, respectively (Fig. 2). In Scopariinae, the clade *Micraglossa* + (*Scoparia* + *Eudonia*) was recovered in all analyses, although with weak support in ML analyses. The corpus bursae covered half with spines, half with scobinate patches (Fig.1, character 26) was suggested as a synapomorphy for the group including these genera (*Caradjaina* **syn.n.** excepted) by Nuss (2003), which argues in favour of this topology. In the

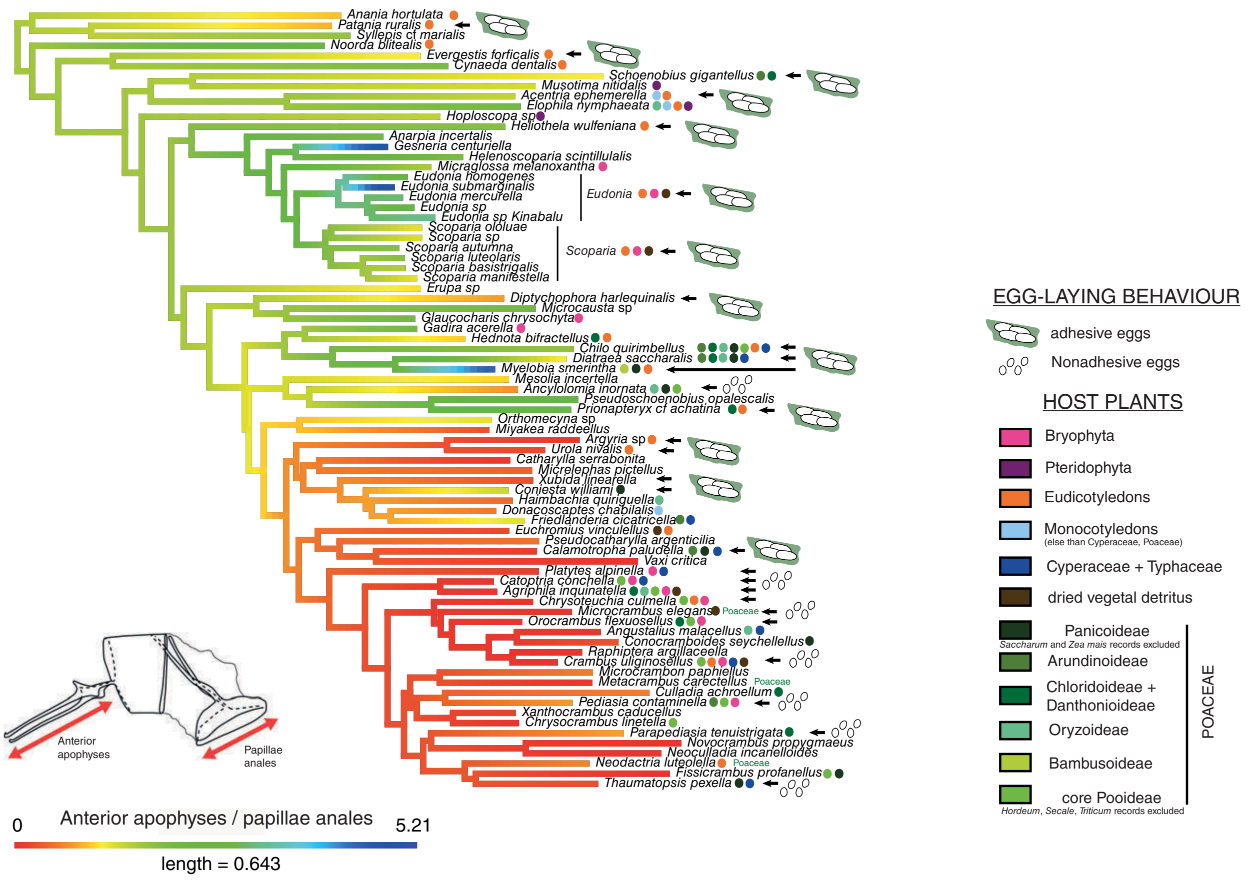


Fig. 4. Ancestral character reconstruction of anterior apophyses lengths compared with papillae anales length on the best-scoring maximum likelihood tree. Host plant and egg adhesiveness records for each species or congeneric species are displayed on the right.

Crambinae, the Ancylolomiini **stat. rev.** showed no support in the ML analysis (BS < 70%). *Ancylolomia* was recovered in the Crambini in the cladistic analysis of Landry (1995) on the basis of the gnathos pointing downward, the papillae anales dorsal connection membranous, and the hindwing cell open. The hindwing cell was coded as 'open' for *Ancylolomia japonica* Zeller in Landry (1995), although it is closed in *A. tentaculella* (Hübner) and was reported to be closed by other authors (de Joannis, 1932; Okano, 1962; Bleszynski, 1965; Kirpichnikova, 1999). Similarities in the morphology of *Prionotalis* and *Ancylolomia* (male genitalia with relatively short valva, strong vinculum, phallus as long as valva, with ductus ejaculatorius branching at anterior apex, female genitalia with papillae anales not coalesced dorsally and ductus seminalis originating on corpus bursae) (Bassi, 2016) support the Ancylolomiini hypothesis recovered here. However, the forewing distal margin produced, the ring-like gnathos without posterior extension and the valva with ventral process shared by *Mesolia*, *Prionapteryx* and *Pseudoschoenobius* are not observed in *Ancylolomia*, suggesting a possible misplacement of this genus as sister to *Prionapteryx* + *Pseudoschoenobius*.

Systematic changes

Our investigations provide the first comprehensive molecular phylogeny for the Crambinae and Scopariinae and the rationale for a number of changes in the classification. The enigmatic Erupini, weakly supported as sister to the Crambinae, do not share the Crambinae synapomorphies – hindwing M_1 near middle of cell and phallus connected medially to juxta – and are thus not considered as such. Their ambiguous position in our analyses restrained us from erecting this tribe as a subfamily for now. The taxa for which the composition is changed here are provided with a new diagnosis in the following, and their composition is summarized in Table S8.

SCOPARIIINAE

Scoparia Haworth, 1811

Diagnosis. Our ancestral character analysis recovered the ventral process of the valva in male genitalia as an apomorphy for the genus. *Scoparia* cannot be separated from *Eudonia* based on external morphology, but has the following combination of characters in genitalia: male genitalia with uncus tip pointed, gnathos tip pointed and directed downwards, sacculus of valva sclerotized, with free distal extension and phallus (most species) with cornuti (Nuss, 1999); female genitalia with anterior and posterior apophyses as long as to twice as long as papillae anales, colliculum short, ductus bursae straight or slightly curved, corpus bursae spinulose on one lateral half, spatulate on other half, with an appendix bursae (absent in *Cholius* **syn.n.**).

Remarks. Molecular data support the monophyly of the clade, including *Caradjaina* and *Scoparia*, but do not support *Scoparia* as a distinct clade from *Caradjaina* (Figs 2, S2). Nuss (1999) highlighted the proximity between *Caradjaina* and *Scoparia* male genitalia, with *Caradjaina* displaying narrower shapes of the uncus, tegumen and base of valva. He suggested that the latter belonged to *Scoparia*, but no *Caradjaina* females were known then. Examination of female genitalia for the first time did not reveal any notable differences between *Caradjaina* and *Scoparia*. Thus, *Caradjaina* **syn.n.** is synonymized here with *Scoparia* and its only described species, *Scoparia kwangtungialis* (Caradja) **comb. rev.**, is transferred back to *Scoparia*. *Cholius* **syn.n.** is recovered in the molecular analysis as an ingroup of *Scoparia* and is thus synonymized here. *Scoparia luteolaris* (Guenée) **comb. rev.** and *S. leucopeplalis* (Hampson) **comb.n.** are transferred to *Scoparia*.

Eudonia Billberg, 1820

Diagnosis. Ancestral character analyses recovered the upward-directed (posterad in several cases) gnathos and the absence of cornuti in male genitalia as well as the long and slender colliculum and the looped ductus bursae in female genitalia as apomorphies for the genus. Further characters allow the segregation of *Eudonia* from other Scopariinae: in male genitalia, uncus tip blunt or notched, valvae generally without sclerotized sacculus – sclerotized in a few species, but without free distal extension; in female genitalia, anterior and posterior apophyses two to six times as long as papillae anales, corpus bursae spinulose on one lateral half, spatulate on other half, with a distinct signum and an appendix bursae.

Remarks. According to our molecular analyses, *Dasyscopa* **syn.n.** and *Dipleurinodes* **syn.n.** are nested within *Eudonia* and are thus synonymized here. *Eudipleurina* Leraut **syn.n.**, not included in our taxon sampling, resembles *Dipleurinodes* by the shared distinct sacculus without free distal extension (Nuss, 1999). It displays all apomorphies of *Eudonia* and is thus synonymized here with this genus. The following species are transferred to *Eudonia*: *Eudonia ambrensis* (Leraut) **comb.n.**, *Eudonia ankaratrella* (Marion) **comb.n.**, *Eudonia axeli* (Nuss) **comb.n.**, *Eudonia barbipennis* (Hampson) **comb.n.**, *Eudonia bueaensis* (Maes) **comb.n.**, *Eudonia comorensis* (Leraut) **comb.n.**, *Eudonia homogenes* (Meyrick) **comb.n.**, *Eudonia mineti* (Leraut) **comb.n.**, *Eudonia nigra* (Leraut) **comb.n.**, *Eudonia phaeopalpia* (Hampson) **comb.n.**, *Eudonia tavetae* (Maes) **comb.n.** and *Eudonia viettei* (Leraut) **comb.n.**

Micraglossa Warren, 1891

Diagnosis. No apomorphies are known for *Micraglossa* (Nuss, 1999). The inwardly directed spine in male genitalia observed in some *Micraglossa* species is a possible synapomorphy. *Micraglossa* can be separated from most other scopariine genera by the presence of golden shiny scales on the head, thorax and abdomen (Nuss, 1999; Li *et al.*, 2010). The genus is thought to be closely related to the Neotropical *Gibeauxia* Leraut, not sampled in this study, with which it shares the golden shiny scales and the presence of an elongated signum in corpus bursae (Nuss, 1999; Li *et al.*, 2010).

Remarks. The Australian *Micraglossa melanoxantha* (Turner) **comb.n.** is here transferred from *Scoparia* to *Micraglossa*.

CRAMBINAE

In light of the phylogenetic results, changes in the tribal classification are needed for all tribes except the Haimbachiini.

Diptychophorini Gaskin, 1972

Type genus. Diptychophora Zeller, 1866

Diagnosis. The moths of this tribe are small, with a forewing length not exceeding *c*. 8 mm and reaching only 3.5 mm in some specimens of *Microcausta*. Apomorphies for the tribe mentioned by Landry (1995), i.e. ratio of the forewing length over its width < 2.0 and the erect terminal scales on the flagellomeres, are not shared by *Gargela*. The forewing outer margin of many Diptychophorini is also often notched near M_1 and M_2, but this is not the case for *Gargela*. Also, the gelechioid-like recurved labial palpi of *Gargela* are a unique feature for a crambine group.

Remarks. The Diptychophorini include 10 genera (Nuss *et al.*, 2019). *Microchilo*, placed by Gaskin (1971) in the Diptychophorini, is recovered in the ‘narrow-winged clade’ (Fig. S2) and thus excluded from this tribe. *Gargela*, which was thought to be related to *Glaucocharis*, *Roxita* Bleszynski (Diptychophorini) and *Calamotropha* (Calamotrophini) based on wing pattern (Song *et al.*, 2009), is placed here confidently in the Diptychophorini.

Ancylolomiini Ragonot, 1889 **stat. rev.**

Type genus. Ancylolomia Hübner, 1825.

Diagnosis. The closed hindwing cell, its M_1 base near the middle of the cell, as well as the large valva, the short and broad tegumen arms with a wide dorsal connection and the ductus ejaculatorius branching at the anterior end of the phallus in male genitalia allow the Ancylolomiini to be segregated from other Crambinae.

Remarks. Ancylolomiini is a senior synonym of Prionapterygini Landry, 1995 **syn.n.** The Nearctic *Eufernaldia* Hulst, and Old World *Surattha* Walker (placed in the Prionapterygini by Landry, 1995), the Palearctic *Prionapteron* Bleszynski and *Talis* Guenée, as well as the Afrotropical *Aurotalis* Bleszynski and *Zovax* Bleszynski are placed here in the Ancylolomiini (Landry, 1995; Bassi, 2013, 2016). *Prionapteron* and *Talis* also share a ringed gnathos and a valval ventral sclerotization in male genitalia with *Mesolia*, *Prionapteryx* and *Pseudoschoenobius*, as well as triangularly shaped papillae anales in female genitalia with *Prionapteryx* and *Pseudoschoenobius*.

Chiloini Heinemann, 1865

Type genus. Chilo Zincken, 1817

Diagnosis. The ancestral character reconstruction recovered the two-armed juxta as the most probable ancestral state of the Chiloini and it thus represents an apomorphy for this tribe. Further characters allow segregation of this tribe from other Crambinae: hindwing cell closed, tympanal organs with marked venulae secundae, pseudosaccus present in male genitalia.

Remarks. In all, 11 genera are assigned here to this tribe: *Chilandrus* Bleszynski, *Chilo*, *Chiqua* Bleszynski, *Diatraea*, *Eschata* Walker, *Gadira*, *Hednota* Meyrick, *Leonardo* Bleszynski, *Malgasochilo* Bleszynski, *Myelobia* and *Tauroscopa* Meyrick. The Myelobiini Minet **syn.n.**. including *Eschata* and *Myelobia*, share the thick venulae secundae and the bifid juxta in male genitalia with other members of the Chiloini. We could not examine specimens or the descriptions of *Hemiptocha* Dognin and *Pseudometachilo* Bleszynski and thus cannot assign them to this tribe with confidence. Klots (1970) provided a brief description of the tribe, although in a more restricted sense, while Gaskin's concept of the tribe is here revised substantially.

Argyriini Klots, 1983

Type genus. Argyria Hübner, 1818

Diagnosis. The following combination of characters allows the segregation of Argyriini from other Crambinae: labial palpi less than twice the eye width, forewing ground colour snow white, forewing R_{S4} starting from cell, hindwing cell open, in male genitalia conspicuous lateral coremata, pseudosaccus absent, in female genitalia anterior apophyses short (Landry, 1995).

Remarks. The Argyriini are presently limited to the two genera *Argyria* Hübner and *Urola* Walker. Bleszynski synonymized *Urola* with *Argyria* (Bleszynski, 1967), and a close relationship between these two genera was suggested by Landry (1995). *Catharylla* and *Micrelephas* could not be reliably assigned to either the Argyriini or the Haimbachiini (Fig. 2), but share all diagnostic features of Argyriini, except for the forewing R_{S4} stalked to $R_{S2} + R_{S3}$ and the absence of lateral coremata in *Catharylla*, and the brown and orange scaling on the forewing in some *Micrelephas* species (Landry, 2003; Landry *et al.*, 2013; Léger *et al.*, 2014). The Australian *Australargyria* Bleszynski and *Neargyrioides* Bleszynski, and the Oriental *Pseudargyria* Okano all share the snow-white colour of the wings, the forewing R_{S4} connected to the cell (connected to $R_{S2} + R_{S3}$ in *Australargyria*), the hindwing cell open and the absence of a pseudosaccus (present in *Pseudargyria*) with the Argyriini, and might belong to this tribe (Okano, 1962; Bleszynski, 1965, 1970b).

Calamotrophini Gaskin, 1988 **stat. rev.**

Type genus. Calamotropha Zeller, 1863

Diagnosis. The combination of the following characters will serve to single out the members of this tribe from other Crambinae: labial palpi more than twice the eye width, forewing with R_{S4} stalked to $R_{S2} + R_{S3}$; in female genitalia, papillae anales with dorsal connection sclerotized and apophyses anterior and posterior short.

Remarks. Calamotropha Zeller, *Pseudocatharylla* Bleszynski and *Vaxi* Bleszynski are included in this tribe. Other Afrotropical genera not included in our sampling, *Chrysocatharylla* Bassi, *Classeya* Bleszynski and *Pseudoclasseya* Bleszynski, have male genitalia similar to those of *Pseudocatharylla* (Bassi, 1999), the latter two sharing asymmetrical male valvae with *Pseudocatharylla*. All three share the hindwing cell open and the forewing R_{S4} vein connected at base with $R_{S2} + R_{S3}$ with the Calamotrophini and are thus placed in this tribe.

Euchromiini Léger, Landry & Nuss **tribe n.**
http://zoobank.org/urn:lsid:zoobank.org:act:1A84282D-930A-4C32-8340-D681BFF27A12.

Type genus. Euchromius Guenée, 1845

Diagnosis. The combination of the following morphological characters are regarded as diagnostic: forewing with single or double yellowish medial fascia, subterminal line starting from tornus and ending at middle of termen above terminal black dots, with a row of large black terminal dots on dorsal half; forewing R_{S4} vein originating from cell, hindwing M_1 vein close to $Sc + R$, hindwing cell open; in male genitalia, gnathos apex pointed downwards, pseudosaccus present; in female genitalia, papillae anales dorsally connected by a membrane (Schouten, 1988, 1992).

Remarks. The Euchromiini encompass the single genus *Euchromius*. *Metaeuchromius* Bleszynski and *Miyakea* Marumo show a similar wing pattern to that of *Euchromius* but the closed hindwing cell, the hindwing M_1 vein placed near the middle of the cell, the gnathos tip pointed upwards and the missing pseudosaccus discriminate them from *Euchromius*.

Crambini Latreille, 1810

Type genus. *Crambus* Fabricius, 1798

Diagnosis. The membranous connection of the papillae anales in female genitalia is recovered as an apomorphy for the tribe. The gnathos tip pointed downwards or posterad in male genitalia is another possible apomorphy, but this state is also observed in the closely related *Euchromius* and *Calamotropha* and might also be the ancestral state of the R_{S4} stalked clade. Further characters allow this tribe to be segregated from other Crambinae: forewing R_{S4} stalked (except some *Platytes* species) with $R_{S2} + R_{S3}$, hindwing cell open; in male genitalia pseudosaccus present; in female genitalia tergite VIII narrow, anterior and posterior apophyses short.

Remarks. Ancylolomia, *Euchromius*, *Micrelephas* and *Miyakea* are excluded from the Crambini. *Microcramboides* Bleszynski **syn.n.** and *Tortriculladia* Bleszynski **syn.n.** are nested within *Microcrambus* and are thus regarded as synonyms. Their original descriptions mentioned that *Microcramboides* and *Tortriculladia* are close to *Microcrambus* based on the genitalia and the sclerites of the male eighth abdominal segment (Bleszynski, 1967). The absence of signa in the female corpus bursae differentiating *Microcrambus* from *Crambus* (Bleszynski, 1963) is shared by *Microcramboides* and *Tortriculladia* and not observed in other members of the '*Crambus* group'. Crambini is the most speciose tribe of Crambinae, containing 61 genera with 783 species.

Evolution of morphological features

Ancestral character-state analyses allow for the discovery of apomorphies for clades and for inferences about the placement of non-assigned taxa and fossils (Smith & Turner, 2005; Beutel & Kristensen, 2012). Among the 27 characters investigated, we recovered 21 synapomorphies supporting clades grouping more than one genus, thereby confirming 10 apomorphies in Landry (1995) and two apomorphies hypothesized in Nuss (1999, 2003). Nine characters provided apomorphies for newly recovered clades among the Crambinae. However, ancestral character reconstruction showed two major limitations: (i) character examination is limited to one or a few species, thereby overlooking trait variation within a taxon (Wiens, 1995); and (ii) ancestral character estimation analyses are based on the assumption that the true phylogenetic tree is used, which can lead to false reconstruction of ancestral character state, even within commonly accepted confident support values (> 90%) (Duchene & Lanfear, 2015).

The uncus and gnathos of the males are used in pairs in contact with the female's segment VIII during copulation in Crambidae (Cordero & Baixeras, 2015). Motion muscles activating the gnathos are mostly absent in the groundplan of Crambidae (Kuznetsov & Stekolnikov, 1979), suggesting a loss of the use of the uncus-gnathos claw function (Kuznetsov & Stekolnikov, 2001). By contrast, muscle M10, which lowers the gnathos by contraction, is present in the following Crambinae and Scopariinae species: *Agriphila straminella* (Denis & Schiffermüller), *Chrysoteuchia culmella* (Linnaeus), *Crambus pratellus* (Linnaeus), *Pediasia matricella* Treitschke, *Euchromius ocelleus* (Haworth) and *Scoparia ancipitella* (La Harpe) (Kuznetsov & Stekolnikov, 1979). All these taxa share a gnathos tip pointed downwards, which suggests a correlation between this trait and the presence of a gnathos-lowering muscle. In the light of our results and those of Regier *et al.* (2012), the presence of this muscle is a possible synapomorphy for the clade, including the Crambinae and Scopariinae. Male genitalia musculature reveals another interesting distribution pattern: the pair of valve extensors (muscles M3) connects the juxta to the anterior or medial part of the vinculum in Crambidae, whereas in *Euchromius ocelleus* and the four Crambini investigated by Kuznetsov & Stekolnikov (1979), M3 muscles attach to the pseudosaccus instead of the vinculum. The crucial role of the pseudosaccus in male genitalic musculature thus explains its conservation in the two groups of Crambinae where it is found.

Our ancestral character reconstruction recovered a loss of signum in the ancestor of the narrow-winged clade and the gain of two signa in the *Crambus* group. Signa are hypothesized to evolve as counter-adaptations against thick spermatophores (Cordero, 2005; Sánchez *et al.*, 2011). The presence of a signum is associated with polyandry, with both regarded as the plesiomorphic conditions in Lepidoptera, whereas the evolution of monandry is associated with the loss of signa (Sánchez *et al.*, 2011). Females of *Parapediasia teterrella* (Zincken) bear no signum and were shown to mate only once, whereas females of *Agriphila plumbifimbriella* (Dyar), which bear one signum, were reported to mate more than once (Marshal, 1988). No extensive data on the reproductive behaviour of the Crambinae are presently available, but the different number of signa observed among the Crambinae could reflect different reproduction behaviours.

Egg-laying behaviour and host plant use

Ecological traits such as nonadhesive eggs and larval life habits were not formerly investigated by ancestral trait reconstruction because of the paucity of available information, but the distribution of these traits on the recovered phylogeny provides insights into the evolution of the Crambinae and Scopariinae. The behaviour of dropping nonadhesive eggs is observed in Crambini and *Ancylolomia*, suggesting at least two independent origins in Crambinae (Fig. 4). Nonadhesive eggs are associated with two modifications of the female oviscapt. First, the dorsal connection of the papillae anales is not sclerotized (Fig. 1, character 18, state 1), which probably facilitates the nontargeted dissemination of eggs. Second, strongly reduced posterior and anterior apophyses as well as short membranes between segments VIII and IX suggest a reduced evertion of the oviscapt during oviposition. The membranous dorsal connection of papillae anales observed in *Euchromius*, *Gadira*, *Miyakea*, *Prionotalis*, *Aurotalis* and *Metaeuchromius* (the latter three were not included in this study) indicate that the females of these species may also lay nonadhesive eggs. Furthermore, the series of steps followed during oviposition seem to differ in species laying nonadhesive eggs. In Lepidoptera species fixing their eggs to a substrate, the oviposition process implies the search for a suitable host plant, with subsequent evaluation of its surface with the antennae, tarsi, proboscis and oviscapt (Chadha & Roome, 1980; Marion-Poll *et al.*, 1992; Renwick & Chew, 1994). Females of *Agriphila plumbifimbriella* and *Parapediasia teterrella* were reported to drop their eggs in flight (Ainslie, 1922; Marshal, 1988), which means that host-searching is either skipped or oviposition is stimulated by habitat characters.

Host plant and larval life habits remain poorly investigated, with the exception of a few species of economic importance (Hill, 1987; Khan *et al.*, 1991; Capinera, 2001; Glime, 2017). Scopariinae are largely moss feeders, with a few *Scoparia* species feeding on dicotyledons (Nuss in Goater *et al.*, 2005). In the Crambinae, the early lineage Diptychophorini are most probably moss feeders, as suggested by the New Zealand *Glaucocharis* reported to feed on leaves of mosses (Gaskin, 1972). Despite the lack of host plant records for the Erupini (Hayden, 2012), moss-feeding habits are observed in the early-diverging lineage of the Crambinae, the Diptychophorini, as well as in *Gadira* and in all early-diverging lineages of the Crambini (*Platytes*, *Agriphila*, *Catoptria*, *Chrysoteuchia*), and suggest moss as the ancestral host plant of the Crambinae and Scopariinae. Crambinae belonging to the narrow-winged clade feed predominantly on Poaceae, with a few species feeding on sedges (*Calamotropha* spp., several Crambini), various dicotyledonous plants (*Argyria*, *Chrysoteuchia*, *Crambus*, *Prionapteryx*) or dry vegetal detritus (*Euchromius*) (Slamka, 2008; Robinson *et al.*, 2010). The wide range of host plants recorded for species of *Chilo* and *Diatraea* are thought to be the result of intense cultivation of cereal crops followed by an increase of their population size, which trigger host plant range expansion in herbivores (Castagneyrol *et al.*, 2016). Crambinae laying nonadhesive eggs (*Ancylolomia* and the Crambini) are reported to feed predominantly on grasses belonging to the ‘core Pooideae’ (Poaceae), i.e. the species-rich clade sister to the Brachypodieae (Saarela *et al.*, 2015). Their larvae live in silken tunnels near the ground, feeding at the base of grasses, unlike other larvae of Crambinae (*Calamotropha*, *Chilo*, *Diatraea*, *Myelobia*, Haimbachiini) which are stem borers in grasses.

Pooideae are thought to have experienced a major radiation in the early Oligocene (34–23 Ma), most likely in the northern hemisphere where they dominate the grass flora (Hartley, 1973; Bouchenak-Khelladi *et al.*, 2010). A host plant shift to Pooideae could explain the high diversity observed in Crambini (916 sp.), as host plant shifts are known to trigger speciation (Forbes *et al.*, 2017), leading to subsequent evolutionary radiations (Fordyce, 2010). Crambini account for 40% of the described crambine species and represent the bulk of crambine diversity in temperate areas (e.g. 80% of the Crambinae fauna in Canada) (Pohl *et al.*, 2018). Our analysis, including part of the diversity of the Crambini (25 of the 61 described genera), recovered the Holarctic genera *Platytes*, *Agriphila* and *Catoptria* as the earliest diverging lineages of Crambini, suggesting that diversification of the tribe took place there. A similar diversification scenario is found in the Satyrinae (Nymphalidae), which diversified on grasses during the drying and cooling period that triggered their expansion in the Oligocene (Peña & Wahlberg, 2008). Interestingly, similar cases of nonadhesive egg-laying behaviours are observed conjointly with the use of Pooideae as host plants in several Satyriinae genera (*Aphantopus*, *Arethusana*, *Brintesia*, *Erebia*, *Hipparchia, Lopinga*, *Maniola*, *Melanargia*, *Minois*, *Pyronia*) (Frohawk, 1924; Forster & Wohlfahrt, 1955; Wiklund, 1984; E. García-Barros, personal communication), suggesting that the evolution of nonadhesive eggs is an adaptation to the switch to Pooideae. Although the lack of fossils prevents us from any speculation about the time of their diversification, Crambini possibly followed a similar evolutionary path to that of the Satyrinae. Future studies with a broader sampling of the tribe covering all genera and biogeographical zones will shed more light on its evolution.

Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Fig. S1. Uncorrected p-distances of the third codon position for each gene plotted against the distance on the best-scoring ML tree of conc6genes.

Fig. S2. Best-scoring ML tree of the whole dataset with best PARTITIONFINDER model applied and bootstrap support values from 1000 replicates displayed on nodes.

Fig. S3. Best-scoring ML tree of the conc6genes_COI1+2 dataset with the best PARTITIONFINDER model applied. Bootstrap support (1000 replicates) displayed above the nodes, posterior probabilities displayed below.

Fig. S4. Node numbers used for ‘ace’ analyses (Table S6) plotted on best-scoring ML tree of the conc6genes dataset with best PARTITIONFINDER model applied.

File S1. R script of the ‘ace’ analysis (APE package; Paradis *et al.*, 2004).

File S2. R script of the ‘fastAnc’ analysis (PHYTOOLS package; Revell, 2012)

File S3. R script of the ‘ace’ function modified by E. Paradis to take uncertain states into account.

Table S1. List of the 111 taxa sampled along with their access numbers at the European Nucleotide Archive (https://www.ebi.ac.uk/ena) for each gene. Subfamilial and tribal assignments follow the current classification (prior to this study) according to GLOBIZ (Nuss *et al.*, 2019). The institute acronyms stand as follows: Muséum d’histoire naturelle de Genève (MHNG), Museum für Naturkunde der Humboldt-Universität Berlin (ZMHB), Senckenberg Museum für Tierkunde Dresden (SMTD), Tiroler Landesmuseum Ferdinandeum, Innsbruck (TLMF), Zoologische Staatsammlung München (ZSM).

Table S2. PCR primers used. PCR product length for newly designed nested primers refer to the PCR product obtained with the corresponding standard primer from Wahlberg & Wheat (2008).

Table S3. PCR mix adapted from Wahlberg & Wheat (2008).

Table S4. PCR programmes adapted from Wahlberg & Wheat (2008) and Regier (2007).

Table S5. Character states matrix.

Table S6. Scores from the 'ace' analysis (ape package) for each node (see Fig. S4).

Table S7. Egg-laying behavior, host plant data and larval life habits in Crambinae, Scopariinae and other Crambidae subfamilies.

Table S8. Revised systematic classification of genera of Crambinae and Scopariinae investigated in this study. Support for systematic positions are provided by the analysis of the morphology only (*), or by the analyses of the morphology and molecular (**).

Acknowledgements

We are thankful to Leif Aarvik, David Agassiz, Tommy Andriollo, Giorgio Baldizzone, Graziano Bassi, Carl Bélanger, Ferenc Buschmann, Eric Drouet, Friedmar Graf, Chris Grinter, Axel Hausmann, James E. Hayden, Robert J. B. Hoare, Eric H. Metzler, Jacques Rochat, László Ronkay and Daniel Rubinoff for providing us with freshly collected specimens. Graziano Bassi and Alma Solis helped with the identification of some specimens.

TL would like to thank the following people for helping with organisation, logistics and export permits in the fieldwork: Stephen Sutton, Richard Mally, Charles S. Vairappan (Institute for Tropical Biology and Conservation, Kota Kinabalu, Malaysia), Ching Y. Chung (Sabah Biodiversity Centre) and the staff of the Sabah Parks on field trip to Borneo, Malaysia; Christoph Neinhuis, Thea Lautenschläger (Technische Universität Dresden) for their collaboration in Angola, as well as José Lau and the staff from the Universidade Kimpa Vita of Ndalatando and Uíge (Angola) on field trip to Angola; Christoph Neinhuis, Sarah Wagner (TU Dresden), Ashley Field, Daven Crayn, David Rentz and the staff of the Australian Tropical Herbarium (James Cook University, Cairns) on a field trip to Queensland, Australia. For help with the laboratory work, we are thankful to Manuela Bartel, Richard Mally, Chistian Kehlmaier, Anke Müller, Anja Rauh (SMTD), Raphaël Covain and Jannik Pralong (MHNG). Francesca Vegliante shared helpful information on the copulatory mechanism in Pyraloidea. We thank Peter Russell and Enrique García-Barros for useful comments on egg evolution and people from Lepiforum.de for documenting the eggs of various Crambinae species. Field trips by TL were funded by the Deutscher Akademischer Austauschdienst (DAAD) (Angola, Australia) and a grant from the Royal Entomological Society in the U.K. (Malaysia). Field trips by MN to Bolivia and Peru were funded by the DAAD, Deutsche Forschungsgemeinschaft (DFG) and the Senckenberg Gesellschaft für Naturforschung. Field trips by BL to Bolivia and Nicaragua were funded by the City of Geneva, which provided additional funds to TL, along with the Senckenberg Gesellschaft für Naturforschung. We thank Andreas Schmitz (MHNG) and two anonymous reviewers for insightful comments on the manuscript. The authors are unaware of any conflicts of interest.

References

Aberer, A.J., Krompass, D. & Stamatakis, A. (2013) Pruning rogue taxa improves phylogenetic accuracy: an efficient algorithm and webservice. *Systematic Biology*, **62**, 162–166.

Ainslie, G.G. (1922) Contribution to a knowledge of the Crambinae. II. *Crambus laqueatellus* Clemens. *Annals of the Entomological Society of America*, **15**, 125–136.

Ainslie, G.G. (1930) *The Bluegrass Webworm*. USDA Technical Bulletin 173: 1–26.

Amsel, H.G. (1961) Die Microlepidopteren der Brandt'schen Iran-Ausbeute. 5. Teil. *Arkiv för Zoologi (N.S.), Stockholm (Ser. 2)*, **13**, 323–445, pls. 1–9.

Bassi, G. (1999) Notes on *Pseudocatharylla* Bleszynski, 1961 (Lepidoptera: Crambidae: Crambinae) with a description of new genera and new species. *Bollettino Del Museo Regionale Di Scienze Naturali Torino*, **16**, 151–188.

Bassi, G. (2013) Notes on some Old World Prionapterygini Landry, 1995 (Lepidoptera: Pyraloidea, Crambidae, Crambinae), with descriptions of new species. *Revue Suisse de Zoologie*, **120**, 131–160.

Bassi, G. (2016) Studies on Afrotropical Crambinae (Lepidoptera, Pyraloidea, Crambidae): notes on the genus *Aurotalis* Bleszyński, 1970. *Revue Suisse de Zoologie*, **123**, 11–20.

Beutel, R.G. & Kristensen, N.P. (2012) Morphology and insect systematics in the era of phylogenomics. *Arthropod Structure & Development*, **41**, 303–305.

Bleszynski, S. (1963) Studies on the Crambidae (Lepidoptera). Part 41. On some tropical Crambidae with descriptions of new genera and species. *Acta Zoologica Cracoviensia*, **8**, 133–181.

Bleszynski, S. (1964) Revision of the world species of the family Crambidae (Lepidoptera). Part 2. Genera: *Pseudocatharylla* Blesz., *Classeya* Blesz., *Pseudoclasseya* Blesz. and *Argentochiloides* Blesz. *Acta Zoologica Cracoviensia*, **9**, 683–760.

Bleszynski, S. (1965) Crambinae. *Microlepidoptera Palearctica*, Vol. **1** (ed. by H.G. Amsel, H. Reisser and F. Gregor). Verlag Georg Fromme & co., Wien.

Bleszynski, S. (1966) Further taxonomic notes on some tropical species. *Acta Zoologica Cracoviensia*, **11**, 451–497.

Bleszynski, S. (1967) Studies on the Crambinae (Lepidoptera). Part 44. New Neotropical genera and species. Preliminary check-list of Neotropical Crambinae. *Acta Zoologica Cracoviensia*, **12**, 39–110.

Bleszynski, S. (1970a) A revision of the world species of *Chilo* Zincken (Lepidoptera: Pyralidae). *Bulletin of the British Museum*, **25**, 101–195, pls 1–5.

Bleszynski, S. (1970b) New genera and species of tropical Crambinae (studies on the Crambinae, Lepidoptera, Pyralidae, part 48). *Tijdschrift voor Entomologie*, **113**, 1–26.

Blomberg, S.P., Garland, J.T. & Ives, A.R. (2003) Testing for phylogenetic signal in comparative data: behavioral traits are more labile. *Evolution*, **57**, 717–745.

Bouchenak-Khelladi, Y., Verboom, G.A., Savolainen, V. & Hodkinson, T.R. (2010) Biogeography of the grasses (Poaceae): a phylogenetic approach to reveal evolutionary history in geographical space and geological time. *Botanical Journal of the Linnean Society*, **162**, 543–557.

Bouckaert, R., Heled, J., Kühnert, D. *et al.* (2014) BEAST 2: a software platform for Bayesian evolutionary analysis. *PLoS Computational Biology*, **10**, e1003537.

Capinera, J. (2001) *Handbook of Vegetable Pests (Academic Press)*. Elsevier, Amsterdam, Netherlands

Castagneyrol, B., Jactel, H., Brockerhoff, E.G., Perrette, N., Larter, M., Delzon, S. & Piou, D. (2016) Host range expansion is density dependent. *Oecologia*, **182**, 779–788.

Chadha, G.K. & Roome, R.E. (1980) Oviposition behaviour and the sensilla of the ovipositor of *Chilo partellus* and *Spodoptera littoralis* (Lepidoptera: Noctuidae). *Journal of Zoology*, **192**, 169–178.

Clarke, J.F.G. (1965) Microlepidoptera of Juan Fernandez Islands. *Proceedings of the United States National Museum, Washington*, **117**, 1–105.

Cordero, C. (2005) The evolutionary origin of signa in female Lepidoptera: natural and sexual selection hypotheses. *Journal of Theoretical Biology*, **232**, 443–449.

Cordero, C. & Baixeras, J. (2015) Sexual selection within the female genitalia in Lepidoptera. *Cryptic Female Choice in Arthropods* (ed. by A. Peretti and A. Aisenberg), pp. 325–350. Springer, Berlin.

Decker, C. (2003) *Talgdrüsenkarzinome und Muir-Torre-Syndrom Mikrosatelliteninstabilitäts-Analysen und Mutationsuntersuchungen am CTNNB1-Gen*. Martin-Luther-Universität Halle-Wittenberg, Halle.

Duchene, S. & Lanfear, R. (2015) Phylogenetic uncertainty can bias the number of evolutionary transitions estimated from ancestral state reconstruction methods. *Journal of Experimental Zoology Part B Molecular and Developmental Evolution*, **324**, 517–524.

Dyar, H.G. & Heinrich, C. (1927) The American moths of the genus *Diatraea* and allies. *Proceedings of the United States National Museum, Washington*, **71**, 1–48, pls 1–20.

Felsenstein, J. (1985) Phylogenies and the comparative method. *The American Naturalist*, **125**, 1–15.

Forbes, A.A., Devine, S.N., Hippee, A.C., Tvedte, E.S., Ward, A.K.G., Widmayer, H.A. & Wilson, C.J. (2017) Revisiting the particular role of host shifts in initiating insect speciation. *Evolution*, **71**, 1126–1137.

Forbes, W.T.M. (1920) Notes on the Crambinae (Lepidoptera). *Journal of the New York Entomological Society*, **28**, 214–227.

Fordyce, J.A. (2010) Host shifts and evolutionary radiations of butterflies. *Proceedings of the Royal Society of London B: Biological Sciences*, **277**, 3735–3743.

Forster, W., & Wohlfahrt, T.A. (1955) *Die Schmetterlinge Mitteleuropas. 2. Tagfalter: Diurna (Rhopalocera und Hesperiidae)*. Franckh'sche Verlagshandlung, Stuttgart.

Frohawk, F.W. (1924) *Natural History of British Butterflies*, Vol. **2**, Hutchinson & Co., London.

Gaskin, D.E. (1972) Revision of New Zealand Diptychophorini (Lepidoptera: Pyralidae: Crambinae). *New Zealand Journal of Science*, **14**, 759–809.

Gaskin, D.E. (1975) Revision of the New Zealand Crambini (Lepidoptera: Pyralidae: Crambinae). *New Zealand Journal of Zoology*, **2**, 265–363.

Gaskin, D.E. (1988) *Crambinae (Lepidoptera; Pyralidae) in Greece with New Records*. The Entomologist's Record and Journal of Variation, **100**, 153–162.

Giegerich, R., Meyer, F., & Schleiermacher, C. (1996) GeneFisher-software support for the detection of postulated genes. In *ISMB* 68–77.

Glime, J. (2017) Chapter 12-14. Terrestrial insects: Holometabola – Lepidoptera: Tortricoidea – Papilionoidea. *Bryophyte Ecology*, Vol. **2** (ed. by J. Glime) Michigan Technological University and the International Association of Bryologists, Houghton. URL http://www.bryoecol.mtu.edu.

Goater, B., Nuss, M. & Speidel, W. (2005) Pyraloidea I (Crambidae: Acentropinae, Evergestinae, Heliothelinae; Schoenobiinae, Scopariinae). *Microlepidoptera of Europe*, Vol. **4** (ed. by P. Huemer and O. Karsholt). Apollo Books, Stenstrup.

Hannemann, H.J. (1964) Kleinschmetterlinge oder Microlepidoptera II. Die Wickler (s.l.) (Cochylidae und Carposinidae). Die Zünslerartigen (Pyraloidea). *Die Tierwelt Deutschlands*, Vol. **50** (ed. by F. Dahl). Gustav Fischer, Jena.

Hartley, W. (1973) Studies on the origin, evolution, and distribution of the Gramineae. V. The subfamily Festucoideae. *Australian Journal of Botany*, **21**, 201–234.

Hayden, J.E. (2012) Revision of *Odilla noralis* Schaus and transfer of Erupini to Midilinae (Lepidoptera: Crambidae). *Annals of Carnegie Museum*, **80**, 309–322.

Hill, D.S. (1987) *Agricultural Insect Pests of Temperate Regions and their Control*. Cambridge University Press, Cambridge.

Hill, D.S. (2008) *Pests of Crops in Warmer Climates and their Control*. Springer Science & Business Media, Berlin.

Huelsenbeck, J.P. & Ronquist, F. (2001) MRBAYES: Bayesian inference of phylogenetic trees. *Bioinformatics*, **17**, 754–755.

Irisarri, I., Singh, P., Koblmüller, S. *et al.* (2018) Phylogenomics uncovers early hybridization and adaptive loci shaping the radiation of Lake Tanganyika cichlid fishes. *Nature Communications*, **9**, 3159.

de Joannis, J. (1932) Clefs ou tables analytiques des genres de Crambidae (Pyralidae) de France et de Belgique. *L'Amateur de Papillons, Paris*, **6**, 6–24.

Kawahara, A.Y. & Breinholt, J.W. (2014) Phylogenomics provides strong evidence for relationships of butterflies and moths. *Proceedings of the Royal Society B: Biological Sciences*, **281**, 20140970.

Khan, Z.R., Litsinger, J.A., Barrion, A.T. *et al.* (1991) *World Bibliography of Rice Stem Borers: 1794–1990*. IRRI, Manila.

Kirpichnikova, V.A. (1999) Pyraloidea. *Key to the insects of Russian Far East*, Vol. **5** (ed. by P.A. Ler), pp. 320–496. Dal'nauka, Vladivostok. (in Russian).

Klopfstein, S., Vilhelmsen, L., Heraty, J.M., Sharkey, M. & Ronquist, F. (2013) The hymenopteran tree of life: evidence from protein-coding genes and objectively aligned ribosomal data. *PLoS One*, **8**, e69344.

Klots, A.B. (1970) North American Crambinae. Notes on the tribe Chiloini and a revision of the genera *Eoreuma* Ely and *Xubida* Schaus (Lepidoptera: Pyralidae). *Journal of the New York Entomological Society*, **78**, 100–120.

Klots, A.B. (1983) Crambinae. *Check List of the Lepidoptera of America North of Mexico including Greenland* (ed. by R.W. Hodges *et al.*), pp. 76–78. E. W. Classey Ltd. and The Wedge Entomological Research Foundation, London.

Knölke, S., Erlacher, S., Hausmann, A., Miller, M.A. & Segerer, A.H. (2004) A procedure for combined genitalia dissection and DNA extraction in Lepidoptera. *Insect Systematics & Evolution*, **35**, 401–409.

Kristensen, N.P. (2004) *Handbook of Zoology, IV Arthropoda: Insecta*, Part 36 Lepidoptera, Moths and Butterflies, 2: Morphology, Physiology, and Development. Walter de Gruyter, Berlin.

Kuznetsov, V.I. & Stekolnikov, A.A. (1979) Functional morphology of the male genitalia of the Pyraloidea (Lepidoptera) of the Palearctica fauna. *Trudy Zoologicheskogo Instituta Leningrad*, **83**, 46–96 (in Russian).

Kuznetsov, V.I. & Stekolnikov, A.A. (2001) New approaches to the system of Lepidoptera of world Fauna. *Rossijskaya Akademia Nauk, Trudy Zoologicheskogo Instituta*, **282**, 1–462 (in Russian).

Landis, J.B., Bell, C.D. & Hernandez, M., *et al.* (2018) Evolution of floral traits and impact of reproductive mode on diversification in the phlox family (Polemoniaceae). *Molecular Phylogenetics and Evolution*, **127**, 878–890.

Landry, B. (1995) *A Phylogenetic Analysis of the Major Lineages of the Crambinae and of the Genera of Crambini of North America (Lepidoptera:Pyralidae)*. Associated Publishers, Gainesville.

Landry, B. (2003) Revision of the Neotropical genus *Micrelephas* (Lepidoptera: Pyralidae: Crambinae). *Tropical Lepidoptera, Gainesville*, **11**, 13–27.

Landry, B., Becker, V.O. & Mally, R. (2013) Breaking the pattern again: additions to *Micrelephas* Dognin, 1905 (Lepidoptera; Pyralidae; Crambinae), including a new species and a key. *Tropical Lepidoptera Research*, **23**, 99–112.

Landry, B., Maes, J., Passoa, S. & Léger, T. (2015) Description of a new species of *Myelobia* Herrich-Schäffer (Lepidoptera, Pyralidae s.l., Crambinae) from Nicaragua feeding on cultivated bamboo, *Guadua aculeata* Rupr. ex E. Fourn. (Poaceae). *Journal of Research on the Lepidoptera*, **48**, 65–81.

Lanfear, R., Calcott, B., Ho, S.Y.W. & Guindon, S. (2012) Partitionfinder: combined selection of partitioning schemes and substitution models for phylogenetic analyses. *Molecular Biology and Evolution*, **29**, 1695–1701.

Lanfear, R., Frandsen, P.B., Wright, A.M., Senfeld, T. & Calcott, B. (2017) PartitionFinder 2: new methods for selecting partitioned models of evolution for molecular and morphological phylogenetic analyses. *Molecular Biology and Evolution*, **34**, 772–773.

Legaspi, J.C., Legaspi, B.C., King, E.G. & Saldaña, R.R. (1997) Mexican rice borer, *Eoreuma loftini* (Lepidoptera: Pyralidae) in the lower Rio Grande Valley of Texas: its history and control. *Subtropical Plant Science*, **49**, 53–64.

Léger, T., Landry, B., Nuss, M. & Mally, R. (2014) Systematics of the Neotropical genus *Catharylla* Zeller (Lepidoptera, Pyralidae s. l., Crambinae). *ZooKeys*, **375**, 15–73.

Leraut, P. (1980) Liste systématique et synonymique des Lépidoptères de France, Belgique et Corse. *Alexanor and Bulletin de la Société Entomologique de France*, 1–334.

Lewvanich, A. (1981) A revision of the Old World species of *Scirpophaga* (Lepidoptera: Pyralidae). *Bulletin of the British Museum of Natural History (Entomology)*, **42**, 185–298.

Li, W., Li, H. & Nuss, M. (2010) Taxonomic revision and biogeography of *Micraglossa* Warren, 1891 from laurel forests in China (Insecta: Lepidoptera: Pyraloidea: Crambidae: Scopariinae). *Arthropod Systematics & Phylogeny*, **68**, 159–180.

Maddison, W. P., & Maddison, D.R. (2017) *Mesquite: A Modular System for Evolutionary Analysis*. Version 3.31. [WWW document]. URL http://www.mesquiteproject.org.

Marion-Poll, F.C., Guillaumin, D. & Masson, C. (1992) Sexual dimorphism of tarsal receptors and sensory equipment of the ovipositor in the European corn borer, *Ostrinia nubilalis*. *Cell and Tissue Research*, **267**, 507–518.

Marshal, L.D. (1988) Small male advantage in mating in *Parapediasia teterrella* and *Agriphila plumbifimbriella* (Lepidoptera: Pyralidae). *American Midland Naturalist*, **119**, 412–419.

Matheny, E.L. & Heinrichs, E.A. (1972) Chorion characteristics of sod webworm eggs. *Annals of the Entomological Society of America*, **65**, 238–246.

Miller, M.A., Pfeiffer, W., & Schwartz, T. (2010) Creating the CIPRES science gateway for inference of large phylogenetic trees. In *Proceedings of the Gateway Computing Environments Workshop (GCE), 2010* (pp. 1–8). New Orleans, Louisiana

Millière, P. (1868) Iconographie et Description de Chenilles et Lépidoptères inédits. *Annales de la Société Linnéenne de Lyon*, **15**, 189–235.

Minet, J. (1982) Les Pyraloidea et leurs principales divisions systématiques (Lep. Ditrysia). *Bulletin de la Société Entomologique de France*, **86**, 262–280.

Müller, J., Müller, K., Neinhuis, C., & Quandt, D. (2005) PhyDE-Phylogenetic Data Editor. URL http://www.phyde.de/.

Munroe, E. (1995) Crambidae (Crambinae, Schoenobiinae, Cybalomiinae, Linostinae, Glaphyriinae, Dichogaminae, Scopariinae, Musotiminae, Midilinae, Nymphulinae, Odontiinae, Evergestinae, Pyraustinae). *Atlas of Neotropical Lepidoptera. Checklist: Part 2, Hyblaeoidea – Pyraloidea - Tortricoidea*, Vol. **3** (ed. by J.B. Heppner), pp. 34–79. Association for Tropical Lepidoptera & Scientific Publishers, Gainesville, Florida.

Munroe, E. & Solis, M.A. (1998) The Pyraloidea. (ed. by N.P. Kristensen), *Lepidoptera, Moths and Butterflies. Volume 1: Evolution, systematics, and biogeography*. In Fischer M., *Handbook of Zoology, Vol. IV Arthropoda: Insecta*, pp. , pp. 233–256. Walter de Gruyter, Berlin.

Mutanen, M., Wahlberg, N. & Kaila, L. (2010) Comprehensive gene and taxon coverage elucidates radiation patterns in moths and butterflies. *Proceedings of the Royal Society B: Biological Sciences*, **277**, 2839–2848.

Nuss, M. (1998) The Scopariinae and Heliothelinae stat. rev. (Lepidoptera: Pyraloidea, Crambidae) of the Oriental region - a revisional synopsis with descriptions of new species from the Philippines and Sumatra. *Nachrichten des Entomologischen Vereins Apollo*, (Suppl., **17**, 475–528.

Nuss, M. (1999) Revision der Gattungen der Scopariinae (Lepidoptera: Pyraloidea, Crambidae). *Nova Supplementa Entomologica*, **13**, 3–151.

Nuss, M. (2003) *Afroscoparia* – a new genus of Scopariine from southern Africa (Insecta: Lepidoptera: Pyraloidea: Crambidae). *Entomologische Abhandlungen*, **61**, 109–115.

Nuss, M., Landry, B., Mally, R. *et al.* (2019). Global Information System on Pyraloidea. www.pyraloidea.org.

Okano, M. (1962) The systematic study on the Japanese Crambinae (Lepidoptera, Pyralidae). Annual Report of the Gakugei Faculty of the Iwate University **20**: 83–137, pl. 1–15.

Pagel, M. (1994) Detecting correlated evolution on phylogenies: a general method for the comparative analysis of discrete characters. *Proceedings of the Royal Society B: Biological Sciences*, **255**, 37–45.

Pagel, M. (1999) Inferring the historical patterns of biological evolution. *Nature*, **401**, 877–884.

Paradis, E., Claude, J. & Strimmer, K. (2004) APE: analyses of phylogenetics and evolution in R language. *Bioinformatics*, **20**, 289–290.

Peña, C. & Wahlberg, N. (2008) Prehistorical climate change increased diversification of a group of butterflies. *Biology Letters*, **4**, 274–278.

Peterson, A. (1963) Egg types among moths of the Pyralidae and Phycitidae-Lepidoptera. *The Florida Entomologist*, **46**, 1–14.

Pohl, G.R., Landry, J.-F., Schmidt, B.C. *et al.* (2018) *Annotated Checklist of the Moths and Butterflies (Lepidoptera) of Canada and Alaska*. Pensoft, Sofia.

Polilov, A.A. (2015) Small is beautiful: features of the smallest insects and limits to miniaturization. *Annual Review of Entomology*, **60**, 103–121.

Ponomarev, A. (2016) *Ancylolomia tentaculella*-Der Versuch, Zucht *Foto* [online forum]. [WWW document]. URL http://www.lepiforum.de/2_forum_2013.pl?page=1;md=read;id=25218. [Accessed on 29 October 2017].

Ragonot, E.L. (1888) Descriptions de genres nouveaux et espèces nouvelles de Lépidoptères. *Annales de la Société Entomologique de France*, **8**, 271–284, pl. 6.

Rambaut, A., Drummond, A.J., Xie, D. *et al.* (2018) *Tracer Version 1.7* [WWW document]. URL http://tree.bio.ed.ac.uk/software/tracer/.

Ratnasingham, S. & Hebert, P.D. (2007) BOLD: the barcode of life data system (http://www. Barcodinglife. Org). *Molecular Ecology Notes*, **7**, 355–364.

Regier, J.C. (2007) Protocols, Concepts, and Reagents for preparing DNA sequencing templates. [WWW document]. URL http://sites.biology.duke.edu/cunningham/pdfs/PCR_primers.pdf.

Regier, J.C., Mitter, C., Solis, M.A. *et al.* (2012) A molecular phylogeny for the pyraloid moths (Lepidoptera: Pyraloidea) and its implications for higher-level classification. *Systematic Entomology*, **37**, 635–656.

Renwick, J.A.A. & Chew, F.S. (1994) Oviposition behavior in Lepidoptera. *Annual Review of Entomology*, **39**, 377–400.

Revell, L.J. (2012) Phytools: an R package for phylogenetic comparative biology (and other things). *Methods in Ecology and Evolution*, **3**, 217–223.

Robinson, G.S., Ackery, P.R., Kitching, I.J., Beccaloni, G.W. & Hernández, L.M. (2010) *HOSTS—A Database of the World's Lepidopteran Hostplants*. Natural History Museum, London.

Robinson, G.S., Tuck, K.R. & Shaffer, M. (1994) *A Field Guide to the Smaller Moths of South-East Asia*. Natural History Museum, London.

Saarela, J.M., Wysocki, W.P., Barrett, C.F. *et al.* (2015) Plastid phylogenomics of the cool-season grass subfamily: clarification of relationships among early-diverging tribes. *AoB Plants*, **7**, plv046.

Sánchez, V., Hernández-Baños, B.E. & Cordero, C. (2011) The evolution of a female genital trait widely distributed in the Lepidoptera: comparative evidence for an effect of sexual coevolution. *PLoS One*, **6**, e22642.

Schouten, R. (1988) Revision of the species of the genus *Euchromius* Guenée, 1845 (Lepidoptera: Pyralidae: Crambinae) occurring in the Afrotropical region. *Zoologische Verhandelingen*, **244**, 1–64.

Schouten, R. (1992) Revision of the genera *Euchromius* Guenée and *Miyakea* Marumo (Lepidoptera: Crambidae: Crambinae). *Tijdschrift voor Entomologie*, **135**, 191–274.

Shibuya, J. (1928) On the Japanese Crambinae. *Journal of the Faculty of Agriculture, Hokkaido Imperial University, Sapporo*, **21**, 121–147, pl. 2.

Slamka, F. (2008) *Crambinae & Schoenobiinae*. Pyraloidea of Europe (Lepidoptera), **2**. František Slamka, Bratislava

Smith, N.D. & Turner, A.H. (2005) Morphology's role in phylogeny reconstruction: perspectives from paleontology. *Systematic Biology*, **54**, 166–173.

Soltis, D.E., Mort, M.E., Latvis, M. *et al.* (2013) Phylogenetic relationships and character evolution analysis of Saxifragales using a supermatrix approach. *American Journal of Botany*, **100**, 916–929.

Song, S., Chen, F. & Wu, C. (2009) A review of the genus *Gargela* Walker in China, with descriptions of ten new species (Lepidoptera: Crambidae, Crambinae). *Zootaxa*, **2090**, 40–56.

Spriggs, E.L., Schmerler, S.B., Edwards, E.J. & Donoghue, M.J. (2018) Leaf form evolution in viburnum parallels variation within individual plants. *The American Naturalist*, **191**, 235–249.

Stamatakis, A. (2006) RAxML-VI-HPC: maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics*, **22**, 2688–2690.

Tingle, J.L., Gartner, G.E.A., Jayne, B.C. & Garland, T. Jr (2017) Ecological and phylogenetic variability in the spinalis muscle of snakes. *Journal of Evolutionary Biology*, **30**, 2031–2043.

Wahlberg, N. & Wheat, C.W. (2008) Genomic outposts serve the phylogenomic pioneers: designing novel nuclear markers for genomic DNA extractions of Lepidoptera. *Systematic Biology*, **57**, 231–242.

Wiens, J. (1995) Polymorphic characters in phylogenetic systematics. *Systematic Biology*, **44**, 482–500.

Wiklund, C. (1984) Egg-laying patterns in butterflies in relation to their phenology and the visual apparency and abundance of their host plants. *Oecologia*, **63**, 23–29.

Wilkinson, M. (1994) Common cladistic information and its consensus representation: reduced Adams and reduced cladistic consensus trees and profiles. *Systematic Biology*, **43**, 343–368.

Wootton, R.J. (1979) Function, homology and terminology in insect wings. *Systematic Entomology*, **4**, 81–93.

Youm, O. & Gilstrap, F.E. (1994) Habitat site selection, crop damage and oviposition preference by *Contesta* [sic] (= *Haimbachia*) *ignefusalis* (Lepidoptera: Pyralidae). *International Journal of Pest Management*, **40**, 231–236.

Accepted 6 February 2019

Chapter 2

Refining the phylogeny of Crambidae with complete sampling of subfamilies (Lepidoptera, Pyraloidea)

Refining the phylogeny of Crambidae with complete sampling of subfamilies (Lepidoptera, Pyraloidea)

Authors: Théo Léger[1], Richard Mally[2], Christoph Neinhuis[3] & Matthias Nuss[4]

1. Museum für Naturkunde – Leibniz-Institut für Evolutions- und Biodiversitätsforschung, Invalidenstr. 43, 10115 Berlin, Germany
2. Slovenská 13 12000 Prague 2 - Vinohrady Czech Republic
3. Technische Universität Dresden, Institute of Botany, Zellescher Weg 20b, 01217 Dresden, Germany
4. Senckenberg Museum für Tierkunde Dresden, Königsbrücker Landstr. 159, 01109 Dresden, Germany
Corresponding author: Théo Léger (theo.leger@mfn.berlin)

Abstract

Crambidae forms with more than 10,000 described species the most species rich pyraloid lineage. They can be best identified by morphological characters of the adult tympanal organ and larval chaetotaxy. We present the first molecular phylogeny of Crambidae including all subfamilies and most tribes. We use available molecular data from two previous studies as well as published transcriptomes and genomes, compiling ten genes totalling 11,247 bp. Up to eight genes are sequenced for thirty-nine additional taxa, with Cathariinae, Cybalomiinae and Linostinae sampled for the first time. Maximum Likelihood and Bayesian analyses recover topologies mostly agreeing with that of previous studies, with several groupings showing better support. Cathariinae and Cybalomiinae are recovered as ingroup of Glaphyriinae, but with weak support. Linostinae is either sister to Glaphyriinae, or to the "CAMMSS clade". Lathrotelinae were recovered monophyletic and as sister to Musotiminae in the Bayesian analysis. Heliothelinae s. l. are polyphyletic: Hoploscopinae **stat. n.** are recovered sister to ((Crambinae + Erupini) + (Scopariinae + Heliothelinae)), while Heliothelinae s. str. are strongly supported as sister to Scopariinae. Evolution of host plant preferences are discussed.

Introduction

With roughly 16,000 described species, Pyraloidea represent one of the most diverse lineages of Lepidoptera (Nuss et al., 2003–2019). The adults bear a paired tympanal organ in the second abdominal segment consisting of two tympanic chambers supporting a tympanum. This feature allows detecting the echolocation sounds of hunting bats and plays a role in acoustic communication in mating (Greenfield, 2014, and references therein). Pyraloids exhibit an unprecedented spectrum of ecological adaptations in larval life habits, including adaptations to freshwater habitats (Acentropinae) or extreme dry environments such as deserts (some Phycitinae). The larval food spectrum spans from detritus, lichens, mosses, lycopods and ferns to mono- and eudicotyledonous plants. A number of species is known as pests of Poaceae (e.g. *Chilo* Zincken, 1817, *Cnaphalocrocis* Lederer, 1863, *Diatraea* Guilding, 1828, *Marasmia* Lederer, 1863, *Ostrinia* Hübner, 1825, *Scirpophaga* Treitschke, 1832), Brassicaceae (*Hellula* Guenée, 1854) and Solanaceae (*Duponchelia* Zeller, 1847, *Hymenia* Hübner, 1825, Lineodini, *Spodalea* Guenée, 1854) (Capinera, 2001; Hill, 1987, 2008; Khan et al., 1991; Landry & Roque-Albelo, 2008; Mally et al., 2019; Solis & Adamski, 1998a). Mutualistic relationships with bees, ants and sloths, or parasitism on other Lepidoptera or Hymenoptera larvae have been reported for some taxa, e.g. *Chalcoela* Zeller, 1872, *Cryptoses* Dyar, 1908, *Dicymolomia* Zeller, 1872, *Galleria* Fabricius, 1798, *Niphopyralis* Hampson, 1893 (Kemner, 1923, Munroe & Solis, 1998, Pauli et al., 2014, Powell et al., 1998, Roepke, 1916)

Morphological differences in the tympanal organ led authors to recognize two main groups designated as Crambidae and Pyralidae (Börner, 1925, Minet, 1982, 1983, 1985). The Crambidae are characterized by a tympanal organ of the "open type", i.e. with a broad anteromedial opening, the presence of a praecinctorium and the conjunctiva and tympanum not in the same plane (Minet, 1982). A further synapomorphy lies in the presence of one or two L setae in the abdominal segment 9 of the larvae (Hasenfuß, 1960). Different hypotheses regarding the phylogeny of the Crambidae flourished during the second half of the 20th century. Roesler (1973) presented hypotheses about their relationships based on adult and immature characters. Kuznetsov & Stekolnikov (1979) formulated a hypothesis on the Crambidae phylogeny based on the muscular anatomy of the male genitalia. Minet (1982, 1985) characterised several subfamilies based on the examination of the tympanal organ. Yoshiyasu (1985) postulated a partly resolved phylogeny based on adult and immature characters for the Japanese Acentropinae and Musotiminae. The first cladistic analysis of Crambidae is that of Solis & Maes (2002) based on 33 morphological characters assembled from previous studies. Their study, however, did not resolve relationships among subfamilies, and no convincing phylogeny was known in the early 2000's.

Regier et al. (2009) and Mutanen et al. (2010) provided the first molecular phylogenies of Lepidoptera including a significant number of Pyraloidea subfamilies (10 and 18 respectively). They confirmed the monophyly of both Crambidae and Pyralidae, forming together the monophyletic Pyraloidea, and provided insights into relationships among crambid subfamilies. Regier et al. (2012) provided the first molecular phylogeny focussing on pyraloid moths, based on five genes for 28 Crambidae and 13 Pyralidae, with up to 14 additional genes sampled for a subset of these taxa. The recovered topologies within the two families disagree with all previous, morphology-based hypotheses. A "wet-habitat clade", comprising the Acentropinae, Midilinae and Schoenobiinae, and a "mustard oil clade" including Evergestinae (syn.), Glaphyriinae and Noordinae (syn.) whose larvae feed upon Brassicales, were among the clades recovered for the first time. Spilomelinae and Pyraustinae were found monophyletic and sister-groups, as were Crambinae and Scopariinae. A phylogeny based on thirteen mitogenomes from five Crambidae subfamilies (Acentropinae, Crambinae, Pyraustinae, Spilomelinae, Schoenobiinae) was published the following year (Ye et al., 2013). The topology notably recovered the Schoenobiinae as sister-group to Crambinae, constrasting with Regier et al. (2012), where they were recovered in a clade with Acentropinae and Midilinae. Finally, recent phylogenies provided insights into the evolution of Pyraustinae and Spilomelinae (Mally et al., 2019), and of Crambinae and Scopariinae (Léger et al., 2019b). Despite great improvements in the understanding of the evolutionary relationships of Pyraloidea, the subfamilies Cathariinae, Cybalomiinae and Linostinae were never included in previous studies, and so far, no supported phylogenetic placements were obtained for Heliothelinae (Léger et al., 2019b) or Lathrotelinae (Mally et al., 2019). This study aims to investigate the phylogenetic placement of Cathariinae, Cybalomiinae, Heliothelinae, Lathrotelinae and Linostinae within Crambidae. A brief summary for these five subfamilies is provided hereafter.

Cathariinae Minet, 1982

These small, blackishly winged moths are found in alpine areas of the Alps and the Pyrenees. Male genitalia lack a gnathos, and females have a reduced tympanal organ. Depending on the taxonomic concept, one or two species are recognized (Leraut, 1997). Larvae are reported feeding on *Cerastium pedunculatum* (Caryophyllaceae), *Saxifraga aphylla*, *Saxiphraga oppositifolia* and *Silene acaulis* (Saxifragaceae) (Schmid, 2019). *Catharia* was originally placed in the Odontiinae (Munroe, 1961) or Pyraustinae (Marion, 1962), before Minet (1982) erected a subfamily to accommodate the genus based on the reduction of the gnathos and tympanal organ. Leraut (1997), however, treats Catharinae as synonym of Odontiinae.

Cybalomiinae Marion, 1955

Cybalomiine moths display yellow to brownish forewings similar to those of some Glaphyriinae. The Cybalomiinae display characteristic fovea between Rs 2+3 and Rs 4 on the forewing, and lateral indentations of sternite 2 (Luquet & Minet, 1982). Larvae are reported to feed on Brassicaceae and Capparaceae (Chrétien, 1911; Lhomme, 1935; Robinson et al., 2010). Marion (1955) described the tribe Cybalomiini as part of the Scopariinae, and Munroe (1959) raised it to the subfamily level. Regier et al. (2012) suspected this subfamily to belong to the Glaphyriinae based on the shared use of Brassicales as larval host plant. The subfamily counts 112 species currently classified in 19 genera which are predominantly found in dry regions of Southern Europe, Africa, Asia and Australia as well as North and South America (Nuss et al., 2003–2019–2019).

Heliothelinae Amsel, 1961

This subfamily comprises two tribes, the Heliothelini and the Hoploscopini, that share the presence of a spine in the corpus bursae of the female genitalia (Nuss, 1998). The Heliothelini are small dark-winged moths with yellow to orange colouration on the hindwings in many species. The diurnal moths are found in dry habitats of the Old World. In contrast, the Hoploscopini display reddish-brown forewings with yellow to red markings. The moths fly at night and are found in tropical mountains of the Oriental and Australasian regions. Larvae of *Heliothela wulfeniana* (Scopoli, 1763) feed on Lamiaceae and Violaceae (Schütze, 1931), while larvae of Hoploscopini are reported from ferns (Mally et al., 2017). Heliothelinae are still a matter of debate, treated by some authors as subgroup of Scopariinae (Hannemann, 1964, Leraut, 1980, Munroe & Solis, 1998, Robinson et al., 1994), while others advocate two separate lineages (Minet, 1982, Nuss, 1998, Nuss, 1999). Heliothelinae were not recovered monophyletic by Léger et al. (2019), but among-subfamilies relationships were poorly supported, precluding the inference of meaningful conclusions. The three Heliothelini and two Hoploscopini genera encompass fifty described species (Nuss et al., 2003–2019–2019), with at least as many species awaiting description in Hoploscopini (Léger et al., 2019a, Robinson et al., 1994).

Lathrotelinae Clarke, 1971

Clarke (1971) described the Lathrotelidae from a single female specimen of *Lathroteles obscura* Clarke, 1971, collected on Rapa Island (French Polynesia). The specimen lacked a tympanal organ but displayed other characters typical for Pyraloidea, so that the author considered it to be closely related to Pyraloidea ("Pyralidae" s. l.). Minet (1991) found strongly reduced tympanal organs of the "crambid type" when examining a male specimen of *L. obscura* and synonymized Lathrotelidae with Nymphulinae (now Acentropinae) based on their similarities in the tympanal organs. The same author reinstated the Lathrotelinae to acommodate this genus, along with *Diplopseustis* Meyrick, 1884, *Diplopseustoides* Guillermet, 2013 and *Sufetula* Walker, 1859, and suggested the two or three lunules on the forewing costa as a synapomorphy for the group (Minet, 2015). This pantropical subfamily currently hosts five genera encompassing 42 species (Nuss et al., 2003–2019–2019).

Linostinae Amsel, 1956

Linostine moths display snow white forewings with finely marked black median and subterminal lines. The subfamily was described by Amsel (1956) to host the genus *Linosta* Möschler, 1882, which includes four neotropical species. The subfamily was revised by Munroe (1959).

Material & Methods

Taxon sampling

Samples were collected as adult moths by light-trapping or at day with a net and preserved either dried or in alcohol. A number of specimens were obtained through loans and donations from colleagues (see Acknowledgements). Specimens were identified based on wing pattern and genitalia, and identification was cross-checked by DNA barcoding with help of the Identification Engine in BOLD (http://boldsystems.org/; Ratnasingham & Hebert, 2007). Dried specimens collected less than two years prior to DNA extraction were considered for molecular genetic analyses. All Crambidae subfamilies were included, with Cathariinae (1 species), Cybalomiinae (4 species), Lathrotelinae (5 species) and Linostinae (1 species) represented for the first time in a molecular phylogeny. PCR-generated molecular sequences from studies of Mutanen et al. (2010) (16 taxa), Regier et al. (2012) (41 taxa) and Heikkilä et al. (2015) (1 taxon) were downloaded from GenBank and added to our molecular dataset. A representative subset of the taxa from phylogenetic studies of Léger et al. (2019) and Mally et al. (2019) were also included. Sequences of interest were retrieved from published transcriptomes of *Cnaphalocrocis medinalis* (Guenée, 1854), *Myelobia smerintha* (Hübner, 1821) (Kawahara & Breinholt, 2014), *Scirpophaga incertulas* (Walker, 1863) (Renuka et al., 2017), as well as from whole genome of *Amyelois transitella* (Walker, 1863) and *Chilo suppressalis* (Walker, 1863) on the LepBase interface (Challis et al., 2016; ensembl.lepbase.org). Taxon sampling is summarized on supplementary Table B.2.

Molecular work

DNA was extracted with the NucleoSpin Tissue kit (Macherey-Nagel, Germany) from abdomens following the non-destructive method of Knölke et al. (Knölke et al., 2004). Seven genes (total = 5,649 bp) from the sampling of Mutanen et al. (2010) were initially considered for amplification: CAD (792 bp), EF-1α (1071 bp), GAPDH (654 bp), IDH (657 bp), RpS5 (576 bp), wingless (402 bp) and the mitochondrial COI (1,440 bp). The dataset of Regier et al. (2012) includes five nuclear genes amplified from cDNA: CAD (2,958 bp), DDC (1,281 bp), enolase (1,134 bp), period (1,074 bp) and wingless (402 bp). Standard primers listed in Wahlberg & Wheat (2008) were used to amplify all markers except MDH from Mutanen et al. (2010). Alternatively, nested primers of Léger et al. (2019) were used for samples that proved difficult to amplify. The Regier and Mutanen datasets show only a small overlap consisting of a fragment of the CAD gene and wingless (total=1,251 bp). Presence of numerous introns in the first part of CAD, as well as in DDC, enolase and period render their amplification from genomic DNA cumbersome. In order to increase the overlap of the Regier dataset with our own molecular dataset and Mutanen dataset, we investigated the intron-exon structure for suitable regions to amplify in the CAD, DDC, enolase and period genes from annotated genomes of *Chilo suppressalis* and *Amyelois transitella* available from LepBase (Challis et al., 2016). The 4th CAD and 5th DDC exons (3142 and 726 bp respectively) were considered for primer design. Eighty percent consensus sequences were generated from the Regier gene datasets via Genefisher2 (Giegerich et al., 1996). Primers were designed by eye on conserved regions and subsequently checked for melting temperature, 3' complementarity, self-annealing and potential hairpin formation on the online platform OligoCalc (www.basic.northwestern.edu/biotools/OligoCalc.html). Two pairs of primers were tested to amplify the first part of the 4th CAD exon in two fragments of 827 and 793 bp respectively. Second fragment was successfully amplified in most of the samples, while amplification of first fragment proved to be difficult and was abandoned in the course of the study. A pair of primers was designed for the amplification of a 547 bp fragment of the 5th DDC exon (Table S1). BIO-X-ACT Short DNA Polymerase (Bioline, UK) was used following the PCR protocol of Wahlberg & Wheat (2008) as in Léger et al. (2019). Hi-Spec Additive (Bioline) was added to samples with lower yields. PCR programmes from Wahlberg & Wheat (2008) with the annealing temperature optimized for each primer set or the TouchDown PCR programme (Regier, 2007) were used as in Léger et al. (2019). Amplification success was checked by electrophoresis on 1 or 2% agarose gels subsequently stained with GelRed and visualised under UV light. For PCR products with weak or multiple bands, bands of interest were excised from the gel and DNA was extracted using Macherey-Nagel's PCR clean-up gel extraction kit. PCR products were cleaned by adding 0.3 μ l ExoSAP-IT (USB, USA) and 1 μ l H2O to 10 μl of PCR product, then following the manufacturer's protocol. Cleaned PCR products were forward-sequenced by Macrogen (Netherlands) or alternatively at the SMTD on a 3730 DNA Analyzer (Applied Biosystems, USA) using the T7 sequencing primer or PCR primers. Reverse sequencing with the T3 sequencing primer or PCR primers was performed for poor quality samples. Samples with ZMBN voucher code (see supplementary Table B.1) were processed according to the protocol of Mally et al. (2019).

Generation of molecular datasets

Targeted genes were retrieved from transcriptomes using reciprocal blasting with BLASTn 2.6 and from whole genomes using the blast tool as provided by the LepBase interface (Challis et al., 2016; ensembl.lepbase.org). DNA sequences from closely related taxa were used as query for both sequence searches. RAxML analysis for each single gene dataset was performed in order to identify and remove potential paralogues. Alignment of most sequence datasets was straightforward and was done by eye in PhyDE 0.9971 (Müller et al., 2005). Due to high occurrence of indels, the period gene was aligned using MAFFT (Katoh & Standley, 2013) as provided online by the European Molecular Biology Laboratory (EMBL, www.ebi.ac.uk). Gene files were concatenated using a bash script. Conspecific sequences from different datasets were combined for following taxa: *Chilo suppressalis* (CsuOGS1.0 and MAS-92-1001-1), *Pyralis farinalis* (Linnaeus, 1758) (MM00051 and CWM-08-2331), *Scirpophaga incertulas* (MAS-92-1003 & SRR1613323) and *Syntonarcha iriastis* Meyrick, 1890 (MTDLEP3002 and AZ-07-2650). Codon positions with undergoing synonymous substitutions tend to evolve faster and have a heterogeneous base composition (Cho et al., 2011, Regier et al., 2009, 2012). Following the approach described in previous studies (Regier et al., 2010, 2012, 2013), we used a bash script to generate an additional dataset "no_syn" with all synonymous substitution at third codon positions discarded. The size of the final datasets was of 11247 bp.

Identification of rogue taxa

A taxon is identified as "rogue" when its topological position varies greatly in the comparison of similar tree reconstructions (Aberer et al., 2013, Wilkinson, 1994). RogueNaRok (Aberer et al., 2013) was used to identify rogue taxa using the following options: majority-rule search, support optimized, maximum dropset size = 2, algorithm = roguenarok.

Phylogenetic analyses

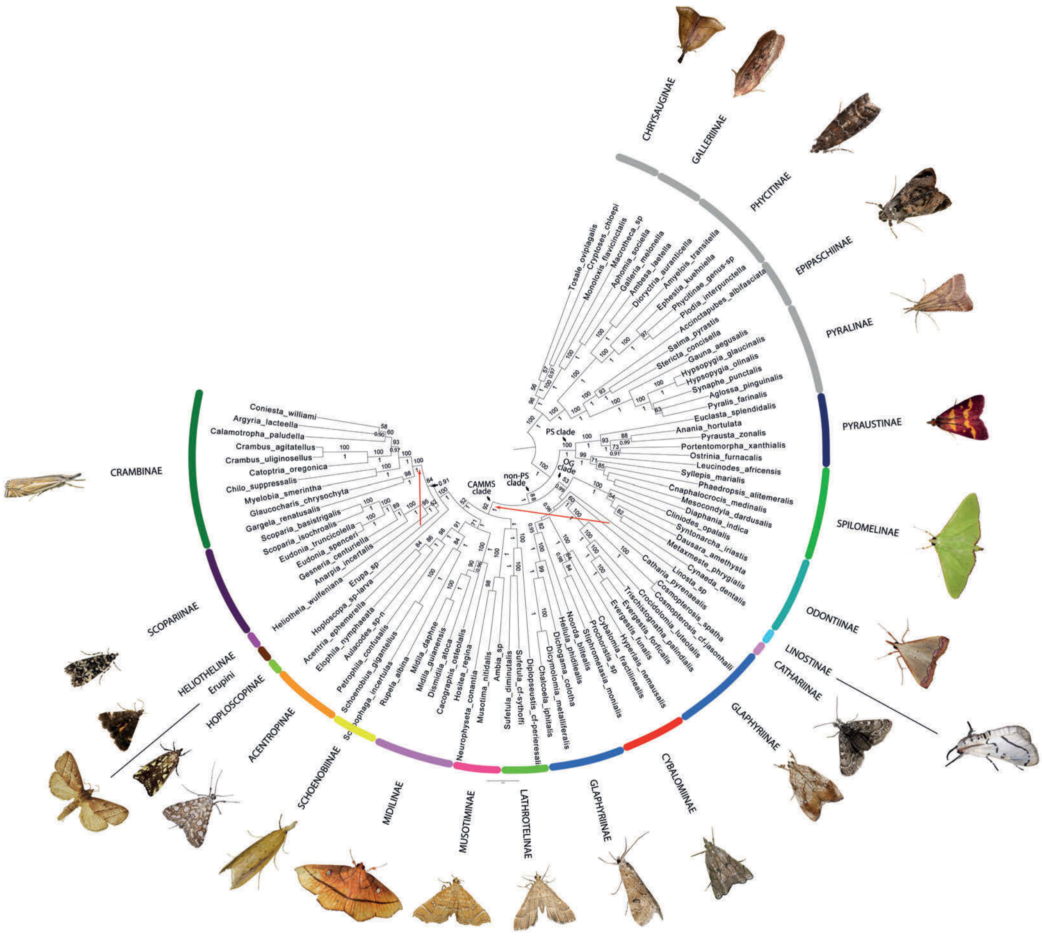
The molecular dataset was searched for the best partition scheme using PartitionFinder 2 (Lanfear et al., 2017) with the AICc model selection and the 'greedy' algorithm (Lanfear et al., 2012). The best model merged the second codon position of CAD, DDC, IDH in a subset and the second codon position of EF-1alpha, GAPDH and RpS5 in another subset, with all other codon position representing their own partition. Maximum Likelihood (ML) analyses were performed on RAxML (Stamatakis, 2006), with the dataset partitioned according to the best PartitionFinder model. Branch support was estimated with 1,000 rapid bootstrap inferences with the GTR+CAT algorithm, and the best tree was estimated with the GTR+GAMMA algorithm. Bayesian inferences (BI) were performed under MrBayes v.3.2.6 (Huelsenbeck & Ronquist, 2001) with the dataset partitioned according to the best PartitionFinder model. The following settings were used: prset revmatpr = dirichlet(1,2,1,1,2,1) (assuming a transition frequency twice as high as transversions), pinvarpr = uniform(0,1), ratepr = variable, brlenspr = unconstrained: exponential (1.0), parameters revmat, tratio, statefreq, shape set unlinked. Number of generations was set to 100,000,000, with burn-in set to 0.25. Good mixing of the Markov Chain Monte Carlo (MCMC) was assessed by visualizing the effective sample size in Tracer (Rambaut et al., 2018). Effective Sample Sizes (ESS) over 200 indicated sufficient sampling. ML and BI analyses were conducted on the CIPRES Portal (Miller et al., 2010).

Results and discussion

Rogue taxa

Hendecasis apicefulva Hampson, 1916 (sample MM13885) is highlighted as most unstable taxon (RogueNaRok raw improvement = 2.514), followed by *Ancylolomia inornata* (Staudinger, 1870) (sample MTDLEP1634; raw improvement = 0.806), and *Niphopyralis chionesis* (sample ANIC002674) together with *Udea ferrugalis* (Hübner, 1796) (sample MTDLEP870) (raw improvement=1.279). *Niphopyralis chionesis* (Spilomelinae) was already known to be problematic by Mally et al. (2019) due to its very long terminal branch in the phylogenetic tree. This peculiar pyraloid moth resembles limacodid moths, and its larvae develop in nests of leafcutter ants. This taxon was acommodated in its own subfamily Wurthiinae before Regier et al. (2012) synonymized the latter with Spilomelinae. Excluding the rogue taxon *H. apicefulva* from our dataset greatly improves the support for the wet-habitat clade (BS=35 vs 71 after removal) and the clade Acentropiinae + Schoenobiinae (BS=67 vs 91). Similarly, removing *A. inornata* from our dataset recovers the "open-cell clade" (sensu Léger et al., 2019b) with great support (BS=31 vs 93).

Figure 2.1: Best-scoring Maximum Likelihood tree of the 10-genes dataset under RaxML with best Partition-Finder model applied. Bootstrap support estimated from 1000 replicates displayed above the nodes, posterior probabilities from the bayesian analysis displayed below the nodes. Species represented and picture credit, clockwise: *Casuaria armata* (© A. Kay, Flickr), *Galleria mellonella* (© D. Hobern), *Dioryctria sp.* (© D. Hobern), *Salma pyrastis* (© D. Hobern), *Synaphe punctalis* (© Riszard, Flickr), *Pyrausta tyralis* (© D. Hobern), *Parotis sp.* (© I. MacMillan), *Autocharis hedyphaes* (© S. & A. Pearson), *Linosta centralis* (© G. Kunz), *Catharia pyrenaealis* (© L. Mikonranta, Flickr), *Crocidolomia pavonana* (© Naturgucker.de, Flickr), *Diplopseutis prophetica* (© D. Ackers), *Hellula rogatalis* (©© D. Hobern), *Musotima ochropteralis* (© D. Hobern), *Midila daphne* (© A. Kay), *Donacaula melinellus* (© M. Krancevic), *Elophila nymphaeata* (© D. Hobern), *Hoploscopa sp.* (© T. Léger), *Erupa sp.* (© T. Léger), *Heliothela ophideresena* (© D. Hobern), *Scoparia sp.*, *Crambus lathionellus* (© F. Bauer).



Phylogenetic analyses

ML and BI (Fig. 2.1) provide largely congruent relationships among subfamilies. Topological incongruences between the ML and the BI analysis show poor support in both analyses. The positions of *Linosta* (Linostinae) and *Erupa* Walker, 1864 (Erupini) differ in both analyses, but none of these placements is strongly supported. 65% of among-subfamilies relationships and 81% of infra-subfamilies relationships show substantial support (BS> 70). Analysis of the no-syn dataset (Suppl. Fig. B2) shows overall lower node support, with substantial support (BS> 70) recovered for 58% of among-subfamilies relationships and 60% of infra-subfamilies relationships. The topology recovered from the no-syn dataset shows ten nodes in discordance with the ML analysis of the standard dataset. Some alternative groupings are recovered with substantial support: *Rupela* (Schoenobiinae) branches at base of the Acentropinae (BS=77) as recovered in Regier et al. (2012), and *Erupa* groups with *Hoploscopa* Meyrick, 1886 (BS=77). These phylogenetic incongruences are discussed in the section “Phylogenetic relationships” below.

Missing data

Our approach of combining datasets from different studies aims to expand gene and taxon sampling. However, merging datasets with different gene samplings may result in blocks of missing data that can result in misleading phylogenetic reconstructions (Lemmon et al., 2009; Simmons, 2012). The analysis excluding the Regier dataset (not shown) does not show any discrepancies compared to the analysis of the complete dataset, but several deep nodes within the Crambidae show a decrease in support. This observation is in line with a previous study analysing the effect of missing data when combining different datasets (Cho et al., 2011).

Phylogenetic relationships

Our analyses confirm the basal split of Pyraloidea into Crambidae and Pyralidae, which is well supported by morphological and molecular evidence (Minet, 1982; Mutanen et al., 2010; Regier et al., 2012). Relationships among the five subfamilies of Pyralidae are widely concordant with the findings of Regier et al. (2012) and are strongly supported (BS> 95). One exception is the clade including Gallerinae and Chrysauginae, which is supported only in half of the analyses of Regier et al. (2012). In our analyses, it is either recovered with strong support (BS=96) or with weak support in the analysis of the conc10genes_nosyn dataset. Chrysauginae are recovered monophyletic, but only BI provides substantial support for it (pp=1.00, BS=56). Chrysauginae were found paraphyletic with respect to Galleriinae in Regier et al. (2012), and the authors raised doubt regarding the monophyly of this group. Solis & Mitter (1992) proposed a sclerotized ring around the base of the larval SD1 seta as apomorphy for the group, and characters of the male forewing venation are suspected to be apomorphic. Crambidae are recovered monophyletic with maximum support (BS=100) and show a basal dichotomy into the “PS clade” comprising Pyraustinae and Spilomelinae (BS=100), and another moderately supported “non-PS clade” including all remaining Crambidae (BS=88), in line with the results from Regier et al. (2012). Relationships within the Spilomelinae are surprisingly poorly resolved, with only the clade referred to as “Euspilomelinae” in Mally and al. (2019) showing substantial support (BS=85). The broad taxon sampling and the integration of morphological characters in the Bayesian reconstruction possibly explain the better branch support observed in Mally et al. (2019).

We find the non-PS clade of Regier et al. (2012), comprising Acentropinae, Crambinae, Glaphyriinae, Midilinae, Musotiminae, Odontiinae, Schoenobiinae and Scopariinae, to also include Cathariinae, Cybalomiinae, Heliothelinae, Hoploscopinae **stat. n.**, Lathrotelinae and Linostinae, with moderate support (BS=88) in the ML analysis. Basal relationships among Cathariinae, Cybalomiinae, Glaphyriinae, Linostinae, Odontiinae and the CAMMSS clade do not show significant support (BS< 50). Linostinae are found to be sister to Glaphyriinae + Cybalomiinae + Cathariinae without support in the ML analysis, while in the BI they are placed as sister to the CAMMSS clade (pp=0.84). The absence of a proboscis and ocelli as well as the reduced labial palpi supported the sister relationship between *Linosta* and *Niphopyralis* in Solis & Maes (2002), but this relationship was questioned by the authors due to the nature of the character changes (three losses) and the different geographical occurrences of these lineages (Neotropics and Oriental-Australasian, respectively). The position of *Niphopyralis* within Spilomelinae (Suppl. Fig. B1) is in line with Regier et al. (2012) and Mally et al. (2019), while *Linosta* is recovered in the “non-PS clade” (with as of yet unresolved sister-group relationship). The reductions of these morphological characters thus appear to be convergent in the light of these results. Our analyses recover Linostinae, Cathariinae and Cybalomiinae in the Odontinae + Glaphyriinae clade (“OG clade”) of Regier et al. (2012), although with low support in the ML analysis (BS=53, pp=0.99). When *Linosta* is excluded from the analysis (not shown), the OG clade shows strong support (BS=98), confirming the rogue behavior of *Linosta* in our analyses. Both analyses recover a clade comprising Cathariinae, Cybalomiinae and Glaphyriinae, but only BI provides strong support for this grouping (pp=0.98; BS=50 when *Linosta* excluded). Glaphyriinae are separated in two clades: *Cosmopterosis* + (*Crocidolomia* + (*Trischistognatha* + *Evergestis*)) (BS=100), and *Noorda* + (*Hellula* +, (*Dichogama* + (*Chalcoela* + *Dicymolomia*))) (BS=82, pp=0.95). Cathariinae are sister to the first clade (BS=60, pp=1; BS=73 when *Linosta* excluded). In the morphologyy, the absence of a gnathos in males of Cathariinae is also reported in many Glaphyriinae, but this character was shown to vary greatly in this group (Munroe, 1972; Regier et al., 2012; Solis & Adamski, 1998b). The biology of the immatures however differ, *Catharia pyrenaealis* larvae feed on *Heliosperma alpestre* (Caryophyllaceae; Krone, 1905) and were also found feeding on *Saxifraga oppositifolia* (Saxifragaceae), *Cerastium pedunculatum* (Caryophyllaceae), *Saxifraga aphylla* (Saxifragaceae), *Silene acaulis* (Caryophyllaceae) (Schmid, 2019). Cathariinae hence do not share the Brassicales-feeding in larval instars with Glaphyriinae and Cybalomiinae. Cybalomiinae, here represented by four genera, are recovered monophyletic (BS=100) and are found nested within Glaphyriinae, but their position remains ambiguous. Larvae of this subfamily almost exclusively feed on Brassicales, a trait shared with most Glaphyriinae, which suggests a common origin of this feeding habit in the two groups. Our results suggest a broad concept of Glaphyriinae including Cathariinae and Cybalomiinae. However, weak support precludes us from any systematic changes for now, but highlights these groups as the ones that are most in need of systematic clarification in future works.

The "CAMMSS clade" sensu Regier et al. (2012), comprising Acentropinae, Crambinae, Midilinae, Musotiminae, Schoenobiinae and Scopariinae, includes here also the Lathrotelinae, Hoploscopinae *stat. n.* and Heliothelinae s. str. (BS=92). Basal relationships between Lathrotelinae, Musotiminae, the "wet habitat clade" of Regier et al. (2012) comprising the Acentropinae, Midilinae and Schoenobiinae, and the clade including Crambinae, Erupini, Heliothelini, Hoploscopini and Scopariinae do not show substantial support in the ML analysis, while BI supports a clade comprising the Lathrotelinae and Musotiminae as sister to all other lineages of the CAMMSS clade. Lathrotelinae are recovered monophyletic (BS=100) and they are confirmed as part of the CAMMSS clade (BS=92) as hypothesized by Minet (2015) based on the shared use of monocotyledons as larval host plants. The author discussed morphological characters shared with Acentropinae, e.g. the dorsal position of the lobulus (=tympanic crest) and the presence of well-developed venulae secundae. The latter character has however been shown to vary greatly in Crambidae (Léger et al., 2019b). Lathrotelinae are found sister to Musotiminae, although without significant support in the ML analysis (BS=42, pp=1.00). The lathroteline genus *Sufetula* shares with Musotiminae the undulating wing margin and the absence of chaetosemata and ocelli. In contrast, Musotiminae lack the CuP on the forewings which are present in Lathrotelinae, and males bear a gnathos (absent in Lathrotelinae) and display secondary sexual characters (absent in Lathrotelinae) (J. Hayden, 2013). Musotiminae are recovered monophyletic with maximal support. The clade comprising Acentropinae, Midilinae and Schoenobiinae refered to as the as "wet habitat clade" by Regier et al. (2012) is recovered monophyletic, however with weak support in the ML analysis (BS=71, pp=1.00). *Hendecasis*, flagged as rogue taxon, is recovered within the wet habitat clade as sister to Midilinae (Suppl. Fig. B1), however without significant support (BS=35). This genus is currently placed in Cybalomiinae, although wing shape and pattern resemble those of musotimine moths. Our analysis refutes this placement, and shows *Hendecasis* to belong to the "CAMMSS clade". Acentropinae and Schoenobiinae form a sister-group with strong support (BS=94). This clade is one of the few relationships within Crambidae which is well supported by morphological evidence (Martínez, 2010; Passoa, 1988; Yoshiyasu, 1985). Monophyly of Acentropinae is well supported (BP=97), while monophyly of Schoenobiinae shows moderate support (BS=84, pp=1.00). However, analysis of the no-syn dataset recovers *Rupela* as nested in the Acentropinae (BP=79). This result is similar to that of Regier et al. (2012), where *Rupela* was recovered as sister to Acentropinae in analyses of their 19-genes dataset, rendering Schoenobiinae paraphyletic. They argued that this position is due to large portions of missing data in their 19-genes dataset. Indeed, nine morphological characters support the monophyly of Schoenobiinae including *Rupela* (Common, 1960; Lewvanich, 1981; Martínez, 2010; Passoa, 1988), while no synapomorphy shared by *Rupela* and Acentropinae is known (Regier et al., 2012). We assume that the weak number of informative sites in the no-syn dataset explains this ambiguous grouping. The clade including the Crambinae and Scopariinae in Regier et al. (2012) is confirmed here and also includes the Erupini and the Heliothelinae, with maximum support (BS=100). The Heliothelinae are polyphyletic: Hoploscopini are recovered as sister to the remaining groups of this clade (BS=84), while Heliothelinae s. str. are found sister to Scopariinae (BS=95). The sclerotized thorn invaginated into the corpus bursae in female genitalia, considered as apomorphic for this group by Nuss (1998), now appears homoplastic in the light of these results. Hoploscopini were found sister to Musotiminae by Léger et al. (Léger et al., 2019b), a topology that found echo in the biology of the immatures, both groups being fern-feeders. Larval morphology of the Hoploscopini suggests close relationship either to the Crambinae or to Acentropinae + Schoenobinae (Mally et al., 2017). The sister relationships between Heliothelinae s. str. and Scopariinae finds echo in the morphology: Minet (1982) showed the Heliothelinae and Scopariinae to have a similar tympanal organ and wing venation, while he recognized substantial differences in male and female genitalia. Nuss (1998) justified the separation of Heliothelinae s. l. from the Scopariinae by the presence of a thorn in the female corpus bursae (absent in Scopariinae) and the lack of an appendix bursae (present in Scopariinae). The latter is however absent in all basal lineages of Scopariinae and does not represent an apomorphy for this group (Léger et al., 2019b). Heliothelinae s. str. also lack the median discoidal X-shaped stigma suggested as synapomorphy for Scopariinae (Nuss, 1999). Habitat and biology of Heliothelinae s. str. and Scopariinae also differ from each other. Heliothelinae s. str. occur in warm and dry lowlands of the Old world and Australia, and their larvae are endophagous on Violaceae. In contrast, Scopariinae occur in moist habitats and their larvae are moss-feeders. The present topology leaves us with a choice of considering Heliothelinae as a separate subfamily or as part of the Scopariinae. Due to morphological and ecological differences of the two taxa, we decide here to keep Heliothelinae s. str. and Scopariinae as separate taxa. As Hoploscopini are recovered as sister to Heliothelinae, Scopariinae and Crambinae, it is raised here to subfamily rank, i.e. Hoploscopinae **stat. n.** The position of Erupini in this clade remains ambiguous. *Erupa* was alternatively placed in Schoenobiinae (Bleszynski, 1966), Crambinae (Lewvanich, 1981, Munroe, 1995) and finally in Midilinae (J. E. Hayden, 2012), and was recovered as sister to Crambinae by Léger et al. (2019a), but only with support from the BI analysis. Current analyses refute a placement of *Erupa* in Midilinae, but detailed relationship remains obscure due to lack of support. Interestingly, the analysis of the no-syn dataset (Suppl. Fig. B2) pairs *Hoploscopa* with *Erupa* (BS=77). This relationship is recovered here for the first time and is in conflict with the result provided by the analysis of the standard dataset. Analysis of the morphology in both groups did not reveal any possible synapomorphy. Noteworthy, the taxon *Odilla* Schaus, 1940, placed by Hayden (2012) along with Erupini in the Midilinae, displays brownish forewings with a white postmedian blot that resemble those of *Perimeceta* species. Inclusion of further taxa such as *Neerupa* Hampson, 1919, *Schoenerupa* Hampson, 1919 (Erupini) and *Perimeceta* Turner, 1915 (Hoploscopinae) might shed more light onto the placement of Erupini.

Host plant utilization

Inclusion of five new lineages in a phylogenetic frame sheds more light into host plant evolution in Crambidae. Host plant patterns and switches are paralleled with other cases in Lepidoptera. In the following, we treat feeding habits by plant group.

Eudicotyledons. Eudicotyledons, or flowering plants, represent the bulk of angiosperms diversity with a diversity estimated to nearly 400’000 species. All eudicotyledons are treated here, except the Brassicales treated in the next paragraph. Odontiinae, Pyraustinae and Spilomelinae feed on a broad spectrum of eudicotyledons (Mally et al., 2019; Munroe & Solis, 1998; Robinson et al., 2010), and Cybalomiinae and Glaphyriinae are specialists on brassicales. Larvae are leaf folders, lear tiers, or bore in fruits or stems (Munroe & Solis, 1998). The dominance of eudicotyledon in the host plants spectrum of the “PS” and the “OG clade” suggest them as the likely ancestral host plant of the Crambidae. Switch to host plants such as monocotyledons, pterydophytes or bryophytes is considered secondary.

Brassicales. Brassicales are characterized by the presence of mustard oils or glucosinolates. These chemical compounds form toxic isothiocyanates when they interact with myrosinases stocked in myrosin cells (Halkier & Gershenzon, 2006). The families Brassicaceae, Capparaceae and Cleomaceae form the bulk of Brassicales diversity. In Crambidae, the Cybalomiinae and Glaphyriinae feed predominantly on Brassicaceae and Capparaceae. Larvae of *Noorda* feed on *Moringa* (Moringaceae) whose species also contain glucosinolates (Fahey et al., 2018). Interestingly, *Trischistognatha* is reported to feed on *Drypetes* (Putranjivaceae), which is the only family outside of the Brassicales that developed mustard oil (Hall et al., 2002). The position of *Trischistognatha* nested within the Glaphyriinae speaks for a host-plant switch from an ancestral Brassicales host-plant to *Drypetes*. A similar host-plant switch to *Drypetes* is observed in Brassicales-feeding Pieridae (Braby & Trueman, 2006). There are notable exceptions in feeding habits of glaphyriine larvae: a few specialists are reported feeding on Cyperaceae (*Typha* spp.) or lichens, or parasiting Lepidoptera or Hymenoptera larvae (Munroe & Solis, 1998). Mechanism of metabolization of glucosinolates is known for other brassicales-feeding Lepidoptera: *Plutella xylostella* (Linnaeus, 1758) and *Pieris rapae* Linnaeus, 1758 use the enzyme glucosinolate sulfatase (Ratzka et al., 2002) or redirect the hydrolysis of the glucosinolates into nitriles (Wittstock et al., 2004). Not much is known about the way Cybalomiinae or Glaphyriinae metabolize glucosinolate, but *Crocidolomia pavonana* (Fabricius, 1794) appears to be resistant to isothiocyanate, while it is lethal to *P. xylostella*, suggesting the existence of a different metabolic pathway of processing glucosinolates (Tadle, 2017). In Crambidae, four other taxa are feeding on Brassicales: two midiline taxa are reported from Capparaceae, while some pest species of *Chilo* and *Talis* (Crambinae) have been recorded from Brassicaceae (Robinson et al., 2010). This implies that the ability to metabolize glucosinolates was retained in these taxa, or that it evolved independently.

Monocotyledons. Monocotyledons encompass 60,000 species and include notably Poaceae, Cyperaceae and Arecaceae used as host plants by a substantial number of Crambidae species. The subfamilies Acentropinae, Crambinae, Lathrotelinae, Midilinae and Schoenobiinae of the CAMMSS clade are predominantly feeding on monocotyledons. Lathrotelinae are reported feeding on *Carex* spp., Cyperaceae (*Diplopseustis*), Arecaceae (*Diplopseustis*, *Sufetula*), Poaceae (e.g. *S. grumalis*, a pest on sugarcane) and recently on Bromeliaceae (*S. anania*) (Gaedike, 2010; Genty & Mariau, 1975; Patrick, 1994; Robinson et al., 2010; Seín, 1930; Solis et al., 2019). In Midilinae, *Cacographis* and *Eupastrania* are reported boring on roots of palm trees (Aracaceae), while *Dolichobela* and *Styphlolepis* were found feeding on Capparaceae. A majority of larvae of Crambinae and Schoenobiinae larvae bore in grasses of the Cyperaceae and Poaceae, with feeding on roots or at base of grasses considered derivated in Crambinae (Léger et al., 2019b). Acentropinae are unique in the adaptation of larvae to live in aquatic habitats. Foodplant include aquatic monocotyledons alongside with aquatic Pterydophyta and dicotyledons. The recovering of the Lathrotelinae within the CAMMSS clade reinforce the hypothesis of a monocotyledon as ancestral host plant of the group, but pterydophytes is another likely ancestral host plant for this clade. Monocots-feeders outside of the CAMMSS clade are scarce. In the Spilomelinae, the *Cnaphalocrocis* group forms a major radiation on monocots (Léger et al., 2019b).

Pteridophyta. Ferns are rather uncommon as host plant in insects (Auerbach & Hendrix, 1980). They contain simple phenolic compounds, tannins and several other chemicals that act as defence against bacteria, fungi and herbivores, but they lack compounds like acetylenes or glucosinolates found in angiosperms (Cooper-Driver, 1985). High concentrations of phytoecdysteroids are found in some fern taxa, e.g. Polypodiaceae (Lafont et al., 2011). Fern-feeding habits are scarcely represented in lepidopteran lineages, and exclusive or nearly-exclusive associations to ferns are observed only in a few lepidopteran lineages, e.g. Callidulidae, Lithinini (Geometridae), *Psychoides* Bruand, 1853 (Tineidae), *Pachyrhabda* Meyrick, 1897 (Oechophoridae) and *Callopistria* Hübner, 1821 (Noctuidae) (Auerbach & Hendrix, 1980; Weintraub et al., 1995). Crambidae exhibit two lineages feeding on ferns: Hoploscopinae and Musotiminae. These two subfamilies currently include 20 and 194 described species, respectively. For Hoploscopinae, ongoing work describes 26 new species and estimates another 30 species awaiting description (Léger et al., 2019a). Hoploscopinae occur in South-East Asia and Melanesia, where diversity of Pteridophyta is at its highest (Ebihara & Kuo, 2012). Our finding of Hoploscopinae and Musotiminae in different clades speaks in favour for an independent evolution of fern feeding in these two groups. Further cases of fern feeding in Crambidae are known from *Epipagis miltochristalis* (Hampson, 1896), *Psara platycapna* (Meyrick, 1897), *Samea multiplicalis* (Guenée, 1854), *Udea decrepitalis* (Herrich-Schäffer, 1848) (all Spilomelinae) and *Phenacodes aleuropa* (Lower, 1903) (Scopariinae) as well as several Acentropinae feeding on aquatic pteridophytes (Robinson et al., 2010).

Bryophyta. Bryophyta forms a paraphyletic assemblage comprising liverworts, mosses and hornworts (Wickett et al., 2014). These groups represent the earliest lineages of land plants and originated in the Carboniferous (Hübers & Kerp, 2012). In Pyraloidea, moss-feeding habits are found in Scopariinae and in some species of crambine *Agriphila* Hübner, 1825, *Catoptria* Hübner, 1825, *Gadira* Walker, 1866 and *Glaucocharis* Meyrick, 1938. The early-branching crambine lineage *Glaucocharis* also feeds on mosses, raising the question whether moss-feeding habits observed in Crambinae and Scopariinae are the result of a single origin, or represent convergence evolution. *Heliothela* Guenée, 1854, recovered sister to Scopariinae in this study, is known to feed upon Lamiaceae and Violaceae, contrasting with moss feeding habits of Scopariinae. Host plants of Erupini are currently unknown, but monocotyledons were suggested by Hayden (2012). Additional host plant data for Erupini as well as for the basal scopariine lineage *Anarpia* Chapman, 1912 (Léger et al., 2019b) would shed light on the evolution of moss feeding habits in Crambinae and Scopariinae. Interestingly, several moss feeding species of *Agriphila*, *Catoptria* (Crambinae) and *Eudonia* Billberg, 1820 (Scopariinae) from New Zealand show congeneric taxa feeding on grasses, and some species have been reported feeding on both plants (Robinson et al., 2010). Larvae of these feed at the base of grasses, suggesting that spatial proximity rather than phytochemistry led these host plant switches to mosses.

Summary and outlook

We provide the first phylogeny comprising all subfamilies of Crambidae and including pyraloid molecular datasets from major previous phylogenetic studies (Heikkilä et al., 2015; Kawahara & Breinholt, 2014; Léger et al., 2019b; Mally et al., 2019; Mutanen et al., 2010; Regier et al., 2012) and from published genomes or transcriptomes (Challis et al., 2016; Renuka et al., 2017) as well as our own sequences. The synergetic effect of these molecular datasets lead to an increase of support for several clades found in Regier et al. (2012), and provide placement for Cathariinae, Cybalomiinae and Linostinae, although without well supported sister-relationships. The Cathariinae and Cybalomiinae are recovered in a clade together with the Glaphyriinae, with which the Cybalomiinae share the Brassicales as host plant. The Heliothelinae s. l. are found to be polyphyletic and are therefore split into Heliothelinae s. str. and Hoploscopinae **stat. n.**, and both are recovered in a well-supported clade together with Crambinae, Erupini and Scopariinae. The exclusion of synonymous mutations results in a different placement of Erupini with respect to Hoploscopinae and for Schoenobiinae with respect to Acentropinae, providing alternative hypotheses to be tested with a greater set of molecular characters. The close relationship between Cybalomiinae and Glaphyriinae suggest one origin of the Brassicales feeding habits in both groups. Fern feeding habits, observed in the Musotiminae and recently reported in the Hoploscopinae (Mally et al., 2017), evolved independently in these two lineages. A common origin of moss-feeding habits in Crambinae and Scopariinae is challenged by the sister-relationship of Scopariinae and Heliothelinae, the latter feeding on Violaceae in larval stages. The hundred taxa included in the present study constitute a tiny fraction of the nearly 16,000 described Pyraloidea. Intra-subfamily relationships of four of the most species-rich subfamilies (Crambinae, Pyraustinae, Scopariinae and Spilomelinae) were the scope of two recent phylogenetic studies (Léger et al., 2019b; Mally et al., 2019) and helped to comprehensively sample these groups in order to span over their molecular diversity. A better understanding of phylogenetic relationships in other species-rich groups like the Acentropinae, Odontiinae, Glaphyriinae, Schoenobiinae by dedicated studies is necessary to better sample these groups in future studies adressing the Crambidae phylogeny. Phylogenomics has been widely used in reconstructing relationships across all Lepidoptera (e.g., Bazinet et al., 2017; Kawahara & Breinholt, 2014; Kawahara et al., 2019), or in butterflies

(Li et al., 2019; Toussaint et al., 2018). With the ever decreasing costs of high-throughput sequencing, the use of genomic methods in future projects on pyraloid phylogeny holds the promise of a hundred-fold increase in the size of dataset and the possibility to include museum specimens of rare taxa.

