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Phylogeny and classification of the Scopulini moths (Lepidoptera: Geometridae, Sterrhinae)

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The phylogenetic relationships of the genera in the geometrid tribe Scopulini (Lepidoptera: Sterrhinae) were examined using 141 characters of adult morphology and ecology. The study material included 92 species, representing all previously recognized genera and covering the morphological variation and full geographical range of the tribe. The cladistic analysis resulted in 20 equally parsimonious trees and a strict consensus cladogram based on these was well resolved. A majority of the recovered synapomorphic characters have been used previously in the taxonomy of the tribe. However, many novel characters were found in the sclerotized structures of the thorax. Many previously recognized genera were found to be nonmonophyletic and based on the present revised, synapomorphy-based classification, the number of recovered genera is reduced considerably. Twenty new generic synonyms and 90 new or revived species combinations are proposed. Seven genera are considered valid, with the large genus *Scopula* Schrank including over 85% of all species in the tribe. The taxonomic history of the tribe is reviewed and the problems of earlier classifications are discussed. A key to the genera is presented, although an informal diagnosis is preferred. All recognized genera are illustrated and a revised world checklist of the Scopulini is presented.

ADDITIONAL KEYWORDS: cladistic analysis – morphology – taxonomy.

INTRODUCTION

The Scopulini – the genus *Scopula* Schrank and its close relatives – is the largest tribe of the geometrid subfamily Sterrhinae, with about 900 described species. Species are found worldwide, although the group is mostly tropical.

The group is diverse in many aspects of morphology and ecology. The moths are typically moderate to small in size compared to other geometrids, with recurrent sexual dimorphism in wing size, shape and pattern. Males usually possess secondary sexual characters, such as coremata on the 2nd and 8th sternites and hair pencils on the hind legs. In the most extreme cases, male hindleg tarsi are absent; the swallowed tibia with a hair pencil is not used for walking but primarily for scent production and distribution (Hashimoto, 1992). Most species are nocturnal, straw-coloured and cryptic, yet there are a number of deviations, especially in the tropical lineages and in the groups that have adopted a diurnal mode of life. For example, species of the diurnal African genus *Aletis* Hübner are brightly coloured and are considered to be model species that are mimicked in appearance by species of the butterfly genus *Euphaedra* Hübner (Nymphalidae) (Staude & Curle, 1997).

The biology of most of the species is unknown. In the better-known western Palaearctic, Japanese, and Nearctic faunas, caterpillars of many species are polyphagous feeders on low herbs, although monophagy is not unusual (McGuffin, 1967; Sugi, 1987; Ebert, 2001). Some specialization in larval host-plants is evident at the generic level; for example, the species of *Problepsis* Lederer tend to feed on Oleaceae and those of *Antitrygodes* Warren on Rubiaceae (Holloway, 1997; Robinson *et al*., 2002). In South-east Asia a few species of *Scopula* have adopted an unusual way of life: the adults feed on mammalian sweat, tears and blood seeping from wounds (Bänziger & Fletcher, 1985), while species of *Zythos* Fletcher have been recorded visiting carrion (Holloway, 1997). A few species are of

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minor pest status, attacking tobacco (Sannino & Balbiani, 1984; Sannino & Espinosa, 1999) and groundnut (Satpathi, 1995). Typically, larvae are narrow and stick-like, and rest at an angle of 45 ° (Sugi, 1987; Ebert, 2001).

There has been only one published study on the systematics of the tribe, a treatment based on Palaearctic material (Sterneck, 1941). Other publications deal with generic or species descriptions, focusing mainly on regional faunas (Covell, 1970; Hausmann, 1994; Yazaki, 1996; Karisch, 2001). Lack of a global view of the tribe's taxonomy has resulted in a relatively restricted generic classification. This is problematic because it can result in an unstable system in a group where new species are constantly being described and ascribed to genera that have traditionally been recognized in each region. A further consequence of regional classification has been a tendency towards describing new genera on an *ad hoc* basis, where new species are identified that do not fit the existing system. Many generic concepts appear to have originated in this way and their status needs to be revised. A similar problem affects the systematics of the Macariini (Scoble & Krüger, 2002).

There has hitherto been no attempt to synthesize and evaluate the findings of these regional studies, or to view the systematics of the tribe from a global perspective. A recent cladistic analysis by Sihvonen & Kaila (2004) attempted to redress this problem for the tribes of Sterrhinae, in the course of which Scopulini was recovered as a monophyletic entity. It was beyond the scope of the analysis, however, to resolve generic relationships within Scopulini.

This is the first published study of the generic relationships of the tribe on a worldwide scale. Its objectives are as follows: (1) to present a testable hypothesis of the tribe's phylogeny; (2) to find characters that can be used to delimit natural, synapomorphy-based groups, and (3) to classify the extant, described fauna. It is hoped that this approach will lead to a more stable system in a species-rich group where generic concepts have hitherto been vague.

Classification of the Scopulini: historical background

I will not discuss in detail here the characters that appear in the original generic descriptions. Most of the latter were made in the 19th century, at a time when methods and generic concepts differed from ours. They often appear to be superficial; in many cases, names were introduced in the form of simple lists.

As already mentioned, the literature dealing with the generic classification and systematics of the tribe is limited, with most of the data drawn from checklists and similar treatments. Careful examination of a few of these (Covell, 1983; Wiltshire, 1994; McQuillan & Edwards, 1996; Viidalepp, 1996; Leraut, 1997; Hacker, 1999) reveals that there appear to be several well-recognized, possibly monophyletic groups within Scopulini such as *Scopula*, *Problepsis* and *Zythos*, although we are left with the problem of inferring whether the order of genera in the checklists reflects their phylogenetic relationships. I now summarize the historical classification of Scopulini in chronological order. Only papers with a broader systematic importance are discussed.

Pierce (1914) arranged the British fauna into tribes based on a detailed examination of genitalic structures, a novel approach at that time. Acidaliinae (Scopulini) consisted of one genus, *Acidalia* (the author was not mentioned in this context, see Appendix under *Scopula*), and the species referred to it are nowadays considered to belong to *Scopula*. He considered *Acidalia* a natural genus due to the peculiar structures of the male and female genitalia. These include *inter alia* extreme fusion of the male genitalia, presence of coremata at the articulation of the sacculus with the tegumen, cerata and mappa on the male's eight sternite, and a spine-like signum on the female genitalia.

In his monograph on the Palaearctic Geometridae, Prout (1912–16) brought together 21 genera that he collectively called the *Acidalia* group (Scopulini). The group was characterized, among other features, by having one or two large areoles, in contrast to the *Cosymbia* group (Cosymbiini) where this structure was either absent or if present, single and very small. In the *Acidalia*-group male antenna were fasciculate and valve simple, whereas in the *Cosymbia*-group they were bipectinated and valve complex. The *Acidalia*-group was divided into sections according to the number of forewing areoles. The two-areole group contained, for example, *Rhodostrophia* Hübner (Rhodostrophiini), as well as genera that are nowadays not considered to be closely related to it, including *Somatina* Guenée (Scopulini).

In the context of these groups, he discussed generic relationships. For example, the one-areole genus *Problepsis* was considered to be a straight derivative of two-areole genus *Somatina*. These two genera were differentiated from *Acidalia* by their larger size, and most species by the absence of spurs on male hind tibia, these being replaced by a hair pencil.

Prout described four new Scopulini genera – *Glossotrophia*, *Antilycauges*, *Holarctias* and *Oar* – the latter three being monotypic. The descriptions were based on external morphological features; for example, the lack of medial spurs on the female hind leg in *Glossotrophia* was considered exceptional. *Antilycauges* was characterized by having numerous short, fasciculated sensilla in the male antenna, an elongated wing cell

(areola), and palpi which were stout and rough scaled. *Holarctias* was differentiated from closely related taxa, namely section *Pylarpe* Herrich-Schäffer of genus *Scopula*, by having a hairy head and body, flat front, small eyes and moderately long palpi with attenuated terminal segments.

Oar was considered an abnormal genus within the *Acidalia*-group and possibly a derivate of *Emmiltis* Hübner (Sterrhini) (see Sihvonen & Kaila, 2004), due to a shortened proboscis. Furthermore, palpi were covered with moderate hair scales and male antenna were characterized by numerous long, fasciculated sensilla. The monotypic genus *Stigma* Alphéraky was considered the closest relative of *Oar*, but differentiated from the latter by having palpi covered with long, erect hair scales. Finally, *Cinglis* Guenée was associated with the *Cosymbia*-group (Cosymbiini) because of its bipectinated antenna and complex valve, although the systematic position was considered preliminary.

In a supplement to his monograph, Prout (1934–39) redefined the generic concepts of the Scopulicae (Scopulini), largely based on external characters, that he had adopted in his earlier work. This redefinition was based on utilization of genitalic structures, relying on Sterneck's revisions of Palaearctic Sterrhinae (Sterneck's manuscript was widely distributed prior to its publication in 1941 and cited by Prout, see below) and on Pierce (1914).

Prout included seven genera in the *Scopula*-group (Scopulini) in the Palaearctic region, characterized by two socii and absence of uncus and gnathos. Further, the valves were described as 'flowing out' (*ausgeflossene*), the male 8th sternite as having mappa and cerata and the female hind leg as having two pairs of spurs except in *Glossotrophia*. At the generic level, no delimiting characters were given to *Scopula*, whereas *Glossotrophia* was considered a natural genus and easy to delimit on the basis of one pair of spurs in the female hind leg. It was noted, however, that the apical portion of the sacculus of the valva (fibula) is melanized in a number of species in *Scopula*, as well as in *Glossotrophia*, thus obscuring the generic boundaries. *Holarctias*, *Oar* and *Stigma* were characterized by absence of cerata, and as having varying degrees of valve differences relative to *Scopula*. Although the aberrant wing venation of *Cinglis* was noted, Prout concluded that this genus is appropriately combined with Scopulini as it shares the typical condition of the male 8th sternite.

Prout (1929–35) subsequently treated the African Scopulini. As with the Palaearctic material, the generic descriptions emphasized differences in wing venation, male antennae, and hindtibial spurs. The majority of the genera that he associated with Scopulini are still treated as such, except *Discomiosis* Prout and *Tricentroscelis* Prout, which are currently associated with Rhodostrophiini (Sihvonen & Kaila, 2004). *Zygophyxia* Prout, on the other hand, was seen as a relative of *Sterrha* (= *Idaea* [Sterrhini]), although it is nowadays considered to be within the concept of the Scopulini (Hacker, 1999; Sihvonen & Kaila, 2004). The monotypic African genera *Isoplenia* Warren and *Isoplenodia* Prout were considered to be close relatives of *Epicosymbia* Warren, based on the pectinated male antennae and two-areole condition of the forewing.

Prout noted the structural similarity between *Scopula* and *Epicosymbia*, especially in features of the male genitalia, although the well-developed uncus of *Epicosymbia* was interpreted as an unusual Scopulini feature. The generic status of *Lissoblemma* Warren was questioned, and Prout speculated that it would perhaps be better placed as a Section within *Somatina*, having in common with many *Somatina* species the bipectinated male antenna and absence of male hind leg spurs. Currently, *Lissoblemma* is associated with Rhodostrophiini (Sihvonen & Kaila, 2004).

Monotypic *Leucoxena* was considered a branch of *Scopula* but retained as a separate genus as the hindwing veins $Sc + R_1$ and Rs were stalked for a longer distance than in the typical *Scopula*. Prout (1929–35) was the first to discuss the Sterrhinae connection of brightly coloured, diurnal species of two-areole genus *Aletis* and one-areole *Cartaletis* Warren, on the basis of wing venation characters and genitalic structures, although he still treated them as Oenochrominae.

Prout's (1920–41) monograph of Indo-Australian fauna was the first comprehensive treatment of Scopulini published in the region. He again adopted the approach he had used with the Palaearctic material. *Antitrygodes* was considered both as an offshoot of *Somatina* and as closely related to *Problepsis*, as it had only one areole present in the forewing. This compact group of cryptically coloured moths differed further from *Somatina* by having a less serrated hindwing margin, although the male genitalia were found to be similar to *Scopula*.

When Turner (1908) described *Autanepsia*, he considered it to be closely related to *Rhodostrophia* because the only species of *Autanepsia* had two areoles. Prout (1920–41) speculated whether *Autanepsia* should be treated as a section of Australian genus *Dithalama* Meyrick or *Somatina*, because it shared with them all the diagnostic characters (apart from its two terminal spurs, absent in the two latter genera). Hairy species of *Dasybela* Turner from Tasmania were noted to have superficial similarity with species of *Holarctias* from the Northern Hemisphere. The compact, small, primarily Malaysian genus *Nobilia* Walker (*Zythos* Fletcher) was diagnosed as having moderately short labial palps, hind tibia of males shortened and without spurs, and two-

areole forewings. Monotypic *Lipomelia* Warren, while smaller than *Nobilia*, was diagnosed as having the same features.

Janse (1933–35) did not discuss the generic relationships of Scopulini, but his work is significant due to the detailed descriptions and illustrations that he provided. Species of *Problepsis*, for example, were shown to have two fused, setose broad lobes, a unique feature that has been shown to support monophyly of the genus (Sihvonen & Kaila, 2004). The genera immediately preceding and following *Scopula* in his publication included those that are still associated with the tribe, except *Discomiosis* (Rhodostrophiini) (Sihvonen & Kaila, 2004).

Sterneck (1941) published the only detailed hypothesis on the relationships of the Scopulini, based on a detailed morphological examination of a large number of taxa from across the Palaearctic region. The study was not limited to Scopulini, but covered all Palaearctic Sterrhinae. He laid the basis for further studies, and the detailed structural descriptions and illustrations that he provided are still widely used (e.g. Hausmann, 1994). He recognized three main lineages within Scopulini. *Holarctias* and *Oar* were treated separately as they lacked cerata and mappa on the male 8th sternite. *Cinglis* was treated in isolation because it had the unusual conditions of fasciculate male antennae with ventrolateral sensilla arranged in multiple rows, and aberrant wing venation (i.e. R_5 being unstalked and rising directly from the areole). The remaining six genera were divided into two groups on the basis of number of forewing areoles, aedeagus shape, and cerata structures. The first group included *Problepsis* and *Somatina* and the second group *Antilycauges*, *Scopula*, *Glossotrophia* and *Stigma*.

When Hausmann (1994) described two new genera, namely *Scopuloides* and *Pseudocinglis*, he emphasized the quantitative differences of proboscis length and wing venation characters, in addition to number of hindtibial spurs. *Scopuloides* was considered a close relative of *Glossotrophia*, sharing with it two spurs in the female hind leg, although it was noted that species of *Scopuloides* also had several features in common with *Scopula*. *Pseudocinglis*, although externally similar to *Glosstorophia*, was considered to be morphologically intermediate between *Cinglis* and *Antilycauges* on the basis of genital and wing venation characters.

Holloway (1997) provided explicit descriptions of Sterrhinae tribes and genera in his treatment of the Bornean fauna, treating the species from that area within a broader taxonomic context. The Problepsini and Aletini were also considered to be within the concept of Scopulini. While he did not discuss generic relationships or apomorphic features, the order in which he presented the genera can be inferred to reflect affinities between them. Differences in the structures of the male's 2nd and 8th sternite, socii and signum were often used in generic delimitations.

In addition to these works, a few taxonomic treatments of single genera, focusing on regional faunas, have been published. These include revisions of Nearctic species of *Scopula* (Covell, 1970), various studies on *Glossotrophia* (Hausmann, 1993a, b, 1994) and Sundanean species of *Zythos* (Yazaki, 1996).

Definition of the study group

The definition of the tribe Scopulini, as used here, follows the cladistic analysis of Sterrhinae by Sihvonen & Kaila (2004). In that paper we described how only a few of the putative characters delimiting the tribe effectively defined parts of it. It was found to include the Aletini and Problepsini, as had already been suggested by Holloway (1996, 1997). The generic relationships within the tribe were largely unresolved. Monophyly was found to be supported by two homoplastic synapomorphies: the absence of a medial ridge on the epinotum of the male metathorax (two occurrences within Sterrhinae) and the ovoid and granulate signum with spines pointing away from the centre (two occurrences and three reversals within Sterrhinae). The Sterrhini were recovered as the sister group of the Scopulini.

Currently, the tribe comprises 25 genera, 12 of which are monotypic (Sihvonen & Kaila, 2004).

MATERIAL AND METHODS

Study material

This was obtained from the following institutions: Australian National Insect Collection, CSIRO Division of Entomology, Canberra, Australia (ANIC); The Natural History Museum, London, UK (BMNH); Finnish Museum of Natural History (Zoological Museum), Helsinki, Finland (ZMH), and Zoologische Staats-Sammlung, München, Germany (ZSBS).

Specimen preparation and photography

The genitalia and abdomen were prepared following methods described by Hardwick (1950). The male vesica was everted via the caecum that was cut open by placing the aedeagus inside a hypodermic syringe (Sihvonen, 2001).

Before preparing the head and thorax, the wings were removed and prepared (as described below), or glued to a piece of plastic with a temporary pin with original labels. The head and thorax, still attached to the original pin, were placed in a 10% potassium

hydroxide (KOH) solution and kept at room temperature for 12–15 h. Following maceration, the original pin was removed and replaced by the temporary one. Scales were removed with a brush, except the male secondary sexual characters such as scent pencils of the hind tibia. The metathorax was separated from the mesothorax at the intersegmental membrane using forceps.

All preparations of genital, abdominal and other structures were preserved temporarily in glycerol, which allowed examination from various perspectives. These were subsequently transferred into ethanol tubes for 24 h to remove the glycerol and then mounted on slides in Euparal (Hardwick, 1950). Glass props were used to support the coverslip. Thoracic preparations were mounted laterally, and metathoracic preparations were mounted with the posterior margin facing the coverslip. All were stained with Chlorazol black.

The wing venation slides were prepared as follows. One pair of wings was removed either by gentle downwards pressure or by lifting with fine forceps. The wings were then placed in a dish containing 99.5% ethanol and scales removed from both surfaces with delicate brushes. They were placed on a slide in a drop of ethanol, which was replaced by a drop of euparal, and covered with a coverslip. The slides were left unstained.

Various structures were prepared using a Wild M5 stereomicroscope (maximum magnification 50×). External characters of adult and immature stages were examined using a Wild M10 (512×). Adult and genital structural characters were examined using a stereomicroscope and a Leitz Diaplan phase contrast compound microscope (1560×). Photographs were taken using a Leica DC300 digital camera and Image Manager software. Image files were processed and the final plates arranged using CorelDraw.

OUTGROUPS

Idaea aversata L. and *I. emarginata* L., from the Sterrhini, the putative sister group (Sihvonen & Kaila, 2004), were used in order to root the tree and polarize the characters (Farris, 1972; Nixon & Carpenter, 1993).

INGROUP

The study material included 90 species, covering the worldwide geographical range of the Scopulini (listed in Table 1). Their identity was checked against external or genital examination of type specimens, apart from a few species found in the Holarctic region, whose identity is well established.

In a phylogenetic analysis of a species-rich group, such as the Scopulini, it is impractical to include all described species. As a consequence, those included in the analysis were chosen according to the following guidelines. First, all type species of the nominal genera were included. If material was not available, I attempted to include species that were morphologically similar. Second, more than one species was included from each genus (unless monotypic) in order to reduce the number of characters that could possibly appear as autapomorphic.

Third, an attempt was made to cover the tribe's morphological diversity as exhaustively as possible. For this purpose 650 species were studied, including genitalia, covering over 70% of the described fauna (see Appendix). In addition, many more were examined externally. Finally, I attempted to include taxa that came from areas where the Scopulini have received comparatively little attention, in particular the Neotropics and the rest of the Southern Hemisphere. The type species of each included genus are illustrated as follows: imagos are shown in Figures 1–25, male genitalia in Figures 30–54, male 8th sternite in Figures 55–79 and female genitalia in Figures 80–99.

PHYLOGENETIC METHODS

The character set summarized in Table 2 was analysed using NONA v. 2.0 (Goloboff, 1999) and all characters were weighted equally. The command sequence used for the matrix, using TBR branch swapping, was hold*; hold/50; mult*200. The initial results were then submitted to more exhaustive searches as recommended in the manual: max*; swap*; altswap*; mswap*2. The trees were saved with sv*, read back into NONA and the command best issued to delete suboptimal cladograms (Nixon & Carpenter, 1996). The final cladograms were saved with sv*, and used for calculation of a strict consensus tree. Final trees, a strict consensus tree and character optimizations were studied using WinClada v.1.00.08 (Nixon, 2002).

CHARACTER DESCRIPTIONS

Where possible, the terminology of the general morphology, including wing venation and thoracic sclerites, was adopted from Scoble (1992), genital terminology from Covell (1970), Klots (1970) and Sibatini (1972). In doubtful cases, descriptive terms were used and were accompanied by illustrations.

There are 141 characters in total: 41 are from wings, 50 from the head, thorax, and abdomen, 49 from genitalia, and one from ecology. One hundred and four characters were binary and the 37 multistate characters were treated as unordered. I attempted to minimize a priori assumptions regarding the value of characters as a source of systematic information; con-

Table 1. Taxa used in the cladistic analysis of the tribe Scopulini and, within square parenthese, the biogeographical area where the type specimen has been described. *Abbreviations:* Af, Africa; As, Asia; Au, Australia; M, Madagascar; N, Nearctic; P, Palaearctic. This gives a rough indication where the species occur. Species are mentioned in their generic combinations prior to analysis

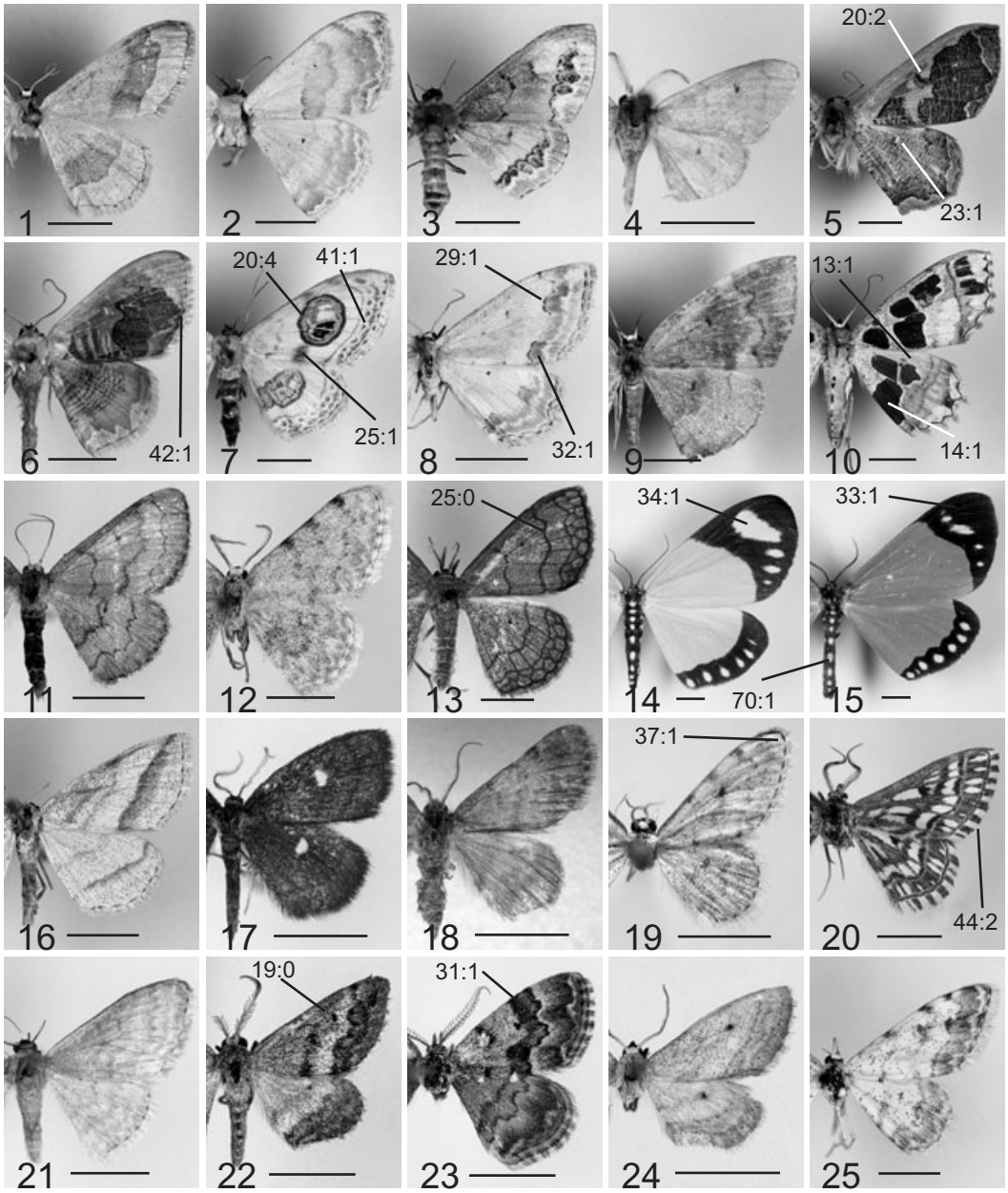
Genus	Species [type specimen locality]
Outgroups (Sterrhini)	
Idaea	*aversata* Linnaeus [P], *emarginata* Linnaeus [P]
Ingroups (Scopulini)	
Aletis	*helcita* (Linnaeus) [Af], *erici* Kirby [Af]
Antilycauges	*pinguis* (Swinhoe) [As]
Antitrygodes	*cuneilinea* (Walker) [As], *divisaria* (Walker) [As], *parvimacula* Warren [As]
Autanepsia	*poliodesma* Turner [Au]
Cartaletis	*gracilis* (Möschler) [Af], *libyssa* (Hopffer) [Af], *variabilis* (Butler) [Af]
Cinglis	*humifusaria* (Eversmann) [P]
Dasybela	*achroa* (Lower) [Au]
Dithalama	*cosmospila* Meyrick [Au], *desueta* (Warren) [Au]
Epicosymbia	*albivertex* (Swinhoe) [As], *dentisignata* (Walker) [Af], *perstrigulata* (Prout) [Af]
Glossotrophia	*adenensis* Wiltshire [Af], *asellaria* (Herrich-Schäffer) [P], *confinaria* (Herrich-Schäffer) [P]
Ignobilia	*urnaria* (Guenée) [As]
Isoplenia	*trisinuata* Warren [Af]
Isoplenodia	*arrogans* Prout [Madagascar]
Leucoxena	*lactea* Warren [Af]
Lipomelia	*subusta* Warren [As]
Oar	*pratana* (Fabricius) [P]
Problepsis	*achlyobathra* Prout [As], *aegretta* Felder & Rogenhofer [Af], *conjunctiva* Warren [As], *clemens* Lucas [Au], *flavistigma* Swinhoe [Af], *ocellata* (Frivaldszky) [P], *plagiata* (Butler) [P]
Pseudocinglis	*benigna* (Brandt) [P], *eurata* (Prout) [P]
Scopula	*achrosta* Prout [As], *actuaria* (Walker) [As], *adelpharia* (Püngeler) [P], *ansorgei* (Warren) [Af], *curvimargo* (Warren) [Af], *decolor* (Staudinger) [P], *deserta* (Warren) [Af], *desita* (Walker) [Au], *donovani* (Distant) [Af], *eburneata* (Guenée) [Neotropics], *emissaria* (Walker) [As], *epigypsa* (Meyrick) [As], *ferrilineata* (Moore) [As], *fimbrilineata* (Warren) [Af], *haemaleata* (Warren) [Af], *imitaria* (Hübner) [P], *immorata* (Linnaeus) [P], *limboundata* (Haworth) [N], *mecysma* (Swinhoe) [As], *opicata* (Fabricius) [As], *ornata* (Scopoli) [P], *pedilata* (Felder & Rogenhofer) [As], *plionocentra* (Prout) [Af], *rhodocraspeda* Prout [Madagascar], *rivularia* (Leech) [P], *rufisalsa* (Warren) [Af], *sentinaria* (Geyer) [N], *silonaria* (Guenée) [Af], *submutata* (Treitschke) [P], *subnictata* (Snellen) [Neotropics], *ternata* Schrank [P], *umbelaria* (Hübner) [P], *vinocinctata* (Guenée) [Neotropics], *virgulata* (Denis & Schiffermüller) [P]
Scopuloides	*fucata* (Püngeler) [P], *origalis* (Brandt) [P]
Somatina	*anthophilata* Guenée [As], *centrophora* Prout [Af], *chalyboeta* (Walker) [Af], *eurymitra* Turner [Au], *indicataria* (Walker) [P], *irregularis* (Warren) [Af], *lia* Prout [Madagascar], *mendicaria* (Leech) [P], *microphylla* (Meyrick) [As], *nigridiscata* (Warren) [As], *nucleata* Warren [Af], *sedata* Prout [Af], *triocellata* (Bastelberger) [Au]
Stigma	*kuldschaensis* Alphéraky [P]
Zygophyxia	*relictata* (Walker) [As], *tornisecta* Prout [Af]
Zythos	*avellanea* (Prout) [As], *obliterata* (Warren) [As], *turbata* (Walker) [As]

sequently, all characters that could be coded unequivocally were included. Many, such as the shape of the base of the male metafurca (Ch. 54, Figs 109, 110), are novel and demonstrate that detailed morphological studies can yield new and phylogenetically significant characters.

Two autapomorphic qualitative characters (Chs. 0 and 58) were included in the analysis. This was because these characters were present in one monotypic genus only, and I wanted to alert lepidopterists to search for these features outside the taxa studied. Furthermore, the inclusion of autapomorphic characters does not affect the calculation of consistency indices (Yeates, 1992). The data set is given in Table 2.

Head

0. *Pilifer*: (0) present; (1) absent.
1. *Sensilla styloconica at distal end of proboscis*: (0) present; (1) absent (morphologically unidentifiable).



Figures 1–25. Type species of genera included in the phylogenetic analysis. The numbers on the figures refer to the numbers of the character states. 1. *Idaea aversata*. 2. *Somatina anthophilata*. 3. *Dithalama cosmospila*. 4. *Isoplenodia arrogans*. 5. *Zythos turbata*. 6. *Lipomelia subusta*. 7. *Problepsis ocellata*. 8. *Scopula ornata*. 9. *Ignobilia urnaria*. 10. *Antitrygodes divisaria*. 11. *Epicosymbia dentisignata*. 12. *Glossotrophia confinaria*. 13. *Isoplenia trisinuata*. 14. *Cartaletis libyssa*. 15. *Aletis helcita*. 16. *Leucoxena lactea*. 17. *Stigma kuldschaensis*. 18. *Dasybela achroa*. 19. *Pseudocinglis eurata*. 20. *Cinglis humifusaria*. 21. *Autanepsia poliodesma*. 22. *Antilycauges pinguis*. 23. *Oar pratana*. 24. *Zygophyxia tornisecta*. 25. *Scopuloides fucata*. Scale bars = 5.0 mm.

2. *Proximal pigment layer of compound eyes*: (0) circular; (1) semicircular (figured in Sihvonen & Kaila, 2004).
3. *Two pores on anterior part of dorsal sclerite between antennae*: (0) absent (morphologically unidentifiable); (1) present.
4. *Two extensions on anterior part of dorsal sclerite between antennae*: (0) absent; (1) present (Fig. 100). Similar protuberant, rounded projections dorsad to antennal opening have been reported from Ennominae (Young & McQuillan, 2003).

