

The phylogenetic systematics of Spilomelinae and Pyraustinae (Lepidoptera: Pyraloidea: Crambidae) inferred from DNA and morphology

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Abstract. Spilomelinae and Pyraustinae form a species-rich monophylum of Crambidae (snout moths). Morphological distinction of the two groups has been difficult in the past, and the morphologically heterogeneous Spilomelinae has not been broadly accepted as a natural group due to the lack of convincing apomorphies. In order to investigate potential apomorphic characters for Spilomelinae and Pyraustinae and to examine alternative phylogenetic hypotheses, we conduct a phylogenetic analysis using 6 molecular markers and 114 morphological characters of the adults representing 77 genera of Spilomelinae and 18 genera of Pyraustinae. The results of the analysis of the combined data strongly suggest that Spilomelinae and Pyraustinae are each monophyletic and sister to each other. Wurthiinae is confirmed as ingroup of Spilomelinae, and *Sufetula* Walker, 1859 as a non-spilomeline. Within Spilomelinae, several well supported clades are obtained, for which we propose a first phylogeny-based tribal classification, using nine available and four new names: Hydririni Minet, 1982 **stat.rev.**, Lineodini Amsel, 1956 **stat.rev.**, Udeini **trib.n.**, Wurthiini Roepke, 1916 **stat.rev.**, Agrotorini Acloque, 1897 **stat.rev.**, Spilomelini Guenée, 1854 **stat.rev.** (= Siginae Hampson, 1918), Herpetogrammatini **trib.n.**, Hymeniini Swinhoe, 1900 **stat.rev.**, Asciodini **trib.n.**, Trichaeini **trib.n.**, Steniini Guenée, 1854 **stat.rev.**, Nomophilini Kuznetsov & Stekolnikov, 1979 **stat.rev.** and Margaroniini Swinhoe & Cotes, 1889 **stat.rev.** (= Dichocrociinae Swinhoe, 1900; = Hapaliadae Swinhoe, 1890; = Margarodidae Guenée, 1854). The available name Syleptinae Swinhoe, 1900 could not be assigned to any of the recovered clades. Three tribes are recognized in Pyraustinae: Euclastini Popescu-Gorj & Constantinescu, 1977 **stat.rev.**, Portentomorphini Amsel, 1956 **stat.rev.** and Pyraustini Meyrick, 1890 **stat.rev.** (= Botydes Blanchard, 1840; = Ennychites Duponchel, 1845). The taxonomic status of *Tetridia* Warren, 1890, found to be sister to all other investigated Pyraustinae, needs further investigation. The four Spilomelinae tribes that are sister to all other, ‘euspilomeline’ tribes share several plesiomorphies with Pyraustinae. We provide morphological synapomorphies and descriptions for Spilomelinae, Pyraustinae and the subgroups recognised therein. These characters allow the assignment of additional 125 genera to Spilomelinae tribes, and additional 56 genera to Pyraustinae tribes.

New and revised combinations are proposed: *Nonazochis* Amsel, 1956 **syn.n.** of *Conchylodes* Guenée, 1854, with *Conchylodes graphialis* (Schaus, 1912) **comb.n.**; *Conchylodes octonalis* (Zeller, 1873) **comb.n.** (from *Lygropia*); *Hyperectis* Meyrick, 1904 **syn.n.** of *Hydriris* Meyrick, 1885, with *Hydriris dioctias* (Meyick, 1904) **comb.n.**, and *Hydriris apicalis* (Hampson, 1912) **comb.n.**; *Conogethes pandamalis* (Walker, 1859) **comb.n.** (from *Dichocrocis*); *Arthromastix pactolalis* (Guenée, 1854) **comb.n.** (from *Syllepte*); *Prophantis coenostolalis* (Hampson, 1899) **comb.n.** (from *Thliptoceras*); *Prophantis xanthomeralis* (Hampson, 1918) **comb.n.** (from *Thliptoceras*); *Prophantis longicornalis* (Mabille, 1900) **comb.n.** (from *Syngamia*); *Charitoprepes apicipicta* (Inoue, 1963) **comb.n.** (from *Heterocnephes*); *Prenesta rubrocinctalis* (Guenée, 1854) **comb.n.** (from *Glyphodes*); *Alytana calligrammalis* (Mabille, 1879) **comb.n.** (from *Analyta*). *Epherema* Snellen, 1892 **stat.rev.** with its type species *E. abyssalis* Snellen, 1892 **comb.rev.** is removed from synonymy with *Syllepte* Hübner, 1823. *Ametrea* Munroe, 1964 and *Charitoprepes* Warren, 1896 are transferred from Pyraustinae to Spilomelinae; *Prooedema* Hampson, 1891 from Spilomelinae to Pyraustinae; *Aporocosmus* Butler, 1886 from Spilomelinae to Odontiinae; *Orthoraphis* Hampson, 1896 from Spilomelinae to Lathrotelinae; *Hydropionea* Hampson, 1917, *Plantegumia* Amsel, 1956 and MUNROE’S (1995) “undescribed genus ex *Boeotarcha* Meyrick” are transferred from Spilomelinae to Glaphyriinae.

Key words. Snout moths, phylogeny, tribal classification, morphology.

1. Introduction

Pyraustinae and Spilomelinae comprise over 5,200 described species worldwide, accounting for about one third of the species in Pyraloidea (NUSS et al. 2003–2019). It is estimated that about 50% of the pyraloid species are still undescribed on a global scale (MUNROE 1972a), and SUTTON et al. (2015) estimated that in Southeast Asia 60% of the species remain to be described. The knowledge about ecology and especially host plant associations of the larvae is rather comprehensive for the species occurring in Europe (e.g. HASENFUSS 1960; EMMET 1988) and North America (e.g. MUNROE 1972a,b, 1974b, 1976a). A review of the known host plant data for the Oriental species has been given by ROBINSON et al. (2001). In recent years, rearing efforts of Lepidoptera caterpillars like those in Papua New Guinea (MILLER et al. 2007) and Costa Rica (JANZEN & HALLWACHS 2009) collected from the local flora have accumulated a large amount of host plant data for tropical Spilomelinae. Altogether, spilomeline larvae feed on a large variety of angiosperms, with varying degrees of host specificity, and a few species feed on gymnosperms (e.g. INOUE & YAMANAKA 2006) and ferns (e.g. FARAHPOUR-HAGANI et al. 2016). Larvae of *Niphopyralis* Hampson, 1893 are associated with weaver ants, living in their nests and feeding on ant larvae (ROEPKE 1916; KEMNER 1923). Several species are known for their economic impact on crops, among them the corn borers of the genus *Ostrinia* Hübner, 1825 (e.g. NAFUS & SCHREINER 1991), the bean pod borer *Maruca vitrata* (Fabricius, 1787) (e.g. SHARMA 1998), the rice leafrollers of the genera *Cnaphalocrocis* Lederer, 1863 and *Marasmia* Lederer, 1863 (e.g. PATHAK & KHAN 1994) as well as the eggplant borers in the genus *Leucinodes* Guenée, 1854 (e.g. MALLY et al. 2015). Corn borers of the genus *Ostrinia* have become model systems in basic and applied research, like for population ecology, genetics and management as well as pheromone research (ELSWORTH et al. 1989; BURGIO & MANI 1995; ONSTAD & GOULD 1998; WANG et al. 1998; ROELOFS et al. 2002; LASSANCE 2010; FUJI et al. 2011).

Though there has been continuous progress in the systematics of Spilomelinae and Pyraustinae, their current classification is still largely based on typological concepts. Spilomelinae and Pyraustinae are not easily distinguishable based on external features and therefore have long been considered as one taxon under the name Pyraustidae, together with distinct groups like Schoenobiinae, Acentropinae, Scopariinae, Odontiinae and Glyphyriinae (MARION 1952). The distinction between Spilomelinae and Pyraustinae began to come into focus through analyses of genitalia by MÜLLER-RUTZ (1929), PIERCE & METCALFE (1938) and MARION (1952, 1954). During the 1970s, the consensus was to classify Pyraustinae into Spilomelini and Pyraustini (MUNROE 1964, 1976a, 1995; MUNROE & SOLIS 1998). In 1982, MINET split Spilomelinae from Pyraustinae, regarding them only distantly related based on the lack of convincing synapomorphies. He considered the bilobed praecin-

torium and the very reduced or absent gnathos, features common to both Spilomelinae and Pyraustinae, as due to parallelism. Furthermore, he considered none of the diagnostic features for Spilomelinae to be uniquely autapomorphic; instead, he diagnosed Spilomelinae by a combination of characters: chaetosemata absent, males without subcostal retinaculum, praecinctorium bilobed, tympanic frame protruding, spinulae distinctly tapered, male genitalia without well-developed gnathos, and female genitalia without large rhombical signum. SOLIS & MAES' (2003) cladistic study based on morphological features of adults also implied that Pyraustinae and Spilomelinae are not closely related. In contrast, a phylogenetic analysis of molecular data by REGIER et al. (2012) supported the monophyly of Pyraustinae + Spilomelinae; the diversity of both groups, however, was poorly sampled, with only two species of Pyraustinae and three species of Spilomelinae included. Wurthiinae, characterised by a number of morphological adaptations to their ant association, was recovered as ingroup of Spilomelinae. Recently, Lathrotelinae was revised and removed from Spilomelinae, comprising *Diplopseustis* Meyrick, 1884, *Diplopseustoides* Guillermet, 2013, *Lathroteles* J.F.G. Clarke, 1971 and *Sufetula* Walker, 1859 (MINET 2015).

The classification of Spilomelinae is confusing. The subfamily includes 4,097 described species in 338 genera (NUSS et al. 2003–2019). Many genera contain only a few species, and 87 genera (26%) are monotypic. In contrast, 20 genera comprise more than 50 species, collectively encompassing 50% of the species. The most species-rich genera are *Udea* Guenée, 1845, *Palpita* Hübner, 1808, *Glyphodes* Guenée, 1854 and the heterogeneous genera *Syllepte* Hübner, 1823 and *Lamprosema* Hübner, 1823. Pyraustinae comprises 1,239 described species in 174 genera, with 94 genera (52%) monotypic and only three genera with more than 50 species: *Loxostege* Hübner, 1825, *Anania* Hübner, 1823 and *Pyrausta* Schrank, 1802 (NUSS et al. 2003–2019). Tribes within Spilomelinae and Pyraustinae have been proposed for recognition in the past, but they usually served to segregate single genera with aberrant morphology, e.g. the long-legged, narrow-winged Lineodini Amsel, 1956, Nomophilini Kuznetsov & Stekolnikov, 1979 and Hydririni Minet, 1982. Therefore, a comprehensive tribal classification has not been thoroughly accepted. MUNROE (1995) classified the Neotropical Spilomelinae into 15 genus groups plus many unplaced genera, but he did not provide diagnoses for these informal genus groups.

The natural relationships among some Spilomelinae genera have been investigated (SUTRISNO 2002a,b, 2003, 2004, 2005, 2006; SUTRISNO et al. 2006; MALLY & NUSS 2010; HAINES & RUBINOFF 2012), but a large-scale phylogenetic analysis that takes the outstanding diversity of Spilomelinae and Pyraustinae into account and identifies main lineages and their phylogenetic relationships has not been published to date.

Our study provides the first phylogenetic intra-subfamily classification of Spilomelinae and Pyraustinae based on analysis of molecular, morphological and eco-

Table 1. Genetically investigated material with accession numbers. Second row of header states the primer pairs used to amplify the respective genetic marker. (NCBI) in columns Origin and Collection refers to sequences obtained from GenBank, and neither origin nor storing collection are known.

DNA sample	Genus	Species	Tribus	Origin	Collection	COI (1440bp)		EF-1a (1071bp)	
						HyblCO/HybNancy	HybJerry/HybPat	HybOscar-6143/Bosie-6144	HybEF51.9/EFcM4
MTD393	<i>Synalphe</i>	<i>punctalis</i> (Fabricius, 1775)	(PYRALINAE)	Germany	MTD	JF497027		MK459848	
MM00051	<i>Pyralis</i>	<i>farinalis</i> (Linnaeus, 1758)	(PYRALINAE)	(NCBI)	(NCBI)		GU828389	GU828925	GU829221
MM09194	<i>Schoenobius</i>	<i>gigantellus</i> (Denis & Schiffermüller, 1775)	(SCHOENOBINAE)	(NCBI)	(NCBI)		GU929806	GU829143	GU829411
MM11223	<i>Clepsidrina</i>	<i>irida</i> Meyrick, 1888	(ACENTROPINAE)	(NCBI)	(NCBI)		GU828852	GU829154	GU829419
MM03362	<i>Crambus</i>	<i>uliginosellus</i> Zeller, 1850	(CRAMBINAE)	(NCBI)	(NCBI)		GU828691	GU829014	GU829302
MM04967	<i>Eudania</i>	<i>truncatella</i> (Stainton, 1849)	(SCOPARIINAE)	(NCBI)	(NCBI)		GU828709	GU828504	GU829032
MTD370	<i>Midia</i>	<i>guyanensis</i> Munroe, 1970	(MIDILINAE)	French Guiana	MTD	MK459667		MK459849	
MTD1307	<i>Sufetula</i>	<i>diminutalis</i> (Walker, 1866)	(LATHROTELINAE)	Germany	MTD	MK459668		MK459850	
ZMBN094	<i>Aetholix</i>	cf. <i>flavibasalis</i> (Guenée, 1854)	Agrotini	Malaysia	ZMBN	MK459669		MK459851	
MTD1016	<i>Agathodes</i>	<i>designalis</i> Guenée, 1854	Margaritini	Peru	ZSM	MK459670		MK459852	
MTD1328 (WPHZ21)	<i>Agroglipia</i>	<i>excelsalis</i> (Walker, 1866)	Margaritini	Australia	UHIM	JX017869		JX017948	MK459853
MTD488A	<i>Agrotera</i>	<i>nemorialis</i> (Scopoli, 1863)	Agrotini	Germany	MTD	MK459671		MK459854	
MTD1354	<i>Anagastria</i>	cf. <i>primordialis</i> (Dyar, 1906)	Steniini	Bolivia	MTD	MK506102	MK459672	MK459855	
MTD798	<i>Antigastra</i>	<i>catalaunalis</i> (Duponchel, 1833)	Margaritini	Morocco	MTD	MK459673		MK459856	
MTD1331	<i>Apilocras</i>	<i>novateautonalis</i> Munroe, 1968	Wurthini	Peru	ZSM	MK506080	MK459674	MK459857	
MTD668	<i>Aristobulea</i>	<i>principis</i> Munroe & Mutuura, 1968	Wurthini	China	MTD	JF852437	MK459675	MK459858	
MTD797	<i>Arnia</i>	<i>nervosalis</i> (Guenée, 1854)	Nomophitini	Morocco	MTD	MK459676		MK459859	
MTD776	<i>Arthromastix</i>	<i>lauralis</i> (Walker, 1859)	Asciodini	Venezuela	MHNG	JF852400	MK459677	MK459860	
MTD1061	<i>Arthromastix</i>	<i>pactolalis</i> (Guenée, 1854)	Asciodini	French Guiana	R. Rougerie	JN305177	MK459678	MK459861	
MTD1325	<i>Asciodes</i>	cf. <i>gordialis</i> Guenée, 1854	Asciodini	Bolivia	MTD	MK506100	MK459679	MK459862	
MTD1019	<i>Asturades</i>	<i>fimbriatralis</i> (Guenée, 1854)	Margaritini	Peru	ZSM	MK506101	MK459680	MK459863	
MTD1347	<i>Ategumia</i>	<i>ebulealis</i> (Guenée, 1854)	Nomophitini	Bolivia	MTD	MK506088	MK459681	MK459864	
MTD1329	<i>Azochis</i>	cf. <i>rufidiscalis</i> Hampson, 1904	Margaritini	Peru	ZSM	MK506095	MK459682	MK459865	
MTD882	<i>Bocchoris</i>	cf. <i>inspersalis</i> (Zeller, 1852)	Nomophitini	Sierra Leone	T. Karisch	MK459683		MK459866	
MTD1281	<i>Botyodes</i>	<i>dinasalis</i> (Walker, 1859)	Margaritini	China	MTD	MK506074	MK459684	MK459867	
MTD1319	<i>Cadarena</i>	<i>putoraria</i> (Hübner, 1825)	Margaritini	Cameroon	MTD	MK506074	MK459684	MK459868	
MTD826	<i>Chaphalocras</i>	cf. <i>medialis</i> (Guenée, 1854)	Spilomeilini	Philippines	MTD	MK459686		MK459869	
MTD1041	<i>Conchylodes</i>	<i>zebra</i> (Sepp, 1850)	Udeini	French Guiana	MTD	MK506103	MK459687	MK459870	
ITBC058	<i>Conogathes</i>	<i>pandamalis</i> (Walker, 1859)	Margaritini	Malaysia	ZMBN	MK459688		MK459871	
MTD649	<i>Cydalima</i>	<i>perspectalis</i> (Walker, 1859)	Margaritini	China	MTD	JF852281	MK459689	MK459872	
MTD1047	<i>Desmia</i>	cf. <i>tages</i> (Cramer, 1777)	Nomophitini	French Guiana	MTD	MK506091	MK459690	MK459873	
MTD1323	<i>Diaphania</i>	<i>hyalinata</i> (Linnaeus, 1767)	Margaritini	Bolivia	MTD	MK506110	MK459691	MK459874	
MTD557	<i>Diasemia</i>	<i>reticularis</i> (Linnaeus, 1761)	Nomophitini	Romania	MTD	MK459692		MK459875	
MTD1357	<i>Diasemiopsis</i>	<i>leodoculis</i> (Walker, 1859)	Nomophitini	Bolivia	MTD	MK506106	MK459693	MK459876	
ZMBN097	<i>Dichocras</i>	cf. <i>zebralis</i> (Moore, 1867)	Margaritini	Malaysia	ZMBN	MK459694		MK459877	
MTD868	<i>Dolicharthria</i>	<i>punctalis</i> (Denis & Schiffermüller, 1775)	Steniini	Spain	MTD	MK459695		MK459878	
MTD786	<i>Duponchella</i>	<i>fovealis</i> Zeller, 1847	Steniini	Morocco	MTD	MK459696		MK459879	
MTD1316	<i>Eporidia</i>	<i>dariusalis</i> Walker, 1859	Spilomeilini	Cameroon	MTD	MK459697		MK459880	

Table 1 continued.

DNA sample	Genus	Species	Tribus	Origin	Collection	COI (1440bp)	EF-1a (1071bp)
MTD1321	<i>Eurhyparodes</i>	cf. <i>lydamis</i> Druce, 1902	Herpetogrammatini	Bolivia	MTD	HybLCD/HybNancy MK506099	HybOscar-6143/Bosie-6144 MK459881
MTD1566	<i>Fibodes</i>	sp.	Margariniini	Angola	MTD	MK459699	MK459882
MTD1318	<i>Ghesquiereilana</i>	cf. <i>hirtusalis</i> (Walker, 1859)	Margariniini	Cameroon	A. Zwick	MK459700	MK459883
MTD1285	<i>Glyphodes</i>	<i>sibillialis</i> Walker, 1859	Margariniini	Peru	ZSM	MK459701	MK459884
MTD0820	<i>Glyphodes</i>	cf. <i>stolalis</i> Guenée, 1854	Margariniini	Philippines	MTD	MK459702	MK459885
MTD1283	<i>Gonocausta</i>	sp.	Hydririni	Bolivia	MTD	MK506090	MK459703
MTD0808	<i>Heritaiodes</i>	<i>derogata</i> (Fabricius, 1775)	Agroterini	Philippines	MTD	MK459704	MK459887
MTD0994	<i>Herpetogramma</i>	<i>phaeopteralis</i> (Guenée, 1854)	Herpetogrammatini	Peru	ZSM	MK506075	MK459705
MTD1337	<i>Hileithia</i>	cf. <i>obliquialis</i> (Schaus, 1912)	Herpetogrammatini	Peru	ZSM	MK506096	MK459706
MTD1282	<i>Hodeberia</i>	<i>testalis</i> (Fabricius, 1794)	Margariniini	Yemen	MTD	MK459707	MK459890
MTD1565	<i>Hydriris</i>	<i>ornatalis</i> (Duponchel, 1832)	Hydririni	Angola	MTD	MK459708	MK459891
MTD1004	<i>Hymenia</i>	<i>perspectalis</i> (Hübner, 1796)	Hymenini	Peru	ZSM	MK506081	MK459892
MTD1043	<i>Lamposema</i>	cf. <i>dorsalis</i> (Walker, 1859)	Hydririni	French Guiana	MTD	MK506082	MK459893
MTD1562	<i>Leucinodes</i>	<i>africanensis</i> Mally et al., 2015	Lineodini	Angola	MTD	LN624711	MK459894
MTD1349	<i>Leucochroma</i>	<i>coropae</i> (Stoll in Cramer & Stoll, 1781)	Margariniini	Bolivia	MTD	MK506087	MK459895
MTD1251	<i>Lineodes</i>	<i>vulnificae</i> Dyar, 1913	Lineodini	Bolivia	MTD	MK506112	MK459896
MTD1284	<i>Liopasia</i>	<i>andrealis</i> Dognin, 1910	Margariniini	Bolivia	MTD	MK506105	MK459897
WPH197	<i>Marasmia</i>	<i>poeyalis</i> (Boisduval, 1833)	Spilomelini	(NCBI)	(NCBI)	JX017856	JX017933
WPH115	<i>Marasmia</i>	<i>trapezalis</i> (Guenée, 1854)	Spilomelini	(NCBI)	(NCBI)	JX017849	JX017926
MTD1341	<i>Maruca</i>	<i>virata</i> (Fabricius, 1787)	Margariniini	Bolivia	MTD	MK506085	MK459898
MTD364	<i>Mecyna</i>	<i>lutealis</i> (Duponchel, 1833)	Nomophiliini	Italy	TLMF	JF497031	MK459899
MTD1340	<i>Megastes</i>	cf. <i>pusialis</i> Snellen, 1875	Margariniini	Bolivia	MTD	MK506098	MK459900
MTD787	<i>Meaasia</i>	<i>suppandalis</i> (Hübner, 1823)	Stenitini	Morocco	MTD	MK459717	MK459901
ZMBN104	<i>Nacoleia</i>	<i>insolitalis</i> (Walker, 1862)	Margariniini	Malaysia	ZMBN	MK459718	MK459902
ZMBN103	<i>Neonanthus</i>	cf. <i>pseudocomortalis</i> Yamanaka & Kirpichnikova, 1993	Agroterini	Malaysia	ZMBN	MK459719	MK459903
MTD1046	<i>Neoleucinodes</i>	<i>dissolvens</i> (Dyar, 1914)	Lineodini	French Guiana	MTD	MK506093	MK459904
MTD152	<i>Niphopyralis</i>	<i>chionosis</i> Hampson, 1919	Wurthini	Australia	ANIC	MK459721	MK459905
MTD782	<i>Nomophila</i>	<i>noctuella</i> (Denis & Schiffermüller, 1775)	Nomophiliini	Morocco	MTD	MK459722	MK459906
MTD1483	<i>Obtusipalpis</i>	<i>parcalis</i> Hampson, 1896	Margariniini	Angola	MTD	MK459723	MK459907
SDA008A	<i>Omiodes</i>	<i>continuatialis</i> (Wallengren, 1860)	Margariniini	Hawaii	UHIM	MK459724	MK459908
WPH252B	<i>Omiodes</i>	<i>humeralis</i> Guenée, 1854	Margariniini	Costa Rica	UHIM	JX017886	JX017965
ZMBN097	<i>Dichocrocis</i>	cf. <i>zebralis</i> (Moore, 1867)	Margariniini	Malaysia	ZMBN	MK459694	MK459877
MTD784	<i>Palpita</i>	<i>vitrealis</i> (Rossi, 1794)	Margariniini	Morocco	MTD	MK459725	MK459910
MM00325	<i>Patania</i>	<i>ruralis</i> (Scopoli, 1763)	Agroterini	(NCBI)	(NCBI)	GU828634	GU828968
MTD1018	<i>Patania</i>	cf. <i>silicalis</i> (Guenée, 1854)	Agroterini	Peru	ZSM	MK506097	MK459911
MTD1324	<i>Phostria</i>	cf. <i>tedea</i> (Stoll in Cramer & Stoll, 1780)	Agroterini	Bolivia	MTD	MK506092	MK459912
MTD1033	<i>Preresta</i>	cf. <i>iphicidalis</i> (Walker, 1859)	Margariniini	French Guiana	MTD	MK506083	MK459913
MTD1342	<i>Preresta</i>	cf. <i>rubrocinctalis</i> (Guenée, 1854)	Margariniini	Bolivia	MTD	MK506078	MK459914

Table 1 continued.

DNA sample	Genus	Species	Tribus	Origin	Collection	COI (1440bp)		EF-1a (1071bp)	
						HyblCO/HybNancy	HybJerry/HybPat	HybOscar-6143/Bosie-6144	HybEF51.9/EFrcM4
MTD1015	<i>Prenesta</i>	<i>scyllalis</i> (Walker, 1859)	Margaronini	Peru	ZSM	HybLCO/HybNancy MK506094	HybJerry/HybPat MK459730	HybOscar-6143/Bosie-6144 MK459915	HybEF51.9/EFrcM4
WPH188	<i>Prophantis</i>	<i>cf. androstigmata</i> (Hampson, 1918)	Trichaeini	(NCBI)	(NCBI)	JX017853	JX017853	JX017930	—
ZMBN017	<i>Prophantis</i>	<i>xanthomeris</i> (Hampson, 1918)	Trichaeini	Angola	MTD	MK459731	MK459731	MK459916	—
MTD650	<i>Pycnarmon</i>	<i>pantherata</i> (Butler, 1878)	Agroterini	China	MTD	MK459732	MK459732	MK459917	—
MTD774	<i>Rhectosemia</i>	<i>multifidialis</i> Lederer, 1863	Lineodini	Venezuela	MHNG	JF852398	MK459733	MK459918	—
MTD0874	<i>Rhinphalea</i>	<i>cf. astrigalis</i> Hampson, 1899	Margaronini	Philippines	MTD	MK459734	MK459734	MK459919	—
ZMBN011	<i>Salbia</i>	<i>haemorrhoidalis</i> (Guenée, 1854)	Spilomelini	Bolivia	MTD	MK506086	MK459735	MK459920	—
MTD1358	<i>Samea</i>	<i>cf. multiplicalis</i> (Guenée, 1854)	Nomophiliini	Bolivia	MTD	MK506079	MK459736	MK459921	—
MTD1235	<i>Samea</i>	<i>eclesialis</i> Guenée, 1854	Nomophiliini	USA	FMNH	MK459737	MK459737	MK459922	—
MTD0872	<i>Siga</i>	<i>liris</i> (Cramer, 1775)	Spilomelini	French Guiana	MHNG	MK459738	MK459738	MK459923	—
MTD1248	<i>Spilomela</i>	<i>perspicata</i> (Fabricius, 1787)	Spilomelini	Peru	ZSM	MK506084	MK459739	MK459924	—
MTD783	<i>Spoladea</i>	<i>recurvalis</i> (Fabricius, 1775)	Spilomelini	Morocco	MTD	MK459740	MK459740	MK459925	—
MTD1320	<i>Sylepis</i>	<i>marialis</i> Poey, 1832	Hymenini	Morocco	MTD	MK459741	MK459741	MK459926	—
MTD1017	<i>Syngamia</i>	<i>florella</i> (Stoll in Cramer & Stoll, 1781)	Hydririni	Bolivia	MTD	LR135741	LR135741	MK459927	—
MTD1315	<i>Terasita</i>	<i>meitucosalis</i> Guenée, 1854	Spilomelini	Peru	ZSM	MK506076	MK459741	MK459927	—
MTD1247	<i>Trichaea</i>	<i>pilicornis</i> Herrich-Schäffer, 1866	Margaronini	Peru	ZSM	MK506111	MK459742	MK459928	—
MTD0870	<i>Udea</i>	<i>ferrugalis</i> (Hübner, 1796)	Trichaeini	Peru	ZSM	MK506089	MK459743	MK459929	—
MTD956	<i>Udea</i>	<i>washingtonalis</i> (Grote, 1882)	Udeini	Morocco	MTD	JF852252	MK459744	MK459930	—
MTD276, MTD357	<i>Udeoides</i>	<i>muscosalis</i> (Hampson, 1913)	Udeini	Canada	MTD	MK459745	MK459745	MK459931	—
MTD1467	<i>Zebrania</i>	<i>phenice</i> (Stoll in Cramer & Stoll, 1782)	Margaronini	Kenya	MTD	JF497033	JF497033	MK459932	—
MTD1338	<i>Achyra</i>	<i>cf. ranalis</i> (Guenée, 1854)	Pyraustini	Angola	MTD	MK459746	MK459746	MK459933	—
MM01851	<i>Anania</i>	<i>hortulata</i> (Linnaeus, 1758)	Pyraustini	Bolivia	MTD	MK506109	MK459747	MK459934	—
MTD553	<i>Anania</i>	<i>verbascalis</i> (Denis & Schiffermüller, 1775)	Pyraustini	(NCBI)	(NCBI)	GU828675	GU828472	GU829003	GU829287
MTD1484	<i>Cryptosara</i>	<i>caritalis</i> (Walker, 1859)	Portentomorphini	Romania	MTD	MK459748	MK459748	MK459935	—
MTD1558	<i>Eucasta</i>	<i>gigantalis</i> Viette, 1957	Euclastini	Angola	MTD	MK459749	MK459749	MK459936	—
MTD1466	<i>Eucasta</i>	<i>splendidalis</i> (Herrich-Schäffer, 1848)	Euclastini	Kenya	NHMO	MK459750	MK459750	MK459937	—
MTD1327 (WPH215)	<i>Hyalobathra</i>	<i>crenulata</i> Sutrisno & Horak, 2003	Euclastini	Bulgaria	S. Beshkov	MK459751	MK459751	MK459938	—
MTD1350	<i>Hyalorista</i>	<i>cf. taeniolalis</i> (Guenée, 1854)	Portentomorphini	Australia	UHIM	JX017826	JX017826	JX017943	MK459939
MTD605	<i>Loxostege</i>	<i>aeruginalis</i> (Hübner, 1796)	Pyraustini	Bolivia	MTD	MK506108	MK459752	MK459940	—
MTD1343	<i>Oenobotys</i>	<i>sp.</i>	Pyraustini	Macedonia	MTD	MK459753	MK459753	MK459941	—
MTD398	<i>Ostrinia</i>	<i>nubilalis</i> (Hübner, 1796)	Pyraustini	Bolivia	MTD	MK506104	MK459754	MK459942	—
ZMBN096	<i>Pagoda</i>	<i>salvialis</i> Walker, 1859	Pyraustini	Germany	MTD	MK459755	MK459755	MK459943	—
MTD906	<i>Paracorsia</i>	<i>repandalis</i> (Denis & Schiffermüller, 1775)	Pyraustini	Malaysia	ZMBN	MK459756	MK459756	MK459944	—
MTD1322	<i>Portentomorpha</i>	<i>xanthialis</i> (Guenée, 1854)	Portentomorphini	Kyrgyzstan	MTD	MK459757	MK459757	MK459945	—
MTD477	<i>Psammotis</i>	<i>pulveralis</i> (Hübner, 1796)	Portentomorphini	Bolivia	MTD	MK506077	MK459758	MK459946	—
MTD1344	<i>Pseudopyrausta</i>	<i>cf. minima</i> (Hedemann, 1894)	Pyraustini	Germany	MTD	MK459759	MK459759	MK459947	—
			Pyraustini	Bolivia	MTD	MK506107	MK459760	MK459948	—

Table 1 continued.

DNA sample	Genus	Species	Tribus	Origin	Collection	COI (144bp)		EF-1a (1071bp)	
MTD953	<i>Pyrausta</i>	<i>purpurealis</i> (Linnaeus, 1758)	Pyraustini	Germany	MTD	HybLCO/HybNancy	HybJerry/HybPat	HybOscar-6143/Bosie-6144	HybEF51.9/EFrcM4
MTD560	<i>Sitachna</i>	<i>verticalis</i> (Linnaeus, 1758)	Pyraustini	Romania	MTD	MK459761	MK459762	MK459949	MK459950
MTD1326 (WPH209)	<i>Tetridia</i>	<i>caletoralis</i> (Walker, 1859)	Tetridini	Australia	UHIM	JX017861	JX017861	JX017938	MK459951
WPH054	<i>Uresiphita</i>	<i>gilvata</i> (Fabricius, 1794)	unplaced	Hawaii	UHIM	JX017825	JX017825	JX017919	—
DNA sample	Genus	Species	Tribus	Origin	Collection	CAD (825bp)	GAPDH (654bp)	IDH (657bp)	RpS5 (576bp)
MTD393	<i>Synaphe</i>	<i>punctalis</i> (Fabricius, 1775)	(PYRALINAE)	Germany	MTD	MK459763	MK460136	MK459952	MK460052
MM00051	<i>Pyralis</i>	<i>farinalis</i> (Linnaeus, 1758)	(PYRALINAE)	(NCBI)	(NCBI)	GU828092	GU829747	GU829979	GU830604
MM09194	<i>Schoenobius</i>	<i>gigantellus</i> (Denis & Schiffermüller, 1775)	(SCHOENOBINAE)	(NCBI)	(NCBI)	GU828306	GU829903	GU830222	GU830790
MM11223	<i>Clepsicosma</i>	<i>iridia</i> Meyrick, 1888	(ACENTROPINAE)	(NCBI)	(NCBI)	GU828315	GU829906	GU830230	GU830800
MM03362	<i>Crambus</i>	<i>uliginosellus</i> Zeller, 1850	(CRAMBINAE)	(NCBI)	(NCBI)	GU828182	GU829811	GU830078	GU830681
MM04967	<i>Eudonia</i>	<i>truncatella</i> (Stainton, 1849)	(SCOPARIINAE)	(NCBI)	(NCBI)	GU828197	GU829823	GU830095	GU830697
MTD0370	<i>Midila</i>	<i>guianensis</i> Munroe, 1970	(MIDLINAE)	French Guiana	MTD	MK459764	MK460137	MK459953	MK460053
MTD1307	<i>Sufetula</i>	<i>diminutalis</i> (Walker, 1866)	(LATHROTELINAE)	Germany	MTD	MK459765	MK460138	MK459954	MK460054
ZMBN094	<i>Aetholix</i>	<i>cf. flavibasalis</i> (Guenée, 1854)	Agrotini	Malaysia	ZMBN	MK459766	MK460139	MK459955	MK460055
MTD1016	<i>Agathodes</i>	<i>designalis</i> Guenée, 1854	Margaronini	Peru	ZSM	MK459767	—	MK459956	MK460056
MTD1328 (WPH221)	<i>Agrioglypta</i>	<i>excelsalis</i> (Walker, 1866)	Margaronini	Australia	UHIM	JX017793	—	MK459957	JX018024
MTD488A	<i>Agrotera</i>	<i>nemoralis</i> (Scopoli, 1863)	Agrotini	Germany	MTD	MK459768	MK460140	MK459958	MK460057
MTD1354	<i>Anagastina</i>	<i>cf. primordialis</i> (Dyar, 1906)	Steniini	Bolivia	MTD	MK459769	MK460141	MK459959	MK460058
MTD798	<i>Antigastrea</i>	<i>catalaunalis</i> (Duponchel, 1833)	Margaronini	Morocco	MTD	MK459770	—	MK459960	MK460059
MTD1331	<i>Apilacrocis</i>	<i>novatautonialis</i> Munroe, 1968	Wurthini	Peru	ZSM	MK459771	—	MK459961	—
MTD688	<i>Aristobulea</i>	<i>principis</i> Munroe & Mutuura, 1968	Wurthini	China	MTD	MK459772	MK460142	MK459962	—
MTD797	<i>Arnia</i>	<i>nervosalis</i> (Guenée, 1854)	Nomophiliini	Morocco	MTD	MK459773	—	—	MK460060
MTD776	<i>Arthromastix</i>	<i>lauralis</i> (Walker, 1859)	Asciodini	Venezuela	MHNG	—	MK460143	MK459963	MK460061
MTD1061	<i>Arthromastix</i>	<i>pactolalis</i> (Guenée, 1854)	Asciodini	French Guiana	R. Rougerie	MK459774	MK460144	MK459964	MK460062
MTD1325	<i>Asciodes</i>	<i>cf. gordialis</i> Guenée, 1854	Asciodini	Bolivia	MTD	MK459775	MK460145	MK459965	MK460063
MTD1019	<i>Asturades</i>	<i>fimbriatralis</i> (Guenée, 1854)	Margaronini	Peru	ZSM	MK459776	—	MK459966	MK460064
MTD1347	<i>Ategumia</i>	<i>ebulealis</i> (Guenée, 1854)	Nomophiliini	Bolivia	MTD	MK459777	—	MK459967	MK460065
MTD1329	<i>Azochis</i>	<i>cf. ruffidiscalis</i> Hampson, 1904	Margaronini	Peru	ZSM	MK459778	MK460146	MK459968	MK460066
MTD882	<i>Baccharis</i>	<i>cf. dispersalis</i> (Zeller, 1852)	Nomophiliini	Sierra Leone	T. Karisch	—	MK460147	—	MK460067
MTD1281	<i>Boydodes</i>	<i>dinaealis</i> (Walker, 1859)	Margaronini	China	MTD	—	—	MK459969	MK460068
MTD1319	<i>Cadarena</i>	<i>puddorana</i> (Hübner, 1825)	Margaronini	Cameroon	A. Zwick	MK459779	MK460148	MK459970	MK460069
MTD826	<i>Chaphalocracis</i>	<i>cf. madhais</i> (Guenée, 1854)	Spilomelini	Philippines	MTD	MK459780	—	MK459971	MK460070
MTD1041	<i>Conchylodes</i>	<i>zebra</i> (Sepp, 1850)	Udeini	French Guiana	MTD	MK459781	MK460149	MK459972	—
ITBC058	<i>Conogathes</i>	<i>pandamalis</i> (Walker, 1859)	Margaronini	Malaysia	ZMBN	MK459782	MK460150	MK459973	MK460071

Table 1 continued.

DNA sample	Genus	Species	Tribus	Origin	Collection	CAD (825bp)	GAPDH (654bp)	IDH (657bp)	RpS5 (576bp)
MTD649	<i>Cydalina</i>	<i>perspectalis</i> (Walker, 1859)	Margaronini	China	MTD	—	MK460151	MK459974	—
MTD1047	<i>Desmia</i>	cf. <i>lagos</i> (Cramer, 1777)	Nomophitini	French Guiana	MTD	MK459783	MK460152	MK459975	MK460072
MTD1323	<i>Diaphania</i>	<i>hyalinata</i> (Linnaeus, 1767)	Margaronini	Bolivia	MTD	MK459784	MK460153	MK459976	MK460073
MTD557	<i>Diasemia</i>	<i>reticularis</i> (Linnaeus, 1761)	Nomophitini	Romania	MTD	MK459785	MK460154	MK459977	MK460074
MTD1357	<i>Diasemiopsis</i>	<i>leodacalis</i> (Walker, 1859)	Nomophitini	Bolivia	MTD	MK459786	MK460155	MK459978	MK460075
ZMBN097	<i>Dichrocrocis</i>	cf. <i>zebralis</i> (Moore, 1867)	Margaronini	Malaysia	ZMBN	MK459787	MK460156	MK459979	MK460076
MTD888	<i>Dolichanthria</i>	<i>punctalis</i> (Denis & Schiffermüller, 1775)	Stenini	Spain	MTD	MK459788	—	MK459980	MK460077
MTD786	<i>Duponchella</i>	<i>fovealis</i> Zeller, 1847	Stenini	Morocco	MTD	MK459789	MK460157	MK459981	MK460078
MTD1316	<i>Eponidia</i>	<i>dariusalis</i> Walker, 1859	Spilomelini	Cameroon	A. Zwick	MK459790	—	MK459982	MK460079
MTD1321	<i>Eurhyparodes</i>	cf. <i>lygdamis</i> Druce, 1902	Herpetogrammatini	Bolivia	MTD	MK459791	MK460158	MK459983	MK460080
MTD1566	<i>Fiodes</i>	sp.	Margaronini	Angola	MTD	MK459792	—	MK459984	MK460081
MTD1318	<i>Ghesquiereiella</i>	cf. <i>hirtusalis</i> (Walker, 1859)	Margaronini	Cameroon	A. Zwick	MK459793	MK460159	MK459985	MK460082
MTD1285	<i>Glyphodes</i>	<i>sibillialis</i> Walker, 1859	Margaronini	Peru	ZSM	MK459794	MK460160	MK459986	MK460083
MTD820	<i>Glyphodes</i>	cf. <i>stolalis</i> Guenée, 1854	Margaronini	Philippines	MTD	MK459795	MK460161	MK459987	MK460084
MTD1283	<i>Gonacausta</i>	sp.	Hydririni	Bolivia	MTD	MK459796	MK460162	MK459988	MK460085
MTD808	<i>Hemtaloces</i>	<i>derogata</i> (Fabricius, 1775)	Agrotini	Philippines	MTD	MK459797	MK460163	MK459989	—
MTD994	<i>Herpetogramma</i>	<i>phaeopteralis</i> (Guenée, 1854)	Herpetogrammatini	Peru	ZSM	MK459798	—	MK459990	MK460086
MTD1337	<i>Hilethia</i>	cf. <i>obliqualis</i> (Schaus, 1912)	Herpetogrammatini	Peru	ZSM	MK459799	MK460164	MK459991	MK460087
MTD1282	<i>Hodeberia</i>	<i>testalis</i> (Fabricius, 1794)	Margaronini	Yemen	MTD	MK459800	MK460165	MK459992	MK460088
MTD1565	<i>Hydriris</i>	<i>ornatalis</i> (Duponchel, 1832)	Hydririni	Angola	MTD	MK459801	MK460166	—	—
MTD1004	<i>Hymenia</i>	<i>perspectalis</i> (Hübner, 1796)	Hymenini	Peru	ZSM	MK459802	MK460167	MK459993	MK460089
MTD1043	<i>Lampyrisma</i>	cf. <i>dorsalis</i> (Walker, 1859)	Hydririni	French Guiana	MTD	MK459803	MK460168	MK459994	MK460090
MTD1562	<i>Leucinodes</i>	<i>africanensis</i> Maly et al., 2015	Lineodini	Angola	MTD	MK459804	—	MK459995	—
MTD1349	<i>Leucochroma</i>	<i>corope</i> (Stoll in Cramer & Stoll, 1781)	Margaronini	Bolivia	MTD	MK459805	MK460169	MK459996	MK460091
MTD1251	<i>Lineodes</i>	<i>vulnificata</i> Dyar, 1913	Lineodini	Bolivia	MTD	MK459806	MK460170	MK459997	MK460092
MTD1284	<i>Liopasia</i>	<i>andrealis</i> Dognin, 1910	Margaronini	Bolivia	MTD	MK459807	MK460171	MK459998	MK460093
WPH197	<i>Marasmia</i>	<i>poeyalis</i> (Boisduval, 1833)	Spilomelini	(NCBI)	(NCBI)	JX017781	—	—	JX018009
WPH115	<i>Marasmia</i>	<i>trapezalis</i> (Guenée, 1854)	Spilomelini	(NCBI)	(NCBI)	JX017777	—	—	JX018002
MTD1341	<i>Maruca</i>	<i>vitratata</i> (Fabricius, 1787)	Margaronini	Bolivia	MTD	MK459808	—	MK459999	MK460094
MTD364	<i>Mecyna</i>	<i>lutealis</i> (Duponchel, 1833)	Nomophitini	Italy	TLMF	—	MK460172	MK460000	MK460095
MTD1340	<i>Megastes</i>	cf. <i>pusialis</i> Snellen, 1875	Margaronini	Bolivia	MTD	MK459809	MK460173	MK460001	MK460096
MTD787	<i>Metasia</i>	<i>suppandalis</i> (Hübner, 1823)	Stenini	Morocco	MTD	MK459810	MK460174	MK460002	MK460097
ZMBN104	<i>Nacoleia</i>	<i>insolitalis</i> (Walker, 1862)	Margaronini	Malaysia	ZMBN	MK459811	—	MK460003	—
ZMBN103	<i>Neaenalthes</i>	cf. <i>pseudocantortalis</i> Yamanaka & Kirpichnikova, 1993	Agrotini	Malaysia	ZMBN	—	MK460175	MK460004	MK460098
MTD1046	<i>Neoleucinodes</i>	<i>dissolvens</i> (Dyar, 1914)	Lineodini	French Guiana	MTD	MK459812	MK460176	MK460005	—
MTD152	<i>Niphopyralis</i>	<i>chionensis</i> Hampson, 1919	Wurthini	Australia	ANIC	MK459813	—	MK460006	MK460099
MTD782	<i>Nomophila</i>	<i>noctuelia</i> (Denis & Schiffermüller, 1775)	Nomophitini	Morocco	MTD	MK459814	MK460177	MK460007	MK460100
MTD1483	<i>Obtusipalpis</i>	<i>paridalis</i> Hampson, 1896	Margaronini	Angola	MTD	MK459815	MK460178	MK460008	MK460101

Table 1 continued.