Acknowledgments

We thank Carl Bélanger, Eric Drouet, Robert Hoare (NZAC), Rolf Mörter, Andreas Segerer (ZSM) and Marja van der Straten (NPPO Wageningen, NL) for providing freshly collected specimens for analysis. We thank Manuela Bartel (MTD) her help with the lab work. Jürgen Schmid provided us host plant records of *Catharia pyrenaealis*. We are indebted to the following people for their help in fieldwork: Thea Lautenschläger (Technische Universität Dresden) as well as the staff from the Universidade Kimpa Vita of Ndalatando and Uíge for collecting in Angola; Stephen Sutton, Charles S. Vairappan (Institute for Tropical Biology and Conservation, Kota Kinabalu, Malaysia), Ching Y. Chung (Sabah Biodiversity Centre) and the staff of the Sabah Parks for collecting in Sabah, Malaysia. Field trips by TL to Angola and Malaysia were funded by the DAAD (Angola) and the Royal Entomological Society (Malaysia). RM thanks the Norwegian Meltzer Research Fund for their grant support of the collecting in Malaysia. Field trips by MN to Bolivia and Peru were funded by the DAAD, Deutsche Forschungsgemeinschaft (DFG) and the Senckenberg Gesellschaft für Naturforschung. TL was funded by the Senckenberg Gesellschaft für Naturforschung.

Bibliography

Aberer, A. J., Krompass, D., & Stamatakis, A. (2013). Pruning rogue taxa improves phylogenetic accuracy: An efficient algorithm and webservice. *Systematic biology*, *62*(1), 162–166.

Amsel, H. G. (1956). Microlepidoptera Venezolana i. *Boletin de Entomologia Venezolana, Maracay*, *10*(1), 1–336.

Auerbach, M. J. & Hendrix, S. D. (1980). Insect-fern interactions: Macrolepidopteran utilization and species-area association. *Ecological Entomology*, *5*(2), 99–104.

Bazinet, A. L., Mitter, K. T., Davis, D. R., Van Nieukerken, E. J., Cummings, M. P., & Mitter, C. (2017). Phylotranscriptomics resolves ancient divergences in the Lepidoptera. *Systematic Entomology*, *42*(2), 305–316. doi:10.1111/syen.12217

Bleszynski, S. (1966). Further taxonomic notes on some tropical species. *Acta Zoologica Cracoviensia*, *11*(15), 451–497.

Börner, C. (1925). 22. Ordn. Lepidoptera, Schmetterlinge. In *Fauna von Deutschland, 3. verbesserte Auflage. – Fauna von Deutschland, ein Bestimmungsbuch unserer heimischen Tierwelt* (Quelle and Meyer, pp. 358–387). Leipzig.

Braby, M. F. & Trueman, J. W. H. (2006). Evolution of larval host plant associations and adaptive radiation in pierid butterflies. *Journal of evolutionary biology*, *19*(5), 1677–1690.

Capinera, J. (2001). *Handbook of vegetable Pests* (Academic Press). Elsevier.

Challis, R. J., Kumar, S., Dasmahapatra, K. K., Jiggins, C. D., & Blaxter, M. (2016). Lepbase: The Lepidopteran genome database. *bioRxiv*, 056994. doi:10.1101/056994

Cho, S., Zwick, A., Regier, J. C., Mitter, C., Cummings, M. P., Yao, J., ... Parr, C. (2011). Can Deliberately Incomplete Gene Sample Augmentation Improve a Phylogeny Estimate for the Advanced Moths and Butterflies (Hexapoda: Lepidoptera)? *Systematic Biology*, *60*(6), 782–796. doi:10.1093/sysbio/syr079

Chrétien, P. (1911). Contribution à la connaissance des Lépidoptères du nord de l'Afrique. *Annales de la Société Entomologique de France, Paris*, *79*, 497–531.

Clarke, J. F. G. (1971). The Lepidoptera of Rapa Island. *Smithsonian Contributions to Zoology, Washington*, *56*, 1–182.

Common, I. F. B. (1960). A revision of the Australian stem borers hitherto referred to *Schoenobius* and *Scirpophaga* (Lepidoptera: Pyralidae, Schoenobiinae). *Australian Journal of Zoology*, *8*, 307–347.

Cooper-Driver, G. (1985). Anti-predation strategies in pteridophytes—a biochemical approach. *Proceedings of the Royal Society of Edinburgh, Section B: Biological Sciences*, *86*, 397–402.

Ebihara, A. & Kuo, L.-Y. (2012). East and Southeast Asian pteridophyte flora and DNA barcoding. In *The Biodiversity Observation Network in the Asia-pacific Region* (pp. 321–327). Springer.

Fahey, J. W., Olson, M. E., Stephenson, K. K., Wade, K. L., Chodur, G. M., Odee, D., ... Hubbard, W. C. (2018). The Diversity of Chemoprotective Glucosinolates in Moringaceae (*Moringa* spp.) *Scientific Reports*, *8*(1), 7994. doi:10.1038/s41598-018-26058-4

Gaedike, R. (2010). Nachtrag 2009 zum verzeichnis der Schmetterlinge Deutschlands (Microlepidoptera). *Entomologische Nachrichten und Berichte*, *54*, 109–122.

Genty, P. & Mariau, D. (1975). Morphologie et biologie du Pyralidae des racines de l'*Elaeis*, *Sufetula diminutalis*. *Oléagineux*, *30*(4), 147–152.

Giegerich, R., Meyer, F., & Schleiermacher, C. (1996). GeneFisher-software support for the detection of postulated genes. In *ISMB* (pp. 68–77).

Greenfield, M. D. (2014). Acoustic communication in the nocturnal Lepidoptera. In *Insect hearing and acoustic communication. Animal signals and communication* (Vol. 1, pp. 81–100). Berlin: Springer.

Halkier, B. A. & Gershenzon, J. (2006). Biology and biochemistry of glucosinolates. *Annual review of plant biology*, *57*, 303–333. doi:10.1146/annurev.arplant.57.032905.105228

Hall, J. C., Sytsma, K. J., & Iltis, H. H. (2002). Phylogeny of Capparaceae and Brassicaceae based on chloroplast sequence data. *American journal of botany*, *89*(11), 1826–1842. doi:10.3732/ajb.89.11.1826

Hannemann, H. J. (1964). Kleinschmetterlinge oder Microlepidoptera II. Die Wickler (s.l.) (Cochylidae und Carposinidae). Die Zünslerartigen (Pyraloidea). In *Die Tierwelt Deutschlands* (Vol. 50). Jena: Gustav Fischer.

Hasenfuß, I. (1960). *Die Larvalsystematik der Zünsler.* Berlin: Academie Verlag.

Hayden, J. (2013). *Sufetula* Walker in Florida (Lepidoptera: Crambidae). *Insecta Mundi, Gainesville, Florida*, *296*, 1–15.

Hayden, J. E. (2012). Revision of *Odilla noralis* Schaus and transfer of Erupini to Midilinae (Lepidoptera: Crambidae). *Annals of Carnegie Museum*, *80*(4), 309–322. doi:10.2992/007.079.0401

Heikkilä, M., Mutanen, M., Wahlberg, N., Sihvonen, P., & Kaila, L. (2015). Elusive ditrysian phylogeny: An account of combining systematized morphology with molecular data (Lepidoptera). *BMC Evolutionary Biology*, *15*(1), 260. doi:10.1186/s12862-015-0520-0

Hill, D. S. (1987). *Agricultural insect pests of temperate regions and their control.* Cambridge: Cambridge University Press.

Hill, D. S. (2008). *Pests of crops in warmer climates and their control.* Springer Science & Business Media.

Hübers, M. & Kerp, H. (2012). Oldest known mosses discovered in Mississippian (late visean) strata of Germany. *Geology*, *40*(8), 755–758. doi:10.1130/G33122.1

Huelsenbeck, J. P. & Ronquist, F. (2001). MRBAYES: Bayesian inference of phylogenetic trees. *Bioinformatics*, *17*(8), 754–755.

Katoh, K. & Standley, D. M. (2013). MAFFT Multiple Sequence Alignment Software version 7: Improvements in Performance and Usability. *Molecular Biology and Evolution*, *30*(4), 772–780. doi:10.1093/molbev/mst010

Kawahara, A. Y. & Breinholt, J. W. (2014). Phylogenomics provides strong evidence for relationships of butterflies and moths. *Proceedings of the Royal Society B: Biological Sciences*, *281*(1788), 20140970. doi:10.1098/rspb.2014.0970

Kawahara, A. Y., Plotkin, D., Espeland, M., Meusemann, K., Toussaint, E. F. A., Donath, A., … dos Reis, M. et al. (2019). Phylogenomics reveals the evolutionary timing and pattern of butterflies and moths. *Proceedings of the National Academy of Sciences*, *116*(45), 22657–22663. doi:10.1073/pnas.1907847116

Kemner, N. V. A. (1923). Hyphaenosymphilie, eine neue, merkwürdige art von myrmekophilie bei einem neuen myrmekophilen schmetterling (wurthia aurivillii n. sp.) aus java. *Arkiv för Zoologi, Stockholm*, *15*(15), 1–28, figs 1–7, pls 1–4.

Khan, Z. R., Litsinger, J. A., Barrion, A. T., Villanueva, F. F. D., Fernandez, N. J., & Taylo, L. D. (1991). *World Bibliography of Rice Stem Borers: 1794-1990.* Manila, The Philippines: IRRI.

Knölke, S., Erlacher, S., Hausmann, A., Miller, M. A., & Segerer, A. H. (2004). A procedure for combined genitalia dissection and DNA extraction in Lepidoptera. *Insect Systematics & Evolution*, *35*(4), 401–409. doi:10.1163/187631204788912463

Kuznetsov, V. I. & Stekolnikov, A. A. (1979). Functional morphology of the male genitalia of the Pyraloidea (Lepidoptera) of the Palearctica fauna. *Trudy zoologicheskogo instituta leningrad*, *83*, 46–96 (in Russian).

Lafont, R., Ho, R., Raharivelomanana, P., & Dinan, L. (2011). Ecdysteroids in ferns: Distribution, diversity, biosynthesis, and functions. In *Working with ferns* (pp. 305–319). New York: Springer.

Landry, B. & Roque-Albelo, L. (2008). The Glaphyriinae (Lepidoptera: Pyralidae) of the Galápagos Islands, Ecuador, with keys to the Neotropical species of *Hellula* Guenée. *Tijdschrift voor Entomologie, 's Gravenhage*, *151*, 193–203. doi:10.1163/22119434-900000264

Lanfear, R., Calcott, B., Ho, S. Y. W., & Guindon, S. (2012). Partitionfinder: Combined selection of partitioning schemes and substitution models for phylogenetic analyses. *Molecular Biology and Evolution*, *29*(6), 1695–1701. doi:10.1093/molbev/mss020

Lanfear, R., Frandsen, P. B., Wright, A. M., Senfeld, T., & Calcott, B. (2017). PartitionFinder 2: New Methods for Selecting Partitioned Models of Evolution for Molecular and Morphological Phylogenetic Analyses. *Molecular Biology and Evolution*, *34*(3), 772–773. doi:10.1093/molbev/msw260

Léger, T., Kehlmaier, C., & Nuss, M. (2019a). Twenty-six new species of *Hoploscopa* (Lepidoptera, Crambidae) from South-East Asia revealed by morphology and DNA barcoding. *Zookeys*, *in press.*

Léger, T., Landry, B., & Nuss, M. (2019b). Phylogeny, character evolution and tribal classification in Crambinae and Scopariinae. *Systematic Entomology*, *44*(4), 757–776. doi:10.1111/syen.12353

Lemmon, A. R., Brown, J. M., Stanger-Hall, K., & Lemmon, E. M. (2009). The Effect of Ambiguous Data on Phylogenetic Estimates Obtained by Maximum Likelihood and Bayesian Inference. *Systematic Biology*, *58*(1), 130–145. doi:10.1093/sysbio/syp017

Leraut, P. (1980). Liste systématique et synonymique des Lépidoptères de France, Belgique et Corse. *Alexanor and Bulletin de la Société entomologique de France*, *Supplement*, 1–334.

Leraut, P. (1997). Liste systématique et synonymique des Lépidoptères de France, Belgique et Corse (deuxième édition). *Alexanor*, *suppl.* 7–526.

Lewvanich, A. (1981). A revision of the Old World species of *Scirpophaga* (Lepidoptera: Pyralidae). *Bulletin of the British Museum (Natural History) Entomology series, London*, *42*(4), 185–298.

Lhomme, L. (1935). Catalogue des Lépidoptères de France et de Belgique. Microlépidoptères. *Le Carriol, Lot.* 1–172.

Li, W., Cong, Q., Shen, J., Zhang, J., Hallwachs, W., Janzen, D. H., & Grishin, N. V. (2019). Genomes of skipper butterflies reveal extensive convergence of wing patterns. *Proceedings of the National Academy of Sciences*, *116*(13), 6232–6237. doi:10.1073/pnas.1821304116

Luquet, G. C. & Minet, J. (1982). Découverte dans le vaucluse d'une nouvelle espèce de Pyrale et désignation de l'espèce-type du genre *Krombia* Chrétien (Lep. Crambidae Cybalomiinae). *Alexanor*, *12*(7), 317–326.

Mally, R., Hayden, J. E., Neinhuis, C., Jordal, B. H., & Nuss, M. (2019). The phylogenetic systematics of Spilomelinae and Pyraustinae (Lepidoptera: Pyraloidea: Crambidae) inferred from DNA and morphology. *Arthropod Systematics & Phylogeny*, *77*(1), 141–204. doi:10.26049/ASP77-1-2019-07

Mally, R., Léger, T., Vairappan, C. S., Sutton, S., & Nuss, M. (2017). Discovery of another fern-feeding group of moths: The larvae of Hoploscopini (Insecta: Lepidoptera: Pyraloidea) from Borneo. *Raffles Bulletin of Zoology*, *65*, 100–108.

Marion, H. (1955). Révision des Pyraustidae de la faune française (suite). *Revue française de Lépidoptérologie, Paris*, *15*(3), 181–188, 221–227.

Marion, H. (1962). Révision des Pyraustidae de France. Nouveau complément au genre *Scoparia*. *Alexanor*, *2*(6), 224–226, pl. 6.

Martínez, E. L. (2010). *A revision of the new world species of Donacaula Meyrick and a phylogenetic analysis of related Schoenobiinae (Lepidoptera: Crambidae)* (Doctoral dissertation, Mississippi State University, Mississippi).

Miller, M. A., Pfeiffer, W., & Schwartz, T. (2010). Creating the CIPRES Science Gateway for inference of large phylogenetic trees. In *Proceedings of the Gateway Computing Environments Workshop (GCE), 2010* (pp. 1–8). New Orleans. doi:10.1109/GCE.2010.5676129

Minet, J. (1982). Les Pyraloidea et leurs principales divisions systématiques (Lep. Ditrysia). *Bulletin de la Société entomologique de France*, *86*, 262–280.

Minet, J. (1983). Étude morphologique et phylogénétique des organes tympaniques des Pyraloidea. 1 - Généralités et homologies. (Lep. Glossata). *Annales de la Société Entomologique de France*, *19*(2), 175–207.

Minet, J. (1985). Étude morphologique et phylogénétique des organes tympaniques des Pyraloidea. 2- Pyralidae, Crambidae, première partie. (Lepidoptera, Glossata). *Annales de la Société entomologique de France*, (21), 69–86.

Minet, J. (1991). Tentative reconstruction of the ditrysian phylogeny (Lepidoptera: Glossata). *Insect Systematics & Evolution*, *22*(1), 69–95.

Minet, J. (2015). Lathrotelidae Clarke, 1971: A rehabilitated name deserving subfamily rank (Lepidoptera, Crambidae). *Bulletin de la Société entomologique de France*, *120*(1), 109–112.

Müller, J., Müller, K., Neinhuis, C., & Quandt, D. (2005). PhyDE-Phylogenetic Data Editor. http://www.phyde.de/.

Munroe, E. (1959). Revision of the genus *Linosta* Möschler (Lepidoptera: Pyralidae) with characterization of the subfamily Linostinae and a new subfamily. *The Canadian Entomologist, Ottawa*, (91), 485–488.

Munroe, E. (1961). Synopsis of the North American Odontiinae, with descriptions of new genera and species (Lepidoptera: Pyralidae). *Memoirs of the Entomological Society of Canada*, *93*(24), 1–93.

Munroe, E. (1972). Pyraloidea, Pyralidae comprising subfamilies Scopariinae, Nymphulinae. In *The Moths of America north of Mexico* (E. W. Classey and R. B. D. Publications Inc., Vol. 13.1.A & 13.1.B, pp. 1–134, 135–250). London.

Munroe, E. (1995). Crambidae (Crambinae, Schoenobiinae, Cybalomiinae, Linostinae, Glaphyriinae, Dichogaminae, Scopariinae, Musotiminae, Midilinae, Nymphulinae, Odontiinae, Evergestinae, Pyraustinae). In *Atlas of Neotropical Lepidoptera. Checklist: Part 2. Hyblaeoidea – Pyraloidea - Tortricoidea 3* (pp. 34–79). Gainesville: Association for Tropical Lepidoptera & Scientific Publishers.

Munroe, E. & Solis, M. A. (1998). The Pyraloidea. In *Lepidoptera, Moths and Butterflies. Volume 1: Evolution, systematics, and biogeography* (de Gruyter, Vol. IV Arthropoda: Insecta, pp. 233–256). Handbook of Zoology. Berlin.

Mutanen, M., Wahlberg, N., & Kaila, L. (2010). Comprehensive gene and taxon coverage elucidates radiation patterns in moths and butterflies. *Proceedings. Biological Sciences*, *277*(1695), 2839–2848. doi:10.1098/rspb.2010.0392

Nuss, M. (1998). The Scopariinae and Heliothelinae stat. rev. (Lepidoptera: Pyraloidea, Crambidae) of the Oriental Region - a revisional synopsis with descriptions of new species from the Philippines and Sumatra. *Nachrichten des entomologischen Vereins Apollo*, *suppl. 17*, 475–528.

Nuss, M. (1999). Revision der Gattungen der Scopariinae (Lepidoptera: Pyraloidea, Crambidae). *Nova Supplementa Entomologica, Berlin*, *13*, 3–151.

Nuss, M., Landry, B., Mally, R., Vegliante, F., Tränkner, A., Bauer, F., … Speidel, W. (2003–2019). Global Information System on Pyraloidea. - www.pyraloidea.org.

Passoa, S. (1988). Systematic positions of *Acentria ephemerella* (Denis & Schiffermüller), Nymphulinae, and Schoenobiinae based on morphology of immature stages (Pyralidae). *Journal of the Lepidopterists' Society*, *42*(4), 247–262.

Patrick, B. (1994). Antipodes Island Lepidoptera. *Journal of the Royal Society of New Zealand*, *24*(1), 91–116.

Pauli, J. N., Mendoza, J. E., Steffan, S. A., Carey, C. C., Weimer, P. J., & Peery, M. Z. (2014). A syndrome of mutualism reinforces the lifestyle of a sloth. *Proceedings of the Royal Society B: Biological Sciences*, *281*(1778), 20133006.

Powell, J. A., Mitter, C., & Farrell, B. (1998). Evolution of Larval Food Preferences in Lepidoptera. In *Handbook of Zoology. Part 35. Insecta, Lepidoptera, Moths and Butterflies* (Vol. 1: Evolution, Systematics and Biogeography, pp. 403–422). Berlin: deGruyter.

Rambaut, A., Drummond, A. J., Xie, D., Baele, G., & Suchard, M. A. (2018). Tracer (Version 1.7). Retrieved from http://tree.bio.ed.ac.uk/software/tracer/

Ratnasingham, S. & Hebert, P. D. N. (2007). BOLD: The barcode of life data system (http://www.Barcodinglife.org). *Molecular Ecology Notes*, *7*, 355–364.

Ratzka, A., Vogel, H., Kliebenstein, D. J., Mitchell-Olds, T., & Kroymann, J. (2002). Disarming the mustard oil bomb. *Proceedings of the National Academy of Sciences of the United States of America*, *99*(17), 11223–11228. doi:10.1073/pnas.172112899

Regier, J. C. (2007). Protocols, Concepts, and Reagents for preparing DNA sequencing templates. URL http://sites.biology.duke.edu/cunningham/pdfs/PCR_primers.pdf.

Regier, J. C., Mitter, C., Solis, M. A., Hayden, J. E., Landry, B., Nuss, M., … Cummings, M. P. (2012). A molecular phylogeny for the pyraloid moths (Lepidoptera: Pyraloidea) and its implications for higher-level classification. *Systematic Entomology*, *37*(4), 635–656. doi:10.1111/j.1365-3113.2012.00641.x

Regier, J. C., Mitter, C., Zwick, A., Bazinet, A. L., Cummings, M. P., Kawahara, A. Y., … Davis, D. R. (2013). A large-scale, higher-level, molecular phylogenetic study of the insect order Lepidoptera (moths and butterflies). *PLoS One*, *8*(3), e58568.

Regier, J. C., Shultz, J. W., Zwick, A., Hussey, A., Ball, B., Wetzer, R., … Cunningham, C. W. (2010). Arthropod relationships revealed by phylogenomic analysis of nuclear protein-coding sequences. *Nature*, *463*, 1079. doi:10.1038/nature08742

Regier, J. C., Zwick, A., Cummings, M. P., Kawahara, A. Y., Cho, S., Weller, S., … Parr, C. (2009). Toward reconstructing the evolution of advanced moths and butterflies (Lepidoptera: Ditrysia): An initial molecular study. *BMC Evolutionary Biology*, *9*(1), 280. doi:10.1186/1471-2148-9-280

Renuka, P., Madhav, M. S., Padmakumari, A. P., Barbadikar, K. M., Mangrauthia, S. K., Vijaya Sudhakara Rao, K., … Ravindra Babu, V. (2017). RNA-seq of Rice Yellow Stem Borer *Scirpophaga incertulas* Reveals Molecular Insights During Four Larval Developmental Stages. *G3: Genes—Genomes—Genetics*, *7*(9), 3031–3045. doi:10.1534/g3.117.043737

Robinson, G. S., Ackery, P. R., Kitching, I. J., Beccaloni, G. W., & Hernández, L. M. (2010). *HOSTS—a Database of the World's Lepidopteran Hostplants*. London: Natural History Museum.

Robinson, G. S., Tuck, K. R., & Shaffer, M. (1994). *A field guide to the smaller moths of South-East Asia*. London: Natural History Museum.

Roepke, W. (1916). Eine neue myrmekophile Lepidoptere aus Java (*Wurthia mymecophila* ngn sp.) *Zoologische Mededelingen*, *2*(15), 141–146.

Roesler, R. U. (1973). *Phycitinae. Microlepidoptera Palaearctica* (G. Fromme). Vienna: H.G. Amsel, F. Gregor, H. Reisser and G. Fromme.

Schmid, J. (2019). *Kleinschmetterlinge der Alpen* (Haupt-Verlag).

Schütze, K. T. (1931). Die Biologie der Kleinschmetterlinge unter besonderer Berücksichtigung ihrer Nährpflanzen und Erscheinungszeiten. In *Handbuch der Microlepidopteren. Raupenkalender-geordnet nach der Illustrierten deutschen Flora* (pp. 1–235). Frankfurt am Main: Verlag des Internationalen Entomologischen Vereins e. V.

Seín, F. (1930). The sugar cane root caterpillar and other new root pests in Puerto Rico. *Journal of the Department of Agriculture of Porto Rico, Rio Piedras*, *14*(3), 167–191, pl. 20–29.

Simmons, M. P. (2012). Misleading results of likelihood-based phylogenetic analyses in the presence of missing data. *Cladistics*, *28*(2), 208–222. doi:10.1111/j.1096-0031.2011.00375.x

Solis, M. A. & Adamski, D. (1998a). Review of the Costa Rican Glaphyriinae (Lepidoptera: Pyraloidea: Crambidae). *J. N.Y. Entomol. Soc. 106*, 1–55.

Solis, M. A. & Adamski, D. (1998b). Review of the Costa Rican Glaphyriinae (Lepidoptera: Pyraloidea: Crambidae). *Journal of the New York Entomological Society*, *106*(1), 1–55.

Solis, M. A., Hayden, J. E., Sanabria, F. V., Gonzalez, F., Ujueta, C. S., & Gulbronson, C. J. (2019). A New Species of *Sufetula* Walker (Lepidoptera: Crambidae) Feeding on the Roots of Pineapple, *Ananas comosus* (l.)(bromeliaceae), from Costa Rica. *Proceedings of the Entomological Society of Washington*, *121*(3), 497–510. doi:10.4289/0013-8797.121.3.497

Solis, M. A. & Maes, K. (2002). Preliminary phylogenetic analysis of the subfamilies of Crambidae (Pyraloidea: Lepidoptera). *Belgian Journal of Entomology*, *4*, 53–95.

Solis, M. A. & Mitter, C. (1992). Review and preliminary phylogenetic analysis of the subfamilies of the Pyralidae (sensu stricto) (Lepidoptera: Pyraloidea). *Systematic Entomology*, *17*, 79–90.

Stamatakis, A. (2006). RAxML-VI-HPC: Maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics*, *22*(21), 2688–2690. doi:10.1093/bioinformatics/btl446

Tadle, F. P. T. (2017). *Choice of feeding sites, growth and survival by Crocidolomia pavonana (f.)* (Doctoral dissertation, University of Queensland, Brisbane).

Toussaint, E. F. A., Breinholt, J. W., Earl, C., Warren, A. D., Brower, A. V., Yago, M., ... Lohman, D. J. (2018). Anchored phylogenomics illuminates the skipper butterfly tree of life. *BMC evolutionary biology*, *18*(1), 101. doi:10.1186/s12862-018-1216-z

Wahlberg, N. & Wheat, C. W. (2008). Genomic outposts serve the phylogenomic pioneers: Designing novel nuclear markers for genomic DNA extractions of Lepidoptera. *Systematic Biology*, *57*(2), 231–242. doi:10.1080/10635150802033006

Weintraub, J. D., Lawton, J. H., & Scoble, M. J. (1995). Lithinine moths on ferns: A phylogenetic study of insect-plant interactions. *Biological Journal of the Linnean Society*, *55*(3), 239–250.

Wickett, N. J., Mirarab, S., Nguyen, N., Warnow, T., Carpenter, E., Matasci, N., ... Gitzendanner, M. A. (2014). Phylotranscriptomic analysis of the origin and early diversification of land plants. *Proceedings of the National Academy of Sciences*, *111*(45), E4859–E4868.

Wilkinson, M. (1994). Common cladistic information and its consensus representation: Reduced Adams and reduced cladistic consensus trees and profiles. *Systematic Biology*, *43*, 343–368.

Wittstock, U., Agerbirk, N., Stauber, E. J., Olsen, C. E., Hippler, M., Mitchell-Olds, T., … Vogel, H. (2004). Successful herbivore attack due to metabolic diversion of a plant chemical defense. *Proceedings of the National Academy of Sciences of the United States of America*, *101*(14), 4859–4864. doi:10.1073/pnas.0308007101

Ye, F., Shi, Y., Xing, L., Yu, H., & You, P. (2013). The complete mitochondrial genome of *Paracymoriza prodigalis* (Leech, 1889)(Lepidoptera), with a preliminary phylogenetic analysis of Pyraloidea. *Aquatic insects*, *35*(3), 71–88. doi:10.1080/01650424.2014.948456

Yoshiyasu, Y. (1985). A systematic study of the Nymphulinae and the Musotiminae of Japan (Lepidoptera: Pyralidae). *Scientific Report of Kyoto Prefectural University, Agriculture*, *37*, 1–162.

Chapter 3

Discovery of another fern-feeding group of moths: the larvae of Hoploscopini (Insecta: Lepidoptera: Pyraloidea) from Borneo.

RAFFLES BULLETIN OF ZOOLOGY **65**: 100–108
Date of publication: 24 May 2017
http://zoobank.org/urn:lsid:zoobank.org:pub:9B3F66A2-2939-48AB-B8E8-FBF63C8235CF

Discovery of another fern-feeding group of moths: the larvae of Hoploscopini (Insecta: Lepidoptera: Pyraloidea) from Borneo

Richard Mally[1*], Théo Léger[2], Charles S. Vairappan[3], Stephen Sutton[3] & Matthias Nuss[2]

Abstract. We report the discovery of Hoploscopini larvae (Lepidoptera: Crambidae: Heliothelinae) on ferns at the southern slopes of Mount Kinabalu (Sabah, Borneo). The COI barcode of the larvae assigns them to the genus *Hoploscopa*. We provide the first detailed description of the larval stage for this tribe. Among Crambidae, these larvae are most similar to Crambinae larvae but differ in the presence of two L setae on A9, a character state that is present in Acentropinae and Schoenobiinae. We discuss the presence and distribution of L setae on A9 in Crambidae. Our observations of these larvae on this host plant and published host plant data support our hypothesis that larvae of the entire tribe Hoploscopini may be fern-feeders.

Key words. larva, chaetotaxy, *Hoploscopa*, fern, DNA barcoding

INTRODUCTION

Hoploscopini is comprised of two genera, *Hoploscopa* Meyrick, 1886 and *Perimeceta* Turner, 1915, with a total of 20 described and more than 60 undescribed species in the Oriental Region, Wallacea, New Guinea and northern Queensland (Robinson et al., 1994; Nuss, 1998, 1999; Nuss et al., 2003–2016). Hoploscopini are still poorly studied, and preimaginal stages as well as larval food plants were unknown until very recently (Miller et al., 2015), but had not been assigned to this tribe. The nocturnal adults are recorded from mountainous habitats and are attracted by artificial light. The forewing length of the moths ranges from 7 to 10 mm in *Hoploscopa* and from 11 to 13 mm in *Perimeceta*. Forewing colouration is reddish-brown with various markings of diagonal stripes, ellipses, or silvery spots (Robinson et al., 1994; Nuss, 1998).

The classification of the group is somewhat controversial. Robinson et al. (1994) established the Hoploscopini within Scopariinae without an explanation for doing so, but Nuss (1998) pointed to the lack of synapomorphies supporting this grouping. Later, Hoploscopini were included in Heliothelinae based on the conspicuous, inwardly directed spine in the corpus bursae of the female genitalia (Nuss, 1998, 1999). The Heliothelinae, originally established as a tribe within Scopariinae (Amsel, 1961) and later elevated to subfamily rank by Minet (1982), were subsequently synonymised with Scopariinae by Munroe & Solis (1998) and retained in synonymy by Solis & Maes (2003). Future phylogenetic analyses may show whether one of these or even another classification might be supported.

The objective of this paper is to record the discovery of five hoploscopine larvae on fern fronds at Mount Kinabalu (Sabah, Borneo) and to compare these findings with the available information of food plants of Hoploscopini.

MATERIAL & METHODS

Five larvae were found on Mount Kinabalu at an altitude of 1,680 m during the night of 13 June 2015 sitting on the undersides of fern fronds, which were unfolded and unwebbed. They were taken with the plants on which they were found for rearing purposes down to Kota Kinabalu at sea level, where rearing efforts were continued using fern species from the lowlands. None of the larvae accepted this alteration in food, climate, and elevation, and all the larvae died. Two of the larvae were kept in 96% natural ethanol for subsequent morphological and genetic analyses and are deposited at the University Museum of Bergen, Norway.

Genetic analysis was performed by extraction of DNA from the whole body of one of the larvae using Qiagen's DNEasy blood & tissue kit. PCR amplification of the DNA barcoding region of the mitochondrial cytochrome C oxidase subunit I (COI) gene was done using the primers LCO (Folmer et al., 1994) and Nancy (Wahlberg & Wheat, 2008) in combination with a universal T7/T3 tail (Wahlberg & Wheat, 2008). We used 25 µl of PCR volume containing 0.75u TaKaRa Ex Taq Hot-Start DNA polymerase, 2.5 µl 10 × buffer, 400 nM of each primer, 800 nM dNTP mix and 2 µl DNA extract.

---

[1] University Museum of Bergen, Natural History Collections, Realfagbygget, Allégaten 41, 5007 Bergen, Norway; Email: richard.mally@uib.no (*corresponding author)

[2] Senckenberg Naturhistorische Sammlungen Dresden, Museum für Tierkunde, Königsbrücker Landstraße 159, 01109 Dresden, Germany; Email: theo.leger@senckenberg.de (TL), matthias.nuss@senckenberg.de (MN)

[3] Institute for Tropical Biology and Conservation, Universiti Malaysia Sabah, Jalan UMS, 88400 Kota Kinabalu, Sabah, Malaysia; Email: csvairappan@gmail.com (CSV); stephensutton7@gmail.com (SS)

ISSN 2345-7600 (electronic) | ISSN 0217-2445 (print)

Cycling conditions were as follows: initial denaturation for 5 min at 95°C, 40 cycles with (1) 30 s at 95°C, (2) 30 s at 48°C, (3) 90 s at 70°C, final extension of 10 min at 70°C. PCR success was evaluated via gel electrophoresis on a 1% agarose gel using GelRed (Biotium). For clean-up of the successfully amplified PCR products, 0.5u of each the Exonuclease (Exo) and Shrimp Alkaline Phosphatase (SAP) enzymes were added to 8 µl of PCR product and the mixture was incubated in a thermocycler for 15 min at 37°C before inactivating the enzymes for 30 min at 80°C. The sequencing PCR was performed with BigDye, using 160 nM of T7/T3 sequencing primers and 0.5–2 µl PCR product. Sequencing was done at the Sequencing Facility, University of Bergen.

The alignment of the DNA sequence data was done with PhyDE version 0.9971 (Müller et al., 2010). MEGA 7 (Kumar et al., 2016) was used to find the best-fitting DNA model, which resulted in the GTR+G+I model. A Maximum Likelihood (ML) analysis of the sequence data was done with RAxML 7.4.2 (Stamatakis, 2006), using the raxmlGUI 1.3 interface (Silvestro & Michalak, 2012). The ML analysis included a bootstrap test with 1,000 replications. The resulting ML tree was edited in TreeGraph version 2.11.1-654 beta (Stöver & Müller, 2010). We used the BIN numbers of the Barcode of Life Database (BOLD, http://v4.boldsystems.org; Ratnasingham & Hebert, 2007) as DNA-barcoded taxa may not have been identified to species level.

In addition to the "BC MTD" Barcode samples provided by MN, BOLD was mined for further relevant records. Due to the different opinions regarding the classification of Hoploscopini we included Scopariinae in our search.

After DNA extraction, the exoskeleton of the larva was cut laterally, flattened, and preserved together with the head capsule in Euparal on a microscopic slide for further examination. The second larva was left intact in order to study the length and direction of the setae. Terminology of larval morphology, especially chaetotaxy, follows Hasenfuss (1963). Thoracic segments are abbreviated as T1–T3, abdominal segments as A1–A10. Drawings were done using Adobe Illustrator CS6, version 16.0.3.

The larval food plant was identified using Raciborski (1898) and Beaman & Edwards (2007).

RESULTS

A total of five individuals of larvae were found on fern fronds at 1,680 m altitude on the southern slope of Mount Kinabalu in Mesilau (see Fig. 1 for two of the larvae). Weather conditions were cloudy, but not rainy, with high humidity and temperature at about 20°C.

Material examined. Two larvae: Malaysia, Sabah, Mount Kinabalu National Park, Mesilau, western edge of Mount Kinabalu Golf Club, 6°01′38″N 116°35′32″E, 1,680 m, 13.vi.2015, leg. Théo Léger & Richard Mally (University Museum of Bergen, Norway).

Fig. 1. Two *Hoploscopa* larvae (centre and right) on the underside of a fragment of their food plant, *Dicranopteris linearis* (Burman, 1768) Underwood, 1907. Scale: one square measures 5 mm.

Molecular identification of the larva. Sequencing of one of the larvae yielded a 655 bp fragment of the 5′ part of the COI gene. A search for similar sequences with the NCBI nucleotide blast tool resulted in a closest match with three specimens of "Scopariinae sp." originating from Papua New Guinea (Miller et al., 2015). The corresponding images of these specimens on BOLD allowed us to identify these three and another seven specimens, altogether forming four barcode-species, as belonging to the genus *Hoploscopa*, and the information was corrected accordingly in the BOLD database.

Subsequently, we analysed all sequences available for *Hoploscopa* and *Perimeceta* available to us on BOLD in a ML analysis. The species whose larva we describe here is sister to the species pair *Hoploscopa* AAU5240 + *Hoploscopa* AAU5241, both from North Sumatra (Sumatera Utara), in the ML tree (Fig. 3). The adult *Hoploscopa* specimens that we collected in Mount Kinabalu National Park (see Fig. 2 for representatives) appear as five separate species (BOLD BINs ADE1420, ADE3896, ADE3897, ADE4123 and ADE4125 in Table 1 and Fig. 3). The larvae could not be matched to any of the adults of the 15 DNA-barcoded species of *Hoploscopa* (Fig. 3).

Perimeceta, the other genus of Hoploscopini with four species included in this analysis, is sister to *Hoploscopa* in the ML tree (Fig. 3).

All included COI barcode sequences (Table 1) are publicly available on NCBI's GenBank and the European Nucleotide Archive (ENA) via the accession numbers as well as on BOLD.

Morphological description of the larvae. The larvae are identified as Pyraloidea by the presence of two setae in the prespiracular group of the prothorax and three subventral setae on abdominal segments 3 to 6 as well as by the crochets forming a complete circle (Solis, 2006).

In the larval key on European Pyraloidea by Hasenfuss (1960), our larvae are identified as Crambidae ("Crambinae" sensu Hasenfuss, 1960), but they match none of the treated subgroups in this family. The closest similarity is found with Crambinae ("Crambini" sensu Hasenfuss, 1960), agreeing

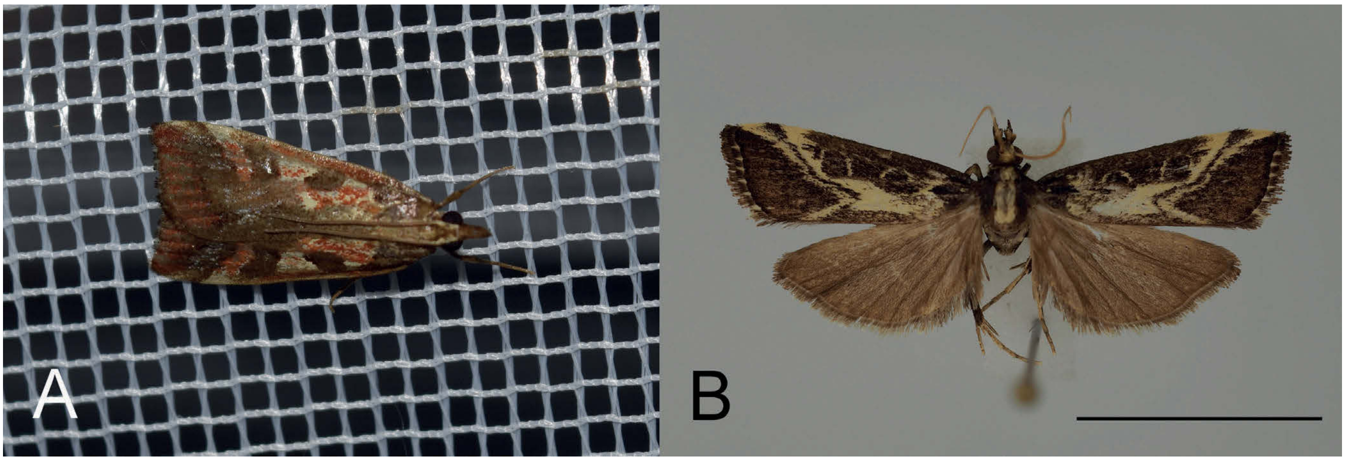


Fig. 2. Adult specimens of *Hoploscopa* from Mount Kinabalu. A, an unidentified specimen taken on 05 June 2015 at night by T. Léger near Mount Kinabalu park headquarters; B, specimen BC MTD Lep 03004 of *Hoploscopa* ADE1420 from the genetic analysis, abdomen removed for DNA extraction and genitalia dissection. Note that neither of the two adult specimens is conspecific with the described larvae. Scale: A, one mesh square measures 1.2 × 1.2 mm; B, scale bar measures 10 mm.

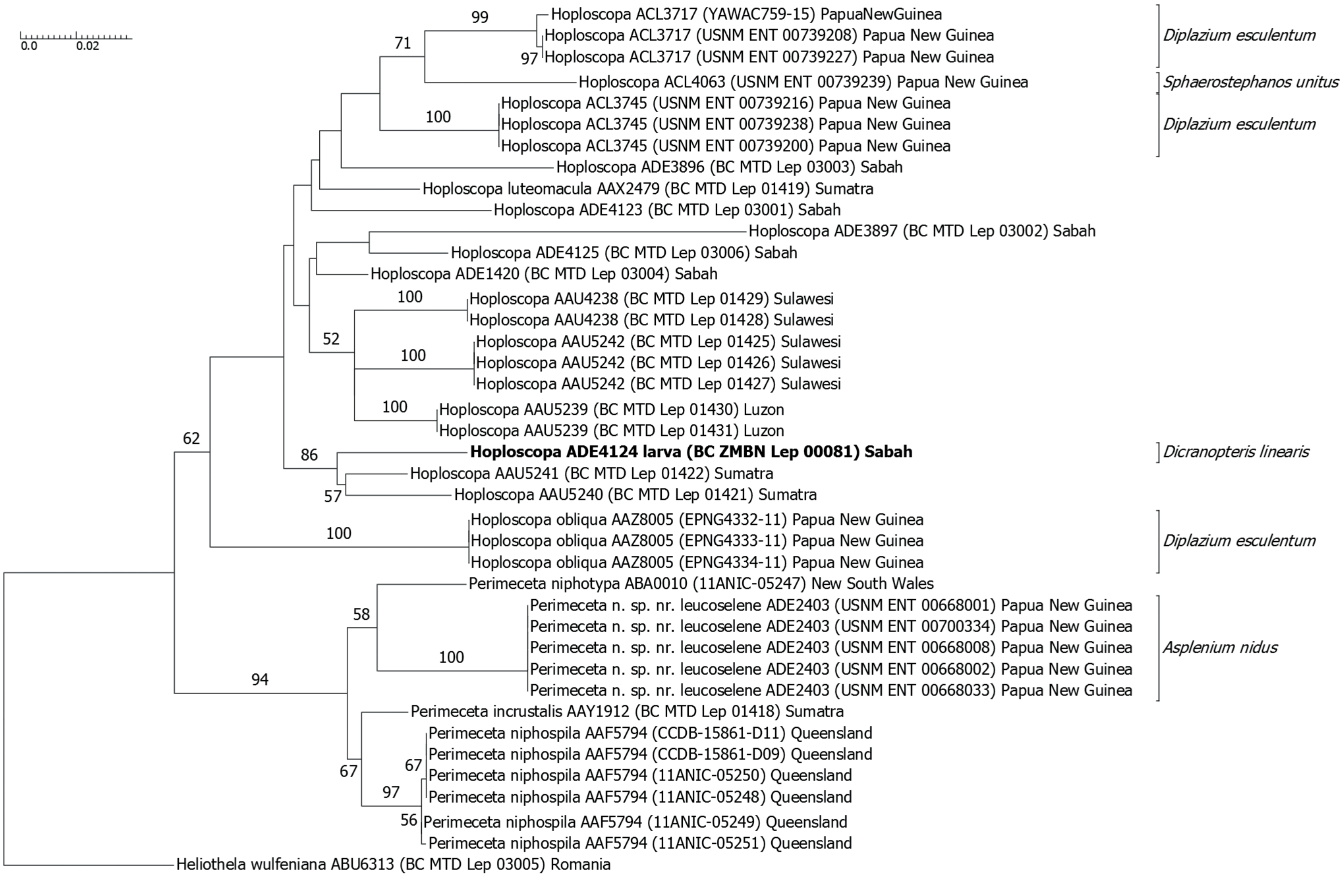


Fig. 3. Maximum likelihood tree of Hoploscopini DNA barcodes (549–654 bp), based on the GTR+G+I model, with *Heliothela wulfeniana* (Heliothelini; 509 bp) as outgroup and the sequenced larva from Mount Kinabalu marked in bold. BOLD BIN numbers are indicated behind the taxon names, followed by the BOLD Sample ID in brackets, and the geographical origin of the sample. Known host plants are indicated on the right; the numbers above the branches represent bootstrap values ≥ 50% based on 1,000 bootstrap replicates. Scale bar represents number of substitutions per site.

in these character states with Hasenfuss' (1960) diagnosis: epicranial index 1–1.7; adfrontals span max half of the length of the coronal suture; AF2 more ventral than P2; stemma 5 posterodorsal of stemma 6; stemmata 4–6–5 in a sharp to right angle; O3 ventral of line connecting stemmata 4 and 5; O3 considerably closer to SO3 than to O2; O1–O2–O3 in a sharp to right angle; A1 with XD2–SD1–SD2 in a right to obtuse angle; L2 macroscopic on meso- and metathorax; abdominal legs normal developed, crochets with two to three hook rows; A1–8 with distance D2–D2 considerably longer than D1–D1, and L1 posterodorsal of L2; on A8 the stigma is located caudal of the lines connecting D1 and SD1 as well as SD1 and L1; A9 with D1 near to and anterodorsally to DS1, and D2 of both sides on a single pinaculum; well developed

Table 1. Samples of DNA barcoded specimens included in this study. For taxa without species identification the respective BOLD BIN number was used as species epithet.

Taxon	BOLD BIN (No. of Sampled Specimens)	Geographical Origin	GenBank Accession Number	BOLD Sample ID
Heliothela wulfeniana	ABU6313 (n = 1)	Romania	KY080439	BC MTD Lep 03005
Hoploscopa luteomacula	AAX2479 (n = 1)	Indonesia, Sumatra	KX843698	BC MTD Lep 01419
Hoploscopa obliqua	AAZ8005 (n = 3)	Papua New Guinea	KX783025 KX783026 KX783027	USNM ENT 00665932 USNM ENT 00514750 USNM ENT 00514731
Hoploscopa ADE4124	ADE4124 (n = 1)	Malaysia, Sabah	KY080442	BC ZMBN Lep 00081
Hoploscopa AAU5242	AAU5242 (n = 3)	Indonesia, Sulawesi	JN272552 JN272553 JN272554	BC MTD Lep 01425 BC MTD Lep 01426 BC MTD Lep 01427
Hoploscopa AAU5239	AAU5239 (n = 2)	Philippines, Luzon	JN272557 JN272558	BC MTD Lep 01430 BC MTD Lep 01431
Hoploscopa AAU4238	AAU4238 (n = 2)	Indonesia, Sulawesi	JN272555 JN272556	BC MTD Lep 01428 BC MTD Lep 01429
Hoploscopa ADE4125	ADE4125 (n = 1)	Malaysia, Sabah	KY080444	BC MTD Lep 03006
Hoploscopa ADE1420	ADE1420 (n = 1)	Malaysia, Sabah	KY080440	BC MTD Lep 03004
Hoploscopa AAU5240	AAU5240 (n = 1)	Indonesia, Sumatra	JN272550	BC MTD Lep 01421
Hoploscopa AAU5241	AAU5241 (n = 1)	Indonesia, Sumatra	JN272551	BC MTD Lep 01422
Hoploscopa ADE4123	ADE4123 (n = 1)	Malaysia, Sabah	KY080441	BC MTD Lep 03001
Hoploscopa ADE3896	ADE3896 (n = 1)	Malaysia, Sabah	KY080445	BC MTD Lep 03003
Hoploscopa ACL3745	ACL3745 (n = 3)	Papua New Guinea	KP850086 KP850401 KP850535	USNM ENT 00739216 USNM ENT 00739238 USNM ENT 00739200
Hoploscopa ACL4063	ACL4063 (n = 1)	Papua New Guinea	KP850867	USNM ENT 00739239
Hoploscopa ACL3717	ACL3717 (n = 3)	Papua New Guinea	KP850187 KP850609 KX842727	USNM ENT 00739208 USNM ENT 00739227 YAWCATCR0759
Hoploscopa ADE3897	ADE3897 (n = 1)	Malaysia, Sabah	KY080443	BC MTD Lep 03002
Perimeceta incrustalis	AAY1912 (n = 1)	Indonesia, Sumatra	KX843699	BC MTD Lep 01418
Perimeceta niphospila	AAF5794 (n = 6)	Australia, Queensland	KF388782 KF391745 JN272547 JN272548 KF390107 KF392415	11ANIC-05248 11ANIC-05249 11ANIC-05250 11ANIC-05251 CCDB-15861-D09 CCDB-15861-D11

Taxon	BOLD BIN (No. of Sampled Specimens)	Geographical Origin	GenBank Accession Number	BOLD Sample ID
Perimeceta niphotypa	ABA0010 (n = 1)	Australia, New South Wales	KF391291	11ANIC-05247
Perimeceta sp. near *leucoselene*	ADE2403 (n = 5)	Papua New Guinea	KY034067 KY034068 KY034066 KY034070 KY034069	USNM ENT 00668001 USNM ENT 00668002 USNM ENT 00668008 USNM ENT 00668033 USNM ENT 00700334

anal plate; A10 with distance II–II smaller than or equal to II–III, IIIa macroscopic. Our larvae differ from Hasenfuss' (1960) diagnosis of Crambinae in these character states: AF2 lateral of bifurcation of epicranial suture (instead of more dorsal than bifurcation); A1 with only two SV setae (instead of three); A9 with L2 present (instead of absent); distance V1–V1 on A10 larger than on A9 (instead of smaller); and on A10 distance V1–VIId smaller than VIIc–VIIb (instead of larger).

Head. (Fig. 4) Orthognathous, brown; epicranial suture present; vertex with microsetae V1–3 in a line; pore Va variable in position, slightly lateral between V2 and V3 or lateral of V3; front with P1 close to AF1, P2 between P1 and V1, pore Pb ventral of P2, pore Pa in the centre of P1, L1 and A3; AF1 slightly dorsal of the centre of adfrontal area, AF2 at level of lower end of central suture, pore AFa between AF1 and AF2, closer to AF2; F1 ventral of AFa halfway of dorsoventral expanse of the frontal area, pore Fa medioventral of F1; ventral clypeus margin slightly undulated, C1 on lateral end, C2 halfway between C1 and sagittal plane dorsal of slight ventrad protrusion; A1, A2 and A3 in an arched line, distance A2–A3 approximately twice the distance A1–A2; L1 central on lateral head, pore La posterodorsal of L1; microseta G1 at level of P1 and L1, pore Ga anteroventral of G1; six stemmata in an oval semicircle, O1 in its centre, O2 posterior of stemma 1, O3 well posterior of stemma 6, pore Oa posteroventral of stemma 6; SO1 ventral of stemma 5 posterior of antennal socket, SO2 ventral of stemma 6, SO3 ventral of pore Oa, pore SOa anterior of SO3.

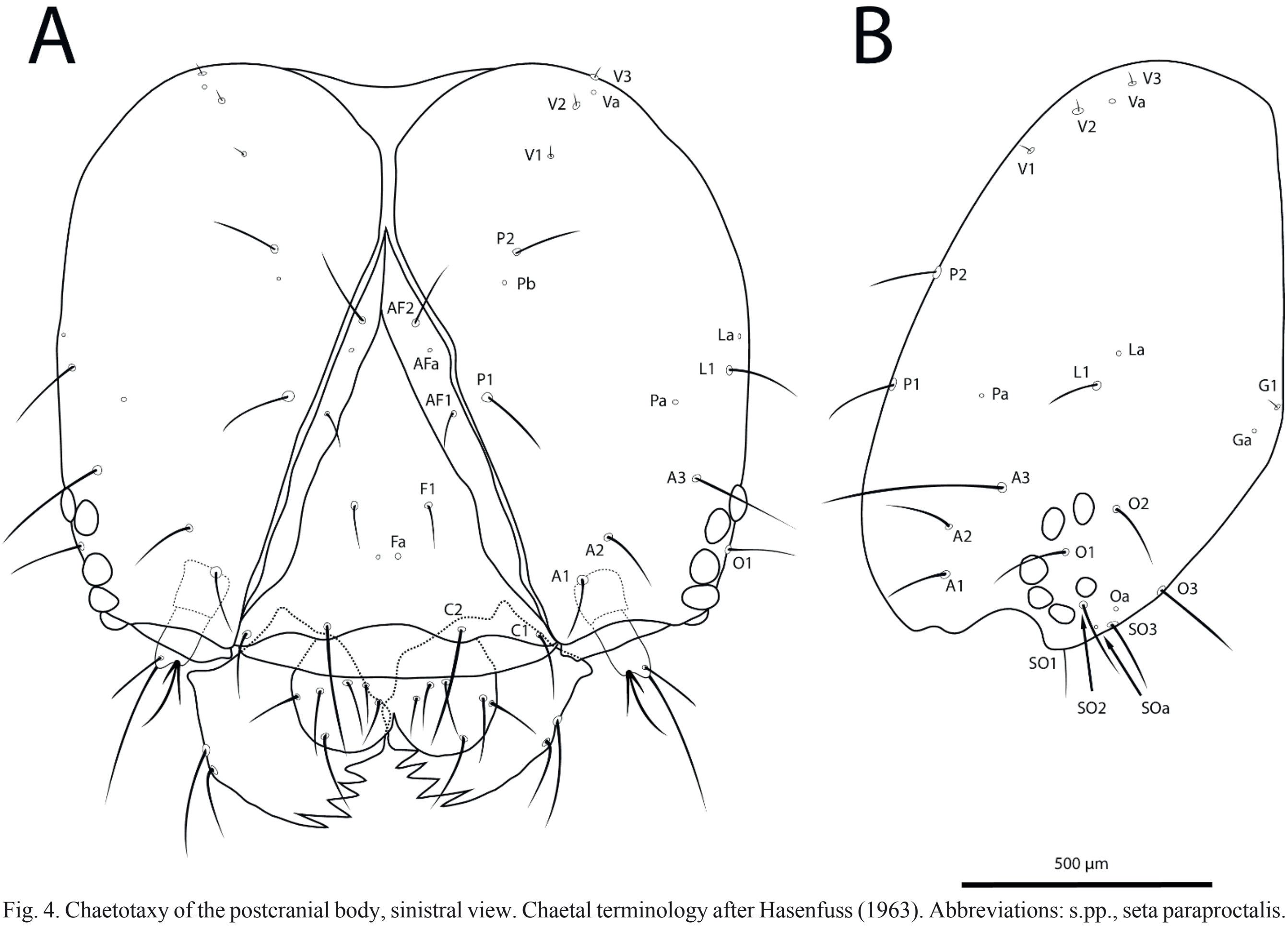


Fig. 4. Chaetotaxy of the postcranial body, sinistral view. Chaetal terminology after Hasenfuss (1963). Abbreviations: s.pp., seta paraproctalis.

Thorax. (Fig. 5) Prothoracic and prespiracular shield as well as dorsal, subdorsal and lateral pinacula strongly sclerotised, black, subventral and ventral pinacula less so. Prothoracic shield with roughly equally long D1 and D2, XD1, XD2, SD1 and SD2, three pores (a–c) present, pore a posterodorsal and pore b posterior of XD1, pore c dorsal of XD2, microseta MXD1 at posterior edge of prothoracic shield between D1 and D2; prespiracular shield anterior to spiracle bisetose (L1–2), extending posteroventrally around spiracle; subventral pinaculum bisetose (SV1–2); coxa of prothoracic leg with five setae, MV2 microseta on anterodorsal end of coxal band, MV3 microseta between the two anterior coxal macrosetae, a third microseta posterodorsally close to posterior coxal macroseta; V1 posteroventral of leg. T2 and T3 identical: bisetose dorsal and subdorsal pinacula (D1+D2, SD1+SD2), D2 about twice the length of D1; MD1 microseta anterior of D2, MSD1–2 microsetae anteroventral of subdorsal pinaculum; two lateral pinacula with anterior bisetose (L1+L2) and the posterior unisetose (L3), posterior lateral pinaculum including L3 is missing on one body side in one of the two investigated specimens; subventral pinacula unisetose (SV1); coxal band with MV2 and MV3 as in prothorax, plus MV1 microseta anterodorsally of MV2; V1 posteroventral of leg.

Abdomen. (Fig. 5) A1–8: Two unisetose (D1, D2) dorsal pinacula and the unisetose (SD1) subdorsal pinaculum strongly sclerotised, subventral pinacula less so; D1, D2 and SD1 about the same length; MD1 microseta anterior to D2 on anterior segment edge; SD2 microseta anterior of spiracle; two lateral pinacula below spiracle, anterodorsal one bisetose (L1–2), the posteroventral unisetose (L3), setae of approximately equal length; subventral group bisetose (SV1, SV3) in A1 and A7, trisetose (SV1–3) in A2 and A3–6 (at anteriodorsal base of prolegs), and unisetose (SV1) in A8 and A9, SV1–2 are absent on left side of A4 in one larva; V1 at posteromedial end of abdominal segments; MV3 microseta on anterior segment edge between subventral group and V1. A9 with a large unpaired dorsal pinaculum covering the dorsum, bearing one long seta (D2) on each side; subdorsal pinaculum trisetose (D1, SD1, L2), with SD1 in a less strongly sclerotised semicircular part of pinaculum; MD1 on anterior segment edge between dorsal and subdorsal pinaculum; lateral pinaculum unisetose (L1); one subventral (SV1) and one ventral (V1) seta, with MV3 on anterior segment edge between SV1 and V1. Unpaired anal shield (segment A10) with four setae (I, II, III, IIIa) on each side, seta I being the shortest; short Seta paraproctalis (S.ppr.) posteroventral of anal shield on dorsal tip of a lanceolate, weakly sclerotised area; V1 close to ventral base of terminal legs. Prolegs on A3–6 with crochets in a complete circle of three concentric rows of outward-directed hooks, the outer circle bearing the shortest hooks and the inner circle the longest; prolegs on A10 forming a semicircle.

Food plant records. The larvae were found on *Dicranopteris linearis* (Burman, 1768) Underwood, 1907 (Gleicheniaceae; Fig. 6). The larvae were sitting on the underside of intact fronds, which did not show any traces of frass. In captivity, they fed on this plant species from the outer edge of the pinnate leaves towards the mid-ribs (Fig. 1). After we left the collecting area at 1,680 m we continued to feed the caterpillars with non-Gleicheniaceae ferns growing in the lowland of Kota Kinabalu, but these were rejected and the larvae died.

The search for related species on BOLD resulted in the recognition of five barcoded Hoploscopinae species collected in Yawan, Papua New Guinea which are found to feed on ferns as well: *Hoploscopa* ACL3745, *Hoploscopa* ACL3717 and *Hoploscopa obliqua* (Rothschild, 1915) feed on *Diplazium esculentum* (Retzius in Retzius & König, 1791) Swartz, 1803 (Athyriaceae), *Hoploscopa* ACL4063 feeds on *Sphaerostephanos unitus* (Linnaeus, 1759) Holttum, 1794 (Thelypteridaceae), and *Perimeceta* sp. near *leucoselene* (Hampson, 1919) feeds on *Asplenium nidus* Linnaeus, 1753 (Aspleniaceae) (S. Miller, C. Redmond & T. Whitfield, pers. comm.; Botanical Research Institute of Texas, 2003–2009).

DISCUSSION

All known larval host plant records for Hoploscopinae belong to six species, and all are included in our analysis (Fig. 3). The larvae are feeding on fern species of

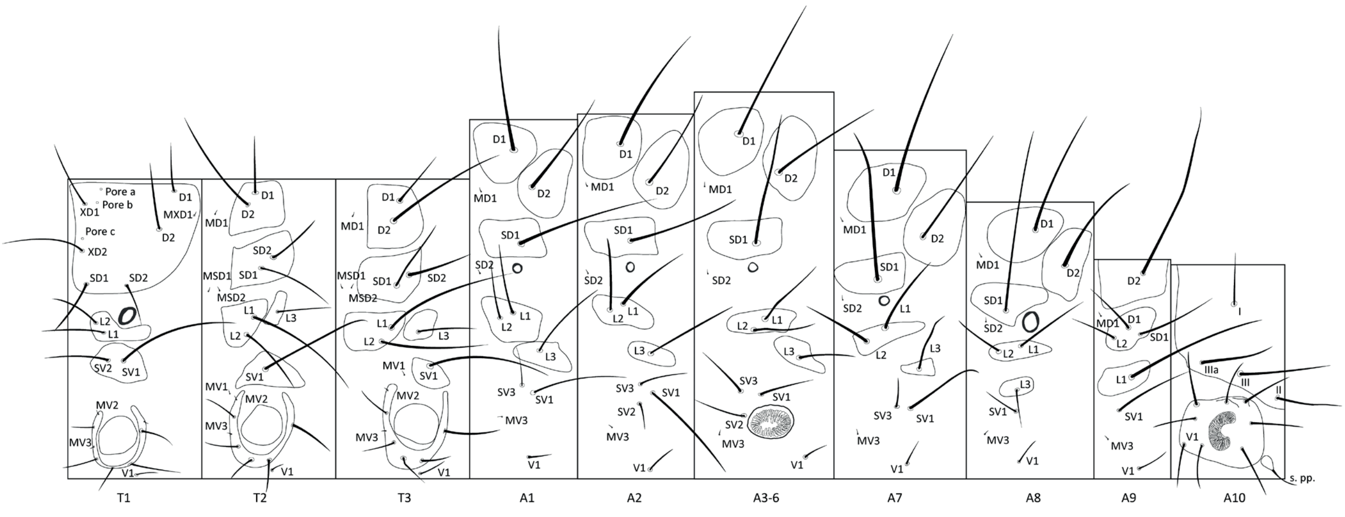


Fig. 5. Chaetotaxy of the postcranial body, sinistral view. Chaetal terminology after Hasenfuss (1963). Abbreviations: s.pp., seta paraproctalis.

Fig. 6. *Dicranopteris linearis* (Burman, 1768) Underwood, 1907, the food plant of the investigated *Hoploscopa* larvae; photo taken at the collecting site of the larvae.

Gleicheniaceae (Gleicheniales), Aspleniaceae, Athyriaceae or Thelypteridaceae (all three Polypodiales). These repeated findings from ferns as food plants suggest that Hoploscopini are fern feeders. This fern-feeding habit contrasts with the feeding habit of the supposed sister-group Heliothelini. For one of its species, *Heliothela wulfeniana* (Scopoli, 1763), the angiosperm genera *Viola* Linnaeus, 1753 (Violaceae) and *Mentha* Linnaeus, 1753 (Lamiaceae) are recorded as larval food plants (Nuss, 2005). Other fern-feeders among Crambidae are known in Musotiminae (e.g. Munroe, 1972; Kirk, 1978; Phillips & Solis, 1996; Solis et al., 2004, 2005a, 2005b; Yen et al., 2004), in *Phenacodes* Turner, 1937, treated in Scopariinae by Munroe (1958) and Munroe & Solis (1998), and provisionally placed in Cybalomiinae by Nuss (1999), and in the Spilomelinae *Herpetogramma sphingealis* Handfield & Handfield, 2011, *H. aeglealis* (Walker, 1859) and *H. platycapna* (Meyrick, 1897) (Kirk, 1978; Solis, 2008; Handfield & Handfield, 2011), *Diasemiopsis ramburialis* (Duponchel, 1833) (Farahpour-Haghani et al., 2016) and *Udea decrepitalis* (Herrich-Schäffer, 1848) (Lhomme, 1935).

Based on the diagnostic characters of the chaetotaxy provided by Hasenfuss (1960), the Crambinae are the group that shares the most larval similarities with *Hoploscopa*. One character that differs in *Hoploscopa* is the presence of an L2 seta on A9, grouped on a pinaculum together with D1 and SD1. Among Crambidae, a second L seta on A9 is yet only known to occur in Acentropinae (Hasenfuss, 1960, 1963) and Schoenobiinae (Passoa & Habeck, 1987; Passoa, 1988). This character state may turn out to be a synapomorphy for a group comprising Acentropinae, Schoenobiinae and Hoploscopini. A comprehensive comparison of the chaetotaxy of all crambid subfamilies is currently not possible, as descriptions of larvae of Cathariinae, Lathrotelinae, Linostinae, Midilinae, and Heliothelini are still lacking.

The molecular data analysis reveals 16 DNA barcode-species for *Hoploscopa*. This is precisely the number of species so far described in the genus, but some known species are recorded from other geographical places (Nuss et al., 2003–2016) and therefore at least some of them are probably not conspecific with those included in our analysis. This, as well as the long terminal branches of some taxa in our analysis, point to a large proportion of still undescribed species in *Hoploscopa*, and in fact Robinson et al. (1994) already report more than 50 undescribed species of *Hoploscopa* based on material in entomological collections. The inability to link the larvae from Mount Kinabalu with any of the collected adults during the same field trip suggests that different *Hoploscopa* species on Mount Kinabalu may have different flight times, or species may not be attracted by artificial light. Future study of altitudinal and chronological occurrence as well as of food plant usage in Hoploscopini will contribute to our understanding of speciation in this still poorly studied group.

ACKNOWLEDGEMENTS

We are thankful for the enormous help and support that we experienced in preparation of and during our work in Sabah from Chung (Sabah Biodiversity Centre) and the staff of Sabah Parks and of Universiti Malaysia Sabah, Kota Kinabalu. Sabah Parks and the Sabah Biodiversity Centre provided permits for conducting research and collecting, and for export of part of the material. We are grateful to Peter Achleitner for his generous hospitality during the first and second author's stay in his house in Mesilau near which we found the larvae. Papua New Guinea data come from a Binatang Research Center program led by Vojtech Novotny (Institute of Entomology, Czech Academy of Sciences, České Budějovice, Czech Republic), George Weiblen (Bell Museum of Natural History, University of Minnesota, U.S.A.), Yves Basset (Smithsonian Tropical Research Institute, Panama), and Scott Miller (National Museum of Natural History, Smithsonian Institution, Washington, D.C., U.S.A.), and supported by the US National Science Foundation (grants DEB-0515678, 0841885 and others) and the Czech Science Foundation (grants 206/09/0115, 14-04258S and others). DNA barcodes for specimens from PNG were provided by Paul Hebert (Department of Integrative Biology, University of Guelph, Ontario, Canada) through a grant from Genome Canada and the Ontario Genomics Institute in support of the iBOL project. George Weiblen, Timothy Whitfeld (Department of Ecology and Evolutionary Biology, Brown University, Rhode Island, U.S.A.), and Conor Redmond (Institute of Entomology, Czech Academy of Sciences, České Budějovice, Czech Republic) provided host plant identifications, and Scott Miller provided insect identifications. Francesca Vegliante (Senckenberg Museum für Tierkunde Dresden, Germany) contributed with valuable discussions and comments on the chaetotaxy. Two reviewers, Alma Solis (U.S. Department of Agriculture, Washington, D.C., U.S.A.) and Christian Schulze (University of Vienna, Austria), provided helpful comments on the manuscript. Collecting on Borneo was supported through a travel grant of the Royal Entomological Society and through the Norwegian Meltzer Research Grant.

LITERATURE CITED

Amsel HG (1961) Die Microlepidopteren der Brandt'schen Iran-Ausbeute 5. Teil. Arkiv för Zoologi Stockholm, 13: 323–445, pls. 1–9.

Beaman JH & Edwards PJ (2007) Ferns of Kinabalu: An Introduction. Natural History Publications (Borneo), Malaysia, 6 + 198 pp.

Botanical Research Institute of Texas (2003–2009) Digital Flora of New Guinea. http://ng.atrium-biodiversity.org/atrium (Accessed 26 July 2016).

Burman NL (1768) Flora Indica: Cui Accedit Series Zoophytorum Indicorum, Nec Non Prodromus Florae Capensis. Apud Cornelium Haek & Johannem Schreuderum, Leiden & Amsterdam, 242 pp.

Duponchel PAJ (1831–1834 ["1831"]) Nocturnes 5(2). Histoire naturelle des Lépidoptères ou Papillons de France, Paris, 8(2): pp. 5–402, pls. 211–236.

Farahpour Haghani A, Jalaeian M & Landry B (2016) *Diasemiopsis ramburialis* (Duponchel) (Lepidoptera, Pyralidae s. l., Spilomelinae) in Iran: first record for the country and first host plant report on water fern (*Azolla filiculoides* Lam., Azollaceae). Nota Lepidopterologica, 39(1): 1–11.

Folmer O, Black M, Hoeh W, Lutz R & Vrijenhoek R (1994) DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. Molecular Marine Biology and Biotechnology, 3(5): 294–299.

Hampson GF (1919) Descriptions of new Pyralidae of the subfamilies Crambinae and Siginae. Annals and Magazine of Natural History, including Zoology, Botany and Geology, London, 9(3): 275–292, 437–457, 533–547.

Handfield L & Handfield D (2011) A new species of *Herpetogramma* (Lepidoptera, Crambidae, Spilomelinae) from eastern North America. ZooKeys, 149: 5–15.

Hasenfuss I (1960) Die Larvalsystematik der Zünsler (Pyralidae). Abhandlungen zur Larvalsystematik der Insekten, 5: 1–263.

Hasenfuss I (1963) Eine Vergleichend-morphologische Analyse der regulären Borstenmuster der Lepidopterenlarven. Studien zur Methodik der vergleichenden Morphologie der Borstenmuster und zur phylogenetischen Deutung der Abwandlungen der regulären Borstenmuster der Lepidopterenlarven. Zeitschrift für Morphologie und Ökologie der Tiere, 52: 197–364.

Herrich-Schäffer GAW (1847–1855, imprint "1849") Systematische Bearbeitung der Schmetterlinge von Europa, zugleich als Text, Revision und Supplement zu Jakob Hübner's Sammlung europäischer Schmetterlinge. 4: Die Zünsler und Wickler. G. J. Manz, Regensburg, pp. [1]–2–288, (Index) [1]–2–48, pls. 1–23 (Pyralidides) + 1–59 (Tortricides).

Holttum RE (1974) Thelypteridaceae of Africa and adjacent islands (Thelypteridaceae van Afrika en omliggende eilande). Journal of South African Botany, 40(2): 123–168.

Kirk AA (1978) The insect fauna of the weed *Pteridium aquilinum* (L.) Kuhn (Polypodiaceae) in Papua New Guinea: A potential source of biological control agents. Journal of the Australian Entomological Society, 16: 403–409.

Kumar S, Stecher G & Tamura K (2016) MEGA7: Molecular Evolutionary Genetics Analysis version 7.0 for bigger datasets. Molecular Biology and Evolution 33(7): 1870–1874.

Lhomme L (1935) Catalogue des Lépidoptères de France et de Belgique. Microlépidoptères. Le Carriol, Lot, 1–172.

Linnaeus C (1753) Species Plantarum, Tomus 2. Impensis Laurentii Salvii, Holmiae, 561–1231.

Linnaeus C (1759) Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Salvius, Holmiae 10(2), 1–4, 825–1384.

Meyrick E (1886) Descriptions of Lepidoptera from the South Pacific. Transactions of the Entomological Society of London, 1886: 189–296.

Meyrick E (1897) On Lepidoptera from the Malay Archipelago. Transactions of the Entomological Society of London, 1897: 69–92.

Miller SE, Rosati ME, Gewa B, Novotny V, Weiblen GD & Hebert PDN (2015) DNA barcodes of Lepidoptera reared from Yawan, Papua New Guinea. Proceedings of the Entomological Society of Washington, 117(2): 247–250.

Minet J (1982) Les Pyraloidea et leurs principales divisions systématiques (Lep. Ditrysia). Bulletin de la Société entomologique de France, Paris, 86(1981): 262–280.

Müller J, Müller K, Neinhuis C & Quandt D (2010) PhyDE – Phylogenetic Data Editor, version 0.9971. http://www.phyde.de (Accessed 31 July 2016).

Munroe EG (1958) The geographic distribution of the Scopariinae (Lepidoptera: Pyralidae). Proceedings of the Tenth International Congress on Entomology, 1956, Montreal, 1: 831–837.

Munroe EG (1972) Pyraloidea, Pyralidae comprising subfamilies Scopariinae, Nymphulinae. In: Dominick RB et al. (eds.), The Moths of America North of Mexico 13(1A).(E. W. Classey and R. B. D. Publications Inc., London, pp. 1–134.

Munroe EG & Solis MA (1998) The Pyraloidea. In: Kristensen NP (ed.), Lepidoptera, Moths and Butterflies, Volume 1: Evolution, systematics, and biogeography. In: Fischer M (ed.), Handbook of Zoology. Volume IV Arthropoda: Insecta, Part 35. Walter de Gruyter, Berlin, pp. 233–256.

Nuss M (1998) The Scopariinae and Heliothelinae stat. rev. (Lepidoptera: Pyraloidea, Crambidae) of the Oriental Region – a revisional synopsis with descriptions of new species from the Philippines and Sumatra. Nachrichten des entomologischen Vereins Apollo, Supplement 17: 475–528.

Nuss M (1999) Revision der Gattungen der Scopariinae (Lepidoptera: Pyraloidea, Crambidae). Nova Supplementa Entomologica, 13: 3–151.

Nuss M (2005) Heliothelinae. In: Goater B, Nuss M & Speidel W, Pyraloidea I. In: Huemer P & Karsholt O (eds.), Microlepidoptera of Europe 4. Apollo Books, Stenstrup, pp. 109–111, 182, 223, 257, pl. 3 fig. 53.

Nuss M, Landry B, Mally R, Vegliante F, Tränkner A, Bauer F, Hayden J, Segerer A, Schouten R, Li H, Trofimova T, Solis MA, De Prins J & Speidel W (2003–2016) Global Information System on Pyraloidea. www.pyraloidea.org (Accessed 04 August 2016).

Passoa S (1988) Systematic positions of *Acentria ephemerella* (Denis & Schiffermüller), Nymphulinae, and Schoenobiinae based on morphology of immature stages (Pyralidae). Journal of the Lepidopterists' Society 42(4): 247–262.

Passoa S & Habeck DH (1987) A description of the larva and pupa of *Rupela albinella*, a pest of rice in Latin America (Lepidoptera: Pyralidae: Schoenobiinae). Florida Entomologist, 70(3): 368–375.

Phillips E & Solis MA (1996) *Neurophyseta* (Lepidoptera: Crambidae) de Costa Rica. Revista de Biología Tropical, 44 (2): 693–717.

Raciborski M (1898) Die Pteridophyten der Flora von Buitenzorg. Flore de Buitenzorg, Volume 1. E. J. Brill, Leiden, pp. I–XII, 1–255.

Ratnasingham S & Hebert PDN (2007) BOLD: The Barcode of Life Data System (http://www.barcodinglife.org). Molecular Ecology Notes, 7(3): 355–364.

Retzius AJ & König JG (1791) Observationes botanicae sex fascicvlis comprehensae. Siegfried Lebrecht Crusium, Lipsiae, 15–40.

Robinson GS, Tuck KR & Shaffer M (1994) A field guide to the smaller moths of South-East Asia. Malaysian Nature Society, Kuala Lumpur, 309 pp.

Rothschild LW (1915) Macrolepidoptera. In: Rothschild W & Durrant JH (eds.), Lepidoptera of the British Ornithologists' Union and Wollaston expeditions in the Snow Mountains, southern Dutch New Guinea. Zoological Museum, Tring, pp. 1–146, pls. 1–2.

Scopoli JA (1763) Entomologia Carniolica exhibens insecta Carnioliae indigena et distributa in ordines, genera, species, varietates, methodo Linneana. Joannis Thomae Trattner, Vienna, 420 pp.

Silvestro D & Michalak I (2012) raxmlGUI: A graphical front-end for RAxML. Organisms Diversity & Evolution, 12: 335–337.

Solis MA (2006) Key to selected Pyraloidea (Lepidoptera) larvae intercepted at U.S. ports of entry: Revision of Pyraloidea in "Keys to some frequently intercepted lepidopterous larvae" by Weisman 1986. USDA Systematic Entomology Laboratory, Lincoln, NE, USA: 1–58.

Solis MA (2008) Pyraloidea and their known hosts (Insecta: Lepidoptera) of Plummers Island, Maryland. Bulletin of the Biological Society of Washington 15: 88–106.

Solis MA & Maes KVN (2003) Preliminary phylogenetic analysis of the subfamilies of Crambidae (Pyraloidea Lepidoptera). Belgian Journal of Entomology, 4(2002): 53–95.

Solis MA, Yen SH & Goolsby JA (2004) Species of *Lygomusotima* new genus and *Neomusotima* Yoshiyasu (Lepidoptera: Crambidae) from Australia and Southeastern Asia feeding on *Lygodium microphyllum* (Schizaeceae). Annals of the Entomological Society of America, 97(1): 64–76.

Solis MA, Davis DR & Nishida K (2005a) Life history and systematics of *Albusambia elaphoglossumae* (Lepidoptera: Crambidae): A new genus and species of musotimine with leaf-mining biology from Costa Rica. International Journal of Tropical Biology, 53 (3–4): 487–501.

Solis MA, Yen SH, Goolsby JH, Wright T, Pemberton R, Winotal A, Chattrukul U, Thagong A & Rimbut S (2005b) *Siamusotima aranea*, a new stem-boring musotimine (Lepidoptera: Crambidae) from Thailand feeding on *Lygodium flexuosum* (Schizaeaceae). Annals of the Entomological Society of America, Washington, 98(6): 887–895.

Stamatakis A (2006) RAxML-VI-HPC: maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. Bioinformatics, 22(21): 2688–2690.

Stöver BC & Müller KF (2010) TreeGraph 2: Combining and visualizing evidence from different phylogenetic analyses. BMC Bioinformatics, 11: 7.

Swartz OP (1803) Observationes botanicae genera et species filicum illustrantes. Journal für die Botanik, 1801(2): 273–312.

Turner AJ (1915) Studies in Australian Lepidoptera. Proceedings of the Royal Society of Queensland, Brisbane, 27: 11–57.

Turner AJ (1937) New Australian Pyraloidea (Lepidoptera). Proceedings of the Royal Society of Queensland, Brisbane, 48(10): 61–88.

Underwood LM (1907) American ferns – VIII. A preliminary review of the North American Gleicheniaceae. Bulletin of the Torrey Botanical Club, 34(5): 243–262.

Wahlberg N & Wheat CW (2008) Genomic outposts serve the phylogenomic pioneers: designing novel nuclear markers for genomic DNA extractions of Lepidoptera. Systematic Biology, 57(2): 231–242.

Walker F (1859) Pyralides. List of the Specimens of Lepidopterous Insects in the Collection of the British Museum, 18: 509–798.

Yen SH, Solis MA & Goolsby JA (2004) *Austromusotima*, a new musotimine genus (Lepidoptera: Crambidae) feeding on Old World climbing fern, *Lygodium microphyllum* (Schizaeaceae). Annals of the Entomological Society of America, Washington, 97(3): 397–410.

Chapter 4

Twenty-six new species of *Hoploscopa* (Lepidoptera, Crambidae) from South-East Asia revealed by morphology and DNA barcoding.

ZooKeys $$: @–@ (2019)
doi: 10.3897/zookeys.@@.36563
http://zookeys.pensoft.net

RESEARCH ARTICLE

A peer-reviewed open-access journal
ZooKeys
Launched to accelerate biodiversity research

Twenty-six new species of *Hoploscopa* (Lepidoptera, Crambidae) from South-East Asia revealed by morphology and DNA barcoding

Théo Léger[1], Christian Kehlmaier[2], Charles S. Vairappan[3], Matthias Nuss[2]

1 *Museum für Naturkunde – Leibniz-Institut für Evolutions- und Biodiversitätsforschung, Invalidenstr., Berlin, Germany* **2** *Senckenberg Museum für Tierkunde Dresden, Königsbrücker Landstr., Dresden, Germany* **3** *Institute for Tropical Biology and Conservation, Universiti Malaysia Sabah, 88400 Kota Kinabalu, Sabah, Malaysia*

Corresponding author: *Théo Léger* (theo.leger@mfn.berlin)

Academic editor: *Colin Plant* | Received 27 May 2019 | Accepted 25 August 2019 | Published @@ @@@@ 2019

http://zoobank.org/DBF339E5-EBBC-4619-9438-8359C769473F

Citation: Léger T, Kehlmaier C, Vairappan CS, Nuss M (2019) Twenty-six new species of *Hoploscopa* (Lepidoptera, Crambidae) from South-East Asia revealed by morphology and DNA barcoding. ZooKeys @@: @–@. https://doi.org/10.3897/zookeys.@@.36563

Abstract

Hoploscopa Meyrick (Lepidoptera: Crambidae) is a fern-feeding genus found in montane areas of South-East Asia and Melanesia, eastwards up to the Samoan Islands. It includes sixteen described species, with at least 70 further undescribed species known from scientific collections. An iterative approach including morphological and molecular characters was used in order to explore the diversity of *Hoploscopa*. The hitherto described species are revised, and descriptions authored by T. Léger and M. Nuss are provided for an additional 26 new species: *H. agtuuganonensis* **sp. nov.**, *H. albipuncta* **sp. nov.**, *H. albomaculata* **sp. nov.**, *H. anacantha* **sp. nov.**, *H. boleta* **sp. nov.**, *H. cynodonta* **sp. nov.**, *H. danaoensis* **sp. nov.**, *H. gombongi* **sp. nov.**, *H. gracilis* **sp. nov.**, *H. ignitamaculae* **sp. nov.**, *H. isarogensis* **sp. nov.**, *H. jubata* **sp. nov.**, *H. kelama* **sp. nov.**, *H. kinabaluensis* **sp. nov.**, *H. mallyi* **sp. nov.**, *H. marijoweissae* **sp. nov.**, *H. matheae* **sp. nov.**, *H. niveofascia* **sp. nov.**, *H. pangrangoensis* **sp. nov.**, *H. parvimacula* **sp. nov.**, *H. pseudometacrossa* **sp. nov.**, *H. sepanggi* **sp. nov.**, *H. sumatrensis* **sp. nov.**, *H. titika* **sp. nov.**, *H. tonsepi* **sp. nov.**, *H. ypsilon* **sp. nov.** Using a protocol specific for the amplification of DNA from old museum specimens, we recovered 101 COI barcodes for all but one of the newly described species, with 76 being larger than 487 bp. Species delimitation analyses suggest cryptic diversity, with six cases reflecting allopatric divergence, and two further cases found in sympatry.

Keywords

ancient DNA, integrative taxonomy, Melanesia, Pyraloidea

Table of Contents

Introduction 3
Materials and methods 4
  Material acquisition 4
  Iterative approach 4
  Molecular work 5
  Data analyses 5
  Species delimitation 6
  Systematic treatment 7
Results 7
  Molecular dataset 7
  Species delimitation 8
  Systematics 8
    Hoploscopa Meyrick, 1886 8
      Hoploscopa albipuncta Léger & Nuss, sp. nov. 12
      Hoploscopa matheae Léger & Nuss, sp. nov. 15
      Hoploscopa sepanggi Léger & Nuss, sp. nov. 17
      Hoploscopa cynodonta Léger & Nuss, sp. nov. 18
      Hoploscopa parvimacula Léger & Nuss, sp. nov. 20
      Hoploscopa kinabaluensis Léger & Nuss, sp. nov. 22
      Hoploscopa luteomacula Nuss, 1998 24
      Hoploscopa obliqua (Rothschild, 1915) 25
      Hoploscopa niveofascia Léger & Nuss, sp. nov. 26
      Hoploscopa gombongi Léger & Nuss, sp. nov. 27
      Hoploscopa tonsepi Léger & Nuss, sp. nov. 28
      Hoploscopa marijoweissae Léger & Nuss, sp. nov. 30
      Hoploscopa titika Léger & Nuss, sp. nov. 31
      Hoploscopa pangrangoensis Léger & Nuss, sp. nov. 32
      Hoploscopa isarogensis Léger & Nuss, sp. nov. 33
      Hoploscopa ypsilon Léger & Nuss, sp. nov. 35
      Hoploscopa danaoensis Léger & Nuss, sp. nov. 36
      Hoploscopa aurantiacalis (Snellen, 1895) 39
      Hoploscopa brunnealis (Snellen, 1895) 40
      Hoploscopa ocellata (Hampson, 1919) 41
      Hoploscopa quadripuncta (Rotschild, 1915) 42
      Hoploscopa semifascia (Hampson, 1919) 43
      Hoploscopa subvariegata (Rotschild, 1915) 44
      Hoploscopa persimilis (Rotschild, 1915) 45
      Hoploscopa diffusa (Hampson, 1919) 46
      Hoploscopa triangulifera (Hampson, 1919) 47
      Hoploscopa astrapias Meyrick, 1886 48
      Hoploscopa anamesa Tams, 1935 50

Hoploscopa nauticorum Tams, 1935 51
Hoploscopa anacantha Léger & Nuss, sp. nov. 52
Hoploscopa kelama Léger & Nuss, sp. nov. 53
Hoploscopa ignitamaculae Léger & Nuss, sp. nov. 55
Hoploscopa albomaculata Léger & Nuss, sp. nov. 63
Hoploscopa sumatrensis Léger & Nuss, sp. nov. 64
Hoploscopa mallyi Léger & Nuss, sp. nov. 65
Hoploscopa gracilis Léger & Nuss, sp. nov. 68
Hoploscopa agtuuganonensis Léger & Nuss, sp. nov. 69
Hoploscopa boleta Léger & Nuss, sp. nov. 70
Hoploscopa pseudometacrossa Léger & Nuss, sp. nov. 72
Hoploscopa metacrossa (Hampson, 1917) 73
Hoploscopa jubata Léger & Nuss, sp. nov. 75
Misplaced species 76
Discussion 88
Acknowledgements 89
References 90
Supplementary material 1 95
Supplementary material 2 95
Supplementary material 3 96
Supplementary material 4 96
Supplementary material 5 96

Introduction

South-East Asia is home to a rich biodiversity encompassing three of the 25 world's biodiversity hotspots (Myers et al. 2000). Pyraloidea is one of the largest superfamilies of Lepidoptera in the Oriental region, with 3,771 known species (Heppner 1998). Much of its diversity for this region remains to be described in this group (Nuss 1998, Sutton et al. 2015). *Hoploscopa* Meyrick best illustrates this knowledge gap, with 16 species currently described and more than 70 species awaiting description (Robinson et al. 1994). *Hoploscopa* moths display elongated brown forewings often with median and postmedian diagonal pale yellow to red markings. The genus is distributed across the Oriental and Australasian regions, ranging from the Malay Peninsula eastwards to the Samoa Islands, but is virtually absent from the tropical rainforests of Northern Queensland, Australia. A recent study reported the larvae to feed on ferns (Mally et al. 2017).

Nuss (1998) synonymised *Syncrotaula* Meyrick, a replacement name for *Eudorina* Snellen, with *Hoploscopa*, and transferred twelve species to it. The author also provided a checklist of the genus and described one new species. Robinson et al. (1994) erected the tribe Hoploscopini within Scopariinae for *Hoploscopa* (= *Syncrotaula*) and *Perimeceta* Turner. Nuss (1998) transferred the Hoploscopini to the Heliothelinae based on the shared inwardly directed spine of the corpus bursae in the female genitalia. *Perimeceta*, the only other genus included in the Hoploscopini, is distributed from Java to South Australia and its larvae also feed on ferns (Miller et al. 2015, Mally et al. 2017). The systematic placement of Hoploscopini is still a matter of debate, with some authors grouping them together with Heliothelini in the Heliothelinae (Nuss 1998), while others consider the Heliothelinae an ingroup of Scopariinae (Leraut 1980, Minet 1982, Munroe and Solis 1998). The first molecular-based phylogeny including representatives of *Hoploscopa* suggest it to represent a separate lineage outside of Scopariinae + Crambinae (Léger et al., 2019).

This paper aims at establishing an iterative approach following Yeates et al. (2011) for species discovery and description in *Hoploscopa*, serving as a first step of a comprehensive revision of the genus. With an iterative approach using morphology and COI barcode, we provide redescriptions for fifteen of the 16 described species and describe 26 new species. Incongruence between morphology and molecular datasets, as well as possible factors that affected the evolution of the group are discussed.

Materials and methods

Material acquisition

Material collected on Borneo, Java, Fiji, the Malay Peninsula, North-Sulawesi, New Guinea, the Philippines, Samoa, Sumatra and Vanuatu was obtained from the Museum für Tierkunde Dresden (**MTD**), the British Natural History Museum, London (**NHMUK**), the United States National Museum, Washington (**USNM**), the Museum für Naturkunde Berlin (**ZMHB**) and the Zoologische Staatsammlung München, Munich (**ZSM**). Examination of the type specimens of the previously described species, all deposited at the NHMUK, was done by TL during a visit at that institution.

Iterative approach

In order to test species hypotheses with two independent sets of characters, we followed the best practice outlined by Schlick-Steiner et al. (2010), here referred to as "iterative taxonomy" (Yeates et al. 2011). This workflow started by sorting undescribed material to morphospecies based primarily on wing pattern, followed by examination of characters in male genitalia that show most variation. Subsequently, for each morphospecies, specimens with slightly differing wing pattern and/or of each collecting locality were selected for amplification of the mitochondrial COI barcode. Finally, morphospecies with at least one obtained COI barcode sequence were considered for species description (with the exception of *H. marijoweissae* sp. nov.). If strong divergence was observed in the COI barcode within a morphospecies, a second more careful examination of the specimens was conducted in the search of diagnostic characters, and COI barcode was sequenced for all specimens of the series. Specimens in poor conditions (i.e., wing pattern faded away, abdomen missing) or new species without male specimens available were not further considered for species description.

Molecular work

One hundred and fifty-seven dried museum specimens were considered for DNA extraction. Assuming a higher degree of degradation due to the age of the dried specimens, DNA extraction and preparation of PCR samples for specimens collected before 1990 (referred to as "old sample") were performed in the clean-room facility of the SGN-SNSD-Mol-lab at MTD. The abdomen (one or two legs if the abdomen could not be used) was carefully removed with sterilised pincers for DNA extraction, following a non-destructive method (Knölke et al. 2004) with the NucleoSpin Tissue kit (Macherey-Nagel, Düren, Germany) according to the manufacturer's protocol. DNA quantity of old samples was measured with a NanoDropOne spectrophotometer. We followed a work flow previously used by other authors (Hebert et al. 2013, Mitchell 2015, Hundsdoerfer et al. 2017) by amplifying up to five short overlapping fragments covering the COI barcode part (see Suppl. material 1: Fig. S1). Primers, amplicon length and amplicon overlap are listed in Suppl. material 2: Table S1. In the first step (recently collected samples only), amplification of the whole COI barcode sequence (658 bp) was attempted with the primer pair HybLCO/HybNancy, each flanked with universal primer tails ("Hyb-") facilitating sequencing (Wahlberg and Wheat 2008). If amplification was not successful, we proceeded in the second step with the amplification of fragments 1a (LepF1/K699) and 1b (f220/LepR1 or HybNancy). The latter reverse primer showed a slightly better performance with respect to the amplification of fragment 1b and was preferentially used. If amplification of fragments 1a or 1b in step two failed, we proceeded in step three with amplification of fragments A, B, C (covering fragment 1a) and C, D, E (covering fragment 1b). PCR-mix included 2 µl of BIORON complete buffer 10× incl. Mg^{2+} (25 mM), 2 µl of each primer at 10pmol/µl, 0.4 µl of dNTP (each 10 mM), 0.2 µl of Taq polymerase BIORON (Bioron DFS Taq, Ludwigshafen, Germany) ,1 µl (recent samples) or 1 to 8 µl (old samples) of DNA (depending on the quantity of DNA measured) and filled up with water to final volume of 20 µl. Alternatively, the AccuStart II GelTrack PCR SuperMix (2×) (Quanta BioSciences, Beverly, USA) ready-to-use mix was used in the following PCR-mix: 6.5 µl AccuStart ready-to-use-mix, 1 µl of each primer, 1–8 µl DNA and filled up with water to final volume of 25 µl. Initial denaturation at 95 °C during 5 min was followed by 42 cycles of 30 sec denaturation at 95 °C, 40 sec hybridisation at 49 °C, 50 sec elongation at 72 °C, with a final elongation at 72 °C for 10 min. Amplification success was checked by electrophoresis on 1 or 2% agarose gels, subsequently stained with GelRed and visualised under UV light. Sequencing was performed by Macrogen (Netherlands) using the original PCR primers or the T7 and T3 sequencing primers (Wahlberg and Wheat 2008). Full COI-barcoding PCR products were sequenced in the forward direction only, while the shorter PCR products were sequenced in both directions.

Data analyses

Sequences were checked by eye and concatenated using PHYDE 0.9971 (Müller et al. 2005). In order to assess the amplification of the correct fragment, sequences were blasted with the blastn program against the nucleotide collection (nt), as provided by the National Center for Biotechnology Information (NCBI). In order to identify potential nuclear pseudogenes, sequences were searched for indels, internal stop codons and double peaks in electropherograms, following Song et al. (Song et al. 2008). Newly generated sequences (including ENA and BOLD accession numbers), as well as sequences retrieved from Barcode of Life Data System (BOLD, http://v4.boldsystems.org/) are reported in Suppl. material 3: Table S2. For the phylogenetic analyses, PartitionFinder2 (Lanfear et al. 2017) was used to determine the best partitioning scheme using the AICc model and the greedy search algorithm (Lanfear et al. 2012). Partition for each of the three codon positions was recovered as the best model and subsequently used for further analyses. Maximum Likelihood (ML) analysis was performed with RAxML (Stamatakis 2006) as implemented on the CIPRES portal (Miller et al. 2010), using the GTR+GAMMA substitution model and the best PartitionFinder scheme. Node support was estimated with 1000 thorough bootstrap replicates using the same algorithm.

Species delimitation

Two different methods were used to investigate species delimitation in our molecular dataset: Automatic Barcode Gap Discovery (ABGD) (Puillandre et al. 2012) and General Mixed Yule-coalescent method (GMYC) (Pons et al. 2006, Fujisawa and Barraclough 2013). These popular methods have been repeatedly used in DNA barcoding studies on Lepidoptera (Kekkonen and Hebert 2014, Dincă et al. 2015, Dumas et al. 2015, Nakahara et al. 2019). We noticed a detrimental effect of non-compliant barcode sequences (< 487 bp) on the estimation of species in densely sampled clades (n > 2), where these sequences were flagged as new species. Consequently, these sequences were removed to generate a COI_487 bp dataset. Distance-based analysis ABGD was calculated using the K80 Kimura distance model and X fixed to 0.5 on the dedicated platform (https://bioinfo.mnhn.fr/abi/public/abgd/abgdweb.html). Genetic distances are referred to as K2P-dist throughout the text.

The ultrametric tree required for the GMYC analysis was generated using BEAST 1.10.4 (Suchard et al. 2018). The COI dataset was partitioned after codon position accordingly to the best PartitionFinder2 scheme. An uncorrelated relaxed clock with lognormal distribution was used and the Speciation: Yule Process model was set as tree prior model and other parameters were left unchanged. MCMC chain was set to 40 million generations, sampled every 1000th generation. Convergence was checked on Tracer (Rambaut et al. 2018) and the first 4 million generations were discarded as burnin. Species delimitation analysis was performed using the GMYC method as implemented in the R-package SPLITS (Ezard et al. 2009, Fujisawa and Barraclough 2013). The single-threshold option was used as suggested in Fujisawa and Barraclough (2013).

Systematic treatment

Genitalia were mounted following the method of Robinson (1976). Photographs of the habitus of imagines were taken with an Olympus E-M1 with the Olympus M. Zuiko Digital ED 60 mm f/2.8 Macro Lens. Photographs of genitalia and measurements were performed on a Nikon Eclipse 90i at the MTD. Images were subsequently enhanced on Adobe Photoshop CS6 and illustrations plates were created on Adobe Illustrator CS6. Collecting data of holotypes was copied exactly as found on the labels, with vertical bars to mark line breaks. Abbreviations or translations are given in square brackets where judged meaningful. Paratype data are reported by country in alphabetical order, with information reported without indication of line change. Collecting localities are reported as written on labels. Dates and collectors' information were standardised and the latter placed in parentheses. The specimen depositories are reported with the use of the corresponding acronyms. GPS coordinates for localities were retrieved from the online platform geographic.org (https://geographic.org/geographic_names/) using the database of the National Geospatial-Intelligence Agency. Specimens whose conspecificity was uncertain were listed under "Other specimens examined". Nomenclature follows that of Landry (1995), except for the use of the term phallus (Kristensen 2003). The colours "bronze", "ochre", and "tawny" refer to the Wikipedia list of colours by shade for brown (https://en.wikipedia.org/wiki/Category:Shades_of_brown). Character description was facilitated by the use of Mesquite (Maddison and Maddison 2017) where each character was given a state, thereby allowing a better visualisation of character state variation as well as warranting consistency among species descriptions.

Results

Molecular dataset

We obtained 101 COI barcodes ranging in length from 261 to 658 bp (mean length = 545 bp), among them 76 barcode "compliant sequences" (> 487 bp) according to Hebert et al. (2013). Ten non-compliant barcode sequences were kept in the final dataset for species with no or one barcode sequence. Fifteen further non-compliant barcode sequences were discarded from the final dataset (see Suppl. material 2: Tab. S1). We recovered the COI barcode for all but one (*H. marijoweissae* sp. nov.) species described in this paper and for seven of the sixteen previously described species. Twenty-five *Hoploscopa* sequences, as well as 13 sequences from the hypothesised sister-group *Perimeceta* were retrieved from BOLD and added to our dataset, totalling 124 COI barcode sequences including nine of the described species. Eleven species were represented by only one barcode sequence. Recovered fragments and total sequence length are summarised in Suppl. material 3: Table S2. The oldest sample from which we could successfully amplify COI sequence data were collected in 1955 (63 years old). The Maximum Likelihood analysis of the COI dataset is illustrated in Fig. 123, with bootstrap support (abbr. BS) more than 50 displayed on nodes. Genetic distances (K2P-dist) between all COI barcodes are reported in Suppl. material 4: Table S3.

Species delimitation

Analysis of the morphology allowed delineation of 39 species. Both ABGD and GMYC analyses highlighted 48 molecular operational taxonomic units (MOTUs) in *Hoploscopa* species, splitting seven of the morphospecies into two MOTUs, and one into three MOTUs (*H. danaoensis* sp. nov.). Six of these splits reflect allopatric divergence. In each of the two species *H. matheae* sp. nov. and *H. parvimacula* sp. nov., there is one female from the Malay Peninsula recovered as a separate MOTU from other specimens from Borneo. In *H. luteomacula*, the two specimens from Borneo are recovered as a distinct MOTU to that of Sumatra. In *H. albipuncta* sp. nov., a female from Luzon (Philippines) was recovered in a MOTU distinct from that including the specimens from Borneo. Genetic differentiation is also observed among Philippines islands: specimens of *H. danaoensis* sp. nov. from Danao, Negros, and Mindanao represent three different MOTUs, while specimens of *H. isarogensis* sp. nov. from Luzon and Leyte are also recovered into two distinct MOTUs.

Sympatric divergence is observed in *H. kinabaluensis* sp. nov. and *H. sumatrensis* sp. nov. *Hoploscopa kinabaluensis* sp. nov. is split into two MOTUs representing sister clades and diverging from each other by 1.7–2.2%. In *H. sumatrensis* sp. nov., two separate MOTUs are recovered by the ML analysis in a clade with DNA samples BC_MTD_LEP01421 (*Hoploscopa* sp. near *sumatrensis*) and BC_ZMBN_Lep00081 (larva of *Hoploscopa* sp.). The two *H. sumatrensis* MOTUs show a divergence of 4.1–6%. Second MOTU, represented by samples MTD8258 and BC_MTD_LEP01422, include only females and need examination of male specimens.

Systematics

Hoploscopa Meyrick, 1886

Haploscopa Hampson, 1897: 223.

Syncrotaula Meyrick, 1933: 378. Type species *Eudorina aurantiacalis* Snellen, 1895, by subsequent designation (for *Eudorina* Snellen, 1895) by Joannis, 1930.

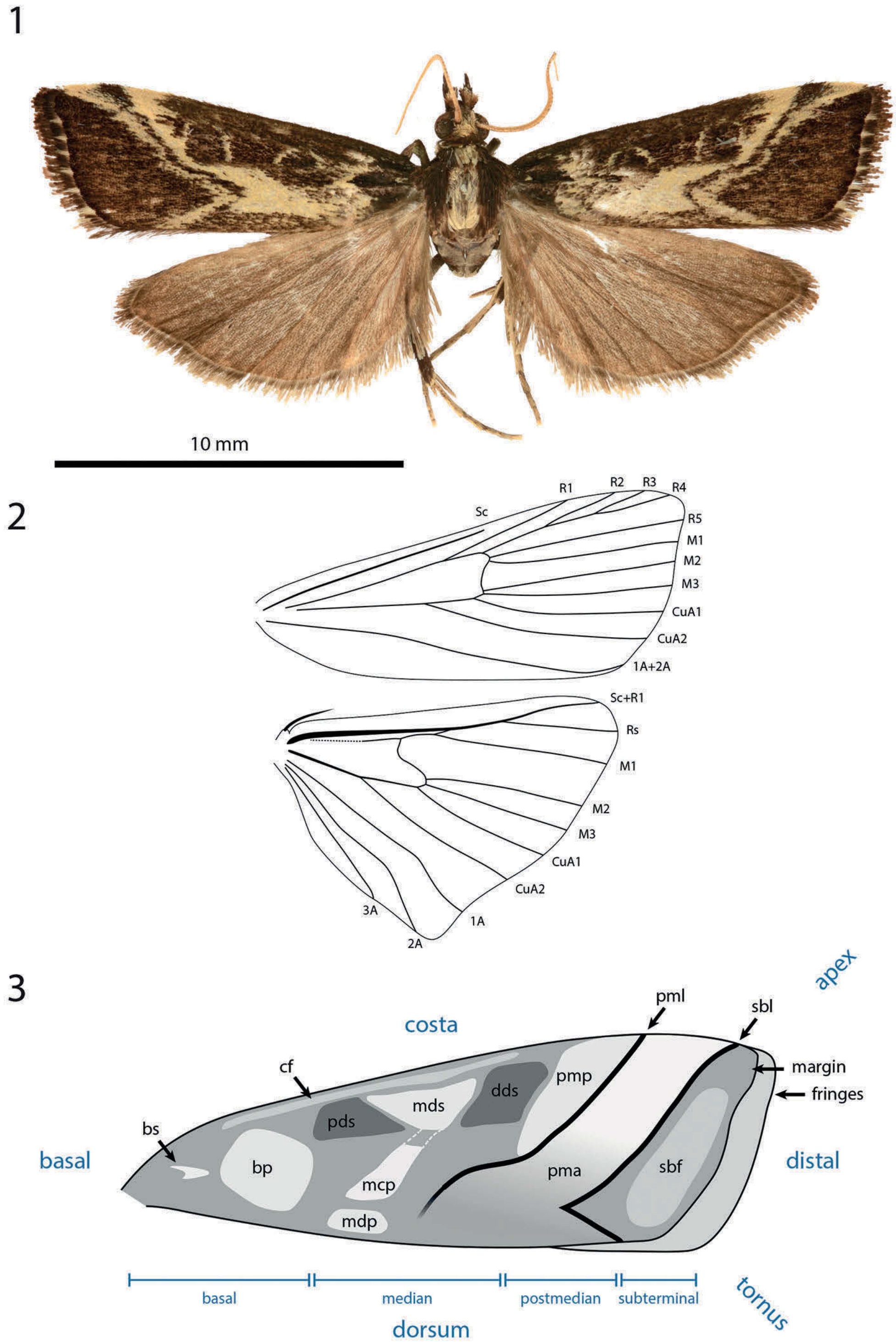
Type species. *Hoploscopa astrapias* Meyrick, 1886, by monotypy.

Diagnosis. *Hoploscopa* displays brown to dark brown forewings, often bearing pale yellow-, yellow-, or red-coloured median and postmedian diagonal stripes. In male genitalia, the uncus is well developed, the gnathos forms a ribbon-like structure, often with a posterior projection, and the vinculum bears laterally a pair of coremata. In female genitalia, the antrum is short, often sclerotised, and the corpus bursae bears a thorn, often with a basal sclerotisation. *Hoploscopa* is morphologically very similar to *Perimeceta*. The forewings of *Perimeceta* are slightly larger, display a yellow to brown ground colour, with one basal elliptic and one postmedian lunule-shaped white spot. In male genitalia, *Perimeceta* shows a spade-shaped uncus, the gnathos arms connect shortly after arising and are expanded posteriorly into an elongated tip, the valva shows a conspicuously rounded ventral margin, and is apically narrowed into a tip, while the ventral margin is more or less straight in *Hoploscopa*. *Perimeceta* exhibits female genitalia similar to those of *Hoploscopa* with a slender ductus bursae and a rounded corpus bursa bearing a thorn. However, the latter displays a membranous antrum in female genitalia, while it is sclerotised in most species of *Hoploscopa*.