Table 2. Data matrix for the cladistic analysis of Scopulini, based on characters from adult morphology and ecology. Missing data are represented by '?'. Characters coded from the literature are within grey tint boxes. Numbers in parentheses after each taxon name indicate the literature reference as follows: (1) Hausmann (1994); (2) Wiltshire (1986); (3) Janse (1933–35); (4) Turner (1908); (5) Prout (1929–35); (6) Prout (1920–41)

TAXA	0123456789111111111122222222223333333333444444444455555555556666666666 0123456789012345678901234567890123456789012345678901234567890123456789
Idaea aversata	0000000000000000000000000000000000000000000000000000000000000000000000
Idaea emarginata	0000000000000000000000001000000000001002010000000000000000000100200
Problepsis ocellata	0001000010000000220140100110000000000000010010000000011?0010001103210
Problepsis conjunctiva	?????0000??000001211411001110000000001001011000000?????????000?000000
Problepsis achlyobathra	?????000100000001211400001100000000001002011000000?????????0001000000
Problepsis plagiata	0001000000000002201411001110000000001001002000000000?0100100011000010
Problepsis clemens	?????000100000001201300001000000000011001001000000?????????001103000
Problepsis aegretta (3)	?????000112000002201301000000000000000001001000000?????????0001??????
Problepsis flavistigma	?????000100000002201301000000000000001001001000000?????????1101100010
Somatina anthophilata	0000000000000000000000000000010000000000000010001200001010??0001100210
Somatina chalyboeta (5)	00000???0??000000000000000000010000000000000100011000010100100011100210
Somatina microphylla	0000100000001000000250100000000000000000010020001200101010011101100210
Somatina nigridiscata	0000000000000000000000000000000000000000000010001200001010011121100210
Somatina indicataria	0001000000000000001000001000100100000000100200012000010000 1?001100210
Somatina mendicaria	?????000000000000000000000000000000000000000010001200?????????001100210
Somatina triocellata	?????000000000002201301000000000000001000000000000000????????0001103210
Somatina centrophora	?????000100000002201301000000000000000110100100012000????????1121100210
Somatina nucleata (5)	?????000000000000001001000000000000000001201100012000??? 0010001000200
Somatina sedata (5)	?????000000000000000000000000000000011100001000121?????????0001100210
Somatina eurymitra	?????0000??000000000200000000001000000000000100012 10????????000?100210
Somatina lia	?????000000000000000000000000000000100000010001200????????0001100210
Somatina irregularis	?????000000000000000000000000001000000000201100000000????????0001100210
Scopula ornata	0000101000000000000000000000001001000000000000000000000011010??0001100210
Scopula decolor	0000000000000000000000000000000000000000002011000000000010?0??1121100210
Scopula imitaria	0001000000000000000000000000000000000001002011000000000101001000 1100210
Scopula ansorgei	0001000001200000000000000000000000000000000001000000010101 00?0001100210
Scopula immorata	0001100100000000000000000000000000000000000000000000000101001000 1100210
Scopula sentinaria	0001010100000000000000000100000000000010000010000000001100011121100210
Scopula rufisalsa	0001001011100000000000000000000000000000000001000000001101001112 1100210
Scopula umbelaria	0001000000000000000000000000000000000000000000000000000?0?0??0001100210
Scopula deserta	0000001001200000000000000100100000000000000010000000010?0010001100210
Scopula donovani	0000001000000000000000000100100000000000000010010000011000011121100210
Scopula lactea	0000001000000000000000000100100000000000000010010000010100111121100210
Scopula silonaria	0001001000000000000000000000000000000000000010000300011111011121100210
Scopula opicata	0000000000000000000250000000000000000010000010000000011000010001100210
Scopula plionocentra	0001001000000000000000000000000000000000000000000000000101001112 1100210
Scopula virgulata	000??000000000000000000000000000000000000000010000000011010011101100210
Scopula submutata	0001000000000000000000000000001000000010000000000000010101001000 1100210
Scopula curvimargo	0001001010000000000000000000000010000100000000000000010100111011 00210
Scopula ternata	0001000000000000000000000000000000000000000010000000010100111121100210
Scopula ferrilineata	000??000000000000000000001000000100000100000100000001010?0010001100210
Scopula limboundata	0000000000000000000000000000001001000000000010000000 10?010000001100210
Scopula epigypsa (6)	0000101000000000000000000000000000000000000010000000001?10??0001 1100210
Scopula mecysma	0001100000000000000000000000000000000010020110000000010?0000001100210
Scopula adelpharia	0000001000000000000000000000000000000000000010000000011000000001100210
Scopula haemaleata (5)	?????000000000000000000000000000000010000010000000?????????? 01??????
Scopula achrosta	?????000000000000000000000001001000000002010000000?????????0001100210
Scopula rivularia	?????000000000000000000000001001000000000010000000?????????0001100210
Scopula actuaria	?????000000000000000000000000000000000000010000000?????????0001???2??
Scopula desita	?????001000000000000000000000000000000000000000000?????????0001000210
Scopula pedilata	?????000000000000000000000000001000000000000000000?????????0001100210
Scopula vinocinctata	?????000000000000001300000000000000001000000100000000?????????0001000210

Table 2. *Continued*

TAXA	0123456789111111111122222222223333333333444444444455555555556666666666 0123456789012345678901234567890123456789012345678901234567890123456789
Scopula eburneata	?????0000000000000000000000000000000000000001000000?????????0001000210
Scopula subnictata	?????0000000000000000000000001001000000000000000000?????????0001100210
Scopula fimbrilineata	?????0000120000000000000000000000000000000000000000000???0010001100210
Scopula rhodocraspeda (5)	?????0000??000000000000001000000000000002011000000?????????0001100210
Pseudocinglis eurata	?????0000000000000000000000000000000010000001000030?????????1121000210
Pseudocinglis benigna	?????0000000000000000000000000000000010000001000030?????????1120??02?0
Cinglis humifusaria	0101000110000000000000001000000000001100?0?2000000001110001112110021 0
Zythos turbata (6)	0000000000020000310120010000001000000001010100012000110100001010001000
Zythos obliterata	?????0000000000031025000000000000000000012011000110 0?????????0101100100
Zythos avellanea	?????0000002000031012001000000100000000101010001200?????????0101100100
Antilycauges pinguis	0000001110000000000000001000000000000000000000000000010000111211002 10
Isoplenodia arrogans (5)	100?????1??000000000000000000000000000?0??000121010101011010 1001001
Isoplenia trisinuata	0000001011100000000000000000000000000010000010001210001010011121100210
Scopuloides fucata (1)	?????0000 0000000000000000000000000000010000001000000?????????112 0???2??
Scopuloides origalis (1)	?????0000??000000000000000000000000001000000100000?????????112 0000210
Antitrygodes divisaria	0001000000001110000110201000000000000000000000000??10?0000001002001
Antitrygodes cuneilinea (6)	?????0000000110000011020000000000000000000000000000001??????000 1001001
Antitrygodes parvimacula	?????0000000111000011020100000000000000000000000000?????????0001002001
Epicosymbia dentisignata (3)	000??0001000000000000000000000000000000002011000111001101 0??111 1100???
Epicosymbia perstrigulata (3)	000??0001000000000000000000000000000000002011000111001 1?0001010 1100210
Epicosymbia albivertex	?????0001000000000000000000000000000000002011000111 0?????????0001100210
Dithalama cosmospila	000??0000000000000000001000000000000000000100012100010100100010000 01
Dithalama desueta	?????0000120000000000000000000000000000000010001110?????????010?100210
Aletis helcita	0011001010000001000250300200000011112220?0111100301001111??1120110210
Aletis erici	?????0101000000100025030020000000111122 20?0111100301?????????1120110210
Stigma kuldschaensis	0101000002??000000010000000000000002220201100000000111000111 2?100210
Cartaletis libyssa	0011001010000001000250300200000011112220?0111101111001111011120110210
Cartaletis variabilis	0011001010000002000250300200000011112220?0111101211001111011120110210
Cartaletis gracilis	?????0101001000200025030020000000111001 00?0011101111?????????1120110210
Leucoxena lactea	0001101010000000000000000000000000000000000010000000011000??1101100210
Oar pratana	0101010110000000000000000000001000000000000200004 00?0?010011121100210
Lipomelia subusta (6)	000000000??2000022010001000000000000000000101000000000101001000 1103201
Autanepsia poliodesma (4)	?????0000??000000000000000000000000000000001000111 0??????????2???????
Ignobilia urnaria	0000000010000000000000000100000000000000?0?1000110001101001000100020 1
Zygophyxia tornisecta (1)	0100001000000000000000000100000000000000000010010000011000011120 100210
Zygophyxia relictata	?????0100000000000000000010010000000000000001001 0000?????????1120100210
Glossotrophia confinaria	0001000000000000000000000000000000000010000001000000000110 10??1110100210
Glossotrophia asellaria	000??0000000000000000000000000000000010000001000000000110100111110100210
Glossotrophia adenensis (2)	?????0000 0000000000000000000000000000010000001000000?????????1110??????
Dasybela achroa	?????0100??000000000000000000000000000000201200000 00??????????2???0210

	1111111111111111111111111111111111111111111 7777777777888888888899999999990000000000111111111122222222223333333334 0123456789012345678901234567890123456789012345678901234567890123456789012345678901234567890
Idaea aversata	0000000000000000000000000000000000000000000000000000000000000000000000000
Idaea emarginata	0000000000000000000000000000000000000000000000000000000000000000000000000
Problepsis ocellata	0000002112100200111001200010121001200000101011100000101000000001002110 0
Problepsis conjunctiva	0??0?021121002000110012100101210012000000010112001001010000000 10???????0
Problepsis achlyobathra	00?0002111000200111001200010121001200000000100120010000100000000 10020100
Problepsis plagiata	0001002112100200011001210010120001200000000101120010010100000001010021100
Problepsis clemens	0000002101000200111001200010121001200000000101020010010100000000 1002110?
Problepsis aegretta	0001001302100200111001200010120001200000000100020010010100000000 1002110?
Problepsis flavistigma	0000102300000200011001200010121001200000000101120010010100000000000 2010?
Somatina anthophilata	0000002400000100013001300010120001210010011000100000001000000011002 1110

Table 2. *Continued*

	1111111111111111111111111111111111111111 7777777777888888888899999999990000000000111111111122222222223333333334 0123456789012345678901234567890123456789012345678901234567890123456789012345678901234567890
Somatina chalyboeta	00000024100001000110013010101200012100101011002000000010000000??????????
Somatina microphylla	02121024000002000110013000101200012000000010012000100010000000110020110
Somatina nigridiscata	00001023000000010130013000101200012100101010003000000010000000010021111?
Somatina indicataria	02120021020102001110013000101200012000000010011000000010000000110020110
Somatina mendicaria	02120023020002001130013000101210012000000010111000000010001000010021110?
Somatina triocellata	00010021120002000110012000101210012000000010102000000010000000010020110
Somatina centrophora	00?01021000002001110012000101210012000000010002000000010000000021010102?
Somatina nucleata	00000023020102000110013000101200012100000010?10100000100010000010010111?
Somatina sedata	00000023020102000110013000101200012100102?11000200011001000000011002111?
Somatina eurymitra	00000024021002001130013000101220012000001010012000000010000000??????????
Somatina lia	00000013000000011110013000101200012100101110012000000010000000011002011?
Somatina irregularis	00000024120012000110013000101200012000000010001100000010000000010020102?
Scopula ornata	00000024120102001110013000111200012000000010001000000010100000010021100
Scopula decolor	00001024020002001110013000101200012000000010001000000010000000010020100
Scopula imitaria	00000024020102001110013000101200012000000010001000000010000000010020100
Scopula ansorgei	00000023010002001110013000101200012010000010011000000010000000010021011?
Scopula immorata	00?01024120102001110013000101200012000000010011000001110000000021021110
Scopula sentinaria	02121013000002001110013000101000012000000010001000000010000000000001111?
Scopula rufisalsa	00001023020002001110013000101200012000000010001000100010000000010020100
Scopula umbelaria	00000024020102001110013000101200012010000011001010000010010000110020110
Scopula deserta	00?00023020102001110013001111100012000000010001010001110000?00010021100
Scopula donovani	00001024020102001110013000111200012100000010001000000010000000010020100
Scopula lactea	00001023020102001110013000101200012000000010001000000010000000000020100
Scopula silonaria	02121023020102001110013000101200012000000010001000000010000000010020100
Scopula opicata	00000024120102001110013000101200012000000100?10000000100000000010011100
Scopula plionocentra	00001024020102001110013000111200012000000010001000000010000000000001010?
Scopula virgulata	00000024120102001110013000101200012000000010001000000010100000010021100
Scopula submutata	00000024020102001110013000111200012000010010010000000010000000000020110
Scopula curvimargo	00?01024020102001110013000101200012000000010001000110010100000001002110?
Scopula ternata	00000024020102001110013000101200012000000010001000000010000000010020100
Scopula ferrilineata	00000024020102001110013000111200012100100010001000000010000000010020100
Scopula limboundata	00000024020102001110013000101200012000000010001000000010000000010020100
Scopula epigypsa	00000023021002001110013000101200012000010010001000000010000000001002010?
Scopula mecysma	00000023020102001110013000101200012000100010011000000010000000010020110
Scopula adelpharia	00000024120102001110013000101200012000000010011000000010000000010010110
Scopula haemaleata	00000024120012000110013000101200012000000010011100000010002000011002110?
Scopula achrosta	00000023020102000110013000101200012000000010001000000010000000001002110?
Scopula rivularia	00000024020102001110013000101200012010000010001010000010010000001002011?
Scopula actuaria	00000024120102001110013000101200012000000010001000000010000000001001011?
Scopula desita	00000023020102000110013000111200012000110010011010001110000000021020112?
Scopula pedilata	00000024020102001110013000101200012000000010011000000010000000001002010?
Scopula vinocinctata	00000023020102001110013000111200012000000010001000000010000000001002010?
Scopula eburneata	00000023010002001110013000111200012000000010000000000010000000000002010?
Scopula subnictata	00000023020102001110013000101200012000010010001000000010000000000001010?
Scopula fimbrilineata	00000023020102001110013000101200012000000011001000000010000000010021110
Scopula rhodocraspeda	00000023020102001110013001101100012000000010001000000010000000??????????
Pseudocinglis eurata	02121023020102001110013000101200112000000010011000000010000?0021100
Pseudocinglis benigna	0??0?02300000200111001300010120011200000001011100000001000010000021100
Cinglis humifusaria	02121023020102001110013000101200112000000010011000001010000100000021100
Zythos turbata	00000013000000011140113010001201212001001010000000001110000000110120120
Zythos obliterata	00000013000000011140113010001201212001001010000000000010000000110120112?
Zythos avellanea	00000013000000011140113000001201212001000010000000000010000000110120120
Antilycauges pinguis	02121024020102001110013000101200012000000010010000000010000000000010100
Isoplenodia arrogans	0??01024020002001110013000101200012000001010001000000011100000???????????

Table 2. *Continued*

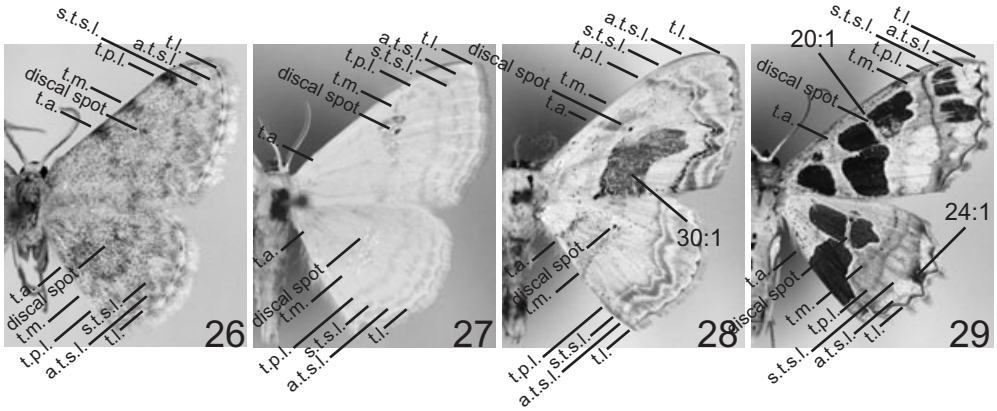
	1111111111111111111111111111111111111111
	7777777777888888888899999999990000000001111111111222222222233333333334
	0123456789012345678901234567890123456789012345678901234567890123456789
Isoplenia trisinuata	02121023020002001110013000101200012100 11??100010000010100000000 1001011?
Scopuloides fucata (1)	0??0?024120?02001????13000101?????2?00???0100?????00???0?0??00?00020110
Scopuloides origalis (1)	02121024120002001110013000101200012000000001000????000010000000 00?2011 0
Antitrygodes divisaria	00010122120102000111013000101200012000011110012000001110000000110021110
Antitrygodes cuneilinea	00010024120102000110012000101200012000010110001000000010000000000211??
Antitrygodes parvimacula	00010122120102000111013000111200012000011?10010000000010000000110021111?
Epicosymbia dentisignata	00001003020102101110011000101200011000000010001000000010000010010011011?
Epicosymbia perstrigulata	0??01003020102101110011000101200011000000010001000000010000010010011011?
Epicosymbia albivertex	00000003020102001110011000101200011000000010 0?10000000100000100100 1011?
Dithalama cosmospila	00000024100000?11200130001012200120000000100120000000111000000100201 10
Dithalama desueta	00001024100000011110013000101220012000001010000000001111100000000002111?
Aletis helcita	10201023020102001110013000101200012100100010001000000010000000010020101
Aletis erici	10201023020102001110013000101200012100100010001000000010000000010021101
Stigma kuldschaensis	00001013000000001110013000101200012000000010011000000010000100 0???????0
Cartaletis libyssa	10201024120102001110013000101200012100100011 0?10000000100000000010020101
Cartaletis variabilis	10201023020102001110013000101200012100100010002000000010000000010020101
Cartaletis gracilis	10201023020102001110013000101200012100100011002000000010000000010020101
Leucoxena lactea	02121013000002001110013000101200012000000010001000000010000000010020100
Oar pratana	02121024020002001110013000101200012000000010011000100010002000000020100
Lipomelia subusta	00000024020000000110013000101200012100100011000000000010000000 1????????
Autanepsia poliodesma	02121024000001001110013000101200012000001010010000000010000000 ????????
Ignobilia urnaria	01000024020102001110013010101200012100100010003000000010002000020021 10?
Zygophyxia tornisecta	02121024120102001110013000111200012000000010011000000010000000 ?0020100
Zygophyxia relictata	0??0?02?1??00?0?11100130001010000120000000100100000011111000000000 2010?
Glossotrophia confinaria	00001024020102001110013000101200012000000010001000000010000000010020110
Glossotrophia asellaria	00001024020002001110013000101200012000000010001000000010000000010020100
Glossotrophia adenensis (2)	0000?024020102001????13000?01?????20000?00100?????00????????00?10020100
Dasybela achroa	02121003010000001110013000101200012000000010001000000011100000 0????????

5. *Scales between antennae*: (0) flat scales only; (1) both flat and hair scales.
6. *Scales among chaetosemata*: (0) absent (Fig. 103); (1) present (Fig. 104).
7. *Male antennal segments dorsally*: (0) unicolorous; (1) bicolorous.
8. *Ventrolateral sensilla on proximal part of male flagellomere*: (0) single row; (1) multiple rows.
9. *Ventrolateral sensilla on medial part of female flagellomere*: (0) present; (1) absent.
10. *Ventrolateral sensilla on proximal part of female flagellomere*: (0) undifferentiated; (1) multiple rows; (2) single row.

Wing pattern

See Figures 26–29 for a few examples of how wing pattern homologies have been interpreted.

11. *Forewing costa*: (0) narrow; (1) wide, dark brown; (2) wide, grey.
12. *Light green colour on wings*: (0) absent; (1) present.
13. *Reticulate pattern*: (0) absent; (1) present (Fig. 10).
14. *Elongated marking on hindwing inner margin*: (0) absent; (1) present (Fig. 10).
15. *Wings unicolorous (without irroration)*: (0) no; (1) yes, orange; (2) yes, light yellow.
16. *Distribution of iridescent scales*: (0) absent; (1) scattered uniformly; (2) restricted to a few rows including discal spots; (3) restricted to a few rows excluding discal spots.
17. *Structure of iridescent scales*: (0) absent; (1) glossy, longitudinally grooved (Fig. 101); (2) glossy, smooth (Fig. 102).
18. *Iridescent scales of cilia*: (0) absent; (1) present.
19. *Forewing discal spot unicolorous, dark*: (0) yes (Fig. 23); (1) no; (2) absent.
20. *Forewing discal spot structure*: (0) spot; (1) cryptic (Fig. 29); (2) lunular (Fig. 5); (3) ocellate, semiround; (4) ocellate, round (Fig. 7); (5) absent.
21. *Forewing discal spot with wide brown margin*: (0) absent; (1) present (Fig. 105).



Figures 26–29. Interpretation of wing pattern homologies. Species are mentioned in their generic combinations prior to analysis. The numbers in the figures refer to the numbers of the character states. 26. *Glossotrophia confinaria*. 27. *Problepsis aegretta*. 28. *Somatina chalyboeta*. 29. *Antitrygodes divisaria*. *Abbreviations:* t.a., transverse anterior line. t.m., transverse median line. t.p.l., transverse posterior line. s.t.s.l., subterminal shade line. a.t.s.l., adterminal shade line. t.l., terminal line. Figures are not to scale.

22. *Hindwing discal spots*: (0) present, dark spot; (1) present, ocellate; (2) present, concolorous with wings; (3) absent.
23. *Pale markings on anterior side of hindwing discal spot*: (0) absent; (1) present (Fig. 5).
24. *Dark patch on hindwing margin at vein M_2*: (0) absent; (1) present (Fig. 29).
25. *Transverse median line*: (0) present, distinct (Fig. 13); (1) present, obscure (Fig. 7); (2) absent.
26. *Dark patch at forewing transverse median line separated by vein CuA_1*: (0) absent; (1) present (Fig. 105).
27. *One dark patch at forewing M_2*: (0) absent; (1) present (Fig. 106).
28. *Transverse posterior line*: (0) continuous; (1) spotted.
29. *Two dark marks on forewings medial of transverse posterior line*: (0) absent; (1) present (Fig. 8).
30. *Shade on forewing termen between transverse anterior and transverse median lines*: (0) absent; (1) present (Fig. 28).
31. *Shade on forewing between transverse median and transverse posterior lines*: (0) absent; (1) present (Fig. 23).
32. *Dark mark at forewing termen*: (0) absent; (1) present (Fig. 8).
33. *Forewing margins wide*: (0) no; (1) yes (Fig. 15).
34. *Forewing margins with white spots*: (0) no; (1) yes (Fig. 14).
35. *Hindwing margins wide*: (0) no; (1) yes.
36. *Hindwing margins with white spots*: (0) no; (1) yes.
37. *Terminal line at forewing apex*: (0) present, not smoothly curved around apex; (1) present, smoothly curved around apex (Fig. 19); (2) absent. A smoothly curving terminal line that continues around the forewing apex has been considered a synapomorphy of *Glossotrophia* (Hausmann, 1993c).
38. *Terminal line continuity at forewing margin*: (0) discontinuous; (1) continuous; (2) absent.
39. *Terminal line width at forewing margin*: (0) equally wide; (1) wider at vein ends; (2) absent.
40. *Spot at vein end at forewing margin*: (0) absent; (1) present.
41. *Subterminal shade line*: (0) present, continuous; (1) present, discontinuous (Fig. 7); (2) absent.
42. *Subterminal shade line and terminal line*: (0) do not touch each other on fore and hindwings; (1) touch each other at fore and hindwings (Fig. 6).
43. *Adterminal shade line*: (0) present (Figs 26–29); (1) absent.
44. *Fringe*: (0) chequered, dark spot at vein end; (1) unicolorous; (2) chequered, white spot at vein end (Fig. 20).

Wing scales

45. *Shape at forewing discal spot area*: (0) margins parallel; (1) tapering towards apex.
46. *Surface at forewing discal spot area*: (0) longitudinally grooved; (1) smooth.

Wing shape

47. *Forewing termen rounded:* (0) no; (1) yes.

Wing venation

48. *Forewing areoles*: (0) one, formed by R veins; (1) two, formed by R veins. Features of wing vena-

tion have been used extensively in the systematics of the Scopulini (e.g. Prout, 1912–16; Forbes, 1948; Hausmann, 1994).

49. *Point of origin of forewing vein R_5*: (0) proximal areole, stalked with veins R_2–R_4; (1) distal areole, distinctly separate from R_2–R_4; (2) distal areole, stalked with R_2–R_4; (3) proximal areole, distinctly separate from R_2–R_4; (4) stalked with M_1. I am aware that characters 49–51 are variable and the division of these into distinct character states may turn out to be artificial if more taxa and material were to be studied.
50. *Point of origin of forewing vein M_1*: (0) proximal areole; (1) distal areole.
51. *Hindwing veins $Sc + R_1$ and Rs*: (0) fused shortly; (1) separate, but connected via a crossvein (R_1?). 51: 1 was earlier considered to be a synapomorphy for the Orthostixinae (Hausmann, 2001).

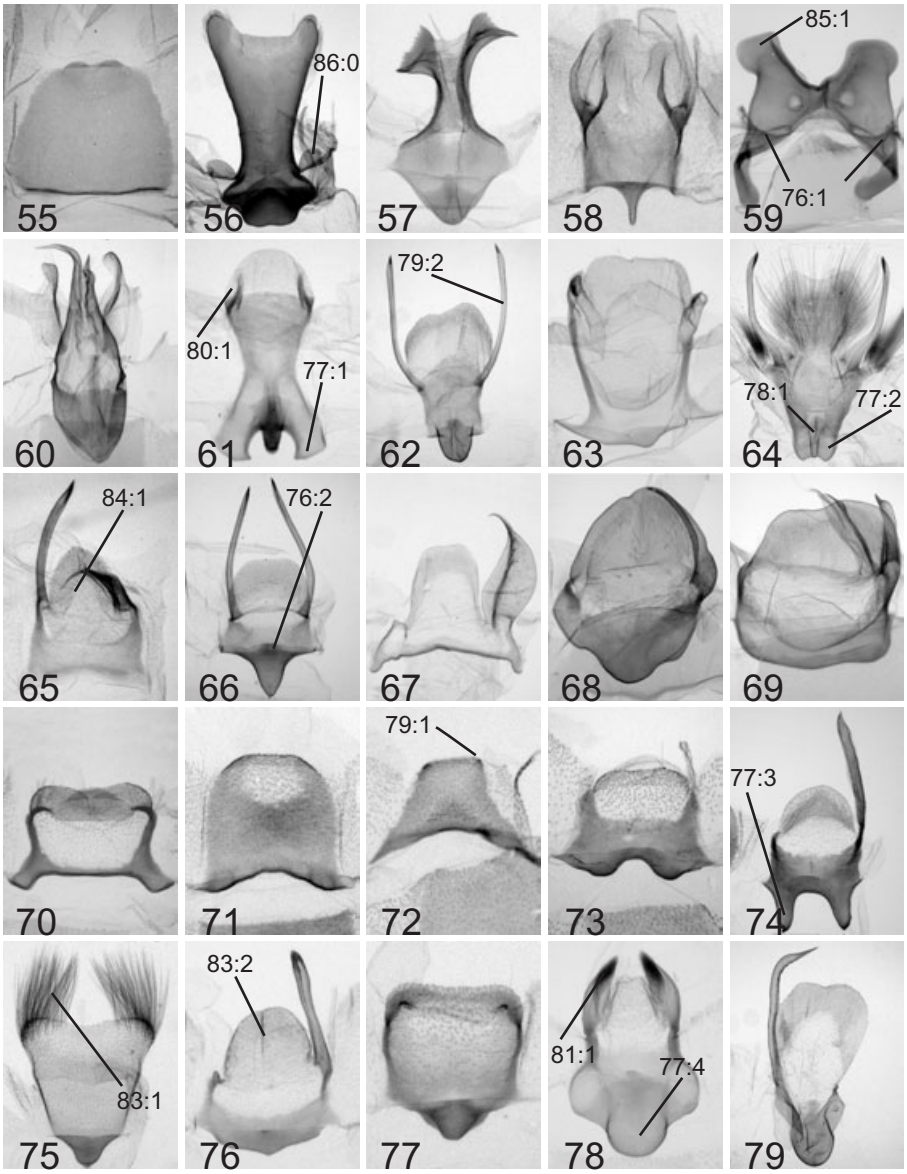
Thorax

52. *Anterior ventral lamina of metathorax metafurca*: (0) present (Fig. 107); (1) absent.
53. *Posterior ventral lamina of metathorax metafurca*: (0) present (Fig. 107); (1) absent.
54. *Base of metathorax metafurca*: (0) margins constricted (Fig. 109); (1) lateral margins basally opened or straight (Fig. 110).
55. *Pouch on posterior margin of male metathorax coxa*: (0) present (Fig. 108); (1) absent. Pouch absent in females.
56. *Membrane sac at posterior part of male metathorax coxa*: (0) absent; (1) present (Fig. 111).
57. *Lateral processes of male metathorax coxa*: (0) elongated (Fig. 109); (1) undifferentiated (Fig. 110). Processes absent in females.
58. *Opening on male metathorax dorsal sclerite*: (0) present (Fig. 112); (1) absent.
59. *Medial ridge in epinotum*: (0) present; (1) absent.
60. *Male hindleg outer margin hair pencil of tibia*: (0) present (Fig. 113); (1) absent.
61. *Male hindleg inner margin hair pencil of tibia*: (0) present (Fig. 113); (1) absent.
62. *Male hindleg distal spurs of tibia*: (0) absent; (1) one; (2) two. The number of male and female hindleg spurs has been used extensively in systematics of the Scopulini (e.g. Janse, 1933–35). Intraspecific variation has been reported to occur in the number of spurs in a few *Glossotrophia* species (Hausmann, 1993c).
63. *Female hindleg medial spurs of tibia*: (0) absent; (1) two; (2) one.
64. *Apical spines on male hindleg tarsus*: (0) absent; (1) present.
65. *Thick spines on anterior side of male hindleg tarsus*: (0) absent; (1) present.
66. *Male hindleg tarsomeres*: (0) not fused; (1) tarsomeres 1–5 fused; (2) tarsomeres 2–5 fused; (3) tarsomeres 4–5 fused.
67. *Male hindleg claws*: (0) absent (Fig. 115); (1) one (Fig. 114); (2) two, separate.
68. *Male hindleg pretarsus arolium*: (0) absent; (1) present.
69. *Male hindleg pretarsus pulvillus*: (0) present (Figs 114, 115); (1) absent.

Abdomen

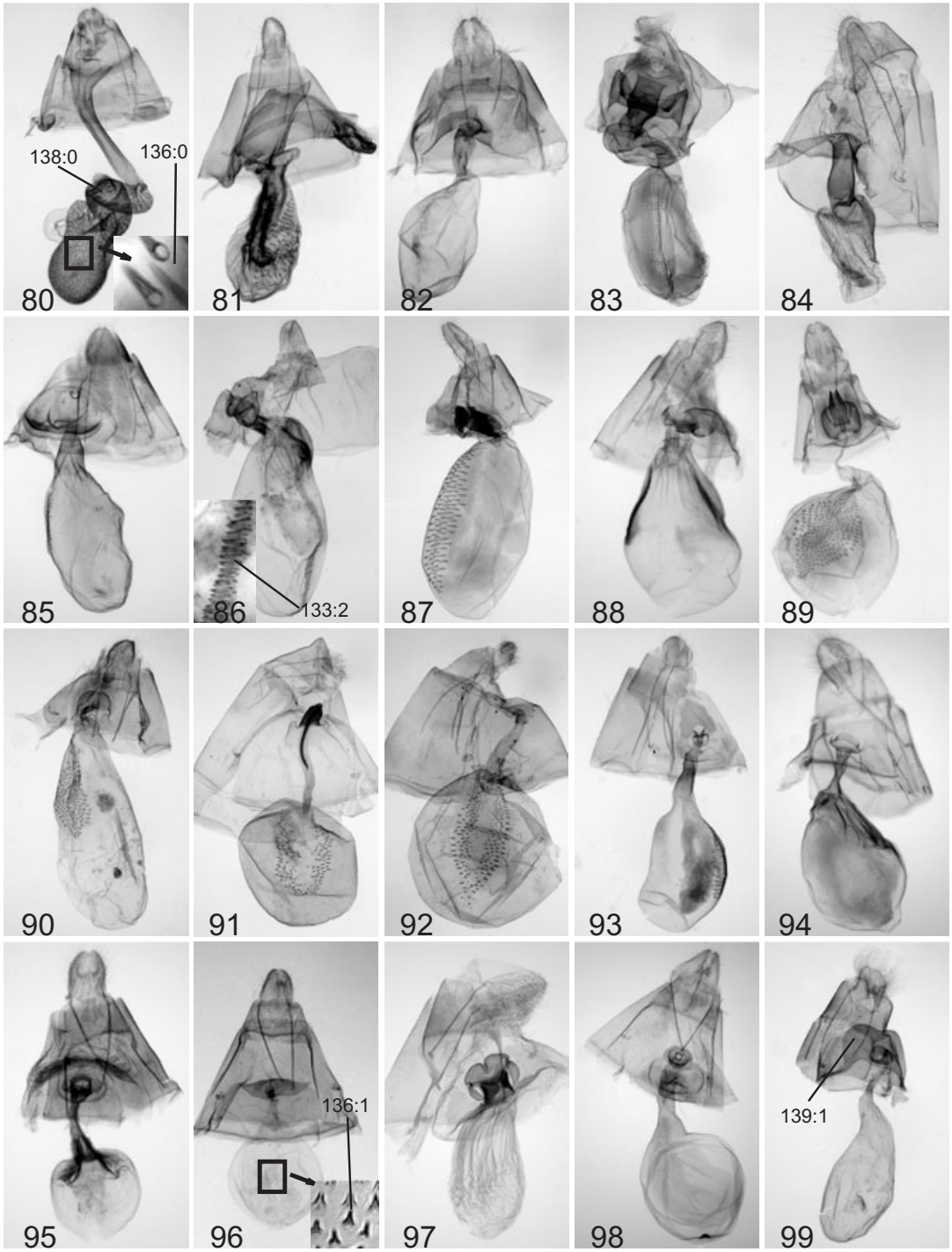
70. Three parallel rows of white spots: (0) no; (1) yes (Fig. 15).
71. *Pouch on male 2nd sternite anteromedially*: (0) round (Fig. 116); (1) posterior margin elongated; (2) absent. The surface of this pouch was found to be variable between species. It is smooth in the majority of taxa. It is not unusual for it to be round, with a granulate surface (e.g. *Scopula eburneata*) or have star-shaped invaginations (e.g. *Scopula achrosta*). In a few species, such as *Aletis helcita* and *Stigma kuldschaensis*, it is covered with stout setae. Due to the quantitative nature of this variation I was unable to code it unambiguously.
72. *Pouch on male 2nd sternite anteromedially*: (0) with one chamber (Fig. 116); (1) absent; (2) with two chambers.
73. *Pouch on male 2nd sternite anteromedially with lateral elongation*: (0) laterally not invaginated; (1) laterally invaginated (Fig. 116); (2) absent.
74. Extensions on male 2nd sternite anterolaterally: (0) present (Fig. 116); (1) absent.
75. *Setae laterally on 6th male segment*: (0) absent; (1) present.
76. *Pouch between male 7th and 8th sternite*: (0) absent; (1) two pouches (Fig. 59); (2) one pouch (Fig. 66).
77. *Male 8th sternite anterior margin*: (0) unmodified; (1) trifurcate, blunt (Fig. 61); (2) trifurcate, round (Fig. 64); (3) bifurcate (Fig. 74); (4) elongated medially (Fig. 78).
78. *Male 8th sternite with two parallel grooves*: (0) absent; (1) present (Fig. 64).
79. *Cerata*: (0) absent; (1) rudimentary (Fig. 72); (2) fully developed (Fig. 62). There exists intraspecific variation in the shape and length of the cerata in many species of *Scopula* and *Glossotrophia* (Hausmann, 1999b). For this reason I did not include quantitative features of these structures in this study.
80. *Cerata fused with mappa*: (0) no; (1) yes (Fig. 61).
81. *Cerata with setae*: (0) no; (1) yes (Fig. 78).
82. *Cerata bifurcate*: (0) no; (1) yes.