DNA sample	Genus	Species	Tribus	Origin	Collection	CAD (825bp)	GAPDH (654bp)	IDH (657bp)	RpS5 (576bp)
SDA008A	<i>Omiodes</i>	<i>continuatialis</i> (Wallengren, 1860)	Margariniini	Hawaii	UHIM	—	HybFrigal/ HybBurre	HybIDHdeg27F/ HybIDHdegR	HybRpS5/ HybRpS5r
WPH252B	<i>Omiodes</i>	<i>humeralis</i> Guenée, 1854	Margariniini	Costa Rica	UHIM	JX017808	MK460180	MK460010	JX018040
MTD784	<i>Palpita</i>	<i>vitrealis</i> (Rossi, 1794)	Margariniini	Morocco	MTD	MK459816	MK460181	MK460011	MK460102
MM0325	<i>Petania</i>	<i>ruralis</i> (Scopoli, 1763)	Agrotini	(NCBI)	(NCBI)	GU828133	GU829772	GU830021	GU830638
MTD1018	<i>Petania</i>	<i>cf. silicalis</i> (Guenée, 1854)	Agrotini	Peru	ZSM	MK459817	MK460182	MK460012	MK460103
MTD1324	<i>Phostria</i>	<i>cf. tedea</i> (Stoll in Cramer & Stoll, 1780)	Agrotini	Bolivia	MTD	MK459818	MK460183	MK460013	MK460104
MTD1033	<i>Prenepta</i>	<i>cf. iphicalis</i> (Walker, 1859)	Margariniini	French Guiana	MTD	MK459819	MK460184	MK460014	MK460105
MTD1342	<i>Prenepta</i>	<i>cf. rubrocinctalis</i> (Guenée, 1854)	Margariniini	Bolivia	MTD	MK459820	—	MK460015	MK460106
MTD1015	<i>Prenepta</i>	<i>scyllalis</i> (Walker, 1859)	Margariniini	Peru	ZSM	MK459821	MK460185	MK460016	MK460107
WPH188	<i>Prophantis</i>	<i>cf. androstigmata</i> (Hampson, 1918)	Trichaeini	(NCBI)	(NCBI)	—	—	—	JX018006
ZMBN017	<i>Prophantis</i>	<i>xanthomeris</i> (Hampson, 1918)	Trichaeini	Angola	MTD	—	—	MK460017	MK460108
MTD650	<i>Pycnarmon</i>	<i>pantherata</i> (Butler, 1878)	Agrotini	China	MTD	MK459822	MK460186	MK460018	MK460109
MTD774	<i>Rhacotsema</i>	<i>multifariata</i> Lederer, 1863	Lineodini	Venezuela	MHNG	MK459823	MK460187	MK460019	—
MTD874	<i>Rhimphalea</i>	<i>cf. astigalis</i> Hampson, 1899	Margariniini	Philippines	MTD	—	MK460188	MK460020	MK460110
ZMBN011	<i>Salbia</i>	<i>haemorrhoidalis</i> (Guenée, 1854)	Spilomelini	Bolivia	MTD	—	MK460189	MK460021	MK460111
MTD1358	<i>Samea</i>	<i>cf. multiplicalis</i> (Guenée, 1854)	Nomophiliini	Bolivia	MTD	—	MK460190	MK460022	MK460112
MTD1235	<i>Samea</i>	<i>ecclesiastis</i> Guenée, 1854	Nomophiliini	USA	FMNH	MK459824	MK460191	MK460023	MK460113
MTD872	<i>Siga</i>	<i>liris</i> (Cramer, 1775)	Spilomelini	French Guiana	MHNG	MK459825	—	MK460024	MK460114
MTD1248	<i>Spilomela</i>	<i>perspicata</i> (Fabricius, 1787)	Spilomelini	Peru	ZSM	MK459826	—	MK460025	MK460115
MTD783	<i>Spoladea</i>	<i>recurvalis</i> (Fabricius, 1775)	Hymeniini	Morocco	MTD	MK459827	MK460192	MK460026	MK460116
MTD1320	<i>Syllepis</i>	<i>marialis</i> Poey, 1832	Hydririni	Bolivia	MTD	LR134539	LR134626	LR134717	LR134887
MTD1017	<i>Syngamia</i>	<i>florella</i> (Stoll in Cramer & Stoll, 1781)	Spilomelini	Peru	ZSM	MK459828	MK460193	MK460027	MK460117
MTD1315	<i>Tersatia</i>	<i>meticalosalis</i> Guenée, 1854	Margariniini	Peru	ZSM	—	—	MK460028	MK460118
MTD1247	<i>Trichaea</i>	<i>pilicornis</i> Herrich-Schäffer, 1866	Trichaeini	Peru	ZSM	MK459829	MK460194	MK460029	MK460119
MTD870	<i>Udea</i>	<i>ferrugalis</i> (Hübner, 1796)	Udeini	Morocco	MTD	MK459830	MK460195	MK460030	—
MTD956	<i>Udea</i>	<i>washingtonalis</i> (Grote, 1882)	Udeini	Canada	MTD	—	MK460196	MK460031	—
MTD276, MTD357	<i>Udeoides</i>	<i>muscosalis</i> (Hampson, 1913)	Udeini	Kenya	MTD	MK459831	MK460197	MK460032	—
MTD1467	<i>Zebronia</i>	<i>phenice</i> (Stoll in Cramer & Stoll, 1782)	Margariniini	Angola	MTD	MK459832	MK460198	MK460033	MK460120
MTD1338	<i>Achyra</i>	<i>cf. rantalis</i> (Guenée, 1854)	Pyraustini	Bolivia	MTD	MK459833	MK460199	MK460034	MK460121
MM01851	<i>Anania</i>	<i>horvulata</i> (Linnaeus, 1758)	Pyraustini	(NCBI)	(NCBI)	GU828170	GU829798	GU830062	GU830669
MTD553	<i>Anania</i>	<i>verbascalis</i> (Denis & Schiffermüller, 1775)	Pyraustini	Romania	MTD	MK459834	MK460200	MK460035	MK460122
MTD1484	<i>Cryptosara</i>	<i>carialis</i> (Walker, 1859)	Portentomorphini	Angola	MTD	MK459835	—	MK460036	MK460123
MTD1558	<i>Eucasta</i>	<i>gigantalis</i> Viette, 1957	Eucastini	Kenya	NHMO	MK459836	—	MK460037	MK460124
MTD1466	<i>Eucasta</i>	<i>splendidalis</i> (Herrich-Schäffer, 1848)	Eucastini	Bulgaria	S. Beshkov	MK459837	—	MK460038	MK460125
MTD1327 (WPH215)	<i>Hyalobathra</i>	<i>crenulata</i> Sutrisno & Horak, 2003	Portentomorphini	Australia	UHIM	JX017788	—	MK460039	JX018019

Table 1 continued.

DNA sample	Genus	Species	Tribus	Origin	Collection	CAD (825bp)	GAPDH (654bp)	IDH (657bp)	RpS5 (576bp)
MTD1350	<i>Hyalorista</i>	<i>cf. taeniolalis</i> (Guenée, 1854)	Pyraustini	Bolivia	MTD	HybCAD743r/ HybCAD1028r	HybFrigga/ HybBurre	HybIDHdeg2F/ HybIDHdegR	HybRpS5r/ HybRpS5r
MTD0605	<i>Loxostege</i>	<i>aeruginalis</i> (Hübner, 1796)	Pyraustini	Macedonia	MTD	MK459838	MK460201	MK460040	MK460126
MTD1343	<i>Oenobotrys</i>	sp.	Pyraustini	Bolivia	MTD	MK459840	—	MK460042	MK460127
MTD388	<i>Ostrinia</i>	<i>nubilalis</i> (Hübner, 1796)	Pyraustini	Germany	MTD	MK459841	—	MK460043	MK460129
ZMBN096	<i>Pagoda</i>	<i>salvealis</i> Walker, 1859	Pyraustini	Malaysia	ZMBN	MK459842	MK460202	MK460044	MK460130
MTD906	<i>Paracorsia</i>	<i>repandalis</i> (Denis & Schiffermüller, 1775)	Pyraustini	Kyrgyzstan	N. Poil	MK459843	MK460203	MK460045	MK460131
MTD1322	<i>Portentomorpha</i>	<i>xanthialis</i> (Guenée, 1854)	Portentomorphini	Bolivia	MTD	MK459844	—	MK460046	MK460132
MTD477	<i>Psammotis</i>	<i>pulveralis</i> (Hübner, 1796)	Pyraustini	Germany	MTD	—	MK460204	MK460047	—
MTD1344	<i>Pseudopyrausta</i>	<i>cf. minima</i> (Hedemann, 1894)	Pyraustini	Bolivia	MTD	MK459845	MK460205	MK460048	MK460133
MTD953	<i>Pyrausta</i>	<i>purpurealis</i> (Linnaeus, 1758)	Pyraustini	Germany	MTD	MK459846	MK460206	MK460049	MK460134
MTD560	<i>Sitachna</i>	<i>verticalis</i> (Linnaeus, 1758)	Pyraustini	Romania	MTD	MK459847	MK460207	MK460050	MK460135
MTD1326 (WPH209)	<i>Tetridia</i>	<i>caletoralis</i> (Walker, 1859)	Tetridini	Australia	UHIM	JX017785	—	MK460051	JX018014
WPH054	<i>Uresiphita</i>	<i>gilvata</i> (Fabricius, 1794)	unplaced	Hawaii	UHIM	JX017770	—	—	JX017996

logical data of a global taxonomic sample. We also discuss the monophyly of the Neotropical genus groups proposed by MUNROE (1995), since these represent the best recent attempt to classify Spilomelinae.

2. Material and methods

2.1. Material

A broad range of Spilomelinae taxa was investigated to reflect the morphological, ecological, evolutionary, and geographical diversity of the group. 86 Spilomelinae species of 77 genera were studied, representing roughly one quarter of the genus-level diversity of Spilomelinae. In addition, we included 20 species of Pyraustinae representing 18 genera. We included 6 representatives of other Crambidae subfamilies as an internal outgroup taxon: *Eudonia truncicolella* (Stainton, 1849) (Scopariinae), *Crambus uliginosellus* Zeller, 1850 (Crambinae), *Schoenobius gigantellus* (Denis & Schiffermüller, 1775) (Schoenobiinae), *Midila guianensis* Munroe, 1970 (Midilinae), *Clepsicosma iridia* Meyrick, 1888 (Acentropinae) and *Sufetula diminutalis* (Walker, 1866) (Lathrotelinae). The phylogeny is rooted with the external outgroup taxon consisting of the Pyralidae *Synaphe punctalis* (Fabricius, 1775) and *Pyralis farinalis* (Linnaeus, 1758) (both Pyralinae). See Table 1 for the list of taxa that were studied both genetically and morphologically. Taxon sampling was primarily determined by the availability of freshly collected material suitable for the sequencing of the genetic markers of interest (see 2.2.1. Molecular methods). The studied taxa were identified to genus- or species level based on morphological investigations including genitalia dissection, as well as comparing the 5' half of the mitochondrial COI gene sequence ('DNA Barcode') with the sequence data available on the Barcode of Life Database (BOLD, <http://v4.boldsystems.org>; Ratnasingham & Hebert 2007). For some taxa of interest, only one specimen was available for both molecular and morphological studies, resulting in the lack of the corresponding sex for investigation of its morphology. Where possible, we compensated for this lack by coding morphological features based on information from published literature (illustrations, descriptions). These cases concerned the following taxa and consulted literature: *Midila guianensis* (MUNROE 1970), *Diasemiopsis leodocusalis* (WALKER, 1859) (MUNROE 1957), *Neoleucinodes dissolvens* (DYAR, 1914) (CAPPs 1948), *Euclasta gigantal* Viette, 1957 (POPESCU-GORJ & CONSTANTINESCU 1977).

Furthermore, we coded the morphology of closely related species for those taxa, where possible. The close relationship of those replacement specimens was evaluated by comparing the available genitalia, and where possible, COI barcode data. Those cases with replacement specimens are (male / female): *Anageshna primordialis* / *A. cf. primordialis*; *Asciodes cf. gordialis* / *A. quietalis*; *Azochis cf. rufidiscalis* / *A. rufidiscalis*; *Megastes cf. pusialis* / *M. pusialis*; *Trichaea pilicornis* / *T. prochyta*; *Hyalorista cf. taeniolalis* / *H. taeniolalis*.

We state author and year of description of all genera and species at their first mention in the text. Taxa identified as ‘cf.’ have the author and year of description of the closest species known to us. A list of investigated genitalia slides is given in Supplement Table S1.

2.2. Methods

2.2.1. Molecular methods

DNA extraction was done using the DNeasy Blood & Tissue kit (Qiagen) or the NucleoSpin Tissue kit (Macherey-Nagel) according to the manufacturers’ protocols. The six genes COI, CAD, EF-1a, GAPDH, IDH and RpS5 were amplified with the following primer pairs: COI in one large fragment with HybLCO (forward) and HybPat (reverse) or as two shorter fragments with HybLCO (forward) and HybNancy (reverse) as well as HybJerry (forward) and HybPat (reverse); CAD with HybCAD743f (forward) and HybCAD1028r (reverse); EF-1a (Elongation Factor 1-alpha) in one large fragment with HybOscar-6143 (forward) and HybEFrcM4 (reverse) or as two shorter, overlapping fragments with HybOscar-6143 (forward) and HybBosie-6144 (reverse) as well as HybEF51.9 (forward) and HybEFrcM4 (reverse); GAPDH with HybFrigga (forward) and HybBurre (reverse); IDH with HybIDHdeg27F (forward) and HybIDHdegR (reverse); RpS5 with HybRpS5f (forward) and HybRpS5r (reverse) (WAHLBERG & WHEAT 2008; HAINES & RUBINOFF 2012). Each primer contains a universal T7 (forward) or T3 (reverse) primer tail at their 5’ end, which was used for sequencing (WAHLBERG & WHEAT 2008).

All gene fragments were amplified in 25 µl reactions. The amplification protocol at the SNSD DNA lab was: 200 nM of each primer, 200 µM dNTP mix, 2.5 µl Taq buffer, 1 mM MgCl₂, 1 u BIO-X-ACT Short DNA Polymerase (Bioform), 2 µl DNA of concentration as extracted, and distilled water added up to 25 µl in total per reaction. At the UiB DNA lab the PCR protocol was: 400nM of each primer, 800 µM dNTP mix, 2.5 µl Taq buffer (incl. MgCl₂), 0.75 u TaKaRa Ex Taq DNA Polymerase, 2 µl DNA of extracted concentration, and distilled water added up to 25 µl in total per reaction.

The PCR programme for mitochondrial COI was: initial phase at 95°C for 5 min, 38–40 cycles at 95°C for 30 s 50°C for 30 s and 72°C for 60 s, final phase at 72°C for 10 min and cooling at 8°C. For the nuclear genes CAD, EF-1a, GAPDH, IDH and RpS5 we ran a touch-down PCR: 24 cycles at 95°C for 30 s 55°C with –0.4°C / cycle for 30 s and 72°C for 60 s + 2 s / cycle, then 12 cycles at 95°C for 30 s 45°C for 30 s and 72°C for 120 s + 3 s / cycle, final phase at 72°C for 10 min and cooling at 8°C.

PCR results were examined via gel electrophoresis on a 1% agarose gel and GelRed as dyeing agent. Successful PCR samples were cleaned with ExoSAP and

subsequently amplified in Sanger-sequencing PCR reactions. Sequencing was done in both directions with the T7 and T3 primers, using the BigDye kit with this setup: 0.5–3.0 µl of PCR sample (depending on the sample’s band thickness on the agarose gel), 160 nM primer, 1 µl buffer, 0.5 µl BigDye, and adding up distilled water to 10 µl in total per reaction. Sequencing was conducted at the sequencing facilities of SNSD and UiB, Dept. of Molecular Biology, or via Macrogen Europe. PCR, clean-up and sequencing PCR at SNSD was performed on a Mastercycler ep gradient s (Eppendorf) or a PCR System 9700 (GeneAmp), at UiB a Bio-Rad 1000 thermal cycler was used for PCR and sequencing PCR, and a MJ Research PTC-200 thermal cycler for PCR clean-up. All sequences were proofread by eye and aligned manually using PhyDE 0.9971 (MÜLLER et al. 2008). All new sequence data have been submitted to an open access nucleotide sequence database (GenBank; <https://www.ncbi.nlm.nih.gov/genbank/>); accession numbers are compiled in Table 1.

2.2.2. Morphological methods

Genitalia were dissected according to ROBINSON (1976), with modifications: The abdomen was cut open along one pleural membrane, cleaned, and embedded in medium under a cover slip to allow clear investigation of the tympanal organs. Female genitalia were stained with Chlorazol Black. Male genitalia were either left unstained or were stained with Chlorazol Black or Eosin Y.

Morphological structures were investigated using Leica M125 and M205C stereomicroscopes. Images were photographed with a Canon EOS 60D in combination with a Canon EF 100mm 1:2,8 Macrolens and Canon EOS Utility Version 2.10.2.0. A Leica CTR6000 Microscope in combination with a Leica DFC420 camera and Leica Application Suite programme (Version 3.8.0) was used to photograph the genitalia.

Observed morphological features were coded according to the morphology character circumscriptions and compiled in a morphomatrix (Table 2) for all investigated taxa. *Clepsicosma iridia* (Acentropinae) was not studied morphologically, and is therefore omitted in Table 2.

Morphological abbreviations in Figs. 3–15: **an.** – antrum; **a.t.** – anal tube; **ap.a.** – apophysis anterioris; **ap.p.** – apophysis posterioris; **apx.** – appendix bursae; **coe.** – coecum of phallus; **col.** – colliculum; **cos.** – costa; **cos.b.** – costa base; **cos.d.** – distal costa; **cos.ex.** – dorsad process of basal costa; **cos.p.** – rod-shaped ventrad process of basal costa; **crn.** – cornutus or cornuti; **c.b.** – corpus bursae; **d.b.** – ductus bursae; **d.s.** – ductus seminalis; **div.** – diverticulum; **fo.ty.** – fornix tympani; **fib.** – fibula; **fla.** – basal antennal flagellomeres; **fr.** – frons; **fre.** – frenulum; **gna.** – gnathos; **h.p.** – hairpencil sclerite(s); **h.p.s.** – hairpencil sclerites of the saccus; **hau.** – haustellum; **jx.** – juxta; **la.p.** – labial palps; **lam.** – lamella antevaginalis of ostium bursae; **lob.** – lobulus of lateral tympanal case; **mx.p.** – maxillary palps; **o.b.** – ostium bursae; **oc.** – ocellus; **p.a.** – papilla anales; **p.ph.** – posterior phallus apodeme; **ped.** – pedicellus; **pl.m.** – pleural membranes; **pl.tu.** – pleural scale tufts of male abdominal segment 7; **pl.sc.** – pleural sclerites of male abdominal segment 8; **ret.** – retinaculum; **s2–s8** – 2nd–8th abdominal sternite; **sac.** – sacculus; **sac.d.** – distal sacculus; **sac.ex.** –

extension of distal sacculus; **sac.pr.** – projection from central sacculus; **sc.** – saccus of vinculum; **sc.v.** – ventral saccus tip; **sca.f.** – raised scales on mesal side of flagellomeres; **se.s.** – sensillar setae of flagellomeres; **sig.** – signum; **t1–t8** – 1st–8th abdominal tergite; **teg.** – tegumen; **teg.h.** – hair-pencils on the dorsolateral tegumen; **tran.** – transtillum arm; **tr.in.** – transtillum inferior sensu MARION 1954; **ty.fr.** – tympanic frame; **unc.** – uncus; **u.ch.** – uncus chaetae; **v.s.** – venula secunda; **v.va.** – ventral valva edge; **ves.** – vesica; **vin.** – vinculum; **vin.d.** – dorsal joint of vinculum with valva.

2.2.3. Phylogenetic analysis

For the phylogenetic analyses, the nucleotide sequences of the genetic data were used. Initial Maximum Likelihood analyses showed that analysis of the amino acid sequences translated from the nucleotide data resulted in poorly resolved topologies with branch supports mostly >> 50 percent; amino acid sequences were therefore disregarded as phylogenetic data source.

The sequence data were investigated for potential substitution saturation in third codon positions (XIA et al. 2003; XIA & LEMEY 2009) using DAMBE5 (XIA 2013). RogueNaRok (ABERER et al. 2013) was used to screen the molecular data for rogue taxa, which were subsequently excluded from the analysis.

We analysed the concatenated molecular and morphological data with two different partitioning schemes: GENES and TIGER. In the GENES scheme, we placed each gene and the morphological data into a separate partition, resulting in 7 partitions. In the TIGER scheme, following ROTA & WAHLBERG (2012), we partitioned the molecular dataset in terms of evolutionary site rates using the programme TIGER (CUMMINS & MCINERNEY 2011). We chose initial partitioning into 10 bins and pooled the bins with < 100 sites with bin 1, resulting in 5 molecular partitions, with bin 1 (incl. bins 2–6, each with < 100 sites) = 1798 sites, bin 7 = 182 sites, bin 8 = 684 sites, bin 9 = 1291 sites, and bin 10 = 1213 sites; morphology was treated as a separate 6th partition.

We used jModeltest v2.1.4 (GUINDON & GASCUEL 2003; DARRIBA et al. 2012) to infer the models that best reflect the sequence evolution of the genetic data. The resulting models for the GENES partitioning are: TIM3+G+I model for the COI partition, SYM+G+I model for the EF-1a partition, TVM+G+I model for the GAPDH partition, and GTR+G+I model for the CAD, IDH and RpS5 partitions. The TIM3 model is not implemented in MrBayes, and for this and the TVM model we used the GTR model instead. We omitted the invariant sites (I) parameter from the models since the parameters G and I are strongly correlated, and fewer parameters improved the analysis time (SULLIVAN & SWOFFORD 2001). The TIGER partitioning scheme was analysed under the GTR+G model. For the morphological partition, we applied the Mk model with gamma rate variation (LEWIS 2001). The concatenated dataset was analysed with MrBayes version 3.2.6 (RONQUIST et al. 2012) on the CIPRES online platform (MILLER et al. 2010) using Extreme Science and Engineering Discovery Environment (XSEDE). Two parallel runs were set up

for 30 Mio. generations, with sampling of every 1,000th generation. The parameters for gamma shape, proportion of invariable sites, character state frequencies and GTR substitution rates were unlinked for the partitions, and the overall rate was allowed to vary across partitions. The initial 25% of the trees were discarded as burn-in. Effective sampling sizes (ESS) and the degree of convergence of the runs were evaluated in Tracer (RAMBAUT et al. 2014). The phylogenetic trees were annotated using TreeGraph 2.14.0-771 beta (STÖVER & MÜLLER 2010).

In addition, a Maximum Likelihood (ML) analysis of the gene-partitioned molecular dataset was done using RAxML-HPC2 (8.2.10) (STAMATAKIS 2014) on XSEDE through the CIPRES V 3.3 online platform (MILLER et al. 2010).

WinClada 1.00.08 (NIXON 2002) was used to derive ancestral morphological characters from the topology that was observed in the majority of analyses. Unambiguous synapomorphies, and in addition those derived from slow optimization (slow optimization or DELTRAN, SWOFFORD & MADDISON 1987) are plotted on the topology and summarized. Apomorphies are included in the diagnoses of clades (see Phylogenetic classification section) except if they are very homoplastic in that clade. Characters were mapped on the consensus of the parsimony cladograms as well as the Bayesian trees for the sake of methodological consistency (ASSIS 2015).

A parsimony analysis was conducted with TNT 1.5 (GOLOBOFF & CATALANO 2016). All states were non-additive and equally weighted, and gaps were treated as missing data. A traditional search plus the parsimony ratchet (NIXON 1999) and branch-swapping was done (commands: mxram 100; cc-; collapse [; rs 1; hold 10000; rat: iter 50; mu: hold 20 replic 100 rat; bb;). Ratchet commands were the default values: stop when 14 substitutions made, 4% upweight and downweight probability, 50 total iterations, alternating equal weights. One hundred replications were done, saving 20 trees per replication. In addition to equal weights, implied weighting (GOLOBOFF 1993) was explored under a range of k-parameter values in TNT with the same search parameters. To try to resolve incongruence among cladograms, we ran the IterPCR script provided by POL & ESCAPA (2009). This script suggests characters to recode, which is not done by the application embedded in TNT 1.5.

3. Results

3.1. Molecular data

We present new genetic data for 100 taxa. In addition, we complemented the genetic data for four taxa from the study of HAINES & RUBINOFF (2012), for which we obtained the original DNA extracts from Will Haines (University of Hawaii): vouchers WPH209, WPH215,

WPH221, and WPH252. COI sequencing was successful for all samples except for the 3' half of '*Thliptoceras xanthomeris*' Hampson, 1918 (DNA voucher ZMBN Lep017). Sequencing success for CAD was 85% (of n = 100 samples), for the 1st part of EF-1a 94% (n=100), for the second part of EF-1a 100% (n=104), for GAPDH 70% (n=104), for IDH 97% (n=104), and for RpS5 85% (n=100). The amplification of RpS5 with the primers of WAHLBERG & WHEAT (2008) failed for all taxa in the tribes Udeini and Lineodini (see Taxonomy for tribes) except for 37% of the sequence length of *Lineodes vulnifica*, probably due to a lack of match between primer and attachment sequence.

The molecular alignment has a length of 5,223 base-pairs (bp), with 1,440 bp accounting for COI, 825 bp for CAD, 1,071 bp for EF-1a, 654 bp for GAPDH, 657 bp for IDH, and 576 bp for RpS5.

The CAD sequence of *Anania verbascalis* (GenBank accession no. MK459834) lacks three codons (9 bp, i.e. three amino acids in the respective protein product) compared to all other CAD sequences incorporated in our dataset. These three codons are present in the congeneric species, *A. hortulata*, and they code for the amino acids Isoleucine-Alanine-Valine. This three-codon deletion is situated in a variable region of the CAD gene, where especially the second codon is coding for a variety of different amino acids among the investigated taxa. A three-codon deletion at the identical location in the CAD sequence was observed in other Pyraustinae taxa believed to be closely related to *Anania* (Kai Chen, pers. comm.), so that this deletion might represent a synapomorphy for these taxa.

The long terminal branch of *Niphopyralis chionesis* Hampson, 1919 in the phylogenetic results of MUTANEN et al. (2010) and REGIER et al. (2012) is suspicious, and we therefore re-sequenced this species from available material (voucher no. MTD152) to evaluate whether the data from the previous studies might be compromised. Our resulting sequence coverage was comparable to that of MUTANEN et al. (2010), where the first half of EF-1a and the entirety of the GAPDH were unsuccessful in sequencing, just as in our results. Our sequenced data largely matches that of the MUTANEN et al. (2010) dataset, with only a few nucleotide differences between the corresponding sequences of the two investigated specimens. This result strongly suggests that the long terminal branch of *N. chionesis* in former studies is not due to sequence contamination. However, since the same DNA lab protocol (WAHLBERG & WHEAT 2008) was used in the MUTANEN et al. (2010) study as well as in the present study, the sequencing of pseudogenes cannot be ruled out, although no reading frame shifts or stop codons occur in any of the investigated *N. chionesis* sequences, suggesting that they code for functional proteins. None of the nucleotide sequences of *N. chionesis* is found to be exceptionally divergent from those of other investigated taxa, and observed nucleotide substitutions relative to the other taxa mostly result in synonymous amino acid codons, i.e. they encode the same amino acid.

3.2. Morphological data

Morphological data was coded from investigation of dried adult specimens and their genitalia. For a complete list of genitalia slides of species investigated in the context of this study (beyond the taxa included in the phylogenetic dataset), see Electronic Supplement File 1.

The morphological investigation resulted in the recognition of 115 variable characters for all 114 taxa. Of these characters, 91 are binary, and 24 are multistate. Nineteen characters code features of the head and thorax including legs and wings, 23 of the abdomen including the tympanal organs but excluding the genitalia, 47 of the male genitalia, 25 of the female genitalia and one character of the locality of larval feeding. Character 115 (locality of larval feeding) was coded from literature data, and the following literature was used: HINCKLEY (1964), GENTY & MARIAU (1975), MUNROE (1976), ALLYSON (1984), COMMON (1990), NUSS (2005), SPEIDEL (2005), SLAMKA (2008, 2013), HAYDEN et al. (2013), LERAUT (2014) and PEREIRA et al. (2014), as well as a personal observation of *Leucinodes africensis* Mally et al., 2015 from Marja van der Straten (pers. comm.).

The morphomatrix is shown in Table 2. The definitions of the morphological characters and their states are as follows:

- 1 Presence of anteriad-directed projection medially on frons: **(0)** absent (Fig. 11C); **(1)** present (Fig. 4B).
- 2 Presence of haustellum: **(0)** absent (Fig. 6A; ROEPKE 1916: fig. 2); **(1)** present (Fig. 4B).
- 3 Presence of transverse rim on anterior or mesal face of pedicellus [male]: **(0)** absent (Fig. 8F); **(1)** present (Fig. 11C).
- 4 Presence of a crest or prong of raised scales on mesal side of flagellomeres [male]: **(0)** absent (Fig. 11C); **(1)** present at ca. 1/3 of antenna length, crest forming a triangular prong proximally (Fig. 11D); **(2)** present in proximal part of antenna (Fig. 8F).
- 5 Length of sensillar setae at basal antennomeres relative to diameter of basal antennomeres [male]: **(0)** ≤ 50% (♂ in Fig. 10I, Fig. 11C); **(1)** > 50% (♂ in Fig. 10H, Fig. 11D).
- 6 Length of cilia at antenna base in female compared to male: **(0)** of equal length (Fig. 10I); **(1)** shorter (Fig. 10H).
- 7 Presence of ocelli: **(0)** absent (Fig. 6B); **(1)** present (Fig. 11C).
- 8 Direction of 3rd labial palpomere: **(0)** dorsal (Fig. 11C); **(1)** porrect (Fig. 4B).
- 9 Intersexual size differences of 3rd labial palpomere: **(0)** well developed in both sexes (MAES 1995: pl. 5); **(1)** short in the male (Fig. 4B); **(2)** short in both sexes (Fig. 6A; ROEPKE 1916: fig. 3).
- 10 Length of maxillary palpi: **(0)** long enough to hypothetically come in contact with each other (Fig. 11C); **(1)** minute to obsolete, cannot hypothetically get in contact with each other (Fig. 6A).

- 11 Presence of broad scale tuft on distal foreleg tibia (not to be confused with epiphysis): **(0)** absent; **(1)** present.
- 12 Presence of tuft of long scales on distal foreleg femur: **(0)** absent; **(1)** present.
- 13 Presence of a longitudinal groove bearing a hair pencil on male midleg tibia: **(0)** absent (FROLOV et al. 2007: fig. 1A); **(1)** present (FROLOV et al. 2007: fig. 1B,C).
- 14 Presence of tibio-abdominal scale brush [male]: longitudinal line of thin, spatulate scales on male hindleg's proximal tibia in contact with an area of ventrad scales on pleural membranes of abdominal segment 2: **(0)** absent; **(1)** present (MEY & SPEIDEL 2010: figs. 5, 10).
- 15 Number of apical spurs on hindtibia: **(0)** 4, a proximal and a distal pair (Fig. 10F, G); **(1)** 2, only a distal pair (as in fig. 10F,G, but without proximal spur pair).
- 16 Length of metatibial proximal inner spur relative to tibial segment between this and the distal spur pair: **(0)** $< 1/2$ (distance "d") (Fig. 10F); **(1)** $\geq 1/2$ (distance "d") (Fig. 10G).
- 17 Presence of field of enlarged, raised scales on male central forewing costa: **(0)** absent (Fig. 7A); **(1)** present (Fig. 9A).
- 18 Form of retinaculum at costal base of forewing underside in males: **(0)** simple brush of straight hairs (Fig. 8I); **(1)** cuticle protruded as a retinacular hook (frenulum hook sensu FORBES 1926: fig. 7; POPESCU-GORJ & CONSTANTINESCU 1977: fig. 3b).
- 19 Number of frenulum bristles in female: **(0)** one (Fig. 4A); **(1)** two (POPESCU-GORJ & CONSTANTINESCU 1977: fig. 3a).
- 20 Splitting of praecinctorium: **(0)** strong (MARION 1954: fig. 2); **(1)** weak to absent (MARION 1954: fig. 1).
- 21 Presence of lobulus on lateral edge of tympanal case: **(0)** absent (Fig. 6C); **(1)** present (Fig. 8A).
- 22 Shape of fornix tympani surface: **(0)** projecting from the tympanic frame (MINET 1983: "cd." in fig. 30; MAES 1985: "f.ty." in pls. 1A, 1D); **(1)** recessed within the frame (MAES 1985: pl. 1E, "f.ty." in pl. 2C).
- 23 Direction of fornix tympani projection: **(0)** ventral (MINET 1983: "cd." in fig. 30); **(1)** lateral (see HAYDEN 2013: figs. 18, 19, 21, 22).
- 24 Presence of venulae secundae: **(0)** absent (Fig. 6C); **(1)** present (Fig. 8A).
- 25 Course of venulae secundae: **(0)** converging (Fig. 5C); **(1)** in posterior half parallel or diverging (Fig. 8A).
- 26 Presence of lateral anterior lobe on each side of anterior edge of male sternite 3: **(0)** absent (Fig. 6C); **(1)** present (Fig. 7G).
- 27 Presence of pleural scale tufts on each side of the male abdomen, one small scale tuft anteriorly on segment 6 and one large scale tuft anteriorly on segment 7: **(0)** absent (Fig. 3H); **(1)** present (Fig. 8H).
- 28 Presence of pleural scale tufts on each side of the male abdomen, one large scale tuft anteriorly on segment 5, one small scale tuft on anterior ends of segments 6 and 7: **(0)** absent (Fig. 12G); **(1)** present (Fig. 13C).
- 29 Presence of large, oval pleural scale tufts on each side of male abdominal segment 7, with a presumably secretory opening in its anterior centre: **(0)** absent (Fig. 3H); **(1)** present (Fig. 14F).
- 30 Outline of central anterior edge of male sternite 7: **(0)** straight to slightly undulate (Fig. 6F); **(1)** anteriorly projecting protuberance or spine (Fig. 3H); **(2)** arch-shaped recession (Fig. 8G).
- 31 Outline of central posterior edge of male sternite 7: **(0)** straight (Fig. 8H); **(1)** with pair of posteriad, curved spines running dorsally of sternite 8 (Fig. 6F); **(2)** with pair of posteriad lobes (Fig. 15E); **(3)** a wide V-shaped recession (Fig. 8E).
- 32 Outline of anterior edge of male tergite 8: **(0)** straight to convex (Fig. 6F); **(1)** with triangular and straight-edged or semicircular indentation (Fig. 3H).
- 33 Sclerotization of male tergite 8: **(0)** homogenous (Fig. 9D); **(1)** heterogenous, i.e. with distinct sclerotization pattern (Fig. 3H).
- 34 Sclerotization pattern on male tergite 8: **(0)** central longitudinal strip; **(1)** longitudinal strip, bifurcating anteriorly into a Y-shape (Fig. 3H).
- 35 Presence of a field of setose scales on the anterior ends of the male tergite 8's Y-shaped sclerotisation: **(0)** absent (Fig. 8H); **(1)** present (Fig. 11F).
- 36 Presence of U-shaped sclerotisation on lateral and anterior edge of male sternite 8: **(0)** absent (Fig. 9D); **(1)** present (Fig. 11F).
- 37 Presence of an anterolaterad sclerotized lobe on each side of anterior edge of male sternite 8, running dorsad of sternite 7: **(0)** absent (Fig. 8H); **(1)** present (Fig. 6G).
- 38 Presence of central hair scale patch(es) on anterior edge of male sternite 8: **(0)** absent (Fig. 8H); **(1)** present (Fig. 3H).
- 39 Presence of median U-shaped recession or deep notch on posterior edge of male sternite 8: **(0)** absent (Fig. 3H); **(1)** present (Fig. 6G).
- 40 Presence of a sclerite on each pleural membrane of male segment 8: **(0)** absent (Fig. 6F); **(1)** present (Figs 3H, 9D).
- 41 Shape of pleural sclerite on male segment 8: **(0)** slim longitudinal strip (Fig. 9D); **(1)** broad semicircle (Fig. 3H).
- 42 Presence of a field of setae anterior on pleurites of male segment 8: **(0)** absent (Fig. 3H); **(1)** present.
- 43 Presence of uncus: **(0)** absent (reduced) (Fig. 3A); **(1)** present (Fig. 3D).
- 44 Shape of uncus: **(0)** conical, non-capitate (Fig. 3D); **(1)** capitate (Fig. 3G).
- 45 Shape of apical uncus: **(0)** single head (Fig. 3D); **(1)** bi- or trifurcate head (Fig. 9E); **(2)** two separate heads (Figs. 9G, 11E).