Description. ***Head.*** Antennae dorsally with pale yellow to brown scales. Ocelli absent. Frons slightly produced, rounded. Proboscis basally white to brown scaled. Maxillary palpi brown to dark brown, first segment pale yellow, inner side brown to pale yellow. Labial palpi porrect, 2–2.9 × diameter of compound eye, brown, white to pale yellow at base, inner side brown to pale yellow.

Thorax (Figs 1–45). Collar white to pale yellow. Frenulum simple in ♂, triple in ♀. Forewing length 7–13 mm, 2.4–2.9 × maximal width, females slightly larger than males. Wing venation (Fig. 2): R1 not connected to Sc; R2, R3 and R4 stalked together; R5 free, arising from upper corner of cell; M1, M2 not stalked; M3 arising from lower corner of cell; CuA1 arising below lower corner; CuA2 at distal 1/3 of cell; 1A+2A arising from cell base; Hindwing Sc+R1 connected to Rs at distal 1/3; M1 connected to Sc+R1 by short vein; cell closed; M2, M3 and CuA1 arising at lower angle of cell; CuA2 arising at middle of cell; 1A, 2A, 3A free. Forewing ground colour brown to dark brown, markings white, yellow or red colour. The pattern elements can be described as follows (Fig. 3):

cf	costal field stretched along costa up to postmedian area;
bs	basal streak small, weakly or not marked;
bp	basal patch often quadrangular, ill-defined;
pds and **dds**	proximal and distal discoidal stigmata along costal field;
mds	the median discoidal stigma trapezoid, with costal edge longer than dorsal one;
mcp and **mdp**	median cubital patch and median dorsal patch in line with median discoidal stigma, often forming together a Y-shape pattern;
pmp	postmedian patch roughly triangular, narrowing at costa;
pml	postmedian line running from costa to middle of dorsum, often barely marked, mostly visible close to costa;
pma	postmedian area often suffused to a various extend with white, yellow or red;
sl	subterminal line running from costa close to apex towards dorsum, often incurved inwards at CuA2;
sbf	subterminal field more or less suffused with brown, red or yellow.



Figures 1–3. Habitus, venation and forewing pattern in *Hoploscopa*. **1** Habitus of *Hoploscopa matheae* sp. nov., holotype, ♀, Malaysia, Sabah, Kundasang, Kinabalu Mt. Lodge veranda, 6°0'42.15"N, 116°32'3.63"E, 1570 m (T. Léger & R. Mally) (genitalia on slide TL315 ♀) **2** wing venation of *Hoploscopa* species: *H. jubata* sp. nov., paratype, ♂, Papua New Guinea, Morobe Prov., nr Bulolo, Mt Susu Nat. Res., *Araucaria* For., 975 m, 27–28 Aug 1983 (S. Miller) (wing preparation TL706) **3** nomenclature used for description of forewing pattern of *Hoploscopa spp.* Abbreviations: bp (basal patch), bs (basal streak), cf (costal field), dds (distal discoidal stigma), mcp (median cubital patch), mds (median discoidal stigma), mpd (median patch at dorsum), pds (proximal discoidal stigma), pma (postmedian area), pml (postmedian line), pmp (postmedian patch), sbf (subterminal field), sbl (subterminal line).

The margin is brown, in some species with spots, fringe unicoloured or chequered.

Hindwing upper side pale yellow to pale brown; underside pale yellow, with brown markings on costa and subterminal line toward costa; males of some species with androconial organ on the upper side at dorsum, consisting of upright scales along CuA2 and 1A veins and a protruded margin between CuA2 and 1A, bearing a patch of greyish scales. Forelegs brown to dark brown. Midlegs with femur brown, tibia and tarsi often pale yellow, speckled with brown. Hindlegs pale yellow on inner side, pale yellow to brown on outer side, tarsi bronze to pale brown.

Tympanal organs (Figs 83–84).

tb	Tympanic bridge deeply divided in the centre;
td	Tympanic drum (Fig. 50) ovoid, antero-ventrally semi-closed, posteriorly not reaching transverse ridge;
tdp	Tympanic depressions broad, opened ventrally;
tm	Tympanum subtriangular;
tr	Transverse ridge (“”) not sclerotised.

Venulae secundae absent.

Abdomen. Pale brown to brown. In males, sternum A8 more or less broadly indented, in some species with small lateral papillae-like projection (Figs 85, 86).

Male genitalia (Figs 46–82).

c	cornutus on phallus elongated, flat, spatula-shaped, except otherwise mentioned;
de	ductus ejaculatorius;
g	Gnathos arms (Fig. 54) originating from the dorsal part of tegumen, forming ring, with or without dorso-median extension;
jx	Juxta basally wide with anterior margin rounded to quadrangular, narrowing at basal 1/4;
s	saccus triangular to quadrangular, pointing dorsally;
ta	Tegumen arms anteriorly sclerotised, with edge marked, posteriorly membranous; dorsally fused into a bridge of various width, articulated or fused to uncus base;
uc	Uncus well-developed, densely haired apically;
v	Valva elongated, hairy, sclerotised, with strongly sclerotised dorsal edge;
vc	Vinculum U-shaped in posterior view, dorso-laterally on each side with anterior projection bearing brush-shaped coremata.

Female genitalia (Figs 87–122).

aa	Anterior apophyses (Fig. 88) bluntly angled at posterior 1/3, bent ventrad;
at	Antrum sclerotised or membranous;

cb	Corpus bursae globular or ovoid, its membrane with a reticulate structure;
cs	Broad sclerotisation of the corpus bursae;
db	Ductus bursae membranous with longitudinal wrinkles, variable in length and shape;
pa	Posterior apophyses slender, straight, directed posterad except otherwise mentioned;
pp	Papillae anales thin in lateral view, dorsally and ventrally connected, setose;
segm. VIII	Segment VIII faintly sclerotised, ventrally membranous; setae scattered across segment, more densely concentrated on posterior margin;
t	thorn on corpus bursae large, sclerotised, inwardly projecting, its base slighly extending outwards into a small sclerotised protuberance.

Distribution. *Hoploscopa* is found from the Malay Peninsula and Sumatra in the West to the Samoa Islands in the East, as well as from the North of Thailand to Vanuatu and Fiji in the South. It is absent from Queensland (Australia) and New Caledonia. It is predominantly found in tropical mountain forests, with only few species encountered in the lowlands.

Biology. Host plant data is available for five *Hoploscopa* species, all feeding on ferns. The larvae of *H. gombongi* sp. nov., *H. obliqua* sp. nov., and *H. tonsepi* sp. nov. from Papua New Guinea are reported from *Diplazium esculentum* (Retzius in Retzius & König, 1791) Swartz, 1803 (Athyriaceae) (Miller et al. 2015, Mally et al. 2017). Another undescribed *Hoploscopa* species (sample USNM_ENT_00739239) from Papua New Guinea is reported from *Sphaerostephanos unitus* (Linnaeus, 1759) Holttum, 1794 (Thelypteridaceae) (ibid). Lastly, one undescribed *Hoploscopa* species from Borneo is reported from the fern *Dicranopteris linearis* (Burman, 1768) Underwood, 1907 (Gleicheniaceae) (Mally et al. 2017).

Hoploscopa albipuncta **Léger & Nuss, sp. nov.**

http://zoobank.org/26FE78DF-5D7E-4034-A730-FA5C7177466E

Figs 4, 46, 87

Material examined. ***Holotype*****:** ♂, with labels: “Malaysia: Sabah, Kinabalu Park H[ead]Q[uarter], | Timpohon Gate, 700m from Liwagu | Trail starting point, near Liwagu River, | 6°1'40"N, 116°32'59"E, 1760m, UV light, | 18.vi.2015, leg. T. Léger & R. Mally”; “TL335 | ♂”. Deposited in ZMHB.

Paratypes**:** 13 ♂, 1 ♀. Malaysia: 8 ♂ (1 with genitalia on slide TL336 ♂), same data as holotype; 3 ♂ (1 with genitalia on slide TL536 ♂), Sabah, Kinabalu National Park, Timpohon Gate, 300 m from Ligawu trail starting point, 6°1'41"N, 116°32'54"E, 1820 m, UV light, 18.vi.2015, leg. T. Léger & R. Mally (MTD); 1 ♂, Sabah, Mesilau, Kopogon, 24.ii.2006, light trap, leg. W. & M. Mey; 1 ♂ (genitalia on slide TL635 ♂), Sabah, Mesilau River, 24–25.ii.2006, light trap, leg. W. & M. Mey; 1 ♀ (DNA voucher MTD7434, genitalia on slide TL609 ♀), Sabah, Mesilau, 2000 m, 14–17.xi.2006, light trap, leg. W. Mey & K. Ebert (ZMHB).

Other specimens examined. 1 ♂. Malaysia: 1 ♂ (DNA voucher ITBC09, genitalia on slide TL309 ♂), same data as holotype.

Diagnosis. *Hoploscopa albipuncta* sp. nov. displays a basal white well-rounded spot on the forewing. In male genitalia, the dorsal margin of the valva is protruded, the juxta displays two conspicuous tips and the phallus bears an anvil-shaped cornutus. In female genitalia, the antrum is membranous and forms a rounded pouch.

Similar species. No similar species known.

Description. ***Head.*** Antennae dorsally with brown scales. Proboscis pale yellow. Maxillary palpi brown, basally light brown. Labial palpi brown, ventrally pale yellow.

Thorax (Fig. 4). Collar white. Forewing length: 9–10 mm (♂ & ♀); forewing ground colour brown; rounded snow white basal cubital spot; median discoidal stigma rhomboid to ellipsoid, dark red, edged with pale yellow; postmedian spot trapezoid, dark red, proximally pale yellow; subterminal line snow white, parallel to termen, slightly angled at M1, broader at costa; fringes brown, with white dots. Hindwing dirty pale yellow. Forelegs bronze. Midlegs brown, with tibia and tarsi segments distally white. Hindlegs brown, with tibia and tarsi segments distally white.

Abdomen. Male sternum A8 posterior margin straight.

Male genitalia (N = 5) (Fig. 46). Uncus long and slender, gently narrowing on basal half, apex tongue-shaped. Gnathos projection broad, triangular, with rounded apex. Valva ventral margin straight, dorsal margin strongly protruded dorsad, apex rounded. Juxta with base rounded, medially narrowed, apex split into two conspicuous tips. Saccus small, pointing dorsad. Phallus with sclerotised, anvil-shaped cornutus.

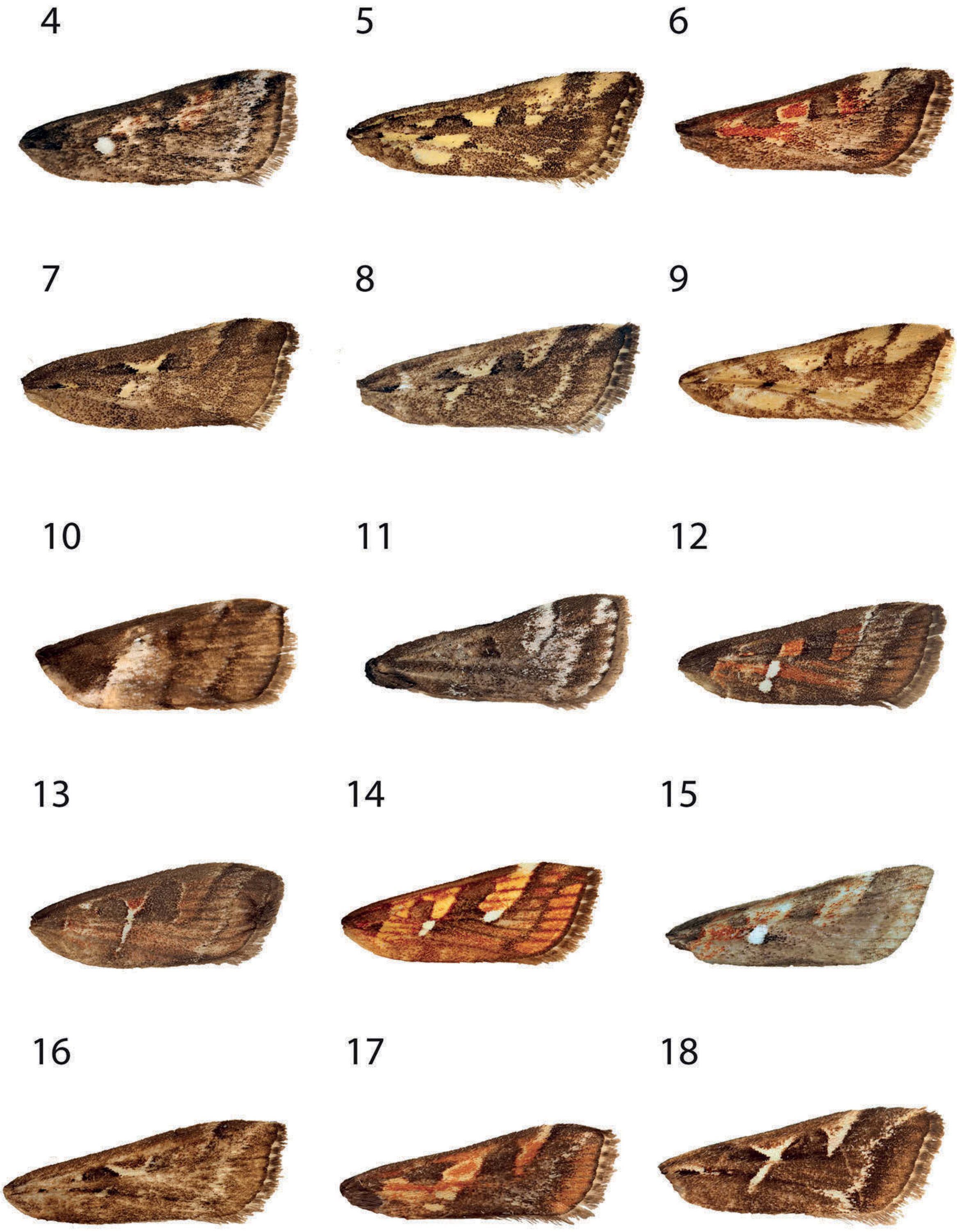
Female genitalia (N = 1) (Fig. 87). Anterior apophyses with dorsal bump at posterior 1/3. Antrum forming a membranous rounded pouch. Ductus bursae long, slender, straight. Corpus bursae small, globular, reticulate, with barely marked sclerotisation at thorn base. Thorn curved, with small dents pointing toward thorn apex on its inner side, glabrous on the outer side.

Distribution. Known from the slopes of the Mount Kinabalu (4,095 m) on Borneo, at altitudes between 1,700 m and 2,000 m.

DNA barcoding. Specimen MTD7430 from Luzon shows an K2P-distance of 4.5–4.9% with the two specimens from Borneo.

Etymology. The species name *albipuncta* refers to the Latin *albus*, white, and *punctus*, forming a point.

Remarks. Two female specimens from the Philippines with similar habitus and genitalia but a COI barcode divergence of 4.5–4.9% are recovered as different MOTU in the species delimitation analyses. Unfortunately, no male was available for this study, thus we refrained from describing a new species based on these two specimens.



Figures 4–18. Habitus of *Hoploscopa* species. **4** *Hoploscopa albipuncta* sp. nov., holotype, ♂, Malaysia, Sabah, Kinabalu Park HQ, Timpohon Gate, 700 m from Liwagu Trail starting point, near Liwagu River, 6°1'40"N, 116°32'59"E, 1760 m, 18.vi.2015 (T. Léger & R. Mally) (genitalia on slide TL335 ♂) **5** *Hoploscopa sepanggi* sp. nov., holotype, ♂, Malaysia, Sabah, Mesilau Nature Resort, 6°2'43.71"N, 116°35'48.03'E, 1925 m, at lamps, 30.v.2015 (T. Léger & R. Mally) **6** *Hoploscopa cynodonta* sp. nov., holotype, ♂, Malaysia, Sabah, Kinabalu Park HQ, junction Kiau View- and Pandanus Trail, 6°0'32.84"N, 116°32'14.94"E, 1690m, UV light, 07.vi.2015 (T. Léger & R. Mally) (genitalia on slide TL327 ♂) **7** *Hoploscopa parvimacula* sp. nov., paratype, ♀, Sabah, Mesilau Nature Resort, 6°2'43.71"N, 116°35'48.03"E, 1925 m, at lamps, 30.v.2015 (T. Léger & R. Mally) (genitalia on slide TL312 ♀.

Hoploscopa matheae Léger & Nuss, sp. nov.

http://zoobank.org/D792135D-FFA9-49ED-8B76-C9802548E8E5

Figs 1, 47, 88

Material examined. ***Holotype***: ♀, with labels: "Malaysia: Sabah, Kundasang, | Kinabalu Mt. Lodge veranda, 6°0'42.15"N, 116°32'3.63"E, 1570 m, at day, 15.vi.2015, | leg. T. Léger & R. Mally"; "DNA barcoding | BC MTD Lep 3004"; "ITBC | 15"; "TL315 | ♀". Deposited in ZMHB.

Paratypes: 1 ♂, 2 ♀. Brunei: 1 ♂ (NHMUK010923334, DNA voucher MTD8245, genitalia on slide TL730 ♂), 1 ♀ (NHMUK010923427), Bukit Retak, LP 238, GR 873804, 1365m, moss forest, 1–4.v.1989, leg. M. G. Allen & K. R. Tuck (NHMUK). Malaysia: 1 ♀ (DNA voucher MTD7426, genitalia on slide TL599 ♀), Sabah, Tawau Hills, Gelas River, 3.iii.2006, leg. W. + M. Mey (ZMHB).

Other specimens examined. 2 ♀. Indonesia: 1 ♀ (NHMUK010923426), Java, Singolangoe, Tengger, 5000 feet, 05.1934 (F. P. A. Kalis) [abdomen missing] (NHMUK). Malaysia: 1 ♀ (NHMUK010923425, DNA voucher MTD8244 & genitalia on slide TL729 ♀), Cameron Highlands, Gunung Brinchang, 15–23.viii.1986 (G. S. Robinson) (NHMUK).

Diagnosis. *Hoploscopa matheae* sp. nov. is unique in the genus by its broad pale yellow forewing fascia crossed by postmedian brown line as well as the basal and distal discoidal spots circled with pale yellow.

Similar species. No similar species known.

Figures 4–18. Continued. **8** *Hoploscopa kinabaluensis* sp. nov., paratype, ♀, Sabah, Kinabalu Park HQ, Timpohon Gate, 700 m from Liwagu trail starting point, near Liwagu River, 6°1'40"N, 116°32'59"E, 1760 m, UV light, 18.vi.2015 (T. Léger & R. Mally) (genitalia on slide TL326 ♀) **9** *Hoploscopa luteomacula* Nuss, paratype, ♀, Indonesia, Sumatra, Barat, N-Padangpanjang, Mt Singgalang, 2100 m, 10–11.ii.1996 (A. Kallies) (genitalia on slide GU prep. Nuss 743) **10** *Hoploscopa obliqua* Rotschild, abdomen missing, Papua New Guinea, Madang Province, Wanang village, 05°15'S, 145°17'E, reared from *Diplazium esculentum*, 12.vi.2007 **11** *Hoploscopa niveofascia* sp. nov., holotype, ♂, Papua New Guinea, Morobe Prov., nr. Bulolo, Mt. Susu Nat. Res., 975 m, 27–28.viii. 1983, *Araucaria* For. (S. Miller) (genitalia on slide TL442 ♂) **12** *Hoploscopa gombongi* sp. nov., paratype, ♂, Papua New Guinea, Yawan village, 06°10'S, 146°5'E, NG Binatang Res. Ctr. (B Gewa, J. Kua, S Sau, A. Kinibel) **13** *Hoploscopa tonsepi* sp. nov., holotype, ♂, Papua New Guinea, Yawan village, 06°10'S, 146°5'E, NG Binatang Res. Ctr. (J. Valeba, J. Auga, M. Dilu, F. Philip, R. Lilip) (genitalia on slide TL655 ♂) **14** *Hoploscopa marijoweissae* sp. nov., ♂, Papua New Guinea: Morobe Province, Mount Kaindi, 2350 m, 11.xii.1976 (G. F. Hevel & R. E. Dietz) (genitalia on slide TL437 ♂) **15** *Hoploscopa titika* sp. nov., holotype, ♂, Sumatra-Holzweg, 25 km SSW-Pematangsiantar, Straße nach Prapat, LF, 13.ii.1996 (A. Kallies) (genitalia on slide TL505 ♂) **16** *Hoploscopa pangrangoensis* sp. nov., paratype, ♀, Indonesia, Java, Mt. Pangrange, SE Bogor, 6.30S 107.10E, 1625 m, primary forest, 16–20.ii.1996 (Siniaev & Afonin) (genitalia on slide TL627 ♀) **17** *Hoploscopa isarogensis* sp. nov., paratype, ♀, Philippines, South Luzon, Mt Isarog, 13°40'N, 123°20'E, 530 m, submontane forest, at light, 22.iii.2000 (M. Nuss) (genitalia on slide TL523 ♀) **18** *Hoploscopa ypsilon* sp. nov., paratype, ♀, Philippines, Luzon, Mountain Province, Chatol, 2100 m, 16–18.xi.1997 (Mey, Ebert & Nuss).

Description. ***Head.*** Antennae dorsally with pale yellow scales. Proboscis dark brown. Maxillary palpi dark brown, basally and inwardly pale yellow. Labial palpi dark brown, ventro-basally pale yellow.

Thorax (Fig. 1). Thorax dark brown, with two pale yellow stripes laterally and one dorsally. Collar pale yellow. Forewing length: 10 mm (♂ & ♀); forewing ground colour dark brown, with darker scales at its base; basally with a roughly defined Z-line pale yellow; basal and distal discoidal patches of a darker brown, circled with pale yellow, median discoidal stigma therebetween dark red in some specimens; broad median triangular pale yellow patch near dorsum, connected distally by a line to postmedian triangular pale yellow patch; subterminal pale yellow line following median line shape, originating at distal 1/4 of dorsum, inwardly incurved costal field between A1+2 and Cu2, costally diverging toward apex; subterminal field broadly marked with scales of a lighter brown; fringes dark brown, with pale yellow dots. Hindwing pale brown. Forelegs dark brown. Midlegs brown; femur and tibia distally pale yellow; tarsi pale yellow. Hindlegs dark brown, femur-tibia articulation pale yellow; tibia distally pale yellow; tarsi bronze.

Abdomen. Male sternum A8 posterior margin straight.

Male genitalia. (*N* = 1) (Fig. 47). Uncus broad, narrowing on distal half, with apex truncate. Gnathos without posterior projection. Valva ventral margin slightly concave, bent dorsad on apical 1/5; dorsal margin conspicuously convex; apex blunt. Juxta with base slightly quadrangular, medially narrow, apically broad, with broadly incurved apex. Saccus not pronounced.

Female genitalia (*N* = 2) (Fig. 88). Anterior apophyses with dorsal tip pointed dorsad at posterior 1/3. Antrum sclerotisation twice as long as broad. Ductus bursae short, wider on posterior 1/4, roughly straight. Corpus bursae pear-shaped, reticulate on posterior half, sclerotised between thorn and corpus opening. Thorn straight, with small dents pointing toward thorn apex, basally with small outwardly projected extension.

Distribution. Known from the Malay Peninsula, and Borneo (Brunei, Mount Kinabalu), at altitudes between 1,300 m and 1,600 m.

DNA barcoding. Specimen MTD8244 from the Malay Peninsula shows an K2P-distance of 2.2% with the two specimens from Borneo. It is recovered as a distinct MOTU in the species delimitation analyses. Specimens from Kinabalu and Tawau Hills share identical COI barcodes. No COI barcode was obtained for the specimen from Brunei (MTD8245).

Etymology. The species is named after Mathéa Léger, sister of the first author.

Remarks. One specimen from the NHMUK collected on Mount Tengger (Indonesia, Java) in 1934 shares a similar wing pattern and thus potentially represents a conspecific specimen. Unfortunately, the abdomen of the specimen was missing. Specimen MTD8244 shows minor differences in wing pattern with those from Borneo: costal field, median discoidal stigma and subterminal field are dark red, and base of thorn on corpus bursae is thinner.

Hoploscopa sepanggi **Léger & Nuss, sp. nov.**

http://zoobank.org/81756486-A524-4D2A-912E-F824C234F835

Figs 5, 48, 89

Material examined. ***Holotype*****:** ♂, with labels: "Malaysia, Sabah, Mesilau Nature Resort | 6°2'43.71"N, 116°35'48.03"E, 1925 m, at | lamps, 30.05.2015, leg. T. Léger & R. Mally". Deposited in ZMHB.

Paratypes**:** 6 ♂, 3 ♀. Malaysia: 1 ♂ (genitalia on slide TL260 ♂) with same data as holotype except 02.vi.2015; 3 ♂ (genitalia on slide TL641 ♂ & TL338 ♂), 1 ♀ (genitalia on slide TL547 ♀), Sabah, Mesilau, logging site 400 m before entrance to Mesilau Nature Resort, 6°2'22"N, 116°35'54"E, 1930 m, UV light, 02.vi.2015, leg. T. Léger & R. Mally; 1 ♀ (genitalia TL337 on slide TL337 ♀), same data except 01.vi.2015; 1 ♂ (DNA voucher MTD7894, genitalia on slide TL671, wing preparation on slide TL237), Sabah, Kinabalu National Park, Timpohon Gate, 300 m from Ligawu trail starting point, 6°1'41"N, 116°32'54"E, 1820 m, UV light, 18.vi.2015, leg. T. Léger & R. Mally; 1 ♂ (DNA voucher MTD LEP 123, genitalia on slide TL365 ♂), 1 ♀, Sabah, Mesilau, 2000 m, 14–17.xi.2006, light trap, leg. W. Mey & K. Ebert (ZMHB).

Other specimens examined. 1 ♂. Malaysia: 1 ♂ (DNA voucher ITBC02, genitalia on slide TL302 ♀), same data as holotype.

Diagnosis. *Hoploscopa sepanggi* sp. nov. bears sulfurous to pale yellow patches on the forewing forming a roughly chequered pattern. In male genitalia, the gnathos projection is slender, ca. half the length of uncus, and the juxta distal half is narrow, with a notched apex.

Similar species. *Hoploscopa luteomacula*. The postmedian cubital and subterminal patch are missing or reduced to traces in *H. sepanggi* sp. nov., while they are well-marked, pale yellow in *H. luteomacula.* The fringes are brown, chequered with yellow in *H. sepanggi* sp. nov., while they are yellow in *H. luteomacula*.

Description. ***Head.*** Antennae dorsally striped with pale yellow and brown scales. Proboscis brown, speckled with pale yellow. Maxillary palpi brown, base and inner side pale yellow. Labial palpi brown, ventral base and inner side pale yellow.

Thorax (Fig. 5). Thorax dorsally pale yellow, laterally brown. Collar pale yellow. Forewing length: 11–12.5 mm (♂), 11.5–13 mm (♀); forewing ground colour brown; basal patch and median discoidal stigma trapezoid, sulphur yellow with dark brown edges; basal and antemedian cubital patches abutting each other, quadrilateral, sulphur yellow with dark brown edges; costal field sulphur yellow; median patch at dorsum oval, sulphur yellow; postmedian patch triangular, sulphur yellow, invaded with longitudinal brown streak on its middle; subterminal line reduced to small interspaced sulphur yellow dashes, with triangular sulphur costal spot; subterminal field broadly marked with pale yellow; fringe chequered pale yellow and brown. Hindwing pale brown. Forelegs dark brown. Midlegs brown, speckled with pale yellow. Hindlegs with femur brown; tibia pale yellow, speckled with brown, distally brown; tarsi bronze.

Abdomen. Male sternum A8 posterior margin bilobed, with pair of lateral papillae-like protuberances.

Male genitalia (*N* = 5) (Fig. 48). Uncus long and slender, gently tapering toward tongue-shaped apex. Gnathos projection slender, ca. half the uncus length. Valva ventral margin gently bent dorsad on distal 1/3, dorsal margin conspicuously convex, apex slightly pointed. Juxta with base roughly quadrangular, medially narrowed, apex faintly notched. Saccus broad, triangular, pointing dorsad.

Female genitalia (*N* = 3) (Fig. 89). Anterior apophyses with small dorsal bump at 1/3. Antrum sclerotisation twice as long as broad. Ductus bursae thin, slender, elbowed at 1/4 and 3/4. Corpus bursae ovoid, reticulated, diffuse sclerotisation between thorn and corpus opening, medially with faintly sclerotised band. Thorn straight, small, with tiny dents pointing toward thorn base, basally with small outwardly projected extension.

Distribution. Known from the slopes of the Mount Kinabalu on Borneo, at altitudes between 1,800 m and 2,000 m.

Etymology. This species is described in honour of the late Malaysian mountain guide Robbie Sepanggi who died on Mount Kinabalu during the 2015 Sabah earthquake while trying to save hikers.

Hoploscopa cynodonta Léger & Nuss, sp. nov.

http://zoobank.org/55B144AD-1AF7-4023-BC82-E5E2750AFE88
Figs 6, 49, 90

Material examined. ***Holotype*:** ♂, with labels: “Malaysia, Sabah, Kinabalu Park H[ead]Q[quarters], | junction Kiau View- and Pandanus | Trail, 6°0'32.84"N, 116°32'14.94"E, | 1690 m, UV light, 07.vi.2015, | leg. T. Léger & R. Mally”; “DNA voucher | Lepidoptera | MTD 2015 | [vertically written:] no. 3066”; “TL327 | ♂”. Deposited in ZMHB.

***Paratypes*:** 4 ♂, 2 ♀. Brunei: 2 ♂ (1 with NHMUK010923398, DNA voucher MTD8233 & genitalia on slide TL746; 1 with NHMUK010923401), 1 ♀ (NHMUK010923400), Ulu Temburong, LP 298, GR 838892, 300 m, 26–30-iv-1989, leg. M. Allen & K. Tuck (NHMUK). Malaysia: 1 ♂ (genitalia on slide TL531 ♂), Sabah, Kinabalu National Park, Timpohon Gate, 700 m from Liwagu Trail starting point, near Liwagu River, 6°1'40"N, 116°32'59"E, 1700 m, 18.vi.2015, leg. Léger & R. Mally (MTD); 1 ♀ (DNA voucher MTD7425 & genitalia on slide TL625 ♀), Sabah, Tawau Hills National Park, Headquarter, waterfall, 23–27.xi.2006, leg. W. Mey & K. Ebert (ZMHB). 1 ♂ (NHMUK010923352), Sabah, Gunung Monkobo, 5.48N, 116.56E, dipterocarp forest, 945m, 14–23.viii.1987, leg. K. Tuck (NHMUK).

Diagnosis. This relatively small-sized species (forewing length 8–10 mm) shows brown forewings with red markings edged with pale yellow. The median discoidal stigma is oval, red, edged with pale yellow, median cubital patch is reduced to a small streak and median dorsal patch is absent. The postmedian patch consists of a mix of red and brown scales, at costa forming triangular pale yellow patch. Male genitalia are unique in the conspicuously incurved ventral margin of the valva, medially extending into a tip pointing ventrad. In female genitalia, the corpus bursae is small, globular, and bears a crest of sclerotised acanthae between thorn and corpus opening.

Similar species. *Hoploscopa isarogensis* sp. nov.; to a lesser extent *H. mallyi* sp. nov., *H. agtuuganonensis* sp. nov., *H. gracilis* sp. nov., *H. ignitamaculae* sp. nov. Median cubital and dorsal patches form with the median discoidal stigma a disrupted pale yellow band (median dorsal patch not marked in *H. mallyi* sp. nov.), and postmedian pale yellow marking at costa is reduced to a blotch in above listed species. *Hoploscopa gracilis* sp. nov. and *H. mallyi* sp. nov. are slightly larger (9–12 mm). Comparison of the male genitalia allows unequivocal separation from these species. In female genitalia, *H. isarogensis* sp. nov. displays a narrower and slightly longer ductus bursae and a larger corpus bursae with large curved thorn, while it is small and straight in *H. cynodonta* sp. nov. Female genitalia of *H. mallyi* sp. nov., *H. agtuuganonensis* sp. nov., and *H. gracilis* sp. nov. share the broad ductus bursae, the small globular corpus bursae with *H. cynodonta* sp. nov. but have a longer ductus bursae, and the sclerotisation of corpus bursae is large and diffuse.

Description. *Head.* Antennae dorsally with pale yellow scales. Proboscis brown to pale brown. Maxillary palpi brown, base and inner side pale yellow. Labial palpi brown, ventrally pale yellow.

Thorax (Fig. 6). Collar white. Forewing length: 8–10 mm (♂), 8 mm (♀); forewing ground colour brown; basal longitudinal red streak basally surrounded with pale yellow U-shaped spot; costal field red; median discoidal stigma oval, red with pale yellow edges; median cubital patch forming longitudinal pale yellow rectangle; postmedian patch red, with basal edge pale yellow, distally abutted with pale yellow triangular costal patch; postmedian line costally marked; postmedian suffusion of pale yellow and pale brown scales, distally edged by pale yellow subterminal line; subterminal field marked with red; fringe chequered pale yellow and brown. Hindwing pale brown. Forelegs and midlegs brown. Hindlegs with femur brown; tibia pale yellow, distally brown; tarsi bronze speckled with pale yellow.

Abdomen. Male sternum A8 posterior margin forming two conspicuous triangular tips, laterally with pair of papillae-like protuberances.

Male genitalia (*N* = 2) (Fig. 49). Uncus medially slightly widened, narrowing toward apex, apex duck beak-shaped, medio-ventrally with a bump and two ridges. Gnathos projection tongue-shaped, ca. 1/4 of uncus length. Valva ventral margin with basal half sclerotised, at 1/4 conspicuously incurved into a semi-circle, protruded medio-ventrally into a tooth-like tip pointing ventrad, with marked ridge on inner side; valva dorsal margin convex, apex truncate. Juxta with base rounded, medially narrowed, apical half laterally protruded, with few scattered hairs, apex broad, not sclerotised. Saccus quadrangular, conspicuously produced anterad.

Female genitalia (*N* = 1) (Fig. 90). Anterior apophyses with small dorsal bump at 1/3. Posterior apophyses bent ventrad. Antrum sclerotisation twice as long as broad, barely sclerotised. Ductus bursae relatively short, broad, with a narrow loop before corpus bursae. Corpus bursae globular, reticulated, with crest of sclerotised acanthae between thorn and corpus opening. Thorn straight, slightly incurved at apex, with small dents pointing toward thorn base.

Distribution. Known on Borneo from Brunei to the Mount Kinabalu, the Mount Monkobo (1,759m) and the Tawau Hills in Sabah (Malaysia), at altitudes between 300 and 1,700 m.

DNA barcoding. Specimens LEP3066 from Mount Kinabalu and MTD7425 from Tawau Hills differ by 0.4%. The nearest neighbour is *H. isarogensis* sp. nov. from the Philippines (K2P-dist = 2.3–3%).

Etymology. Formed by apposition of the Greek words *cyno-*, of the dog, and *odous*, tooth, referring to the conspicuous tooth-like extension on the ventral margin of the valva in male genitalia.

Hoploscopa parvimacula Léger & Nuss, sp. nov.

http://zoobank.org/4E445DD3-8C71-40DE-9EDB-870935206EDE

Figs 7, 50, 91

Material examined. ***Holotype***: ♂, with labels: "Malaysia, Sabah, Mesilau, logging | site 400m before entrance to Mesilau | Nature Resort, 6°2'21.97"N, 116°35'54.12"E, 1930m, UV light, | 02.vi.2015, leg. T. Léger & R. Mally"; "DNA voucher | Lepidoptera | MTD2016 | [vertically written:] n°. 3196 "; "TL510 | ♂". Deposited in ZMHB.

Paratypes: 7 ♂, 2 ♀. Malaysia: 1 ♂ (DNA voucher MTD7888 & genitalia on slide TL552 ♂) with same data as holotype, 2 ♂ (DNA vouchers MTD7884 & MTD7885, genitalia on slides TL673 ♂ & TL261 ♂), 1 ♀ (DNA voucher MTD7883 & genitalia on slide TL551 ♀) with same data as holotype except 02.vi.2015; 1 ♂ (DNA voucher MTD7886, genitalia on slide TL537 ♂), Sabah, Mesilau Nature Resort, 6°2'44"N, 116°35'48"E, 1925 m, at lamps, 30.v.2015, leg. T. Léger & R. Mally; 1 ♀ (DNA voucher ITBC12, DNA barcoding voucher BC MTD LEP3003, genitalia on slide TL312 ♀), same data except 01.vi.2015; 2 ♂ (DNA vouchers MTD7895 & MTD7896, genitalia on slides TL550 ♂ & TL549 ♂), Sabah, Kinabalu National Park, Timpohon Gate, 300 m from Liwagu trail starting point, 6°1'41"N, 116°32'54"E, 1820 m, UV light, 18.vi.2015, leg. T. Léger & R. Mally; 1 ♂ (DNA voucher MTD7890, genitalia on slide TL672 ♂), Sabah, Kundasang, Kinabalu Mountain Lodge veranda, 6°0'42"N, 116°32'4"E, 1570 m, at light, 18.vi.2015, leg. T. Léger & R. Mally (ZMHB).

Diagnosis. *Hoploscopa parvimacula* sp. nov. displays brown forewings with reduced pale yellow markings. The median discoidal stigma forms a crescent shape, and the median cubital patch forms a streak not connected to the median discoidal stigma. The postmedian patch and postmedian area are faintly marked with pale yellow. In male genitalia, the gnathos projection is distally spatula-shaped, reaching ca. 2/3 of the uncus length, and the juxta displays blunt lateral projections and a truncate apex.

Similar species. *Hoploscopa kinabaluensis* sp. nov., *H. pangrangoensis* sp. nov. The forewings of *H. kinabaluensis* sp. nov. display more contrasting postmedian patch and subterminal line, and a subterminal field suffused with pale yellow. In *H. pangrangoensis* sp. nov., the median cubital patch is almost absent and the subterminal line is more strongly pronounced. In male genitalia, base of gnathos projection is narrower and the cornutus displays a narrow bump at apex in *H. kinabaluensis* sp. nov. The finger-like gnathos projection of *H. pangrangoensis* sp. nov. is narrower than that of *H. parvimacula* sp. nov. and reaches only half the uncus length. In female genitalia, ductus bursae of *H. kinabaluensis* sp. nov. is twice as long as in other species, with a loop on its middle and a large bow before corpus bursae. In *H. pangrangoensis* sp. nov., colliculum is membranous with longitudinal sclerotised lines, corpus bursae is larger and thorn is smaller.

Description. ***Head.*** Antennae dorsally striped with brown and bronze scales. Proboscis pale yellow, speckled with pale brown. Maxillary palpi dark brown, base and inner side pale yellow. Labial palpi dark brown, ventro-basally pale yellow.

Thorax (Fig. 7). Collar pale yellow. Forewing length: 9–10 mm (♂ & ♀); forewing ground colour brown; basal dark brown dash, distally pale yellow; basal and distal discoidal stigmata dark brown; median patches Y-shaped, pale yellow, disrupted with brown at vein, edged basally and distally with dark brown; postmedian patch of a lighter brown, with pale yellow triangular costal spot distally edged with dark brown; subterminal line pale yellow, distally dark brown; fringe brown, with pale yellow dots. Hindwing pale brown. Forelegs brown. Midlegs with femur brown; tibia pale yellow, speckled with brown; tarsi bronze. Hindlegs with femur brown; tibia pale yellow, speckled with brown; tarsi pale yellow to pale brown.

Abdomen. Male sternum A8 posterior margin bilobed, with pair of lateral papillae-like protuberances.

Male genitalia (*N* = 8) (Fig. 50). Uncus medially broadened, narrowing on distal half, apex slightly obtuse. Gnathos projection ca. 2/3 of uncus length, spatula-shaped. Valva ventral margin straight, gently bent dorsad on distal 1/4, dorsal margin convex, apex rounded or slightly pointed. Juxta slender, base roughly quadrangular, apex truncate. Saccus small, pointing dorsad.

Female genitalia (*N* = 2) (Fig. 91). Anterior apophyses with dorsal bump at posterior 1/3. Antrum sclerotisation twice as long as broad. Ductus bursae short and straight, slightly bent before corpus bursae. Corpus bursae pear-shaped, posterior half reticulated, anterior half membranous, with diffuse sclerotisation between thorn and corpus opening, medially with faintly marked sclerotised band. Thorn short and straight, with small dents pointing toward thorn apex.

Distribution. Known from Mount Kinabalu on Borneo, at altitudes between 1,550 and 1,950 m.

DNA barcoding. Sample MTD8229 of *H. parvimacula* sp. nov. shows a K2P-dist of 3.1–3.4% with samples from Borneo and is recovered as separate MOTU.

Phylogenetic relationships. The specimen MTD8229 is recovered as sister to *H. parvimacula* sp. nov. (BS = 97).

Etymology. Refers to the Latin *parvus*, for small, and *macula*, for spot, referring to the Y-shaped median markings that are smaller than in other similar species.

Remarks. The specimen with DNA voucher MTD8229 belongs to a series of females from the Malay Peninsula, which are morphologically similar to *H. parvimacula* sp. nov. and deposited at NHMUK. Since no males of the same series were available for investigations, we restrained from drawing further conclusions here.

Hoploscopa kinabaluensis **Léger & Nuss, sp. nov.**

http://zoobank.org/F75F92C1-7C04-4BE9-A602-0FE822BF66D2

Figs 8, 51, 92

Type material. ***Holotype*:** ♀, with labels: "Malaysia, Sabah, Kundasang | Kinabalu Mt. Lodge veranda, | 6°0'42.15"N, 116°32'3.63"E, | 1570m, at light, 16.vi.2015, | leg. T. Léger & R. Mally"; "DNA voucher | Lepidoptera | MTD 2015 | [vertically written:] no. 3064"; "TL325 ♀". Deposited in ZMHB.

***Paratypes*:** 3 ♂, 4 ♀. Malaysia: 1 ♂ (DNA voucher MTD7889, genitalia on slide TL667 ♂), same data as holotype; 1 ♂ (DNA voucher MTD7893 & genitalia on slide TL342 ♂), 1 ♀ (DNA voucher MTD LEP3065 & genitalia on slides TL326 ♀), Sabah, Kinabalu National Park, Timpohon Gate, 700 m from Liwagu trail starting point, near Liwagu River, 6°1'40"N, 116°32'59"E, 1760 m, UV light, 18.vi.2015, leg. T. Léger & R. Mally; 1 ♂ (DNA voucher MTD7897, genitalia on slide TL341 ♂), Sabah, Kinabalu National Park, Timpohon Gate, 300 m from Liwagu trail starting point, 6°1'41"N, 116°32'54"E, 1820 m, UV light, 18.vi.2015, leg. T. Léger & R. Mally; 1 ♀ (DNA voucher MTD7882, TL666 ♀), Sabah, Kinabalu National Park Headquarters, junction Kiau View- and Pandanus Trail, 6°0'32.84"N, 116°32'15"E, 1690 m, UV light, 07.vi.2015, leg. T. Léger & R. Mally; 1 ♀ (DNA voucher MTD7887, genitalia on slide TL662 ♀), Sabah, Kundasang, road 200 m before Kinabalu Mt. Lodge, 6°0'37"N, 116°32'4"E, 1535m, UV light, 03.vi.2015, leg. T. Léger & R. Mally (MTD).

Other specimens examined. 1 ♂, 2 ♀. Malaysia: 1 ♂ (DNA voucher MTD7892, genitalia on slide TL546 ♂), 1 ♀ (DNA voucher MTD7891 & genitalia on slide TL674 ♀), Sabah, Kinabalu National Park, Timpohon Gate, 700 m from Liwagu trail starting point, near Liwagu River, 6°1'40"N, 116°32'59"E, 1760 m, UV light, 18.vi.2015 (T. Léger & R. Mally); 1 ♀ (NHMUK 010923435, DNA voucher MTD8232 & genitalia on slide TL745 ♀), Sabah, Gunung Monkobo, dipterocarp forest, 975m, 5.48N, 116.56E (7–13.viii.1987) (NHMUK).

Diagnosis. The forewing median markings form an interrupted pale yellow Y, and postmedian patch and subterminal line are pale yellow, well-marked. In male genitalia, the gnathos projection is ca. 2/3 of uncus length, spatula-shaped, broadening toward apex, and the cornutus displays a small but conspicuous bump. Female genitalia show a long ductus bursae broadly curved twice and a large pear-shaped corpus bursae.

Similar species. *Hoploscopa parvimacula* sp. nov. (q.v.), *H. brunnealis*, *H. danaoensis* sp. nov., *H. metacrossa*. These species share similar forewing markings with

H. kinabaluensis sp. nov. Male genitalia of these species show a gnathos projection larger at base, of constant width, reaching ca. half of uncus length, and a cornutus lacking the apical bump. In female genitalia, the shorter ductus bursae is nearly straight.

Description. *Head.* Antennae dorsally striped with pale yellow and bronze scales. Proboscis brown speckled with pale yellow. Maxillary palpi brown, base and inner side pale yellow. Labial palpi brown, ventral base and inner side pale yellow.

Thorax (Fig. 8). Thorax dorsally pale yellow, laterally brown. Collar pale yellow. Forewing length: 9.0–10.5 mm (♂), 10–11 mm (♀); forewing ground colour brown; basal dark brown dash, distally pale yellow; median discoidal stigma and median cubital patch forming together a pale yellow-coloured Y, disrupted with brown at vein, edged basally and distally with dark brown; postmedian patch roughly triangular, pale yellow, invaded with brown, edged with dark brown; subterminal line thick, pale yellow; fringe chequered pale yellow and brown. Hindwing pale brown. Forelegs brown. Midlegs with femur brown; tibia brown, inwardly pale yellow; tarsi bronze. Hindlegs with femur brown; tibia pale yellow, speckled with brown; tarsi bronze, speckled with brown.

Abdomen. Male sternum A8 posterior margin broadly indented, with pair of lateral papillae-like protuberances.

Male genitalia ($N = 4$) (Fig. 51). Uncus broad, gently narrowing on distal half, apex obtuse. Gnathos projection ca. 2/3 of uncus length, narrow at base, widening toward apex, apex spatula-shaped. Valva ventral margin straight, gently bent dorsad on distal 1/3, dorsal margin convex, apex rounded or slightly pointed. Juxta slender, base roughly quadrangular, apex slightly incurved. Saccus small, pointing dorsad. Phallus with elongated cornutus, at posterior end with narrow bump pointing dorsad.

Female genitalia ($N = 5$) (Fig. 92). Anterior apophyses with tip or bump at posterior 1/3. Antrum sclerotisation ca. twice as long as broad. Ductus bursae long, slender, with one loop, curved before corpus bursae. Corpus bursae conspicuously ovoid, reticulated, with sclerotisation between thorn and corpus opening and faintly marked sclerotised band medially. Thorn long, slightly curved, with small dents pointing toward thorn apex.

Distribution. Known from the slopes of Mount Kinabalu and Mount Monkobo on Borneo, from altitudes between 975 m and 1,850 m.

DNA barcoding. Two MOTUs diverging by 1.7–2.2% are recovered in *H. kinabaluensis* sp. nov. These two lineages are found in sympatry at Mount Kinabalu.

Etymology. The species name *kinabaluensis* refers to Mount Kinabalu on Borneo, where the species occurs.

Remarks. The two barcode lineages show no differences in wing pattern and female genitalia. Only minor differences are found in male genitalia, with the apex of the gnathos projection slightly narrower and the basal margin of the juxta slightly incurved in the second lineage. Since second MOTU is only represented by three specimens including only one male, we restrained ourselves from describing a new species here.

Hoploscopa luteomacula Nuss, 1998

Figs 9, 52, 93

Material examined. ***Holotype*****:** ♂, with labels: "Holotypus"; "Sumatra, Barat | N-Padangpanjang | Mt. Singgalang 2100m | 10–11.ii.1996, L[icht]F[ang] [light trap] | leg. A. Kallies"; "HOLOTYPE | Hoploscopa luteomacula | det. Nuss, 1996"; "GU 744 | prep. Nuss 1996"; "Coll. M. Nuss | Geschenk 2000 | Museum für Tier- | kunde Dresden". Deposited in MTD.

Paratype**:** 2 ♀. Indonesia: 1 ♀ (genitalia on slide GU 743, DNA barcode BC MTD 01419), same data as holotype; 1 ♀ (genitalia in capsule under specimen), Sumatra, Holzweg 2, 25km SSW-Pematangsiantar, Strasse nach Prapat [road to Prapat], 25.x.1989, leg. E. W. Diehl (MTD).

Other material examined. 1 ♂, 1 ♀. Brunei: ♀ (NHMUK010923403, DNA voucher MTD8234 & genitalia on slide TL747 ♀), Ulu Temburong, LP 298, GR 838892, 300m, 26–30.iv.1989 (M. G. Allen & K. R. Tuck). Malaysia: 1 ♂ (DNA voucher MTD LEP 3195 & genitalia on slide TL525 ♂), Sabah, Kundasang, road 200m before Kinabalu Mt. Lodge, 6°0'37.38"N, 116°32'0.35"E", 1535m, UV light, 03.vi.2015, leg. T. Léger & R. Mally (ZMHB).

Diagnosis. *Hoploscopa luteomacula* displays broad pale yellow patches in the forewing. In male genitalia, the uncus is rectangular with a truncate apex, the gnathos forms a tongue-shaped projection ca. 1/4 of the uncus length, the juxta is medially conspicuously narrowed and displays a duck-shaped apex.

Similar species. No similar species known.

Description. ***Head.*** Antennae dorsally pale yellow. Proboscis pale yellow. Maxillary palpi brown, base and inner side pale yellow. Labial palpi brown, ventral base and inner side pale yellow.

Thorax (Fig. 9). Thorax brown, dorsally pale yellow. Collar pale yellow. Forewing length: 9–11 mm (♂ & ♀); forewing ground colour brown, with markings pale yellow; basal patch large, rhomboid, slightly encroached with brown near dorsum; small basal discoidal spot; median discoidal stigma trapezoid; costal field pale yellow, speckled with brown; median cubital and dorsal patches rhomboid; postmedian patch quadrangular to elliptic, dorsally invaded with brown; postmedian cubital patch rhomboid; subterminal costal patch triangular; subterminal field more or less broadly marked with pale yellow; fringes pale yellow, sometimes with tiny brown dots, apex brown. Hindwing pale yellow to pale brown. Forelegs femur pale yellow; tibia brown, inner side pale yellow; tarsi pale yellow speckled with bronze. Midlegs with femur pale yellow; tibia and tarsi brown. Hindlegs pale yellow.

Male genitalia (*N* = 1) (Fig. 52). Uncus large, rectangular, slightly narrowed at apical 1/4, apex truncate. Gnathos projection tongue-shaped, ca. 1/3 of uncus length. Valva ventral margin nearly straight, dorsal margin convex, apex blunt. Juxta with large rounded base, medially conspicuously narrowed, apex duck beak-shaped. Saccus small, pointing dorsad.

Female genitalia (*N* = 1) (Fig. 93). Anterior apophyses with dorsal bump at posterior 1/3. Antrum sclerotisation reduced to sclerotised ring. Ductus bursae short, nearly straight. Corpus bursae large, pear-shaped, reticulated on posterior half, anterior half membranous, with faint sclerotisation between thorn and corpus opening. Thorn nearly straight, with dents pointing toward thorn apex, basally with small outwardly projected extension.

Distribution. Known from Sumatra (Indonesia) at altitudes between 1,200 m and 2,100 m.

DNA barcoding. Specimens MTD8234 and MTD LEP 3195 from Borneo show an K2P-distance of 2.5–4.4% with the specimen from Sumatra and are recovered as a distinct MOTU.

Remarks. Deep barcode divergence between morphologically similar specimens from Borneo and Sumatra might represent phylogeographic variability or distinct species. Additional material from both regions and a broader set of characters is needed to test these hypotheses.

Hoploscopa obliqua (Rothschild, 1915)

Figs 10, 53, 94

Material examined. ***Holotype*:** ♂, with labels: "Holo- | type" [round label, red ringed]; "Utakwa R[iver]., | Dutch N[ew]. Guin[ea]., | 3000 f[ee]t., Jan[uary]. 1913. | A.F.R. Wollaston."; "437"; "Eudorina | obliqua | Type Rotsch[ild]." [handwritten]; "♂ | Pyralidae | Brit[ish].Mus[eum]. | Slide N°. | 20252"; "N,HMUK 010923283" [barcode appended]. Deposited in NHMUK.

Other specimens examined. Papua New Guinea: 2 specimens [abdomens lost] (1 with DNA voucher "USNM ENT 00665932", 1 with DNA voucher "USNM ENT 00514731"), 1 ♀ (DNA voucher "USNM ENT 00514750", genitalia on slide TL656 ♀), Madang Province, Wanang village, 05°15'S, 145°17'E, 1700 m, reared from *Diplazium esculentum*, 12.vi.2007, leg. Auga, Molem, Tamtiai, Lilip, Ibalim, Posman, Rimandai, Brus, Novotny, Hrcek (USNM).

Diagnosis. The antennae striped with white and the antemedian oblique white streak extended distally into white suffusion in the forewing are unique to this species. In male genitalia, the gnathos projection forms a broad plate with a small apical tip. In female genitalia, the antrum is membranous, the ductus bursae is long and corpus bursae is densely covered with erect papillae on one half.

Similar species. No similar species known.

Description. ***Head.*** Antennae dorsally striped with brown and white. Proboscis brown. Maxillary palpi brown, base pale brown, apex white. Labial palpi brown with white apex.

Thorax (Fig. 10). Collar white. Forewing length: 8–9 mm (♂ & ♀); forewing ground colour brown; basal area of a darker brown; antemedian oblique thick white streak running from dorsum to upper margin of cell, distally extended into white suffusion; postmedian patch reduced to costal white blotch; postmedian line of a darker brown at costa; barely marked subterminal white line incurved inwards at CuA2, running up to M2; fringes pale brown. Hindwing pale brown. Fore- and midlegs brown, tibia and tarsi segments distally white. Hindlegs brown.

Male genitalia (N = 1) (Fig. 53). Uncus medially conspicuously widened, narrowed at apical 1/4, apex spatulate. Gnathos projecting into a broad spatula-shaped plate with small apical tip on its middle. Valva ventral margin gently bent dorsad on distal 1/3, dorsal margin convex, apex pointed. Juxta slender, with base rounded, apex obtuse. Saccus small, pointing dorsad.

Female genitalia (N = 1) (Fig. 94). Anterior apophyses bent ventrad at 1/3. Antrum membranous. Ductus bursae long, straight. Corpus bursae globular, with one half reticulated, one half with erect papillae, with sclerotised bump on each side of thorn. Thorn straight, broad at base, tapering at mid-length, with small dents pointing toward thorn apex. Phallus with club-shaped cornutus.

Distribution. Known from the Papua (Indonesia) and Madang Provinces (Papua New Guinea) on New Guinea, at altitudes between 1,000 m and 1,700 m.

Phylogenetic relationships. *Hoploscopa niveofascia* sp. nov. is recovered as sister group in the ML analysis of the COI barcode (BS = 95).

Remarks. Nuss (1998) transferred this species from *Eudorina* to *Hoploscopa*.

Hoploscopa niveofascia Léger & Nuss, sp. nov.

http://zoobank.org/4112C427-AF2B-4CAE-BDB3-E94033B8E8C2

Figs 11, 56

Material examined. ***Holotype***: ♂, with labels: "Papua New Guinea | Morobe Prov[ince]., n[ea]r. Bulolo | Mt. Susu Nat[ional]. Res[erve]., 975m | 27–28 Aug.1983, S. Miller | UV Lite, Araucaria For[est]"; "DNA voucher | Lepidoptera | MTD2016 | [vertically written:] no. 3162"; "TL442 | ♂". Deposited in USNM.

Diagnosis. *Hoploscopa niveofascia* sp. nov. displays snow white postmedian patch, subterminal line and well-marked marginal spots on the forewing. In male genitalia, the uncus is broad, with straight lateral margin and a blunt apex. Female genitalia not known.

Similar species. *Hoploscopa diffusa*. *Hoploscopa niveofascia* sp. nov. shares with *H. diffusa* the white markings of the forewing. However, postmedian patch of *H. diffusa* is broadly marked with brown, marginal spots are reduced to small dots, and fringes exhibit white spots, while fringes are brown in *H. niveofascia* sp. nov.

Description. ***Head.*** Antennae dorsally dark brown. Proboscis white. Maxillary palpi dark brown, basally pale brown. Labial palpi dark brown, ventro-basally white.

Thorax (Fig. 11). Thorax dark brown with mesodorsal transversal white line. Collar white. Forewing length: 9.5 mm; forewing ground colour dark brown; basal area without marked patches, white scales scattered near dorsum; median discoidal stigma darker coloured, rectangular, basally and distally thinly edged with white; postmedian patch diffuse, white; postmedian line marked on costal half; subterminal line thick, zigzagging, disrupted distally at M1; margin with large white spots; fringes bronze. Fore- and midlegs dark brown, with tibia and tarsi segments distally white. Hindlegs brown to bronze.

Abdomen. Male sternum A8 posterior margin straight.

Male genitalia (N = 1) (Fig. 56). Uncus broad with straight lateral margin, apex truncate, medially slightly incurved. Gnathos reduced to thin band without posterior projection. Valva ventral margin bent dorsad on distal half, dorsal margin slightly convex, apex pointed. Juxta elongated, with base rounded, medially narrowing, apex blunt. Saccus small, pointing dorsad.

Female genitalia Not known.

Distribution. Known from Mount Susu (975 m) in the Morobe Province (Papua New Guinea).

Phylogenetic relationships. *Hoploscopa obliqua* is recovered as sister group in the ML analysis of the COI barcode (BS = 95).

Etymology. From the Latin *niveus*, snowy, and *fascia*, band, referring to the snow-white markings on the forewing.

Hoploscopa gombongi Léger & Nuss, sp. nov.

http://zoobank.org/74AD0BB2-8718-42BA-88A3-0C6236302D18

Figs 12, 54, 96

Material examined. ***Holotype***: ♂, with labels: [exuvia pinned under the specimen] “Sp. PYRA-106 | YS.2H.3826 | CATY 001 L[ength] 9mm | YC 29975 Leaf M [circled] Y | Roll [circled] - Tie - Chew - Skel | 10-SEP-2012 [handwritten]”; “Papua New Guinea | Yawan village | 06°10'S, 146°5'E [1700m] | L[e]g[i]t B Gewa, J. Kua, | S Sau, A. Kinibel | NG Binatang Res[earch]. C[en]t[e]r.”; “USNM ENT: PNG | Madang Ecology Project | [barcode] | 00739216” [DNA voucher]; “DNA 2013”; “TL | 653 ♂”. Deposited in USNM.

Paratypes: 1 ♂, 2 ♀. Papua New Guinea: 1 ♂ (“YC29970”, DNA voucher “00739200”), 1 ♀ (“YC29974”, DNA voucher “00739238”, genitalia on slide TL654 ♀), same data as holotype except “L=19mm”, “Chew” (♂), “Leaf Y”, “L=14mm”, “Tie” (♀), leg. M. Rimandai, S. Sau, A. Kinibel, M. Jimbudo; 1 ♀ (“YC28238”, DNA voucher “00739199” & MTD7872, genitalia on slide TL657 ♀), same data as holotype except “Chew”, “L=15mm”, 11.ix.2012, leg. M. Rimandai, S. Sau, A. Kinibel, M. Jimbudo (USNM).

Diagnosis. The well-marked median cubital and dorsal snow-white patches on the forewing segregate this species from its congeners. Median discoidal stigma is trapezoid, reddish brown, postmedian patch is reddish brown, distally edged by thin white streak. In male genitalia, the narrow uncus-tegumen connection and the broadly indented uncus apex is unique to this species. In female genitalia, papillae anales are thick, not connecting dorsally and ventrally, corpus bursae is small, globular, with a long straight thorn.

Similar species. No similar species known.

Description. ***Head.*** Antennae dorsally brown. Proboscis pale brown. Maxillary palpi dark brown, base and inner side pale yellow to light brown. Labial palpi dark brown, ventro-basally pale yellow.

Thorax (Fig. 12). Collar white. Forewing length 10–11 mm (♂), 9–10 mm (♀); forewing ground colour dark brown; cubital reddish brown fascia running from basal to postmedian area; basal and distal discoidal patches of a darker brown; rhombical reddish orange median discoidal stigma therebetween, basally and distally thinly edged with pale yellow; median cubital and dorsal patches white, elongated, slightly disrupted at 1A+2A; median reddish brown streak running between CuA1 and CuA2 parallel to cubital fascia; postmedian roughly quadrangular reddish brown patch, crossed with brown lines, with slender white streak abutting dorsally, running up to costa; postmedian line thin, marked on costal half; postmedian fascia white, speckled with brown; subterminal line thin, white, running more or less straight from dorsum distal 1/4 to apex; subterminal field faintly marked with reddish brown; fringes brown, with pale yellow dots. Hindwing pale yellow, slightly darker at apex. Legs brown, tibia distally pale yellow, tarsi brown to pale brown.

Abdomen. Male sternum A8 posterior margin bilobed.

Male genitalia (*N* = 1) (Fig. 54). Uncus slender, entirely sclerotised, forming narrow connection to tegumen, narrowed on its middle, apex large, broadly indented. Gnathos reduced to barely sclerotised band. Tegumen arms dorso-posteriorly not fused. Valva slender, ventral margin nearly straight, gently bent dorsad on distal 1/4, dorsal margin convex, valva apex pointed. Juxta with base rounded, medially slightly narrowed with weakly sclerotised edges, apex broadly rounded, flanked on each side with sclerotised bump covered with setae. Saccus not pronounced. Phallus apically with sclerotised spine.

Female genitalia (*N* = 2) (Fig. 96). Papillae anales thick, dorsally and ventrally not connected. Posterior apophyses bent dorsad. Anterior apophyses widened at posterior 1/3, with tip pointed dorsad. Antrum sclerotisation as long as broad. Ductus bursae long, more or less straight. Corpus bursae small, globular, reticulated, with sclerotisation between thorn and corpus opening. Thorn straight, with small dents pointing toward thorn base, basally with small outwardly projected extension.

Distribution. Known from Yawan village (1,700 m) in the Eastern Highlands Province (Papua New Guinea).

Biology. The moths were reared from the fern *Diplazium esculentum* (Retzius in Retzius & König, 1791) Swartz, 1803 (Athyriaceae) (S. Miller, C. Redmond & T. Whitfield, pers. comm.).

Etymology. The species epithet *gombongi* comes from "gombong", the name for fern in the Yau language (https://www.ethnologue.com/language/yuw), referring to the larval host plant. This name was suggested by Vojtěch Novotný and Gibson Mayiah.

Hoploscopa tonsepi Léger & Nuss, sp. nov.

http://zoobank.org/B0664603-AEC3-4D7B-8A99-146A6359A88C

Figs 13, 55, 101

Material examined. ***Holotype*:** ♂, with labels: [exuvia in a capsule pinned under the specimen] "Sp. PYRA-106 | YP.4B.4041 | CATY 002 L 11 mm | YC 30471 Leaf M [circled] Y | Roll - Tie - Chew [circled] - Skel | 13 OCT 2012 [handwritten]"; "Papua New Guinea | Yawan village | 06°10'S, 146°5'E [1700m] | L[e]g[i]t J. Valeba, J. Auga | M. Dilu, F. Philip, R. Lilip | NG Binatang Res[earch]. C[en]t[e]r."; "USNM ENT: PNG | Madang Ecology Project | [barcode] | 00739227" [DNA voucher]; "DNA 2013"; "TL | 655 ♂". Deposited in USNM.

Paratypes**:** 2 ♂, 1 ♀. Papua New Guinea: 1 ♂ ("YC30467", DNA voucher MTD7874 & "00739207", genitalia on slide TL661 ♂), same data as holotype except "CATY 001, L = 15 mm"; 1 ♀ ("YC30472", DNA voucher "00739208"), same data as holotype except "CATY 001, L = 15 mm", leg. B. Gewa, J. Kua, S. Sau, A. Kinibel; 1 ♀ ("YC30473", DNA voucher "00739234" & MTD7873, genitalia on slide TL658 ♀), same data as holotype except "L = 10 mm" "Roll", leg. B. Gewa, J. Kua, S. Sau, A. Kinibel (USNM).

Diagnosis. *Hoploscopa tonsepi* sp. nov. displays a triangular reddish brown median discoidal stigma with white edges, extending toward dorsum into narrow white cubital streak. In male genitalia, the two-armed uncus with two small tips on its middle is unique to this species. In female genitalia, the absence of posterior apophyses, the short ductus bursae and the small corpus bursae without thorn are atypical for the genus and observed only in this species.

Similar species. No similar species known.

Description. ***Head.*** Antennae dorsally striped with brown and bronze scales. Proboscis pale yellow, brown at base. Maxillary palpi dark brown, base and inner side pale yellow to light brown. Labial palpi dark brown, ventro-basally pale yellow.

Thorax (Fig. 13). Collar pale yellow. Forewing length: 9–10 mm (♂ & ♀); forewing ground colour brown, broadly suffused with reddish brown; basal oblique thin white streak; cubital reddish brown fascia running from basal to postmedian area; basal and distal discoidal patches of a darker brown, basally and distally thinly edged with white; median discoidal stigma reddish brown, with V-shaped white edge, together with narrow white cubital streak forming a Y; postmedian patch roughly triangular, reddish brown, crossed with brown lines, abutted with pale yellow blotch at costa; postmedian line broad, marked on costal half; postmedian suffusion faintly marked, pale yellow; subterminal line pale yellow, diffuse, running more or less straight from dorsum distal 1/4 to apex; subterminal field marked with reddish brown; fringes brown, with pale yellow dots. Hindwing pale brown, darker at apex. Forelegs dark brown; tibia dark brown, distally pale yellow; tarsi pale yellow. Midlegs with femur dark brown; tibia pale yellow, speckled with brown, distally brown; tarsi pale yellow. Hindlegs brown; tibia and tarsi segments distally pale yellow.

Abdomen. Male sternum A8 posterior margin bilobed.

Male genitalia (*N* = 2) (Fig. 55). Uncus broad, entirely sclerotised, on distal half extending into two arms with rounded tip, with small dent on inner side, margin between arms with two small tips on its middle. Gnathos projection plump, ca. 2/3 of uncus length. Valva slender, ventral margin nearly straight, dorsal margin slightly convex, apex pointed. Juxta with base roughly rounded, medially narrowed, apex blunt, slightly incurved. Saccus slightly quadrangular. Coecum penis reduced to a short protrusion.

Female genitalia (*N* = 1) (Fig. 101). Papillae anales thick, dorsally and ventrally not connected. Posterior apophyses absent. Anterior apophyses without bump at posterior 1/3. Antrum sclerotisation short. Ductus bursae short, slender, straight. Corpus bursae very small, ovoid, covered with tiny papillae. Corpus sclerotisation and thorn absent.

Distribution. Known from the Yawan village (1,700 m) in the Eastern Highlands Province (Papua New Guinea).

Biology. The moths were reared from *Diplazium esculentum* (Retzius in Retzius & König, 1791) Swartz, 1803 (Athyriaceae) (S. Miller, C. Redmond, & T. Whitfield, pers. comm.).

Etymology. Named after Tonsep, a village leader from Papua New Guinea who locally conducted the project on which the larvae were collected and reared to adults.

Hoploscopa marijoweissae Léger & Nuss, sp. nov.

http://zoobank.org/D8FBB3AC-2B4B-436E-B939-70FB9B5E9336

Figs 14, 57, 95

Material examined. ***Holotype*:** ♂, with labels: "M[oun]t. Goliath [Mount Yamin], | 5000 f[ee]t., Centr[al]. Dutch N[ew]. Guinea, | ca. 139° long, | February 1911, | (A. S. Meek)."; "N,HMUK 010923397" [barcode appended]; "TL | 710 ♂". Deposited in NHMUK.

***Paratypes*:** 1 ♂, 1 ♀. Indonesia: 1 ♂ (NHMUK010923399), 1 ♀ (NHMUK010923351, genitalia on slide TL 709 ♀), same data as holotype (NHMUK).

Other specimens examined. 1 ♂. Papua New Guinea: 1 ♂, (DNA voucher MTD LEP 3157 & genitalia on slide TL437 ♂) Morobe Province, Mount Kaindi, 2350 m, 11.xii.1976, leg. G. F. Hevel & R. E. Dietz (USNM).

Diagnosis. This species is recognisable by the brown forewings broadly suffused with copper-coloured scales giving them a shiny appearance. Median cubital patch is white, discoidal stigma and postmedian patch are yellow, the latter marked with white toward dorsum and at costa. In male genitalia, uncus is elongated, with a truncate apex, and gnathos projection is ca. half the length of uncus, with truncate apex. In female genitalia, antrum is barely sclerotised, ductus bursae is long, slender and straight and corpus bursae is large, globular, with a small slightly curved thorn.

Similar species. No similar species known.

Description. ***Head.*** Antennae dorsally bronze. Proboscis pale yellow. Maxillary palpi brown, inner side pale brown. Labial palpi brown, ventrally pale yellow, inner side pale brown.

Thorax (Fig. 14). Collar pale yellow. Forewing length 11 mm (♂), 12 mm (♀); forewing ground colour brown; broad basal yellow band stretching from subdorsum to costa, with crossing veins copper-coloured, edged with copper; costal field copper; median discoidal stigma yellow with copper edges, costally filled with copper, forming together with cubital trapezoid white patch a canine tooth shape; postmedian patch broad, yellow, basally encroached with copper, crossing veins copper-coloured, with white blotch at costa; postmedian line broad, marked on costal half; broad copper postmedian fascia with crossing veins brown; subterminal field marked with a mix of yellow and copper scales; fringe brown, with white dots. Hindwing white to pale brown. Forelegs brown. Midlegs with femur brown; tibia pale yellow, apically brown; tarsi pale yellow to pale brown. Hindlegs with femur brown; tibia pale yellow, speckled with brown; tarsi pale brown.

Abdomen. Male sternum A8 posterior margin bilobed.

Male genitalia (*N* = 1) (Fig. 57). Uncus long and slender, with straight lateral margin, apex blunt. Gnathos projection ca. half the length of uncus, blunt. Valva ventral margin nearly straight, in basal half slightly concave, dorsal margin conspicuously rounded, apex pointed. Juxta with base rounded, notched on its middle, medially narrowed, apex rounded, faintly notched on its middle. Saccus triangular. Phallus with truncate cornutus.

Female genitalia (*N* = 1) (Fig. 95). Anterior apophyses conspicuously widened at posterior 1/3, with tip pointing dorsad. Antrum sclerotisation weak, ca. as long as broad. Ductus bursae straight, slender. Corpus bursae large, globular, posterior half reticulated, anterior half membranous, with weak sclerotisation between corpus opening and thorn. Thorn long, slightly curved, with small dents pointing toward thorn base, basally with small outwardly projected extension.

Distribution. Known from Mount Yamin (Indonesia: Papua), and Mount Kaindi (Papua New Guinea: Morobe Province), at altitudes between 1,700 m and 2,350 m.

Etymology. Dedicated to the late Marijo Weiss, a close friend of Théo Léger's family.

Remarks. The specimen from Mount Kaindi is very similar to those from Mount Yamin but its postmedian fascia of the forewing is yellow and copper instead of dark copper, and uncus and gnathos projection are slightly longer in male genitalia.

Hoploscopa titika **Léger & Nuss, sp. nov.**

http://zoobank.org/8B31F2F7-6FD3-4C8D-85E2-43D87F3EEF3E

Figs 15, 58

Material examined. ***Holotype*****:** ♂, with labels: "Sumatra-Holzweg | 25 km SSW-Pematangsiantar | straße nach Prapat [road to Prapat], L[icht]F[ang] [light trap] | 13.ii.1996, leg. A. Kallies"; "coll[ection]. M. Nuss | Geschenk 2000 | Museum für Tier- | kunde Dresden"; "DNA voucher | Lepidoptera | MTD 2016 | [vertically written:] no. 3206"; "TL505 | ♂". Deposited in MTD.

Diagnosis. *Hoploscopa titika* sp. nov. is recognisable by its well-marked white quadrangular median cubital spot on the forewing. In male genitalia, the gnathos projection is reduced to a small ridge, and the dorsal margin of the valva is rounded, broadly sclerotised. Female genitalia not known.

Similar species. No similar species known.

Description. ***Head.*** Antennae dorsally with pale yellow to bronze scales. Proboscis white. Maxillary palpi brown, inner side white to pale brown. Labial palpi brown, ventro-basally white.

Thorax (Fig. 15). Collar white. Forewing length: 9 mm; forewing ground colour brown; basal patch extending from dorsum to subcosta, red, with small basal pale yellow spot; median discoidal stigma triangular, white, filled with red and pale yellow scales, with white trapezoid cubital patch abutting dorsally; postmedian patch roughly quadrangular, white, filled with red and pale yellow scales; subterminal line diffuse, white; subterminal field marked with red and pale yellow; fringe missing on specimen. Forelegs lost. Mid- and hindlegs white to pale yellow.

Abdomen. Male sternum A8 posterior margin bilobed, with pair of lateral papillae-like protuberances.

Male genitalia (*N* = 1) (Fig. 58). Uncus long and slender, gently tapering toward apex, apex tongue-shaped. Gnathos projection limited to small ridge. Valva broad, ventral margin bent dorsad on distal 1/3, dorsal margin conspicuously convex, apex pointed. Juxta with base rounded, medially straight, apex blunt. Saccus small, pointing dorsad. Phallus apically with sclerotised spine.

Female genitalia. not known.

Distribution. Known from North Sumatra (Indonesia).

Etymology. The species name *titika* comes from the Indonesian word "titik" meaning spot or dot, referring to the white median cubital spot of the forewing.

Hoploscopa pangrangoensis Léger & Nuss, sp. nov.

http://zoobank.org/B24AA14E-0E31-4CF0-BCDC-85DB29385473
Figs 16, 59, 97

Material examined. *Holotype*: ♀, with labels: "Indonesia, Java, M[oun]t. Pangrange | 30 km S[outh]E[ast] Bogor, 1625 m | primary forest 16–20.ii.1996 | 6.30S 107.10E leg. Siniaev & Afonin"; "Lepidoptera | date: i.2018 | MTD 7433 | [vertically written:] DNA-voucher"; "TL | 636 ♀". Deposited in ZMHB.

***Paratypes*:** 4 ♂, 1 ♀. Indonesia: 2 ♂ (1 with genitalia on slide TL659 ♂), 1 ♀ (DNA voucher MTD7431, genitalia on slide TL627 ♀), same data as holotype; 2 ♂ (1 with genitalia on slide TL660 ♂), same data as holotype except 21–26.ii.1996 (ZMHB).

Diagnosis. The forewing markings of *H. pangrangoensis* sp. nov. are reduced to a small crescent-shaped median discoidal stigma; median cubital and dorsal patches are not marked, and postmedian patch is reduced to a blotch at costa. In male genitalia, the uncus is medially widened and the gnathos projection shows a finger-like projection ca. half the length of uncus. In female genitalia, the thin longitudinal sclerotised lines of the antrum are unique to this species.

Similar species. *Hoploscopa parvimacula* sp. nov. (q.v.), *H. sumatrensis* sp. nov. *Hoploscopa sumatrensis* sp. nov. shares with *H. pangrangoensis* sp. nov. the crescent-shaped pale yellow median discoidal stigma on the forewing and the small median cubital patch. However, median discoidal stigma and postmedian patch are filled with reddish brown in *H. sumatrensis* sp. nov.. In male genitalia, the gnathos projection reaches 4/5 of the uncus length in *H. sumatrensis* sp. nov. In female genitalia, antrum of *H. sumatrensis* sp. nov. is completely sclerotised.

Description. *Head.* Antennae dorsally striped with brown and bronze scales. Proboscis pale brown. Maxillary palpi brown, ventro-basally pale yellow. Labial palpi brown, base and inner side pale yellow.

Thorax (Fig. 16). Collar pale yellow. Forewing length: 10–11 mm (♂ & ♀); forewing ground colour brown; basal dark brown dash distally pale yellow; small pale yellow spot at base of cell; basal and distal discoidal patches dark brown; median discoidal stigma forming costa facing C, white to pale yellow; median cubital blotch pale yellow; postmedian pale yellow streak at costa, distally with dark brown streak; postmedian area speckled with pale yellow; subterminal line pale yellow, diffuse; fringes brown, with pale yellow dots. Hindwing pale brown. Forelegs brown, tarsi pale brown. Midlegs with femur brown; tibia brown speckled with pale yellow; tarsi pale yellow speckled with bronze. Hindlegs with femur brown; tibia pale yellow, speckled with pale brown; tarsi pale yellow.

Abdomen. Male sternum A8 posterior margin notched, with pair of lateral papillae-like protuberances.

Male genitalia (*N* = 2) (Fig. 59). Uncus medially widened, narrowed on apical 1/4, apex blunt. Gnathos projection finger-shaped, ca. half the length of uncus. Valva ventral margin straight, gently bent dorsad on distal 1/3, dorsal margin conspicuously convex; apex slightly pointed. Juxta with base quadrangular, medially narrowing, apex roughly rounded. Saccus triangular, conspicuously pointing dorsad.

Female genitalia (*N* = 2) (Fig. 97). Anterior apophyses with dorsal bump at posterior 1/3. Antrum elongated, membranous, with thin longitudinal sclerotised lines, anteriorly with minute sclerotised markings. Ductus bursae bent posterad before corpus opening. Corpus bursae pear-shaped, reticulated, with sclerotisation between thorn and corpus opening and faintly marked sclerotised band medially. Thorn straight, with small dents pointing toward thorn apex.

Distribution. Known from the slopes of Mount Pangrango (3019 m) on Java (Indonesia), at an altitude of 1,625 m.

Etymology. Named after Mount Pangrango, a dormant stratovolcano on Java, where the specimens were collected.

Hoploscopa isarogensis Léger & Nuss, sp. nov.

http://zoobank.org/C77DFE2E-3B02-4738-8F3E-E8139D571FEB

Figs 17, 60, 100

Material examined. ***Holotype*:** ♀, with labels: “Philippines, South Luzon | M[oun]t Isarog | 13°40'N, 123°20'E, 530 m | submontane forest, at light | 22.iii.2000, leg. M. Nuss”; “DNA Barcode | BC MTD 01431”; “DNA voucher | Lepidoptera | MTD 2016 | [vertically written:] no. 3198”; “TL514 | ♀”. Deposited in MTD.

***Paratypes*:** 2 ♂, 7 ♀. Philippines: 1 ♂ (DNA vouchers MTD LEP14 & MTD LEP3209, genitalia on slide TL507 ♂), 5 ♀ (1 with DNA voucher MTD LEP43 & MTD LEP3208, genitalia on slide TL528 ♀; 1 with DNA barcode BC MTD 01430; 1 with DNA voucher MTD LEP3199 & genitalia on slide TL520 ♀, 1 with DNA voucher MTD LEP3200 & genitalia on slide TL523 ♀), same data as holotype; 1 ♂, 1 ♀ (♂ with genitalia on slide TL762 ♂), same date and locality as holotype, leg. Mey &

Ebert; 1 ♀ (DNA voucher MTD7422 & genitalia on slide TL621 ♀), Laguna, Pangil, 50 m, 11.iv.1997, leg. Mey & Speidel (MTD).

Other specimens examined. 2 ♂, 7 ♀. Philippines: 1 ♂ (DNA voucher MTD7420 & genitalia on slide TL626 ♂), 6 ♀ (4 with DNA voucher MTD7418, MTD8143, MTD8144, MTD8146, MTD8148 and genitalia on slide TL630♀, TL704 ♀, TL705 ♀, TL720 ♀, TL719 ♀ respectively, 2 with DNA voucher MTD8145 & MTD8147), Leyte, Lake Danao, 650 m, 14.-17.4.1997, leg. W. Mey & W. Speidel (ZMHB); 1 ♂ (DNA voucher MTD7423 & genitalia on slide TL631 ♂), Mindoro, Mt Baco Pass, 1150 m, 14.i.1998 (Mey & Samarita); 1 ♀ (DNA voucher MTD7424 & genitalia voucher on slide TL619 ♀), Mindoro, Mt Halcon, 1300 m, 15–17.i.1998 (Mey & Samarita) (ZMHB);

Diagnosis. *Hoploscopa isarogensis* sp. nov. is a relatively small brown-winged species (forewing length = 7–9.5 mm) with red markings edged yellow. Median discoidal stigma, cubital and dorsal patches form together a disrupted band, and postmedian patch is red with a pale yellow blotch at costa. In male genitalia, the apex of the uncus is duck beak-shaped, with a small marked bump on its ventral side, and gnathos projection is ca. 1/3 of uncus length, with an indented apex. In female genitalia, the corpus bursae displays a clearly delimited sclerotisation between the thorn and the corpus opening, and bears a long, thick, curved thorn.

Similar species. *Hoploscopa cynodonta* sp. nov. (q.v.), *H. ignitamaculae* sp. nov. (q.v.), *H. agtuuganonensis* sp. nov. The forewings of *H. agtuuganonensis* sp. nov. display a trapezoid median discoidal stigma, and median markings are only slightly disrupted, while they are well separated in *H. isarogensis* sp. nov. In male genitalia, gnathos projection reaches 2/3 of uncus length and has a truncate apex. In female genitalia, ductus bursae is long, broad, with one loop, while it is shorter, slender and straight in *H. isarogensis* sp. nov., and the small corpus bursae displays one plump thorn with a small sclerotisation at its base.

Description. *Head.* Antennae dorsally brown. Proboscis pale yellow. Maxillary palpi brown, base and inner side pale brown. Labial palpi brown, ventrobasally pale yellow.

Thorax (Fig. 17). Collar white. Forewing length: 7–8 mm (♂), 8–9.5 mm (♀); forewing ground colour brown; broad basal patch pale yellow to yellow, crossed by longitudinal reddish brown fascia running up to centre of wing; costal field reddish brown; median discoidal stigma rhomboid to elliptic, pale yellow, filled with reddish brown; cubital and dorsal pale yellow patches forming with median discoidal stigma an oblique band disrupted at veins; postmedian patch roughly triangular, reddish brown, more or less speckled with pale yellow, with pale yellow blotch at costa; subterminal line pale yellow, conspicuously incurved inwards at CuA2; subterminal field marked with reddish brown; fringe brown, with pale yellow dots. Hindwing pale brown. Forelegs brown. Midlegs brown, inner side pale yellow. Hindlegs brown, tibia marked with pale yellow.

Abdomen. Male sternum A8 posterior margin broadly indented, with pair of lateral papillae-like protuberances.

Male genitalia (*N* = 2) (Fig. 60). Uncus long, medially broadened, narrowed at apical 1/4, apex duck beak-shaped, medio-ventrally with a small bump projecting ventrad. Gnathos projection ca. 1/3 of the uncus length, with apex notched. Valva ventral margin nearly straight, gently bent dorsad on distal 1/4, dorsal margin slightly convex, apex truncated. Juxta broad, with base rounded, medially slightly narrowed, apex split into two weakly sclerotised tips. Saccus quadrangular.

Female genitalia (*N* = 6) (Fig. 100). Anterior apophyses with small dorsal bump at posterior 1/3. Antrum sclerotisation short, ca. as wide as long. Ductus bursae nearly straight. Corpus bursae globular and reticulated but in some specimens with a rounded pouch-like extension, with well-marked sclerotisation between thorn and ductus bursae opening, medially with faintly sclerotised band. Thorn sabre-like, curved, with small dents pointing toward thorn base.

Distribution. Known from the Luzon and Mindoro islands (Philippines), between sea level and 1,150 m.

DNA-barcoding. Specimens from Luzon and Leyte show an K2P-distance of 3.4–3.9% and are recovered in two MOTUs.

Etymology. Named after Mount Isarog (1966 m), a volcano on Luzon Island (Philippines) where the species is found.

Remarks. Minor differences were observed in male and female genitalia of the specimens from Leyte. However, with only one male from Leyte on hand, we refrained from drawing further conclusions here.

Hoploscopa ypsilon **Léger & Nuss, sp. nov.**

http://zoobank.org/06694A15-8524-4AB3-AAC0-2874511AC4F3

Figs 18, 61, 98

Material examined. ***Holotype***: ♂, with labels: “Philippinen, Luzon | M[oun]t[ai]n. Prov[ince]., Barlig | 1650 m, 14–15.XI.97 | leg. Mey, Ebert, Nuß”; “DNA voucher | Lepidoptera | date: ix.2018 | MTD8138 | [vertically written:] DNA-voucher”; “TL699 | ♂”. Deposited in ZMHB.

Paratypes: 9 ♂, 15 ♀. Philippines: 4 ♂, 10 ♀ (1 with DNA voucher MTD7429 & genitalia on slide TL623 ♀), same data as holotype; 3 ♂ (1 with genitalia on slide TL677 ♂), 5 ♀ (1 with DNA voucher MTD7427 & genitalia on slide TL620 ♀, 1 with DNA voucher MTD7428 & genitalia on slide TL637 ♀), Luzon, Mountain Province, Chatol, 2100 m, 16–18.xi.1997, leg. Mey, Ebert & Nuss; 1 ♂ (DNA voucher 7435 & genitalia on slide TL624 ♂), Luzon, Ifugao, Mount Polis, 2000 m, 13.xi.1997, leg. Mey, Ebert & Nuss; 1 ♂ (DNA voucher MTD8137), Luzon, Santa Fe, Bald Mountain, 1150 m, 11–13.xi.1997, leg. Mey, Ebert & Nuss (ZMHB).

Diagnosis. *Hoploscopa. ypsilon* sp. nov. displays well-marked white coloured markings on the forewing. Median discoidal stigma and cubital patch are Y-shaped, postmedian patch is triangular and subterminal line is conspicuously incurved inwards at CuA2. In male genitalia, the gnathos forms a short, broadly rounded projection.

Similar species. *Hoploscopa danaoensis* sp. nov. This species displays pale yellow markings on the forewing, the postmedian area is more or less broadly suffused with pale yellow, with subterminal line only slightly incurved inwards at CuA2. In male genitalia, *H. danaoensis* sp. nov. has a tongue-shaped projection ca. half the uncus length. Female genitalia are very similar to those of *H. danaoensis* sp. nov. and cannot be confidently separated.

Description. ***Head.*** Antennae dorsally with brown scales. Proboscis brown, speckled with pale yellow. Maxillary palpi brown, inner side and base pale yellow. Labial palpi brown, ventral base and tip pale yellow.

Thorax (Fig. 18). Collar pale yellow. Forewing length: 9–10 mm (♂), 9.5–11 mm (♀); forewing ground colour dark brown; basal dark brown blotch with oblique white streak abutting at costa; median discoidal stigma V-shaped, white, edged with darker brown, together with white cubital streak forming a Y; postmedian patch triangular, white, invaded with light brown toward costa, edged with darker brown; subterminal line white, conspicuously incurved inwards at CuA2; fringes brown, with pale yellow dots. Hindwing pale brown, darker at apex. Forelegs brown; tarsi brown to pale brown. Midlegs with femur brown; tibia brown, speckled with pale yellow; tarsi pale yellow. Hindlegs with femur brown; tibia brown speckled with pale yellow, distally pale yellow; tarsi pale yellow.

Abdomen. Male sternum A8 posterior margin bilobed.

Male genitalia (*N* = 3) (Fig. 61). Uncus long, slightly narrowed on apical 1/4, apex duck beak-shaped. Gnathos projection broad, very short, with broadly rounded apex. Valva ventral margin gently bent dorsad on distal 1/3, dorsal margin conspicuously convex, apex slightly pointed. Juxta with base rounded, medially slightly narrowed, apex broadly incurved. Saccus small, quadrangular.

Female genitalia (*N* = 3) (Fig. 98). Anterior apophyses with dorsal bump at 1/3. Antrum sclerotisation short, ca. as wide as long. Ductus bursae kinked before corpus opening. Corpus bursae pear-shaped, reticulated, with sclerotisation between thorn and corpus opening and faintly marked sclerotised band medially. Thorn small, straight, with small dents pointing toward thorn apex.

Distribution. Known from the Ifugao, the Mountain and the Nueva Vizcaya Provinces on the Luzon island (Philippines), at altitudes between 1,150–2,100 m.

DNA barcoding. The highest intraspecific divergence is 0.7%. The nearest neighbor is *H. danaoensis* sp. nov. (2.9–3.1%).

Etymology. The species name *ypsilon*, for the Greek letter Y, refers to the shape of the median markings on the forewing.

Hoploscopa danaoensis Léger & Nuss, sp. nov.

http://zoobank.org/CE945458-F671-4EE7-8E5B-FA18C6CC58AC

Figs 19, 62, 99

Material examined. ***Holotype*:** ♂, with labels: "Philipinen [sic], Leyte | Lake Danao, 650 m | 14.-17.4.1997 | leg. Mey & Speidel"; "DNA voucher | Lepidoptera | date: i.2018 | MTD7419 | [vertically written:] DNA-voucher"; "TL | 632 ♂". Deposited in ZMHB.

Paratypes**:** 6 ♂, 11 ♀. Philippines: 6 ♂ (2 with genitalia on slide TL721 ♂ & TL722 ♂), 11 ♀ (1 with DNA voucher MTD7421 & genitalia on slide TL618 ♀, 1 with DNA voucher MTD8142 & genitalia on slide TL703, 1 with DNA voucher MTD8141 & genitalia on slide TL702 ♀), same data as holotype (ZMHB).

Other specimens examined. 2 ♂, 9 ♀. Philippines: 1 ♂ (genitalia on slide TL681 ♂), 1 ♀ (DNA voucher MTD7417 & genitalia on slide TL615 ♀), Mindanao, 1050 m, Mt Agtuuganon, 28.v.-7.vi.1996, leg. W. Mey; 1 ♂ (DNA voucher MTD8140 & genitalia on slide TL701 ♂), 8 ♀ (DNA voucher MTD8139 & genitalia on slide TL700 ♀), Negros, Patag, Lake Danao, 1400m, 21.5.96, leg. W. Mey (ZMHB).

Diagnosis. The forewings of *H. danaoensis* sp. nov. displays pale yellow median markings forming a Y. In male genitalia, the uncus displays a straight lateral margin and an obtuse apex, and the tongue-shaped gnathos projection reaches ca. half of the uncus length. The juxta is progressively narrowing toward the notched apex. Female genitalia are very similar to several other *Hoploscopa* species, e.g., *H. ypsilon* sp. nov., *H. parvimacula* sp. nov**.**

Similar species. *Hoploscopa brunnealis* (q.v.), *H. ypsilon* sp. nov. (q.v.), *H. metacrossa* (q.v.).

Description. *Head.* Antennae dorsally with brown scales. Proboscis pale brown, of a darker brown at base. Maxillary palpi brown, basally pale yellow, inner side pale brown. Labial palpi brown, ventro-basally pale yellow, inner side speckled with pale yellow.

Thorax (Fig. 19). Collar pale yellow. Forewing length: 8 mm (♂), 8–9 mm (♀); forewing ground colour brown; basal dark brown blotch distally pale yellow; median discoidal stigma V-shaped, white to pale yellow, with dark brown basal and distal edges; cubital patch elongated, white to pale yellow, together with median discoidal stigma forming a Y; postmedian patch roughly triangular, white to pale yellow, broadly invaded with brown, edged with darker brown; postmedian line marked on costal half; subterminal line thick, white to pale yellow, incurved inwards at CuA2, angled at M1; fringes brown, with diffuse pale yellow dots. Hindwing pale brown. Forelegs brown, tarsi pale brown. Midlegs with femur brown; tibia brown, speckled with pale yellow, distally pale yellow; tarsi pale yellow. Hindlegs with femur brown; tibia pale yellow, speckled with pale brown; tarsi pale brown.

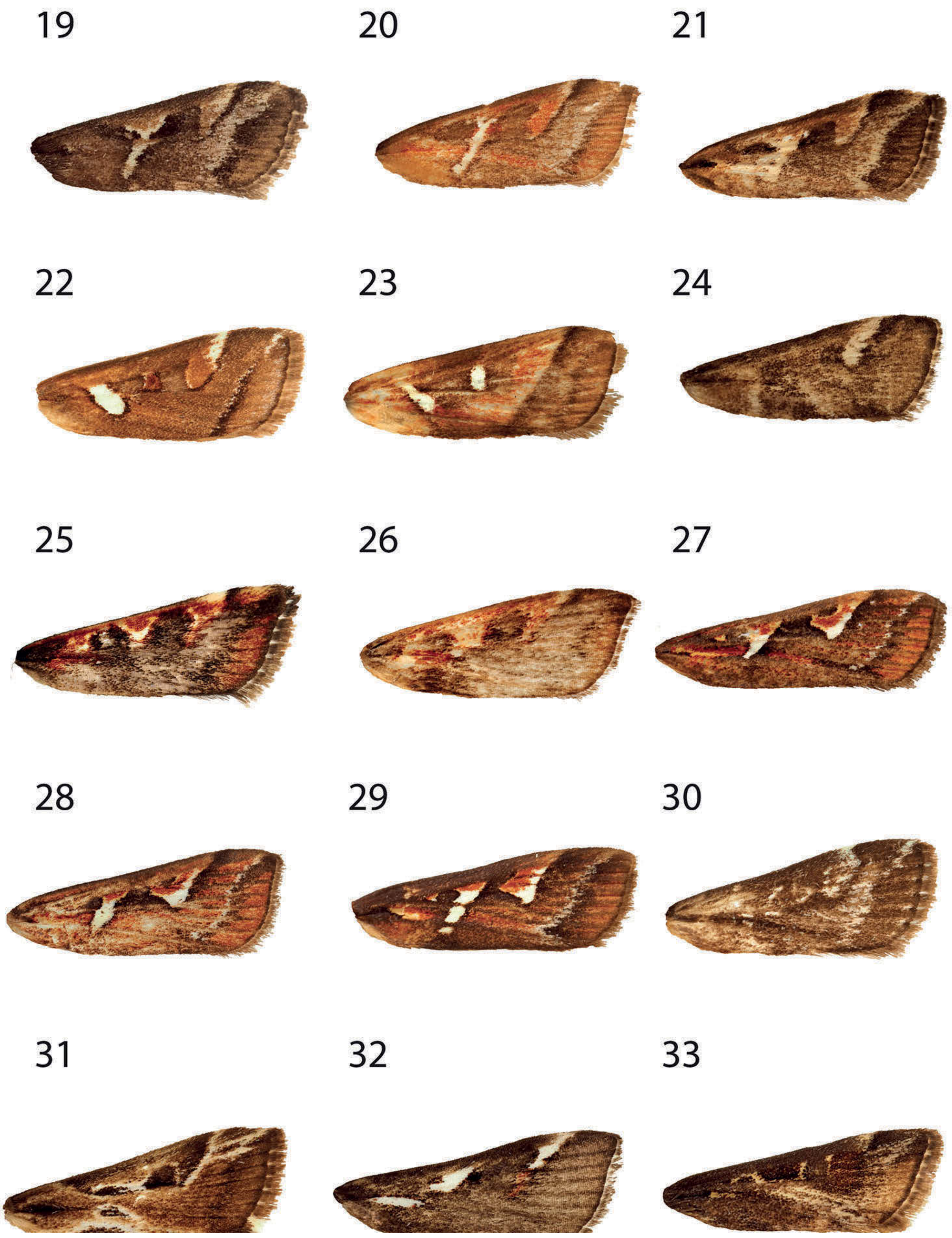
Abdomen. Male sternum A8 posterior margin straight.

Male genitalia ($N = 1$) (Fig. 62). Uncus long with straight lateral margin, apex obtuse. Gnathos projection tongue-shaped, ca. half the uncus length. Valva ventral margin gently bent dorsad on distal 1/3, dorsal margin conspicuously convex, apex slightly pointed. Juxta with base quadrangular, tapering toward apex, apex notched. Saccus small, pointing dorsad.

Female genitalia ($N = 1$) (Fig. 99). Anterior apophyses with dorsal bump at posterior 1/3. Antrum short, as long as broad. Ductus bursae short, straight, kinked before corpus bursae. Corpus bursae broad, pear-shaped, reticulated, with elongated sclerotisation between thorn and corpus opening, medially with sclerotised band. Thorn straight, with small dents pointing toward thorn apex.

Distribution. Known from Lake Danao (650 m) on Leyte island (Philippines).

DNA barcoding. Morphologically similar specimens from Mindanao and Negros are recovered in two separate MOTUs and show a divergence of 3.9–4.2% with *H. danaoensis* sp. nov.



Figures 19–33. Habitus of *Hoploscopa* species **19** *Hoploscopa danaoensis* sp. nov., paratype, ♂, Philippines, Leyte, Lake Danao, 650 m, 14–17.iv.1997 (Mey & Speidel) **20** *Hoploscopa aurantiacalis* Snellen lectotype, ♀, NHMUK010923286, Indonesia, Java occ., Pengaleng, 4000 ft, 1893 (genitalia on slide Pyralidae Brit. Mus. Slide N° 20246) **21** *Hoploscopa brunnealis* Snellen, lectotype, ♀, NHMUK010923292, Indonesia, Java occ., Pengaleng, 4000 ft, 1893 (genitalia on slide Pyralidae Brit. Mus. Slide N° 20247) **22** *Hoploscopa ocellata* Hampson, holotype, ♀, NHMUK010923358, Indonesia, Moluccas, Batchian, iii.1892 (W. Doherty) (genitalia on slide Pyralidae Brit. Mus. Slide N° 20258) **23** *Hoploscopa quadripuncta* Rotschild, holotype, ♂, NHMUK010923357, Indonesia, Papua, Utakwa River, 3000 ft, i.1913 (A.F.R. Wollaston) (genitalia on slide Pyralidae Brit. Mus. Slide N° 20257)

Etymology. Named after Lake Danao on Leyte where the species is found.

Remarks. Minor differences were observed in male genitalia of the specimens from Mindanao and Negros. However, we only had one male on hand for each series. In absence of further evidence, we refrained from describing further species here.

Hoploscopa aurantiacalis (Snellen, 1895)

Figs 20, 102

Material examined. ***Lectotype*:** ♀, with labels: "Lecto- | type" [purple ringed]; "SYN- | TYPE" [blue ringed]; "F1893 | Java occ. | Pengaleng | 4000' F[ee]t" [handwritten, label squared with silver]; "Syncrotaula | aurantiacalis | Snellen | det. M. Shaffer, 1967" [handwritten]; "Lectotype | Eudorina | aurantiacalis | Snellen | det. M. Nuß" [handwritten]; "99.113."; "♀ | Pyralidae | Brit[ish].Mus[eum]. | Slide N°. | 20246"; "GU Nr 659 | prep. M. Nuß"; "N,HMUK 010923286" [barcode appended]. Deposited in NHMUK.

Diagnosis. The median discoidal stigma, cubital and dorsal patches of the forewings form an oblique thin white streak. In female genitalia, the membranous pouch anterad from the antrum and the leaf-shaped sclerotisation of the corpus bursae allows to recognise this species. Male genitalia are not known.

Similar species. No similar species known.

Description. ***Head.*** Antennae dorsally brown. Proboscis pale yellow. Maxillary palpi brown, base pale yellow, inner side pale brown. Labial palpi brown, ventral base and inner side pale yellow.

Figures 19–33. Continued. **24** *Hoploscopa semifascia* Hampson, ♀, NHMUK010923321, Papua New Guinea, Southern Highlands, Bosavi, 570 m, 6.i.1986 (D. Agassiz) (genitalia on slide TL740 ♀) **25** *Hoploscopa subvariegata* Rothschild, ♂, Morobe Province, near Wau, Mt. Kaindi, 2360 m, 27–28. vii.1983 (S. E. & P. M. Miller) (genitalia on slide TL642 ♂) **26** *Hoploscopa persimilis* Rothschild, lectotype, ♂, NHMUK010923328, Indonesia, Papua, Utawka River, 3000 ft., i.1913 (A.F.R. Wollaston) (genitalia on slide Pyralidae Brit. Mus. Slide N° 20255) **27** *Hoploscopa astrapias* Meyrick, lectotype, ♀, NHMUK010923383, Fiji, Vunîdawa, 2.i.1932 (genitalia on slide Pyralidae Brit. Mus. Slide N° 20241) **28** *Hoploscopa anamesa* Tams, ♀, NHMUK010923466, Vanuatu, Aneityum Island, Red Crest, 3 m NE of Anelgauhat, 1200 ft, vi.1955 (E. Cheesman) (genitalia on slide TL718 ♀) **29** *Hoploscopa nauticorum* Tams, allotype, ♀, Samoan, Upolu Island, Malololelei, 2000 ft, 21.ii.1925 (P. A. Buxton & G. H. Hopkins) **30** *Hoploscopa diffusa* Hampson, lectotype, ♂, NHMUK010923338, Papua New Guinea, Fergusson Island, x-xi.1894 (A. S. Meek) (genitalia on slide Pyralidae Brit. Mus. Slide N° 1014 ♂) **31** *Hoploscopa triangulifera* Hampson, ♀, NHMUK010923453, Biagi, Mambare R., 1600 m, iii.1906 (A. S. Meek) (genitalia on slide TL712 ♀) **32** *Hoploscopa anacantha* sp. nov., holotype, ♂, NHMUK010923444, Indonesia, North Sumatra, Dumoga-Bone N. P., Gunung Mogogonipa, summit, 1008 m, 18–20.x.1985 (genitalia on slide TL759 ♂) **33** *Hoploscopa kelama* sp. nov., paratype, ♂, NHMUK010923342 , Indonesia, North Sulawesi, Dumoga-Bone National Park, Clarke Camp, lower montane forest, 1140 m, x.1985 (Royal Entomological Society of London, Project Wallace) (genitalia on slide TL759 ♂).

Thorax (Fig. 20). Collar white. Forewing length: 10 mm; forewing ground colour brown; basal longitudinal red fascia dorsally edged with pale yellow, running up to postmedian area; costal field reddish brown; median oblique white streak extending from cell down to dorsal area, slightly split costally; postmedian patch reddish brown speckled with white, with costal white blotch; postmedian line marked on costal half; postmedian suffusion white; subterminal line white; subterminal field broadly marked with reddish brown; margin brown, chequered with pale yellow. Hindwing pale brown. Fore- and midlegs brown to bronze. Hindlegs with femur bronze, tibia pale yellow speckled with bronze, tarsi bronze.

Male genitalia. Not known.

Female genitalia (*N* = 1) (Fig. 102). Anterior apophyses bent ventrad at 1/3, without bump. Antrum sclerotisation short, broad. Ductus bursae short, with a rounded pouch at base, one loop on its middle. Corpus bursae rounded, extending lateral into a broad pouch, posterior half reticulated, anterior half with erect papillae, with leaf-shaped sclerotisation at corpus opening. Thorn long, flattened, straight, thinly indented.

Distribution. Recorded from West Java (Indonesia), at an altitude of 1,300 m.

Remarks. Nuss (1998) transferred this species from *Eudorina* to *Hoploscopa* and designated the lectotype.

Hoploscopa brunnealis (Snellen, 1895)

Figs 21, 103

Argyria xiphotoma Meyrick, 1938

Material examined. *Lectotype*: ♀, with labels: “Lecto- | type” [round label, purple ringed]; “SYN- | TYPE” [round label, ringed blue]; “F1893 | Java occ[idental]. | Pengaleng | 4000’ F[ee]t” [handwritten, squared with silver]; “99.113.” [handwritten] | “Syncrotaula | brunnealis | Snellen [handwritten] | det. M. Shaffer, 1967”; “Lectotype | Eudorina | brunnealis | Snellen | det. M. Nuß” [handwritten]; “GU Nr. 660 | prep. M. Nuß”; “♀ | Pyralidae | Brit[ish].Mus[eum]. | Slide N°. | 20247”; "N,HMUK 010923292” [barcode appended]. Deposited in NHMUK.

Diagnosis. *Hoploscopa brunnealis* displays a forewing pattern very similar to that of *H. danaoensis* sp. nov., with a median pale yellow Y, a postmedian pale yellow patch invaded with brown or tawny and a pale yellow subterminal line. In female genitalia, the antrum sclerotisation is short, the ductus bursae is short, straight, and the corpus bursae is pear-shaped, with a small straight thorn. Male genitalia are not known.

Similar species. *Hoploscopa danaoensis* sp. nov., *H. metacrossa* (q.v.), *H. parvimacula* sp. nov. (q.v.). Female genitalia of se species display a larger antrum sclerotisation.

Description. *Head.* Antennae dorsally with bronze scales. Proboscis pale brown to pale yellow. Maxillary palpi brown, base and inner side pale yellow. Labial palpi brown, ventral base and inner side pale yellow.

Thorax (Fig. 21). Forewing length: 10 mm; ground colour brown; basal dash dark brown distally pale yellow; costal field tawny; median discoidal stigma and median cubital patch forming together a pale yellow-coloured Y, with basal and distal edges dark brown; postmedian patch tawny speckled with pale yellow, distally pale yellow, with costal pale yellow blotch; postmedian area suffused with pale yellow; subterminal line pale yellow; fringes brown, with pale yellow dots.

Male genitalia. Not known.