Figures 30–54. Male genitalia and aedeagus of type species of genera included in the phylogenetic analysis. The numbers in the figures refer to the numbers of the character states. 30. *Idaea aversata* (slide number) PS704. 31. *Somatina anthophilata* (slide number) BMNH GEO20369. 32. *Dithalama cosmospila* PS707. 33. *Isoplenodia arrogans* BMNH GEO20527. 34. *Zythos turbata* BMNH GEO20371. 35. *Lipomelia subusta* BMNH GEO20530. 36. *Problepsis ocellata* BMNH GEO20370. 37. *Scopula ornata* PS692. 38. *Ignobilia urnaria* BMNH GEO20531. 39. *Antitrygodes divisaria* BMNH GEO20375. 40. *Epicosymbia dentisignata* BMNH GEO20365. 41. *Glossotrophia confinaria* BMNH GEO20382. 42. *Isoplenia trisinuata* BMNH GEO20363. 43. *Cartaletis libyssa* BMNH GEO20372. 44. *Aletis helcita* BMNH GEO20360. 45. *Leucoxena lactea* BMNH GEO20376. 46. *Stigma kuldschaensis* PS859. 47. *Dasybela achroa* PS897. 48. *Pseudocinglis eurata* PS894. 49. *Cinglis humifusaria* PS648. 50. *Autanepsia poliodesma* BMNH GEO20526. 51. *Antilycauges pinguis* BMNH GEO20381. 52. *Oar pratana* PS714. 53. *Zygophyxia tornisecta* BMNH GEO20380. 54. *Scopuloides origalis* PS58 (male of *S. fucata* type species of the genus was not available for study). Figures are not to scale.

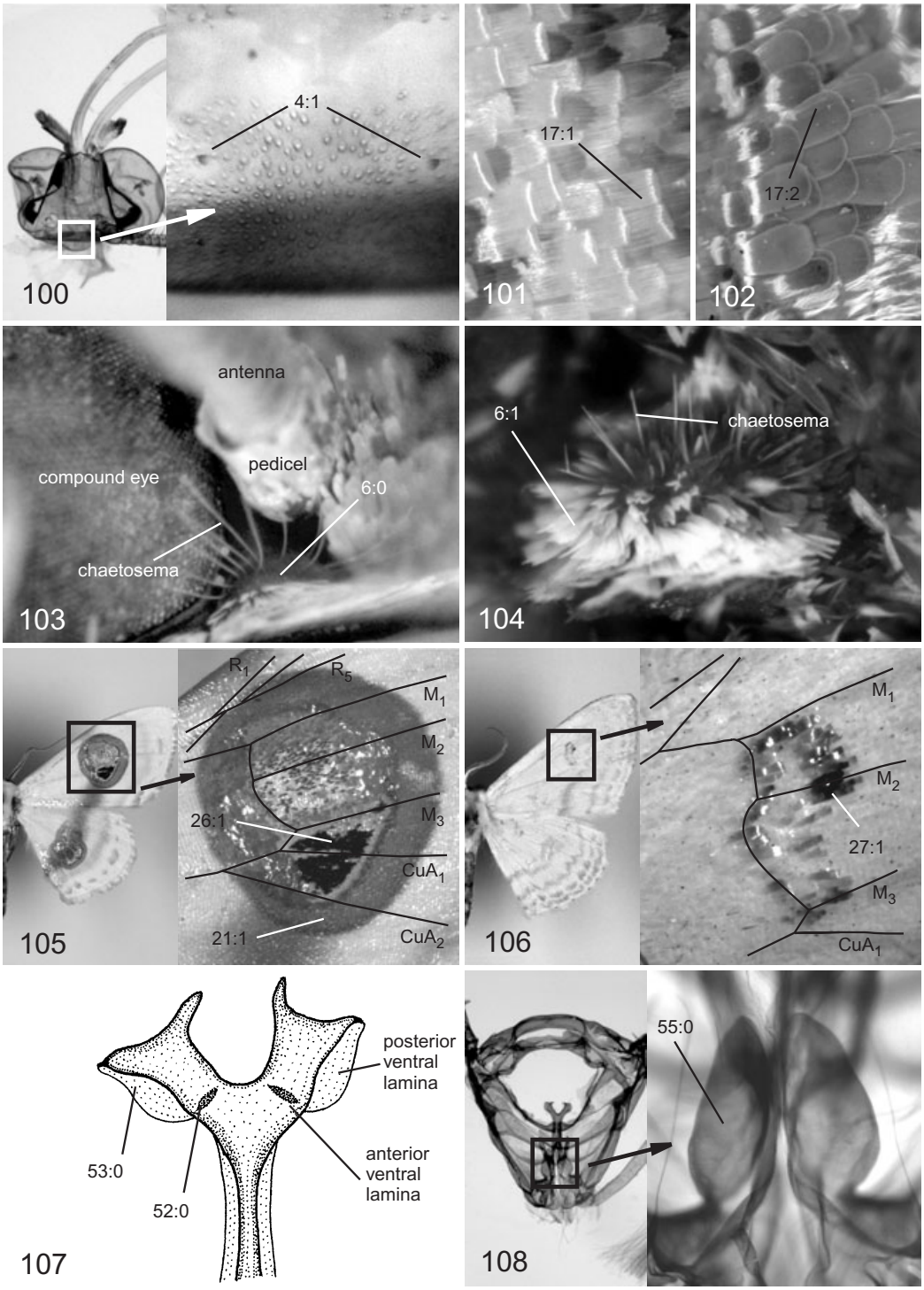


Figures 55–79. Male 8th sternite of type species of genera included in the phylogenetic analysis. The numbers in the figures refer to the numbers of the character states. 55. *Idaea aversata* (slide number) PS704. 56. *Somatina anthophilata* (slide number) BMNH GEO20369. 57. *Dithalama cosmospila* PS707. 58. *Isoplenodia arrogans* BMNH GEO20527. 59. *Zythos turbata* BMNH GEO20371. 60. *Lipomelia subusta* BMNH GEO20530. 61. *Problepsis ocellata* BMNH GEO20370. 62. *Scopula ornata* PS692. 63. *Ignobilia urnaria* BMNH GEO20531. 64. *Antitrygodes divisaria* BMNH GEO20375. 65. *Epicosymbia dentisignata* BMNH GEO20365. 66. *Glossotrophia confinaria* BMNH GEO20382. 67. *Isoplenia trisinuata* BMNH GEO20363. 68. *Cartaletis libyssa* BMNH GEO20372. 69. *Aletis helcita* BMNH GEO20360. 70. *Leucoxena lactea* BMNH GEO20376. 71. *Stigma kuldschaensis* PS859. 72. *Dasybela achroa* PS897. 73. *Pseudocinglis eurata* PS894. 74. *Cinglis humifusaria* PS648. 75. *Autanepsia poliodesma* BMNH GEO20526. 76. *Antilycauges pinguis* BMNH GEO20381. 77. *Oar pratana* PS714. 78. *Zygophyxia tornisecta* BMNH GEO20380. 79. *Scopuloides origalis* PS58 (the male of *S. fucata*. the type species of the genus. was not available for study). Figures are not to scale.

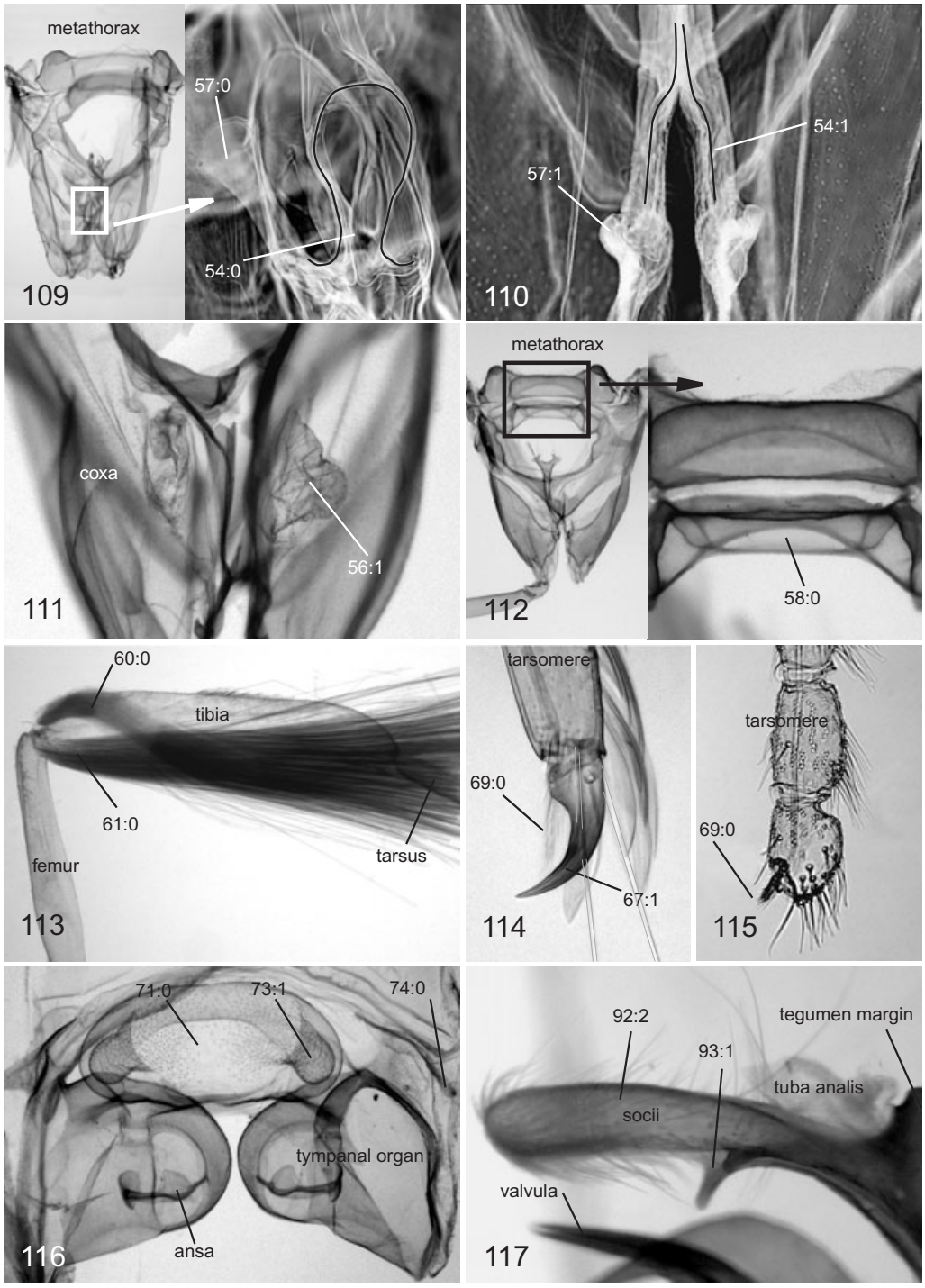
83. *Mappa*: (0) absent; (1) setose (Fig. 75); (2) bare (Fig. 76).
84. *Posterior margin of mappa separate*: (0) no; (1) yes (Fig. 65).
85. *Posterior part of male 8th sternite sclerotized*: (0) no; (1) yes (Fig. 59).
86. *Posterolateral appendices on male 8th sternite*: (0) present (Fig. 56); (1) absent.



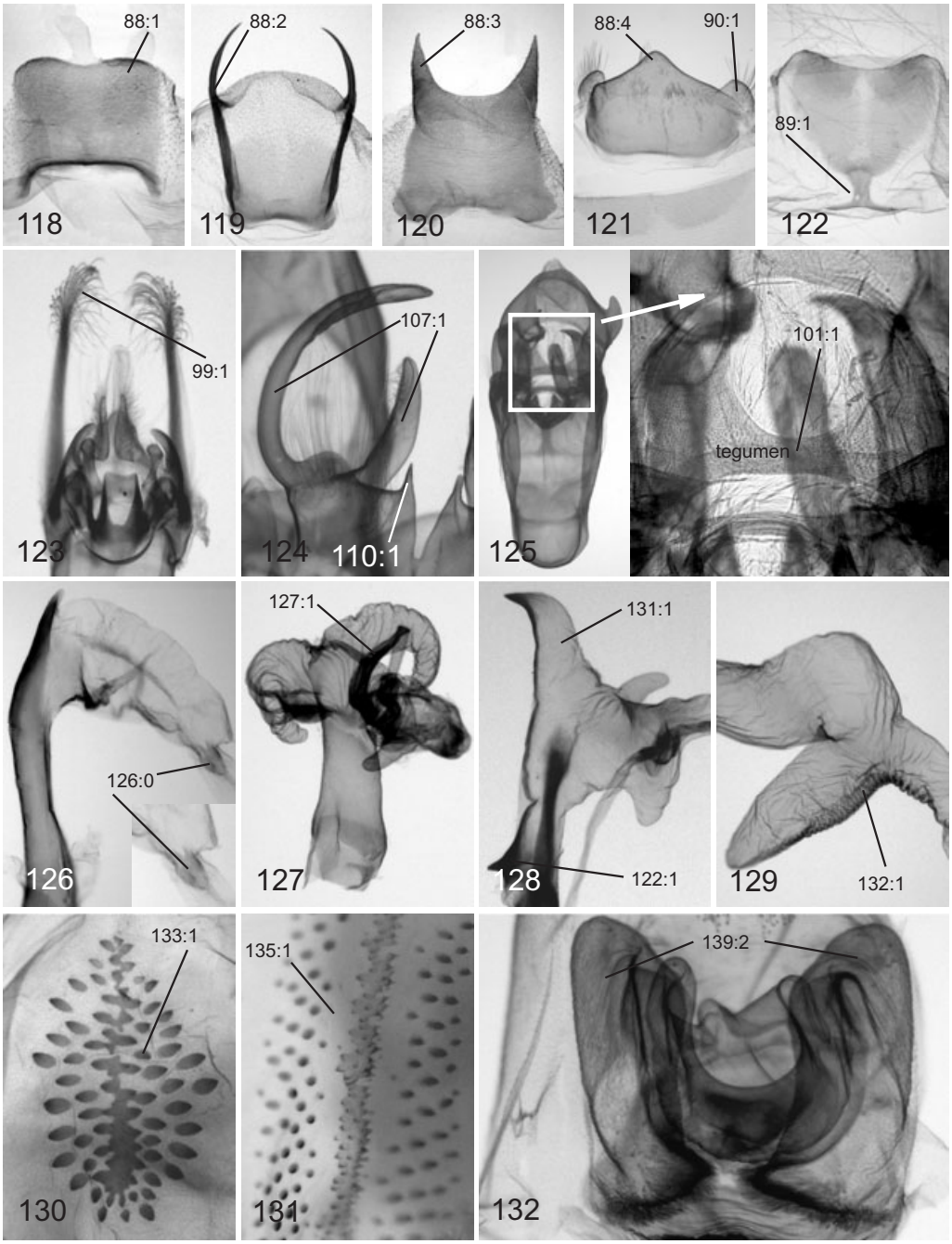
Figures 80–99. Female genitalia of type species of genera included in the phylogenetic analysis. The numbers in the figures refer to the numbers of the character states. 80. *Idaea aversata* (slide number) PS828. 81. *Somatina anthophilata* (slide number) BMNH GEO20472. 82. *Dithalama cosmospila* PS832. 83. *Zythos turbata* BMNH GEO20483. 84. *Problepsis ocellata* BMNH GEO20485. 85. *Scopula ornata* PS835. 86. *Ignobilia urnaria* (insert: signum) BMNH GEO20532. 87. *Antitrygodes divisaria* BMNH GEO20480. 88. *Epicosymbia dentisignata* BMNH GEO20462. 89. *Glossotrophia confinaria* BMNH GEO20476. 90. *Isoplenia trisinuata* BMNH GEO20464. 91. *Cartaletis libyssa* BMNH GEO20468. 92. *Aletis helcita* BMNH GEO20469. 93. *Leucoxena lactea* BMNH GEO20478. 94. *Pseudocinglis eurata* PS895. 95. *Cinglis humifusaria* PS644. 96. *Antilycauges pinguis* BMNH GEO20479 (insert: corpus bursae spines). 97. *Oar pratana* PS804. 98. *Zygophyxia tornisecta* BMNH GEO20474. 99. *Scopuloides fucata* PS59. Figures are not to scale.



Figures 100–108. Characters used in the cladistic analysis. Species are mentioned in their generic combinations prior to analysis. The numbers in the figures refer to the numbers of the character states. 100. Extensions on the anterior part of dorsal sclerite between antennae. *Somatina microphylla* (slide number) PS711. 101. Structure of iridescent scales. *Zythos turbata*. 102. Structure of iridescent scales. *Problepsis conjunctiva*. 103. Chaetosemata. *Zythos avellanea*. 104. Scales among chaetosemata. *Cartaletis variabilis*. 105. Dark patch at forewing transverse median line that is separated by vein CuA1 (veins drawn on top). *Problepsis conjunctiva*. 106. Dark patch at forewing M2 (veins drawn on top). *Problepsis centrophora*. 107. Anterior and posterior ventral lamina of metathorax metafurca. *Scopula imitaria* PS779. 108. Pouch on posterior margin of male metathorax coxa. *Problepsis ocellata* (slide number) BMNH GEO20421.



Figures 109–117. Characters used in the cladistic analysis. Species are mentioned in their generic combinations prior to analysis. The numbers in the figures refer to the numbers of the character states. 109. Base of male metafurca (posterior view). *Idaea aversata* (slide number) PS766. 110. Base of male metafurca (posterior view). *Cartaletis variabilis* (slide number) BMNH GEO20575. 111. Membranous sac at posterior part of male metathoracic coxa (dorsal view). *Scopula silonaria* BMNH GEO20433. 112. Opening on dorsal sclerite of male metathorax (dorsal view). *Scopula ternata* PS718. 113. Hair pencils of tibia on outer and inner margin of male hindleg. *Ignobilia urnaria* BMNH GEO20579. 114. Pretarsus of male hindleg. *Zythos turbata* BMNH GEO20443. 115. Pretarsus of male hindleg. *Problepsis achlyobathra* BMNH GEO20724. 116. Pouch on male 2nd sternite with lateral invaginations. *Antitrygodes parvimacula* PS883. 117. Lateral appendices of socii. *Problepsis plagiata* PS709.



Figures 118–132. Characters used in the cladistic analysis. Species are mentioned in their generic combinations prior to analysis. The numbers in the figures refer to the numbers of the character states. 118. Posterior margin of male 8th tergite. *Scopula submutata* (slide number) PS693. 119. Posterior margin of male 8th tergite. *Dithalama cosmospila* PS707. 120. Posterior margin of male 8th tergite. *Somatina eurymitra* PS888. 121. Posterior margin of male 8th tergite. *Zythos avellanea* PS879. 122. Posterior margin of male 8th tergite. *Antitrygodes divisaria* (slide number) BMNH GEO20375. 123. Apex of coremata. *Scopula rhodocraspeda* BMNH GEO20700. 124. Position of sacculus. *Zythos obliterata* BMNH GEO20591. 125. Dorsally fused anterior margins of tegumen (dorsal view). *Zythos turbata* BMNH GEO20371. 126. Plate-shaped sclerotization at proximal end of ductus ejaculatorius. *Antilycauges pinguis* BMNH GEO20381. 127. Sclerotization of vesica. *Scopula rivularia* BMNH GEO20684. 128. Dorsal diverticulum of vesica with sharp sclerotization at apex. *Problepsis plagiata* PS709. 129. Parallel folds of vesica. *Zythos turbata* BMNH GEO20371. 130. Signum. *Somatina indicataria* PS834. 131. Bare zone of signum. *Zythos obliterata* BMNH GEO20592. 132. Flexible lamella antevaginalis divided into two parts. *Zythos avellanea* PS880.

87. *Male 8th tergite*: (0) unmodified, membranous; (1) modified.
88. *Male 8th tergite posterior margin*: (0) unmodified; (1) concave, with two round lateral lobes (Fig. 118); (2) concave, with two sclerotized lateral spines (Fig. 119); (3) concave, with two sharp lateral projections (Fig. 120); (4) convex (Fig. 121).
89. Male 8th tergite laterally constricted: (0) no; (1) yes (Fig. 122).
90. Male 8th tergite with two membranous appendices on posterolateral margin: (0) no; (1) yes (Fig. 121).

Male genitalia

91. *Uncus*: (0) present; (1) absent.
92. *Socii*: (0) absent; (1) fused at apex, dorsal of tuba analis (Fig. 40); (2) fused at apex, ventral of tuba analis (Fig. 117); (3) separate (Fig. 43). The fused, setose structure lying ventrad of the tuba analis in *Problepsis* has been considered to be a subscaphium (Holloway, 1997). Based on its position, general appearance and the fact that the tuba analis is visible dorsad of this fused structure, I consider the structure to be socii. In *Epicosymbia*, socii are fused, but lie dorsad of the tuba analis. I also consider *Cinglis* and *Pseudoscinglis* to have socii, contrary to Hausmann's (1994) interpretation. The paired, asymmetrical structures found on the tegumen margin in *Zythos* are here considered to be socii, although the usual setae are absent.
93. *Socii with two lateral appendices*: (0) no; (1) yes (Fig. 117).
94. *Socii asymmetrical*: (0) no; (1) yes.
95. *Socii widest at apex*: (0) no; (1) yes.
96. *Socii setae*: (0) absent; (1) present.
97. *Socii crossed*: (0) no; (1) yes.
98. *Gnathos*: (0) present; (1) absent.
99. *Coremata*: (0) absent; (1) present, apex turned ventrally (Fig. 123); (2) present, apex straight.
100. *Ventral margin of tegumen*: (0) unmodified (straight); (1) modified, dentate; (2) modified, round lobe.
101. *Anterior margins of tegumen fused dorsally*: (0) no; (1) yes (Fig. 125).
102. *Transtilla*: (0) anterior margin connected to valvula via a membrane; (1) anterior margin sclerotized to valvula; (2) absent.
103. *Transtilla wide plate*: (0) yes; (1) no.
104. *Valva*: (0) sacculus and valvula fused, line of fusion not visible; (1) sacculus and valvula fused, line of fusion visible; (2) sacculus and valvula separate.
105. *Sacculus of valva*: (0) symmetrical; (1) asymmetrical (Fig. 44).
106. *Right sacculus of valva bifurcate*: (0) no; (1) yes.
107. *Valvula of valva ventral of sacculus*: (0) no; (1) yes (Fig. 124).
108. *Valvula of valva*: (0) symmetrical; (1) asymmetrical.
109. *Valvula apex of valva*: (0) nondentate; (1) dentate.
110. *Medial margin of sacculus upturned*: (0) no; (1) yes.
111. *Curved lobe on lateral margin of sacculus*: (0) no; (1) yes (Fig. 39).
112. *Vinculum size*: (0) small; (1) enlarged.
113. *Vinculum shape*: (0) symmetrical; (1) asymmetrical (Fig. 43).
114. *Vinculum margin*: (0) convex (Fig. 41); (1) concave (Fig. 36).
115. *Posteriorly directed lobe on top of vinculum with a medial ridge*: (0) absent; (1) present (Fig. 49).
116. *Anterior margin of juxta with wing-like processes*: (0) absent; (1) apex free (Fig. 52); (2) apex fused to sacculus of valva; (3) one apex free, other apex fused.
117. *Anterior margin of juxta with long processes laterally*: (0) absent; (1) present.
118. *Right arm of wing-like juxta processes longer*: (0) no; (1) yes.
119. *Only anterior margin of wing-like juxta processes sclerotized*: (0) no; (1) yes.
120. *Lobes of aedeagus*: (0) absent; (1) present.
121. *Round lobe on dorsal side of aedeagus*: (0) absent; (1) present.
122. *Distal part of aedeagus*: (0) smooth; (1) with sclerotized spines (Fig. 128).
123. *Apex of aedeagus with several separate spines*: (0) no; (1) yes.
124. *Vesica spiral*: (0) yes; (1) no.
125. *Sclerotizations of vesica*: (0) present; (1) absent.
126. *Plate-shaped sclerotization at proximal end of ductus ejaculatorius*: (0) present (Fig. 126); (1) absent.
127. *Long, curved structure on vesica*: (0) absent; (1) present (Fig. 127).
128. *Several teeth on vesica*: (0) absent; (1) present, on a plate; (2) present, separate.
129. *Long, curved cornutus at proximal end of ductus ejaculatorius*: (0) absent; (1) present (Fig. 46).
130. *Plate-shaped sclerotization on apical diverticulum*: (0) absent; (1) present (Fig. 40).
131. *Long diverticulum dorsally with sharp sclerotization at apex*: (0) absent: (1) present (Fig. 128).
132. *Parallel folds on vesica*: (0) absent; (1) present (Fig. 129).

Female genitalia

133. *Signum*: (0) absent; (1) spines separate, point away from centre (Fig. 130); (2) spines fused, point away from centre (Fig. 86).
134. *Fused signum spines visible at edges only*: (0) no; (1) yes.
135. *Bare zone at signum laterally at both sides of median ridge*: (0) no; (1) yes (Fig. 131).
136. *Long spines on inner surface of corpus bursae*: (0) present, hollow (Fig. 80); (1) present, solid (Fig. 96); (2) absent.
137. *Proximal part of corpus bursae sclerotized*: (0) no; (1) yes.
138. *Spirals of ductus bursae*: (0) one (Fig. 80); (1) less than one.
139. *Lamella antevaginalis flap-like, flexible*: (0) no; (1) yes, one plate (Fig. 99); (2) yes, divided into two parts (Fig. 132).

Ecology

140. *Species diurnal only*: (0) no; (1) yes.

RESULTS

The initial search of 141 characters resulted in 20 equally parsimonious cladograms (L = 853, CI = 0.22; RI = 0.59). More efficient search strategies did not find any more equally parsimonious cladograms, nor did the 'best' command eliminate any of the original trees. A strict consensus tree of these appears in Figure 133 (L = 876, CI = 0.21; RI = 0.58). Figure 134 shows one of the original trees (19 of 20) with the characters plotted. This is shown to give an indication of the supporting characters and to show how certain genera may be related, in contrast to the unresolved nodes of the strict consensus cladogram. The strict consensus cladogram is simplified to show the generic relationships within Scopulini in Figure 135.

In total, 22 characters were found to support the monophyly of the Scopulini (Fig. 134, Table 3). This is partially artificial since only two taxa from the putative sister group (Sterrhini) were used as outgroup. Cladistic analysis of Sterrhinae tribes has revealed that many of the synapomorphies supporting monophyly of the Scopulini would not do so if more outgroup taxa were included in the analysis (Sihvonen & Kaila, 2004).

According to this analysis there are two main lineages within Scopulini (Figs 133, 135; for supporting characters, see Diagnoses). The first includes *Isoplenodia*, *Dithalama*, *Somatina* and *Zythos*. *Dithalama* was found to be paraphyletic with regard to *Isoplenodia*, and the relationships of *Somatina* and *Zythos* are

Table 3. Synapomorphies for the tribe Scopulini that are supported under all optimizations, taken from the strict consensus cladogram of Figure 133. 'Char.' refers to the character number and state. Unique synapomorphies are shown in bold

Char.	Synapomorphies
44: 1	**Fringe unicolorous**
54: 1	**Lateral margins of metathoracic metafurca basally opened or straight** (Fig. 110)
56: 1	Presence of membranous sac at posterior end of male metathoracic coxa (1 reversal) (Fig. 111)
59: 1	**Absence of medial ridge on epinotum of male metathoracic dorsal sclerite**
63: 1	**Tibia of female hindleg with two medial spurs (i.e. 2 + 2 spurs)**
68: 1	Presence of male hindleg pretarsus arolium (1 reversal)
76: 2	**One pouch between male's 7th and 8th sternites** (Fig. 66)
77: 3	Anterior margin of male 8th sternite bifurcate (5 reversals)
77: 4	Anterior margin of male 8th sternite elongated medially (5 reversals)
87: 1	**Male's 8th tergite modified**
88: 1	**Posterior margin of male 8th tergite concave, with two round lateral lobes** (Figs 118, 122)
91: 1	**Absence of uncus**
92: 3	**Separate socii**
98: 1	**Absence of gnathos**
99: 2	**Apex of coremata straight**
103: 1	**Narrow transtilla**
104: 2	**Sacculus and valvula of valva separate**
112: 1	**Enlarged vinculum**
116: 1	Anterior margin of juxta with wing-like processes, apex free (4 occurrences) (Fig. 52)
124: 1	**Vesica not spiral**
133: 1	**Separate signum spines, pointing away from centre** (Fig. 130)
136: 2	**Absence of long spines on inner surface of corpus bursae**
138: 1	Spirals of ductus bursae less than one

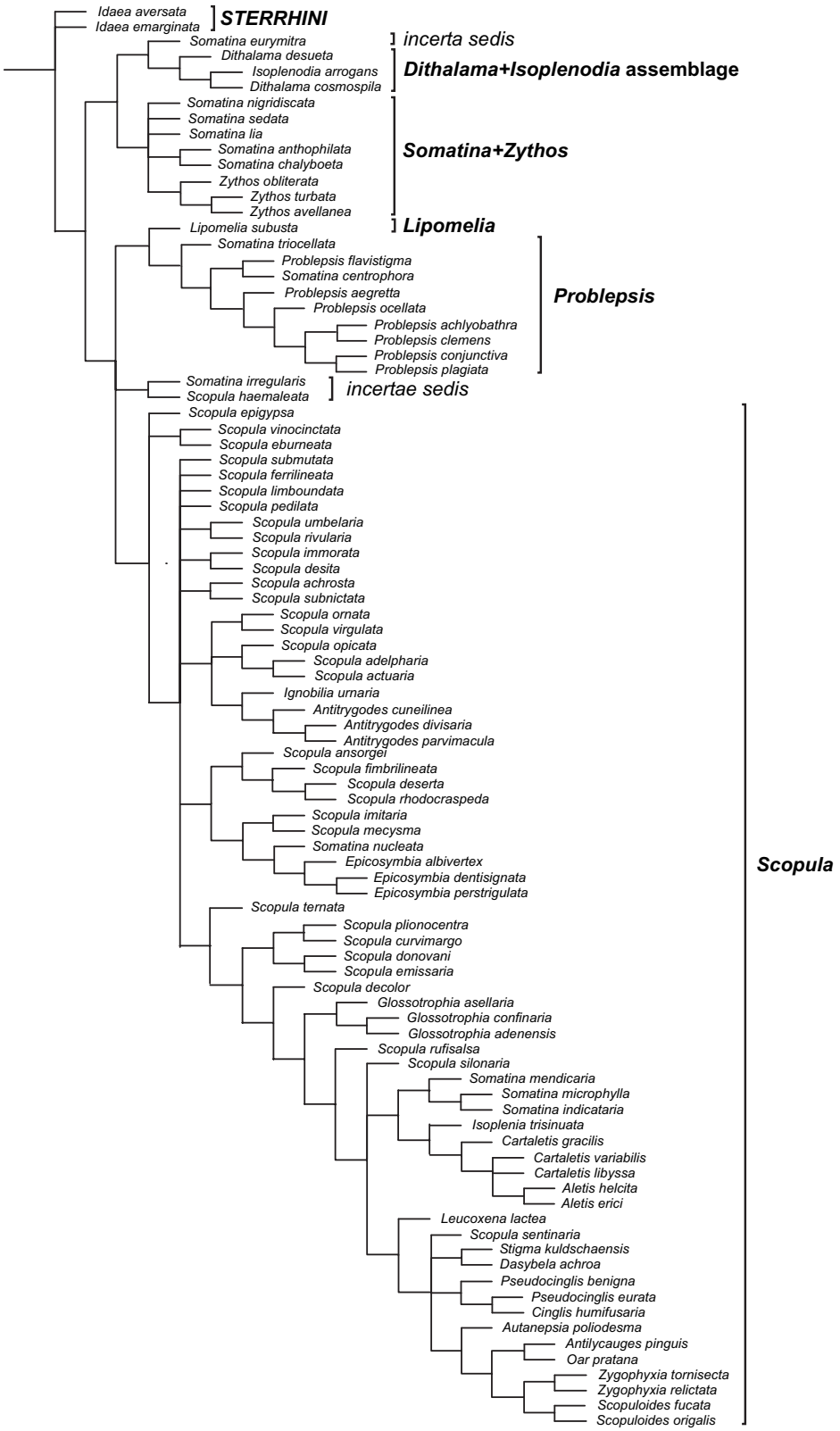


Figure 133. Strict consensus of 20 equally parsimonious cladograms. based on 141 characters of adult morphology and ecology (L = 876, CI = 0.21; RI = 0.58). Species are mentioned in their generic combinations prior to analysis. Names on the right-hand margin indicate genera as recognized here.

unresolved. One taxon, *Somatina eurymitra*, is *incerta sedis* (see Diagnosis of *Somatina*). The second lineage includes *Lipomelia*, *Problepsis* and *Scopula*. *Lipomelia* and *Problepsis* were recovered as sister groups. The sister group of *Scopula* is unknown, as there is a trichotomy in this lineage involving *Lipomelia*, *Problepsis*, *Scopula*, while two taxa (*Somatina irregularis* and *Scopula haemaleata*) are *incertae sedis* (see Diagnoses of *Somatina* and *Scopula*).