- 46 Presence of chaetae on surface of uncus head(s): **(0)** absent (Fig. 15C); **(1)** present (Fig. 3D).
- 47 Structure of uncus head chaetae: **(0)** simple, not apically split (Figs. 7D, 14C); **(1)** bifurcate (Fig. 9I); **(2)** multifurcate (POPESCU-GORJ & CONSTANTINESCU 1977: fig. 7d); **(3)** short, flat, spatulate (Fig. 14C).
- 48 Location of setae on uncus: **(0)** dorsal (Fig. 13A); **(1)** dorsal & lateral (Fig. 5E); **(2)** dorsal & ventral (MALLY & NUSS 2010: fig. 2B); **(3)** ventral (Fig. 9E); **(4)** lateral (SLAMKA 2008: pl. 29 fig. 182).
- 49 Attachment of uncus to tegumen: **(0)** broad, point of attachment constricted (Fig. 4E); **(1)** broad, smooth transition (Fig. 4F); **(2)** narrow, offset (MUNROE 1976b: pl. u fig. 6a; MALLY & NUSS 2010: fig. 2C).
- 50 Region between subscaphium and dorsal tegumen: **(0)** membranous (Fig. 9G); **(1)** sclerotized as gnathos (sensu MAES 1998) (Fig. 3G); **(2)** sclerotized as pseudognathos (sensu MAES 1998) (Figs. 4E, 5D).
- 51 Shape of transtillum arms: **(0)** triangular (tapering towards apex) (Fig. 4E); **(1)** rounded (Fig. 3G); **(2)** strap-like (apex blunt or pointed) (Figs. 8B, 11E); **(3)** large rectangular, medioventrally with finger-like process (“transtillum inferior” sensu MARION 1954) (Fig. 15D; MARION 1954: fig. 11); **(4)** rhomboidal (= triangular with cut apex) (Fig. 15C).
- 52 Connection point of transtillum arms: **(0)** narrow (Fig. 3G); **(1)** broad (Fig. 11E).
- 53 Presence of long dorsad chaetae on surface of transtillum arms: **(0)** absent (Fig. 3G); **(1)** present (Fig. 15D).
- 54 Presence of lobar processes carrying hair-pencils on the dorsolateral tegumen sides: **(0)** absent (Fig. 13B); **(1)** present (Fig. 3A).
- 55 Depth of gap/split of juxta: **(0)** < 10% of dorsoventral length of juxta (Fig. 3G); **(1)** 10–60% of dorsoventral length of juxta (Fig. 5D); **(2)** > 60% of dorsoventral length of juxta to complete division into two juxta arms (Figs. 3A, 6E).
- 56 Saccus shape: **(0)** U-shaped (Fig. 3A); **(1)** (sharply) V-shaped (Fig. 4F); **(2)** stout, almost rectangular (Fig. 5E); **(3)** narrow elongate (Fig. 9H).
- 57 Presence of constriction at basal saccus: **(0)** absent (Fig. 3A); **(1)** present (Fig. 13A).
- 58 Ratio between saccus length and sacculus breadth: **(0)** ≤ 1 (Fig. 3A); **(1)** > 1 (Fig. 13B).
- 59 Presence of protruding keel on ventral saccus tip: **(0)** absent (Fig. 3A); **(1)** present (Fig. 4F).
- 60 Presence of partly sclerotized, chaetose hairpencil articulating with the anterior edge of the vinculum-tegumen connection: **(0)** absent (Fig. 7C); **(1)** present (Figs. 13A, 10C, 14E).
- 61 Number of hairpencil sclerites on each side of the genitalia: **(0)** one (Figs. 13A, 10C, 14E); **(1)** two or more (articulated with each other via membranes) (Fig. 9H).
- 62 Presence of more than one kind of hairpencil chaetae: **(0)** absent (Fig. 14E); **(1)** present (CLARKE 1986: fig. 34a; KIMURA et al. 2002: figs. 1–4).
- 63 Presence of a pair of sclerotized, hair-studded hair-pencils articulating with the anteromedian edge of the saccus: **(0)** absent (Fig. 5E); **(1)** present (Fig. 3G).
- 64 Presence of fibula emerging from central inner valva: **(0)** absent (Fig. 3D); **(1)** present (Fig. 4F).
- 65 Presence of fibula emerging from dorsal valva base near costa base: **(0)** absent (Fig. 3D); **(1)** present (Figs. 4E, 10C).
- 66 General shape of fibula: **(0)** broad triangular (Fig. 8B); **(1)** elongate triangular, at least twice as long as broad (Fig. 4F); **(2)** elongate needle-like to claw-shaped (Figs. 4E, 7D); **(3)** as long as broad, circular to squarish (Fig. 12C).
- 67 General orientation of fibula: **(0)** ventrally directed towards sacculus or distal sacculus (Figs. 4E, 8B); **(1)** directed towards ventral sacculus base (Fig. 7C); **(2)** directed towards distal valva (Fig. 3A); **(3)** directed dorsally, towards tegumen/uncus (Fig. 3G).
- 68 Presence of chaetae on fibula surface: **(0)** absent (Fig. 4E); **(1)** present (Figs. 7C, 15D).
- 69 Structure of apex of chaetae on fibula surface: **(0)** simple (Figs. 7C, 15D); **(1)** some simple, some multifid (= editum of Pyraustinae) (YANG et al. 2012: uppermost arrow in fig. 7A–D); **(2)** spatulate (CLARKE 1986: fig. 34a).
- 70 Presence of raised ridge running from basal to dorsodistal sacculus: **(0)** absent (Fig. 5D); **(1)** present (Fig. 12D).
- 71 Presence of finger-like process studded with simple chaetae emerging from central sacculus: **(0)** absent (Fig. 5D); **(1)** present (Fig. 9H).
- 72 Presence of extension (process in some cases) at dorsodistal sacculus: **(0)** absent (Fig. 4E); **(1)** present (Fig. 4F).
- 73 Spatial association of fibula with dorsodistal sacculus (or its extension): **(0)** distant (Fig. 4F); **(1)** closely associated, overlapping (Fig. 4E); **(2)** fibula and dorsodistal sacculus fused (Fig. 11E).
- 74 Presence of inflation of basal costa: **(0)** absent (Fig. 4E); **(1)** present (Fig. 8B).
- 75 Joint of basal valva costa (with vinculum) extended into an elongate, rod-shaped process: **(0)** absent (Fig. 4F); **(1)** present (Fig. 8B).
- 76 Presence of long, sometimes loosely arranged chaetae on surface of costal base: **(0)** absent (Fig. 4E); **(1)** present (Figs. 3A, 5E).
- 77 Presence of a knee-like bend of 60–80° in the post-basal costa: **(0)** absent (Fig. 4E); **(1)** present (Fig. 13B).
- 78 General shape of post-basal costa (not the entire dorsal valva edge): **(0)** concave (Fig. 3A); **(1)** straight (Fig. 5E); **(2)** convex (Figs. 8B, 9F,G).
- 79 Presence of a setose dorsad process on the basal costa: **(0)** absent (Fig. 3A); **(1)** present (Fig. 11E).
- 80 General structure of distal costa: **(0)** tubular (Fig. 3A); **(1)** broadening (Fig. 12E).
- 81 Costa following the course of (= in alignment with) the dorsal valva edge (all the way) into subapical

- valva region: **(0)** absent (Fig. 9H); **(1)** present (Fig. 4E).
- 82** Presence of detached costa from valval area, the costa protruding freely dorsad instead: **(0)** absent (Fig. 7C); **(1)** present (Fig. 15C; MUNROE 1976b: pl. u fig. 6a; SHAFFER & MUNROE 2007: figs. 130, 133).
- 83** Presence of a recess in the course of the ventral valva edge: **(0)** absent (Fig. 4F); **(1)** present (Fig. 7D).
- 84** Presence of a coecum on the phallus apodeme: **(0)** absent (Figs. 8C, 12D); **(1)** present (Figs. 3B, 4G).
- 85** Length of phallus coecum relative to phallus apodeme length: **(0)** < 10% (Fig. 4G); **(1)** ≥ 10% (Fig. 3B).
- 86** Presence of reduction of phallus apodeme sclerotisation to a ventral, longitudinally sclerotized strip (the rest of the apodeme being more or less membranous): **(0)** absent (Figs. 4G, 15D); **(1)** present (Figs. 7D, 10C, 13F).
- 87** Presence of a distinct sclerite in the posterior phallus apodeme: **(0)** absent (Fig. 13F); **(1)** present (Fig. 4G).
- 88** Presence of sclerotisation on surface of vesica: **(0)** absent (Fig. 7F); **(1)** present (Fig. 3B).
- 89** Type of vesica sclerotisation: **(0)** single cornutus (Fig. 3B); **(1)** multiple cornuti (Fig. 13F); **(2)** granulated area (Fig. 3B).
- 90** Orientation of everted papillae anales: **(0)** postero-ventrad (Fig. 3F); **(1)** ventrad (Fig. 4H); **(2)** posteriad (Fig. 5F).
- 91** Dorsal end of papillae anales larger than ventral end: **(0)** absent (Fig. 3F); **(1)** present (Fig. 13E).
- 92** Ventral end of papillae anales larger than dorsal end: **(0)** absent (Fig. 3F); **(1)** present (Fig. 14G).
- 93** Presence of a strongly sclerotized frame (= lamella antevaginalis) around the ostium bursae: **(0)** absent (Fig. 5F); **(1)** present (Fig. 3F).
- 94** Presence of strong sclerotisation in the antrum: **(0)** absent, with antrum more or less membranous (Fig. 11H); **(1)** present (Fig. 4H).
- 95** Presence of a longitudinal membranous strip in the antrum sclerotisation: **(0)** absent (Fig. 9J); **(1)** present (Figs. 5F, 10D,E).
- 96** Presence of thickened mesocuticle in the antrum: **(0)** absent (Fig. 11G); **(1)** present (Fig. 4H).
- 97** Presence of a cone-shaped central structure (*Anania*-type) in the antrum: **(0)** absent (Fig. 11G); **(1)** present (Fig. 15F; TRÄNKNER et al. 2009: arrows in figs. 18–21).
- 98** Presence of a lateral blind-end evagination (diverticulum) in the colliculum: **(0)** absent (Fig. 13D); **(1)** present (Fig. 13E).
- 99** Presence of a strongly sclerotised colliculum anterior of antrum and posterior of attachment of ductus seminalis: **(0)** absent (Fig. 11G); **(1)** present (Fig. 5F).
- 100** Presence of a longitudinal membranous strip in the colliculum sclerotisation: **(0)** absent (Fig. 13D); **(1)** present (Fig. 5F).
- 101** Presence of thickened mesocuticle in the colliculum: **(0)** absent (Fig. 5F); **(1)** present (Fig. 14G).
- 102** Point of attachment of ductus seminalis to female genital tract: **(0)** at posterior ductus bursae, at or near colliculum (Fig. 5G); **(1)** at anterior ductus bursae (Fig. 7E); **(2)** at corpus bursae (Fig. 12F).
- 103** Demarcation between corpus bursae and ductus bursae: **(0)** distinct by narrow anterior ductus transforming into wide corpus bursae (Fig. 3E); **(1)** indistinct or absent by wide anterior ductus transforming into equally wide corpus bursae, i.e. fluent transformation of d.b. to c.b.) (Figs. 3F, 10E).
- 104** Presence of sclerotisation in ductus bursae: **(0)** absent (Fig. 3E); **(1)** present (Fig. 5F).
- 105** Intensity of ductus bursae sclerotisation: **(0)** weak (granulose texture) (Fig. 13E); **(1)** strong (Fig. 5F).
- 106** Presence of sclerotisation in corpus bursae: **(0)** absent (Fig. 9J); **(1)** present (Fig. 3F).
- 107** Structure of corpus bursae sclerotisation: **(0)** a granulose area (Figs. 11G–H); **(1)** one or more clearly delimited sclerites (= signum, Pl. signa) (Fig. 3F).
- 108** Number of signa: **(0)** one (Fig. 3E); **(1)** two or more (Fig. 3F).
- 109** Shape of anterior-most signum: **(0)** circular, spinose, can be invaginated as a spine (Fig. 8K); **(1)** longitudinal slim, strip-like (Fig. 13E); **(2)** elongate rhombical to ovate (longitudinal axis longer than transverse one) (Fig. 5F); **(3)** transverse rhombical to cross-shaped (longitudinal axis shorter than or equally long as transverse one) (Figs. 3E, 15F–G); **(4)** patch of protruding teeth/spikes (Fig. 3F); **(5)** transverse, smooth or dentate line or arch, with or without central posteriad leg (if present, then signum Y-shaped) (Figs. 10E, 11H); **(6)** broad, medially constricted, resembling puckered lips (Figs. 14G,H).
- 110** Shape of second signum (located posterior of first signum): **(0)** circular, spinose, can be invaginated as a spine (Fig. 8K); **(1)** longitudinal slim, strip-like (Fig. 5F); **(2)** elongate rhombical to ovate (SHAFFER & MUNROE 2007: figs. 299, 300); **(3)** patch of protruding teeth/spikes (Fig. 3F).
- 111** Presence of a third, slim, strip-like signum posterior of the two anterior signa: **(0)** absent (Fig. 8J); **(1)** present (Fig. 8K).
- 112** Presence of appendix bursae on anterior ductus bursae: **(0)** absent (Fig. 8K); **(1)** present (Figs. 14G, 15G).
- 113** Presence of appendix bursae on corpus bursae: **(0)** absent (Fig. 8K); **(1)** present (Figs. 3F, 15F).
- 114** Point of attachment of appendix bursae on corpus bursae: **(0)** lateral (Figs. 3F, 15F); **(1)** posterior (Fig. 9J); **(2)** anterior (Fig. 5G).
- 115** Locality of larval feeding: **(0)** concealed in rolled/spun leaves or in a web (LEUTHARDT et al. 2010: fig. 1; HAYDEN et al. 2017: fig. 19); **(1)** on leaf/fruit surface (upper/underside) (HAYDEN et al. 2013: *Lineodes fontella*); **(2)** boring in stems and/or branches (SOURAKOV 2011: figs. 6A, 7A, 10B); **(3)** boring in

flowers, pods and fruits (SOURAKOV 2011: figs. 3, 4); **(4)** on/in roots (GENTY & MARIAN 1975: figs. 3–5, 7); **(5)** on dead and decaying plant matter (MURPHY 1990: pl. 15 fig. J).

3.3. Phylogenetic results

The investigation of the gene data with DAMBE5 showed no signs for significant substitution saturation in the three different codon positions of COI, CAD, EF-1a and GAPDH. Codon positions nt1 and nt2 of IDH and RpS5 showed no significant saturation, whereas in nt3 of these two genes, some substitution saturation was observed. This low level of substitution saturation was accepted as of minor influence for the phylogenetic analysis of these data, so that no codon position was removed from the final dataset. This decision was supported by trial analyses of the dataset with nt3 removed from IDH and RpS5 which showed a very similar topology and comparable node support.

In phylogenetic pre-analyses, several taxa had conspicuously unstable positions in the phylogeny. These most problematic ‘rogue’ taxa were identified using RogueNaRok and excluded from final analyses. One exception was *Niphopyralis chionesis*, which we decided to keep in the dataset despite its long terminal branch in the phylogenetic results.

Differences in the coverage of morphological data coding affect the performance of the phylogenetic analyses: MrBayes analyses containing morphological data for the outgroup taxa performed worse than analyses that only comprised morphological data for Pyraustinae and Spilomelinae and where outgroups were coded as ‘?’. When outgroup morphological data is included in the analysis, the parallel MrBayes runs do not converge properly and the effective sample size is low for a number of parameters. All phylogenetic results stated and discussed below are therefore based on the datasets that only comprise the morphological data for Spilomelinae, Pyraustinae and *Sufetula*. The potential causes and implications of outgroup coding are elaborated in the Discussion section.

The parallel runs of all MrBayes analyses converged sufficiently after 30 Mio. generations, and ESS were (mostly well) above 100. The analyses of the different datasets result in highly similar topologies, and branch support from the analyses of the molecular data alone and those of the combined molecular and morphological data are almost identical (Fig. 1). The additional morphological data in the analysis of the combined dataset does not result in improved resolution or branch support as compared to the results of the molecular dataset. Branching differences are found in the position of the clade Spilomelini (see dotted arrow in Fig. 1), and within the clade Margaroniini. Pyralidae, Pyralinae, and Crambidae are each monophyletic with high branch supports. In the Crambidae outgroup, *Sufetula* (Lathroteli-

nae) is sister to the “CAMMSS Clade” sensu REGIER et al. (2012), with a clade *Crambus* (Crambinae) + *Eudonia* (Scopariinae) sister to the “Wet Habitat Clade” (sensu REGIER et al. 2012) *Clepsicosma* + (*Midila* + *Schoenobius*), the latter belonging to Acentropinae, Midilinae and Schoenobiinae, respectively. Sister to the Crambidae outgroup is the “PS Clade” (sensu REGIER et al. 2012) of Pyraustinae and Spilomelinae. Both Pyraustinae and Spilomelinae are highly supported (1 PP) monophyletic and moderately-supported (0.93–0.95 PP) sister to each other.

Within Pyraustinae, *Tetridia* is sister to all other taxa. The two *Euclasta* species form a monophylum (Euclastini) that is sister to the remainder of Pyraustinae. A clade *Uresiphita* + (*Portentomorpha* + (*Cryptosara* + *Hyalobathra*)) is sister to the remainder of Pyraustinae (Pyraustini). *Ostrinia* is sister to a clade *Pagyda* + *Paracorsia*, which is sister to the remainder of Pyraustinae. *Achyra* + (*Loxostege* + *Sitochroa*) is sister to a clade *Oenobotys* + (*Hyalorista* + *Pyrausta*) and its sister group of *Psammotis*, *Pseudopyrausta* and *Anania*. *Anania*, with two sampled species, is monophyletic except in the phylogram of the GENES-partitioned genetic dataset, where *A. hortulata* is sister to *Psammotis*, and *A. verbascalis* sister to *Pseudopyrausta*, all with PP < 0.9.

The phylogenetic relationships within Spilomelinae are as follows: Hydririni + ((Udeini + Lineodini) + (Wurthiini + (Agroterini + (Margaroniini + (Spilomelini + (Herpetogrammatini + ((Hymeniini + Asciodini) + (Trichaeini + (Steniini + Nomophilini))))))))), with the exception of the GENES-partitioned analyses, where Spilomelini is in an unsupported (0.67–0.72 PP) sister-group relationship with Margaroniini (indicated by dotted arrow in Fig. 1). Hydririni comprises *Hydriris* + (*Lamprosema* + (*Gonocausta* + *Syllepis*)). Udeini comprises *Conchylodes* + (*Udeoides* + *Udea*). Lineodini comprises *Lineodes* + (*Rhectosemia* + (*Leucinodes* + *Neoleucinodes*)). Wurthiini comprises *Apilocrocis* + (*Aristeubulea* + *Niphopyralis*). Agroterini comprises *Pycnarmon* + ((*Neoanalthes* + (*Aetholix* + *Agrotera*)) + (*Haritalodes* + (*Phostria* + *Patania*))). Margaroniini forms a large polytomy with several moderately to well-supported monophyla, which are: *Asturodes* + *Maruca*; *Omiodes*; *Prentesia*; *Liopasia* + (*Agathodes* + *Terastia*); *Hodebertia* + (*Antigastra* + *Zebronia*); (*Azochis* + *Conogethes*) + *Ghesquierellana* + *Megastes*); (*Agrioglypta* + *Obtusipalpis*) + (*Dichocrocis* cf. *zebralis* + *Glyphodes*). Additional taxa in Margaroniini with unresolved or unsupported (PP < 0.9) relationships are: *Cydalima*, *Filodes*, *Rhimphalea*, *Diaphania*, *Palpita*, *Botyodes*, *Cadarena*, *Leucochroma*, *Nacoleia insolitalis*. Spilomelini comprises (*Siga* + *Eporidia*) + (*Spilomela* + (*Salbia* + (*Marasmia* + *Cnaphalocrocis*))). Herpetogrammatini comprises *Eurhynparodes* + (*Herpetogramma* + *Hileithia*). Hymeniini comprises *Hymenia* + *Spoladea*. Asciodini comprises *Asciodes* + *Arthromastix*. Trichaeini comprises *Trichaea* + *Prophantis*. Steniini comprises (*Dolicharthria* + *Metasia*) + (*Duponchelia* + *Anageshna*). Nomophilini com-

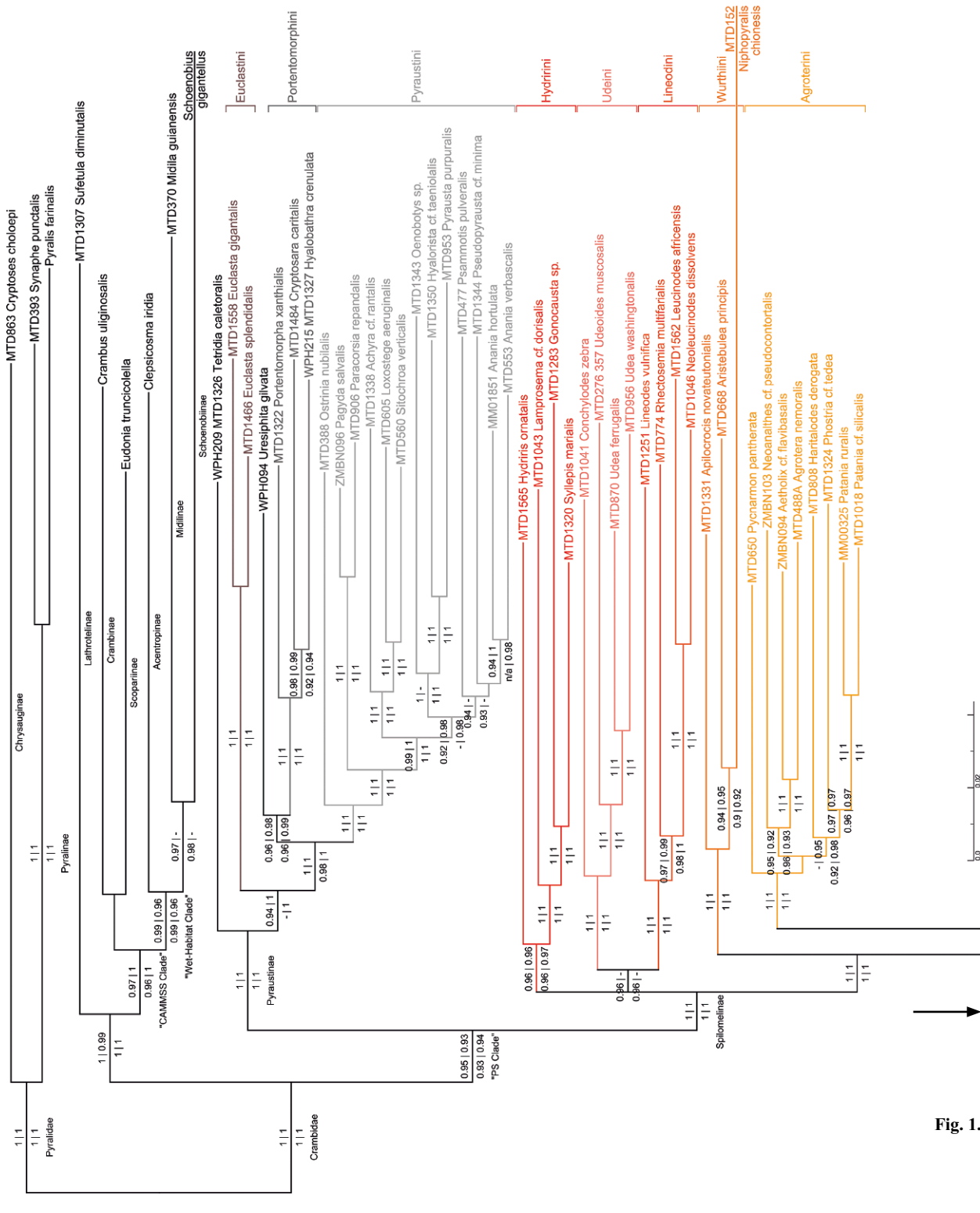


Fig. 1.

prises (*Syngamia* + (*Ategumia* + (*Bocchoris* + (*Diasemia* + *Diasemiopsis*)))) + (*Desmia* + (*Mecyna* + (*Samea* + *Nomophila*)))).

Parsimony analysis resulted in three cladograms of 35,100 steps. The strict consensus (Fig. 2) has 35,153 steps. Condensing these cladograms with “collapse” did not lengthen them, so filtering with the command “best” was not necessary. *Niphopyralis* groups with *Sufetula*.

The topology of the outgroup CAMMSS clade is different than that in REGIER et al. (2012). Euclastini diverges first in Pyraustinae. The second-diverging clade is Portentomorphi including *Portentomorpha*, *Hyalobathra*, and *Cryptosara*. The topology within Pyraustini is substantially different. *Tetridia* and *Uresiphita* are subordinate in Pyraustini, sister to *Pseudopyrausta* and *Ostrinia*, respectively.

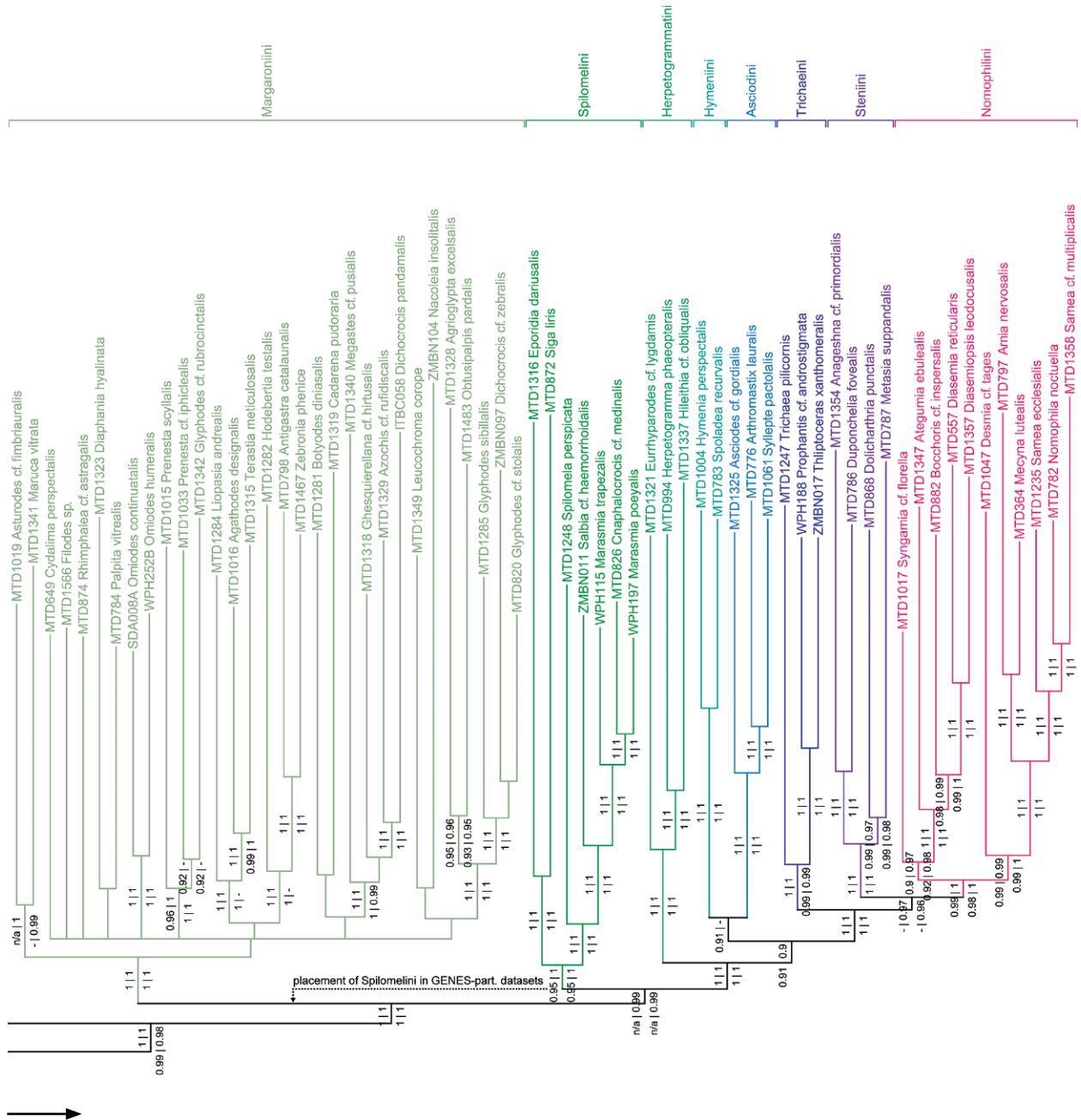


Fig. 1. Bayesian consensus phylogram of the three parallel runs of the TIGER-partitioned MrBayes analysis of the molecular+morphology dataset (“mol+morph-TIGER”). Numbers at internal branches are PP ≥ 0.9 , above branches “mol+morph-GENES | mol+morph-TIGER”, below branches “mol-GENES | mol-TIGER”; nodes without posterior probabilities indicate PP ≥ 0.9 in all four analyses. Scale bar represents substitutions per site. Clade names in quotation marks correspond to those in REGIER et al. (2012). — **Abbreviations:** n/a – node not present; PP – posterior probability. — **Symbols:** - PP < 0.9.

The three unweighted cladograms differ in only two clades: 1) whether *Lineodes* or *Rhectosemia* is the first-diverging genus of Lineodini, and 2) the topology (Steniini + (Nomophilini + Trichaeini)) versus (Nomophilini + (Steniini + Trichaeini)), with Nomophilini in a reduced sense including *Syngamia* but not the *Ategumia* clade. Other differences are 1) the grouping of *Desmia* with Trichaeini and 2) the *Ategumia* clade (with *Bocchoris*,

Diasemia and *Diasemiopsis*) consistently being sister to the clade of the other three tribes (Steniini, Trichaeini, and Nomophilini s.str.).

IterPCR (POL & ESCAPA 2009) did not suggest any taxa or characters to recode. Implied weighting with k-parameter values of 9 through 13 found cladograms (not shown) with *Niphopyralis* sister to *Aristebulea principis* Munroe & Mutuura, 1968, but the topologies are oth-

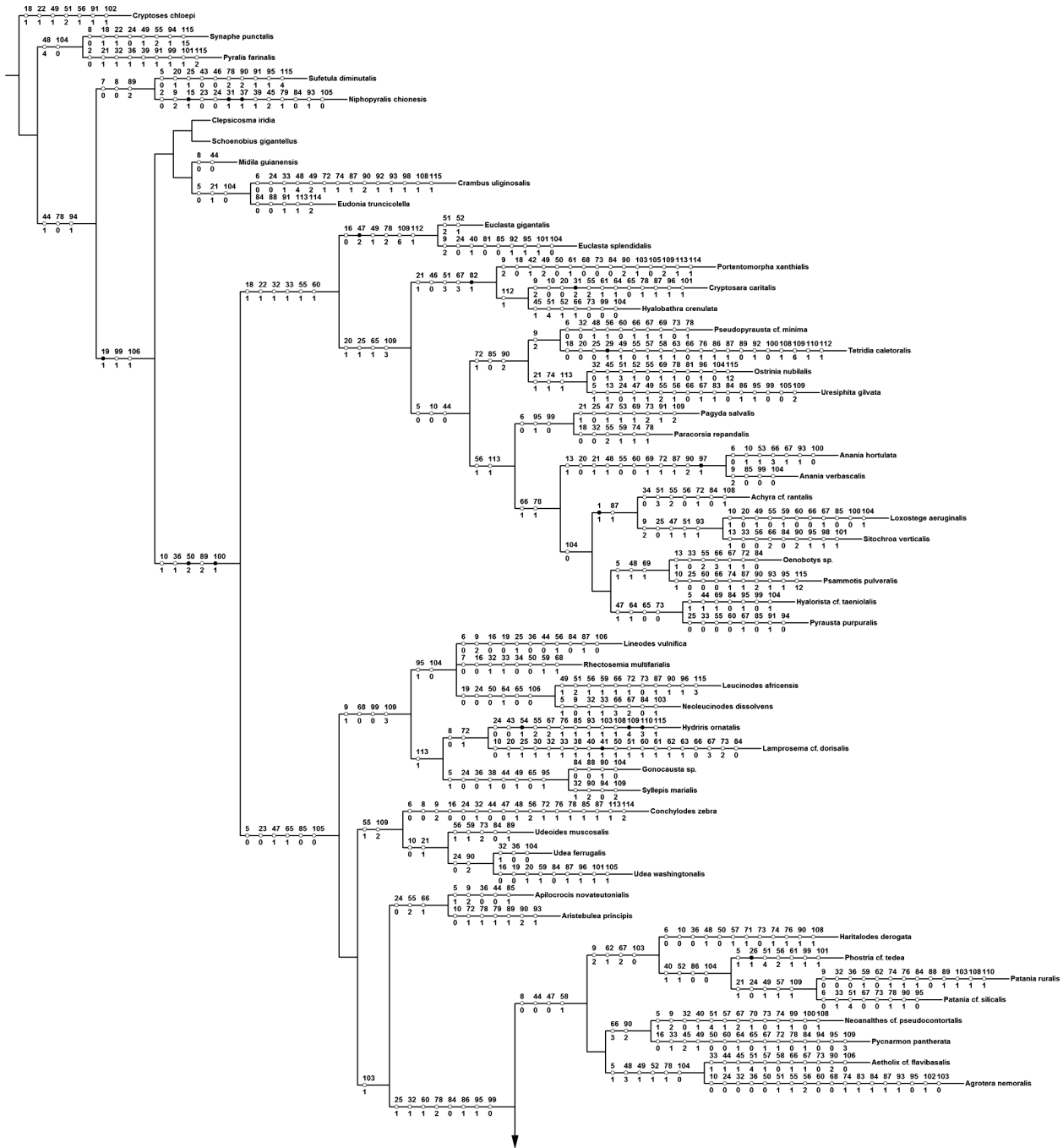


Fig. 2. Strict consensus of three parsimony cladograms of 35,100 steps, with morphological characters mapped with slow optimization. — **Symbols:** ● unique apomorphies; ○ homoplastic apomorphies.

erwise similar to the equal-weights results. The lengths range from 35,159 to 35,192 steps.

Among the genera with more than one sampled species, *Eucleasta*, *Udea*, *Patania* and *Omiodes* are monophyletic. *Marasmia*, *Prenesta* and *Samea* are paraphyletic, and *Glyphodes* and *Dichocrocis* are polyphyletic.

The morphological data were mapped with WinClada on the Bayesian consensus (Fig. 1, synapomorphies not shown) and the parsimony consensus (Fig. 2) using slow optimization (= delayed transformation, DELTRAN). The results are stated in the diagnoses of the clades in the taxonomy section. Although consensus trees are typi-

cally longer than the shortest actual cladograms, the extra steps did not occur along the particular clades that we are interested in diagnosing.

4. Phylogenetic classification

In this section we focus on the taxonomic circumscription of Spilomelinae and Pyraustinae and the clades found therein. We state synapomorphies and / or characters derived from slow optimization in the “Synapomor-

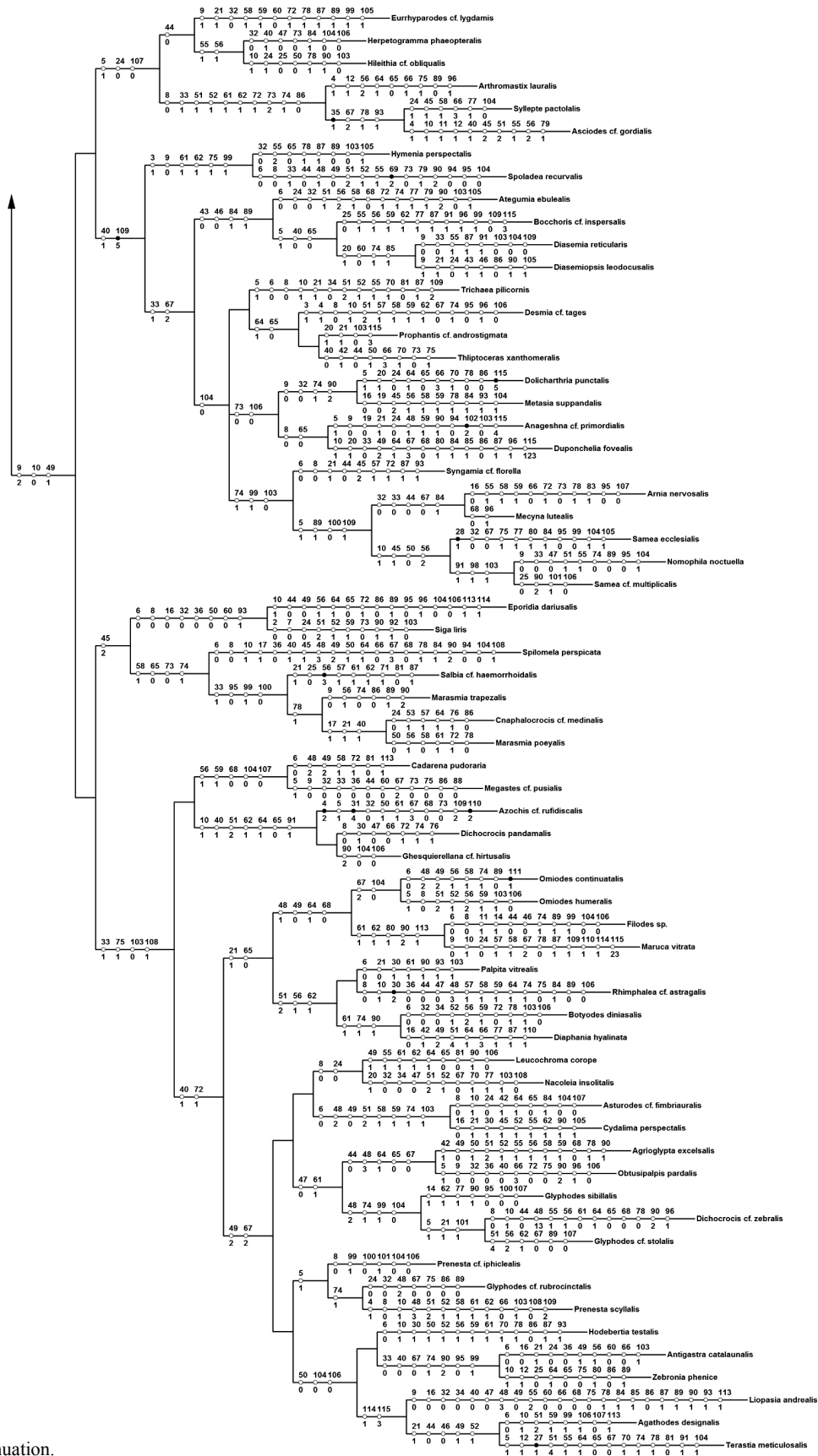


Fig. 2 – Continuation.

phies” paragraphs. Representatives of all proposed tribes are illustrated in Figs. 3–15. The morphological characters indicated in the figures do not necessarily represent

apomorphies for the respective tribe. A checklist of all Spilomelinae and Pyraustinae genera that are placed in tribes is given in the Appendix.

4.1. Spilomelinae + Pyraustinae (PS) Clade

Synapomorphies. No unambiguous synapomorphies were found, as most of the Crambidae outgroup taxa were left uncoded. Under slow optimization, the following three characters are found: 36:1, U-shaped sclerotisation of lateral and anterior edge of male sternite 8 present (also present in Schoenobiinae: *Schoenobius*); 65:1, presence of fibula emerging from dorsal valva base near costa base; 106:1, sclerotisation in corpus bursae present.

Description. The uncus has bifid chaetae. These distinctive chaetae are present in many Pyraustinae as well as in most Spilomelinae. Bifid chaetae are lost in some spilomeline groups which have normal, hair-like monofilament chaetae on the uncus instead (e.g. *Conchylodes* genus group in Udeini, Agrotorini, several Margarini).

The costa of the valva is straight to concave. All investigated Pyraustinae as well as the non-euspilomeline clades (Hydririni, Udeini, Lineodini, Wurthiini) exhibit male genitalia with a straight or concave costa (we only refer to the costa here, and not to the whole dorsal valva edge). Most other Spilomelinae have a convex costa.

The gnathos is reduced to a transverse strap, laterally fused to the tegumen, and usually without a central process. This is the “pseudognathos” of MAES (1998a), which SOLIS & METZ (2011) homologized with the gnathos: the structure is simply reduced and fused. A few Pyraustinae and Spilomelinae do have a central process like that in most other Crambidae, such as *Munroeodes* Amsel, 1957, *Sarabotys* Munroe, 1964, *Phaedropsis* Warren, 1890, *Patania* Moore, 1888, *Syllepte amando* (Cramer, 1779), *Deuterophysa* Warren, 1889 and *Mimudea* Warren, 1892. MUNROE (1964) considered this process to be primitive and indicative of relationship with Evergestini, but our results indicate that such processes are secondarily derived and homoplastic.

The phallus apodeme is evenly sclerotized. All investigated Pyraustinae (except *Uresiphita*) and the non-euspilomeline clades exhibit this character. In the euspilomeline clades, the sclerotisation of the phallus apodeme is usually reduced to a longitudinal ventral strip stretching the length of the phallus; this character is reversed in several Spilomelinae in the euspilomeline clades.

The signum is rhombiform. This distinctive signum is a traditional character of Pyraustinae s.str. (MUNROE 1976a). It is a single sclerite with two axes, a major and minor one, and has short spines or granules. Apart from Pyraustinae, this signum type is found in modified forms in the non-euspilomeline clades (see below). *Lamprosema victoriae* Dyar, 1923 has a very rhombiform signum, as do other *Lamprosema* spp. and *Gonocausta sabinalis* Dyar, 1914. In other Hydririni and in Udeini, the minor transverse axis is nearly absent, and the whole is elongate and zipper-shaped (*Syllepsis*, *Udea*, *Conchylodes*, *Rhectosemia*) to nearly circular (*Choristostigma*); we refer to

this signum type with the minor transverse axis reduced or absent as “ediacaroid” signum, after the Ediacaran biota from the late Proterozoic Eon, which show similar body shapes that likewise vary from nearly circular to elongate.

The corpus bursae has an appendix bursae. An appendix is present in most investigated Pyraustinae and in most Hydririni as well as in *Conchylodes* and *Sisyraera* (Udeini). This character is absent in all other investigated Spilomelinae except for several Margarini and *Eporidia* (Spilomelini), where it might be a secondary development.

Remarks. Immature stages of Pyraustinae and Spilomelinae have not been studied in a phylogenetic context, and characters consistently separating the two groups are not known (ALLYSON 1981, 1984).

4.2. Spilomelinae Guenée, 1854

Type genus: *Spilomela* Guenée, 1854
= Sylleptinae Swinhoe, 1900

Synapomorphies. 10:1, maxillary palpi minute to obsolete, cannot hypothetically come in contact with each other; 23:0, fornix tympani projecting in ventral direction (unique); 105:0, ductus bursae sclerotisation weak or with granulose texture.

Description. The fornix tympani projects ventrad from the tympanic frame. The retinacular hook (frenulum hook sensu FORBES 1926) is lost. Females have two frenular bristles, while the number of female frenular bristles varies in Pyraustinae.

Systematics. Spilomelinae includes a monophylum that we refer to as “euspilomeline clade” (Greek *eu-* good, true), characterised by two morphological synapomorphies (see below). In contrast, the tribes Hydririni, Udeini, Lineodini and Wurthiini represent a paraphylum, of which Wurthiini is sister to the euspilomeline clade. Because of this paraphyly, we refrain from proposing a name for the group, and refer to them as the non-euspilomeline clades.