Female genitalia (*N* = 1) (Fig. 103). Anterior apophyses without dorsal bump at posterior 1/3, Antrum sclerotisation short. Ductus bursae short, slender, more or less straight. Corpus bursae pear-shaped, with posterior half reticulated, anterior half membranous, with faintly marked sclerotisation between thorn and corpus opening, medially with faintly marked sclerotised band. Thorn small, straight, with small dents pointing toward thorn base.

Distribution. Recorded from West Java (Indonesia) at an altitude of 1,300 m.

Remarks. Nuss (1998) transferred this species from *Eudorina* to *Hoploscopa* and designated the lectotype. *Argyria xiphotoma* Meyrick, 1938 is synonymised with *Hoploscopa brunnealis* in the same paper.

Hoploscopa ocellata (Hampson, 1919)

Figs 22, 104

Material examined. ***Holotype*:** ♀, with labels: “Holo- | type” [round label, red ringed]; “Batchian [Bacan islands] | Mar[ch]. 1892 | W. Doherty”; “Pyrocrambia | ocellata | type ♀. H[a]mps[o]n.” [handwritten]; “♀ | Pyralidae | Brit[ish].Mus[eum]. | Slide N°. | 20258”; "N,HMUK 010923358” [barcode appended]. Deposited in NHMUK.

Diagnosis. The large oblique elliptic white patch at base of the forewing, the median trapezoid and postmedian semi-elliptic tawny patches are unique to *H. ocellata*. In female genitalia, the long, wrinkled and multicoiled ductus bursae, the ovoid corpus bursae bearing long acanthae, and the long glabrous thorn unequivocally segregates *H. ocellata* from other *Hoploscopa* species. Male genitalia are not known.

Similar species. No similar species known.

Description. ***Head.*** Antennae dorsally brown. Proboscis pale yellow. Maxillary palpi brown, basally pale yellow. Labial palpi brown, ventro-basally pale yellow.

Thorax (Fig. 22). Collar white. Forewing length: 10 mm; forewing ground colour brown; large elliptic white basal patch with dark brown edges; basal and distal discoidal patches of a darker brown; median discoidal stigma there between trapezoid to square, tawny, basally thinly edged with white; postmedian patch semi-elliptic, tawny, distally with white costal streak; subterminal line more or less straight, disrupted at M1, white, distally dark brown on dorsal 2/3; subterminal field suffused with white; fringes brown with lighter spots. Hindwing pale brown. Fore- and hindlegs brown, with tibia and tarsi segments distally white. Midlegs lost.

Male genitalia. Not known.

Female genitalia (*N* = 1) (Fig. 104). Papillae anales thin, dorsally and ventrally not connected. Anterior apophyses bent ventrad at 1/3, without bump. Antrum membranous. Ductus bursae long, narrow, wrinkled, multi-coiled. Corpus bursae ovoid, with one half reticulate, the other half densely covered with long acanthae, medially with sclerotised band. Thorn long, slender, straight, without dents.

Distribution. Recorded from Bacan island in the Moluccas (Indonesia).

Remarks. Nuss (1998) transferred this species from *Eudorina* to *Hoploscopa*.

Hoploscopa quadripuncta (Rotschild, 1915)

Figs 23, 63, 105

Material examined. ***Holotype*:** ♂, with labels: “Holo- | type” [round label, red ringed]; “Utakwa [sic, Oetakwa] R[iver]., | Dutch N[ew]. Guin[ea]., | 3000 f[ee]t., Jan. 1913. | A.F.R. Wollaston.”; “Eudorina | quadripuncta | Type Rotsch[ild].”; “436”; “♂ | Pyralidae | Brit[ish].Mus[eum]. | Slide N°. | 20257”; "N,HMUK 010923357” [barcode appended]. Deposited in NHMUK.

Other specimens examined. 3 ♂, 1 ♀. Indonesia: 1 ♂ (NHMUK010923460, DNA voucher MTD8249 & genitalia on slide TL734 ♂), Moluccas, Seram, Gunung Kobipoto, north slopes, 570 m (NHMUK010923460), lowland forest, viii-ix.1987, leg. J. D. Holloway, D. T. Jones et al.; 1 ♂ (NHMUK010923459, DNA voucher MTD8248 & genitalia on slide TL733 ♂), same data except 900 m. Papua New Guinea: 1 ♂, 1 ♀, Hydrographers Mountains, 830 m, i.1918, Rothschild bequest (NHMUK).

Diagnosis. The white-coloured basal patch and median discoidal stigma as well as the oblique postmedian line allows separation of *H. quadripuncta* from its congeneric species. In male genitalia, uncus apex is cuneate and gnathos projection is ogive-shaped. In female genitalia, the thorn of the corpus bursae is long, slender, curved, and shows a well-marked rounded sclerotisation at its base.

Similar species. No similar species known.

Description. ***Head.*** Antennae dorsally bronze. Proboscis white. Maxillary palpi brown, base and inner side pale brown. Labial palpi brown, ventral base and inner side white.

Thorax (Fig. 23). Collar pale yellow. Forewing length: 8.5–10 mm (♂), 10 mm (♀); forewing ground colour brown; basal quadrangular oblique white patch, basally and distally edged with dark brown, with tawny to reddish brown fascia along CuA2 spreading distally into postmedian area up to costa; median white rounded patch edged with dark brown; postmedian line oblique straight thick; fringes brown. Hindwing pale brown. Forelegs brown. Midlegs with femur brown, tibia and tarsi pale yellow. Hindlegs pale brown.

Abdomen. Male sternum A8 posterior margin notched.

Male genitalia (*N* = 3) (Fig. 63). Uncus long and slender, narrowed at apical 1/4, apex cuneate. Gnathos projection ogival, ca. 1/3 of uncus length. Valva slender, ventral margin straight on basal 2/3, bent dorsad on apical 1/3, dorsal margin convex, apex pointed. Juxta with base rounded, medially narrowed, apex broad, weakly sclerotised.

Saccus broad, triangular, pointing dorsad. Phallus with flat spatula-shaped cornutus, apically with narrow bump.

Female genitalia (Fig. 105). Anterior apophyses conspicuously widened at posterior 1/3. Antrum with a narrow weakly sclerotised ring. Ductus bursae short, straight. Corpus bursae ovoid, posterior half reticulated, anterior half membranous, sclerotised between thorn and corpus opening, medially with faintly sclerotised band. Thorn long, curved, with small dents pointing toward thorn base on posterior edge, basally with conspicuous outwardly directed plump extension.

Distribution. Recorded from the Oetakwa River (Papua: Indonesia) in New Guinea, also known from the Oro Province (Papua New Guinea) and the Moluccas (Indonesia), at altitudes between 500 m and 1,000 m.

Remarks. Nuss (1998) transferred this species from *Eudorina* to *Hoploscopa*. Other specimens examined from the Moluccas and Papua New Guinea display the same pattern as the holotype from Western New Guinea, however a small difference in the shape of the gnathos projection is observed: it is pointed in the holotype, while it is rounded in the other specimens. Unfortunately, no COI barcode was available for the holotype.

Hoploscopa semifascia **(Hampson, 1919)**

Figs 24, 106

Material examined. ***Holotype***: ♀, with labels: “Holo- | type” [round label, red ringed]; “Fak-Fak | Dutch NewGuinea | Dec’[19]07 | 1700 f[ee]t | (Pratt)”; “1913-216.”; “Eudorina | semifascia | type ♀ H[a]mps[o]n” [handwritten]; “♀ | Pyralidae | Brit[ish]. Mus[eum]. | Slide N°. | 20253”; "N,HMUK 010923320” [barcode appended]. Deposited in NHMUK.

Other specimens examined. 2♀; PAPUA NEW GUINEA: 1♀ (NHMUK010923321, DNA voucher MTD8242, genitalia on slide TL740 ♀), Southern Highlands, Bosavi, 570 m, 6.i.1986, leg. D. Agassiz (NHMUK); 1 ♀ (DNA voucher MTD LEP 3158, genitalia on slide TL438 ♀), Morobe Province, Wau, Wau Ecology Institute, 24–26.viii.1983, 1360 m, leg. S. E. & P. M. Miller (USNM).

Diagnosis. The forewings of *H. semifascia* display an antemedian dark brown fascia edged with pale yellow and a marked postmedian pale yellow patch. Median markings are completely lacking. In female genitalia, the thorn is long, thin, curved in distal half, with a small, well-marked sclerotisation at its base. Male genitalia not known.

Similar species. No similar species known.

Description. ***Head.*** Antennae dorsally striped with bronze and brown scales. Proboscis pale yellow. Maxillary palpi brown, base and inner side pale yellow. Labial palpi brown, base pale yellow, inner side pale yellow to pale brown.

Thorax (Fig. 24). Collar white. Forewing length: 7 mm; forewing ground colour brown; antemedian broad transversal dark brown fascia, basal edge pale yellow, incurved inwardly on costal half, distal edge oblique, pale yellow; postmedian elongated pale yellow patch with dark brown edges; fringes brown, with pale yellow spots. Hindwing pale brown. Forelegs brown. Midlegs brown; tarsi pale brown. Hindlegs with femur brown; tibia pale yellow, speckled with brown; tarsi pale brown.

Male genitalia. Not known.

Female genitalia (*N* = 3) (Fig. 106). Anterior apophyses widened at posterior 1/3, with tip pointed dorsad. Antrum sclerotisation short, ca. as long as broad. Ductus bursae short, slightly curved twice. Corpus bursae reticulated, with small rounded sclerotisation at thorn base. Thorn long and slender, curved, glabrous, basally with small outwardly projected extension.

Distribution. Recorded from Fak-Fak (Papua, Indonesia), also known from the Southern Highlands and the Morobe Province (Papua New Guinea) at altitudes between 550 m and 1,400 m.

DNA barcoding. The K2P-distance between specimens MTD LEP 3158 from the Morobe Province and MTD8242 from the Southern Highlands (Papua New Guinea) is 0.5%.

Remarks. Nuss (1998) transferred this species from *Eudorina* to *Hoploscopa*. Other specimens examined from Papua New Guinea display the same pattern and identical genitalia as the holotype from Western New Guinea.

Hoploscopa subvariegata **(Rotschild, 1915)**

Figs 25, 64, 109

Material examined. *Holotype*: ♀, with labels: "Holo- | type" [round label, red ringed]; "Angabunga R[iver]., | affl[uent]. of St. Joseph | R., Brit[ish].N[ew].Guinea, | 6000 f[ee]t, upwards. | Nov.[19]04.-Febr.[19]05. | (A. S. Meek)."; "Eudorina | subvariegata | Type Rotsch[ild]." [handwritten]; "♀ | Pyralidae | Brit[ish].Mus[eum]. | Slide N°. | 20254"; "N,HMUK 010923326" [barcode appended]. Deposited in NHMUK.

Other specimens examined. 14 ♂, 4 ♀. Papua New Guinea: 9 ♂ (2 with genitalia on slide TL478 ♂ & TL642 ♂), 1 ♀ (genitalia on slide TL521 ♀), Morobe Province, near Wau, Mt. Kaindi, 2360 meters, 27–28 July 1983, leg. S. E. & P. M. Miller; 1 ♂ (genitalia on slide TL534 ♂), same data except 29–30.viii.1983; 1 ♂, 1♀, same locality, 11.xii.1976, leg. G. F. Hevel & R. E. Dietz; 2 ♂ (1 with DNA voucher 3156, genitalia on slide TL436 ♂), 1 ♀, same locality, 3.x.1992, leg. V. O. Becker); 1 ♂, 1 ♀ (genitalia on slide TL471 ♀), Morobe Province, Biaro Road, 2000 m, 25.ix.1992, leg. V. O. Becker (USNM).

Diagnosis. *Hoploscopa subvariegata* displays four roughly triangular yellow spots filled with reddish brown on forewing costa. In male genitalia, uncus is long and slender with truncate apex, gnathos projection is tongue-shaped, reaching 1/3 of uncus length, and dorsal margin of the valva is conspicuously protruded dorsad. In female genitalia, ductus bursae is long and straight, corpus bursae is large, globular and bears a small, slightly curved thorn with leaf-shaped sclerotisation at its base.

Similar species. *Hoploscopa persimilis*. The latter species lacks the subterminal triangular yellow blotch at forewing costa. In the male genitalia of *H. persimilis*, uncus apex is duck-shaped, gnathos projection forms a small triangular tip, and valva dorsal margin is not protruded.

Description. ***Head.*** Antennae dorsally with bronze scales. Proboscis pale yellow, basally brown. Maxillary palpi brown. Labial palpi brown, ventro-basally pale yellow.

Thorax (Fig. 25). Collar white. Forewing length: 10 mm (♂), 9.5–12 mm (♀); forewing ground colour brown to dark brown; basal area reddish brown, basally with small yellow dash, at costa with V-shaped yellow patch filled with reddish brown; antemedian cubital snow-white dot; costal field reddish brown; median discoidal stigma V-shaped, white, yellow toward costa, filled with reddish brown; postmedian patch reddish brown, with white to yellow basal edge and pale yellow to yellow costal blotch; subterminal costal spot pale yellow to yellow, encroached with reddish brown; subterminal field reddish brown; margin brown, with white dots. Hindwing dirty white, bronze toward margin. Forelegs femur and tibia brown; tarsi pale yellow. Midlegs with femur brown; tibia pale yellow, dorso-distally brown; tarsi pale yellow. Hindleg femur brown; tibia pale yellow, dorso-distally brown; tarsi pale yellow to pale brown.

Abdomen. Male sternum A8 posterior margin bilobed.

Male genitalia ($N = 4$) (Fig. 64). Uncus long and slender, gently tapering toward apex, apex roughly truncate. Gnathos projection tongue-shaped, ca. 1/3 of uncus length. Valva ventral margin nearly straight, dorsal margin strongly protruded dorsad, apex truncate. Juxta with broad rounded base, medially wide, apex broadly incurved, weakly sclerotised. Saccus broad, triangular, pointing dorsad.

Female genitalia ($N = 2$) (Fig. 109). Anterior apophyses with dorsal small tip at posterior 1/3. Antrum sclerotisation short, ca. as long as broad. Ductus bursae long, slender, straight. Corpus bursae large, globular, posterior half scobinate, anterior half membranous, with sclerotisation between thorn and corpus opening, medially with faintly marked sclerotised band. Thorn slightly curved, with small dents pointing toward thorn base.

Distribution. Recorded from the Angabunga River in the Central Province (Papua New Guinea), also known from Mount Kaindi, Morobe Province, at altitudes between 2,000 m and 2,360 m.

Remarks. Nuss (1998) transferred this species from *Eudorina* to *Hoploscopa*. Other specimens examined from Papua New Guinea display the same pattern and identical genitalia as the holotype from Western New Guinea.

Hoploscopa persimilis (Rotschild, 1915)

Figs 26, 65

Material examined. ***Lectotype*:** ♂, with labels: "Lecto- | type" [round label, purple ringed]; "Utakwa [sic, Oetakwa] R[iver]., | Dutch N[ew]. Guin[ea]., | 3000f[ee]t., Jan[uary]. 1913. | A.F.R. Wollaston."; "439"; "Eudorina | persimilis | Type Rotsch[ild]."; "Lectotype | Eudorina | persimilis | Rothschild | det. Nuß" [handwritten]; "♂ | Pyralidae | Brit[ish].Mus[eum]. | Slide N°. | 20255"; "N,HMUK 010923328" [barcode appended].

Diagnosis. *Hoploscopa persimilis* displays three nearly triangular yellow spots filled with reddish brown on the costa of the forewing. In male genitalia, uncus is long, slender, with duck-shaped apex, gnathos is projected into a small, triangular pointed tip, and valva dorsal margin is conspicuously convex. Female genitalia not known.

Similar species. *Hoploscopa subvariegata* (q.v.).

Description. ***Head.*** Not examined.

Thorax (Fig. 26). Collar pale yellow. Forewing length: 9 mm; forewing ground colour brown; basal patch elongated, reddish brown, basally crossed by transverse pale yellow streak; costal field reddish brown; median discoidal stigma trapezoid, pale yellow, with basal and distal edges reddish brown; postmedian patch triangular, pale yellow and reddish brown, distally with costal pale yellow blotch; subterminal field tawny; fringes brown with pale yellow spots. Hindwing pale yellow. Legs missing or badly preserved.

Male genitalia (N = 1) (Fig. 65). Uncus long, slender, slightly narrowed on apical 1/4, apex duck beak-shaped. Gnathos projection triangular. Valva ventral margin nearly straight, dorsal margin conspicuously convex, apex roughly rounded. Juxta not clearly visible on the slide. Saccus broad, triangular, pointing dorsad. Phallus apically with sclerotised spine.

Female genitalia. Not known.

Distribution. Described from the Oetakwa River on New Guinea (Indonesia: Papua), at an altitude of 1,000 m.

Remarks. Nuss (1998) transferred this species from *Eudorina* to *Hoploscopa* and designated the lectotype. The worn-out specimens hampered accurate description.

Hoploscopa diffusa (Hampson, 1919)

Figs 30, 66

Material examined. ***Lectotype*:** ♂, with labels: "Lecto- | type" [round label, purple ringed]; "Syn- | type" [round label, blue ringed]; "Fergusson I., | X, XI. [18]94 | (A. S. Meek)."; "97–80"; "Pyrocrambia | diffusa. | type ♂. H[a]mpson." [handwritten]; "Pyralidae | Brit[ish].Mus[eum]. | Slide N°. | 1014 ♂"; "Lectotype | Eudorina | diffusa | Hampson | det. Nuß" [handwritten]; "N,HMUK 010923338 [barcode appended]". Deposited in NHMUK.

Other specimens examined. 2 ♂. Papua New Guinea: 2 ♂ (1 with NHMUK010923439 & genitalia on slide TL715 ♂, 1 with NHMUK010923440 & genitalia on slide TL716 ♂), same data as holotype (NHMUK).

Diagnosis. *Hoploscopa diffusa* displays a brown forewing with postmedian patch, part of postmedian area and subterminal line white coloured, and fringes marked with white dots. In male genitalia, gnathos projection is triangular with rounded tip, valva dorsal margin is conspicuously protruded and juxta is tongue-shaped. Female genitalia not known.

Similar species. *Hoploscopa niveofascia* sp. nov. (q.v.).

Description. ***Head.*** Antennae dorsally with brown scales. Proboscis white. Maxillary palpi brown, pale brown at base. Labial palpi brown, ventro-basally white.

Thorax (Fig. 30). Collar white. Forewing length: 9 mm; forewing ground colour dark brown; small white dots scattered in basal and median area; postmedian patch white, filled with brown, with white costal blotch; postmedian line marked on costal half; postmedian area medially suffused with white scales; subterminal line white, shifted distally at M1; margin with white and black spots; fringe brown, with white dots; hindwing pale brown. Fore- and midlegs brown; tibia and tarsi segments distally white. Hindlegs similar, of a lighter brown.

Abdomen. Male sternum A8 posterior margin notched, with pair of lateral papillae-like protuberances.

Male genitalia (*N* = 3) (Fig. 66). Uncus long, narrowed apical 1/4, apex duck beak-shaped. Gnathos projection triangular, with rounded apex. Valva broad, ventral margin conspicuously bent dorsad on apical 1/4, dorsal margin strongly protruding dorsad, apex pointed. Juxta with base rounded, of constant width, apex rounded. Saccus small, pointing dorsad. No cornutus visible on the slide.

Female genitalia. Not known.

Distribution. Recorded from Fergusson Island (Papua New Guinea).

Remarks. Nuss (1998) transferred this species from *Eudorina* to *Hoploscopa* and designated the lectotype.

Hoploscopa triangulifera (Hampson, 1919)

Figs 31, 67, 110

Material examined. ***Holotype*:** ♂, with labels: “Holo- | type” [round label, red ringed]; “Fergusson I[sland]. | [word crossed] xii.[18]95, | (A, S, Meek).”; “.97.204.”; “Eudorina |triangulifera | type ♂. H[a]mps[o]n”[handwritten]; “Body re-affixed | 6.xii.[19]40 R.S.C.” [handwritten]; “♀ | Pyralidae | Brit[ish].Mus[eum]. | Slide N°. | 20256”; "N,HMUK010923353”[barcode appended]. Deposited in NHMUK.

Other specimens examined. 2♂, 2♀. Papua New Guinea: 1♂ (NHMUK010923452, genitalia on slide TL750 ♂), same locality as holotype, xi-xii.1894; 1♂ (genitalia on slide TL711 ♂, NHMUK010923454), 1♀ (genitalia on slide TL712 ♀, NHMUK010923453), Biagi, Mambare R., 1600 m, iii.1906, leg. A. S. Meek; 1♀ (NHMUK010923455), Dampier Island [Karkar], ii-iii.1914 (NHMUK).

Diagnosis. The large median dorsal patch with costal margin rounded on the forewing is unique to *H. triangulifera*. In male genitalia, the gnathos shows no distal projection, and the saccus is broad, quadrangular. In female genitalia, ductus bursae is short and slender, corpus bursae is large, globular, and bears a long curved thorn.

Similar species. No similar species known.

Description. ***Head.*** Antennae dorsally pale yellow. Proboscis brown. Maxillary palpi brown, inner side pale brown. Labial palpi brown, ventral base pale yellow, inner side pale brown.

Thorax (Fig. 31). Thorax brown, dorsally pale yellow. Collar pale yellow. Forewing length: 7–8 mm (♂), 8–9 mm (♀); forewing ground colour brown; basal and distal discoidal stigmata dark brown; median discoidal stigma forming roughly defined white X; median cubital patch elliptic, dark brown with white edges; large median dark brown patch on dorsum with rounded pale yellow costal margin; postmedian patch triangular, dark brown; postmedian line pale yellow, marked on costal half; pale yellow and brown postmedian fascia on costal half in some specimens, edged distally by white subterminal line; fringes brown with white spots. Hindwing pale brown. Forelegs bronze, tarsi speckled with pale yellow. Midlegs with femur bronze; tibia brown, distally pale yellow; tarsi bronze. Hindlegs with femur bronze; tibia brown, basally and distally pale yellow; tarsi bronze.

Male genitalia (*N* = 2) (Fig. 67). Uncus broad, narrowing on distal half, apex truncate. Gnathos projection limited to small ridge. Valva ventral margin nearly straight, dorsal margin conspicuously convex, apex pointed. Juxta with broad rounded base, medially wide, apex broadly incurved, weakly sclerotised. Saccus broad, quadrangular.

Female genitalia (*N* = 2) (Fig. 110). Anterior apophyses without dorsal bump at posterior 1/3. Antrum sclerotisation ca. twice as long as broad. Ductus bursae very short, straight, slender. Corpus bursae kidney shaped, reticulated, with sclerotisation between thorn and corpus opening, and faintly marked sclerotised band medially. Thorn long, incurved, with small dents pointing toward thorn base on inner side, glabrous on outer side.

Distribution. Known from the Madang, the Northern and the Milne Bay Provinces (Papua New Guinea) at altitudes of ca. 1,600 m.

Remarks. Nuss (1998) transferred this species from *Eudorina* to *Hoploscopa*. The handwritten label from Hampson stipulates that the type is a male, while the abdomen dissected shows it is a female. The abdomen was re-affixed to the specimen, suggesting that either the sex wasn't identified properly by Hampson or that the wrong abdomen was reaffixed to the specimen.

Hoploscopa astrapias Meyrick, 1886

Figs 27, 68, 107

Material examined. ***Lectotype*:** ♀, with labels: "Lecto- | type" [round label, purple ringed]; "Vunîdawa | Fiji | HP. 2. 1. [19]32" [handwritten]; "Hoploscopa Meyr." [handwritten]; "astrapias Meyr." [handwritten]; "Hoploscopa | astrapias | 1/1 Meyrick [handwritten] | E. Meyrick det. | in Meyrick Coll."; "Lectotype | Hoploscopa | astrapias | Meyrick | det. M. Nuß" [handwritten]; "Meyrick Coll. | B. M. 1938-290."; "♀ | Pyralidae | Brit[ish].Mus[eum]. | Slide N°. | 20241"; "GU 654 | Hoploscopa | astrapias | Matthias Nuß"; "N,HMUK 010923383" [barcode appended]. Deposited in NHMUK.

Other specimens examined. 1 ♂, 1 ♀. FIJI: 1 ♂ (DNA voucher MTD8251, genitalia on slide TL724 ♂), 1 ♀ (DNA voucher MTD8250, genitalia on slide TL723 ♀), Viti Levu, Nandarivatu, 820 m, 14.9.1955, leg. H. W. Simmonds (NHMUK).

Diagnosis. The forewings of *H. astrapias* display a median cubital triangular white patch and a bean-shaped postmedian patch reddish brown with yellow edges, distally with thick white streak. In male genitalia, the uncus is slender, elongated, the gnathos is reduced to a ring without posterior projection and the valva is slender, with an evenly rounded apex. In female genitalia, the corpus bursae is large, spherical, and bears a large, straight, glabrous thorn.

Similar species. *Hoploscopa anamesa*, *H. nauticorum* but the latter can be separated from *H. astrapias* and *H. anamesa* based on the forewing: median markings form an elongated white streak running down to dorsal area, disrupted at veins (forming roughly triangular white patch not extending beyond CuA2 in the two other species), and the postmedian patch is quadrangular. In male genitalia, the bristles at uncus apex observed in *H. nauticorum* are absent or reduced in *H. astrapias* and *H. anamesa*, and the valva dorsal margin is strongly produced dorsad on basal half, with a more pointed apex in *H. nauticorum* (dorsal margin slightly convex in two other species, apex evenly rounded). Forewing and male genitalia of *H. astrapias* and *H. anamesa* do not provide unambiguous diagnostic characters to separate them. Median cubital patch of *H. anamesa* is slightly thicker than that of *H. astrapias* in specimens examined. Female genitalia allow clear segregation of these two species: antrum is membranous in *H. anamesa*, while it is lightly sclerotised, twice as long as broad in *H. astrapias*, and ductus bursae is long, gently coiled twice in *H. anamesa*, while it is short and broadly curved in *H. astrapias*.

Description. ***Head.*** Antennae dorsally with brown scales. Proboscis white to pale yellow. Maxillary palpi brown, base and inner side pale brown. Labial palpi brown, ventro-basally pale yellow to white.

Thorax (Fig. 27). Collar white. Forewing length: 10–11 mm (♂ & ♀); forewing ground colour brown; basal yellow streak along 1A+2A, abutted with cubital reddish brown fascia running up to median area, disrupted by median cubital patch; costal field reddish brown; median discoidal stigma trapezoid, reddish brown, edged basally and distally with yellow, median cubital patch triangular, snow white, together with median discoidal stigma forming a canine tooth shape; post-median patch bean-shaped, reddish brown with yellow edges, with thick snow white streak abutting dorsally; post-median area suffused with reddish brown; subterminal line white, not reaching dorsum; subterminal field broadly marked with reddish brown; fringes brown. Hindwing pale yellow, bronze toward distal margin. Forelegs brown. Midlegs brown to bronze; tibia medially white. Hindlegs brown to bronze, tibia base dorsally pale yellow.

Male genitalia ($N = 1$) (Fig. 68). Uncus long, slender, with straight lateral margin, apex narrow, tongue-shaped, dorsally with sclerotised bristles. Gnathos projection limited to small ridge. Valva slender, ventral margin nearly straight, dorsal margin convex, apex rounded. Juxta broad, with base rounded, apex weakly sclerotised, slightly incurved. Saccus small, pointing dorsad. Phallus with broad flat spatula-shaped cornutus.

Female genitalia ($N = 1$) (Fig. 107). Anterior apophyses with dorsal bump at posterior 1/3. Antrum lightly sclerotised, twice as long as broad. Ductus bursae short, broadly curved. Corpus bursae globular, with posterior half reticulated, anterior half membranous, with weak sclerotisation between thorn and corpus opening. Thorn long and slender, straight, glabrous.

Distribution. Known from the island of Viti Levu (Fiji), at altitudes between 0 and 800 m.

DNA barcoding. *Hoploscopa astrapias* shows a divergence of 3.9% with *H. anamesa* and 3.3–4.7% with *H. nauticorum*.

Phylogenetic relationships. *Hoploscopa astrapias*, *H. anamesa*, and *H. nauticorum* are recovered together in the ML analysis of the COI barcode (BS = 61). This topology is congruent with the morphology of these three species: the forewings display a snow white transversal median line and postmedian streak; in male genitalia, the uncus is elongated, slender, the gnathos is reduced to a sclerotised band without posterior projection, the phallus bears a broad, flattened, spatula-shaped cornutus; in female genitalia, the corpus bursae is globular and bears a long and slender straight thorn. Within this clade, a close relationship between *H. astrapias* and *H. anamesa* is supported by both morphology and molecular data (BS = 78).

***Hoploscopa anamesa* Tams, 1935**

Figs 28, 69, 108

Material examined. ***Lectotype*:** ♀, with labels: “LECTO- | TYPE” [round label, purple ringed]; “SYN- | TYPE” [round label, blue ringed]; "N,ew Hebrides: | Tanna. | ix.1930. | L.E.Cheesman. | B.M.1931-30.”; “Lectotype | Hoploscopa | astrapias | anamesa | Tams | det. Nuß” [handwritten]; "N,HMUK 010923391” [barcode appended]. Deposited in NHMUK.

Other specimens examined. 2 ♂, 2 ♀. VANUATU: 1 ♂ (NHMUK010923465), 1 ♀ (NHMUK010923466, genitalia on slide TL718 ♀), Aneityum Island, Red Crest, 3 [k]m NE of Anelgauhat, 1200ft, vi.1955, leg. E. Cheesman; 1 ♂ (NHMUK010923471, DNA voucher MTD8254, genitalia on slide TL727 ♂), 1 ♀ (NHMUK010923470, DNA voucher MTD8255, genitalia on slide TL728 ♀), Aneityum Island, Agathis Camp, 1150 ft, 21.vii.1971, leg. G. S. Robinson (NHMUK).

Diagnosis. *Hoploscopa anamesa* (Fig. 28) display forewing and male genitalia similar to those of *H. astrapias*. Female genitalia differ from those of *H. astrapias* in following characters: antrum not sclerotised; ductus bursae long and coiled. Corpus bursae and thorn similar to *H. astrapias*.

Similar species. *Hoploscopa astrapias* and *H. nauticorum* (q.v.).

Description. ***Head.*** Antennae dorsally with brown scales. Proboscis white to pale yellow. Maxillary palpi brown, base and inner side pale brown. Labial palpi brown, ventro-basally pale yellow to white.

Thorax (Fig. 28). Collar white. Forewing length: 10–11 mm (♂ & ♀); forewing ground colour brown; basal yellow streak along 1A+2A, abutted by cubital reddish brown fascia running up to median area, disrupted by median cubital patch; costal field reddish brown; median discoidal stigma trapezoid, reddish brown, edged basally and distally with yellow; median cubital patch thick, streak-like, snow white; postmedian patch bean-shaped, reddish brown with yellow edges, dorsally abutted by thick snow white streak; postmedian area suffused with reddish brown; subterminal line white, not reaching dorsum; subterminal field broadly marked with reddish brown; fringes brown. Hindwing pale yellow, bronze toward distal margin. Forelegs brown. Midlegs brown to bronze; tibia medially white. Hindlegs brown to bronze, tibia base dorsally pale yellow.

Male genitalia (*N* = 1) (Fig. 69). Uncus long, slender, with straight lateral margin, apex narrow, tongue-shaped, dorsally with sclerotised bristles. Gnathos projection limited to small ridge. Valva slender, ventral margin nearly straight, dorsal margin convex, apex rounded. Juxta broad, with base rounded, apex weakly sclerotised, blunt. Saccus small, pointing dorsad. Phallus with broad flat spatula-shaped cornutus.

Female genitalia (*N* = 1) (Fig. 108). Anterior apophyses with dorsal protuberance at posterior 1/3. Antrum membranous. Ductus bursae long, coiled. Corpus bursae globular, with posterior half reticulated, anterior half membranous, with weak sclerotisation between thorn and corpus opening. Thorn long and slender, straight, glabrous.

Distribution. Known from the Fiji (see Remarks), the Aneityum and Tanna islands on Vanuatu, at an altitude of ca. 350 m.

Phylogenetic relationships. *Hoploscopa astrapias* is recovered as sister species (BS = 78).

Remarks. Nuss (1998) raised *H. anamesa* from subspecies of *H. astrapias* to species. He stated that this species occurs in sympatry with *H. astrapias* on Fiji.

Hoploscopa nauticorum Tams, 1935

Figs 29, 70

Material examined. ***Holotype*:** ♂, with labels: “Holo- | type [round label, red ringed]”; “SAMOAN IS. [typographed]| Malololelei | Upolu | 24.ii.24. [handwritten]| P.A.Buxton”; “SAMOA: | Brit.-Mus. | 1935-315.”; “Hoploscopa | astrapias | nauticorum Tams [typographed] | Holotype ♂ ”; “♂ | Pyralidae | Brit[ish].Mus[eum]. | Slide N°. | 20242”; “GU Nr. 655 | prep. M. Nuß”; "N,HMUK 010923388 [barcode appended]”. Deposited in NHMUK.

***Allotype*:** ♀, with labels: “Allo- | type [round label, red ringed]”; “SAMOAN IS. [typographed] | Upolu Is[land] | Malololelei | 21.ii.1925 | 2,000 f[ee]t | P.A. Buxton | and G. H. Hopkins [handwritten]”; “SAMOA: | Brit. Mus. | 1935-315.”; “Hoploscopa | astrapias | nauticorum Tams [typographed] | Paratype. | Allotype ♀ [handwritten]”; "N,HMUK 010923389 [barcode appended]”. Deposited in NHMUK.

Other specimens examined. 2 ♂. SAMOA: 2 ♂ (DNA vouchers MTD8252 & MTD8253, genitalia on slide TL725 ♂ & TL726 ♂), West Samoa, Upolu, Tiavi, 600 m, 24.viii.1974, leg. G. S. Robinson (NHMUK).

Diagnosis. The forewings of *H. nauticorum* display snow white median, cubital and dorsal markings together forming a streak disrupted with brown at veins, and a postmedian triangular reddish brown patch, distally with snow white streak. In male genitalia, the small sclerotised bristles on dorsal side of the uncus apex are unique to this species. Female genitalia were not investigated.

Similar species. *Hoploscopa astrapias* (q.v.), *H. anamesa* (see *H. astrapias*).

Description. ***Head.*** Antennae dorsally bronze. Proboscis brown, speckled with pale yellow. Maxillary palpi dark brown, basally pale yellow, inner side brown. Labial palpi dark brown, ventral base pale yellow.

Thorax (Fig. 29). Collar pale brown. Forewing length: 10–11 mm; forewing ground colour dark brown; basal yellow streak along 1A + 2A, abutted to cubital reddish brown fascia running up to postmedian area, disrupted by median cubital patch; small reddish blotch at base of cell, with minute snow white dot; median discoidal stigma trapezoid, reddish brown, basally and distally edged with yellow, with snow white streak abutting dorsally, running down to dorsal area, disrupted at veins; postmedian patch quadrangular, reddish brown, dorso-distally with thick snow white streak; subterminal line white, indented inwardly at CuA2; subterminal field reddish brown; fringe brown. Hindwing pale yellow, bronze toward distal margin. Forelegs brown, tarsi speckled with pale yellow. Midlegs brown; tibia base speckled with pale yellow. Hindlegs brown.

Abdomen. Male sternum A8 posterior margin broadly indented, with pair of lateral papillae-like protuberances.

Male genitalia (*N* = 3) (Fig. 70). Uncus long and slender, gently tapering toward apex, apex narrow, tongue-shaped, dorsally with few small sclerotised bristles. Gnathos without posterior projection. Valva ventral margin nearly straight, dorsal margin strongly protruding dorsad on basal half, apex rounded. Saccus broad, medially slightly incurved. Phallus with broad, flat, spatula-shaped cornutus.

Female genitalia. Not investigated.

Distribution. Known from the island of Upolu on Samoa, at an altitude of ca. 600 m.

Phylogenetic relationships. *Hoploscopa nauticorum* is recovered as sister to *H. astrapias* and *H. anamesa* in the ML analysis of the COI barcode (BS = 61).

Remarks. Nuss (1998) raised *H. nauticorum* from subspecies of *H. astrapias* to species.

Hoploscopa anacantha Léger & Nuss, sp. nov.

http://zoobank.org/58D67EDA-0687-479C-87A3-854F58BC369C

Figs 32, 71, 111

Material examined. ***Holotype***: ♂, with labels: "G[unung]. Mogogonipa | summit, 1008m. | 18–20.x.1985"; "INDONESIA : | SULAWESI UTARA, | Dumoga-Bone N[ational]. P[ark]. [Bogani Nani Wartabone National Park] | October 1985."; "R[oyal]. Ent[omological]. Soc[iety]. Lond[on]. | PROJECT WALLACE | B.M. 1985-10"; "N,HMUK010923444 [barcode appended]"; "TL 759 | ♂". Deposited in NHMUK.

Paratypes: 3♂, 3♀ INDONESIA: 2♂ (NHMUK010923449 & NHMUK010923343), Sulawesi Utara, Danau Mooat, site 22, PHPA chalet, open habitat, 1080 m, 31.viii.1985, leg. J. D. Holloway; ♂ (NHMUK010923446 &

genitalia on slide TL760 ♂), 1 ♀ (NHMUK010923445), Sulawesi Utara, Dumoga-Bone National Park [Bogani Nani Wartabone National Park], "Clarke" Camp, lower montane forest, 1140 m, leg. Royal Entomological Society of London; 2 ♀ (1 with NHMUK010923447, DNA voucher MTD8247 & genitalia on slide TL732 ♀, 1 with NHMUK010923448), Sulawesi Utara, Danau Mooat, near Kotamobagu, 1200 m, 27–28.ix.1985, leg. Royal Entomological Society of London (NHMUK).

Diagnosis. *Hoploscopa anacantha* sp. nov. displays dark brown forewings with basal, median and postmedian white streak-like markings. In male genitalia, the gnathos projection forms a conspicuous triangle ca. half the uncus length. In female genitalia, the elongated bulging sclerotisation without thorn on corpus bursae is unique to this species.

Similar species. No similar species known.

Description. ***Head.*** Antennae dorsally dark brown. Proboscis white. Maxillary palpi dark brown, basally white. Labial palpi dark brown, ventro-basally white.

Thorax (Fig. 32). Collar white. Forewing length: 9 mm (♂), 9–10 mm (♀); forewing ground colour dark brown; basal cubital streak and median triangular to streak-like patch white, edged with darker brown and few reddish brown scales; postmedian streak white, reddish brown toward middle of wing; fringes dark brown, with white dots. Hindwing pale brown. Legs brown.

Abdomen. Male sternum A8 posterior margin notched, laterally with pair of papillae-like protuberances.

Male genitalia ($N = 2$) (Fig. 71). Uncus long, slender, with straight lateral margin, apex blunt. Gnathos projection broad, triangular, ca. half the uncus length, with small rounded apex. Valva ventral margin nearly straight, dorsal margin convex, apex pointed. Juxta with base quadrangular, medially narrowed, apex wide, truncate. Saccus small, quadrangular.

Female genitalia ($N = 1$) (Fig. 111). Anterior apophyses without bump at posterior 1/3. Antrum sclerotisation short, as long as broad. Ductus bursae long, broadly curved before corpus opening. Corpus bursae globular, covered with erect papillae, reticulated at corpus opening, with well-marked elongated bulging sclerotisation running from corpus opening to middle of corpus bursae. Thorn absent.

Distribution. Known from North Sulawesi (Indonesia) at altitudes between 1,000 m and 1,200 m.

Phylogenetic relationships. This species is recovered sister to an undescribed *Hoploscopa* species (DNA voucher MTD8238) from North Sulawesi.

Etymology. From the Greek *a-*, *an-*, without, and *acantha*, spine, referring to the absence of thorn on the corpus bursae of female genitalia. This name was suggested by Francesca Vegliante.

Hoploscopa kelama Léger & Nuss, sp. nov.

http://zoobank.org/69D2A893-2F5A-4E90-9E82-8C6FD059A364

Figs 33, 72, 112

Material examined. ***Holotype***: ♀, with labels: "[Indonesia] North-Sulawesi, Danau Mooat | east of Kotamobagu, 1150m | 30–31.iii.2000, at light | leg. A. Kallies &

S. Naumann"; "DNA voucher | Lepidoptera | MTD 2016 | no. 3214 [vertically written]"; "TL | 532 ♀". Deposited in MTD.

***Paratypes*:** 6 ♂, 2 ♀. 1 ♂ (DNA voucher MTD LEP3215, genitalia on slide TL511 ♂), same data as holotype; 2 ♀ (1 with DNA voucher MTD7878 & genitalia on slide TL665 ♀, 1 with DNA voucher 7879 & genitalia on slide TL474 ♀), same collecting locality as holotype, 25–26.iii.2000, leg. A. Kallies & C. Zorn (MTD); 2 ♂ (NHMUK010923443, NHMUK010923341), North Sulawesi, Danau Mooat, near Kotamobagu, 1200 m, 27–28.ix.1985, leg. Royal Entomological Society of London, Project Wallace; 3 ♂ (NHMUK010923342, NHMUK010923442, NHMUK010923441), North Sulawesi, Dumoga-Bone National Park [Bogani Nani Wartabone National Park], Clarke Camp, lower montane forest, 1140 m, x.1985, leg. Royal Entomological Society of London, Project Wallace (NHMUK).

Diagnosis. *Hoploscopa kelama* sp. nov. displays basal and distal discoidal dark brown spots edged with pale yellow, as well as a pale yellow cubital double line on the forewing. In female genitalia, the very small thorn located at the corpus bursae opening is unique to this species.

Similar species. *Hoploscopa boleta* sp. nov., *H. pseudometacrossa* sp. nov. Both species display light brown median discoidal stigma and postmedian patch and lack the double pale yellow cubital line observed in *H. kelama* sp. nov. Examination of genitalia allows unambiguous separation of these species from *H. kelama* sp. nov.: male genitalia of both species show a slender uncus bearing thick setae, ventrally marked with three small ridges, and female genitalia show a larger thorn located on posterior half of corpus bursae.

Description. ***Head.*** Antennae dorsally striped with brown and ochreous scales. Proboscis brown. Maxillary palpi brown, basally pale yellow, inner side pale brown. Labial palpi brown, ventro-basally pale yellow.

Thorax (Fig. 33). Collar white. Forewing length: 8–9.5 mm (♂ & ♀); forewing ground colour brown to dark brown; basal dash black at base, distally pale yellow; basal discoidal patch forming dorsally opened pale yellow C filled with dark brown; distal discoidal patch dark brown, quadrangular, with basal and distal edges pale yellow; double cubital pale yellow-coloured line running from median area distally to tornus; small postmedian costal pale yellow blotch; subterminal line pale yellow, barely or not marked on its middle, forming diffuse pale yellow patch near apex; fringes brown, with pale yellow dots. Hindwing pale brown. Forelegs brown. Mid- and hindlegs with femur brown; tibia dark brown, distally pale yellow; tarsi brown.

Abdomen. Male sternum A8 posterior margin notched, with pair of lateral papillae-like protuberances.

Male genitalia (*N* = 1) (Fig. 72). Uncus long and slender, medially slightly widened, conspicuously narrowed at apical 1/4, apex duck beak-shaped, with small median bump. Gnathos projection limited to a small ridge. Valva ventral margin nearly straight, dorsal margin slightly convex, apex pointed. Juxta slender, with base slightly quadrangular, medially narrowed, apex broadly incurved, weakly sclerotised. Saccus quadrangular.

Female genitalia (*N* = 3) (Fig. 112). Anterior apophyses with small dorsal bump at posterior 1/3. Antrum sclerotisation broad, ca. twice as long as broad. Ductus bursae long, broad, looped once, kinked at corpus opening. Corpus bursae with posterior half reticulated, anterior half membranous. Thorn located on ductus bursae shortly ahead of corpus opening, very small, with dents pointing toward thorn apex.

Distribution. Known from North Sulawesi (Indonesia) at altitudes between 1,000 m and 1,200 m.

Phylogenetic relationships. The ML analysis of the COI barcode recovered *H. kelama* sp. nov. in a clade with *H. albomaculata* sp. nov. and *H. ignitamaculae* sp. nov., but without significant support (BS = 30). These three species vary greatly in their wing pattern but show similarities in the morphology of the genitalia: the uncus apex is duck-shaped, with a small tip on its middle in male genitalia; in female genitalia, the ductus bursae is long and broad, the corpus bursae is globular, with an elongated, well-marked sclerotisation. *Hoploscopa kelama* sp. nov. and *H. ignitamaculae* sp. nov. share a small-sized thorn on corpus bursae. Hoploscopa *anacantha* sp. nov. shares a wing pattern similar to that of *H. albomaculata* sp. nov., and displays an elongated, marked sclerotisation like in the other three species above, although without thorn.

Etymology. The species epithet *kelama* comes from the Indonesian "kelam" meaning dark.

Hoploscopa ignitamaculae Léger & Nuss, sp. nov.

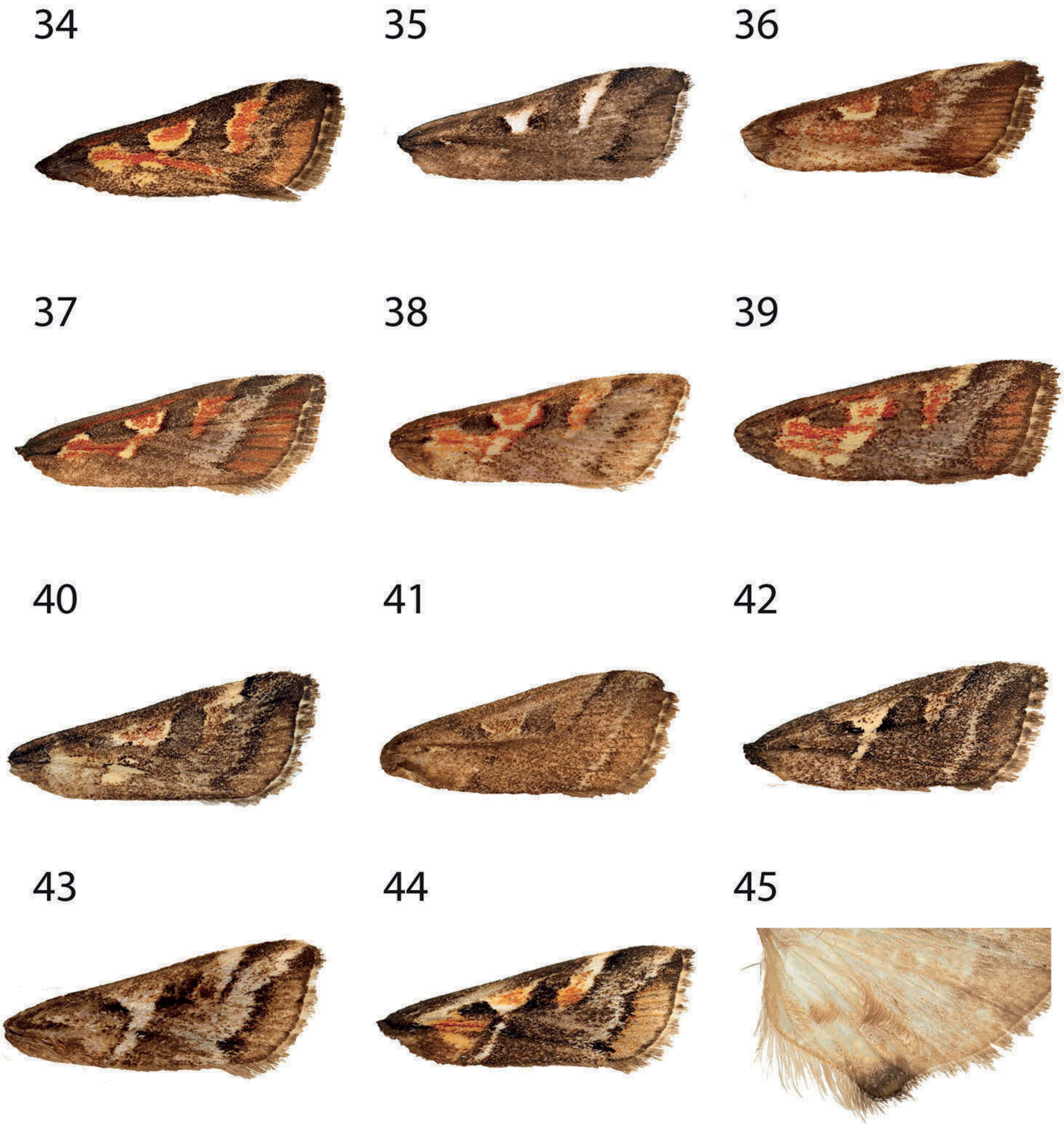
http://zoobank.org/DB39215F-2066-454D-BEAE-BE7D0E523CF4

Figs 34, 73, 113

Material examined. ***Holotype***: ♀, with labels: "[Indonesia] North-Sulawesi, Tangkoko- | Batuangus-Dua-Saudara Reserve | near Batuputih, primary forest | 600m, 21.iii.2000, at light | leg. A. Kallies & C. Zorn"; "DNA barcode | BC MTD 01427". Deposited in MTD.

Paratypes: 6 ♂, 14 ♀. Indonesia: 4 ♂ (3 with genitalia on slide TL475 ♂, TL480 ♂, TL545 ♂), 7 ♀ (1 with DNA voucher MTD LEP82, genitalia on slide TL364 ♀; 1 with DNA barcode BC MTD 01425), same data as holotype; 3 ♀ (1 with DNA voucher MTD LEP3216, DNA barcoding BC MTD 01426; 1 with DNA voucher MTD LEP3218, genitalia on slide TL516 ♀), North Sulawesi, Danau Mooat, east of Kotamobagu, 1000 m, 25–26.iii.2000, at light, leg. A. Kallies & C. Zorn; 1 ♂ (DNA voucher MTD LEP3217 & genitalia on slide TL509 ♂) with same collecting locality, 30–31.iii.2000, leg. A. Kallies & S. Naumann (MTD); 1 ♂ (NHMUK010923412), North Sulawesi, Dumoga-Bone National Park [Bogani Nani Wartabone National Park], Clarke Camp, lower montane forest, 1140 m, ix.1985, leg. Royal Entomological Society of London, Project Wallace; 1 ♀ (NHMUK010923411), same data except Plot B, lowland forest, 300 m; 2 ♀ (NHMUK010923410, NHMUK010923413), same data except Gunung Mogogonipa, summit, 1008m, 22–23.ix.1985 (NHMUK).

Diagnosis. The forewings of *H. ignitamaculae* sp. nov. display marked basal, median and postmedian reddish orange markings edged with yellow; postmedian patch with undulated basal margin. In male genitalia, uncus is medially widened, apex is duck-shaped, ventrally with small bump, and gnathos is projecting into a short, pointed tip. In female genitalia, the well-delimited elongated sclerotisation of the corpus bursae with the small slightly curved thorn on its middle is unique to this species.



Figures 34–45. Habitus of *Hoploscopa* species. **34** *Hoploscopa ignitamaculae* sp. nov., paratype, ♂, North Sulawesi, Danau Mooat, east of Kotamobagu, 1000 m, 30–31.iii.2000 (A. Kallies & C. Zorn) (genitalia on slide TL509 ♂) **35** *Hoploscopa albomaculata* sp. nov., paratype, ♀, Indonesia, North Sulawesi, Danau Mooat, east of Kotamobagu, 1000 m, 25–26.iii. 2000, (A. Kallies & C. Zorn) (genitalia on slide TL540 ♀) **36** *Hoploscopa sumatrensis* sp. nov., holotype, ♂, Indonesia, Sumatra-Holzweg, 25 km SSW-Pematangsiantar, Strasse nach Prapat, 6–26.i.1996 (A. Kallies) (genitalia on slide TL755 ♂) **37** *Hoploscopa mallyi* sp. nov., paratype, ♂, Malaysia, Sabah, Mt Kinabalu, Mesilau, 2000 m, 14–17.xi.2006 (W. Mey & K. Ebert) **38** *Hoploscopa gracilis* sp. nov., holotype, ♂, Indonesia, Sumatra-Holzweg, 25 km SSW-Pematangsiantar, Straße nach Prapat, 13.ii.1996 (A. Kallies) (genitalia on slide TL754 ♂) **39** *Hoploscopa agtuuganonensis* sp. nov., holotype, ♀, Philippines, Mindanao, Mt Agtuuganon, 1050 m, 28.v–7.vi.1996 (W. Mey) (genitalia on slide TL616 ♀) **40** *Hoploscopa boleta* sp. nov., paratype, ♀, Papua New Guinea, Morobe, Mt Kaindi, 2360 m, 3.x.1992 (V. O. Becker) (genitalia on slide TL448 ♀) **41** *Hoploscopa pseudometacrossa* sp. nov., holotype, ♀, Papua New Guinea, W. Hhl, Prv, near Mt. Hagen, Kuk Ag, Res. Sta., 1600 m, 19–20.viii.1983 (Scott E. & Pamela Miller) (genitalia on slide TL689 ♀) **42** *Hoploscopa metacrossa* Hampson, ♀, Papua New Guinea, Morobe Province, near Bulolo, Mt Susu National Reserve, *Araucaria* forest, 975 m, 27–28.viii.1983 (S. Miller).

Similar species. *Hoploscopa isarogensis* sp. nov. Forewing markings of *H. isarogensis* sp. nov. tend more to red. Postmedian patch is triangular with a straight basal margin, and subterminal line is often markedly pale yellow.

Description. *Head.* Antennae dorsally with bronze scales. Proboscis white to pale yellow. Maxillary palpi brown, basally pale yellow. Labial palpi brown, ventral base and inner side pale yellow.

Thorax (Fig. 34). Collar white. Forewing length: 8.0–9.5 mm (♂ & ♀); forewing ground colour brown; basal patch yellow, with cubital reddish orange streak starting from its middle, running distally up to postmedian area; costal field reddish orange; median discoidal stigma trapezoid, reddish orange, edged with yellow; median cubital and dorsal patches yellow, not connected; postmedian patch reddish orange, basal margin undulated, yellow, costal blotch yellow; subterminal field brown to tawny; fringes brown with pale yellow spots. Hindwing pale brown. Forelegs brown. Midlegs brown; tibia distally pale yellow. Hindlegs with femur brown; tibia pale yellow speckled with brown; tarsi brown.

Abdomen. Male sternum A8 posterior margin broadly incurved, with pair of lateral papillae-like protuberances.

Male genitalia (*N* = 4) (Fig. 73). Uncus long, medially widened, apex duck beak-shaped, ventrally with a small bump. Gnathos projection triangular, slender, ca. 1/4 of uncus length, with rounded apex. Valva ventral margin nearly straight, dorsal margin convex, apex pointed. Juxta with rounded base, narrowing on basal half, apex blunt. Saccus slightly quadrangular.

Female genitalia (*N* = 2) (Fig. 113). Anterior apophyses with dorsal bump at posterior 1/3. Antrum sclerotisation short, ca. as long as wide. Ductus bursae broad, kinked at anterior and posterior 1/4. Corpus bursae globular, posterior half reticulated, anterior half with erect papillae, with elongated sclerotised area running from corpus opening to its middle. Thorn on middle of sclerotisation, very small, slightly curved, with dents pointing toward thorn base.

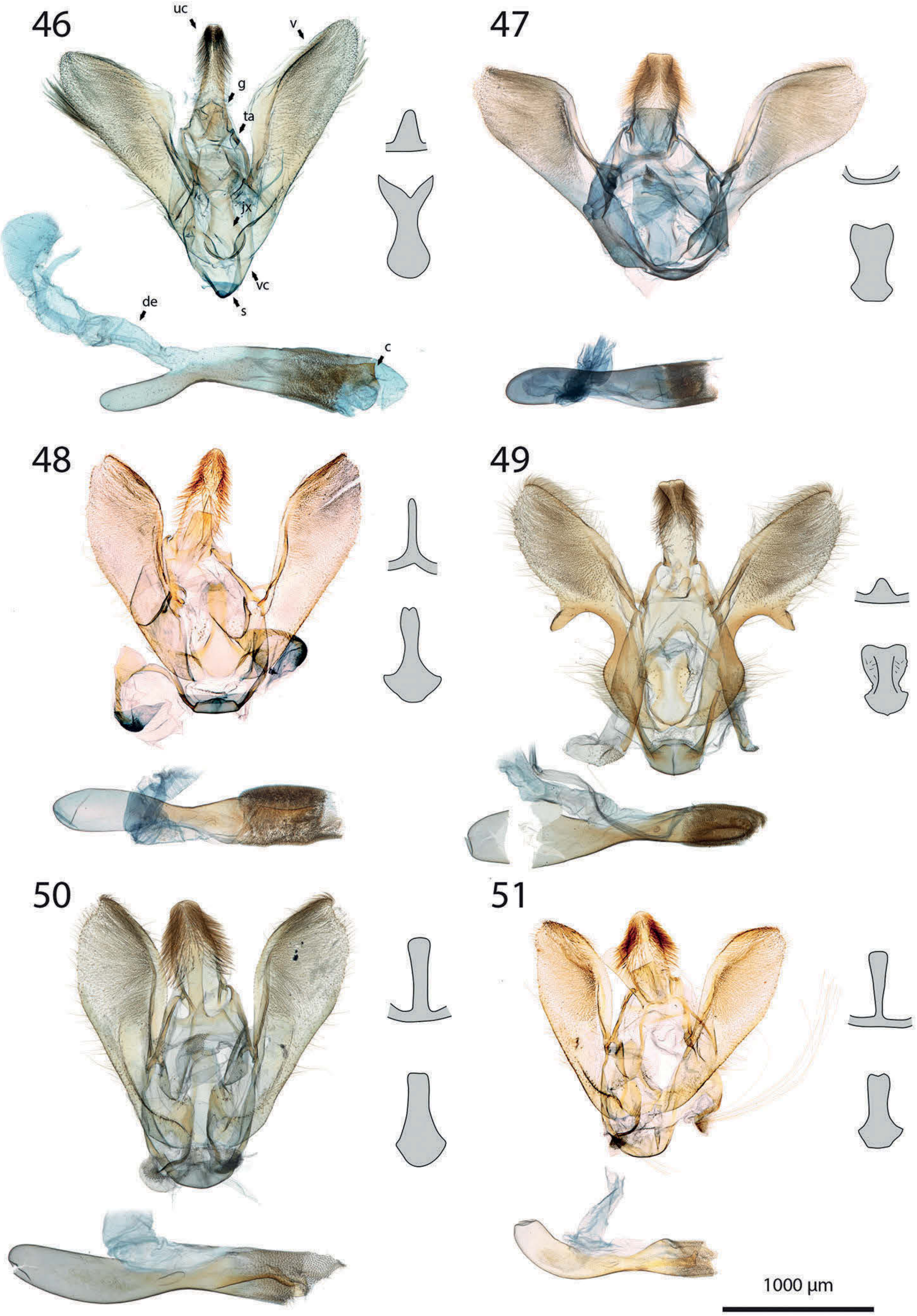
Distribution. Known from North Sulawesi (Indonesia) at altitudes between 300 m and 1,150 m.

Phylogenetic relationships. See *H. kelama* sp. nov.

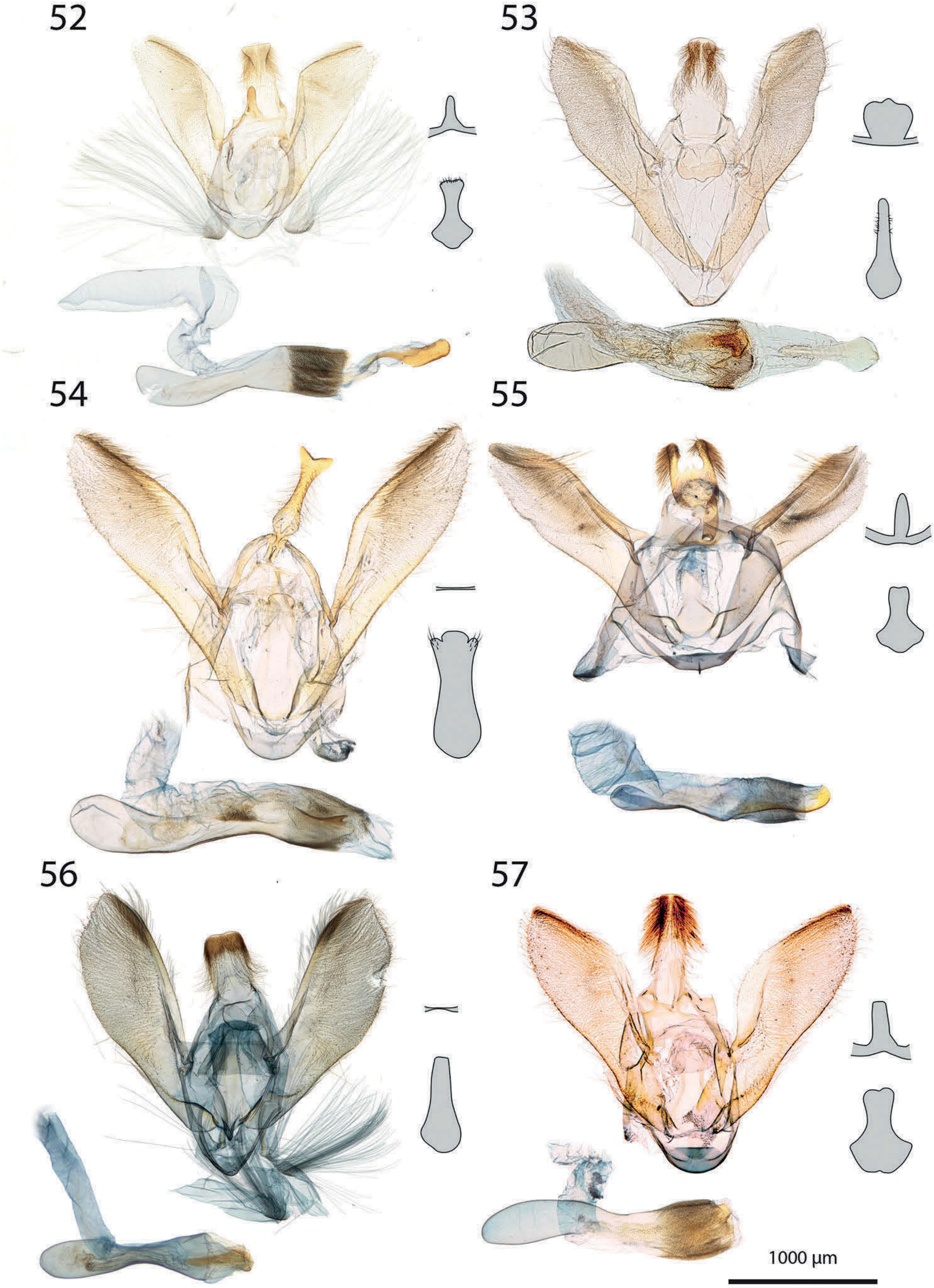
Etymology. From the Latin *ignitus*, set on fire, and *macula*, spot or blot, in reference to the red and yellow spots of the forewing.

Remarks. Specimen MTD8238 shows a forewing pattern resembling that of *H. ignitamaculae* sp. nov., but with markings reduced. However, the thorn is absent in female genitalia.

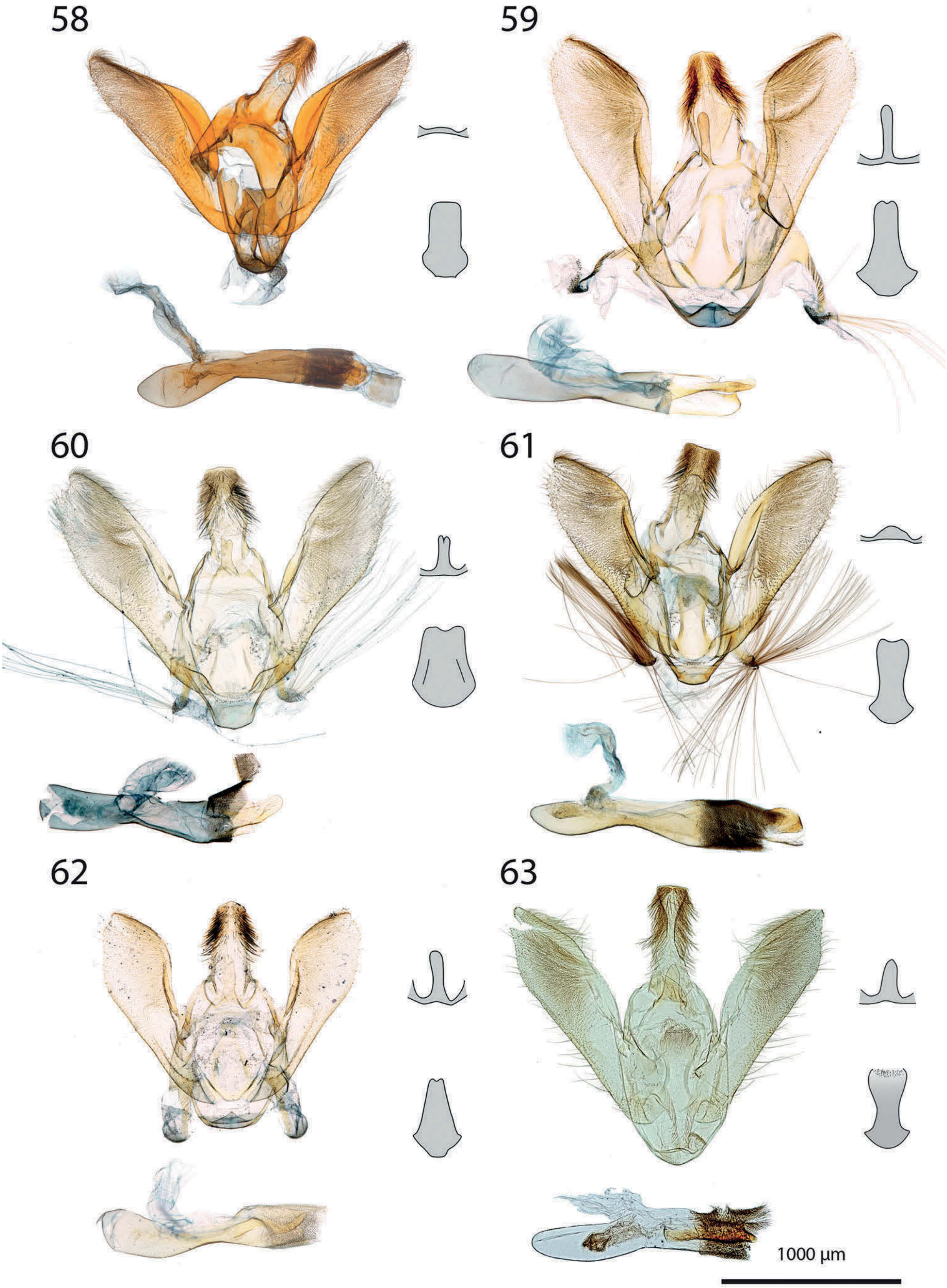
Figures 34–45. Continued. **43** *Hoploscopa jubata* sp. nov., paratype, ♂, Papua New Guinea, Morobe Province, near Bulolo, Mt Susu National Reserve, *Araucaria* forest, 975 m, 27–28.viii.1983 (S. Miller) **44** *Hoploscopa jubata* sp. nov. , paratype, ♀, Morobe Province, near Bulolo, Mt Susu National Reserve, *Araucaria* forest, 975 m, 27–28.viii.1983 (S. Miller) **45** Hindwing scent organ in *Hoploscopa metacrossa*. Paratype, ♂, Papua New Guinea, Morobe Province, Wau, 1200 m, 8–14.xii.1976 (G. F. Hevel & R. E. Dietz) (genitalia on slide TL443 ♂).



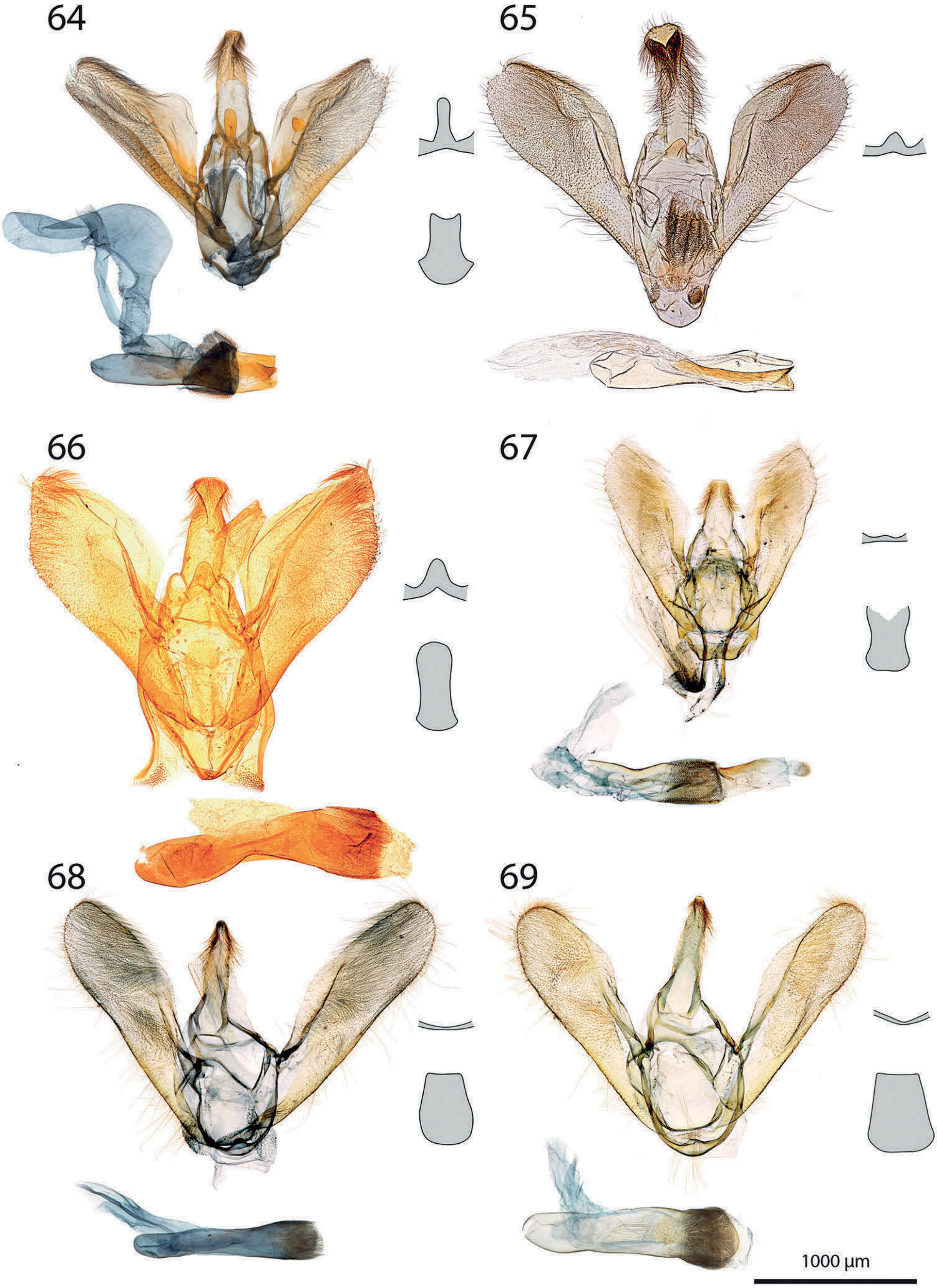
Figures 46–51. Male genitalia features of *Hoploscopa*. For each figure left above: genitalia without phallus; left below: phallus; right above: gnathos drawing; right below: juxta drawing. **46** *Hoploscopa albipuncta* sp. nov., paratype, TL336 ♂ (genitalia without phallus), TL635 ♂ (phallus) **47** *Hoploscopa matheae* sp. nov., paratype, TL730 ♂ **48** *Hoploscopa sepanggi* sp. nov., paratype, TL641 ♂ **49** *Hoploscopa cynodonta* sp. nov., paratype, TL531 ♂ **50** *Hoploscopa parvimacula* sp. nov., holotype, TL510 ♂ **51** *Hoploscopa kinabaluensis* sp. nov., paratype, TL342 ♂. Abbreviations: c (cornutus), de (ductus ejaculatorius), g (gnathos), jx (juxta), s (saccus), ta (tegumen arm), v (valva), vc (vinculum), uc (uncus).



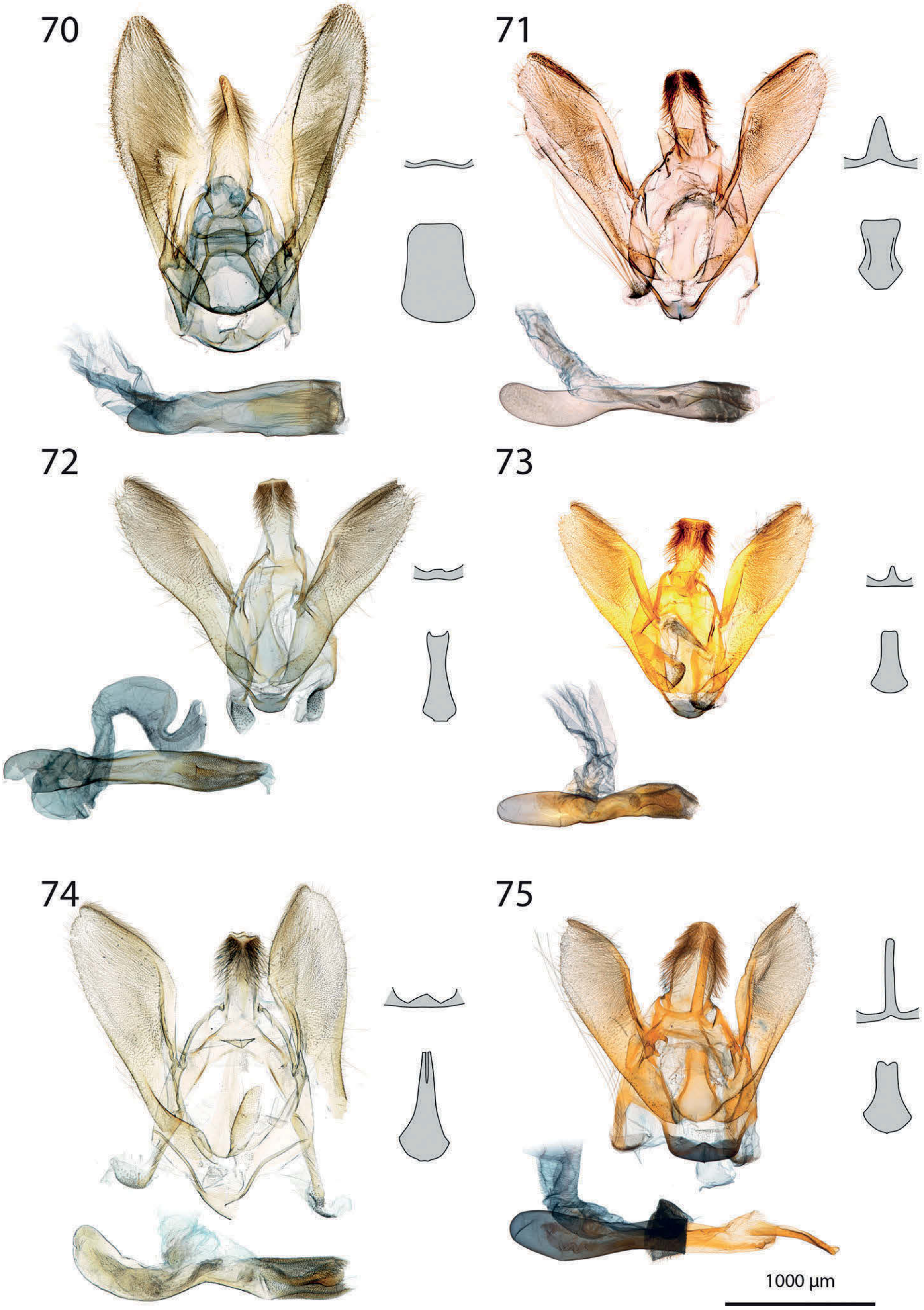
Figures 52–57. Male genitalia features of *Hoploscopa*. **52** *Hoploscopa luteomacula* Nuss, holotype, GU prep. Nuss 744 ♂ **53** *Hoploscopa obliqua*, holotype, Pyralidae Brit. Mus. Slide N° BMNH20252 ♂ (phallus with juxta attached) **54** *Hoploscopa gombongi* sp. nov., holotype, TL653 ♂ **55** *Hoploscopa tonsepi* sp. nov., paratype, TL661 ♂ **56** *Hoploscopa niveofascia* sp. nov., holotype, TL442 ♂ **57** *Hoploscopa marijoweissae* sp. nov., holotype, TL710 ♂.



Figures 58–63. Male genitalia features of *Hoploscopa*. **58** *Hoploscopa titika* sp. nov., holotype, TL505 ♂ (apical part of juxta attached to phallus) **59** *Hoploscopa pangrangoensis* sp. nov., paratype, TL659 ♂ **60** *Hoploscopa isarogensis* sp. nov., paratype, TL762 ♂ **61** *Hoploscopa ypsilon* sp. nov., paratype, TL624 ♂ **62** *Hoploscopa danaoensis* sp. nov., holotype, TL632 ♂ **63** *Hoploscopa quadripuncta*, holotype, Pyralidae Brit. Mus. Slide N° BMNH20257 ♂.



Figures 64–69. male genitalia features of *Hoploscopa*. 64. *Hoploscopa subvariegata*, TL534 ♂. **65** *Hoploscopa persimilis*, lectotype, Pyralidae Brit. Mus. Slide N° BMNH20255 ♂ (no juxta drawing) **66** *Hoploscopa diffusa*, holotype, Pyralidae Brit. Mus. Slide N° BMNH1014 ♂ **67** *Hoploscopa triangulifera*, TL711 ♂ **68** *Hoploscopa astrapias*, TL724 ♂ **69** *Hoploscopa anamesa*, TL727 ♂.



Figures 70–75. Male genitalia features of *Hoploscopa*. **70** *Hoploscopa nauticorum*, TL725 ♂ **71** *Hoploscopa anacantha* sp. nov., holotype, TL759 ♂ **72** *Hoploscopa kelama* sp. nov., paratype, TL511 ♂ **73** *Hoploscopa ignitamaculae* sp. nov., paratype, TL545 ♂ **74** *Hoploscopa albomaculata* sp. nov., paratype, TL363 ♂ **75** *Hoploscopa sumatrensis* sp. nov., paratype, TL538 ♂.

Hoploscopa albomaculata **Léger & Nuss, sp. nov.**

http://zoobank.org/E458DE68-F0CC-48B1-91D2-8F94B21D51DB

Figs 35, 74, 114

Material examined. ***Holotype*:** ♀, with labels: "[Indonesia] North Sulawesi, Danau Mooat | east of Kotamobagu, 1000m | 25.–26. iii. 2000, at light | leg. A. Kallies & C. Zorn"; "DNA Barcode | BC MTD 01429"; "TL544 | ♀". Deposited in MTD.

***Paratypes*:** 9 ♂, 5 ♀. Indonesia: 5 ♂ (4 with genitalia on slides TL473 ♂, TL479 ♂, TL543 ♂, TL646 ♂), 3 ♀ (1 with DNA voucher MTD LEP57 & MTD LEP3213, genitalia on slide TL529 ♀), same data as holotype; 2 ♂ (1 with DNA voucher MTD LEP81, genitalia on slide TL363 ♂), 1 ♀ (DNA barcoding BC MTD 01428, genitalia on slide TL540 ♀), same locality as holotype, 30–31.iii.2000, leg. A. Kallies & S. Naumann (MTD); 1 ♂ (NHMUK010923450), 1 ♀ (NHMUK010923355), North Sulawesi, Danau Mooat, 1200 m, near Kotamobagu, 27–28.ix.1985 (♂), 9.xi.1985 (♀), leg. Royal Entomological Society of London, Project Wallace; 1 ♂ (NHMUK010923451), same data, Site 22, 1080 m, PHPA chalet, open habitat, 31.viii.1985, leg. J. D. Holloway (NHMUK).

Diagnosis. *Hoploscopa albomaculata* sp. nov. is unique by virtue of its median trapezoid and postmedian streak-like white patches on the forewing. In male genitalia, the gnathos projection is reduced to a small triangular tip, and the juxta is elongated, slender, with a deeply indented apex. In female genitalia, ductus bursae is long, broad and curvy, and corpus bursae displays well-delimited sclerotised band and a straight thorn.

Similar species. No similar species known.

Description. ***Head.*** Antennae dorsally with brown scales. Proboscis pale yellow to pale brown. Maxillary palpi brown, base and inner side pale yellow. Labial palpi brown, ventral base and inner side pale yellow.

Thorax (Fig. 35). Collar pale yellow. Forewing length: 9 mm (♂), 9–10 mm (♀); forewing ground colour brown; small basal white dash edged with dark brown; median trapezoid white patch, with basal and distal edges dark brown; postmedian white streak, pale yellow at costa, edges dark brown; subterminal line dark brown, basally faintly marked with pale yellow; fringes basally pale yellow, distally brown. Hindwing pale brown. Forelegs bronze. Mid- and hindlegs with femur brown; tibia pale yellow speckled with brown; tarsi bronze.

Abdomen. Male sternum A8 posterior margin bilobed, laterally with pair of papillae-like protuberances.

Male genitalia ($N = 5$) (Fig. 74). Uncus medially slightly widened, narrowed at apical 1/4, apex roughly truncate, ventrally with a triangular tip pointing posterad. Gnathos projection wide, triangular. Valva ventral margin nearly straight, dorsal margin conspicuously convex, apex pointed. Juxta slender, with base rounded, narrowing toward apex, apex deeply indented. Saccus small, pointing dorsad.

Female genitalia ($N = 3$) (Fig. 114). Anterior apophyses without dorsal bump at posterior 1/3. Ductus bursae long, slender, gently curved twice. Antrum sclerotisation short, ca. as long as wide. Corpus bursae small, globular, reticulated, with marked elongated sclerotisation from corpus opening to thorn. Thorn straight, with small dents pointing toward thorn apex.

Distribution. Known from North Sulawesi (Indonesia) at altitudes between 1,000 m and 1,200 m.

Phylogenetic relationships. See *H. kelama* sp. nov.

Etymology. From the Latin *albus*, white, and *maculatus*, covered with spots.

Hoploscopa sumatrensis Léger & Nuss, sp. nov.

http://zoobank.org/22F33777-64CB-4E37-9AB2-41A52020ABEB

Figs 36, 75, 83, 115

Material examined. ***Holotype***: ♂, with labels: "Sumatra-Holzweg | 25km SSW-Pematangsiantar | Straße nach Prapat [road to Prapat] | 6.-26.i.1995, leg. A. Kallies"; "coll[ection]. M. Nuss | Geschenk 2000 | Museum für Tier- | kunde Dresden"; "DNA voucher | Lepidoptera | date: xi.2018 | MTD8260 | [vertically written:] DNA | -voucher"; "TL755 | ♂". Deposited in MTD.

Paratypes: 3 ♂, 4 ♀. Indonesia. 3 ♂ (DNA vouchers MTD9119, MTD9129 & MTD9121 and genitalia on slides TL761 ♂, TL763 ♂, TL538 ♂), 3 ♀ (DNA vouchers MTD LEP 3205, MTD8257, MTD8262 & genitalia on slides TL524 ♀, TL752 ♀, TL757 ♀), same data as holotype; 1 ♀ (DNA voucher MTD7880 & genitalia on slide TL670 ♀), Sumatra, Asahan, Huta Padang, 1990, leg. E. W. Diehl (MTD).

Other specimens examined. 4 ♀, 2 ♀ (DNA vouchers MTD LEP 3202, MTD 8258 & genitalia on slides TL530 ♀, TL753 ♀), same data as holotype; 1 ♀ (DNA voucher MTD LEP 3210 & genitalia on slide TL522 ♀), same data as holotype except 23.viii.1989, leg. E. W. Diehl; 1 ♀ (DNA voucher MTD8261 & genitalia on slide TL756 ♀), same data as holotype except 13.ii.1996 (MTD).

Diagnosis. The forewings of *H. sumatrensis* sp. nov. display a pale yellow crescent-shaped median discoidal stigma filled with reddish brown, as well as a postmedian area broadly suffused with pale yellow. In male genitalia, the gnathos projection is slender, ca. 4/5 of uncus length, with a tongue-shaped apex, and the juxta has a rounded base and a notched apex. In female genitalia, the short and slender ductus bursae bent before corpus and the pear-shaped corpus bursae with small straight thorn resemble those of other *Hoploscopa* species, e.g., *H. danaoensis* sp. nov. and *H. parvimacula* sp. nov.

Similar species. *Hoploscopa pangrangoensis* sp. nov. (q.v.).

Description. ***Head.*** Antennae dorsally with brown scales. Proboscis pale yellow to brown. Maxillary palpi brown, base and inner side pale yellow. Labial palpi brown, ventral base and inner side pale yellow.

Thorax (Fig. 36). Collar pale yellow. Forewing length: 9–10 mm (♂ & ♀); forewing ground colour brown; small basal dark brown dash distally pale yellow; base of dorsum with patch of pale yellow scales; cubital reddish brown fascia running up to median area; median discoidal stigma reddish brown, edged with crescent-shaped pale yellow patch; postmedian patch reddish brown, with pale yellow blotch at costa; subterminal line broad, pale yellow; subterminal field tawny to brown; fringes brown, with pale yellow dots. Hindwing pale yellow. Forelegs bronze. Midlegs with femur brown; tibia pale yellow to brown; tarsi bronze. Hindlegs brown; tibia pale yellow speckled with brown; tarsi bronze.

Abdomen (Fig. 83). Male sternum A8 posterior margin bilobed.

Male genitalia (*N* = 4) (Fig. 75). Uncus medially broad, narrowed at apical 1/4, apex tongue-shaped. Gnathos projection slender, ca. 4/5 of uncus length, apex tongue-shaped. Valva ventral margin straight, bent dorsad on distal 1/4, dorsal margin convex, apex pointed. Juxta base rounded, distal half narrowed, apex notched. Saccus triangular, pointed.

Female genitalia (*N* = 4) (Fig. 115). Anterior apophyses with dorsal tip at posterior 1/3. Antrum sclerotisation short. Ductus bursae short, kinked before corpus opening. Corpus bursae large, pear-shaped, with sclerotisation between thorn and corpus opening and a median sclerotised band. Thorn small, straight, with small dents.

Distribution. Known from North Sumatra (Indonesia).

DNA barcoding. Two MOTUs are found in morphologically identical specimens with same collecting data. The K2P-distance between the two MOTUs is 4.1–6%. The first MOTU, which is the one of the type material, shows an intraspecific variation of 0.7%. The second MOTU is found in three females (samples BC MTD LEP01422, MTD8258 and MTD8261) and shows an intraspecific divergence of 0.6%.

Etymology. Named after the island of Sumatra where the species is encountered.

Remarks. Future examination of male specimens from the second lineage will help to determine whether or not it represents a separate species.

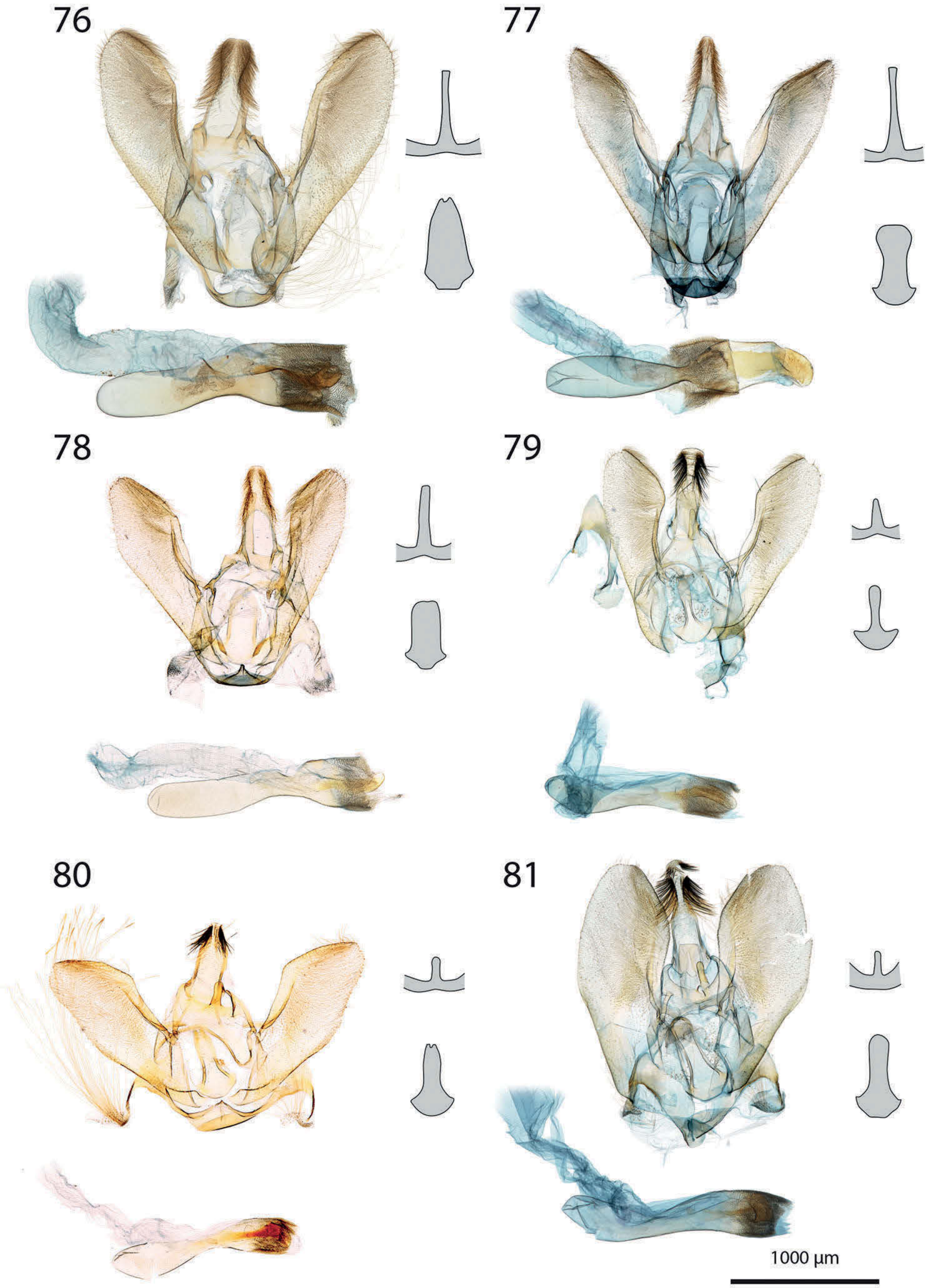
Hoploscopa mallyi **Léger & Nuss, sp. nov.**

http://zoobank.org/13552C8E-ED5E-447B-859A-8402DD48BA72

Figs 37, 76, 116

Material examined. ***Holotype***: ♀. “Borneo, Mt Kinabalu | Headquarter, 1600m | 10–13.XI.2006, L[icht]F[ang] | leg. W. Mey & K. Ebert”; “Liwagu River | 1500m, Turm”; “DNA voucher | Lepidoptera | M. Nuss 2007 | [vertically written:] no. 124”; “TL366 | ♀”. Deposited in ZMHB.

Paratypes: 4 ♂, 2 ♀. Malaysia: 1 ♂, 1 ♀ (genitalia on slides TL533 ♂ and TL340 ♀ respectively), Sabah, Kinabalu National Park Headquarters, 250 m from Pandanus Trail starting point, 6°0'34"N, 116°32'20"E 1640 m, UV light, 07.vi.2015, leg. T. Léger & R. Mally; 2 ♂ (1 with genitalia on slide TL339 ♂), Sabah, Mesilau logging site, 400 m before entrance to Mesilau Nature Reserve, 6°2'22"N, 116°35'54"E, 1930 m, UV light, 02.vi.2015, T. Léger & R. Mally; 1 ♀ (DNA voucher 3197, genitalia on slide TL513 ♀), Sabah, Kinabalu Park Headquarters, ca. 300 m from starting point of Kiau View Trail, 6°0'25"N, 116°32'21"E, 1660 m, UV light, 06.vi.2015, T. Léger & R. Mally (MTD); 1 ♂, Borneo, Mt Kinabalu, Mesilau, 2000 m, 14–17.xi.2006, W. Mey & K. Ebert (ZMHB).



Figures 76–81. Male genitalia features of *Hoploscopa*. **76** *Hoploscopa mallyi* sp. nov., paratype, TL339 ♂ **77** *Hoploscopa gracilis* sp. nov., paratype, TL539 ♂ **78** *Hoploscopa agtuuganonensis* sp. nov., paratype, TL675 ♂ **79** *Hoploscopa boleta* sp. nov., holotype, TL440 ♂ **80** *Hoploscopa pseudometacrossa* sp. nov., paratype, TL441 ♂ (uncus apex missing) **81** *Hoploscopa metacrossa*, TL443 ♂.

Diagnosis. The forewings of *H. mallyi* sp. nov. display pale yellow crescent-shaped median discoidal stigma filled with red, together with median cubital patch forming a Y. In male genitalia, gnathos projection is long, slender, ca. 2/3 the uncus length, and juxta is ogive-shaped, with a slightly indented apex. In female genitalia, ductus bursae is long, broad and forms two large curves. Corpus bursae is small, globular, with one short curved thorn.

Similar species. *Hoploscopa agtuuganonensis* sp. nov., *H. gracilis* sp. nov. In *H. agtuuganonensis* sp. nov., median discoidal stigma together with cubital and dorsal patches forms a band progressively narrowing toward dorsum (median cubital patch reduced to small streak, median dorsal patch absent in *H. mallyi* sp. nov.). *Hoploscopa gracilis* sp. nov. displays wing pattern similar to *H. mallyi* sp. nov. and can be best separated by examination of genitalia: uncus is slenderer, valva apex is pointed (rounded in *H. mallyi* sp. nov.) and juxta displays a broad duck beak-shaped apex. In female genitalia, ductus bursae shows a narrow loop at posterior 1/3, and thorn is less curved in *H. gracilis* sp. nov.

Description. ***Head.*** Antennae dorsally with brown scales. Proboscis brown to pale brown scaled. Maxillary palpi brown, base and inner side pale yellow. Labial palpi brown, ventral base and inner side pale yellow.

Thorax (Fig. 37). Collar pale yellow. Forewing length: 10–12 mm (♂), 11–12 mm (♀); forewing ground colour brown; basal longitudinal red streak basally edged with pale yellow; costal field red; median discoidal stigma crescent-shaped, pale yellow, filled with red; median cubital patch streak-like, pale yellow, together with discoidal stigma forming a Y; postmedian patch triangular, red, basal edge partially pale yellow, with pale yellow blotch at costa; postmedian area suffused with pale yellow and iridescent scales; subterminal field marked with red; fringes brown with pale yellow dots. Hindwing pale brown. Forelegs brown. Midlegs brown; femur and tibia distally pale yellow. Hindlegs with femur brown; tibia pale yellow speckled with brown; tarsi pale yellow to pale brown.

Male genitalia (N = 2) (Fig. 76). Uncus slender, medially narrowed, apex spatulate. Gnathos projection slender, ca. 2/3 of uncus length. Valva ventral margin gently bent dorsad on distal 1/3, dorsal margin convex, apex rounded. Juxta ogival, with base quadrangular, medially as wide as base, narrowing toward apex, apex narrow, notched. Saccus triangular, pointing dorsad.

Female genitalia (N = 3) (Fig. 116). Anterior apophyses with dorsal bump at posterior 1/3. Antrum sclerotisation forming a short ring. Ductus bursae long, broad, forming two large curves. Corpus bursae small, globular, reticulate, sclerotised between thorn and corpus opening, medially with broad faintly sclerotised band. Thorn sabre-like, curved, with small dents pointing toward thorn base, basally with conspicuous outwardly projected extension.

Distribution. Known from the slopes of Mount Kinabalu on Borneo, at altitudes between 1,600 m and 2,000 m.

Phylogenetic relationships. This species is recovered in a clade with *H. agtuuganonensis* sp. nov. and *H. gracilis* sp. nov. in the ML analysis of the COI barcode (BS = 92). The morphology of these species is in agreement with the molecular findings: in male genitalia, gnathos projection is long and slender; in female genitalia, the antrum sclerotisation is short, the ductus bursae is relatively broad, looped or with conspicuous curves, and the corpus bursae is small, globular.

Etymology. This species is dedicated to our colleague and friend Richard Mally, an eminent lepidopterologist.

Hoploscopa gracilis Léger & Nuss, sp. nov.

http://zoobank.org/CDC1F535-1AB1-469F-B6DE-082810E8E28F

Figs 38, 77, 117

Material examined. ***Holotype*:** ♂, with labels: "Sumatra-Holzweg | 25km SSW-Pematangsiantar | Straße nach Prapat [road to Prapat], L[icht]F[ang] [light trap] | 13.ii.1996, leg. A. Kallies"; "coll[ection]. M. Nuss | Geschenk 2000 | Museum für Tier- | kunde Dresden"; "DNA voucher | Lepidoptera | date: xi.2018 | MTD8259 | [vertically written:] DNA- | voucher"; "TL754 | ♂". Deposited in MTD.

***Paratypes*:** 4 ♂, 2 ♀. Indonesia: 2 ♂ (1 with DNA voucher MTD7876 & genitalia on slide TL664 ♂, 1 with DNA voucher MTD LEP 3203 & genitalia on slide), North Sumatra, Sipirok, 1450 m, 27–28.i.1995, leg. A. Kallies; 1 ♂ (DNA voucher MTD8256 & genitalia on slide TL751 ♂), North Sumatra, Mount Sibayak, 03°14'19"N, 98°29'52"E, 1900 m, 02.iii.2002, leg. U. Buchsbaum; 1 ♂ (genitalia on slide TL539 ♂), 1 ♀ (DNA voucher MTD8263 & genitalia on slide TL758 ♀), North Sumatra, Mount Sibayak, 03°14'13"N, 98°29'41"E, 1750 m, 07.vii.2000, leg. U. Buchsbaum; 1 ♀ (DNA voucher MTD LEP 3204 & genitalia on slide TL527 ♀), North Sumatra, Dairi, near Sumbul, 2°46'N, 98°32'E, 1670 m, 20.ii.1999, leg. U. Buchsbaum.

Other specimens investigated. 1 ♀. Malaysia: 1 ♀ (NHMUK010923415, DNA voucher MTD8239 & genitalia on slide TL737 ♀), West Malaysia, Cameron Highlands, Gunung Brinchang, 1980 m, 23–31.x.1989 (G. S. Robinson & M. A. Tobin) (NHMUK).

Diagnosis. *Hoploscopa gracilis* sp. nov. displays pale yellow crescent-shaped median discoidal stigma filled with reddish brown, together with median cubital patch forming a Y. In male genitalia, uncus is long and slender, valva is slender with pointed apex, and juxta displays a broad duck beak-shaped apex. In female genitalia, the ductus bursae is long, forming one loop on its middle, and the corpus bursae is small, globular, with one short slightly curved thorn.

Similar species. *Hoploscopa agtuuganonensis* sp. nov., *H. mallyi* sp. nov. (q.v.). Median markings of the forewing form a band progressively narrowing toward dorsum in *H. agtuuganonensis* sp. nov. In male genitalia, uncus of *H. agtuuganonensis* sp. nov. is larger, valva has a rounded apex and juxta apex is tongue-shaped. Female genitalia of *H. agtuuganonensis* sp. nov. are very similar to those of *H. gracilis* sp. nov. but differ by a more marked corpus sclerotisation and a thicker thorn.

Description. ***Head.*** Antennae dorsally ochreous to brown. Proboscis pale yellow. Maxillary palpi brown, base and inner side pale yellow. Labial palpi brown, ventral base and inner side pale yellow.

Thorax (Fig. 38). Collar pale yellow. Forewing length: 9 mm (♂), 11 mm (♀); forewing ground colour brown; broad elongated basal patch reddish brown with basal edge pale yellow, distally running up to median cubital patch; costal field reddish brown; median discoidal stigma reddish brown, edged with costa facing pale yellow C; trapezoid oblique pale yellow cubital patch disrupted at 1A+2A, together with median discoidal stigma forming a Y; postmedian triangular patch reddish brown, speckled with pale yellow, distally with costal pale yellow blotch; postmedian area suffused with a mix of pale yellow and iridescent scales; subterminal field marked with reddish brown; fringes brown, with pale yellow dots. Hindwing pale yellow. Forelegs brown. Midlegs brown; tibia distally pale yellow. Hindlegs brown, tibia pale yellow speckled with brown.

Abdomen. Male sternum A8 posterior margin notched, with pair of very small papillae-like protuberances.

Male genitalia ($N = 4$) (Fig. 77). Uncus long and slender, gently tapering toward apex, apex spatulate. Gnathos projection slender, ca. 2/3 of uncus length, with truncate apex. Valva slender, ventral margin nearly straight, gently bent dorsad on distal 1/4, dorsal margin convex, apex pointed. Juxta with base rounded, medially straight, widening at distal 1/3, apex duck beak-shaped. Saccus triangular, conspicuously pointing dorsad.

Female genitalia ($N = 2$) (Fig. 117). Anterior apophyses with dorsal bump at posterior 1/3. Antrum sclerotisation as long as wide. Ductus bursae long, with one loop, curved before corpus opening. Corpus bursae small, globular, reticulated, with sclerotisation between thorn and corpus opening and faintly sclerotised band medially. Thorn small, plump, slightly curved, with small dents pointing toward thorn base, basally with small outwardly projected extension.

Distribution. Known from North Sumatra, at altitudes between ca. 1,200 m to 1,900 m.

DNA barcoding. The species shows an intraspecific variation of 0.9%

Phylogenetic relationships. See *H. mallyi* sp. nov.

Etymology. From the Latin *gracilis*, slender, narrow, referring to the slender shape of the uncus, the gnathos projection, and the valva in male genitalia.

Hoploscopa agtuuganonensis Léger & Nuss, sp. nov.

http://zoobank.org/EA83FE68-F42D-4481-AB44-D1258E5DEBD4

Figs 39, 78, 118

Material examined. ***Holotype***: ♀, with labels: "Philippinen | Mindanao, 1050m | Mt Agtuuganon | 28.5–7.6.[19]96, leg. MEY"; "DNA voucher | Lepidoptera | date: i.2018 | MTD7416 | [vertically written:] DNA-voucher"; "TL | 616 ♀". Deposited in ZMHB.

Paratypes: 12 ♂. Philippines: 12 ♂(1 with DNA voucher MTD8149 & genitalia on slide TL708 ♂, 2 with genitalia on slide TL675 ♂, TL676 ♂), 4 ♀ (1 with DNA voucher MTD7415 & genitalia on slide TL617 ♀), same data as holotype (ZMHB).

Diagnosis. In *H. agtuuganonensis* sp. nov., median markings of the forewing form together a pale yellow band progressively narrowing toward dorsum, faintly disrupted with red at veins. In male genitalia, uncus is long, slender, narrowed at apical 1/4 and gnathos projection is long and slender. In female genitalia, ductus bursae is long, broad, with one loop, and corpus bursae is small, globular, with one short plump thorn.

Similar species. *Hoploscopa isarogensis* sp. nov. (q.v.), *H. mallyi* sp. nov. (q.v.), *H. gracilis* sp. nov. (q.v.).

Description. *Head.* Antennae dorsally striped with brown and pale yellow scales. Proboscis pale yellow to pale brown. Maxillary palpi brown, base and inner side pale yellow. Labial palpi brown, ventral base and inner side pale yellow.

Thorax (Fig. 39). Collar pale yellow to white. Forewing length: 8–9 mm (♂), 9 mm (♀); forewing ground colour brown; basal reddish brown quadrangular patch basally edged with pale yellow, crossed by longitudinal pale yellow streak, with median cubital and dorsal patches abutting dorsally; costal field reddish brown; median discoidal stigma trapezoid, pale yellow, filled with reddish brown, basal and distal edges marked with reddish brown, together with two pale yellow cubital patches forming a broad band narrowing toward dorsum; postmedian patch triangular, reddish brown, more or less speckled with pale yellow, with pale yellow blotch at costa; postmedian area suffused with pale yellow; subterminal line pale yellow; subterminal field reddish brown; fringes brown, with large pale yellow spots. Hindwing pale brown. Fore- and midlegs brown. Hindlegs with femur brown; tibia pale yellow speckled with brown; tarsi brown.

Abdomen. Male sternum A8 posterior margin bilobed.

Male genitalia (N = 2) (Fig. 78). Uncus long and slender, gently tapering toward apex, narrowed at apical 1/4, apex spatulate. Gnathos projection slender, ca. 2/3 of uncus length. Valva ventral margin straight, bent dorsad on distal 1/3, dorsal margin convex, apex rounded. Juxta with base quadrangular, with straight lateral margin, apex blunt. Saccus triangular, conspicuously pointing dorsad.

Female genitalia (N = 3) (Fig. 118). Anterior apophyses with dorsal tip at basal 1/3. Antrum sclerotisation short, ca. as long as broad. Ductus bursae long, broad, with one loop. Corpus bursae small, globular, reticulated, with roughly defined sclerotisation between thorn and corpus opening. Thorn plump, straight, with small dents pointing toward thorn base, basally with small outwardly projected extension.

Distribution. Known from the slopes of Mount Agtuuganon (1,660 m) on Mindanao Island (Philippines), at an altitude of 1,050 m.