The relationships of species groups within *Scopula* are largely unresolved, but the species groups themselves often have many supporting synapomorphies. Many characters showed extensive homoplasy, for example the presence of a posteriorly directed lobes on top of the vinculum (Ch. 115, CI = 0.05; RI = 0.37, Fig. 49) and the presence of sclerotized spines on the distal part of the aedeagus, i.e. carina (Ch. 122, CI = 0.09; RI = 0.28).

DISCUSSION

Generic classification of the Scopulini

The classification proposed here diverges markedly from previous classifications (see 'Systematic Treatment' and Appendix). This is not surprising if we consider that there has not been a previous attempt to study systematically the material throughout the morphological and geographical range of the tribe.

The generic concepts adopted here inevitably result in groupings that contain externally different species. This is most pronounced within *Scopula*, as it is considered to include species from previously recognized genera such as *Glossotrophia*, *Antitrygodes* and *Aletis*. However, from the morphological point of view, the recognized genera appear to represent rather well the material I have examined. In most instances the main groups were fairly apparent from morphological study and comparison, and these groupings were confirmed later by cladistic analysis.

Characters and taxon sampling

The cladistic analysis was based on 141 characters, coded from adult morphology and ecology. Although the analysis covered the morphology very extensively, much promising phylogenetic information was observed that could not be incorporated into the data matrix. In most cases this was due to the quantitative nature of the morphological variation, which prevented unambiguous coding. For example, the shape of the pouch, situated on the posterior margin of the male metathoracic coxa (Ch. 55, Fig. 108), was found to be an area of extensive variation, in addition to the shape of the vesica, and length and arrangement of antennal sensilla in males. A further example is the shape of the outer membrane of the anterior opening of the aedeagus that encloses the ductus ejaculatorius. Unfortunately, this membrane was routinely removed before I realized its possible phylogenetic significance (Rose, 1985). Due to the shortage of material, immature stages were not included in the study, and they certainly need to be studied more extensively in the future.

Many characters previously used extensively in systematics of the Scopulini were found to be homoplastic. One example is the number of forewing areoles. *Problepsis* and *Scopula* have been considered to be one-areole genera, whereas the two-areole condition was found to be true for *Somatina* (e.g. Sterneck, 1941; Prout, 1920–41). However, two areoles are also present in a few taxa of *Problepsis* and *Scopula* (Ch. 48, CI = 0.14; RI = 0.76). In addition, the putative features of *Glossotrophia* (i.e. the absence of medial spurs of the female hindtibia and the presence of a dark terminal line that curves around the forewing apex) appeared homoplastic, as already noted by Hausmann (1993c). Clearly, if species are associated with certain genera on the basis of one homoplastic character alone, nonmonophyletic groupings result.

The number of analysed taxa is potentially adequate to recover the major groupings of the Scopulini and reveal the morphological variation within them. The number need not be increased markedly in future studies. The geographical coverage of taxa analysed was also extensive and adequate to recover the generic relationships. However, more taxa and characters are going to be needed to establish the relationships of species within the large genus *Scopula*; these were largely unresolved in the analysis.

From cladogram to classification

Transforming the information provided by cladograms into a formal classification is problematic because there is no objective way to define what constitutes a category, such as a genus. For the classification to have validity, one should attempt to delimit the category at the generic level and above so that they maximise their value in communication. If the categories are too narrowly or widely delimited, they may fail to adequately convey the relatedness of species.

This project has been undertaken with the aim of providing a more stable classification for the Scopulini. The problem with previous classifications has been the lack of global perspective, resulting in relatively restricted generic schemes. The present approach has involved drawing together information from earlier studies and adding new observations. As a result, many new generic synonyms and species combinations are proposed. A similar approach was used by Scoble & Krüger (2002) when they classified the world fauna of Macariini.

Figure 134. Cladogram 19 of 20 based on 141 characters from adult morphology and ecology (L = 853, CI = 0.22; RI = 0.59). Numbers above hash marks indicate character numbers and below character states. Black bars indicate unique and white bars non-unique synapomorphies. Species are mentioned in their generic combinations prior to analysis. Names on the right-hand margin indicate genera as recognized here.

Groups of species are here recognized as genera if they are monophyletic and supported by synapomorphies that are unique or have low homoplasy. I have emphasized similarities rather than differences. I have also tried to avoid making new generic synonyms if the material studied is somehow contradictory or insufficient. One could argue that instead of proposing new generic synonyms for *Scopula* (see Appendix), I could have retained many of the traditional genera. However, had I done so, it would have either rendered the remaining taxa paraphyletic or split lineages into a large number of small, often new, genera. Furthermore, a classification where genera are very narrowly delimited can lead to the frequent addition of new genera when new species with slightly differing character combinations are discovered.

In the present paper, some genera are recognized that contain externally very different species, while others are more homogeneous. This is because I have tried to identify and name only monophyletic groupings rather than artificial classes. It may be argued that this approach can result in a reduction both of taxonomic resolution and of the overall comprehensiveness of the classification. However, as species groups within genera can still be recognized, identified and named, this need not be the case.

Finally, it is worth emphasizing that the majority of the genera of Scopulini were described in the 19th century. Generic taxonomy, for example, was based on comparison of external features alone. It is only natural that with recent advances, such as high-magnification microscopes, synapomorphy-based

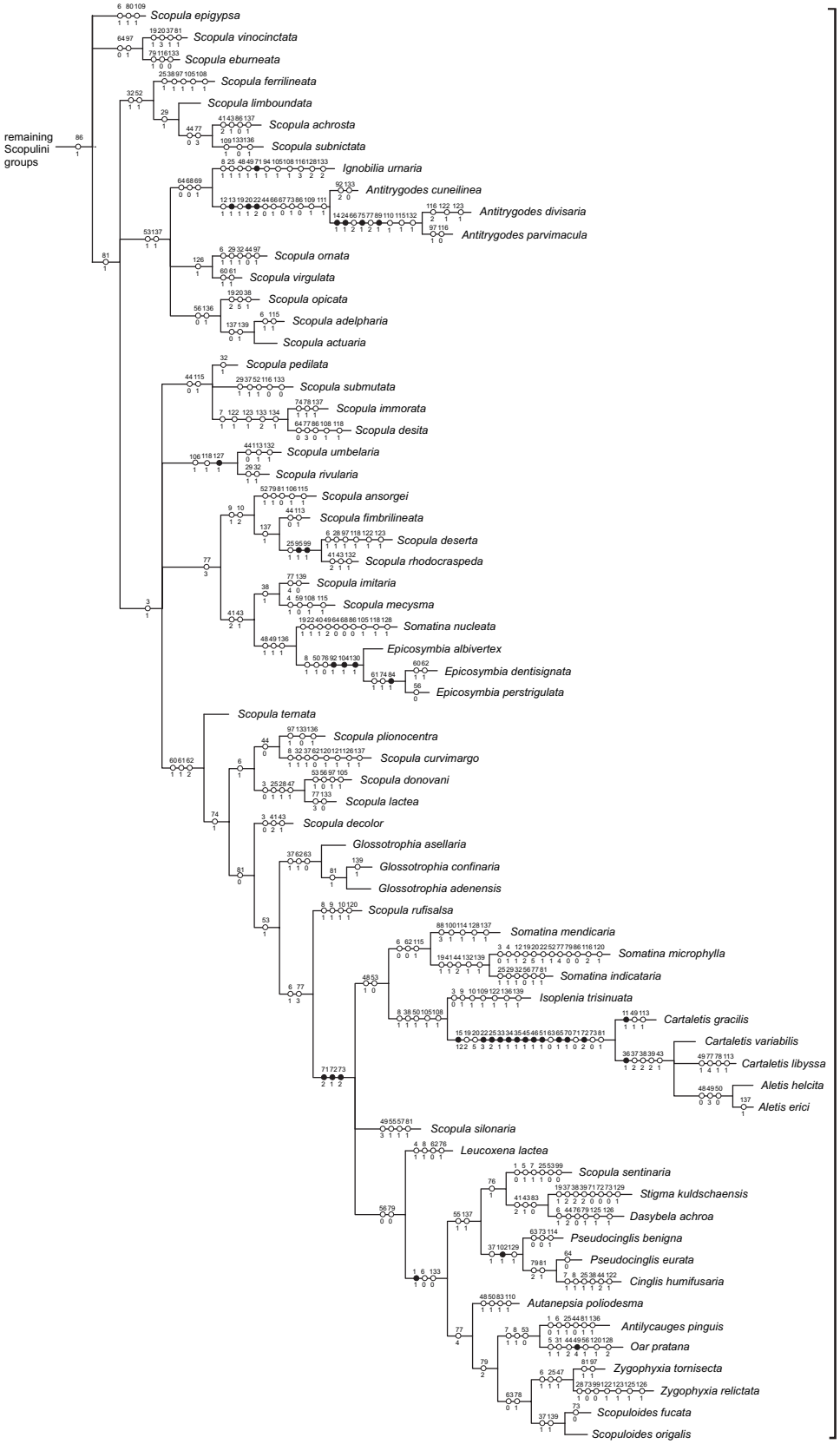


Figure 134. *Continued*

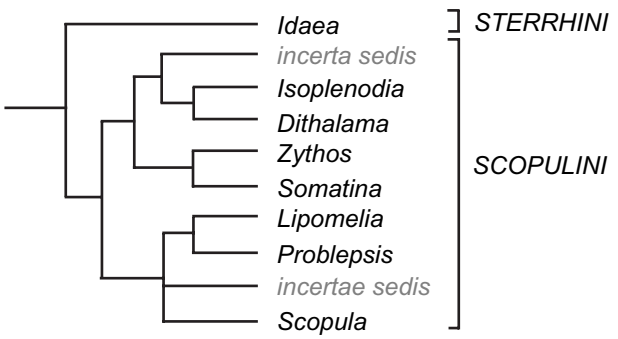


Figure 135. A simplified cladogram of Figure 133 transformed to show generic relationships within the Scopulini. Taxa of uncertain generic association (*incertae sedis*) are shown in grey.

phylogenetic reasoning and parsimony software, results may be obtained that contradict the earlier classifications.

Consequently, the proposed classification has one large genus, *Scopula*, that contains 800 valid species, i.e. over 85% of the described fauna. *Problepsis*, *Zythos* and *Somatina* are middle-sized genera that include together over 100 species. *Dithalama* tentatively contains four species, whereas *Lipomelia* is monotypic. *Isoplenodia* is tentatively retained as a valid, monotypic genus although its recognition makes *Dithalama* paraphyletic. More material on *Dithalama* and *Isoplenodia* is needed to better resolve the relationships. A few species are *incertae sedis*, but they are retained in their traditional generic positions until further evidence is available (see Appendix).

Future research

Although this work has hopefully clarified many problems endemic to the systematics of the Scopulini, further large-scale research is needed to test the validity of the results and to establish a more precise understanding of generic relationships. Emphasis should be placed on the study of immature stages, in addition to a detailed morphological study of adults. The use of molecular characters is likely to be useful when attempting to solve intra- and intergeneric relationships, although it is difficult to obtain material that extensively covers the study group. It would be important also to study possible associations of a few Neotropical genera, i.e. *Acratodes* Guenée, *Haemalea* Hübner, *Leptostales* Möschler, *Proutoscia* Schaus, and *Pseudasellodes* Warren (Sihvonen & Kaila, 2004) with the Scopulini.

As is evident from this study, species-level revisions of many genera in the tribe are still needed (see also Hausmann, 1999b). No doubt many species are still misplaced, although they can be associated with related species with the help of the generic diagnoses provided here. For example, *Somatina* is a nonmonophyletic assemblage of species, whose generic association with *Scopula*, *Dithalama* and *Problepsis* needs to be revised.

Most importantly, a worldwide taxonomic revision of *Scopula*, the largest genus of the tribe, is essential. Many species of this genus are difficult to identify based on external features alone, and the lack of comprehensive identification literature has resulted in extensive synonymy. This practice still continues. If the defect is not corrected, future research on this group will be bedevilled with nomenclatorial problems arising from synonymies. The example of *Scopula floslactata* is a case in point. In addition to the valid species name, this species was described 12 (!) times between 1763 and 1951. One can only imagine how much time it has taken for later authors to correct mistakes.

I hope that this study and the proposed classification will provide a solid basis for future research on Scopulini systematics and taxonomy. Comprehensive identification tools, whether in the form of literature or internet-based databases, are urgently required. Once completed, they will provide a basis for applied studies on these moths, including the reconstruction of evolutionary issues such as the evolution of lacriphagy (Bänziger & Fletcher, 1985) and the shift from nocturnal to diurnal modes of life.

SYSTEMATIC TREATMENT

Diagnoses for the tribe Scopulini and its genera

A generic key to the male Scopulini is given, although it must be borne in mind that many characters are homoplastic. Use of a key that relies on a single or a few possibly homoplastic characters can result in arbitrary generic or even tribal combinations because no all-inclusive external features have yet been allocated that can be applied in order to separate species between Scopulini, Sterrhini and Cosymbiini. A key to the females is not provided due to the lack of material. A less formal approach to identify the Scopulini and component genera is more effective than a dichotomous key. The reader is referred to characteristic tribal and generic features that are *italicized* in the diagnoses (see also Table 3). Many species can be assigned to genera by focusing on these few italicized characters alone. It must be remembered that even though some genera and species can be recognized from external features, in most cases it is necessary to study the genitalia. Important structures relating to generic placement are found also in the male coxa, hindleg and 8th sternite and tergite.

GENERIC KEY TO ADULT MALES OF SCOPULINI

1. Hindtibia with two claws or claws absent 2
– Hindtibia with one claw (Fig. 114) . . . . . *Zythos*
2. Subterminal shaded line and terminal line not touching each other on fore- and hindwings 3
– Subterminal shaded line and terminal line touching each other on fore- and hindwings (Fig. 6) . . . . . *Lipomelia*
3. Discal spots nonocellate and/or socii separate or fused at apex, dorsad of tuba analis 4
– Discal spots ocellate (Fig. 7) and/or socii fused at apex, ventral of tuba analis (Fig. 117) . . . . . *Problepsis*
4. Pilifer present; opening on metathorax dorsal sclerite present (Fig. 112) 5
– Pilifer absent; opening on metathorax dorsal sclerite absent . . . . . *Isoplenodia*
5. 8th tergite without two concave, sclerotized lateral spines 6
– 8th tergite with two concave, sclerotized lateral spines (Fig. 119) . . . . . *Dithalama*
6. 8th sternite's posterolateral appendices usually absent; lateral pouches between sternites 3 and 4 absent 7
– 8th sternite's posterolateral appendices present (Fig. 56); lateral pouches between sternites 3 and 4 present; forewing with two areoles . . . . . *Somatina*
7. Usually cerata (Fig. 62) and mappa (Fig. 76) present; valvae symmetrical; forewing with one areole; 8th tergite posterior margin concave with two round lateral lobes (Figs 118, 122) . . . . . *Scopula*

SCOPULINI DUPONCHEL, 1845

Definition of the tribe is based on a cladistic analysis of the Sterrhinae by Sihvonen & Kaila (2004), where two synapomorphies were found: the signum of the female genitalia being ovoid, granulate, with spines pointing away from the centre (Fig. 130), and the absence of a medial ridge on the epinotum of the male metathorax (character state 'present' is figured in Sihvonen & Kaila, 2004). In that analysis neither of these characters was considered to be unique to the tribe, see Results. In the present study it was found that they were unique. In addition, 20 other characters, 18 of which are unique, are proposed as possible tribal synapomorphies (Table 3). The male 8th tergite with the posterior margin concave with two round lateral lobes (88: 1, Figs 118, 122), may be a true synapomorphic character. Also characteristic are the absence of uncus and gnathos, and the presence of socii.

Wings

Wingspan *c.* 11–70 mm, usually 25–40 mm. Shape usually triangular, forewing apex elongated or termen occasionally rounded; hindwing margin often concave between vein ends or elongated at M_3. Facies very variable; many are *straw-coloured, with numerous wavy transverse lines running from forewing to hindwing, and with small, dark discal spots* (e.g. Figs 8, 21); ocellate discal markings and various other fasciae on white or grey background are also common; iridescent scales present in many species; forewings with fine striae and wide, dark medial band are not unusual; underside often fuscous, above patterns weakly repeated underside; underside ground colour uniform ochreous in some; transverse lines variably developed, usually all present, occasionally absent; sub- and adterminal shaded lines usually present, occasionally pronounced; terminal line continuous, discontinuous or absent; fringes unicolorous or chequered. Forewings with one or two areoles; R_5 from proximal or distal areole, either free or stalked with R_2–R_4 or stalked with M_1. Hindwing $Sc + R_1$ and Rs fused shortly or Sc and Rs separate but connected via R_1.

Head

Labial palpus upturned, 3-segmented, organ of vom Rath distinct. Pilifer present, rarely absent. Proboscis fully developed; variably shaped sensilla styloconica at distal end, absent in many species. Frons convex. Two openings or extensions on anterior part of dorsal sclerite between antennae either present or absent. Compound eye round to elliptic; proximal pigment layer circular or semicircular. Scales between antennae flat or flat and hair-like. *Male antenna usually fasciculate*, occasionally bipectinate to two-thirds; if bipectinate, proximal rami sometimes elongated; sensilla in single or multiple rows. Female antenna usually fasciculate, simple, occasionally sensilla

arranged in single or even multiple rows. Antennal segments dorsally uni- or bicolorous. Chaetosemata usually from naked surface, occasionally from scaled surface.

Thorax

Foreleg with well-developed epiphysis; tibial spurs absent; thick spines on tarsus usually absent. Midleg with two tibial spurs, symmetrical or asymmetrical; tarsus normally developed, 5-segmented, thick spines usually absent, sometimes present. *Male hindleg tibia often with outer and/or inner hair pencil* proximally (Fig. 113), or absent; distal spurs two, one or absent; *reduction in tarsus length common*; all or part of tarsus segments may be fused; yet usually fully developed, 5-segmented; thick spines usually absent; two apical spines present in most species; usually two claws, symmetrical or asymmetrical, occasionally one or absent; arolium and pulvillus usually present. Female hindleg tibia usually with 2 + 2 spurs, occasionally with one medial spur or absent altogether; hindleg tarsus normally developed. Anterior and posterior ventral lamina of male metafurca usually present, occasionally absent; *margins of metafurca basally opened or straight* (Fig. 110); *pouch on posterior margin of metathorax coxa usually present* (Fig. 108), semiround, occasionally pronounced; medial ridge absent on epinotum of male metathorax dorsal sclerite; lateral processes of male coxa elongated in many species, variable in size and shape, rarely absent; absent in females.

Abdomen

Male 2nd sternite usually with distinct, round pouch (Fig. 116) between tympanal organs, posterior margin often invaginated, occasionally with two chambers, surface smooth, with fine ornaments or stout setae; anterolateral extensions present or absent. Male 6th segment occasionally with setae. *Membranous sac between male 7th and 8th sternite usually present* (Fig. 66). Male 8th sternite very variable; anterior margin convex, concave, tri- or bifurcate; *cerata and mappa present in many species* (Figs 62, 76); posterior margin membranous or sclerotized; posterolateral appendices occasionally present. *Male 8th tergite variable; posterior margin usually concave, with two round lateral lobes* (Figs 118, 122). Female abdomen simple, without modifications.

Male genitalia

Genitalia capsule appearing *ovoid* when viewed ventrally, characterized by enlarged vinculum and usually short, separate valvula and sacculus of valva. *Uncus and gnathos absent. Socii usually setose, separate*; occasionally fused at apex, lying ventrally or dorsally of tuba analis. Ventral margin of tegumen straight or with various processes, sometimes with distinct teeth. *Valvula and sacculus of valva usually separate* (e.g. Fig. 41), fused in a few cases; sacculus lying ventrally of valvula; both processes often asymmetrical; valvula curved ventrally, weakly sclerotized, setose, sometimes strongly sclerotized, acute; sacculus wide at base, tapering towards apex, blunt or acute; lateral and ventral extensions in many species. *Coremata present* (Fig. 123) at lateral end of transtilla, often pronounced or even bent ventrally; lost easily, but surface of genitalia distinctly granulate. Dorsal part of *juxta* tunnel-shaped; ventral part *often with wing-like processes* (Fig. 52), often asymmetrical. Transtilla usually present, occasionally anterior margins of tegumen fused replacing it. *Vinculum enlarged, often with posteriorly directed lobe on top* (Fig. 49). Aedeagus shape and size variable, often with dorsal lobes or carina at apex; caecum small or moderate; *outer membrane of aedeagus expanded to semiround sac* covering proximal end of ductus ejaculatorius; vesica very variable; simple sac with moderate diverticula or very complex with numerous coiled, twisted diverticula; *plate-shaped sclerotization at proximal end of ductus ejaculatorius usually present* (Fig. 126); otherwise variably sclerotized, occasionally with distinct cornuti. Spermatophore elongated sac, size and shape variable; occasionally frenum distinct, curved structure.

Note: special care is needed to interpret homologies of the male genital structures. Socius, and especially valvula, sacculus and juxta often replace each other functionally. For example, the left arm of the juxta in *Somatina anthophilata* Guenée has functionally replaced the left sacculus of the valva, the latter being diminished in size.

Female genitalia

Papillae anales longitudinally grooved, setose, sometimes bilobed into rounded dorsal and shorter, narrower ventral part. Apophyses posteriores usually longer than apophyses anteriores. Lamella postvaginalis pronounced in some species, usually weakly developed or absent. Ostium bursae cup-shaped, a complex of structures, occasionally simple or virtually absent. *Lamella antevaginalis usually flap-like* (Figs 99, 132), flexible or undeveloped in those species that have a well-developed lamella postvaginalis. Ductus bursae membranous or variably sclerotized; ductus seminalis arises from ductus bursae, corpus bursae neck or corpus bursae. Corpus bursae sac-like, occasionally heavily folded; *signum an ovoid field of separate spines* (Fig. 130), pointing

away from centre, either fused or absent along medial axis in some species; spines on inner surface of corpus bursae common.

Distribution and species diversity
Virtually cosmopolitan with 912 described species and many more undescribed.

Immature stages
Due to the shortage of material, it was not possible to include immature stages in the cladistic analysis. Patocka (2003: 270), who worked with Central European fauna only, was able to find only quantitative delimiting pupal features for Scopulini. He diagnosed the pupa as follows: the 'front leg verges on antennae as far as the compound eye extends'. In the Rhodostrophini, by contrast, the 'front leg verges on antennae beyond the compound eye'. In addition, cremaster setae D2 of Scopulini are closer to each other than in Rhodostrophiini.

The *Glossotrophia* species group of *Scopula* has the unique condition of a free and loped elongated proboscis extending beyond the distal part of the pupa (Hausmann, 2001; Patocka, 2003). Chaetotaxy and pupal characters are described under generic concepts, where data are available. The narrow larvae of many species rest in a stick-like posture at an angle of 45 °. Some specialization in larval host-plants can be seen: Oleaceae in *Problepsis* and Rubiaceae in some *Somatina*. However, frequent polyphagy in *Scopula* and the worldwide distribution of the tribe make generalizations difficult.

Biology
Species can be found in forested and open habitats. A few *Scopula* species are known to be of minor pest status (see Introduction).

Comments on systematics
In total, 22 characters were found to support the monophyly of Scopulini (Fig. 134, Table 3). This is partially artificial since only two taxa from the putative sister group, Sterrhini, were used as outgroup. It is known from the cladistic analysis of the tribes of Sterrhinae (Sihvonen & Kaila, 2004) that many of the characters that appear here as synapomorphies supporting the monophyly of Scopulini would not do so if more outgroup taxa were present. Scopulini also includes Aletini (Hampson, 1918) and Problepsini (Wiltshire 1990) as indicated by Holloway (1996, 1997). Both of these tribes share with Scopulini their characteristic structural features, including those of male 8th sternite, male and female genitalia and wing venation.

THE *DITHALAMA, ISOPLENODIA, SOMATINA* AND *ZYTHOS* GROUP OF GENERA

This group of four genera is characterized by five synapomorphies (Figs 133–135): presence of two forewing areoles formed by R veins (48: 1, six occurrences and one reversal); forewing vein R_5 runs from the distal areole and is stalked with veins R_2–R_4 (49: 2, eight occurrences); posterolateral appendices are absent on male 8th sternite (86: 1, five occurrences and six reversals); the medial margin of the sacculus is upturned (110: 1, four occurrences); lamella antevaginalis is flap-like, flexible, formed by one plate (139: 1, 13 occurrences and two reversals). Within the group, the relationships are not resolved. *Somatina eurymitra* is *incerta sedis* and recognition of *Isoplenodia* renders *Dithalama* paraphyletic. These three taxa form the sister group to *Somatina* + *Zythos*.

Comments on systematics
This group of genera, although not found to be supported by unique synapomorphies (Figs 134, 135), appears to be rather distinctive. Cerata are absent in most cases, and the species have two areoles in the forewings. In the other group of genera (i.e. *Scopula*, *Lipomelia* and *Problepsis*) the cerata are fully developed and in most species the forewings have only one areole .

DITHALAMA MEYRICK, 1888 (FIGS 3, 32, 57, 82, 119, APPENDIX)

Diagnosis: description is based on type species only (see 'Comments on systematics', below). Monophyly supported by five synapomorphies: transverse median line of wings is obscure (25: 1, 12 occurrences); posterior margin of male 8th tergite is concave, with two sclerotized lateral spines (88: 2, unique, Fig. 119); medial margin of sacculus is not upturned (110: 0, three occurrences); presence of posteriorly directed lobe on top of vinculum with a medial ridge (115: 1, 15 occurrences); apices of wing-like juxta processes are fused to sacculus of valva (116: 2, seven occurrences).

Imago: wingspan 19–24 mm. Male antenna fasciculate, sensilla in single rows; female antenna fasciculate, simple. Pilifer present. Wing patterns variable, transverse lines ranging from almost straight to hardly recognizable; discal spot dark; terminal line discontinuous; wing patterns repeated on underside but indistinct. Forewing with two areoles; R_5 from distal areole, either stalked with R_2–R_4 or straight from

accessory cell. Outer margin hair pencil of male hindleg tibia present, inner either present or absent; distal spurs of hindleg tibia absent; tarsomeres shortened but not fused; claws either two in number or absent. Female hindleg tibia with two pairs of spurs.

Male abdomen and genitalia: pouch on male 2nd sternite round; anterolateral extensions present or absent. One membranous pouch between male 7th and 8th sternite. Male 8th sternite sclerotized; anterior margin elongated medially; laterally turned extensions or two blunt lobes on posterior margin; *cerata, mappa and membranous posterolateral appendices absent* (Fig. 57). Posterior margin of male 8th tergite concave with two sharp cerate-like projections or with two round lateral lobes (Fig. 119). Socii separate, setose. *Ventral margin of tegumen with round lobes*, separate or fused. Valvae symmetrical, variably sclerotized, anterior margin of sacculus medially upturned or levelled. Transtilla present. Anterior margin of juxta with wing-like processes, apex fused to sacculus of valva or absent. Vinculum enlarged. Aedeagus straight with one or several teeth, carina, at distal end; vesica simple, curved sac, without sclerotizations.

Female genitalia: lamella antevaginalis sclerotized, flap-like, flexible, medially elongated. Ostium bursae weakly sclerotized; ductus bursae wide, proximal part either membranous or sclerotized; ductus seminalis arises from ductus bursae. Corpus bursae elongated sac; signum either granulate, spines point away from centre or absent; long spines on inner surface of corpus bursae absent.

Distribution and species diversity: Australia and Tasmania. Four species identified tentatively (McQuillan & Edwards, 1996). See Appendix under *Dithalama*.

Immature stages: unknown.

Biology: unknown, although *D. cosmospila* is suspected to live on *Eucalyptus* (Prout, 1920–41).

Comments on systematics: the genus is in need of revision, as was already noted by Prout (1920–41). He speculated that *Dithalama* is closely related to *Somatina* and *Autanepsia*, and the latter monotypic genus should perhaps be combined with *Dithalama*. In this analysis *Dithalama* was recovered as paraphyletic with regard to *Isoplenodia*. The *Dithalama* + *Isoplenodia* connection, although not discussed earlier, is supported by a number of character absences (Fig. 134). In addition to *Dithalama* + *Isoplenodia*, the secondary loss of sclerotizations of vesica (125: 1), which is a derived feature in this analysis, has occurred outside of these taxa only in Tasmanian species *Dasybela achroa* and South African species *Zygophyxia relictata*, which were found to be unrelated to *Dithalama*. Absence of male hindleg claws (67: 0), pretarsus arolium (68: 0) and pulvillus (69: 1), on the other hand, are found also in a number of taxa in *Zythos*, *Problepsis* and *Antitrygodes*.

ISOPLENODIA PROUT, 1932
(FIGS 4, 33, 58)

Diagnosis: monophyly supported by eight synapomorphies: absence of pilifer (character and character state 0: 1, unique); ventrolateral sensilla on proximal part of male flagellomere are in multiple rows (8: 1, nine occurrences); absence of anterior ventral lamina of metathoracic metafurca (52: 1, six occurrences); absence of opening on male metathoracic dorsal sclerite (58: 1, character state 'present' shown in Fig. 112, unique); fusion of male hindleg tarsomeres 1–5 (66: 1, two occurrences); cerata are fully developed (79: 2, three occurrences, two reversals); mappa is bare 83: 2 (four occurrences); ventral margin of tegumen is unmodified, straight (100: 0, three reversals).

Imago: wingspan *c.* 16 mm. Head smooth-scaled; male antenna fasciculate; sensilla arranged in multiple rows, proximal row elongated. *Pilifer absent*. Wings light brown, transverse lines weakly expressed; discal spot dark; terminal line discontinuous, equally wide; underside light fuscous. Forewing with two areoles; R_5 from distal areole, stalked with R_2–R_4. *Opening on male metathorax dorsal sclerite absent*. Outer margin hair pencil of male hindleg tibia short; inner absent; tarsomere segments 1–5 fused, claws absent. Female hind tibia with 2 + 2 spurs.