4.2.1. Non-euspilomeline clades

The non-euspilomeline clades are characterised by pleiomorphies shared with Pyraustinae: the pleural membranes of the male abdominal segment 8 lack a longitudinal sclerotized strip; the valva costa is straight or concave; the phallus apodeme is evenly sclerotized; and the signum is “ediacaroid”. Several taxa exhibit an appendix bursae.

4.2.2. Hydririni + Lineodini

Synapomorphies. 9:1, intersexual size difference of 3rd labial palpomere, short in male.

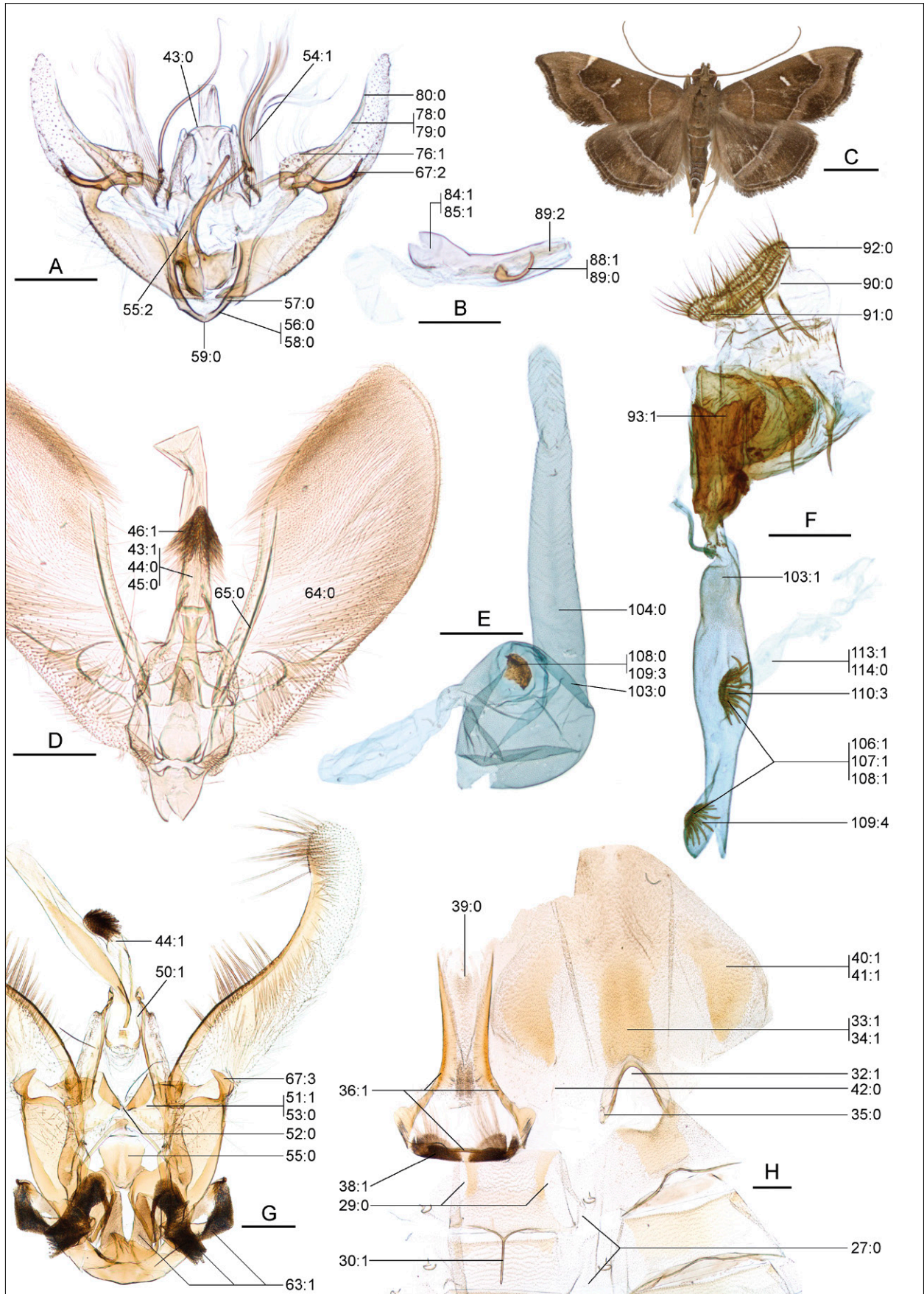


Fig. 3. Hydririni. **A:** male genitalia of *Hydriris ornatalis*. **B:** phallus of *H. ornatalis*. **C:** adult male of *Lamprosema* sp., a representative of the core-*Lamprosema* group. **D:** male genitalia of *Syllepsis marialis*. **E:** anterior part of female genitalia of *Gonocausta* sp. **F:** female genitalia of *H. ornatalis*. **G:** male genitalia of *L. cf. dorisalis*. **H:** posterior abdomen (spread) of *L. cf. dorisalis*. — **Scale bars:** A, B, D–H – 500 µm; C – 5 mm.

4.2.3. Hydririni Minet, 1982 stat.rev.

Type genus: *Hydriris* Meyrick, 1885

Synapomorphies. 113:1, appendix bursae present on corpus bursae (see remarks below). Most Hydririni exhibit the unique apomorphy 38:1, central hair scale patch(es) on anterior edge of male sternite 8 present. In the parsimony trees, only 113:1 is an apomorphy of Hydririni.

Description. The genitalia morphology is heterogeneous: the valvas are slender to broad (*Syllepsis*), and the uncus and gnathos are reduced (*Choristostigma* Warren, 1892, *Hydriris* Meyrick, 1885, *Hyperectis* Meyrick, 1904) to well-developed. *Choristostigma*, *Hydriris*, *Hyperectis*, *Nehydriris* Munroe, 1974a and *Rhectothyris* Warren, 1890 have a dorsolateral tegumen exhibiting lobar processes with a field of long, thin hair-pencils, with a long phallus caecum, and with a single straight or hooked cornutus. The hairs on the anterior edge of male sternite 8 are absent in *Choristostigma*, *Ommatospila* and *Hydriris ornatalis* but present in *H. aonialis*. Some taxa have an appendix bursae emerging laterally from the corpus bursae as in Pyraustinae: Pyraustini (see below). The signum is ediacaroid, circular to elongate with the minor transverse axis varying from broad (*Lamprosema* Hübner, 1823, *Gonocausta* Lederer, 1863) to short, or forming circle(s) of radiating spines (*Choristostigma*, *Hydriris*, *Nehydriris*). *Ommatospila* has a circular ediacaroid signum and an opposing signum consisting of a field of spines, like in *Choristostigma* and *Hydriris*.

Systematics. MINET (1982) established Hydririni in Glaphyriinae and included only *Hydriris* in this tribe. MUNROE (1995) returned *Hydriris* to Spilomelinae. Beside *Hydriris*, MUNROE (1995) placed in his *Hydriris* genus group also *Choristostigma*, *Geshna* Dyar, 1906 and *Nehydriris*.

According to our phylogenetic analysis, *Hydriris* (7 spp.), *Gonocausta* Lederer, 1863 (4 spp.), *Lamprosema* (72 spp.) and *Syllepsis* Poey, 1832 (7 spp.) belong to Hydririni. Furthermore, based on morphological characters we place *Choristostigma* (10 spp.), *Nehydriris* (1 sp.), *Ommatospila* Lederer, 1963 (3 spp.) and *Rhectothyris* (1 sp.) here. According to morphological characters, *Geshna* does not belong to Hydririni, but to Spilomelini (see below).

Hyperectis dioctias Meyrick, 1904, the type species of *Hyperectis*, is depicted in ZIMMERMAN (1958). From there it is evident that this genus is misplaced in Pyraustinae and that the genitalia are close to those of *Hydriris ornatalis* (Duponchel, 1832) and *H. aonialis* (Walker, 1859), and that the genus is not distinguishable from *Hydriris*. We therefore synonymize *Hyperectis* Meyrick, 1904 **syn.n.** with *Hydriris*, and transfer the two species *Hydriris dioctias* Meyrick, 1904 **comb.n.**, and *Hydriris apicalis* (Hampson, 1912) **comb.n.**

Food plants. The known larval food plants are Sapindaceae (*Gonocausta*, *Lamprosema*, *Syllepsis*) and single cases of Fabaceae (*Lamprosema*), Anacardiaceae and Lamiaceae (both *Syllepsis*) (JANZEN & HALLWACHS 2009).

Hydriris ornatalis larvae feed on the leaf undersides of *Ipomoea batatas* (Convolvulaceae) and related plants, later instars skeletonize the leaves (HINCKLEY 1964).

Remarks. The genitalia of *Syllepsis* and *Gonocausta* are highly similar, and a future revision might evaluate these two genera as congeneric. *Lamprosema* contains numerous misplaced Old-World species and needs revision. We verify the congenerity of the taxon used in our analyses with *Lamprosema lunulalis* Hübner, 1823 from Suriname, the type species of the genus.

An appendix bursae is also observed in *Conchylodes* and *Sisyrcera* (Udeini) as well as in Pyraustinae. Under a slightly different basal branching sequence, the appendix bursae could be recovered as a synapomorphy of Pyraustinae and Spilomelinae but lost in most Spilomelinae. However, the best topology in this study indicates separate origins.

Some of the characters by which MINET (1982) placed Hydririni in Glaphyriinae are homoplastic. Spatulate hind wing scales are paralleled with Glaphyriinae, and SOLIS & ADAMSKI (1998) found that such scales are variable even within Glaphyriinae. The spinose signa of *H. ornatalis* resemble the spinose sclerotizations of many Neotropical glaphyriines, but *H. aonialis* has a lenticular ediacaroid signum.

4.2.4. Lineodini Amsel, 1956 stat.rev.

Type genus: *Lineodes* Guenée, 1854

Synapomorphies. 104:0, sclerotisation in ductus bursae absent. Slow optimization only: 8:1, direction of 3rd labial palpomere correct (paralleled in other early-diverging clades; not found in the parsimony trees); 95:1, longitudinal membranous strip in the antrum sclerotisation present. Fast optimization only: 19:0, female with only one frenular bristle (HAYDEN et al. 2013); 106:0, signum absent (not with slow optimization due to position of *Rhectosemia*).

Description. The wings are moderately broad (*Leucinodes*) to narrow and almost pterophorid-like in *Lineodes* Guenée, 1854 and *Atomopteryx* Walsingham, 1891. The sacci tympani are ventrally open (HAYDEN et al. 2013). The valvae are very slender to relatively broad, triangular or paddle-shaped, and the valva apex is rounded to somewhat acute; the costa is straight to concave; the fibula is either slender and emerging from the costa base, shorter and emerging more from the centre of the valva, or entirely absent in *Euleucinodes* Capps, 1948 and *Proleucinodes* Capps, 1948 (see CAPPS 1948). The sacculus is simple or (in *Leucinodes* Guenée, 1854) with a distal sacculus process in close association with the fibula. The posterior phallus is unmodified or with sclerotized appendages (in *Leucinodes*, see MALLY et al. 2015). The posterior ductus bursae, colliculum and antrum in *Leucinodes* and *Neoleucinodes* Capps, 1948 often have a thickened mesocuticle and partial sclerotisation (HAYDEN et al. 2013; MALLY et al. 2015).

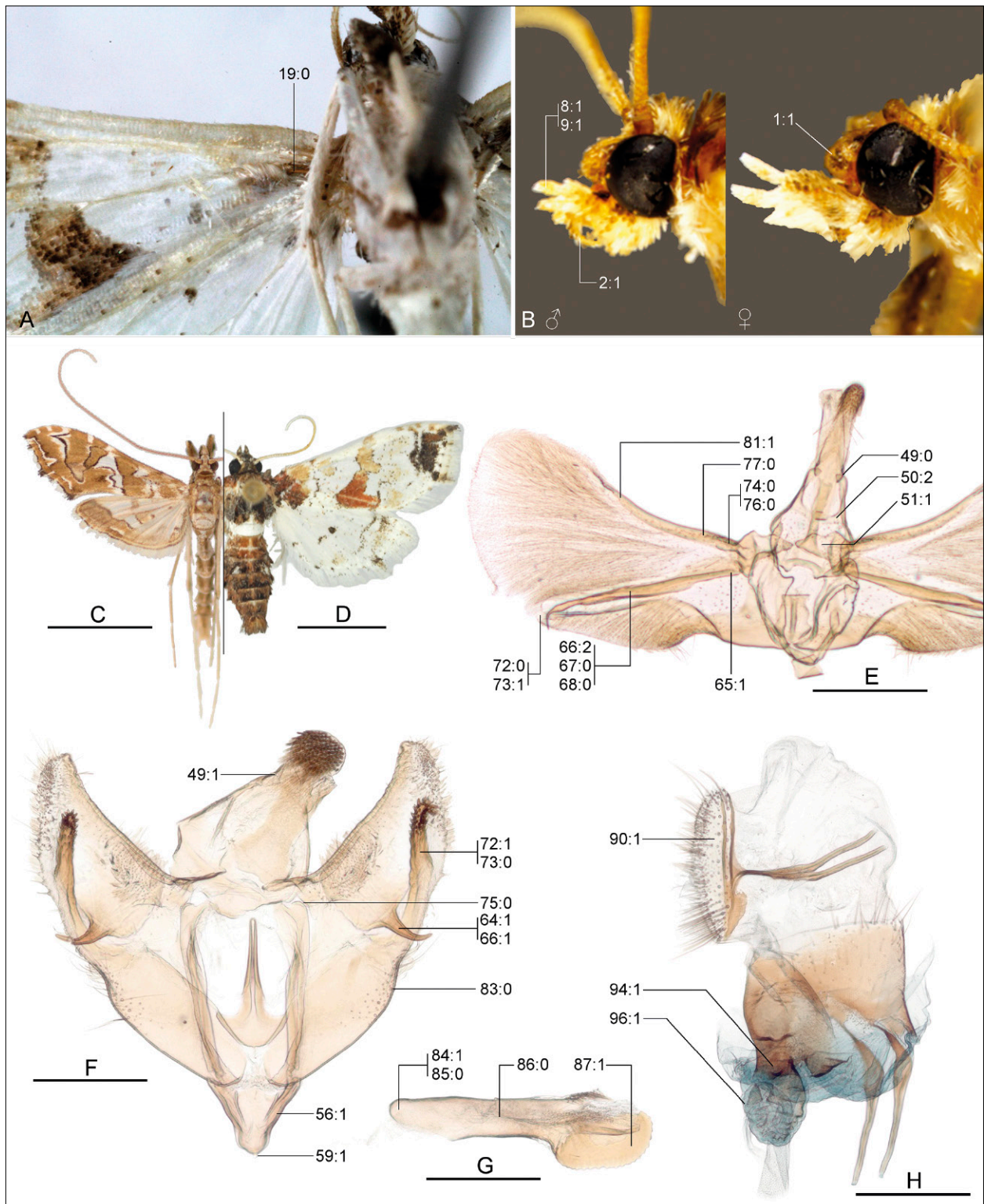


Fig. 4. Lineodini. **A:** ventral view of wings on frenulum bristle of female *Leucinodes orbonalis*. **B:** head of *Le. orbonalis*, male (left) and female (right) (modified from Figs. 11–12 of MALLY et al. 2015). **C:** adult male of *Lineodes vulnifica*. **D:** adult female of *Le. Africensis*. **E:** male genitalia of *Li. vulnifica*. **F:** male genitalia of *Le. africensis*. **G:** phallus of *Le. africensis*. **H:** posterior part of female genitalia of *Le. pseudorbonalis*. — **Scale bars:** C, D – 5 mm; E–H (same scale) – 500 μ m.

Systematics. Lineodini was originally proposed for *Lineodes* (38 spp.) and *Atomopteryx* (10 spp.) (= *Stenoptycha* Zeller, 1863) (AMSEL 1956); it is expanded here to contain *Leucinodes* (20 spp.), *Neoleucinodes* (9 spp.) and *Rhctosemia* Lederer, 1863 (12 spp.) according to

our phylogenetic analysis as well as to contain *Euleucinodes* (1 sp.) and *Proleucinodes* (4 spp.), and to confirm *Atomopteryx* based on morphological characters.

With the exception of *Leucinodes*, all these genera were included by MUNROE (1995) in his *Udea* genus

group, plus *Lamprosema* and *Udea*, which however belong to Hydririni (see above) and Udeini, respectively (see below).

The position of *Rhectosemia* in the phylogram (Fig. 1) diverging after *Lineodes* disagrees with morphology. Females of some examined species of *Rhectosemia* have two frenular bristles, and they have a signum that is usually narrow and elongate. These are plesiomorphies in contrast to the synapomorphies of the other genera: one bristle in both sexes and the loss of the signum.

Food plants. Almost all known larval food plants are Solanaceae, the larvae either boring into the fruits (*Leucinodes*, *Neoleucinodes*) or feeding on leaves and fruit surfaces (*Atomopteryx*, *Lineodes*) (HAYDEN et al. 2013). Several species of this group are pests on solanaceous crops, e.g. *Neoleucinodes elegantalis* on tomato (*Solanum lycopersicum*), and *Leucinodes* spp. on eggplant (*Solanum melongena*) (HAYDEN et al. 2013; MALLY et al. 2015). JANZEN & HALLWACHS (2009) report two *Neoleucinodes* species from *Heliconia* spp. (Heliconiaceae).

Remarks. Character 95:1, the presence of a longitudinal membranous strip in the antrum sclerotisation, is also present in Hydririni: *Gonocausta*, *Syllepis*. The reduction to one frenular bristle in females is also present in members of the *Udea itysalis* and *U. alpinalis* species groups (sensu MALLY & NUSS 2011) (Udeini), in *Metasia supbandalis* (Steniini), *Diasemiopsis ramburialis* (Duponchel, 1833) (Diasemiini) and *Niphopyralis* (Wurthiini). We find Lineodini and Udeini (see below) to be sister groups in the Bayesian analyses. However, they do not share any synapomorphies with each other, also not under slow optimization. Lineodini and Hydririni are sister-groups in parsimony analysis, sharing 9:1, 68:0, 99:0, and 109:3.

4.2.5. Udeini Mally, Hayden, Neinhuis, Jordal & Nuss trib.n.

Type genus: *Udea* Guenée, 1845 (in Duponchel)

Synapomorphies. 55:1, depth of gap/split of juxta being 10–60% of dorsoventral length of juxta; 99:1, strongly sclerotised colliculum anterior of the antrum and posterior of the attachment of the ductus seminalis present (not found with parsimony); 109:2, signum elongate rhombical to ovate, longer than wide (found with parsimony).

Description. The uncus varies from uncapitate in the *Udea* group (*Deana* Butler, 1879, *Mnesictena* Meyrick, 1884, *Tanaophysa* Warren, 1892, *Udea* Guenée in Duponchel, 1845, *Udeoides* Maes, 2006) to conical (*Conchylodes* Guenée, 1854), reduced to triangle in *Sisyracera* Möscher, 1890 and *Ercta* Walker, 1859, and reduced to a transverse arching band in *Cheverella* Landry, 2011. The uncus dorsally has bifurcate chaetae in the *Udea* group, but the chaetae are simple and located dorsally and ventrally in *Conchylodes*, *Sisyracera* and *Cheverella*, and lost in *Ercta*. The costa of the valva is slightly concave; the ventral sacculus edge is parallel to the costa

(inflated in *Cheverella*), the valva apical of the sacculus tapers towards a rounded apex. The female genitalia have an elongate signum that is rhombical, lanceolate or ediacaroid in shape. In all *Udea* species groups sensu MALLY & NUSS (2011) except the *U. ferrugalis* species group, an accessory signum in the conjunction of ductus- and corpus bursae is present. *Conchylodes*, *Ercta* and *Sisyracera* have a membranous appendix bursae, attached anteriorly in *Conchylodes* and *Ercta* and posteriorly in *Sisyracera*. The antrum is strongly sclerotized, weakly in *Cheverella*. **Systematics.** MINET (1982) associated *Udea* (214 spp.) with Pyraustinae, a decision followed by LERAUT (1997, 2012). In contrast, our phylogenetic analysis supports *Udea* as belonging to Spilomelinae, forming a monophylum together with *Udeoides* (5 spp.) and *Conchylodes* (21 spp.); furthermore, based on morphological characters, we place *Cheverella* (1 sp.), *Deana* (1 sp.), *Ercta* (7 spp.), *Mnesictena* Meyrick, 1884 (7 spp.), *Sisyracera* (3 spp.) and *Tanaophysa* (2 spp.) in this monophylum.

Udeini was proposed by LERAUT (1997) in Pyraustinae, but without a description to differentiate the taxon, a requirement by the International Code of Zoological Nomenclature (RIDE et al. 1999, International Commission on Zoological Nomenclature: article 13.1) for names published after 1930. Therefore, the family-group name Udeini was not available prior to our proposal and formal description.

The genitalia of *Azochis graphialis* Schaus, 1912, type species of *Nonazochis* Amsel, 1956, resemble those of *C. diphteralis* (Geyer, 1826), not justifying the separation of the two genera. We therefore synonymize the monotypic *Nonazochis* Amsel, 1956 **syn.n.** with *Conchylodes* Guenée, 1854, and transfer *Conchylodes graphialis* (Schaus, 1912) **comb.n.** *Conchylodes octonalis* (Zeller, 1873) **comb.n.** is transferred from *Lygropia* Lederer, 1863 based on characters in common with *Conchylodes*: upward-curved transtilla arms, white wings with spots (orange in *C. octonalis*, black in congeners), corpus bursae with anterior appendix bursae, larvae feeding on Boraginaceae (POWELL & OPLER 2009).

Food plants. The food plant spectrum is broad in Udeini, and several *Udea* species such as *U. ferrugalis*, *U. lutealis*, *U. olivalis*, *U. prunalis* and *U. rubigalis* are pronouncedly polyphagous (WEIGEL et al. 1925; LHOMME 1935). *Mnesictena flavidalis* is recorded from *Muehlenbeckia* (Polygonaceae), *M. notata* from *Urtica* and *Australina* (Urticaceae) (ROBINSON et al. 2010). The larvae of *Conchylodes ovulalis* (Guenée, 1854) are recorded to feed on *Platanus* (Platanaceae) (SOLIS 2008), other *Conchylodes* species feed on Asteraceae, Cordiaceae, Malvaceae, Boraginaceae and Annonaceae (JANZEN & HALLWACHS 2009). *Sisyracera* and *Cheverella* are on Boraginaceae (DYAR 1917; WOLCOTT 1950; LANDRY et al. 2011).

Remarks. The genus *Mnesictena* was synonymised with *Udea* by MUNROE (1983), followed by SHAFFER et al. (1996). The type species of both genera were studied by MALLY & NUSS (2011) and found to be not congeneric, supporting DUGDALE'S (1988) view of keeping them as separate groups, but the authors did not reinstate *Mne-*

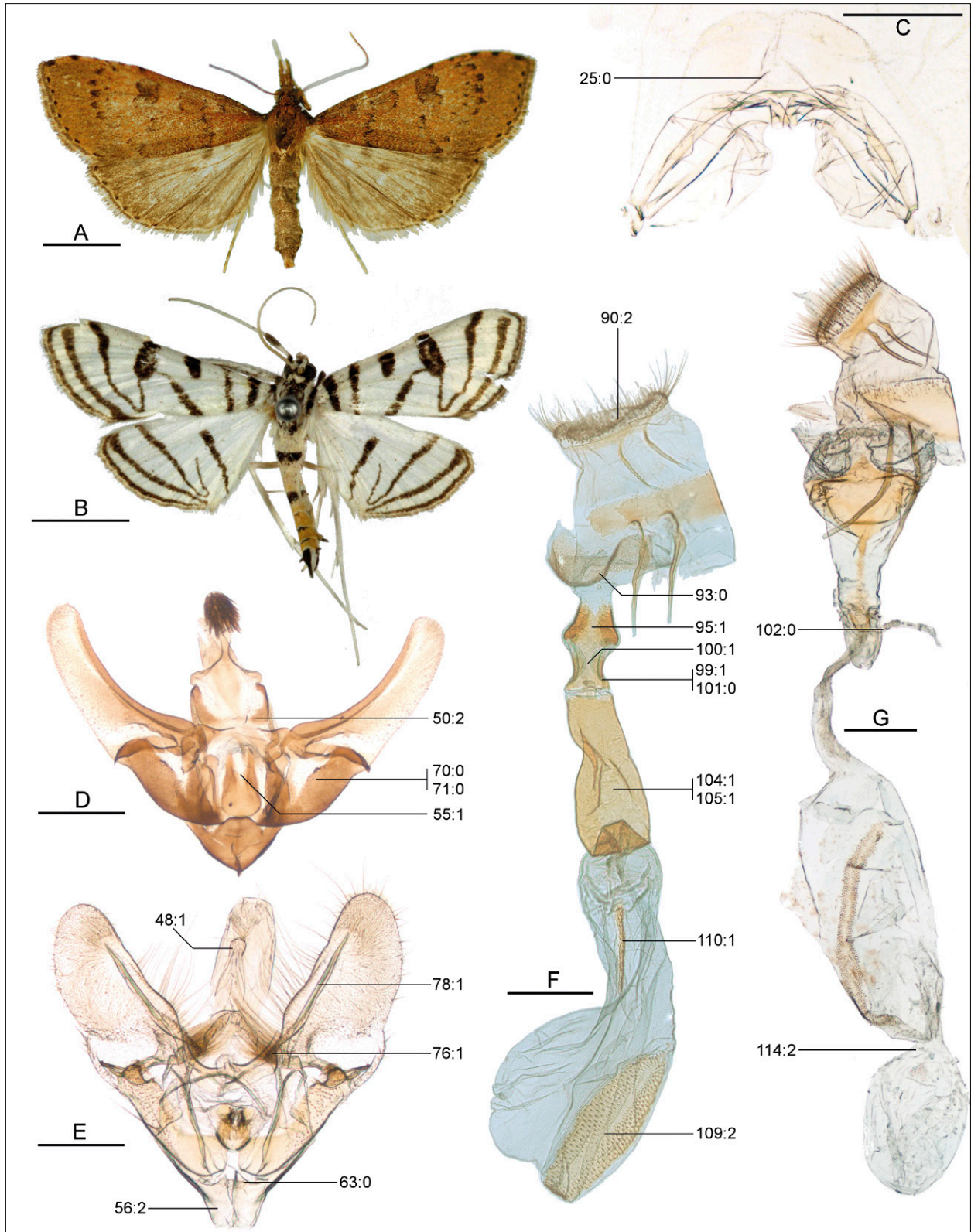


Fig. 5. Udeini. **A:** adult female of *Udea maderensis*. **B:** adult male of *Conchylodes ovulalis*. **C:** tympanal organs of male *Udeoides muscosalis*. **D:** male genitalia of *U. rhododendronalis*, phallus omitted. **E:** male genitalia of *C. zebra*, phallus omitted. **F:** female genitalia of *U. rhododendronalis*. **G:** female genitalia of *C. zebra*. — **Scale bars:** A, B – 5 mm; C–G – 500 µm.

sictena as bona genus. We leave this issue to a thorough future study of the relationships within Udeini.

Sisyrcera and *Cheverella* are problematic Neotropical genera. MUNROE (1995) left *Sisyrcera* unplaced, and

the relationship of *Cheverella*, a Galápagos endemic, prompted lengthy discussion in LANDRY et al. (2011), who decided that the *Hydriris* or *Siga* groups were the most likely places. Their relationship with *Conchylodes*

seems more plausible to us. The larvae of all three genera feed on Boraginaceae. The moths are white with black spotted lines (dense reticulate pattern in *Sisyracera*) and have ascending labial palpi. The valvae are attenuate, and the uncus is reduced or lost, bearing only fine chaetae. *Sisyracera* shares with *Conchylodes* an appendix bursae. The homoplasies to be accounted for are the change of the signum in *Sisyracera* and *Cheverella* (signum absent in the former, a small thorn in the latter) and loss of the valva fibula in *Sisyracera*. The robust valvae and inflated sacculus of *Cheverella* can be explained as part of the internally feeding larval syndrome, which is paralleled in the *Beebea* group (Asciodini) and among the internally feeding Margaroniini that had been classified in MUNROE's (1995) polyphyletic *Polygrammodes* group.

Microphysetica Hampson, 1917 belongs to Hydririni or Udeini. Females have a rhombiform signum and appendix bursae but not the tubular colliculum of Udeini. Males have sternite 8 like *Udea* and *Choristostigma*: centrally membranous but without a distinctive anterior scale field, and the juxta is mesally weak but not split into distinct arms.

4.2.6. Wurthiini + euspilomeline clades

Synapomorphies. 109:0, shape of anterior-most signum: circular, spinose, or invaginated as a spine, without obvious axes. 103:1, indistinct division of the ductus bursae and corpus bursae (only found with parsimony).

4.2.7. Wurthiini Roepke, 1916 stat.rev.

Type genus: *Wurthia* Roepke, 1916 = *Niphopyralis* Hampson, 1893

Synapomorphies. 55:2, depth of gap/split of juxta ranging from more than 60% of dorsoventral length of juxta to complete division into two juxta arms; 66:1, general shape of fibula elongate, length at least twice the width, apically rounded (may be curved). Slow optimization only: 24:0, venulae secundae absent.

Description. The male genitalia have a broad triangular, ventrally directed fibula; the mesal sides of the sacculi are produced as two strongly sclerotized arms which dorsally end in a broad, spinulose tip or a slim, needle-shaped projection (not split in *Mimetebulea* Munroe & Mutuura, 1968); the mediodorsal sacculus has a medially directed process (absent in *Apilocrocis* Amsel, 1956 and *Diaphantania* Möschler, 1890). In the female genitalia, the lamella antevaginalis forms a strongly sclerotised antrum frame; the signum is rounded, small (*Aristebulea* Munroe & Mutuura, 1968, *Pseudebulea* Butler, 1881) to relatively large (*Apilocrocis*, *Diaphantania*), and absent in *Mimetebulea* and *Niphopyralis*. Under fast optimization, the loss of venulae secundae (24:0) is shared with various Hydririni, Lineodini and Udeini.

Systematics. Based on our phylogenetic results, we place *Apilocrocis* (11 spp.), *Aristebulea* (2 spp.) and

Niphopyralis (= *Wurthia*) (8 spp.) in Wurthiini. Furthermore, based on morphological investigation, we place *Diaphantania* (3 spp.), *Mimetebulea* (1 sp.) and *Pseudebulea* (4 spp.) in this tribe. This group can be considered as an enlargement of MUNROE's (1995) *Diaphantania* genus group.

Food plants. Food plants are not known for most Wurthiini. The larvae of *Apilocrocis glaucosia* (Hampson, 1912) feed on *Celtis iguanea* (Ulmaceae) (JANZEN & HALLWACHS 2009). *Niphopyralis* larvae live as brood parasites in nests of ants of the genera *Oecophylla* Smith, 1860 and *Polyrhachis* Smith, 1857 and feed on eggs, larvae, and pupae of their hosts (ROEPKE 1916; KEMNER 1923).

Remarks. The placement of *Niphopyralis* in Spilomelinae was a surprising discovery of REGIER et al. (2012), but its particular association with *Aristebulea* and *Apilocrocis* in our analysis allows a radical but satisfying reinterpretation of the aberrant male genitalia (Fig. 6E). The genitalia have been previously illustrated in MAES (1998a), who interpreted the gnathos as consisting of two separate, articulated arms. This condition occurs in other lepidopteran superfamilies (e.g. Papilionoidea), but it is not common in Pyraloidea (to our knowledge, occurring elsewhere only in Heliothelinae). In our interpretation, these two separate processes are the distal halves of the true valvae. They are small and displaced dorsad, but they have the same shape as the valvae in other wurthiines: distally attenuate with a triangular swelling at the base of the costa (like that in *Diaphantania impulsalis* (Herrich-Schäffer, 1871) and *Aristebulea principis*). The valva of other Wurthiini genera is divided by a membranous cleft between the sacculus and distal half; this cleft reaches the outer margin in *Apilocrocis* and nearly so in the other genera. We interpret the sclerotised structures flanking the juxta in *Niphopyralis* as the valva sacculi, each with a median process similar to those in *Aristebulea*, *Mimetebulea*, *Pseudebulea*, *Diaphantania* and *Apilocrocis*. It is not entirely clear whether the elongate processes in the ventral region of the genitalic capsule arise from the sacculi or from the juxta (as coded in the character list 55:2). We further interpret the pair of weakly setose structures atop the tegumen to be the uncus in normal position, even though the other members of the tribe have a single-headed uncus with bifid chaetae. The gnathos is absent.

4.2.8. Euspilomeline clades

Synapomorphies. 86:1, reduction of phallus apodeme to a ventral, longitudinally sclerotized strip along the manica (the rest of the apodeme being more or less membranous). In addition, the parsimony trees add many more synapomorphies: 32:1, male tergite 8 with anterior edge emarginate; 60:1, partly sclerotized hair pencils present on anterior edge of vinculum-tegumen connection; 78:2, valva with convex costa; 84:0, phallus without coecum; 95:1, antrum with longitudinal membranous strip; and 99:0, a strongly sclerotised colliculum between antrum and ductus seminalis absent.

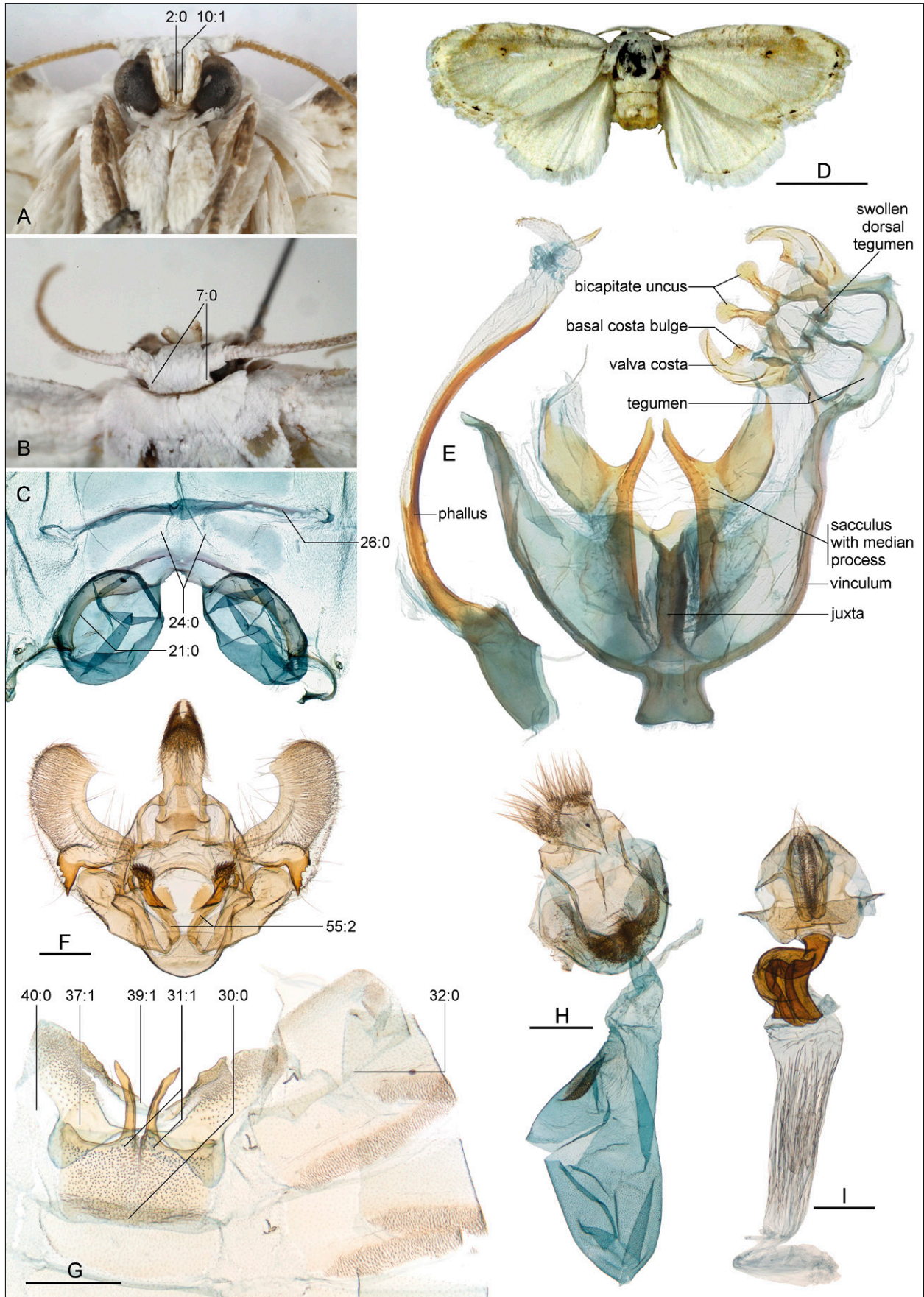


Fig. 6. Wurthiini. **A:** head of female *Niphopyralis* sp., ventral view. **B:** head of female *Niphopyralis* sp., dorsal view. **C:** tympanal organs of male *Niphopyralis* sp. **D:** adult female of *Niphopyralis* sp., posterior abdomen removed. **E:** male genitalia of *Niphopyralis* sp. **F:** male genitalia of *Apilocrocis novateutonialis*, phallus omitted. **G:** posterior abdomen of male *N. chionesis*. **H:** female genitalia of *Diaphantania impulsalis*. **I:** female genitalia of *N. chionesis*. — **Scale bars:** D – 5 mm; F–I – 500 µm.

In this monophylum, the postmedial (PM) lines of both wings are usually more jagged than in Pyraustinae and among the early-diverging spilomeline clades. Especially the hindwing PM line is usually boldly marked and projects distad on the M and CuA veins, whereas in Pyraustinae, the hindwing PM line tends to be faint and a smooth arc. In Pyraustinae, only very rarely does the forewing PM line jut basad on the anal fold or is drawn costad toward the discal spot (but see *Pseudopyrausta*). In general, the hindwing PM line is similar to the forewing PM line, so the combination of boldness and jaggedness distinguishes it. Although the jagged shape is common in the euspilomeline clade, it is also present in *Aristebulea* and *Pseudebulea* (Wurthiini).

4.2.9. Agrotterini Acloque, 1897 stat.rev.

Type genus: *Agrotera* Schrank, 1802

Synapomorphies. 47:0, structure of uncus head chaetae simple, not split; 58:1, ratio between saccus length and sacculus breadth > 1 (elongate saccus, often with bulbous apex). The parsimony trees add 8:0, sclerotization on vesica absent; and 44:0, conical (non-capitate) uncus. Slow optimization only: 8:0, 3rd labial palpomere directed dorsally.

Description. The labial palps are upturned. The uncus has a broad base, usually truncate to variously reduced, at the extreme being a squat, transversely rectangular square. The gnathos has a well-developed medial process in some genera (see e.g. LERAUT 2005b: figs. 14–17). The valvae are more or less rectangular, with costal and ventral margins parallel, or slightly ovate; the saccus is notably elongate, often distally bulbous. The female genitalia have round and granular signa, single or double, rarely extended as horns (*Framinghamia* Strand, 1920, *Phostria oajacalis* (Walker, 1866)).

The upturned 3rd labial palpomere is a synapomorphy for this tribe in the DELTRAN analysis, but it is shared with various other tribes, such as Asciodini, the *Siga* group of Spilomelini, *Spoladea*, and some Nomophilini and Steniini. The presence of simple, unsplit uncus chaetae is paralleled in some Pyraustinae, Margaroniini and Udeini, and in *Nomophila* Hübner, 1825. In many genera, the tegumen mesally extends anteriorly, like an extended roof. This unique structure may characterize a clade in Agrotterini. In some genera, the papillae anales face ventrad at a right angle to the axis of the ovipositor; this state is paralleled in some Margaroniini.

Systematics. According to our phylogenetic results, Agrotterini comprises *Aetholix* Lederer, 1863 (4 spp.), *Agrotera* (27 spp.), *Haritalodes* Warren, 1890 (11 spp.), *Neonanthus* Yamanaka & Kirpichnikova, 1993 (8 spp.), *Patania* Moore, 1888 (= *Pleuroptya* Meyrick, 1890) (41 spp.), *Phostria* Hübner, 1819 (87 spp.) and ‘*Pycnarmon*’ *pantherata* Butler, 1878 which is not congeneric with *P. jaguaralis* (Guenée, 1854), the type species of the polyphyletic genus *Pycnarmon* Lederer, 1863 (59 spp.).

The placement of *Pycnarmon* among the euspilomeline clades is still uncertain. Based on morphological characteristics, we further place the following genera in Agrotterini: *Aiyura* Munroe, 1974a (2 spp.), *Bocchoropsis* Amsel, 1956 (2 spp.), *Chalcidoptera* Butler, 1887 (15 spp.), *Chilochromopsis* Munroe, 1964 (1 sp.), *Coenostolopsis* Munroe, 1960 (3 spp.), *Diastictis* Hübner, 1818 (12 spp.), *Framinghamia* (2 spp.), *Glaucopteryx* Maes, 2008 (1 sp.), *Goliathodes* Munroe, 1974a (1 sp.), *Gypodes* Munroe, 1976 (1 sp.), *Lygropia* Lederer, 1863 (68 spp.), *Lypotigris* Hübner, 1825 (1 sp.), *Micromartinia* Amsel, 1957 (1 sp.), *Microthyris* Lederer, 1863 (7 spp.), *Nagiella* Munroe, 1976 (4 spp.), *Nosophora* Lederer, 1863 (26 spp.), *Notarcha* Meyrick, 1884 (18 spp.), *Pantographa* Lederer, 1863 (9 spp.), *Phaedropsis* Warren, 1890 (24 spp.), *Phryganodes* Guenée, 1854 (26 spp.), *Tetracona* Meyrick, 1884 (2 spp.) and *Ulopeza* Zeller, 1852 (16 spp.).

Nagiella has been considered either a valid genus (MUNROE 1976b; KIRTI & SODHI 2001; ROSE 2001; ULLAH et al. 2017) or a synonym of *Pleuroptya* (= *Patania*) (INOUE 1982; LERAUT 1997). We concur with MUNROE’s (1976b) separation of *Nagiella* from *Patania*. ULLAH et al. (2017) describe a fourth species in this genus. For the generic diagnosis see MUNROE (1976b).