Phylogenetic relationships. See *H. mallyi* sp. nov.

Etymology. Named after Mount Agtuuganon on Mindanao Island (Philippines), where the specimens were collected.

Hoploscopa boleta Léger & Nuss, sp. nov.

http://zoobank.org/D717911D-F973-4401-BC2B-873E5ACED283

Figs 40, 79, 119

Material examined. *Holotype*: ♂, with labels: "Co[lection] BECKER | PNG 1562", " Papua New Guinea | Morobe, M[oun]t Kaindi | 2360m 3.x.1992 | V. O. Becker

Col[lection]; " DNA voucher | Lepidoptera | MTD2016 | [vertically written:] no. 3160"; "TL440 | ♂". Deposited in USNM.

***Paratypes*:** 2 ♀. Papua New Guinea: 1 ♀ (DNA voucher MTD LEP3168, genitalia on slide TL448 ♀), same data as holotype; 1 ♀ (DNA voucher MTD LEP 3159), same locality as holotype, 27–28.vii.1983, leg. S.E. & P. M. Miller (USNM).

Diagnosis. The forewings of *H. boleta* sp. nov. display median discoidal stigma and postmedian patch of a lighter brown, the latter with a well-marked pale yellow blotch at costa. In male genitalia, the conspicuous basal lateral projections of the juxta resemble the shape of a mushroom. Female genitalia are somewhat similar to those of other *Hoploscopa* species, e.g., *H. parvimacula* sp. nov., and *H. danaoensis* sp. nov., with a short straight ductus bursae, a pear-shaped corpus bursae, and a small straight thorn.

Similar species. *Hoploscopa pseudometacrossa* sp. nov., to a lesser extent *H. kelama* sp. nov. (q.v.). In *H. pseudometacrossa* sp. nov., forewing median discoidal stigma and postmedian patch are barely marked, and postmedian pale yellow blotch at costa is much smaller. In male genitalia, gnathos of *H. pseudometacrossa* sp. nov. displays a thumb-like projection, juxta shows less prominent lateral projections and an indented apex. In female genitalia, corpus bursae is larger than that of *H. boleta* sp. nov.

Description. *Head.* Antenna dorsally striped with ochreous and bronze scales. Proboscis pale yellow, basally brown. Maxillary palpi brown, base and inner side pale yellow. Labial palpi brown, ventro-basally pale yellow.

Thorax (Fig. 40). Collar pale yellow. Forewing length: 9–10 mm (♂ & ♀); forewing ground colour brown; basal dash dark brown, distally pale yellow; basal and distal discoidal patches quadrangular, dark brown, basally and distally edged with pale yellow; median discoidal stigma there between trapezoid, light brown; dorsal median patch broad, pale yellow; postmedian patch light brown, with pale yellow blotch at costa; postmedian area suffused with pale yellow near costa; subterminal line dark brown, diffuse; fringe brown, with pale yellow dots. Hindwing pale yellow, darker at apex. Forelegs brown, tarsi bronze. Mid- and hindlegs with femur brown, tibia pale yellow, speckled with brown, tarsi bronze.

Abdomen. Male sternum A8 posterior margin broadly indented.

Male genitalia (N = 1) (Fig. 79). Uncus slender, conspicuously narrowed at apical 1/4, apex duck beak-shaped, bearing thick setae, ventrally with three small ridges. Gnathos projection ca. 1/3 of the uncus length, tongue-shaped, gently narrowing toward apex. Valva ventral margin nearly straight, dorsal margin slightly convex, apex slightly blunt. Juxta with base rounded with two conspicuous lateral projections, abruptly narrowed at basal 1/3, apex spatulate, similar to the shape of a mushroom. Saccus small, pointing dorsad.

Female genitalia (N = 2) (Fig. 119). Anterior apophyses with dorsal bump at posterior 1/3. Antrum sclerotisation twice as long as broad. Ductus bursae short, nearly straight. Corpus bursae globular, posterior half reticulated, medially with erect acanthae, anterior half membranous, with sclerotisation between thorn and corpus opening, medially with a sclerotised band. Thorn straight, with small dents pointing toward thorn base.

Distribution. Known from Mount Kaindi in the Morobe Province (Papua New Guinea), at an altitude of 2,360 m.

Phylogenetic relationships. This species displays an uncus apex similar to those of *H. jubata* sp. nov., *H. metacrossa*, and *H. pseudometacrossa* sp. nov. and is possibly related to them.

Etymology. From the Latin *boletus*, in reference to the mushroom shape of the juxta.

Hoploscopa pseudometacrossa **Léger & Nuss, sp. nov.**

http://zoobank.org/E21452AB-8784-4A67-B270-1802A4D7293A

Figs 41, 80, 120

Material examined. ***Holotype***: ♀, with labels: "Papua New Guinea: W[estern]. H[ig]hl[and] | Pr[o]v[ince], n[ea]r Mt. Hagen, Kuk Ag | Res[earch]. Sta[tion]., 1600m, UV Lite | 19–20 August 1983 | Scott E. & Pamela Miller"; "DNA voucher | Lepidoptera | date: i.2018 | MTD 7898 | [vertically written:] DNA-voucher"; "TL689 | ♀". Deposited in USNM.

Paratypes: 1 ♂, 1 ♀. Papua New Guinea: 1 ♂, 1 ♀ (♂ with DNA voucher MTD LEP3161 & genitalia on slide TL441 ♂; ♀ with DNA voucher MTD LEP3155 & genitalia on slide TL435 ♀), same data as holotype (USNM).

Diagnosis. The forewings of *H. pseudometacrossa* sp. nov. display barely marked median discoidal stigma and postmedian patch, while basal and distal discoidal patches are dark brown. Male hindwing displays an androconial organ on the dorsum. In male genitalia, the gnathos shows a short, thumb-like projection, and the juxta is slender, with notched apex. In female genitalia, the ductus bursae is relatively short-sized, the corpus bursae is large, spherical, with a small straight thorn.

Similar species. *Hoploscopa boleta* sp. nov. (q.v.), *H. metacrossa*, *H. kelama* sp. nov. (q.v.). Forewing median discoidal stigma forms a pale yellow Y with median cubital patch in *H. metacrossa*. In male genitalia, gnathos projection of *H. metacrossa* is thinner, valva is larger, and juxta apex is rounded. Female genitalia are very similar, but the antrum sclerotisation is shorter, and the corpus bursae smaller in *H. metacrossa*.

Description. ***Head.*** Antennae dorsally with bronze to brown scales. Proboscis pale yellow to brown. Maxillary palpi brown, base and inner side pale yellow. Labial palpi brown, ventro-basally pale yellow.

Thorax (Fig. 41). Collar pale yellow. Forewing length: 9–10 mm (♂ & ♀); forewing ground colour brown; basal dash dark brown, distally pale yellow; basal and distal discoidal stigma quadrangular, dark brown; median discoidal stigma faded, basally and distally thinly edged with pale yellow; postmedian patch faded, with distal edge dark brown, at costa with pale yellow blotch; postmedian line marked on costal half; postmedian area suffused with pale yellow near costa; subterminal line pale yellow; fringe brown, with pale yellow dots. Hindwing pale brown; in males, presence of an androconial organ on the dorsum of the hindwing. Forelegs brown. Mid- and hindlegs with femur brown, tibia brown speckled with pale yellow, tarsi bronze.

Abdomen. Male sternum A8 posterior margin broadly indented, with pair of lateral papillae-like protuberances.

Male genitalia (*N* = 1) (Fig. 80). Uncus slender, narrowed on apical 1/4which bears thick setae, apex missing on available slide. Gnathos projection thumb-shaped, ca. 1/4 of uncus length. Valva ventral margin bent dorsad on distal half, dorsal margin medially angled, apex roughly rounded. Juxta with base rounded, medially narrowed, apex notched. Saccus broad, triangular, pointing dorsad.

Female genitalia (*N* = 2) (Fig. 120). Anterior apophyses with dorsal bump at posterior 1/3. Antrum sclerotisation twice as long as broad. Ductus bursae short, more or less straight. Corpus bursae large, posterior half reticulated, medially covered with erect acanthae, anterior half membranous, with weak sclerotisation at thorn base. Thorn straight, with small dents pointing toward thorn base, basally with small outwardly projected extension.

Distribution. Known from Mount Hagen in the Morobe Province (Papua New Guinea), at an altitude of 1,600 m.

Phylogenetic relationships. The hindwing scent scales observed in males of *H. jubata* sp. nov., *H. pseudometacrossa* sp. nov., and *H. metacrossa* suggest a close relationship between these three species.

Etymology. The name is made by the apposition of the prefix *pseudo-* from the Greek *pseudes*, false and *metacrossa*, referring to the resemblance of this species with *H. metacrossa*.

Hoploscopa metacrossa (Hampson, 1917)

Figs 42, 45, 81, 84, 86, 121

Material examined. ***Holotype*****:** ♂, with labels: "Holo- | type" [round label, red ringed]; "Fak-Fak | Dutch NewGuinea | Dec'[19]07 | 1700f[ee]t | (Pratt)"; "1913-216"; "Scoparia | metacrossa | type ♂. H[a]mps[o]n." [handwritten]; "Pyralidae | Brit[ish]. Mus[eum]. | Slide N°. | 3612"; "N,HMUK 010923297" [barcode appended]. Deposited in NHMUK.

Other specimens examined. 12 ♂, 38 ♀. Papua New Guinea: 10 ♂ (3 with DNA vouchers MTD7899, MTD7900, MTD7901 and genitalia on slides TL690 ♂, TL691 ♂, TL692 ♂ respectively; 1 with genitalia on slide TL482 ♂), 25 ♀ (1 with genitalia on slide TL481 ♀), Morobe Province, near Bulolo, Mt Susu National Reserve, *Araucaria* forest, 975m, 27–28.viii.1983, leg. S. Miller; 1 ♂ (genitalia on slide TL472 ♂), 9 ♀ (2 with DNA vouchers MTD LEP 3166, MTD LEP 3167 and genitalia on slides TL446 ♀, TL447 ♀), Morobe Province, Wau, Wau Ecological Institute, montane forest, 1200 m, 12–24.vii.1983 (2 ♀), 25–31.vii.1983 (1 ♂, 3 ♀), 1–10.viii.1983 (1 ♀), 23–31.viii.1983 (3 ♀), leg. S. E. & P. M. Miller; 4 ♀, same collecting data except "trap at zoo pond", 25–27.vii.1983; 1 ♂ (DNA voucher MTD LEP 3163 & genitalia on slide TL443 ♂), Morobe Province, Wau, 1200 m, 8–14.xii.1976, leg. G. F. Hevel & R. E. Dietz (USNM).

Diagnosis. The forewings of *H. metacrossa* display Y-shaped median and a postmedian pale yellow patches observed in several other *Hoploscopa* species (e.g., *H. danaoensis* sp. nov.). Male hindwing displays an androconial organ on the dorsum. The strongly sclerotised tympanic drum in tympanal organs of males is only observed in this species. In male genitalia, gnathos is projected into a small, slender, tongue-shaped tip, and valva is broad, with a rounded ventral margin. In female genitalia, antrum sclerotisation is as long as wide, ductus bursae is short, straight and the corpus bursae is large.

Similar species. *Hoploscopa brunnealis*, *H. danaoensis* sp. nov., *H. kinabaluensis* sp. nov. (q.v.), *H. pseudometacrossa* sp. nov. (q.v.). Males of *H. metacrossa* are easily separated from similar species (except *H. pseudometacrossa* sp. nov.) by the presence of scent organs on the hindwing, the sclerotised tympanic drum, and the characteristic spatulate uncus apex with ventral ridges. Female genitalia of the four above-mentioned species are similar, but ductus bursae is bent before corpus bursae in these species (nearly straight in *H. metacrossa*) and corpus bursae are smaller than that of *H. metacrossa*.

Description. ***Head.*** Antennae dorsally brown. Proboscis pale yellow to brown. Maxillary palpi brown, base and inner side pale yellow. Labial palpi brown, ventral base and inner side pale yellow.

Thorax (Fig. 42, 45). Collar pale yellow. Forewing length: 9–10 mm (♂ & ♀); forewing ground colour brown; basal dark brown spot distally pale yellow; median discoidal stigma trapezoid, pale yellow, together with cubital pale yellow patches forming a Y; postmedian patch pale yellow speckled with brown, distal edge dark brown; postmedian line marked on costal half; postmedian area variously suffused with pale yellow; subterminal line pale yellow; fringes brown with pale yellow dots. Hindwing pale brown; in males, presence of an androconial organ on the dorsum of the hindwing. Forelegs brown. Mid- and hindlegs with femur brown; tibia pale yellow, speckled with brown; tarsi brown.

Abdomen (Fig. 84, 86). Male sternum A8 posterior margin broadly indented, with pair of lateral papillae-like protuberances.

Male genitalia (*N* = 3) (Fig. 81). Uncus slender, narrowed at apical 1/4, apex spatulate, bearing thick setae, ventrally with five small ridges. Gnathos projection ca. 1/4 of uncus length, slender, tongue-shaped. Valva ventral margin curved dorsad on distal half, dorsal margin conspicuously convex, apex rounded. Juxta with base rounded or slightly quadrangular, narrowing at basal 1/4, apex tongue-shaped. Saccus triangular, conspicuously pointing dorsad. Phallus with elongated, flat, spatula-shaped cornutus with subapical tip.

Female genitalia (*N* = 3) (Fig. 121). Anterior apophyses with dorsal bump at posterior 1/3. Antrum sclerotisation short, ca. as long as wide. Ductus bursae short, nearly straight. Corpus bursae spherical, reticulated, with sclerotisation between thorn and corpus opening and faintly marked sclerotisation medially. Thorn straight, with small dents pointing toward thorn base, basally with small outwardly projected extension.

Distribution. Known from the Papua (Indonesia) and the Morobe Provinces (Papua New Guinea) in New Guinea, at altitudes between 600 and 1,200 m.

Phylogenetic relationships. See *H. boleta* sp. nov. and *H. pseudometacrossa* sp. nov.

Remarks. Nuss (1998) transferred this species from *Eudorina* to *Hoploscopa*.

Hoploscopa jubata **Léger & Nuss, sp. nov.**

http://zoobank.org/F81F0837-5324-4B81-AC72-B0519F850301

Figs 2, 43, 44, 82, 122

Material examined. ***Holotype***: ♂, with labels: "Papua New Guinea | Morobe Prov[ince]., n[ea]r Bulolo | Mt Susu Nat[ional]. Res[erve]., 975m | 27–28 Aug.1983, S. Miller | UV Lite, Araucaria For[est]."; " DNA voucher | Lepidoptera | MTD2016 | [vertically written:] no. 3164"; "TL444 | ♂". Deposited in USNM.

Paratypes: 4 ♂, 24 ♀. Papua New Guinea. 4 ♂ (1 with genitalia on slide TL447 ♂, 1 with genitalia on slide TL542 ♂, 1 with wing preparation TL706), 21 ♀ (1 with DNA voucher MTD LEP3165 & genitalia on slide TL445 ♂, 2 with genitalia on slide TL476 ♀ & TL541 ♀), same data as holotype. 1 ♀, Morobe Province, Wau, Wau Ecological Institute, 12–24.vii.1983; 1 ♀, same data except 1–10.viii.1983; 1 ♀, Morobe Province, Wau, 1200 m, 8–14.xii.1976, at black light, leg. G. F. Hevel & R. E. Dietz (USNM).

Diagnosis. The forewings of *H. jubata* sp. nov. display white and orange markings. Median markings together form a white Y, at costa filled with orange, and postmedian area is broadly suffused with white (male) or reddish orange (female). Male hindwing displays an androconial organ on the dorsum. In male genitalia, gnathos projection is slender, ca. 1/3 of the uncus length, and juxta displays two conspicuous lateral projections at base, and a deeply indented apex. In female genitalia, the four loops formed by the ductus bursae is unique to this species.

Similar species. No similar species known.

Description. ***Head.*** Antennae dorsally brown. Proboscis brown. Maxillary palpi brown, base and inner side pale yellow. Labial palpi brown, ventral base and inner side pale yellow.

Thorax (Figs 2, 43, 44). Collar brown. Forewing length: 9–10 mm (♂ & ♀); forewing ♂ ground colour dark brown; basal narrow white streak, distally marked with yellow and orange; costa medially with mix of brown and pale yellow scales; median discoidal stigma white, filled with few red and yellow scales, together with cubital and dorsal patch forming a white Y; postmedian patch brown speckled with red, more or less marked, distally with costal white streak; postmedian line marked on costal half; postmedian area with broad white suffusion; subterminal line conspicuously incurved inward at CuA2, white; fringe chequered brown and pale yellow; forewing ♀ (Fig. 44) ground colour dark brown; yellow basal patch crossed by orange streak; median trapezoid white patch, more or less filled with yellow and red scales, together with cubital and dorsal white patches forming a Y; postmedian patch roughly oval, reddish orange, basally edged with yellow, distally with costal white streak; postmedian line marked on costal half; postmedian area faintly speckled with white between postmedian patch and subterminal line; subterminal line white, incurved inwards at CuA2; subterminal field marked with reddish orange and yellow; fringe brown with pale yellow dots. Hindwing pale yellow; in males, presence of an androconial organ on the dorsum of the hindwing. Forelegs bronze. Midlegs with femur brown; tibia brown, distally pale yellow; tarsi bronze. Hindlegs with femur brown; tibia pale yellow, speckled with brown; tarsi bronze.

Abdomen. Male tergite I, II partially sclerotised; tergite III sclerotised, with two shallow depressions on each side of middle, bearing patches of modified scales. Sternum A8 posterior margin straight.

Male genitalia (*N* = 3) (Fig. 82). Uncus long and slender, basally narrow, medially slightly widening, narrowed at apical 1/4, apex spatula-shaped, ventrally with eight small ridges. Gnathos projection slender, ca. 1/3 of the uncus length. Valva gently bending dorsad from distal 1/3, dorsal margin slightly convex, apex roughly truncate, hair concentrated on median line on inner side of valvae, forming a furrow ring. Juxta mushroom-shaped, with base roughly rounded, slightly concave on its middle, with two conspicuous lateral extensions pointing outward, conspicuously narrowed at basal 1/4, apex split into two conspicuously pointed tips. Saccus broad, triangular, pointing dorsad.

Female genitalia (*N* = 3) (Fig. 122). Anterior apophyses with dorsal bump at posterior 1/3. Antrum sclerotisation short, ca. as long as broad. Ductus bursae very long, forming four conspicuous loops. Corpus bursae small, globular, reticulated, medially with light broad sclerotised patch, with weak rounded sclerotisation at corpus opening. Thorn gently curved, with small dents pointing toward thorn base, basally with small outwardly projected extension.

Distribution. Known from Wau and from Mount Susu in the Morobe Province (Papua New Guinea), at altitudes between 950 m and 1,200 m.

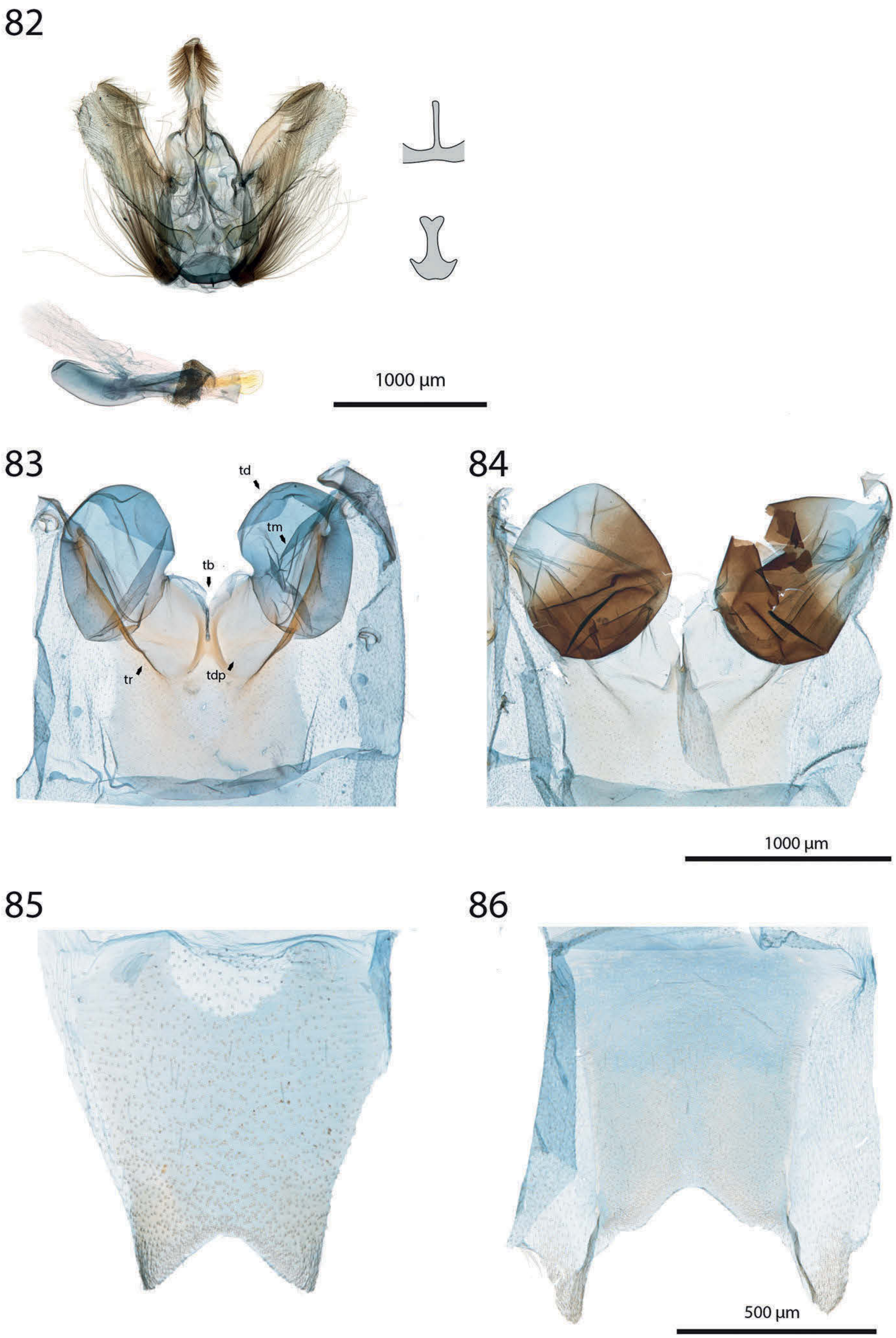
Phylogenetic relationships. See *H. boleta* sp. nov. and *H. pseudometacrossa* sp. nov.

Etymology. From the Latin *jubatus*, having a mane, referring to the dense hair covering on the inner side of the male genitalia.

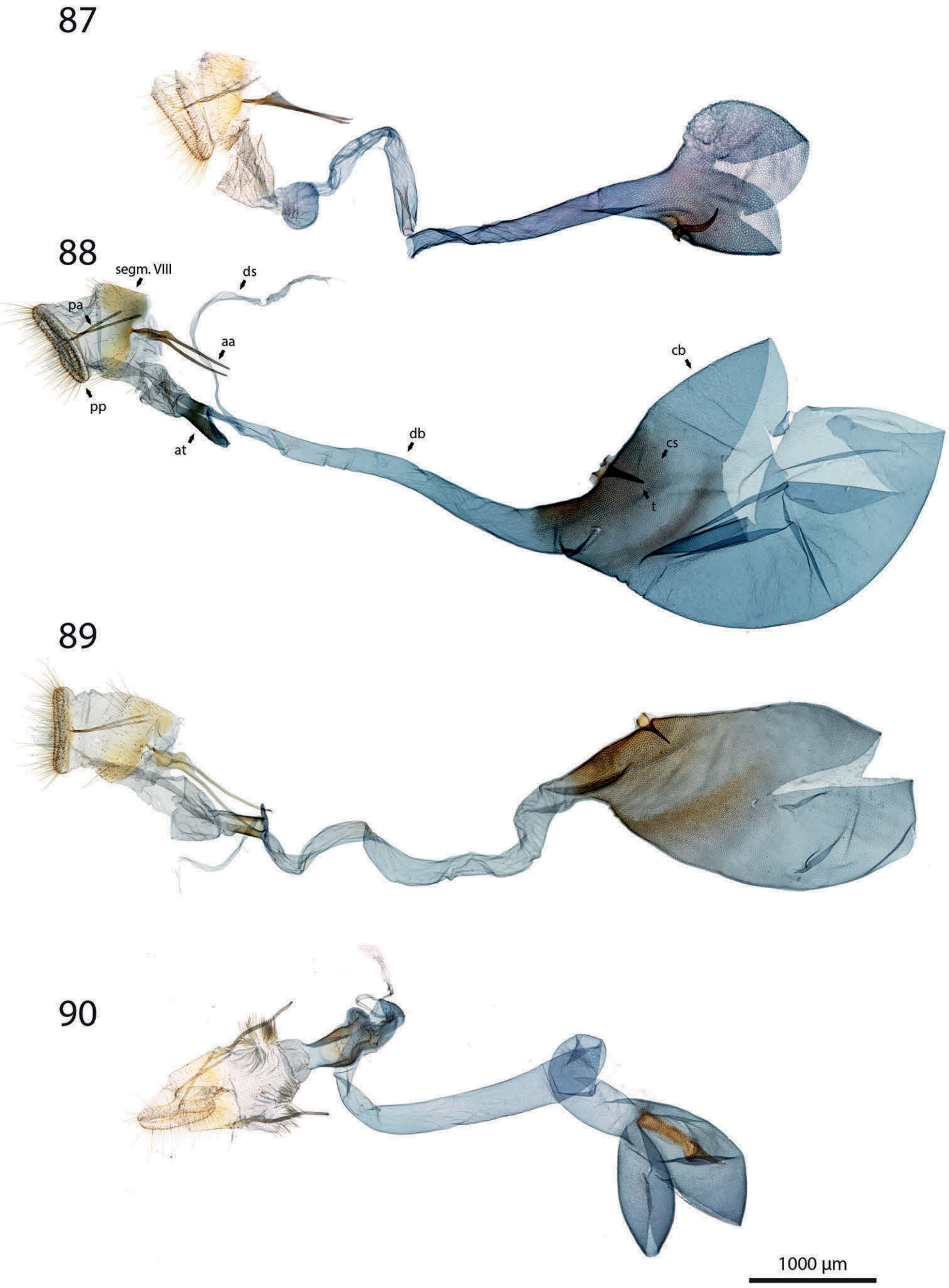
Remarks. This species is the only one known from the genus to exhibit a pronounced sexual dimorphism.

Misplaced species

Hoploscopa mediobrunnea (De Joannis, 1929) from Vietnam has been provisionally placed in *Hoploscopa* by Nuss (1998). He justified his choice as follows: ""Since *Eudorina* Snellen is a homonym of *Eudorina* Ehrenberg, 1832 (Protozoa), I place *E. mediobrunnea* here preliminarily in *Hoploscopa*. With the white discocellular stigma and the white fasciata adjacent to the median space, the wing pattern of this species look similar to the Musotiminae genus *Uthinia*. In contrast to *Uthinia*, *H. mediobrunnea* shows porrect labial palpi, a long ductus bursae, and the ductus seminalis originates near the antrum. The corpus bursae shows three round signa, with inwardly directed tiny spines arising from their edges." (Nuss, 1998). Its wing shape and the female genitalia are different from all *Hoploscopa* species we have examined to date, and we therefore assume that *H. mediobrunnea* belongs to a different genus.

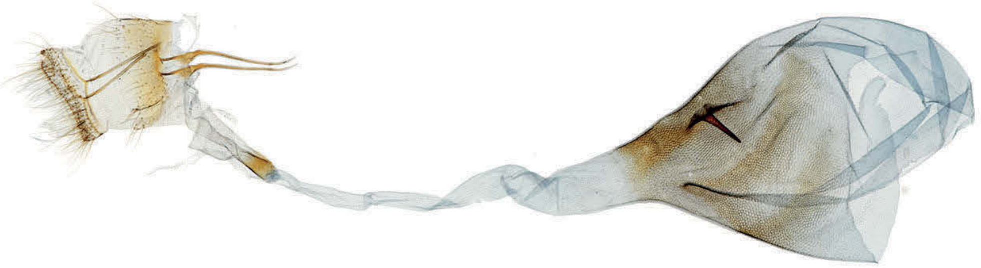


Figures 82–86. Male genitalia and abdomen features of *Hoploscopa*. **82** *Hoploscopa jubata* sp. nov., paratype, TL542 ♂ **83** Tympanal organs of *Hoploscopa sumatrensis* sp. nov., paratype, TL538 ♂ **84** Male tympanal organs of *Hoploscopa metacrossa*, TL472 ♂ **85** Sternite VIII of *Hoploscopa* sp. near *isarogensis*, TL626 ♂ **86** Sternite VIII of *Hoploscopa metacrossa*, TL443 ♂. Abbreviations: tb (tympanic bridge), td (tympanic drum), tdp (tympanic depression), tm (tympanum), tr (transverse ridge).

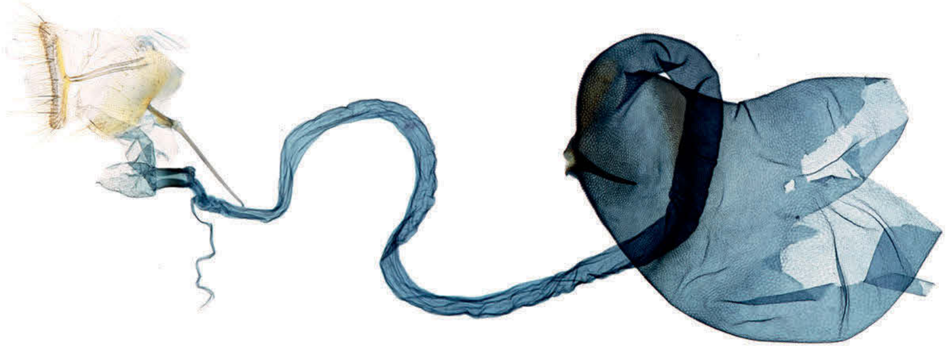


Figures 87–90. Female genitalia features of *Hoploscopa*. **87** *Hoploscopa albipuncta* sp. nov., paratype, TL609 ♀ **88** *Hoploscopa matheae* sp. nov., paratype, TL599 ♀ **89** *Hoploscopa sepanggi* sp. nov., paratype, TL547 ♀ **90** *Hoploscopa cynodonta* sp. nov., paratype, TL625 ♀. Abbreviations: aa (anterior apophyses), at (antrum), cb (corpus bursae), cs (corpus sclerotization), db (ductus bursae), ds (ductus seminalis), pa (posterior apophyses), pp (papillae anales), segm. VIII (segment VIII), t (thorn).

91

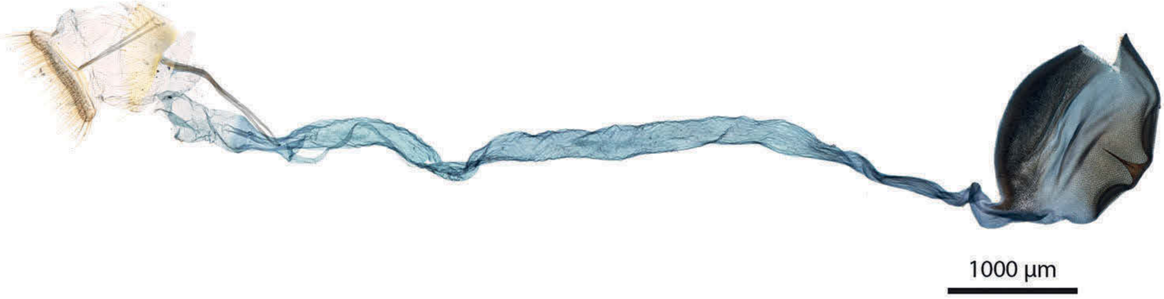


92

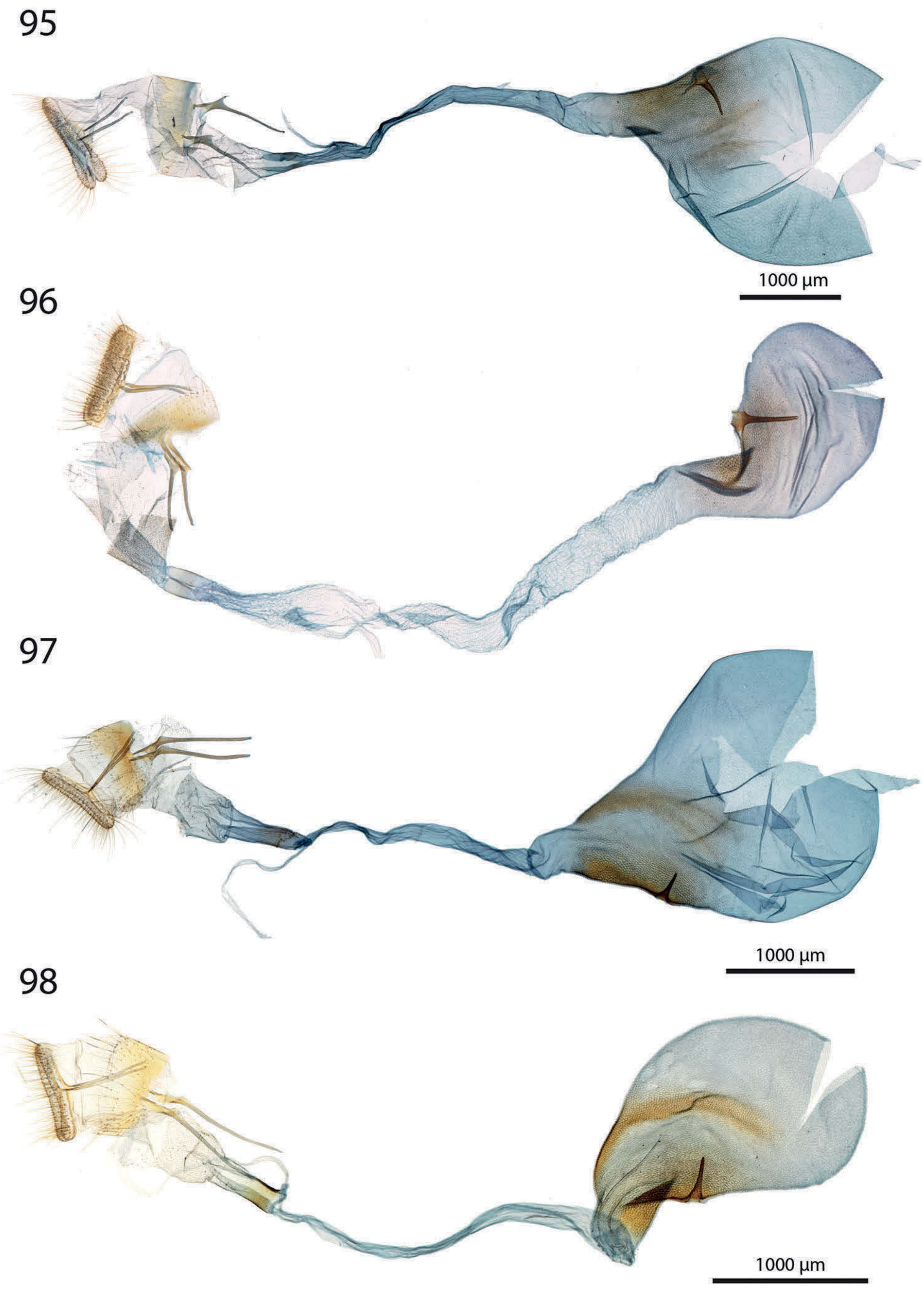


93

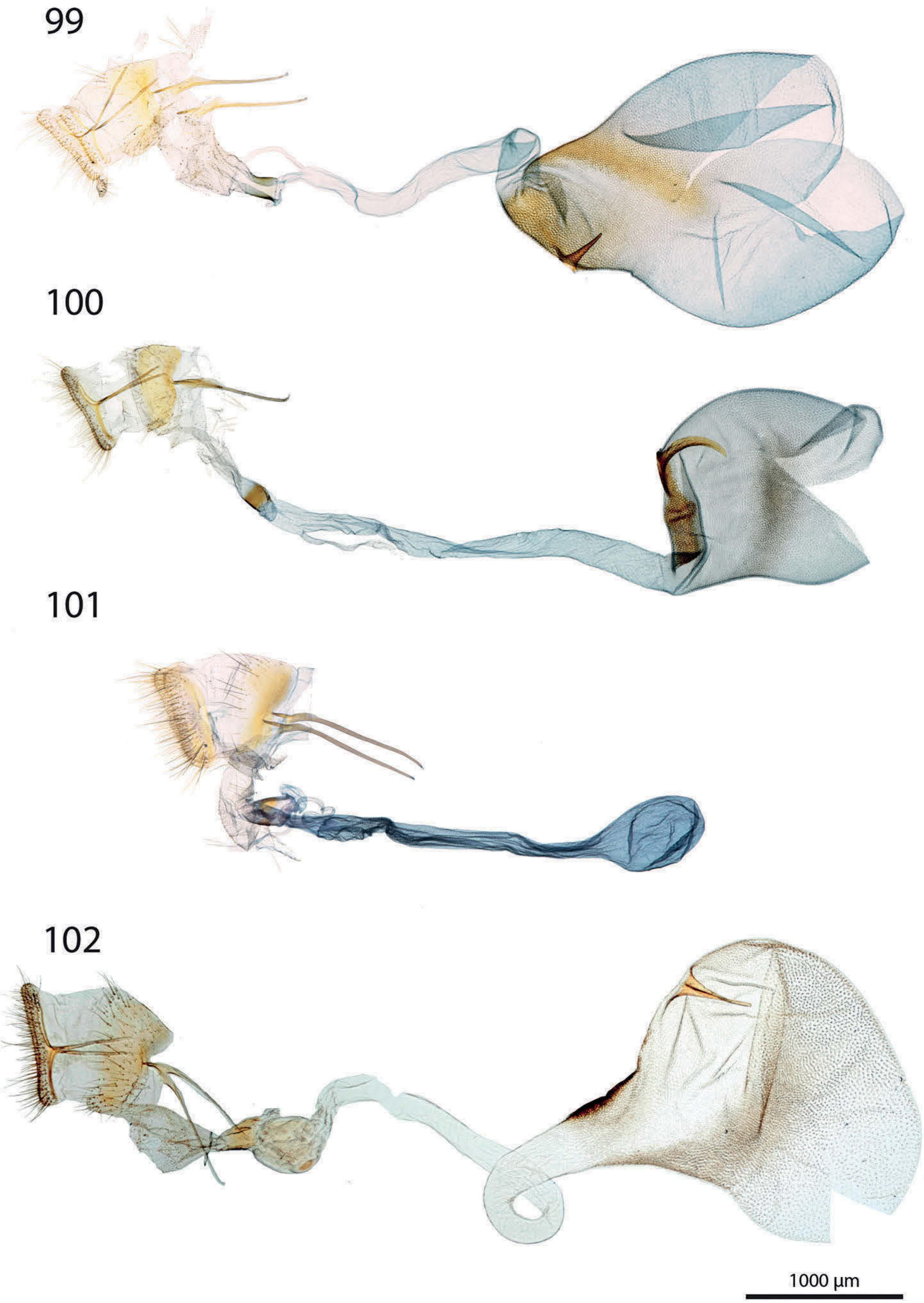
94



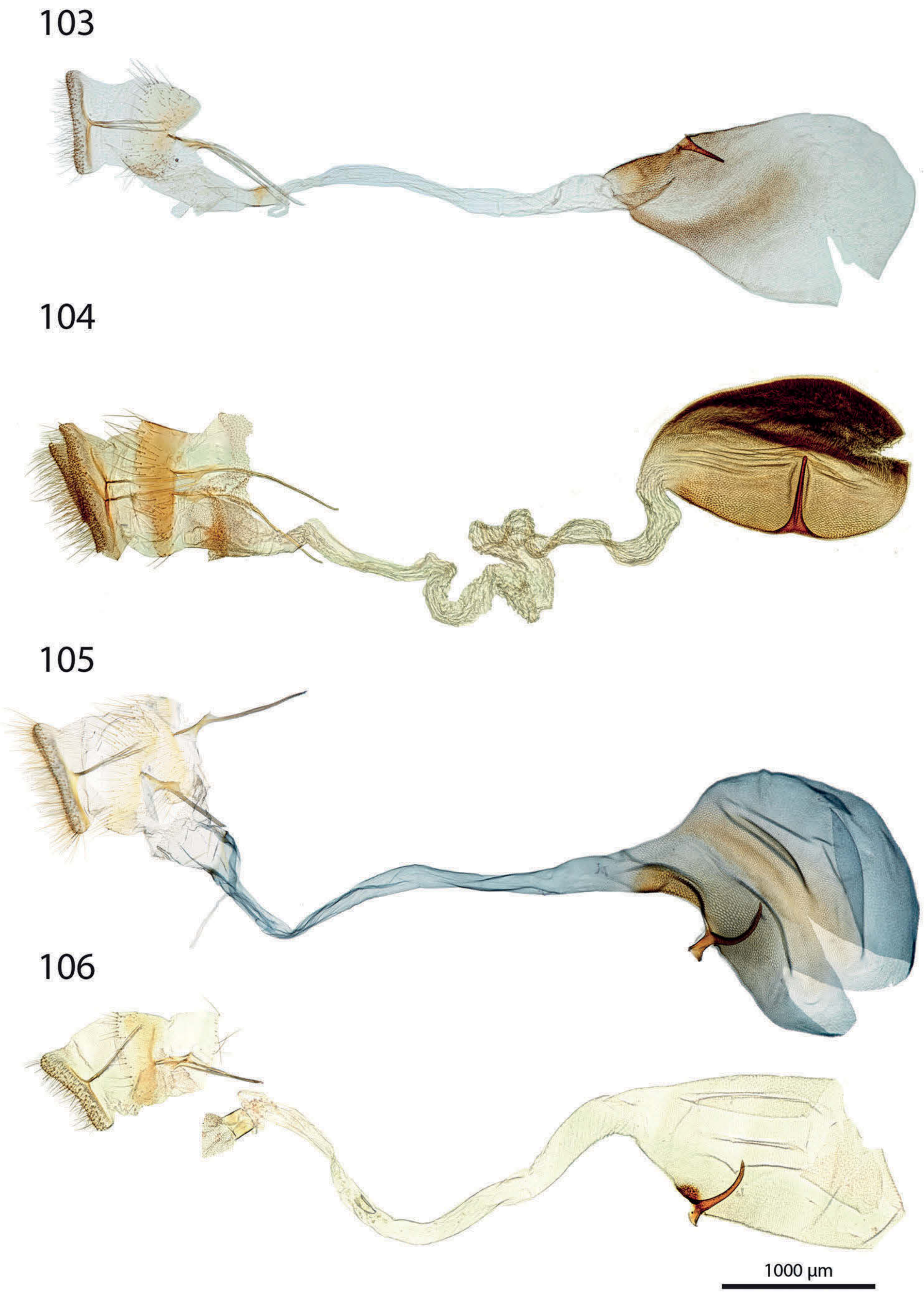
Figures 91–94. Female genitalia features of *Hoploscopa*. **91** *Hoploscopa parvimacula* sp. nov., paratype, TL551 ♀ **92** *Hoploscopa kinabaluensis* sp. nov., TL674 ♀ **93** *Hoploscopa luteomacula*, paratype, GU prep. Nuss 743 ♀ **94** *Hoploscopa obliqua*, paratype, TL656 ♀.



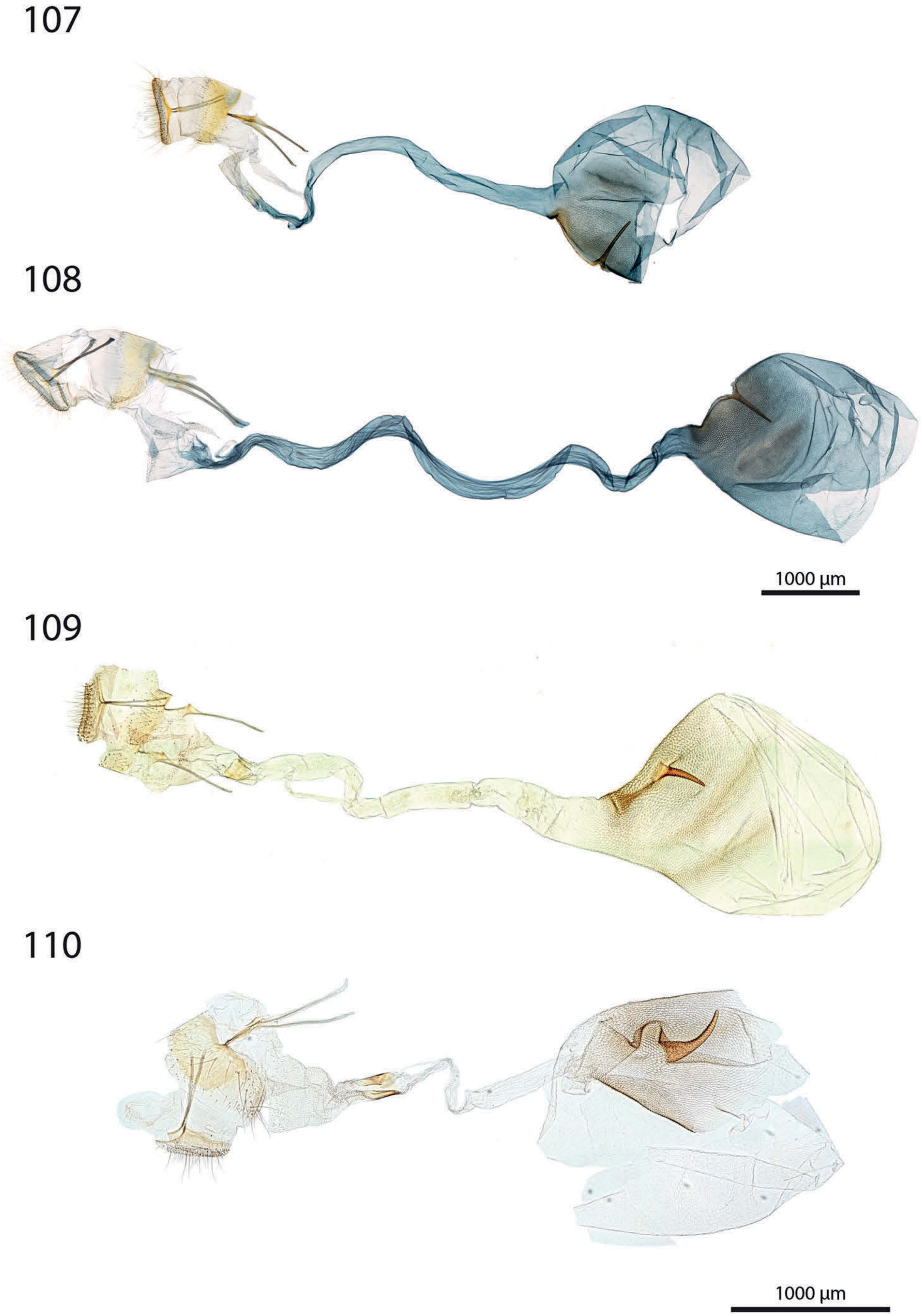
Figures 95–98. Female genitalia features of *Hoploscopa*. **95** *Hoploscopa marijoweissae* sp. nov., paratype, TL709 ♀ **96** *Hoploscopa gombongi* sp. nov., paratype, TL654 ♀ **97** *Hoploscopa pangrangoensis* sp. nov., paratype, TL627 ♀ **98** *Hoploscopa ypsilon* sp. nov., paratype, TL620 ♀.



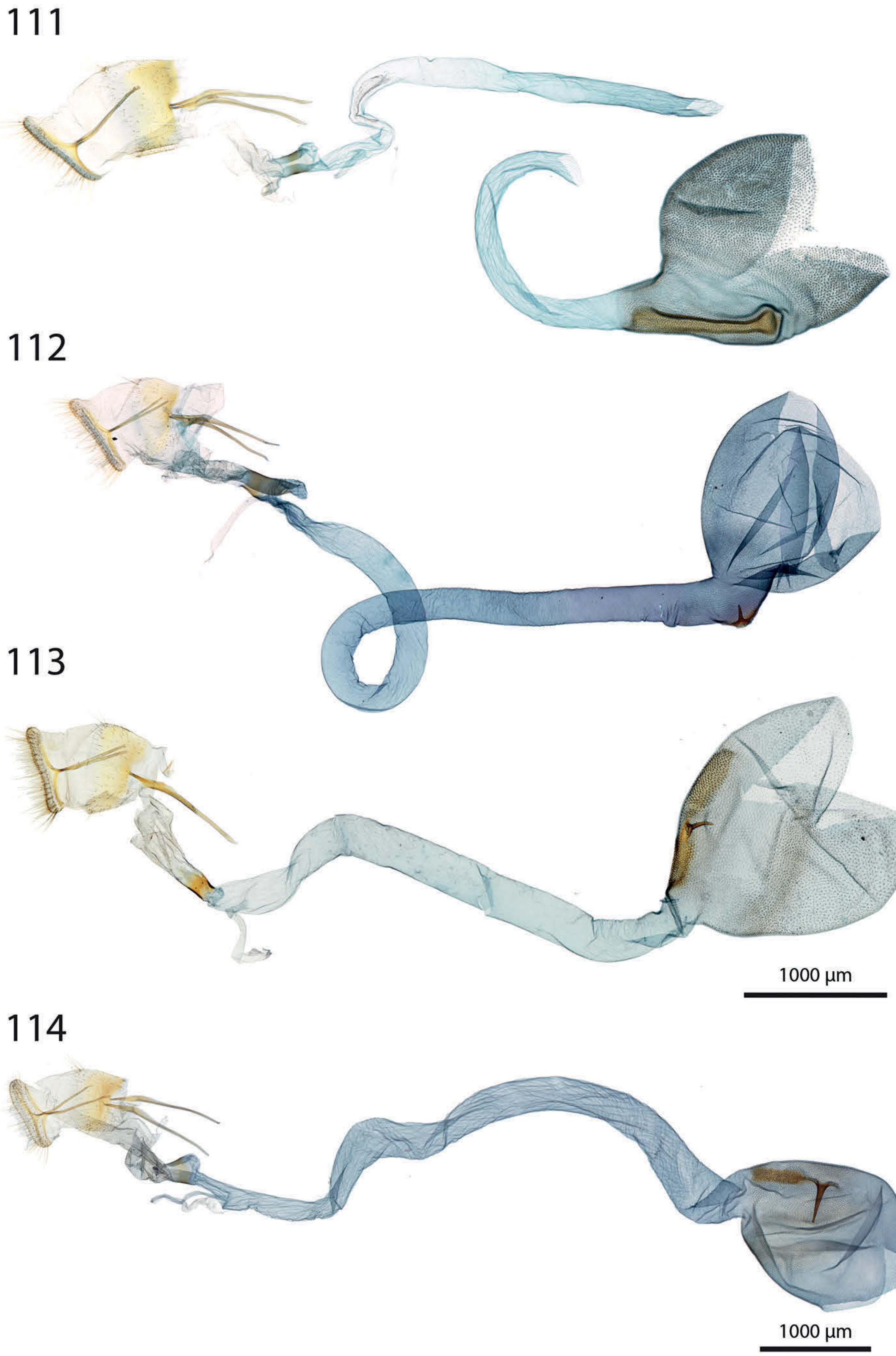
Figures 99–102. Female genitalia features of *Hoploscopa*. **99** *Hoploscopa danaoensis* sp. nov., paratype, TL618 ♀ **100** *Hoploscopa isarogensis* sp. nov., holotype, TL514 ♀ **101** *Hoploscopa tonsepi* sp. nov., paratype, TL658 ♀ **102** *Hoploscopa aurantiacalis*, lectotype, Pyralidae Brit. Mus. Slide N° BMNH20246 ♀.



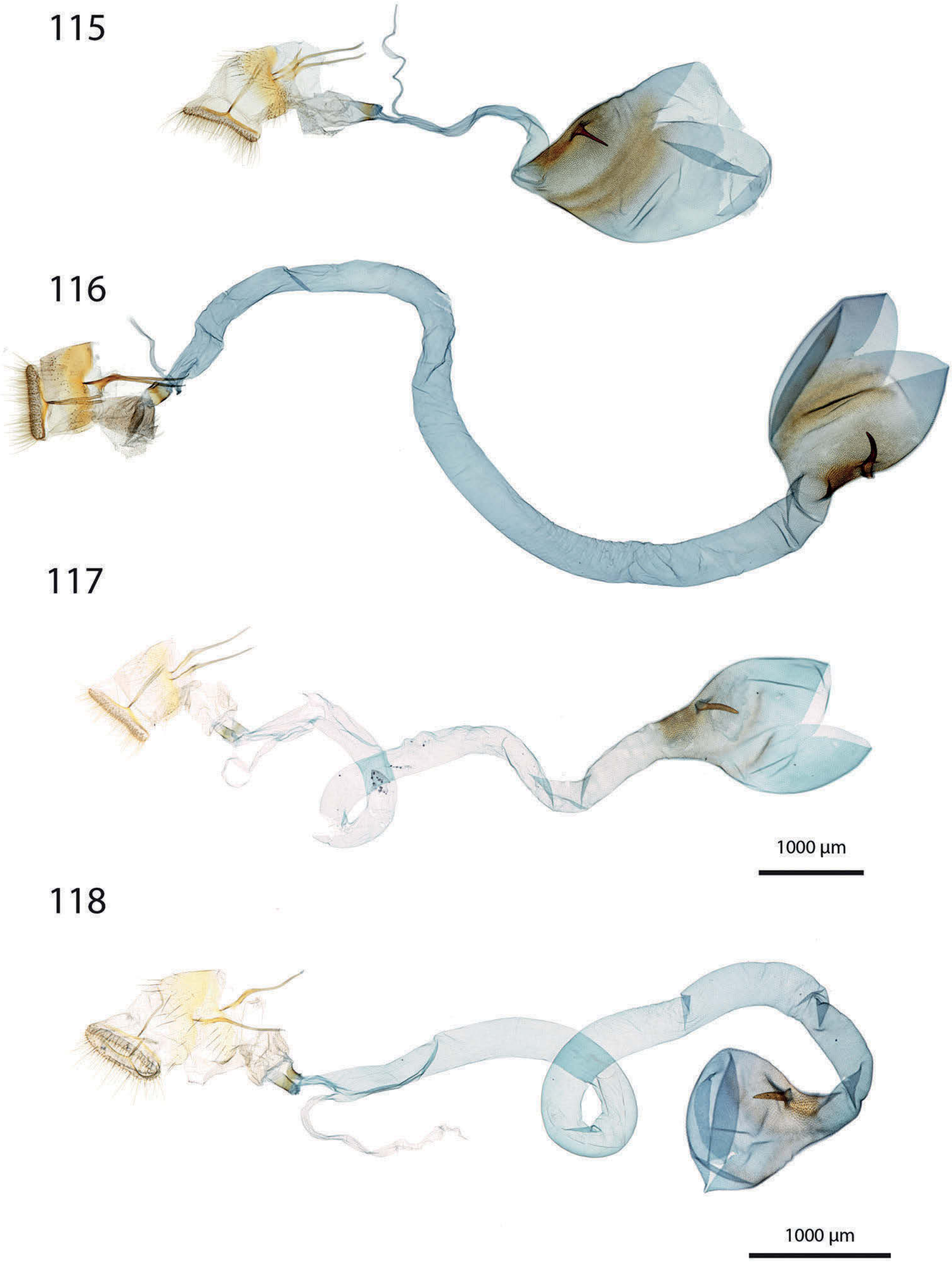
Figures 103–106. Female genitalia features of *Hoploscopa*. **103** *Hoploscopa brunnealis*, lectotype, Pyralidae Brit. Mus. Slide N° BMNH20247 ♀ **104** *Hoploscopa ocellata*, holotype, Pyralidae Brit. Mus. Slide N° BMNH20258 ♀ **105** *Hoploscopa quadripuncta*, TL713 ♀ **106** *Hoploscopa semifascia*, holotype, Pyralidae Brit. Mus. Slide N° BMNH20253 ♀.



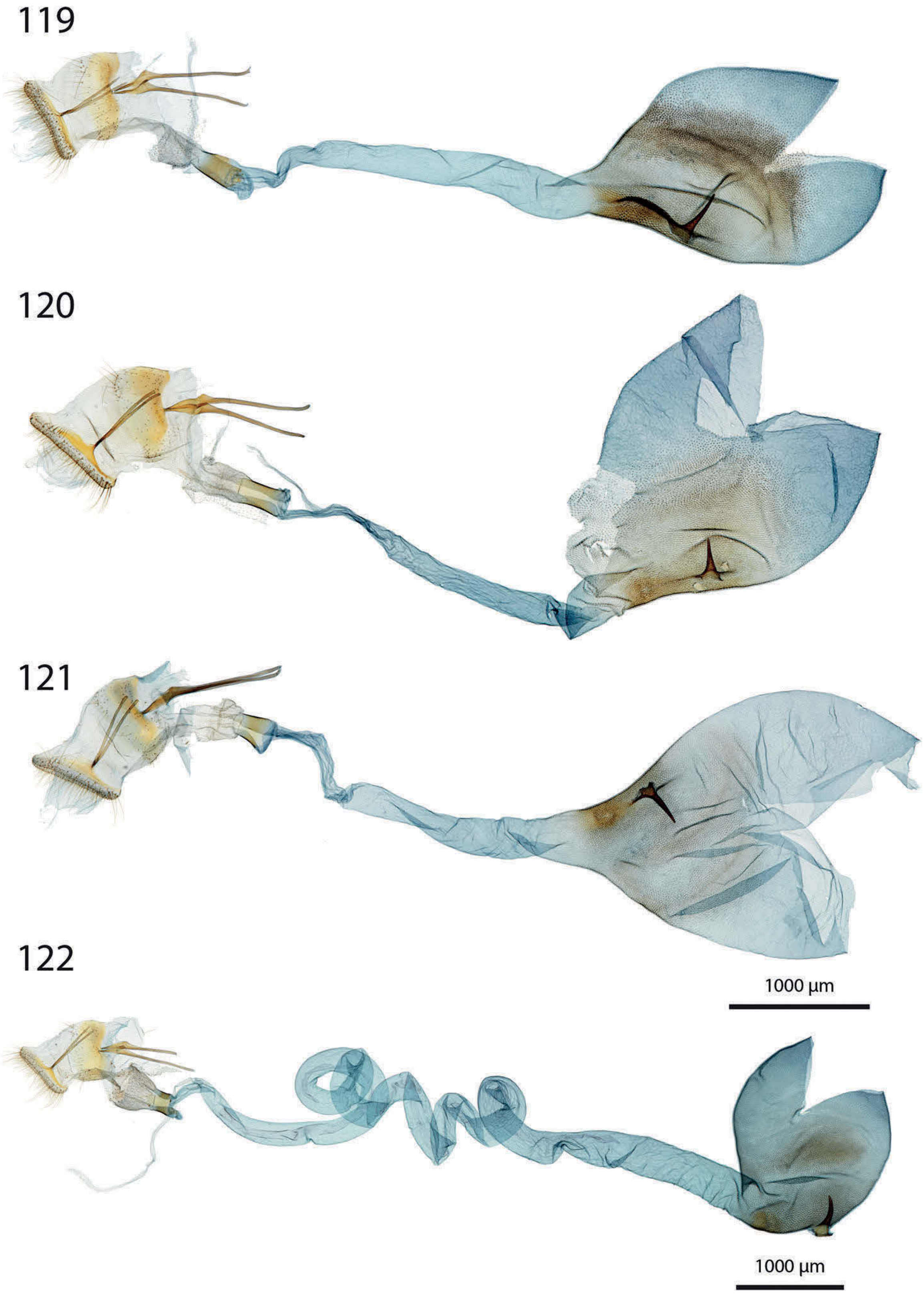
Figures 107–110. Female genitalia features of *Hoploscopa*. **107** *Hoploscopa astrapias*, TL23 ♀ **108** *Hoploscopa anamesa*, TL718 ♀ **109** *Hoploscopa subvariegata*, lectotype, Pyralidae Brit. Mus. Slide N° BMNH20254 ♀ **110** *Hoploscopa triangulifera*, holotype, Pyralidae Brit. Mus. Slide N° BMNH20256 ♀.



Figures 111–114. Female genitalia features of *Hoploscopa*. **111** *Hoploscopa anacantha* sp. nov., paratype, TL732 ♀ **112** *Hoploscopa kelama* sp. nov., paratype, TL665 ♀ **113** *Hoploscopa ignitamaculae* sp. nov., paratype, TL364 ♀ **114** *Hoploscopa albomaculata* sp. nov., paratype, TL529 ♀.



Figures 115–118. Female genitalia features of *Hoploscopa*. **115** *Hoploscopa sumatrensis* sp. nov., paratype, TL530 ♀ **116** *Hoploscopa mallyi* sp. nov., paratype, TL513 ♀ **117** *Hoploscopa gracilis* sp. nov., paratype, TL527 ♀ **118** *Hoploscopa agtuuganonensis* sp. nov., holotype, TL616 ♀.



Figures 119–122. Female genitalia features of *Hoploscopa*. **119** *Hoploscopa boleta* sp. nov., paratype, TL448 ♀ **120** *Hoploscopa pseudometacrossa* sp. nov., paratype, TL435 ♀ **121** *Hoploscopa metacrossa*, paratype, TL446 ♀ **122** *Hoploscopa jubata* sp. nov., paratype, TL445 ♀.

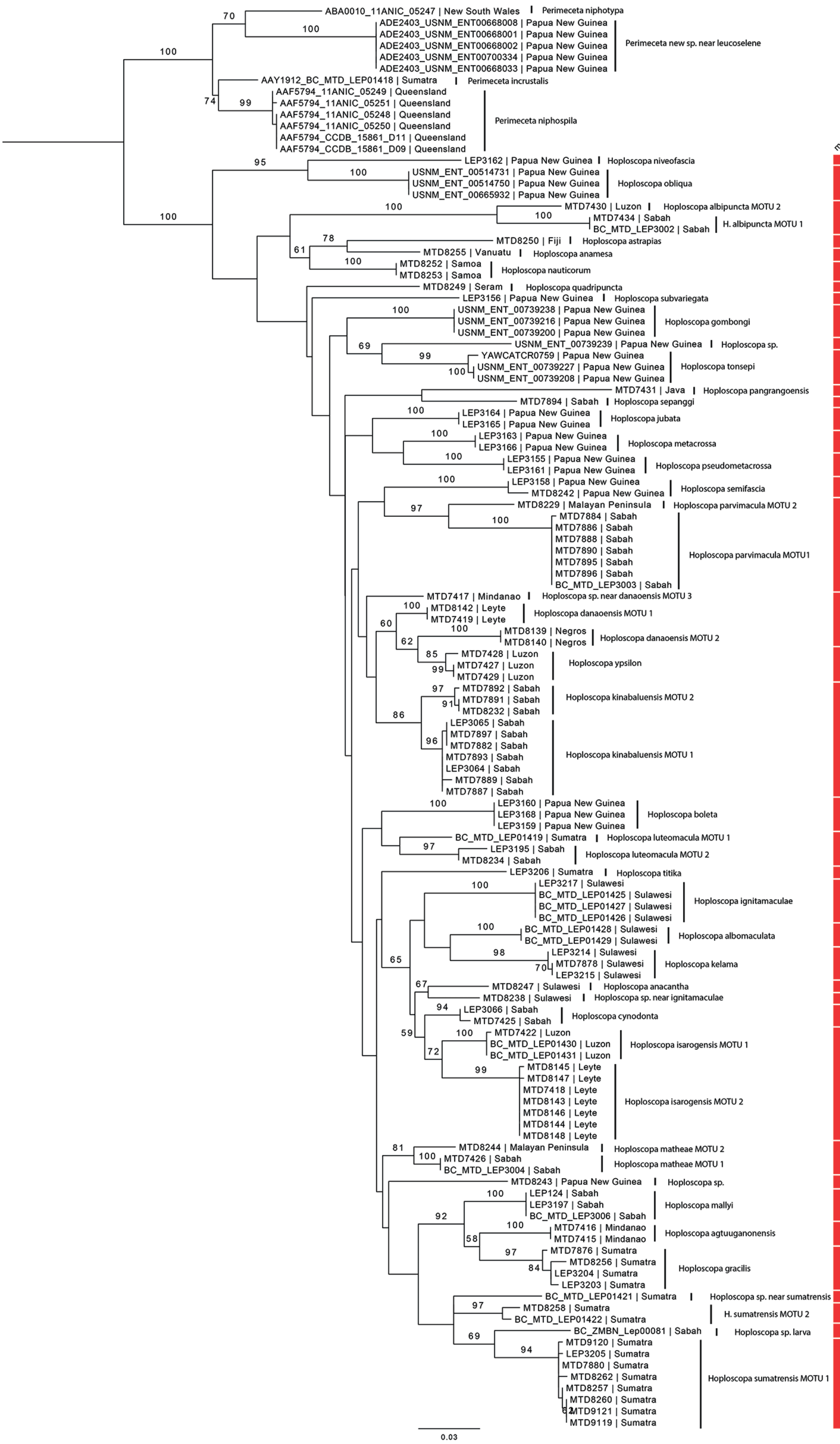


Figure 123. RaxML analysis of the COI barcode dataset partitionned after codon positions. Node support estimated with 1000 thorough bootstrap replicates under the GTR+GAMMA substitution model. Columns on the right display species delimitation inferred from the morphology (red), the ABGD (pink), and GMYC (green) methods.

Discussion

Our iterative taxonomic revision resulted in the discovery and description of 26 new species as well as the redescription of 15 species. Thirty of 38 morphospecies were concordant with species delimitation based on the COI barcode. Distinct genetic divergence (i.e., more than 2%) among populations of different islands, with minor morphological differences in wing pattern or male genitalia, suggests reproductive isolation through allopatric effects. In *H. matheae* sp. nov. and *H. parvimacula* sp. nov., specimens from Borneo and from Malaysia Peninsula form two distinct MOTUs that deserve closer examination. Cryptic divergence between Borneo and Malayan Peninsula has been found in other studies, e.g., ants (Quek et al. 2007, Feldhaar et al. 2010), bats (Francis et al. 2010), and birds (Lohman et al. 2011). Similarly, specimens of *H. danaoensis* sp. nov. and *H. isarogensis* sp. nov. from different Philippines islands display distinct genetic differentiation suggesting allopatric differentiation. Cryptic diversity among populations of different Philippines islands has also been reported in birds (Lohman et al. 2010). We found specimens from Eastern New Guinea resembling the type specimens of *H. quadripuncta* and *H. semifascia* from Western New Guinea, but displaying minor differences in male genitalia in each case. This suggests potential east-west differentiation along the Cordillera, as observed in birds (Joseph et al. 2001). Molecular investigations of specimens from Western New Guinea should be performed to test this hypothesis. High DNA barcode divergence in geographically distant species reveals the need for a better sampling with higher geographical coverage to investigate both intraspecific and interspecific variation (Bergsten et al. 2012, Talavera et al. 2013).

Two cases of high genetic divergence found in sympatric populations deserve closer attention. The first case involves *H. sumatrensis* sp. nov. from north Sumatra, where two mitochondrial lineages differ by 4.1–6%. In the second case, a divergence of 1.7–2.2% is observed in sympatric specimens of *H. kinabaluensis* sp. nov. on Mount Kinabalu. Closer examination of the morphology did not reveal any differences in either case. Inclusion of nuclear markers is needed in order to test if these mitochondrial lineages reflect different species or cases of introgression, symbiont infection, or maternal lineage sorting (Funk and Omland 2003, Hurst and Jiggins 2005, Harrison and Larson 2014). Notably, introgression has been reported in Lepidoptera (Zakharov et al. 2009; Cong et al. 2017), including Crambidae (Mally et al. 2018).

The investigated material more than doubled the number of *Hoploscopa* species. With 41 species now described, we still have not reached the saturation phase in species discovery for this group. For example, morphology of the female genitalia and molecular data support specimens MTD8238 and MTD8243 as different species, for which male specimens remain to be discovered. Similarly, molecular data and images of the habitus support specimen USNM_ENT_00739239 as a new but yet undescribed species. Unfortunately, this specimen could not be located (Scott Miller, pers. comm.). Additionally, the nine cases of morphospecies split into two or more MOTUs suggest putative new cryptic species and require further examination. In the NHMUK collection, we estimate at least a further 30 species await description. The presumed sister-group *Perimeceta* is probably less diverse, with four described species to date and an estimated twelve undescribed species in the collections of the NHMUK.

Hoploscopa is predominantly found in montane wet forests of South-East Asia at altitudes above 1,000 m, while species from higher latitudes tend to stretch their altitudinal distribution down to the lowlands, e.g., on the Philippines (*H. danaoensis* sp. nov., *H. isarogensis* sp. nov.) and the Melanesian islands (*H. astrapias*, *H. anamesa*, *H. nauticorum*). Mountain of South-East Asia are also home to other species-rich crambid groups, e.g., *Glaucocharis*, *Micraglossa*, and *Scoparia* (Gaskin 1985, Nuss 1998). Based on our data, we hypothesise isolation through elevation, higher specialisation, and seasonality as three potential factors driving the diversification of *Hoploscopa*. Isolation through elevation promotes species diversity and endemism (Steinbauer et al. 2016). The study of Merckx et al. (2015) on a broad range of taxonomic groups from Mount Kinabalu suggested endemic species on tropical mountains to originate either from long-distance dispersal (eccentric species) or from colonisation from local lowlands (centric species). All seven new species from Mount Kinabalu described in this paper do not share morphological similarities and no close relationships was recovered among them. On the contrary, *H. mallyi* sp. nov. from Mt Kinabalu forms a well-supported clade with *H. agtuuganonensis* sp. nov. from Mindanao and *H. gracilis* sp. nov. from Sumatra and represents a possible case of long-distance dispersal across islands. Colonisation from local lowland is also conceivable in *Hoploscopa*: *H. cynodonta* sp. nov. is reported at an altitude of 300 m in Brunei, and other *Hoploscopa* specimens have been collected at altitudes of 500 m at the foot of Mount Kinabalu (Schulze 2000). Secondly, on-site specialisation on host plant is another possible driver of speciation. Moths were shown to be high specialists in tropical mountains (Rodríguez-Castañeda et al. 2010). Larvae of *Hoploscopa* feed on ferns, which show a high species diversity in montane wet forests (Ebihara and Kuo 2012). Current host plant records report five *Hoploscopa* species to feed on ferns belonging to three distinct genera (Mally et al. 2017). Ferns are scarcely used by Lepidoptera (Weintraub et al. 1995) and thus represent a large palette of potential larval food. Finally, there is a possible seasonality occurring in *Hoploscopa* species. The *Hoploscopa* larva described by Mally et al. (2017) and collected during a field trip on Mount Kinabalu did not match any of the eight species we collected there, although we cannot rule out the possibility that we simply did not collect it. Seasonality is observed in Pyraloidea from lowlands surrounding Mount Kinabalu (Schulze and Fiedler 2003) but no studies are available on the seasonality of moths at higher elevations in South-East Asia. Further systematic work on *Hoploscopa*, phylogeographic investigations, as well as accumulation of host plant will assist in completing a more comprehensive picture of its diversity.

Acknowledgements

We are grateful to Ulf Buchsbaum (ZSM), David Lees (NHMUK), Wolfram Mey (ZMHB) and Scott Miller (USNM) for the specimens loaned for investigation. TL is grateful to David Lees and Geoff Martin for the assistance provided during his stay at the NHMUK. For assistance provided on the 2015 field work on Mount Kinabalu (Malaysia, Sabah), TL would like to thank Stephen Sutton, Richard Mally, Prof. S. Vairappan (Institute for Tropical Biology and Conservation, Kota Kinabalu, Malaysia), Ching Y. Chung (Sabah Biodiversity Center), and the staff of the Sabah Parks. Manuela Bartel (MTD) performed PCR and sample preparation for several specimens. We thank the SGN-SNSD-Mol-Lab for allowing access to their facilities for the molecular work. We are very grateful to Richard Mally and Nathalie Yonow for carefully reviewing our manuscript. Material for *Hoploscopa gombongi* sp. nov., *H. obliqua* sp. nov., and *H. tonsepi* sp. nov. originates from the Binatang Research Center program led by Vojtěch Novotný (Institute of Entomology, Czech Academy of Sciences, České Budějovice, Czech Republic), George Weiblen (Bell Museum of Natural History, University of Minnesota, USA), Yves Basset (Smithsonian Tropical Research Institute, Panama), and Scott Miller (National Museum of Natural History, Smithsonian Institution, Washington, DC, USA), and was supported by the US National Science Foundation (grants DEB-0515678, 0841885 and others) and the Czech Science Foundation (grants 206/09/0115, 14-04258S and others). DNA barcodes for these specimens were provided by Paul Hebert (Department of Integrative Biology, University of Guelph, Ontario, Canada) through a grant from Genome Canada and the Ontario Genomics Institute in support of the iBOL project. We thank Vojtěch Novotný, Gibson Mayiah, Stephen Sutton, and Francesca Vegliante for suggestions of names for some of the newly described species.

References

Bergsten J, Bilton DT, Fujisawa T, Elliott M, Monaghan MT, Balke M, Hendrich L, Geijer J, Herrmann J, Foster GN (2012) The effect of geographical scale of sampling on DNA barcoding. Systematic biology 61: 851–869. https://doi.org/10.1093/sysbio/sys037

Cong Q, Shen J, Borek D, Robbins RK, Opler PA, Otwinowski Z, Grishin NV (2017) When COI barcodes deceive: complete genomes reveal introgression in hairstreaks. Proceedings of the Royal Society B: Biological Sciences 284: 20161735. https://doi.org/10.1098/rspb.2016.1735

Dincă V, Montagud S, Talavera G, Hernández-Roldán J, Munguira ML, García-Barros E, Hebert PDN, Vila R (2015) DNA barcode reference library for Iberian butterflies enables a continental-scale preview of potential cryptic diversity. Scientific Reports 5: 12395. https://doi.org/10.1038/srep12395

Dumas P, Barbut J, Le Ru B, Silvain J-F, Clamens A-L, d'Alençon E, Kergoat GJ (2015) Phylogenetic Molecular Species Delimitations Unravel Potential New Species in the Pest Genus *Spodoptera* Guenée, 1852 (Lepidoptera, Noctuidae). PLOS ONE 10: 1–20. https://doi.org/10.1371/journal.pone.0122407

Ebihara A, Kuo L-Y (2012) East and Southeast Asian pteridophyte flora and DNA barcoding. In: The Biodiversity Observation Network in the Asia-Pacific Region. Springer, Tokyo, 321–327. https://doi.org/10.1007/978-4-431-54032-8_23

Ezard T, Fujisawa T, Barraclough TG (2009) Splits: species' limits by threshold statistics. R package version 1.0-14/ r31. http://R-Forge.R-project.org/projects/splits/

Feldhaar H, Gadau J, Fiala B (2010) Speciation in obligately plant-associated *Crematogaster* Ants: host distribution rather than adaption towards specific hosts drives the process. In: Glaubrecht M (Ed.) Evolution in Action. Springer, Berlin, Heidelberg. https://doi.org/10.1007/978-3-642-12425-9_10

Francis CM, Borisenko AV, Ivanova NV, Eger JL, Lim BK, Guillén-Servent A, Kruskop SV, Mackie I, Hebert PDN (2010) The role of DNA barcodes in understanding and conservation of mammal diversity in southeast Asia. PloS ONE 5: e12575–e12575. https://doi.org/10.1371/journal.pone.0012575

Fujisawa T, Barraclough TG (2013) Delimiting species using single-locus data and the Generalized Mixed Yule Coalescent approach: a revised method and evaluation on simulated data sets. Systematic biology 62: 707–724. https://doi.org/10.1093/sysbio/syt033

Funk DJ, Omland KE (2003) Species-level paraphyly and polyphyly: frequency, causes, and consequences, with insights from animal mitochondrial DNA. Annual Review of Ecology, Evolution, and Systematics 34: 397–423. https://doi.org/10.1146/annurev.ecolsys.34.011802.132421

Gaskin DE (1985) Morphology and Reclassification of the Australasian, Melanesian and Polynesian *Glaucocharis* Meyrick (Lepidoptera: Crambinae: Diptychophorini). Australian Journal of Zoology, Supplementary Series 33: 1–75. https://doi.org/10.1071/AJZS115

Hajibabaei M, Smith MA, Janzen DH, Rodriguez JJ, Whitfield JB, Hebert PD (2006) A minimalist barcode can identify a specimen whose DNA is degraded. Molecular Ecology Notes 6: 959–964. https://doi.org/10.1111/j.1471-8286.2006.01470.x

Harrison RG, Larson EL (2014) Hybridization, introgression, and the nature of species boundaries. Journal of Heredity 105: 795–809. https://doi.org/10.1093/jhered/esu033

Hausmann A, Miller SE, Holloway JD, Dewaard JR, Pollock D, Prosser SW, Hebert PD (2016) Calibrating the taxonomy of a megadiverse insect family: 3000 DNA barcodes from geometrid type specimens (Lepidoptera, Geometridae). Genome 59: 671–684. https://doi.org/10.1139/gen-2015-0197

Hebert PD, Zakharov EV, Prosser SW, Sones JE, McKeown JT, Mantle B, La Salle J (2013) A DNA "Barcode Blitz": Rapid digitization and sequencing of a natural history collection. PLoS One 8: e68535. https://doi.org/10.1371/journal.pone.0068535

Heppner JB (1998) Classification of Lepidoptera. Part. 1 Introduction. Holarctic Lepidoptera 5, Suppl. 1: iv + 148 + 6 pp.

Hundsdoerfer AK, Päckert M, Kehlmaier C, Strutzenberger P, Kitching IJ (2017) Museum archives revisited: Central Asiatic hawkmoths reveal exceptionally high late Pliocene species diversification (Lepidoptera, Sphingidae). Zoologica Scripta 46: 552–570. https://doi.org/10.1111/zsc.12235

Hurst GD, Jiggins FM (2005) Problems with mitochondrial DNA as a marker in population, phylogeographic and phylogenetic studies: the effects of inherited symbionts. Proceedings of the Royal Society B: Biological Sciences 272: 1525–1534. https://doi.org/10.1098/rspb.2005.3056

Joseph L, Slikas B, Alpers D, Schodde R (2001) Molecular systematics and phylogeography of New Guinean logrunners (Orthonychidae). Emu 101: 273–280. https://doi.org/10.1071/MU01008

Kekkonen M, Hebert PD (2014) DNA barcode-based delineation of putative species: efficient start for taxonomic workflows. Molecular ecology resources 14: 706–715. https://doi.org/10.1111/1755-0998.12233

Knölke S, Erlacher S, Hausmann A, Miller MA, Segerer AH (2004) A procedure for combined genitalia dissection and DNA extraction in Lepidoptera. Insect Systematics & Evolution 35: 401–409. https://doi.org/10.1163/187631204788912463

Kristensen NP (2003) 4. Skeleton and muscles: adults. Handbook of Zoology, Vol. IV, Part 36, Lepidoptera, Moths and Butterflies, Vol. 2, Morphology, Physiology, and Development. De Gruyter, Berlin, 39–131.

Kumar S, Stecher G, Li M, Knyaz C, Tamura K (2018) MEGA X: Molecular Evolutionary Genetics Analysis across Computing Platforms. Molecular Biology and Evolution 35: 1547–1549. https://doi.org/10.1093/molbev/msy096

Landry B (1995) A phylogenetic analysis of the major lineages of the Crambinae and of the genera of Crambini of North America (Lepidoptera:Pyralidae). Memoirs on Entomology International. Associated Publishers, Gainesville, 242 pp.

Lanfear R, Calcott B, Ho SYW, Guindon S (2012) Partitionfinder: combined selection of partitioning schemes and substitution models for phylogenetic analyses. Molecular Biology and Evolution 29: 1695–1701. https://doi.org/10.1093/molbev/mss020

Lanfear R, Frandsen PB, Wright AM, Senfeld T, Calcott B (2017) PartitionFinder 2: New methods for selecting partitioned models of evolution for molecular and morphological phylogenetic analyses. Molecular Biology and Evolution 34: 772–773. https://doi.org/10.1093/molbev/msw260

Leraut P (1980) Liste systématique et synonymique des Lépidoptères de France, Belgique et Corse. Alexanor and Bulletin de la Société entomologique de France Supplement: 1–334.

Léger T, Landry B, Nuss M (2019) Phylogeny, character evolution and tribal classification in Crambinae and Scopariinae (Lepidoptera, Crambidae). Systematic Entomology 44: 757–776. https://doi.org/10.1111/syen.12353

Lohman DJ, de Bruyn M, Page T, von Rintelen K, Hall R, Ng PK, Shih H-T, Carvalho GR, von Rintelen T (2011) Biogeography of the Indo-Australian archipelago. Annual Review of Ecology, Evolution, and Systematics 42: 205–226. https://doi.org/10.1146/annurev-ecolsys-102710-145001

Lohman DJ, Ingram KK, Prawiradilaga DM, Winker K, Sheldon FH, Moyle RG, Ng PK, Ong PS, Wang LK, Braile TM (2010) Cryptic genetic diversity in "widespread" Southeast Asian bird species suggests that Philippine avian endemism is gravely underestimated. Biological Conservation 143: 1885–1890. https://doi.org/10.1016/j.biocon.2010.04.042

Maddison WP, Maddison DR (2017) Mesquite: a modular system for evolutionary analysis – Version 3.31. http://www.mesquiteproject.org

Mally R, Huemer P, Nuss M (2018) Deep intraspecific DNA barcode splits and hybridisation in the *Udea alpinalis* group (Insecta, Lepidoptera, Crambidae) – an integrative revision. ZooKeys 746: 51–90. https://doi.org/10.3897/zookeys.746.22020

Mally R, Léger T, Vairappan CS, Sutton S, Nuss M (2017) Discovery of another fern-feeding group of moths: the larvae of Hoploscopini (Insecta: Lepidoptera: Pyraloidea) from Borneo. Raffles Bulletin of Zoology 65: 100–108.

Merckx VSFT, Hendriks KP, Beentjes KK, Mennes CB, Becking LE, Peijnenburg KTCA, Afendy A, Arumugam N, de Boer H, Biun A, Buang MM, Chen P-P, Chung AYC, Dow R, Feijen FAA, Feijen H, Soest CF, Geml J, Geurts R, Gravendeel B, Hovenkamp P, Imbun P, Ipor I, Janssens SB, Jocqué M, Kappes H, Khoo E, Koomen P, Lens F, Majapun RJ, Morgado LN, Neupane S, Nieser N, Pereira JT, Rahman H, Sabran S, Sawang A, Schwallier RM, Shim P-S, Smit H, Sol N, Spait M, Stech M, Stokvis F, Sugau JB, Suleiman M, Sumail S, Thomas DC, van Tol J, Tuh FYY, Yahya BE, Nais J, Repin R, Lakim M, Schilthuizen M (2015) Evolution of endemism on a young tropical mountain. Nature 524: 347. https://doi.org/10.1038/nature14949

Miller MA, Pfeiffer W, Schwartz T (2010) Creating the CIPRES Science Gateway for inference of large phylogenetic trees. Proceedings of the Gateway Computing Environments Workshop (GCE), New Orleans, 1–8. https://doi.org/10.1109/GCE.2010.5676129

Miller SE, Rosati ME, Gewa B, Novotny V, Weiblen GD, Hebert PD (2015) DNA Barcodes of Lepidoptera Reared from Yawan, Papua New Guinea. Proceedings of the Entomological Society of Washington 117: 247–250. https://doi.org/10.4289/0013-8797.117.2.247

Minet J (1982) Les Pyraloidea et leurs principales divisions systématiques (Lep. Ditrysia). Bulletin de la Société entomologique de France 86: 262–280.

Mitchell A (2015) Collecting in collections: a PCR strategy and primer set for DNA barcoding of decades-old dried museum specimens. Molecular ecology resources 15: 1102–1111. https://doi.org/10.1111/1755-0998.12380

Müller J, Müller K, Neinhuis C, Quandt D (2005) PhyDE-Phylogenetic Data Editor.

Munroe E, Solis MA (1998) The Pyraloidea. Lepidoptera, Moths and Butterflies. Vol 1: Evolution, Systematics, and Biogeography. Handbook of Zoology, Berlin, 233–256.

Myers N, Mittermeier RA, Mittermeier CG, Da Fonseca GA, Kent J (2000) Biodiversity hotspots for conservation priorities. Nature 403: 853. https://doi.org/10.1038/35002501

Nakahara S, Lamas G, Tyler S, Marín MA, Huertas B, Willmott KR, Mielke OHH, Espeland M (2019) A revision of the new genus *Amiga* Nakahara, Willmott & Espeland, gen. n., described for *Papilio arnaca* Fabricius, 1776 (Lepidoptera, Nymphalidae, Satyrinae). ZooKeys 821: 85–152. https://doi.org/10.3897/zookeys.821.31782

Nuss M (1998) The Scopariinae and Heliothelinae stat. rev. (Lepidoptera: Pyraloidea, Crambidae) of the Oriental Region – a revisional synopsis with descriptions of new species from the Philippines and Sumatra. Nachrichten des entomologischen Vereins Apollo suppl. 17: 475–528.

Pons J, Barraclough TG, Gomez-Zurita J, Cardoso A, Duran DP, Hazell S, Kamoun S, Sumlin WD, Vogler AP (2006) Sequence-based species delimitation for the DNA taxonomy of undescribed insects. Systematic biology 55: 595–609. https://doi.org/10.1080/10635150600852011

Prosser SW, deWaard JR, Miller SE, Hebert PD (2016) DNA barcodes from century-old type specimens using next-generation sequencing. Molecular Ecology Resources 16: 487–497. https://doi.org/10.1111/1755-0998.12474

Puillandre N, Lambert A, Brouillet S, Achaz G (2012) ABGD, Automatic Barcode Gap Discovery for primary species delimitation. Molecular Ecology 21: 1864–1877. https://doi.org/10.1111/j.1365-294X.2011.05239.x

Quek S-P, Davies SJ, Ashton PS, Itino T, Pierce NE (2007) The geography of diversification in mutualistic ants: a gene's-eye view into the Neogene history of Sundaland rain forests. Molecular Ecology 16: 2045–2062. https://doi.org/10.1111/j.1365-294X.2007.03294.x

Rambaut A, Drummond AJ, Xie D, Baele G, Suchard MA (2018) Tracer. http://tree.bio.ed.ac.uk/software/tracer/

Robinson GS (1976) The preparation of slides of Lepidoptera genitalia with special reference to the Microlepidoptera. Entomologist's Gazette 27: 127–132.

Robinson GS, Tuck KR, Shaffer M (1994) A field guide to the smaller moths of South-East Asia. Natural History Museum, London, 308 pp.

Rodríguez-Castañeda G, Dyer LA, Brehm G, Connahs H, Forkner RE, Walla TR (2010) Tropical forests are not flat: how mountains affect herbivore diversity. Ecology letters 13: 1348–1357. https://doi.org/10.1111/j.1461-0248.2010.01525.x

Schlick-Steiner BC, Steiner FM, Seifert B, Stauffer C, Christian E, Crozier RH (2010) Integrative taxonomy: a multisource approach to exploring biodiversity. Annual review of entomology 55: 421–438. https://doi.org/10.1146/annurev-ento-112408-085432

Schulze CH (2000) Auswirkungen anthropogener Störungen auf die Diversität von Herbivoren: Analyse von Nachtfalterzönosen entlang von Habitatgradienten in Ost-Malaysia. Universität Bayreuth.

Schulze CH, Fiedler K (2003) Vertical and temporal diversity of a species-rich moth taxon in Borneo. In: Basset Y, et al. (Eds) Arthropods of Tropical Forests: Spatio-temporal Dynamics and Resource Use in the Canopy. Cambridge University Press, 69–85.

Song H, Buhay JE, Whiting MF, Crandall KA (2008) Many species in one: DNA barcoding overestimates the number of species when nuclear mitochondrial pseudogenes are coamplified. Proceedings of the national academy of sciences 105: 13486–13491. https://doi.org/10.1073/pnas.0803076105

Stamatakis A (2006) RAxML-VI-HPC: maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. Bioinformatics 22: 2688–2690. https://doi.org/10.1093/bioinformatics/btl446

Steinbauer MJ, Field R, Grytnes J-A, Trigas P, Ah-Peng C, Attorre F, Birks HJB, Borges PA, Cardoso P, Chou C-H (2016) Topography-driven isolation, speciation and a global increase of endemism with elevation. Global Ecology and Biogeography 25: 1097–1107. https://doi.org/10.1111/geb.12469

Suchard MA, Lemey P, Baele G, Ayres DL, Drummond AJ, Rambaut A (2018) Bayesian phylogenetic and phylodynamic data integration using BEAST 1.10. Virus Evolution 4: vey016. https://doi.org/10.1093/ve/vey016

Sutton S, Barlow H, Whitaker T (2015) An exciting new book. Pyraloid Planet 9: 2–3.

Talavera G, Dincă V, Vila R (2013) Factors affecting species delimitations with the GMYC model: insights from a butterfly survey. Methods in Ecology and Evolution 4: 1101–1110. https://doi.org/10.1111/2041-210X.12107

Wahlberg N, Wheat CW (2008) Genomic outposts serve the phylogenomic pioneers: designing novel nuclear markers for genomic DNA extractions of Lepidoptera. Systematic Biology 57: 231–242. https://doi.org/10.1080/10635150802033006

Weintraub JD, Lawton JH, Scoble MJ (1995) Lithinine moths on ferns: a phylogenetic study of insect-plant interactions. Biological Journal of the Linnean Society 55: 239–250. https://doi.org/10.1111/j.1095-8312.1995.tb01062.x

Yeates DK, Seago A, Nelson L, Cameron SL, Joseph LEO, Trueman JW (2011) Integrative taxonomy, or iterative taxonomy? Systematic Entomology 36: 209–217. https://doi.org/10.1111/j.1365-3113.2010.00558.x

Zakharov EV, Lobo NF, Nowak C, Hellmann JJ (2009) Introgression as a likely cause of mtDNA paraphyly in two allopatric skippers (Lepidoptera: Hesperiidae). Heredity 102: 590 pp. https://doi.org/10.1038/hdy.2009.26

Supplementary material 1

Figure S1. Scheme summarising the approach followed for amplification of the COI barcode from old material

Authors: Théo Léger, Christian Kehlmaier, Charles Vairappan, Matthias Nuss

Data type: molecular data

Link: https://doi.org/10.3897/zookeys.@@.36563.suppl1

Supplementary material 2

Table S1. Primers sequences with characteristics and chemical properties

Authors: Théo Léger, Christian Kehlmaier, Charles Vairappan, Matthias Nuss

Data type: molecular data

Link: https://doi.org/10.3897/zookeys.@@.36563.suppl2

Supplementary material 3

Table S2. List of DNA samples of *Hoploscopa* moths and allies used in this study

Authors: Théo Léger, Christian Kehlmaier, Charles Vairappan, Matthias Nuss

Data type: molecular data

Link: https://doi.org/10.3897/zookeys.@@.36563.suppl3

Supplementary material 4

Table S3. Distance matrix calculated under MEGA (Kumar et al. 2018) using the Maximum Composite Likelihood algorithm

Authors: Théo Léger, Christian Kehlmaier, Charles Vairappan, Matthias Nuss

Data type: molecular data

Link: https://doi.org/10.3897/zookeys.@@.36563.suppl4

Supplementary material 5

Table S4. Collecting localities of the *Hoploscopa* specimens examined

Authors: Théo Léger, Christian Kehlmaier, Charles Vairappan, Matthias Nuss

Data type: species data

Link: https://doi.org/10.3897/zookeys.@@.36563.suppl5

Chapter 5

Conclusion and outlook

The presented work gives a first detailed phylogeny of the Crambinae, Scopariinae and Heliothelinae s. str. as well as new insights into the phylogenetic placement, the host plants, the larval morphology and the species diversity of Hoploscopinae. The analysis of a six-genes dataset resolved most relationships within Crambinae and Scopariinae and resulted in a revised tribal and generic classification, respectively. However, this dataset failed at resolving relationships among subfamilies and in species-rich groups such as the Crambini and *Eudonia*. Analyses of our ten-genes dataset combined with other data (Mutanen et al., 2010; Regier et al., 2012) as well as published transcriptomes or genomes (Challis et al., 2016; Kawahara & Breinholt, 2014; Renuka et al., 2017) provided the first phylogeny for all Crambidae subfamilies. The Heliothelinae were recovered as polyphyletic, with Heliothelinae s. str. sister to the Scopariinae and Hoploscopinae stat. n. as a separate lineage sister to (Heliothelinae + Scopariinae) + Crambinae. Cathariinae and Cybalomiinae were found related to the Glaphyriinae, as suggested by the Brassicales host plants shared between Cybalomiinae and Glaphyriinae. However, the lack of basal support prevented us from proposing taxonomic changes. The Lathrotelinae were confirmed monophyletic and could be confidently assigned to the CAMMSS clade while the Linostinae were recovered within the non-PS clade, although its position within this clade varied among analyses.

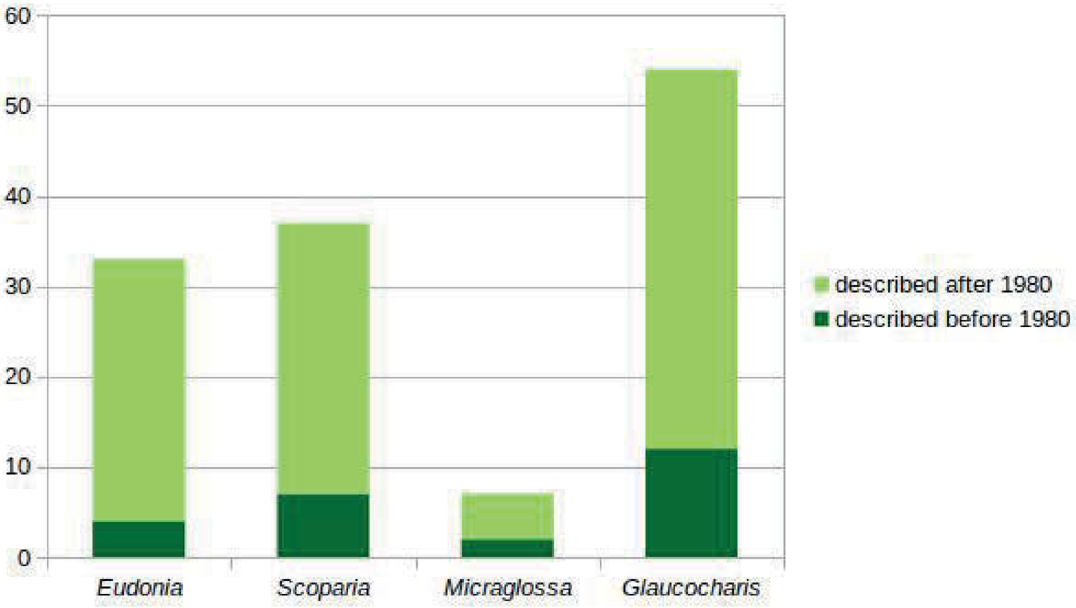
The difficulty in confidently placing Cathariinae, Cybalomiinae and Linostinae in a phylogenetic framework here reflects the limits of the multigene datasets generated using a "first generation" Sanger sequencing approach and suggests the inclusion of a greater number of molecular markers in order to increase branch support. NGS methods such as Target Enrichment, Transcriptome Sequencing, Shotgun Sequencing or Whole Genome Sequencing provide hundreds of markers for phylogenetic analyses and there is an evergrowing number of studies on biodiversity using them (Matos-Maraví et al., 2019). These genomic methods have been successfully used in several phylogenetic studies on Lepidoptera (e.g., Bazinet et al., 2017; Kawahara & Breinholt, 2014; Kawahara et al., 2019; Li et al., 2019; Toussaint et al., 2018) and are envisioned as the next step in pyraloid phylogeny. The use of fragmented DNA as a template for some of these methods (e.g. Shotgun Sequencing, Target Enrichment) opens the gate for phylogenetics to be applied to museum material (e.g., St Laurent et al., 2018 Li et al., 2019). This is especially relevant in times where fieldwork in tropical countries becomes increasingly difficult (Prathapan et al., 2018).

Ancestral character reconstruction in Crambinae and Scopariinae confirmed the apomorphic status of twelve characters, while nine other characters provided new apomorphies. For instance, the "open cell" in the hindwing of several Crambinae have been used by several authors for a tentative classification of the group, and was shown in this study to represent an apomorphy for the newly recovered “open-cell clade”. Other characters previously used to define taxonomic groups were shown to be homoplastic in the light of the phylogenetic tree, as exemplified by the snow white color of the forewings proposed as an apomorphy for the Argyriini (Munroe, 1995), which turned out to represent convergence patterns in the light of the present results. Li et al. (2019) found a similar convergence in wing pattern in Hesperiidae that misled specialists in their classification. Sampling of several taxa per genus in *Eudonia*, *Microcrambus* and *Scoparia* in the presented work highlighted seven genera as in-groups of the three above-mentioned genera and led to their synonymization. We expect further cases in future works enlarging the generic sampling. Finally, morphological traits could be associated with variations in life history. The reduction of the anterior apophyses as well as the non-coalesced papillae anales in the female oviscapt of the Crambini correlate with the behaviour of laying non-adhesive eggs and the use of cool-season grasses (Pooideae) as host plants. Also, variations in genitalic characters such as the tip of the gnathos in males or the number of signa on the corpus bursae in females suggest different modus operandi in the poorly known mating process of the Crambinae and provide ground for future research.

The third paper of this work provide the first host plant record for the Hoploscopinae. A review of the records in the world lepidopteran hostplants database (Robinson et al., 2010) and in additional literature provides host records for an estimated 246 species of Crambinae, Heliothelinae, Hoploscopinae and Scopariinae. This represents less than 10% of the 2700 species described in all four subfamilies. Tropical regions are especially understudied in this matter: tropical species constitute only a third of the 246 species with host plant records, and the majority of their host plants records are crops. This highlights the scarcity of our knowledge on the interactions of most pyraloid species with their ecosystems and advocate the need of more studies addressing trophic interactions (Wilson, 2017). DNA barcoding has been shown to efficiently uncover interactions between insects and host plants (Baker et al., 2016), and was used in this work to confidently assign the larvae collected on ferns to the genus *Hoploscopa*. Large-scale projects on Lepidoptera-host plant associations in groups such as Geometridae and Pyraloidea (Hausmann et al., 2019; Miller et al., 2015, 2016; Segar et al., 2017) shows the way to efficiently tackle trophic interactions in largely unknown ecosystems.

New species are described at a regular pace, with 32 to 115 species described each year in the period of 2006-2015 (Nuss et al., 2003–2019), depending on the productivity and disposition of pyraloid taxonomists. Tackling the diversity of *Hoploscopa* with morphology and DNA barcoding resulted in the description of 26 new species, increasing the number of species placed in the genus to 41. Another 30 still undescribed species are known from scientific collections. This magnitude fits within the range of the expansion factors estimated from diverse genera of Scopariinae and Crambinae in China and summarized in Fig. 5.1. Evaluating the number of species remaining to be described is a delicate task as some groups have been revised regionally or globally, while others are in a poor taxonomical state. Also, the species diversity depends on factors such as ecological adaptations and dispersal abilities that vary strongly among taxa. *Hoploscopa* and Scopariinae both share the montane rain forests of South-East Asia as habitat, but use different larval host plants, ferns and mosses, respectively. When using a factor 4.4 to estimate the number of undescribed species in *Hoploscopa* as a proxi to estimate the diversity in Scopariinae in South-East Asia and Melanesia, the fifteen scopariine species of *Eudonia*, *Micraglossa* and *Scoparia* presently described from these regions (Nuss et al., 2003–2019) suggest that another 70 species remain to be described from there. When applying the factors calculated for these three genera in China (Fig. 5.1), the number of species awaiting description in South-East Asia ranges between 38 and 109.

Figure 5.1: Diagramm displaying the number of species brought by revisions of four mountain-dwelling pyraloid groups in China



DNA barcoding is a long established method enabling rapid survey of the diversity in poorly known groups (Miller et al., 2016, Srivathsan et al., 2019). Our integrative approach, referred to as "iterative", consisted in a first screen and sorting of *Hoploscopa* specimens after morphology, followed by sequencing of the DNA barcode for few representative of each morphospecies. However, some morphospecies unveil unexpected diversity in COI barcode, as illustrated by *Hoploscopa kinabaluensis* and *H. sumatrensis*, where morphologically identical specimens from the same locality were recovered into two clusters. This diversity might go unnoticed when only few specimens of each morphospecies are selected for DNA barcoding. A decrease in costs of DNA barcoding enables the use of a reverse workflow where material is first sorted using DNA barcoding, afterwhat few specimens of each operational taxonomic units (OTUs) are investigated morphologically (Wang et al., 2018). Current costs of Sanger analysis of 6\$/specimen represent the DNA extraction ($\sim$ 2.5\$), PCR costs ($\sim$ 1.5\$) and unidirectional sequencing ($\sim$ 2\$). High-throughput sequencing of tagged amplicons shows a drop of sequencing price to 0.20\$/specimen when samples are massively processed, representing a total cost of 1\$/specimen (Hebert et al., 2018). A method using MinION reports a cost of 0.55\$/specimens (Srivathsan et al., 2019). Alternatively, the use of short barcodes (313bp) has been shown to effectively sort specimens without a decrease of performance in comparison to full length COI barcode, and results in a cost of less than 0.5\$/specimen (Wang et al., 2018). Yet, DNA barcoding does not always agree with morphological delimitations. Incongruences can result from errors due to wrong morphological assignment, contamination in PCR or artefacts in the analysis with short sequences (Srivathsan et al., 2019). When these incongruences persist in independent replicates, biological phenomenons such as incomplete lineage sorting or introgression can underlie these patterns. Inclusion of a set of nuclear markers is advised in these cases (Schlick-Steiner et al., 2010).

While DNA barcoding ensure the use of an universal marker across Lepidoptera, analysis of morphology suffers a lack of standard across groups (Avise & Mitchell, 2007). In the present work, the use of software Mesquite (W. P. Maddison & D. R. Maddison, 2017) facilitated the investigation of morphological characters by allowing rapid visualization of character diversity and warrantying consistency in the description of these characters. However, performance decreases when this information is transcribed into the manuscript, suggesting no current solution to drastically increase the speed of species descriptions without encroaching on quality. Taxonomical works providing description for a large number of taxa often rely on short concise diagnostical descriptions (e.g., Butcher et al., 2012; Riedel et al., 2013b, 2014, Riedel & Narakusumo, 2019). Another issue slowing down taxonomic work is the necessary laborious detective work through old literature of variable quality and the equally necessary examination of type specimens, often spread across museums (Riedel et al., 2013a). Digitization initiatives in museums such as IdigBio (www.idigbio.org) and DISSCO (www.dissco.eu), especially for type specimens, will bridge the literature with physical specimens, while molecular characterization of museum material (Hausmann et al., 2016, Prosser et al., 2016) will link Linnean taxonomy with DNA barcoding and endorse species discovery.

We now have a fairly good knowledge of the phylogenetic relationships within Crambidae, as well as for the large clades Crambinae + Scopariinae and Pyraustinae + Spilomelinae (Léger et al., 2019; Mally et al., 2019). Further species-rich groups, such as Acentropinae (767 spp.), Epipaschiinae (718 spp.), Pyralinae (962 spp.) and Phycitinae (3131 spp.), are in great need of systematic revision and should be the focus of future studies. Future works will benefit from the use of genomic methods in a taxon-, collection- or region-based approach and will provide new insights into the phylogenetic relationships of pyraloid moths, fostering our understanding of the evolution of morphological and ecological characters as well as accelerating species discovery. The advances in the field of "museomics" will contribute to the discovery of evolutionary lineages we are not aware of yet. These endeavors go hand in hand with the ambitious project by Lewin et al. (2018) to provide a genome for each living species.

Bibliography

Avise, J. C. & Mitchell, D. (2007). Time to standardize taxonomies. *Systematic Biology*, *56*(1), 130–133.

Baker, C. C. M., Bittleston, L. S., Sanders, J. G., & Pierce, N. E. (2016). Dissecting host-associated communities with DNA barcodes. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences*, *371*, 20150328. doi:10.1098/rstb.2015.0328

Bazinet, A. L., Mitter, K. T., Davis, D. R., Van Nieukerken, E. J., Cummings, M. P., & Mitter, C. (2017). Phylotranscriptomics resolves ancient divergences in the Lepidoptera. *Systematic Entomology*, *42*(2), 305–316. doi:10.1111/syen.12217

Butcher, B. A., Smith, M. A., Sharkey, M. J., & Quicke, D. L. (2012). A turbo-taxonomic study of Thai *Aleiodes* (*Aleiodes*) and *Aleiodes* (*Arcaleiodes*)(Hymenoptera: Braconidae: Rogadinae) based largely on COI barcoded specimens, with rapid descriptions of 179 new species. *Zootaxa*, *3457*(1), 232.