Male abdomen and genitalia: anterolateral extensions on male 2nd sternite absent. One membranous pouch between male 7th and 8th sternite. Anterior margin of male 8th sternite elongated medially; cerata symmetrical; mappa constricted at base; membranous, posterolateral appendices absent. Posterior margin of male 8th tergite concave. Socii rudimentary, short. Ventral margin of tegumen straight. Valvae symmetrical, soft, setose, valvula and sacculus separate. Anterior margin of sacculus medially upturned, covered with pointing setae. Transtilla present. Juxta weakly sclerotized, narrow at base, but with long wing-like processes. *Vinculum enlarged, dorsally narrow, v-shaped* (Fig. 33). Aedeagus curved ventrally, with long caecum; without sclerotizations.

Female genitalia: unknown.

Distribution and species diversity: known from Madagascar only. One species.

Immature stages: unknown.

Biology: unknown.

Comments on systematics: the genus is retained as valid but only tentatively (see comments on *Dithalama*). Prout speculated that *Isoplenodia* might be of a close relative of the African genera *Epicosymbia* and *Isoplenia*, on the basis of two forewing areoles, and long ciliated male antenna. This was not supported in this analysis and the condition of two forewing areoles (48: 1) was shown to be a very homoplastic character. *I. arrogans* was found to have cerata-like structures laterally on the male 8th sternite, but these are immobile and without apical setae, contrary to other studied material. Examination of female structures could give further clues about the systematic position of this species.

Somatina Guenée, [1858]
(Figs 2, 27, 31, 56, 81, 120, Appendix)

Diagnosis: monophyly supported by three synapomorphies: sacculi of valva are asymmetrical (105: 1, seven occurrences); valvuli of valva are asymmetrical (108: 1, seven occurrences); anterior margin of juxta is with wing-like processes, apex is fused to sacculus of valva (116: 2, seven occurrences).

Imago: wingspan 23–33 mm. Male antenna fasciculate; proximal row of sensilla sometimes weakly elongated, those sensilla in single rows. Female antenna fasciculate, simple. Pilifer present. Wing patterns variable, colour ranging from white to reddish-yellow, greyish-brown in many species; often irrorated with dark scales; dark band on forewing termen between transverse anterior and median lines in many species; transverse lines dentate, straight or sometimes modified, taking unusual forms; discal spot weak, dark; iridescent scales usually absent, glossy in few species; terminal line usually discontinuous, equally wide; patterns often repeated on underside, fuscous, sometimes absent. *Forewing with two areoles*; R_5 from distal areole, stalked with R_2–R_4 or straight from cell. Outer and inner margin hair pencil of male hindleg tibia usually present, outer concealed in a furrow formed by long scales in many species; apical spurs usually absent, sometimes two; tarsomeres normally developed, 5-segmented; two claws. Female hind tibia with 2 + 2 spurs.

Male abdomen and genitalia: pouch on male 2nd sternite round, posterior margin often invaginated; anterolateral extensions usually present. Small lateral pouches between sternites 3 and 4 rarely present. Usually one, sometimes two membranous pouches between male 7th and 8th sternite. Male 8th sternite variable, x-shaped and heavily sclerotized in many species; anterior margin elongated medially or bifurcate; *cerata usually absent* (Fig. 56), sometimes present as fully developed; *mappa absent, setose or bare*; posterolateral appendices usually present. *Male 8th tergite posterior margin concave, with two round lobes or sharp projections* (Fig. 120). Socii separate, covered with long setae. Ventral margin of tegumen unmodified, rarely with small round or elongated projections. *Sacculus and valvula of valva separate, with pronounced asymmetry*; valvula shape varies from wide, blunt-ended to narrow, long, with sharp apex; medial and lateral margin of sacculus often with upturned projections. Anterior margin of juxta with wing-like processes, *apex rarely free, instead fused to sacculus* in most species, and sometimes asymmetrical; sometimes juxta processes functionally replacing sacculus of valva. Transtilla narrow weakly sclerotized band, rarely wide. Vinculum enlarged, symmetrical and usually convex. Aedeagus bent, sometimes with small projections near apex; *vesica complex, with several large, often twisted diverticula* (Fig. 31); variably sclerotized but rarely with distinct cornuti.

Female genitalia: lamella postvaginalis usually absent; lamella antevaginalis large, sclerotized, medially invaginated, flap-like structure in most species. Ostium bursae weakly sclerotized. Ductus bursae usually coiled, weakly sclerotized. Ductus seminalis opens from corpus bursae neck. Corpus bursae ovoid sac; signum elongated, made of separate spines, rather large compared to size of corpus bursae.

Distribution and species diversity: from Africa to the Oriental region and Australia. Forty-four species and several subspecies, although see 'Comments on systematics'.

Immature stages: I have been unable to find any references. Nakamura (1994) described the pupa of *Somatina indicataria* (Walker), but the taxon is considered to belong to *Scopula* in the present study.

Biology: S. anthophilata has been recorded from *Gardenia jasminoides* and *Randia dumetorum* (Rubiaceae) and *Rosa* (Rosaceae). *Somatina omicraria* and *S. virginalis* have been recorded from the Oleaceae genus *Jasminum* (Robinson *et al*., 2002).

Comments on systematics: Sterrhinae species with two areoles on the forewings have traditionally been considered to belong to *Somatina*, in contrast to *Problepsis* and *Scopula*, which have one areole. Since this character was shown to be homoplastic in the present study (48: 1), and as both states occur in many lineages, *Somatina* was considered to be a polyphyletic assemblage of species, as noted by Inoue (1992), with many species formerly ascribed to it shown to belong to either *Problepsis* or *Scopula*.

While the remaining species should be revised against the generic descriptions given here and, if necessary, transferred to the appropriate genera (see

Appendix for examples), *Somatina* is, however, likely to be a monophyletic group of species. It has a number of characteristic, although not unique, features. One such feature is the anterior margin of the juxta that is fused to sacculus of the valva (116: 2). The male of *S. anthophilata*, the type species of the genus, has small lateral pouches between sternites 3 and 4 (Holloway, 1997), although as these were not seen in other studied taxa, this autapomorphy was not coded. Traditionally, *Somatina* has been considered a close relative of *Scopula* or *Problepsis* (e.g. Prout, 1920–41, 1934–39), but in the present study species of the redefined genus are associated with *Zythos*. This connection is supported by the sclerotized posterior part of male 8th sternite (85: 1, Fig. 59), which is found elsewhere only in *Dithalama desueta*, and by the presence of parallel folds on the vesica (132: 1, 129), found also in a few *Scopula* taxa. Several characters, e.g. the structure of the socii and signum, indicate a close relationship with *Scopula*.

Somatina irregularis and *S. eurymitra* were considered *incertae sedis*, but were retained in their traditional generic combinations, as they did not group together with the recognized genera. *Somatina irregularis* grouped together with *Scopula haemaleata*, sharing with it a number of unique features, such as a bifurcated cerata (82: 1) and a juxta with long processes laterally (117: 1). *Somatina eurymitra*, meanwhile, showed affinities with *Somatina* and *Problepsis*; for example, the male 8th tergite is concave with two sharp lateral projections (88: 3), a feature typical of *Somatina*, while the cerata fused with the mappa (80: 1) is a common condition in *Problepsis*. Females of *S. eurymitra* were not available for study. It remains to be tested whether these taxa actually represent larger monophyletic groups.

ZYTHOS FLETCHER, 1979
(FIGS 5, 34, 59, 83, 101, 103, 114, 121, 124, 125, 129, 131, 132, APPENDIX)

Diagnosis: monophyly supported by 20 synapomorphies: iridescent scales of wings are restricted to a few rows, excluding discal spots (16: 3, unique); iridescent scales of wings are glossy and longitudinally grooved (17: 1, unique, Fig. 101); discal spot of forewing is not unicolorous and dark (19: 1, six occurrences);discal spot of forewing is lunular (20: 2, two occurrences); presence of a spot at vein endings at forewing margin (40: 1, two occurrences); absence of hair pencil on inner margin of male hind tibia (61: 1, seven occurrences); male hindleg is with one claw only (67: 1, unique, Fig. 114); absence of pretarsus arolium on male hindleg (68: 0, six reversals); two pouches are present between male 7th and 8th sternites (76: 1, four occurrences, Fig. 59); absence of posterolateral appendices on male 8th sternite (86: 1, five occurrences, five reversals); posterior margin of male 8th tergite is convex (88: 4, unique, Fig. 121), posterolateral margin of male 8th tergite has two membranous appendices (90: 1, Fig. 121); absence of setae on socii (96: 0, unique); anterior margins of tegumen are dorsally fused (101: 1, unique, Fig. 125); absence of transtilla (102: 2, unique); valva have symmetrical sacculi (105: 0, two occurrences); valvula of valva lies ventral of sacculus (107: 1, unique, Fig. 124); valvuli of valvae are symmetrical (108: 0, two occurrences); anterior margin of juxta is without wing-like processes (116: 0, nine occurrences); signum has a bare zone laterally on both sides of median ridge (135: 1, unique, Fig. 131).

Imago: wingspan 32–40 mm. Male antennae fasciculate, sensilla in single rows; female antennae fasciculate, simple. Pilifer present. *Sensilla styloconicae forming serrate lining at distal end of proboscis*. Chaetosemata prominent. Wing pattern variable, often with fine striations on extensive areas of wings; costa and middle parts often olive grey; often with longitudinally grooved iridescent scales on outer half of forewing, excluding discal spots (Fig. 101); subterminal shaded line and terminal line touching each other at fore- and hindwings in many species; discal spots dark, often lunular on forewings; pale markings on anterior side of hindwing discal spots in many species; terminal line discontinuous, equally wide, *dark spot at vein end at forewing margin*; underside often unicolorous, ranging from light brown to light orange. Forewings with two areoles; R_5 from distal areole, either stalked with R_2–R_4 or straight from accessory cell. Hair pencil of outer margin of male hindleg tibia present, point of origin prominent; inner margin hair pencil absent; tarsomeres normally developed; *one claw* (Fig. 114); arolium absent; pulvillus present. Female hindleg tibia with 2 + 2 spurs.

Male abdomen and genitalia: pouch on male 2nd sternite round, large; anterolateral extensions present. Two membranous pouches between male 7th and 8th sternite. Male 8th sternite heavily sclerotized, anterior margin bifurcate; posterior margin with blunt extensions or medial projections; cerata, mappa and membranous posterolateral appendices absent (Fig. 59). *Male 8th tergite posterior margin convex, with two membranous appendices on posterolateral margin* (Fig. 121). Genitalia capsule oval. *Socii wide, separate, without setae*. Ventral margin of tegumen slightly curved inwards. Valvae symmetrical, valvula and sacculus separate; anterior margin of sacculus medially upturned or levelled; *valvula moved ventrad of sacculus* (Fig. 124), often curved dorsally. *Transtilla absent; instead, anterior margins of tegumen are fused dorsally* (Fig. 125). Anterior margin of juxta without wing-like processes. Vinculum enlarged. Aedeagus

almost straight, apex with small blunt extension; vesica prominent, long, often with long lateral diverticulum and sclerotized parallel folds.

Female genitalia: lamella antevaginalis flap-like, flexible, medially either concave or bilobed. Ostium bursae heavily sclerotized. Ductus bursae membranous, coiled; ductus seminalis arises from ductus bursae. Corpus bursae an elongate sac; *signum often with narrow medial, sclerotized strip followed by bare zone* (Fig. 131) and granulate field of separate spines on both sides laterally.

Immature stages: unknown.

Distribution and species diversity: from India to Papua New Guinea. Morphologically, a compact genus with 11 species.

Biology: adults occur predominantly in the understorey of lowland rain forests and have been collected from carrion-baited pitfall traps (Holloway, 1997). The serrated distal end of the proboscis indicates an adaptation to piercing. Frequently taken from secondary forests as well (Chey, 1994).

Comments on systematics: Prout (1920–41), followed by Holloway (1997), considered *Zythos* to be a close relative of *Ignobilia* on the basis of striated facies and pale underside of wings. In the present study *Zythos* is associated with *Somatina* (see Discussion under that genus).

THE *LIPOMELIA, PROBLEPSIS* AND *SCOPULA* GROUP OF GENERA

This group of genera is characterized by one synapomorphy (Figs 133–135): the fully developed cerata (79: 2, six occurrences, six reversals). Within the group, the relationships are not resolved. *Lipomelia* and *Problepsis* form a compact group, *Somatina irregularis* and *Scopula haemaleata* are *incertae sedis*, and externally heterogeneous *Scopula* is characterized by a combination of features.

Comments on systematics

See the *Dithalama, Isoplenodia, Somatina* and *Zythos* group of genera.

LIPOMELIA WARREN, 1893 (FIGS 6, 35, 60, APPENDIX)

Diagnosis: monophyly supported by ten synapomorphies: forewing costa is wide and grey (11: 2, two occurrences); presence of pale markings on anterior side of hindwing discal spot (23: 1, two occurrences); subterminal shade line and terminal line are touching each other at fore- and hindwings (42: 1, two occurrences, Fig. 6); absence of male hindleg pretarsus arolium (68: 0, six reversals); absence of male hindleg pretarsus pulvillus (69: 1, three occurrences); sacculi of valva are asymmetrical (105: 1, seven occurrences); valvuli of valva are asymmetrical (108: 1, seven occurrences); vinculum is asymmetrical (113: 1, six occurrences); anterior margin of juxta is without wing-like processes (116: 0, nine occurrences); presence of parallel folds on vesica (132: 1, seven occurrences).

Imago: wingspan *c.* 25 mm. Head smooth-scaled; male antennae fasciculate, sensilla in single rows. Pilifer present. Wings brown, base striated, dark area between transverse posterior line and subterminal shade line at forewings; transverse lines cryptic, *subterminal shade line and terminal line touching each other at fore- and hindwings* (Fig. 6); discal spots white, with iridescent scales, surface smooth; pale markings on anterior side of hindwing discal spots; terminal line discontinuous, equally wide; underside fuscous. Forewings with one areole; R_5 stalked with R_2–R_4. Outer and inner margin hair pencil of male hindleg tibia well developed; distal spurs of hindleg tibia absent; tarsomeres short, segments 4–5 fused; *two claws; arolium and pulvillus absent*. Female hindleg tibia with 2 + 2 spurs (Prout, 1920–41).

Male abdomen and genitalia: round pouch and anterolateral extensions on male 2nd sternite present. One membranous pouch between male 7th and 8th sternite. Male 8th sternite anterior margin elongated medially; *cerata present, coalescent at base* (Fig. 60); mappa absent; membranous posterolateral appendices present. Male 8th tergite posterior margin concave. Socii short, setose, separate. Ventral margin of tegumen straight. *Valvae asymmetrical*, valvula and sacculus separate, ventral margin of left sacculus bifurcate. Transtilla present. Anterior margin of juxta with wing-like processes absent. Aedeagus curved dorsally; plate-shaped sclerotization at proximal end of ductus ejaculatorius; cornutus absent; vesica simple, large lateral diverticulum at base with sclerotized parallel folds, small diverticulum dorsally.

Female genitalia: unknown.

Distribution and species diversity: from India to Taiwan. One species.

Immature stages: unknown.

Biology: unknown.

Comments on systematics: when Warren (1893) described *Lipomelia*, he did not discuss its systematic position. Prout (1920–41) considered it a close relative of *Scopula* on the basis of one areole on the forewing and male genital characters, although he noted that

the facies of *L. subusta* resembles that of *Zythos* spp. In the present study, *Lipomelia* is associated with *Problepsis* on the basis of forewing iridescent scale characters. One of these characters, i.e. the structure of iridescent scales being glossy and smooth (17: 2, Figs 102, 134) is a unique synapomorphy of this clade. I have chosen not to synonymize *Lipomelia* with *Problepsis*, however, because the former lacks several characteristic features of the latter, e.g. ocellate discal spots on both pairs of wings (cf. Figs 6, 7), fused socii lying ventral to tuba analis (cf. Figs 35, 36, 117), and male 8th sternite anterior margin not being trifurcate and blunt (cf. Figs 60, 61). Male genitalia of *Lipomelia*, including 8th sternite, were found to be structurally similar to those of *Scopula*.

PROBLEPSIS LEDERER, 1853 (FIGS 7, 27, 36, 61, 84, 102, 105, 106, 108, 115, 117, 128, APPENDIX)

Diagnosis: monophyly supported by five synapomorphies: discal spot of forewing is ocellate and round (20: 3, three occurrences, Fig. 7); discal spot of hindwing is ocellate (22: 1, three occurrences); socii are fused at apex, lying ventral of tuba analis (92: 2, two occurrences, Fig. 117); ventral margin of tegumen is dentate (100: 1, two occurrences); anterior margin of juxta is with wing-like processes, apex is fused to sacculus of valva (116: 2, five occurrences).

Imago: wingspan 25–50 mm. Male antennae fasciculate; sensilla in single or multiple rows, proximal row elongated in many species. Female antennae fasciculate, simple; sensilla in single rows. Pilifer present. Wings pale to white, greyish in few species; *ocellated discal spots* (Fig. 7) distinct; smooth, glossy, *iridescent scales often present in discal spots or scattered throughout wings* (Figs 102, 105, 106); transverse median line often wide, indistinct; subterminal shade line discontinuous, spotted; terminal line continuous or discontinuous, equally wide or wider at vein ends. Patterns not repeated or weakly expressed on underside. Forewings often with one areole, sometimes two; R_5 from proximal or distal areole, stalked with R_2–R_4. Outer margin hair pencil of male hindleg tibia present or absent; inner margin hair pencil often moderate, sometimes massive or absent; tarsomeres often reduced in length, 5-segmented or segments 4–5 fused; claws either two in number or absent. Female hind tibia with 2 + 2 spurs.

Male abdomen and genitalia: pouch on male 2nd sternite round, posterior margin often invaginated; anterolateral extensions present or absent. One or two membranous pouches between male 7th and 8th sternite. Male 8th sternite elongated; anterior margin often trifurcate, blunt or sometimes bifurcate; cerata absent, rudimentary or fully developed, often fused to mappa; mappa present, bare; membranous posterolateral appendices present or absent. Male 8th tergite posterior margin concave. *Socii fused at apex, ventral of tuba analis* (Fig. 117), setose, sometimes with two lateral appendices. *Ventral margin of tegumen sometimes unmodified, dentate in most species*. Valvula and sacculus of valva separate, symmetrical, long, tapering towards apex, acute; medial margin of sacculus rarely upturned. Transtilla variably sclerotized, often invaginated medially. Anterior margin of juxta with wing-like processes, often anterior margin sclerotized only, apex fused to sacculus of valva, sometimes free. Vinculum enlarged, symmetrical, anterior margin often concave. Aedeagus often slightly bent, apex with one or several teeth; vesica large, complex, variably sclerotized, rarely with distinct cornuti; several diverticula, sometimes long and prominent.

Female genitalia: lamella postvaginalis sclerotized in many species; *lamella antevaginalis often absent*, sometimes weakly developed, rarely flap-like, flexible. Ostium bursae often sclerotized; *ductus bursae sclerotized, straight, wide* (Fig. 84) in most species. Ductus seminalis arises from ductus bursae or corpus bursae neck. Corpus bursae ovoid, membranous sac. Signum absent sometimes, usually an ovoid patch of separate or fused spines, small compared to size of corpus bursae.

Distribution and species diversity: most species occur from sub-Saharan Africa to Indonesia and Australia. Only a few reach the Palaearctic region. Fifty-one species and several subspecies.

Immature stages: the only larval description is based on a species from south India, whose identity is uncertain. It is possibly *P. deliaria* Guenée (Bell in Holloway, 1997). The Japanese species illustrated in Sugi (1987) rest at 45 ° from the substrate, usually in the mid-rib of a leaf. Based on limited Japanese material (Nakamura, 1994), *the pupal cremaster has one pair of setae only*. Pupation takes place in a loose cocoon incorporating particles of earth, usually on the soil surface.

Biology: all host-plant records relate to Oleaceae (Holloway, 1997). These include *Olea* (Holloway, 1997), *Ligustrum* (Sugi, 1987) and *Jasminum* (Singh, 1957). Many species are from lowland forest, including cultivated areas and dry heath, but Holloway (1997) reports species taken at heights of almost 1800 m in Borneo. In north-east China, *P. phoebearia* Erschov and *P. plagiata* (Butler) were taken from a lamp on a warm, south-facing sandy grove (pers. observ.).

Comments on systematics: traditionally, *Problepsis* has been delimited to include species that have one forewing areole, large ocellated discal spots with iridescent scales and no spurs on male hind legs. Its closest relatives were assumed to be *Antitrygodes, Scopula* and *Somatina* (Sterneck, 1941; Prout, 1934–39; Holloway, 1997). In the present study, the clade comprising *Lipomelia* + *Problepsis* was found to be the closest relative of *Scopula*, in addition to two taxa *incertae sedis* (Fig. 133). Ocellated discal spots, whether round or semiround (20: 3 or 20: 4), were found to be a unique synapomorphy of *Problepsis*. Number of forewing areoles was shown to be a homoplastic character (Ch. 48), and although the majority of *Problepsis* species have one, two are also found, e.g. in *P. centrophora* (Prout). Absence of male hindleg spurs was found to be a plesiomorphic feature in Scopulini (62: 0). Fused socii of male genitalia (92: 2), which lie ventral to tuba analis, was found to be a diagnostic character delimiting the genus; it is present in all studied *Problepsis* taxa, and found outside of it in *Antitrygodes cuneilinea* (Walker) only. It is possible that a few *Problepsis* species are misplaced in *Somatina*, see Appendix. See also Discussion under *Lipomelia*.

SCOPULA SCHRANK, 1802
(FIGS 8–26, 29, 37–54, 62–79, 85–100, 104, 107, 110–113, 116, 118, 122, 123, 126, 127, 130, APPENDIX)

Diagnosis: monophyly supported by one synapomorphy: absence of posterolateral appendices on male 8th sternite (86: 1, five occurrences).

Imago: wingspan 11–70 mm, usually 25–35 mm. Male antennae fasciculate; sensilla in single or multiple rows, proximal row sometimes elongated markedly; rarely bipectinate. Female antennae usually fasciculate, simple, occasionally sensilla arranged in single or even multiple rows. Pilifer present. Wings very variable, no single character can be used to define this group; almost all colours are found, but *usually straw or grey-brown* are dominant; often irrorated, sometimes unicolorous; *iridescent scales absent*; *three wavy transverse lines running from forewing to hindwing* are common, dentate in many species, reduced to series of spots in other or absent; sometimes two dark marks on forewings medial to transverse posterior line and another dark mark at forewing termen; few species with reticulate pattern; few with wide dark areas on outer third of wings; terminal line at forewings usually discontinuous, equally wide; smoothly curved around forewing apex occasionally or absent. *Discal spot usually dark, small*; cryptic in some, rarely absent; fringe usually unicolorous, occasionally chequered. Patterns usually repeated on underside, weak, sometimes absent. *Forewings usually with one areole*, sometimes two; R_5 usually from proximal areole, either stalked with R_2–R_4 or free, sometimes from distal areole, stalked with R_2–R_4 or free or even from M_1. Hindwing $Sc + R_1$ and Rs usually stalked for short distance, then divergent or sometimes connected by R_1. Outer and inner margin hair pencil of male hindleg tibia either present or absent; sometimes pronounced; if absent, replaced with two spurs at distal end in many species, occasionally one or absent; tarsomeres usually normally developed, sometimes reduced in length, 5-segmented; rarely segments 1–5 or 2–5 fused; two claws, absent in few groups. Female hindleg tibia with 2 + 2 spurs, sometimes only two distally.

Male abdomen and genitalia: pouch on male 2nd sternite round, posterior margin occasionally invaginated or rarely elongated, surface smooth or with fine decorations, one- or occasionally two-chambered; occasionally laterally elongated; with or without pointing setae, sometimes absent; anterolateral extensions present or absent. Sometimes tufts of setae on male 6th and 7th segments laterally. Usually one membranous pouch between male 7th and 8th sternite, rarely two or absent. Male 8th sternite anterior margin often medially elongated, sometimes cup-like or bifurcate, rarely trifurcate; *cerata usually present, asymmetrical, free* (Fig. 62), with apical setae, or rarely fused to mappa, sometimes seen as bifurcate, rudimentary or absent; *mappa usually present, bare* (Fig. 76), sometimes setose or posterior margin separate, rarely absent; *posterolateral appendices usually absent*, pronounced occasionally; posterior margin of male 8th sternite not sclerotized. *Male 8th tergite posterior margin usually concave with two round lobes* (Figs 118, 122) or rarely with sharp projections; laterally constricted in few species. *Socii size and shape variable, typically separate at apex*, setose, well developed, slightly upturned, occasionally reduced to tuft of setae, rarely massive, or in few instances *fused at apex, dorsal of tuba analis*. Tegumen ventral margin usually unmodified, rarely with lateral nondentate projections. Transtilla present, usually U-shaped, occasionally W-shaped; weakly sclerotized. Sacculus and valvula of valva separate, partially fused in few instances; size and shape very variable; symmetrical in most cases but pronounced asymmetry not unusual; *valvula usually soft, blunt-ended* (e.g. Fig. 48), bent ventrally, setose, blunt-ended, often with apical spines; sacculus usually more sclerotized, tapering towards apex, sometimes acute or dark; bifurcate in some species; occasionally rudimentary; various projections may arise from lateral and ventral margins. *Anterior margin of juxta typically with wing-like projections* (Fig. 52), sometimes absent; apex usually free, but both or one extensions fused to sacculus in few

species; often asymmetrical, size and shape variable; juxta often tube-shaped, well sclerotized with cup-like extension ventrally. Vinculum enlarged, margin typically convex, rarely concave; symmetrical, sometimes asymmetrical; cup-shaped and turned ventrally in few species. Aedeagus size and shape variable, in many instances narrow and straight or wide and slightly bent; caecum usually a continuation of aedeagus, enlarged occasionally; sharp projections at apex (carina) sometimes; apex sharp or blunt; vesica size and shape variable; often simple sac, with small diverticula and plate-shaped sclerotization at proximal end of ductus ejaculatorius; or large, complex, with elongated, twisted diverticula, variably sclerotized; distinct cornuti usual but more often sclerotizations are less definitive; pronounced plate-shaped sclerotizations at distal end of vesica occasionally; all instances between extremities occur.

Female genitalia: papillae anales often round, ventral margin upturned occasionally. Lamella postvaginalis usually weakly developed, irregular plate or made of parallel folds or absent. *Lamella antevaginalis usually sclerotized, flap-like, semiround* (Fig. 99), posterior margin invaginated in few species; horseshoe-shaped in others, laterally wider; asymmetry usual; normally bare but occasionally heavily setose. Ostium bursae usually sclerotized, with lateral extensions, reaching proximal part of ductus bursae, dorsally membranous. Ductus bursae variable in length, width, shape and amount of sclerotization; membranous and coiled in many cases, or short and wide, or indistinct. Ductus seminalis arises from ductus bursae, corpus bursae neck or corpus bursae. Corpus bursae elongated sac, usually smooth but heavily wrinkled in others. *Signum usually present as an elongated patch of separate spines* (Fig. 130), sometimes two patches, which may be fused medially along axis, sometimes spines fused forming long and narrow band. Usually corpus bursae with spines on inner surface, length and density variable.

Distribution and species diversity: virtually ubiquitous. The genus has successfully colonized even the remotest islands in Polynesia and New Zealand (Holloway, 1997; Dugdale, 1988). About 800 described species and numerous subspecies. See 'Comments on systematics' under *Somatina*.

Immature stages: material is scarce in museums and pertinent literature is scattered, often dealing with single species. Too little is known to make comprehensive conclusions. The most detailed descriptions can be found in McGuffin (1967: 12), who dealt with Canadian species. Their application to the world-fauna may be questionable, but they provide a good starting point: 'Egg round, somewhat longer than wide, usually larger at one end than at other (figs 77, 84c) with longitudinal ridges and cross striae; white, cream coloured, or light green; turning pink, scarlet, brown, or black; attached to leaves of food plant or laid loosely on ground near food plant.' The illustrations of eggs of Palaearctic *Scopula* species fit the description well (Sannino & Balbiani, 1984; Sannino & Espinosa, 1999). The caterpillar is usually long, slender, green or brown in colour, with longitudinal patterns. The resting posture is either stick-like, at an angle of 45 °, or ventrally bent to form a complete loop (Sugi, 1987; Murase, 1998; Ohbayashi, 2000; Tominaga, 2000; Ebert, 2001). According to McGuffin (1967: 12): '20–30 annulets on each anterior abdominal segment; cuticle smooth at 50×; body setae short, with blunt tips; setae on legs relatively long, pointed; prolegs of mature larva with 6–10 crochets in two incompletely separated groups (fig. 82g).' If disturbed, the larvae of many Palaearctic species drop down and make several powerful side-to-side movements (pers. observ.).

Many species are polyphagous, and recorded host-plants range from woody to herbaceous taxa. They include Scrophulariaceae (*Striga*), Sterculiaceae (*Theobroma*), Asteraceae (*Lactuca*), Polygonaceae (*Rumex*), Lamiaceae(*Thymus*), Poaceae (*Zea*), Moraceae (*Ficus*) Rosaceae (*Filipendula, Sorbus*), Liliaceae (*Litanthus*) and Ericaceae (*Vaccinium*) for *Scopula*; Rubiaceae (*Adina*, *Breonia*, *Mitragyna*, *Hymenodictyon* and *Mussaenda*) and Marantaceae (*Maranta*) for the *Antitrygodes*-group; Rubiaceae (*Oxyanthus, Randia*) and Sapindaceae (*Blighia*) for the *Aletis*-group (Staude, 1999; Tanahara, 1999; Robinson *et al*., 2002); Lamiaceae (*Thymus*), Caryophyllaceae (*Dianthus, Gypsophila*) and Brassicaceae (*Alyssum*) for the *Glossotrophia*-group (King, 2000; Hausmann & Dötterl, 2003) and Rubiaceae (*Pygmaeothamnus*) for the *Epicosymbia*-group (Staude, 1999). A few species are known to be of minor pest status, attacking tobacco (Sannino & Balbiani, 1984; Sannino & Espinosa, 1999) and groundnut (Satpathi, 1995).

Pupal cremaster has usually four pairs of setae, terminal pair usually much enlarged (Khotko, 1977; Patocka, 1994), reduced to two in *S. indicataria* (Nakamura, 1994). In the *Glossotrophia*-group the proboscis case extends beyond the cremaster, curving inwards (King, 2000; Hausmann, 2001).

Biology: Scopula includes species of both forested and open habitats as shown in the host-plant list. A number of species have been recorded feeding as adults on the tears, sweat and blood seeping from wounds of large mammals in South-east Asia (Bänziger & Fletcher, 1985). Many species are day-active, and the species of the African *Aletis* and *Cartaletis* groups are exclusively diurnal.

Parasitoids: Homolobus truncator (Say) (Braconidae: Homolobinae) has been reported to parasitize the larva of *S. annae* (Mentzer) of the *Glossotrophia* group (King, 2000).

Distinct species groups can be defined within *Scopula*. Their description is, however, beyond the scope of this paper. They include the *Antitrygodes*, *Epicosymbia*, *Glossotrophia* and *Aletis* groups.

Comments on systematics: Scopula is the largest and externally most heterogeneous genus of the tribe. Although only one character was found to support the monophyly of this genus, overall support is nevertheless not as weak as it may appear from the cladogram. Having studied a large number of species across different biogeographical regions, I have seen that the moths of this genus have many characteristic features such as separate sacculus and valvula of the valva, urceolate shaped juxta and spined signum, in addition to diagnostic structures of the male 8th sternite and tergite. All were found to be homoplastic, and accordingly, many are present in the majority of species, although one or a few may be absent in any given species. For example, the absence of ceras in many apical species such as *Scopula sentinaria*, *Stigma kuldschaensis* and *Dasybela achroa* was found to be due to secondary losses (79: 0, CI = 0.09, RI = 0.51). It is thus difficult to define this genus in terms of unique features; instead, *Scopula* can be characterized by a combination of characters, as already noted by Covell (1970). Many distinctive species groups within *Scopula* were found, but their relationships remain unresolved, probably due to the high degree of homoplasy that the characters display (Fig. 134).

All the synonymized genera were found to have diagnostic structural characters of *Scopula*, although some of the taxa were found to have very divergent external appearance from the type species of the genus, *S. ornata* (Appendix).

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APPENDIX

Preliminary revised checklist of the genera and species of the Scopulini

The definition of the tribe Scopulini follows Sihvonen & Kaila (2004). The concept also includes Aletini and Problepsini (Holloway, 1996, 1997). The checklist is largely based on Scoble (1999); this publication is recommended for readers who require further details. Species and subspecies (the latter indented) are listed in alphabetical order under their revised generic names. An asterisk indicates that the species has been studied by the author (external and genital characters). Synonyms are also indented. Comments are printed in a smaller font within square parentheses. While the need for replacement names as a result of primary or secondary homonymy is clear, they have not been proposed here due to the fact that in many cases type specimens were not studied. As not all putatively valid species were included in the study, several monophyletic groups may eventually be recovered that do not appear as such in the list. This is especially true of the *Somatina* species assemblage, where numerous species await combination with the appropriate genera; instances are mentioned in the comments.