This diverse, globally distributed tribe generally corresponds to MUNROE’s (1995) *Syllepte* group. We conjecture that he placed the *Phaedropsis* and *Syllepte* groups first in his checklist because some have a gnathos in the traditional sense, i.e. with a well-developed medial process, which would seem to be the primitive state. In our analysis, this process is secondarily derived, since none of the non-euspilomeline clades have it (the gnathos being a simple, transverse band). This process is also present in two genera of uncertain placement: *Mimudea* Warren, 1892, and *Deuterophysa* Warren, 1889.

Species of *Phaedropsis* are hardly separable from the type species of *Lygropia*, *Asopia unicoloralis* Guenée, 1854. *Lygropia* and *Phostria* are major dustbin genera of this tribe, holding many explicitly misplaced species (MUNROE 1995).

In many genera, especially in the Old World, the forewing costa bears a light-colored triangular spot. This is the “*Nosophora-Chalcidoptera*” group referred to by MUNROE (1974a). In some taxa, the spot is so strongly developed that it extends to the tornus and fills most of the forewing (e.g. some misplaced ‘*Leucinodes*’ species, ‘*Syllepte*’ *dottoalis* Schaus, 1927).

Food plants. Larvae are generally leaf-tiers. Larvae of *Patania silicalis* and *P. sabinusalis* have been reared on Urticaceae (KIMBALL 1965; MILLER et al. 2007; SOLIS 2008), *P. silicalis* furthermore on *Polygonum* (Polygonaceae), *Ipomoea* and *Merremia* (Convolvulaceae), *Rivina* (Petiveriaceae) and *Bougainvillea* (Nyctaginaceae) (HEPPNER & HABECK 1976; BENDICHO-LOPEZ 1998); *P. ruralis* feeds on *Urtica* (Urticaceae), *Humulus* (Cannabaceae), *Chenopodium*, *Atriplex* (Amaranthaceae), *Filipendula* (Rosaceae) and *Ribes* (Grossulariaceae) (LHOMME 1935); Central American *Patania* species (as *Pleuroptya*) are recorded from Acanthaceae, Rubiaceae

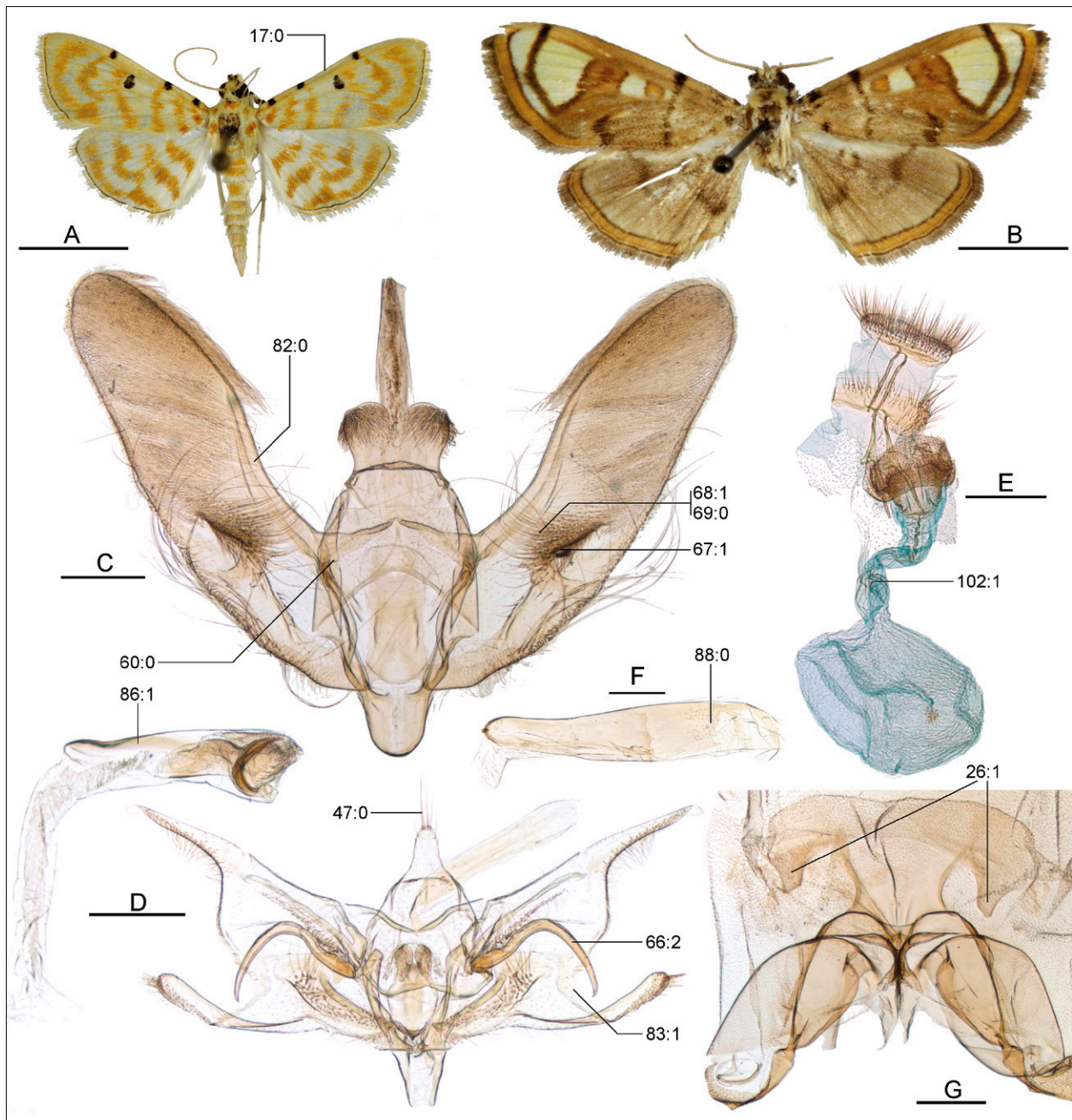


Fig. 7. Agrototerini. **A:** adult male of *Notarcha* cf. *quaternalis*. **B:** adult male of *Pycnarmon pantherata*, abdomen removed. **C:** male genitalia of *P. pantherata*, phallus omitted. **D:** male genitalia of *Agrotera nemoralis*. **E:** female genitalia of *A. nemoralis*. **F:** phallus of *Patania ruralis*. **G:** tympanal organs of male *Phostria temira*. — **Scale bars:** A, B – 5 mm; C–G – 500 μ m.

and Urticaceae (JANZEN & HALLWACHS 2009). Known food plants for *Phostria* larvae are mainly Convolvulaceae, Malvaceae and Rubiaceae (JANZEN & HALLWACHS 2009). *Agrotera nemoralis* feeds on *Carpinus*, *Betula*, *Corylus* (Betulaceae), *Castanea* and *Quercus* (Fagaceae) (MELZER & NUSS 2009), while two Australasian *Agrotera* species are reported to feed on *Syzygium* spp. (Myrtaceae) (MILLER et al. 2007). *Haritalodes* is recorded from Malvaceae, Amaranthaceae and Moraceae (GHESQUIÈRE 1942; MILLER et al. 2007); *Diastictis* on Asteraceae (POWELL & OPLER 2009); *Framinghamia* on *Salix* (Salicaceae); *Phaedropsis* on Polygonaceae and Malvaceae (JANZEN & HALLWACHS 2009).

Significant host associations are with Malvaceae s.l. (*Pantographa*, *Haritalodes*, *Phaedropsis*), Convolvulaceae (*Phostria tedeia*-group, *Lygropia tripunctata*-group, *Microthyris* incl. *Cyclocena*; see HAYDEN & DICKEL 2014) and Rubiaceae ('*Pilocrocis*' *xanthozonalis*-group). **Remarks.** The mimetic '*Pilocrocis*' *xanthozonalis*-group belongs here, and its species are misplaced in the Herpetogrammatini genus *Pilocrocis*.

The Australian species of *Agrotera* have recently been revised by CHEN et al. (2017), who removed *Leucinodella* Strand, 1918, *Nistra* Walker, 1859, *Sagariphora* Meyrick, 1894 and *Tetracona* from synonymy with *Agrotera*; the former three genera can currently not be placed in any

of the proposed tribes, but *Tetracona* is placed in Agrotini, close to *Aetholis* (CHEN et al. 2017).

4.2.10. Margaroniini Swinhoe & Cotes, 1889 stat.rev.

Type genus: *Margaronia* Hübner, 1825
= Dichocrociinae Swinhoe, 1900: 478
= Hapaliadae Swinhoe, 1890: 268
= Margarodidae Guenée, 1854: 286

Synapomorphies. 33:1, sclerotization of male tergite 8: heterogenous, i.e. with distinct sclerotization pattern; 72:1, extension (process in some cases) at dorsodistal sacculus present (not found with parsimony); 75:1, joint of basal valva costa (with vinculum) extended into an elongate, rod-shaped process present; 103:0, demarcation between corpus bursae and ductus bursae distinct, with a narrow anterior ductus transforming into a wide corpus bursae (only found with parsimony); 108:1, two signa. Slow optimization only: 40:1, sclerite on each pleural membrane of male segment 8 present (not found with parsimony); 95:1, longitudinal membranous strip in the antrum sclerotisation present (not found with parsimony).

Description. The adult moths are mostly medium-sized to large. Many genera have the scape and pedicel of the male antenna modified. Males of many genera have a large, black tuft of fine, hairlike sex-scales on A8. The tegumen is often spacious in sagittal dimension (hampering the planar mounting of the genitalia on a glass slide). The uncus is conical or uncapitate and long-necked (bifurcate in *Cydalima perspectalis*), with simple or bifurcate chaetae, often with both, or without chaetae. The anterior tegumen-vinculum connection usually has an attached pad of hairpencils, the pad structure ranging from a simple sclerotized base with one kind of simple hairs to several membrane-connected sclerites with several differently structured hairs. The valva is commonly broad and oval, with one fibula about halfway to the apex. The sacculus is comma-shaped, broadest at the anteroventral valva base, arching and tapering distad (broadening in *Liopasia* and *Obtusipalpis*), its distal apex usually ending in a ridge or sclerotized process in close spatial association with the distal fibula. The vesica of the phallus has a granulated area and/or one to several bodkin-shaped cornuti. The corpus bursae often has a pair of circular signa, which can be flat or invaginated to form spikes, or signum absent. The ductus bursae is granular in many genera (e.g. *Cydalima*).

The heterogenous sclerotization of male tergite 8 (33:0) may be shared also with Asciodini, *Spoladea*, Trichaeini, and some Steniini.

The base of the valva costa simple, not rod-shaped, in several genera: the stout-bodied *Liopasia* Möschler, 1882, *Megastes* Guenée, 1854 and *Obtusipalpis* Hampson, 1896, and in '*Glyphodes*' *rubrocinctalis* (Guenée, 1854) and *Zebronia phenice* (Stoll, 1782). The rod-shaped state is paralleled in Hymeniini, *Arthromastix lauralis* (Walker,

1859), *Samea ecclesialis* Guenée, 1854 and *Prophantis xanthomerialis* Hampson, 1918 **comb.n.**)

Systematics. Based on our phylogenetic findings we associate these taxa with Margaroniini: *Agathodes* Guenée, 1854 (16 spp.), *Agrioglypta* Meyrick, 1932 (11 spp.), *Antigastra* Lederer, 1863 (2 spp.), *Asturodes* Amsel, 1956 (1 sp.), *Azochis* Walker, 1859 (16 spp.), *Botyodes* Guenée, 1854 (10 spp.), *Cadarena* Moore, 1886 (1 sp.), *Conogethes pandamalis* (Walker, 1859) **comb.n.**, *Cydalima* Lederer, 1863 (9 spp.), *Diaphania* Hübner, 1818 (95 spp.), *Dichocrocis* cf. *zebralis* (Moore, 1867), *Filodes* Guenée, 1854 (16 spp.), *Ghesquierellana* Berger, 1955 (5 spp.), *Glyphodes* Guenée, 1854 (156 spp.), *Hodebertia* Leraut, 2003 (1 sp.), *Liopasia* (15 spp.), *Leucochroma* Guenée, 1854 (6 spp.), *Maruca* Walker, 1859 (4 spp.), *Megastes* (16 spp.), '*Nacoleia*' *insolitalis* (Walker, 1862), *Obtusipalpis* (6 spp.), *Omiodes* Guenée, 1854 (98 spp.), *Palpita* Hübner, 1808 (162 spp.), *Prenesta* Snellen, 1875 (18 spp.), *Pygospila* Guenée, 1854 (10 spp.), *Rhimphalea* Lederer, 1863 (12 spp.), *Terastia* Guenée, 1854 (7 spp.), *Zebronia* Hübner, 1821 (6 spp.). '*Nacoleia*' *insolitalis* is misplaced in *Nacoleia* Walker, 1859, and its correct generic affiliation remains uncertain. '*Dichocrocis*' *pandamalis* is misplaced in *Dichocrocis*; its correct placement is in *Conogethes* Meyrick, 1884, where it is transferred here (see above). *Dichocrocis* Lederer, 1863 (53 spp.) is considered polyphyletic and needs revision; maculation and male genitalia of the type species *D. frenatalis* Lederer, 1863 indicate a placement among the euspilomeline groups, probably near or in Steniini, but this needs further investigation.

'*Glyphodes*' *rubrocinctalis* is misplaced in *Glyphodes*; in our phylogenetic analysis (Fig. 1) it is subordinate in *Prenesta*. The male genitalia are smaller than those of the type species of *Prenesta*, *P. scyllalis*, but they are similar in structure, and the moths share distinctive red and yellow maculation. We therefore transfer *Prenesta rubrocinctalis* (Guenée, 1854) **comb.n.** from *Glyphodes*.

Furthermore, we assign the following taxa based on morphological investigation: *Alytana* J.C. Shaffer & Munroe, 2007 (2 sp.), *Anarmodia* Lederer, 1863 (24 spp.), *Aphytoceros* Meyrick, 1884 (3 spp.), *Arthroschista* Hampson, 1893 (2 spp.), *Caprinia* Walker, 1859 (11 spp.), *Chabulina* J.C. Shaffer, & Munroe, 2007 (2 spp.), *Charitoprepes* Warren, 1896 (2 sp.), *Chrysophyllis* Meyrick, 1934 (1 sp.), *Chrysothyridia* Munroe, 1967 (2 spp.), *Cirrhochrista* Lederer, 1863 (38 spp.), *Colomychus* Munroe, 1956 (2 spp.), *Compacta* Amsel, 1956 (4 spp.), *Condylorrhiza* Lederer, 1863 (4 spp.), *Conogethes* (16 spp.), *Didymostoma* Warren, 1892 (2 spp.), *Dysallacta* Lederer, 1863 (3 spp.), *Endocrossis* Meyrick, 1889 (4 spp.), *Eusabena* Snellen, 1901 (4 spp.), *Glyphodella* J.C. Shaffer, & Munroe, 2007 (3 spp.), *Hedyleptopsis* Munroe, 1960 (1 sp.), *Heterocnephes* Lederer, 1863 (4 spp.), *Hoterodes* Guenée, 1854 (5 spp.), *Loxmaionia* Schaus, 1913 (1 sp.), *Marwitzia* Gaede, 1917 (3 spp.), *Megaphysa* Guenée, 1854 (1 sp.), *Meroctena* Lederer, 1863 (4 spp.), *Nolckenia* Snellen, 1875 (1 sp.), *Omphisa* Moore, 1886 (10 spp.), *Pachynoa* Lederer, 1863 (12 spp.), *Paro-*

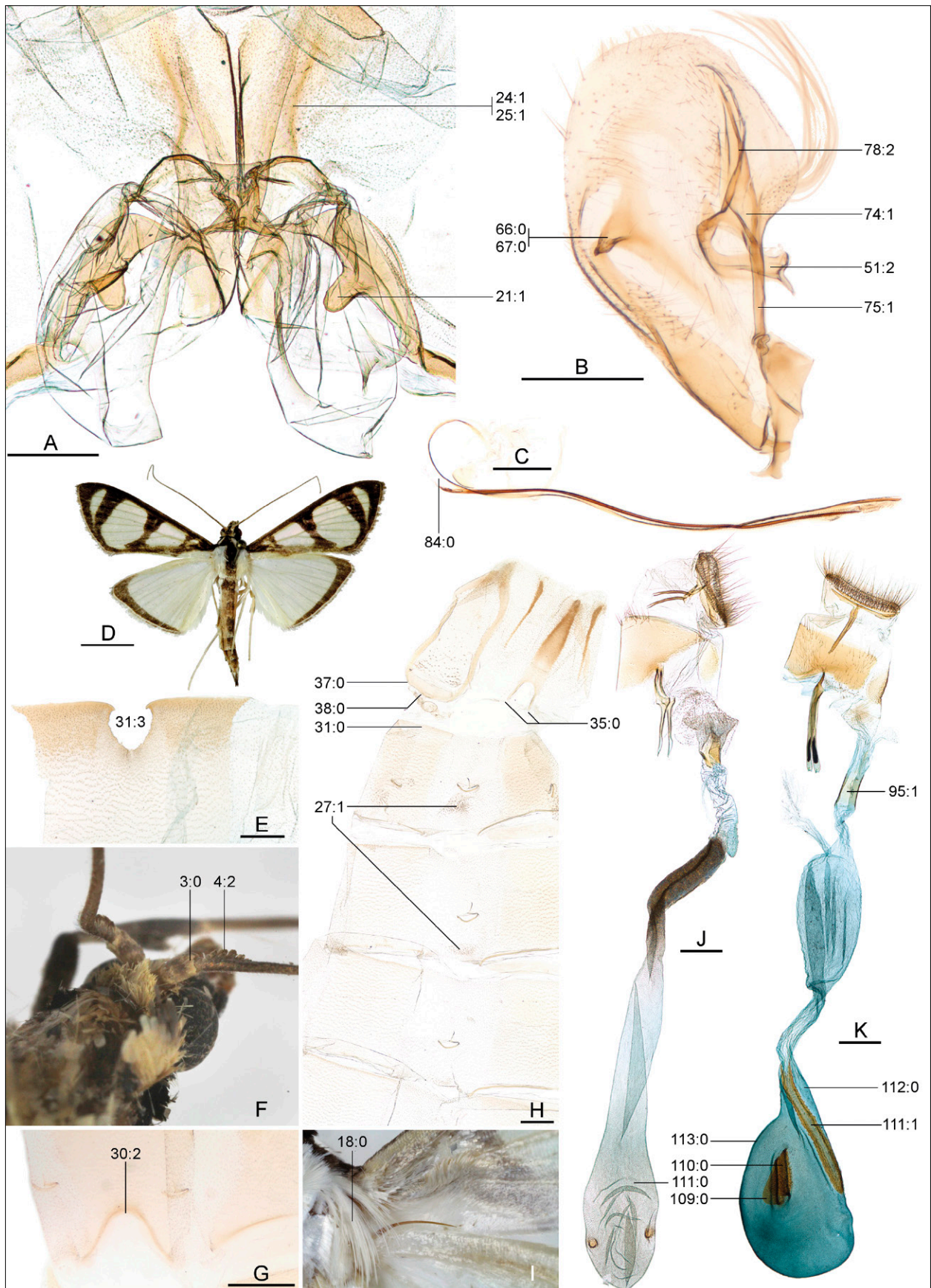


Fig. 8. Margaroniini. **A:** tympanal organs of female *Cydalima perspectalis*. **B:** left valva of male genitalia of *Conogethes pandamalis*. **C:** phallus of male *C. pandamalis*. **D:** male adult of *Glyphodes prothymalis*. **E:** 7th sternite of male *Azochis* cf. *rufidiscalis*. **F:** head of male *Azochis* sp. **G:** 7th abdominal sternite of male *Rhimphalea* cf. *astrigalis*. **H:** dissected abdomen of male *Terastia meticulosalis*. **I:** ventral wing side of male *G. prothymalis* with frenulum bristle. **J:** female genitalia of *C. perspectalis*. **K:** female genitalia of *Omiodes continuatalis*. — **Scale bars:** A–C, E, G, H, J, K – 500 µm; D – 5 mm.

tis Hübner, 1831 (37 spp.), *Poliobotys* J.C. Shaffer & Munroe, 2007 (1 sp.), *Polygrammodes* Guenée, 1854 (78 spp.), *Polygrammopsis* Munroe, 1960 (1 sp.), *Radessa* Munroe, 1977 (2 spp.), *Rhagoba* Moore, 1888 (2 spp.), *Sinomphisa* Munroe, 1958 (3 spp.), *Sparagmia* Guenée, 1854 (1 sp.), *Stemorrhages* Lederer, 1863 (8 spp.), *Synclera* Lederer, 1863 (13 spp.), *Syngamilyta* Strand, 1920 (5 spp.), *Talanga* Moore, 1885 (9 spp.), *Tessema* J.F.G. Clarke, 1986 (1 sp.), *Tyspanodes* Warren, 1891 (20 spp.), *Uncobotyodes* Kirti & Rose, 1990 (1 sp.).

Tyspanodes is not a natural group, and at least *T. exalthealis* (Walker, 1859) is misplaced here; we did not investigate the type species, *T. nigrolinealis* (Moore, 1867), but we can confidently place *T. hillalis* Schaus, 1927, *T. hypsalis* Warren, 1891 and *T. celebensis* Munroe, 1960 in Margaroniini.

Heterocnephes apicipicta Inoue, 1963 is misplaced in *Heterocnephes* and transferred to the monotypic *Charitoprepes* as *Charitoprepes apicipicta* (Inoue, 1963) **comb.n.** The type species *C. lubricosa* Warren, 1896 shares with *C. apicipicta* the wing pattern and the structure of the male genitalia (cf. INOUE 1963; KIM et al. 2014). *Alytana calligrammalis* (Mabille, 1879) **comb.n.** is transferred from *Analyta*, a transfer that had not been formerly proposed by SHAFFER & MUNROE (2007) in their description of *Alytana*.

Food plants. We arrange food plant records, where available, according to the clades found within Margaroniini as shown in Fig. 1: *Astrodes fimbriauralis* is recorded from *Colubrina* (Rhamnaceae); *Maruca vitrata* is a pest species on various Fabaceae such as *Lablab*, *Phaseolus*, *Pisum*, *Psophocarpus*, *Sesbania* and *Vigna*, but has also been recorded from Rubiaceae, Solanaceae, Poaceae and Euphorbiaceae (ROBINSON et al. 2010). *Cydalima* mainly feeds on Apocynaceae (*C. laticostalis* (Guenée, 1854)), Buxaceae (*C. perspectalis* (Walker, 1859)) or Rhamnaceae (*C. mysteris* Meyrick, 1886) (ROBINSON et al. 2010). *Filodes* feeds on *Thunbergia* (Acanthaceae) (ROBINSON et al. 2010). *Diaphania* species mostly feed on Cucurbitaceae; *Palpita* is primarily on Oleaceae, but *P. flegia*, probably the first-diverging member with a plesiomorphic male antennal scape, feeds on Apocynaceae (MOORE 1884–1887; HINCKLEY 1964; KIMBALL 1965; CLAVIJO ALBERTOS 1990; SOLIS 2006, 2008; ROBINSON et al. 2010). *Omiodes* species feed on a variety of host plants, and two species (*O. diemenalis* (Guenée, 1854), *O. indicata* (Fabricius, 1775)) are widespread pests on Fabaceae; the larvae of the Hawaiian *Omiodes* clade feed on monocotyledonous plants, except *O. monogona* Moore, 1888, which feeds on Fabaceae (ROBINSON et al. 2010; HAINES & RUBINOFF 2012). *Omiodes stigmosalis* Warren, 1892, a borer in fig fruits (JANZEN & HALLWACHS 2009), is misplaced in *Omiodes* but has the characters of Margaroniini. *Prenesta* is recorded mainly from Apocynaceae and Moraceae (JANZEN & HALLWACHS 2009). Larvae of *Liopasia*, *Agathodes* and *Terastia* commonly feed on *Erythrina* (Fabaceae) (HINCKLEY 1864; KIMBALL 1965; SOURAKOV 2012; PEREIRA et al. 2014). *Antigastra catalaunalis* (Duponchella, 1833) and *Zebronia phenice* (Stoll in Cramer & Stoll,

1782) are leaf-tiers on Lamiales: The former, best known as a pest of sesame (Pedaliaceae), also feeds on Bignoniaceae (*Tecoma stans*) and Plantaginaceae (POWELL & OPLER 2009). The latter feeds on Bignoniaceae but was also recorded on *Gossypium* (Malvaceae) and *Ricinus* (Euphorbiaceae) (ROBINSON et al. 2010). *Hodebertia testalis* (Fabricius, 1794) larvae predominantly feed on Asclepiadaceae (ROBINSON et al. 2010). *Botyodes* feeds on Flacourtiaceae, Moraceae, *Salix* (Salicaceae) and several other hosts (NAKAMURA & OHGUSHI 2004; ROBINSON et al. 2010). *Cadarena pudoraria* (Hübner, 1825) and the closely related ‘*Glyphodes*’ (or ‘*Pyrausta*’) *perlegans* (Hampson, 1898) group are recorded from Passifloraceae, *C. pudoraria* also from *Gossypium* and *Sida* (Malvaceae) (JANZEN & HALLWACHS 2009; ROBINSON et al. 2010; DE PRINS & MAZZEI 2016). *Ghesquierellana hirtusalis* (Walker, 1859) larvae feed on *Ficus* (Moraceae) and *Gossypium* (Malvaceae); *Megastes* on *Ipomoea* (Convolvulaceae); *Azochis* on *Ficus* (Moraceae); *Conogethes* larvae are recorded from a wide range of plants, e.g. Pinaceae, Gnetaceae, Malvaceae, Sapindaceae, Euphorbiaceae and Zingiberaceae (ROBINSON et al. 2010; SHASHANK et al. 2018). ‘*Nacoleia*’ *insolitalis* from *Sandoricum* (Meliaceae) (ROBINSON et al. 2010). The known larval host plants of the *Glyphodes* genus group sensu SUTRISNO (2002b) (*Glyphodes*, *Dysallacta*, *Talanga*, *Agrioglypta*) are primarily the latex-containing Moraceae and Apocynaceae (KIMBALL 1965; COMMON 1990; ROBINSON et al. 2010). *Obtusipalpis* is recorded from Rubiaceae, Moraceae and Rutaceae (ROBINSON et al. 2010).

Host plants for other genera placed in Margaroniini are: *Arthroschista* and *Parotis* on Rubiaceae, the latter also on Apocynaceae, on which *Pygospila* and *Stemorrhages* mainly feed; *Cirrhochrista* on Moraceae; *Condylorrhiza* on Salicaceae; *Eusabena* on *Hoya* (Asclepiadaceae); *Anarmodia* and *Sparagmia* on Araliaceae; *Synclera* on *Gouania* and *Zizyphus* (Rhamnaceae) (MANN & BRAR 1980; JANZEN & HALLWACHS 2009; ROBINSON et al. 2010; HAYDEN et al. 2017).

The most general trend in this group is feeding on latex-bearing plants, especially Apocynaceae and Moraceae. The habit of boring in tubers of *Ipomoea* (Convolvulaceae) by *Megastes*, *Polygrammodes eleuata*, and *Omphisa anastomosalis* (Guenée, 1854) is explained by the presence of latex in these roots. Nevertheless, many genera and genus groups diverge from the pattern and radiate on non-latex-bearing plants, e.g. some *Polygrammodes* in roots of *Vernonia*, *Sinomphisa* in Bignoniaceae, and *Omphisa fuscidentalis* (Hampson, 1896) in bamboo. **Remarks.** Margaroniini roughly reflects a combination of MUNROE’s (1995) *Diaphania* and *Polygrammodes* groups. The assumed close relationship for *Agathodes*, *Terastia* and *Liopasia* (MUNROE 1960; SOURAKOV et al. 2015) has been confirmed by our results. Females of the *Agathodes* genus group exhibit an appendix bursae (absent in some species); the larvae are feeding on *Erythrina* (Fabaceae) (PEREIRA et al. 2014).

The possible sister group relationship between *Omiodes* and *Cnaphalocrocis* Lederer, 1863, as suggested by

HAINES & RUBINOFF (2012), could not be confirmed. We treat *Cnaphalocrocis* as a member of Spilomelini (see below), whereas *Omiodes* belongs to Margaroniini. The sister group of *Omiodes* remains to be discovered.

CLAVIJO ALBERTOS (1990) observed and described the “anepisternal scale organ” in males of many genera of Spilomelinae. Apparently, this is a tymbal organ (NAKANO et al. 2012b). Among Spilomelinae, ultrasound production is reported from the Margaroniini *Conogethes punctiferalis* (Guenée, 1854), *Glyphodes pyloalis* Walker, 1859 and *Palpita nigropunctalis* (Bremer, 1864) as well as in *Spoladea recurvalis* (Fabricius, 1775) (Hymeniini) (NAKANO et al. 2009, 2012a).

4.2.11. Spilomelini Guenée, 1854 stat.rev.

Type genus: *Spilomela* Guenée, 1854
= Siginae Hampson, 1918

Synapomorphies. 45:2, apical uncus bifurcate. The uncus is bicapitate with bulbous heads.

Description. Small (15 mm wingspan) to large (90 mm wingspan) moths. Spilomelini shares the bicapitate uncus with Asciodini and some Steniini such as *Metasia* and *Loxostegopsis*. The costa of the valva is straight to slightly concave or convex. This tribe consists of two distinct clades: the *Cnaphalocrocis* group and the *Siga* group.

In the *Cnaphalocrocis* group, adults are small to medium-sized. Most genera are brown and drab in colour, whereas *Spilomela* has contrasting maculation; the wings' transverse lines consist of straight segments and angulate junctions. Males have a field of enlarged, raised scales on the centre of the forewing costa (absent in several taxa). Sacci tympani are small and closely set. In the male genitalia, the flattened uncus is weakly bifid, the head consisting of two connected, flat pads or fields of chaetae rather than clearly separate parts; the uncus is lost in *Geshna*. The sacculus ends distally with a small fibula-like process pointing inward toward the center of the valva. Some taxa have a fibula in the center of the valva. In *Spilomela perspicata*, the details of the male genitalia are distorted by elongation, but the uncus is apically bifid on close inspection. In females, the colliculum is cylindrical and open dorsally or entire. The colliculum is often extended as extra sclerotization on the adjacent ductus bursae. The ductus bursae is usually very short and has fine spinules or striations next to the colliculum. The signum typically is a granulose circle or a small thorn, but *Palpusia* species have two long, sickle-shaped signa, and *Spilomela receptalis* (Walker, 1859) has two shorter sickles; signa are absent in *Rhectocraspeda* and *Spilomela perspicata* (Fabricius, 1787) itself, which in addition has a very long, unsclerotized ductus bursae.

The *Siga* group includes medium-sized to large and thick-bodied moths. The proboscis is lost in *Siga*, otherwise normally developed. The sacci tympani are exposed as a shallow zona glabra, and the fornix tympani is circularly rounded without an angle. The male genitalia have

the uncus entirely split into two separate unci (unsplit in *Zeuzerobotys*), bearing bifid chaetae; the costal margin of the valva is approximately straight or only slightly convex near the base, never strongly convex, distally straight or slightly concave; the apical half of the valva is bluntly attenuate, slightly to markedly narrower than basal half of valva with its inflated sacculus; there is one ventrally directed, hook-shaped to spatulate fibula emerging from centre of valva. The combination of the bifid uncus and the shape of the valva distinguish members of the *Siga* group from robust-bodied Margaroniini. The ductus bursae is as long as or shorter than corpus bursae, and the corpus bursae is spherical, rarely ovate, without signa.

Systematics. Based on our phylogenetic analyses, we place the following taxa in Spilomelini: *Cnaphalocrocis* group with *Cnaphalocrocis* (27 spp.), *Marasmia* Lederer, 1863 (9 spp.), *Salbia* Guenée, 1854 (35 spp.) and *Spilomela* Guenée, 1854 (8 spp.); *Siga* group with *Eporidia* Walker, 1859 (1 sp.) and *Siga* Hübner, 1820 (2 spp.), as presumed by MUNROE (1958).

Based on morphological investigation, we further assign *Aethaloessa* Lederer, 1863 (3 spp.), *Geshna* Dyar, 1906 (1 sp.), *Marasmianympha* Munroe, 1991 (1 sp.), *Orphanostigma* Warren, 1890 (6 spp.), *Palpusia* Amsel, 1956 (10 spp.) and *Rhectocraspeda* Warren, 1892 (2 spp.) to the *Cnaphalocrocis* group, and *Cirrhocephalina* Munroe, 1995 (5 spp.), *Scaptesyloides* Munroe, 1976 (2 spp.) and *Zeuzerobotys* Munroe, 1963 (1 sp.) to the *Siga* group, following MUNROE (1963; 1976b; 1995) and LANDRY et al. (2011) (but see Remarks).

Food plants. The hosts of the *Cnaphalocrocis* group are heterogeneous, but the group includes a major radiation on monocots, especially on Gramineae. The larvae of *Aethaloessa*, *Cnaphalocrocis*, *Marasmia* and *Salbia* are mainly leaf-rollers on Poaceae, *Salbia* larvae are also recorded from Verbenaceae and to a lesser amount from Gesneriaceae and Fabaceae, and *Aethaloessa floridalis* (Zeller, 1852) from Urticaceae (JANZEN & HALLWACHS 2009; ROBINSON et al. 2010). *Rhectocraspeda* is found on *Piper* (Piperaceae), *Columnnea* (Gesneriaceae) and Solanaceae, *Geshna* on *Canna* (Cannaceae), *Lilium* (Liliaceae), *Thalia geniculata* (Marantaceae) and *Zantedeschia* (Araceae), *Palpusia* on Convolvulaceae and Rubiaceae, and *Orphanostigma* on Lamiaceae, Asteraceae and Malvaceae (KIMBALL 1965; HEPPNER 2003; JANZEN & HALLWACHS 2009; ROBINSON et al. 2010). *Spilomela* larvae are reported from Dilleniaceae, Ulmaceae and Rubiaceae (JANZEN & HALLWACHS 2009).

In the *Siga* group, the hosts are unknown for *Siga* and *Eporidia*, the two genera included in our phylogenetic analysis.

Remarks. The genus *Spilomela* is polyphyletic and needs revision. We base our conclusions on the type species, *S. perspicata*.

The *Siga* group shares with Asciodini a similar morphology of the male genitalia, especially the overall robust form and bifid uncus. We transfer several genera to Asciodini (below). Together with *Siga* and *Eporidia*, the genera that we retain in the *Siga* group on morphologi-

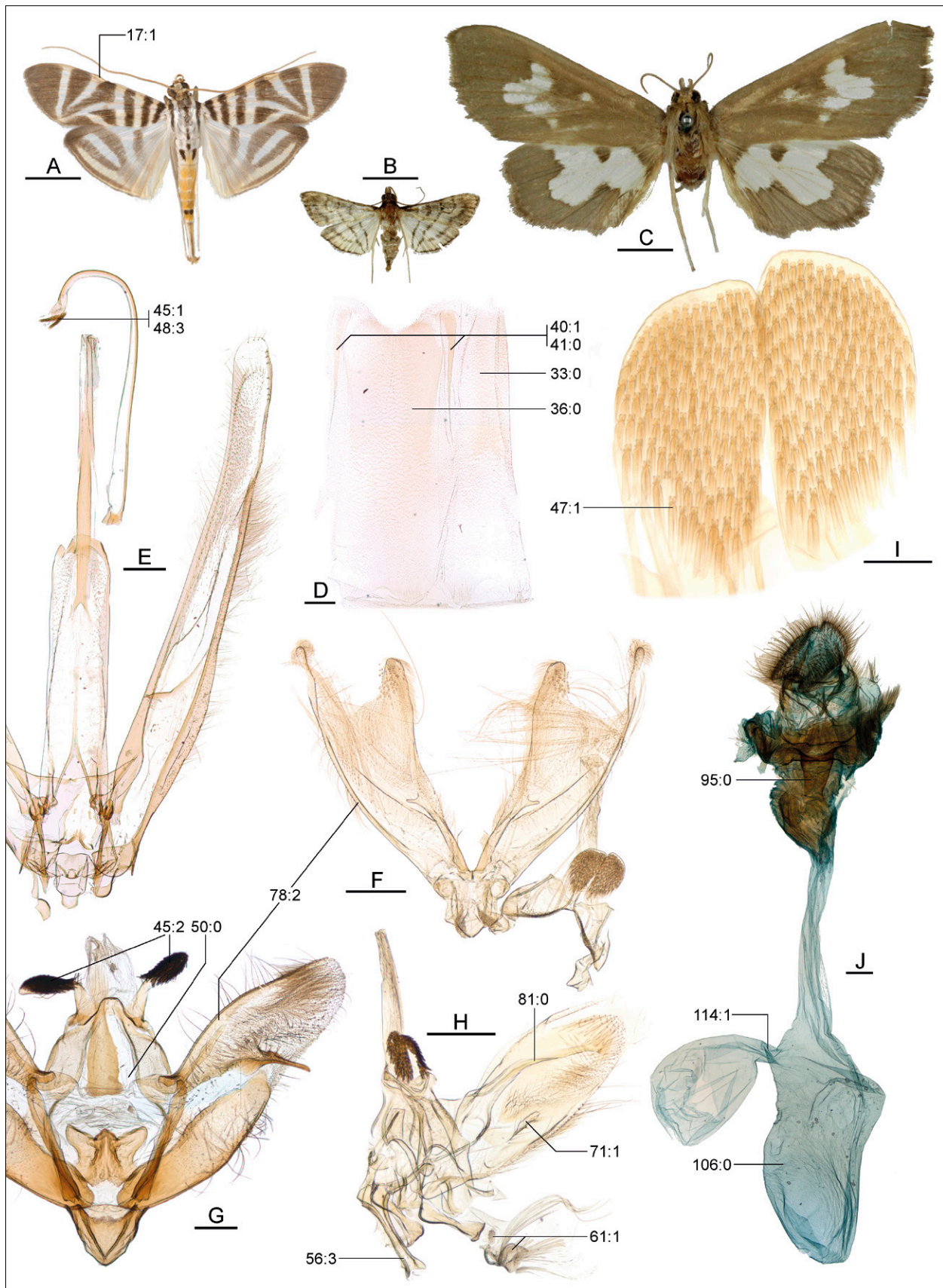


Fig. 9. Spilomelini. **A:** adult male of *Spilomela perspicata*. **B:** adult female of *Marasmia poeyalis*. **C:** adult female of *Eporidia dariusalis*, abdomen removed. **D:** 8th abdominal segment of male *S. perspicata*. **E:** male genitalia of *S. perspicata*, uncus detached from tegumen, phallus omitted. **F:** male genitalia of *M. poeyalis*, valvae embedded inverted in the preparation with the costa facing outward, phallus omitted. **G:** male genitalia of *E. dariusalis*, phallus omitted. **H:** male genitalia of *Salbia* cf. *haemorrhoidalis*, one valva and phallus omitted. **I:** uncus heads of the male genitalia of *M. poeyalis*. **J:** female genitalia of *E. dariusalis*. — **Scale bars:** A–C (same scale) – 5 mm; D–H, J – 500 µm; I – 100 µm.

cal grounds (*Cirrhocephalina*, *Scaptesyloides*, and *Zeuzerobotys*) share the same shape of fibula and valva, and non-inflated transtilla. The colliculum of *Siga*, *Eporidia*, and *Scaptesyloides* is entire and bulges ventrad rather like a pot-belly or a pitcher plant (*Nepenthes*) (female genitalia not observed for *Cirrhocephalina* and *Zeuzerobotys*). The loss of the proboscis in *Siga* is paralleled in Wurthini: *Niphopyralis*.

The monotypic *Gesha* is included because the larvae feed on *Canna*, the wing pattern is typical of the *Cnaphalocrocis* group, and the genitalia share characters with some *Salbia* species, namely swellings on the base of the valva costa (also in *S. mizaralis* (Druce, 1899)) and the broad, triangular uncus. The loss of bifid uncus chaetae and the movement of the fibula to a central position on the valva are homoplasies.

4.2.12. Herpetogrammatini Mally, Hayden, Neinhuis, Jordal & Nuss trib.n.

Type genus: *Herpetogramma* Lederer, 1863

Synapomorphies. 5:1, length of sensillar setae at basal antennomeres relative to diameter of basal antennomeres in male > 50%; 107:0, corpus bursae sclerotisation consisting of a granulose area. Slow optimization only: 8:1, 3rd labial palpomere porrect. The parsimony trees imply one apomorphy: 44:0, a conical, non-capitate uncus; characters 5:1 and 107:0 are synapomorphies with Asciodini.

Description. The uncus is conical, non-capitate, slender to broad, with dorsally attached chaetae that are bifid in *Eurrhyarodes* and *Hileithia* and hairlike in all other genera examined; the uncus is broadly attached to the tegumen, that is, the tegumen grades evenly into the uncus without “shoulders”. Character 44:0, shape of uncus conical, non-capitate, is absent in several species of *Blepharomastix* such as *B. ranalis* (Guenée, 1854), an apparent reversal of the tribe’s synapomorphy. The valvae are ovate with a convex to straight costa and rounded to acute apex; the sacculus is weakly developed or absent; the fibula is long and emerges from near costa base, pointing towards the centre of the ventral valva edge, or the fibula is reduced to a fold or lost entirely (*Cryptobotys*, *Pilocrocis*, some *Herpetogramma* spp.); the juxta is compact, dorsally split; the saccus is V-shaped, its tip often somewhat offset; the hairpencils are simple (one sclerite bearing one kind of simple chaetae) or absent. The phallus coecum is short or absent; the phallus apodeme is membranous apart from a ventral longitudinal sclerotized strip; the vesica is granulose, often with a dense patch of small cornuti. The corpus bursae is membranous or posteriorly with a granulose area, and the signum is single or absent: when most developed, it is a round, granulose rhomboid with transverse axis dominant (*Cryptobotys*, *Herpetogramma* spp.), or reduced to a transverse line (*Pilocrocis ramentalis* Lederer, 1863, *Blepharomastix ranalis*), a round dome, or a longitudinal

elongate signum (*Hileithia* spp.); the signum is absent or rudimentary in *Eurrhyarodes*, but with posterior wall of corpus bursae sclerotized; the corpus bursae is well distinguished from the long, slender, membranous or partly sclerotized ductus bursae; the colliculum is membranous or with a sclerotisation partially encompassing the ductus; the antrum is weakly to strongly sclerotized, simple. **Systematics.** Based on our phylogenetic results, we place *Eurrhyarodes* Snellen, 1880 (12 spp.), *Herpetogramma* Lederer, 1863 (100 spp.) and *Hileithia* Snellen, 1875 (19 spp.) here. Furthermore, *Blepharomastix* Lederer, 1863 (85 spp.), *Cryptobotys* Munroe, 1956 (2 spp.) and *Pilocrocis* Lederer, 1863 (65 spp.) are assigned to Herpetogrammatini based on morphological characters.