Challis, R. J., Kumar, S., Dasmahapatra, K. K., Jiggins, C. D., & Blaxter, M. (2016). Lepbase: The Lepidopteran genome database. *bioRxiv*, 056994. doi:10.1101/056994

Hausmann, A., Diller, J., Moriniere, J., Höcherl, A., Floren, A., & Haszprunar, G. (2019). DNA Barcoding of fogged caterpillars in Peru: A novel approach for unveiling host-plant relationships of tropical moths (Insecta, Lepidoptera). *bioRxiv*. doi:10.1101/799221

Hausmann, A., Miller, S. E., Holloway, J. D., Dewaard, J. R., Pollock, D., Prosser, S. W., & Hebert, P. D. N. (2016). Calibrating the taxonomy of a megadiverse insect family: 3000 DNA barcodes from geometrid type specimens (Lepidoptera, Geometridae). *Genome*, *59*(9), 671–684. doi:10.1139/gen-2015-0197

Hebert, P. D. N., Braukmann, T. W., Prosser, S. W., Ratnasingham, S., deWaard, J. R., Ivanova, N. V., . . . Sones, J. E. (2018). A Sequel to Sanger: Amplicon sequencing that scales. *BMC genomics*, *19*(1), 219. doi:10.1186/s12864-018-4611-3

Kawahara, A. Y. & Breinholt, J. W. (2014). Phylogenomics provides strong evidence for relationships of butterflies and moths. *Proceedings of the Royal Society B: Biological Sciences*, *281*(1788), 20140970. doi:10.1098/rspb.2014.0970

Kawahara, A. Y., Plotkin, D., Espeland, M., Meusemann, K., Toussaint, E. F. A., Donath, A., . . . dos Reis, M. et al. (2019). Phylogenomics reveals the evolutionary timing and pattern of butterflies and moths. *Proceedings of the National Academy of Sciences*, *116*(45), 22657–22663. doi:10.1073/pnas.1907847116

Léger, T., Landry, B., & Nuss, M. (2019). Phylogeny, character evolution and tribal classification in Crambinae and Scopariinae. *Systematic Entomology*, *44*(4), 757–776. doi:10.1111/syen.12353

Lewin, H. A., Robinson, G. E., Kress, W. J., Baker, W. J., Coddington, J., Crandall, K. A., . . . Zhang, G. (2018). Earth BioGenome Project: Sequencing life for the future of life. *Proceedings of the National Academy of Sciences*, *115*(17), 4325. doi:10.1073/pnas.1720115115

Li, W., Cong, Q., Shen, J., Zhang, J., Hallwachs, W., Janzen, D. H., & Grishin, N. V. (2019). Genomes of skipper butterflies reveal extensive convergence of wing patterns. *Proceedings of the National Academy of Sciences*, *116*(13), 6232–6237. doi:10.1073/pnas.1821304116

Maddison, W. P. & Maddison, D. R. (2017). Mesquite: A modular system for evolutionary analysis. version 3.31 http://www.mesquiteproject.org.

Mally, R., Hayden, J. E., Neinhuis, C., Jordal, B. H., & Nuss, M. (2019). The phylogenetic systematics of Spilomelinae and Pyraustinae (Lepidoptera: Pyraloidea: Crambidae) inferred from DNA and morphology. *Arthropod Systematics & Phylogeny*, *77*(1), 141–204. doi:10.26049/ASP77-1-2019-07

Matos-Maraví, P., Ritter, C. D., Barnes, C. J., Nielsen, M., Olsson, U., Wahlberg, N., … Antonelli, A. (2019). Biodiversity seen through the perspective of insects: 10 simple rules on methodological choices and experimental design for genomic studies. *PeerJ*, *7*, e6727. doi:10.7717/peerj.6727

Miller, S. E., Hausmann, A., Hallwachs, W., & Janzen, D. H. (2016). Advancing taxonomy and bioinventories with DNA barcodes. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences*, *371*(1702), 20150339. doi:10.1098/rstb.2015.0339. JSTOR: 27481791

Miller, S. E., Rosati, M. E., Gewa, B., Novotny, V., Weiblen, G. D., & Hebert, P. D. N. (2015). DNA Barcodes of Lepidoptera Reared from Yawan, Papua New Guinea. *Proceedings of the Entomological Society of Washington*, *117*(2), 247–250. doi:10.4289/0013-8797.117.2.247

Munroe, E. (1995). Crambidae (Crambinae, Schoenobiinae, Cybalomiinae, Linostinae, Glaphyriinae, Dichogaminae, Scopariinae, Musotiminae, Midilinae, Nymphulinae, Odontiinae, Evergestinae, Pyraustinae). In *Atlas of Neotropical Lepidoptera. Checklist: Part 2. Hyblaeoidea – Pyraloidea - Tortricoidea 3* (pp. 34–79). Gainesville: Association for Tropical Lepidoptera & Scientific Publishers.

Mutanen, M., Wahlberg, N., & Kaila, L. (2010). Comprehensive gene and taxon coverage elucidates radiation patterns in moths and butterflies. *Proceedings. Biological Sciences*, *277*(1695), 2839–2848. doi:10.1098/rspb.2010.0392

Nuss, M., Landry, B., Mally, R., Vegliante, F., Tränkner, A., Bauer, F., … Speidel, W. (2003–2019). Global Information System on Pyraloidea. - www.pyraloidea.org.

Prathapan, K. D., Pethiyagoda, R., Bawa, K. S., Raven, P. H., Rajan, P. D., Acosta, L. E., … Pérez González, A. (2018). When the cure kills – cbd limits biodiversity research. *Science*, *360*(6396), 1405–1406. doi:10.1126/science.aat9844

Prosser, S. W., deWaard, J. R., Miller, S. E., & Hebert, P. D. N. (2016). DNA barcodes from century-old type specimens using next-generation sequencing. *Molecular Ecology Resources*, *16*(2), 487–497. doi:10.1111/1755-0998.12474

Regier, J. C., Mitter, C., Solis, M. A., Hayden, J. E., Landry, B., Nuss, M., … Cummings, M. P. (2012). A molecular phylogeny for the pyraloid moths (Lepidoptera: Pyraloidea) and its implications for higher-level classification. *Systematic Entomology*, *37*(4), 635–656. doi:10.1111/j.1365-3113.2012.00641.x

Renuka, P., Madhav, M. S., Padmakumari, A. P., Barbadikar, K. M., Mangrauthia, S. K., Vijaya Sudhakara Rao, K., … Ravindra Babu, V. (2017). RNA-seq of Rice Yellow Stem Borer *Scirpophaga incertulas* Reveals Molecular Insights During Four Larval Developmental Stages. *G3: Genes—Genomes—Genetics*, *7*(9), 3031–3045. doi:10.1534/g3.117.043737

Riedel, A. & Narakusumo, R. P. (2019). One hundred and three new species of *Trigonopterus* weevils from Sulawesi. *ZooKeys*, *828*, 1–153. doi:10.3897/zookeys.828.32200

Riedel, A., Sagata, K., Suhardjono, Y. R., Tänzler, R., & Balke, M. (2013a). Integrative taxonomy on the fast track - towards more sustainability in biodiversity research. *Frontiers in Zoology*, *10*(1), 15. doi:10.1186/1742-9994-10-15

Riedel, A., Sagata, K., Surbakti, S., Tänzler, R., & Balke, M. (2013b). One hundred and one new species of *Trigonopterus* weevils from New Guinea. *ZooKeys*, *280*, 1–150. doi:10.3897/zookeys.280.3906

Riedel, A., Tänzler, R., Balke, M., Rahmadi, C., & Suhardjono, Y. R. (2014). Ninety-eight new species of *Trigonopterus* weevils from Sundaland and the Lesser Sunda Islands. *ZooKeys*, *467*, 1–162. doi:10.3897/zookeys.467.8206

Robinson, G. S., Ackery, P. R., Kitching, I. J., Beccaloni, G. W., & Hernández, L. M. (2010). *HOSTS—a Database of the World's Lepidopteran Hostplants*. London: Natural History Museum.

Schlick-Steiner, B. C., Steiner, F. M., Seifert, B., Stauffer, C., Christian, E., & Crozier, R. H. (2010). Integrative taxonomy: A multisource approach to exploring biodiversity. *Annual review of entomology*, *55*, 421–438. doi:10.1146/annurev-ento-112408-085432

Segar, S. T., Volf, M., Isua, B., Sisol, M., Redmond, C. M., Rosati, M. E., . . . Novotny, V. (2017). Variably hungry caterpillars: Predictive models and foliar chemistry suggest how to eat a rainforest. *Proceedings. Biological sciences*, *284*(1866). doi:10.1098/rspb.2017.1803

Srivathsan, A., Hartop, E., Puniamoorthy, J., Lee, W. T., Kutty, S. N., Kurina, O., & Meier, R. (2019). Rapid, large-scale species discovery in hyperdiverse taxa using 1d MinION sequencing. *bioRxiv*. doi:10.1101/622365

St Laurent, R. A., Hamilton, C. A., & Kawahara, A. Y. (2018). Museum specimens provide phylogenomic data to resolve relationships of sack-bearer moths (Lepidoptera, Mimallonoidea, Mimallonidae). *Systematic entomology*, *43*(4), 729–761. doi:10.1111/syen.12301

Toussaint, E. F. A., Breinholt, J. W., Earl, C., Warren, A. D., Brower, A. V., Yago, M., . . . Lohman, D. J. (2018). Anchored phylogenomics illuminates the skipper butterfly tree of life. *BMC evolutionary biology*, *18*(1), 101. doi:10.1186/s12862-018-1216-z

Wang, W. Y., Srivathsan, A., Foo, M., Yamane, S. K., & Meier, R. (2018). Sorting specimen-rich invertebrate samples with cost-effective NGS barcodes: Validating a reverse workflow for specimen processing. *Molecular ecology resources*, *18*(3), 490–501. doi:10.1111/1755-0998.12751

Wilson, E. O. (2017). Biodiversity research requires more boots on the ground. *Nature Ecology & Evolution*, *1*(11), 1590–1591. doi:10.1038/s41559-017-0360-y

Appendix A

Phylogeny, tribal classification and character evolution in Crambinae and Scopariinae (Lepidoptera: Pyraloidea)

Figure A.1: Uncorrected p-distances of the 3rd codon position for each gene plotted against the distance on the best scoring ML tree of conc6genes.

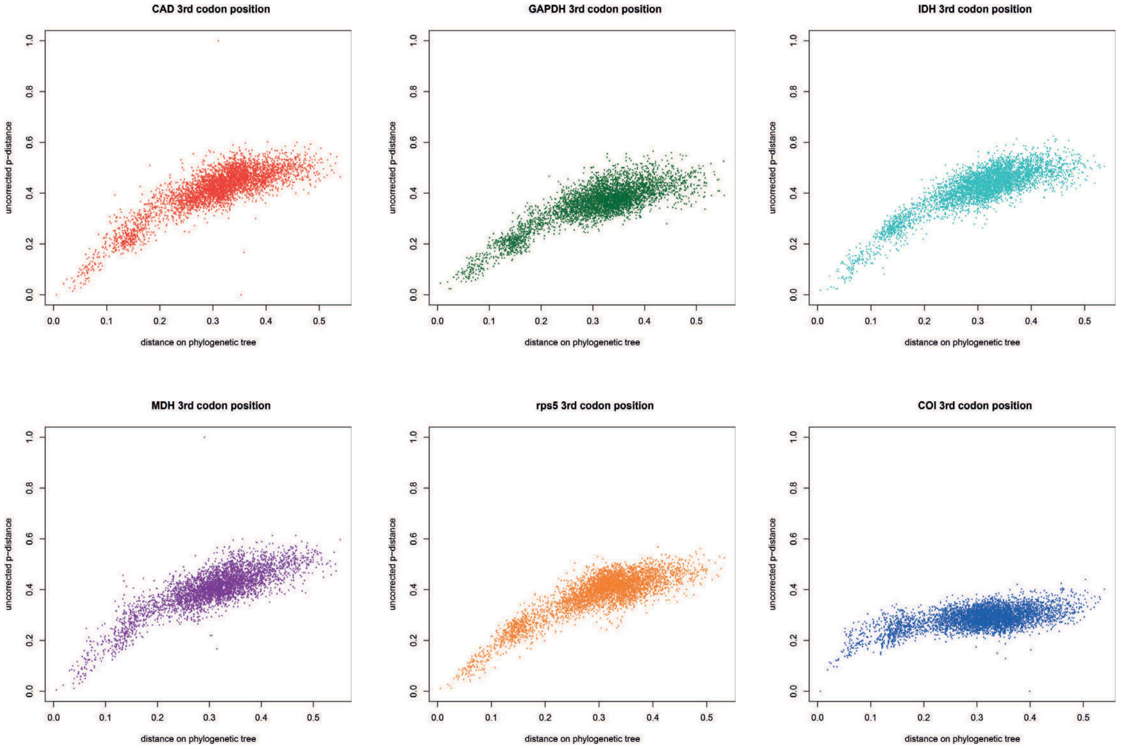


Figure A.2: Best-scoring ML tree of the whole dataset with best Partition Finder model applied and bootstrap support values from 1000 replicates displayed on nodes.

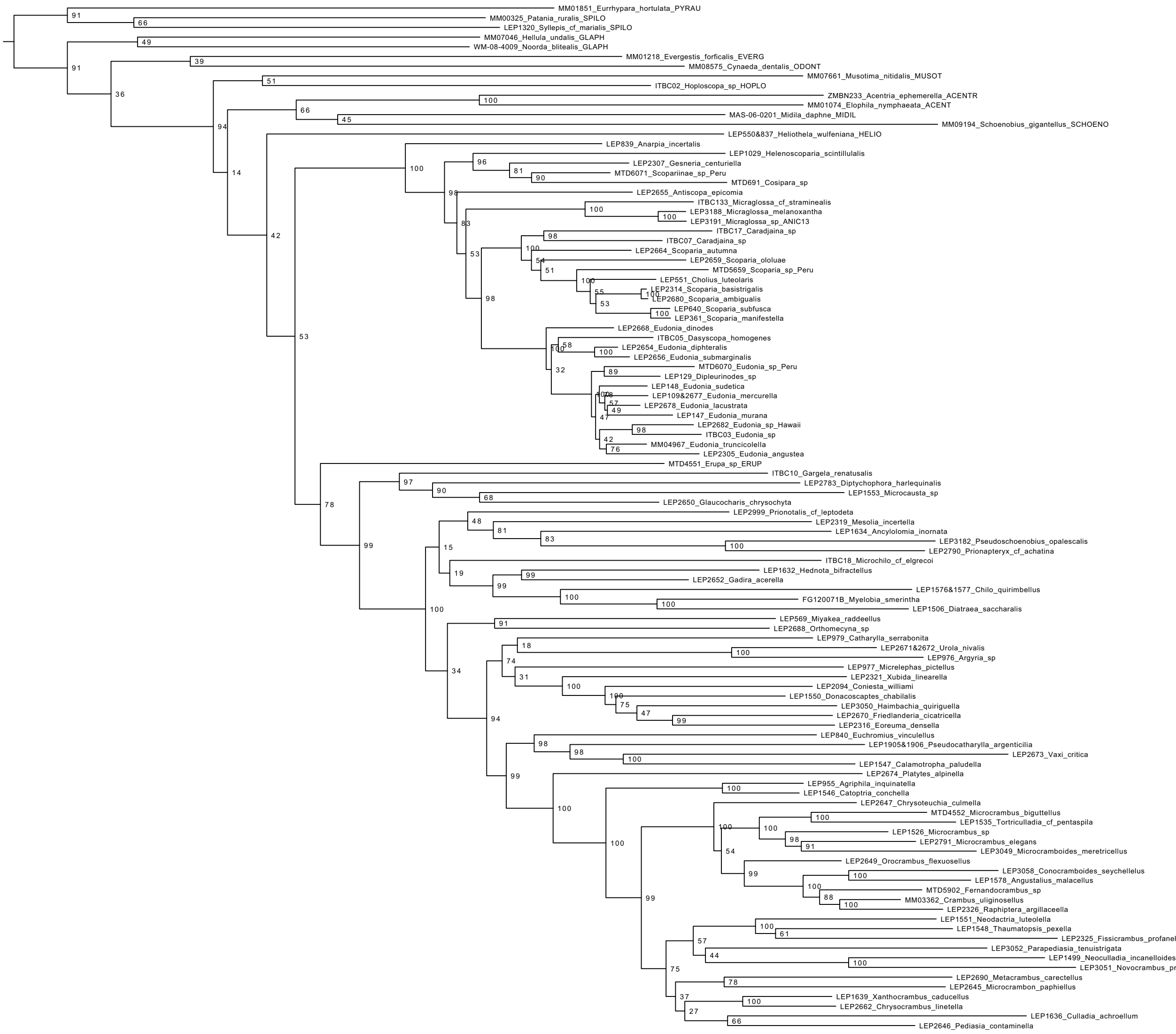


Figure A.3: Best-scoring ML tree of the conc6genes_COI1+2 dataset with the best Partition Finder model applied. Bootstrap support (1000 replicates) displayed above the nodes, posterior probabilities displayed below.

Figure A.4: Nodes numbers used for ace analyses (Table S6) plotted on best-scoring ML tree of the conc6genes dataset with best Partition Finder model applied.

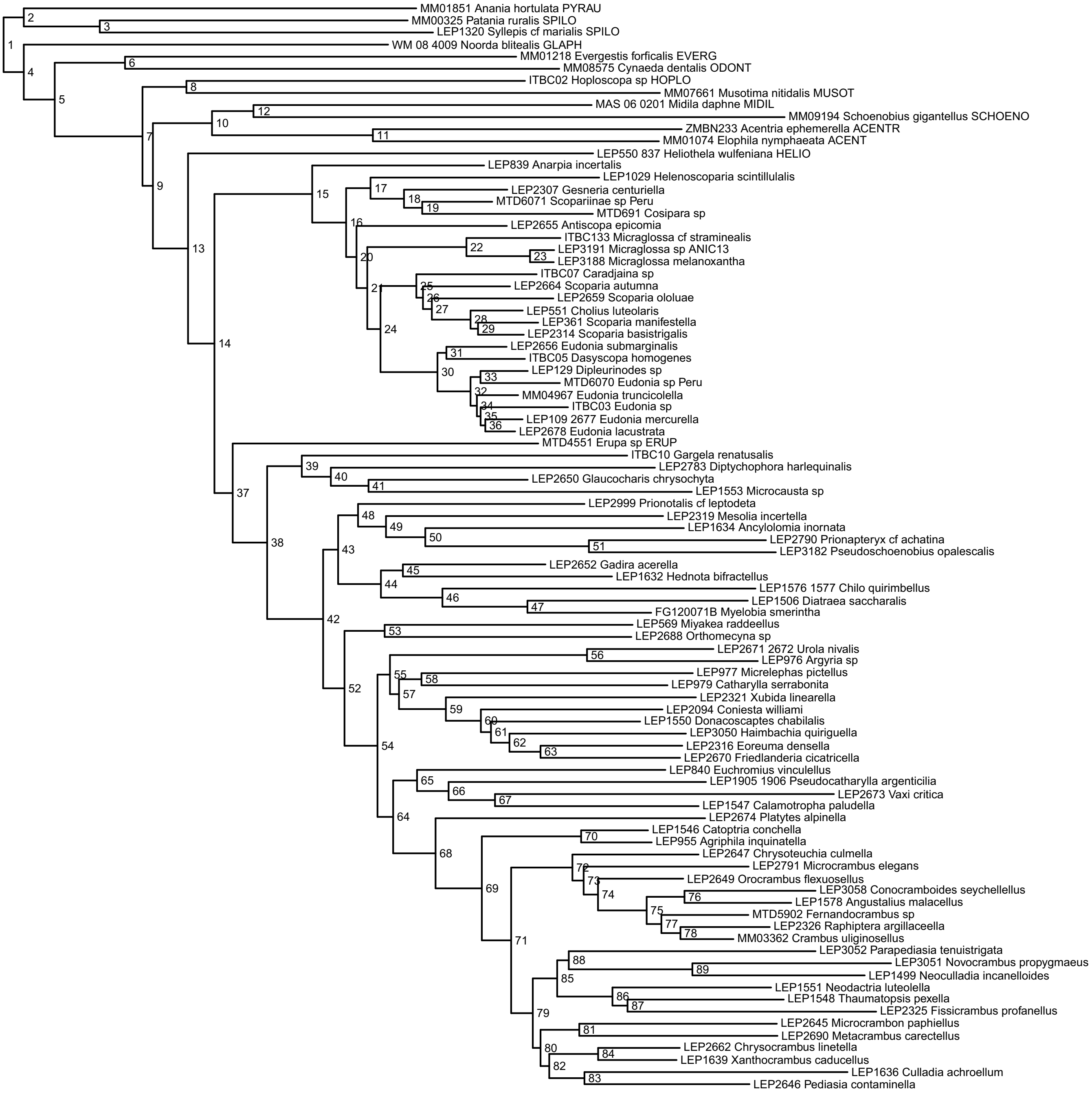


Table A.1: List of the 111 taxa sampled along with their access numbers at the European Nucleotide Archive (https://www.ebi.ac.uk/ena) for each gene. Subfamilial and tribal assignments follows the current classification (prior to this study) according to GLOBIZ (Nuss et al., 2018). The institute acronyms stand as follows: Muséum d'histoire naturelle de Genève (MHNG), Museum für Naturkunde der Humboldt-Universität Berlin (ZMHB), Senckenberg Museum für Tierkunde Dresden (SMTD), Tiroler Landesmuseum Ferdinandeum, Innsbruck (TLMF), Zoologische Staatsammlung München (ZSM).

	species	Voucher code	Locality	Depository / reference	Tissue used	CAD (795bp)	GAPDH (654bp)	IDH (678bp)	MDH (680bp)	rps5 (558bp)	COI 1st part (609bp)	COI 2nd part (743bp)
Acentropinae	Acentria ephemerella	ZMBN233	Germany	SMTD	abdomen	LR134540	X	LR134718	X	LR134888	LR135742	LR135742
	Elophila nymphaeata	MM01074	Finland	Mutanen et al., 2010	3-4 abdomen segments	GU828154	GU829784	GU830044	GU830363	GU830655	GU828657	GU828455
Erupini	Erupa sp.	MTD4551	Peru	SMTD	abdomen, dried	LR134543	LR134629	LR134721	LR134807	LR134890	LR214889	LR135659
Glaphyriinae	Evergestis forficalis	MM01218	Finland	Mutanen et al., 2010	abdomen	GU828159	GU829789	GU830049	GU830368	GU830659	GU828662	GU828460
	Hellula undalis	MM07046		Mutanen et al., 2010		KT713810	GU829851	GU830143	GU830459	X	X	GU929732
	Noorda blitealis	WM-08-4009	Namibia	Mutanen et al., 2010		KT713809	X	GU830246	GU830558	X	GU828868	GU929828
Heliothelinae	Heliothela wulfeniana	LEP550	Romania	SMTD	abdomen, dried	LR134541	LR134627	LR134719	X	X	LR214888	LR135658
	Heliothela wulfeniana	LEP837	Romania	SMTD	abdomen, dried	X	X	X	LR134805	X	X	X
	Hoploscopa sp.	ITBC02	Malaysia	SMTD	abdomen, alcohol	LR134542	LR134628	LR134720	LR134806	LR134889	LR135696	LR135696
Midilinae	Midila daphne	MAS-06-0201	Costa Rica	Mutanen et al., 2010		GU828074	X	GU829957	GU830284	GU830589	GU828567	GU828368
Musotiminae	Musotima nitidalis	MM07661	Australia	Mutanen et al., 2010	3 legs	GU828285	GU829888	GU830197	GU830515	GU830769	GU828816	GU929784

Continued on next page

Table A.1 – *Continued from previous page*

	species	Voucher code	Locality	Depository / reference	Tissue used	CAD (795bp)	GAPDH (654bp)	IDH (678bp)	MDH (680bp)	rps5 (558bp)	COI 1st part (609bp)	COI 2nd part (743bp)
Odontiinae	Cynaeda dentalis	MM08575	Finland	Mutanen et al., 2010	legs	GU828293	GU829894	GU830205	GU830522	X	GU828824	GU929791
Pyraustinae	Anania hortulata	MM01851	Finland	Mutanen et al., 2010	piece of abdomen	GU828170	GU829798	GU830062	GU830380	GU830669	GU828675	GU828472
Schoenobiinae	Schoenobius gigantellus	MM09194	Finland	Mutanen et al., 2010	legs	GU828306	GU829903	GU830222	GU830533	GU830790	GU828842	GU929806
Spilomelinae	Patania ruralis	MM00325	Finland	Mutanen et al., 2010	Head + 2 legs	GU828133	GU829772	GU830021	GU830342	GU830638	GU828634	GU828432
	Syllepis cf. marialis	LEP1320	Bolivia	SMTD	abdomen, dried	LR134539	LR134626	LR134717	X	LR134887	LR135741	LR135741
Crambinae	Ancylolomia inornata	LEP1634	Italy	Coll. G. Baldizzone	abdomen, dried	LR134562	LR134649	LR134739	LR134826	X	LR214893	LR135663
	Diatraea saccharalis	LEP1506	Bolivia	MHNG	abdomen, dried	LR134551	LR134637	LR134729	LR134815	LR134898	LR135701	LR135701
	Gadira acerella	LEP2652	New Zealand	MHNG	abdomen, dried	LR134577	LR134664	LR134754	LR134841	LR134923	LR214900	LR135670
	Gargela renatusalis	ITBC10	Malaysia	MHNG	abdomen, alcohol	LR134596	LR134683	LR134773	LR134860	LR134943	LR135729	LR135729
	Hednota bifractellus	LEP1632	Australia	ZSM	abdomen, dried	LR134561	LR134648	X	LR134825	LR134909	LR135708	LR135708
	Orthomecyna sp.	LEP2688	USA	MHNG	abdomen, dried	LR134583	LR134670	LR134760	LR134847	LR134929	LR135722	LR135722
	Prionotalis cf. leptodeta	LEP2999	Angola	SMTD	abdomen, alcohol	LR134587	LR134675	LR134764	LR134851	LR134934	LR135743	LR135743

Continued on next page

Table A.1 – *Continued from previous page*

	species	Voucher code	Locality	Depository / reference	Tissue used	CAD (795bp)	GAPDH (654bp)	IDH (678bp)	MDH (680bp)	rps5 (558bp)	COI 1st part (609bp)	COI 2nd part (743bp)
Argyriini	Argyria sp.	LEP976	Brazil	MHNG	thorax, alcohol	LR134547	LR134633	LR134725	LR134811	LR134894	HG793013	HG793013
	Catharylla serrabonita	LEP979	Brazil	MHNG	thorax, alcohol	LR134549	LR134635	LR134727	LR134813	LR134896	HG793017	HG793018
	Pseudocatharylla argenticilia	LEP1905	Angola	SMTD	abdomen, dried	LR134565	LR134652	LR134742	LR134829	LR134911	X	X
Argyriini	Pseudocatharylla argenticilia	LEP1906	Angola	SMTD	abdomen, dried	X	X	X	X	X	LR214894	LR135664
	Urola nivalis	LEP2671	Canada	MHNG	abdomen, alcohol	LR134580	LR134667	LR134757	X	LR134926	LR135719	LR135719
	Urola nivalis	LEP2672	Canada	MHNG	abdomen, alcohol	X	X	X	LR134844	X	X	X
	Vaxi critica	LEP2673	Canada	MHNG	abdomen, alcohol	LR134581	LR134668	LR134758	LR134845	LR134927	LR135720	LR135720
Calamotrophini	Calamotropha paludella	LEP1547	Switzerland	MHNG	abdomen, alcohol	LR134554	LR134641	LR134732	LR134818	LR134902	LR135703	LR135703
Chiloini	Chilo quirimbellus	LEP1576	Angola	SMTD	abdomen, dried	X	LR134646	X	X	LR134907	LR135706	LR135706
	Chilo quirimbellus	LEP1577	Angola	SMTD	abdomen, dried	LR134559	X	LR134737	LR134823	X	X	X
Crambini	Agriphila inquinatella	LEP955	Germany	SMTD	abdomen, dried	LR134546	LR134632	LR134724	LR134810	LR134893	LR135699	LR135699
	Angustalius malacellus	LEP1578	Angola	SMTD	abdomen, dried	LR134560	LR134647	LR134738	LR134824	LR134908	LR135707	LR135707
	Catoptria conchella	LEP1546	Italy	MHNG	abdomen, alcohol	LR134553	LR134640	LR134731	LR134817	LR134901	LR214890	LR135660
	Chrysocrambus linetella	LEP2662	Switzerland	MHNG	abdomen, dried	LR134578	LR134665	LR134755	LR134842	LR134924	LR135717	LR135717
	Chrysoteuchia culmella	LEP2647	France	MHNG	abdomen, alcohol	LR134574	LR134661	LR134751	LR134838	LR134920	LR135714	LR135714
	Conocramboides seychellellus	LEP3058	La Réunion	J. Rochat	abdomen, alcohol	LR134592	LR134680	LR134769	LR134856	LR134939	LR214902	LR135672

Continued on next page

Table A.1 – *Continued from previous page*

	species	Voucher code	Locality	Depository / reference	Tissue used	CAD (795bp)	GAPDH (654bp)	IDH (678bp)	MDH (680bp)	rps5 (558bp)	COI 1st part (609bp)	COI 2nd part (743bp)
Crambini	Crambus uliginosellus	MM03362	Finland	Mutanen et al., 2010	2 legs	GU828182	GU829811	GU830078	GU830395	GU830681	GU828691	GU828487
	Culladia achroellum	LEP1636	La Réunion	MHNG	abdomen, alcohol	LR134563	LR134650	LR134740	LR134827	X	LR135709	LR135709
	Euchromius vinculellus	LEP840	Morocco	SMTD	abdomen, dried	LR134545	LR134631	LR134723	LR134809	LR134892	LR135698	LR135698
	Fernandocrambus sp.	MTD5902	Peru	SMTD	abdomen, dried	LR134595	LR134682	LR134772	LR134859	LR134942	LR214905	LR135675
	Fissicrambus profanellus	LEP2325	USA	SMTD	abdomen, alcohol	LR134570	LR134657	LR134747	LR134834	LR134916	LR214897	LR135667
	Metacrambus carectellus	LEP2690	Italy	MHNG	abdomen, dried	X	LR134671	X	LR134848	LR134930	X	X
	Micrelephas pictellus	LEP977	Brazil	MHNG	thorax, alcohol	LR134548	LR134634	LR134726	LR134812	LR134895	HG793012	HG793012
	Microcramboides meretricellus	LEP3049	Nicaragua	MHNG	abdomen, dried	LR134588	LR134676	LR134765	LR134852	LR134935	LR135725	LR135725
	Microcrambon paphiellus	LEP2645	La Réunion	MHNG	abdomen, alcohol	LR134572	LR134659	LR134749	LR134836	LR134918	LR214898	LR135668
	Microcrambus biguttellus	MTD4552	USA	SMTD	abdomen, dried	LR134594	LR134681	LR134771	LR134858	LR134941	LR214904	LR135674
	Microcrambus elegans	LEP2791	Canada	MHNG	abdomen, alcohol	LR134586	LR134674	LR134763	LR134850	LR134933	LR135724	LR135724
	Microcrambus sp.	LEP1526	Bolivia	MHNG	abdomen, dried	X	LR134638	X	X	LR134899	X	X
	Miyakea raddeellus	LEP569	China	SMTD	abdomen, dried	LR134544	LR134630	LR134722	LR134808	LR134891	LR135697	LR135697
	Neoculladia incanelloides	LEP1499	Bolivia	MHNG	abdomen, dried	LR134550	LR134636	LR134728	LR134814	LR134897	LR135700	LR135700
	Neodactria luteolella	LEP1551	Canada	MHNG	abdomen, alcohol	LR134557	LR134644	LR134735	LR134821	LR134905	LR214891	LR135661
	Novocrambus propygmaeus	LEP3051	Nicaragua	MHNG	abdomen, dried	LR134590	LR134678	LR134767	LR134854	LR134937	LR135727	LR135727
	Orocrambus flexuosellus	LEP2649	New Zealand	MHNG	abdomen, dried	LR134575	LR134662	LR134752	LR134839	LR134921	LR135715	LR135715
	Parapediasia tenuistrigata	LEP3052	Nicaragua	MHNG	abdomen, dried	LR134591	LR134679	LR134768	LR134855	LR134938	LR135728	LR135728
	Pediasia contaminella	LEP2646	Switzerland	MHNG	abdomen, alcohol	LR134573	LR134660	LR134750	LR134837	LR134919	LR214899	LR135669

Continued on next page

Table A.1 – *Continued from previous page*

	species	Voucher code	Locality	Depository / reference	Tissue used	CAD (795bp)	GAPDH (654bp)	IDH (678bp)	MDH (680bp)	rps5 (558bp)	COI 1st part (609bp)	COI 2nd part (743bp)
Crambini	Platytes alpinella	LEP2674	Hungary	MHNG	abdomen, alcohol	LR134582	LR134669	LR134759	LR134846	LR134928	LR135721	LR135721
	Raphiptera argillaceella	LEP2326	USA	SMTD	abdomen, alcohol	LR134571	LR134658	LR134748	LR134835	LR134917	LR135713	LR135713
	Thaumatopsis pexella	LEP1548	Canada	MHNG	abdomen, alcohol	LR134555	LR134642	LR134733	LR134819	LR134903	LR135704	LR135704
	Tortriculladia cf. pentaspila	LEP1535	Brazil	MHNG	abdomen, dried	LR134552	LR134639	LR134730	LR134816	LR134900	LR135702	LR135702
	Xanthocrambus caducellus	LEP1639	Switzerland	MHNG	abdomen, alcohol	LR134564	LR134651	LR134741	LR134828	LR134910	LR135710	LR135710
Diptychophorini	Diptychophora harlequinalis	LEP2783	USA	MHNG	abdomen, alcohol	LR134584	LR134672	LR134761	LR134849	LR134931	LR135723	LR135723
	Glaucocharis chrysochyta	LEP2650	New Zealand	MHNG	abdomen, dried	LR134576	LR134663	LR134753	LR134840	LR134922	LR135716	LR135716
	Microcausta sp.	LEP1553	French Guiana	MHNG	abdomen, alcohol	LR134558	LR134645	LR134736	LR134822	LR134906	LR214892	LR135662
	Microchilo cf. elgrecoi	ITBC18	Malaysia	MHNG	abdomen, dried	LR134597	LR134684	LR134774	LR134861	LR134944	LR135730	LR135730
Haimbachiini	Coniesta williami	LEP2094	Angola	SMTD	abdomen, dried	LR134566	LR134653	LR134743	LR134830	LR134912	LR214895	LR135665
	Donacoscaptes chabilalis	LEP1550	Brazil	MHNG	abdomen, alcohol	LR134556	LR134643	LR134734	LR134820	LR134904	LR135705	LR135705
	Eoreuma densella	LEP2316	USA	SMTD	abdomen, alcohol	LR134567	LR134654	LR134744	LR134831	LR134913	LR135711	LR135711
	Friedlanderia cicatricella	LEP2670	France	MHNG	abdomen, dried	LR134579	LR134666	LR134756	LR134843	LR134925	LR135718	LR135718
	Haimbachia quiriguella	LEP3050	Nicaragua	MHNG	abdomen, dried	LR134589	LR134677	LR134766	LR134853	LR134936	LR135726	LR135726
	Xubida linearella	LEP2321	USA	SMTD	abdomen, alcohol	LR134569	LR134656	LR134746	LR134833	LR134915	LR135712	LR135712
Myelobiini	Myelobia smerintha	FG120071B	French Guiana	Kawahara & Breinholt, 2014	thorax		SRS620579	SRS620579	SRS620579	SRS620579	SRS620579	SRS620579

Continued on next page

Table A.1 – *Continued from previous page*

	species	Voucher code	Locality	Depository / reference	Tissue used	CAD (795bp)	GAPDH (654bp)	IDH (678bp)	MDH (680bp)	rps5 (558bp)	COI 1st part (609bp)	COI 2nd part (743bp)
Prionapterygini	Mesolia incertella	LEP2319	USA	SMTD	abdomen, alcohol	LR134568	LR134655	LR134745	LR134832	LR134914	LR214896	LR135666
	Prionapteryx cf. achatina	LEP2790	USA	MHNG	abdomen, alcohol	LR134585	LR134673	LR134762	X	LR134932	LR214901	LR135671
	Pseudoschoenobius opalescalis	LEP3182	USA	E. Metzler	abdomen, dried	LR134593	X	LR134770	LR134857	LR134940	LR214903	LR135673
Scopariinae	Anarpia incertalis	LEP839	Morocco	SMTD	abdomen, dried	LR134604	LR134692	LR134782	LR134868	LR134951	LR214906	LR135676
	Antiscopa epicomia	LEP2655	New Zealand	MHNG	abdomen, dried	LR134610	LR134698	LR134787	LR134872	LR134956	LR214911	LR135681
	Caradjaina sp.	ITBC07	Malaysia	SMTD	abdomen, alcohol	LR134623	LR134714	LR134802	LR134885	LR134973	LR135740	LR135740
	Caradjaina sp.	ITBC17	Malaysia	SMTD	abdomen, dried	LR134624	LR134715	LR134803	LR134886	LR134974	LR214926	LR135694
	Cholius luteolaris	LEP551	Romania	SMTD	abdomen, dried	LR134602	LR134690	LR134780	LR134866	LR134949	LR135735	LR135735
	Cosipara sp.	MTD691	Peru	SMTD	abdomen, dried	LR134618	LR134708	LR134796	LR134880	LR134967	LR214922	LR135690
	Dasyscopa homogenes	ITBC05	Malaysia	SMTD	abdomen, alcohol	LR134622	LR134713	LR134801	LR134884	LR134972	LR135739	LR135739
	Dipleurinodes sp.	LEP129		ZMHB	abdomen, dried	X	LR134686	LR134776	LR134862	LR134945	X	X
	Eudonia angustea	LEP2305	France	SMTD	abdomen, dried	LR134606	LR134694	LR134783	X	LR134952	LR214907	LR135677
	Eudonia dinodes	LEP2668	New Zealand	MHNG	abdomen, dried	LR134614	LR134702	LR134791	LR134875	LR134960	LR214915	LR135684
	Eudonia diphteralis	LEP2654	New Zealand	MHNG	abdomen, dried	LR134609	LR134697	LR134786	LR134871	LR134955	LR214910	LR135680
	Eudonia lacustrata	LEP2678	Bulgaria	SMTD	abdomen, dried	LR134615	LR134703	LR134792	LR134877	LR134962	LR214917	LR135686
	Eudonia mercurella	LEP109	Germany	SMTD	whole voucher, dried	LR134598	LR134685	LR134775	X	X	LR135731	LR135731
	Eudonia mercurella	LEP2677	Germany	SMTD	abdomen, dried	X	X	X	LR134876	LR134961	LR214916	LR135685
	Eudonia murana	LEP147		SMTD	abdomen, dried	LR134599	LR134687	LR134777	LR134863	LR134946	LR135732	LR135732

Continued on next page

Table A.1 – *Continued from previous page*

	species	Voucher code	Locality	Depository / reference	Tissue used	CAD (795bp)	GAPDH (654bp)	IDH (678bp)	MDH (680bp)	rps5 (558bp)	COI 1st part (609bp)	COI 2nd part (743bp)
Scopariinae	Eudonia sp.	LEP2682	USA	MHNG	abdomen, alcohol	X	LR134705	X	X	LR134964	LR214919	LR135688
	Eudonia sp.	MTD6070	Peru	SMTD	abdomen, dried	X	LR134709	LR134797	LR134881	LR134968	LR214923	LR135691
	Eudonia sp.	ITBC03	Malaysia	SMTD	abdomen, alcohol	LR134621	LR134712	LR134800	LR134883	LR134971	LR135738	LR135738
	Eudonia submarginalis	LEP2656	New Zealand	MHNG	abdomen, dried	LR134611	LR134699	LR134788	X	LR134957	LR214912	LR135682
	Eudonia sudetica	LEP148	Austria	SMTD	abdomen, dried	LR134600	LR134688	LR134778	LR134864	LR134947	LR135733	LR135733
	Eudonia truncicolella	MM04967	Finland	Mutanen et al., 2010	legs	GU828197	GU829823	GU830095	GU830413	GU830697	GU828709	GU828504
	Gesneria centuriella	LEP2307	Canada	MHNG	abdomen, dried	LR134607	LR134695	LR134784	LR134869	LR134953	LR214908	LR135678
	Helenoscoparia scintillulalis	LEP1029	St-Helena	SMTD	abdomen, dried	LR134605	LR134693	X	X	X	LR135737	LR135737
	Micraglossa cf. stramineralis	ITBC133	Malaysia	SMTD	abdomen, dried	LR134625	LR134716	LR134804	X	LR134975	LR214927	LR135695
	Micraglossa sp.	LEP3188	Australia	SMTD	abdomen, alcohol	LR134617	LR134706	LR134794	LR134879	LR134965	LR214920	X
	Scoparia ambigualis	LEP3191	Australia	SMTD	abdomen, dried	X	LR134707	LR134795	X	LR134966	LR214921	LR135689
	Scoparia autumna	LEP2680	Germany	SMTD	abdomen, dried	LR134616	LR134704	LR134793	LR134878	LR134963	LR214918	LR135687
	Scoparia basistrigalis	LEP2664	New Zealand	MHNG	abdomen, dried	LR134613	LR134701	LR134790	LR134874	LR134959	LR214914	LR135683
	Scoparia manifestella	LEP2314	Germany	SMTD	abdomen, dried	LR134608	LR134696	LR134785	LR134870	LR134954	LR214909	LR135679
	Scoparia melanoxantha	LEP361	Italy	TLMF	abdomen, dried	LR134601	LR134689	LR134779	LR134865	LR134948	LR135734	LR135734
	Scoparia ololuae	LEP2659	Kenya	D. Agassiz Coll.	abdomen, dried	LR134612	LR134700	LR134789	LR134873	LR134958	LR214913	X
	Scoparia sp.	MTD5659	Peru	SMTD	abdomen, dried	LR134620	LR134711	LR134799	X	LR134970	LR214925	LR135693
	Scoparia subfusca	LEP640	Romania	SMTD	abdomen, dried	LR134603	LR134691	LR134781	LR134867	LR134950	LR135736	LR135736
	Scopariinae sp.	MTD6071	Peru	SMTD	abdomen, dried	LR134619	LR134710	LR134798	LR134882	LR134969	LR214924	LR135692

Table A.2: PCR primers used. PCR product length for newly designed nested primers refer to the PCR product obtained with the corresponding standard primer from Wahlberg & Wheat (2008).

Gene	Primer	Direction	Sequence (5' -¿ 3')	Annealing temperature	PCR product length (bp)	Reference
GAPDH	Frigga	Forward	AARGCTGGRGCTGAATATGT	55	691	Wahlberg & Wheat, 2008
GAPDH	Burre	Reverse	GWTTGAATGTACTTGATRAGRTC	55	691	Wahlberg & Wheat, 2008
GAPDH	GAPDHf96	Forward	YTCYTGCACYACCAACTG	55	508	this study
GAPDH	GAPDHr610	Reverse	TCRTTGTCRTACCARCTGAT	55	646	this study
RpS5	RpS5f	Forward	ATGGCNGARGARAAYTGGAAYGA	55	613	Wahlberg & Wheat, 2008
RpS5	RpS5r	Reverse	CGGTTRGAYTTRGCAACACG	55	613	Wahlberg & Wheat, 2008
RpS5	RpS5f3	Forward	GAYATTCCYGAAATCAAACT	55	535	this study
RpS5	RpS5r538	Reverse	TCCARCTCRTCCTTYTTYTT	55	592	this study
IDH	IDHdeg27F	Forward	GGWGAYGARATGACNAGRATHATHTGG	55	711	Wahlberg & Wheat, 2008
IDH	IDHdegR	Reverse	TTYTTRCAIGCCCANACRAANCCNCC	55	711	Wahlberg & Wheat, 2008
IDH	IDHf169	Forward	ATGTGGAARAGYCCYAATGG	53	490	this study
IDH	IDHr626	Reverse	CAATCARYCTRTGCTCATACC	53	658	this study
MDH	MDHf	Forward	GAYATNGCNCCNATGATGGGNGT	55	733	Wahlberg & Wheat, 2008
MDH	MDHr	Reverse	AGNCCYTCNACDATYTTCCAYTT	55	733	Wahlberg & Wheat, 2008
MDH	MDHf73	Forward	GCYATGCCYAGAAGAGAAGG	55	595	this study
MDH	MDHr490	Reverse	ACAGCWGCACCWCKCTTRTG	55	535	this study
CAD	CAD743f	Forward	GGNGTNACNACNGCNTGYTTYGARCC	55	850	Wahlberg & Wheat, 2008
CAD	CAD1028r	Reverse	TTRTTNGGNARYTGNCCNCCCAT	55	850	Wahlberg & Wheat, 2008
CAD	CADf19	Forward	AGYTCNATGAAAAGYGTNGG	55	754	this study
CAD	CADr604	Reverse	CATCCHACWGCACACCAATC	55	661	this study
COI	LCO	Forward	GGTCAACAAATCATAAAGATATTGG	50	676	Wahlberg & Wheat, 2008
COI	Nancy	Reverse	CCTGGTAAAATTAAAATATAAACTTC	50	676	Simon & al., 1994
COI	Jerry	Forward	CAACAYTTATTTTGATTTTTTGG	50	829	Wahlberg & Wheat, 2008
COI	Pat	Reverse	ATCCATTACATATAATCTGCCATA	50	829	Wahlberg & Wheat, 2008

Table A.3: PCR mix adapted from Wahlberg & Wheat (2008).

Reagents	20 μ l reaction (without Hi-Spec Additive)	20 μ l reaction (with Hi-Spec Additive)
H2O (ultraclean)	11.5	10.5
10x OptiBuffer	2	2
MgCl2 (50 mM)	1	1
F primer (10 pmol/μ l)	2	2
R primer (10 pmol/μ l)	2	2
5xHi Spec. Additive	-	1
dNTP (each 10 mM)	0.4	0.4
BIO-X-ACT Short Taq DNA polymerase (4u/μ l)	0.12	0.12
DNA (μ l)	1	1

Table A.4: PCR programs adapted from Wahlberg & Wheat (2008) and Regier (2007).

Program	Steps	Temperature	Time
Wahlberg & Wheat (2008)	initial	95°C	5 min
	38 cycles	95°C	30 sec
		50-55°C (see primer pair)	40 sec
		72°C	1 min 30 sec
	final	72°C	10 min
	cooling	8°C	∞
Touchdown (Regier, 2007)	38 cycles	95°C	30 sec
		55°C, -0,4°C/cycle	30 sec
		70°C	1 min, +2 sec/cycle
		Go to 1, 24x	
		95°C	30 sec
		45°C	30 sec
		70°C	2 min, + 3 sec/cycle
		Go to 5, 12x	
	final	70°C	10 min
	cooling	8°	∞

Table A.5: Character states matrix

char. N°	character description	Anania hortulata	Syllepis cf marialis	Patania ruralis	Noorda blitealis	Cynaeda dentalis	Evergestis forficalis	Musotima nitidalis	Hoploscopa sp.
1	Forewing Rs veins	0	?	0	0	0	0	?	0
2	Forewing Rs4 vein	0	?	0	0	0	0	?	0
3	Forewing distal margin	0	0	0	0	0	0	0	0
4	Hindwing M1 - Sc+R connection	0	?	0	0	0	0	0	0
5	Hindwing cell	0	?	0	0	0	0	0	0
6	Hindwing M2-M3-CuA1-CuA2	0	?	0	0	0	0	0	0
7	Tympanic pockets	?	1	1	0	0	0	0	0
8	Venulae secundae	?	0	1	0	0	1	0	0
9	Uncus	0	0	0	0	0	0	0	0
10	Gnathos arms projection	0	0	1	0	0	0	0	0
11	Gnathos tip	1	1	2	1	1	1	1	0
12	Valva ventral process	0	0	0	0	0	0	1	0
13	Pseudosaccus	0	0	0	0	0	0	0	0
14	Juxta	0	0	0	0	0	0	1	0
15	Attachment of the aedeagus	0	0	?	0	0	0	1	0
16	Opening of the ductus ejaculatorius	0	0	0	0	0	0	1	0
17	Cornuti	0	0	1	0	1	0	1	0
18	Papillae anales dorsal connection	0	0	0	0	1	0	0	0
19	Papillae anales shape	0	0	0	0	0	0	0	0
20	Posterior apophyses	0	0	0	0	0	0	0	0
21	Setation on segment VIII	0	0	0	0	0	0	0	0
22	Intersegmental membrane VIII-IX structure	0	0	0	0	0	0	1	1
23	Colliculum	0	0	0	0	0	0	0	0
24	Ductus bursae	1	0	1	0	0	0	0	0
25	Signum on corpus bursae	1	1	1	?	0	2	1	1
26	Corpus bursae wall structure	0	0	0	0	0	0	0	0
27	Appendix bursae	1	1	0	0	0	0	0	0

Continued on next page

Table A.5 – *Continued from previous page*

char. N°	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27
Elophila nymphaeata	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
Acentria ephemerella	0	0	0	?	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Schoenobius gigantellus	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Midila daphne	0	1	0	0	0	0	0	0	1	0	1	0	0	0	?	0	1	0	0	0	0	?	0	0	0	0	0
Heliothela wulfeniana	0	0	0	0	?	?	0	0	0	0	0	?	0	1	?	?	?	0	0	0	0	0	0	0	1	0	0
Anarpia incertalis	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	?	0	1	0	0
Helenoscoparia scintillulalis	0	0	0	0	0	0	0	1	0	0	0	0	0	0	?	0	1	0	0	0	0	0	?	0	0	0	0
Gesneria centuriella	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Cosipara sp.	0	0	0	0	1	0	0	0	0	1	2	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0
Scopariinae sp. Peru	?	?	?	?	?	?	0	0	0	0	1	0	0	0	0	0	0	?	?	?	?	?	?	?	?	?	?
Antiscopa epicomia	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
Micraglossa cf straminealis	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Micraglossa melanoxantha	0	0	0	0	0	0	0	0	?	?	?	?	?	?	?	?	?	0	0	0	0	0	?	0	1	1	0
Micraglossa sp. ANIC13	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	?	?	?	?	?	?	?	?	?	?
Caradjaina sp.	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1
Scoparia autumna	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	?	0	0	1	1
Scoparia ololuae	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	0	0	0	0	0	1	1	1	1
Cholius luteolaris	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0

Continued on next page

Table A.5 – *Continued from previous page*

char. N°	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27
Scoparia basistrigalis	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Scoparia manifestella	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Dasyscopa homogenes	0	0	0	0	0	0	0	0	?	?	?	?	?	?	?	?	?	0	0	0	0	0	1	1	1	0	1
Eudonia submarginalis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1	1	1	1
Eudonia sp. Peru	0	0	0	0	0	0	?	?	0	0	0	0	0	0	0	0	1	?	?	?	?	?	?	?	?	?	?
Dipleurinodes sp.	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	1	1	1	1	1
Eudonia truncicolella	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	?	1	1	1	1
Eudonia sp. (ITBC03)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	?	1	1	1
Eudonia lacustrata	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	1	1	1	1	1
Eudonia mercurella	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1	1	1	1
Erupa sp.	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0
Gargela renatusalis	0	0	0	1	0	0	0	0	0	0	0	0	0	1	?	0	0	0	0	0	0	0	0	0	2	?	0
Diptychophora harlequinalis	1	0	0	1	0	0	0	0	0	0	0	0	0	1	1	0	1	1	0	0	0	0	0	0	1	0	0
Microcausta sp.	1	0	0	1	0	1	1	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0
Glaucocharis chrysochyta	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0
Hednota bifractellus	0	0	0	1	0	0	1	1	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Gadira acerella	0	0	0	1	0	0	1	1	0	0	0	0	1	1	1	0	0	1	0	0	0	0	0	0	0	0	0
Chilo quirimbellus	0	0	0	0	0	0	1	1	0	0	0	0	1	1	1	0	1	0	0	0	0	0	0	0	1	0	0

Continued on next page

Table A.5 – *Continued from previous page*

char. N°	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27
Myelobia smerintha	0	0	0	0	0	0	0	1	0	0	0	0	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0
Diatraea saccharalis	0	0	0	0	0	0	0	1	0	0	0	0	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0
Prionotalis cf leptodeta	0	0	0	?	?	?	0	0	0	0	1	0	1	0	1	1	1	1	0	0	0	0	0	0	?	0	0
Mesolia incertella	0	1	1	1	0	0	1	0	1	1	?	1	1	0	?	1	0	0	0	0	0	0	0	0	0	0	0
Ancylolomia inornata	0	1	0	1	0	0	1	0	0	0	1	0	1	0	0	1	1	1	0	0	0	0	0	0	0	0	0
Pseudoschoenobius opalescalis	0	0	1	1	0	1	1	0	0	1	?	1	0	?	1	1	0	0	1	0	0	0	0	0	0	0	0
Prionapteryx cf achatina	0	0	1	1	0	1	1	0	0	1	?	1	0	?	1	1	0	0	1	0	0	1	0	0	0	0	0
Orthomecyna sp.	0	0	0	1	0	1	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	?	0	0
Miyakea raddeellus	0	0	0	1	0	0	1	0	0	0	0	0	0	0	1	1	0	1	0	0	0	0	0	0	0	0	0
Argyria sp.	0	0	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Urola nivalis	0	0	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Catharylla serrabonita	0	1	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0
Micrelephas pictellus	0	0	0	0	1	0	1	0	0	0	0	0	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0
Xubida linearella	0	0	0	0	1	0	0	1	0	0	0	0	0	0	1	0	1	0	0	1	0	0	0	0	0	0	0
Coniesta williami	0	0	0	0	1	0	0	1	1	0	0	?	?	?	1	?	?	0	0	1	1	1	0	0	1	0	0
Donacoscaptes chabilalis	0	0	0	0	1	0	0	1	1	0	0	0	0	0	1	0	0	0	0	0	1	1	0	0	0	0	0
Haimbachia quiriguella	0	0	0	0	1	0	0	1	1	0	0	0	0	0	1	0	1	0	0	1	1	1	0	0	?	0	0

Continued on next page

Table A.5 – *Continued from previous page*

char. N°	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27
Friedlanderia cicatricella	0	0	0	?	1	?	0	1	1	0	0	0	0	0	1	0	1	0	0	1	0	0	0	0	0	0	0
Eoreuma densella	0	0	0	0	1	0	0	1	1	0	0	0	0	0	1	0	1	0	0	1	1	1	0	0	0	0	0
Euchromius vinculellus	0	0	0	0	1	0	1	0	0	0	1	0	1	0	1	0	0	1	0	0	0	0	0	0	0	0	0
Pseudocatharylla argenticilia	0	1	0	0	1	0	1	0	0	0	0	0	1	0	?	0	0	0	0	0	0	0	0	0	0	0	0
Calamotropha paludella	0	1	0	0	0	0	1	1	0	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	1	0	0
Vaxi critica	0	1	0	0	1	0	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Platytes alpinella	1	2	0	0	1	1	1	0	0	0	1	0	1	?	1	0	1	1	0	1	0	0	0	0	2	0	0
Agriphila inquinatella	0	1	0	0	1	0	1	0	0	0	1	0	1	0	1	0	0	1	0	0	0	0	0	0	1	0	0
Catoptria conchella	0	1	0	0	1	0	1	0	0	0	1	0	1	0	1	0	1	1	0	0	0	0	0	0	1	0	0
Chrysoteuchia culmella	0	1	0	0	1	0	1	0	0	0	1	0	1	0	1	0	0	1	0	0	0	0	0	0	2	0	0
Microcrambus elegans	0	1	0	0	1	0	1	0	0	0	1	0	1	0	1	0	0	1	0	1	0	0	0	0	0	0	0
Orocrambus flexuosellus	0	1	0	0	1	0	1	1	0	0	1	0	1	?	1	0	1	1	0	0	0	0	0	0	2	0	0
Angustalius malacellus	0	1	0	0	1	0	1	0	0	1	?	0	1	?	1	0	0	1	0	?	0	0	0	0	2	0	0
Conocramboides seychellellus	0	1	0	0	1	0	1	0	0	0	1	0	1	0	1	0	0	1	0	0	0	0	0	0	1	0	0
Fernandocrambus sp.	1	2	0	0	1	0	1	1	0	0	1	0	1	0	1	0	0	1	0	0	0	0	0	0	2	0	0
Crambus uliginosellus	0	1	0	0	1	0	1	0	0	0	1	1	1	0	1	0	0	1	0	0	0	0	0	0	2	0	0
Raphiptera argillaceella	2	2	0	0	1	1	1	0	0	2	2	0	1	0	1	0	1	1	0	0	0	0	0	0	2	0	0
Metacrambus carectellus	0	1	0	0	1	0	1	1	0	0	1	0	1	0	1	?	1	1	0	0	0	0	0	0	?	0	0

Continued on next page

Table A.5 – *Continued from previous page*

char. N°	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27
Microcrambon paphiellus	0	1	0	0	1	0	1	0	0	0	1	0	1	?	?	0	0	1	0	0	0	0	0	0	0	0	0
Pediasia contaminella	0	1	0	0	1	0	1	1	0	0	0	0	1	0	1	0	0	1	0	1	0	0	0	0	0	0	0
Culladia achroellum	1	2	0	0	1	0	1	0	0	0	1	0	1	0	1	0	0	1	0	0	0	0	0	0	0	0	0
Xanthocrambus caducellus	0	1	0	0	1	0	1	0	0	0	1	1	?	?	?	0	0	1	0	1	0	0	0	0	0	0	0
Chrysocrambus linetella	0	1	0	0	1	0	1	0	0	0	1	0	1	0	1	0	1	1	0	0	0	0	0	0	2	0	0
Neodactria luteolella	0	1	0	0	1	0	1	1	0	0	1	0	1	0	1	0	0	1	0	0	0	0	0	0	0	0	0
Fissicrambus profanellus	0	1	0	0	1	0	1	0	0	0	1	1	1	0	1	0	0	1	0	0	0	0	0	0	0	0	0
Thaumatopsis pexella	0	1	0	0	1	0	1	1	0	0	1	0	1	0	1	0	0	1	0	0	0	0	0	0	0	0	0
Parapediasia tenuistrigata	0	1	0	0	1	0	1	0	0	0	1	0	1	0	1	0	0	1	0	0	0	0	0	0	0	0	0
Neoculladia incanelloides	1	2	0	0	1	1	0	0	0	0	1	0	1	?	1	0	0	1	0	?	0	0	0	0	0	0	0
Novocrambus propygmaeus	1	2	0	0	1	1	0	0	0	0	1	0	1	0	1	0	?	1	0	?	0	0	0	0	0	0	0

Table A.6: Scores from the ace analysis (ape package) for each node (see Fig. S4).

char. N°	character description	state	node number						
			1	2	3	4	5	6	7
1	Forewing Rs veins	0	1.000	1.000	0.998	1.000	1.000	1.000	1.000
		1	0.000	0.000	0.001	0.000	0.000	0.000	0.000
		2	0.000	0.000	0.001	0.000	0.000	0.000	0.000
2	Forewing Rs4 vein	0	1.000	1.000	0.997	1.000	1.000	0.999	1.000
		1	0.000	0.000	0.003	0.000	0.000	0.001	0.000
3	Forewing distal margin	0	1.000	1.000	1.000	1.000	1.000	1.000	1.000
		1	0.000	0.000	0.000	0.000	0.000	0.000	0.000
4	Hindwing M1 - Sc+R connection	0	1.000	1.000	0.999	1.000	1.000	1.000	1.000
		1	0.000	0.000	0.001	0.000	0.000	0.000	0.000
5	Hindwing cell	0	1.000	1.000	0.999	1.000	1.000	1.000	1.000
		1	0.000	0.000	0.001	0.000	0.000	0.000	0.000
6	Hindwing M2-M3-CuA1-CuA2	0	1.000	1.000	0.997	1.000	1.000	1.000	1.000
		1	0.000	0.000	0.003	0.000	0.000	0.000	0.000
7	Tympanic pockets	0	0.844	0.727	0.287	0.961	0.993	0.995	1.000
		1	0.156	0.273	0.713	0.039	0.007	0.005	0.000
8	Venulae secundae	0	0.935	0.916	0.853	0.954	0.961	0.896	0.996
		1	0.065	0.084	0.147	0.046	0.039	0.104	0.004
9	Uncus	0	1.000	1.000	1.000	1.000	1.000	1.000	1.000
		1	0.000	0.000	0.000	0.000	0.000	0.000	0.000
10	Gnathos arms projection	0	0.999	0.999	0.977	1.000	1.000	1.000	1.000
		1	0.001	0.001	0.023	0.000	0.000	0.000	0.000
11	Gnathos tip	0	0.066	0.059	0.067	0.072	0.110	0.081	0.702
		1	0.934	0.941	0.933	0.928	0.890	0.919	0.298
12	Valva ventral process	0	0.999	0.999	0.998	1.000	1.000	0.998	1.000
		1	0.001	0.001	0.002	0.000	0.000	0.002	0.000
13	Pseudosaccus	0	1.000	1.000	1.000	1.000	1.000	1.000	1.000
		1	0.000	0.000	0.000	0.000	0.000	0.000	0.000
14	Juxta	0	1.000	1.000	0.999	1.000	1.000	0.999	1.000
		1	0.000	0.000	0.001	0.000	0.000	0.001	0.000
15	Attachment of the aedeagus	0	1.000	1.000	0.999	1.000	1.000	1.000	1.000
		1	0.000	0.000	0.001	0.000	0.000	0.000	0.000
16	Opening of the ductus ejaculatorius	0	1.000	1.000	1.000	1.000	1.000	1.000	1.000
		1	0.000	0.000	0.000	0.000	0.000	0.000	0.000
17	Cornuti	0	0.745	0.733	0.652	0.760	0.767	0.695	0.812
		1	0.255	0.267	0.348	0.240	0.233	0.305	0.188
18	Papillae anales dorsal connection	0	1.000	1.000	0.999	1.000	0.999	0.972	1.000
		1	0.000	0.000	0.001	0.000	0.001	0.028	0.000
19	Papillae anales shape	0	1.000	1.000	1.000	1.000	1.000	1.000	1.000
		1	0.000	0.000	0.000	0.000	0.000	0.000	0.000
20	Posterior apophyses	0	1.000	1.000	1.000	1.000	1.000	1.000	1.000
		1	0.000	0.000	0.000	0.000	0.000	0.000	0.000
21	Setation on segment VIII	0	1.000	1.000	1.000	1.000	1.000	1.000	1.000
		1	0.000	0.000	0.000	0.000	0.000	0.000	0.000
22	Intersegmental membrane VIII-IX structure	0	1.000	1.000	1.000	1.000	1.000	1.000	0.997
		1	0.000	0.000	0.000	0.000	0.000	0.000	0.003
23	Colliculum	0	1.000	1.000	1.000	1.000	1.000	1.000	1.000
		1	0.000	0.000	0.000	0.000	0.000	0.000	0.000
24	Ductus bursae	0	0.942	0.893	0.876	0.992	0.999	1.000	1.000
		1	0.058	0.107	0.124	0.008	0.001	0.000	0.000
25	Signum on corpus bursae	0	0.019	0.014	0.011	0.024	0.030	0.138	0.022
		1	0.969	0.977	0.981	0.962	0.953	0.723	0.976
		2	0.012	0.009	0.008	0.014	0.017	0.140	0.002
26	Corpus bursae wall structure	0	1.000	1.000	1.000	1.000	1.000	1.000	1.000
		1	0.000	0.000	0.000	0.000	0.000	0.000	0.000
27	Appendix bursae	0	0.951	0.908	0.896	0.995	1.000	1.000	1.000
		1	0.049	0.092	0.104	0.005	0.000	0.000	0.000

Continued on next page

Table A.6 – *Continued from previous page*

	char. N°	1			2		3		4		5		6		7		8		9		10		11		12		13		14		15		16		17		18		19		20		21		22		23		24		25			26		27	
	state	0	1	2	0	1	0	1	0	1	0	1	0	1	0	1	0	1	0	1	0	1	0	1	0	1	0	1	0	1	0	1	0	1	0	1	0	1	0	1	0	1	0	1	0	1	0	1	0	1	0	1	2	0	1	0	1
node number	8	0.999	0.001	0.001	0.998	0.002	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	0.999	0.001	0.991	0.009	1.000	0.000	1.000	0.000	0.697	0.303	0.981	0.019	1.000	0.000	0.987	0.013	0.994	0.006	0.992	0.008	0.766	0.234	0.999	0.001	1.000	0.000	1.000	0.000	1.000	0.000	0.466	0.534	1.000	0.000	1.000	0.000	0.019	0.976	0.005	1.000	0.000	1.000	0.000
	9	1.000	0.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	0.997	0.003	1.000	0.000	1.000	0.000	0.754	0.246	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	0.818	0.182	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	0.027	0.972	0.002	1.000	0.000	1.000	0.000
	10	1.000	0.000	0.000	0.998	0.002	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	0.960	0.040	1.000	0.000	1.000	0.000	0.778	0.222	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	0.718	0.282	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	0.634	0.350	0.016	1.000	0.000	1.000	0.000
	11	1.000	0.000	0.000	0.999	0.001	0.999	0.001	0.998	0.002	1.000	0.000	0.999	0.001	0.998	0.002	0.843	0.157	1.000	0.000	1.000	0.000	0.921	0.079	0.997	0.003	1.000	0.000	0.999	0.001	1.000	0.000	1.000	0.000	0.609	0.391	0.999	0.001	1.000	0.000	0.999	0.001	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	0.872	0.107	0.021	1.000	0.000	1.000	0.000
	12	1.000	0.000	0.000	0.975	0.025	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	0.999	0.001	0.937	0.063	0.990	0.010	1.000	0.000	0.742	0.258	0.998	0.002	1.000	0.000	0.999	0.001	0.999	0.001	1.000	0.000	0.657	0.343	0.999	0.001	1.000	0.000	1.000	0.000	1.000	0.000	0.999	0.001	1.000	0.000	1.000	0.000	0.708	0.270	0.022	1.000	0.000	1.000	0.000
	13	1.000	0.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	0.998	0.002	1.000	0.000	1.000	0.000	0.816	0.184	1.000	0.000	1.000	0.000	0.999	0.001	0.999	0.001	1.000	0.000	0.854	0.146	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	0.011	0.989	0.001	1.000	0.000	1.000	0.000
	14	1.000	0.000	0.000	1.000	0.000	1.000	0.000	0.999	0.001	1.000	0.000	1.000	0.000	1.000	0.000	0.999	0.001	1.000	0.000	1.000	0.000	0.828	0.172	1.000	0.000	1.000	0.000	1.000	0.000	0.998	0.002	1.000	0.000	0.887	0.113	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	0.007	0.992	0.000	1.000	0.000	1.000	0.000
	15	1.000	0.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	0.999	0.001	1.000	0.000	1.000	0.000	0.162	0.838	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	0.968	0.032	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	0.002	0.998	0.000	1.000	0.000	1.000	0.000
	16	1.000	0.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	0.129	0.871	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	0.984	0.016	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	0.004	0.996	0.000	1.000	0.000	1.000	0.000
	17	1.000	0.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	0.996	0.004	1.000	0.000	1.000	0.000	0.119	0.881	0.999	0.001	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	0.964	0.036	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	0.007	0.993	0.001	1.000	0.000	1.000	0.000
	18	1.000	0.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	0.996	0.004	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	0.024	0.976	0.995	0.005	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	0.969	0.031	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	0.002	0.997	0.001	1.000	0.000	1.000	0.000
	19	1.000	0.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	0.900	0.100	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	0.998	0.002	0.020	0.980	0.998	0.002	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	0.954	0.046	0.999	0.001	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	0.004	0.994	0.002	1.000	0.000	1.000	0.000
	20	1.000	0.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	0.131	0.869	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	0.986	0.014	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	0.006	0.994	0.000	0.985	0.015	0.999	0.001
	21	1.000	0.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	0.113	0.887	0.999	0.001	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	0.981	0.019	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	0.999	0.001	0.005	0.995	0.000	0.013	0.987	0.983	0.017

Continued on next page

Table A.6 – *Continued from previous page*

	char. N°	1			2		3		4		5		6		7		8		9		10		11		12		13		14		15		16		17		18		19		20		21		22		23		24		25			26		27	
	state	0	1	2	0	1	0	1	0	1	0	1	0	1	0	1	0	1	0	1	0	1	0	1	0	1	0	1	0	1	0	1	0	1	0	1	0	1	0	1	0	1	0	1	0	1	0	1	0	1	0	1	2	0	1	0	1
node number	22	1.000	0.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	0.999	0.001	1.000	0.000	1.000	0.000	0.008	0.992	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	0.985	0.015	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	0.068	0.928	0.004	0.000	1.000	1.000	0.000
	23	1.000	0.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	0.004	0.996	0.999	0.001	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	0.987	0.013	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	0.997	0.003	1.000	0.000	0.019	0.978	0.003	0.000	1.000	1.000	0.000
	24	1.000	0.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	0.118	0.882	0.987	0.013	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	0.958	0.042	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	0.935	0.065	0.004	0.996	0.000	0.000	1.000	0.031	0.969
	25	1.000	0.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	0.003	0.997	0.014	0.986	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	0.988	0.012	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	0.934	0.066	0.019	0.981	0.000	0.000	1.000	0.000	1.000
	26	1.000	0.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	0.000	1.000	0.001	0.999	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	0.989	0.011	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	0.947	0.053	0.050	0.950	0.000	0.000	1.000	0.000	1.000
	27	1.000	0.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	0.000	1.000	0.000	1.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	0.982	0.018	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	0.946	0.054	0.052	0.948	0.000	0.000	1.000	0.000	1.000
	28	1.000	0.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	0.000	1.000	0.000	1.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	0.999	0.001	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	0.179	0.820	0.001	0.000	1.000	0.001	0.999
	29	1.000	0.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	0.000	1.000	0.000	1.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	0.999	0.001	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	0.824	0.174	0.001	0.000	1.000	0.000	1.000
	30	1.000	0.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	0.969	0.031	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	0.087	0.913	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	0.000	1.000	0.001	0.999	0.000	1.000	0.000	0.000	1.000	0.000	1.000
	31	1.000	0.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	0.973	0.027	0.999	0.001	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	0.079	0.921	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	0.001	0.999	0.000	1.000
	32	1.000	0.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	0.001	0.999	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	0.000	1.000	0.000	1.000
	33	1.000	0.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	0.990	0.010	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	0.001	0.999	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	0.000	1.000	0.000	1.000
	34	1.000	0.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	0.000	1.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	0.000	1.000	0.000	1.000
	35	1.000	0.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	0.000	1.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	0.000	1.000	0.000	1.000

Continued on next page

Table A.6 – *Continued from previous page*

	char. N°	1			2		3		4		5		6		7		8		9		10		11		12		13	
	state	0	1	2	0	1	0	1	0	1	0	1	0	1	0	1	0	1	0	1	0	1	0	1	0	1	0	1
node number	36	1.000	0.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	0.996	0.004	1.000	0.000
	37	1.000	0.000	0.000	1.000	0.000	1.000	0.000	0.965	0.035	1.000	0.000	1.000	0.000	0.998	0.002	0.997	0.003	1.000	0.000	1.000	0.000	0.938	0.062	1.000	0.000	1.000	0.000
	38	1.000	0.000	0.000	1.000	0.000	1.000	0.000	0.060	0.940	1.000	0.000	1.000	0.000	0.979	0.021	1.000	0.000	1.000	0.000	1.000	0.000	0.994	0.006	1.000	0.000	1.000	0.000
	39	0.997	0.003	0.000	1.000	0.000	1.000	0.000	0.036	0.964	1.000	0.000	1.000	0.000	0.990	0.010	0.999	0.001	1.000	0.000	1.000	0.000	0.998	0.002	1.000	0.000	1.000	0.000
	40	0.956	0.044	0.000	1.000	0.000	1.000	0.000	0.035	0.965	0.999	0.001	0.999	0.001	0.990	0.010	0.999	0.001	1.000	0.000	1.000	0.000	0.998	0.002	1.000	0.000	1.000	0.000
	41	0.953	0.047	0.000	1.000	0.000	1.000	0.000	0.052	0.948	0.983	0.017	0.993	0.007	0.982	0.018	0.998	0.002	1.000	0.000	1.000	0.000	0.998	0.002	1.000	0.000	1.000	0.000
	42	1.000	0.000	0.000	1.000	0.000	1.000	0.000	0.031	0.969	1.000	0.000	1.000	0.000	0.019	0.981	0.999	0.001	1.000	0.000	1.000	0.000	0.996	0.004	1.000	0.000	0.951	0.049
	43	1.000	0.000	0.000	1.000	0.000	1.000	0.000	0.019	0.981	1.000	0.000	1.000	0.000	0.012	0.988	0.989	0.011	1.000	0.000	1.000	0.000	0.989	0.011	1.000	0.000	0.024	0.976
	44	1.000	0.000	0.000	1.000	0.000	1.000	0.000	0.022	0.978	1.000	0.000	1.000	0.000	0.010	0.990	0.099	0.901	1.000	0.000	1.000	0.000	0.999	0.001	1.000	0.000	0.000	1.000
	45	1.000	0.000	0.000	1.000	0.000	1.000	0.000	0.005	0.995	1.000	0.000	1.000	0.000	0.004	0.996	0.057	0.943	1.000	0.000	1.000	0.000	0.999	0.001	1.000	0.000	0.000	1.000
	46	1.000	0.000	0.000	1.000	0.000	1.000	0.000	0.905	0.095	1.000	0.000	1.000	0.000	0.096	0.904	0.037	0.963	1.000	0.000	1.000	0.000	0.998	0.002	1.000	0.000	0.000	1.000
	47	1.000	0.000	0.000	1.000	0.000	1.000	0.000	0.993	0.007	1.000	0.000	1.000	0.000	0.877	0.123	0.011	0.989	1.000	0.000	1.000	0.000	0.998	0.002	0.999	0.001	0.000	1.000
	48	1.000	0.000	0.000	0.996	0.004	0.998	0.002	0.011	0.989	1.000	0.000	0.999	0.001	0.013	0.987	0.996	0.004	1.000	0.000	0.994	0.006	0.754	0.246	0.988	0.012	0.013	0.987
	49	1.000	0.000	0.000	0.931	0.069	0.863	0.137	0.001	0.999	1.000	0.000	0.998	0.002	0.003	0.997	0.998	0.002	0.999	0.001	0.865	0.135	0.690	0.310	0.866	0.134	0.012	0.988

	char. N°	14		15		16		17		18		19		20		21		22		23		24		25			26		27	
	state	0	1	0	1	0	1	0	1	0	1	0	1	0	1	0	1	0	1	0	1	0	1	0	1	2	0	1	0	1
node number	36	1.000	0.000	1.000	0.000	1.000	0.000	0.000	1.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	0.000	1.000	0.000	1.000
	37	1.000	0.000	0.971	0.029	1.000	0.000	0.876	0.124	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	0.012	0.987	0.001	1.000	0.000	1.000	0.000
	38	0.999	0.001	0.018	0.982	1.000	0.000	0.888	0.112	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	0.048	0.947	0.005	1.000	0.000	1.000	0.000
	39	0.979	0.021	0.009	0.991	1.000	0.000	0.856	0.144	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	0.028	0.962	0.010	1.000	0.000	1.000	0.000
	40	0.978	0.022	0.001	0.999	1.000	0.000	0.812	0.188	0.997	0.003	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	0.012	0.984	0.005	1.000	0.000	1.000	0.000
	41	0.992	0.008	0.000	1.000	1.000	0.000	0.798	0.202	0.999	0.001	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	0.007	0.990	0.003	1.000	0.000	1.000	0.000
	42	1.000	0.000	0.000	1.000	0.951	0.049	0.898	0.102	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	0.994	0.006	0.000	1.000	0.000	1.000	0.000
	43	0.996	0.004	0.000	1.000	0.930	0.070	0.878	0.122	0.999	0.001	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	0.999	0.001	0.000	1.000	0.000	1.000	0.000
	44	0.023	0.977	0.000	1.000	0.951	0.049	0.845	0.155	0.999	0.001	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	0.999	0.001	0.000	1.000	0.000	1.000	0.000
	45	0.008	0.992	0.000	1.000	0.988	0.012	0.876	0.124	0.985	0.015	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	0.999	0.001	0.000	1.000	0.000	1.000	0.000
	46	0.004	0.996	0.000	1.000	0.905	0.095	0.511	0.489	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	0.982	0.015	0.004	1.000	0.000	1.000	0.000
	47	0.001	0.999	0.000	1.000	0.065	0.935	0.228	0.772	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	0.994	0.004	0.002	1.000	0.000	1.000	0.000
	48	0.999	0.001	0.000	1.000	0.074	0.926	0.834	0.166	0.991	0.009	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	0.998	0.001	0.001	1.000	0.000	1.000	0.000
	49	0.999	0.001	0.003	0.997	0.008	0.992	0.820	0.180	0.991	0.009	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	0.999	0.001	0.000	1.000	0.000	1.000	0.000

Continued on next page

Table A.6 – *Continued from previous page*

	char. N°	1			2		3		4		5		6		7		8		9		10		11		12		13	
	state	0	1	2	0	1	0	1	0	1	0	1	0	1	0	1	0	1	0	1	0	1	0	1	0	1	0	1
node number	50	1.000	0.000	0.000	0.924	0.076	0.858	0.142	0.000	1.000	1.000	0.000	0.978	0.022	0.001	0.999	0.997	0.003	1.000	0.000	0.852	0.148	0.600	0.400	0.841	0.159	0.025	0.975
	51	1.000	0.000	0.000	0.995	0.005	0.017	0.983	0.000	1.000	1.000	0.000	0.064	0.936	0.001	0.999	0.994	0.006	1.000	0.000	0.043	0.957	0.574	0.426	0.089	0.911	0.959	0.041
	52	1.000	0.000	0.000	1.000	0.000	1.000	0.000	0.039	0.961	0.993	0.007	1.000	0.000	0.012	0.988	1.000	0.000	1.000	0.000	1.000	0.000	0.997	0.003	1.000	0.000	0.967	0.033
	53	1.000	0.000	0.000	1.000	0.000	1.000	0.000	0.010	0.990	0.998	0.002	0.986	0.014	0.031	0.969	0.998	0.002	1.000	0.000	1.000	0.000	0.997	0.003	1.000	0.000	0.992	0.008
	54	1.000	0.000	0.000	0.993	0.007	1.000	0.000	0.999	0.001	0.001	0.999	1.000	0.000	0.001	0.999	1.000	0.000	1.000	0.000	1.000	0.000	0.988	0.012	1.000	0.000	0.962	0.038
	55	1.000	0.000	0.000	0.998	0.002	1.000	0.000	1.000	0.000	0.000	1.000	1.000	0.000	0.001	0.999	0.996	0.004	1.000	0.000	1.000	0.000	0.998	0.002	1.000	0.000	0.999	0.001
	56	1.000	0.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	0.000	1.000	1.000	0.000	0.001	0.999	0.996	0.004	1.000	0.000	1.000	0.000	0.997	0.003	0.999	0.001	1.000	0.000
	57	1.000	0.000	0.000	0.998	0.002	1.000	0.000	1.000	0.000	0.000	1.000	1.000	0.000	0.006	0.994	0.982	0.018	1.000	0.000	1.000	0.000	0.999	0.001	1.000	0.000	1.000	0.000
	58	1.000	0.000	0.000	0.989	0.011	1.000	0.000	1.000	0.000	0.000	1.000	1.000	0.000	0.004	0.996	0.986	0.014	1.000	0.000	1.000	0.000	0.998	0.002	1.000	0.000	1.000	0.000
	59	1.000	0.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	0.000	1.000	1.000	0.000	0.915	0.085	0.160	0.840	0.951	0.049	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000
	60	1.000	0.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	0.000	1.000	1.000	0.000	0.998	0.002	0.011	0.989	0.008	0.992	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000
	61	1.000	0.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	0.000	1.000	1.000	0.000	1.000	0.000	0.003	0.997	0.000	1.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000
	62	1.000	0.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	0.000	1.000	1.000	0.000	1.000	0.000	0.001	0.999	0.000	1.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000
	63	1.000	0.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	0.000	1.000	0.999	0.001	1.000	0.000	0.001	0.999	0.000	1.000	1.000	0.000	0.999	0.001	1.000	0.000	1.000	0.000

	char. N°	14		15		16		17		18		19		20		21		22		23		24		25			26		27	
	state	0	1	0	1	0	1	0	1	0	1	0	1	0	1	0	1	0	1	0	1	0	1	0	1	2	0	1	0	1
node number	50	0.998	0.002	0.008	0.992	0.002	0.998	0.769	0.231	0.979	0.021	0.997	0.003	1.000	0.000	1.000	0.000	0.999	0.001	1.000	0.000	1.000	0.000	0.998	0.001	0.001	1.000	0.000	1.000	0.000
	51	0.935	0.065	0.000	1.000	0.000	1.000	0.876	0.124	0.998	0.002	0.010	0.990	1.000	0.000	1.000	0.000	0.959	0.041	1.000	0.000	1.000	0.000	0.995	0.002	0.002	1.000	0.000	1.000	0.000
	52	1.000	0.000	0.000	1.000	0.949	0.051	0.902	0.098	0.999	0.001	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	0.998	0.002	0.000	1.000	0.000	1.000	0.000
	53	1.000	0.000	0.000	1.000	0.256	0.744	0.829	0.171	0.982	0.018	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	0.988	0.007	0.006	1.000	0.000	1.000	0.000
	54	1.000	0.000	0.000	1.000	1.000	0.000	0.917	0.083	0.999	0.001	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	0.000	1.000	0.000	1.000	0.000
	55	1.000	0.000	0.000	1.000	1.000	0.000	0.881	0.119	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	0.000	1.000	0.000	1.000	0.000
	56	1.000	0.000	0.000	1.000	1.000	0.000	0.928	0.072	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	0.996	0.002	0.002	1.000	0.000	1.000	0.000
	57	1.000	0.000	0.000	1.000	1.000	0.000	0.833	0.167	1.000	0.000	1.000	0.000	0.997	0.003	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	0.999	0.001	0.000	1.000	0.000	1.000	0.000
	58	0.992	0.008	0.000	1.000	1.000	0.000	0.801	0.199	1.000	0.000	1.000	0.000	0.999	0.001	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	0.979	0.018	0.003	1.000	0.000	1.000	0.000
	59	1.000	0.000	0.000	1.000	1.000	0.000	0.569	0.431	1.000	0.000	1.000	0.000	0.098	0.902	0.967	0.033	0.926	0.074	1.000	0.000	1.000	0.000	0.999	0.001	0.000	1.000	0.000	1.000	0.000
	60	1.000	0.000	0.000	1.000	1.000	0.000	0.474	0.526	1.000	0.000	1.000	0.000	0.042	0.958	0.007	0.993	0.020	0.980	1.000	0.000	1.000	0.000	0.997	0.003	0.000	1.000	0.000	1.000	0.000
	61	1.000	0.000	0.000	1.000	1.000	0.000	0.447	0.553	1.000	0.000	1.000	0.000	0.041	0.959	0.002	0.998	0.008	0.992	1.000	0.000	1.000	0.000	0.998	0.001	0.000	1.000	0.000	1.000	0.000
	62	1.000	0.000	0.000	1.000	1.000	0.000	0.283	0.717	1.000	0.000	1.000	0.000	0.004	0.996	0.001	0.999	0.008	0.992	1.000	0.000	1.000	0.000	0.998	0.001	0.001	1.000	0.000	1.000	0.000
	63	1.000	0.000	0.000	1.000	1.000	0.000	0.175	0.825	1.000	0.000	1.000	0.000	0.001	0.999	0.005	0.995	0.015	0.985	1.000	0.000	1.000	0.000	0.999	0.001	0.000	1.000	0.000	1.000	0.000

Continued on next page

Table A.6 – *Continued from previous page*

	char. N°	1			2		3		4		5		6		7		8		9		10		11		12		13		14		15		16		17		18		19		20		21		22		23		24		25			26		27	
	state	0	1	2	0	1	0	1	0	1	0	1	0	1	0	1	0	1	0	1	0	1	0	1	0	1	0	1	0	1	0	1	0	1	0	1	0	1	0	1	0	1	0	1	0	1	0	1	0	1	0	1	2	0	1	0	1
node number	64	1.000	0.000	0.000	0.479	0.521	1.000	0.000	1.000	0.000	0.000	1.000	1.000	0.000	0.000	1.000	1.000	0.000	1.000	0.000	1.000	0.000	0.664	0.336	1.000	0.000	0.020	0.980	1.000	0.000	0.000	1.000	1.000	0.000	0.936	0.064	0.946	0.054	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	0.999	0.001	0.001	1.000	0.000	1.000	0.000
	65	1.000	0.000	0.000	0.454	0.546	1.000	0.000	1.000	0.000	0.000	1.000	1.000	0.000	0.000	1.000	0.998	0.002	1.000	0.000	1.000	0.000	0.644	0.356	1.000	0.000	0.006	0.994	1.000	0.000	0.000	1.000	1.000	0.000	0.943	0.057	0.947	0.053	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	0.998	0.002	0.001	1.000	0.000	1.000	0.000
	66	1.000	0.000	0.000	0.079	0.921	1.000	0.000	1.000	0.000	0.001	0.999	1.000	0.000	0.000	1.000	0.986	0.014	1.000	0.000	1.000	0.000	0.663	0.337	1.000	0.000	0.005	0.995	0.999	0.001	0.000	1.000	1.000	0.000	0.940	0.060	0.989	0.011	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	0.989	0.009	0.002	1.000	0.000	1.000	0.000
	67	1.000	0.000	0.000	0.028	0.972	1.000	0.000	1.000	0.000	0.017	0.983	1.000	0.000	0.000	1.000	0.918	0.082	1.000	0.000	1.000	0.000	0.629	0.371	0.999	0.001	0.011	0.989	0.988	0.012	0.000	1.000	1.000	0.000	0.922	0.078	0.995	0.005	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	0.928	0.062	0.010	1.000	0.000	1.000	0.000
	68	0.999	0.001	0.000	0.253	0.747	1.000	0.000	1.000	0.000	0.000	1.000	0.997	0.003	0.000	1.000	0.999	0.001	1.000	0.000	1.000	0.000	0.144	0.856	1.000	0.000	0.001	0.999	1.000	0.000	0.000	1.000	1.000	0.000	0.916	0.084	0.111	0.889	1.000	0.000	0.998	0.002	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	0.934	0.017	0.049	1.000	0.000	1.000	0.000
	69	1.000	0.000	0.000	0.006	0.994	1.000	0.000	1.000	0.000	0.000	1.000	1.000	0.000	0.000	1.000	1.000	0.000	1.000	0.000	1.000	0.000	0.009	0.991	1.000	0.000	0.000	1.000	1.000	0.000	0.000	1.000	1.000	0.000	0.950	0.050	0.003	0.997	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	0.914	0.034	0.052	1.000	0.000	1.000	0.000
	70	1.000	0.000	0.000	0.000	1.000	1.000	0.000	1.000	0.000	0.000	1.000	1.000	0.000	0.000	1.000	1.000	0.000	1.000	0.000	1.000	0.000	0.001	0.999	1.000	0.000	0.000	1.000	1.000	0.000	0.000	1.000	1.000	0.000	0.766	0.234	0.000	1.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	0.030	0.966	0.004	1.000	0.000	1.000	0.000
	71	1.000	0.000	0.000	0.000	1.000	1.000	0.000	1.000	0.000	0.000	1.000	1.000	0.000	0.000	1.000	1.000	0.000	1.000	0.000	1.000	0.000	0.000	1.000	1.000	0.000	0.000	1.000	1.000	0.000	0.000	1.000	1.000	0.000	0.986	0.014	0.000	1.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	0.930	0.012	0.059	1.000	0.000	1.000	0.000
	72	1.000	0.000	0.000	0.000	1.000	1.000	0.000	1.000	0.000	0.000	1.000	1.000	0.000	0.000	1.000	0.999	0.001	1.000	0.000	1.000	0.000	0.000	1.000	1.000	0.000	0.000	1.000	1.000	0.000	0.000	1.000	1.000	0.000	0.981	0.019	0.000	1.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	0.174	0.002	0.824	1.000	0.000	1.000	0.000
	73	1.000	0.000	0.000	0.000	1.000	1.000	0.000	1.000	0.000	0.000	1.000	1.000	0.000	0.000	1.000	0.998	0.002	1.000	0.000	1.000	0.000	0.000	1.000	1.000	0.000	0.000	1.000	1.000	0.000	0.000	1.000	1.000	0.000	0.975	0.025	0.000	1.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	0.162	0.001	0.836	1.000	0.000	1.000	0.000
	74	1.000	0.000	0.000	0.000	1.000	1.000	0.000	1.000	0.000	0.000	1.000	1.000	0.000	0.000	1.000	0.987	0.013	1.000	0.000	1.000	0.000	0.000	1.000	1.000	0.000	0.000	1.000	1.000	0.000	0.000	1.000	1.000	0.000	0.951	0.049	0.000	1.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	0.030	0.001	0.970	1.000	0.000	1.000	0.000
	75	1.000	0.000	0.000	0.000	1.000	1.000	0.000	1.000	0.000	0.000	1.000	1.000	0.000	0.000	1.000	0.996	0.004	1.000	0.000	1.000	0.000	0.000	1.000	1.000	0.000	0.000	1.000	1.000	0.000	0.000	1.000	1.000	0.000	0.987	0.013	0.000	1.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	0.001	0.001	0.998	1.000	0.000	1.000	0.000
	76	1.000	0.000	0.000	0.000	1.000	1.000	0.000	1.000	0.000	0.000	1.000	1.000	0.000	0.000	1.000	0.999	0.001	1.000	0.000	0.988	0.012	0.004	0.996	1.000	0.000	0.000	1.000	0.999	0.001	0.000	1.000	1.000	0.000	0.986	0.014	0.000	1.000	1.000	0.000	0.999	0.001	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	0.003	0.022	0.975	1.000	0.000	1.000	0.000
	77	0.996	0.003	0.002	0.000	1.000	1.000	0.000	1.000	0.000	0.000	1.000	1.000	0.000	0.000	1.000	0.993	0.007	1.000	0.000	1.000	0.000	0.000	1.000	0.999	0.001	0.000	1.000	1.000	0.000	0.000	1.000	1.000	0.000	0.985	0.015	0.000	1.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	0.000	0.000	1.000	1.000	0.000	1.000	0.000

Continued on next page

Table A.6 – *Continued from previous page*

	char. N°	1			2		3		4		5		6		7		8		9		10		11		12		13	
	state	0	1	2	0	1	0	1	0	1	0	1	0	1	0	1	0	1	0	1	0	1	0	1	0	1	0	1
node number	78	0.994	0.002	0.004	0.000	1.000	1.000	0.000	1.000	0.000	0.000	1.000	0.996	0.004	0.000	1.000	0.998	0.002	1.000	0.000	1.000	0.000	0.001	0.999	0.981	0.019	0.000	1.000
	79	1.000	0.000	0.000	0.000	1.000	1.000	0.000	1.000	0.000	0.000	1.000	1.000	0.000	0.000	1.000	0.999	0.001	1.000	0.000	1.000	0.000	0.000	1.000	1.000	0.000	0.000	1.000
	80	1.000	0.000	0.000	0.000	1.000	1.000	0.000	1.000	0.000	0.000	1.000	1.000	0.000	0.000	1.000	0.999	0.001	1.000	0.000	1.000	0.000	0.000	1.000	1.000	0.000	0.000	1.000
	81	1.000	0.000	0.000	0.000	1.000	1.000	0.000	1.000	0.000	0.000	1.000	1.000	0.000	0.000	1.000	0.962	0.038	1.000	0.000	1.000	0.000	0.001	0.999	1.000	0.000	0.000	1.000
	82	1.000	0.000	0.000	0.000	1.000	1.000	0.000	1.000	0.000	0.000	1.000	1.000	0.000	0.000	1.000	0.998	0.002	1.000	0.000	1.000	0.000	0.001	0.999	1.000	0.000	0.000	1.000
	83	0.996	0.004	0.000	0.001	0.999	1.000	0.000	1.000	0.000	0.000	1.000	1.000	0.000	0.000	1.000	0.946	0.054	1.000	0.000	1.000	0.000	0.048	0.952	1.000	0.000	0.000	1.000
	84	1.000	0.000	0.000	0.000	1.000	1.000	0.000	1.000	0.000	0.000	1.000	1.000	0.000	0.000	1.000	0.999	0.001	1.000	0.000	1.000	0.000	0.000	1.000	0.971	0.029	0.000	1.000
	85	1.000	0.000	0.000	0.000	1.000	1.000	0.000	1.000	0.000	0.000	1.000	1.000	0.000	0.001	0.999	0.992	0.008	1.000	0.000	1.000	0.000	0.000	1.000	1.000	0.000	0.000	1.000
	86	1.000	0.000	0.000	0.000	1.000	1.000	0.000	1.000	0.000	0.000	1.000	1.000	0.000	0.000	1.000	0.642	0.358	1.000	0.000	1.000	0.000	0.000	1.000	0.998	0.002	0.000	1.000
	87	1.000	0.000	0.000	0.000	1.000	1.000	0.000	1.000	0.000	0.000	1.000	1.000	0.000	0.000	1.000	0.631	0.369	1.000	0.000	1.000	0.000	0.001	0.999	0.993	0.007	0.000	1.000
	88	0.996	0.004	0.000	0.000	1.000	1.000	0.000	1.000	0.000	0.000	1.000	0.992	0.008	0.010	0.990	0.993	0.007	1.000	0.000	1.000	0.000	0.000	1.000	1.000	0.000	0.000	1.000
	89	0.051	0.948	0.001	0.043	0.957	1.000	0.000	1.000	0.000	0.000	1.000	0.086	0.914	0.882	0.118	0.995	0.005	1.000	0.000	1.000	0.000	0.003	0.997	0.999	0.001	0.000	1.000

	char. N°	14		15		16		17		18		19		20		21		22		23		24		25			26		27	
	state	0	1	0	1	0	1	0	1	0	1	0	1	0	1	0	1	0	1	0	1	0	1	0	1	2	0	1	0	1
node number	78	1.000	0.000	0.000	1.000	1.000	0.000	0.959	0.041	0.000	1.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	0.000	0.000	1.000	1.000	0.000	1.000	0.000
	79	1.000	0.000	0.000	1.000	1.000	0.000	0.991	0.009	0.000	1.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	0.999	0.000	0.001	1.000	0.000	1.000	0.000
	80	1.000	0.000	0.000	1.000	1.000	0.000	0.985	0.015	0.000	1.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	0.999	0.000	0.001	1.000	0.000	1.000	0.000
	81	0.999	0.001	0.000	1.000	1.000	0.000	0.900	0.100	0.000	1.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	0.991	0.004	0.005	1.000	0.000	1.000	0.000
	82	1.000	0.000	0.000	1.000	1.000	0.000	0.980	0.020	0.000	1.000	1.000	0.000	0.995	0.005	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	0.999	0.000	0.001	1.000	0.000	1.000	0.000
	83	1.000	0.000	0.000	1.000	1.000	0.000	0.967	0.033	0.000	1.000	1.000	0.000	0.977	0.023	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	0.998	0.001	0.001	1.000	0.000	1.000	0.000
	84	0.999	0.001	0.000	1.000	1.000	0.000	0.880	0.120	0.000	1.000	1.000	0.000	0.979	0.021	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	0.964	0.002	0.034	1.000	0.000	1.000	0.000
	85	1.000	0.000	0.000	1.000	1.000	0.000	0.990	0.010	0.000	1.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	0.000	1.000	0.000	1.000	0.000
	86	1.000	0.000	0.000	1.000	1.000	0.000	0.984	0.016	0.000	1.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	0.000	1.000	0.000	1.000	0.000
	87	1.000	0.000	0.000	1.000	1.000	0.000	0.979	0.021	0.000	1.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	0.999	0.000	0.000	1.000	0.000	1.000	0.000
	88	1.000	0.000	0.000	1.000	1.000	0.000	0.981	0.019	0.000	1.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	0.000	1.000	0.000	1.000	0.000
	89	0.996	0.004	0.000	1.000	1.000	0.000	0.883	0.117	0.000	1.000	1.000	0.000	0.960	0.040	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	0.996	0.002	0.002	1.000	0.000	1.000	0.000

Table A.7: Egg-laying behavior, host plant data and larval life habits in Crambinae, Scopariinae and other Crambidae subfamilies. The HOSTS database refers to the World's Lepidoptera Hostplants Database of Robinson et al. (2010; https://www.nhm.ac.uk/our-science/data/hostplants/)

	Genus	Species	Host plant taxonomical rank	Host plant species	Egg-laying behaviour	Egg type	Larval life habits	References
Acentropinae	*Acentria*	*ephemerella*	Ceratophyllaceae, Haloragaceae, Hydrocharitaceae, Lythraceae, Polygonaceae, Potamogetonaceae	*Elodea canadensis, Hydrocharis morsus-ranae, Najas marina, Zannichellia palustris, Polygonum amphibium, Ceratophyllum demersum, Trapa natans, Myriophyllum sp., Potamogeton pectinatus*	115-250 eggs/female, deposited in a mass, layers, or series	greenish, oval, slightly wider at one end	lives in a flat case of leaves. First instar miner or feeding freely on the leaves. In later instars make its way into the stalk of the host plant for hibernation.	Heinemann, 1865; Sorhagen, 1886; Disqué, 1890; Buckler, 1901; Haupt, 1906; Nigmann, 1908; Berg, 1941; Speidel, 2004
	Acentria	*nivea*	Ceratophyllaceae, Elatinaceae, Haloragaceae, Hydrocharitaceae, Portulacaceae, Potamogetonaceae	*Elodea canadensis, Hydrilla verticillata, Potamogeton, Portulaca, Ceratophyllum, Elatine americana, Myriophyllum sibiricum*				HOSTS database
	Chrysendeton	*kimballi*			occur in very small irregular clusters, glued together	0.45×0.3mm, scale-like		Peterson, 1963
	Elophila	*africalis*	Araceae	*Pistia stratiotes, Azolla pinnata*				HOSTS database
	Elophila	*difflualis*	Menyanthaceae, Potamogetonaceae, Poaceae: Oryzoideae	*Potamogeton, Nymphoides, Oryza sativa, Azolla pinnata, Salvinia cucullata*				HOSTS database
	Elophila	*icciusalis*			occur singly and scattered	0.6×0.4mm		Peterson, 1963
	Elophila	*interruptalis*	Nymphaeaceae	*Nymphaea*				HOSTS database
	Elophila	*manilensis*	Araceae	*Pistia stratiotes, Salvinia cucullata*				HOSTS database
	Elophila	*nigralbalis*	Salviniaceae	*Azolla pinnata*				HOSTS database

Continued on next page

Table A.7 – *Continued from previous page*

	Genus	Species	Host plant taxonomical rank	Host plant species	Egg-laying behaviour	Egg type	Larval life habits	References
Acentropinae	*Elophila*	*nymphaeata*	Alismataceae, Boraginaceae, Hydrocharitaceae, Menyanthaceae, Nymphaeaceae, Plantaginaceae, Typhaceae, Poaceae: Oryzoideae	*Alisma plantago-aquatica, Hydrocharis morsus-ranae, Nymphoides peltata, Myosotis laxa, Calltriche palustris, Nuphar lutea, Nymphaea alba, Oryza sativa, Sparganium emersum, Potamogeton natans, Catabrosa aquatica*			First instar mining; then building a case with leaf fragments. Larva is hydrophylic during first two instars, eats small holes in the surface of the leaf. Spins its case to the lower part of stalk for hibernation and penetrates into it.	Treitschke, 1829; Sorhagen, 1886; Leech, 1886; Buckler, 1901; Wörz, 1949; Reichholf, 1978; Speidel, 1984; Speidel, 2004; HOSTS database
	Elophila	*obliteralis*			small clusters <12 eggs, very adhesive, glued together	0.4×0.5mm, ovoid, slightly pliable		Peterson, 1963
	Elophila	*responsalis*	Araceae, Nymphaeaceae, Oleaceae, Pontederiaceae	*Pistia stratiotes, Eichhornia, Jasminum bifarium, Nymphaea, Azolla pinnata, Marsilea, Salvinia auriculata*				HOSTS database
	Elophila	*turbata*	Salviniaceae; Marsileaceae	*Azolla pinnata, Marsilea quadrifolia*				HOSTS database
Crambinae: Ancylolomiini	*Ancylolomia*	*chrysographellus*	Poaceae: Oryzoideae, Panicoideae	*Oryza sativa, Imperata cylindrica, Paspalum dilatatum*			stem borer	Khan, 1991; HOSTS database
	Ancylolomia	*disparalis*	Poaceae	*"grasses"*				Ylla et al., 2008; Slamka, 2008
	Ancylolomia	*indica*	Poaceae: Oryzoideae, Panicoideae	*Oryza sativa, Saccharum officinarum*				HOSTS database
	Ancylolomia	*inornata*	Poaceae: Oryzoideae, Panicoideae	*Oryza sativa, Sorghum, Zea mays*				HOSTS database
	Ancylolomia	*japonica*	Poaceae: Oryzoideae	*Oryza sativa*				HOSTS database
	Ancylolomia	*locupletella*	Poaceae: Panicoideae	*Spinifex squarrosus*				HOSTS database
	Ancylolomia	*palpella*	Poaceae: Pooideae	*Brachypodium spp.*			lives in silken galleries at the base of grasses	Slamka, 2008

Continued on next page

Table A.7 – *Continued from previous page*

	Genus	Species	Host plant taxonomical rank	Host plant species	Egg-laying behaviour	Egg type	Larval life habits	References
Crambinae: Ancylolomiini	*Ancylolomia*	*tentaculella*	Poaceae: Pooideae	*Dactylis glomerata*	eggs seem to be freely laid, not adhesive		lives in vertical tunnel 3-4cm long at the base of stems of large grasses	Goater, 1984; Slamka, 2008; www.lepiforum.de
	Ancylolomia	*tripolitella*	Poaceae	̈grasses”				Ylla et al., 2008; Slamka, 2008
	Prionapteryx	*indentella*	Poaceae: Chloridoideae	*Buchloe dactyloides*			inhabit vertical silken tunnels in the soil.	Sorensen
	Prionapteryx	*invectalis*	Fagales	*Casuarina*	Females dig the ground with their robust ovipositor and lay a single egg. Eggs adhesive			HOSTS database
	Prionapteryx	*nebulifera*	Ericaceae	*Gaylussacia, Leiophyllum buxifolium*			lives in tunnels on stems of the plants	HOSTS database
	Talis	*quercella*	Asteraceae, Brassicaceae, Cannabaceae, Poaceae: Panicoideae	*Brassica, Cannabis sativa, Helianthus annuus, Zea mays*, ”grasses”			lives on the roots of grasses	Slamka, 2008; HOSTS database
	Zovax	*vangoghi*	Poaceae: Oryzoideae	*Oryza*				HOSTS database
Crambinae: Argyriini	*Argyria*	*divisella*	Fabaceae	*Glycine max*				HOSTS database
	Argyria	*lacteella*	Fabaceae	*Phaseolus lunatus*	eggs laid with an adhesive	0.6×0.4mm; much smaller than those of *U. nivalis*; tiny reticulations on the chorion		Peterson, 1963; HOSTS database

Continued on next page

Table A.7 – *Continued from previous page*

	Genus	Species	Host plant taxonomical rank	Host plant species	Egg-laying behaviour	Egg type	Larval life habits	References
Argyriini	*Urola*	*nivalis*	Oleaceae	*Oleaceae*, "grasses"	occur singly or in small clusters (Peterson, 1963)	1.1×0.7mm; light yellowish-green, upper surface with small wrinkles and tiny reticulations		
Crambinae: Calamotrophini	*Calamotropha*	*atkinsoni*	Cyperaceae	*Actinoscirpus grossus*				HOSTS database
	Calamotropha	*corticellus*	Cyperaceae	*Rhynchospora corymbosa*				HOSTS database
	Calamotropha	*leptogrammella*	Cyperaceae, Poaceae: Panicoideae	*Cyperus rotundus*, *Paspalum dilatatum*				HOSTS database
	Calamotropha	*lupatus*	Typhaceae	*Typha latifolia*, "grasses"				HOSTS database
	Calamotropha	*paludella*	Typhaceae, Poaceae: Arundinoideae	*Phragmites spp.*, *Typha latifolia*	eggs laid with an adhesive in cluster of 3-5	egg flattened, laid in cluster of 3-5	leaf and stems borer	Slamka, 2008; HOSTS database www.lepiforum.de
	Calamotropha	*shichito*	Cyperaceae	*Cyperus serotinus*				HOSTS database
	Calamotropha	*unicolorellus*	Cupressaceae, Cyperaceae	*Cupressus*, *Cyperus tegetum*				HOSTS database
Crambinae: Chiloini	*Chilo*	*agamemnon*	Poaceae: Oryzoideae, Panicoideae, Pooideae	*Oryza sativa*, *Echinochloa crus-galli*, *Saccharum officinarum*, *Zea mays*, *Elymus repens*				HOSTS database
	Chilo	*auricilia*	Poaceae: Chloridoideae, Oryzoideae, Panicoideae	*Eleusine coracana*, *Oryza sativa*, *Andropogon sorghum*, *Cymbopogon citratus*, *Hemarthria altissima*, *Miscanthus fusca*, *Saccharum officinarum*, *Sorghum*, *Zea mays*			stem borer	Khan, 1991; HOSTS database
	Chilo	*bandra*	Poaceae: Panicoideae	*Saccharum officinarum*				HOSTS database
	Chilo	*batri*	Poaceae: Panicoideae	*Saccharum officinarum*				HOSTS database
	Chilo	*christophi*	Poaceae: Arundinoideae, Oryzoideae	*Phragmites communis*, *Oryza sativa*				HOSTS database