Scopulini
Scopulini Duponchel, 1845 [1844–46] (as Scopulites). Type species: *Phalaena paludata* Linnaeus, 1767, a junior synonym of *Phalaena ornata* Scopoli, 1763 [Portugal].
Aletini Hampson, 1918 (as Aletinae). Type species: *Papilio helcita* Linnaeus, 1763. Indiis [incorrect locality, probably tropical Africa].
Problepsini Wiltshire, 1990. Type species: *Caloptera ocellata* Frivaldszky, 1845. [Greece].

Dithalama
Dithalama Meyrick, 1888. Type species: *Dithalama cosmospila* Meyrick, 1888. Australia.
cosmospila Meyrick, 1888*
desueta (Warren, 1902)*

Dithalama is possibly a non-monophyletic assemblage of species (see Diagnosis and *Isoplenodia* below). The following unstudied *Dithalama* taxa are left tentatively under their current generic combination, waiting for their status to be revised against the diagnosis provided for *Dithalama.*

persalsa (Warren, 1902)
ioparia (Swinhoe, 1902)
punctilinea Swinhoe, (1902)
tetrasticha (Lower, 1902

Isoplenodia
Isoplenodia Prout, 1932. Type species: *Isoplenodia arrogans* Prout, 1932. Madagascar.
The generic status of *Isoplenodia* Prout and especially its relationship to *Dithalama* warrants further investigation (see *Dithalama*). It is retained tentatively as a valid genus because females, which often are phylogenetically informative, were not available for study. *Isoplenodia* may turn out to be a junior synonym of *Dithalama*.

arrogans Prout, 1932*

Somatina
Somatina Guenée, [1858]. Type species: *Somatina anthophilata* Guenée, [1858]. [India].
Nebessa Walker, 1869. Type species: *Nebessa chalyboeta* Walker, 1869. Congo.
Somatinopsis Warren, 1896. Type species: *Somatinopsis nigridiscata* Warren, 1896. Indonesia.
Somatodes Guenée, [1858] [misspelling of *Somatina*]

Somatina is possibly a non-monophyletic assemblage of species. The following taxa have been checked and agree with the diagnosis provided.

anthophilata Guenée, [1858]*
chalyboeata (Walker, 1869)*
densifasciaria Inoue, 1992*
[*S. densifasciaria* Inoue shares the diagnostic conditions of *Somatina*, for example the posterior margin on the male 8th tergite that is concave with two sharp projections (character 88: 3) (Inoue, 1992). It is externally similar to *S. rosacea* Swinhoe.]
discata Warren, 1909*
[*S. discata* Warren, 1909 is possibly a junior synonym of *Somatina nigridiscata* Warren, 1896, based on examination of the genitalia of the type material from The Natural History Museum, London: *Somatina discata* holotype (slide BMNH GEO 19799) and *Somatinopsis nigridiscata* holotype (slide BMNH GEO 19798)].
lia Prout, 1915*
nigridiscata (Warren, 1896)*
[See *S. discata* Warren, 1909.]
sedata Prout, 1922*

The following taxa are left tentatively within their current generic combination, awaiting comprehensive revision.

accraria Swinhoe, 1904
[*Somatina accraria* Swinhoe, 1904 should probably be combined with the genus *Problepsis*. It is for the time being retained in *Somatina*, however, as I have not yet prepared type specimens of this species, deposited at BMNH. *S. accraria* is closely related to *S. figurata* Warren (Prout, 1929–35; Janse, 1933–35); see latter for further comments.]
apicipuncta Prout, 1915
centrofasciaria (Leech, 1897)
[Only a female type specimen of this taxon is known, deposited at BMNH. Prout (1920–41, 1934–39) speculated that it should perhaps be combined with *Discoglypha* Warren 1896.]
ctenophora Prout, 1915*
[*S. ctenophora* Prout, 1915 should probably be combined with *Problepsis*. Janse (1933–35) illustrated the male genitalia, which share several features of *Problepsis*, e.g. socii fused at apex, lying ventral to the tuba analis. *S. ctenophora* is for the time being retained in *Somatina*,

however, as I have not yet prepared the type specimen of this species, deposited at BMNH.]

eurymitra Turner, 1926 *incerta sedis**

[*Somatina eurymitra* Turner, 1926 is *incertae sedis*, but retained in *Somatina* until a revision is done. It may not be congeneric with *Somatina*, as my cladistic results indicate that it is the sister taxon to the *Dithalama* + *Isoplenodia* clade (Figs 133, 134).]

figurata Warren, 1897*

rufitacta Warren, 1905

ssp. *candida* Prout, 1932

ssp. *transfigurata* Prout, 1922

[*Somatina figurata* Warren, 1897 should probably be combined with *Problepsis*. Janse (1933–35) illustrates the male genitalia, which share several features of *Problepsis*, e.g. socii fused at apex, lying ventral to the tuba analis, and distal part of aedeagus that has a distinct sclerotized spine (character 122: 1). *S. figurata* is for the time being retained in *Somatina,* however, as I have not yet prepared the type specimen of this species, deposited at BMNH.]

fletcheri Herbulot, 1958

fraus Prout, 1916

fungifera Warren, 1909

hombergi Herbulot, 1967

impunctulata (Warren, 1901)

[Only the male type specimen of this taxon is known, deposited at BMNH. Prout (1929–35) speculated that it should perhaps be combined with *Scopula* Schrank, 1802.]

ioscia Prout, 1932

irregularis (Warren, 1898) *incerta sedis**

[*Cosymbia? irregularis* (Warren, 1898) is retained in *Somatina* awaiting a revision of the genus. I have found that it shares two unique synapomorphies with *Scopula haemaleata* (Warren, 1898). It is unknown whether this clade represents a larger species group. The synapomorphies may prove to be homoplastic if more taxa are included in a cladistic analysis.]

lemairei Herbulot, 1978

macroanthophilata Xue, 1992

maeandrata Prout, 1925

mozambica (Thierry-Mieg, 1905)

[*Somatina mozambica* (Thierry-Mieg), which was originally combined with *Problepsis* but later transferred to *Somatina*, based on its two-areole forewing (Prout, 1929–35), may eventually be recombined with *Problepsis*. I have shown this character to be homoplastic and the genus *Problepsis*, among others, has one or two areoles. Characters mentioned in the description of the species, e.g. weakly developed ocellated discal spots that have metallic (= iridescent) scales suggest affinity with *Problepsis* (Thierry-Mieg, 1905). I have not dissected the genitalia, and the depository of the type specimen is unknown.]

obscuriciliata Wehrli, 1924

omicraria (Fabricius, 1798)

[*Somatina omicraria* (Fabricius) may eventually be combined with *Problepsis*. Characters such as weakly developed ocellated discal spots that have silvery (= iridescent) scales and forewing venation (Prout, 1920–41) suggest affinity with *Problepsis*. I have not dissected the genitalia; type specimen is at ZMUC.]

cana Hampson, 1895

extrusata (Walker, 1861)

ossicolor Warren, 1898

plynusaria (Walker, [1863])

congruaria (Walker, 1869)

postlineata (Warren, 1899)

[Prout (1920–41) speculated that this taxon should perhaps be combined with *Scopula* Schrank, 1802. I have not dissected the genitalia; type specimens are at BMNH.]

probleptica Prout, 1917

[*Somatina probleptica* Prout may eventually be combined with *Problepsis*. Characters such as well developed ocellated discal spots that have silvery (= iridescent) scales and forewing venation suggest affinity with *Problepsis*, as already indicated by Prout (1929–35). I have not dissected the genitalia; type specimen is at BMNH.]

prouti Janse, 1934*

[*Somatina prouti* Janse, 1934 should probably be combined with *Problepsis*. Janse (1933–35) illustrated the male genitalia, which shares features of *Problepsis*, in addition to wings that have weakly ocellated discal spots with iridescent scales not seen in *Somatina*. *Somatina prouti* has two areoles on the forewing and this has been considered a *Somatina* feature. My cladistic analysis shows that this character is homoplastic and that *Problepsis*, among others, has one or two areoles. Female is unknown. *Somatina prouti* is for the time being retained in *Somatina*, however, awaiting a comprehensive revision.]

purpurascens Moore, [1887]

pythiaria (Guenée, [1858])

[*Argyris pythiaria* Guenée may eventually be combined with *Problepsis*. Characters illustrated and mentioned in the description of species, for example weakly developed ocellated discal spots that have lead metallic (= iridescent) scales suggest affinity with *Problepsis* (Guenée, 1858). I have not dissected the genitalia; lectotype female is deposited at MNHN.]

rhodochila Prout, 1932

rosacea Swinhoe, 1894*

ssp. *anaemica* Prout, 1914

[*Somatina rosacea* Swinhoe has several features, including genitalia, that it shares with either *Somatina* or *Scopula*, thus making its generic combination difficult to judge. It also demonstrates that the generic association of *Somatina* species needs to be studied further.]

rufifascia Warren, 1896

maculata Warren, 1898

rubridisca Swhinhoe, 1900

sordida Warren, 1898

sanctithomae Herbulot, 1958

sublucens (Warren, 1907)*

[Only the female of *S. sublucens* (Warren) was available for study (BMNH 20648). As features like spinose signum show affinity with *Scopula*, the generic combination of this species remains to be tested.]

subviridata (Warren, 1901)

syneorus Prout, 1915

transvehens Prout, 1918

[*Somatina transvehens* Prout may eventually be combined with *Problepsis*. Characters such as weakly developed ocellated discal spots that have silvery (= iridescent) scales and forewing venation suggest affinity with *Problepsis*, as already indicated by Prout (1920–41). I have not dissected the genitalia; type specimen is in BMNH.]

vestalis (Butler, 1875)*

[*Somatina vestalis* (Butler, 1875) should probably be combined with *Problepsis*. Janse (1933–35) illustrates the male genitalia, which share several features of *Problepsis*, e.g. socii fused at apex, lying ventral to the tuba analis. In addition, the wings have weakly ocellated discal spots with iridescent scales not seen in *Somatina*. *S. vestalis* has two

areoles on the forewing and this has been considered a feature of the genus. My cladistic analysis shows that this character is homoplastic and that *Problepsis*, among others, has one or two areoles. Female genitalia (slide BMNH GEO 4274) also suggest affinity with *Problepsis*. *S. vestalis* is for the time being retained in *Somatina*, however, as I have not yet prepared the type specimen of this species, deposited at BMNH.]

virginalis Prout, 1917*

[*Somatina virginalis* Prout, 1917 should probably be combined with *Problepsis*. Wings have weakly ocellated discal spots with iridescent scales not seen in *Somatina*. *S. virginalis* has two areoles on its forewing and this has been considered a feature of the genus. My cladistic analysis shows that this character is homoplastic and that *Problepsis*, among others, has one or two areoles. Female genitalia (slide BMNH GEO 4275) also suggest affinity with *Problepsis*. *Somatina virginalis* is for the time being retained in *Somatina*, however, as I have not yet prepared type specimen of this species, deposited at BMNH.]

wiltshirei Prout, 1938

Zythos

Zythos Fletcher, 1979. Type species: *Nobilia turbata* Walker, 1862. Malaysia. [Replacement name for *Nobilia* Walker, 1861].

Nobilia Walker, 1861. Type species: *Nobilia turbata* Walker, 1862. Malaysia. [Junior homonym of *Nobilia* Gray, 1855 (Mollusca).]

aphrodite (Prout, 1932)*

ssp. *rooki* (Prout, 1938)

avellanea (Prout, 1932)*

clypeata Yazaki, 1996*

cupreata (Pagenstecher, 1888)

nebulosa (Warren, 1897)

erotica (Prout, 1932)*

fastigata (Prout, 1938)*

modesta Yazaki, 1996*

molybdina (Prout, 1938)

ssp. *tombarensis* (Prout, 1938)

obliterata (Warren, 1897)*

simplaria (Snellen, 1899)

strigata (Warren, 1896)*

ssp. *rubescens* (Prout, 1938)

turbata (Walker, 1862)*

strigularia (Snellen, [1886])

Lipomelia

Lipomelia Warren, 1893. Type species: *Lipomelia subusta* Warren, 1893. India.

Defoa Swinhoe, 1893. Type species: *Defoa ustata*, a junior synonym of *Lipomelia subusta* Warren, 1893. [India].

subusta Warren, 1893*

ustata (Swinhoe, 1893)

Problepsis

Problepsis Lederer, 1853. Type species: *Caloptera ocellata* Frivaldszky, 1845. [Greece]. [Replacement name for *Caloptera* Frivaldszky, 1845.]

Argyris Guenée, [1858]. Type species: *Argyris ommatophoraria* Guenée, [1858], a junior synonym of *Problepsis ocellata* Frivaldszky, 1845. [Lebanon.]

Caloptera Frivaldszky, 1845. Type species: *Caloptera ocellata* Frivaldszky, 1845. [Greece]. [Junior homonym of *Caloptera* Gistl, 1834 (Coleoptera).]

Problepsiodes Warren, 1899. Type species: *Problepsis conjunctiva* Warren, 1893. India.

achlyobathra Prout, 1928*

ssp. *emphyla* Prout, 1938*

ssp. *violescens* Prout, 1934

aegretta Felder & Rogenhofer, 1875*

egretta Hale-Carpenter, 1932 [misspelling of *aegretta*]

ssp. *insculpta* Prout, 1917

albidior Warren, 1899*

ssp. *matsumurai* Prout, 1938

apollinaria (Guenée, [1858])*

ssp. *aphylacta* Prout, 1938

ssp. *candidior* Prout, 1917

ssp. *deparcata* Prout, 1925

ssp. *hemicyclata* Warren, 1897

ssp. *wilemani* West, 1930

argentea Warren, 1900

asira Wiltshire, 1982*

borneamagna Holloway, 1997*

centrophora (Prout, 1915) **comb. nov.***

[*Somatina centrophora* Prout, 1915 is transferred from *Somatina* to *Problepsis*.]

clemens Lucas, 1890*

margaritata Warren, 1896

conjunctiva Warren, 1893*

ssp. *subjunctiva* Warren, 1893

craspediata Warren, 1897

ssp. *frosti* Prout, 1938

ssp. *rotifera* Prout, 1916

crassinotata Prout, 1917*

deducta Herbulot, 1962

deliaria Guenée, [1858]*

delphiaria Guenée, ([1858])*

ssp. *auriculifera* Warren, 1897

argentisquama (Warren, 1899)*

diazoma Prout, 1938

digammata Kirby, 1896*

digammata Warren, 1897

[Junior primary homonym and a junior synonym of *P. digammata* Kirby, 1896. *P. digammata* Warren, 1897 was erroneously listed as a junior synonym of *P. aegretta aegretta* Felder & Rogenhofer, 1875 (Vári, Kroon & Krüger, 2002).]

digrammata Prout, 1933 [misspelling of *digammata*]

discophora Fixsen, 1887*

superans coreana Bryk, 1949

ssp. *kardakoffi* Prout, 1938*

erythra Wiltshire, 1982*

eucircota Prout, 1913*

evanida Prout, 1932

exanimata Prout, 1935

flavistigma Swinhoe, 1904*

ssp. *dilatistigma* Prout, 1917

herbuloti Viette, 1968

insignita Prout, 1938

korinchiana Rothschild, 1920*
latonaria Guenée, ([1858])*
longipannis Prout, 1917
lucifimbria (Warren, 1902)
magna Warren, 1906*
maxima Thierry-Mieg, 1905
meroearia Saalmüller, 1884*
mayottaria (Oberthür, 1923)
metallopictata (Pagenstecher, 1888)
venus Thierry-Mieg, 1905
minuta Inoue, 1958*
mitis Joannis, 1932
neumanni Prout, 1932
ocellata (Frivaldszky, 1845)*
ommatophoraria Guenée, ([1858])
ssp. *cinerea* (Butler, 1886)*
ochripicta Warren, 1901
paredra Prout, 1917*
phoebearia Erschov, 1870*
[Replacement name for *Argyris deliaria* Bremer, 1864.]
deliaria (Bremer, 1864)
[Junior primary homonym of *Argyris deliaria* Guenée, [1858].]
plagiata (Butler, 1881)*
riminota Prout, 1938
plenorbis Prout, 1917*
rorida Prout, 1932*
sancta Meyrick, 1888
shirozui Inoue, 1986*
similinotata Prout, 1917*
subreferta Prout, 1935
superans Butler, 1885*
ssp. *summa* Prout, 1935
transposita Warren, 1903
triocellata Bastelberger, 1908. **comb. rev.***
[*Problepsis triocellata* (Bastelberger, 1908) is transferred from *Somatina* to *Problepsis*.]
ssp. *scenica* (Prout, 1938)
vulgaris Butler, 1889*
attenuata Warren, 1909

Scopula

Scopula Schrank, 1802. Type species: *Phalaena paludata* Linnaeus, 1767, a junior synonym of *Phalaena ornata* Scopoli, 1763. [Portugal].
Acidalia Bruand, 1846. Type species: *Geometra strigaria* Hübner, [1799], a junior synonym of *Geometra virgulata* [Denis & Schiffermüller], 1775. [Austria]. [Junior homonym of *Acidalia* Hübner, [1819] 1816 (Lepidoptera: Nymphalidae).]
Acidalia Treitschke, 1825. Type species: *Geometra strigaria* Hübner, [1799], a junior synonym of *Geometra virgulata* [Denis & Schiffermüller], 1775. [Austria]. [Junior homonym of *Acidalia* Hübner, [1819] 1816 (Lepidoptera: Nymphalidae).]
Acidalina Staudinger, 1898. Type species: *Acidalina decolor*, Staudinger, 1898. Algeria.
Aletis Hübner, [1820]. Type species: *Papilio helcita* Linnaeus, 1763. Indiis [incorrect locality, probably tropical Africa]. **syn. nov.**
Anacosymbia Prout, 1913. Type species: *Anacosymbia perstrigulata* Prout, 1913. [South Africa] **syn. nov.**
Antanepsia Turner, 1908. Type species: *Autanepsia poliodesma* Turner, 1908. Australia [missspelling of *Autanepsia*]
Antilycauges Prout, 1913. Type species: *Emmiltis pinguis* Swinhoe, 1902. [Taiwan]. **syn. nov.**
Antitrygodes Warren, 1895. Type species: *Macaria divisaria* Walker, 1861. [India]. **syn. nov.**
Autanepsia Turner, 1908. Type species: *Autanepsia poliodesma* Turner, 1908. Australia. **syn. nov.**
Calothysanis Hübner, [1823] 1816. Type species: *Geometra imitaria* Hübner, [1799] 1796. Europe.
Cartaletis Warren, 1894. Type species: *Aletis libyssa* Hopffer, 1858. Mozambique. **syn. nov.**
Chlorocraspedia Warren, 1899. Type species: *Chlorocraspedia ansorgei* Warren, 1899. Uganda.
Cinglis Guenée, [1858]. Type species: *Fidonia humifusaria* Eversmann, 1837. [Russia]. **syn. nov.**
Craspedia Hübner, [1825] 1816: Type species: *Phalaena ornata* Scopoli, 1763. [Italy].
Csopula Fischer von Röslerstamm, 1842. [misspelling of *Scopula*].
Cymatida Sodoffsky, 1837. Type species: *Geometra strigaria* Hübner, [1799] 1796, a junior synonym of *Geometra virgulata* [Denis & Schiffermüller], 1775. [Austria]. [Unnecessary replacement name for *Acidalia* Treitschke, 1825].
Cymatoides Agassiz, 1847. [Emendation of *Cymatida* Sodoffsky, 1837].
Dasybela Turner, 1908. Type species: *Emmiltis achroa* Lower, 1902. Australia. **syn. nov.**
Dasybella Turner, 1908 [misspelling of *Dasybela*]
Dosithea Duponchel, 1829. Type species: *Phalaena ornata* Scopoli, 1763. [Portugal].
Dosithoea Rambur, 1833 [misspelling of *Dosithea*]
Epicosymbia Warren, 1897. Type species: *Epicosymbia perrufa* Warren, 1897, a junior synonym of *Acidalia? dentisignata* Walker, [1863]. [South Africa]. **syn. nov.**
Eucidalia Sterneck, 1941. Type species: *Phalaena immorata* Linnaeus, 1758. Europe.
Glossotrophia Prout, 1913. Type species: *Acidalia confinaria* Herrich-Schäffer, 1847. Hungary. **syn. nov.**
Holarctias Prout, 1913. Type species: *Haematopis sentinaria* Geyer, 1837. [Canada].
Ignobilia Prout, 1932. Type species: *Ephyra urnaria* Guenée, [1858]. Borneo. **syn. nov.**
Induna Warren, 1897. Type species: *Induna rufisalsa* Warren, 1897. [South Africa].
Isoplenia Warren, 1897. Type species: *Isoplenia trisinuata* Warren, 1897. [South Africa]. **syn. nov.**
Leucoxena Warren, 1900. Type species: *Leucoxena lactea* Warren, 1900. [Kenya]. **syn. nov.**
Leptaletis Warren, 1894. Type species: *Aletis variabilis* Butler, 1878. [Angola]. **syn. nov.**
Leptomeris Hübner, [1825] 1816. Type species: *Geometra umbelaria* Hübner, [1813] 1796. Europe.
Lipocentris Warren, 1905. Type species: *Lipocentris rubriceps* Warren, 1905. Angola.

Longula Staudinger, 1892. Type species: *Longula extraordinaria* Staudinger, 1892, a junior synonym of *Lycauges donovani* Distant, 1892. [Lebanon].
Lycauges Butler, 1879. Type species: *Lycauges lactea* Butler, 1879, a junior synonym of *Acidalia emissaria* Walker, 1861. Japan.
Oar Prout, 1913. Type species: *Phalaena pratana* Fabricius, 1794. [North Africa]. **syn. nov.**
Phyletis Guenée, [1858]. Type species: *Phyletis silonaria* Guenée, [1858]. [Ethiopia].
Pigia Guenée, [1858]. Type species: *Pigia infantularia* Guenée, [1858], a junior synonym of *Phalaena opicata* Fabricius, 1798. [Sri Lanka].
Pleionocentra Warren, 1898. Type species: *Scopula plionocentra* Prout, 1920. [*Geometra minorata sensu* Warren, nec Boisduval 1833]. Niger.
Prasonesis Meyrick, 1889. Type species: *Prasonesis microphylla* Meyrick, 1889. [Papua New Guinea]. **syn. nov.**
Pseudocinglis Hausmann, 1994. Type species: *Glossotrophia eurata* Prout, 1913. Turkmenistan. **syn. nov.**
Psilephyra Bastelberger, 1909. Type species: *Psilephyra bilineata* Bastelberger, 1909, a junior synonym of *Induna curvimargo* Warren, 1900. [Tanzania].
Pylarge Herrich-Schäffer, 1855. Type species: *Idaea commutata* Freyer, [1832] 1833, a junior synonym of *Scopula ternata*, Schrank, 1802. [Germany].
Runeca Moore, 1888. *Type species: Runeca ferrilineata* Moore, 1888. India.
Sarodria Sodoffsky, 1837. [Unnecessary replacement name for *Scopula* Schrank, 1802.]
Sarothria Agassiz, 1847. [Emendation of *Sarodria* Sodoffsky, 1937].
Scopuloides Hausmann, 1994. Type species: *Acidalia fucata* Püngeler, 1909. [Kyrgyzstan] **syn. nov.**
Sphecodes Hübner, 1822. Type species: *Geometra arcuaria* Hübner, [1799] 1796. [Junior homonym of *Sphecodes* Latreille, 1804 (Hymenoptera)]. [Germany].
Stigma Alphéraky, 1883. Type species: *Stigma kuldschaensis* Alphéraky, 1883. [China]. **syn. nov.**
Synelys Hulst, 1896. Type species: *Acidalia enucleata* Guenée, [1858], a junior synonym of *Phalaena limboundata* Haworth, 1809. [North America].
Trichoclada Meyrick, 1886. Type species: *Trichoclada epigypsa* Meyrick, 1886. [Fiji].
Triorisma Warren, 1897. Type species: *Triorisma violacea* Warren, 1897. [India].
Ustocidalia Sterneck, 1932. Type species: *Acidalia adelpharia* Püngeler, 1894. [Israel].
Zygophyxia Prout, 1916. Type species: *Zygophyxia tornisecta* Prout, 1916. Somalia. **syn. nov.**

ablativa (Dognin, 1911)
abolita Herbulot, [1956]
abornata (Guenée, [1858])
accentuata (Guenée, [1858])*
  accenturiata (Walker, 1861) [misspelling of *accentuata*]
  dentigerata Walker, ([1863])
  exgiuaria Prout, 1932 [misspelling of *exiguaria*]
  exiguaria (Walker, 1860)
  exiquaria Janse, 1917 [misspelling of *exiguaria*]
  rudisaria (Walker, 1861)*
accessaria (Herrich-Schäffer, 1852)
  recessaria (Guenée, [1858])*
[Unnecessary replacement name for *Acidalia accessaria* Herrich-Schäffer, 1852.]
acentra (Warren, 1897)*
acharis Prout, 1938
achroa (Lower, 1902) **comb. nov.***
[*Emmiltis achroa* Lower, 1902 is transferred from *Dasybela* to *Scopula*.]
achrosta Prout, 1935*
acidalia (Holland, 1894)
acinosa (Prout, 1932) **comb. nov.**
[*Antitrygodes acinosa* Prout, 1932 is transferred from *Antitrygodes* to *Scopula*.]
actuaria (Walker, 1861)*
  ssp. *nigranalis* (Warren, 1896)
  parumnotata (Warren, 1898)
  ssp. *sheljuzhkoi* Wiltshire, 1967
acutanellus Herbulot, 1992*
acyma Prout, 1932*
addictaria (Walker, 1861)*
adelpharia (Püngeler, 1894)*
  ssp. *pharaonis* Sterneck, 1933*
adenensis (Wiltshire, 1986) **comb. nov.***
[*Glossotrophia adenensis* Wiltshire, 1986 is transferred from *Glossotrophia* to *Scopula*.]
adeptaria (Walker, 1861)*
  eximia (Warren, 1898)
  tainanensis (Wileman & South, 1917)
  ssp. *tenuipes* (Turner, 1914)
aegrefasciata Sihvonen, 2001*
aemulata (Hulst, 1896)*
  tawneata (Cassino, 1931)
aequidistans (Warren, 1896)
aequifasciata (Christoph, 1881)
aequifasciaria (Hedemann, 1881)
[Unjustified emendation of *Acidalia aequifasciata* Christoph, 1881.]
aetheomorpha Prout, 1917
afghana (Ebert, 1965)*
africana Berio, 1937*
agglomerata Herbulot, 1992*
agnes (Butler, 1886)
agrapta (Warren, 1902)
agrata (Felder & Rogenhofer, 1875) **comb. nov.***
[*Trygodes agrata* Felder & Rogenhofer, 1875 is transferred from *Antitrygodes* to *Scopula*.]
agutsaensis Vasilenko, 1997
alargata (Dognin, 1901)
alba (Hausmann, 1993) **comb. nov.***
[*Glossotrophia alba* Hausmann, 1993 is transferred from *Glossotrophia* to *Scopula*. Junior secondary homonym of *Aletis alba* Druce, 1896, requiring a replacement name.]
  ssp. *africana* (Hausmann, 1993)*
  [Junior secondary homonym of *Scopula africana* Berio, 1937, requiring a replacement name.]
  ssp. *brunellii* (Hausmann, 1993)*

ssp. *capriata* (Hausmann, 1993)*
ssp. *zahmi* (Hausmann, 1993)*
albiceraria (Herrich-Schäffer, 1847)*
sulphuraria (Freyer, 1847)
ssp. *vitellinaria* (Eversmann, 1851)*
mannerheimatia (Erschov, 1871)
albida (Warren, 1899)*
pura (Swinhoe, 1909)
albidaria (Staudinger, 1901)
ssp. *sankana* Prout, 1938
albidulata (Warren, 1897)
albiflava (Warren, 1896)*
albilarvata (Warren, 1899)
albivertex (Swinhoe, 1892) **comb. nov.***
[*Idaea albivertex* Swinhoe, 1892 is transferred from *Epicosymbia* to *Scopula*.]
ssp. *ancillaria* (Warren, 1895)
albomaculata (Moore, 1888)
alboverticata (Warren, 1895)
aleuritis (Turner, 1908)
alfierii (Wiltshire, 1949) **comb. nov.**
[*Glossotrophia alfierii* Wiltshire, 1949 is transferred from *Glossotrophia* to *Scopula*.]
alma Prout, 1920*
alstoni Prout, 1919*
amala (Meyrick, 1886)
lacteisabulosa (Rothschild, 1915)
parasira (Meyrick, 1889)
[*Scopula (Acidalia) parasira* Meyrick, 1889 was listed as a valid species in Scoble (1999) by mistake (Linda Pitkin, pers. comm.).]
amazonata (Guenée, [1858])
ambigua Prout, 1935*
amphiphracta Prout, 1938
amseli Wiltshire, 1967*
anaitisaria (Walker, 1861)
anatreces Prout, 1920
ancellata (Hulst, 1887)*
ssp. *catenes* (Druce, 1892)
andalusiaria (Wagner, 1935) **comb. nov.***
[*Cinglis andalusiaria* Wagner, 1935 is transferred from *Cinglis* to *Scopula*. This species' status needs to be revised. It is considered to be a valid species by Redondo & Gáston (1999) and Scoble (1999), whereas Müller (1996) treats it as a subspecies of *Scopula [Cinglis] humifusaria* (Eversmann, 1837).]
andresi (Draudt, 1912)
angusticallis Prout, 1935
aniara Prout, 1934
anisopleura Inoue, 1982*
annae (Mentzer, 1990) **comb. nov.***
[*Glossotrophia annae* Mentzer, 1990 is transferred from *Glossotrophia* to *Scopula*.]
annexata Prout, 1938*
annubiata (Staudinger, 1892)*
annularia (Swinhoe, 1890)*
nigropunctata (Guenée, [1858])
[Junior secondary homonym of *Phalaena nigropunctata* Hufnagel, 1767, requiring a replacement name.]
ssp. *reducta* Rothschild, 1920*
anoista (Prout, 1915)
ansorgei (Warren, 1899)*
ansulata (Lederer, 1871)*
ssp. *adulteraria* (Erschov, 1874)
ssp. *characteristica* (Alphéraky, 1883)
ssp. *eberti* Wiltshire, 1967
[*Scopula eberti* Wiltshire, 1967 was downgraded to a subspecies of *Scopula ansulata* (Lederer, 1871) by Hausmann & László (1999).]
antankarana Herbulot, [1956]
antiloparia (Wallengren, 1863)*
[*Acidalia (Scopula) antiloparia* Wallengren, 1863 is possibly a junior synonym of *Geometra (Scopula) minorata* Boisduval, 1833, based on genital examination of type material at The Natural History Museum, London, and Universitets Zoologiska Institut, Uppsala, Sweden. Prout (1929–35) suggested that *A. antiloparia* (Wallengren) could be conspecific with *Scopula sincera* (Warren, 1901). The opinion was based on a description of *A. antiloparia*, not on examination of the types.]
anysima Prout, 1938
aphercta Prout, 1932
apicipunctata (Christoph, 1881)*
arenaria (Leech, 1897)*
apparitaria (Walker, 1861)*
approbata (Warren, 1900)*
atomaria (Warren, 1897)*
responsaria (Walker, 1861)
trias (Warren, 1904)*
floccularia (Herrich-Schäffer, 1870)
[*Acidalia floccularia* Herrich-Schäffer, 1870 is considered to be a junior synonym of *Scopula apparitaria* (Walker, 1861) (Becker, 2002).]
arcuaria (Hübner, [1799])
arenosaria (Staudinger, 1879)
argentidisca (Warren, 1902)*
naias (Warren, 1903)
argillina (Lower, 1915) **comb. nov.**
[*Emmiltis argillina* Lower, 1915 is transferred from *Dasybela* to *Scopula*.]
argyroleuca (Hampson, 1910)*
asellaria (Herrich-Schäffer, 1847) **comb. nov.***
[*Acidalia asellaria* Herrich-Schäffer, 1847 is transferred from *Glossotrophia* to *Scopula*.]
dentatolineata insularis (Wehrli, 1926)
ssp. *dentatolineata* (Wehrli, 1926)*
ssp. *gerstbergeri* (Hausmann, 1993)*
ssp. *isabellaria* (Milliére, 1868)*
ssp. *lenzi* (Hausmann, 1993)*
ssp. *philipparia* (Prout, 1913)*
ssp. *romanaria* (Milliére, 1869)*
ssp. *tripolitana* (Turati, 1930)*
asiatica (Brandt, 1938) **comb. nov.***
[*Glossotrophia asiatica* Brandt, 1938 is transferred from *Glossotrophia* to *Scopula*.]
asopiata (Guenée, [1858])*
discrimaria (Walker, 1861)
asparta Prout, 1938*
aspiciens Prout, 1926
aspilataria (Walker, 1861)
asthena Inoue, 1943*