MUNROE (1995) further places the monotypic *Pelinopsis* Dognin, 1905 in his *Herpetogramma* group. As we did not study this taxon, we keep it unplaced.

Food plants. The known food spectrum of the larvae comprises Acanthaceae (*Hileithia*, *Pilocrocis*, *Eurrhyarodes splendens* Druce, 1895), Actinidiaceae (*Pilocrocis*), Malvaceae (*Hileithia*) and Urticaceae (*Pilocrocis*) (HEPPNER 2003; SOLIS 2008; JANZEN & HALLWACHS 2009). ‘*Pilocrocis*’ *milvinalis* (Swinhoe, 1886) is reported from Apocynaceae, Fabaceae and Rubiaceae, *P. pterygodia* Hampson, 1912 from Lamiaceae (ROBINSON et al. 2010). *Eurrhyarodes bracteolalis* (Zeller, 1852) is recorded from *Solanum* (Solanaceae) and *Oryza* (Poaceae) (ROBINSON et al. 2010), *Blepharomastix ranalis* from *Chenopodium* (Amaranthaceae) (SOLIS 2008). The species-rich genus *Herpetogramma* (100 spp.; NUSS et al. 2003–2019) contains species with a variety of food plants ranging from ferns to angiosperms (SOLIS 2008; JANZEN & HALLWACHS 2009).

Remarks. The mimetic ‘*Pilocrocis*’ *xanthozonalis* Hampson, 1912 group (including *P. cyrisalis* (Druce, 1895)) feeds on Rubiaceae; this group is misplaced in *Pilocrocis* and belongs to Agrotorini, based on the extended tegumen, naked uncus, and twin tack-shaped signa.

4.2.13. Hymeniini + Asciodini

Synapomorphies. 61:1, two or more hairpencil sclerites on each side of the genitalia (articulated with each other via membranes); 62:1, more than one kind of hairpencil chaetae present.

4.2.14. Hymeniini Swinhoe, 1900 stat.rev.

Type genus: *Hymenia* Hübner, 1825

Synapomorphies. 3:1, transverse rim on anterior or mesal face of pedicellus in male present; 9:0, size of 3rd labial palpomere well developed in both sexes; 75:1, joint of basal valva costa (with vinculum) extended into an elongate, rod-shaped process. Slow optimization only: 40:1, sclerite present on each pleural membrane of male segment 8.

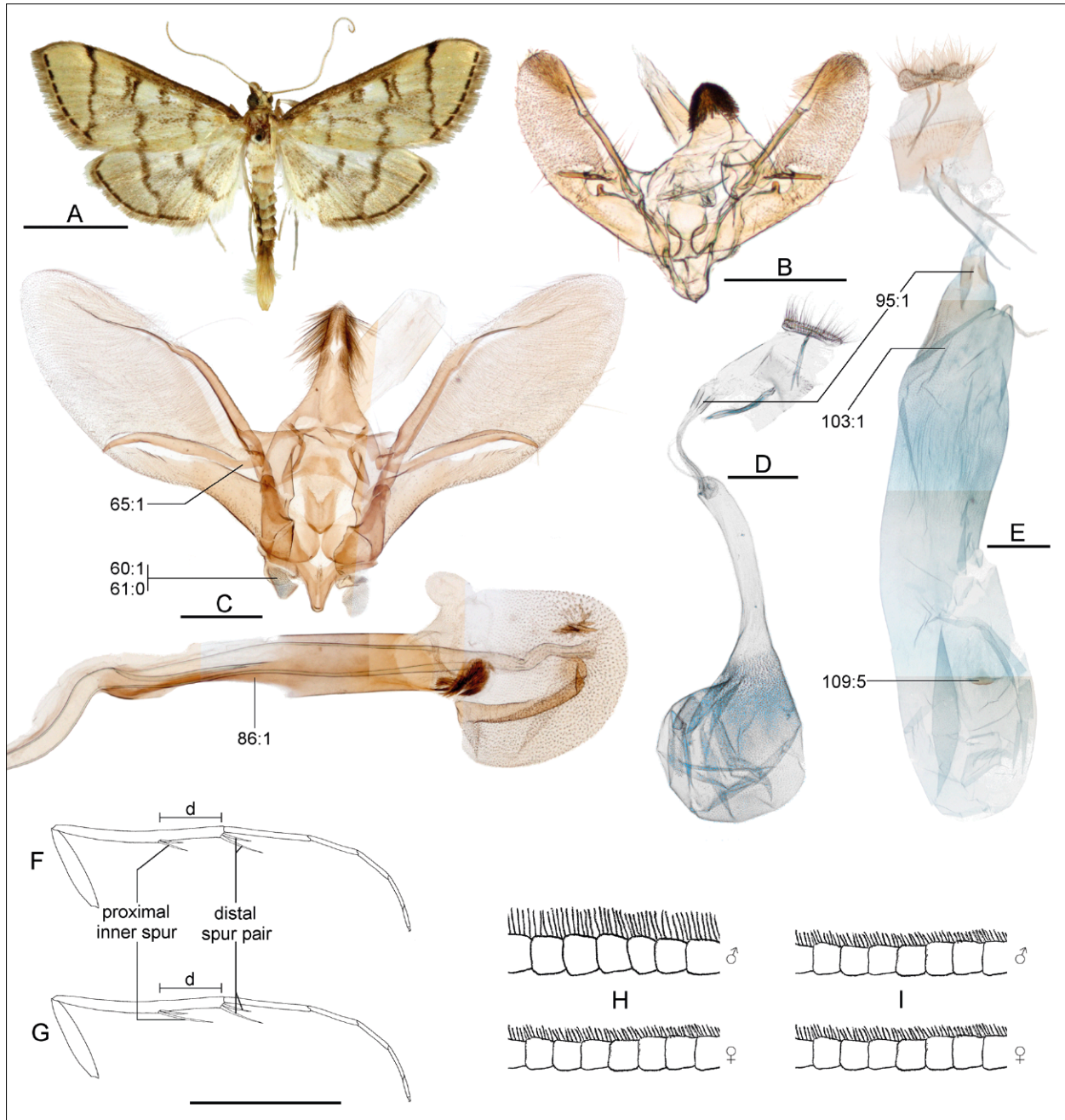


Fig. 10. Herpetogrammatini. **A:** adult male of *Blepharomastix ranalis*. **B:** male genitalia of *Eurrhyparodes lygdamis*, phallus omitted. **C:** male genitalia of *Herpetogramma licarsisalis*, vesica of phallus everted. **D:** female genitalia of *Hileithia* cf. *obliquialis*. **E:** female genitalia of *H. licarsisalis*. **F–G:** schematic hindlegs, modified from LEWVANICH 1981, Fig. 18. **H–I:** schematic antennae. — **Scale bars:** A, G, H – 5 mm; B–E – 500 μ m.

The modified antenna base in males is apomorphic: the pedicellus is erect, long, with oblong scales emerging from its distal margin (*Hymenia perspectalis* (Hübner, 1796)) or medially and posteriorly from its base (*Spoladea recurvalis*); the anterior (*H. perspectalis*) or medial edge (*S. recurvalis*) of the pedicellus is raised to a transverse rim; the basal flagellomeres have a pointy protrusion on anterior side; and the flagellum is directed posteriad, giving the antenna a geniculate appearance.

The parsimony trees do not have 40:1, but they add 61:1, two or more hairpencil sclerites on each side of the genitalia, articulated with each other via membranes;

62:1, more than one kind of hairpencil chaetae present; and 99:1, strongly sclerotized colliculum.

Description. The imagines are small (forewing length about 9 mm) with dark brown wings contrasted with white forewing markings in the median and postmedian lines, and a white transverse band in the hindwing; the head and legs are contrastingly marked. The basal valva costa is extended into an elongate, ventrad rod that serves as dorsal joint with the vinculum. The hairpencils are complex, consisting of several sclerotized pads partly with parallel lines of sclerotized ridges, bearing distinct bundles of long, characteristically bent chaetae; the anterior

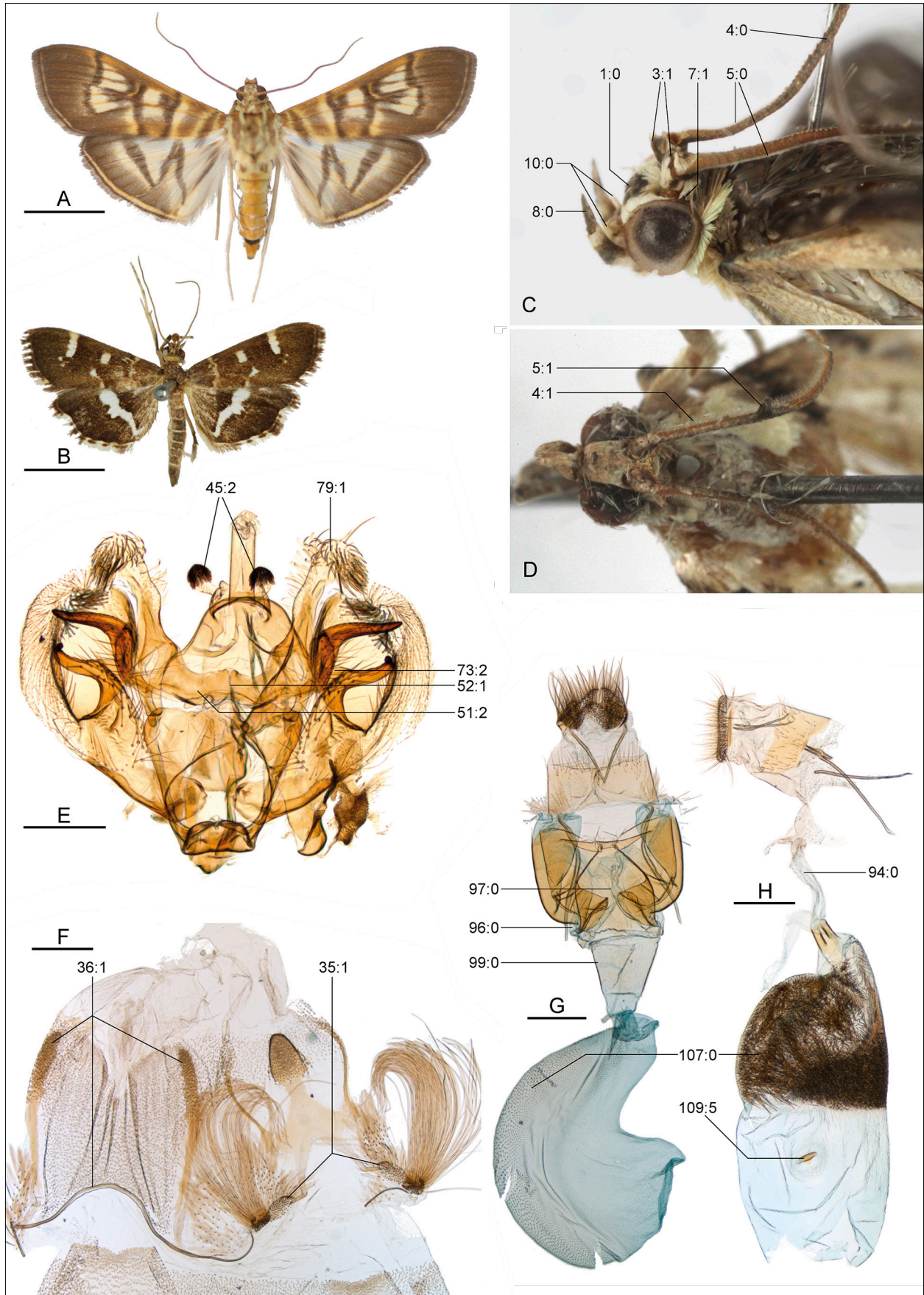


Fig. 11. Hymeniini (B, C, H) and Asciodini (A, D–G). **A:** adult female of *Arthromastix lauralis*. **B:** male of *Hymenia perspectalis*. **C:** head of male *H. perspectalis*. **D:** head of male *Asciodes* cf. *gordialis*. **E:** male genitalia of *As.* cf. *gordialis*, phallus omitted. **F:** 8th abdominal segment of *As.* cf. *gordialis*. **G:** female genitalia of *Ar. pactolalis*. **H:** female genitalia of *Spoladea recurvalis*. — **Scale bars:** A, B – 5 mm; E–H – 500 μ m.

half of corpus bursae has a short (*S. recurvalis*) or long (*H. perspectalis*) transverse ridged signum, the posterior half of the corpus bursae granulose (*H. perspectalis*) or densely studded with needle-like spikes (*S. recurvalis*); the antrum has a longitudinal, non-sclerotized strip.

Hymeniini exhibits a typical wing pattern with a dark to light brown ground colour interrupted by a broad white postmedial line on fore- and hindwing; abdomen dorsally brown with a white band on the segments' posterior margin.

Systematics. Based on our phylogenetic analyses, we place *Hymenia* Hübner, 1825 (3 spp.) and *Spoladea* Guenée, 1854 (2 spp.) in Hymeniini. *Hymenia* and *Spoladea* represent a part of MUNROE'S (1995) polyphyletic *Hymenia* genus group.

Food plants. The spotted beet webworm moth, *Hymenia perspectalis* (Hübner, 1796), and the Hawaiian beet webworm moth, *Spoladea recurvalis*, are polyphagous, their larvae feeding on a large variety of food plants, among them several important crops like *Amaranthus*, *Beta*, *Solanum tuberosum*, *Spinacia*, *Xanthosoma* and *Zea mays* (SOLIS 2006, 2008).

Remarks. The extension of the basal valva costa into an elongate, ventrad rod, serving as dorsal joint with the vinculum, is also present in most investigated Margaroniini, in *Arthromastix lauralis* (Asciodini), *Samea ecclesialis* Guenée, 1854 (Nomophilini), and *Prophantis xanthomeris* (Trichaeini).

The imagines of *Hymenia* and *Spoladea* are very similar externally, and the generic names have been used interchangeably in the literature. Despite these superficial similarities between the adults of *Spoladea* and *Hymenia*, their genitalia are significantly different, and the two genera should be kept separate.

4.2.15. Asciodini Mally, Hayden, Neinhuis, Jordal & Nuss trib.n.

Type genus: *Asciodes* Guenée, 1854

Synapomorphies. 5:1, sensillar setae on basal antennomeres of male > 50% relative to diameter of basal antennomeres; 72:1, extension (process in some cases) of dorsodistal sacculus present; 74:1, basal costa inflated; 86:0, phallus apodeme sclerotisation reduced to a ventral, longitudinally sclerotized strip; 107:0, corpus bursae with a granulose sclerotised area. Slow optimization only: 52:1, connection point of transtillum arms broad; 73:2, fibula and dorsodistal sacculus fused.

The parsimony trees do not have 107:0, but they add five synapomorphies: 8:0, dorsal direction of 3rd labial palpomere; 33:1, male tergite 8 with heterogenous, distinct sclerotization pattern; 51:1, transtillum arms rounded; 61:1, two or more hairpencil sclerites on each side of the genitalia, articulated with each other via membranes; and 62:1, more than one kind of hairpencil chaetae present.

Description. Males of some genera exhibit modified antennomeres halfway along the flagellum. In the forewing

of many genera, the postmedial line is roundly concave where it crosses the anal fold, rather than angulate. The sacci tympani are hemispherical and clearly defined; they are smaller and deeper than in most Spilomelinae. The uncus head is bicapitate or has two separate heads (with a single head and a central dorsoventral, chaetae-free strip in *Arthromastix lauralis* (Walker, 1859) and *Ceratocilia sixolalis* (Schaus, 1912)); the costa base and vinculum saccus are inflated; the transtilla is large and circular or strap-like, with a broad median connection (slim in *C. sixolalis*). The fibula in the center of the valva is connected to the sacculus by a distinct "arch" bowing transversely across the valva. This arch may bear from one to three digitate processes, or none (*Bicilia*). Signa are usually either absent (most genera) or present as one arcuate line (*Psara*, *Sathria*, *Bicilia*). The ostium bursae and ductus bursae are variously sclerotized. Minimally, the colliculum is smooth, elongate, and entire (not ventrally membranous). In some genera, the ostium is flanked by two plates or entirely surrounded by wrinkled sclerites, and the colliculum may be fused with more extensive sclerotization along the ductus bursae, which is always shorter than the corpus bursae. The posterior end of the corpus bursae is often sclerotized with granules or spinules.

Systematics. Based on our phylogenetic results we place *Arthromastix* Warren, 1890 (2 spp.), *Asciodes* Guenée, 1854 (5 spp.) and *Arthromastix pactolalis* (Guenée, 1854) comb.n. here. Furthermore, based on common morphological features, we assign *Beebea* Schaus, 1923 (1 sp.), *Bicilia* Amsel, 1956 (4 spp.), *Ceratocilia* Amsel, 1956 (8 spp.), *Ceratoclasia* Lederer, 1863 (9 spp.), *Laniifera* Hampson, 1899 (1 sp.), *Laniipriva* Munroe, 1976 (1 sp.), *Loxomorpha* Amsel, 1956 (4 spp.), *Maracayia* Amsel, 1956 (2 spp.), *Psara* Snellen, 1875 (36 spp.) and *Sathria* Lederer, 1863 (3 spp.) to Asciodini.

We transfer five genera from MUNROE'S (1995) *Siga* group: *Beebea*, *Laniifera*, *Laniipriva*, *Loxomorpha* and *Maracayia*. Males of all the species have the fibula connected to the sacculus by an arch, valvae oval in shape or with a basally inflated costa, enlarged transtilla bases (except *Loxomorpha*), and the forewing PM line rounded basad on the anal fold. Females have a sclerotized lamella postvaginalis, except in *Laniipriva*. The known larvae feed on Cactaceae (Caryophyllales) as borers or webworms. The robust form of the genitalia obscures a key morphological character – the sacculus-fibula arch – but it is visible in careful dissection. Unlike most Asciodini, the hairpencils are either very simple tufts of hairs or absent, and male antennae are not modified. Like in Margaroniini and Spilomelini, the large size of imagines and "robust" genitalia are syndromatic of the internally feeding larval habit. *Laniipriva* is problematic because the female genitalia illustrated by MUNROE (1976b: fig. 21) have an unarmed ostium and a bulged colliculum like in the *Siga* group, but the female maculation (ibid. fig. 6) is typical of Asciodini.

Ceratocilia (considering *C. sixolalis*) may have a basal position in this tribe, with its simple transtilla and hairpencils.

Food plants. Asciodini larvae commonly feed on herbaceous Caryophyllales. *Asciodes gordialis* Guenée, 1854 feeds mainly on Nyctaginaceae (*Bougainvillea Mirabilis*, *Pisonia*), as does *Ceratocilia sixolalis* (Nees, *Pisonia*); two undetermined *Ceratocilia* species were reared from Rubiaceae, though (KIMBALL 1965; JANZEN & HALLWACHS 2009; ROBINSON et al. 2010). *Arthromastix lauralis* feeds on *Trichostigma octandrum* (Phytolaccaceae) (BENDICHO-LOPEZ 1998). *Bicilia* is recorded from *Petiveria* and *Rivina* (Petiveriaceae) (BENDICHO-LOPEZ 1998; JANZEN & HALLWACHS 2009). *Psara* feeds on Amaranthaceae, Nyctaginaceae, Nelumbonaceae, Phytolaccaceae, *P. obscuralis* also on Convolvulaceae (JANZEN & HALLWACHS 2009; ROBINSON et al. 2010). *Laniifera cyclades* (Druce, 1895), *Beebea guglielmi* Schaus, 1923, *Loxomorpha*, and *Maracayia* species feed on Cactaceae, especially *Opuntia*, with records of *Maracayia* on other Caryophyllales (MANN 1969; JANZEN & HALLWACHS 2009; LARA-VILLALÓN et al. 2016).

Remarks. The upturned palpi (8:0) and heterogenous male tergite 8 (33:1) are shared with some other taxa (see diagnoses of Agrotini and Margaroniini). An extension of the sacculus (72:1) is shared with *Eurrhyarodes*, but in that genus, it is a free process, not fused with the fibula.

This group of uncolorful moths, as circumscribed here, is a Neotropical radiation on Caryophyllales. MUNROE'S (1995) association of the gracile external feeders is one of his more perceptive groupings; we doubt that he had knowledge of the host records available to us now. Munroe probably associated the large-bodied *Beebea* and *Laniifera* with *Siga* on overall habitus, and he left *Loxomorpha* and *Maracayia* unplaced.

Hymeniini species, although polyphagous, prefer Amaranthaceae and Chenopodiaceae. Therefore, the sister-group relationship of Asciodini and Hymeniini under some results (Bayesian and implied-weights parsimony under $k = 9 - 13$) suggests that feeding on Caryophyllales is a synapomorphy of the two tribes.

4.2.16. Trichaeini + (Steniini + Nomophilini)

Synapomorphies. 109:5 (unique), anterior-most signum a transverse, smooth or dentate arch, with or without central posteriad leg (if present, then signum Y-shaped) (not found with parsimony). Slow optimization only: 33:1, sclerotization of male tergite 8 heterogeneous (in parsimony trees); 67:2, fibula directed towards distal valva; 78:2, general shape of post-basal costa (not the entire dorsal valva edge) convex (not found with parsimony); 104:0, sclerotisation in ductus bursae absent.

4.2.17. Trichaeini Mally, Hayden, Neinhuis, Jordal & Nuss trib.n.

Type genus: *Trichaea* Herrich-Schäffer, 1866

Synapomorphies. 70:1, raised ridge running from basal to dorsodistal sacculus present.

Description. The valvae are weakly sclerotized, lens-shaped, often with fluting on ventral half of valva (cf. Odontiinae); the fibula is strongly sclerotized (*Trichaea*) to weak, bearing simple hairs (absent in some *Prophantis* spp.); the sacculus is scaly; a ridge-like protrusion is running from near the sacculus base to the valva centre. The corpus bursae has a slim longitudinal signum, its anterior end split into two anterolateral legs in some *Prophantis* species; the ductus bursae is broad, narrowing at the posterior end.

Systematics. Based on our phylogenetic analyses, we place *Prophantis* Warren, 1896 (8 spp.) and *Trichaea* Herrich-Schäffer, 1866 (11 spp.) in Trichaeini.

MUNROE (1967) points to the distinctness of *Thliptoceras* and *Prophantis*, with several misplaced species attributable to *Prophantis*. Our phylogenetic results reveal that the African *T. xanthomeris* is one of these cases. Here, we remove this and another African species from *Thliptoceras* and transfer them to *Prophantis*: *Prophantis xanthomeris* (Hampson, 1918) **comb.n.**, and *Prophantis coenostolalis* (Hampson, 1899) **comb.n.** Furthermore, the African *Prophantis longicornalis* (Mabille, 1900) **comb.n.** is transferred from *Syngamia* Guenée, 1854. '*Thliptoceras fenestratum* Aurivillius, 1910 is also misplaced and belongs to one of the non-euspilomeline clades, probably Udeini.

In the parsimony analysis, *Desmia* falls in Trichaeini, but it is not supported by any unambiguous morphological characters.

A few Neotropical taxa with mimetic maculation and Rubiaceae-feeding larvae should be investigated as possible members of Trichaeini, but we leave them incertae sedis because the morphological evidence is weak and we did not sequence them. They include *Erilusa* Walker, 1866 and species misplaced elsewhere, such as *Phostria delilalis* (Walker, 1859) and *Pilocrocis xanthozonalis* Hampson, 1912. Females of *Erilusa* and *P. xanthozonalis* have a large, complete colliculum, a short, granulose ductus bursae, and two small, round signa, characters that relate them to *Prophantis*. In *Erilusa*, the uncus is uncapitate and the elliptic, dentate fibula is not connected to the sacculus, which exclude it from Asciodini. The uncus varies from capitate in *Erilusa* to reduced and triangular in *P. xanthozonalis*, but the uncus is likewise variably reduced in Trichaeini. *Sacculosia* Amsel, 1956 (1 sp.) shares a fibula and fluted valva similar to *Trichaea*, but more information is needed in order to investigate this hypothetical relationship.

Food plants. *Prophantis smaragdina* (Butler, 1875), *P. octoguttalis* (C. Felder, R. Felder & Rogenhofer, 1875) and *P. longicornalis* are recorded as pests on *Coffea arabica* (Rubiaceae) and referred to as '[coffee] berry moths'; alternative hosts are *Tricalysia* and *Bertiera zaluzania*, *Ixora coccinea*, *Gardenia* (Rubiaceae), *Duranta plumieri* (Verbenaceae) and *Triclisia* (Menispermaceae) (WALLER et al. 2007; GUILLERMET 2009). HINCKLEY (1964) reports an undescribed *Prophantis* from Fiji boring in *Gardenia* flowers and shoots.

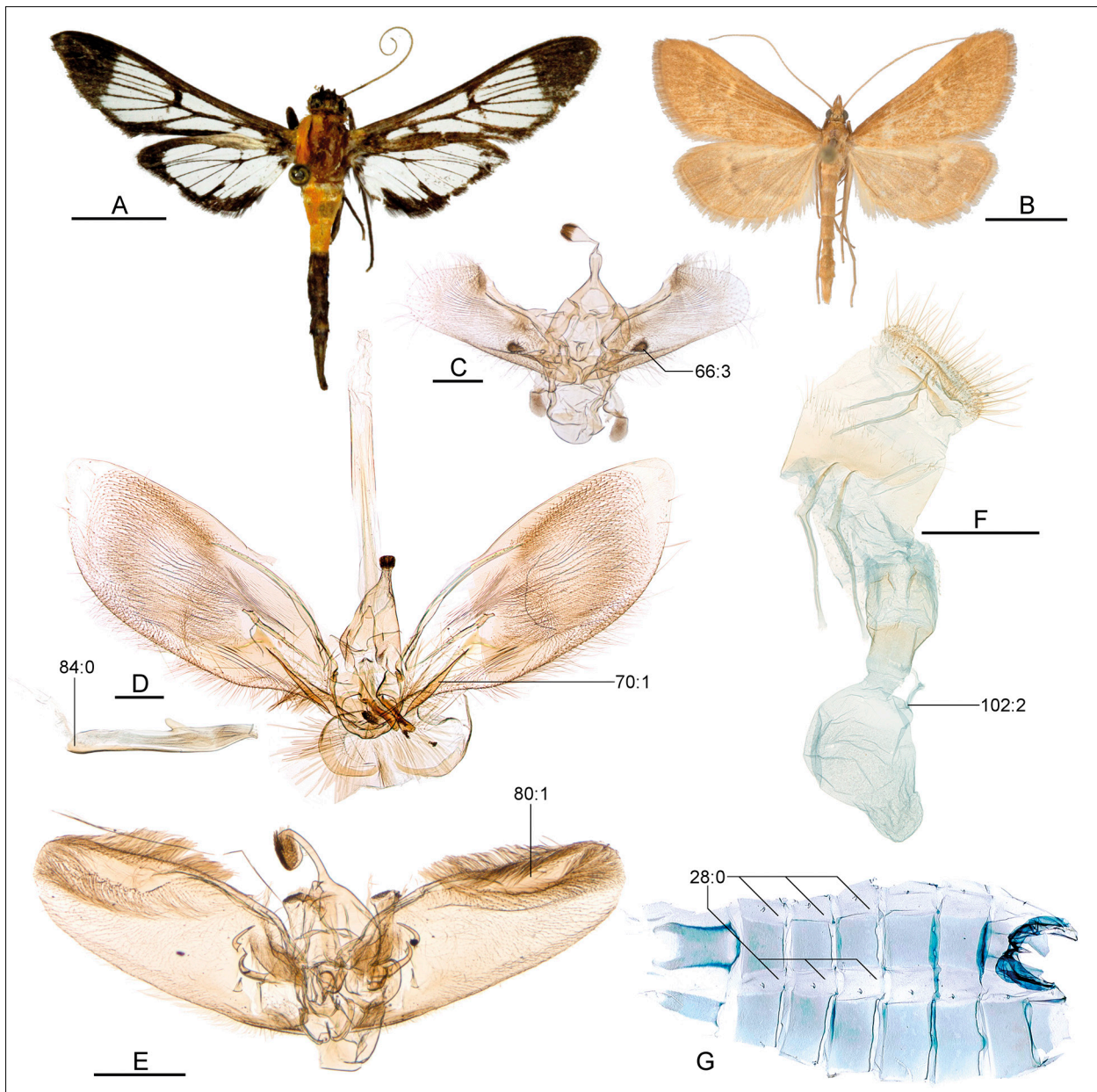


Fig. 12. Trichaeini (A, D) and Steniini (B, C, E–G). **A:** adult male of *Trichaea* sp. **B:** adult male of *Dolicharthria aetnealis*. **C:** male genitalia of *Do. punctalis*, phallus omitted. **D:** male genitalia of *T. pilicornis*. **E:** male genitalia of *Duponchelia fovealis*, phallus omitted. **F:** female genitalia of *Du. fovealis*. **G:** abdomen of male *Penestola bufalis*. — **Scale bars:** A, B – 5 mm; C–F – 500 μ m.

JANZEN & HALLWACHS (2009) report *Trichaea* larvae from *Psychotria* spp., *Morinda panamensis* and *Margaritopsis microdon* (Rubiaceae), with a single record on each Urticaceae and Celastraceae. Feeding on Rubiaceae is shared with Nomophilini (see also remarks there).

Remarks. The slim longitudinal signum of some *Prophantis* species with its anterior end split into two anterolateral legs is paralleled in *Syngamia* (Nomophilini).

4.2.18. Steniini Guenée, 1854 stat.rev.

Type genus: *Stenia* Guenée, [1845] = *Dolicharthria* Stephens, 1834

Synapomorphies. 106:0, sclerotisation in corpus bursae absent. Slow optimization only: 73:0, fibula and dorso-

distal sacculus (or its extension) distant from each other, non-overlapping. The parsimony trees imply the same, with both characters unambiguous.

Description. Imagines often have long legs; males have a slender, long abdomen. The uncus is single or bicapitate (*Loxostegopsis*, *Tatobotys*) or entirely split (*Metasia*) and has bifid chaetae. The valva costa is concave or straight, in some taxa weakly convex, and the valva is simple with usually zero or one fibula originating from base of valva, or in the *Duponchelia* group (sensu HAYDEN 2011) with two or three small fibulae at the base of the valva; the phallus has a caecum. The signum is absent, except in *Bradina*, *Diathrausta*, and *Perisyntrocha*, where it is a toothed arc. The ostium and ductus bursae lack any other sclerotization.

In the *Duponchelia* group, Rs_1 is stalked with Rs_{2+3} in the forewing, and a fovea in the male forewing at the distal end of the discal cell is a recurrent character in several but not all species; a pair of elongate hairpencils is present dorsal of the vinculum; the ductus bursae is very short; the larvae have the mesothoracic SD2 seta fine and hairlike.

Systematics. Based on our phylogenetic results, we place *Anageshna* Munroe, 1956 (1 sp.), *Dolicharthria* Stephens, 1834 (24 spp.), *Duponchelia* Zeller, 1847 (5 spp.) and *Metasia* Guenée, 1854 (88 spp.) in Steniini. Furthermore, based on morphology we place *Apogeshna* Munroe, 1956 (3 spp.), *Bradina* Lederer, 1863 (87 spp.), *Epherema* Snellen, 1892 **stat.rev.** (1 sp.), *Hymenoptychis* Zeller, 1852 (4 spp.), *Loxostegopsis* Dyar, 1917 (6 spp.), *Penestola* Möschler, 1890 (3 spp.), *Steniodes* Snellen, 1875 (9 spp.), *Symmoraema* Meyrick, 1894 (1 sp.) and *Tatobotys* Butler, 1881 (11 spp.) here. *Bradina* is unusual in possessing a signum, which could be plesiomorphic. The genera *Duponchelia*, *Hymenoptychis*, *Penestola* and *Tatobotys* are considered to be closely related: they have two or three small fibulae, a pair of narrow vincular androconia, forewing Rs_1 stalked with Rs_{2+3} and frequently a fovea, and the larvae are semiaquatic in swamps. We did not examine the type species of *Nacoleia*, *N. rhoeoalis* (Walker, 1859), but certain important species in this large genus (84 spp.) such as *N. octasema* (Meyrick, 1886) and *N. charesalis* (Walker, 1859) belong to Steniini based on the position of the fibula, absence of a signum, and saprophagous larval habits.

Pileocera Lederer, 1863 (93 spp.) probably belongs to Steniini. We have not studied the type species *P. violalis* Lederer, 1863, but *P. signiferalis* (Wallengren, 1860) as illustrated by CLARKE (1986: figs. 56, 57) shares the maculation, a broad and deep saccus, ornate valvae, complex hairpencils, and a corpus bursae with spicules but no single signum. It is related to a group of Steniini that have a broad saccus and ornate valvae that includes certain *Steniodes* species (*S. mendica* (Hedemann, 1894), *S. acuminalis* (Dyar, 1914)), *Camptomastix* Warren, 1892 and *Symmoraema* Meyrick, 1894. *Lipararchis* Meyrick, 1934 (2 spp.) might belong here too.

Food plants. Little is known about the feeding habits of Steniini. *Dolicharthria punctalis* (Denis & Schiffermüller, 1775) preferably on wilting leaves of different plants (HASENFUSS 1960). *Metasia corsicalis* (Duponchel, 1833) is reported to feed on detritus (LERAUT 2012). *Nacoleia charesalis* feeds on rotting leaves and bores in turmeric stems, and *N. octasema* consumes inflorescences of bananas (PAINE 1964; HIREMATH et al. 1990; KUMAR et al. 1996; TOMINAGA 2002). The absence of records by itself suggests that the saprophagous habit is common, because such larvae would be easy to overlook. One group is particularly interesting: the larvae of the *Duponchelia* group (sensu HAYDEN 2011) are detritivores in marshes and intertidal environments of mangrove swamps (MURPHY 1990). They are often associated with the *Avicennia* zone of mangrove forests, which is inundated at high tides. The larvae live on the ground and feed on rich soil and juicy

fallen plant matter (e.g. HINCKLEY 1964). *Duponchelia fovealis* Zeller, 1847 as a pest is spread through the plant nursery trade as it feeds on organic potting soil and succulent stems and foliage.

4.2.19. Nomophilini Kuznetsov & Stekolnikov, 1979 stat.rev.

Type genus: *Nomophila* Hübner, 1825

Synapomorphies. No unambiguous synapomorphies could be found for this tribe as circumscribed in the Bayesian results. Slow optimization only: 74:1, basal costa inflated. Two sister clades are present in Nomophilini, *Syngamia* + (*Ategumia* + (*Bocchoris* + (*Diasemia* + *Diasemiopsis*))) and *Desmia* + ((*Mecyna* + *Arnia*) + (*Samea* + *Nomophila*)). In the former clade, no synapomorphies or characters from slow optimization are found, but the latter clade is characterised by the synapomorphies 67:0, fibula ventrally directed towards sacculus or distal sacculus, and 95:0, longitudinal membranous strip in the antrum sclerotisation absent.

Nomophilini as circumscribed here is not monophyletic in the parsimony trees.

A core Nomophilini s.str. consisting of *Mecyna*, *Nomophila*, and *Samea* (without *Desmia* or *Syngamia*) has several synapomorphies in both the Bayesian and parsimony trees: 5:1, sensilla of male antennae elongate; 89:1, vesica with multiple cornuti; 100:0, colliculum evenly sclerotized all around, without membranous strip; and 109:1, signum longitudinal and granular.

Description. Small to medium-sized moths. The wing pattern is reticulated in many Neotropical genera. The *Diasemia* group have sacci tympani normally developed (*Bocchoris*), small (*Ategumia*) or absent (*Diasemia*, *Diasemiopsis*), with the fornix tympani in contact with the tympanic frame all around. The male genitalia have a conical to capitate uncus (reduced in *Ategumia*, *Diasemia* and *Bocchoris*), uni- to bicapitate, uncus head naked or with simple and/or bifurcate chaetae; the valvae are ovate, mostly with a convex costa; the fibula is well-developed, straight to arched and emerging from near the costa base (small in *Desmia*, absent in *Bocchoris*, *Diasemia* and *Diasemiopsis*). In the female genitalia, the corpus bursae has a granulose central area or an elongate signum, longitudinal or transverse in orientation, in *Diasemia* and *Bocchoris* invaginated to form a spine; the colliculum is sclerotized, in *Nomophila* and ‘*Samea*’ *multiplicalis* (Guenée, 1854) with an apomorphic blind anterolaterad evagination (diverticulum sensu MUNROE 1973); the antrum is strongly sclerotized, broad tubular or barrel-shaped.

Systematics. Based on our phylogenetic results we place *Arnia* Guenée, 1849 (1 sp.), *Ategumia* Amsel, 1956 (10 spp.), *Bocchoris* Moore, 1885 (31 spp.), *Desmia* Westwood, 1832 (89 spp.), *Diasemia* Hübner, 1825 (13 spp.), *Diasemiopsis* Munroe, 1957 (2 spp.), *Mecyna* Doubleday, 1849 (34 spp.), *Nomophila* Hübner, 1825 (14 spp.), *Samea* Guenée, 1854 (28 spp.) and *Syngamia* (25 spp.)

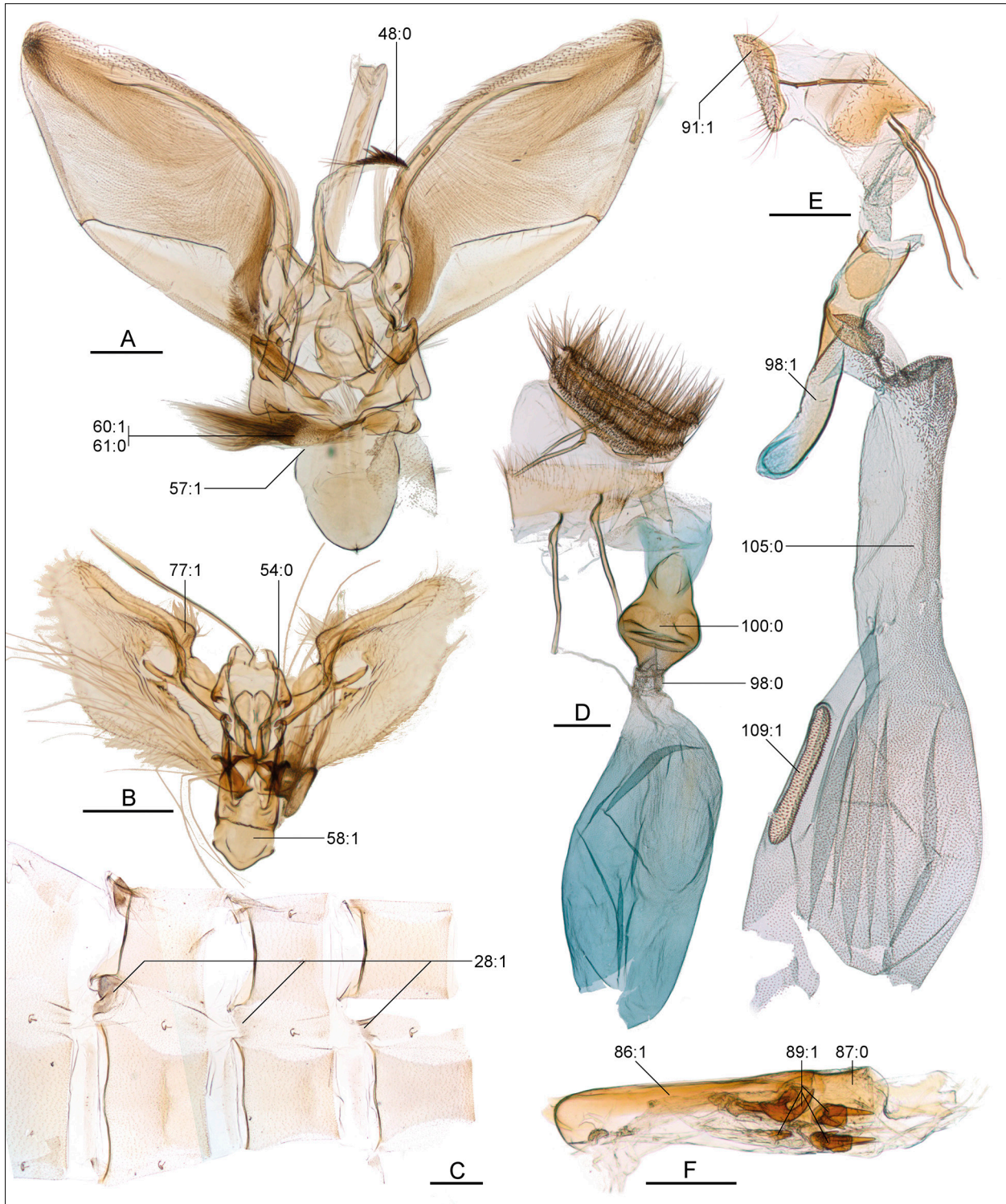


Fig. 13. Nomophilini. **A:** male genitalia of *Desmia tages*, phallus omitted. **B:** male genitalia of *Ategumia ebulealis*, phallus omitted. **C:** abdomen segments 4–7 of male *Samea ecclesialis*. **D:** female genitalia of *Desmia* sp. **E:** female genitalia of *Nomophila noctuella*. **F:** phallus of *Mecyna lutealis*. — **Scale bars:** 500 µm.

here. Furthermore, we place *Crocidocnemis* Warren, 1889 (2 spp.), *Diacme* Warren, 1892 (10 spp.), *Diasemiodes* Munroe, 1957 (4 spp.), *Diathrausta* Lederer, 1863 (20 spp.), *Epipagis* Hübner, 1825 (14 spp.), *Mimophobetron* Munroe, 1950 (1 sp.), *Mimorista* Warren, 1890 (15 spp.), *Niphograptia* Warren, 1892 (1 sp.), *Nothomastix* Warren, 1890 (5 spp.), *Parapilocrocis* Munroe, 1967 (3

spp.), *Pardomima* Warren, 1890 (16 spp.), *Perisyntrocha* Meyrick, 1894 (4 spp.), *Pessocosma* Meyrick, 1884 (4 spp.) and *Sameodes* Snellen, 1880 (15 spp.) in Nomophilini based on morphological characters.