Continued on next page

Table A.7 – *Continued from previous page*

	Genus	Species	Host plant taxonomical rank	Host plant species	Egg-laying behaviour	Egg type	Larval life habits	References
Crambinae: Chiloini	*Chilo*	*diffusilinea*	Poaceae: Oryzoideae, Panicoideae	*Oryza sativa, Pennisetum glaucum, Sorghum*			stem borer	Khan, 1991; HOSTS database
	Chilo	*erianthalis*	Poaceae: Panicoideae	*Saccharum sp.*				HOSTS database
	Chilo	*ikri*	Poaceae: Panicoideae	*Andropogon, Miscanthus fusca, Saccharum officinarum*				HOSTS database
	Chilo	*infuscatellus*	Poaceae: Oryzoideae, Panicoideae	*Oryza sativa, Saccharum officinarum, Sorghum*				HOSTS database
	Chilo	*kanra*	Poaceae: Panicoideae	*Miscanthus fusca, Saccharum officinarum*				HOSTS database
	Chilo	*luteellus*	Poaceae: Arundinoideae, Panicoideae	*Phragmites australis, Zea mays*				HOSTS database
	Chilo	*niponella*	Poaceae: Arundinoideae	*Phragmites australis*				HOSTS database
	Chilo	*orichalcociliella*	Poaceae: Chloridoideae, Panicoideae	*Eleusine coracana, Panicum, Pennisetum, Saccharum officinarum, Sorghum, Zea mays*				HOSTS database
	Chilo	*panici*	Poaceae: Panicoideae	*Panicum miliaceum*				HOSTS database
	Chilo	*partellus*	Poaceae: Oryzoideae, Panicoideae	*Oryza sativa, Coix lacryma-jobi, Panicum maximum, Pennisetum americanum, Saccharum officinarum, Sorghum bicolor, Zea mays*			stem borer	Khan, 1991; HOSTS database
	Chilo	*phragmitellus*	Poaceae: Arundinoideae, Oryzoideae, Pooideae	*Phragmites australis, Oryza sativa, Glyceria maxima*	eggs laid in group with an adhesive	flattened, marked with a faint texture	stem borer	Fletcher, 1914, Peterson, 1963; Slamka, 2008; HOSTS database
	Chilo	*plejadellus*	Poaceae: Oryzoideae	*Oryza sativa*	laid in clusters of 10-12	Scale-like, overlap like shingles, yellow		Peterson, 1963; HOSTS database

Continued on next page

Table A.7 – *Continued from previous page*

	Genus	Species	Host plant taxonomical rank	Host plant species	Egg-laying behaviour	Egg type	Larval life habits	References
Crambinae: Chiloini	*Chilo*	*polychrysa*	Cyperaceae, Poaceae: Oryzoideae, Panicoideae, Pooideae	*Cyperus digitatus, Scirpus, Oryza sativa, O., Echinochloa crus-galli, Hymenachne amplexicaulis, Saccharum officinarum, Sacciolepis myosuroides, Zea mays, Triticum*				HOSTS database
	Chilo	*pulverosellus*	Poaceae: Panicoideae	*Zea mays*				Slamka, 2008
	Chilo	*sacchariphagus*	Poaceae: Oryzoideae, Panicoideae	*Oryza sativa, Andropogon sorghum, Miscanthus fusca, Pennisetum americanum, Saccharum officinarum, Sorghum bicolor, Zea mays*				HOSTS database
	Chilo	*suppressalis*	Brassicaceae, Solanaceae, Poaceae: Chloridoideae, Oryzoideae, Panicoideae, Pooideae	*Andropogon sorghum, Brassica oleracea, Brachiaria mutica, Coix lacryma-jobi, Cymbopogon citratus, Echinochloa crusgalli, Eleusine coracana, Lycopersicon esculentum, Miscanthus fusca, Oryza sativa, Panicum miliaceum, Paspalum conjugatum, Pennisetum americanum, Saccharum officinarum, Solanum melongena, Sorghum bicolor, Triticum, Zea mays*	eggs laid in clusters of up to 70, fish scale-like	0.9×0.5mm, turning from translucent-white to dark-yellow	larvae cluster between the leaf sheaths and stems, then burrow into the stems to feed	Slamka, 2008; HOSTS database
	Chilo	*terrenellus*	Poaceae: Panicoideae	*Saccharum officinarum*				HOSTS database
	Chilo	*tumidicostalis*	Poaceae: Panicoideae	*Saccharum officinarum*				HOSTS database
	Chilo	*zacconius*	Poaceae: Oryzoideae, Panicoideae	*Oryza sativa, Echinochloa pyramidalis, Panicum maximum, Rottboellia exaltata, Zea mays*				HOSTS database
	Chilo	*zizaniae*	Poaceae: Oryzoideae	*Zizania latifolia*				HOSTS database

Continued on next page

Table A.7 – *Continued from previous page*

	Genus	Species	Host plant taxonomical rank	Host plant species	Egg-laying behaviour	Egg type	Larval life habits	References
Crambinae: Chiloini	*Diatraea*	*albicrinella*	Poaceae: Panicoideae	*Panicum grande, Saccharum officinarum*				HOSTS database
	Diatraea	*amazonica*	Poaceae: Panicoideae	*Paspalum fasciculatum*				HOSTS database
	Diatraea	*amnemonella*	Poaceae: Panicoideae	*Saccharum officinarum*				HOSTS database
	Diatraea	*bellifactella*	Poaceae: Panicoideae	*Saccharum officinarum*				HOSTS database
	Diatraea	*brunnescens*	Poaceae: Panicoideae	*Pennisetum bambusiforme*				HOSTS database
	Diatraea	*busckella*	Poaceae: Panicoideae	*Saccharum officinarum*				HOSTS database
	Diatraea	*cayenella*	Poaceae: Panicoideae	*Andropogon, Saccharum officinarum*				HOSTS database
	Diatraea	*centrellus*	Poaceae: Panicoideae	*Paspalum, Saccharum officinarum*				HOSTS database
	Diatraea	*considerata*	Poaceae: Panicoideae	*Saccharum officinarum*				HOSTS database
	Diatraea	*crambidoides*	Poaceae: Panicoideae	*Saccharum officinarum, Tripsacum dactyloides, Zea mays*				HOSTS database
	Diatraea	*dyari*	Poaceae: Panicoideae	*Saccharum officinarum*				HOSTS database
	Diatraea	*evanescens*	Poaceae: Panicoideae	*Paspalum scrobiculatum, Sorghum*	clusters of 6-10 eggs	0.8×0.6mm, scale-like		Peterson, 1963; HOSTS database
	Diatraea	*flavipennella*	Poaceae: Panicoideae	*Saccharum officinarum*				HOSTS database
	Diatraea	*grandiosella*	Poaceae: Panicoideae	*Saccharum officinarum, Zea mays*				HOSTS database
	Diatraea	*guatemala*	Poaceae: Panicoideae	*Saccharum officinarum*				HOSTS database
	Diatraea	*impersonatellus*	Poaceae: Panicoideae	*Andropogon schoenanthus, Paspalum virgatum, Saccharum officinarum*				HOSTS database
	Diatraea	*indigenella*	Poaceae: Panicoideae	*Saccharum officinarum*				HOSTS database
	Diatraea	*lineolata*	Poaceae: Oryzoideae, Panicoideae	*Oryza sativa, Paspalum virgatum, Saccharum officinarum, Tripsacum latifolium, Zea mays*				HOSTS database
	Diatraea	*lisetta*			clusters of 8-10	0.8×0.6mm; eggs scale-like, cream-white		Peterson, 1963
	Diatraea	*magnifactella*	Poaceae: Panicoideae	*Saccharum officinarum*				HOSTS database
	Diatraea	*minimifacta*	Poaceae: Panicoideae	*Saccharum officinarum*				HOSTS database

Continued on next page

Table A.7 – *Continued from previous page*

	Genus	Species	Host plant taxonomical rank	Host plant species	Egg-laying behaviour	Egg type	Larval life habits	References
Crambinae: Chiloini	*Diatraea*	*muellerella*	Poaceae: Panicoideae	*Saccharum officinarum*				HOSTS database
	Diatraea	*myersi*	Poaceae: Panicoideae	*Paspalum fasciculatum, Saccharum officinarum*				HOSTS database
	Diatraea	*pedibarbata*	Cyperaceae, Typhaceae, Poaceae: Panicoideae	*Cyperus, Paspalum, Typha*				HOSTS database
	Diatraea	*postlineella*	Poaceae: Panicoideae	*Zea mays*				HOSTS database
	Diatraea	*rosa*	Poaceae: Panicoideae	*Saccharum officinarum*				HOSTS database
	Diatraea	*rufescens*	Poaceae: Panicoideae	*Saccharum officinarum*				HOSTS database
	Diatraea	*saccharalis*	Platanaceae, Poaceae: Arundinoideae, Chloridoideae, Oryzoideae, Panicoideae, Pooideae	*Andropogon squarrosa, Arundo donax, Avena sativa, Brachiaria muticum, Echinochloa colonum, E., Hymenachne amplexicaulis, Leptochloa, Melinis repens, Oryza sativa, Panicum maximum, Paspalum fasciculatum, Pennisetum latifolium, Platanus occidentalis, Saccharum officinarum, Sorghum bicolor, Stenotaphrum secundatum, Tripsacum dactyloides, Zea mays*	clusters of 10-50, eggs laid in group with an adhesive, overlapping like fish scales, deposited on upper and lower surface of leaves	1.2×0.8mm; flattened, marked with a faint texture	borer in the salk of sugarcane	Peterson, 1963; Passoa, 1985; Capinera, 2001; HOSTS database
	Diatraea	*savannarum*	Poaceae: Panicoideae	*Saccharum officinarum*				HOSTS database
	Diatraea	*schausella*	Poaceae: Panicoideae	*Setaria poiretiana*				HOSTS database
	Diatraea	*strigipennella*	Poaceae: Panicoideae	*Saccharum officinarum*				HOSTS database
	Diatraea	*suffusella*	Poaceae: Panicoideae	*Saccharum officinarum*				HOSTS database
	Diatraea	*tabernella*	Poaceae: Panicoideae	*Saccharum officinarum*				HOSTS database
	Diatraea	*veracruzana*	Poaceae: Panicoideae	*Saccharum officinarum*				HOSTS database
	Gadira	*acerella*	Bryophyta	"moss"				Patrick et al., 2011
	Hednota	*bivittella*	Lomandraceae	*Lomandra,*				HOSTS database
	Hednota	*crypsichroa*	Poaceae: Pooideae	*Hordeum vulgare, Secale cereale*				HOSTS database

Continued on next page

Table A.7 – *Continued from previous page*

	Genus	Species	Host plant taxonomical rank	Host plant species	Egg-laying behaviour	Egg type	Larval life habits	References
Crambinae: Chiloini	*Hednota*	*longipalpella*	Poaceae: Pooideae	*Hordeum vulgare, Secale cereale, Triticum*				HOSTS database
	Hednota	*panteucha*	Poaceae: Pooideae	*Hordeum vulgare, Secale cereale, Triticum aestivum*		0.7×0.5mm, ovale, with longitudinal ridges	makes silken tunnels in the soil	Koch, 1965; HOSTS database
	Hednota	*pedionoma*	Poaceae: Pooideae	*Hordeum vulgare, Secale cereale, Triticum aestivum*				HOSTS database Koch, 1965
	Hednota	*pleniferella*	Poaceae					HOSTS database
	Hednota	*recurvella*	Dasypogonaceae, Iridaceae	*Dasypogon, Patersonia*				HOSTS database
	Hednota	*tritalis*	Poaceae: Chloridoideae	*Cynodon dactylon*			makes silken tunnels in the soil	Koch, 1965
	Myelobia	*atrosparsellus*	Poaceae: Panicoideae	*Gynerium sagittatum*				HOSTS database
	Myelobia	*bimaculata*	Poaceae: Panicoideae	*Saccharum officinarum*				HOSTS database
	Myelobia	*nicaraguensis*	Poaceae: Bambusoideae	*Guadua aculeata*	eggs laid in clusters with an adhesive	flattened, with a faint texture	Stem borer, larva feeds on branches, not emerging shoots	Landry et al., 2015
	Myelobia	*paleacea*	Euphorbiaceae, Poaceae: Bambusoideae	*Mabea, Merostachys claussenii, Chusquea bambusoides*				HOSTS database
	Myelobia	*smerintha*	Poaceae: Bambusoideae	*Bambusa targoara, B., Chusquea bambusoides, Merostachys claussenii*				Dyar, 1917; Forbes, 1926; Landry et al., 2015; HOSTS database
Crambinae: Crambini	*Agriphila*	*aeneociliella*	Poaceae: Pooideae	*Bromus inermis*			lives in spined tubes at the bases of grasses	Slamka, 2008
	Agriphila	*cyrenaicella*	Poaceae					Slamka, 2008
	Agriphila	*geniculea*					lives in silken galleries at the base of grasses	Slamka, 2008
	Agriphila	*inquinatella*	Brachytheciaceae, Poaceae: Pooideae	*Brachythecium spp., Festuca ovina, Poa*			hibernates in silken galleries at the bases of grasses (feeds on roots and base of stems)	Slamka, 2008; HOSTS database

Continued on next page

Table A.7 – *Continued from previous page*

	Genus	Species	Host plant taxonomical rank	Host plant species	Egg-laying behaviour	Egg type	Larval life habits	References
Crambinae: Crambini	*Agriphila*	*latistria*	Poaceae: Pooideae	*Bromus*			lives in silken tube at the bases of grasses	Slamka, 2008
	Agriphila	*plumbifimbriella*			Non-adhesive eggs dropped during slow, undulating flight			Marshall, 1988
	Agriphila	*poliella*	Poaceae: Pooideae	*Festuca vallesiaca, Poa annua*			lives in silken galleries at the base of grasses	Slamka, 2008
	Agriphila	*ruricolella*	Poaceae: Panicoideae	*Zea mays* "turfgrass", detritophagous	non-adhesive eggs dropped during slow, undulating flight			Marshall, 1988; HOSTS database
	Agriphila	*selasella*	Poaceae: Chloridoideae, Pooideae	*Spartina, Festuca ovina, Hordeum, Poa, Puccinellia maritima, Glyceria*			hibernates in silken tube covered by grass fragments at the base of grasses	Slamka, 2008; HOSTS database
	Agriphila	*straminella*	Poaceae: Pooideae	*Festuca ovina, Hordeum vulgare, Poa pratensis, Triticum*			lives in silken galleries at the base of grasses	Slamka, 2008; HOSTS database
	Agriphila	*tristella*	Poaceae: Pooideae	*Avenella flexuosa, Deschampsia caespitosa, Poa*			hibernates in silken tube covered by grass fragments at the base of grasses	Slamka, 2008
	Agriphila	*vulgivagellus*	Poaceae: Oryzoideae	*Oryza sativa,*	Non-adhesive eggs dropped during slow, undulating flight	0.5×0.35mm; 21 irregular, longitudinal ridges, white to orange		Peterson, 1963; Marshall, 1988; HOSTS database
	Angustalius	*malacelloides*	Poaceae: Oryzoideae	*Oryza sativa*				HOSTS database
	Angustalius	*malacellus*	Cyperaceae, Poaceae: Oryzoideae, Panicoideae	*Cyperus, Oryza sativa, Saccharum officinarum, Sorghum, Zea mays*				HOSTS database
	Catoptria	*conchella*	Bryophyta	"moss"			lives on moss covered stones and old trees	Slamka, 2008

Continued on next page

Table A.7 – *Continued from previous page*

	Genus	Species	Host plant taxonomical rank	Host plant species	Egg-laying behaviour	Egg type	Larval life habits	References
Crambinae: Crambini	*Catoptria*	*confusella*	Bryophyta	“moss”			lives under mosses on stones	Slamka, 2008
	Catoptria	*falsella*	Brachytheciaceae, Pottiaceae	*Brachythecium rutabulum, Barbula, Tortula intermedia*	egg non-adhesive, deposited singly		moving in a tube of silk where pupation occurs later	Slamka, 2008; www.lepiforum.de
	Catoptria	*fulgidella*	Asteraceae, Cyperaceae, Poaceae: Pooideae	*Gnaphalium, Carex arenaria, Festuca*				Slamka, 2008
	Catoptria	*furcatella*	Lycopodiaceae, Poaceae: Pooideae	*Lycopodium, Festuca ovina*				Slamka, 2008
	Catoptria	*luctiferella*	Bryophyta	“moss”				Slamka, 2008
	Catoptria	*lythargyrella*	Poaceae: Pooideae	*Festuca*	eggs non-adhesive		builds a silken tunnel among roots	Schwarz, 1964
	Catoptria	*maculalis*	Bryophyta	“moss”			silken tube on mosses	Slamka, 2008
	Catoptria	*margaritella*	Bryophyta	“moss”			silken tube on roots of grasses	Slamka, 2008
	Catoptria	*myella*	Bryophyta	“moss”			lives in or under moss growing on stones	Slamka, 2008
	Catoptria	*osthelderi*	Bryophyta	“moss”				Slamka, 2008
	Catoptria	*pauperella*	Poaceae: Pooideae	*Festuca*				Slamka, 2008
	Catoptria	*permutatella*	Bryophyta	“moss”				Slamka, 2008
	Catoptria	*petrificella*			egg non-adhesive, deposited singly			www.lepiforum.de
	Catoptria	*pinella*	Cyperaceae, Poaceae: Pooideae	*Carex, Eriophorum vaginatum, Deschampsia caespitosa*				HOSTS database
	Catoptria	*pyramidella*	Bryophyta	“moss”			hibernates on mosses	Slamka, 2008
	Catoptria	*staudingeri*	Bryophyta	“moss”				Slamka, 2008
	Catoptria	*verella*	Bryophyta	“moss”	eggs seem to be adhesive		lives on mosses in the ground and on the stems and branches of trees (old apple, plum, poplar)	Slamka, 2008; www.lepiforum.de
	Chrysocramboides	*craterellus*	Poaceae					Slamka, 2008
	Chrysocrambus	*dentuellus*	Poaceae: Pooideae	*Festuca ovina*				Slamka, 2008

Continued on next page

Table A.7 – *Continued from previous page*

	Genus	Species	Host plant taxonomical rank	Host plant species	Egg-laying behaviour	Egg type	Larval life habits	References
Crambinae: Crambini	*Chrysocrambus*	*sardiniellus*			eggs deposited singly, completely non-adhesive			www.lepiforum.de
	Chrysoteuchia	*culmella*	Hylocomiaceae, Poaceae: Pooideae	*Ctenidium, Agrostis, Dactylis, Festuca*			lives in roots and stems. Do not produce silken galleries as majority of Crambinae	Slamka, 2008; www.lepiforum.de
	Chrysoteuchia	*toparia*	Ericaceae, Pinaceae, Polygonaceae, Poaceae: Pooideae	*Rumex, Abies, Pseudotsuga, Vaccinium macrocarpon, Agrostis gigantea, Dactylis glomerata, Festuca rubra, Poa pratensis*	egg non-adhesive, deposited singly			Matheny
	Conocramboides	*seychellelus*	Poaceae: Panicoideae	*Ischaemum aristatum*				HOSTS database
	Crambus	*agitatellus*	Poaceae	”turfgrass”				Solis, 2008
	Crambus	*alboclavellus*			egg non-adhesive, deposited singly			Matheny
	Crambus	*decorellus*			egg non-adhesive, deposited singly			Matheny
	Crambus	*divus*	Arecaceae	*Juania australis*			larva feeds on new leaves	Clarke, 1965 and reference therein
	Crambus	*ericellus*	Ericaceae, Poaceae: Pooideae	*Calluna vulgaris, Erica arborea, Aira, Corynephorus, Deschampsia flexuosa, Festuca ovina*				Gozmany, 1963; Slamka, 1997; Slamka, 2008; HOSTS database
	Crambus	*hamellus*	Poaceae: Pooideae	*Deschampsia*				Slamka, 2008
	Crambus	*heringiellus*	Hypnaceae	*Hypnum*			inhabits long tube constructed from moss-fragments and frass	Slamka, 2008
	Crambus	*laqueatellus*	Poaceae: Panicoideae, Pooideae	“moss”, *Deschampsia caespitosa, Zea mays*	egg non-adhesive, deposited singly			Matheny
	Crambus	*lathionellus*	Poaceae: Pooideae	*Aira, Deschampsia caespitosa*			hibernates in spun-tube	Slamka, 2008

Continued on next page

Table A.7 – *Continued from previous page*

	Genus	Species	Host plant taxonomical rank	Host plant species	Egg-laying behaviour	Egg type	Larval life habits	References
Crambinae: Crambini	*Crambus*	*pascuellus*	Fabaceae, Poaceae: Pooideae	“moss”, *Poa, Trifolium*	egg non-adhesive, deposited singly	oval with obvious ridges	lives in silken galleries near the ground on various grasses	Matheny
	Crambus	*perlellus*	Poaceae: Pooideae	*Deschampsia, Festuca*			hibernates in a tubular silken gallery on bases of stems of grasses	Slamka, 2008; HOSTS database
	Crambus	*praefectellus*	Poaceae: Panicoideae	*Zea mays, Detritophagous*	egg non-adhesive, deposited singly			Matheny
	Crambus	*pratellus*	Poaceae: Pooideae	*Deschampsia*			lives on shoots of grasses, inhabits spun-tube covered by detritus fragments	Slamka, 2008
	Crambus	*quinquareatus*			eggs deposited singly, completely non-adhesive	rounded, with 20 longitudinal ridges, cream to red		Peterson, 1963
	Crambus	*satrapellus*			eggs deposited singly, completely non-adhesive	0.4×0.32mm, rounded, with 16 longitudinal ridges, white to red		Peterson, 1963
	Crambus	*silvellus*	Cyperaceae	*Carex*			lives in a web on sedges. Pupates in a cocoon in the soil	Slamka, 2008
	Crambus	*sperryellus*						HOSTS database
	Crambus	*tristellus*	Bryophyta	“moss”			makes silken galleries on mosses	Shield, 1856; Glime, 2017
	Crambus	*tutillus*						HOSTS database
	Crambus	*uliginosellus*						Slamka, 2008
	Culladia	*cuneiferellus*	Poaceae: Chloridoideae	*Cynodon*				HOSTS database
	Culladia	*signifer*	Poaceae: Chloridoideae	*Eleusine indica*				HOSTS database
	Euchromius	*bellus*	-	*dry leaves*			detritophageous	Slamka, 2008

Continued on next page

Table A.7 – *Continued from previous page*

	Genus	Species	Host plant taxonomical rank	Host plant species	Egg-laying behaviour	Egg type	Larval life habits	References
Crambinae: Crambini	*Euchromius*	*gozmanyi*	Amaranthaceae	*Salicornia*			detritophageous	Slamka, 2008
	Euchromius	*ocelleus*	-	*dry leaves*			detritophageous	Lhomme, 1935-1946; Capps, 1966; Schouten, 1992; Slamka, 2008
	Euchromius	*ramburiellus*	-	*dry leaves*			detritophageous	Slamka, 2008
	Fernandocrambus	*harpipterus*						HOSTS database
	Fissicrambus	*mutabilis*	Poaceae: Panicoideae, Pooideae	*Avena sativa, Dactylis glomerata, Digitaria sanguinalis, Hordeum vulgare, Phleum pratense, Poa pratensis, Secale cereale, Zea mays*		0.45×0.3mm; 15 longitudinal ridges, color greenish white to orange	larva feeds above ground on the leaves of a more or less restricted range of grasses	Peterson, 1963; HOSTS database
	Metacrambus	*carectellus*	Poaceae	”grasses”			“larva lives on grass”	Slamka, 2008
	Micrelephas	*pictellus*	Euphorbiaceae	*Hyeronima alchorneoides*				Landry, 2003
	Microcrambus	*elegans*	Poaceae: Panicoideae	*Zea mays* “turfgrass”, detritophagous	eggs deposited singly, non-adhesive; 20-40 eggs deposited	0.4×0.2mm; 14 longitudinal ridges; color white to light orange		Peterson, 1963; Allyson, 1986; Solis, 2008;
	Microcrambus		Poaceae: Panicoideae	”turfgrass”	eggs deposited singly, non-adhesive; 20-40 eggs deposited	0.4×0.2mm; 14 longitudinal ridges; color white to light orange		HOSTS database
	Neodactria	*caliginosella*	Apiaceae, Plantaginaceae, Solanaceae, Poaceae: Panicoideae, Pooideae	*Daucus carota, Nicotiana, Plantago lanceolata, Triticum, Zea mays*				Dominick, 1964; Landry, 1995; HOSTS database
	Neodactria	*luteolella*	Poaceae: Panicoideae	*Zea mays*, ”turfgrass”				HOSTS database
	Neodactria	*zeellus*	Poaceae: Panicoideae	*Zea mays*				HOSTS database
	Ocrocrambus	*callirrhous*	Poaceae: Pooideae	*Festuca novaezealandiae*				White, 1963, Gaskin, 1975

Continued on next page

Table A.7 – *Continued from previous page*

	Genus	Species	Host plant taxonomical rank	Host plant species	Egg-laying behaviour	Egg type	Larval life habits	References
Crambinae: Crambini	*Ocrocrambus*	*cyclopicus*	Poaceae: Pooideae	*Arrhenatherum elatius, Bromus mollis*			"grass bases"	Gaskin, 1975; Patrick et al, 2011
	Ocrocrambus	*enchophorus*	Poaceae: Pooideae	*Bromus catharticus, Festuca arundinacea, Poa caespitosa*				Gaskin, 1975
	Ocrocrambus	*flexuosellus*	Ditrichaceae, Poaceae: Pooideae	*Ceratodon purpureus, Dactylis glomerata, Festuca rubra var., Phleum pratense, Poa annua*		0.4×0.3mm, oblate, 11-17 vertical ribs, creamy yellow to pinkish	tunnel through grass roots and soil	Watt, 1914; Hudson, 1928; Kesley, 1957 ; Cumber
	Ocrocrambus	*heliotes*				0.44×0.3mm, oblate, 20-26 vertical ribs, creamy white to orange		Gaskin, 1975
	Orocrambus	*angustipennis*	Poaceae: Danthonioideae	*Cortaderia selloana*			in growing stems and blades	Gaskin, 1975
	Orocrambus	*lewisi*	Poaceae: Pooideae	*Poa nemoralis*				White, 1963; Gaskin, 1975
	Orocrambus	*mylites*	Poaceae: Danthonioideae	*Chionochloa australis*				Gaskin, 1975
	Orocrambus	*ramosellus*	Poaceae: Pooideae	*Agrostis tenuis, Alopecurus pratensis, Bromus catharticus, Festuca novazealandiae, Poa annua, Poa nemoralis*		0.45×0.35mm, oblate, 18-22 vertical ribs, creamy white to orange	"grass bases"	White, 1963; Gaskin, 1975; Patrick et al, 2011
	Orocrambus	*simplex*	Poaceae: Pooideae	*Poa nemoralis*		0.5×0.38mm, oblate, 14-19 vertical ribs, pale yellow to orange		Gaskin, 1975, HOSTS database

Continued on next page

Table A.7 – *Continued from previous page*

	Genus	Species	Host plant taxonomical rank	Host plant species	Egg-laying behaviour	Egg type	Larval life habits	References
Crambinae: Crambini	*Orocrambus*	*vittellus*	Poaceae: Pooideae	*Agrostis tenuis*		0.5×0.3mm, oblate, 14-22 vertical ribs, orange-brown to brown	"grass bases"	White, 1963; Gaskin, 1975; Patrick et al, 2011
	Parapediasia	*ligonellus*	Poaceae: Chloridoideae	*Zoysia matrella*				HOSTS database
	Parapediasia	*teterrella*	Poaceae: Pooideae	*Festuca, Poa pratensis*	lay non-adhesive eggs while perched or while flying			Ainslie, 1930; Marshal, 1988; HOSTS database
	Pediasia	*aridella*	Poaceae: Pooideae	*Puccinellia maritima*			lives in silken gallery covered by fragments at the base of the stems	Slamka, 2008; HOSTS database
	Pediasia	*caliginosella*			egg non-adhesive, deposited singly			Matheny
	Pediasia	*dorsipunctellus*	Poaceae					HOSTS database
	Pediasia	*fascelinella*	Poaceae: Pooideae	*Corynephorus canescens, Deschampsia, Elytrigia junceiforme*				Slamka, 2008
	Pediasia	*jucundella*	Poaceae: Pooideae	*Triticum*				Slamka, 2008
	Pediasia	*luteella*	Poaceae: Pooideae	*Festuca ovina, Poa, Triticum*				Slamka, 2008
	Pediasia	*luteolella*			egg non-adhesive, deposited singly			Matheny
	Pediasia	*mutabilis*			egg non-adhesive, deposited singly			Matheny
	Pediasia	*paludella*	Poaceae: Pooideae	*Festuca ovina, Poa*			hibernates in silken gallery vertically placed among stems of grasses	Slamka, 2008

Continued on next page

Table A.7 – *Continued from previous page*

	Genus	Species	Host plant taxonomical rank	Host plant species	Egg-laying behaviour	Egg type	Larval life habits	References
Crambinae: Crambini	*Pediasia*	*pedriolella*	Poaceae: Pooideae	*Agropyron junceum*			lives in long silken tube in the ground near the bases of grasses	Slamka, 2008
	Pediasia	*trisecta*	Solanaceae, Poaceae: Panicoideae, Pooideae	*Zea mays, Festuca rubra, Poa pratensis, Nicotiana*	egg non-adhesive, deposited singly	0.65×0.35mm, 16 longitudinal ribs, greenish white to yellow		Peterson, 1963; Matheny
	Pediasia	*truncatella*	Sphagnaceae, Poaceae: Arundinoideae	*Molinia, Sphagnum*			tyrphophilous	Slamka, 2008
	Platytes	*alpinella*	Pottiaceae	*Barbula ruraliformis, Tortula*	egg non-adhesive, deposited singly			Slamka, 2008; Léger, personal observation, 2018
	Platytes	*cerussella*	Cyperaceae, Poaceae: Pooideae	*Carex arenaria, Festuca*	eggs non-adhesive, <100 eggs		feed on roots of small, stiff grasses growing on sand and shingle	Schwarz, 1964; Goater, 1986; Slamka, 2008
	Thaumatopsis	*edonis*			egg non-adhesive, deposited singly			Matheny
	Thaumatopsis	*pectinifer*	Cyperaceae, Poaceae: Panicoideae	*Cyperus, Paspalum stramineum, Paspalum stramineum*			larvae feed just below the soil surface from silken tubes	Landry, 1995 and reference therein
	Thysanotia	*chrysonuchella*	Poaceae: Pooideae	*Festuca ovina*			lives on grasses; inhabits its silken galery at the bases of stems	Slamka, 2008
	Xanthocrambus	*saxonellus*			eggs non-adhesive, <100 eggs			Schwarz, 1964

Continued on next page

Table A.7 – *Continued from previous page*

	Genus	Species	Host plant taxonomical rank	Host plant species	Egg-laying behaviour	Egg type	Larval life habits	References
Crambinae: Diptychophorini	*Diptychophora*	*sp.*			eggs glued to the substrate			Landry, personal observation, 2018
	Glaucocharis	*bipunctella*	Hepaticophyta	*liverwort cushions*				Beever
	Glaucocharis	*elaina*	Funariaceae	*Funaria*				Gaskin, 1971
	Glaucocharis	*epiphaea*	Polytrichaceae	*Dawsonia superba*			chews off tips of leaves shoots, with refuge tunnels made with silk, leaf fragments and frass	Beever
	Glaucocharis	*metallifera*	Bryophyta	"moss"				Hudson, 1928
	Glaucocharis	*microdora*	Bryophyta	"moss"				Hudson, 1928
Crambinae: Haimbachiini	*Bissetia*	*steniella*	Poaceae: Panicoideae	*Saccharum*				
	Coniesta	*ignefusalis*	Poaceae: Panicoideae	*Andropogon, Oryza sativa, Panicum maximum, Pennisetum americanum, Saccharum officinarum, Sorghum bicolor, Zea mays*	eggs laid between leaf sheath and the stem in batches of 20-50	Scale-like, creamy-yellow	tunnel in leaf sheaths and in underlying stem	Haris, 1962; HOSTS database
	Donacoscaptes	*berthellus*	Poaceae: Panicoideae	*Saccharum officinarum*				HOSTS database
	Donacoscaptes	*infusellus*	Pontederiaceae	*Eichhornia crassipes, Pontederia cordata*				HOSTS database
	Donacoscaptes	*tauromma*	Poaceae: Panicoideae	*Saccharum spontaneum*				HOSTS database
	Eoreuma	*loftini*	Poaceae: Oryzoideae, Panicoideae	*Cymbopogon citratus, Oryza sativa, Panicum miliaceum, Saccharum officinarum, Sorghum, Zea mays*	eggs adhesive, laid in masses of 5-100, between layers of dry leaf tissue near the plante base	flattened and sometimes marked with a faint texture	early instars feed on and inside the leaf sheaths, producing a red hole; larvae tunnel into the stem both vertically and horizontally	Johnson, 1981; Legaspi et al., 1997;
	Friedlanderia	*cicatricella*	Cyperaceae, Poaceae: Arundinoideae	*Phragmites australis, Schoenoplectus lacustris*				Slamka, 2008
	Haimbachia	*quiriguella*	Poaceae: Oryzoideae	*Oryza*				Capps, 1965
	Pseudobissetia	*terrestrella*	Poaceae: Panicoideae	*Zea mays*				Slamka, 2008
	Thopeutis	*forbesellus*	Cyperaceae	*Juncus, Scirpus*				Frohne 1939; Dyar

Continued on next page

Table A.7 – *Continued from previous page*

	Genus	Species	Host plant taxonomical rank	Host plant species	Egg-laying behaviour	Egg type	Larval life habits	References
Crambinae: Haimbachiini	*Xubida*	*panalope*			eggs laid singly or in clusters, coated with thin, somewhat opaque, white adhesive	1×0.7mm, scale-like, translucent		Peterson, 1963
	Xubida	*rutubella*	Poaceae: Panicoideae	*Saccharum*				Agnew et al., 1998
	Hellula	*phidilealis*			eggs adhesive, laid singly or in small clusters	eggs are ovoid		Peterson, 1963
Glaphyriinae	*Evergestis*	*africalis*	Brassicaceae	*Brassica*				HOSTS database
	Evergestis	*bifascialis*	Brassicaceae	*Brassica, Raphanus*				HOSTS database
	Evergestis	*extimalis*	Brassicaceae	*Brassica rapa, Diplotaxis tenuifolia, Iberis, Sinapis, Sisymbrium*			larva occurs singly or in groups in spun-together shoot tips; boring fruits or eating the seeds; hibernates in a cocoon in or on the soil.	Zocchi, 1951; Goater, Nuss & Speidel, 2004; HOSTS database
	Evergestis	*forficalis*	Apiaceae, Brassicaceae	*Apium graveolens, Armoracia rusticana, Brassica oleracea, Raphanus sativus*	eggs laid in mass of 10 eggs glued on the host plant		larva in a spinning under the leaves, making windows and holes; hibernates in a tough subterranean cocoon	Goater, Nuss & Speidel, 2004; HOSTS database; www.lepiforum.de
	Evergestis	*funalis*	Portulacaceae	*Portulaca*				HOSTS database
	Evergestis	*infirmalis*	Brassicaceae	*Brassica*				HOSTS database
	Evergestis	*limbata*	Brassicaceae, Fabaceae	*Allaria petiolata, Genista tinctoria*				HOSTS database
	Evergestis	*pallidata*	Brassicaceae	*Armoracia rusticana, Barbarea vulgaris, Brassica rapa, Diplotaxis tenuifolia, Raphanus sativus*				HOSTS database
	Evergestis	*pechi*	Brassicaceae	*Diplotaxis pendula, Sisymbrium irio*			larva feeds on the flowers	Chrétien, 1917; Goater, 2004

Continued on next page

Table A.7 – *Continued from previous page*

	Genus	Species	Host plant taxonomical rank	Host plant species	Egg-laying behaviour	Egg type	Larval life habits	References
Glaphyriinae	*Evergestis*	*politalis*	Brassicaceae	*Biscutella didyma*			larva gregarious at the base of different Cruciferae, feeding on leaves at base of stem	Lhomme, 1935; Goater, Nuss & Speidel, 2004; HOSTS database
	Evergestis	*renatalis*	Brassicaceae	*Sisymbrium*				HOSTS database
	Evergestis	*rimosalis*	Brassicaceae	*Brassica oleracea, Rorippa*				HOSTS database
	Noorda	*blitealis*	Moringaceae	*Moringa oleifera*	eggs laid on ventral surface of leaves; 75-170 eggs/female	eggs round to spherical in shape	larvae remain on a thin siklen web on the underside of the leaf and feed on the leaflets	Selvi
Heliothelinae	*Heliothela*	*wulfeniana*	Violaceae	*Viola arvensis*	eggs glued singly on the upper side of the leaf		first instar larvae mine in the leaves, second instar feed through the stem of the leaf into the hollow stem	Jensen, 1968; Nuss, 2004; www.lepiforum.de
	Hoploscopa	*sp.*	Gleicheniaceae	*Dicranopteris linearis*			larva feeds on leaves	Mally et al., 2017
Musotiminae	*Lygomusotima*	*stria*			eggs laid singly or in small clusters, mostly on the new growth	translucent pale yellow in clusters	early instars skeletonize leaves, whereas 4th instars consume entire leaves	Solis et al, 2004
	Musotima	*aduncalis*	Aspleniaceae; Pteridaceae	*Adiantum, Asplenium*				HOSTS database
	Musotima	*dryopterisivora*	Dryopteridaceae	*Dryopteris cf. chinensis*				Nakamura, 1977
	Musotima	*nitidalis*	Dennstaedtiaceae; Pteridaceae	*Adiantum, Histiopteris, Pteridium*				HOSTS database
	Musotima	*ochropteralis*	Pteridaceae	*Adiantum*				HOSTS database
	Musotima	*suffusalis*	Pteridaceae	*Adiantum*				HOSTS database
	Neomusotima	*conspurcatalis*			eggs laid singly or in small clusters, mostly on the new growth	translucent pale yellow in clusters	early instars skeletonize leaves, whereas 4th instars consume entire leaves	Solis et al, 2004
	Panotima		Dennstaedtiaceae	*Pteridium aquilinum*				Lawton et al., 1988

Continued on next page

Table A.7 – *Continued from previous page*

	Genus	Species	Host plant taxonomical rank	Host plant species	Egg-laying behaviour	Egg type	Larval life habits	References
Odontiinae	*Siamusotima*	*aranea*	Lygodiaceae	*Lygodium flexuosum*	eggs are laid on the upper surface of the leaf		stem borer.	Solis et al, 2005
	Metaxmeste	*schrankiana*	Ericaceae	*Vaccinium*			larva lives in a tube, feeds on leaves	Slamka, 2008
	Cynaeda	*dentalis*	Boraginaceae	*Anchusa officinalis*, *Echium vulgare*, *Heliotropium europaeum*, *Onosma*			first instars mining basal leaves, later feeds on leaves, lives also in lower part of stem	Slamka, 2008; HOSTS database
Pyraustinae	*Anania*	*hortulata*					larva lives in rolled or spun leaves; feeds along leaf margins.	Slamka, 2013
	Ostrinia	*palustralis*			eggs glued in cluster of 6-20 on host plant	eggs flattened		www.lepiforum.de
	Pyrausta	*magniferalis*			eggs in clusters of 3-20, adhesive	0.7×0.5mm, scale-like		Peterson, 1963
	Sericoplaga	*maclurae*			eggs in clusters of 15-25	0.65×0.55mm		Peterson, 1963
	Sitochroa	*verticalis*			eggs glued in cluster on host plant			www.lepiforum.de
Schoenobiinae	*Donacaula*	*cf aquilellus*	Poaceae: Chloridoideae					HOSTS database
	Donacaula	*dodatellus*	Cyperaceae, Poaceae: Oryzoideae	*Actinoscirpus grossus*, *Oryza sativa*				HOSTS database
	Donacaula	*forficella*	Cyperaceae, Poaceae: Arundinoideae, Oryzoideae, Pooideae	*Carex*, *Phragmites*, *Oryza sativa*, *Glyceria sativa*				HOSTS database
	Donacaula	*maximella*	Poaceae: Oryzoideae	*Zizaniopsis miliacea*				HOSTS database
	Donacaula	*mucronella*	Cyperaceae, Poaceae: Arundinoideae, Pooideae	*Carex riparia*, *Phragmites*, *Glyceria maxima*				HOSTS database
	Donacaula	*niloticus*	Cyperaceae	*Cyperus*				HOSTS database

Continued on next page

Table A.7 – *Continued from previous page*

	Genus	Species	Host plant taxonomical rank	Host plant species	Egg-laying behaviour	Egg type	Larval life habits	References
Schoenobiinae	*Patissa*	*flavicostella*			in clusters of 12 or more	0.7×0.5mm, scale-like, in rows, yet never overlap		Peterson, 1963
	Schoenobius	*gigantella*	Poaceae: Arundinoideae, Pooideae	*Phragmites australis, Glyceria maxima*	eggs glued in clusters			HOSTS database
	Schoenobius	*melinellus*			single layered masses of 12-18 eggs	0.85×0.7, broadly oval		Peterson, 1963
	Schoenobius	*scirpus*	Cyperaceae	*Scirpus grossus*				Chen
	Schoenobius	*sordidellus*			single or two layered masses of about 90 eggs	ovoid, nearly colorless	Peterson, 1963	
Scopariinae	*Cosipara*	*sp.*	Bryophyta	*“moss”*				Munroe, 1972; Glime, 2017
	Eudonia	*alpina*	Bryophyta	“moss”				HOSTS database
	Eudonia	*angustea*	Brachytheciaceae, Pottiaceae	*Homalothecium sericeum, Tortula muralis, Syntrichia ruraliformis, Pseudocrossidium revolutum, Pseudocrossidium revolutum, Tortula muralis*			pupation in a slight web among moss	Goater, Nuss & Speidel, 2004
	Eudonia	*aspidota*	Bryophyta	“moss”				Patrick et al., 2011; Glime, 2017
	Eudonia	*bisinualis*	Poaceae					HOSTS database
	Eudonia	*bucolica*	Bryophyta	“moss”				HOSTS database
	Eudonia	*campbellensis*	Apiaceae, Caryophyllaceae	*Azorella selago, Colobanthus muscoides*, “moss”				Patrick, 1994
	Eudonia	*dactyliopa*	Bryophyta	“moss”				HOSTS database
	Eudonia	*delunella*	Leucodontaceae	*Leucodon sciuroides, lichens*			lichens, mosses growing on ash, apple, elm	Goater, Nuss & Speidel, 2004 & Speidel, 2004
	Eudonia	*dinodes*	Bryophyta	“moss”				Patrick et al., 2011
	Eudonia	*diphteralis*	Poaceae					HOSTS database

Continued on next page

Table A.7 – *Continued from previous page*

	Genus	Species	Host plant taxonomical rank	Host plant species	Egg-laying behaviour	Egg type	Larval life habits	References
Scopariinae	*Eudonia*	*lacustrata*	Brachytheciaceae, Ditrichaceae, Hypnaceae, Lembophyllaceae, Pottiaceae	*Brachythecium rutabulum, Ceratodon purpureus, Eurhynchium praelongum,, Hypnum cupressiforme, Isothecium alopecuroides, Polytrichum commune, Tortella tortuosa*	eggs glued to the substrate		mosses on *Sambucus nigra*	Schwarz, 1965; Goater, Nuss & Speidel, 2004
	Eudonia	*lineola*	Parmeliaceae, Teloschistaceae	*Melanelia olivacea, Parmelia parietina, Xanthoria parietina*				Goater, Nuss & Speidel, 2004 & Speidel, 2004
	Eudonia	*lycopodiae*	Lycopodiaceae	*Lycopodium cernuum*				HOSTS database
	Eudonia	*mawsoni*	Apiaceae, Asteraceae, Caryophyllaceae, Dicranaceae, Hypnaceae, Jungermanniaceae, Montiaceae, Polytrichaceae, Ptychomniaceae, Rubiaceae, Sphagnaceae, Thuidiaceae	*Azorella macquarensis, Pleurophyllum hookeri, Colobanthus muscoides, Montia fontana, Dicranoloma sp, Coprosoma perpusilla, Hypnum sp., Thuidium furfurosum, Jamesoniella colorata, Polytrichaceae sp., Ptychomnion aciculare, Sphagnum falcatulum*				Jackson, 1995
	Eudonia	*mercurella*	Brachytheciaceae, Hypnaceae	*Isothecium alopecuroides, Hypnum cupressiforme*				Goater, Nuss & Speidel, 2004
	Eudonia	*minualis*	Bryophyta	“moss”				Patrick et al., 2011; Glime, 2017
	Eudonia	*murana*	Bryaceae, Dicranaceae, Grimmiaceae, Hypnaceae	*Bryum capillare, Dicranum scoparium, Grimmia pulvinata, Racomitrium, Hypnum cupressiforme*				Goater, Nuss & Speidel, 2004
	Eudonia	*pallida*	Amblystegiaceae, Hylocomiaceae	*Calliergonella cuspidata, Pleurozium schreberi*	eggs laid singly or in batch, fixed to substrate	ovoid, flattened, finely reticulate		Goater, Nuss & Speidel, 2004

Continued on next page

Table A.7 – *Continued from previous page*

	Genus	Species	Host plant taxonomical rank	Host plant species	Egg-laying behaviour	Egg type	Larval life habits	References
Scopariinae	*Eudonia*	*phaeoleuca*	Bryophyta	"moss"				Goater, Nuss & Speidel, 2004
	Eudonia	*philerga*	Bryophyta	"moss"				Patrick et al., 2011; Glime, 2017
	Eudonia	*psammitis*	Apiaceae, Caryophyllaceae	*Azorella selago*, *Colobanthus muscoides*, "moss"				Patrick, 1994
	Eudonia	*sabulosellus*			eggs laid just below ground level (to a depth of 10 mm) adhering to grass or moss stems			Cowley, 1987
	Eudonia	*steropaea*	Leucobryaceae	*Campylopus*				Hoare, 2011; Glime, 2017
	Eudonia	*strigalis*	Bryophyta	moss				Beadle
	Eudonia	*submarginalis*	Poaceae	"grass"				HOSTS database
	Eudonia	*sudetica*	Bryophyta	"moss"				Goater, Nuss & Speidel, 2004
	Eudonia	*truncicolella*	Aulacomniaceae, Brachytheciaceae, Dicranaceae, Hylocomiaceae, Hypnaceae	*Aulacomnium palustre, Campylopus, Dicranum scoparium, Dicranum polysetum, Scleropodium purum, Pleurozium schreberi, Hypnum cupressiforme, Hypnum jutlandicum*				Goater, Nuss & Speidel, 2004
	Micraglossa	*aurata*	Mniaceae, Plagiochilaceae, Radulaceae	*Trachycystis microphylla, Plagiochila sciophila, Radula japonica*				Murase, 2005
	Scoparia	*ambigualis*	Dicranaceae, Hylocomiaceae, Hypnaceae, Lembophyllaceae, Oxalidaceae	*Dicranum scoparium, Rhytidiadelphus loreus, Hypnum jutlandicum, Isothecium myosuroides, Oxalis acetosella, lichens, detritophagous*	ova laid in straight rows of 2-6 eggs fixed to the substrate	asymmetrically ovoid, slightly dimpled	lives under lichens and mosses on Quercus, Fagus and rocks	Goater, Nuss & Speidel, 2004
	Scoparia	*ancipitella*	Mniaceae, Polytrichaceae	*Mnium hornum, Polytrichum commune*				Goater, Nuss & Speidel, 2004

Continued on next page

Table A.7 – *Continued from previous page*

	Genus	Species	Host plant taxonomical rank	Host plant species	Egg-laying behaviour	Egg type	Larval life habits	References
Scopariinae	*Scoparia*	*basistrigalis*	Brachytheciaceae, Ditrichaceae	*Ceratodon purpureus, Eurhynchium praelongum, Brachythecium rutabulum*				Goater, Nuss & Speidel, 2004
	Scoparia	*pyralella*	Asteraceae	*Senecio jacobaea, detritophagous*				Goater, Nuss & Speidel, 2004
	Scoparia	*subfusca*	Asteraceae	*Picris hieracioides, Tussilago*			scores and channel the surface of the roots, occasionally making short tunnels through it	Goater, Nuss & Speidel, 2004
Spilomelinae	*Anania*	*funebris*	Asteraceae, Fabaceae	*Solidago virga-aurea, Genista trinctoria*				HOSTS database
	Anania	*verbascalis*	Asteraceae, Lamiaceae, Scrophulariaceae	*Aster multiflorus, Helianthus annuus, Leucanthemum vulgare, Xanthium strumarium, Teucrium scorodonia, Verbascum thapsus*				HOSTS database
	Herpetogramma	*bipunctalis*			small clusters of ~10 eggs	Scale-like		Peterson, 1963
	Hymenia	*fasciales*			laid singly on oak foliage	Scale-like, translucent		Peterson, 1963
	Loxogeste	*similalis*			round clusters of 10-50 or more overlapping ova	0.73×0.55mm, scale-like		Peterson, 1963
	Nomophila	*noctuella*			singly or in clusters of 4-20 eggs	0.6×0.4mm		Peterson, 1963
	Patania	*ruralis*	Asteraceae, Fabaceae, Urticaceae, Poaceae: Panicoideae	*Lactuca sativa, Glycine max, Zea mays, Urtica dioica*	eggs glued singly on Urticaceae		larva lives in rolled-up leaves; it makes a window, the hole before feeding along the margin of the leaf	HOSTS database; www.lepiforum.de
	Pilocrocis	*ramentalis*			glued in clusters of ~35 eggs	0.7×0.55mm, scale-like		Peterson, 1963
	Samea	*ecclesialis*			occur in small groups of ~6-15	0.7×0.4mm, scale-like		Peterson, 1963

Continued on next page

Table A.7 – *Continued from previous page*

	Genus	Species	Host plant taxonomical rank	Host plant species	Egg-laying behaviour	Egg type	Larval life habits	References
Spilomelinae	*Udea*	*carniolica*			eggs glued in cluster of ∼13			www.lepiforum.de
	Udea	*murinalis*			eggs glued in cluster of ∼5			www.lepiforum.de
	Udea	*rubigalis*			eggs in clusters of 6-12, covered with elongated mass with needle-like, light-brown structures	0.65×0.6mm, milky-white to yellowish		Peterson, 1963

Appendix B

Refining the phylogeny of Crambidae with complete sampling of subfamilies (Lepidoptera, Pyraloidea)

Table B.1: PCR primers used for this work

Gene	Primer	Sequence (5' -> 3')	Direction	Annealing temperature	PCR product length (bp)	Reference
CAD	CAD743f	GGNGTNACNACNGCNTGYTTYGARCC	F	55	850	Wahlberg & Wheat, 2008
CAD	CADf19	AGYTCNATGAAAAGYGTNGG	F	55	754	Léger et al. (2019)
CAD	CAD1028r	TTRTTNGGNARYTGNCCNCCCAT	R	55	850	Wahlberg & Wheat, 2008
CAD	CADr604	CATCCHACWGCACACCAATC	R	55	661	Léger et al. (2019)
CAD	CAD_exon4f2	TRGGNACYCCNATHCARTC	F	55	754	This study
CAD	CAD_exon4r2	ACYTCNCCNACRCTTTTCAT	R	55	754	This study
COI	LCO	GGTCAACAAATCATAAAGATATTGG	F	50	676	Wahlberg & Wheat, 2008
COI	Nancy	CCTGGTAAAATTAAAATATAAACTTC	R	50	676	Simon et al., 1994
COI	Jerry	CAACAYTTATTTTGATTTTTTGG	F	50	829	Wahlberg & Wheat, 2008
COI	Pat	ATCCATTACATATAATCTGCCATA	R	50	829	Wahlberg & Wheat, 2008
DDC	DDC Wahlberg3.2sF	TGGYTICAYGTIGAYGCNGCNTAYGC	F	55	621	Wahlberg & Wheat, 2008
DDC	DDC_exon3r	GNGARCAAATHGCTAAYCTTA	R	55	621	This study
EF-1alpha	Oscar	GGCCCAAGGAAATGGGCAAGGG	F	58	750	Haines & Rubinoff, 2012
EF-1alpha	Bosie	CCGGCGACGTAACCACGACGC	R	58	750	Haines & Rubinoff, 2012
EF-1alpha	EF51.9	CARGACGTATACAAAATCGG	F	50	511	Cho et al., 1995
EF-1alpha	EFrcM4	ACAGCVACKGTYTGYCTCATRTC	R	50	511	Cho et al., 1995
GAPDH	Frigga	AARGCTGGRGCTGAATATGT	F	55	691	Wahlberg & Wheat, 2008
GAPDH	GAPDHf96	YTCYTGCACYACCAACTG	F	55	508	Léger et al. (2019)
GAPDH	Burre	GWTTGAATGTACTTGATRAGRTC	R	55	691	Wahlberg & Wheat, 2008
GAPDH	GAPDHr610	TCRTTGTCRTACCARCTGAT	R	55	646	Léger et al. (2019)
IDH	IDHdeg27F	GGWGAYGARATGACNAGRATHATHTGG	F	55	711	Wahlberg & Wheat, 2008
IDH	IDHdegR	TTYTTRCAIGCCCANACRAANCCNCC	R	55	711	Wahlberg & Wheat, 2008
IDH	IDHf169	ATGTGGAARAGYCCYAATGG	F	53	490	Léger et al. (2019)
IDH	IDHr626	CAATCARYCTRTGCTCATACC	R	53	658	Léger et al. (2019)
RpS5	RpS5f	ATGGCNGARGARAAYTGGAAYGA	F	55	613	Wahlberg & Wheat, 2008
RpS5	RpS5f3	GAYATTCCYGAAATCAAACT	F	55	535	Léger et al. (2019)
RpS5	RpS5r	CGGTTRGAYTTRGCAACACG	R	55	613	Wahlberg & Wheat, 2008
RpS5	RpS5r538	TCCARCTCRTCCTTYTTYTT	R	55	592	Léger et al. (2019)
wingless	LepWg1	GARTGYAARTGYCAYGGYATGTCTGG	F	50	400	Brower & DeSalle, 1998
wingless	LepWg2	ACTICGCARCACCARTGGAATGTRCA	R	50	400	Brower & DeSalle, 1998

Table B.2: List of the 100 taxa sampled along with the study where they were used and their access numbers in respective depositories. For sequences extracted from published genomes or transcriptomes, the sequence length is given. Subfamilial and tribal assignments follows the current classification (prior to this study) according to GLOBIZ (Nuss, 2003-2019).

	Species	Voucher code	Study	COI (1440bp)	EF-1alpha (1071bp)	GAPDH (654bp)	IDH (657bp)	rps5 (576bp)	wingless (402bp)	CAD (2958bp)	DDC (1281bp)	enolase (1134bp)	period (1074bp)
Acentropinae	Acentria ephemerella	ZMBN233	Léger (2019) - this study	LR135742, LR135742	LR743320FT, LR743352FT	X	LR134718	LR134888	LR743192FT	LR743218FT, LR134540	LR743264FT	X	X
	Aulacodes sp-n	KN-06-0005	Regier (2012)	657	X	X	X	X	JQ786692	JQ784336	JQ785699	JQ789358	JQ785295
	Elophila nymphaeata	MM01074	Mutanen (2010)	GU828657, GU828455	GU828988, GU829272	GU829784	GU830044	GU830655	GU829543	GU828154	X	X	X
	Petrophila confusalis	RR-98-1148	Regier (2012)	657	X	X	X	X	GQ283876	GQ283562	GQ283641	GQ283723	GQ283799
Catharinae	Catharia pyrenaealis	MTDLEP116	this study	LR743376FT, LR743399FT	LR743329FT, LR743359FT	LR743166FT	LR743152FT	LR743128FT	LR743200FT	LR743229FT, LR743246FT	LR743275FT	X	X
Chrysauginae	Cryptoses chloepi	MTDLEP863	this study	LR743374FT, LR743397FT	LR743327FT, LR743358FT	LR743164FT	LR743150FT	X	LR743198FT	X	X	X	X
	Monoloxis flavicinctalis	05-srnp-24832	Regier (2012)	X	X	X	X	X	GQ283868	GQ283554	GQ283636	GQ283716	GQ283794
	Tosale oviplagalis	MM07088	Mutanen (2010)	GU828764, GU929738	GU829077, GU829360	GU829855	GU830149	X	GU829626	X	X	X	X
Crambinae	Ancylolomia inornata	MTDLEP1634	Léger (2019) - this study	LR214893, LR135663	LR743356FT	LR134649	LR134739	X	X	LR134562	X	X	X
	Argyria sp.	MTDLEP976	Léger (2019) - this study	HG793013, HG793013	LR743357FT	LR134633	LR134725	LR134894	LR743195FT	LR743222FT, LR134547	LR743268FT	X	X
	Calamotropha paludella	MTDLEP1547	Léger (2019) - this study	LR135703, LR135703	LR743348FT	LR134641	LR134732	LR134902	X	LR743214FT, LR134554	LR743260FT	X	X
	Catoptria oregonica	RR-98-1176	Regier (2012)	X	X	X	X	X	GQ283832	GQ283516	GQ283603	GQ283680	GQ283762
	Chilo suppressalis	CsuOGS1.0	Lepbase	1440	1071	X	657	576	X	X	X	X	X
	Chilo suppressalis	MAS-92-1001-1	Regier (2012)	X	X	X	X	X	JQ786745	JQ784428	JQ785784	JQ789442	JQ785349
	Coniesta williami	MTDLEP2094	Léger (2019) - this study	LR214895, LR135665	X	LR134653	LR134743	LR134912	X	LR743223FT, LR134566	LR743269FT	X	X
	Crambus agitatellus	JWB-08-0114	Regier (2012)	X	X	X	X	X	X	JQ784371	JQ785733	X	JQ785313

Continued on next page

Table B.2 – *Continued from previous page*

	Species	Voucher code	Study	COI (1440bp)	EF-1alpha (1071bp)	GAPDH (654bp)	IDH (657bp)	rps5 (576bp)	wingless (402bp)	CAD (2958bp)	DDC (1281bp)	enolase (1134bp)	period (1074bp)
Crambinae	Crambus uliginosellus	MM03362	Mutanen (2010)	GU828691, GU828487	GU829014, GU829302	GU829811	GU830078	GU830681	GU829571	GU828182	X	X	X
	Gargela renatusalis	ITBC10	Léger (2019) - this study	LR135729, LR135729	LR743326FT	LR134683	LR134773	LR134943	X	LR743227FT, LR134596	LR743273FT	X	X
	Glaucocharis chrysochyta	MTDLEP2650	Léger (2019) - this study	LR135716, LR135716	X	LR134663	LR134753	LR134922	X	LR743224FT, LR134576	LR743270FT	X	X
	Myelobia smerintha	FG120071B	Kawahara & Breinholt (2014)	SRS620579	1071	SRS620579	SRS620579	SRS620579	X	X	980	X	1008
Cybalomiinae	Cybalomia fractilinealis	MTDLEP903	this study	LR743377FT, LR743400FT	LR743330FT, LR743360FT	LR743167FT	LR743153FT	X	X	X	X	X	X
	Hendecasis apicefulva	MM13885	Heikkila (2015)	1385	829	X	X	575	349	400	X	X	X
	Hyperlais nemausalis	MTDLEP1305	this study	LR743378FT, LR743401FT	LR743331FT, LR743361FT	LR743175FT	LR743154FT	LR743129FT	X	LR743230FT, LR743247FT	X	X	X
	Prochoristis sp	MTDLEP902	this study	LR743379FT, LR743402FT	LR743332FT, LR743362FT	LR743182FT	LR743155FT	LR743130FT	LR743201FT	LR743248FT	X	X	X
	Stiphrometasia monialis	MTDLEP904	this study	LR743380FT, LR743403FT	LR743333FT, LR743363FT	LR743183FT	LR743156FT	LR743131FT	LR743202FT	LR743231FT, LR743249FT	LR743276FT	X	X
Epipaschiinae	Accinctapubes albifasciata	05-srnp-46779	Regier (2012)	X	X	X	X	X	GQ283822	GQ283505	GQ283592	GQ283669	GQ283752
	Salma pyrastis	MJM-97-0297	Regier (2012)	X	X	X	X	X	JQ787035	JQ784826	JQ786143	JQ789773	JQ785592
	Stericta concisella	MM07502	Mutanen (2010)	GU828772, GU929745	GU829083, GU829364	GU829859	GU830154	X	GU829634	KT713807	X	X	X
Galleriinae	Aphomia sociella	MM01875	Mutanen (2010)	GU828676, GU828473	GU829004, GU829288	GU829799	GU830063	GU830670	GU829560	GU828171	X	X	X
	Galleria melonella	CWM-08-2532	Regier (2012)	X	X	X	X	X	JQ786829	JQ784545	JQ785888	JQ789539	JQ785415
	Macrotheca sp	RR-98-1123	Regier (2012)	X	X	X	X	X	GQ283865	GQ283551	GQ283634	GQ283713	GQ283791
Glaphyriinae	Chalcoela iphitalis	CWM-06-1016	Regier (2012)	657	X	X	X	X	JQ786721	JQ784395	JQ785755	JQ789411	JQ785328
	Cosmopterosis cf-jasonhalli	ZMBN231	this study	LR743381FT, LR743404FT	LR743334FT, LR743364FT	LR743171FT	LR743157FT	LR743132FT	X	LR743232FT	LR743277FT	X	X
	Crocidolomia luteolalis	AZ-07-2685	Regier (2012)	657	X	X	X	X	JQ786710	JQ784378	JQ785739	JQ789394	JQ785316

Continued on next page

Table B.2 – *Continued from previous page*

	Species	Voucher code	Study	COI (1440bp)	EF-1alpha (1071bp)	GAPDH (654bp)	IDH (657bp)	rps5 (576bp)	wingless (402bp)	CAD (2958bp)	DDC (1281bp)	enolase (1134bp)	period (1074bp)
Glaphyriinae	Dichogama colotha	05-srnp-18221	Regier (2012)	X	X	X	X	X	X	JQ784451	JQ785805	JQ789464	JQ785365
	Dicymolomia metalliferalis	RR-99-1228	Regier (2012)	657	X	X	X	X	JQ786765	JQ784460	JQ785812	JQ789470	JQ785370
	Evergestis forficalis	MM01218	Mutanen (2010)	GU828662, GU828460	GU828993	GU829789	GU830049	GU830659	GU829548	GU828159	X	X	X
	Evergestis funalis	RR-98-1157	Regier (2012)	657	X	X	X	X	JQ786804	JQ784514	JQ785859	JQ789512	JQ785397
	Hellula phidilealis	MTDLEP119	this study	LR743370FT, LR743390FT	LR743315FT, LR743346FT	LR743172FT	LR743143FT	X	X	LR743213FT, LR743239FT	LR743259FT	X	X
	Noorda blitealis	WM-08-4009	Mutanen (2010) - Regier (2012)	GU828868, GU929828	GU829170, GU829430	X	GU830246	X	JQ786932	JQ784674	JQ786007	JQ789647	JQ785500
	Trischistognatha palindialis	ZMBN232	this study	LR743375FT, LR743398FT	LR743328FT	LR743186FT	LR743151FT	LR743127FT	LR743199FT	LR743228FT	LR743274FT	X	X
Heliothelinae	Heliothela wulfeniana	MTDLEP550	Léger (2019) - this study	LR214888, LR135658	LR743321FT, LR743353FT	LR134627	LR134719	X	X	LR743219FT, LR134541	LR743265FT	X	X
	Hoploscopa sp-larva	ZMBN107	this study	LR743373FT, LR743395FT	LR743322FT, LR743354FT	LR743173FT	LR743148FT	LR743125FT	LR743193FT	LR743220FT, LR743244FT	LR743266FT	X	X
Lathrotelinae	Diplopseustis cf-perieresalis	ZMBN68	this study	LR743382FT, LR743405FT	LR743335FT, LR743365FT	LR743169FT	LR743158FT	LR743133FT	LR743203FT	LR743250FT	LR743278FT	X	X
	Sufetula cf-sythoffi	ZMBN57	this study	LR743383FT, LR743406FT	LR743336FT, LR743366FT	LR743185FT	X	LR743134FT	LR743204FT	LR743233FT, LR743251FT	LR743279FT	X	X
	Sufetula diminutalis	MTDLEP1307	this study	MK459668	MK459850	MK460138	MK459954	MK460054	X	LR743215FT, MK459765	LR743261FT	X	X
Linostinae	Linosta sp	MTD4865	this study	LR743384FT, LR743407FT	LR743337FT	LR743177FT	LR743159FT	LR743135FT	LR743205FT	LR743234FT	X	X	X
Midilinae	Cacographis osteolalis	MAS-91-0407-1	Regier (2012)	X	X	X	X	X	JQ786735	JQ784413	X	JQ789428	JQ785341
	Dismidila atoca	MAS-06-0202	Regier (2012)	657	X	X	X	X	JQ786764	JQ784459	JQ785811	X	X
	Erupa sp	MTD4551	Léger (2019) - this study	LR214889, LR135659	LR743325FT	LR134629	LR134721	LR134890	LR743197FT	LR743226FT, LR134543	LR743272FT	X	X
	Hositea regina	ZMBN230	this study	LR743385FT, LR743408FT	X	LR743174FT	LR743160FT	LR743136FT	LR743206FT	X	LR743280FT	X	X

Continued on next page

Table B.2 – *Continued from previous page*

	Species	Voucher code	Study	COI (1440bp)	EF-1alpha (1071bp)	GAPDH (654bp)	IDH (657bp)	rps5 (576bp)	wingless (402bp)	CAD (2958bp)	DDC (1281bp)	enolase (1134bp)	period (1074bp)
Midilinae	Midila daphne	MAS-06-0201	Mutanen (2010) - Regier (2012)	GU828567, GU828368	GU828909, GU829204	X	GU829957	GU830589	JQ786914	JQ784653	JQ785991	X	X
	Midila guianensis	MTDLEP370	this study	MK459667	MK459849	MK460137	MK459953	MK460053	X	MK459764	X	X	X
Musotiminae	Ambia sp	MTDLEP3055	this study	LR743386FT, LR743410FT	LR743339FT	LR743180FT	LR743162FT	LR743138FT	LR743207FT	X	X	X	X
	Musotima nitidalis	MM07661	Mutanen (2010)	GU828816, GU929784	GU829121, GU829396	GU829888	GU830197	GU830769	GU829670	GU828285	X	X	X
	Neurophyseta conantia	MAS-91-0601	Regier (2012)	X	X	X	X	X	JQ786929	JQ784670	JQ786004	JQ789644	JQ785498
Odontiinae	Cliniodes opalalis	05-srnp-7932	Regier (2012)	657	X	X	X	X	JQ786723	JQ784397	JQ785757	JQ789413	JQ785330
	Cynaeda dentalis	MTDLEP139	this study	LR743369FT, LR743388FT	LR743310FT, LR743341FT	LR743168FT	LR743140FT	LR743117FT	LR743188FT	LR743209FT, LR743236FT	LR743255FT	X	X
	Dausara amethysta	ITBC98	this study	LR743387FT, LR743411FT	LR743340FT, LR743368FT	X	LR743163FT	LR743139FT	LR743208FT	LR743235FT, LR743253FT	LR743281FT	X	X
	Metaxmeste phrygialis	MTDLEP843	this study	LR743372FT	LR743319FT, LR743351FT	LR743178FT	LR743147FT	LR743124FT	X	LR743217FT, LR743243FT	LR743263FT	X	X
	Syntonarcha iriastis	AZ-07-2650	Regier (2012)	X	X	X	X	X	X	JQ784835	X	JQ789781	JQ785599
	Syntonarcha iriastis	MTDLEP3002	this study	LR743371FT	X	LR743533	LR743534	LR743121FT	X	X	X	X	X
Phycitinae	Ambesa laetella	RR-98-1191	Regier (2012)	X	X	X	X	X	JQ786672	JQ784307	JQ785674	JQ789330	JQ785278
	Amyelois transitella	GCA-001186105	Lepbase	X	1071	654	657	576	402	2928	1278	1134	1011
	Dioryctria auranticella	RR-98-1142	Regier (2012)	X	X	X	X	X	JQ786758	JQ784446	JQ785801	JQ789459	JQ785361
	Ephestia kuehniella	MM00141	Mutanen (2010)	GU828613, GU828411	GU828947, GU829239	GU829761	GU830001	GU830622	GU829507	GU828114	X	X	X
	Phycitinae genus-sp	NB-06-0053	Regier (2012)	X	X	X	X	X	JQ786836	JQ784553	JQ785896	JQ789545	JQ785420
	Plodia interpunctella	RFD-96-1255	Regier (2012)	X	X	X	X	X	GQ283881	GQ283567	GQ283646	GQ283728	AF063440

Continued on next page

Table B.2 – *Continued from previous page*

	Species	Voucher code	Study	COI (1440bp)	EF-1alpha (1071bp)	GAPDH (654bp)	IDH (657bp)	rps5 (576bp)	wingless (402bp)	CAD (2958bp)	DDC (1281bp)	enolase (1134bp)	period (1074bp)
Pyralinae	Aglossa pinguinalis	MM00106	Mutanen (2010)	GU828599, GU828398	GU828933	GU829753	GU829988	X	GU829495	GU828100	X	X	X
	Gauna aegusalis	MJM-97-0311	Regier (2012)	X	X	X	X	X	GQ283855	GQ283541	GQ283625	GQ283703	GQ283782
	Hypsopygia glaucinalis	AYK-04-0881-10	Regier (2012)	X	X	X	X	X	JQ786951	JQ784700	JQ786032	JQ789672	JQ785516
	Hypsopygia olinalis	AM-93-0021	Regier (2012)	X	X	X	X	X	JQ786846	JQ784567	JQ785910	JQ789557	JQ785429
	Pyralis farinalis	CWM-08-2331	Regier (2012)	X	X	X	X	X	JQ786824	JQ784539	JQ785882	JQ789533	JQ785410
	Pyralis farinalis	MM00051	Mutanen (2010)	GU828590, GU828389	GU828925, GU829221	GU829747	GU829979	GU830604	GU829487	GU828092	1053	X	X
	Synaphe punctalis	MTDLEP393	this study	JF497027	MK459848	MK460136	MK459952	MK460052	JF497068	MK459763	LR743256FT	X	X
Pyraustinae	Anania hortulata	MM01851	Mutanen (2010)	GU828675, GU828472	GU829003, GU829287	GU829798	GU830062	GU830669	GU829559	GU828170	X	X	X
	Euclasta splendidalis	MTDLEP1466	this study	MK459751	MK459938	LR743170FT	MK460038	MK460125	LR743194FT	LR743221FT, MK459837	LR743267FT	X	X
	Ostrinia furnacalis	MAS-92-0801	Regier (2012)	657	X	X	X	X	X	X	JQ786036	JQ789677	JQ785519
	Portentomorpha xanthialis	MTDLEP1322	this study	MK506077, MK459758	MK459946	LR743181FT	MK460046	MK460132	X	MK459844	X	X	X
	Pyrausta zonalis	RR-98-1141	Regier (2012)	653	X	X	X	X	JQ786986	JQ784753	JQ786076	JQ789714	JQ785550
Schoenobiinae	Rupela albina	MAS-91-0209	Regier (2012)	X	X	X	X	X	GQ283889	GQ283575	GQ283653	GQ283736	AF063444
	Schoenobius gigantellus	MM09194	Mutanen (2010)	GU828842, GU929806	GU829143, GU829411	GU829903	GU830222	GU830790	GU829691	GU828306	X	X	X
	Scirpophaga incertulas	MAS-92-1003	Regier (2012)	X	X	X	X	X	X	X	X	X	X
	Scirpophaga incertulas	SRR1613323	Renuka (2017)	1256	1047	548	323	565	401	2923	1276	X	X
Scopariinae	Anarpia incertalis	MTDLEP839	Léger (2019) - this study	LR214906, LR135676	LR743324FT	LR134692	LR134782	LR134951	LR743196FT	LR743225FT, LR134604	LR743271FT	X	X
	Eudonia spenceri	RR-98-1146	Regier (2012)	620	X	X	X	X	X	GQ283580	GQ283658	GQ283741	GQ283812

Continued on next page

Table B.2 – *Continued from previous page*

	Species	Voucher code	Study	COI (1440bp)	EF-1alpha (1071bp)	GAPDH (654bp)	IDH (657bp)	rps5 (576bp)	wingless (402bp)	CAD (2958bp)	DDC (1281bp)	enolase (1134bp)	period (1074bp)
Scopariinae	Eudonia truncicolella	MM04967	Mutanen (2010)	GU828709, GU828504	GU829032, GU829321	GU829823	GU830095	GU830697	GU829585	GU828197	X	X	X
	Gesneria centuriella	MTDLEP2307	Léger (2019) - this study	LR214908, LR135678	X	LR134695	LR134784	LR134953	X	LR134607	LR743254FT	X	X
	Scoparia basistrigalis	MTDLEP2314	Léger (2019) - this study	LR214909, LR135679	LR743313FT, LR743344FT	LR134696	LR134785	LR134954	X	LR743211FT, LR134608	LR743257FT	X	X
	Scoparia isochroalis	SWC-06-0240	Regier (2012)	657	X	X	X	X	JQ787033	JQ784823	JQ786140	JQ789771	JQ785590
Spilomelinae	Cnaphalocrocis medinalis	SRR64791	Kawahara & Breinholt (2014)	1039	983	648	569	209	X	168	1039	1065	398
	Diaphania indica	AYK-04-5705	Regier (2012)	657	X	X	X	X	X	JQ784462	JQ785814	JQ789472	JQ785372
	Leucinodes africensis	MTDLEP1562	this study	LN624711, MK459711	MK459894	LR743176FT	MK459995	LR743123FT	X	LR743216FT, MK459804	LR743262FT	X	X
	Mesocondyla dardusalis	Ppy224	Regier (2012)	X	X	X	X	X	GQ283885	GQ283571	GQ283650	GQ283732	AF063443
	Niphopyralis chionesis	ANIC002674	Mutanen (2010)	GU828537, GU828339	GU829183, GU829183	X	GU829928	GU830572	GU829444	GU828048		X	X
	Niphopyralis chionesis	AZ-07-2642	Regier (2012)	X	X	X	X	X	JQ786937	JQ784682	JQ786015	JQ789654	JQ785504
	Phaedropsis alitemeralis	MAS-91-0122	Regier (2012)	X	X	X	X	X	GQ283884	GQ283570	GQ283649	GQ283731	AF063442
	Syllepis marialis	MTDLEP1320	Léger (2019) - this study	LR135741, LR135741	LR743314FT, LR743345FT	LR134626	LR134717	LR134887	LR743191FT	LR743212FT, LR134539	LR743258FT	X	X
	Udea ferrugalis	MTDLEP870	this study	JF852252, MK459744	MK459930	MK460195	MK460030	LR743118FT	LR743189FT	LR743210FT, MK459830	X	X	X

Figure B.1: Best-scoring ML tree of the whole dataset with best Partition Finder model applied and bootstrap support values from 1000 replicates displayed on nodes

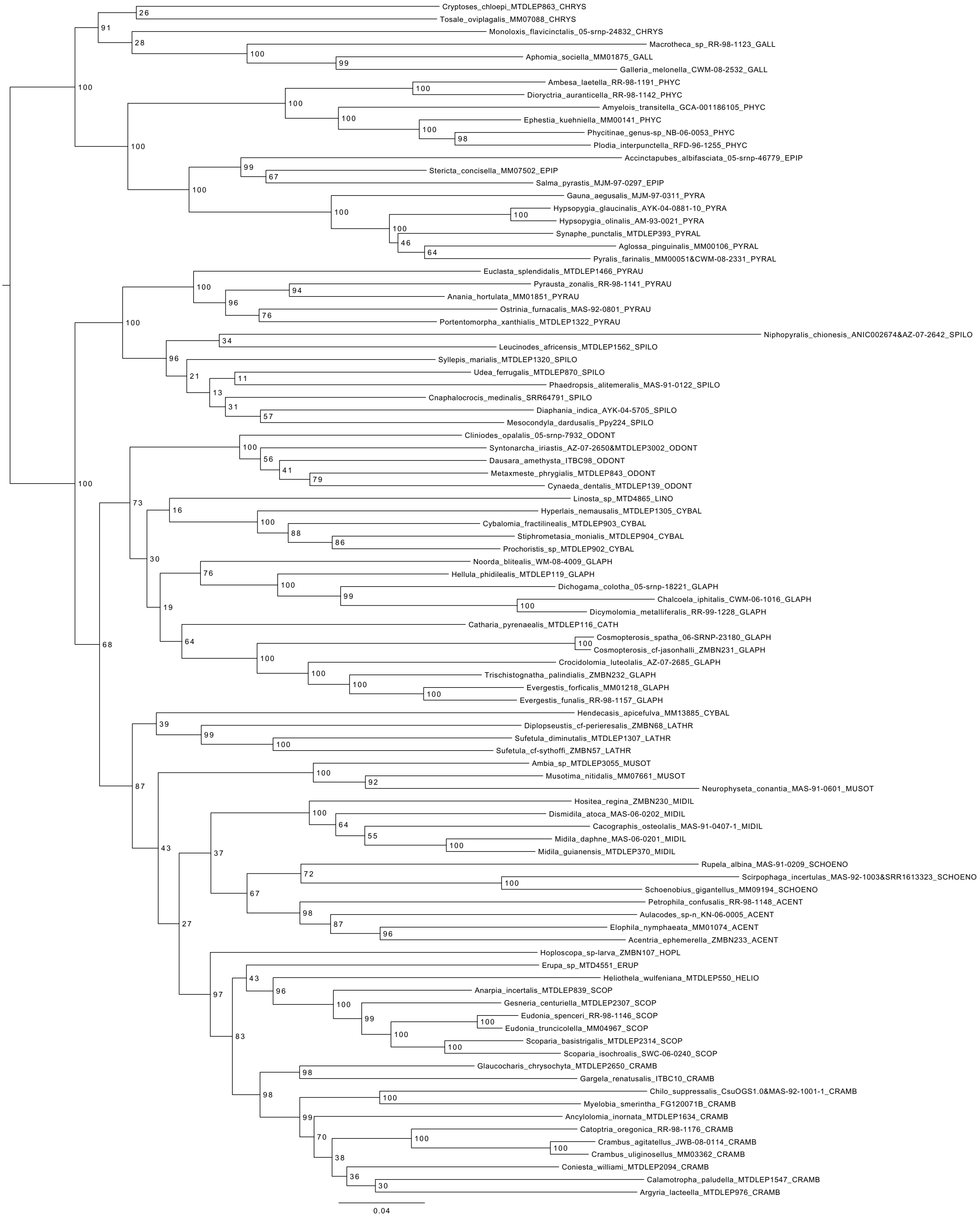
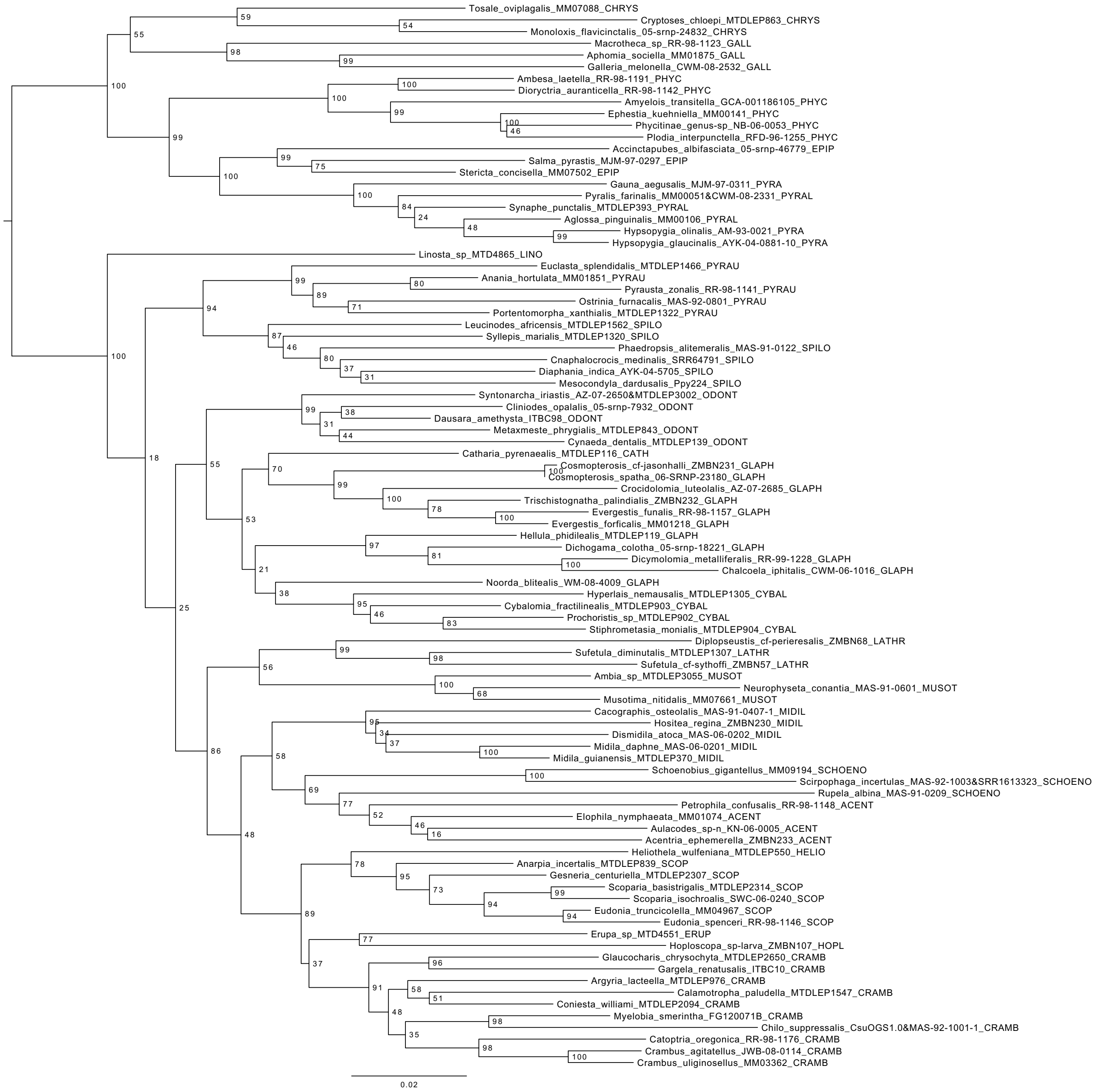


Figure B.2: Best-scoring ML tree of the conc10genes_nosyn dataset with best Partition Finder model applied and bootstrap support values from 1000 replicates displayed on nodes



Appendix C

Twenty-six new species of *Hoploscopa* (Lepidoptera, Crambidae) from South-East Asian revealed by morphology and DNA barcoding.

Figure C.1: Scheme summarising the approach followed for amplification of the COI barcode from old material.

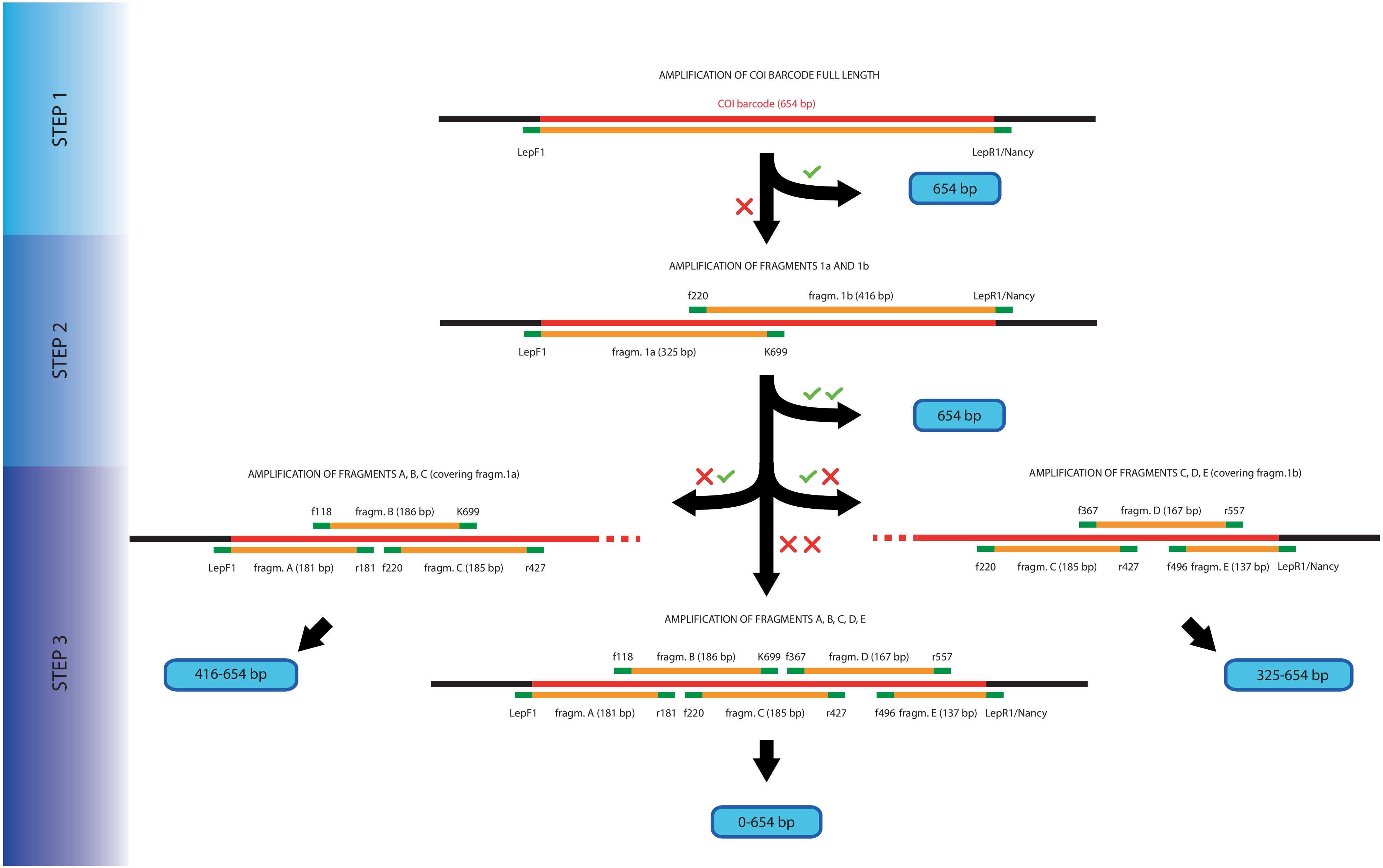


Table C.1: Primers sequences with characteristics and chemical properties.

Gene	Fragment N°	Fragment length (length without primers between brackets)	Primer	Overlap with preceding fragment	Overlap with following fragment	Tm used	Sequence	References
COI Barcode part	1a	371 (325)	LepF1	-	83bp	49°	ATTCAACCAATCATAAAGATATTGG	Hebert et al. 2004
			K699				WGGGGGGTAAACTGTTCATCC	http://www.nymphalidae.net/Molecular.htm
COI Barcode part	1b	464 (416)	f220	83bp	-	49°	CCYGAYATAGCYTTYCCMCGAA	This study
			LepR1				TAAACTTCTGGATGTCCAAAAAATCA	Hebert et. al. 2004
COI Barcode part	A	228 (181)	LepF1	-	42bp	49°	ATTCAACCAATCATAAAGATATTGG	Hebert et. al. 2004
			r181				GWACTARTCAATTTCCRAATCC	This study
COI Barcode part	B	228 (186)	f118	42bp	83bp	49°	ACYATTGTWACAGCYCAYGCT	This study
			K699				WGGGGGGTAAACTGTTCATCC	http://www.nymphalidae.net/Molecular.htm
COI Barcode part	C	233 (185)	f220	83bp	37bp	49°	CCYGAYATAGCYTTYCCMCGAA	This study
			r427				GTTGTAATAAARTTAATDGCYCCTAA	This study
COI Barcode part	D	210 (167)	f367	37bp	36bp	49°	AGAGGWAGHTCWGTAGATTTAGC	This study
			r557				ARTATDGTAATAGCTCCHGCTA	This study
COI Barcode part	E	188 (137)	f496	36bp	-	49°	CCWYTATTTATTTGAGCTGTWGGAA	This study
			LepR1				TAAACTTCTGGATGTCCAAAAAATCA	Hebert et. al. 2004

Table C.2: List of DNA samples of *Hoploscopa* species and allies used in this study.

	Voucher N°	Species	Origin and Institution storage	LepF1/LepR1	Fragm 1a (LepF1/K699)	Fragm 1b (f220/LepR1)	Fragm. A (LepF1/r181)	Fragm. B (f118/K699)	Fragm. C (f220/r427)	Fragm. D (f367/r557)	Fragm. E (f496/LepR1)	COI barcode length (bp)	GenBank accession	BOLD sample	Tissue
This study	MTD7415	*H. agtuuganonensis*	PHIL: Mindanao, Mt Agtuuganon, 126.205833E 7.781389N, 1050m, 7.6.1996 (W. Mey) [MFNB]	-	X	OK						416	LR699226FT	HOPLO080-19	abdomen
	MTD7416	*H. agtuuganonensis*	PHIL: Mindanao, Mt Agtuuganon, 126.205833E 7.781389N, 1050m, 7.6.1996 (W. Mey) [MFNB]	-	OK	OK						614	LR699227FT	HOPLO081-19	abdomen
	MTD7434	*H. albipuncta*	MALAYSIA: Sabah, Mesilau Nature Resort, 116.596111E 6.044722N, 2000m, 17.11.2006 (W. Mey & K. Ebert) [MFNB]	OK								526	LR699228FT	HOPLO003-19	abdomen
	MTD7430	*H. albipuncta MOTU 2*	PHIL: Luzon, Mt Province, Bontoc, Barlig, 121.149413E 17.076131N 1650m, 15.11.1997 (W. Mey, K. Ebert & M. Nuss) [MFNB]	-	OK	OK						614	LR699229FT	HOPLO001-19	abdomen
	MTD8247	*H. anacantha*	INDONESIA: North Sulawesi, Danau Mooat, near Kotamobagu, 1200m, 27-28.ix.1985 [NHMUK]	-	OK	X	OK	OK	OK	OK	X	528	LR699230FT	HOPLO082-19	abdomen
	MTD8255	*H. anamesa*	VANUATU: Aneityum Island, Agathis Camp, 1150’, 21.vii.1971 (G. Robinson) [NHMUK]	-	X	X	X	X	OK	OK	OK	341	LR699231FT	HOPLO093-19	abdomen
	MTD8250	*H. astrapias*	FIJI: Viti Levu, 2700’, Nandarivatu, 14.ix.1955 (H. Simmonds) [NHMUK]	-	X	X	X	X	OK	OK	OK	415	LR699232FT	HOPLO094-19	abdomen
	LEP3159	*H. boleta*	PNG: Morobe Prov., near Wau, Mt. Kaindi, 2360m, 27-28.vii.1983 (S. E. & P. M. Miller) [USNM]	-	OK	X			OK	OK	OK	649	LR699233FT	HOPLO043-19	abdomen
	LEP3160	*H. boleta*	PNG: Morobe Prov., Mt Kaindi, 2360m, 3.x.1992 (V. O. Becker) [USNM]	-	OK	X			OK	X	OK	561	LR699234FT	HOPLO044-19	abdomen
	LEP3168	*H. boleta*	PNG: Morobe Prov., Mt. Kaindi, 2360m, 3.x.1992 (V. O. Becker) [USNM]	-	OK	X			OK	OK	OK	658	LR699235FT	HOPLO045-19	abdomen

Continued on next page

Table C.2 – *Continued from previous page*

	Voucher N°	Species	Origin and Institution storage	LepF1/LepR1	Fragm 1a	Fragm 1b	Fragm. A	Fragm. B	Fragm. C	Fragm. D	Fragm. E	COI bar-code length (bp)	Gen- Bank accession	BOLD sample ID	Tissue
This study	LEP3066	*H. cynodonta*	MALAYSIA: Sabah, Kinabalu Park HQ, junction Kiau View- and Pandanus Trail, 6°0'32.84N 116°32'14.94E, 1690m, UV light, 07.06.2015 (T. Léger & R. Mally) [MTD]	OK								614	LR699236FT	HOPLO031-19	abdomen
	MTD7425	*H. cynodonta*	MALAYSIA: Sabah, Tawau, Tawau Hills National Park, 117.952219E 4.436889N, 11.27.2006 (W. Mey & K. Ebert) [MFNB]	OK								548	LR699237FT	HOPLO030-19	abdomen
	MTD7419	*H. danaoensis*	PHIL: Leyte, Ormoc, Lake Danao, 124.69E 11.06N, 650m, 17.4.1997 (W. Mey & W. Speidel) [MFNB]	-	OK	OK						617	LR699238FT	HOPLO077-19	abdomen
	MTD8142	*H. danaoensis*	PHIL: Leyte, Ormoc, Lake Danao, 124.69E 11.06N, 650m, 17.4.1997 (W. Mey & W. Speidel) [MFNB]	-	OK	OK						620	LR699239FT	HOPLO079-19	abdomen
	MTD8139	*H. danaoensis MOTU 2*	PHIL: Negros, Patag, Lake Danao, 1400m, 21.5.1996 (W. Mey) [MFNB]	-	OK	OK						638	LR699240FT	HOPLO091-19	abdomen
	MTD8140	*H. danaoensis MOTU 2*	PHIL: Negros, Patag, Lake Danao, 1400m, 21.5.1996 (W. Mey) [MFNB]	-	OK	OK						416	LR699241FT	HOPLO092-19	abdomen
	MTD7417	*H. danaoensis MOTU 3*	PHIL: Mindanao, Mt Agtuuganon, 126.205833E 7.781389N, 1050m, 7.6.1996 (W. Mey) [MFNB]	-	OK	OK						614	LR699242FT	HOPLO076-19	abdomen
	LEP3203	*H. gracilis*	INDONESIA: Sumatra, Sipirok, 1450m, 27-28.i.1995 (A. Kallies) [MTD]	X	OK	OK						630	LR699243FT	HOPLO054-19	abdomen
	LEP3204	*H. gracilis*	INDONESIA: Sumatra, Dairi Ost a, near Sumbul, 2°46'N 98°32'E, 1670m, 20.ii.1999 (U. Buchsbaum) [MTD]	OK								516	LR699244FT	HOPLO055-19	abdomen
	MTD7876	*H. gracilis*	INDONESIA: Sumatra, Sipirok, 99.25E 1.6N, 1450m (A. Kallies) [MTD]	-	OK	OK						612	LR699245FT	HOPLO056-19	abdomen
	MTD8256	*H. gracilis*	INDONESIA: Sumatra, Mount Sibayak, ca. 1900 müNN, 03°14'19N/098°29'52E, 02.03.2002 (U. Buchsbaum) [MTD]	-	OK	OK						580	LR699246FT	HOPLO057-19	abdomen
	LEP3217	*H. ignitamaculae*	INDONESIA: North Sulawesi, Danau Mooat, east of Kotamobagu, 1150m, 30-31.iii.2000 (A. Kallies & S. Naumann) [MTD]	OK								517	LR699247FT	HOPLO051-19	abdomen

Continued on next page

Table C.2 – *Continued from previous page*

	Voucher N°	Species	Origin and Institution storage	LepF1/LepR1	Fragm 1a	Fragm 1b	Fragm. A	Fragm. B	Fragm. C	Fragm. D	Fragm. E	COI barcode length (bp)	GenBank accession	BOLD sample ID	Tissue
This study	MTD7422	*H. isarogensis*	PHIL: Luzon, Pangil, Laguna Pangil, 121.436735E 14.358491N, 50m, 4.11.1997 (W. Mey & W. Speidel) [MFNB]	-	OK	OK						614	LR699248FT	HOPLO018-19	abdomen
	MTD7418	*H. isarogensis MOTU 2*	PHIL: Leyte, Ormoc, Lake Danao, 124.69E 11.06N, 650m, 17.4.1997 (W. Mey & W. Speidel) [MFNB]	-	OK	OK						615	LR699249FT	HOPLO090-19	abdomen
	MTD8143	*H. isarogensis MOTU 2*	PHIL: Leyte, Ormoc, Lake Danao, 124.69E 11.06N, 650m, 17.4.1997 (W. Mey & W. Speidel) [MFNB]	-	OK	OK						618	LR699250FT	HOPLO084-19	abdomen
	MTD8144	*H. isarogensis MOTU 2*	PHIL: Leyte, Ormoc, Lake Danao, 124.69E 11.06N, 650m, 17.4.1997 (W. Mey & W. Speidel) [MFNB]	-	OK	OK						638	LR699251FT	HOPLO085-19	abdomen
	MTD8145	*H. isarogensis MOTU 2*	PHIL: Leyte, Ormoc, Lake Danao, 124.69E 11.06N, 650m, 17.4.1997 (W. Mey & W. Speidel) [MFNB]	-	OK	OK						614	LR699252FT	HOPLO086-19	abdomen
	MTD8146	*H. isarogensis MOTU 2*	PHIL: Leyte, Ormoc, Lake Danao, 124.69E 11.06N, 650m, 17.4.1997 (W. Mey & W. Speidel) [MFNB]	-	OK	OK						622	LR699253FT	HOPLO087-19	abdomen
	MTD8147	*H. isarogensis MOTU 2*	PHIL: Leyte, Ormoc, Lake Danao, 124.69E 11.06N, 650m, 17.4.1997 (W. Mey & W. Speidel) [MFNB]	-	OK	OK						617	LR699254FT	HOPLO088-19	abdomen
	MTD8148	*H. isarogensis MOTU 2*	PHIL: Leyte, Ormoc, Lake Danao, 124.69E 11.06N, 650m, 17.4.1997 (W. Mey & W. Speidel) [MFNB]	-	OK	OK						638	LR699255FT	HOPLO089-19	abdomen
	LEP3164	*H. jubata*	PNG: Morobe Prov., near Bulolo, Mt Susu Nat. Res., 975m., 27-28.viii.1983, Araucaria Forest (S. Miller) [USNM]	-	OK	X			OK	OK	OK	574	LR699256FT	HOPLO046-19	abdomen
	LEP3165	*H. jubata*	PNG: Morobe Prov., near Bulolo, Mt Susu Nat. Res., 975m., 27-28.viii.1983, Araucaria Forest (S. Miller) [USNM]	-	OK	OK			OK	OK	X	658	LR699257FT	HOPLO047-19	abdomen
	LEP3214	*H. kelama*	INDONESIA: North Sulawesi, Danau Mooat, east of Kotamobagu, 1150m, 30-31.iii.2000 (A. Kallies & S. Naumann) [MTD]	OK	OK	OK						637	LR699258FT	HOPLO061-19	abdomen

Continued on next page

Table C.2 – *Continued from previous page*

	Voucher N°	Species	Origin and Institution storage	LepF1/LepR1	Fragm 1a	Fragm 1b	Fragm. A	Fragm. B	Fragm. C	Fragm. D	Fragm. E	COI barcode length (bp)	GenBank accession	BOLD sample ID	Tissue
This study	LEP3215	*H. kelama*	INDONESIA: North Sulawesi, Danau Mooat, east of Kotamobagu, 1150m, 30-31.iii.2000 (A. Kallies & S. Naumann) [MTD]	-	OK	OK						620	LR699259FT	HOPLO062-19	abdomen
	MTD7878	*H. kelama*	INDONESIA: North Sulawesi, Danau Moat, east of Kotamobagu, 124.45E 0.75N, 1000m (A. Kallies & C. Zorn) [MTD]	-	OK	OK						586	LR699260FT	HOPLO060-19	abdomen
	LEP3064	*H. kinabaluensis MOTU 1*	MALAYSIA: Sabah, Kundasang, Kinabalu Mt. Lodge veranda, 6°0'42.15N 116°32'3.63E, 1570 m, at light, 16.06.2015 (T. Léger & R. Mally) [MTD]	OK								563	LR699261FT	HOPLO020-19	abdomen
	LEP3065	*H. kinabaluensis MOTU 1*	MALAYSIA: Sabah, Kinabalu Park HQ, Timpohon Gate, 700 m from Liwagu Trail starting Point, near Liwagu River, 6°1'40N 116°32'59E, 1700 m, 18.06.2015 (T. Léger & R. Mally) [MTD]	OK								609	LR699262FT	HOPLO021-19	abdomen
	MTD7882	*H. kinabaluensis MOTU 1*	MALAYSIA: Sabah, Kundasang, Kinabalu Park HQ, junction Kiau View and Pandanus trail, 116.5375E 6.009167N, 1690m (T. Léger & R. Mally) [MTD]	OK								605	LR699263FT	HOPLO022-19	abdomen
	MTD7887	*H. kinabaluensis MOTU 1*	MALAYSIA: Sabah, Kundasang, 200m before Kinabalu Mountain Lodge, 6°0'37"N 116°32'0"E, 1535m, UV light, 03.vi.2015 (T. Léger & R. Mally) [MTD]	OK								546	LR699264FT	HOPLO023-19	abdomen
	MTD7889	*H. kinabaluensis MOTU 1*	MALAYSIA: Sabah, Kundasang, Kinabalu Mt. Lodge veranda, 6°0'42.15N 116°32'3.63E, 1570 m, at light, 16.06.2015 (T. Léger & R. Mally) [MTD]	OK								561	LR699265FT	HOPLO024-19	abdomen
	MTD7893	*H. kinabaluensis MOTU 1*	MALAYSIA: Sabah, Kinabalu Park HQ, Timpohon Gate, 700 m from Liwagu Trail starting Point, near Liwagu River, 6°1'40N 116°32'59E, 1700 m, 18.06.2015 (T. Léger & R. Mally) [MTD]	X	OK	OK						613	LR699266FT	HOPLO027-19	abdomen

Continued on next page

Table C.2 – *Continued from previous page*

	Voucher N°	Species	Origin and Institution storage	LepF1/LepR1	Fragm 1a	Fragm 1b	Fragm. A	Fragm. B	Fragm. C	Fragm. D	Fragm. E	COI barcode length (bp)	Gen- Bank accession	BOLD sample ID	Tissue
This study	MTD7897	*H. kinabaluensis MOTU 1*	MALAYSIA: Sabah, Kinabalu Park HQ, Timpohon Gate, 300 m from Liwagu Trail starting Point, 6°1'41N 116°32'54E, 1820m, 18.06.2015 (T. Léger & R. Mally) [MTD]	OK								560	LR699267FT	HOPLO028-19	abdomen
	MTD7891	*H. kinabaluensis MOTU 2*	MALAYSIA: Sabah, Kinabalu Park HQ, Timpohon Gate, 700 m from Liwagu Trail starting Point, near Liwagu River, 6°1'40N 116°32'59E, 1700 m, 18.06.2015 (T. Léger & R. Mally) [MTD]	OK								603	LR699268FT	HOPLO025-19	abdomen
	MTD7892	*H. kinabaluensis MOTU 2*	MALAYSIA: Sabah, Kinabalu Park HQ, Timpohon Gate, 700 m from Liwagu Trail starting Point, near Liwagu River, 6°1'40N 116°32'59E, 1700 m, 18.06.2015 (T. Léger & R. Mally) [MTD]	X	OK	OK						594	LR699269FT	HOPLO026-19	abdomen
	MTD8232	*H. kinabaluensis MOTU 2*	MALAYSIA: Sabah, Gunong Monkobo, dipterocarp forest, 116.56E 5.48N, 975m, 7-13.viii.1987 (K. Tuck) [NHMUK]	X	OK	X			OK	OK	OK	613	LR699270FT	HOPLO029-19	abdomen
	LEP3195	*H. luteomacula MOTU 2*	MALAYSIA: Sabah, Kundasang, road 200m before Kinabalu Mt. Lodge, 6°0'37.38N 116°32'0.35E, 1535m, 03.05.2015 (T. Léger & R. Mally) [MTD]	OK								608	LR699271FT	HOPLO066-19	abdomen
	MTD8234	*H. luteomacula MOTU 2*	BRUNEI: Ulu Temburong, LP 298, GR838892, 300m, 26-30.iv.1989 (K. Tuck) [NHMUK]	-	OK	X			OK	OK	X	495	LR699272FT	HOPLO067-19	abdomen
	LEP124	*H. mallyi*	MALAYSIA: Sabah, Kinabalu HQ, 1600m, 10-13.xi.2006 (W. Mey & K. Ebert) [MFNB]	OK								582	LR699273FT	HOPLO004-19	abdomen
	LEP3197	*H. mallyi*	MALAYSIA: Sabah, Kinabalu Park HQ, ca. 300M from starting point of Kiau View Trail, 6°0'25N 116°32'21E, 1160m, UV light, 06.06.2015 (Leger &) [MTD]	OK								613	LR699274FT	HOPLO005-19	abdomen
	MTD7426	*H. matheae*	MALAYSIA: Sabah, Tawau, Tawau Hills National Park, 117.952219E 4.436889N, 11.27.2006 (W. & M. Mey) [MFNB]	OK								593	LR699275FT	HOPLO006-19	abdomen