astrabes Prout, 1932
asymmetrica Holloway, 1997*
atramentaria (Bastelberger, 1909)
atricapilla Prout, 1934*
ssp. *harithensis* Wiltshire, 1990
atriceps (Hampson, 1895)*
atridiscata (Warren, 1897)*
attentata (Walker, 1861)*
nicobarica Prout, 1938*
axiata (Püngeler, 1909)
axiotis (Meyrick, 1888)
batesi Prout, 1932
beccarii (Prout, 1915)
beckeraria (Lederer, 1853)*
ssp. *amataria* (Wehrli, 1927)
ssp. *assimilaria* Prout, 1913
ssp. *hermonicola* Hausmann, 1997*
ssp. *rebeli* (Prout, 1913)*
[Replacement name for *Scopula agraria* Rebel, 1908.]
agraria Rebel, 1908
[Junior secondary homonym of *Acidalia agraria* Joannis, 1891.]
benenotata Prout, 1932
benguetensis Prout, 1931
benigna (Brandt, 1941) **comb. nov.***
[*Glossotrophia benigna* Brandt, 1941 is transferred from *Pseudocinglis* to *Scopula*.]
ssp. *nigromaculata* (Hausmann, 1994)*
benitaria (Barnes & McDunnough, 1913)*
bifalsaria (Prout, 1913)*
[Replacement name for *Acidalia falsaria* Leech, 1897.]
falsaria (Leech, 1897)
[Junior primary homonym of *Acidalia falsaria* Herrich-Schäffer, 1852.]
ssp. *falsificata* Prout, 1934
[Replacement name for *Acidalia grisescens* Prout, 1916.]
bifalsaria grisescens Prout, 1916
[Junior secondary homonym of *Acidalia grisescens* Staudinger, 1852.]
bigeminata (Warren, 1897)*
fumosaria (Swinhoe, 1904)
bimacularia (Leech, 1897)*
bispurcata (Warren, 1898)*
bistrigata (Pagenstecher, 1907)
brachypus Prout, 1926*
brookesae Holloway, 1976*
bullata (Vojnits, 1986) **comb. nov.***
[*Glossotrophia bullata* Vojnits, 1986 is transferred from *Glossotrophia* to *Scopula*.]
buraimana (Wiltshire, 1949) **comb. nov.***
[*Glossotrophia buraimana* Wiltshire, 1949 is transferred from *Glossotrophia* to *Scopula*.]
alfierii montana (Wiltshire, 1980)
butleri (Prout, 1913)*
[Replacement name for *Craspedia insolata* Butler, 1889.]
insolata (Butler, 1889)*
[Junior secondary homonym of *Acidalia insolata* Felder & Rogenhofer, 1875.]
ssp. *aequibrachiata* Holloway, 1997*
satsumaria (Leech, 1897)*
butyrosa (Warren, 1893)*
caberaria Herbulot, 1992*
cacuminaria (Morrison, 1874)*
cacuminata (Packard, 1876)
[Unjustified emendation of *Acidalia cacuminaria* Morrison, 1874.]
caducaria (Swinhoe, 1904)*
caeria Prout, 1938
caesaria (Walker, 1861)*
caesarea (Fuchs, 1902) [misspelling of *caesaria*]
faeculentaria (Mabille, 1880)
obturbata (Walker, 1861)
perfectaria (Walker, 1861)*
rufimixtaria (Warren, 1900)
ssp. *walkeros* Wiltshire, [1981]
cajanderi (Herz, 1903)*
anaitaria (Herz, 1903)*
elwesi achlyoides Prout, 1935*
elwesi sajanensis Prout, 1935*
septentrionicola McDunnough, 1939*
calcarata Fletcher, 1958*
caledonica Holloway, 1979
callibotrys (Prout, 1918) **comb. nov.***
[*Antitrygodes callibotrys* Prout, 1918 is transferred from *Antitrygodes* to *Scopula*.]
calothysanis Herbulot, 1965
calotis (Dyar, 1912)
campbelli Prout, 1920*
candida Prout, 1934
candidaria (Warren, 1902)*
[Junior secondary homonym of *Acidalia candidaria* Packard, 1873, requiring a replacement name.]
canularia (Herrich-Schäffer, 1870)
capnosterna Prout, 1938
carnosa Prout, 1925*
cassiaria (Swinhoe, 1904)
cassioides Prout, 1932
castissima (Warren, 1897)
exangulata (Warren, 1899)
cavana (Druce, 1892)
celebraria (Walker, 1861)
cervinata (Warren, 1905)
chalcographata (Brandt, 1938) **comb. nov.***
[*Glossotrophia chalcographata* Brandt, 1938 is transferred from *Glossotrophia* to *Scopula*.]
ssp. *sinaica* (Rebel, 1948)
chionaeata (Herrich-Schäffer, 1870)
[*Acidalia chionaeata* Herrich-Schäffer, 1870 is removed from synonymy with *Scopula eburneata* (Guenée), and considered to be a valid species (Becker, 2002).]
chrysoparalias (Prout, 1917) **comb. nov.**
[*Anacosymbia chrysoparalias* Prout, 1917 is transferred from *Epicosymbia* to *Scopula*.]
chydaea Prout, 1938
cineraria (Leech, 1897)*
cinnamomata Fletcher, 1955*
circumpunctata (Warren, 1898)
clandestina Herbulot, [1956]
clarivialis Prout, 1931*

cleoraria (Walker, 1861)*
ssp. *effrenata* (Walker, [1863])
coangulata Prout, 1920*
coenona (Turner, 1908)
colonaria (Herrich-Schäffer, 1852)
colymbas Herbulot, 1994*
comes Prout, 1927
commaria (Swinhoe, 1904)
compensata (Walker, 1861)*
obluridata (Hulst, 1887)
complanata (Warren, 1896)*
concinnaria (Duponchel, 1842)*
hesperidata (Staudinger, 1871)
concinnata (Guenée, [1858])
[Unnecessary replacement name for *Dosithea concinnaria* Duponchel, 1842.]
ssp. *universaria* (Zerny, 1927)
concolor (Warren, 1905) **comb. nov.**
[*Cartaletis concolor* Warren, 1905 is transferred from *Cartaletis* to *Scopula*.]
concurrens (Warren, 1897)
conduplicata (Warren, 1904)
confertaria (Walker, 1861)*
internexata (Warren, 1904)*
confinaria (Herrich-Schäffer, 1847) **comb. nov.***
[*Acidalia confinaria* Herrich-Schäffer, 1847 is transferred from *Glossotrophia* to *Scopula*.]
corrivularia (Milliére, 1869)
ssp. *aetnaea* (Prout, 1935)*
ssp. *prouti* (Hausmann, 1993)*
[Junior secondary homonym of *Scopula prouti* Djakonov, 1935, requiring a replacement name.]
ssp. *sacraria* (Bang-Haas, 1910)
ssp. *scoblei* (Hausmann, 1993)*
ssp. *uberaria* (Zerny, 1933)
confusa (Butler, 1878)*
congruata (Zeller, 1847)*
decorata leukiberica (Wehrli, 1927)
violata ablutata (Dannehl, 1927)
coniargyris Prout, 1932
coniaria (Prout, 1913)*
[Replacement name for *Acidalia pulveraria* Leech, 1897.]
pulveraria (Leech, 1897)
[Junior primary homonym of *Acidalia pulveraria* Snellen, 1872.]
ssp. *okinawensis* Prout, 1920
conotaria (Schaus, 1901)
conscensa (Swinhoe, 1886) **comb. nov.***
[*Eupithecia conscensa* Swinhoe, 1886 is transferred from *Zygophyxia* to *Scopula*.]
consimilata (Warren, 1896)*
aggravata (Warren, 1897)
perfilata Prout, 1920*
seductilis Prout, 1931*
conspersa (Warren, 1900) **comb. nov.**
[*Epicosymbia conspersa* Warren, 1900 is transferred from *Epicosymbia* to *Scopula*.]
conspicillaria Karisch, 2001*
contramutata Prout, 1920
convergens (Warren, 1904)*
convergens Bryk, 1949
[Junior secondary homonym of *Emmiltis convergens* Warren, 1904, requiring a replacement name.]
convictorata (Snellen, 1874)
cornishi Prout, 1932
corrivalaria (Kretschmar, 1862)*
ssp. *eccletica* Prout, 1935*
corrupta Prout, 1931*
costata (Moore, [1887])
coundularia (Warren, 1898)
crassipuncta (Warren, 1901)
crawshayi Prout, 1932*
cumulata (Alphéraky, 1883)*
beckeraria cretaria (Staudinger, 1892)
ssp. *alaiana* Viidalepp, 1988
cuneilinea (Walker, [1863]) **comb. nov.***
[*Geometra cuneilinea* Walker, [1863] is transferred from *Antitrygodes* to *Scopula*.]
curvimargo (Warren, 1900)*
bilineata (Bastelberger, 1909)*
nubicincta (Hampson, 1910)*
dapharia (Swinhoe, 1904)*
dargei Herbulot, 1992*
declinata Herbulot, 1972
decolor (Staudinger, 1898)*
decorata ([Denis & Schiffermüller], 1775)*
caerulata (Gmelin, 1790)
cinerata (Fabricius, 1781)
decoraria (Hübner, [1799])
ornataria (Esper, [1806])
violata (Thunberg, 1784)
ssp. *armeniaca* (Thierry-Mieg, 1916)
ssp. *drenowskii* Sterneck, 1941*
ssp. *eurhythma* Prout, 1935
ssp. *przewalskii* Viidaleppp, 1975
defectiscripta (Prout, 1914)*
defixaria (Walker, 1861)*
martharia (Walker, 1866)
deflavaria (Warren, 1896)*
ssp. *calorifica* (Warren, 1898)
ssp. *relevata* Prout, 1938
deflavarioides Holloway, 1997*
dehortata (Dognin, 1901)
deiliniata (Warren, 1897)
deliciosaria (Walker, 1861)*
delitata (Prout, 1913)*
delospila (Warren, 1907)
demissaria (Walker, [1863])
densicornis (Warren, 1897)
fumigrisea (Warren, 1898)
dentilinea (Warren, 1897) **comb. nov.***
[*Antitrygodes dentilinea* Warren, 1897 is transferred from *Antitrygodes* to *Scopula*.]
dentisignata (Walker, [1863]) **comb. nov.***
[*Acidalia? dentisignata* Walker, [1863] is transferred from *Epicosymbia* to *Scopula*.]
denticulata Prout, 1933

[*Epicosymbia denticulata* Prout, 1933 (in Prout, 1929–35) is a typographical error for *Acidalia*? *dentisignata* Walker, [1863].]
perrufa (Warren, 1897)
derasata (Walker, [1863])*
[According to Janse (1933–35), *Scopula (Acidalia) derasata* Walker, [1863] is probably an aberration of *Scopula (Geometra) minorata* Boisduval, 1833. The male genitalia are shown on plate IX, fig. 3 in that publication.]
deserta (Warren, 1897)*
desita (Walker, 1861)*
vibrata (Lucas, 1900)
ssp. *luzonica* Prout, 1931
despoliata (Walker, 1861)
crurata (Warren, 1901)
destituta (Walker, 1866)*
cretata (Warren, 1900)
detentata Prout, 1926*
dhofarata Wiltshire, 1986*
didymosema (Lower, 1893)
diffinaria (Prout, 1913) **comb. nov.***
[*Glossotrophia diffinaria* Prout, 1913 is transferred from *Glossotrophia* to *Scopula*.]
dignata (Guenée, [1858])*
dimoera Prout, 1922
dimoeroides Herbulot, [1956]
dimorphata (Snellen, 1881)*
ssp. *hainanica* Prout, 1938*
ssp. *suffidaria* (Swinhoe, 1902)
disclusaria (Christoph, 1881)
discrepans Prout, 1916*
ssp *infirmata* Prout, 1938
dismutata (Guenée, [1858])
catenularia (Walker, 1861)
disparata (Hampson, 1903) **comb. nov.***
[*Craspedia disparata* Hampson, 1903 is transferred from *Glossotrophia* to *Scopula*.]
ssp. *somaliata* (Prout, 1916)*
dissonans (Warren, 1897)*
divisaria (Walker, 1861) **comb. nov.***
[*Macaria divisaria* Walker, 1861 is transferred from *Antitrygodes* to *Scopula*.]
ssp. *perturbata* (Prout, 1914)*
dohertyi (Warren, 1897)
donaria (Schaus, 1901)
donovani (Distant, 1892)*
extraordinaria (Staudinger, 1892)
extremata (Warren, 1897)
dorsinigrata (Warren, 1904)
dotina Prout, 1938
dubernardi (Oberthür 1923)*
duplicipuncta (Prout, 1913)
duplinupta Inoue, 1982*
dux Prout, 1927*
dysmorpha (Prout, 1915) **comb. nov.**
[*Antitrygodes dysmorpha* Prout, 1915 is transferred from *Antitrygodes* to *Scopula*.]
eburneata (Guenée, [1858])*
blandula (Warren, 1906)
subsignaria (Walker, 1861)
eclipes (Prout, 1910)*
ectopostigma Prout, 1932
elegans (Prout, 1915)
elegantula Herbulot, 1978
eleina Prout, 1938
elisabethae Prout, 1934*
elwesi Prout, 1922
[The inclusion of this species within *Scopula* remains tentative (Sihvonen, 2001).]
emissaria (Walker, 1861)*
defamataria (Walker, 1861)
mollis (Warren, 1896)
ssp. *lactea* (Butler, 1879)*
ssp. *proxima* (Butler, 1886)
memma (Prout, 1913)*
ssp. *jordani* (West, 1930)*
emutaria (Hübner, [1809])*
ssp. *subroseata* (Haworth, 1809)
enucloides (Schaus, 1901)
epigypsa (Meyrick, 1886)*
cernea (Druce, 1888)
nivipennis (Butler, 1886)
epiorrhoe Prout, 1935*
episcia (Meyrick, 1888)
episticta Turner, 1942
erebospila (Lower, 1902)
erici (Kirby, 1896) **comb. nov.***
[*Aletis erici* Kirby, 1896 is transferred from *Aletis* to *Scopula*.]
ssp. *euparypha* (Prout, 1913)
erinaria (Swinhoe, 1904)*
ssp. *isolata* Prout, 1920
isolatata Vári & Kroon, 1986 [misspelling of *isolata*]
erlangeri (Prout, 1932) **comb. nov.**
[*Zygophyxia erlangeri* Prout, 1932 is transferred from *Zygophyxia* to *Scopula*.]
erubescens (Warren, 1895)*
erymna Prout, 1928
euchroa Prout, 1925*
eulomata (Snellen, 1877)*
compressaria (Warren, 1900)
eunupta Vasilenko, 1998*
euphemia Prout, 1920
eurata (Prout, 1913) **comb. nov.***
[*Glossotrophia eurata* Prout, 1913 is transferred from *Pseudocinglis* to *Scopula*.]
extimaria (Walker, 1861)*
falcataria (Warren, 1901)
falcovitshi Viidalepp, 1992 **comb. nov.**
[*Scopula falcovitshi* Viidalepp, 1992 is transferred from *Pseudocinglis* to *Scopula*. Hausmann & László (1999) transferred *Scopula falcovitshi* to *Pseudocinglis*.]
falsaria (Herrich-Schäffer, 1852) **comb. nov.**
[*Acidalia falsaria* Herrich-Schäffer, 1852 is transferred from *Glossotrophia* to *Scopula*.]
farinaria (Leech, 1897)
fernaria Schaus, 1940
ferrilineata (Moore, 1888)*

ferruginea (Hampson, 1893)*
fibulata (Guenée, [1858])*
fimbrilineata (Warren, 1902)*
niobe (Fawcett, 1916)
protuberans (Warren, 1909)
ssp. *immaculata* (Warren, 1905)*
flaccata (Staudinger, 1898)*
ssp. *languidata* (Prout, 1913)*
flaccidaria (Zeller, 1852)*
flavifurfurata Prout, 1920
flavinsolata Holloway, 1997*
flavissima (Warren, 1898)
flavorosearia (Shchetkin, 1956)
flexio Prout, 1917
floslactata (Haworth, 1809)*
brunneata (Goeze, 1781)
cariata (Schrank, 1802)
concatenata (Hufnagel, 1767)
dentilinearia (Borkhausen, 1794)
fulvicans (Fourcroy, 1785)
fulvostriata (Goeze, 1781)
lactata (Haworth, 1809)*
lactata scotica Cockayne, 1951*
remutaria (Hübner, [1799])
spataceata (Scopoli, 1763)
strigata (Fourcroy, 1785)
sublactata (Haworth, 1809)
ssp. *claudata* Prout, 1913*
[Viidalepp (1996) treated this taxon as a valid species.]
fluidaria (Swinhoe, 1886)
forbesi (Druce, 1884) **comb. nov.**
[*Aletis forbesi* Druce, 1884 is transferred from *Cartaletis* to *Scopula*.]
flexilimes (Warren, 1897)
formosana Prout, 1934*
[Replacement name for *Scopula orientalis* Prout, 1914.]
moorei orientalis Prout, 1914
[Junior secondary homonym of *Acidalia orientalis* Alphéraky, 1875.]
fragilis (Warren, 1903)
francki Prout, 1935*
frigidaria (Möschler, 1860)*
arcticaria (Walker, [1863])
defixaria (Walker, 1861: 796)
[Junior primary homonym of *Acidalia defixaria* Walker, 1861: 731, requiring a replacement name.]
impauperata (Walker, 1861)*
okakaria (Packard, 1867)
ssp. *schoyeni* (Sparre-Schneider, 1883)
froitzheimi Wiltshire, 1967
fucata (Püngeler, 1909) **comb. nov.***
[*Acidalia fucata* Püngeler, 1909 is transferred from *Scopuloides* to *Scopula*.]
kirghisica (Viidalepp, 1988)*
fulminataria (Turati, 1927)
fulvicolor Hampson, 1899
fumosaria (Prout, 1913)
[Junior secondary homonym of *Emmiltis fumosaria* Swinhoe, 1904, requiring a replacement name.]
furfurata (Warren, 1897)*
fuscata (Hulst, 1887)*
[Junior secondary homonym of *Phalaena fuscata* Fabricius, 1794, requiring a replacement name.]
fuscescens Prout, 1934
fuscobrunnea (Warren, 1901)
fuscifusa (Prout, 1911)
galactina Fletcher, 1978*
gastonaria (Oberthür, 1876)*
gastonaria candicans (Prout, 1913)*
gastonaria obscuraria (Bang-Haas, 1910)
ssp. *luteofasciata* (Rothschild, 1913)
gazellaria (Wallengren, 1863)*
gazella (Distant, 1892)
griselineata Janse, 1917 [misspelling of *griseolineata*]
griseolineata (Warren, 1900)
gibbivalvata Herbulot, 1972
gilva Sato, 1993*
glaucescens Herbulot, 1978
gnou Herbulot, 1985*
gracilis (Möschler, 1887) **comb. nov.***
[*Amnemopsyche gracilis* Möschler, 1887 is transferred from *Cartaletis* to *Scopula*.]
alba (Druce, 1896)
pallida (Warren, 1894)
[Junior secondary homonym of *Idaea pallida* Warren, 1888, requiring a replacement name.]
ssp. *landbecki* (Prout, 1919)
ssp. *variegata* (Prout, 1916)
[Junior secondary homonym of *Phalaena variegata* Scopoli, 1763, requiring a replacement name.]
gracilis (Brandt, 1941) **comb. nov.***
[*Glossotrophia gracilis* Brandt, 1941 is transferred from *Glossotrophia* to *Scopula*. Junior secondary homonym of *Amnemopsyche gracilis* Möschler, 1887, requiring a replacement name.]
graphidata Prout, 1920
grasuta (Schaus, 1901)
griseolineata (Rothschild, 1915)*
[Junior secondary homonym of *Sterrha griseolineata* Warren, 1900, requiring a replacement name.]
grisescens (Staudinger, 1892)
guancharia (Alphéraky, 1889)*
ssp. *illustris* Pinker, 1968 [1969]
ssp. *mus* Pinker, 1968 [1969]
ssp. *uniformis* Pinker, 1968 [1969]
gyalararia (Franzenau, 1856)
habilis (Warren, 1899)*
hackeri Hausmann, 1999*
haemaleata (Warren, 1898) *incerta sedis**
[*Craspedia haemaleata* (Warren, 1898) is retained in *Scopula* until a comprehensive revision on the genus *Scopula* is done. My results show that it shares two unique synapomorphies with *Somatina irregularis* Warren, 1898. It is unknown whether this clade represents a larger species group. The synapomorphies may prove to be homoplastic if more taxa were included in a cladistic study.]
haematophaga Bänziger & Fletcher, 1985*
haeretica Herbulot, [1956]
halimodendrata (Erschov, 1874)
hanna (Butler, 1878)*

heba Prout, 1920*
hectata (Guenée, [1858])*
heidra Debauche, 1938*
helcita (Linnaeus, 1763) **comb. nov.***
[*Papilio (Danaus) helcita* Linnaeus, 1763 is transferred from *Aletis* to *Scopula*.]
druryi (Butler, 1878)
fascelis (Linnaeus, 1764)
fuscofasciatus (Goeze, 1779)
helcitaria (Turton, 1802)
[Unjustified emendation of *Papilio (Danaus) helcita* Linnaeus, 1763.]
macularia (Fabricius, 1781)
rubricaput (Swinhoe, 1904)
ssp. *contractimargo* (Prout, 1916)
ssp. *dissoluta* (Gaede, 1917)
herbuloti Karisch, 2001*
[Junior secondary homonym of *Antitrygodes herbuloti* Viette, 1977, requiring a replacement name.]
herbuloti (Viette, 1977) **comb. nov.***
[*Antitrygodes herbuloti* Viette, 1977 is transferred from *Antitrygodes* to *Scopula*.]
hesycha Prout, 1919*
hoerhammeri Brandt, 1941
homaema Prout, 1920
homodoxa (Meyrick, 1886)*
honestata (Mabille, 1869)
horichroea (Prout, 1916)
humifusaria (Eversmann, 1837) **comb. nov.***
[*Fidonia humifusaria* Eversmann, 1837 is transferred from *Cinglis* to *Scopula*. See *Scopula andalusiaria* (Wagner, 1935).]
humilis (Prout, 1913)*
hyphenophora (Warren, 1896)*
ssp. *ambiguiceps* Prout, 1938
hypocallista (Lower, 1900)
hypochra (Meyrick, 1888)*
ichinosawana (Matsumura, 1925)*
ssp. *honshuensis* Inoue, 1982
idearia (Swinhoe, 1886)*
idnothogramma Prout, 1938
ignobilis (Warren, 1901)*
imitaria (Hübner, [1799])*
ssp. *syriacaria* (Culot, 1918)
immistaria (Herrich-Schäffer, 1852)*
ssp. *beshkovi* Gelbrecht & Hausmann, 1997*
immorata (Linnaeus, 1758)*
contaminata (Scopoli, 1763)
festucaria (Brahm, 1791)
fuscata (Fabricius, 1794)
graminata (Hufnagel, 1767)
immoraria (Hübner, [1799])
myrtillata (Dadd, 1911)
ssp. *duercki* Sheljuzhko, 1955
immutata (Linnaeus, 1758)*
pallidata (Borkhausen, 1794)
impersonata (Walker, 1861)*
ssp. *accurataria* (Christoph, 1881)*
muscularia (Staudinger, 1897)
ssp. *macescens* (Butler, 1879)*
impicta Prout, 1922
[Janse (1933–35) considered *Scopula impicta* Prout, 1922 an aberrative form of *Scopula picta* (Warren, 1897) as a result of careful comparison of genitalia.]
improba (Warren, 1899)
impropriaria (Walker, 1861)
tricincta (Warren, 1906)
inactuosa Prout, 1920*
inangulata (Warren, 1896)*
incalcarata Fletcher, 1958*
incanata (Linnaeus, 1758)*
adjunctaria (Boisduval, 1840)
demutaria (Bruand, 1846)
mediata (Fabricius, [1776])
mutata (Treitschke, 1828)
mutataria (Duponchel, 1830)
variegata (Scopoli, 1763)
ssp. *ibericata* (Reisser, 1935)
ssp. *rubeni* Viidalepp, 1979
indicataria (Walker, 1861) **comb. nov.***
[*Argyris indicataria* Walker, 1861 is transferred from *Somatina* to *Scopula*. The affinity of *Argyris indicataria* with *Scopula* was suggested by Inoue (1992).]
ssp. *morata* (Prout, 1938)
ssp. *sufflava* (Prout, 1938)
inductata (Guenée, [1858])*
anticaria (Walker, 1860)
consecutaria (Walker, 1866)*
delicata (Cassino, 1931)
oliveata (Cassino, 1931)
sobria (Walker, 1866)*
suppressaria (Walker, [1863])
infantilis Herbulot, 1970
inficita (Walker, 1866)
ssp. *philippina* Prout, 1931*
inflexibilis Prout, 1931*
infota (Warren, 1897)
ssp. *perfumosa* (Warren, 1904)
innocens (Butler, 1886)*
innominata Schaus, 1940
inscriptata (Walker, [1863])*
acentra (Warren, 1911)
[Junior secondary homonym of *Craspedia acentra* Warren, 1897, requiring a replacement name.]
insincera Prout, 1920
instructata (Walker, 1863)
[Janse (1933–35) considered *Scopula instructata* (Walker, 1863) a possible junior synonym of *Scopula minorata* (Boisduval, 1833).]
intensata (Moore, 1887)
ssp. *ochriata* Prout, 1938
internata (Guenée, [1858])*
illiturata (Walker, [1863])
pudens (Warren, 1905)
pulverosaria (Walker, [1863])*
strigulifera (Walker, 1861)*
ssp. *praeruptorum* Prout, 1920*
internataria (Walker, 1861)*
tremula (Bastelberger, 1909)

ssp. *punctistriata* (Mabille, 1880)
cuspidata (Mabille, 1900)
internataria eucentra Prout, 1928
inustaria (Herrich-Schäffer, 1847)
iranaria Bytinski-Salz & Brandt, 1937
irrorata (Bethune-Baker, 1891)*
irrubescens Prout, 1934
[Replacement name for *Synelys irrufata* Warren, 1906.]
irrufata (Warren, 1906)
[Junior secondary homonym of *Sterrha irrufata* Warren, 1906.]
irrufata (Warren, 1905)*
isodesma (Lower, 1903)
isomala Prout, 1932*
isomerica Prout, 1922
iterata Herbulot, 1978
jacta (Swinhoe, 1885) **comb. nov.***
[*Idaea jacta* Swinhoe, 1885 is transferred from *Glossotrophia* to *Scopula*.]
jejuna Prout, 1932
johnsoni Fletcher, 1958*
julietae Robinson, 1975*
junctaria (Walker, 1861)*
ssp. *johnstonaria* McDunnough, 1941
ssp. *quinquelinearia* (Packard, 1871)*
impunctata (Warren, 1904)*
vestalialis (Barnes & McDunnough, 1913)
juruana (Butler, 1881)
inquinatula (Warren, 1905)
virginea (Warren, 1897)
kagiata (Bastelberger, 1909)*
karischi Herbulot, 1999*
kashmirensis (Moore, 1888)*
ssp. *gooraisensis* Prout, 1935
ssp. *quettensis* Prout, 1935*
kawabei Inoue, 1982*
klaphecki Prout, 1922
immutata chinensis (Sterneck, 1927)
kohor Herbulot & Viette, 1952
kounden Herbulot, 1992*
kuldschaensis (Alphéraky, 1883) **comb. nov.***
[*Stigma kuldschaensis* Alphéraky, 1883 is transferred from *Stigma* to *Scopula*.]
ssp. *negrita* (Thierry-Mieg, 1905)
atraria (Bang-Haas, 1906)
lacriphaga Bänziger & Fletcher, 1985*
lactaria (Walker, 1861)*
intervulsata (Walker, 1861)
tectaria (Walker, 1866)
ssp. *gaboosi* Hausmann, 1998*
lactarioides Brandt, 1941
lactea (Warren, 1900) **comb. nov.***
[*Leucoxena lactea* Warren, 1900 is transferred from *Leucoxena* to *Scopula*. Junior secondary homonym of *Lycauges lactea* Butler, 1879, requiring a replacement name.]
laevipennis (Warren, 1897)*
uninotata (Warren, 1897)
laresaria Schaus, 1940
larseni (Wiltshire, 1982) **comb. nov.***
[*Zygophyxia larseni* Wiltshire, 1982 is transferred from *Zygophyxia* to *Scopula*.]
latelineata (Graeser, 1892)*
lathraea Prout, 1922
latifera (Walker, 1869)
latimediata Fletcher, 1958*
latitans Prout, 1920*
[Replacement name for *Acidalia reconditaria* Snellen, 1872.]
reconditaria (Snellen, 1872)
[Junior primary homonym of *Acidalia reconditaria* Walker, 1861.]
lautaria (Hübner, [1831])*
minutularia (Hulst, 1880)
myrmidonata (Guenée, [1858])
lechrioloma (Turner, 1908)
legrandi Herbulot, [1963]
lehmanni Hausmann, 1991*
[Described as *Scopula immistaria* ssp. *lehmanni* Hausmann, 1991, but raised to species rank by Gelbrecht & Hausmann (1997).]
leucoloma Prout, 1932
ssp. *altimontana* Herbulot, 1972
ssp. *permutans* Herbulot, 1972
leucopis Prout, 1926*
leuculata (Snellen, 1874)
nigricosta (Dognin, 1911)
leuraria (Prout, 1913)*
libyssa (Hopffer, 1858) **comb. nov.***
[*Aletis libyssa* Hopffer, 1858 is transferred from *Cartaletis* to *Scopula*.]
ssp. *ethelinda* (Kirby, 1896)
helcita latifasciata (Gaede, 1917)
monteironis nigriventris (Gaede, 1917)
ssp. *monteironis* (Druce, 1883)
monteironis entebbena (Strand, 1921)
ssp. *natalensis* (Prout, 1917)
[Junior secondary homonym of *Glossotrophia natalensis* Prout, 1915, requiring a replacement name.]
libyssa fusciventris (Gaede, 1917)
limbata (Wileman, 1915)*
limboundata (Haworth, 1809)*
continuaria (Walker, 1866)*
enucleata (Guenée, [1858])*
mensurata (Walker, 1866)*
nigrodiscalis (Hulst, 1898)
reconditaria (Walker, 1861)
restrictata (Walker, 1861)*
limosata Fletcher, 1963*
linearia (Hampson, 1891)*
liotis (Meyrick, 1888)
compensata (Walker, 1861)
longicerata Inoue, 1955*
longitarsata Prout, 1932*
loxographa Turner, 1941
loxosema (Turner, 1908)
lubricata (Warren, 1905)*
ludibunda (Prout, 1915)*
lugubriata Fletcher, 1958*
luridata (Zeller, 1847)*
coenosaria (Lederer, 1855)
luridaria (Herrich-Schäffer, 1852)