Arnia Guenée, 1849 was synonymized with *Stenia* Duponchel, 1845 (a synonym of *Dolicharthria* Stephens, 1834) by REBEL (1901), a decision that was revoked by

AMSEL (1952). We find *Arnia* as sister to *Mecyna*, and they share a number of morphological features, such as shape of uncus and fibula, multiple dentiform cornuti in the phallus, a central granulose area in the corpus bursae, and a short broad, sclerotized ductus bursae.

Food plants. Larvae are leaf-rollers mainly on Fabaceae, Onagraceae, Rubiaceae and Vitaceae, with occasional records from Begoniaceae, Cordiaceae and Malvaceae (KIMBALL 1965; ALLYSON 1984; SOLIS 2008; JANZEN & HALLWACHS 2009; HAYDEN 2014). *Ategumia* feeds mainly on Melastomataceae, furthermore on Rubiaceae and Bignonaceae, with single records on Fabaceae, Piperaceae and Urticaceae (JANZEN & HALLWACHS 2009). *Bocchoris inspersalis* (Zeller, 1852) is reported from Malvaceae, Fabaceae and Amaranthaceae (GHESQUIÈRE 1942; WAGNER et al. 2008; ROBINSON et al. 2010). *Diasemia* is recorded from Asteraceae, Plantaginaceae and Lecythidaceae (GHESQUIÈRE 1942; ROBINSON et al. 2010), *Syngamia* mainly on Rubiaceae, with further records on Acanthaceae and Asteraceae (JANZEN & HALLWACHS 2009), *Pardomima* was recorded from coffee (Rubiaceae) (MARTIN 1955). Larvae of the monotypic *Mimophobetron* feed on different species of Rubiaceae (JANZEN & HALLWACHS 2009). *Nothomastix klossi* is recorded from *Psychotria* (Rubiaceae) (MILLER et al. 2007).

'*Samea*' *multiplicalis* (Guenée, 1854) and *Niphograptata alboguttalis* (Warren, 1889), whose larvae are used in biological control of aquatic weeds, may represent an aquatic lineage, related to *Crociodocnemis*, whose larvae are not known. Furthermore, *Diasemiopsis ramburialis* was reported to feed on leaves of the aquatic fern *Azolla filiculoides* (Salviniaceae) (FARAHPOUR-HAGHANI et al. 2016).

In the clade Trichaeini + (Nomophilini + Steniini), the larvae of most Trichaeini and of several Nomophilini (especially the early-diverging *Desmia* and *Syngamia*) feed on Rubiaceae. Considering this relationship, we hypothesize that this is the primitive host family for Nomophilini or maybe for the entire clade Trichaeini + (Nomophilini + Steniini), and that Nomophilini has radiated onto other hosts. However, larvae of Steniini, as far as known, are detritivorous.

Remarks. The common form of the male genitalia of Nomophilini is fairly nondescript, with few striking characters: the uncus is usually simple or weakly bifid, the valvae are elliptical, and there is one curved fibula or none. However, particular genera or genus groups show interesting characters, such as modification or loss of the uncus (*Nomophila*, *Ategumia*), distally concave valva (*Samea cancellalis*, *Diacme*), or one pair of apical cornuti in several genera (e.g. *Mecyna*, *Mimorista*, *Samea*, *Epipagis*). Likewise, the shape of the signum may be informative above the genus level. The maculation of the "core" Nomophilini is characteristically chequered, but other taxa (*Desmia*, *Syngamia*, *Mimophobetron*) show other patterns. The "core" Nomophilini is well-characterized by female genitalia. The colliculum is tubular with one or two lateral pockets, and the signa have two forms: commonly a longitudinal granular strip or (much

less commonly) a transverse "moustache" with two more or less connected sections, found in *Samea castellalis* Guenée, 1854 and *Sameodes cancellalis* (Zeller, 1852). An inflated basal costa (74:1) is shared with some Steniini (*Dolicharthria* and *Metasia*).

Samea is paraphyletic with respect to *Nomophila* in our phylogenetic results. Both *S. multiplicalis* and most species of *Nomophila* (see MUNROE 1973) have a large, deeply arched fibula, uncus without large bifid chaetae, and the colliculum extended into a diverticulum.

Nomophila was revised by MUNROE (1973), the African *Pardomima* species by MARTIN (1955), *Syngamia florella* (Stoll in Cramer & Stoll, 1781) and its variations by HEPPNER (2010). This tribe generally corresponds to the *Samea* group of MUNROE (1995).

A simple tubular colliculum and transverse signum (similar to that in *S. castellalis*) are also found in *Diasemiodes*, *Diathrausta*, and *Perisyntrocha* (MUNROE 1956), so Nomophilini seems to be a better tribe for these genera than Steniini. On the other hand, the absence of checkered maculation suggests that further investigation is needed.

4.2.20. Munroe's (1995) *Eulepte* group

Apart from *Syllepte* (see below), only the core of MUNROE'S (1995) *Eulepte* group is not represented in our molecular sampling (three other genera are transferred to Hydririni). For this reason, we do not formally propose it as a tribe. The genera *Eulepte* Hübner, 1825 (6 spp.), *Praeacrosipila* Amsel, 1956 (4 spp.), *Leucochromodes* Amsel, 1956 (8 spp.), and *Mesocondyla* Lederer, 1863 (2 spp.) have oval to moderately attenuate valvae, uncus with bifid chaetae, and a pair of simple vincular androconia with long, hairlike setae. The saccus is elongate in *Mesocondyla* and *Eulepte*, and perhaps most distinctively, most taxa (except *M. dardusalis*) have two inwardly curved fibulae closely set together: one an extension of the sacculus, the other from the face of the valva, just inside and curving in parallel with the saccular fibula. The ductus bursae is elongate in *Eulepte* and *Mesocondyla*, short in *Leucochromodes* and *Praeacrosipila*, and the signum is absent or double. The maculation is yellow with a darker postmedial area, which however also occurs in other taxa (e.g. *Lygropia* species). *Zenamorpha discophoralis* (Hampson, 1899) is another possible member of this group, considering the male genitalia, although it could also belong to Trichaeini.

4.2.21. *Syllepte* Hübner, 1823

Syllepte, the type genus of "Sylleptinae", is a large polyphyletic genus within Spilomelinae, containing 199 valid species (NUSS et al. 2003–2019). The identity of the genus is ambiguous as the type material of its type species, *Syllepte incomptalis* Hübner, 1823 (and not *Phalaena amando* Cramer, 1779, as erroneously stated by KIRTI

& GILL 2007), is lost (GROLL 2017). The illustrations of the male specimens of this species depicted in HÜBNER (1819–1823: 18, pl. [50] figs. 285, 286) are difficult to associate to any known species. The maculation resembles, to some degree, *Bocchoropsis* Amsel, 1956 and specimens of the *Polygrammodes eleuata* (Fabricius, 1777) species group.

4.2.22. Genera removed from Spilomelinae

Aporocosmus Butler, 1886 is transferred to Odontiinae, where it is related to *Thesaurica* Turner, 1915. *Orthoraphis* Hampson, 1896 is transferred to Lathrotelinae.

Hydropionea Hampson, 1917, *Plantegumia* Amsel, 1956 and MUNROE'S (1995) "undescribed genus ex *Boeotarcha* Meyrick" appear to form a group of aberrant Glaphyriinae. MUNROE (1995) probably placed them in Spilomelinae because the males have the gnathos reduced to a transverse band or absent. However, the males possess a retinacular hook, but they do not have the synapomorphies of Pyraustinae. We transfer them to Glaphyriinae s.l. (REGIER et al. 2012). This is supported by 1) narrow valvae with apically separate costa and sacculus, and 2) tympanal organs with large, mesal sacci tympani and large puteoli. A species of *Hydropionea* has been raised on *Capparis uniflora* (JANZEN & HALLWACHS 2009), which fits with Glaphyriinae s.l., a clade best defined as a radiation on mustard-oil producing Brassicales (REGIER et al. 2012).

Phaedropsis leialis (Dognin, 1906) and *Lygropia murinalis* Schaus, 1912 are related and misplaced in Spilomelinae. They have a male retinacular hook, tympanal organs with the fornix at the same level as the venula prima, gnathos with medial process, unmodified valvae, and an ediacaroid signum. This combination of characters is very puzzling; we tentatively place them in Pyraustinae incertae sedis. The host (*Gouania* Jacq.: Rhamnaceae; JANZEN & HALLWACHS 2009) is not informative.

Certain species belong to Pyraustinae incertae sedis. *Lygropia fusalis* Hampson, 1904 and related species are Pyraustinae, based on the editum of comb-tipped scales on the sella, concave costa, the deeply invaginated sacci tympani, and data from the nuclear EF-1a gene. *Blepharomastix haedulalis* (Hulst, 1886) is another with typically pyraustine male genitalia. Females of both taxa have no signum, so their placement in Pyraustinae was overlooked.

4.3. Pyraustinae Meyrick, 1890

Type genus: *Pyrausta* Schrank, 1802

Synapomorphies. 22:1, fornix tympani surface recessed within the frame (unique); 33:1, heterogenous sclerotization of male tergite 8, i.e. with distinct sclerotization

pattern; 55:1, juxta split 10–60% of its length (only in the parsimony trees); 60:1, partly sclerotized chaetose hairpencils articulating with the anterior edge of the vinculum tegumen connection present; 99:1, strongly sclerotized colliculum anterior of the antrum and posterior of the attachment of the ductus seminalis present (not found with parsimony). Slow optimization only: 8:1, direction of third labial palpomere porrect (not found with parsimony); 32:1, anterior edge of male tergite 8 deeply emarginate (only in the parsimony trees); 109:6, anterior-most signum broad, medially constricted, resembling puckered lips (unique; not found with parsimony).

Description. A retinacular hook (frenulum hook sensu FORBES 1926) is present in the male forewing of 13 of the 18 investigated Pyraustinae. The mesothoracic tibia in males has a hidden hairpencil (OHNO 2000; FROLOV et al. 2007). The fornix tympani is recessed within tympanic frame. The hemispherical sacci tympani tend to be large and deep, especially in Pyraustini and Portentomorphini. The shape and large size is paralleled in some Odontiinae. The degree at which the praecinctorium of the tympanal organ is bilobed is neither distinctive for Spilomelinae nor for Pyraustinae, so that this character is unreliable for distinguishing the two subfamilies. Male genitalia have a transtilla inferior (sensu MARION 1954; absent from *Tetridia* and many other taxa) and a sella (sensu MARION 1952) on the inner surface of the valva, often with strong piliform or spatulate hairs (editum sensu MARION 1952); the editum is absent from many taxa. The female genitalia have a long, coiled ductus bursae (absent in several taxa, e.g. *Nascia*, *Ostrinia*, *Uresiphita*). Deciduous cornuti are present.

Appendix bursae present, emerging from the anterior ductus bursae (and not from the corpus bursae) in *Tetridia*, Euclastini and Portentomorphini, or laterally from the corpus bursae in Pyraustini and *Uresiphita*. Signum broad rhombical (Pyraustini), 'puckered lips'-shaped in Euclastini and *Tetridia* Warren, 1890, or ediacaroid in Portentomorphini and *Uresiphita*.

The shapes of the teguminal ridges in SOLIS & MAES (2003: character 9) seem to be good for diagnosing tribes.

Remarks. Plesiomorphic characters shared with the non-euspilomeline clades in Spilomelinae are: absence of a sclerotized strip on the pleural membranes of segment 8 (present in Euclastini); costa straight to concave; saccus of vinculum broadest at the base, without a basal constriction. Deciduous cornuti are paralleled in the Spilomelinae '*Syllepte*' *adductalis* (Walker, 1859) and *Pycnarmon pantherata* (Agroterini). The ediacaroid signum of Portentomorphini and *Uresiphita* is shared with the non-euspilomeline Spilomelinae.

4.3.1. *Tetridia* Warren, 1890

Autapomorphies. 29:1, large, oval pleural scale tufts on each side of the male abdominal segment 7 present, with an opening in its anterior centre (unique); 57:1, basal saccus constricted; 58:1, ratio between saccus length

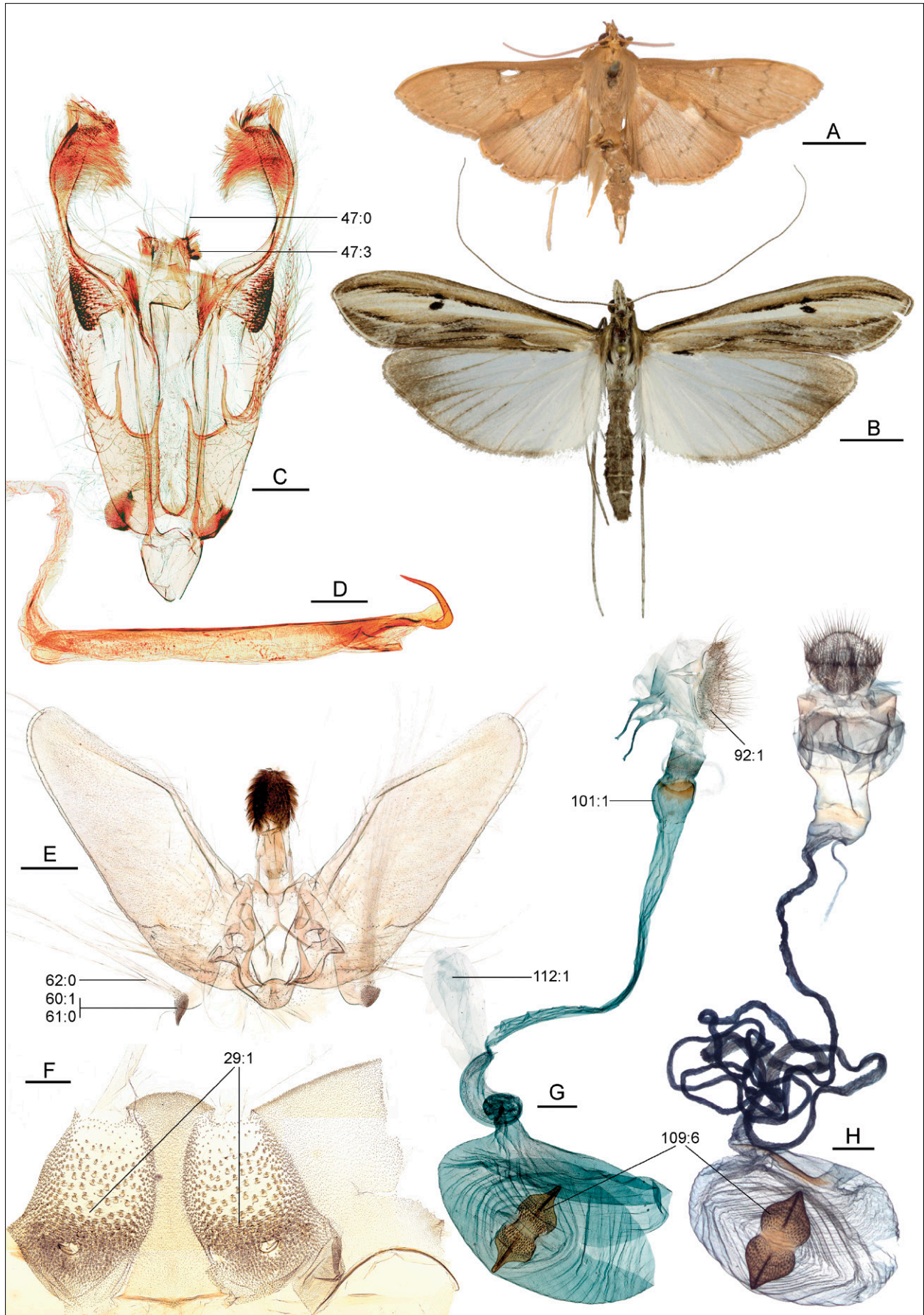


Fig. 14. *Tetridia* (A, C, D, F, H) and *Euclastini* (B, E, G). **A:** adult male of *Tetridia vinacealis*. **B:** adult female of *Euclasta gigantealis*. **C:** male genitalia of *T. vinacealis*. **D:** phallus of *T. vinacealis*. **E:** male genitalia of *E. splendida*. **F:** 7th abdominal segment of male *T. vinacealis*. **G:** female genitalia of *E. splendida*. **H:** female genitalia of *T. vinacealis*. — **Scale bars:** A, B – 5 mm; C–H – 500 μ m.

and sacculus breadth > 1; 63:1, presence of a pair of sclerotized, hair-studded hairpencils articulating with the anteromedian edge of the sacculus; 66:0, general shape of fibula broadly triangular; 72:1, extension (process in some cases) of dorsodistal sacculus present; 76:1, long, sometimes loosely arranged chaetae on surface of costal base present; 86:1, phallus apodeme sclerotisation reduced to a ventral, longitudinally sclerotized strip; 87:1, a distinct sclerite in the posterior phallus apodeme present; 89:0, vesica with single cornutus; 92:1, ventral end of papillae anales larger than dorsal end; 100:0, longitudinal membranous strip in the colliculum sclerotisation absent; 108:1, two or more signa; 110:1, second signum (located posterior of first signum) slim, strip-like. Slow optimization only: 25:0, venulae secundae convergent; 49:1, uncus attached to tegumen as a broad, smooth transition; 90:2, orientation of everted papillae anales posterior; 112:1, appendix bursae present on anterior ductus bursae.

Description. The antennae are longer than the forewing. The uncus has spatulate chaetae in addition to simple, hair-like chaetae; the sacculus broad and triangular, occupying the ventral valva base, and the centre of the dorsal sacculus edge has a robust spine pointing dorsally towards the uncus, and a second, more fragile, curved spine further towards the distal sacculus; the ventral vinculum anteromedially has paired hairpencil-like structures. The signum is broad, medially constricted, resembling puckered lips ('spectacles-shaped' in POPESCU-GORJ & CONSTANTINESCU 1977); the appendix bursae emerges at the anterior end of the ductus bursae. The tegumen ridges cannot be discerned, because the scale-bearing lateral fields of the tegumen are expanded and compress the mesal area into a narrow strip. Therefore, the ridges could be either absent or fused.

Systematics. So far, we place only two species of *Tetridia* here, the type species *T. vinacealis* (Moore, 1877), and *T. caletoralis* (Walker, 1859).

The identity of *T. caletoralis* is still not fully clear, as the type material at NHMUK could not be traced. We used the DNA extract of voucher specimen WPH209 from HAINES & RUBINOFF (2012) for our molecular dataset, but specimens available for morphological study could not be confirmed as conspecific with specimen WPH209, which had no genitalia left for investigation. Instead, for the morphological investigation we used DNA-barcoded material that was in the nearest neighbour BIN of specimen WPH209 in the Barcode of Life Database (BOLD).

KIRTI & GILL (2007) transferred *T. caletoralis* to *Patania*, based on material from the Natural History Museum London. We have seen the NHMUK Pyralidae slide no. 19900 (male) to which KIRTI & GILL (2007) likely refer and agree that this taxon belongs to *Patania* or at least to Agrotini. However, we have doubts about the correct identification of the material referred to by KIRTI & GILL (2007), and we have not seen the specimen from which NHMUK Pyralidae slide no. 19900 originates. SHIBUYA (1928) mentions four characters in which *T. vinacealis*, the type species of *Tetridia*, differs from *T. caletoralis*:

body and wings fuscous; legs ferruginous; both wings with a series of terminal black spots; ante- and postmedian lines on the forewing distinctly different in the dorsal half. KIRTI & GILL (2007), on the other hand, state that "this species [*T. caletoralis*] drastically differs from the type species of the genus *Tetridia* Warren i.e., *vinacealis* Moore" (KIRTI & GILL 2007: p. 266). Many adult Pyraustinae and Spilomelinae exhibit a wing pattern similar to that of *T. vinacealis*, and we assume that KIRTI & GILL (2007) misidentified their material. A revision of the genus might bring certainty on this matter and might answer the question whether this taxon should be placed in a separate tribe.

Food plants. *Tetridia caletoralis* is recorded from *Shorea robusta* (Dipterocarpaceae) (ROBINSON et al. 2010).

Remarks. The paired hairpencil-like structures attached anteromedially to the vinculum are a plesiomorphy shared with *Lamprosema* in Spilomelinae: Hydririni; the 'puckered lips'-shaped signum is shared with Euclastini; the attachment of the appendix bursae to the anterior end of the ductus bursae is shared with Euclastini and Portentomorphini.

4.3.2. Euclastini Popescu-Gorj & Constantinescu, 1977 stat.rev.

Type genus: *Euclasta* Lederer, 1855

Synapomorphies. 10:1, length of maxillary palpi minute to obsolete, cannot hypothetically come in contact with each other (not found with parsimony); 16:0, metatibial proximal inner spur shorter than half of tibial segment between this and the distal spur pair; 47:2, multifurcate structure of uncus head chaetae (unique); 65:0, absence of fibula emerging from dorsal valva base near costa base (not found with parsimony); 78:2, general shape of post-basal costa (not the entire dorsal valva edge) convex. Slow optimization only: 18:1, scale brush at costal base of forewing underside in males formed into a retinacular hook (not found with parsimony); 44:1, shape of uncus capitata (not found with parsimony); 49:1, attachment of uncus to tegumen broad, smooth transition; 109:6, shape of anterior-most signum broad and medially constricted (only in the parsimony trees); 112:1, appendix bursae present on anterior ductus bursae.

Description. The imagines are long-legged and gracile with narrow, apically rounded forewings with brown dorsal ground colour, traversed by a whitish band from wing base to apex, and two dark discal spots. The forewings are held parallel to the frontally raised body when resting, somewhat resembling *Lineodes* (Spilomelinae: Lineodini). The uncus has a bulbous head with multifid chaetae; the valvae are trapezoid, with the straight ventral valva edge parallel to the straight costa that spans the basal half of the dorsal valva edge; and the distal dorsal valva edge runs more or less straight towards valva apex. The fibula is absent. The signum is broad, medially constricted and laterally slimly extended, resembling puck-

ered lips ('spectacles-shaped' in POPESCU-GORJ & CONSTANTINESCU 1977); the appendix bursae emerges at the anterior end of the ductus bursae.

The tegumen ridges are closely parallel, connected by anterior crossbar at junction of V, like a two-legged "Y". **Systematics.** *Euclasta* (17 spp.) is the only included genus.

Food plants. All known host plant records are from Apocynaceae, with *Euclasta splendidalis* (Herrich-Schäffer, 1848) on *Periploca graeca*, *E. warreni* Distant, 1892 on *Acokanthera oppositifolia* and *E. maceratalis* Lederer, 1863 on *Gymnanthera nitida* (POPESCU-GORJ & CONSTANTINESCU 1977; COMMON 1990).

Remarks. The valva shape is somewhat paralleled in *Chilopionea* Munroe, 1964 and some species of *Chilochroma* Amsel, 1956 (Pyraustini). The 'puckered lips'-shaped signum is shared with *Tetridia*, and the origin of the appendix bursae at the anterior end of the ductus bursae is shared with Portentomorphini and *Tetridia*.

MAES (2000) postulates a close relationship between *Paschiodes* Hampson, 1913, *Duzulla* Amsel, 1952 and *Euclasta*. We have not studied *Duzulla* and the figure and description in AMSEL (1952) are inconclusive, and we therefore refrain from speculation. We have seen material of *Paschiodes*, and the presence of bifid chaetae (instead of multifid chaetae as in Euclastini) makes this relationship unlikely. Only one of the five species of *Paschiodes* (*P. ugandae* Maes, 2005) exhibits an appendix bursae, and this emerges from the side of the corpus bursae, a character corresponding to Pyraustini and to *Uresiphita* (see remarks under Portentomorphini). Until an analysis on the phylogenetic relationship of *Paschiodes* is done, we refrain from placing the genus in one of the proposed tribes.

Saucrobotys resembles *Euclasta* in the bulbous uncus head, the valva shape and the absence of a fibula and sella in the male genitalia, and in the appendix bursae emerging from the anterior end of the ductus bursae as well as the 'puckered lips'-shaped signum. The uncus chaetae are bisetose and not multisetose as in *Euclasta*. *Saucrobotys* larvae also feed on Apocynaceae, with *S. futilalis* (Lederer, 1863) on *Apocynum* and *Asclepias syriaca*, where the larvae live gregarious in a nest made from leaves and silk; the plant associations for larvae and pupae of *S. fumoferalis* (Hulst, 1886) are doubtful (MUNROE 1976a). Because of the bisetose uncus chaetae, we refrain from placing *Saucrobotys* in Euclastini. *Euclasta* has been revised by POPESCU-GORJ & CONSTANTINESCU (1977), the two species of *Saucrobotys* are treated in MUNROE (1976a).

4.3.3. (Portentomorphini + *Uresiphita*) + Pyraustini

Synapomorphies. 20:1, splitting of praecinctorium weak to absent. 25:1, Course of venulae secundae parallel or diverging in posterior half (only in parsimony trees); 65:1, fibula emerging from dorsal valva base near

costa base (only in parsimony trees); Slow optimization only: 109:3, anterior-most signum transverse rhombical to cross-shaped, with longitudinal axis shorter than or equally long as transverse one.

4.3.4. Portentomorphini + *Uresiphita*

Synapomorphies. 46:0, chaetae on surface of uncus head(s) absent; 61:1, two or more hairpencil sclerites on each side of the genitalia (articulated with each other via membranes); 82:1, costa detached from valval area, the costa protruding freely dorsad (unique). Slow optimization only: 21:1, lobulus on lateral edge of tympanal case present; 44:1, shape of uncus capitate; 114:1, posterior point of attachment of appendix bursae on corpus bursae.

4.3.5. Portentomorphini Amsel, 1956 stat.rev.

Type genus: *Portentomorpha* Amsel, 1956

Synapomorphies. 5:1, sensillar setae of males at basal antennomeres > 50% relative to diameter of basal antennomeres (not found with parsimony); 46:0, chaetae absent from surface of uncus head(s); 67:3, fibula generally oriented dorsally towards tegumen or uncus. Slow optimization only: 51:3, transtillum arms large rectangular, medioventrally with finger-like process (transtilla inferior sensu MARION 1954). The parsimony trees add two characters: 21:1 and 82:1.

Description. The male genitalia have the costa detached from the valva and projecting freely dorsad, bearing a terminal field of setae. A thin, elongate, curved, often articulated fibula emerges from the centre of the dorsal valva edge, reaching dorsad; the actual valva consists of the far dorsad reaching sacculus which ends in a terminal setose field in the valva apex; the sacculus is large and membranous. The uncus is narrow, naked, and often distally forked. In addition to these synapomorphies, the appendix bursae emerges at the anterior end of the ductus bursae close to the transition into the corpus bursae, in *Pioneabathra* J.C. Shaffer & Munroe, 2007 laterally attached to the corpus bursae. The signum is a four-armed star in *Hyalobathra* Meyrick, 1885 and *Cryptosara* E. L. Martin in Marion, 1957, an ediacaroid sclerite in *Portentomorpha*, and in *Pioneabathra* and *Isocentris filalis* (Guenée, 1854) there are two large, opposing granulose areas. The maculation is basically yellow but often has a distinctively red or orange postmedial area (or entirely pink: e.g. *Hyalobathra unicolor* (Warren, 1895)). The tegumen is short and evenly sclerotized, without dorsal ridges.

Systematics. Based on our phylogenetic results we place *Hyalobathra* (21 spp.), *Cryptosara* (3 spp.) and *Portentomorpha* (1 sp.) in Portentomorphini. MUNROE (1976a) recognizes a group of related genera comprising *Portentomorpha*, *Cryptosara*, *Isocentris* Meyrick, 1887 (7 spp.) and *Hyalobathra*. We concur with MUNROE'S (1976a)

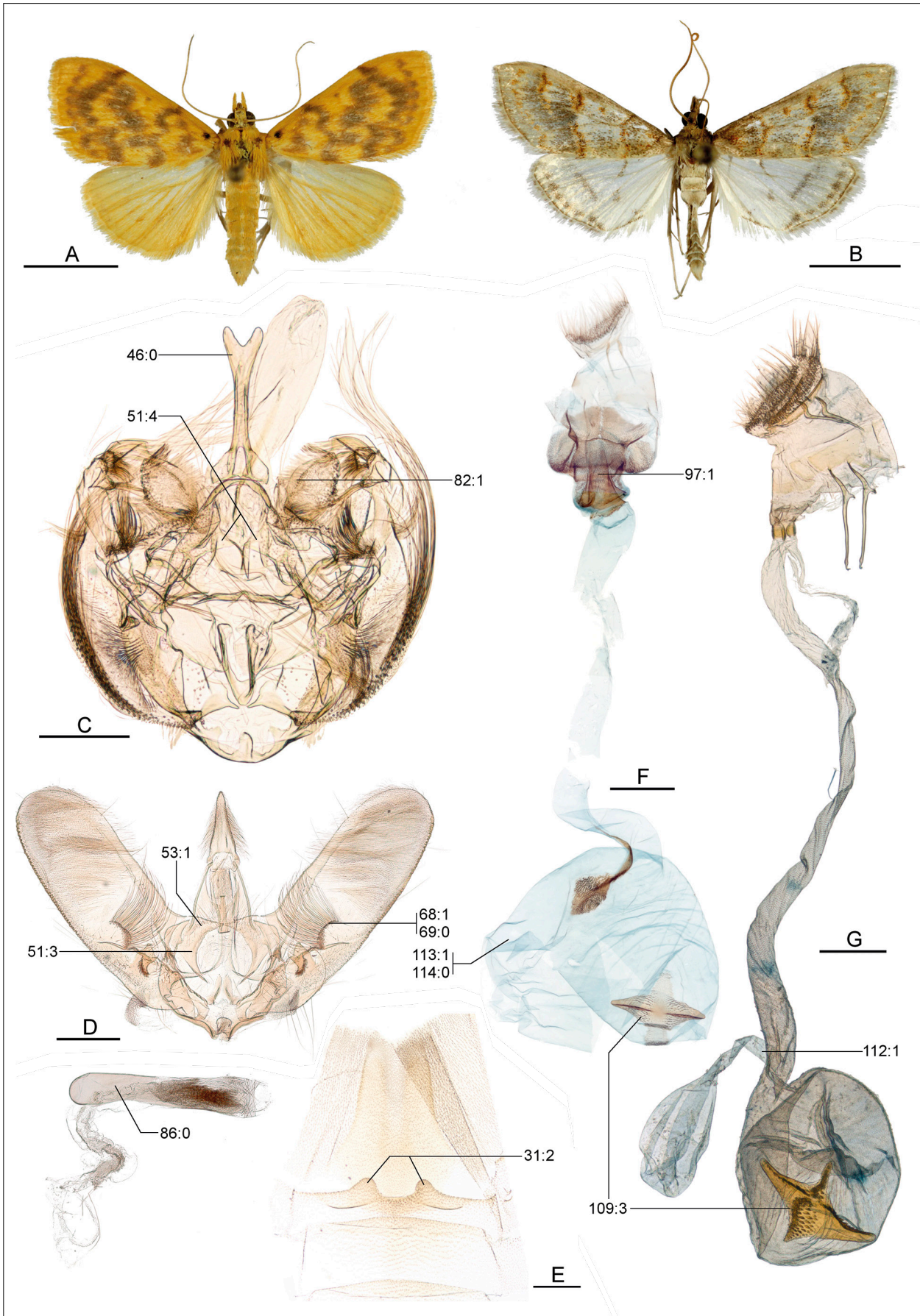


Fig. 15. Portentomorphini (A, C, E, G) and Pyraustini (B, D, F). **A:** adult female of *Pioneabathra olesialis*. **B:** adult male of *Pagyda* sp. **C:** male genitalia of *Hyalobathra illectalis*, phallus omitted. **D:** male genitalia of *Achyra nudalis*. **E:** sternites 6–8 of male *Cryptosara caritalis*. **F:** female genitalia of *Anania coronata*. **G:** female genitalia of *H. illectalis*. — **Scale bars:** A, B – 5 mm; C–G – 500 µm.

composition of this group, here defined as Portentomorphini, and further include the African monotypic genus *Pioneabathra*.

Food plants. Most food plant records are from Phyllanthaceae (Malpighiales): The monotypic *Portentomorpha* feeds on *Margaritaria nobilis*, *Hyalobathra* species on *Glochidion* and *Phyllanthus*, but they are also recorded from *Abrus* (Fabaceae) and *Helianthus* (Asteraceae); *Iso-centris filalis* (Guenée, 1854) and the monotypic *Pioneabathra* on *Flueggea*, the latter also on *Solanum* (SUTRISNO & HORAK 2003; JANZEN & HALLWACHS 2009; ROBINSON et al. 2010).

Remarks. The origin of the appendix bursae at the anterior end of the ductus bursae is shared with *Tetridia* and *Euclastini*.

We consistently find *Uresiphita* Hübner, 1825 to be sister to Portentomorphini in our phylogenetic analyses. *Uresiphita* does not share any of the unusual synapomorphies of the other Portentomorphini, and we therefore do not include it in the tribe. Slow optimization in WinClada results in the following three synapomorphies: 5:1, length of sensillar setae at basal antennomeres relative to diameter of basal antennomeres (male) > 50%; 21:1, lobules on lateral edge of tympanal case present; 54:2, depth of gap or split of juxta > 60% of dorsoventral length of juxta to complete division into two juxta arms. Furthermore, *Uresiphita* shares with Portentomorphini the elongate ediacaroid signum. Species of *Uresiphita* mainly feed on Fabaceae (MUNROE 1976a).

Herpetobotys Maes, 2001 (3 spp.) shares the ediacaroid signum and the emergence of the appendix bursae at the anterior ductus bursae with *Uresiphita*, but the male genitalia are different. For now, we leave *Uresiphita* and *Herpetobotys* incertae sedis in Pyraustinae.

The Australian species of *Hyalobathra* have been revised by SUTRISNO & HORAK (2003).

4.3.6. Pyraustini Meyrick, 1890 stat.rev.

Type genus: *Pyrausta* Schrank, 1802
= *Botydes* Blanchard, 1840
= *Ennychites* Duponchel, 1845

Synapomorphies. 9:0, third labial palpomere well developed in both sexes; 78:1, general shape of post-basal costa (not the entire dorsal valva edge) straight; 113:1, appendix bursae on corpus bursae present. Slow optimization only: 18:1, retinacular hook present in males. The parsimony trees imply a very different diagnosis: 5:0, basal antennomeres of male with sensillae ≤ 50% their diameter; 10:0, maxillary palpi long enough to contact each other; 44:0, uncus conical, not capitate.

Description. The uncus is broad to elongate conical, without a prominent neck constriction and bulbous head; the uncus has fine setae or robust bifurcate chaetae; many taxa with a lobate process (sella sensu MARION 1952) on the central inner valva, carrying long monofilament or multifid chaetae (editum sensu MARION 1952). The signum is broad and rhombical, with the transverse axis

longer than the longitudinal axis. The tegumen ridges are parallel, widely spaced, and not connected.

Systematics. According to our phylogenetic results, we place the following taxa in Pyraustini: *Achyra* Guenée, 1849 (19 spp.), *Anania* (117 spp.), *Hyalorista* Warren, 1892 (5 spp.), *Loxostege* (90 spp.), *Oenobotys* Munroe, 1976 (5 spp.), *Ostrinia* Hübner, 1825 (21 spp.), *Pagyda* Walker, 1859 (26 spp.), *Paracorsia* Marion, 1959 (1 sp.), *Psammotis* Hübner, 1825 (8 spp.), *Pseudopyrausta* Amsel, 1956 (6 spp.), *Pyrausta* (341 spp.) and *Sitochroa* Hübner, 1825 (10 spp.).

Based on morphology, we furthermore place the following genera in Pyraustini: *Adoxobotys* Munroe, 1978 (3 spp.), *Aglaops* Warren, 1892 (4 spp.), *Anamalaia* Munroe & Mutuura, 1969 (1 sp.), *Arenochroa* Munroe, 1976 (1 sp.), *Aurorobotys* Munroe & Mutuura, 1971 (2 spp.), *Callibotys* Munroe & Mutuura, 1969 (3 spp.), *Carminibotys* Munroe & Mutuura, 1971 (1 sp.), *Ceuthobotys* Munroe, 1978 (1 sp.), *Chilochroma* Amsel, 1956 (4 spp.), *Chilocorsia* Munroe, 1964 (1 sp.), *Chilopionea* Munroe, 1964 (1 sp.), *Circobotys* Butler, 1879 (19 spp.), *Crocidophora* Lederer, 1863 (24 spp.), *Crypsitya* Meyrick, 1894 (8 spp.), *Cybalobotys* Maes, 2001 (3 spp.), *Deltobotys* Munroe, 1964 (3 spp.), *Demobotys* Munroe & Mutuura, 1969 (2 spp.), *Ecpyrrhorhoe* Hübner, 1825 (12 spp.), *Epicorsia* Hübner, 1818 (9 spp.), *Epiparbatia* Caradja, 1925 (2 spp.), *Eumorphobotys* Munroe & Mutuura, 1969 (2 spp.), *Fumibotys* Munroe, 1976 (1 sp.), *Gynenomus* Munroe & Mutuura, 1968 (2 spp.), *Hahncappsia* Munroe, 1976 (39 spp.), *Helvibotys* Munroe, 1976 (5 spp.), *Limbobotys* Munroe & Mutuura, 1970 (5 spp.), *Munroeodes* Amsel, 1957 (4 spp.), *Nascia* J. Curtis, 1835 (3 spp.), *Nadeloides* Klima, 1939 (2 spp.), *Neoepicorsia* Munroe, 1964 (7 spp.), *Neohelvibotys* Munroe, 1976 (9 spp.), *Nephelobotys* Munroe & Mutuura, 1970 (1 sp.), *Nomis* Motschulsky, 1861 (4 spp.), *Oronomus* Munroe & Mutuura, 1968 (1 sp.), *Palepicorsia* Maes, 1995 (1 sp.), *Paranomus* Munroe & Mutuura, 1968 (4 spp.), *Paratalanta* Meyrick, 1890 (9 spp.), *Parbatia* Moore, 1888 (6 spp.), *Perispasta* Zeller, 1876 (1 sp.), *Placosaris* Meyrick, 1897 (20 spp.), *Powysia* Maes, 2006 (1 sp.), *Prooedema* Hampson, 1896 (1 sp.), *Protepicorsia* Munroe, 1964 (13 spp.), *Pseudopicorsia* Munroe, 1964 (4 spp.), *Pseudognathobotys* Maes, 2001 (2 spp.), *Pseudopagyda* Slamka, 2013 (3 spp.), *Pseudopolygrammodes* Munroe & Mutuura, 1969 (1 sp.), *Pyrasia* M. O. Martin, 1986 (1 sp.), *Sarabotys* Munroe, 1964 (2 spp.), *Sclerocona* Meyrick, 1890 (1 sp.), *Sinibotys* Munroe & Mutuura, 1969 (5 spp.), *Thivolleo* Maes, 2006 (4 spp.), *Thliptoceras* Warren, 1890 (31 spp.), *Toxobotys* Munroe & Mutuura, 1968 (3 spp.), *Vittabotys* Munroe & Mutuura, 1970 (1 sp.) and *Xanthostege* Munroe, 1976 (2 spp.).

Food plants. *Achyra*, *Anania*, *Hyalorista*, *Loxostege* and *Sitochroa* are polyphagous on a variety of host plants (MUNROE 1976a; ROBINSON et al. 2010; JANZEN & HALLWACHS 2009). The Central American species of *Pyrausta* mainly feed on Lamiaceae, Verbenaceae, Amaranthaceae (JANZEN & HALLWACHS 2009). *Oenobotys* is recorded from *Eupatorium* (Asteraceae) (MUNROE 1976a).

Pagyda species feed on Verbenaceae and Scrophulariaceae, *Psammotis* on Lamiaceae, and *Pseudopyrausta* on *Lantana* (Verbenaceae) (ROBINSON et al. 2010). The monotypic *Paracorsia* is mainly found on Fabaceae (*Genista*, *Ulex*, *Cytisus*, *Phaseolus*), but also on Scrophulariaceae (*Verbascum*) (LHOMME 1935).

Remarks. Our concept of Pyraustini still comprises the majority of the genera and species of Pyraustinae. Although we do not further subdivide the tribe, many characters would provide good evidence. For example, the spatulate scales of the editum characterize many genera. *Achyra*, *Loxostege*, *Powysia* and *Sitochroa* share a unique apomorphic anterior directed projection medially on the frons (1:1). Species of *Anania* share a unique synapomorphic cone-shaped central structure in the antrum (97:1) (LERAUT 2005a; TRÄNKNER et al. 2009).