Continued on next page

Table C.2 – *Continued from previous page*

	Voucher N°	Species	Origin and Institution storage	LepF1/LepR1	Fragm 1a	Fragm 1b	Fragm. A	Fragm. B	Fragm. C	Fragm. D	Fragm. E	COI barcode length (bp)	Gen- Bank accession	BOLD sample ID	Tissue
This study	MTD8244	*H. matheae MOTU 2*	W-MALAYSIA: Pahang, Cameron Highlands, Gunung Brinchang, 15-23.viii.1986 (G. Robinson) [NHMUK]	-	X	X	OK	OK	OK	OK	X	600	LR699276FT	HOPLO007-19	abdomen
	LEP3163	*H. metacrossa*	PNG: Morobe Prov., Wau, 1200m, 8-14.xii.1976 (G. F. Hevel & R. E. Dietz) [USNM]	-	OK	X			OK	OK	OK	611	LR699277FT	HOPLO095-19	abdomen
	LEP3166	*H. metacrossa*	PNG: Morobe Prov., Wau, Wau Ecol. Inst., 25-31.vii.1983, 1200m, Montane Forest (S. E. & P. M. Miller) [USNM]	-	OK	X			OK	OK	OK	658	LR699278FT	HOPLO096-19	abdomen
	MTD8252	*H. nauticorum*	SAMOA: Upolu Island, Tiavi, 1800', 24.viii.1974 (G. Robinson) [NHMUK]	-	X	X	X	X	OK	OK	OK	463	LR699279FT	HOPLO097-19	abdomen
	MTD8253	*H. nauticorum*	SAMOA: Upolu Island, Tiavi, 1800', 24.viii.1974 (G. Robinson) [NHMUK]	-	X	X	OK	X	X	OK	OK	449	LR699280FT	HOPLO098-19	abdomen
	LEP3162	*H. niveofascia*	PNG: Morobe Prov., near Bulolo, Mt Susu Nat. Res., 975m., 27-28.viii.1983, Araucaria Forest (S. Miller) [USNM]	-	OK	X			OK	OK	OK	658	LR699281FT	HOPLO042-19	abdomen
	MTD7431	*H. pangrangoensis*	INDONESIA: Java, Bogor, 106.929159E 6.783761S, 1625m, 20.2.1996 (Siniaev & Afonin) [MFNB]	-	X	OK						416	LR699282FT	HOPLO073-19	abdomen
	MTD7884	*H. parvimacula*	MALAYSIA: Sabah, Mesilau logging site, 400m before entrance to Mesilau Nature Reserve, 6°2'21.97N 116°35'54.12E, 1930 m, UV light, 02.06.2015 (T. Léger & R. Mally) [MTD]	OK								553	LR699283FT	HOPLO010-19	abdomen
	MTD7886	*H. parvimacula*	MALAYSIA: Sabah, Mesilau Nature Resort, 01.06.2015 (T. Léger & R. Mally) [MTD]	OK								558	LR699284FT	HOPLO012-19	abdomen
	MTD7888	*H. parvimacula*	MALAYSIA: Sabah, Mesilau logging site, 400m before entrance to Mesilau Nature Reserve, 6°2'21.97N 116°35'54.12E, 1930 m, UV light, 01.06.2015 (T. Léger & R. Mally) [MTD]	X	OK	OK						614	LR699285FT	HOPLO013-19	abdomen
	MTD7890	*H. parvimacula*	MALAYSIA: Sabah, Kundasang, Kinabalu Mt. Lodge veranda, 6°0'42.15N 116°32'3.63E, 1570 m, at light, 17.06.2015 (T. Léger & R. Mally) [MTD]	OK								604	LR699286FT	HOPLO014-19	abdomen

Continued on next page

Table C.2 – *Continued from previous page*

	Voucher N°	Species	Origin and Institution storage	LepF1/LepR1	Fragm 1a	Fragm 1b	Fragm. A	Fragm. B	Fragm. C	Fragm. D	Fragm. E	COI barcode length (bp)	Gen- Bank accession	BOLD sample ID	Tissue
This study	MTD7895	*H. parvimacula*	MALAYSIA: Sabah, Kinabalu Park HQ, Timpohon Gate, 300 m from Liwagu Trail starting Point, 6°1'41N 116°32'54E, 1820m, 18.06.2015 (T. Léger & R. Mally) [MTD]	X	OK	OK						611	LR699287FT	HOPLO015-19	abdomen
	MTD7896	*H. parvimacula*	MALAYSIA: Sabah, Kinabalu Park HQ, Timpohon Gate, 300 m from Liwagu Trail starting Point, 6°1'41N 116°32'54E, 1820m, 18.06.2015, leg. Leger & Mally [MTD]	X	OK	OK						613	LR699288FT	HOPLO016-19	abdomen
	MTD8229	*H. parvimacula MOTU 2*	W-MALAYSIA: Pahang, Cameron Highlands, Gunong Brinchang, 1800m, 26.x.1989 (G. Robinson & M. Tobin) [NHMUK]	-	X	X	X	X	OK	OK	OK	367	LR699289FT	HOPLO008-19	abdomen
	LEP3155	*H. pseudometacrossa*	PNG: Western Highland Prov., nr Mt. Hagen, Kuk Ag Res. Sta., 1600m, 19-20.viii.1983 (S. E. & P. Miller) [USNM]	-	OK	X			OK	OK	OK	657	LR699290FT	HOPLO048-19	abdomen
	LEP3161	*H. pseudometacrossa*	PNG: Western Highland Prov., nr Mt. Hagen, Kuk Ag Res. Sta., 1600m, 19-20.viii.1983 (S. E. & P. Miller) [USNM]	-	OK	X			OK	OK	OK	654	LR699291FT	HOPLO049-19	abdomen
	MTD8249	*H. quadripuncta*	INDONESIA: Seram, Gunung Kobipoto, north slopes, 570m, lowland forest, viii-ix.1987 (J. Holloway) [NHMUK]	-	X	X	OK	OK	OK	X	OK	509	LR699292FT	HOPLO099-19	abdomen
	LEP3158	*H. semifascia*	PNG: Morobe Prov., Wau, Wau Ecol. Inst., 24-26.viii.1983, 1360m (S. E. & P. M. Miller) [USNM]	-	OK	X			OK	X	OK	468	LR699293FT	HOPLO101-19	abdomen
	MTD8242	*H. semifascia*	PNG: Southern Highlands Prov., Bosavi, 2300ft, 6.i.1986 (D. Agassiz) [NHMUK]	-	X	OK	X	OK				519	LR699294FT	HOPLO100-19	abdomen
	MTD7894	*H. sepanggi*	MALAYSIA: Sabah, Kinabalu Park HQ, Timpohon Gate, 300 m from Liwagu Trail starting Point, 6°1'41N 116°32'54E, 1820m, 18.06.2015 (T. Léger & R. Mally) [MTD]	OK								562	LR699295FT	HOPLO017-19	abdomen
	MTD8243	*H. sp.*	PNG: Southern Highlands Prov., Tari, 5300ft, 1.i.1986 (D. Agassiz) [NHMUK]	-	OK	X			X	X	OK	382	LR699296FT	HOPLO053-19	abdomen

Continued on next page

Table C.2 – *Continued from previous page*

	Voucher N°	Species	Origin and Institution storage	LepF1/LepR1	Fragm 1a	Fragm 1b	Fragm. A	Fragm. B	Fragm. C	Fragm. D	Fragm. E	COI barcode length (bp)	Gen- Bank accession	BOLD sample ID	Tissue
This study	MTD8238	*H. sp. near ignitamaculae*	INDONESIA: North Sulawesi, Danau Mooat, near Kotamobagu, 1200m, 27-28.ix.1985 [NHMUK]	-	OK	X			OK	OK	OK	615	LR699297FT	HOPLO050-19	abdomen
	LEP3156	*H. subvariegata*	PNG: Morobe Prov., Mt. Kaindi, 2360m, 3.x.1992 (V. O. Becker) [USNM]	-	OK	X			OK	OK	OK	613	LR699298FT	HOPLO102-19	abdomen
	LEP3205	*H. sumatrensis MOTU 1*	INDONESIA: Sumatra, 25 km SSW-Pematangsiantar Strasse nach Prapat, 6-26.i.1995 (A. Kallies) [MTD]	-	OK	OK						623	LR699299FT	HOPLO038-19	abdomen
	MTD7880	*H. sumatrensis MOTU 1*	INDONESIA: Sumatra, Asahan Huta Padang, 99.26E 2.785N, 251m (E. W. Diehl) [MTD]	-	OK	OK						599	LR699300FT	HOPLO037-19	abdomen
	MTD8257	*H. sumatrensis MOTU 1*	INDONESIA: Sumatra, 25 km SSW-Pematangsiantar Strasse nach Prapat, 6-26.i.1995 (A. Kallies) [MTD]	-	OK	OK						501	LR699301FT	HOPLO039-19	abdomen
	MTD8260	*H. sumatrensis MOTU 1*	INDONESIA: Sumatra, 25 km SSW-Pematangsiantar Strasse nach Prapat, 6-26.i.1995 (A. Kallies) [MTD]	-	OK	OK						518	LR699302FT	HOPLO040-19	abdomen
	MTD8262	*H. sumatrensis MOTU 1*	INDONESIA: Sumatra, 25 km SSW-Pematangsiantar Strasse nach Prapat, 6-26.i.1995 (A. Kallies) [MTD]	-	OK	OK						610	LR699303FT	HOPLO041-19	abdomen
	MTD9119	*H. sumatrensis MOTU 1*	INDONESIA: Sumatra, 25 km SSW-Pematangsiantar Strasse nach Prapat, 6-26.i.1995 (A. Kallies) [MTD]	-	OK	OK						638	LR699304FT	HOPLO034-19	abdomen
	MTD9120	*H. sumatrensis MOTU 1*	INDONESIA: Sumatra, 25 km SSW-Pematangsiantar Strasse nach Prapat, 6-26.i.1995 (A. Kallies) [MTD]	-	OK	OK						638	LR699305FT	HOPLO035-19	abdomen
	MTD9121	*H. sumatrensis MOTU 1*	INDONESIA: Sumatra, 25 km SSW-Pematangsiantar Strasse nach Prapat, 6-26.i.1995 (A. Kallies) [MTD]	-	OK	OK						577	LR699306FT	HOPLO036-19	legs
	MTD8258	*H. sumatrensis MOTU 2*	INDONESIA: Sumatra, 25 km SSW-Pematangsiantar Strasse nach Prapat, 6-26.i.1995 (A. Kallies) [MTD]	-	OK	OK						630	LR699307FT	HOPLO032-19	abdomen
	LEP3206	*H. titika*	INDONESIA: Sumatra, Holzweg 25km SSW-Pematangsiantar Straße nach Prapat, LF, 13.ii.1996 (A. Kallies) [MTD]	OK								561	LR699308FT	HOPLO064-19	abdomen

Continued on next page

Table C.2 – *Continued from previous page*

	Voucher N°	Species	Origin and Institution storage	LepF1/LepR1	Fragm 1a	Fragm 1b	Fragm. A	Fragm. B	Fragm. C	Fragm. D	Fragm. E	COI barcode length (bp)	GenBank accession	BOLD sample ID	Tissue
This study	MTD7427	*H. ypsilon*	PHIL: Luzon, Mt Province, Bontoc, Chatol, 121.199089E 17.077205N, 2100m, 18.11.1997 (W. Mey, K. Ebert & M. Nuss) [MFNB]	-	OK	OK						614	LR699309FT	HOPLO068-19	abdomen
	MTD7428	*H. ypsilon*	PHIL: Luzon, Mt Province, Bontoc, Chatol, 121.199089E 17.077205N, 2100m, 18.11.1997 (W. Mey, K. Ebert & M. Nuss) [MFNB]	-	OK	OK						614	LR699310FT	HOPLO069-19	abdomen
	MTD7429	*H. ypsilon*	PHIL: Luzon, Mt Province, Bontoc, Barlig, 121.149413E 17.076131N 1650m, 15.11.1997 (W. Mey, K. Ebert & M. Nuss) [MFNB]	-	OK	OK						613	LR699311FT	HOPLO070-19	abdomen
Mally et al., 2017	BC_MTD LEP3002	*H. albipuncta*	MALAYSIA: Sabah, Kinabalu Park HQ, Timpohon Gate, UV light, 18.06.2015 (T. Léger & R. Mally) [MTD]	OK								614	KY080443	BC_MTD LEP3002	abdomen
	BC_MTD LEP01428	*H. albomaculata*	INDONESIA: North Sulawesi, Danau Mooat, east of Kotamobagu, 1000m, 30-31.iii.2000 (A. Kallies & S. Naumann) [MTD]	OK								658	JN272555	BC_MTD LEP01428	abdomen
	BC_MTD LEP01429	*H. albomaculata*	INDONESIA: North Sulawesi, Danau Mooat, east of Kotamobagu, 1000m, 25-26.iii.2000, at light, leg. A. Kallies & C. Zorn [MTD]	OK								658	JN272556	BC_MTD LEP01429	abdomen
	BC_MTD LEP01425	*H. ignitamaculae*	INDONESIA: North-Sulawesi, Tangkoko-Batuangus-Dua-Saudara Reserve, near Batuputih, primary forest, 600m, 21.iii.2000 (A. Kallies & C. Zorn) [MTD]	OK								658	JN272552	BC_MTD LEP01425	abdomen
	BC_MTD LEP01426	*H. ignitamaculae*	INDONESIA: North Sulawesi, Danau Mooat, east of Kotamobagu, 1000m, 30-31.iii.2000 (A. Kallies & S. Naumann) [MTD]	OK								658	JN272553	BC_MTD LEP01426	abdomen

Continued on next page

Table C.2 – *Continued from previous page*

	Voucher N°	Species	Origin and Institution storage	LepF1/LepR1	Fragm 1a	Fragm 1b	Fragm. A	Fragm. B	Fragm. C	Fragm. D	Fragm. E	COI barcode length (bp)	Gen- Bank accession	BOLD sample ID	Tissue
Mally et al., 2017	BC_MTD LEP01427	*H. ignitamaculae*	INDONESIA: North-Sulawesi, Tangkoko-Batuangus-Dua-Saudara Reserve, near Batuputih, primary forest, 600m, 21.iii.2000 (A. Kallies & C. Zorn) [MTD]	OK								658	JN272554	BC_MTD LEP01427	abdomen
	BC_MTD LEP01430	*H. isarogensis*	PHIL: South Luzon, Mt isarogis, 13°40' N 123°20'E, 530m, submontane forest, 22.iii.2000 (M. Nuss) [MTD]	OK								658	JN272557	BC_MTD LEP01430	legs
	BC_MTD LEP01431	*H. isarogensis*	PHIL: South Luzon, Mt isarogis, 13°40' N 123°20'E, 530m, submontane forest, 22.iii.2000 (M. Nuss) [MTD]	OK								658	JN272558	BC_MTD LEP01431	legs
	BC_MTD LEP01419	*H. luteomacula*	INDONESIA: Sumatra, Barat, N-Padangpanjang, Mt. Singgalang, 2100m, 10-11.ii.1996 (A. Kallies) [MTD]	OK								658	KX843698	BC_MTD LEP01419	legs
	BC_MTD LEP3006	*H. mallii*	MALAYSIA: Sabah [MTD]	OK								631	KY080444	BC_MTD LEP3006	abdomen
	BC_MTD LEP3004	*H. matheae*	MALAYSIA: Sabah, Kinabalu Mountain Lodge, 13.06.2015 (T. Léger & R. Mally) [MTD]	OK								627	KY080440	BC_MTD LEP3004	abdomen
	BC_MTD LEP3003	*H. parvimacula*	MALAYSIA: Sabah, Mesilau Nature Resort, 01.06.2015 (T. Léger & R. Mally) [MTD]	OK								613	KY080445	BC_MTD LEP3003	abdomen
	BC_MTD LEP01421	*H. sp. near sumatrensis*	INDONESIA: Sumatra, Barat, N-Padangpanjang, Mt Singgalang 2100m, 10-11.ii.1996 (A. Kallies) [MTD]	OK								658	JN272550	BC_MTD LEP01421	legs
	BC_ZMBN LEP00081	*H. sp_larva*	MALAYSIA: Sabah, Mount Kinabalu National Park, Mesilau, western edge of Mt Kinabalu Golf Club, 6°01'38"N 116°35'32"E, 1680 m, 13.vi.2015 (T. Léger & R. Mally) [ZMBN]	OK								655	KY080442	BC_ZMBN LEP00081	abdomen
	BC_MTD LEP01422	*H. sumatrensis MOTU 2*	INDONESIA: Sumatra, Holzweg 25km SSW-Pematangsiantar Straße nach Prapat, 6.-26.i.1995 (A. Kallies) [MTD]	OK								658	JN272551	BC_MTD LEP01422	legs

Continued on next page

Table C.2 – *Continued from previous page*

	Voucher N°	Species	Origin and Institution storage	LepF1/LepR1	Fragm 1a	Fragm 1b	Fragm. A	Fragm. B	Fragm. C	Fragm. D	Fragm. E	COI barcode length (bp)	Gen- Bank accession	BOLD sample ID	Tissue
Miller et al., 2015	USNM_ENT 00739200	*H. gombongi*	PNG: Morobe Prov., Yawan village, 146.083333E 6.166667S, 1700m, 10.09.2012 (M. Rimandai, S. Sau, A. Kinibel, M. Jimbudo) [USNM]	OK								654	KP850535	USNM_ENT 00739200	legs
	USNM_ENT 00739238	*H. gombongi*	PNG: Morobe Prov., Yawan village, 146.083333E 6.166667S, 1700m, 10.09.2012 (M. Rimandai, S. Sau, A. Kinibel, M. Jimbudo) [USNM]	OK								654	KP850401	USNM_ENT 00739238	legs
	USNM_ENT 00739216	*H. gombongi*	PNG: Morobe Prov., Yawan village, 146.083333E 6.166667S, 1700m, 10.09.2012 (B. Gewa, J. Kua, S. Sau, A. Kinibel) [USNM]	OK								654	KP850086	USNM_ENT 00739216	legs
	USNM_ENT 00665932	*H. obliqua*	PNG: Madang Prov., Wanang village, 05°15'S 145°17'E, 12.06.2007 (Auga, Molem, Tamtiai, Lilip, Ibalim, Posman, Rimandai, Brus, Novotny, Hrcek) [USNM]	OK								654	KX783025	USNM_ENT 00665932	legs
	USNM_ENT 00514731	*H. obliqua*	PNG: Madang Prov., Wanang village, 05°15'S 145°17'E, 12.06.2007 (Auga, Molem, Tamtiai, Lilip, Ibalim, Posman, Rimandai, Brus, Novotny, Hrcek) [USNM]	OK								654	KX783027	USNM_ENT 00514731	legs
	USNM_ENT 00514750	*H. obliqua*	PNG: Madang Prov., Wanang village, 05°15'S 145°17'E, 12.06.2007 (Auga, Molem, Tamtiai, Lilip, Ibalim, Posman, Rimandai, Brus, Novotny, Hrcek) [USNM]	OK								654	KX783026	USNM_ENT 00514750	legs
	USNM_ENT 00739239	*H. sp.*	PNG: Morobe Prov., Yawan village, 146.083333E 6.166667S, 1700m, 10.09.2012 (M. Rimandai, S. Sau, A. Kinibel, M. Jimbudo) [USNM]	OK								627	KP850867	USNM_ENT 00739239	legs
	USNM_ENT 00739227	*H. tonsepi*	PNG: Morobe Prov., Yawan village, 146.083333E 6.166667S, 1700m, 13.10.2012 (J. Valeba, J. Auga, M. Dilu, F. Philip, R. Lilip) [USNM]	OK								654	KP850609	USNM_ENT 00739227	legs
	USNM_ENT 00739208	*H. tonsepi*	PNG: Morobe Prov., Yawan village, 146.083333E 6.166667S, 1700m, 13.10.2012 (J. Valeba, J. Auga, M. Dilu, F. Philip, R. Lilip) [USNM]	OK								654	KP850187	USNM_ENT 00739208	legs

Continued on next page

Table C.2 – *Continued from previous page*

	Voucher N°	Species	Origin and Institution storage	LepF1/LepR1	Fragm 1a	Fragm 1b	Fragm. A	Fragm. B	Fragm. C	Fragm. D	Fragm. E	COI barcode length (bp)	Gen- Bank accession	BOLD sample ID	Tissue
This study (not barcode compliant)	YAWCATCR 0759	*H. tonsepi*	PNG: Morobe Prov., Yawan village, 146.083333E 6.166667S, 1700m, 17.11.2012 (J. Valeba, J. Auga, M. Dilu, F. Philip, R. Lilip) [USNM]	OK								658	KX842727	YAWCATCR 0759	legs
	MTD7421	*H. danaoensis*	PHIL: Leyte, Ormoc, Lake Danao, 124.69E 11.06N, 650m, 17.4.1997 (W. Mey & W. Speidel) [MFNB]	-	X	OK						416		HOPLO078-19	abdomen
	MTD7872	*H. gombongi*	PNG: Morobe Prov., Yawan village, 146.083333E 6.166667S, 1700m, 10.09.2012 (M. Rimandai, S. Sau, A. Kinibel, M. Jimbudo) [USNM]	OK								461		HOPLO074-19	abdomen
	MTD8259	*H. gracilis*	INDONESIA: Sumatra, 25 km SSW-Pematangsiantar Strasse nach Prapat, 13.ii.1996 (A. Kallies) [MTD]	-	X	OK						342		HOPLO058-19	abdomen
	MTD8239	*H. gracilis*	W-MALAYSIA: Pahang, Cameron Highlands, Gunong Brinchang, 1800m, 23-31.x.1989 (G. Robinson & M. Tobin) [NHMUK]	-	X	X	OK	OK	X	X	OK	462		HOPLO059-19	abdomen
	LEP3218	*H. ignitamaculae*	INDONESIA: North Sulawesi, Danau Mooat, east of Kotamobagu, 1000m, 25-26.iii.2000(A. Kallies & C. Zorn) [MTD]	OK								452		HOPLO052-19	abdomen
	MTD7423	*H. isarogensis*	PHIL: Mindoro, Mt. Iglit-Baco National Park, Mt Baco pass, 121.180408E 12.741742N, 1050m, 14.1.1998 (W. Mey & Samarita) [MFNB]	-	X	OK						416		HOPLO019-19	abdomen
	LEP3196	*H. parvimacula*	MALAYSIA: Sabah, Mesilau logging site, 400m before entrance to Mesilau Nature Reserve, 6°2'21.97N 116°35'54.12E, 1930 m, UV light, 02.06.2015 (T. Léger & R. Mally) [MTD]	OK								442		HOPLO009-19	abdomen
	MTD7885	*H. parvimacula*	MALAYSIA: Sabah, Mesilau logging site, 400m before entrance to Mesilau Nature Reserve, 6°2'21.97N 116°35'54.12E, 1930 m, UV light, 02.06.2015 (T. Léger & R. Mally) [MTD]	X	X	OK						415		HOPLO011-19	abdomen

Continued on next page

Table C.2 – *Continued from previous page*

	Voucher N°	Species	Origin and Institution storage	LepF1/LepR1	Fragm 1a	Fragm 1b	Fragm. A	Fragm. B	Fragm. C	Fragm. D	Fragm. E	COI barcode length (bp)	Gen- Bank accession	BOLD sample ID	Tissue
This study (not barcode compliant)	MTD7420	*H. isarogensis MOTU 2*	PHIL: Leyte, Ormoc, Lake Danao, 124.69E 11.06N, 650m, 17.4.1997 (W. Mey & W. Speidel) [MFNB]	-	OK	X						266		HOPLO083-19	abdomen
	MTD8236	*H. sp. near luteomacula*	W-MALAYSIA: Perak, Taiping, Maxwell's Hill, 1150m, 18-20.x.1989 (G. S. Robinson & T. A. Tobin) [NHMUK]		X	OK	X	X				408		HOPLO065-19	abdomen
	LEP3207	*H. sp.*	INDONESIA: Sumatra, Holzweg 2 25km SSW-Pematangsiantar Straße nach Prapat, 19.iii.1990 (E. W. Diehl) [MTD]	-	OK	X						281		HOPLO063-19	abdomen
	MTD8261	*H. sumatrensis MOTU 2*	INDONESIA: Sumatra, 25 km SSW-Pematangsiantar Strasse nach Prapat, 13.ii.1996 (A. Kallies) [MTD]	-	OK	OK						471		HOPLO033-19	abdomen
	MTD7873	*H. tonsepi*	PNG: Morobe Prov., Yawan village, 146.083333E 6.166667S, 1700m (B. Gewa, J. Kua, S. Sau, A. Kinibel) [USNM]	OK								454		HOPLO075-19	abdomen
	MTD8137	*H. ypsilon*	PHIL: Luzon, Santa Fe, Bald Mountain, 1150m, 11-13.xi.1997 (W. Mey, K. Ebert & M. Nuss) [MFNB]	-	OK	X						261		HOPLO071-19	abdomen
	MTD8138	*H. ypsilon*	PHIL: Luzon, Mt Province, Barlig, 121.149413E 17.076131N 1650m, 15.11.1997 (W. Mey, K. Ebert & M. Nuss) [MFNB]	-	OK	X						285		HOPLO072-19	abdomen

Table C.3: K2P-distances calculated on the ABGD online server (https://bioinfo.mnhn.fr/abi/public/abgd/abgdweb.html) using the Kimura 2-parameters algorithm.

	MTD7415	MTD7416	MTD7434	BC_MTD_LEP3002	MTD7430	BC_MTD_LEP01428	BC_MTD_LEP01429	MTD8247	MTD8255	MTD8250	LEP3159	LEP3160	LEP3168	MTD7425	LEP3066	MTD7419	MTD8142	MTD7417	MTD8139	MTD8140	USNM_ENT_00739200	USNM_ENT_00739238	USNM_ENT_00739216	LEP3203	LEP3204	MTD7876	MTD8256	LEP3217	BC_MTD_LEP01425
MTD7415																													
MTD7416	0.00																												
MTD7434	0.08	0.10																											
BC_MTD_LEP3002	0.08	0.11	0.00																										
MTD7430	0.07	0.11	0.05	0.05																									
BC_MTD_LEP01428	0.05	0.07	0.10	0.11	0.10																								
BC_MTD_LEP01429	0.05	0.07	0.10	0.11	0.10	0.00																							
MTD8247	0.03	0.06	0.06	0.07	0.07	0.04	0.04																						
MTD8255	0.05	0.05	0.06	0.06	0.06	0.05	0.05	0.04																					
MTD8250	0.07	0.07	0.07	0.07	0.06	0.07	0.07	0.04	0.04																				
LEP3159	0.06	0.09	0.10	0.12	0.11	0.09	0.09	0.05	0.05	0.06																			
LEP3160	0.05	0.08	0.09	0.10	0.11	0.08	0.08	0.05	0.03	0.05	0.00																		
LEP3168	0.06	0.09	0.10	0.12	0.12	0.09	0.09	0.05	0.05	0.06	0.00	0.00																	
MTD7425	0.04	0.06	0.09	0.09	0.08	0.04	0.04	0.03	0.05	0.07	0.06	0.05	0.06																
LEP3066	0.04	0.07	0.09	0.10	0.09	0.05	0.05	0.03	0.05	0.07	0.07	0.06	0.07	0.00															
MTD7419	0.04	0.07	0.10	0.11	0.10	0.07	0.07	0.05	0.05	0.07	0.06	0.05	0.06	0.04	0.05														
MTD8142	0.04	0.07	0.10	0.11	0.10	0.07	0.07	0.05	0.05	0.07	0.06	0.05	0.06	0.04	0.05	0.00													
MTD7417	0.04	0.07	0.10	0.11	0.09	0.06	0.06	0.04	0.05	0.06	0.06	0.06	0.07	0.05	0.05	0.04	0.04												
MTD8139	0.05	0.08	0.10	0.12	0.11	0.08	0.08	0.06	0.06	0.07	0.07	0.06	0.07	0.06	0.06	0.04	0.04	0.05											
MTD8140	0.05	0.05	0.09	0.09	0.08	0.05	0.05	0.03	0.06	0.07	0.05	0.04	0.05	0.05	0.05	0.02	0.02	0.03	0.00										
USNM_ENT_00739200	0.04	0.06	0.10	0.11	0.10	0.08	0.08	0.06	0.05	0.06	0.08	0.08	0.08	0.06	0.07	0.06	0.06	0.06	0.08	0.05									
USNM_ENT_00739238	0.04	0.06	0.10	0.11	0.10	0.08	0.08	0.06	0.05	0.06	0.08	0.08	0.08	0.06	0.07	0.06	0.06	0.06	0.08	0.05	0.00								
USNM_ENT_00739216	0.04	0.06	0.10	0.11	0.10	0.08	0.08	0.06	0.05	0.06	0.08	0.08	0.08	0.06	0.07	0.06	0.06	0.06	0.08	0.05	0.00	0.00							
LEP3203	0.02	0.05	0.09	0.11	0.11	0.08	0.08	0.07	0.05	0.07	0.09	0.08	0.09	0.05	0.06	0.07	0.07	0.07	0.08	0.05	0.08	0.08	0.08						
LEP3204	0.02	0.03	0.09	0.09	0.09	0.06	0.06	0.05	0.04	0.06	0.07	0.06	0.07	0.05	0.05	0.05	0.05	0.06	0.06	0.05	0.06	0.06	0.06	0.00					
MTD7876	0.02	0.04	0.09	0.10	0.11	0.07	0.07	0.07	0.05	0.06	0.08	0.07	0.08	0.05	0.06	0.06	0.06	0.07	0.07	0.05	0.07	0.07	0.07	0.01	0.00				
MTD8256	0.02	0.04	0.09	0.10	0.10	0.08	0.08	0.06	0.04	0.06	0.08	0.07	0.08	0.05	0.06	0.05	0.05	0.06	0.07	0.04	0.07	0.07	0.07	0.01	0.00	0.01			
LEP3217	0.04	0.05	0.09	0.09	0.08	0.05	0.05	0.03	0.07	0.08	0.08	0.07	0.08	0.04	0.04	0.06	0.06	0.06	0.06	0.05	0.06	0.06	0.06	0.06	0.06	0.06	0.05		
BC_MTD_LEP01425	0.04	0.07	0.09	0.10	0.10	0.06	0.06	0.04	0.07	0.08	0.09	0.08	0.09	0.04	0.05	0.07	0.07	0.07	0.08	0.05	0.08	0.08	0.08	0.08	0.06	0.07	0.07	0.00	
BC_MTD_LEP01426	0.04	0.07	0.09	0.10	0.10	0.06	0.06	0.04	0.07	0.08	0.09	0.08	0.09	0.04	0.05	0.07	0.07	0.07	0.08	0.05	0.08	0.08	0.08	0.08	0.06	0.07	0.07	0.00	0.00

Continued on next page

Table C.3 – *Continued from previous page*

	MTD7415	MTD7416	MTD7434	BC_MTD_LEP3002	MTD7430	BC_MTD_LEP01428	BC_MTD_LEP01429	MTD8247	MTD8255	MTD8250	LEP3159	LEP3160	LEP3168	MTD7425	LEP3066	MTD7419	MTD8142	MTD7417	MTD8139	MTD8140	USNM_ENT_00739200	USNM_ENT_00739238	USNM_ENT_00739216	LEP3203	LEP3204	MTD7876	MTD8256	LEP3217	BC_MTD_LEP01425
BC_MTD_LEP01427	0.04	0.07	0.09	0.10	0.10	0.06	0.06	0.04	0.07	0.08	0.09	0.08	0.09	0.04	0.05	0.07	0.07	0.07	0.08	0.05	0.08	0.08	0.08	0.08	0.06	0.07	0.07	0.00	0.00
MTD8238	0.04	0.07	0.09	0.10	0.10	0.05	0.05	0.03	0.05	0.07	0.08	0.07	0.08	0.03	0.03	0.06	0.06	0.05	0.07	0.04	0.06	0.06	0.06	0.07	0.05	0.07	0.06	0.04	0.05
MTD7422	0.04	0.07	0.09	0.10	0.09	0.05	0.05	0.03	0.05	0.07	0.07	0.07	0.07	0.02	0.03	0.06	0.06	0.05	0.07	0.04	0.07	0.07	0.07	0.07	0.06	0.07	0.06	0.04	0.05
BC_MTD_LEP01430	0.04	0.07	0.09	0.10	0.09	0.05	0.05	0.03	0.05	0.07	0.08	0.07	0.08	0.02	0.03	0.06	0.06	0.05	0.07	0.04	0.08	0.08	0.08	0.07	0.05	0.06	0.07	0.04	0.05
BC_MTD_LEP01431	0.04	0.07	0.09	0.10	0.09	0.05	0.05	0.03	0.05	0.07	0.08	0.07	0.08	0.02	0.03	0.06	0.06	0.05	0.07	0.04	0.08	0.08	0.08	0.07	0.05	0.06	0.07	0.04	0.05
MTD8143	0.06	0.08	0.11	0.12	0.11	0.05	0.05	0.04	0.05	0.07	0.08	0.07	0.08	0.03	0.04	0.07	0.07	0.07	0.07	0.05	0.07	0.07	0.07	0.08	0.07	0.07	0.07	0.05	0.06
MTD8144	0.06	0.08	0.11	0.12	0.11	0.05	0.05	0.04	0.05	0.07	0.08	0.07	0.08	0.03	0.04	0.07	0.07	0.07	0.08	0.05	0.08	0.08	0.08	0.08	0.07	0.07	0.08	0.05	0.06
MTD8145	0.06	0.09	0.11	0.11	0.11	0.05	0.05	0.04	0.05	0.07	0.08	0.07	0.08	0.04	0.04	0.07	0.07	0.07	0.08	0.06	0.08	0.08	0.08	0.08	0.07	0.08	0.07	0.06	0.06
MTD8146	0.06	0.08	0.11	0.12	0.11	0.05	0.05	0.04	0.05	0.07	0.08	0.07	0.08	0.03	0.04	0.07	0.07	0.07	0.07	0.05	0.08	0.08	0.08	0.08	0.07	0.07	0.07	0.05	0.06
MTD8147	0.06	0.08	0.11	0.11	0.11	0.05	0.05	0.04	0.05	0.07	0.08	0.07	0.08	0.03	0.04	0.07	0.07	0.07	0.07	0.06	0.07	0.07	0.07	0.08	0.07	0.07	0.07	0.05	0.06
MTD8148	0.06	0.08	0.11	0.12	0.11	0.05	0.05	0.04	0.05	0.07	0.08	0.07	0.08	0.03	0.04	0.07	0.07	0.07	0.08	0.05	0.08	0.08	0.08	0.08	0.07	0.07	0.08	0.05	0.06
MTD7418	0.06	0.08	0.11	0.12	0.11	0.05	0.05	0.04	0.05	0.07	0.08	0.07	0.08	0.03	0.04	0.07	0.07	0.07	0.07	0.05	0.07	0.07	0.07	0.08	0.07	0.07	0.07	0.05	0.06
LEP3164	0.04	0.07	0.08	0.10	0.09	0.06	0.06	0.05	0.05	0.05	0.05	0.05	0.05	0.05	0.06	0.05	0.05	0.05	0.05	0.03	0.06	0.06	0.06	0.07	0.06	0.07	0.06	0.05	0.06
LEP3165	0.05	0.07	0.10	0.12	0.10	0.07	0.07	0.05	0.05	0.06	0.07	0.06	0.07	0.05	0.06	0.05	0.05	0.05	0.06	0.04	0.07	0.07	0.07	0.08	0.06	0.07	0.07	0.06	0.07
MTD7878	0.05	0.08	0.09	0.10	0.09	0.05	0.05	0.04	0.05	0.08	0.09	0.08	0.09	0.05	0.05	0.08	0.08	0.06	0.08	0.06	0.08	0.08	0.08	0.08	0.07	0.08	0.08	0.05	0.06
LEP3214	0.05	0.08	0.09	0.10	0.10	0.05	0.05	0.04	0.05	0.08	0.09	0.08	0.09	0.05	0.05	0.08	0.08	0.06	0.09	0.06	0.09	0.09	0.09	0.09	0.07	0.08	0.08	0.05	0.06
LEP3215	0.05	0.08	0.09	0.10	0.09	0.05	0.05	0.04	0.05	0.08	0.09	0.08	0.09	0.05	0.05	0.08	0.08	0.06	0.08	0.06	0.09	0.09	0.09	0.08	0.07	0.08	0.08	0.05	0.06
LEP3064	0.03	0.06	0.09	0.10	0.09	0.07	0.07	0.04	0.05	0.07	0.06	0.06	0.06	0.04	0.05	0.03	0.03	0.03	0.05	0.03	0.05	0.05	0.05	0.06	0.05	0.06	0.05	0.05	0.06
LEP3065	0.04	0.07	0.10	0.10	0.10	0.08	0.08	0.05	0.05	0.07	0.07	0.07	0.07	0.05	0.05	0.04	0.04	0.04	0.05	0.03	0.06	0.06	0.06	0.07	0.06	0.07	0.06	0.06	0.07
MTD7882	0.04	0.07	0.10	0.10	0.10	0.08	0.08	0.05	0.05	0.07	0.07	0.07	0.07	0.05	0.05	0.04	0.04	0.04	0.05	0.03	0.06	0.06	0.06	0.07	0.06	0.07	0.06	0.06	0.07
MTD7887	0.04	0.06	0.10	0.10	0.09	0.06	0.06	0.04	0.05	0.07	0.06	0.06	0.06	0.05	0.05	0.03	0.03	0.03	0.04	0.03	0.05	0.05	0.05	0.06	0.05	0.05	0.05	0.06	0.06
MTD7889	0.05	0.07	0.10	0.10	0.09	0.07	0.07	0.04	0.06	0.07	0.06	0.06	0.06	0.05	0.05	0.03	0.03	0.04	0.05	0.04	0.06	0.06	0.06	0.06	0.06	0.06	0.05	0.06	0.06
MTD7893	0.04	0.07	0.10	0.10	0.10	0.08	0.08	0.05	0.05	0.07	0.07	0.07	0.07	0.05	0.05	0.04	0.04	0.03	0.05	0.03	0.06	0.06	0.06	0.07	0.05	0.06	0.06	0.06	0.07
MTD7897	0.04	0.06	0.10	0.10	0.09	0.07	0.07	0.04	0.05	0.07	0.06	0.06	0.06	0.05	0.05	0.03	0.03	0.03	0.04	0.03	0.05	0.05	0.05	0.06	0.06	0.06	0.05	0.06	0.06
MTD7891	0.05	0.08	0.09	0.10	0.10	0.08	0.08	0.05	0.05	0.07	0.07	0.07	0.07	0.05	0.05	0.04	0.04	0.04	0.06	0.04	0.07	0.07	0.07	0.07	0.05	0.07	0.06	0.06	0.07
MTD7892	0.05	0.08	0.09	0.10	0.10	0.08	0.08	0.05	0.06	0.08	0.07	0.06	0.07	0.05	0.05	0.04	0.04	0.04	0.06	0.04	0.07	0.07	0.07	0.07	0.05	0.06	0.06	0.06	0.07
MTD8232	0.05	0.08	0.09	0.10	0.10	0.08	0.08	0.05	0.05	0.07	0.07	0.07	0.07	0.05	0.05	0.04	0.04	0.04	0.06	0.04	0.07	0.07	0.07	0.07	0.05	0.07	0.06	0.06	0.08
BC_MTD_LEP01419	0.05	0.07	0.10	0.11	0.11	0.06	0.06	0.05	0.05	0.07	0.05	0.04	0.05	0.05	0.05	0.05	0.05	0.05	0.07	0.05	0.07	0.07	0.07	0.08	0.06	0.06	0.07	0.07	0.08
LEP3195	0.04	0.06	0.11	0.12	0.10	0.07	0.07	0.04	0.04	0.06	0.06	0.06	0.06	0.05	0.06	0.06	0.06	0.06	0.07	0.05	0.06	0.06	0.06	0.07	0.06	0.06	0.06	0.07	0.07
MTD8234	0.02	0.04	0.07	0.08	0.08	0.04	0.04	0.04	0.03	0.04	0.04	0.04	0.04	0.03	0.04	0.04	0.04	0.04	0.05	0.03	0.04	0.04	0.04	0.05	0.04	0.04	0.05	0.05	0.06
LEP124	0.02	0.04	0.08	0.10	0.10	0.05	0.05	0.04	0.05	0.06	0.06	0.06	0.06	0.04	0.05	0.06	0.06	0.06	0.06	0.04	0.05	0.05	0.05	0.04	0.03	0.04	0.04	0.04	0.05
LEP3197	0.02	0.04	0.09	0.10	0.10	0.06	0.06	0.04	0.05	0.07	0.07	0.07	0.07	0.05	0.05	0.06	0.06	0.06	0.06	0.05	0.05	0.05	0.05	0.04	0.03	0.04	0.04	0.05	0.06
BC_MTD_LEP3006	0.02	0.04	0.09	0.10	0.10	0.06	0.06	0.05	0.05	0.07	0.08	0.07	0.08	0.05	0.05	0.06	0.06	0.06	0.07	0.05	0.06	0.06	0.06	0.05	0.03	0.04	0.05	0.05	0.06
MTD7426	0.03	0.05	0.09	0.10	0.09	0.06	0.06	0.03	0.05	0.06	0.06	0.05	0.06	0.04	0.04	0.04	0.04	0.04	0.05	0.04	0.05	0.05	0.05	0.05	0.05	0.05	0.05	0.04	0.05

Continued on next page

Table C.3 – *Continued from previous page*

	MTD7415	MTD7416	MTD7434	BC_MTD_LEP3002	MTD7430	BC_MTD_LEP01428	BC_MTD_LEP01429	MTD8247	MTD8255	MTD8250	LEP3159	LEP3160	LEP3168	MTD7425	LEP3066	MTD7419	MTD8142	MTD7417	MTD8139	MTD8140	USNM_ENT_00739200	USNM_ENT_00739238	USNM_ENT_00739216	LEP3203	LEP3204	MTD7876	MTD8256	LEP3217	BC_MTD_LEP01425
BC_MTD_LEP3004	0.03	0.05	0.09	0.10	0.09	0.06	0.06	0.03	0.05	0.06	0.06	0.06	0.06	0.04	0.04	0.05	0.05	0.04	0.06	0.04	0.06	0.06	0.06	0.06	0.05	0.05	0.05	0.04	0.05
MTD8244	0.02	0.05	0.07	0.08	0.08	0.05	0.05	0.04	0.04	0.06	0.06	0.06	0.06	0.03	0.03	0.05	0.05	0.04	0.06	0.03	0.05	0.05	0.05	0.06	0.04	0.05	0.06	0.04	0.05
LEP3163	0.05	0.07	0.10	0.11	0.09	0.06	0.06	0.04	0.04	0.06	0.06	0.06	0.06	0.05	0.06	0.06	0.06	0.05	0.06	0.04	0.07	0.07	0.07	0.07	0.06	0.07	0.06	0.06	0.07
LEP3166	0.05	0.07	0.10	0.11	0.09	0.06	0.06	0.04	0.04	0.06	0.07	0.06	0.07	0.05	0.06	0.06	0.06	0.05	0.07	0.04	0.08	0.08	0.08	0.08	0.06	0.07	0.07	0.06	0.07
MTD8252	0.05	0.07	0.08	0.08	0.07	0.06	0.06	0.04	0.03	0.05	0.06	0.06	0.06	0.05	0.05	0.05	0.05	0.06	0.06	0.05	0.06	0.06	0.06	0.06	0.06	0.06	0.05	0.06	0.06
MTD8253	0.04	0.06	0.05	0.06	0.05	0.06	0.06	0.03	0.02	0.03	0.06	0.05	0.06	0.03	0.04	0.04	0.05	0.04	0.06	0.03	0.05	0.05	0.05	0.06	0.04	0.05	0.06	0.04	0.06
LEP3162	0.06	0.09	0.11	0.13	0.10	0.11	0.11	0.07	0.06	0.08	0.11	0.10	0.11	0.08	0.09	0.10	0.10	0.10	0.12	0.08	0.10	0.10	0.10	0.11	0.08	0.10	0.09	0.07	0.09
USNM_ENT_00665932	0.06	0.09	0.10	0.12	0.11	0.10	0.10	0.07	0.05	0.07	0.11	0.10	0.11	0.07	0.08	0.10	0.10	0.09	0.12	0.08	0.10	0.10	0.10	0.12	0.08	0.10	0.10	0.08	0.11
USNM_ENT_00514731	0.06	0.09	0.10	0.12	0.11	0.10	0.10	0.07	0.05	0.07	0.11	0.10	0.11	0.07	0.08	0.10	0.10	0.09	0.12	0.08	0.10	0.10	0.10	0.12	0.08	0.10	0.10	0.08	0.11
USNM_ENT_00514750	0.06	0.09	0.10	0.12	0.11	0.10	0.10	0.07	0.05	0.07	0.11	0.10	0.11	0.07	0.08	0.10	0.10	0.09	0.12	0.08	0.10	0.10	0.10	0.12	0.08	0.10	0.10	0.08	0.11
MTD7431	0.07	0.07	0.09	0.09	0.09	0.07	0.07	0.04	0.07	0.08	0.06	0.06	0.07	0.07	0.07	0.06	0.06	0.06	0.06	0.06	0.07	0.07	0.07	0.06	0.06	0.06	0.06	0.08	0.08
MTD7884	0.08	0.09	0.11	0.12	0.12	0.09	0.09	0.06	0.06	0.09	0.08	0.07	0.08	0.08	0.08	0.07	0.07	0.07	0.07	0.05	0.08	0.08	0.08	0.09	0.09	0.09	0.08	0.08	0.08
MTD7886	0.07	0.09	0.11	0.11	0.11	0.08	0.08	0.06	0.06	0.08	0.08	0.07	0.08	0.07	0.07	0.06	0.06	0.07	0.06	0.05	0.08	0.08	0.08	0.09	0.08	0.08	0.07	0.08	0.08
MTD7888	0.07	0.10	0.11	0.12	0.12	0.10	0.10	0.07	0.06	0.09	0.09	0.08	0.09	0.08	0.09	0.08	0.08	0.07	0.07	0.05	0.08	0.08	0.08	0.10	0.09	0.09	0.09	0.08	0.09
MTD7890	0.07	0.10	0.11	0.12	0.12	0.10	0.10	0.07	0.06	0.09	0.09	0.08	0.09	0.08	0.09	0.07	0.07	0.07	0.07	0.05	0.08	0.08	0.08	0.10	0.09	0.09	0.09	0.08	0.09
MTD7895	0.07	0.10	0.11	0.12	0.12	0.10	0.10	0.07	0.06	0.09	0.09	0.08	0.09	0.08	0.09	0.08	0.08	0.07	0.07	0.05	0.08	0.08	0.08	0.10	0.09	0.09	0.09	0.08	0.09
MTD7896	0.07	0.10	0.11	0.12	0.12	0.10	0.10	0.07	0.06	0.09	0.09	0.08	0.09	0.08	0.09	0.08	0.08	0.07	0.07	0.05	0.08	0.08	0.08	0.10	0.09	0.09	0.09	0.08	0.09
BC_MTD_LEP3003	0.07	0.10	0.11	0.12	0.12	0.10	0.10	0.07	0.06	0.09	0.09	0.08	0.09	0.08	0.09	0.08	0.08	0.07	0.07	0.05	0.08	0.08	0.08	0.10	0.09	0.09	0.09	0.08	0.09
MTD8229	0.04	0.04	0.08	0.08	0.07	0.05	0.05	0.02	0.05	0.06	0.05	0.04	0.05	0.04	0.04	0.03	0.03	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04
LEP3155	0.06	0.08	0.10	0.12	0.12	0.08	0.08	0.05	0.05	0.07	0.07	0.07	0.07	0.06	0.07	0.06	0.06	0.06	0.08	0.05	0.07	0.07	0.07	0.08	0.06	0.07	0.08	0.07	0.08
LEP3161	0.05	0.08	0.10	0.12	0.12	0.08	0.08	0.05	0.05	0.07	0.07	0.07	0.07	0.06	0.07	0.06	0.06	0.06	0.08	0.05	0.07	0.07	0.07	0.08	0.06	0.07	0.08	0.07	0.08
MTD8249	0.03	0.05	0.06	0.07	0.08	0.07	0.07	0.05	0.02	0.04	0.05	0.05	0.05	0.04	0.05	0.04	0.04	0.05	0.05	0.02	0.06	0.06	0.06	0.06	0.04	0.05	0.06	0.04	0.07
MTD8242	0.06	0.08	0.11	0.11	0.10	0.08	0.08	0.04	0.06	0.08	0.07	0.06	0.07	0.07	0.06	0.06	0.06	0.06	0.07	0.06	0.07	0.07	0.07	0.08	0.08	0.08	0.07	0.07	0.07
LEP3158	0.04	0.07	0.08	0.09	0.09	0.07	0.07	0.05	0.04	0.06	0.07	0.07	0.07	0.05	0.05	0.05	0.05	0.06	0.07	0.03	0.06	0.06	0.06	0.08	0.06	0.07	0.06	0.05	0.06
MTD7894	0.05	0.07	0.10	0.11	0.11	0.07	0.07	0.05	0.05	0.07	0.08	0.06	0.08	0.07	0.07	0.06	0.06	0.06	0.07	0.04	0.07	0.07	0.07	0.07	0.06	0.07	0.07	0.07	0.08
BC_MTD_LEP01421	0.05	0.07	0.11	0.12	0.12	0.08	0.08	0.06	0.06	0.08	0.10	0.08	0.10	0.06	0.07	0.08	0.08	0.07	0.08	0.05	0.09	0.09	0.09	0.08	0.07	0.07	0.07	0.07	0.08
BC_ZMBN_Lep00081	0.05	0.07	0.11	0.12	0.10	0.08	0.08	0.06	0.05	0.07	0.08	0.08	0.09	0.06	0.06	0.06	0.06	0.06	0.08	0.05	0.08	0.08	0.08	0.07	0.06	0.07	0.07	0.08	0.09
MTD8243	0.01	0.04	0.06	0.07	0.07	0.04	0.04	0.03	0.02	0.04	0.04	0.04	0.04	0.03	0.04	0.04	0.04	0.04	0.04	0.02	0.04	0.04	0.04	0.04	0.03	0.04	0.04	0.03	0.04
USNM_ENT_00739239	0.06	0.10	0.10	0.12	0.11	0.10	0.10	0.06	0.06	0.06	0.09	0.08	0.09	0.07	0.09	0.07	0.07	0.07	0.09	0.06	0.07	0.07	0.07	0.10	0.08	0.09	0.09	0.09	0.11
LEP3156	0.06	0.09	0.10	0.12	0.12	0.09	0.09	0.06	0.06	0.08	0.08	0.08	0.08	0.06	0.07	0.06	0.06	0.07	0.07	0.04	0.08	0.08	0.08	0.08	0.06	0.08	0.07	0.07	0.09
MTD8258	0.03	0.06	0.09	0.10	0.11	0.07	0.07	0.06	0.05	0.07	0.08	0.08	0.08	0.05	0.06	0.07	0.07	0.06	0.07	0.04	0.07	0.07	0.07	0.06	0.05	0.06	0.06	0.06	0.08
BC_MTD_LEP01422	0.04	0.07	0.10	0.10	0.11	0.07	0.07	0.06	0.05	0.08	0.08	0.07	0.08	0.05	0.06	0.07	0.07	0.06	0.07	0.04	0.08	0.08	0.08	0.07	0.05	0.06	0.06	0.06	0.07
MTD9119	0.05	0.07	0.11	0.13	0.11	0.07	0.07	0.06	0.06	0.08	0.09	0.07	0.09	0.06	0.07	0.07	0.07	0.06	0.07	0.04	0.08	0.08	0.08	0.09	0.07	0.08	0.08	0.07	0.09
MTD9120	0.05	0.07	0.11	0.13	0.11	0.07	0.07	0.05	0.05	0.08	0.08	0.07	0.09	0.06	0.07	0.07	0.07	0.06	0.07	0.04	0.08	0.08	0.08	0.08	0.07	0.08	0.07	0.07	0.08

Continued on next page

Table C.3 – *Continued from previous page*

	MTD7415	MTD7416	MTD7434	BC_MTD_LEP3002	MTD7430	BC_MTD_LEP01428	BC_MTD_LEP01429	MTD8247	MTD8255	MTD8250	LEP3159	LEP3160	LEP3168	MTD7425	LEP3066	MTD7419	MTD8142	MTD7417	MTD8139	MTD8140	USNM_ENT_00739200	USNM_ENT_00739238	USNM_ENT_00739216	LEP3203	LEP3204	MTD7876	MTD8256	LEP3217	BC_MTD_LEP01425
MTD9121	0.05	0.06	0.11	0.12	0.10	0.06	0.06	0.05	0.06	0.08	0.08	0.07	0.08	0.06	0.07	0.07	0.07	0.06	0.06	0.04	0.07	0.07	0.07	0.08	0.07	0.08	0.07	0.07	0.08
MTD7880	0.05	0.07	0.11	0.12	0.11	0.06	0.06	0.05	0.05	0.08	0.07	0.06	0.08	0.06	0.06	0.06	0.06	0.06	0.06	0.04	0.07	0.07	0.07	0.08	0.07	0.07	0.07	0.07	0.08
LEP3205	0.05	0.07	0.11	0.13	0.11	0.07	0.07	0.05	0.05	0.08	0.08	0.07	0.08	0.06	0.07	0.07	0.07	0.06	0.07	0.04	0.07	0.07	0.07	0.08	0.07	0.08	0.07	0.07	0.08
MTD8257	0.04	0.05	0.08	0.10	0.08	0.07	0.07	0.04	0.05	0.06	0.08	0.06	0.08	0.05	0.06	0.06	0.06	0.05	0.05	0.03	0.07	0.07	0.07	0.06	0.05	0.06	0.06	0.05	0.07
MTD8260	0.04	0.05	0.09	0.11	0.09	0.05	0.05	0.04	0.05	0.06	0.07	0.06	0.07	0.05	0.06	0.06	0.06	0.05	0.05	0.03	0.06	0.06	0.06	0.06	0.05	0.06	0.07	0.06	0.07
MTD8262	0.04	0.06	0.11	0.12	0.11	0.07	0.07	0.06	0.05	0.07	0.08	0.07	0.09	0.06	0.07	0.07	0.07	0.06	0.07	0.04	0.08	0.08	0.08	0.08	0.06	0.07	0.07	0.07	0.09
LEP3206	0.04	0.07	0.11	0.11	0.10	0.06	0.06	0.05	0.05	0.07	0.07	0.06	0.07	0.05	0.05	0.06	0.06	0.06	0.07	0.05	0.06	0.06	0.06	0.07	0.06	0.07	0.06	0.06	0.06
USNM_ENT_00739227	0.06	0.09	0.10	0.12	0.11	0.09	0.09	0.06	0.05	0.06	0.08	0.07	0.08	0.08	0.08	0.07	0.07	0.07	0.08	0.05	0.08	0.08	0.08	0.09	0.07	0.08	0.08	0.08	0.10
USNM_ENT_00739208	0.06	0.09	0.10	0.12	0.11	0.09	0.09	0.06	0.05	0.06	0.08	0.07	0.08	0.08	0.08	0.07	0.07	0.07	0.08	0.05	0.08	0.08	0.08	0.09	0.07	0.08	0.08	0.08	0.10
YAWCATCR0759	0.05	0.08	0.11	0.12	0.11	0.08	0.08	0.06	0.05	0.06	0.08	0.08	0.08	0.07	0.08	0.07	0.07	0.06	0.08	0.05	0.08	0.08	0.08	0.09	0.07	0.08	0.08	0.08	0.10
MTD7427	0.05	0.09	0.10	0.11	0.10	0.07	0.07	0.05	0.05	0.07	0.07	0.07	0.07	0.05	0.06	0.03	0.03	0.04	0.04	0.02	0.07	0.07	0.07	0.08	0.06	0.07	0.07	0.07	0.08
MTD7428	0.05	0.09	0.10	0.11	0.10	0.07	0.07	0.05	0.06	0.07	0.06	0.06	0.07	0.05	0.06	0.03	0.03	0.05	0.04	0.02	0.07	0.07	0.07	0.08	0.06	0.07	0.07	0.07	0.08
MTD7429	0.05	0.09	0.10	0.11	0.10	0.07	0.07	0.05	0.05	0.07	0.07	0.07	0.07	0.05	0.06	0.03	0.03	0.04	0.04	0.02	0.07	0.07	0.07	0.08	0.06	0.07	0.07	0.07	0.08

Table C3 (suite). K2P-distances calculated on the ABGD online server (https://bioinfo.mnhn.fr/abi/public/abgd/abgdweb.html) using the Kimura 2-parameters algorithm.

	BC_MTD_LEP01425	BC_MTD_LEP01426	BC_MTD_LEP01427	MTD8238	MTD7422	BC_MTD_LEP01430	BC_MTD_LEP01431	MTD8143	MTD8144	MTD8145	MTD8146	MTD8147	MTD8148	MTD7418	LEP3164	LEP3165	MTD7878	LEP3214	LEP3215	LEP3064	LEP3065	MTD7882	MTD7887	MTD7889	MTD7893	MTD7897	MTD7891	MTD7892	MTD8232
BC_MTD_LEP01425																													
BC_MTD_LEP01426	0.00																												
BC_MTD_LEP01427	0.00	0.00																											
MTD8238	0.05	0.05	0.05																										
MTD7422	0.05	0.05	0.05	0.04																									
BC_MTD_LEP01430	0.05	0.05	0.05	0.03	0.00																								
BC_MTD_LEP01431	0.05	0.05	0.05	0.03	0.00	0.00																							
MTD8143	0.06	0.06	0.06	0.05	0.04	0.03	0.03																						
MTD8144	0.06	0.06	0.06	0.05	0.04	0.04	0.04	0.00																					
MTD8145	0.06	0.06	0.06	0.05	0.04	0.04	0.04	0.00	0.00																				
MTD8146	0.06	0.06	0.06	0.05	0.04	0.04	0.04	0.00	0.00	0.00																			
MTD8147	0.06	0.06	0.06	0.05	0.04	0.04	0.04	0.00	0.00	0.00	0.00																		
MTD8148	0.06	0.06	0.06	0.05	0.04	0.04	0.04	0.00	0.00	0.00	0.00	0.00																	
MTD7418	0.06	0.06	0.06	0.05	0.04	0.03	0.03	0.00	0.00	0.00	0.00	0.00	0.00																
LEP3164	0.06	0.06	0.06	0.06	0.06	0.05	0.05	0.06	0.06	0.06	0.06	0.06	0.06	0.06															
LEP3165	0.07	0.07	0.07	0.06	0.06	0.07	0.07	0.07	0.07	0.07	0.07	0.07	0.07	0.07	0.00														
MTD7878	0.06	0.06	0.06	0.05	0.06	0.06	0.06	0.07	0.07	0.07	0.07	0.07	0.07	0.07	0.07	0.08													
LEP3214	0.06	0.06	0.06	0.05	0.06	0.06	0.06	0.07	0.07	0.07	0.07	0.07	0.07	0.07	0.07	0.08	0.00												
LEP3215	0.06	0.06	0.06	0.05	0.06	0.06	0.06	0.07	0.07	0.07	0.07	0.07	0.07	0.07	0.07	0.08	0.00	0.00											
LEP3064	0.06	0.06	0.06	0.05	0.05	0.05	0.05	0.06	0.06	0.06	0.06	0.06	0.06	0.06	0.05	0.06	0.06	0.06	0.06										
LEP3065	0.07	0.07	0.07	0.06	0.06	0.06	0.06	0.07	0.07	0.07	0.07	0.07	0.07	0.07	0.06	0.06	0.07	0.07	0.07	0.00									
MTD7882	0.07	0.07	0.07	0.06	0.06	0.06	0.06	0.07	0.07	0.07	0.07	0.07	0.07	0.07	0.06	0.06	0.07	0.07	0.07	0.00	0.00								
MTD7887	0.06	0.06	0.06	0.05	0.05	0.05	0.05	0.06	0.06	0.06	0.06	0.06	0.06	0.06	0.05	0.05	0.06	0.06	0.06	0.00	0.00	0.00							
MTD7889	0.06	0.06	0.06	0.05	0.05	0.05	0.05	0.06	0.06	0.06	0.06	0.06	0.06	0.06	0.05	0.06	0.07	0.06	0.07	0.00	0.00	0.00	0.00						
MTD7893	0.07	0.07	0.07	0.06	0.06	0.06	0.06	0.07	0.07	0.07	0.07	0.06	0.07	0.07	0.06	0.06	0.07	0.07	0.07	0.00	0.00	0.00	0.00	0.00					
MTD7897	0.06	0.06	0.06	0.05	0.05	0.05	0.05	0.06	0.06	0.06	0.06	0.06	0.06	0.06	0.05	0.05	0.06	0.06	0.06	0.00	0.00	0.00	0.00	0.00	0.00				
MTD7891	0.07	0.07	0.07	0.06	0.06	0.06	0.06	0.07	0.07	0.08	0.07	0.07	0.07	0.07	0.06	0.06	0.07	0.07	0.07	0.02	0.02	0.02	0.02	0.02	0.02	0.02			
MTD7892	0.07	0.07	0.07	0.06	0.06	0.06	0.06	0.07	0.07	0.07	0.07	0.07	0.07	0.07	0.06	0.06	0.07	0.07	0.07	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.00		
MTD8232	0.08	0.08	0.08	0.06	0.06	0.06	0.06	0.07	0.07	0.08	0.07	0.07	0.07	0.07	0.06	0.07	0.07	0.07	0.07	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.00	0.00	
BC_MTD_LEP01419	0.08	0.08	0.08	0.06	0.06	0.06	0.06	0.07	0.08	0.07	0.07	0.07	0.08	0.07	0.05	0.06	0.08	0.08	0.08	0.05	0.05	0.05	0.05	0.05	0.05	0.05	0.06	0.05	0.06
LEP3195	0.07	0.07	0.07	0.07	0.06	0.06	0.06	0.07	0.07	0.07	0.07	0.07	0.07	0.07	0.06	0.06	0.08	0.08	0.08	0.05	0.06	0.06	0.05	0.06	0.06	0.05	0.06	0.06	0.06

Continued on next page

Table C.4 – *Continued from previous page*

	BC_MTD_LEP01425	BC_MTD_LEP01426	BC_MTD_LEP01427	MTD8238	MTD7422	BC_MTD_LEP01430	BC_MTD_LEP01431	MTD8143	MTD8144	MTD8145	MTD8146	MTD8147	MTD8148	MTD7418	LEP3164	LEP3165	MTD7878	LEP3214	LEP3215	LEP3064	LEP3065	MTD7882	MTD7887	MTD7889	MTD7893	MTD7897	MTD7891	MTD7892	MTD8232
MTD8234	0.06	0.06	0.06	0.05	0.04	0.04	0.04	0.05	0.05	0.05	0.05	0.05	0.05	0.05	0.04	0.05	0.05	0.05	0.05	0.05	0.05	0.05	0.04	0.04	0.05	0.04	0.05	0.05	0.05
LEP124	0.05	0.05	0.05	0.06	0.05	0.04	0.04	0.06	0.06	0.06	0.06	0.06	0.06	0.06	0.05	0.06	0.07	0.07	0.07	0.05	0.05	0.05	0.05	0.05	0.05	0.05	0.06	0.06	0.06
LEP3197	0.06	0.06	0.06	0.06	0.05	0.05	0.05	0.07	0.07	0.07	0.07	0.07	0.07	0.07	0.06	0.07	0.07	0.07	0.07	0.05	0.06	0.06	0.05	0.06	0.06	0.05	0.06	0.06	0.06
BC_MTD_LEP3006	0.06	0.06	0.06	0.06	0.05	0.05	0.05	0.07	0.07	0.07	0.07	0.07	0.07	0.07	0.06	0.07	0.07	0.07	0.07	0.05	0.06	0.06	0.05	0.06	0.06	0.05	0.06	0.06	0.06
MTD7426	0.05	0.05	0.05	0.04	0.04	0.04	0.04	0.05	0.05	0.05	0.05	0.05	0.05	0.05	0.04	0.05	0.07	0.06	0.07	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.05	0.05	0.05
BC_MTD_LEP3004	0.05	0.05	0.05	0.05	0.04	0.04	0.04	0.05	0.05	0.05	0.05	0.05	0.05	0.05	0.05	0.05	0.07	0.07	0.07	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.05	0.05	0.05
MTD8244	0.05	0.05	0.05	0.04	0.04	0.05	0.05	0.05	0.05	0.05	0.05	0.05	0.05	0.04	0.05	0.05	0.05	0.05	0.05	0.03	0.04	0.04	0.04	0.04	0.04	0.04	0.05	0.05	0.05
LEP3163	0.07	0.07	0.07	0.06	0.05	0.05	0.05	0.07	0.07	0.07	0.07	0.07	0.07	0.07	0.04	0.05	0.07	0.07	0.07	0.06	0.06	0.06	0.05	0.06	0.06	0.05	0.07	0.06	0.07
LEP3166	0.07	0.07	0.07	0.06	0.05	0.06	0.06	0.07	0.07	0.07	0.07	0.07	0.07	0.07	0.04	0.05	0.07	0.07	0.07	0.06	0.06	0.06	0.05	0.06	0.06	0.05	0.07	0.06	0.07
MTD8252	0.06	0.06	0.06	0.06	0.06	0.05	0.05	0.06	0.06	0.06	0.06	0.06	0.06	0.06	0.06	0.06	0.06	0.07	0.07	0.05	0.06	0.06	0.06	0.06	0.06	0.06	0.07	0.07	0.07
MTD8253	0.06	0.06	0.06	0.04	0.05	0.06	0.06	0.05	0.05	0.05	0.05	0.05	0.05	0.05	0.04	0.05	0.05	0.05	0.05	0.04	0.05	0.05	0.04	0.04	0.05	0.04	0.05	0.05	0.05
LEP3162	0.09	0.09	0.09	0.09	0.09	0.10	0.10	0.10	0.11	0.10	0.10	0.10	0.11	0.10	0.10	0.11	0.10	0.10	0.10	0.09	0.10	0.09	0.08	0.09	0.10	0.08	0.10	0.10	0.10
USNM_ENT_00665932	0.11	0.11	0.11	0.08	0.09	0.10	0.10	0.11	0.11	0.11	0.11	0.11	0.11	0.11	0.09	0.10	0.08	0.09	0.09	0.08	0.09	0.09	0.07	0.08	0.09	0.08	0.10	0.10	0.10
USNM_ENT_00514731	0.11	0.11	0.11	0.08	0.09	0.10	0.10	0.11	0.11	0.11	0.11	0.11	0.11	0.11	0.09	0.10	0.08	0.09	0.09	0.08	0.09	0.09	0.07	0.08	0.09	0.08	0.10	0.10	0.10
USNM_ENT_00514750	0.11	0.11	0.11	0.08	0.09	0.10	0.10	0.11	0.11	0.11	0.11	0.11	0.11	0.11	0.09	0.10	0.08	0.09	0.09	0.08	0.09	0.09	0.07	0.08	0.09	0.08	0.10	0.10	0.10
MTD7431	0.08	0.08	0.08	0.07	0.07	0.07	0.07	0.07	0.07	0.07	0.07	0.07	0.07	0.07	0.05	0.07	0.06	0.06	0.06	0.06	0.06	0.06	0.06	0.06	0.06	0.06	0.06	0.06	0.06
MTD7884	0.08	0.08	0.08	0.08	0.09	0.08	0.08	0.09	0.09	0.09	0.09	0.09	0.09	0.09	0.06	0.07	0.09	0.09	0.09	0.07	0.08	0.08	0.08	0.08	0.08	0.08	0.08	0.08	0.08
MTD7886	0.08	0.08	0.08	0.08	0.08	0.08	0.08	0.09	0.09	0.09	0.09	0.09	0.09	0.09	0.06	0.07	0.09	0.09	0.09	0.07	0.08	0.08	0.08	0.08	0.08	0.08	0.08	0.08	0.08
MTD7888	0.09	0.09	0.09	0.09	0.09	0.09	0.09	0.10	0.10	0.10	0.10	0.10	0.10	0.10	0.07	0.08	0.10	0.10	0.10	0.08	0.08	0.08	0.08	0.08	0.08	0.08	0.09	0.08	0.09
MTD7890	0.09	0.09	0.09	0.09	0.09	0.09	0.09	0.10	0.10	0.10	0.10	0.10	0.10	0.10	0.07	0.08	0.10	0.10	0.10	0.08	0.08	0.08	0.08	0.08	0.08	0.08	0.09	0.08	0.09
MTD7895	0.09	0.09	0.09	0.09	0.09	0.09	0.09	0.10	0.10	0.10	0.10	0.10	0.10	0.10	0.07	0.08	0.10	0.10	0.10	0.08	0.08	0.08	0.08	0.08	0.08	0.08	0.09	0.08	0.09
MTD7896	0.09	0.09	0.09	0.09	0.09	0.09	0.09	0.10	0.10	0.10	0.10	0.10	0.10	0.10	0.07	0.08	0.10	0.10	0.10	0.08	0.08	0.08	0.08	0.08	0.08	0.08	0.09	0.08	0.09
BC_MTD_LEP3003	0.09	0.09	0.09	0.09	0.09	0.09	0.09	0.10	0.10	0.10	0.10	0.10	0.10	0.10	0.07	0.08	0.10	0.10	0.10	0.08	0.08	0.08	0.08	0.08	0.08	0.08	0.09	0.08	0.09
MTD8229	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.05	0.05	0.06	0.05	0.05	0.05	0.05	0.04	0.04	0.05	0.05	0.05	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04
LEP3155	0.08	0.08	0.08	0.07	0.07	0.07	0.07	0.07	0.08	0.08	0.08	0.08	0.08	0.07	0.06	0.07	0.09	0.09	0.09	0.06	0.06	0.06	0.06	0.06	0.07	0.06	0.07	0.06	0.07
LEP3161	0.08	0.08	0.08	0.07	0.07	0.07	0.07	0.07	0.08	0.08	0.08	0.08	0.08	0.07	0.06	0.07	0.09	0.09	0.09	0.06	0.06	0.06	0.06	0.06	0.07	0.06	0.07	0.06	0.07
MTD8249	0.07	0.07	0.07	0.05	0.06	0.06	0.06	0.06	0.06	0.06	0.06	0.06	0.06	0.06	0.04	0.06	0.06	0.06	0.06	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04
MTD8242	0.07	0.07	0.07	0.06	0.07	0.07	0.07	0.09	0.09	0.09	0.09	0.09	0.09	0.09	0.05	0.06	0.09	0.09	0.09	0.06	0.07	0.07	0.06	0.07	0.06	0.07	0.07	0.07	0.07
LEP3158	0.06	0.06	0.06	0.06	0.06	0.07	0.07	0.07	0.07	0.07	0.07	0.07	0.07	0.07	0.05	0.06	0.07	0.07	0.07	0.06	0.06	0.06	0.06	0.06	0.06	0.06	0.06	0.06	0.06
MTD7894	0.08	0.08	0.08	0.07	0.07	0.07	0.07	0.08	0.08	0.08	0.08	0.08	0.08	0.08	0.06	0.07	0.08	0.08	0.08	0.06	0.06	0.06	0.06	0.06	0.06	0.06	0.06	0.06	0.06
BC_MTD_LEP01421	0.08	0.08	0.08	0.06	0.06	0.07	0.07	0.07	0.08	0.07	0.07	0.07	0.08	0.07	0.08	0.09	0.08	0.09	0.08	0.07	0.07	0.07	0.07	0.07	0.07	0.07	0.08	0.08	0.08
BC_ZMBN_Lep00081	0.09	0.09	0.09	0.06	0.07	0.07	0.07	0.07	0.08	0.08	0.07	0.08	0.08	0.07	0.07	0.08	0.08	0.09	0.08	0.07	0.07	0.07	0.07	0.07	0.07	0.07	0.07	0.07	0.07
MTD8243	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.05	0.05	0.05	0.05	0.05	0.05	0.05	0.04	0.05	0.04	0.04	0.04	0.04	0.04	0.04	0.03	0.03	0.04	0.03	0.04	0.04	0.04

Continued on next page

Table C.4 – *Continued from previous page*

	BC_MTD_LEP01425	BC_MTD_LEP01426	BC_MTD_LEP01427	MTD8238	MTD7422	BC_MTD_LEP01430	BC_MTD_LEP01431	MTD8143	MTD8144	MTD8145	MTD8146	MTD8147	MTD8148	MTD7418	LEP3164	LEP3165	MTD7878	LEP3214	LEP3215	LEP3064	LEP3065	MTD7882	MTD7887	MTD7889	MTD7893	MTD7897	MTD7891	MTD7892	MTD8232
USNM_ENT_00739239	0.11	0.11	0.11	0.08	0.09	0.10	0.10	0.11	0.11	0.11	0.11	0.11	0.11	0.11	0.07	0.08	0.10	0.10	0.10	0.07	0.08	0.08	0.07	0.07	0.08	0.07	0.08	0.08	0.08
LEP3156	0.09	0.09	0.09	0.07	0.08	0.08	0.08	0.09	0.09	0.09	0.09	0.09	0.09	0.09	0.07	0.07	0.08	0.08	0.08	0.06	0.07	0.07	0.05	0.06	0.07	0.06	0.07	0.07	0.07
MTD8258	0.08	0.08	0.08	0.06	0.06	0.07	0.07	0.07	0.07	0.07	0.07	0.07	0.07	0.07	0.07	0.08	0.07	0.08	0.08	0.06	0.07	0.07	0.06	0.06	0.06	0.06	0.06	0.06	0.06
BC_MTD_LEP01422	0.07	0.07	0.07	0.05	0.05	0.07	0.07	0.06	0.07	0.07	0.06	0.07	0.07	0.06	0.06	0.07	0.07	0.08	0.07	0.06	0.07	0.07	0.06	0.06	0.07	0.06	0.06	0.06	0.06
MTD9119	0.09	0.09	0.09	0.06	0.07	0.07	0.07	0.07	0.08	0.07	0.07	0.07	0.08	0.07	0.06	0.07	0.08	0.09	0.08	0.06	0.07	0.07	0.06	0.06	0.07	0.06	0.07	0.07	0.07
MTD9120	0.08	0.08	0.08	0.06	0.06	0.07	0.07	0.07	0.08	0.07	0.07	0.07	0.08	0.07	0.06	0.07	0.08	0.09	0.08	0.06	0.07	0.07	0.06	0.06	0.07	0.06	0.07	0.07	0.07
MTD9121	0.08	0.08	0.08	0.06	0.06	0.06	0.06	0.07	0.07	0.07	0.07	0.07	0.07	0.07	0.06	0.06	0.08	0.08	0.08	0.06	0.07	0.07	0.06	0.06	0.06	0.06	0.07	0.07	0.07
MTD7880	0.08	0.08	0.08	0.06	0.06	0.06	0.06	0.07	0.07	0.07	0.07	0.07	0.07	0.07	0.06	0.06	0.08	0.08	0.08	0.06	0.07	0.07	0.06	0.06	0.07	0.06	0.07	0.07	0.07
LEP3205	0.08	0.08	0.08	0.06	0.07	0.07	0.07	0.07	0.07	0.07	0.07	0.07	0.07	0.07	0.06	0.07	0.08	0.08	0.08	0.06	0.07	0.07	0.06	0.06	0.07	0.06	0.07	0.07	0.07
MTD8257	0.07	0.07	0.07	0.05	0.05	0.06	0.06	0.06	0.06	0.06	0.06	0.06	0.06	0.06	0.04	0.06	0.06	0.07	0.06	0.04	0.05	0.05	0.04	0.04	0.05	0.05	0.06	0.06	0.06
MTD8260	0.07	0.07	0.07	0.06	0.06	0.06	0.06	0.07	0.07	0.07	0.07	0.07	0.07	0.07	0.05	0.05	0.07	0.07	0.07	0.05	0.06	0.06	0.05	0.05	0.06	0.05	0.06	0.06	0.06
MTD8262	0.09	0.09	0.09	0.06	0.07	0.07	0.07	0.07	0.08	0.07	0.07	0.07	0.08	0.07	0.06	0.07	0.08	0.09	0.08	0.06	0.07	0.07	0.06	0.06	0.07	0.06	0.07	0.07	0.07
LEP3206	0.06	0.06	0.06	0.06	0.06	0.06	0.06	0.07	0.07	0.07	0.07	0.07	0.07	0.07	0.06	0.07	0.07	0.07	0.07	0.05	0.06	0.06	0.06	0.06	0.06	0.06	0.06	0.06	0.06
USNM_ENT_00739227	0.10	0.10	0.10	0.08	0.08	0.09	0.09	0.10	0.10	0.10	0.10	0.10	0.10	0.10	0.05	0.07	0.09	0.10	0.10	0.07	0.07	0.07	0.07	0.07	0.07	0.07	0.08	0.08	0.08
USNM_ENT_00739208	0.10	0.10	0.10	0.08	0.08	0.09	0.09	0.10	0.10	0.10	0.10	0.10	0.10	0.10	0.05	0.07	0.09	0.10	0.10	0.07	0.07	0.07	0.07	0.07	0.07	0.07	0.08	0.08	0.08
YAWCATCR0759	0.10	0.10	0.10	0.08	0.09	0.09	0.09	0.10	0.10	0.10	0.10	0.10	0.10	0.10	0.05	0.07	0.09	0.09	0.09	0.07	0.07	0.07	0.06	0.07	0.07	0.07	0.08	0.08	0.08
MTD7427	0.08	0.08	0.08	0.07	0.07	0.07	0.07	0.08	0.08	0.08	0.08	0.08	0.08	0.08	0.06	0.07	0.09	0.09	0.09	0.04	0.04	0.04	0.03	0.04	0.04	0.04	0.05	0.05	0.05
MTD7428	0.08	0.08	0.08	0.07	0.07	0.07	0.07	0.08	0.08	0.08	0.08	0.07	0.08	0.08	0.06	0.07	0.09	0.09	0.09	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.05	0.05	0.05
MTD7429	0.08	0.08	0.08	0.07	0.07	0.07	0.07	0.08	0.08	0.08	0.08	0.08	0.08	0.08	0.06	0.07	0.09	0.09	0.09	0.04	0.04	0.04	0.03	0.04	0.04	0.04	0.05	0.05	0.05

Table C3 (suite). K2P-distances calculated on the ABGD online server (https://bioinfo.mnhn.fr/abi/public/abgd/abgdweb.html) using the Kimura 2-parameters algorithm.

	MTD8232	BC_MTD_LEP01419	LEP3195	MTD8234	LEP124	LEP3197	BC_MTD_LEP3006	MTD7426	BC_MTD_LEP3004	MTD8244	LEP3163	LEP3166	MTD8252	MTD8253	LEP3162	USNM_ENT_00665932	USNM_ENT_00514731	USNM_ENT_00514750	MTD7431	MTD7884	MTD7886	MTD7888	MTD7890	MTD7895	MTD7896	BC_MTD_LEP3003	MTD8229	LEP3155	LEP3161
MTD8232																													
BC_MTD_LEP01419	0.06																												
LEP3195	0.06	0.04																											
MTD8234	0.05	0.02	0.01																										
LEP124	0.06	0.06	0.05	0.04																									
LEP3197	0.06	0.07	0.06	0.04	0.00																								
BC_MTD_LEP3006	0.06	0.07	0.06	0.04	0.00	0.00																							
MTD7426	0.05	0.05	0.04	0.03	0.04	0.04	0.04																						
BC_MTD_LEP3004	0.05	0.05	0.04	0.03	0.04	0.04	0.05	0.00																					
MTD8244	0.05	0.05	0.04	0.03	0.03	0.03	0.04	0.02	0.02																				
LEP3163	0.07	0.06	0.06	0.04	0.05	0.06	0.06	0.04	0.04	0.04																			
LEP3166	0.07	0.06	0.06	0.04	0.05	0.06	0.07	0.04	0.04	0.05	0.00																		
MTD8252	0.07	0.07	0.07	0.04	0.06	0.06	0.06	0.05	0.05	0.04	0.05	0.05																	
MTD8253	0.05	0.05	0.05	0.03	0.04	0.05	0.05	0.04	0.04	0.04	0.04	0.05	0.00																
LEP3162	0.10	0.11	0.09	0.07	0.08	0.08	0.09	0.08	0.09	0.08	0.09	0.09	0.08	0.07															
USNM_ENT_00665932	0.10	0.10	0.09	0.07	0.09	0.09	0.09	0.08	0.09	0.08	0.08	0.08	0.07	0.07	0.08														
USNM_ENT_00514731	0.10	0.10	0.09	0.07	0.09	0.09	0.09	0.08	0.09	0.08	0.08	0.08	0.07	0.07	0.08	0.00													
USNM_ENT_00514750	0.10	0.10	0.09	0.07	0.09	0.09	0.09	0.08	0.09	0.08	0.08	0.08	0.07	0.07	0.08	0.00	0.00												
MTD7431	0.06	0.07	0.06	0.04	0.06	0.06	0.06	0.05	0.05	0.05	0.07	0.07	0.07	0.05	0.09	0.10	0.10	0.10											
MTD7884	0.08	0.08	0.07	0.06	0.08	0.09	0.09	0.06	0.06	0.07	0.08	0.08	0.08	0.06	0.11	0.11	0.11	0.11	0.09										
MTD7886	0.08	0.07	0.07	0.06	0.08	0.09	0.09	0.06	0.06	0.07	0.07	0.07	0.08	0.05	0.11	0.11	0.11	0.11	0.09	0.00									
MTD7888	0.09	0.08	0.08	0.07	0.08	0.09	0.09	0.07	0.07	0.07	0.08	0.08	0.08	0.06	0.12	0.13	0.13	0.13	0.09	0.00	0.00								
MTD7890	0.09	0.08	0.08	0.07	0.08	0.09	0.09	0.07	0.07	0.07	0.08	0.08	0.08	0.06	0.12	0.13	0.13	0.13	0.09	0.00	0.00	0.00							
MTD7895	0.09	0.08	0.08	0.07	0.08	0.09	0.09	0.07	0.07	0.07	0.08	0.08	0.08	0.06	0.12	0.13	0.13	0.13	0.09	0.00	0.00	0.00	0.00						
MTD7896	0.09	0.08	0.08	0.07	0.08	0.09	0.09	0.07	0.07	0.07	0.08	0.08	0.08	0.06	0.12	0.13	0.13	0.13	0.09	0.00	0.00	0.00	0.00	0.00					
BC_MTD_LEP3003	0.09	0.08	0.08	0.07	0.08	0.09	0.09	0.07	0.07	0.07	0.08	0.08	0.08	0.06	0.12	0.13	0.13	0.13	0.09	0.00	0.00	0.00	0.00	0.00	0.00				
MTD8229	0.04	0.05	0.05	0.03	0.04	0.04	0.04	0.04	0.04	0.03	0.04	0.04	0.04	0.04	0.06	0.06	0.06	0.06	0.06	0.03	0.03	0.03	0.03	0.03	0.03	0.03			
LEP3155	0.07	0.06	0.06	0.04	0.06	0.07	0.07	0.06	0.06	0.06	0.05	0.05	0.06	0.06	0.12	0.10	0.10	0.10	0.07	0.08	0.08	0.09	0.09	0.09	0.09	0.09	0.04		
LEP3161	0.07	0.06	0.06	0.04	0.06	0.07	0.07	0.06	0.06	0.06	0.05	0.05	0.06	0.06	0.12	0.10	0.10	0.10	0.07	0.08	0.08	0.09	0.09	0.09	0.09	0.09	0.04	0.00	
MTD8249	0.04	0.05	0.05	0.04	0.04	0.05	0.05	0.03	0.04	0.05	0.05	0.06	0.04	0.04	0.08	0.08	0.08	0.08	0.04	0.05	0.05	0.06	0.06	0.06	0.06	0.06	0.02	0.07	0.07

Continued on next page

Table C.5 – *Continued from previous page*

	MTD8232	BC _MTD _LEP01419	LEP3195	MTD8234	LEP124	LEP3197	BC _MTD _LEP3006	MTD7426	BC _MTD _LEP3004	MTD8244	LEP3163	LEP3166	MTD8252	MTD8253	LEP3162	USNM _ENT _00665932	USNM _ENT _00514731	USNM _ENT _00514750	MTD7431	MTD7884	MTD7886	MTD7888	MTD7890	MTD7895	MTD7896	BC _MTD _LEP3003	MTD8229	LEP3155	LEP3161
MTD8242	0.07	0.07	0.07	0.05	0.06	0.07	0.07	0.07	0.07	0.06	0.06	0.06	0.07	0.03	0.09	0.08	0.08	0.08	0.09	0.08	0.08	0.08	0.08	0.08	0.08	0.08	0.05	0.07	0.07
LEP3158	0.06	0.05	0.06	0.05	0.06	0.06	0.07	0.06	0.06	0.06	0.06	0.06	0.05	0.03	0.09	0.09	0.09	0.09	0.05	0.06	0.06	0.06	0.06	0.06	0.06	0.06	0.02	0.06	0.06
MTD7894	0.06	0.06	0.07	0.06	0.06	0.07	0.07	0.06	0.06	0.06	0.07	0.07	0.07	0.06	0.09	0.09	0.09	0.09	0.05	0.09	0.09	0.09	0.09	0.09	0.09	0.09	0.05	0.07	0.07
BC_MTD_LEP01421	0.08	0.08	0.07	0.06	0.06	0.06	0.06	0.06	0.06	0.07	0.07	0.08	0.07	0.06	0.12	0.12	0.12	0.12	0.07	0.10	0.10	0.10	0.10	0.10	0.10	0.10	0.06	0.09	0.09
BC_ZMBN_Lep00081	0.07	0.07	0.06	0.04	0.06	0.06	0.07	0.06	0.06	0.07	0.07	0.07	0.06	0.05	0.12	0.11	0.11	0.11	0.08	0.09	0.09	0.10	0.10	0.10	0.10	0.10	0.04	0.08	0.08
MTD8243	0.04	0.03	0.03	0.02	0.03	0.03	0.03	0.03	0.03	0.03	0.04	0.04	0.04	0.03	0.05	0.04	0.04	0.04	0.04	0.05	0.05	0.06	0.06	0.06	0.06	0.06	0.02	0.04	0.04
USNM_ENT_00739239	0.08	0.08	0.07	0.05	0.08	0.09	0.10	0.08	0.09	0.08	0.08	0.09	0.08	0.06	0.12	0.11	0.11	0.11	0.08	0.09	0.09	0.10	0.09	0.10	0.10	0.10	0.05	0.08	0.08
LEP3156	0.07	0.07	0.07	0.06	0.06	0.07	0.07	0.06	0.06	0.07	0.08	0.08	0.07	0.05	0.10	0.10	0.10	0.10	0.07	0.07	0.07	0.08	0.08	0.08	0.08	0.08	0.04	0.08	0.08
MTD8258	0.06	0.07	0.05	0.04	0.05	0.05	0.05	0.05	0.05	0.05	0.06	0.07	0.07	0.05	0.10	0.10	0.10	0.10	0.06	0.08	0.08	0.08	0.08	0.08	0.08	0.08	0.05	0.08	0.08
BC_MTD_LEP01422	0.06	0.07	0.05	0.04	0.05	0.06	0.06	0.05	0.05	0.05	0.06	0.06	0.06	0.05	0.11	0.11	0.11	0.11	0.06	0.08	0.08	0.09	0.09	0.09	0.09	0.09	0.05	0.08	0.08
MTD9119	0.07	0.08	0.07	0.05	0.06	0.06	0.07	0.06	0.06	0.07	0.06	0.07	0.07	0.07	0.12	0.11	0.11	0.11	0.08	0.08	0.08	0.09	0.09	0.09	0.09	0.09	0.05	0.09	0.09
MTD9120	0.07	0.08	0.07	0.05	0.06	0.06	0.06	0.06	0.06	0.06	0.06	0.07	0.06	0.06	0.12	0.10	0.10	0.10	0.08	0.08	0.08	0.09	0.09	0.09	0.09	0.09	0.05	0.09	0.09
MTD9121	0.07	0.07	0.06	0.04	0.06	0.06	0.06	0.06	0.06	0.06	0.06	0.06	0.06	0.06	0.10	0.09	0.09	0.09	0.08	0.08	0.08	0.09	0.09	0.09	0.09	0.09	0.05	0.08	0.08
MTD7880	0.07	0.07	0.07	0.05	0.06	0.06	0.06	0.06	0.06	0.06	0.06	0.06	0.06	0.05	0.10	0.09	0.09	0.09	0.08	0.08	0.08	0.09	0.09	0.09	0.09	0.09	0.05	0.08	0.08
LEP3205	0.07	0.07	0.07	0.05	0.06	0.06	0.06	0.06	0.06	0.06	0.06	0.06	0.06	0.06	0.10	0.10	0.10	0.10	0.08	0.08	0.08	0.09	0.09	0.09	0.09	0.09	0.05	0.08	0.08
MTD8257	0.06	0.07	0.06	0.04	0.05	0.05	0.06	0.05	0.05	0.05	0.05	0.06	0.05	0.07	0.08	0.08	0.08	0.08	0.06	0.06	0.06	0.07	0.07	0.07	0.07	0.07	0.05	0.08	0.08
MTD8260	0.06	0.06	0.06	0.04	0.05	0.05	0.05	0.05	0.05	0.05	0.05	0.05	0.06	0.06	0.08	0.07	0.07	0.07	0.06	0.07	0.07	0.08	0.08	0.08	0.08	0.08	0.05	0.08	0.08
MTD8262	0.07	0.08	0.07	0.05	0.06	0.06	0.07	0.06	0.06	0.07	0.06	0.07	0.07	0.07	0.11	0.10	0.10	0.10	0.07	0.08	0.08	0.08	0.08	0.08	0.08	0.08	0.05	0.09	0.09
LEP3206	0.06	0.06	0.06	0.05	0.06	0.06	0.06	0.05	0.05	0.05	0.06	0.06	0.07	0.05	0.08	0.08	0.08	0.08	0.06	0.09	0.09	0.09	0.09	0.09	0.09	0.09	0.05	0.06	0.06
USNM_ENT_00739227	0.08	0.08	0.07	0.06	0.07	0.08	0.08	0.07	0.07	0.07	0.07	0.08	0.07	0.07	0.11	0.10	0.10	0.10	0.07	0.09	0.09	0.10	0.10	0.10	0.10	0.10	0.04	0.08	0.08
USNM_ENT_00739208	0.08	0.08	0.07	0.06	0.07	0.08	0.08	0.07	0.07	0.07	0.07	0.08	0.07	0.07	0.11	0.10	0.10	0.10	0.07	0.09	0.09	0.10	0.10	0.10	0.10	0.10	0.04	0.08	0.08
YAWCATCR0759	0.08	0.08	0.07	0.05	0.07	0.08	0.08	0.07	0.07	0.07	0.07	0.07	0.07	0.07	0.11	0.10	0.10	0.10	0.07	0.09	0.08	0.10	0.10	0.10	0.10	0.10	0.04	0.08	0.08
MTD7427	0.05	0.06	0.06	0.05	0.06	0.07	0.07	0.05	0.06	0.05	0.07	0.07	0.06	0.05	0.10	0.10	0.10	0.10	0.06	0.07	0.07	0.08	0.08	0.08	0.08	0.08	0.03	0.07	0.07
MTD7428	0.05	0.06	0.07	0.05	0.06	0.07	0.07	0.05	0.06	0.06	0.07	0.07	0.06	0.05	0.11	0.10	0.10	0.10	0.06	0.07	0.07	0.08	0.08	0.08	0.08	0.08	0.04	0.06	0.06
MTD7429	0.05	0.06	0.06	0.05	0.06	0.07	0.07	0.05	0.06	0.05	0.07	0.07	0.06	0.05	0.10	0.10	0.10	0.10	0.06	0.07	0.07	0.08	0.08	0.08	0.08	0.08	0.03	0.07	0.07

Table C3 (suite). K2P-distances calculated on the ABGD online server (https://bioinfo.mnhn.fr/abi/public/abgd/abgdweb.html) using the Kimura 2-parameters algorithm.

	LEP3161	MTD8249	MTD8242	LEP3158	MTD7894	BC _MTD _LEP01421	BC _ZMBN _Lep00081	MTD8243	USNM _ENT _00739239	LEP3156	MTD8258	BC _MTD _LEP01422	MTD9119	MTD9120	MTD9121	MTD7880	LEP3205	MTD8257	MTD8260	MTD8262	LEP3206	USNM _ENT _00739227	USNM _ENT _00739208	YAWCATCR0759	MTD7427	MTD7428	MTD7429
LEP3161																											
MTD8249	0.07																										
MTD8242	0.07	0.06																									
LEP3158	0.06	0.07	0.00																								
MTD7894	0.07	0.04	0.08	0.06																							
BC_MTD_LEP01421	0.09	0.07	0.09	0.08	0.08																						
BC_ZMBN_Lep00081	0.08	0.07	0.08	0.07	0.08	0.06																					
MTD8243	0.04	0.05	0.04	0.05	0.04	0.04	0.05																				
USNM_ENT_00739239	0.08	0.06	0.07	0.08	0.09	0.11	0.09	0.07																			
LEP3156	0.08	0.05	0.07	0.06	0.07	0.09	0.08	0.04	0.09																		
MTD8258	0.08	0.06	0.07	0.07	0.07	0.05	0.06	0.04	0.10	0.08																	
BC_MTD_LEP01422	0.08	0.06	0.07	0.07	0.07	0.05	0.06	0.04	0.10	0.08	0.01																
MTD9119	0.09	0.06	0.08	0.07	0.07	0.06	0.05	0.04	0.11	0.08	0.06	0.06															
MTD9120	0.09	0.06	0.08	0.07	0.07	0.06	0.05	0.04	0.10	0.08	0.06	0.06	0.00														
MTD9121	0.08	0.05	0.08	0.06	0.07	0.05	0.04	0.04	0.10	0.08	0.05	0.05	0.00	0.00													

Continued on next page

Table C.6 – *Continued from previous page*

	LEP3161	MTD8249	MTD8242	LEP3158	MTD7894	BC _MTD _LEP01421	BC _ZMBN _Lep00081	MTD8243	USNM _ENT _00739239	LEP3156	MTD8258	BC _MTD _LEP01422	MTD9119	MTD9120	MTD9121	MTD7880	LEP3205	MTD8257	MTD8260	MTD8262	LEP3206	USNM _ENT _00739227	USNM _ENT _00739208	YAWCATCR0759	MTD7427	MTD7428	MTD7429
MTD7880	0.08	0.05	0.08	0.06	0.07	0.06	0.05	0.04	0.09	0.08	0.06	0.05	0.00	0.00	0.00												
LEP3205	0.08	0.05	0.08	0.06	0.07	0.06	0.05	0.04	0.10	0.08	0.06	0.06	0.00	0.00	0.00	0.00											
MTD8257	0.08	0.05	0.06	0.05	0.06	0.04	0.04	0.02	0.08	0.07	0.04	0.04	0.00	0.00	0.00	0.00	0.00										
MTD8260	0.08	0.04	0.07	0.05	0.06	0.05	0.04	0.02	0.08	0.07	0.05	0.05	0.00	0.00	0.00	0.00	0.00	0.00									
MTD8262	0.09	0.06	0.08	0.07	0.07	0.06	0.05	0.04	0.10	0.08	0.05	0.06	0.01	0.00	0.00	0.00	0.00	0.00	0.00								
LEP3206	0.06	0.06	0.07	0.05	0.07	0.07	0.07	0.04	0.08	0.08	0.07	0.07	0.07	0.06	0.06	0.06	0.06	0.05	0.06	0.06							
USNM_ENT_00739227	0.08	0.06	0.08	0.08	0.08	0.10	0.10	0.06	0.07	0.09	0.09	0.10	0.10	0.10	0.09	0.09	0.09	0.08	0.07	0.09	0.07						
USNM_ENT_00739208	0.08	0.06	0.08	0.08	0.08	0.10	0.10	0.06	0.07	0.09	0.09	0.10	0.10	0.10	0.09	0.09	0.09	0.08	0.07	0.09	0.07	0.00					
YAWCATCR0759	0.08	0.06	0.08	0.07	0.07	0.10	0.09	0.06	0.07	0.09	0.10	0.10	0.10	0.09	0.08	0.09	0.09	0.07	0.07	0.09	0.07	0.01	0.01				
MTD7427	0.07	0.06	0.07	0.06	0.07	0.08	0.07	0.04	0.08	0.07	0.07	0.07	0.07	0.07	0.07	0.07	0.07	0.05	0.06	0.07	0.06	0.07	0.07	0.07			
MTD7428	0.06	0.06	0.07	0.06	0.06	0.08	0.07	0.04	0.08	0.07	0.07	0.07	0.07	0.07	0.07	0.07	0.07	0.06	0.06	0.07	0.06	0.07	0.07	0.07	0.01		
MTD7429	0.07	0.06	0.07	0.06	0.07	0.08	0.07	0.04	0.08	0.07	0.07	0.07	0.07	0.07	0.07	0.07	0.07	0.05	0.06	0.07	0.06	0.07	0.07	0.07	0.00	0.01	

Table C.7: Collecting localities of the *Hoploscopa* specimens examined. Historic localities are approximative.

species	latitude	longitude	geographical location	country	detailed locality
H. agtuuganonensis	7.78	126.21	Mindanao	Philippines	Mount Agtuuganon
H. albipuncta	6.042	116.596	Borneo	Malaysia	Kopogon
H. albipuncta	6.045	116.595	Borneo	Malaysia	Mesilau Nature Resort
H. albipuncta	6.028	116.548	Borneo	Malaysia	Timpohon Gate, 300m after Ligawu trail start
H. albipuncta	6.0277	116.549	Borneo	Malaysia	Timpohon Gate, 700m after Ligawu trail start
H. albomaculata	0.76	124.46	North Sulawesi	Indonesia	Lake Danau Mooat
H. anacantha	0.56	123.68	North Sulawesi	Indonesia	Dumoga-Bone NP [Bogani Nani Wartabone NP]
H. anacantha	0.76	124.46	North Sulawesi	Indonesia	Lake Danau Mooat
H. anacantha	0.45	123.93	North Sulawesi	Indonesia	Mount Mogogonipa
H. anamesa	-20.2	169.81	Aneityum	Vanuatu	Aneityum
H. anamesa	-20.23	169.76	Aneityum	Vanuatu	Anelgauhat
H. anamesa	-19.5	169.3	Tanna	Vanuatu	Tanna
H. astrapias	-17.56	177.96	Fiji	Fiji	Nandarivatu
H. astrapias	-17.82	178.32	Fiji	Fiji	Vunîdawa
H. aurantiacalis	-7.175	107.57	Pengaleng	Indonesia	Pengaleng
H. boleta	-7.35	146.68	Papua	Papua New Guinea	Mount Kaindi
H. brunnealis	-7.175	107.57	Pengaleng	Indonesia	Pengaleng
H. cynodonta	4.555	115.154	Borneo	Brunei	Ulu Temburong
H. cynodonta	6.009	116.537	Borneo	Malaysia	Kiau View-Pandanus Trail
H. cynodonta	5.48	116.56	Borneo	Malaysia	Mount Monkobo
H. cynodonta	4.467	117.917	Borneo	Malaysia	Tawau Hills HQ
H. cynodonta	6.0277	116.549	Borneo	Malaysia	Timpohon Gate, 700m after Ligawu trail start
H. danaoensis	11.07	124.69	Leyte	Philippines	Lake Danao
H. diffusa	-9.5	150.66	Papua	Papua New Guinea	Fergusson Island
H. gombongi	-6.2	146.1	Papua	Papua New Guinea	Yawan village
H. gracilis	2.77	98.53	Sumatra	Indonesia	Dairi
H. gracilis	3.24	98.51	Sumatra	Indonesia	Mount Sibayak
H. gracilis	2.755	99	Sumatra	Indonesia	Road from Pematangsiantar to Prapat
H. gracilis	1.617	99.267	Sumatra	Indonesia	Sipirok
H. ignitamaculae	0.56	123.68	North Sulawesi	Indonesia	Dumoga-Bone NP [Bogani Nani Wartabone NP]
H. ignitamaculae	0.76	124.46	North Sulawesi	Indonesia	Lake Danau Mooat
H. ignitamaculae	0.45	123.93	North Sulawesi	Indonesia	Mount Mogogonipa
H. ignitamaculae	1.51	125.18	North Sulawesi	Indonesia	Tangkoko Batuangus Nature Reserve
H. isarogensis	13.66	123.33	Luzon	Philippines	Mount Isarog
H. jubata	-7.22	146.61	Papua	Papua New Guinea	Mount Susu NP
H. jubata	-7	146	Papua	Papua New Guinea	Wau Ecology Institute
H. kelama	0.56	123.68	North Sulawesi	Indonesia	Dumoga-Bone NP [Bogani Nani Wartabone NP]
H. kelama	0.76	124.46	North Sulawesi	Indonesia	Lake Danau Mooat
H. kinabaluensis	6.009	116.537	Borneo	Malaysia	Kiau View-Pandanus Trail
H. kinabaluensis	6.0116	116.534	Borneo	Malaysia	Kinabalu Mountain Lodge
H. kinabaluensis	6.028	116.548	Borneo	Malaysia	Timpohon Gate, 300m after Ligawu trail start
H. kinabaluensis	6.0277	116.549	Borneo	Malaysia	Timpohon Gate, 700m after Ligawu trail start
H. luteomacula	-0.4	100.35	Sumatra	Indonesia	Mount Singgalang
H. luteomacula	2.755	99	Sumatra	Indonesia	Road from Pematangsiantar to Prapat

Continued on next page

Table C.7 – *Continued from previous page*

species	latitude	longitude	geographical location	country	detailed locality
H. mallyi	6.0394	116.598	Borneo	Malaysia	Mesilau logging site
H. mallyi	6.045	116.595	Borneo	Malaysia	Mesilau Nature Resort
H. mallyi	6.009	16.538	Borneo	Malaysia	Pandanus trail, 250m after start
H. mallyi	6.01	116.54	Borneo	Malaysia	Sabah, Kundasang, Kinabalu NP Headquarters
H. mallyi	6.028	116.548	Borneo	Malaysia	Timpohon Gate, 300m after Ligawu trail start
H. marijoweissae	-4.4	139.7	Papua	Indonesia	Mount Goliath [Mount Yamin]
H. matheae	4.33	115.29	Borneo	Brunei	Bukit Retak
H. matheae	6.011	116.534	Borneo	Malaysia	Kinabalu Mountain Lodge
H. matheae	4.467	117.917	Borneo	Malaysia	Tawau Hills HQ
H. metacrossa	-2.91	132.3	Papua	Indonesia	Fak-Fak
H. metacrossa	-7.22	146.61	Papua	Papua New Guinea	Mount Susu NP
H. metacrossa	-7	146	Papua	Papua New Guinea	Wau Ecology Institute
H. nauticorum	-13.9	-171.75	Upolu	Samoa	Malololelei
H. nauticorum	-13.92	171.75	Upolu	Samoa	Tiavi
H. niveofascia	-7.22	146.61	Papua	Papua New Guinea	Mount Susu NP
H. obliqua	-4.48	137.34	Papua	Indonesia	Utakwa [Oetakwa] river
H. obliqua	-5.25	145.283	Papua	Papua New Guinea	Wanang village
H. ocellata	-0.61	127.3	Moluccas	Indonesia	Batchian [Bacan islands]
H. pangrangoensis	-6.77	106.96	Java	Indonesia	Mount Pangrango
H. parvimacula	6.0116	116.534	Borneo	Malaysia	Kinabalu Mountain Lodge
H. parvimacula	6.0394	116.598	Borneo	Malaysia	Mesilau logging site
H. parvimacula	6.045	116.595	Borneo	Malaysia	Mesilau Nature Resort
H. parvimacula	6.028	116.548	Borneo	Malaysia	Timpohon Gate, 300m after Ligawu trail start
H. persimilis	-4.48	137.34	Papua	Indonesia	Utakwa [Oetakwa] river
H. pseudometacrossa	-5.58	144.07	Papua	Papua New Guinea	Mount Hagen
H. quadripuncta	-3.08	129.53	Moluccas	Indonesia	Mount Kobipoto
H. quadripuncta	-4.48	137.34	Papua	Indonesia	Utakwa [Oetakwa] river
H. quadripuncta	-9	148.37	Papua	Papua New Guinea	Hydrographers Range
H. semifascia	-2.91	132.3	Papua	Indonesia	Fak-Fak
H. semifascia	-6.58	142.83	Papua	Papua New Guinea	Bosavi (Mount)
H. semifascia	-7	146	Papua	Papua New Guinea	Wau Ecology Institute
H. sepanggi	6.0394	116.598	Borneo	Malaysia	Mesilau logging site
H. sepanggi	6.045	116.595	Borneo	Malaysia	Mesilau Nature Resort
H. sepanggi	6.028	116.548	Borneo	Malaysia	Timpohon Gate, 300m after Ligawu trail start
H. subvariegata	-8.8	146.5	Papua	Papua New Guinea	Angabunga river
H. subvariegata	-7.35	146.68	Papua	Papua New Guinea	Mount Kaindi
H. sumatrensis	2.755	99	Sumatra	Indonesia	Road from Pematangsiantar to Prapat
H. titika	2.755	99	Sumatra	Indonesia	Road from Pematangsiantar to Prapat
H. tonsepi	-6.2	146.1	Papua	Papua New Guinea	Yawan village
H. triangulifera	-4.63	145.97	Papua	Papua New Guinea	Dampier Island [Karkar]
H. triangulifera	-9.5	150.66	Papua	Papua New Guinea	Fergusson Island
H. triangulifera	-8.45	147.81	Papua	Papua New Guinea	Mambare River
H. ypsilon	17.04	121.1	Luzon	Philippines	Barlig (Chatol)
H. ypsilon	16.97	121.03	Luzon	Philippines	Mount Polis
H. ypsilon	16.16	120.94	Luzon	Philippines	Santa Fe