[Unjustified emendation of *Idaea luridata* Zeller, 1847.]
luridaria formosaria (Herrich-Schäffer, 1852)
ssp. *distracta* (Butler, 1881)*
ssp. *sternecki* Prout, 1935*
[Replacement name for *Acidalia chinensis* Sterneck, 1931.]
coenosaria chinensis (Sterneck, 1931)
[Junior primary homonym of *Acidalia chinensis* Sterneck, 1927.]
lutearia (Leech, 1897)
luteicollis Prout, 1938
luteolata (Hulst, 1880)*
subfuscata (Taylor, 1906)
luxipuncta Prout, 1932*
lydia (Butler, 1886)
jessica (Butler, 1886)
prosaula (Guest, 1887)
macrocelis (Prout, 1915)
macronephes Fletcher, 1958*
magnidiscata (Warren, 1904)*
magnipunctata Fletcher, 1958*
malagasy (Viette, 1977) **comb. nov.***
[*Antitrygodes malagasy* Viette, 1977 is transferred from *Antitrygodes* to *Scopula*.]
malayana Bänziger & Fletcher, 1985*
manengouba Herbulot, 1992*
manes Djakonov, 1936
manifesta (Prout 1911)*
mappata (Guenée, [1858])
marcidaria (Leech, 1897)*
margaritaria (Warren, 1900)
marginepunctata (Goeze, 1781)*
aniculosata (Rambur, 1829)
apertaria (Walker, [1863])
coniugata (Borkhausen, 1794)
marginepunctata griseofasciata (Turati, 1915)
marginepunctata madoniata (Fuchs, 1901)
pastoraria (Joannis, 1891)
ssp. *subatrata* (Wagner, 1919)
ssp. *terrigena* Prout, 1935
mascula (Bastelberger, 1909)*
mecysma (Swinhoe, 1894)*
ssp. *mesites* Prout, 1935*
medioumbrata (Turati, 1930)
[*Ptychopoda medioumbrata* (Turati, 1930) was transferred from *Idaea* to *Scopula* by Raineri (1996).]
megalocentra (Meyrick, 1888)
megalostigma (Prout, 1915)
melanopis (Prout, 1929) **comb. nov.**
[*Cartaletis melanopis* Prout, 1929 is transferred from *Cartaletis* to *Scopula*.]
melanstigma Prout, 1938*
melinau Holloway, 1997*
mendax Herbulot, 1954
mendicaria (Leech, 1897) **comb. nov.***
[*Acidalia mendicaria* Leech, 1897 is transferred from *Somatina* to *Scopula*.]
mentzeri (Hausmann, 1993) **comb. nov.***
[*Glossotrophia mentzeri* Hausmann, 1993 is transferred from *Glossotrophia* to *Scopula*.]
menytes Prout, 1935
merina Herbulot, [1956]
mesophaena Prout, 1923
metacosmia Prout, 1932*
micara (Schaus, 1901)
michinoku Sato, 1994*
micrata (Guenée, [1858])
microphylla (Meyrick, 1889) **comb. nov.***
[*Prasonesis microphylla* Meyrick, 1889 is transferred from *Somatina* to *Scopula*.]
catacissa (Turner, 1908)
minoa (Prout, 1916)*
minorata (Boisduval, 1833)
[See *Scopula antiloparia* (Wallengren, 1863), *Scopula derasata* Walker, [1863] and *Scopula instructata* (Walker, 1863).]
consentanea (Walker, 1861)
conscutanea Walker, [1863] [misspelling of *consentanea*]
holobapharia (Mabille, 1900)*
luculata (Guenée, [1858])
mauritiata (Guenée, [1858])
mombasae (Warren, 1904)*
ssp. *corcularia* (Rebel, 1894)
ssp. *ochroleucaria* (Herrich-Schäffer, 1847)*
ssp. *tripolitana* (Sterneck, 1933)
[Junior secondary homonym of *Glossotrophia tripolitana* Turati, 1930, requiring a replacement name.]
minuta (Warren, 1900)
misera (Walker, 1866)*
ssp. *subtincta* (Warren, 1896)
denubilata (Warren, 1902)
mishmica Prout, 1938*
modesta (Moore, [1887])
latimarginaria (Hampson, 1891)
modicaria (Leech, 1897)*
virginaria (Imaidzumi, 1941)
moinieri Herbulot, 1966
molaris Prout, 1922
mollicula Prout, 1932
monosema Prout, 1923
monotropa Prout, 1925
montivaga Prout, 1922
moorei (Cotes & Swinhoe, 1888)*
[Replacement name for *Anisodes similaria* Moore, 1868.]
similaria (Moore, 1868)*
[Junior primary homonym of *Anisodes similaria* Walker, [1863].]
ssp. *metarsia* Prout, 1938
moralesi (Rungs, 1945)
mustangensis Yazaki, 1995*
nacida (Dognin, 1901)
ssp. *cinerosaria* (Warren, 1904)
napariata (Guenée, [1858])*
ssp. *acrates* Prout, 1938
natalensis (Prout, 1915) **comb. nov.***
[*Glossotrophia natalensis* Prout, 1915 is transferred from *Glossotrophia* to *Scopula*.]
natalica (Butler, 1875)*
diffusizana (Hampson, 1910)

natalata Fletcher, 1978 [misspelling of *natalica*]
nebulata Fletcher, 1963*
nemoraria (Hübner, [1799])*
aliata (Herrich-Schäffer, 1847)
nemorivagata Wallengren, 1863*
bonaventura (Warren, 1897)
neophyta Prout, 1922
neoxesta (Meyrick, 1888)
nepalensis Inoue, 1982
nepheloperas (Prout, 1916)*
nephotropa Prout, 1931
nesciaria (Walker, 1861)*
negataria (Walker, 1861)
ssp. *absconditaria* (Walker, 1861)*
nesciaroides Holloway, 1997*
nigralba Herbulot, 1978
nigricornis Herbulot, 1992*
nigricosta (Prout, 1916) **comb. nov.**
[*Cartaletis nigricosta* Prout, 1916 is transferred from *Cartaletis* to *Scopula*. Junior secondary homonym of *Synelys nigricosta* Dognin, 1911, requiring a replacement name.]
nigridentata (Warren, 1896)*
[*nigrifrons* Pajni & Walia]
[Rose (1985), in his study on systematics of genus *Scopula*, refers to *S. nigrifrons* Pajni & Walia from India without detailed reference. I have not managed to locate the description for this name from the literature, and therefore I consider the name tentatively invalid.]
nigrinotata (Warren, 1897)*
ssp. *nachtigali* Herbulot, 1965*
[*Scopula nachtigali* Herbulot, 1965 was downgraded to a subspecies of *Scopula nigrinotata* (Warren, 1897) by Hausmann (1999a).]
nigristellata (Warren, 1898)
ssp. *nivimontium* Prout, 1938
nigrocellata (Warren, 1899)
nigrociliata Ebert, 1965*
nigropunctata (Hufnagel, 1767)*
exemptaria (Hübner, [1823])
inspersata (Schrank, 1802)
nemorata (Borkhausen, 1794)
tristriaria (Fabricius, 1794)
ssp. *chosensis* Bryk, 1949
ssp. *imbella* (Warren, 1901)*
ssp. *subcandidata* (Walker, [1863])
ssp. *subimbella* Inoue, 1958
nipha Fletcher, 1955*
nitidata (Warren, 1905) **comb. nov.***
[*Cosymbia*? *nitidata* Warren, 1905 is a replacement name for *Isoplenia albivertex* Warren, 1900. *Cosymbia*? *nitidata* Warren, 1905 is transferred from *Epicosymbia* to *Scopula*.]
albivertex (Warren, 1900)
[Junior secondary homonym of *Idaea albivertex* Swinhoe, 1892.]
nitidissima Prout, 1920
nivearia (Leech, 1897)*
nivellearia (Oberthür, 1922)
ssp. *pseudhonestata* (Wehrli, 1926)*
normalis Herbulot, [1956]
nostima Prout, 1938
nubifera Hausmann, 1998*
nucleata (Warren, 1905) **comb. nov.***
[*Somatina nucleata* Warren, 1905 is transferred from *Somatina* to *Scopula*.]
nupta (Butler, 1878)*
analogia Inoue, 1954*
seminupta Sterneck, 1941*
[Unnecessary replacement name for *Asthena nupta*, Butler, 1878.]
obliquifascia Herbulot, 1999
obliquiscripta (Warren, 1897)*
obliquisignata (Bastelberger, 1909)
obliviaria (Walker, 1861)
chlorochrea (Warren, 1900)
ocellata (Warren, 1899)*
ocellicincta (Warren, 1901)
ocheracea (Hampson, 1891)
ochreofusa (Warren, 1899)*
ochreolata (Warren, 1905)
ochricrinita Prout, 1920*
ochrifrons Prout, 1920
oenoloma Prout, 1932
oliveta Prout, 1920
omana Wilthsire, 1977
omissa (Warren, 1906)
omnisona Prout, 1915
ssp. *septentrionis* Herbulot, 1972
ophthalmica Prout, 1920*
opicata (Fabricius, 1798)*
infantularia (Guenée, [1858])
vanaria (Walker, 1861)
opperta Prout, 1920*
oppilata (Walker, 1861)*
crossophragma (Meyrick, 1886)
stipataria (Walker, 1861)
oppunctata (Warren, 1902)
ssp. *plenistigma* (Warren, 1905)
optivata (Walker, 1861)*
ssp. *youngi* Holloway, 1977
orbeorum (Hausmann, 1996) **comb. nov.***
[*Glossotrophia orbeorum* Hausmann, 1993 is transferred from *Glossotrophia* to *Scopula*.]
ordinaria (Dyar, 1912)
ordinata (Walker, 1861)*
candidaria (Packard, 1873)
puraria (Walker, 1861)*
orientalis (Alphéraky, 1876)*
origalis (Brandt, 1941) **comb. nov.***
[*Glossotrophia origalis* Brandt, 1941 is transferred from *Scopuloides* to *Scopula*.]
ssp. *danieli* (Wiltshire, 1966)*
ssp. *safida* (Wiltshire, 1966)*
ssp. *vantshica* (Viidalepp, 1988)*
ornata (Scopoli, 1763)*
instilata (Hufnagel, 1767)
institata (Rottemburg, 1777)
interrupta (Goeze, 1781)
intersecta (Fourcroy, 1785)
paludalis (Schrank, 1802)
paludata (Linnaeus, 1767)

ssp. *enzela* Prout, 1935*
ssp. *subornata* Prout, 1913*
cinis Inoue, 1946*
orthoscia (Meyrick, 1888)*
oryx Herbulot, 1985*
ossicolor (Warren, 1897)
submarginata (Warren, 1898)
ourebi Herbulot, 1985*
oxysticha Prout, 1938
oxystoma Prout, 1929
paetula Prout, 1919
palleuca Prout, 1925*
pallida (Warren, 1888)*
peralba (Swinhoe, 1893)*
pallidiceps (Warren, 1898)*
pallidilinea (Warren, 1897)
palpata (Prout, 1932) **comb. nov.***
[*Zygophyxia palpata* Prout, 1932 is transferred from *Zygophyxia* to *Scopula*. It is possibly a junior synonym of *Zygophyxia tornisecta* Prout, 1916, based on examination of the genitalia of type material at BMNH: *Z. tornisecta* paratype (slide BMNH GEO 9485) and *Z. palpata* holotype (slide BMNH GEO 9486).]
palpifera Prout, 1925*
paneliusi Herbulot, 1957
ssp. *subirrorata* Herbulot, 1957
paradela Prout, 1920
paradelpharia Prout, 1920*
parallelaria (Warren, 1901)*
parodites Prout, 1931*
parvimacula (Warren, 1896) **comb. nov.***
[*Antitrygodes parvimacula* Warren, 1896 is transferred from *Antitrygodes* to *Scopula*.]
ssp. *erythroconia* (Prout, 1938)
ssp. *kirwiriensis* (Prout, 1938)
ssp. *papuana* (Prout, 1938)
ssp. *privativa* (Prout, 1917)
patularia (Walker, 1866)*
opsinaria (Swinhoe, 1892)*
pauperata (Walker, 1861)*
oedocnemis Prout, 1926*
pedilata (Felder & Rogenhofer, 1875)*
pelloniodes Prout, 1922*
pellonoides Prout, 1922 [misspelling of *pelloniodes*]
penricei Prout, 1920
penultima Herbulot, 1992*
peractaria (Walker, 1866)
perialurga (Turner, 1922)
perlata (Walker, 1861)
recessata (Walker, 1861)
perlimbata (Snellen, 1874)
ssp. *atridiscata* (Warren, 1904)
[Junior secondary homonym of *Craspedia atridiscata* Warren, 1897, requiring a replacement name.]
permutata (Staudinger, 1897)*
ssp. *gnophosaria* (Leech, 1897)
perornata (Thierry-Mieg, 1905)
perpunctata Herbulot, 1992*
personata (Prout, 1913)*
perstrigulata (Prout, 1913) **comb. nov.***
[*Anacosymbia perstrigulata* Prout, 1913 is transferred from *Epicosymbia* to *Scopula*.]
pertinax (Prout, 1916)*
phallarcuata Holloway, 1997*
phyletis (Prout, 1913)*
phyxelis Prout, 1938*
picta (Warren, 1897)*
fulvilinea (Warren, 1914)
pinguis (Swinhoe, 1902) **comb. nov.***
[*Emmiltis pinguis* Swinhoe, 1902 is transferred from *Antilycauges* to *Scopula*.]
pirimacula (Prout, 1916) **comb. nov.**
[*Antitrygodes pirimacula* Prout, 1916 is transferred from *Antitrygodes* to *Scopula*.]
pithogona Prout, 1938*
placida (Warren, 1905)
planidisca (Bastelberger, 1908)
planipennis (Warren, 1900)*
plantagenaria (Hulst, 1887)*
canthema (Schaus, 1901)
hieronyma, Prout, 1922*
plionocentra Prout, 1920*
plumbearia (Leech, 1891)*
poliodesma (Turner, 1908) **comb. nov.***
[*Autanepsia poliodesma* Turner, 1908 is transferred from *Autanepsia* to *Scopula*.]
polystigmaria (Hampson, 1903)
elyra (Swinhoe, 1905)
polyterpes Prout, 1920
praecanata (Staudinger, 1896)*
praesignipuncta Prout, 1920*
pratana (Fabricius, 1794) **comb. nov.***
[*Phalaena pratana* Fabricius, 1794 is transferred from *Oar* to *Scopula*.]
ectypata (Mabille, 1888)
megearia (Oberthür, 1881)
pratanaria (Turton, 1802)
reaumuraria (Milliére, 1864)
ssp. *mortuaria* (Staudinger, 1898)
ssp. *occidens* (Prout, 1935)
ssp. *oppressa* (Walker, 1870)
megiaria obscuraria (Bethune-Baker, 1894)
nigrescens (Hampson, 1896)
preumenes Prout, 1938*
prisca Herbulot, [1956]
privata (Walker, 1861)
semicostata (Warren, 1904)
promethes Prout, 1928
propinquaria (Leech, 1897)*
prosoeca (Turner, 1908)
prosthiostigma Prout, 1938*
protecta Herbulot, [1956]
proterocelis Prout, 1920
prouti Djakonov, 1935*
prouti kurilula Bryk, 1942
proximaria (Leech, 1897)*
ssp. *indigenata* (Wileman, 1911)
pruinata Fletcher, 1958*

psephis Prout, 1935
pseudagrata Holloway, 1997*
pseudoafghana Ebert, 1965*
pseudocorrivalaria (Wehrli, 1932)*
pseudodoxa Prout, 1920
pseudophema Prout, 1920
pudicaria (Motschulsky, [1861])*
puerca (Dognin, 1901)
pulchellata (Fabricius, 1794)*
  discata (Warren, 1897)
  grandicularia (Swinhoe, 1886)
  ligataria (Walker, 1861)*
  metaspilaria (Walker, 1861)
  nictata (Guenée, [1858])*
  perlineata (Walker, 1861)*
  perlineata obdiscata Prout, 1938
  perlineata spilotis Prout, 1938
  spatiosaria (Walker, 1866)
  spilodorsata (Warren, 1895)*
  spilodorsata cosmeta Prout, 1938*
  ssp. *rufinubes* (Warren, 1900)*
  ssp. *semperi* Prout, 1938
  ssp. *takowensis* Prout, 1938*
pulverosa Prout, 1934*
  straminea Prout, 1926
punctatissima (Bastelberger, 1911)
  quadrimacula (Wileman, 1915)
puncticosta (Walker, 1869)
punctilineata (Warren, 1897)*
purata (Guenée, [1858])*
  nigrocandida (Hulst, 1898)
pyraliata (Warren, 1898)
pyrrhochra (Prout, 1916)
quadratisparsa Holloway, 1976*
quadrifasciata (Bastelberger, 1909)*
  glaucocyma (Hampson, 1910)
quadrilineata (Packard, 1876)*
  persimilis (Hulst, 1898)*
quinquefasciata Holloway, 1979
quinquestriata (Warren, 1896)
quintaria (Prout, 1916)
  ssp. *principis* Prout, 1932
radiata (Warren, 1897)
rantaizanensis (Wileman, 1915)
rebaptisa Herbulot, 1985
  turlini Herbulot, 1985
  [Junior primary homonym of *Scopula turlini* Herbulot, 1978, requiring a replacement name.]
rectisecta Prout, 1920
recurvata Herbulot, 1992*
recurvinota (Warren, 1902)
recusataria (Walker, 1861)
regenerata (Fabricius, 1794)
relictata (Walker, 1866) **comb. nov.***
[*Acidalia? relictata* Walker, 1866 is transferred from *Zygophyxia* to *Scopula*.]
  demissus (Swinhoe, 1887)
  ooptera (Turner, 1922)
remotata (Guenée, [1858])*
restricta Holloway, 1997 **comb. nov.***
[*Antitrygodes restricta* Warren is a manuscript name. It is explicitly mentioned as such in Prout (1934–35: 162: '*restricta* Warr., MS. (in Mus. Brit.) (Celebes)') and Prout (1920–41: 192: '*restricta* Warr., M. S.'), where he treated it as a synonym of *A. agrata* Felder & Rogenhofer, 1875. As these works state that the name is disclaimed for nomenclatural purposes it is not available (ICZN 1999: Article 8.3), nor does it meet the requirements of Article 13.1 (ICZN, 1999). The name *A. restricta* Prout does not meet the requirements of Article 13.1 (ICZN 1999) either. Holloway (1997) considered *A. restricta* Prout to be a valid name, and revised it as a distinct species from *A. agrata* as *A. restricta* Prout stat. nov. Holloway's (1997: 69) short description of the male genitalia (slide BMNH GEO 18401) and diagnosis with closely related species meet the requirements of ICZN (1999: Articles 13, 15), so Holloway is to be considered the author of *A. restricta*. *A. restricta* Holloway, 1997 is transferred from *Antitrygodes* to *Scopula*.]
rhodinaria (Rebel, 1907)*
rhodocraspeda Prout, 1932*
risa Wiltshire, 1982*
rivularia (Leech, 1897)*
roezaria (Swinhoe, 1904)
romanarioides (Rothschild, 1913) **comb. nov.***
[*Acidalia romanarioides* Rothschild, 1913 is transferred from *Glossotrophia* to *Scopula*.]
roseocincta (Warren, 1899) **comb. nov.***
[*Eois roseocincta* Warren, 1899 is transferred from *Zygophyxia* to *Scopula*.]
rossi (Prout, 1913)*
rostrilinea (Warren, 1900)
rubellata (Staudinger, 1871)
rubiginata (Hufnagel, 1767)*
  domialla (Fourcroy, 1785)
  rubricaria (Hübner, [1799])
  rubricata ([Denis & Schiffermüller], 1775)
  subangularia (Herrich-Schäffer, [1839])
  variata (Villers, 1789)
  vittata (Thunberg, 1784)
  ssp. *ochraceata* (Staudinger, 1901)
rubraria (Doubleday, 1843)*
  acidaliaria (Walker, 1862)
  attributa (Walker, 1861)
  figlinaria (Guenée, [1858])*
  repletaria (Walker, 1861)
rubriceps (Warren, 1905)
rubrocinctata (Guenée, [1858])
  rufifimbria (Warren, 1905)
rubrosignaria (Mabille, 1900)*
  ssp. *sanguinolenta* Herbulot, 1972
ruficolor Prout, 1916
rufigrisea Prout, 1913*
rufisalsa (Warren, 1897)*
  ssp. *pallidisalsa* Prout, 1932*
rufistigma (Warren, 1895)*
rufolutaria (Mabille, 1900)
  gaudialis Prout, 1928
rufomixtaria (Graslin, 1863) **comb. nov.***

[*Acidalia rufomixtaria* Graslin, 1863 is transferred from *Glossotrophia* to *Scopula*.]
rufomixtata (Staudinger, 1871)
ssp. *saharensis* (Hausmann, 1993)*
rufotinctata (Prout, 1913) **comb. nov.***
[*Glossotrophia rufotinctata* Prout, 1913 is transferred from *Glossotrophia* to *Scopula*.]
sagittilinea (Warren, 1897)*
sanguinifissa Herbulot, [1956]
sanguinisecta (Warren, 1897)*
muscosaria (Warren, 1902)
ssp. *subcatenata* Prout, 1932
saphes Prout, 1920
sapor (Druce, 1910) **comb. nov.**
[*Aletis sapor* Druce, 1910 is transferred from *Cartaletis* to *Scopula*.]
sarcodes Prout, 1935
sarfaitensis Wiltshire, 1982*
sauteri Prout, 1922*
scialophia Prout, 1919
scotti Debauche, 1937*
ssp. *turlini* Herbulot, 1978
sebata Fletcher, 1958*
seclusa Herbulot, 1972
seclusoides Herbulot, 1978
sedataria (Leech, 1897)
segregata Prout, 1919*
semignobilis Inoue, 1942*
semispurcata (Warren, 1898)*
semitata (Prout, 1913) **comb. nov.***
[*Glossotrophia semitata* Prout, 1913 is transferred from *Glossotrophia* to *Scopula*.]
ssp. *ariana* (Ebert, 1965)*
ghirshmani (Wiltshire, 1966)*
tangii (Ebert, 1965)*
ssp. *fumata* (Hausmann, 1993)*
ssp. *taurica* (Wehrli, 1930)*
sentinaria (Geyer, 1837)*
gracilior (Butler, 1893)*
spuriaria (Christoph, 1858)
ssp. *rufinaria* (Staudinger, 1861)*
rufociliaria (Bremer, 1864)*
ssp. *rufinularia* (Staudinger, 1901)*
separata (Walker, 1875)*
atlantica (Walker, 1875)
seras Prout, 1938
serena Prout, 1920*
serratilinea (Warren, 1907)*
sevandaria (Swinhoe, 1904)
peararia (Swinhoe, 1904)
seydeli Prout, 1934*
subsincera Herbulot, 1954
shiskensis (Matsumura, 1925)
siccata McDunnough, 1939*
sideraria (Guenée, [1858])*
bucephalaria (Barnes & McDunnough, 1918)
[Junior primary homonym of *Acidalia bucephalaria* Chrétien, 1909, requiring a replacement name.]
californiaria (Packard, 1871)
californiata (Packard, 1876)
[Unjustified emendation of *Acidalia californiaria* Packard, 1871.]
chretieni (Barnes & Benjamin, 1923)
magnetaria (Guenée, [1858])
pacificaria (Packard, 1871)
rubrolinearia (Packard, 1873)
rubrolineata (Gummpenberg, 1892)
silonaria (Guenée, [1858])*
sticticata (Warren, 1901)
similata (Le Cerf, 1924) **comb. nov.***
[*Glossotrophia similata* Le Cerf, 1924 is transferred from *Glossotrophia* to *Scopula*.]
simplificata Prout, 1928
sincera (Warren, 1901)*
See *Scopula antiloparia* (Wallengren, 1863).
sinnaria (Swinhoe, 1904)*
sinuaria Janse, 1935 [misspelling of *sinnaria*]
ssp. *bisinuata* (Warren, 1905)
sinopersonata (Wehrli, 1932)
sjostedti Djakonov, 1936
sordaria Karisch, 2001*
sordida (Warren, 1895)*
sparsipunctata (Mabille, 1900)*
ssp. *menaiensis* Legrand, 1958
spectrum (Prout, 1923) **comb. nov.**
[*Epicosymbia spectrum* Prout, 1923 is transferred from *Epicosymbia* to *Scopula*.]
spinosicrista Herbulot, 1992*
spissitarsata (Warren, 1899)*
spoliata (Walker, 1861)*
pygarata (Wallengren, 1863)
stenoptera Prout, 1922
stenoptila (Prout, 1916) **comb. nov.***
[*Zygophyxia stenoptila* Prout, 1916 is transferred from *Zygophyxia* to *Scopula*.]
stephanitis Prout, 1932
stigmata (Moore, 1888)*
straminea (Felder & Rogenhofer, 1875)*
melliflua Warren, 1897
subaequalis (Prout, 1917) **comb. nov.**
[*Antitrygodes subaequalis* Prout, 1917 is transferred from *Antitrygodes* to *Scopula*.]
subcandida Prout, 1938*
subcarnea Prout, 1934*
subdecorata (Warren, 1896)*
subgastonaria Wiltshire, 1982*
sublinearia (Walker, 1866)*
ssp. *ida* Robinson, 1975*
ssp. *massimensis* Prout, 1938
sublobata (Warren, 1898)*
khakiata (Warren, 1905)*
sublutescens Prout, 1920
submutata (Treitschke, 1828)*
gianellaria (Turati, 1905)
submutaria (Boisduval, 1840)
[Unjustified emendation of *Idaea submutata* Treitschke, 1828.]
submutataria (Herrich-Schäffer, 1847)
[Unjustified emendation of *Idaea submutata* Treitschke, 1828.]

ssp. *mudrica* Koutsaftikis, 1973
ssp. *roseonitens* Wagner, 1926
ssp. *submutulata* Rebel, 1902*
ssp. *taftanica* Brandt, 1941
ssp. *taurilibanotica* Wehrli, 1932
submutata syrilibanotica Wehrli, 1933
subnictata (Snellen, 1874)*
ssp. *cuphoptera* Prout, 1938
subobliquata (Prout, 1913)*
subobliqua Prout, 1928 [misspelling of *subobliquata*]
subpartita Prout, 1919*
subpectinata (Prout, 1915)*
subperlaria (Warren, 1897)
displicitata (Kheil, 1909)
sufficiens (Warren, 1897)
ssp. *acutangula* Swinhoe, 1909
subpulchellata Prout, 1920*
subpunctaria (Herrich-Schäffer, 1847)*
cerusaria Harpe, 1850
[Unnecessary replacement name for *Acidalia subpunctaria* Herrich-Schäffer, 1847.]
depunctata (Guenée, [1858])
[Replacement name for [*Phalaena*] *punctata* Clerck, 1759.]
punctata (Scopoli, 1763)
[Junior primary homonym of [*Phalaena*] *punctata* Clerck, 1759.]
subquadrata (Guenée, [1858])*
tortuosaria (Möschler, 1890)
subrubellata Sterneck, 1941*
subserena Wiltshire, 1990*
subtaeniata (Bastelberger, 1908)
subtilata (Christoph, 1867)*
subtracta Prout, 1935
succrassula Prout, 1931*
suda Prout, 1932*
suffecta Prout, 1938
suffundaria (Walker, 1861)
suna Prout, 1934
superciliata (Prout, 1913)*
superior (Butler, 1878)*
sancta (Butler, 1881)
supernivearia Inoue, 1963*
supina Prout, 1920*
sybillaria (Swinhoe, 1902)*
synethes (Turner, 1922)
szechuanensis (Prout, 1913)*
tahitiensis Orhant, 2003*
taifica Wiltshire, 1982*
takao Inoue, 1954*
tanalorum Herbulot, 1972
technessa Prout, 1932
tenera (Warren, 1899)
tensipallida Prout, 1938
tenuimargo (Prout, 1916) **comb. nov.**
[*Cartaletis tenuimargo* Prout, 1916 is transferred from *Cartaletis* to *Scopula*.]
tenuimedia Prout, 1938*
tenuiscripta Prout, 1917*
tenuisocius Inoue, 1942*
tenuispersata (Fuchs, 1902)*
terminata (Wiltshire, 1966) **comb. nov.***
[*Glossotrophia terminata* Wiltshire, 1966 is transferred from *Glossotrophia* to *Scopula*.]
ssp. *machadoi* (Hausmann, 1993)*
ternata Schrank, 1802*
aequicerata Träff, 1965*
commutaria (Boisduval, 1840)
[Emendation of *Idaea commutata* Freyer, [1832].]
commutata (Freyer, [1832])
fumata (Stephens, 1831)
gypsaria (Boisduval, 1840)
nitidaria (Boisduval, 1840)
saltuata (Speyer, 1839)
simplaria (Freyer, 1852)
terrearia (Mabille, 1900)
empera Prout, 1928
tersicallis Prout, 1929
tessellaria (Boisduval, 1840)*
pulverulentaria (Sélys-Longchamps, 1844)
tabianaria (Turati, 1905)
ssp. *proutiana* Sheljuzhko, 1955
thrasia Prout, 1938
thysanopus (Turner, 1908)*
timandrata (Walker, 1861)*
rufilinearia (Walker, 1861)*
timboensis Prout, 1938
timia (Prout, 1916)
toquilla (Fletcher, 1978) **comb. nov.***
[*Zygophyxia toquilla* Fletcher, 1978 is transferred from *Zygophyxia* to *Scopula*.]
tornisecta (Prout, 1916) **comb. nov.***
[*Zygophyxia tornisecta*, Prout, 1916 is transferred from *Zygophyxia* to *Scopula*. See *Scopula palpata* (Prout, 1932).]
tosariensis Prout, 1923
toxophora Prout, 1919
traducta Prout, 1938
transcaspica Prout, 1935*
[Described as *Scopula submutata transcaspica* Prout, 1935; raised to species rank by Hausmann & László (1999). The page containing the description of *S. transcaspica* (Prout, 1934–39) was dated 1935, not 1939, as indicated by Hausmann & László.]
transcaspia Scoble, 1999 [misspelling of *transcaspica*]
transmeata (Prout, 1931) **comb. nov.**
[*Zygophyxia transmeata* Prout, 1931 is transferred from *Zygophyxia* to *Scopula*.]
transsecta (Warren, 1898)*
dissimulans (Warren, 1899)
trapezistigma Prout, 1938
tricommata (Warren, 1899)
trisinuata (Warren, 1897) **comb. nov.***
[*Isoplenia trisinuata* Warren, 1897 is transferred from *Isoplenia* to *Scopula*.]
tsekuensis Prout, 1935
tumiditibia Prout, 1920
turbidaria (Hübner, [1819])*
lutosata (Ramber, 1866)
macraria (Guenée, [1858])

ssp. *steinbacheri* Prout, 1935
ssp. *turbulentaria* (Staudinger, 1870)
collata (Warren, 1901)
habenata (Warren, 1901)
turbidaria syriturcica (Wehrli, 1934)
umbelaria (Hübner, [1813])*
compararia (Herrich-Schäffer, 1847)
sylvestrata (Borkhausen, 1794)
ssp. *graeseri* Prout, 1935*
ssp. *majoraria* (Leech, 1897)*
umbilicata (Fabricius, 1794)*
crenatilinea (Warren, 1901)*
cugia (Schaus, 1901)
indoctaria (Walker, 1861)*
nigroapicata (Thierry-Mieg, 1892)
umbilicata peruviana Prout, 1922*
umbratilinea (Warren, 1901)*
undilinea (Warren, 1900)*
undulataria (Moore, 1888)*
unicornata (Warren, 1900)*
unilineata (Warren, 1896)
unisignata Prout, 1926
urnaria (Guenée, [1858]) **comb. nov.***
[*Ephyra urnaria* Guenée, [1858] is transferred from *Ignobilia* to *Scopula*.]
usticinctaria (Walker, 1861)*
uvarovi (Wiltshire, 1952) **comb. nov.**
[*Glossotrophia uvarovi* Wiltshire, 1952 is transferred from *Glossotrophia* to *Scopula*.]
vacuata (Guenée, [1858])*
vagata (Walker, 1861)
valentinella Karisch, 2001
variabilis (Butler, 1878) **comb. nov.***
[*Aletis variabilis* Butler, 1878 is transferred from *Cartaletis* to *Scopula*.]
agis (Druce, 1910)
thestis (Druce, 1910)
vicina (Thierry-Mieg, 1907) **comb. nov.***
[*Trygodes vicina* Thierry-Mieg, 1907 is transferred from *Antitrygodes* to *Scopula*. This taxon was treated as *Antitrygodes agrata* ssp. *vicina* Thierry-Mieg, 1907 in Scoble (1999), but raised to species rank by Holloway (1997).]
vicina (Gaede, 1917) **comb. nov.**
[*Aletis vicina* Gaede, 1917 is transferred from *Aletis* to *Scopula*. *Aletis vicina* Gaede, 1917 is a junior secondary homonym of *Trygodes vicina* Thierry-Mieg, 1907, requiring a replacement name.]
viettei Herbulot, 1992*
vigensis Prout, 1938
vigilata (Prout, 1913)*
ssp. *turatii* (Wagner, 1926)
vinocinctata (Guenée, [1858])*
violacea (Warren, 1897)
virginalis (Fourcroy, 1785)*
caricaria (Reutti, 1853)
immaculataria (Villers, 1789)
phlearia (Reutti, 1853)
virgulata ([Denis & Schiffermüller], 1775)*
strigaria (Hübner, [1799])
sulcaria (Hübner, [1825])
[Unnecessary replacement name for *Geometra strigaria* Hübner?, [1799].]
ssp. *albicans* Prout, 1934*
ssp. *rossica* (Djakonov, 1926)
ssp. *substrigaria* (Staudinger, 1900)
ssp. *subtilis* Prout, 1935
vitellina Herbulot, 1978
vitiosaria (Swinhoe, 1904)
vittora (Schaus, 1901)
vojnitsi Inoue, 1992*
voluptaria Prout, 1938*
walkeri (Butler, 1883)
[Replacement name for *Acidalia extimaria* Walker, 1861: 794.]
extimaria (Walker, 1861:794)
[Junior primary homonym of *Acidalia extimaria* Walker, 1861: 782.]
rufilinea (Warren, 1895)
wegneri Prout, 1935*
wittei Debauche, 1938
xanthocephalata (Guenée, [1858])*
xanthomelaena Fletcher, 1957*
yamanei Inoue, 1978
yihe Yang, 1978
zophodes Prout, 1935