5. Discussion

The phylogenetic analysis of our dataset results in the same relationships among Crambidae as found by REGIER et al. (2012) based on a different set of molecular markers that overlaps with our dataset in part of the CAD gene. Because of the low number of Crambidae outgroup taxa in our dataset, comparison with the topology of REGIER et al. (2012) is only possible to a limited degree, but our results reflect their findings where the “Wet Habitat Clade” is sister to the clade of Crambinae + Scopariinae.

REGIER et al. (2012) did not include a representative of the *Sufetula* genus group in their analysis. We include *Sufetula* in our dataset, and we find it to fall outside of Spilomelinae, agreeing HAYDEN (2013) and MINET (2015) who argued for the exclusion of the *Sufetula* group from Spilomelinae. Instead, *Sufetula* is sister to the “CAMMSS clade” minus Musotiminae sensu REGIER et al. (2012). MINET (2015) re-established the name Lathrotelinae on a subfamily rank for the *Sufetula* group and placed the taxon near Acentropinae based on shared characters of the sternum on abdominal segment A2 and the ovipositor. A phylogenetic analysis of a larger taxon sampling of Crambidae, including all currently accepted subfamilies, is necessary to investigate the relationship of Lathrotelinae within Crambidae. In his morphology-based phylogenetic analysis of Australian Spilomelinae, SUTRISNO (2002a) finds *Diploseustis*, now in Lathrotelinae (MINET 2015), as subordinate in Spilomelinae, and sister to the monotypic *Aboetheta*.

Wurthiinae, with the single genus *Niphopyralis* (= *Wurthia*), was originally described in Arctiidae (ROEPKE 1916). KEMNER (1923) synonymised the group with Schoenobiinae, where MUNROE (1958) retained it, while LEWVANICH (1981) transferred it to Pyraustinae (s.l.). REGIER et al. (2012) found *Niphopyralis* to be ingroup of a strongly supported Spilomelinae, and consequently synonymized Wurthiinae with Spilomelinae. We confirm that *Niphopyralis* belongs in Spilomelinae and assign it

to Wurthiini based on our phylogenetic results. As in the studies of MUTANEN et al. (2010) and REGIER et al. (2012), this taxon exhibits a very long terminal branch in our phylogenetic results (Fig. 1). The RogueNaRok analysis marked *Niphopyralis* as rogue taxon, but we decided to keep it in the dataset as we wanted to investigate its relationship with other Spilomelinae (see 3.3.). Most of the observed substitutions in *N. chionesis* relative to other investigated taxa are synonymous, i.e. they do not cause a change in the translated amino acid.

We find little congruence between our phylogenetic results and those of the study by SUTRISNO (2002a) based on 42 external and genital characters of adult moths of selected Australian Spilomelinae, partly due to the little taxon overlap between the two datasets. SUTRISNO (2002a) proposed two synapomorphies for Spilomelinae, namely a strongly bilobed praecinctorium and the absence of a retinacular hook. We find the former character to not be consistent among Spilomelinae; the latter character is indeed not found among Spilomelinae, but present in most Pyraustinae, although it is reduced in many taxa. The common findings in both phylogenies are: *Isocentris* + *Hyalobathra*, which we place in Portentomorphini; *Hymenia* + *Spoladea*, both in Hymeniini; *Hymenoptychis* + *Tatobotys* (misspelled as ‘*Tatabotys*’ in SUTRISNO 2002a) are placed in Steniini. Furthermore, *Agrioglypta*, *Chrysothyridia*, *Didymostoma*, *Dysallacta*, *Glyphodes*, *Synclera* and *Talanga* form a monophylum in SUTRISNO (2002a), and we place all seven genera in Margaroniini. We also find the synapomorphies proposed by SUTRISNO (2002a) among our synapomorphies for this clade, i.e. a heterogeneous sclerotization of male tergite 8 (character 33:1), and two signa (character 108:1).

Our phylogenetic results largely reflect those of the study of HAINES & RUBINOFF (2012) on *Omiodes*. In their phylogram (fig. 2 therein), nine of our proposed Spilomelinae tribes can be identified: Udeini (*Udea*), Agroterini (*Patania*, *Pleuroptya*), Spilomelini (*Cnaphalocrocis*, species misplaced in ‘*Phostria*’), Hymeniini (*Spoladea*), Herpetogrammatini (*Herpetogramma*), Trichaeini (*Prophantis*), Nomophilini (*Nomophila*, *Sameodes*), Steniini (*Bradina*, *Piletocera*), and Margaroniini (‘*Omiodes*’ *basalticalis* and its sister clade). Interestingly, HAINES & RUBINOFF (2012) found a clade comprising the still unplaced genera *Prorodes*, *Syllepte* and *Coptobasis* as sister to *Bradina* + *Piletocera*.

The GENES- and TIGER-partitioned results differ in topology, the most fundamental difference being the placement of Spilomelini, which in the GENES-partitioned analyses is sister to Margaroniini (with PP << 0.9; see dotted line in Fig. 1). Other differences include the lack of support (i.e. PP < 0.9) in TIGER-partitioned analyses for the monophyla *Midila* + *Schoenobius*, (*Psammotis* + *Pseudopyrausta* + *Anania*), and Udeini + Lineodini.

WAHLBERG et al. (2005) reported synergistic effects of combined morphological and molecular data for their phylogenetic analysis of Papilionoidea, and in their review of studies using these two kinds of data, WORTLEY & SCOTLAND (2006) find that most often node resolution

and support increase with the addition of morphological data to a genetic dataset. In our results, the phylogram is nearly fully resolved, and most nodes have high support even in the dataset only comprising the molecular data (see posterior probabilities below branches in Fig. 1). The only significant exception is within the Margaroniini clade, where resolution is poor, and observed relationships as well as their support vary across the differently partitioned analyses. In contrast to previous authors, the addition of morphological data to our molecular dataset does not result in an increase in topology resolution or branch support.

Based on the poor performance of preliminary analyses which included the morphological coding of the Crambidae outgroup, we decided to omit this part of the data. The problems mainly concerned the convergence of the parallel MrBayes runs and resulted in ESS < 100 for several parameters and a somewhat different topology, where Pyraustinae is sister to a monophylum of Spilomelinae and the Crambidae outgroup. Due to the insufficient ESS, this alternative topology was rejected. Furthermore, the choice and circumscription of the morphological characters focus on Spilomelinae and Pyraustinae, and for many characters, we are not confident about drawing homologies with other groups of Crambidae. At the same time, other crambids exhibit characters that are not present in Spilomelinae and Pyraustinae, e.g. the well-developed gnathos of Scopariinae, Crambinae, Schoenobiinae, Glaphyriinae and other groups. It is unlikely to get meaningful results for the phylogeny of Spilomelinae if morphology is coded, for example, based on the characters defined by LANDRY (1995) for Crambini, or by SUTRISNO (2002b) for the Australian *Glyphodes* species and resembling genera. Consequently, a morphomatrix that covers characters from all Crambidae taxa and that is based on a less biased taxon sampling would be necessary to better reflect the morphological diversity of the focus group and to lead to more meaningful phylogenetic results.

In contrast to the other excluded Crambidae outgroup taxa, we choose to retain the Lathrotelinae *Sufetula* in the final morphological data matrix in order to investigate its placement in the phylogeny based on all available data. *Sufetula* was recently removed from Spilomelinae (MINNET 2015), and we concur with this decision as we find the genus to not belong to Spilomelinae in our phylogenetic results.

Pyraustinae and Spilomelinae are both strongly supported monophyletic and sister to each other, as found by REGIER et al. (2012), but opposed to SOLIS & MAES (2003) who found the two groups distantly related. The difference in the structure of the fornix tympani, recessed within the tympanic frame in Pyraustinae and projecting ventrally beyond the tympanic frame in Spilomelinae, is the most consistent character for distinguishing the two groups, and underlines the importance of the tympana for pyraloid systematics. FORBES (1926: p. 332) mentions that the absence or presence of the retinacular hook separates Pyraustinae (s.l.) into two “mainly if not wholly

natural lines”, i.e. Spilomelinae and Pyraustinae sensu stricto. We concur with FORBES (1926), and furthermore consider the presence of a retinacular hook the plesiomorphic character state as it is found in a number of taxa in the sister group of Spilomelinae + Pyraustinae, e.g. in Scopariinae (NUSS 2005), Crambinae (LANDRY 1995) and Schoenobiinae (LEWVANICH 1981); see SAUTER (1973) for a detailed study on this character among Pyraloidea. The retinacular hook is absent in all investigated Spilomelinae, and it may therefore serve as a diagnostic character for the group. In other subfamilies, however, the presence or absence of this structure in males is highly variable at the generic (SOLIS & MAES 2003) or species level (NUSS 2005).

Character 115 (locality of larval feeding) is the only character of the immature life stage, and the only character not concerning morphology. We chose to include this character as we considered it as potentially carrying phylogenetic information. Although data coverage for this character is only about 40%, some statements can be made from the data: For most taxa, there is no apparent association between phylogenetic lineage and larval feeding locality. The majority of coded taxa has larvae that feed concealed in rolled or spun leaves or in a web (character state 115:0). This is the main feeding locality for Margaroniini larvae, although some (*Agathodes*, *Liopasia*, *Maruca*, *Terastia*) are partly or entirely borers in stems, branches, flowers, pods and/or fruits. An interesting association of potential phylogenetic value is the feeding of *Dolicharthria* larvae on decaying or dead plant matter (115:5), a behaviour that is observed in other Steniini as well (see ‘Food plants’ in 4.2.18.).

Larval host plants and feeding modes (internal vs. external; leaf rolling, leaf webbing etc.) are considered a useful source for future research on phylogenetic relationships among Spilomelinae and Pyraloidea in general. A study by SEGAR et al. (2017) on phylogenetic predictions of host plant use in Pyraloidea and Geometridae found that host plant preference is phylogenetically relatively conserved in snout moths. The host plants associations of the taxa studied here support this observation, e.g. Lineodini almost exclusively feeding on Solanaceae, Asciodini commonly on Caryophyllales, and most Portentomorphini on Phyllanthaceae.

The majority of investigated Pyraustinae genera is placed in Pyraustini, a rather homogenous group which mainly varies in the shape of the valva and of the sclerotised processes on the inner valva surface, as well as in the uncus shape, although the spectrum of uncus variation is far narrower than in Spilomelinae. MUNROE (1995) was uncertain about the inclusion of the Neotropical *Portentomorpha* and the related Old World *Hyalobathra* into his concept of Pyraustinae (Pyraustini sensu MUNROE 1995). In our phylogenetic results, both genera are part of Pyraustinae, and they are placed in Portentomorphini. However, we find *Hyalobathra* to be closer related to the African *Cryptosara*. *Tetridia*, the sister to all other phylogenetically investigated Pyraustinae, requires taxonomical revision (see Systematics under 4.3.1.).

Spilomelinae is found highly supported monophyletic in our analysis, supporting MUNROE'S (1995) opinion of Spilomelinae being "at least in large part" monophyletic, while contradicting MINET (1982) and SOLIS & MAES (2003) who perceived Spilomelinae as a para- or polyphyletic assemblage. The only uniquely derived apomorphy common to all investigated Spilomelinae is the ventrad projecting fornix tympani, a character present in MINET'S (1982) circumscription of the group. A (strongly) bilobed praecinctorium, considered diagnostic by MINET (1982) and SUTRISNO (2002a), is found to be homoplastic. It is absent in several investigated Spilomelinae and present in a number of Pyraustinae, and therefore of no diagnostic use. According to SOLIS & MAES (2003) a bilobed praecinctorium is also present in Midilinae. Absence characters like the lack of chaetosemata, the subcostal retinacular hook, and a well-developed gnathos in males, as well as the large rhombical signum in females are not exclusive for Spilomelinae. The loss of the retinacular hook is a synapomorphy of Spilomelinae, but it is paralleled in some Pyraustinae. The character of distinctly tapered spinulae (MINET 1982) was not investigated. According to ALLYSON (1981, 1984), there are no diagnostic morphological characters distinguishing larvae of Pyraustinae from those of Spilomelinae.

In our phylogenetic results, the tribe Margaroniini comprises the most sampled species. This could be due to a sampling bias, but the large number of taxa attributed to the tribe (currently 67 genera with 1,044 species) supports this view of Margaroniini being the most diverse clade in Spilomelinae. Margaroniini is predominantly tropical and subtropical in distribution. Apart from comprising a large number of genera, the tribe also contains many species-rich genera, like *Palpita*, *Glyphodes*, *Omiodes* and *Diaphania*.

We find several well-supported relationships among Margaroniini: the larvae of *Liopasia*, *Terastia* and *Agathodes* all feed on *Erythrina*, and imagines of the three moth genera share a similar wing pattern (SOURAKOV et al. 2015). We find the three genera to be closely related, with *Liopasia* being sister to *Agathodes* + *Terastia*, as reported by SOURAKOV et al. (2015). The *Glyphodes* group, as circumscribed by SUTRISNO (2002b) and SUTRISNO et al. (2006), further includes *Obtusipalpis* as well as the *Dichocrocis zebraalis* species complex. *Conogethes pandamalis*, related to the species complex of the yellow peach moth *C. punctiferalis*, is found to be sister to the Neotropical genus *Azochis*. They share a similar anatomy of the uncus, tegumen and valvae, and a similar structure of the hairpencil scales. The phylogenetic relationships to species with a highly similar wing pattern, like the African *Marwitzia* species (MAES 1998b) or species of the Neotropical *Polygrammodes eleuata* complex, is not known.

The sister group of *Omiodes*, as investigated by HAINES & RUBINOFF (2012), is still not known due to the extensive polytomy in Margaroniini. We can, however, rule out *Cnaphalocrocis* as sister group, which we place in Spilomelini.

The poorly resolved relationships among Margaroniini should be addressed through the choice of better-suited genetic markers, e.g. DDC which has a substitution rate similar to COI (WAHLBERG & WHEAT 2008). Furthermore, the morphological dataset can be improved to incorporate additional characters, e.g. structure of the hairpencil pads and scales, shape and sclerotisation patterns of the valvae, and shape and structure of the tegumen and uncus.

With the morphological dataset at hand and the phylogenetic results, we start to gain a better understanding of functional morphology of the genitalia and character correlations. In most investigated Spilomelinae, the presence of sclerotised membraneous strips on the pleural membranes of the male abdominal segment 8 corresponds with the presence of hairpencils, and we assume that the strips might serve as muscular attachment sites for retraction of the hairpencils. In Pyraustinae, this correlation is absent, and we find sclerites on the pleurites of the male segment 8 only in *Euclasta*, although most pyraustines exhibit 'simple' hairpencils, i.e. a single small hairpencil pad on each side of the anterior vinculum-tegumen connection, studded with one type of hairpencil scales. The longitudinal membranous strip in the female genitalia's antrum possibly functions as a stretching zone during copulation, when the male transfers the spermatophore. This character is present in species with narrow antrum while it is rarely found in species with a broad antrum; it occurs in both Spilomelinae and Pyraustinae. We find the fibula and the distal sacculus often in close spatial association, and the ventral valva margin is often less sclerotised in this area, suggesting that this complex might function as a bendable joint during copulation, when the male clasps the female genital with its valvae. MINET et al. (2014) identified the same weak flexure on the sacculus as a character of Noctuidae s. str. including Dyopsinae. In the future, emphasis should be put on studying the muscular attachment regions of this supposed point for valval bending, as well as of the vinculum and tegumen (see KUZNETZOV & STEKOLNIKOV 1979a,b). Like for most other characters studied, investigation of musculature and nervature is essential to better understand their function and homology. Furthermore, the ontogenetic origins of the fibula should be investigated as it is not clear whether the sclerotised protrusions on the inner side of the valva that are found in most species of Spilomelinae are homologous. We assume that protrusions emerging from the costa are not homologous with those arising from the central inner valva, and we consequently code them as separate characters.

The morphological circumscription of the observed tribes in Spilomelinae and Pyraustinae allows for the assignment of additional taxa in those tribes through morphological investigation, without the strict requirement of molecular data. These morphological diagnoses allow the assignment of additional 125 genera to Spilomelinae tribes, and additional 56 genera to Pyraustinae tribes. 135 genera of Spilomelinae and 103 genera of Pyraustinae remain unassigned to any of the proposed tribes. Among the

Table 3. Correlation of MUNROE's (1995) proposed Spilomelinae genus groups to the Spilomelinae tribes proposed herein.

MUNROE's (1995) genus groups	proposed tribes	unplaced genera	other family groups
<i>Phaedropsis</i> group	Agroterini		
<i>Syllepte</i> group	Agroterini	<i>Syngropia</i> , <i>Praephostria</i> , <i>Syllepte</i> , <i>Tractoceras</i>	
<i>Herpetogramma</i> group	Herpetogrammatini	<i>Pelinopsis</i>	
<i>Hydrinis</i> group	Hydririni apart from <i>Geshna</i> (Spilomelini)		
<i>Udea</i> group	Lineodini apart from <i>Lamprosema</i> (Hydririni) and <i>Udea</i> (Udeini)		
<i>Hymenia</i> group	<i>Ercta</i> : Udeini ; <i>Spilomela</i> : Spilomelini ; <i>Blepharomastix</i> : Herpetogrammatini ; <i>Hymenia</i> , <i>Spoladea</i> : Hymeniini ; <i>Anageshna</i> , <i>Apogeshna</i> , <i>Duponchelia</i> , <i>Loxostegopsis</i> , <i>Parastenia</i> (= <i>Dolicharthria</i>), <i>Penestola</i> , <i>Steniodes</i> : Steniini ; <i>Desmia</i> , <i>Diasemiodes</i> , <i>Diasemiopsis</i> , <i>Diathrausta</i> : Nomophilini	<i>Saccolisia</i>	
<i>Diaphania</i> group	Margaroniini	<i>Chromodes</i>	
<i>Polygrammodes</i> group	Margaroniini		
<i>Siga</i> group	<i>Cirrhocephalina</i> , <i>Siga</i> , <i>Zeuserobotys</i> : Spilomelini ; <i>Beebea</i> , <i>Laniifera</i> , <i>Laniipriva</i> : Asciodini		
<i>Eulepte</i> group	<i>Gonocausta</i> , <i>Ommatospila</i> , <i>Syllepis</i> : Hydririni	<i>Eulepte</i> , <i>Praeacrosipila</i> , <i>Leucochromodes</i> , <i>Mesocondyla</i>	
<i>Samea</i> group	Nomophilini	<i>Stenorista</i>	
<i>Psara</i> group	Asciodini		
<i>Conchylodes</i> group	<i>Conchylodes</i> : Udeini	<i>Pycnarmon</i>	
<i>Syngamia</i> group	<i>Marasmia</i> , <i>Salbia</i> : Spilomelini ; <i>Syngamia</i> : Nomophilini		<i>Sufetula</i> to Lathrotelinae (MINET 2015)
<i>Diaphantania</i> group	Wurthiini		
unplaced genera	<i>Nonazochis</i> (= <i>Conchylodes</i>), <i>Sisyrcera</i> , <i>Tanaophysa</i> : Udeini ; <i>Bocchoropsis</i> , <i>Coenostolopsis</i> , <i>Cyclocena</i> (HAYDEN & DICKELE 2014: syn. of <i>Microthyris</i>), <i>Gypodes</i> : Agroterini ; <i>Analyta</i> , <i>Caprinia</i> , <i>Meroctena</i> , <i>Tyspanodes</i> : Margaroniini ; <i>Palpusia</i> , <i>Rhectocraspeda</i> : Spilomelini ; <i>Eurhyarodes</i> : Herpetogrammatini ; <i>Bicilia</i> , <i>Loxomorpha</i> , <i>Maracayia</i> : Asciodini ; <i>Trichaea</i> : Trichaeini ; <i>Bradina</i> : Steniini ; <i>Bocchoris</i> , <i>Parapilocrocis</i> : Nomophilini	<i>Agrammia</i> , <i>Carthade</i> , <i>Coelorrhyncidia</i> , <i>Corremata</i> , <i>Daulia</i> , <i>Deuterophysa</i> , <i>Dichocrocis</i> , <i>Goniorhynchus</i> , <i>Heterudea</i> , <i>Hylea</i> , <i>Ischnurges</i> , <i>Luma</i> , <i>Mabra</i> , <i>Massepha</i> , <i>Metoea</i> , <i>Metraeopsis</i> , <i>Microphysetica</i> , <i>Mimudea</i> , <i>Pectinobotys</i> , <i>Piletocera</i> , <i>Piletosoma</i> , <i>Platygraphis</i> , <i>Plectrona</i> , <i>Syntrita</i> , <i>Tanaophysopsis</i> , <i>Trithyris</i>	<i>Ennomosia</i> to Glaphyriinae (HAYDEN & DICKELE 2014); <i>Hydropionea</i> and <i>Plantegumia</i> to Glaphyriinae; <i>Orthoraphis</i> to Lathrotelinae

unassigned Spilomelinae genera, the most species-rich are *Syllepte* (198 spp.), *Nacoleia* (84 spp.), *Pycnarmon* (59 spp.), *Dichocrocis* (53 spp.) and *Mimudea* Warren, 1892 (42 spp.), while 76 genera contain only one to two species, respectively. In Pyraustinae, the most species-rich unassigned genera are *Semniomima* Warren, 1892 (15 spp.), *Calamochrous* Lederer, 1863 (13 spp.) and *Paliga* Moore, 1886 (12 spp.). In the European fauna of Spilomelinae and Pyraustinae, only *Uresiphita* remains unplaced as sister to Portentomorphini. In the Nearctic region, *Daulia*, *Deuterophysa*, *Eulepte*, *Microphysetica*, *Stenochora* and *Syllepte* are still unplaced. Furthermore, the majority of genera from MUNROE's (1995) Neotropical genus groups are placed in tribes (Table 3).

Ultimately, the type species of every spilomeline and pyraustine genus should be investigated and placed into the phylogenetic framework. The morphological circumscription of the observed tribes in Spilomelinae and Pyraustinae allows for the assignment of additional taxa in those tribes through morphological investigation, without the strict requirement of molecular data. This should be applied to the 132 Spilomelinae genera and 103 Pyraustinae genera which are not yet assigned to any of the tribes. A concerted effort among systematists to morphologically investigate those unplaced genera and to assign them to the proposed tribes is feasible and desirable. This effort will likely result in the recognition of

taxa that do not fit into this system of tribes. Such taxa can be morphologically coded as well as sequenced for the six genetic markers used in this study. Their phylogenetic placement can then be inferred through a combination with the data presented here. We therefore provide a 'modular' dataset where taxa of interest can be added in order to refine the circumscription of the proposed tribes and to widen our understanding of the phylogenetic relationships of Spilomelinae and Pyraustinae. The resulting improved understanding of Spilomelinae and Pyraustinae genera is expected to promote taxonomic revisions of genera and species groups as well as ecological and applied research on the pyraloids.

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8. Appendix

Checklist of Spilomelinae and Pyraustinae tribes, associated genera and species numbers:

SPILOMELINAE

Hydririni: *Choristostigma* Warren, 1892 (10 spp.) — *Gonocausa* Lederer, 1863 (4 spp.) — *Hydriris* Meyrick, 1885 (7 spp.) — *Lamprosema* Hübner, 1823 (72 spp.) [polyphyletic] — *Nehydriris* Munroe, 1974 (1 sp.) — *Ommatospila* Lederer, 1963 (3 spp.) — *Rhectothyris* Warren, 1890 (1 sp.) — *Syllepsis* Poey, 1832 (7 spp.)

Lineodini: *Atomopteryx* Walsingham, 1891 (10 spp.) — *Euleucinodes* Capps, 1948 (1 sp.) — *Leucinodes* Guenée, 1854 (20 spp.) [MALLY et al. 2015; misplaced spp. in Asia and Australia] — *Lineodes* Guenée, 1854 (39 spp.) — *Neoleucinodes* Capps, 1948 (9 spp.) — *Proleucinodes* Capps, 1948 (4 spp.) — *Rhectosemia* Lederer, 1863 (12 spp.)

Udeini: *Cheverella* B. Landry, 2011 (1 sp.) — *Conchylodes* Guenée, 1854 (21 spp.) [paraphyletic?] — *Deana* Butler, 1879 (1 sp.) — *Ercta* Walker, 1859 (7 spp.) — *Mnesictena* Meyrick, 1884 (7 spp.) — *Sisyraera* Möschler, 1890 (3 spp.) — *Tanaophysa* Warren, 1892 (2 spp.) — *Udea* Guenée, 1845 (in Duponchel) (214 spp.) [e.g. MUNROE 1966, INOUE et al. 2008, MALLY & NUSS 2011] — *Udeoides* Maes, 2006 (5 spp.)

Wurthiini: *Apilocrocis* Amsel, 1956 (11 spp.) — *Aristebulea* Munroe & Mutuura, 1968 (2 spp.) — *Diaphantania* Möschler, 1890 (3 spp.) — *Mimetebulea* Munroe & Mutuura, 1968 (1 sp.) — *Niphopyralis* Hampson, 1893 (8 spp.) — *Pseudebulea* Butler, 1881 (4 spp.)

Agroterini: *Aetholix* Lederer, 1863 (4 spp.) — *Agrotera* Schrank, 1802 (24 spp.) [CHEN et al. 2017] — *Aiyura* Munroe, 1974 (2

spp.) — *Bocchoropsis* Amsel, 1956 (2 spp.) — *Chalcidoptera* Butler, 1887 (15 spp.) — *Chilochromopsis* Munroe, 1964 (1 sp.) — *Coenostolopsis* Munroe, 1960 (3 spp.) — *Diastictis* Hübner, 1818 (12 spp.) — *Framinghamia* Strand, 1920 (1 sp.) — *Glaucobotys* Maes, 2008 (1 sp.) — *Goliathodes* Munroe, 1974 (1 sp.) — *Gypodes* Munroe, 1976 (1 sp.) — *Haritalodes* Warren, 1890 (11 spp.) — *Lygropia* Lederer, 1863 (68 spp.) — *Lypotigris* Hübner, 1825 (1 sp.) — *Micromartinia* Amsel, 1957 (1 sp.) — *Microthyris* Lederer, 1863 (7 spp.) — *Nagiella* Munroe, 1976 (4 spp.) — *Neonanalthes* Yamanaka & Kirpichnikova, 1993 (8 spp.) — *Nosophora* Lederer, 1863 (26 spp.) — *Notarcha* Meyrick, 1884 (18 spp.) — *Pantographa* Lederer, 1863 (9 spp.) — *Patania* Moore, 1888 (40 spp.) — *Phaedropsis* Warren, 1890 (24 spp.) — *Phostria* Hübner, 1819 (87 spp.) — *Phyrganodes* Guenée, 1854 (26 spp.) — *Tetracona* Meyrick, 1884 (2 spp.) [CHEN et al. 2017] — *Ulopeza* Zeller, 1852 (16 spp.)

Margaroniini: *Agathodes* Guenée, 1854 (16 spp.) — *Agrioglypta* Meyrick, 1932 (11 spp.) [SUTRISNO 2002a,b, 2005, SUTRISNO et al. 2006] — *Alytana* J. C. Shaffer, & Munroe, 2007 (2 spp.) — *Analyta* Lederer, 1863 (10 spp.) — *Anarmodia* Lederer, 1863 (24 spp.) — *Antigastra* Lederer, 1863 (2 spp.) — *Aphytoceros* Meyrick, 1884 (3 spp.) — *Arthroschista* Hampson, 1893 (2 spp.) — *Asturodes* Amsel, 1956 (1 sp.) — *Azochis* Walker, 1859 (16 spp.) — *Botyodes* Guenée, 1854 (10 spp.) — *Cadarena* Moore, 1886 (1 sp.) — *Caprinia* Walker, 1859 (11 spp.) — *Chabulina* J. C. Shaffer, & Munroe, 2007 (2 spp.) — *Charitoprepes* Warren, 1896 (2 spp.) — *Chrysophyllis* Meyrick, 1934 (1 sp.) — *Chrysothyridia* Munroe, 1967 (2 spp.) — *Cirrhochrista* Lederer, 1863 (38 spp.) — *Colomychus* Munroe, 1956 (2 spp.) — *Compacta* Amsel, 1956 (4 spp.) — *Condylorrhiza* Lederer, 1863 (4 spp.) — *Conogthes* Meyrick, 1884 (16 spp.) [e.g. INOUE & YAMANAKA 2006, SHASHANK et al. 2015, 2018] — *Cydalima* Lederer, 1863 (9 spp.) [STRELTZOV 2008, MALLY & NUSS 2010] — *Diaphania* Hübner, 1818 (95 spp.) [CLAVIJO ALBERTOS 1990] — *Didymostoma* Warren, 1892 (2 spp.) [SUTRISNO 2002a] spp.) — *Dysallacta* Lederer, 1863 (3 spp.) [SUTRISNO 2002a] — *Endocrossis* Meyrick, 1889 (4 spp.) — *Eusabena* Snellen, 1901 (4 spp.) — *Filodes* Guenée, 1854 (16 spp.) — *Ghesquierellana* Berger, 1955 (5 spp.) — *Glyphodella* J. C. Shaffer & Munroe, 2007 (3 spp.) — *Glyphodes* Guenée, 1854 (156 spp.) [SUTRISNO 2002a,b, 2003, 2006, SUTRISNO et al. 2006] — *Hedyleptopsis* Munroe, 1960 (1 sp.) — *Heterocnephes* Lederer, 1863 (4 spp.) — *Hodebertia* Leraut, 2003 (1 sp.) — *Hoterodes* Guenée, 1854 (5 spp.) — *Leucochroma* Guenée, 1854 (6 spp.) — *Liopasia* Möschler, 1882 (15 spp.) — *Loxmaionia* Schaus, 1913 (1 sp.) — *Maruca* Walker, 1859 (4 spp.) — *Marwitzia* Gaede, 1917 (3 spp.) — *Megaphysa* Guenée, 1854 (1 sp.) — *Megastes* Guenée, 1854 (16 spp.) — *Meroctena* Lederer, 1863 (4 spp.) — *Nolkenia* Snellen, 1875 (1 spp.) — *Obtusipalpis* Hampson, 1896 (6 spp.) — *Omiodes* Guenée, 1854 (98 spp.) [polyphyletic, HAINES & RUBINOFF 2012] — *Omphisa* Moore, 1886 (10 spp.) — *Pachynoa* Lederer, 1863 (12 spp.) — *Palpita* Hübner, 1808 (162 spp.) [INOUE 1996, 1997, 1999] — *Parotis* Hübner, 1831 (37 spp.) — *Poliobotys* J. C. Shaffer & Munroe, 2007 (1 sp.) — *Polygrammodes* Guenée, 1854 (78 spp.) — *Polygrammopsis* Munroe, 1960 (1 sp.) — *Prenesta* Snellen, 1875 (18 spp.) — *Pygospila* Guenée, 1854 (10 spp.) — *Radessa* Munroe, 1977 (2 spp.) — *Rhagoba* Moore, 1888 (2 spp.) — *Rhimphalea* Lederer, 1863 (12 spp.) — *Sinomphisa* Munroe, 1958 (3 spp.) — *Sparagnia* Guenée, 1854 (1 sp.) — *Stemorrhages* Lederer, 1863 (8 spp.) — *Synclera* Lederer, 1863 (13 spp.) — *Syngamilyta* Strand, 1920 (5 spp.) — *Talanga* Moore, 1885 (9 spp.) [SUTRISNO 2002a,b, 2005, SUTRISNO et al. 2006] — *Terastia* Guenée, 1854 (7 spp.) — *Tessema* J. F. G. Clarke, 1986 (1 sp.) — *Tyspanodes* Warren, 1891 (20 spp.) — *Uncobotyodes* Kirti & Rose, 1990 (1 sp.) — *Zebironia* Hübner, 1821 (6 spp.)

Spilomelini: *Aethaloessa* Lederer, 1863 (3 spp.) — *Cirrhocephalina* Munroe, 1995 (5 spp.) — *Cnaphalocrocis* Lederer, 1863 (27 spp.) — *Eporidia* Walker, 1859 (1 sp.) — *Geshna* Dyar, 1906 (1 sp.) — *Marasmia* Lederer, 1863 (9 spp.) — *Marasmianympha* Munroe, 1991 (1 sp.) — *Orphanostigma* Warren, 1890 (6 spp.) — *Palpusia* Amsel, 1956 (10 spp.) — *Rhectocraspeda* Warren,

1892 (2 spp.) — *Salbia* Guenée, 1854 (35 spp.) — *Scaptesyloides* Munroe, 1976 (2 spp.) — *Siga* Hübner, 1820 (2 spp.) — *Spilomela* Guenée, 1854 (8 spp.) — *Zeuzerobotys* Munroe, 1963 (1 sp.)

Herpetogrammatini: *Blepharomastix* Lederer, 1863 (85 spp.) — *Cryptobotys* Munroe, 1956 (2 spp.) — *Eurrhyarodes* Snellen, 1880 (12 spp.) — *Herpetogramma* Lederer, 1863 (100 spp.) — *Hileithia* Snellen, 1875 (19 spp.) — *Pilocrocis* Lederer, 1863 (65 spp.)

Hymeniini: *Hymenia* Hübner, 1825 (3 spp.) — *Spoladea* Guenée, 1854 (2 spp.)

Asciodini: *Arthromastix* Warren, 1890 (2 spp.) — *Asciodes* Guenée, 1854 (5 spp.) — *Beebea* Schaus, 1923 (1 sp.) — *Bicilia* Amsel, 1956 (4 spp.) — *Ceratocilia* Amsel, 1956 (8 spp.) — *Ceratoctasis* Lederer, 1863 (9 spp.) — *Erilusa* Walker, 1866 (3 spp.) [tentative placement] — *Lanifera* Hampson, 1899 (1 sp.) — *Lanipriva* Munroe, 1976 (1 sp.) — *Loxomorpha* Amsel, 1956 (4 spp.) — *Maracayia* Amsel, 1956 (2 spp.) — *Psara* Snellen, 1875 (36 spp.) — *Sathria* Lederer, 1863 (3 spp.)

Trichaeni: *Prophantis* Warren, 1896 (8 spp.) — *Sacculosia* Amsel, 1956 (1 sp.) — *Trichaea* Herrich-Schäffer, 1866 (11 spp.) — *Zenamorpha* Amsel, 1956 (2 spp.)

Steniini: *Anageshna* Munroe, 1956 (1 sp.) — *Apogeshna* Munroe, 1956 (3 spp.) — *Bradina* Lederer, 1863 (87 spp.) — *Dolicharthria* Stephens, 1834 (24 spp.) — *Duponchelia* Zeller, 1847 (5 spp.) — *Epherema* Snellen, 1892 (1 sp.) — *Hymenoptychis* Zeller, 1852 (4 spp.) — *Loxostegopsis* Dyar, 1917 (6 spp.) — *Metasia* Guenée, 1854 (88 spp.) — *Penestola* Möschler, 1890 (3 spp.) — *Steniodes* Snellen, 1875 (9 spp.) — *Symmoracma* Meyrick, 1894 (1 sp.) — *Tatobotys* Butler, 1881 (11 spp.)

Nomophilini: *Arnia* Guenée, 1849 (1 sp.) — *Ategumia* Amsel, 1956 (10 spp.) — *Bocchoris* Moore, 1885 (31 spp.) — *Crociodonemis* Warren, 1889 (2 spp.) — *Desmia* Westwood, 1832 (89 spp.) — *Diacme* Warren, 1892 (10 spp.) — *Diasemia* Hübner, 1825 (13 spp.) — *Diasemiodes* Munroe, 1957 (4 spp.) — *Diasemiopsis* Munroe, 1957 (2 spp.) — *Diathrausta* Lederer, 1863 (20 spp.) — *Epipagis* Hübner, 1825 (14 spp.) — *Mecyna* Doubleday, 1849 (34 spp.) — *Mimophobeton* Munroe, 1950 (1 sp.) — *Mimorista* Warren, 1890 (15 spp.) — *Niphograptia* Warren, 1892 (1 sp.) — *Nomophila* Hübner, 1825 (14 spp.) [MUNROE 1973] — *Nothomastix* Warren, 1890 (5 spp.) — *Parapilocrocis* Munroe, 1967 (3 spp.) — *Pardomima* Warren, 1890 (16 spp.) — *Perisyntrocha* Meyrick, 1894 (4 spp.) — *Pessocosma* Meyrick, 1884 (4 spp.) — *Samea* Guenée, 1854 (28 spp.) — *Sameodes* Snellen, 1880 (15 spp.) — *Syngamia* Guenée, 1854 (25 spp.)

PYRAUSTINAE

Euclastini: *Euclasta* Lederer, 1855 (17 spp.) [POPESCU-GORJ & CONSTANTINESCU 1977]

Portentomorphini: *Cryptosara* E. L. Martin in Marion, 1957 (3 spp.) — *Hyalobathra* Meyrick, 1885 (21 spp.) [SUTRISNO & HORAK 2003] — *Isocentris* Meyrick, 1887 (7 spp.) — *Pioneabathra* J. C. Shaffer & Munroe, 2007 (1 sp.) — *Portentomorpha* Amsel, 1956 (1 sp.)

Pyraustini: *Achyra* Guenée, 1849 (19 spp.) — *Adoxobotys* Munroe, 1978 (3 spp.) — *Aglaops* Warren, 1892 (4 spp.) — *Anamalaia* Munroe & Mutuura, 1969 (1 sp.) — *Anania* Hübner, 1823 (117 spp.) — *Arenochroa* Munroe, 1976 (1 sp.) — *Aurorobotys* Munroe & Mutuura, 1971 (2 spp.) — *Callibotys* Munroe & Mutuura, 1969 (3 spp.) — *Carminibotys* Munroe & Mutuura, 1971 (1 sp.) — *Ceuthobotys* Munroe, 1978 (1 sp.) — *Chilochroma* Amsel, 1956 (4 spp.) — *Chilocorsia* Munroe, 1964 (1 sp.) — *Chilopionea* Munroe, 1964 (1 sp.) — *Circobotys* Butler, 1879 (19 spp.) — *Crociodophora* Lederer, 1863 (24 spp.) — *Crypsityta* Meyrick, 1894 (8 spp.) — *Cybalobotys* Maes, 2001 (3 spp.) — *Deltobotys* Munroe, 1964 (3 spp.) — *Demobotys* Munroe & Mutuura, 1969 (2 spp.) — *Ecyrrhorhoe* Hübner, 1825 (12 spp.) — *Epicorsia* Hübner, 1818 (9 spp.) — *Epiparbatia* Caradja, 1925 (2 spp.) — *Eumorphobotys* Munroe & Mutuura, 1969 (2 spp.) — *Fumibotys* Munroe, 1976 (1 sp.) — *Gynenomis* Munroe & Mutuura, 1968 (2 spp.)

— *Hahncappsia* Munroe, 1976 (39 spp.) — *Helvibotys* Munroe, 1976 (5 spp.) — *Hyalorista* Warren, 1892 (5 spp.) — *Limbobotys* Munroe & Mutuura, 1970 (5 spp.) — *Loxostege* Hübner, 1825 (90 spp.) — *Munroeodes* Amsel, 1957 (4 spp.) — *Nascia* J. Curtis, 1835 (3 spp.) — *Nadeloides* Klima, 1939 (2 spp.) — *Neopicrocorsia* Munroe, 1964 (7 spp.) — *Neohelvibotys* Munroe, 1976 (9 spp.) — *Nephelobotys* Munroe & Mutuura, 1970 (1 sp.) — *Nomis* Motschulsky, 1861 (4 spp.) — *Oenobotys* Munroe, 1976 (5 spp.) — *Oronomis* Munroe & Mutuura, 1968 (1 sp.) — *Ostrinia* Hübner, 1825 (21 spp.) — *Pagyda* Walker, 1859 (26 spp.) — *Palepicrocorsia* Maes, 1995 (1 sp.) — *Paracorsia* Marion, 1959 (1 sp.) — *Paranomus* Munroe & Mutuura, 1968 (4 spp.) — *Paratalanta* Meyrick, 1890 (9 spp.) — *Parbattia* Moore, 1888 (6 spp.) — *Perispasta* Zeller, 1876 (1 sp.) — *Placosaris* Meyrick, 1897 (20 spp.) — *Powysia*

Maes, 2006 (1 sp.) — *Prooedema* Hampson, 1891 (1 sp.) — *Protepicorsia* Munroe, 1964 (13 spp.) — *Psammotis* Hübner, 1825 (8 spp.) — *Pseudepicorsia* Munroe, 1964 (4 spp.) — *Pseudognathobotys* Maes, 2001 (2 spp.) — *Pseudopagyda* Slamka, 2013 (3 spp.) [CHEN & ZHANG 2017] — *Pseudopolygrammodes* Munroe & Mutuura, 1969 (1 sp.) — *Pseudopyrausta* Amsel, 1956 (6 spp.) — *Pyrasia* M. O. Martin, 1986 (1 sp.) — *Pyrausta* Schrank, 1802 (341 spp.) — *Sarobotys* Munroe, 1964 (2 spp.) — *Sclerocona* Meyrick, 1890 (1 sp.) — *Sinibotys* Munroe & Mutuura, 1969 (5 spp.) — *Sitochroa* Hübner, 1825 (10 spp.) — *Thivolleo* Maes, 2006 (4 spp.) — *Thliptoceras* Warren, 1890 (31 spp.) — *Toxobotys* Munroe & Mutuura, 1968 (3 spp.) — *Vittabotys* Munroe & Mutuura, 1970 (1 sp.) — *Xanthostege* Munroe, 1976 (2 spp.)

Electronic Supplement Files

at <http://www.senckenberg.de/arthropod-systematics>

File 1: mally&al-spilomelinaephylogeny-asp2019-electronic-supplement-1.xlsx — **Table S1.** List of examined genitalia slides. — DOI: 10.26049/ASP77-1-2019-07/1

File 2: mally&al-spilomelinaephylogeny-asp2019-electronic-supplement-2.pdf — **Fig. S1.** Maximum Likelihood cladogram of the GENES-partitioned RAxML analysis of the molecular dataset. Numbers at internal branches are bootstrap values (BS) $\geq 50\%$ inferred from 1,000 thorough bootstrap replicates. — DOI: 10.26049/ASP77-1-2019-07/2

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